

CLADOGRAMS, PHYLOGENIES AND THE VERACITY OF THE CONODONT FOSSIL RECORD

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Abstract: Traditionally, conodont intrarelationships have been reconstructed following the evolutionary palaeontology paradigm, which lacks a formal methodology, renders hypotheses unrepeatable and takes little account of the imperfect nature of the fossil record. Cladistics provides a prescriptive approach to phylogeny reconstruction and, it is argued, a rigorous method of character analysis that is not incompatible with the aims of evolutionary palaeontology. To demonstrate this, we use the Silurian family Kockelellidae as an example of how cladistics can be used to reconstruct relative relationships, and how such hypotheses can be converted to phylogenies. We follow traditional, cladistic approaches to assessing the completeness of the fossil record and find that failure to conduct this within a milieu of absolute, rather

than merely relative, relationships leads to spurious inferences of gaps in the fossil record. This appears to be a problem that is widespread in theory, but peculiar to species in practice, and parallels the observation that cladograms of fossil species tend to exhibit poorer correlation to stratigraphy than do cladograms of fossil higher taxa. We conclude that cladistics provides the only appropriate framework within which to conduct character analysis; phylogenies can be developed from cladograms but very often this additional inferential step is entirely superfluous to the aims of evolutionary studies.

Key words: phylogeny, stratigraphy, completeness, fossil record, conodont.

IN COMMON with other fossil groups of biostratigraphic utility, attempts at reconstructing conodont phylogeny have traditionally adopted a bottom-up approach, through the reconstruction of lineages from stratigraphically ordered collections by phenetic means or, more usually, based on the subjective perception of shape changes. Justification for the progressive linkage of such lineages becomes increasingly vague and subjective as potential relatives are identified on the basis of similarities and differences, where both the taxa and the characters are considered only from within a pool of candidates circumscribed by stratigraphy. This approach, often referred to as 'stratophenetics' (*non sensu* Gingerich 1979), is multifarious, hardly phenetic and is indistinguishable from the evolutionary palaeontology approach of, for example, Simpson (1974). However, all practitioners are united in the perspective that where the fossil record is sufficiently complete, stratigraphic data should be used *a priori* to constrain morphological comparisons in attempting to uncover phylogeny.

This approach is not without its problems, chief among which are concerns over how we determine whether the fossil record is sufficiently complete to justify applying the principles of evolutionary palaeontology. No

guidelines are provided for a threshold before which the approach is redundant and, of even greater concern, no guidance is given on how to determine completeness. In practice, it appears that biostratigraphic utility provides confidence in the completeness of the fossil record as a record of the evolutionary history of a group. There is no doubt that the conodont fossil record is of great biostratigraphic value. After all, conodonts are the zone fossils of choice throughout much of the Palaeozoic and early Mesozoic, providing the basis of zonation schemes so refined that in certain intervals they surpass even the correlative power of famed biostratigraphic tools such as the graptolites and trilobites. Thus it has been assumed, both implicitly and explicitly, that the conodont fossil record is sufficiently complete that stratigraphic data can be used in reconstructing phylogeny. However, biostratigraphic utility is not enough in itself. It requires as a minimum only the qualities of repeatability and reproducibility in the chronological distribution of taxa (Sweet and Donoghue 2001) and this does not necessarily equate to 'completeness' in the fossil record of a taxon, or taxa. Even as a maximum we may expect that biostratigraphic utility equates to completeness in the fossil record of a taxon, but this may not be the same as achieving

completeness for all taxa, or even representation of all taxa, as well as a record of morphological intermediates, assuming that such populations or individuals existed. These are prerequisites of attempts to reconstruct absolute evolutionary relationships such as ancestry and descent, which are the base currency of phylogenies steeped in the biostratigraphic tradition.

There are good reasons to doubt the completeness of the conodont fossil record. For instance, in graphical correlation, if biostratigraphic sections were complete, it would be expected that first and last appearance data would plot precisely on the line of correlation, but this expectation is never met (Cooper and Lindholm 1990, based on a graptolite database, is probably as good an approximation as is realizable). It is possible that a complete record may be achieved by piecing together a number of incomplete sections, but this assumes that a complete record is available to be sampled. This is an unrealistic assumption because of systematic biases in facies preservation in the rock record, and the impact that this has on the fossil record of organisms whose distribution is controlled by extrinsic variables (ecology, facies; Holland 1995, 2000; Smith 2001). The effects of such biases on the meaning of the conodont fossil record are potentially strongly limiting and yet their presence is only just beginning to be recognized (Donoghue *et al.* 2003; Barrick and Männik 2005; Lehnert *et al.* 2005).

The problem with the evolutionary palaeontology approach does not, however, begin and end with completeness of the record. In particular, the approach of confining consideration of relationships to within a time interval is problematic for a number of reasons: (1) the time interval is entirely arbitrary and never more than implicit; (2) because it fails to assess the relative importance of morphological similarities and/or differences between taxa within a fully historical context, which is the only appropriate means of determining the phylogenetic significance of characters; (3) because potential relatives are expected only to be found within a given time frame, it is an implicit assumption that gaps in the fossil record must be less than the span of this time frame; thus, this approach provides no scope for identifying bias and degrees of completeness in the fossil record because it has already been assumed that gaps in the record are negligible. Although techniques providing an aphylogenetic *a priori* assessment of fossil record completeness have been in development for many years (Paul 1982; Strauss and Sadler 1989; Marshall 1990, 1994, 1997; Weiss and Marshall 1999; Tavaré *et al.* 2002), they have not yet been employed to provide constraint in such approaches.

Above all else, the evolutionary palaeontology approach lacks a formal methodology and, as such, it is impossible to differentiate shared derived from shared primitive characters. Also there is no means of objectively choosing

between competing hypotheses of relationships on the basis of morphology, nor of differentiating between morphological and stratigraphic data when attempting to judge the relative merits of competing hypotheses. Ultimately, because of the lack of clarity over how morphological characters are weighed against one another and stratigraphy, and because of the general failure to specify the stratigraphic context within which relatives can be identified, the 'analyses' are effectively unrepeatable and unreproducible. These are both qualities that are basic expectations (though not necessarily requisites) of scientific hypotheses. This is not to say that a hypothesis that arises from such an analysis, the phylogeny itself, is unscientific; all phylogenetic hypotheses are testable and are therefore scientific.

Many attempts have been made to formalize the evolutionary palaeontology approach (see Schoch 1986 for an excellent summary) but they remain vague. The most objective formalization is to be found in stratophenetics *sensu stricto* (Gingerich 1979) and a number of phylogenetic lineages of conodonts have been constructed following these established, or similar, procedures (e.g. Barnett 1971, 1972; Dzik and Trammer 1980; Murphy and Cebecioglu 1986, 1987; Dzik 1991, 1994, 1997, 1999, 2002, 2005). As seductively persuasive as many of these lineages are, the hypotheses of ancestor–descendant (direct) relationships between 'populations' or species do not preclude the possible existence of unrecognized, unsampled or, indeed, unsampleable intermediate taxa. Moreover, the potential for discovery of new taxa is inversely proportional to sampling density. As such, the recognized ancestor–descendant pairings can vary in meaning from direct relations to the pairing of taxa that are only very remotely related, and can be considered ancestors and descendants of one another in only the very vaguest sense (cf. Engelmann and Wiley 1977; Schoch 1986; Nelson 1989). Another limitation of stratophenetic studies is that they are usually limited to individual rock successions where the appearance and disappearance of taxa can represent migration, rather than evolutionary events. Finally, the characters considered in stratophenetic studies are generally limited to one, or just a few, and are chosen over other potential variates on a subjective and often unstated basis. These problems notwithstanding, stratophenetically derived lineages of conodonts are rare and have been limited to the species level and, more usually, below. Such evidence is wanting for most species, and our current understanding of the interrelationships of conodonts at the generic level and above is replete with uncertainty (see Sweet 1988, for the very best current assessment).

Dzik (1991, 2005) has attempted to formalize a methodology for evolutionary palaeontology in 'chronophylogenetics', but this still lacks any formal criteria for reconciling

between competing data and datasets, and considers the significance of subjectively chosen characters within unspecified and arbitrarily circumscribed time frames, rather than within a fully historical context. The chief advantage of this methodology, as set out, is that it makes falsifiable predictions, such as morphological intermediates, through retrodiction. However, this is a quality of all phylogenetic hypotheses, rather than of a specific methodology, and is actually better suited to hypotheses that can be correlated directly to the morphological data on which they are based, in contrast to chronophyletics.

Cladistics

In contradistinction, cladistics provides a formal methodology for the treatment of characters in phylogenetic reconstruction. In eschewing stratigraphic data *a priori*, it provides a means of assessing the phylogenetic significance of characters in a context that is both atemporal and, at the same time, fully historical. In so doing, cladistic hypotheses and stratigraphic data provide a means of reciprocal testing *a posteriori*. For a variety of reasons, it is more appropriate to reconstruct relative, rather than direct relationships; these are just as testable and more likely to survive testing – thus, evolutionary studies of character evolution based on such hypotheses are less likely to be revised fundamentally with a new discovery. The data and character definitions on which cladistic hypotheses are based are (generally!) also presented for scrutiny, facilitating tests of both repeatability and reproducibility, in addition to tests of the hypotheses based on the data.

However, the cladistic approach is not beyond criticism. For instance, it can be and has been argued that:

1. *Characters and character states are artefacts of analysis, not properties of organisms.* This is a moot point, but even so, it is a limitation of all approaches to phylogenetic reconstruction, not just cladistics.
2. *Convergence (homoplasy) is so rife that it is not possible to reconstruct relationships independently of stratigraphic data.* It is unlikely that convergence is ever so prevalent that it affects all aspects of morphology. Indeed, if homoplasy were so widespread, it would be a wonder that fossils are of any use in biostratigraphy. Cladistics provides a means of discriminating homology and homoplasy, assuming that homology is dominant over homoplasy, but this is difficult to test (it is possible to compare statistical support for phylogenetic solutions to real and random datasets, e.g. see Donoghue 2001, but the assumption remains). It is possible to partition cladistic analyses by temporal interval (Fortunato 1998) although this removes the global test of homology provided by a fully historical (temporally unconstrained) analysis (cf. Donoghue *et al.* 1989). Because both stratophenetic and evolutionary palaeontological analyses rely heavily on morphological data they are just as subject to convergence as cladistic analyses and so stratigraphic data do not provide a solution to this potential problem.
3. *Characters have different degrees of phylogenetic significance.* This is true, and character selection is the most severe form of character weighting. For those characters included, it is not possible to determine objectively an appropriate weighting scheme without reference to a phylogeny; successive weighting (*a posteriori* reweighting) of cladistic analyses currently provides such a means, and Bayesian approaches are likely to provide more sophisticated approaches in the near future. Subjective methods of *a priori* weighting have always been available.
4. *Cladistics requires and can only reconstruct cladogenic, or divergent, speciation events.* This is a misconception of the goal of cladistics, which is to resolve relative relationships (in the non-familial sense), not to replace absolute, or direct, relationships, and cladistic analyses should be considered an interim step of rigorous character analysis towards the ultimate goal of phylogeny reconstruction. The successive branching between taxa in a cladogram reflects only the nested degrees of relationship between taxa, not (necessarily) the evolutionary process or pattern that underlies their distinction. The process of converting a cladogram to a phylogeny is non-trivial, and will be explored below, but there is no impediment to the conversion of a cladogram to a phylogenetic tree with an architecture common to those derived from evolutionary palaeontology, stratophenetics or chronophyletics.
5. *Evolution does not (always) proceed parsimoniously.* Quite likely, but parsimony is a universal scientific principle, not a tool employed solely by cladists, and it is the same principle employed in evolutionary palaeontology, stratophenetic and chronophyletic analyses when attempting to discriminate between competing hypotheses. Nevertheless, this raises an important point with respect to cladistics, which is that aside from the shibboleth, the key to cladistics is that it forces practitioners of cladistic methodology to confront their assumptions and provide justification for any hypothesis that they wish to present that is more extravagant than the most parsimonious solution. Thus, it is possible to provide uneven weights to the characters, it is possible to choose a tree that is less parsimonious but in greater concordance with stratigraphy, and it is

even possible to recognize taxa as ancestors within cladograms, but *a priori* justification needs to be provided for these extra assumptions. Even if justification is not forthcoming, the explicit acceptance of specific assumptions requires that their impact is considered in contrast to the most parsimonious solution, and the analysis is rendered repeatable and reproducible.

Thus, cladistics provides the most appropriate framework within which to attempt to resolve the interrelationships and systematics of conodonts. But it should go further, by attempting to uncover conodont phylogeny, and by considering the absolute relationships of taxa. This approach can provide a more defensible, stable framework on which to base evolutionary studies that require absolute rather than merely relative relationships. It can also provide a means of assessing the completeness of the conodont fossil record to determine whether there is some justification for the *a priori* use of stratigraphic data in phylogeny reconstruction. Determination of the fidelity with which the conodont fossil record reflects the evolutionary history of the group can further provide a measure of which questions asked of it can actually be answered. On a more general level, such studies will also provide a measure of whether the fossil records of biostratigraphically important groups are more complete than those of groups in which stratigraphic occurrence is an unquestioned guide to phylogenetic relations.

No such studies of the conodont fossil record have yet been undertaken and in this contribution we aim to reconstruct the phylogeny and assess the veracity of the fossil record of a putative clade of taxa that has been used widely in biostratigraphy, including a number of taxa employed in global biozonation.

THE CONODONT FAMILY KOCKELLELLIDAE KLAPPER, 1981

The Silurian conodont family Kockellellidae was chosen as the subject of this study because it is widely regarded as monophyletic, because there is an established scheme of interrelationships for contrast that has been developed over a number of years in the biostratigraphic tradition (Barrick and Klapper 1976; Serpagli and Corradini 1999), and because its fossil record has been intensively studied and utilized in biostratigraphy. Indeed, many of the member taxa contribute to the global zonation scheme for the Silurian.

At least two genera, *Kockellella* (17 species, three in open nomenclature, five subspecies) and *Ancoradella* (one species), have been assigned to the family Kockellellidae (e.g. Sweet 1988), although Fordham

(1991) has argued for the inclusion of *Polygnathoides* (one species). Despite an absence of natural assemblages, multielement reconstructions are available for the vast majority of these taxa, produced on the basis of recurrent associations (Walliser 1964; Klapper and Philip 1971; Barrick and Klapper 1976). Because the morphology of the elements constituting the apparatuses is conservative both within and without the family, their positional homologies can be inferred with reference to taxa that are known from natural assemblages, such as *Ozarkodina* (Pollock 1969; Mashkova 1972; Nicoll 1985; Nicoll and Rexroad 1987) and, thence, to more distantly related taxa such as members of the outgroup (Purnell and Donoghue 1998; Purnell *et al.* 2000). Positional homologies are expressed following the notation scheme of Purnell *et al.* (2000).

PHYLOGENETIC ANALYSIS

Taxa included in the analysis

Outgroup. Taxa representative of each of the three orders of 'complex' conodonts have been included among the outgroup. Specific taxa are selected either because of the degree to which they represent particular clades, or because they have previously been implicated in the origin, ancestry or diversification of the Kockellellidae. For instance, Sweet (1988) has suggested that *Ozarkodina hassi* and *Plectodina tenuis* are ancestral to *Kockellella*; species of *Oulodus* have been included in the analysis because Klapper and Murphy (1974) and Barrick and Klapper (1976) have suggested similarity to the S and M elements in *Kockellella variabilis variabilis*, possibly belying close phylogenetic relations; *Ancoradella ploeckensis* and *Polygnathoides siluricus* have been included in the analysis as well as they are supposedly closely related to *Kockellella* (Link and Druce 1972; Sweet 1988; Fordham 1991; Serpagli and Corradini 1999).

Ancoradella ploeckensis Walliser, 1964 following the reconstruction of Männik and Malkowski (1998: $P_1 = Pa$, $P_2 = Pb$, $S_0 = Sa$, $S_{1/2} = Sb$, $S_{3/4} = Sc$, $M = ?$).

Oulodus rohneri Ethington and Furnish, 1959 following the reconstruction of Nowlan and Barnes (1981: $P_1 =$ priniodiniform, $P_2 =$ oulodiform, $S_0 =$ trichonodelliform, $S_{1/2} =$ zygognathiform, $S_{3/4} =$ eoligonodiniform, $M =$ cyrtioniodiform).

Oulodus ulrichi (Stone and Furnish, 1959) following the reconstruction of Nowlan and Barnes (1981: $P_1 =$ priniodiniform, $P_2 =$ oulodiform, $S_0 =$ trichonodelliform, $S_{1/2} =$ zygognathiform, $S_{3/4} =$ eoligonodiniform, $M =$ cyrtioniodiform).

Ozarkodina confluens (Branson and Mehl, 1933) following the reconstruction of Jeppsson (1974: $P_1 = sp$, $P_2 = oz$, $S_0 = tr$, $S_{1/2} = pl$, $S_{3/4} = hi$, $M = ne$).

Ozarkodina excavata excavata (Branson and Mehl, 1933) following the reconstruction of Jeppsson (1974: $P_1 = sp$, $P_2 = oz$, $S_0 = tr$, $S_{1/2} = pl$, $S_{3/4} = hi$, $M = ne$).

Ozarkodina hassi (Pollock, Rexroad and Nicoll, 1970) following the reconstruction of Armstrong (1990: $P_1 = Pa$, $P_2 = Pb$, $S_0 = Sa$, $S_{1/2} = Sb$, $S_{3/4} = Sc$, $M = M$).

Polygnathoides siluricus Branson and Mehl, 1933 following the reconstruction of Jeppsson (1983: $P_1 = sp$, $P_2 = oz$, $S_{1/2} = pl$, $S_{3/4} = hi$, $M = ne$).

Plectodina tenuis Branson and Mehl, 1933 following the reconstruction of Sweet (1979: $P_1 = Pa$, $P_2 = Pb$, $S_0 = Sa$, $S_{1/2} = Sb$, $S_{3/4} = Sc$, $M = M$).

Ingroup

Kockelella abrupta (Aldridge, 1972) only known element represents the P_1 position. *K. abrupta* has previously been synonymized with *K. manitoulinensis* (McCracken and Barnes 1981; Zhang and Barnes 2002; contra Armstrong 1990), but without a reconstructed multielement apparatus such a step is premature and this taxon has been considered as distinct for the purpose of this study.

Kockelella amsdeni Barrick and Klapper, 1976 following the multielement reconstruction of Barrick and Klapper (1976: $P_1 = Pa$, $P_2 = Pb$, $S_0 = Sa$, $S_{1/2} = Sb$, $S_{3/4} = Sc$, $M = M$).

Kockelella corpulenta (Viira, 1975) only known element represents the P_1 position. *K. corpulenta* has previously been synonymized with *Kockelella walliseri* (Jeppsson 1983, 1997; contra Kleffner 1994; Serpagli and Corradini 1999), but without a multielement reconstruction such a step is premature and this taxon has been considered as distinct for the purpose of this study.

Kockelella crassa (Walliser, 1964) following the reconstruction of Serpagli and Corradini (1999: $P_1 = Pa$, $P_2 = Pb$, $S_0 = ?$, $S_{1/2} = ?$, $S_{3/4} = ?$, $M = ?$). The remaining positions within the apparatus were considered by Serpagli and Corradini (1999) to have been filled by elements that are indistinguishable from their homologues in *Kockelella variabilis variabilis*. However, in the absence of documentary support, the morphology of these elements must be considered unknown.

Kockelella latidentata Bischoff, 1986 ($P_1 = Pa$, $P_2 = ?$, $S_0 = ?$, $S_{1/2} = ?$, $S_{3/4} = ?$, $M = ?$). The validity of this taxon is uncertain due to the very close similarity of the Pa element to the Pa of *Kockelella ranuliformis* (L. Jeppsson, pers. comm. 2001, 2002). The elements assigned Pb and Sb by Bischoff (1986) may more appropriately be assigned to species of *Oulodus* and *Ozarkodina*, respectively.

Kockelella maenniki Serpagli and Corradini, 1999 following the original reconstruction ($P_1 = Pa$, $P_2 = ?$, $S_0 = ?$, $S_{1/2} = ?$, $S_{3/4} = ?$, $M = M$). The remaining positions within the apparatus were considered by Serpagli and Corradini (1999) to have been filled by elements that are indistinguishable from their homologues in *Kockelella variabilis variabilis*. However, in the absence of documentary support, the morphology of these elements must be considered unknown.

?*Kockelella manitoulinensis* (Pollock, Rexroad and Nicoll, 1970) following the reconstruction of Zhang and Barnes (2002: $P_1 = Pa$, $P_2 = Pb$, $S_0 = Sa$, $S_{1/2} = Sb$, $S_{3/4} = Sc$, $M = M$). Zhang and Barnes (2002) queried the assignment of this taxon to

Kockelella because the element assigned to the P_1 position is typical neither of *Kockelella* nor *Ozarkodina*.

Kockelella ortus ortus (Walliser, 1964) following the reconstruction of Jeppsson (1997: $P_1 = Pa$, $P_2 = Pb$, $S_0 = ?$, $S_{1/2} = ?$, $S_{3/4} = ?$, $M = M$).

Kockelella ortus absidata Barrick and Klapper, 1976 following the reconstruction by Klapper *et al.* (1981: $P_1 = Pa$, $P_2 = Pb$, $S_0 = ?$, $S_{1/2} = Sb$, $S_{3/4} = Sc$, $M = M$). The M element of Rexroad *et al.* (1978) corresponds well with that found in association with *K. o. absidata* from both the type collection and collections from Dingle (Aldridge 1980) and Gotland (Jeppsson, unpublished collections), but it does not correspond to the M element of *Kockelella variabilis variabilis* (contra Barrick and Klapper 1976; Serpagli and Corradini 1999), even though the two morphotypes have, hitherto, been assigned to the same form species (*Neoproniodus multiformis*).

Kockelella ortus sardoa Serpagli and Corradini, 1999 following the original reconstruction ($P_1 = Pa$, $P_2 = ?$, $S_0 = ?$, $S_{1/2} = ?$, $S_{3/4} = ?$, $M = M$). The remaining positions within the apparatus were considered by Serpagli and Corradini (1999) to have been filled by elements that are indistinguishable from their homologues in *Kockelella variabilis variabilis*. However, in the absence of documentary support, the morphology of these elements must be considered unknown.

Kockelella patula Walliser, 1964 following the reconstruction by Barrick and Klapper (1976: $P_1 = Pa$, $P_2 = Pb$, $S_0 = Sa$, $S_{1/2} = Sb$, $S_{3/4} = Sc$, $M = M$). The multielement reconstruction of Walliser (1972) is an unreliable synonymy list of form taxa lacking citation to specific specimens.

Kockelella ranuliformis (Walliser, 1964) following the reconstruction by Barrick and Klapper (1976: $P_1 = Pa$, $P_2 = Pb$, $S_0 = Sa$, $S_{1/2} = Sb$, $S_{3/4} = Sc$, $M = M$).

Kockelella stauros Barrick and Klapper, 1976 following the original multielement reconstruction ($P_1 = Pa$, $P_2 = Pb$, $S_0 = Sa$, $S_{1/2} = Sb$, $S_{3/4} = Sc$, $M = M$).

Kockelella variabilis ichnusae Serpagli and Corradini, 1999 ($P_1 = Pa$, $P_2 = ?$, $S_0 = ?$, $S_{1/2} = ?$, $S_{3/4} = ?$, $M = M$). The remaining positions within the apparatus were considered by Serpagli and Corradini (1999) to have been filled by elements that are indistinguishable from their homologues in *Kockelella variabilis variabilis*. However, in the absence of documentary support, the morphology of these elements must be considered unknown.

Kockelella variabilis variabilis Walliser, 1957 following the reconstruction of Aldridge (1980: $P_1 = Pa$, $P_2 = Pb$, $S_0 = Sa$, $S_{1/2} = Sb$, $S_{3/4} = Sc$, $M = M$). This apparatus was also reconstructed by Walliser (1964) as 'Conodonten apparat G'.

Kockelella walliseri (Helfrich, 1975) following the reconstructions of Bischoff (1986: $P_1 = Pa$, $P_2 = Pb$, $S_0 = Sa$, $S_{1/2} = Sb$, $S_{3/4} = Sc$, $M = M$) and Kleffner (1994: $P_1 = Pa$, $P_2 = Pb$, $S_0 = Sa$, $S_{1/2} = Sb$, $S_{3/4} = Sc$, $M = ?$).

Taxa excluded from the analysis

Three taxa assigned to *Kockelella* in open nomenclature (*Kockelella* n. sp. A Klapper and Murphy, 1974, *Kockelella* sp. A Barrick, 1983 and *Kockelella* sp. A Bischoff, 1986) are known from Pa ($= P_1$) elements alone. They are excluded from the analysis because they

are considered to fall within the range of variation of established taxa.

Kockelella suglobovi Mashkova, 1979 exhibits only a superficial similarity to members of the Kockelellidae and may be more appropriately assigned to *Pterospathodus*, which is only remotely related to *Kockelella* (Aldridge and Smith 1993) and has a distinct apparatus composition (Männik 1998). Thus, *K. suglobovi* has been excluded from the analysis.

Characters and coding

The data matrix (Table 1) is composed of 49 discrete unordered morphological characters coded using a contingent coding strategy. This particular coding strategy was adopted because it is more biologically meaningful, theoretically defensible and practically valid than other commonly adopted coding strategies such as strict binary and inappropriate multistate coding (Hawkins *et al.* 1997; Lee and Bryant 1999; Strong and Lipscomb 1999; Forey and Kitching 2000; Hawkins 2000; Jenner 2002). The coding strategy is only operationally significant when a character is composed of more than two character states, some of which are not logically equivalent, such as absence of process versus presence in the form of a platform versus presence in the form of a blade. Clearly, two of these states are different forms of 'process present', and the failure to reflect this in the design of the character leads to a loss of phylogenetic information and may lead to spurious phylogenetic hypotheses that require biologically incongruent character state transformations. There are many coding solutions to this problem, but contingent coding splits the character into two, one character pertaining to the presence or absence of a process, and a second character concerned with whether the process, if present, is manifest as a platform or a blade; if no process is present, the character is inapplicable, and the character state score will be the same as for missing data, '?'. Although this violates the cladistic axiom that all characters should be logically and biologically independent, it is an essentially theoretical problem, the significance of which is vastly outweighed by the advantages that the coding strategy bring to analyses in terms of facilitating only biologically valid character transformations, maximizing character congruence, and providing the most exacting test of homology.

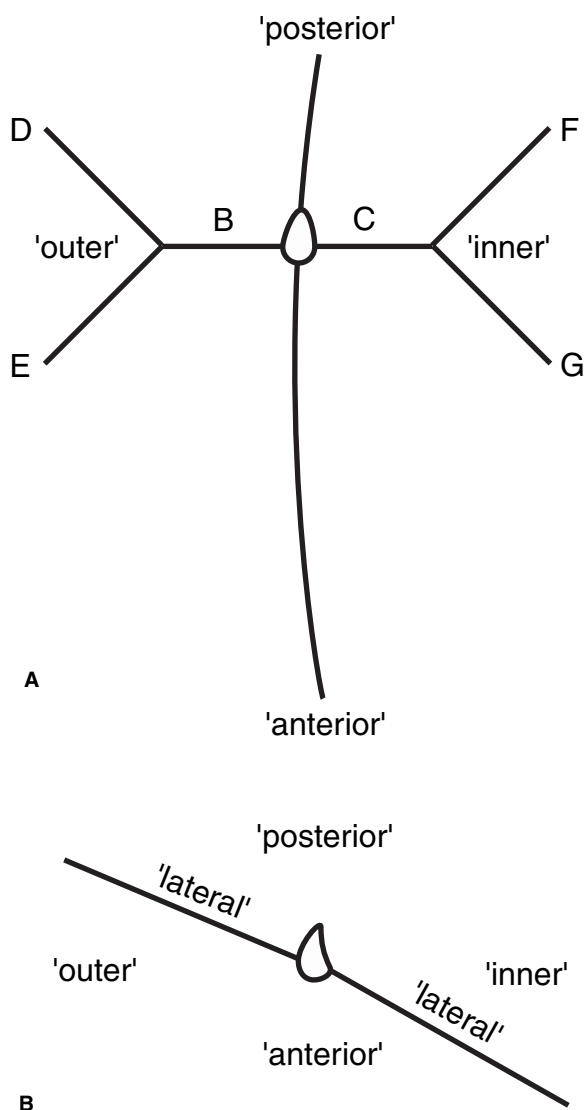
Character coding is based on published and unpublished conodont collections from Oklahoma (USA), Gotland (Sweden), Dingle (Ireland), Britain and Sardinia (Italy), and from taxonomic descriptions and figures in the published literature. The usefulness of published taxonomic descriptions is limited, however, because of the tendency to emphasize taxonomic differences rather than similarities (possible homologous characters). The element notation scheme of Purnell *et al.* (2000) has been

adopted herein to convey positional homologies between element morphotypes. Due to the morphological similarities of elements occupying $S_{1,2}$ and $S_{3,4}$ positions within the ingroup these have been coded as $S_{1/2}$ and $S_{3/4}$, respectively.

A note on homology

Homology is the backbone of any cladistic analysis. Positional homologies are well understood among the major groups of 'complex' conodonts (prioniodontids, prioniodinids and ozarkodinids; prioniodontids *sensu* Donoghue *et al.* 2000) and have previously been thoroughly discussed (e.g. Purnell 1993; Aldridge *et al.* 1995; Purnell and Donoghue 1998; Purnell *et al.* 2000). The homology of individual processes, however, has rarely been discussed (e.g. Donoghue 2001) and by convention processes are recognized and described according to their disposition relative to a landmark rather than in an attempt explicitly (or even implicitly) to identify homology with another process in an element in an homologous position in another taxon. Thus, traditional concepts of process homology are largely phenetic and it is necessary to tease apart the homologies that underlie this phenetic classification scheme using ancillary data sources, such as patterns of ontogenetic development, to distinguish structures that are merely 'similar' from those that are 'the same' in a historical sense. For instance, we can consider homology between the elements occupying the P_1 positions in *Oulodus* and *Kockelella variabilis*. Both taxa possess two primary 'lateral' processes (primary in the conventional sense that the processes join the cusp), but are these processes homologous? The 'lateral' processes of the *Oulodus* P_1 element are manifest at every ontogenetic stage, while in the P_1 element of *K. variabilis*, the 'anterior' and 'posterior' processes begin to develop first; 'lateral' processes are not present in juveniles, and begin to develop much later, as evidenced by ontogenetic suites of specimens (e.g. Serpagli and Corradini 1999). On ontogenetic grounds, therefore, it appears more likely that the 'lateral' processes of *Oulodus* P_1 elements are homologous to the 'anterior' and 'posterior' processes of *K. variabilis*, and that the primary 'lateral' processes of *K. variabilis* are neomorphisms. Thus, we have devised a scheme for identifying homology of post-first generation processes (Text-fig. 1) that serves to obviate false statements of homology between the 'lateral' processes of *Ancoradella*, *Oulodus*, *Plectodina* and *Kockelella*, which we consider on ontogenetic grounds to be not the same, but merely similar.

Whether the first generation processes of these taxa should be considered homologous is best reflected upon after the result of a phylogenetic analysis. However,



TEXT-FIG. 1. Scheme of process homology followed showing the relationship between conventional terminology and our revised terminology. A, the scheme for taxa with lateral processes, but lacking first generation lateral processes. B, the conventional scheme applied to taxa with first generation 'lateral' processes.

within the context of this analysis, to do so would be phylogenetically uninformative, as all of the taxa considered possess these putative homologies. It would be necessary to resort to an additional tier of homological statements considering homology of position of these processes, following the traditional sense of orientation relative to the cusp, which would result in codings common to presence/absence of 'anterior', 'posterior', 'lateral' first generation processes. Thus we have chosen to follow convention in identifying homology of first generation processes.

1. P₁ 'anterior' process: absent (0), present (1). For identification of P₁ process homologies see Text-figure 3.
2. P₁ 'posterior' process: absent (0), present (1). Contrary to the conventional interpretation, a 'posterior' process can be demonstrated to be present in the P₁ element of *Kockella ranuliformis* on the basis that the tip of the basal cavity lies 'anterior' to the 'posterior'-most denticles.
3. P₁ process B: absent (0), present (1). See Text-figure 1.
4. P₁ process C: absent (0), present (1). See Text-figure 1.
5. P₁ process D: absent (0), present (1). See Text-figure 1.
6. P₁ process E: absent (0), present (1). See Text-figure 1.
7. P₁ process F: absent (0), present (1). See Text-figure 1.
8. P₁ process G: absent (0), present (1). See Text-figure 1.
9. P₁ element planate with a recessive basal margin: absent (0), present (1).
10. P₁ basal margin of the 'posterior' process is in the same plane as the basal margin of the 'anterior' process: absent (0), present (1). This character is coded inapplicable in taxa with a recessive basal margin as these taxa do not possess a comparable basal margin.
11. P₁ 'posterior' process free: absent (0), present (1). The 'posterior' process has no basal flare. This character is coded inapplicable in taxa with a recessive basal margin as these taxa do not possess a basal cavity and, consequently, cannot have a basal flare.
12. P₁ cusp is larger than other denticles: absent (0), present (1).
13. P₁ cusp is erect in gerontic specimens: absent (0), present (1).
14. P₁ 'posterior' process significantly proportionately shorter than the 'anterior' process: absent (0), present (1).
15. P₁ small ridge connects the cusp with the first denticle on B and/or C process(es): absent (0) present (1)
16. P₁ fan: absent (0), present (1). A fan is considered present when the 'anterior'-most denticles on the 'anterior' process are bigger than remaining denticles (Murphy and Valenzuela-Ríos 1999).
17. P₁ denticles on the 'anterior' process: erect (0), directed toward the cusp (1). The orientation of the denticles is considered relative to the basal margin of the process.
18. P₁ basal cavity extends under the 'posterior' process: absent (0), present (1).
19. P₁ basal cavity extends under the 'posterior' process as a shallow groove: absent (0), present (1).
20. P₁ basal cavity deepens under the 'posterior' process: absent (0), present (1).
21. P₁ basal cavity rounded in outline: absent (0), present (1).
22. P₁ basal cavity outline constrained by process disposition: absent (0), present (1).
23. P₁ ventral constriction of the basal cavity: absent (0), present (1).
24. P₁ basal cavity extends and deepens under the B and/or C processes: absent (0), present (1).
25. P₁ 'anterior' margin of the platform is approximately perpendicular to the 'anterior-posterior' axis of the element: absent (0), present (1).

26. P₁ 'outer lateral' margin of the basal flare is approximately planar and parallel/subparallel to the 'anterior-posterior' of the element: absent (0), present (1).
27. P₂ 'anterior' process absent: (0), present (1).
28. P₂ 'posterior' process: absent (0), present (1).
29. P₂ 'inner lateral' process: absent (0), present (1). The 'lateral' process in *K. crassa* (but not present in the holotype of the form taxon) appears to be secondarily derived from a 'posterior' process and, thus, is not homologous to either of the 'lateral' processes in either *Oulodus* or *Plectodina*.
30. P₂ 'outer lateral' process: absent (0), present (1).
31. P₂ denticles fused on the 'anterior' process: absent (0), present (1).
32. P₂ denticle spacing on the 'posterior' process: close (0), wide (1).
33. P₂ denticles are fused on the 'posterior' process: absent (0), present (1).
34. P₂ bar extends higher on the 'anterior' process than the bar on the 'posterior' process: absent (0), present (1).
35. P₂ basal cavity extends shallowly and broadly under the 'posterior' process: absent (0), present (1).
36. P₂ twisted basal cavity: absent (0), present (1).
37. P₂ 'outer' basal cavity flare: absent (0), present (1).
38. M 'outer-lateral' process: absent (0), present (1).
39. M element: dolabrate (0), makellate (1).
40. M 'inner-lateral' process of makellate elements: straight (0), bowed/curved (1).
41. M small, constricted basal cavity: absent (0), present (1).
42. M 'inner' basal cavity flare: absent (0), present (1).
43. M 'posterior' basal cavity flare extends under the 'inner-lateral' process: absent (0), present (1).
44. M basal cavity extends broadly and shallowly under the 'inner-lateral' process: absent (0), present (1).
45. M spacing of denticles on the 'inner-lateral' process: close (0), wide (1).
46. M denticles are reclined on the 'inner-lateral' process: absent (0), present (1).
47. S₀ denticles are discretely spaced: absent (0), present (1).
48. S_{1/2} spacing of denticles on the 'inner-lateral' process: wide (0), close (1).
49. S_{3/4} spacing of denticles on the 'posterior' process: wide (0), close (1).

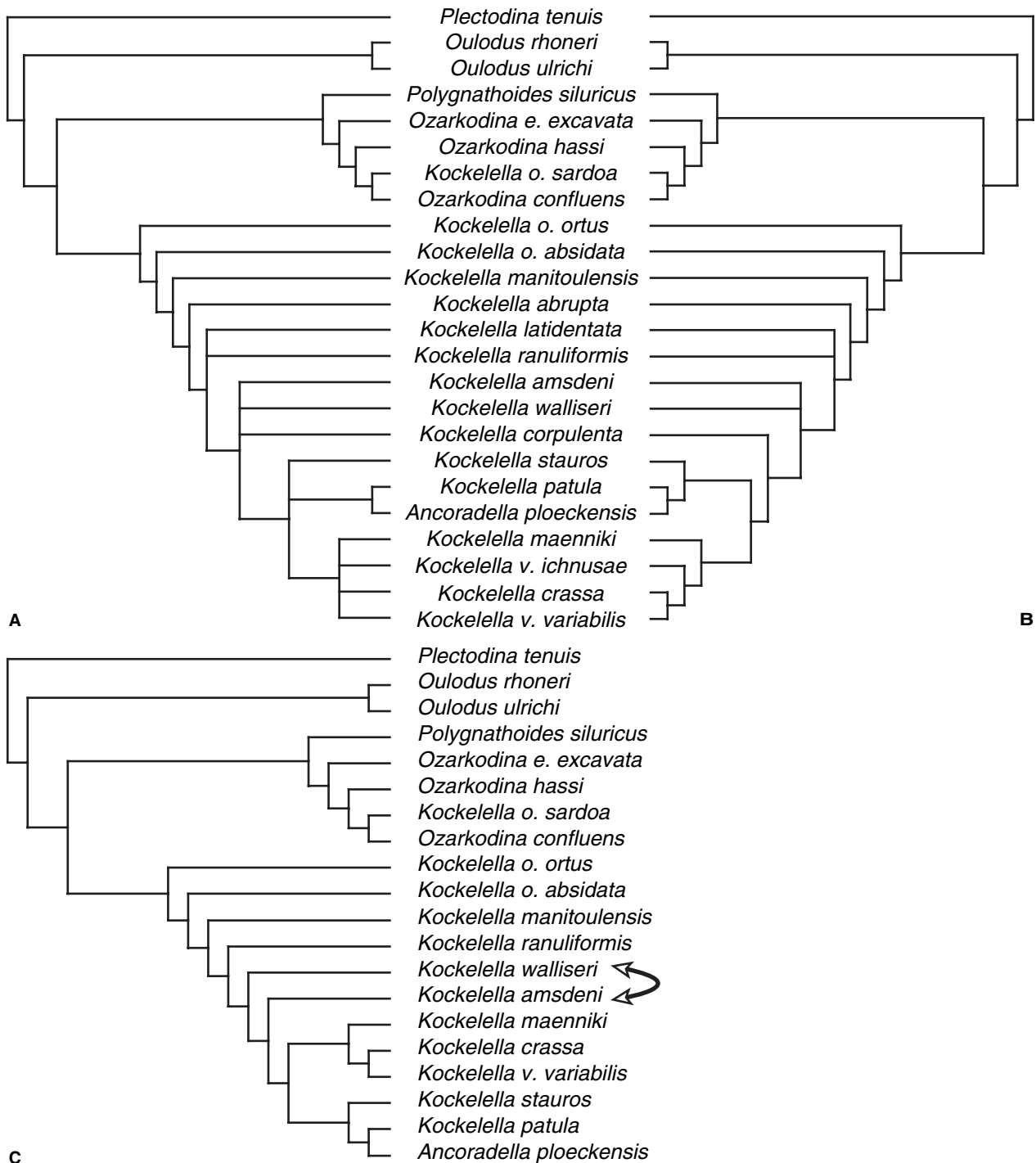
Search techniques

Cladistic analyses were undertaken using PAUP 4.0b10 (Swofford 2002) using 'branch-and-bound' and heuristic (random sequence addition, 100 replicates, ten trees retained at each step, steepest descent on) search options; character evolution was resolved using MacClade 4.05 (Maddison and Maddison 2002). *Plectodina tenuis* was designated as the root in all analyses. Although all characters were unordered and unweighted in primary analyses, these results were subjected to *a posteriori* reweighting in all instances. This methodology, which is equivalent to

the successive weighting technique of Farris (1969), assigns a weight to each character based upon on how well they perform in the primary, unweighted analysis, such that a character exhibiting perfect/good fit to the tree(s) derived from the primary analysis will be assigned a high weighting, while a character exhibiting poor fit to the primary tree(s) will be assigned a low/no weight. The weighted dataset is then reanalysed and the process repeated until assigned weights cease to vary between analyses. The methodology achieves results that are both internally consistent and least affected by spurious hypotheses of homology (Platnick *et al.* 1991, 1996; Goloboff 1993). Furthermore, *a posteriori* reweighting provides a test of minimal trees achieved through consensus of poorly fitting characters (Platnick *et al.* 1991; Kitching *et al.* 1998).

Results, experimental analysis of the dataset, and discussion

The primary unweighted analysis of the dataset yielded 48 equally most-parsimonious trees (CI 0.4667; RI 0.7143; RCI 0.3333; 105 steps; strict consensus presented in Text-fig. 2A), which differ primarily in the interrelationships of *Kockelella ranuliformis* and *K. latidentata*, *K. amsdeni*, *K. corpulenta*, and *K. walliseri*, and a clade of four taxa: *K. crassa*, *K. maenniki*, *K. variabilis ichnusae* and *K. variabilis variabilis*. Successive weighting yielded nine equally most-parsimonious trees (CI 0.7091; RI 0.9003; RCI 0.6384; 33.23254 steps; strict consensus presented in Text-fig. 2B) that differ only in the interrelationships of two pairings, *K. ranuliformis* and *K. latidentata*, and *K. walliseri* and *K. corpulenta*; all nine tree topologies are found among the 48 most-parsimonious trees recovered from the primary, unweighted, analysis. The nine competing trees represent every possible solution to the interrelationships within each of these two pairings, all of which are supported by zero length branches. Almost all of the unresolved components of the consensus trees are attributable to poorly known taxa. *K. corpulenta*, *K. v. ichnusae*, *K. latidentata* and *K. abrupta* (the last not contributing to conflict) are known from just one among the eight paired and one unpaired element positions that comprise the apparatus of kockelellid conodonts. Thus, rather than character conflict, the basis of poor resolution lies in an absence of data. To constrain the influence of the rogue taxa, they were excluded from the dataset and the analysis repeated, yielding two equally most-parsimonious trees that differed only in the relative relationships of *K. walliseri* and *K. amsdeni*, which are resolved in reciprocal positions in the two trees (CI 0.4757; RI 0.6949; RCI 0.3306; 103 steps; Text-fig. 2C). Reweighting yields a single most-parsimonious tree (CI 0.7175; RI 0.8936; RCI



TEXT-FIG. 2. Trees derived from stratigraphically unconstrained analysis of the cladistic dataset. A, strict consensus of 48 trees derived from preliminary, unweighted analysis of the dataset. B, strict consensus of nine trees derived from analysis of the dataset reweighted *a posteriori* according to the Rescaled Consistency Index (RCI) values for the characters in the preliminary unweighted analysis. C, tree derived from unweighted analysis of the dataset, excluding those taxa known only from P₁ elements; the two trees differed in the relative positions of *Kockelella walliseri* and *Kockelella amsdeni*; *a posteriori* reweighting resulted in a single tree in which *K. amsdeni* was resolved as the more derived of the two taxa.

0.6412; 32.75476 steps; Text-fig. 2C) in which *K. amsdeni* is resolved as more derived than *K. walliseri*, compatible with one of the trees obtained from reweighting of the pruned dataset, and all nine of the trees arrived at from reweighting of the complete dataset (and, in corollary, nine of the 48 trees obtained from analysis of the original unweighted complete dataset). The alternative tree topology (Text-fig. 2C) is not compatible with any of the nine trees obtained from reweighting of the complete dataset, but is compatible with 15 trees that are slightly longer (CI 0.6896; RI 0.8907; RCI 0.6142; 34.17004 steps).

The difference in the original 48 trees represents a conflation of the conflicting positions of *K. amsdeni*, *K. variabilis ichnusae*, and the two pairs *K. ranuliformis* and *K. latidentata*, and *K. walliseri* and *K. corpulenta*. The phylogenetic positions of *K. amsdeni* and *K. vs. ichnusae* are resolved through successive weighting, reducing the competing topologies to nine, representing all possible solutions to the two remaining unresolved taxon pairs. Resolution within the two taxon pairs cannot be obtained because none of the competing solutions is supported by data. Thus, the nine trees are identified as optimal for the purposes of the analysis.

The results confirm that the vast majority of taxa assigned hitherto to the family Kockelellidae, and the genus *Kockelella*, constitute a monophyletic group, and that the Kockelellidae are members of the Order Ozarkodinida. However, there are some exceptions. *Polygnathoides*, a putative member of the ingroup, is resolved as part of the outgroup, in a position which suggests that it is a plesiomorphic member of the Order Ozarkodinida and that its similarities to members of the Kockelellidae are little more than ozarkodinid symplesiomorphies. *Ancoradella* is resolved as a member of the ingroup, confirming earlier suggestions to this effect (Link and Druce 1972; Serpagli and Corradini 1999) and rendering *Kockelella* paraphyletic; we suggest that this monospecific genus should in future be considered a junior synonym of *Kockelella*, though this judgement should await a full multielement reconstruction of *Ancoradella ploeckensis*. *Kockelella ortus sardoa* is also resolved among the outgroup, and among species of *Ozarkodina* in particular; it is more appropriately assigned to *Ozarkodina*. *Kockelella ortus absidata* and *K. ortus ortus* are resolved as successive sister taxa to all other members of the Kockelellidae and can be included within the clade. However, it is possible that this hypothesis will not stand up to scrutiny using additional outgroup taxa, specifically including more species of *Ozarkodina*. *K. o. absidata* and *K. o. ortus* are retained within the concept of the Kockelellidae for the purposes of this study. Finally, we note that none of the putative ancestors of the Kockelellidae are resolved as close relatives.

The results of the analysis are also interesting in more general terms, with reference to the question of whether

multielement taxonomy is necessary for phylogenetic reconstruction. Donoghue (2001) demonstrated that although contemporary conodont phylogenies are based almost exclusively on the characteristics of the P₁ element position, at least with regard to the Late Devonian palma-tolepidids, the majority of phylogenetically informative characters are to be found in element positions other than the P₁. Of the 49 phylogenetic informative characters utilized in this analysis, only 26 are based on P₁ element position, a clear indication that although this element position is integral to phylogenetic reconstruction, alone it is not sufficient in this endeavour. The remaining 23 characters are concentrated on the P₂ position especially. Most of the synapomorphies of the Kockelellidae are present on the P₁ element, re-enforcing the importance of characteristics of this element position not only for taxonomy, but also in the systematics of Kockelellidae.

CLADOGRAM-STRATIGRAPHY CONGRUENCE: CLADISTIC ASSESSMENT OF FOSSIL RECORD COMPLETENESS

The fit of stratigraphy to a cladogram can be determined both qualitatively and quantitatively by calibrating the branches of a cladogram to the stratigraphic range of the taxa that the branches subtend ('X-trees' in the terminology of Eldredge 1979); successive sister taxa and sister groups then provide a series of corroborative tests of the early fossil record of one another. Because sister taxa derive from a common ancestor, the first appearance of both lineages in the fossil record should be synchronous. Thus, gaps in the early fossil record of taxa (so-called 'ghost lineages'; Norell 1992) can be inferred.

This can be assessed qualitatively, but a variety of metrics are also available to assess quantitatively the degree of congruence. The most widely employed of these are the Stratigraphic Consistency Index (SCI; Huelsenbeck 1994) and the Relative Completeness Index (RCI; Benton and Storrs 1994); more recently, the Gap Excess Ratio (GER) has been developed by Wills (1999). The SCI assesses the degree to which the hierarchical branching of a cladogram is congruent with the appearance of taxa in the fossil record (Huelsenbeck 1994).

$$\text{SCI} = \frac{\text{number of stratigraphically consistent nodes}}{\text{total number of nodes}}$$

The Relative Completeness Index (RCI; Benton and Storrs 1994) goes beyond determining whether or not cladogram branching order is stratigraphically consistent and actually attempts to measure the overall level of inconsistency in a tree. This is achieved by quantifying the ghost range implied by the difference in age between the ages of the

origin of branches subtending sister taxa, and dividing this value by the observed range length. The RCI is given by the complement of this value expressed as a percentage.

$$\text{RCI} = \left\{ 1 - \frac{\Sigma(\text{implied ghost range})}{\Sigma(\text{stratigraphic range})} \right\} \times 100\%$$

Thus, while the RCI is based on the identification and existence of ghost ranges and attempts to quantify degree of incompleteness, the SCI refers only to the known stratigraphic ranges of taxa and assesses only gross congruence between cladogram branching order and appearance of taxa in the fossil record.

The Gap Excess Ratio (GER; Wills 1999) combines aspects of both SCI and RCI into a metric that expresses the proportion of total implied ghost range necessitated by the constraints of a cladogram. The GER is calculated as follows:

$$\text{GER} = 1 - \frac{(\text{MIG} - G_{\min})}{(G_{\max} - G_{\min})}$$

where MIG is the sum of the implied ghost ranges, G_{\min} is the sum of minimum possible ghost ranges (i.e. the implied ghost ranges from a hypothesis of relationships based solely upon stratigraphic order) and G_{\max} is the maximum possible sum of ghost ranges (obtained by summing the difference in origination times between the oldest taxon and all other taxa). GER values range between 0.00 and 1.00, where MIG is equal to G_{\max} (worst possible) and G_{\min} (best possible), respectively.

SCI, RCI and GER metrics were calculated using GHOST 2.4 (Wills 1999). The stratigraphic ranges of taxa are determined on a presence/absence basis with reference to a timescale divided into time bins of equal length, referred to below as temporal spacing. Because the taxa included in the analysis have been used widely in biostratigraphy their stratigraphic ranges are more finely and accurately resolved than is normally possible. Thus, the temporal spacing applied herein is considerably shorter than has been utilized hitherto in assessments of cladogram-stratigraphy congruence (e.g. Wills 2001) and is based on the graphic correlation composite standard developed for the Silurian by Kleffner (1995), revised after the time scale of Tucker and McKerrow (1995), where each time unit averages to approximately 300,000 years. The stratigraphic ranges of taxa are taken from Aldridge (1972), Barrick and Klapper (1976), Kleffner (1995), Jeppson (1997), Serpagli and Corradini (1999) and Zhang and Barnes (2002). Stratigraphy and data files used in GHOST analyses are presented in the Appendix (section 1).

Results

The stratigraphy-calibrated consensus cladogram for *Kockelella* is presented in Text-figure 3. This reveals signifi-

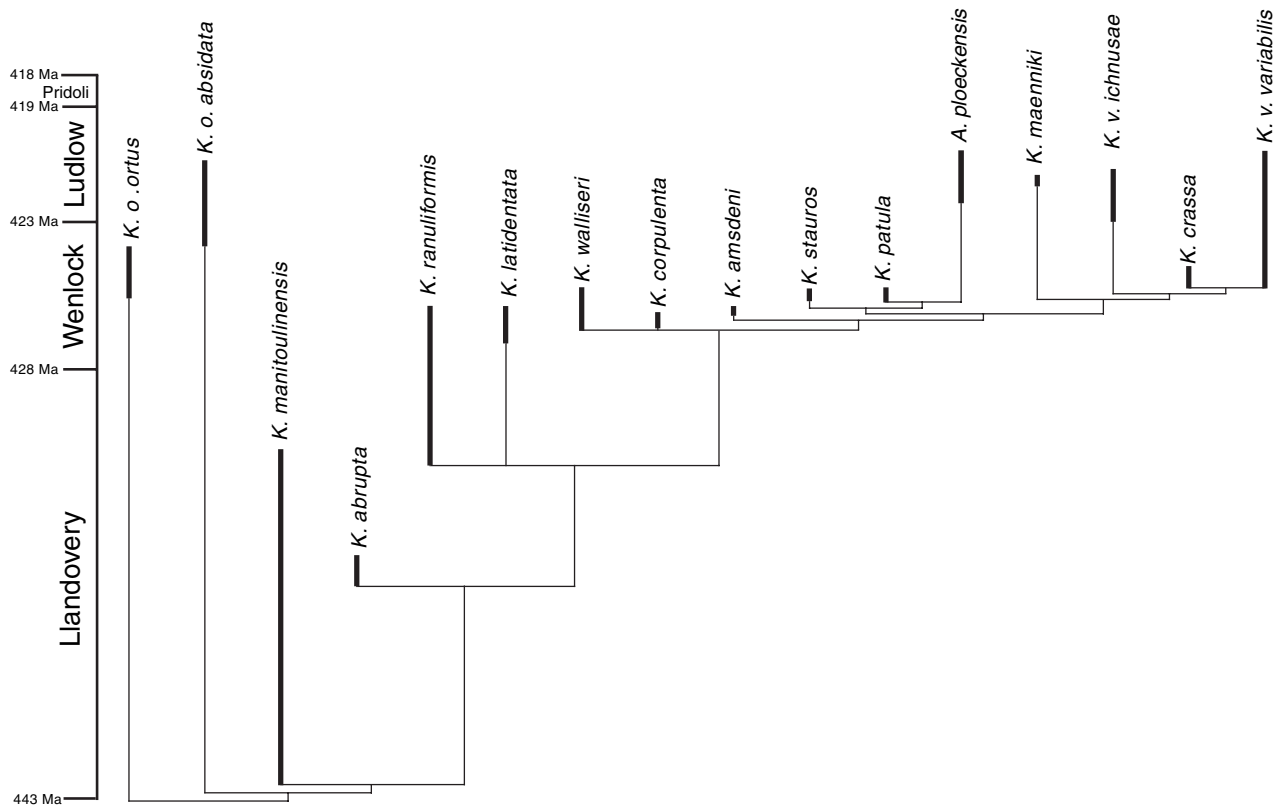
ficant ghost lineages throughout the tree, and particularly along the branches subtending the taxa *Kockelella abrupta*, *K. ranuliformis*, *K. walliseri* and their respective sister groups, implying that there are very significant gaps in the fossil record of the Kockelellidae. Results of the quantitative assessments of cladogram-stratigraphy congruence for the nine optimal trees are presented in Table 2; these exhibit SCI values in the range 0.42–0.5 indicating that half, or slightly fewer, of the nodes in the cladogram are stratigraphically consistent; significance values of 1.5–16.5 indicate that some of these trees (2, 4, 5, 7, 8) exhibit significant ($P > 0.95$) stratigraphic congruence (relative to the permuted dataset) while the others exhibit a level of congruence that is certainly not significantly worse than can be achieved by randomly reassigning the data across respective trees. RCI values of –49 to –59 for the various trees indicate that the fossil record of the Kockelellidae is more gap than record. GER values of 0.78–0.80 indicate that the sum of ghost lineages required by these trees is not close to the minimum possible given the tree topology, but they are nevertheless high. Results from the permutation test for the RCI and GER analyses indicate that all trees are significantly better than randomized data ($P > 0.95$).

The results of this now standard approach to assessing fossil record completeness are somewhat contradictory. The contrasting signal from the SCI and GER metrics could indicate a rich, but significantly incomplete fossil record, the depressed SCI arising from a number of taxa with origination dates that approximate one another. However, the RCI appears to indicate that the kockelellid fossil record is only a very poor reflection of its evolutionary history. In either instance, the low SCI values indicate that stratigraphic data should definitely not be used as a guide to phylogeny reconstruction. However, because fossil record completeness is not the only variable in cladogram-stratigraphy incongruence, it is worth considering alternative explanations before reaching a conclusion.

Causes of incongruence between cladograms and stratigraphic data

Benton *et al.* (1999) identified some major causes of incongruence between cladistic hypotheses and stratigraphic data: (1) cladogram quality; (2) fossil record quality; (3) sampling density; and (4) stratigraphic problems and taxonomic focus. These are explored below as potential explanations of cladogram-stratigraphy incongruence in the fossil record of *Kockelella*.

Cladogram quality. The veracity of any hypothesis of relationships can always be questioned. However, in compar-



TEXT-FIG. 3. 'X'-tree for the Kockelellidae based upon the strict consensus of the nine optimal trees. Resolution of the polytomies has little implication for the extent of the total inferred ghost lineages.

ison with previously published hypotheses of relationships within *Kockelella* (Barrick and Klapper 1976; Serpagli and Corradini 1999) the hypothesis of relationships presented here provide the best explanation of the available morphological data.

Fossil record quality. All three cladogram-stratigraphy congruence metrics imply surprisingly low values for a group widely appreciated for its rich and well-documented fossil record. It is not possible to preclude the possibility that inaccurate dating of fossils is a contributing factor towards incongruence, given that the conodonts themselves invariably provide the dating, but this risk has been minimized by employing most of the stratigraphic range data from a graphical correlation composite standard (Kleffner 1995). While we have gone some way to control for, and exclude, the possibility of imperfect sampling of the fossil record, the possibility remains that there are systematic biases affecting the rock record itself, which particularly affect the fossil record of organisms whose distribution was facies controlled (Holland 1995), which appears to have been the case in *Kockelella* (Aldridge and Mabillard 1981; Armstrong 1990).

Sampling density. The nature of the relationship between cladogram-stratigraphy congruence metrics and sampling density (e.g. the number of taxa included in an analysis) remains problematic (Benton *et al.* 1999). However, analyses including all taxa, as here, must provide the most realistic assessment of fossil record quality. Tree balance is another known bias of these metrics such that the full range of SCI values is not open to fully balanced trees, and fully imbalanced (pectinate) trees will always show the minimum MIG and, thus, exhibit low RCI values (Sidall 1996, 1997; Wills 1999). All of our trees are extremely, but not completely, imbalanced and so it is possible that this is a contributing factor towards the low (negative) RCI scores.

Stratigraphic problems and taxonomic focus. Duration of taxa and temporal spacing of nodes affect both the SCI and the RCI (Hitchin and Benton 1997; Benton *et al.* 1999). If the nodes in the cladogram are dated too precisely, very low SCI and RCI values can be obtained, whereas if all nodes are found at the same temporal level, i.e. dated less precisely, misleadingly high scores can result (Benton *et al.* 1999). To test whether this applied to our analysis, the temporal spacing was increased and the

TABLE 2. Cladogram-congruence metric scores for the cladograms derived from stratigraphically constrained and unconstrained analysis. These metrics were calculated using GHOSTS 2.4 (Wills 1999).

Tree no.	Raw RCI	RCI & GER Sig.	Raw SCI	SCI Sig.	Raw GER
Unconstrained – fine time bins					
1	-59	2.7	0.428571	7.6	0.78389
2	-49	2.2	0.5	2.5	0.803536
3	-59	2.8	0.428571	16.5	0.78389
4	-59	2.8	0.428571	4.3	0.78389
5	-59	2.8	0.428571	4.3	0.78389
6	-59	2.8	0.428571	7.6	0.78389
7	-49	1.8	0.5	1.5	0.803536
8	-49	1.8	0.5	1.7	0.803536
9	-59	2.8	0.428571	8.2	0.78389
Unconstrained –coarse time bins					
1	-42.105263	2.8	0.428571	10.3	0.779923
2	-33.333333	2.1	0.5	4.2	0.799228
3	-42.105263	3	0.428571	22.6	0.779923
4	-42.105263	2.6	0.428571	6.3	0.779923
5	-42.105263	2.5	0.428571	6	0.779923
6	-42.105263	2.7	0.428571	10.6	0.779923
7	-33.333333	2.1	0.5	2.2	0.799228
8	-33.333333	2.1	0.5	2.1	0.799228
9	-42.105263	2.7	0.428571	11.2	0.779923
Constrained –fine time bins					
1	-18.75	1.4	0.6	0.7	0.846715
2	-17.857143	1.1	0.6	0.4	0.84854
3	-10.714286	0.8	0.6	0.6	0.863139
4	-18.75	1	0.6	0.7	0.846715
5	-18.75	1.1	0.6	0.5	0.846715
6	-9.821429	0.5	0.6	0.4	0.864964
7	-17.857143	0.8	0.6	0.6	0.84854
8	-10.714286	0.6	0.6	0.5	0.863139
9	-18.75	0.8	0.6	0.6	0.846715

cladogram-stratigraphy congruence metrics recalculated; the results are presented in Table 2. Less precisely dated nodes result in a modest increase of the RCI, and although SCI values are unchanged, fewer trees exhibit SCI values that are significantly better than random (2, 7, 8). Neither of these factors indicates that the temporal resolution of the analysis is introducing artefacts into the analysis. Another possible bias, identified by Benton and Storrs (1994), arises in the analysis of low-level taxonomic groups, such as species, where artificially low RCI values are achieved when range lengths approach the finest level of stratigraphic resolution. Given that the stratigraphic ranges of almost all the taxa included in our analysis extend through more than one time bin, this potential bias can be excluded.

Other sources of error: artefact. None of the potential biases outlined by Benton *et al.* (1999) obviously provides an adequate explanation for the mismatch between cladograms and stratigraphic data. An alternative interpretation

is that some ghost lineages are artefacts of cladistic analysis. This can arise for two (or more) reasons. First, spurious ghost lineages can be inferred because one of the basic assumptions of cladistic analysis, the monophyly of component taxa, has not been met. Thus, the inclusion of paraphyletic taxa leads to the inference of a ghost lineage in their sister group of duration equal to their own known stratigraphic range. Secondly, spurious ghost lineages can also be inferred where cladograms, which are only intended as explanations of the distributions of synapomorphies, are reinterpreted as phylogenies without further qualification other than calibrating the branching events to time using stratigraphic range data from the fossil record (so-called X trees; Eldredge 1979). This enforces a model or phylogenesis limited to cladogenesis, which may not be entirely appropriate (Bretsky 1979, among many others); this can be particularly problematic when undertaking cladistic analyses at the species level (see also Wagner 1995, 1998; Foote 1996; Paul 1998, 2003). In such instances, indices based on the existence of such ghost

lineages would not be an appropriate measure of the quality of the fossil record. Both factors would lead to disparity in the signal from RCI and GER metrics.

Before considering whether the analysis has been affected by such artefacts, the problem arises as to how to distinguish spurious ghost lineages from real gaps in the fossil record. It has been suggested that confidence intervals may be the most appropriate means of verifying ghost lineages. However, confidence intervals and the results of cladogram-stratigraphy congruence tests are not logically equable. Confidence intervals differ in that they do not incorporate phylogenetic assumptions in their formulation and assess the veracity of the fossil record on a taxon by taxon basis, providing inference of gaps in the range of known taxa. Meanwhile, cladogram-stratigraphy congruence tests assess the overall completeness of the fossil record, providing inference not only of gaps in the range of known taxa but also of the existence of unrecognized and unknown taxa, such as known taxa that have not, hitherto, been recognized as members of a particular in-group, or taxa that have yet to be discovered.

Thus, confidence intervals do not provide an appropriate test of ghost lineages inferred from cladogram-stratigraphy congruence tests. However, in contrasting the results of the two methods, it is possible to discriminate which component of an inferred ghost lineage can be attributed to one of these two types of fossil record incompleteness: (1) gaps in the fossil record of known taxa, determined directly from confidence intervals, and (2) gaps in the fossil record due to unrecognized or unknown taxa, determined by subtracting confidence intervals on range extensions from inferred ghost lineages.

CONFIDENCE INTERVALS

Confidence intervals estimate the 'true' stratigraphic range of a taxon within given a level of statistical confidence (e.g. 95%) and follow the common sense principle that the greater the number of stratigraphic/chronological levels at which a taxon has been recovered, the lower the probability that future discoveries will lie far beyond the currently known distribution. Strauss and Sadler (1989) provide the following formula for their calculation, expressed as a fraction of the known stratigraphic range:

$$(1 - \text{confidence level})^{-1/(\text{number of known fossiliferous horizons})} - 1.$$

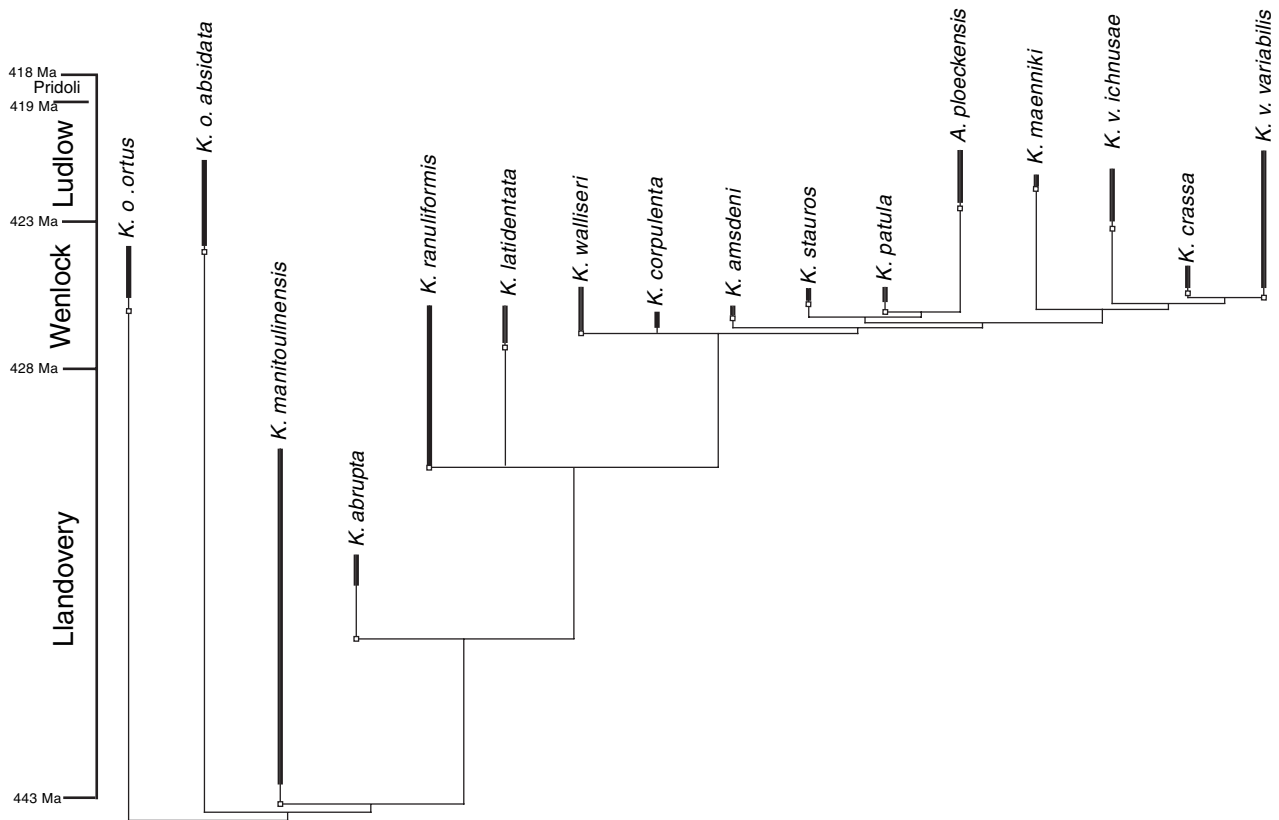
The calculation of confidence intervals requires a number of assumptions and, where these assumptions are not met, there are a variety of techniques that can be implemented to overcome such limitations. At the simplest level, the calculation assumes constant fossil recovery

potential, but techniques have been developed where recovery potential may vary, or where the assumption of continuous sampling is not achieved. Thus, it is possible to account for variable recovery potential that may result from, for example, biases in facies preservation arising from changes in relative sea level and affecting the distribution of organisms whose distribution is facies controlled (Holland 1995, 2000; Marshall 1997; Tavaré *et al.* 2002). It is also possible to account for strategies other than continuous sampling, which is particularly prevalent in micropalaeontology where sections are routinely sampled as a series of arbitrarily spaced discrete horizons (Weiss and Marshall 1999). Sampling strategies that are biased by the requirements of laboratory techniques, such as the sampling restricted to carbonates, also violate the constant recovery potential assumption and should be accounted for in confidence interval calculations. However, the assumptions required of such techniques are both non-trivial and overly simplistic, and can only be readily applied to stratigraphic ranges in local sections and are, thus, not compatible with our aim of assessing the degree to which a composite of global records reflects the evolutionary history of particular taxa. We follow the general method of confidence interval calculation with the caveat that some of the assumptions on which it is based may not be met and that our confidence intervals may be longer or shorter than would otherwise be anticipated.

A database of known stratigraphic occurrences of species of kockelellid on which confidence intervals were calculated, using the general method, is presented in the Appendix (section 2). Occurrences unsupported by illustrated examples of the taxonomic concepts followed were not included in the database. Stratigraphic occurrences in which the total number of fossiliferous horizons is unstated were recorded in the database as single occurrences.

Results and discussion

Confidence intervals on the stratigraphic ranges of in-group members of the Kockelellidae are presented in Text-figure 4 and the Appendix (section 2). These reveal that although the expected stratigraphic ranges of all taxa consistently exceed the observed stratigraphic range, in the vast majority of taxa these coincide approximately, thus providing confidence in the veracity of these taxa as zone fossils and their utility in biostratigraphy, which has been assumed previously only on the basis of repeatability and reproducibility. However, there are very significant exceptions to this overall observation. Most notably, the expected stratigraphic range of *Kockella abrupta* exceeds the known observed stratigraphic ranges by millions of years, indicating that we can have



TEXT-FIG. 4. 'X'-tree for the Kockelellidae based upon the strict consensus of the nine optimal trees. Small open boxes represent 95 per cent confidence intervals on the time of first appearance of the component taxa.

little confidence that future discoveries of this taxon will lie within or close to the known limits on its stratigraphic distribution.

Neither cladogram-stratigraphy congruence nor confidence intervals indicate that the fossil record of *Kockelella* is complete, but the results of these analyses infer degrees of incompleteness that vary very widely. Confidence intervals on the stratigraphic ranges of individual taxa in all instances indicate some prolongation of the known record, although in almost all instances the confidence intervals are sufficiently short to be considered beyond stratigraphic resolution. Even in those instances where a significant (i.e. greater than 5% of the known range) range extension is inferred, these are very minor in comparison with the ghost lineages inferred from stratigraphically calibrated cladograms, which suggest that the fossil record for this group represents considerably less than half of its evolutionary history, as evidenced by negative RCI values. Given the disparity in magnitude of the inferred missing record it must be concluded that the vast majority of the sum of the ghost lineages cannot be attributed to gaps in the fossil records of known taxa. Thus, the vast majority of the total sum of inferred ghost lineages must be attributed to hitherto unrecognized and/or unknown and/or to an analytical artefact. It is

potentially possible to evaluate, at least qualitatively, the probability that the remaining ghost lineages represent either unknown/unrecognized taxa or an analytical artefact with reference to the discovery curve for *Kockelella*.

DISCOVERY CURVES

Discovery curves are usually employed in ecological or palaeoecological studies as a means of determining the degree to which sampling of taxa is representative. As collecting of individuals begins, it is expected that the rate of discovery of new species will be very high, but as collecting continues the rate of new discoveries will slow progressively. Thus, in a cumulative plot of new discoveries against time, it is expected that the curve will be steep initially, reflecting the high probability of new discoveries through continued collecting in a poorly sampled record, eventually shallowing asymptotically and reflecting the reduced probability of new discoveries as the record is progressively more completely sampled. The utility of discovery curves has long been appreciated outside of palaeoecology and they have proven instructive in assessing the degree to which existing sampling of a group is representative of its fossil record (Paul 1982; though not necessar-

ily its evolutionary history as the fossil record itself can be affected by systematic bias, e.g. Holland 1995).

Text-figure 5A is a cumulative plot of *Kockelella* species descriptions against their date of publication (compiled on the basis of the data presented in the Appendix, section 2). The steep curve suggests that the diversity of *Kockelella* has been only very partially sampled and that continued collecting will be rewarded with the discovery of many more species. However, this plot is potentially misleading because it incorporates new taxa that were known from earlier discoveries (synonyms), and previously assigned to form taxa; these clearly do not represent discoveries of new taxa as a result of continued collecting effort, but are merely the recognition of additional taxa among the existing database. The revised plot (Text-fig. 5B), which dates the discovery of new taxa to the earliest description of an assigned synonym, suggests that sampling of the record has matured. This plot can be filtered further for taxa that have been erected as a result of splitting known taxa hitherto assigned to *Kockelella*, as these new taxa cannot be considered 'genuinely new'. The flat profile of the revised curve (Text-fig. 5C) further suggests that the sampling of *Kockelella* is mature and that continued effort will not prove profitable.

Finally, to exclude further the possibility of artefacts in the discovery curve, it is worth considering whether the flattening of the filtered discovery curves, reflecting the continued lack of new discoveries, is an artefact of diminishing collector effort, rather than from diminishing returns of continued effort maintained at approximately the same level. This possibility can be tested by plotting collector effort, represented by number of new publications describing new records of *Kockelella*, against time. The resulting plot (Text-fig. 5D; data from the Appendix, section 2) reveals that collector effort has been episodic over time but that, most significantly, there is no evidence of diminishing collector effort co-ordinate with diminishing discoveries of new taxa.

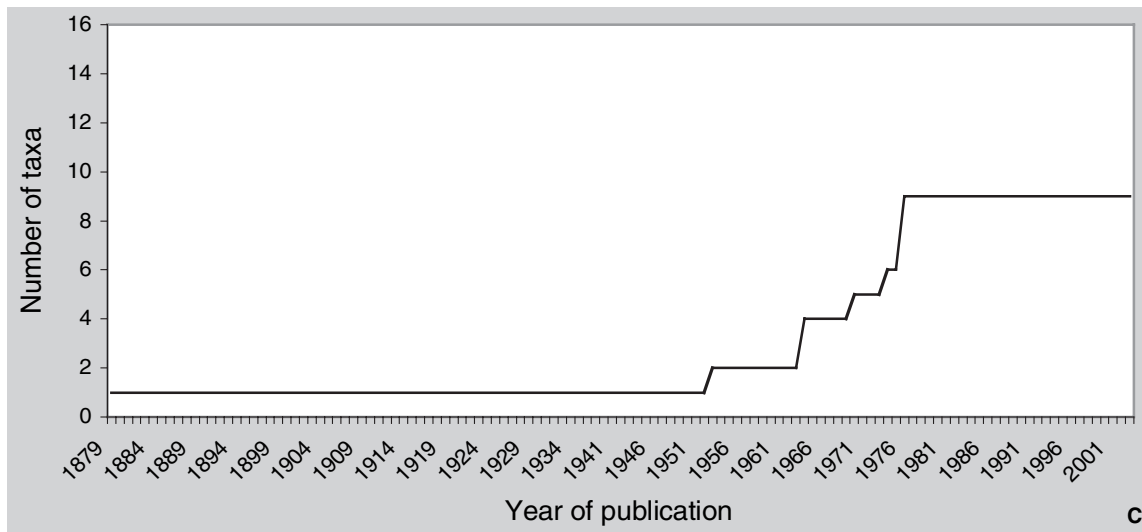
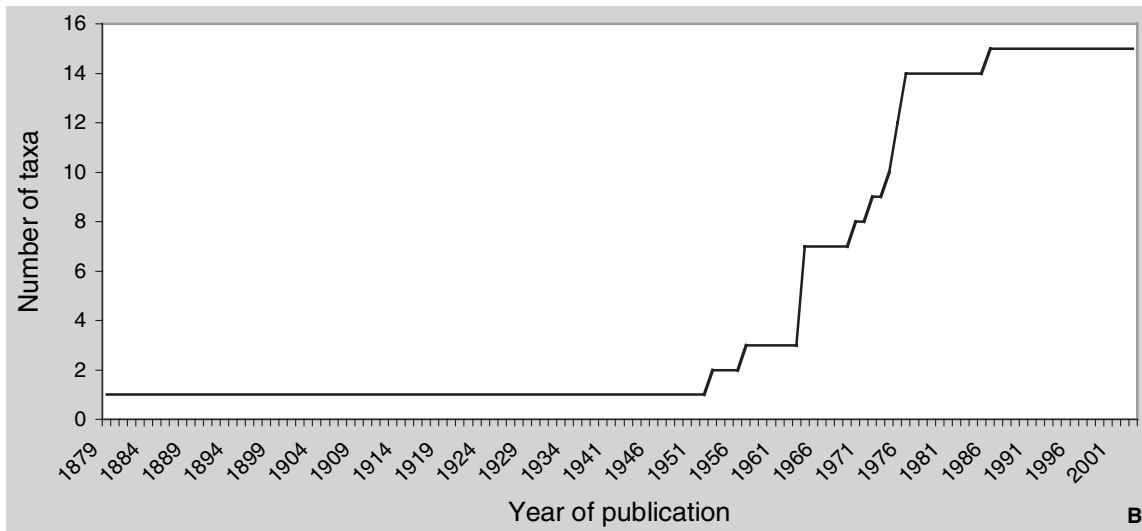
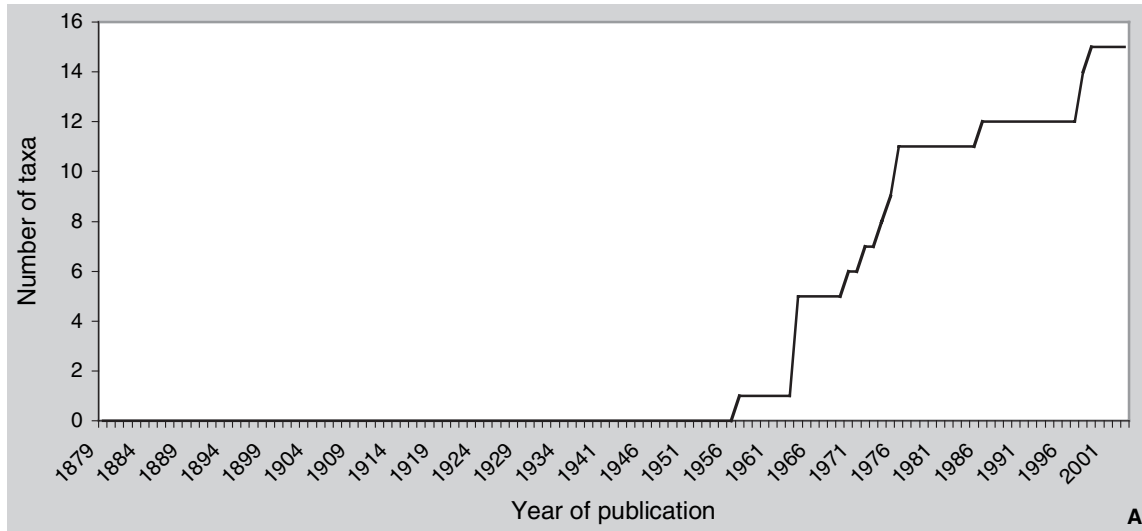
With all artefacts and potential artefacts controlled for, we may conclude from the shape of the discovery curves that knowledge of the fossil record of *Kockelella* is now mature. Thus, it is unlikely that the vast majority of the ghost lineages (that portion remaining after subtraction of confidence intervals) are valid. Thus, it is pertinent to consider sources of analytical artefacts, rather than fossil record completeness, as an explanation.

ANALYTICAL ARTEFACTS IN GHOST LINEAGE INFERENCE: CLADOGRAMS VERSUS PHYLOGENIES

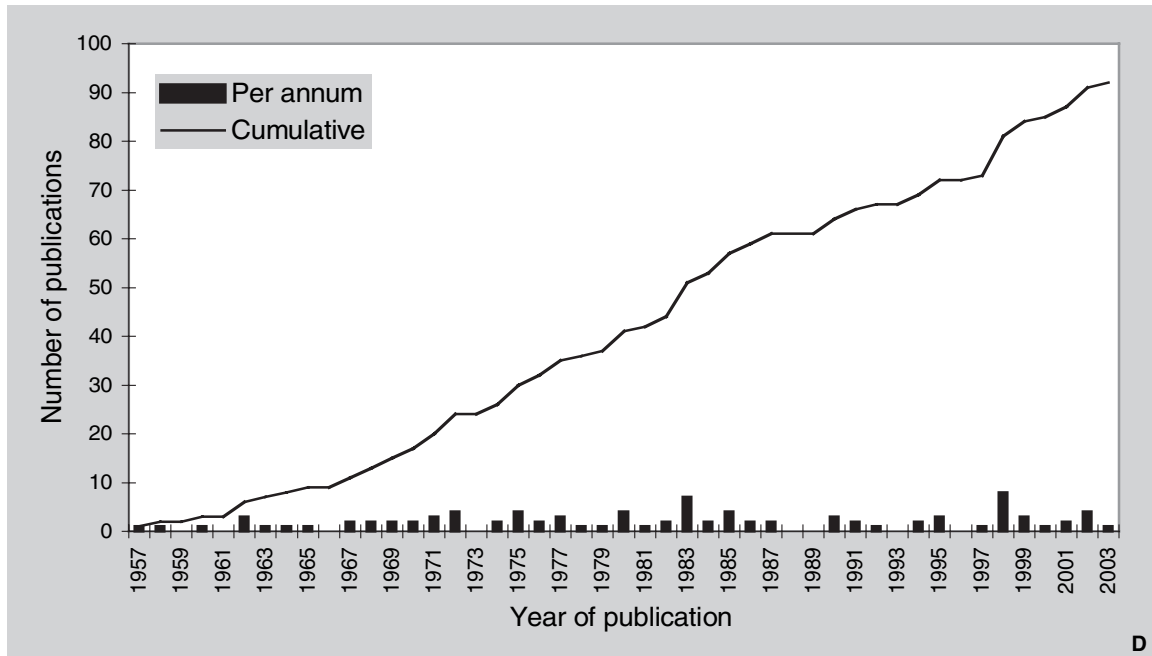
At least one further possibility remains, that incongruence between cladograms and stratigraphic data arises because

cladograms are abstractions of phylogenetic trees and spurious ghost lineages are inferred because of the artefact of considering only relative relationships, to the exclusion of absolute relations. The problem, or lack thereof, in considering direct, or ancestor–descendant, relationships in phylogenetic analysis is an old one (e.g. Engelmann and Wiley 1977 versus Szalay 1977; Eldredge 1979 versus Bretsky 1979). In general, absolute relationships are superfluous, such as in attempts to trace character evolution, where it is more appropriate to follow the evolution of characters through the inferred conditions of hypothetical common ancestors of successive sister groups. This practice neither denies the contribution of potential ancestors (conventionally identified as taxa lacking autapomorphies, e.g. Engelmann and Wiley 1977; Smith 1994), nor is it handicapped by potentially spurious identifications of ancestors. Absolute relationships are also of little concern when attempting to uncover the interrelationships, or when assessing the completeness of the fossil record of higher taxa, which do not have ancestors (Engelmann and Wiley 1977).

However, in attempting to assess fossil record completeness at the species level and/or in attempting to constrain the time of origin of a group, a consideration of absolute relationships is a necessity. This is because, unlike higher taxa, populations and, perhaps, species can be considered to have ancestors (Engelmann and Wiley 1977; but see Nelson 1989). Thus, it is not possible to assume monophyly of taxa at the species level, which is one of the basic requirements of both cladistic analysis and ghost lineage inference. Analyses of the completeness of the fossil record at species level are likely therefore to be subject to the same kind of artefact introduced by paraphyletic higher taxa, and the controls routinely employed to test for paraphyly in higher taxa are not readily applicable to species. Although species cannot strictly be considered ancestral because they arise from differentiation among populations rather than from other species (Wiley 1981), it is a reality that many, particularly fossil, species will include ancestral populations. Such taxa will be found among metataxa, i.e. plesiomorphic grades of organisms united by convention, rather than biological integrity, which cannot be further subdivided on the basis of available evidence (but which may be further resolved on the basis of additional data). Metataxa are recognized operationally on the basis of an absence of autapomorphies, and potentially ancestral groups can be identified among metataxa on the basis of stratigraphic evidence (Smith 1994). Such consideration of potentially ancestral groups, regardless of whether any are identified, has the effect of producing what Eldredge (1979) termed an 'A' tree, which is equivalent to a traditional phylogenetic tree. More to the point, it has the effect of



TEXT-FIG. 5



TEXT-FIG. 5. A–C, discovery curves for the Kockelellidae; D, research effort over time for the Kockelellidae. A, cumulative plot of the discovery of new species and subspecies of kockelellid. B, cumulative plot of the discovery of new species and subspecies of kockelellid, corrected such that the date of discovery of new taxa is referred to the date of description of the earliest synonym. C, cumulative plot of the discovery of new species and subspecies of kockelellid, corrected such that the date of discovery of new taxa is referred to the date of description of the earliest synonym, and such that only genuinely new discoveries are considered (i.e. by excluding ‘new’ taxa identified by massaging the concept of existing taxa). D, research effort, measured according to the number of publications describing ‘new’ collections of kockelellids, plotted per annum and as a cumulative total.

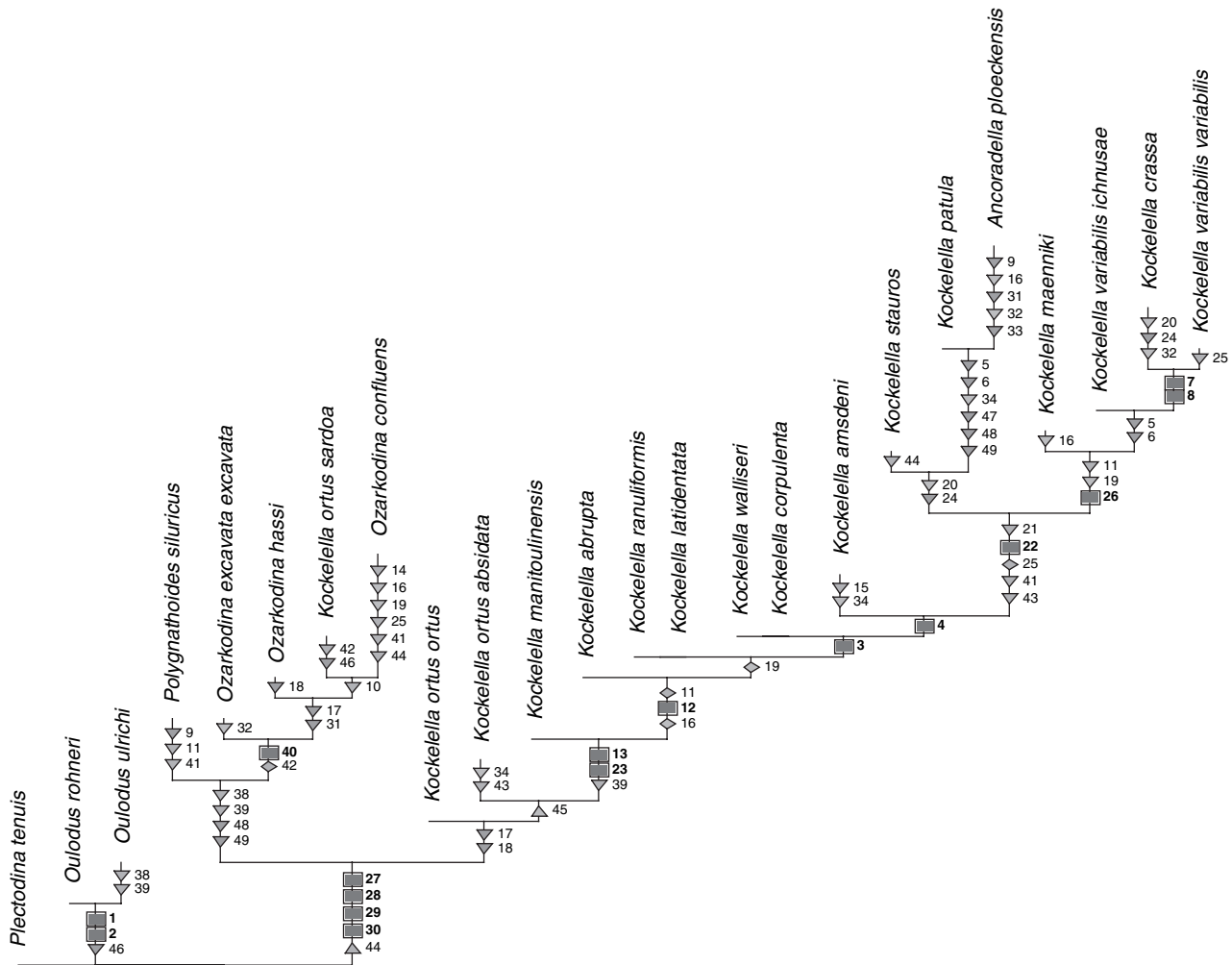
excluding ghost lineage artefacts from assessment of fossil record completeness.

Returning to *Kockelella*, it is possible to identify a number of metataxa by examining the character change tree for terminal branches lacking apomorphies (autapomorphies) (Text-fig. 6); these are *K. abrupta*, *K. corpulenta*, *K. latidentata*, *K. manitoulinensis*, *K. ortus ortus*, *K. patula* and *K. variabilis ichnusae*. Among these species, the stratigraphic range of *K. v. ichusae* is incompatible with its identification as including groupings potentially ancestral to its sister group. *K. latidentata* and *K. corpulenta* are problematic in that they not only operationally lack autapomorphies but also all possible cladistic solutions to their relationship to *K. ranuliformis* and *K. walliseri*, respectively, are supported by zero-length branches. However, their morphology plus stratigraphic range are compatible only with a sister-taxon relationship within their respective taxon pairings, or as more derived than their respective taxon pairs and ancestral to their sister-groups. Given that *K. latidentata* can only be distinguished from *K. ranuliformis*, and *K. corpulenta* from *K. walliseri* on the basis of gerontic specimens (i.e. juveniles of *K. latidentata* and *K. corpulenta* fall within the taxonomic concept of *K. ranuliformis* and *K. walliseri*, respectively), and that the

operationally apparent autapomorphies of *K. ranuliformis* and *K. walliseri* pertain to unknown characteristics of *K. latidentata* and *K. corpulenta*, the solution most parsimonious with stratigraphic data (equally parsimonious with morphological data) is to consider *K. ranuliformis* as ancestral to *K. latidentata* and *K. walliseri* as ancestral to *K. corpulenta*. The resulting ‘A’-tree (Text-fig. 7) demonstrates the effect upon inferred ghost ranges of considering metataxa; the total sum of implied gap in the record is significantly diminished through the abolition of a ghost lineage subtending the sister groups to *K. manitoulinensis*, *K. abrupta* and *K. patula*.

Remaining ghost lineages and the addition of ad hoc assumptions

Significant ghost lineages remain that are not corroborated by confidence intervals. In particular, these include the ghost lineage subtending the sister-group to *Kockelella ranuliformis* and *Kockelella latidentata*, which is imposed exclusively by the stratigraphic range of *K. ranuliformis*, interpreted previously as the direct ancestor of many members of its sister-group. These hypotheses of ancestry



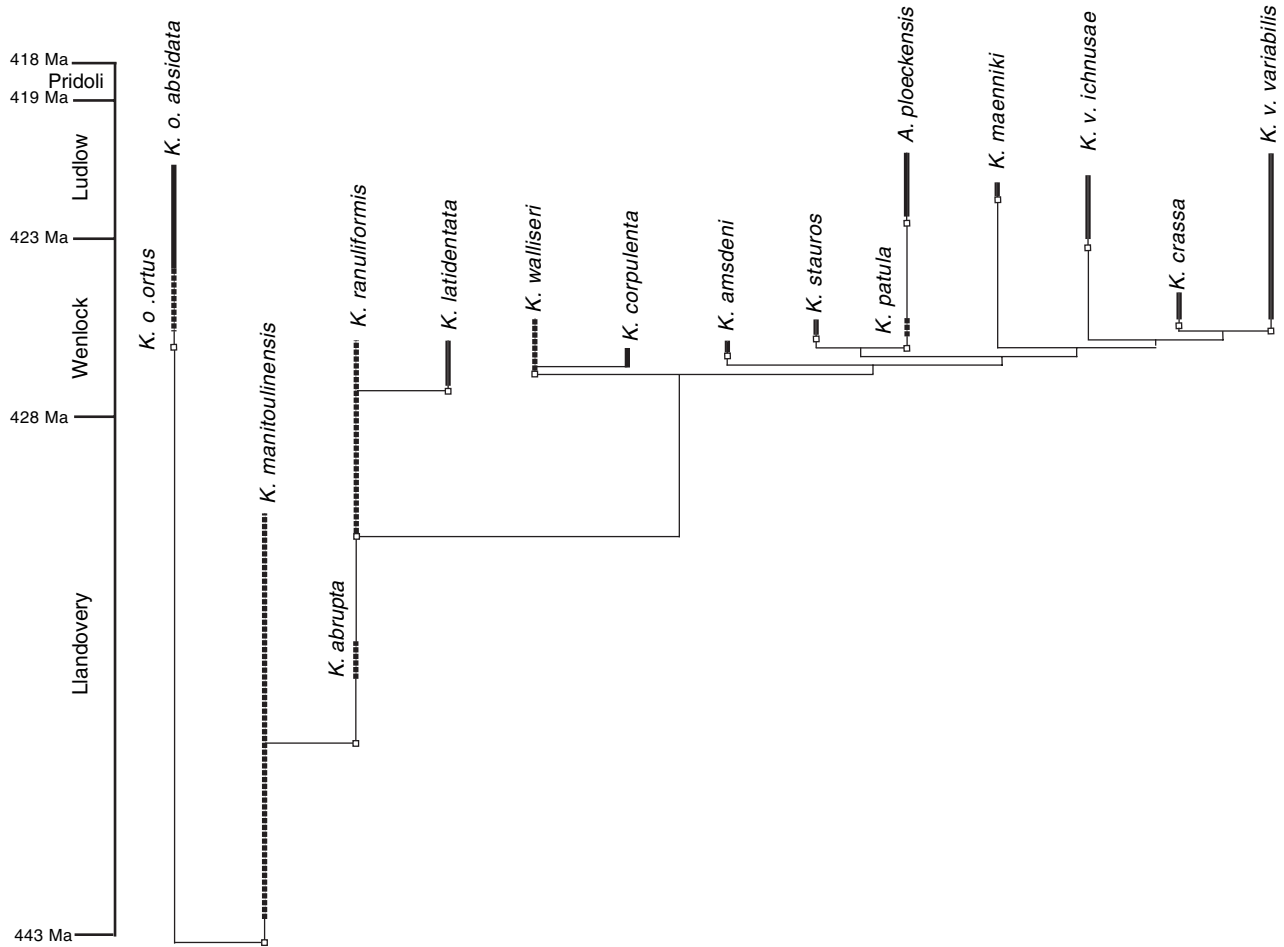
TEXT-FIG. 6. Character changes for the consensus of the nine optimal trees derived from stratigraphically unconstrained analysis. Rectangles represent synapomorphies, triangles represent homoplastic character changes (upward facing triangles reflect character changes that are reversed above, downward facing triangles represent character changes that are reversed outside the clade/taxon in question), diamonds represent homoplastic character changes above and outside; in all instances the number adjacent to the character symbol represents the number in the character descriptions.

are precluded on the identification of a single, homoplastic, autapomorphy of *K. ranuliformis*, the presence of a deeply excavated basal cavity extending beneath the 'posterior' process of the P_1 element (character 20).

Kockelella variabilis ichnusae has previously been identified as a descendant of *K. variabilis variabilis* (Serpagli and Corradini 1999) and within such a framework, a plausible case could also be made for *Kockelella maenniki*; such hypotheses of relationship would erase significant, uncorroborated, ghost lineages, but appear to be precluded by the absence of processes F and G from the P_1 elements of *K. maenniki* and *K. v. ichnusae*. These characters are acquired during the latest stages of ontogeny of the P_1 elements of *K. v. variabilis* (and its sister taxon, *Kockelella crassa*), after passing through a sequence common to the P_1 elements of *K. maenniki* and *K. v. ichnusae*. Thus, it is

possible that the absence of these characters could be the result of secondary loss through pedomorphosis.

Either or all of these additional assumptions could be accepted in reconstructing the phylogeny of *Kockelella* and in attempting to assess the completeness of its fossil record. This would serve to bring the phylogenetic scheme into still closer accord with stratigraphic data than was indicated by the original X tree, at the cost of a few additional steps in the parsimony argument. After all, we acknowledge that evolution may proceed less frugally than strict parsimony. However, ghost lineages inferred elsewhere in the phylogeny of *Kockelella* cannot be as easily explained away and if we are to accept the existence of such gaps, it is perhaps more advisable and scientific to challenge our desire to tidy away such aberrations and to challenge their existence, by increasing the sampling den-



TEXT-FIG. 7. 'A'-tree for the Kockelellidae. Metataxa are denoted by coarse dashed lines; thin solid lines and boxes represent confidence intervals on the first appearance of a taxon.

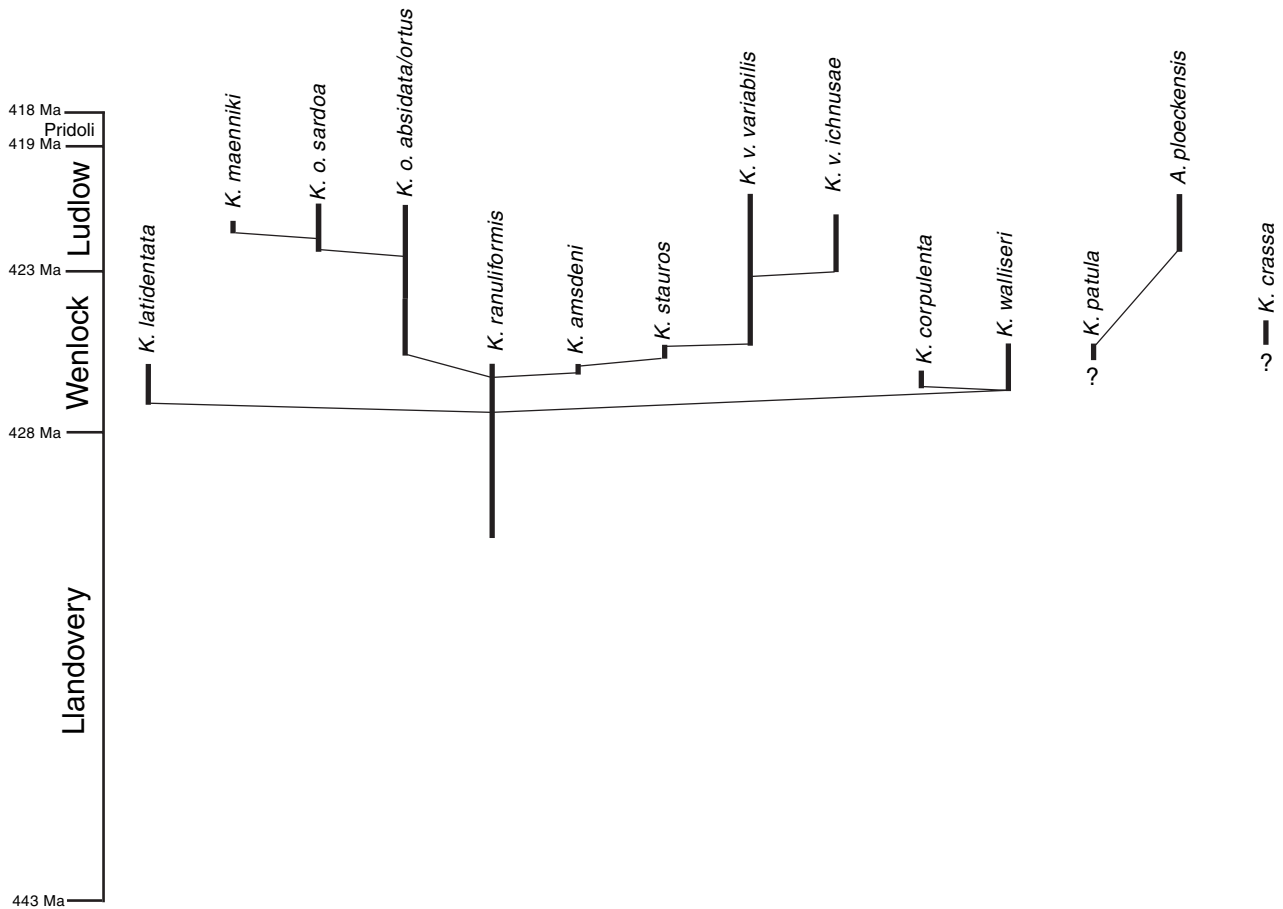
sity of the fossil record, by challenging the cladistic hypothesis with full multielement reconstructions for those taxa whose apparatus is currently known only in part, and through more refined taxonomic analysis of identified metataxa.

Comparison with established phylogenies of the Kockelellidae

It is pertinent to consider the results of the phylogenetic analysis with respect to phylogenies derived hitherto following the practice of evolutionary palaeontology. Two attempts have been made to devise a phylogeny for *Kockelella*, first by Barrick and Klapper (1976), then subsequently developed more fully by Serpagli and Corradini (1999); because the latter encompasses the former we shall confine comparison to the Serpagli and Corradini (1999) phylogeny (Text-fig. 8).

The first point to note is that even the phylogeny devised by evolutionary palaeontological principles indicates that the fossil record of the Kockelellidae is incomplete. This is particularly obvious in the case of *Kockelella crassa* and its proposed descendants, and *Kockelella patula* and its proposed ancestor and descendant. These inferred gaps notwithstanding, the Serpagli and Corradini (1999) phylogeny requires far fewer gaps in the known fossil record of the Kockelellidae than do either the X- or the A-trees presented herein.

Greater stratigraphic congruence, but at what price? To constrain the impact of increased stratigraphic congruence upon morphological evolution, we devised a cladogram compatible with the Serpagli and Corradini (1999) phylogeny (Text-fig. 9A) and implemented it as a constraint on the analysis of the cladistic dataset, with the aim of finding the shortest compatible trees. In doing so we excluded *K. crassa* from the constraint tree because Serpagli and Corradini (1999) were com-



TEXT-FIG. 8. Phylogeny for the Kockelellidae according to Serpagli and Corradini (1999), stratigraphic ranges of certain taxa corrected and plotted according to a revised timescale.

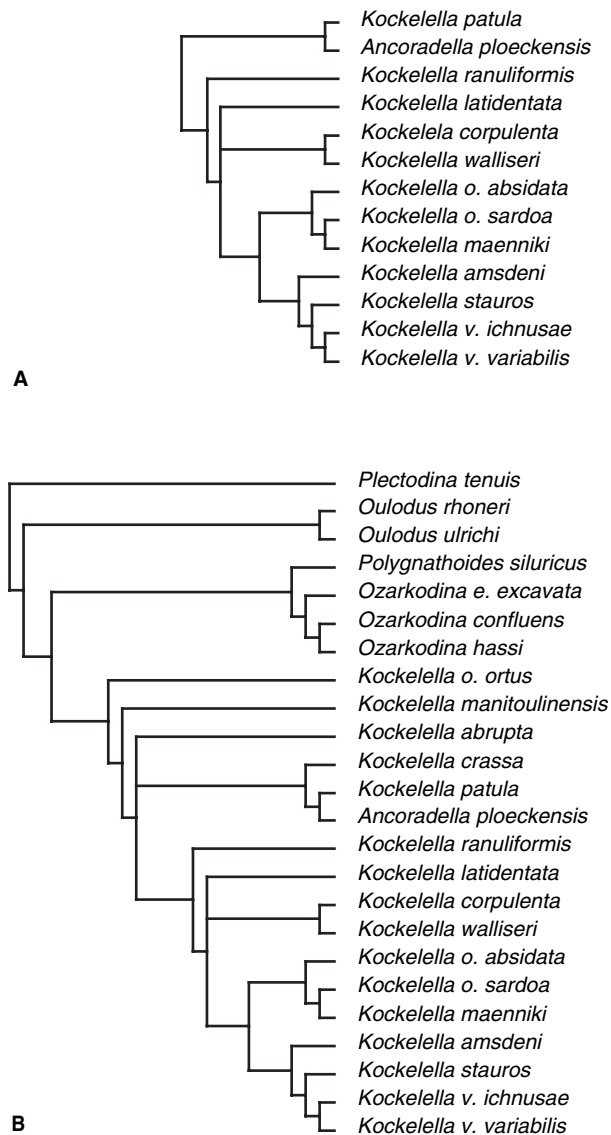
pletely unable to resolve its relationships to any other formal member of the Kockelellidae. Thus, during the subsequent constraint analysis, resolution of the interrelationships of *K. crassa* is unconstrained; this diminishes the severity of the morphological-congruence test of the Serpagli and Corradini (1999) phylogeny. *Kockelella patula* and *Ancoradella ploeckensis* were placed at the base of the constraint tree to reflect the view that they represent a 'different stock' to the remainder of the Kockelellidae (Serpagli and Corradini 1999, p. 277). Constrained analysis of the dataset produced nine equally most-parsimonious trees at 135 steps (CI 0.3630; RI 0.5612; RC 0.2037; the strict consensus is presented in Text-fig. 9B). This is 27 per cent longer than the most-parsimonious trees derived from the unconstrained analysis; it is also a good deal less parsimonious than the *ad hoc* solutions to greater stratigraphic congruence discussed above. These trees do perform marginally better in all stratigraphic congruence metrics (all trees achieving significant congruence in all metrics; Table 2; GHOST file presented in

Appendix, section 1), although this is not altogether surprising given that they were constructed in large part on the basis of stratigraphic data.

To put the disparity in tree length into perspective, we can compare differences in the levels of homoplasy in morphological evolution as implied by the constrained and unconstrained most-parsimonious solutions to the levels expected of a dataset containing the same number of taxa. Based on an empirical study, Sanderson and Donoghue (1989) resolved that there is a positive relationship between the number of taxa included in a cladistic dataset and the consistency index, which is the reciprocal of inferred levels of homoplasy. The expected consistency index can be calculated as follows:

$$\text{CI} = 0.90 - 0.022(\text{number of taxa}) + 0.000213(\text{number of taxa})^2.$$

For the cladistic dataset presented herein the expected consistency index value is 0.494688. The value of the consistency index for the most-parsimonious trees derived



TEXT-FIG. 9. A, constraint tree compatible with the Serpagli and Corradini (1999) kockelellid phylogeny. B, strict consensus of the nine optimal trees compatible with the constraint tree and according to the same data matrix utilized in the stratigraphically unconstrained analyses.

from the unconstrained analysis is slightly less than this expected value (CI 0.4667), but it falls well within the range of variation seen in the dataset upon which Sanderson and Donoghue's regression line is derived. In contrast, the consistency index value for the most-parsimonious trees from the constrained analysis (CI 0.3630) is considerably lower than the expected value, falling outside the envelope delimited by the Sanderson and Donoghue (1989) dataset.

This all appears to bear out a perception among evolutionary palaeontologists that homoplasy is rife, partic-

ularly in groups utilized in biostratigraphy, and a major limitation on phylogenetic inference (e.g. Lazarus and Prothero 1984). However, levels of inferred homoplasy are contingent upon a particular hypothesis of relationships and it is just as likely that the prevalence of homoplasy is not so great, that many inferred homoplasies are misidentified homologies, precluded from interpretation as such by a misplaced reliance upon the *a priori* use of stratigraphic constraint in phylogenetic reconstruction.

Is the fossil record of conodonts any more or less complete than any other fossil group?

At the outset of this analysis we observed that the conodont fossil record is generally considered sufficiently complete for stratigraphic data to be not just useful but vital guides to reconstructing evolutionary relationships. In the absence of any other supporting evidence, this implicit assumption must be based in biostratigraphic experience; indeed it is an assumption common to all fossil groups that are exploited for their biostratigraphic utility. The fossil record of groups that lack biostratigraphic utility, such as most vertebrate clades, is generally considered with considerable circumspection and the drive for an atemporal approach to phylogenetic reconstruction has been most forcibly argued for by specialists in these fields. But, using the same atemporal approaches to phylogenetic reconstruction, are the fossil records of groups that are biostratigraphically useful, such as conodonts, any better than those that are not? Of course, our analysis represents just one small clade that may hardly be representative of conodonts let alone all such groups exploited for their biostratigraphical utility. Nevertheless, it is interesting to compare the stratigraphic congruence metrics derived from cladistic analysis of this entire clade to the average results derived from the fossil record. These results compare favourably to an average of stratigraphic congruence analyses, based on 1000 cladograms derived from a full range of fossil groups (Benton *et al.* 2000); the SCI of our unconstrained analysis is slightly lower than the average (0.42–0.5 vs. 0.55), while the GER of our unconstrained analysis is significantly higher than the average (0.78–0.8 vs. 0.56). The RCI of our unconstrained analysis deviates significantly from the fossil record average (–49 to –59 vs. +31); the reason for this lies, almost certainly, with the number of metataxa included in our analysis, which introduce ghost lineage artefacts, and also contribute to a depressed SCI, as discussed above. The disparity in results is based, more than anything, in the disparity in the taxonomic scale of our analysis versus those included in the study by Benton *et al.* (2000). Although, metataxa are not the preserve of fossil species (Smith 1994), they have been

more readily identified among higher taxa, and revised. Thus, analyses of higher taxa, and of distantly related lower taxa, are much less likely to be prone to the kinds of analytical artefacts discussed herein.

CONCLUDING DISCUSSION

We hope to have shown that the fossil record of the conodont clade *Kockelella* is incomplete. This has been demonstrated through the use of phylogenetic (cladogram-stratigraphy congruence) and aphylogenetic (confidence interval) approaches to assessing the completeness of the fossil record. Given the close temporal proximity in the origination of many taxa included in these analyses, both approaches indicate that stratigraphic data are a poor guide to relationships. Nevertheless, the two approaches reach conclusions concerning the extent to which the fossil record of the Kockelellidae is incomplete, which differ by as much as an order of magnitude. It is possible that this discrepancy arises because aphylogenetic methods assess only the quality of the record of a known taxon, while phylogenetic methods assess this and also allow for the existence of unknown taxa and for known taxa of unrecognized significance. However, we have resolved that much of the discrepancy arises from the use of raw cladograms, calibrated to time and stratigraphy (so-called 'X-trees'), but without further qualification, in assessing the completeness of the fossil record. This is a problem because many fossil taxa are metataxa (Smith 1994) that, if left unrecognized and unconsidered, can lead to spurious inference of missing fossil record. The consideration of metataxa as paraphyletic assemblages of hitherto unrecognized component monophyletic taxa and, potentially, ancestors, leads to the conversion of X-trees to A-trees, which are equivalent to phylogenies in the general sense. Confidence intervals can then be used to determine the likely time of origination of descendants from among metataxa, therein controlling for incompleteness in the record.

By implication, clade-stratigraphy congruence metrics are handicapped if they fail to entertain the presence of metataxa. Indeed, in light of the potential artefact introduced by metataxa, the utility of such metrics is reduced to assessing the relative merits of competing cladograms, as the implied ghost lineages of X-trees will vastly exceed that implied by A-trees. However, although metataxa are not the preserve of species (Smith 1994), metataxa of higher taxonomic status are, in practice, more readily identifiable because their paraphyletic nature is implicit in their definition and, as such, they are usually removed or remedied *a priori* to preclude the introduction of the artefact in cladistic analyses. Thus it is unlikely that most assessments of fossil record quality that entertain higher taxa, or consider

only distantly related species as proxies for higher taxa, are subject to this kind of artefact. This equates well with the observation that species-level cladograms of fossil taxa exhibit significantly poorer correlation to stratigraphic data than do cladograms of higher taxa (Benton and Storrs 1994). Comprehensive species-level analyses of fossil clades are relatively uncommon, at present, but those that have been undertaken with the aim of assessing fossil record quality should be re-evaluated in this light. This is particularly so in instances where a high inferred fossil record quality is relied upon for accessory theories, such as the fossil record of the synapsid–diapsid divergence and its widespread use in molecular clock calibration.

Finally, we hope to have shown that the commonplace criticisms of cladistics are misplaced, conflate theory with practice, and character analysis with phylogeny reconstruction. Cladistic analysis is not incompatible with recognition of ancestor–descendant lineages, it is just that for most practical purposes such hypotheses of relationships are a superfluous inferential step. Clearly then, cladistic analysis does not prescribe cladogenesis as the sole mechanism of evolutionary change; in fact it does not prescribe any pattern of evolutionary change as it is not the objective of cladistic analysis to reveal anything concerning evolutionary processes, although these may be inferred through the construction of phylogenies – which are abstractions of cladograms. Furthermore, cladistic analyses do not preclude the use of stratigraphic data in phylogeny reconstruction; whether stratigraphic data are employed or eschewed in the process of phylogenetic reconstruction is quite a distinct matter. Only cladistics provides a framework within which the consequences of increased stratigraphic congruence upon diminished comparative anatomy can be readily determined and weighed. Above all else, cladistics is not (necessarily) incompatible with the evolutionary palaeontological approach to phylogeny reconstruction, in any of its many guises. Rather, it provides the prescriptive method of character analysis that evolutionary palaeontology traditionally lacks.

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APPENDIX

1. Files used in the GHOST analyses

Optimal trees derived from stratigraphically unconstrained analysis of the cladistic dataset:

16

1. (((B(((H(((KL)M)N)((GO)I)))F)E)(DC)))A)Q)P)
2. (((B(((H(((KL)M)N)((GO)I)))FE))D)C))A)Q)P)
3. (((B(((H(((KL)M)N)((GO)I)))FE))DC))A)Q)P)
4. (((B(((H(((KL)M)N)((GO)I)))E)F)C)D))A)Q)P)
5. (((B(((H(((KL)M)N)((GO)I)))F)E)C)D))A)Q)P)
6. (((B(((H(((KL)M)N)((GO)I)))E)F)(DC)))A)Q)P)
7. (((B(((H(((KL)M)N)((GO)I)))F)E)D)C))A)Q)P)
8. (((B(((H(((KL)M)N)((GO)I)))E)F)D)C))A)Q)P)
9. (((B(((H(((KL)M)N)((GO)I)))FE))C)D))A)Q)P)

Optimal trees derived from analysis of the cladistic dataset while implementing a constraint tree compatible with the phylogeny of Serpagli and Corradini (1999):

17

1. (P(A((K(GO))(B(C((D(FE))((Q(JN))(H(I(ML))))))))))
2. (P(A((K(GO))(B(C(D((FE))((Q(JN))(H(I(ML))))))))))
3. (P(A(B((K(GO))(C((D(FE))((Q(JN))(H(I(ML))))))))))
4. (P(A((B(K(GO)))(C((D(FE))((Q(JN))(H(I(ML))))))))))
5. (P(A((K(GO))(B(C((FE)D((Q(JN))(H(I(ML))))))))))
6. (P(A(B((K(GO))(C(D((FE))((Q(JN))(H(I(ML))))))))))
7. (P(A((B(K(GO)))(C(D((FE))((Q(JN))(H(I(ML))))))))))
8. (P(A(B((K(GO))(C((FE)D((Q(JN))(H(I(ML))))))))))
9. (P(A((B(K(GO)))(C((FE)D((Q(JN))(H(I(ML))))))))))

Stratigraphic ranges formatted in accordance with the relevant Ghost 2.4 stratigraphy files:

Taxon code	Taxon	Start (fine)	End (fine)	Start (coarse)	End (coarse)
A	<i>Kockelella manitoulinensis</i>	bbb	fff	aba	dad
B	<i>Kockelella abrupta</i>	dcc	eae	cbc	ccb
C	<i>Kockelella ranuliformis</i>	eed	gag	dad	eee
D	<i>Kockelella latidentata</i>	fef	gag	dcc	eee
E	<i>Kockelella walliseri</i>	ffe	gga	dcc	eae
F	<i>Kockelella corpulenta</i>	ffe	ggg	dcc	eee
G	<i>Kockelella patula</i>	ffe	ggg	dcc	eee
H	<i>Kockelella amsdeni</i>	ggg	gag	eee	eee
I	<i>Kockelella stauros</i>	gag	gga	eee	eae
J	<i>Kockelella ortus sardoa</i>	gga	hhh	–	–
K	<i>Kockelella crassa</i>	gga	ggb	eae	eea
L	<i>Kockelella variabilis variabilis</i>	gga	hhh	eae	eec
M	<i>Kockelella variabilis ichnusae</i>	ggd	hhh	eeb	eec
N	<i>Kockelella maenniki</i>	ggf	gfg	ece	eec
O	<i>Acoradella ploeckensis</i>	ggd	hah	eeb	eec
P	<i>Kockelella ortus ortus</i>	gga	gcg	eae	eea
Q	<i>Kockelella ortus absidata</i>	ggc	hhh	ebe	eec

Stratigraphy files

Fine	Coarse
61	29
aaa	61
aba	60
aab	59
bbb	58
bab	57
bba	56
ccc	55
cac	54
cca	53
cbc	52
ccb	51
cab	50
cba	49
ddd	48
dad	47
dda	46
dbd	45
dbb	44
dcd	43
dcc	42
eee	41
eae	40
eea	39
ebe	38
eeb	37
ece	36
eec	35
ede	34
eed	33
fff	32

Stratigraphy files (continued)

Fine	Coarse
faf	31
ffa	30
fbf	29
ffb	28
fcf	27
ffc	26
fdf	25
ffd	24
fef	23
ffe	22
ggg	21
gag	20
gga	19
gbg	18
ggb	17
gcg	16
ggc	15
gdg	14
ggd	13
geg	12
gge	11
gfg	10
ggf	9
hhh	8
hah	7
hha	6
hbh	5
hbb	4
hch	3
hhc	2
hdh	1

2. *Dataset used in the compilation of confidence intervals, discovery curves and plot of research effort*
 Many of the publications are not scored as recording new occurrences of kockellelids because the taxonomic assignments to species level and below were not verifiable (no figures). These publications were nevertheless included in the research effort plot.

		Number of fossiliferous horizons per taxon															
Author(s)	Year	<i>Anc. ploeck-ensis</i>	<i>Ko. abrupta</i>	<i>Ko. amsdeni</i>	<i>Ko. corpu-lenta</i>	<i>Ko. crassa</i>	<i>Ko. latit-dentata</i>	<i>Ko. maenmiki</i>	<i>Ko. manitou-ortus</i>	<i>Ko. absidata</i>	<i>Ko. ortus</i>	<i>Ko. patula</i>	<i>Ko. ranuli-formis</i>	<i>Ko. staurus</i>	<i>Ko. variabilis</i>	<i>Ko. variabilis</i>	<i>Ko. walliseri</i>
Walliser	1957																5
Kockel	1958																
Remack-Petitot	1960																
Walliser	1962																
Reichstein	1962																
Ethington and Furnish	1962																
Rhodes and Newall	1963																
Walliser	1964	7			1						1	3	3				35
van den Boogaard	1965																
Igo and Koike	1967																
Flajs	1967																
Nicoll and Rexroad	1968												6				
Igo and Koike	1968																
Drygant	1969										1	1	1				
Fähreus	1969	1															
Serpagli	1970				2												4
Pollock <i>et al.</i>	1970							1									
Drygant	1971																
Schönlaub	1971																
Rexroad and Craig	1971															1	
Link and Druce	1972	3			2						3					3	
Miller	1972																
Aldridge	1972		4										7				
Walliser	1972																
Walmsley <i>et al.</i>	1974												1				
Klapper and Murphy	1974	5			1												
Schönlaub	1975													5			
Schönlaub and Zezula	1975																
Helfrich	1975																8
Viira	1975				1												
Barrick and Klapper	1976			7						13		2	30	8		2	4
Flajs and Schönlaub	1976																
Mashkova	1977												1				

(continued)

		Number of fossiliferous horizons per taxon															
Author(s)	Year	<i>Ant. ploeckensis</i>	<i>Ko. abrupta</i>	<i>Ko. amsdeni</i>	<i>Ko. corpu-lenta</i>	<i>Ko. crassa</i>	<i>Ko. lati-dentata</i>	<i>Ko. maenniki</i>	<i>Ko. manitou-linensis</i>	<i>Ko. ortus absidata</i>	<i>Ko. ortus ortus</i>	<i>Ko. patula</i>	<i>Ko. ranuli-formis</i>	<i>Ko. stauros ichnusae</i>	<i>Ko. variabilis variabilis</i>	<i>Ko. walliseri</i>	
Kleffner	1994		1										10	1		6	
Jeppsson <i>et al.</i>	1995																
Simpson and Talent	1995	4															
Simpson	1995												6		17		
Jeppsson	1997												1				
Sarmiento <i>et al.</i>	1998																
Männik and Malkowski	1998																
Serpagli and Corradini	1998																
Loydell <i>et al.</i>	1998					1											
Norford <i>et al.</i>	1998																
Serpagli <i>et al.</i>	1998							1									
Corradini <i>et al.</i> (a)	1998																
Corradini <i>et al.</i> (b)	1998																
Ferretti <i>et al.</i>	1998																
Benfrika	1999																
Serpagli and Corradini	1999																
Cockle	1999																
Jeppsson and Aldridge	2000																
Johnson <i>et al.</i>	2001	1															
Zhang and Barnes	2002																
Sanz-Lopez <i>et al.</i>	2002																
Männik	2002																
Loydell <i>et al.</i>	2002																
Jeppsson and Calner	2003																
Total number of horizons		30	4	17	1	9	25	18	50	45	9	7	142	16	26	103	51
Confidence interval (%)		10·8	171	20·6	–	45·4	13·2	19·2	6·3	7·0	45·4	64·8	2·1	22·1	12·7	3·0	6·2