BETWEEN DEATH AND DATA: BIASES IN INTERPRETATION OF THE FOSSIL RECORD OF CONODONTS

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Abstract: The fossil record of conodonts may be among the best of any group of organisms, but it is biased nonetheless. Pre- and syndepositional biases, including predation and scavenging of carcasses, current activity, reworking and bioturbation, cause loss, redistribution and breakage of elements. These biases may be exacerbated by the way in which rocks are collected and treated in the laboratory to extract elements. As is the case for all fossils, intervals for which there is no rock record cause inevitable gaps in the stratigraphic distribution of conodonts, and unpreserved environments lead to further impoverishment of the recorded spatial and temporal distributions of taxa. On the other hand, because they are resistant to abrasion and can withstand considerable metamorphism conodonts can preserve evidence of otherwise lost sequences or environments through reworking.

We have conducted a preliminary investigation into how the various forms of gross collecting bias arising from period to period variation in intensity of research effort and in preserved outcrop area have affected the conodont fossil record. At the period level, we are unable to reject the hypothesis that sampling, in terms of research effort, is biased. We have also found evidence of a relationship between outcrop area

and standing generic diversity. Analysis of epoch/stage-level data for the Ordovician–Devonian interval suggests that there is generally no correspondence between research effort and generic diversity, and more research is required to determine whether this indicates that sampling of the conodont record has reached a level of maturity where few genera remain to be discovered. One area of long-standing interest in potential biases and the conodont record concerns the pattern of recovery of different components of the skeleton through time. We have found no evidence that the increasing abundance of P elements relative to S and M elements in later parts of the conodont record reflects evolutionary changes in the composition of the apparatus.

Ignoring the biases and incompleteness of the conodont fossil record will inevitably lead to unnecessary errors and misleading or erroneous conclusions. Taking biases into account has the potential to enhance our understanding of conodonts and their application to geological and biological questions of broad interest.

Key words: completeness, gaps, microfossil, preservation, taphonomy, vertebrate skeletons.

OUR purpose with this contribution is to introduce and provide an overview of an issue that underlies all palaeontological study and provides the common theme of this collection of papers: how we interpret the fossil record. To what extent do perceived changes in morphology, skeletal composition, abundance and diversity through time reflect changes in biology and evolutionary history and how has this primary signal been biased by post-mortem processes? How do biases affect the ways in which we use the record for evolutionary, biological and biostratigraphic purposes?

Conodonts provide a particularly interesting window through which to view the sometimes uneasy relationship between interpretations of the fossil record and hypotheses

of bias. The quality of the conodont fossil record is generally held to be among the best of any group of organisms (Foote and Sepkoski 1999; Sweet and Donoghue 2001), and because of their near ubiquity and ease of recovery from marine strata of Late Cambrian to latest Triassic age conodonts have attained an almost unrivalled reputation for biostratigraphic utility. This in turn has fuelled a widespread tacit assumption that because conodont biostratigraphy works, biases in their fossil record cannot be significant (Donoghue 2001*a,b*; Wickström and Donoghue, 2005). The record must be 'close enough' to the original signal.

Yet few would argue that post-mortem factors have not played some role in shaping what we see, and it must

therefore be true that if the record as we perceive it reflects both biological-evolutionary patterns and post-mortem biases, failure to take both into account will decrease the reliability and accuracy of any interpretations. Every fossil sample lies somewhere in a spectrum that ranges from complete preservation to complete loss, and the papers in this volume explore the fertile ground of interactions between bias and biology.

Biases, for the purpose of this paper, are taken as factors that distort or selectively filter the patterns of spatial and temporal distribution of fossils, as revealed through analysis of collections, causing them to deviate from a perfect record of 'true' biological and evolutionary history. This is more than taphonomy, as we include other biasing factors such as sampling, collecting and processing methods, and consider how assumptions and methods, especially phylogenetic methods, can bias interpretations.

Any simple classification will inevitably underemphasize the complex interactions and feedbacks that occur between biases, but in order to provide a framework for discussion and to be consistent with the overall structure of this collection of papers we consider biases primarily in terms of when they exert their influence, as summarized in Text-figure 1. It is important to note that not all conodonts are equally susceptible to different biases, with various aspects of conodont biology and evolution making some species, or some types of elements within the apparatus more likely to be lost. Similarly, different elements or species may be more susceptible to bias at different stages in the transition from death to data, and

biases at one stage can make elements more or less susceptible to the effects of bias during subsequent stages. We have attempted to highlight these factors in Text-figure 1 and in the discussion below. We also present a more detailed discussion of the potential effects of biology and bias on the relative abundance of different components of the conodont skeleton in collections of isolated elements.

PRE- AND SYNDEPOSTIONAL NON-PRESERVATION AND SELECTIVE LOSS

Predation and scavenging

Numerous examples of elements or apparatuses preserved within predators and scavengers (Scott 1969, 1973; Melton and Scott 1973; Nicoll 1977; Conway Morris 1990; Purnell 1993; Purnell and Donoghue 1998) or in coprolites (Higgins 1981) demonstrate that conodonts were food for other animals. It is possible that many elements in conodont collections have passed through the guts of other animals, but there has been no systematic study of how this may have affected what is preserved. Given the well-known effects on the enamel of gnathostome teeth of passage through a gut (Fisher 1981), it is likely that conodont elements, composed primarily of enamel-like tissues (Donoghue 1998, 2001*c*), could be partially or completely dissolved in the process of digestion by some conodont eaters. Fragmentation is also possible. Species with small elements, or the more gracile
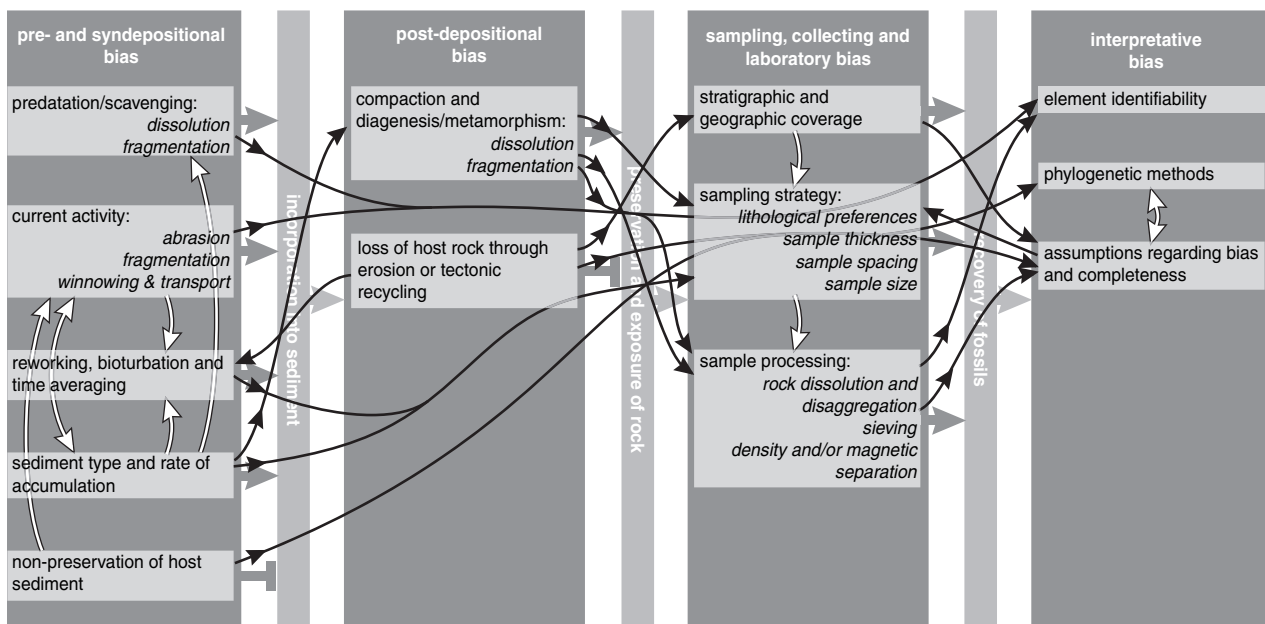
TEXT-FIG. 1. Biases that act to distort recovery of conodont elements. The diagram summarizes when different biases exert their influence and indicates how they interact.

elements in an apparatus are more likely to be lost or fragmented during digestion. Compaction of a coprolitic mass may also result in higher levels of fragmentation because of the close juxtaposition of elements. On the other hand, incorporation of elements into a coprolite may enhance their chances and quality of preservation if it is mineralized or lithified before significant sedimentary compaction.

Current activity

That conodont elements were subject to post-mortem current sorting has long been recognized (e.g. Ellison 1968; von Bitter 1972). More recent experimental work confirmed that the susceptibility of elements to current entrainment, transport and sorting is correlated with their hydrodynamic properties, which in turn are correlated with size and shape (Broadhead et al. 1990; McGoff 1991). Studies by Broadhead and Driese (1994) indicated that elements carried in aqueous suspension with carbonate grains are relatively resistant to abrasion and are unlikely to be destroyed, even after prolonged transport. Simulated aeolian transport with quartz grains, however, resulted in significant abrasion of elements. This work also suggests that current activity does not cause significant breakage of elements. Current sorting is likely to amplify the effects of any differential fragmentation of elements resulting from other predepositional factors, such as predation, leading to increased levels of bias.

Reworking, bioturbation and time-averaging

The effects of bioturbation on element fragmentation are unknown. Its potential for producing time-averaged faunas, however, is beyond doubt. Of particular concern is the fact that bioturbation may have been most intense where it is least evident; the lack of any clear burrowing may indicate that a bed and its conodont elements have been completely homogenized by bioturbation (Droser and Bottjer 1986), possibly resulting in the amalgamation of depositional events (and conodont populations) spanning many thousands of years. Reworking and winnowing may also lead to time-averaging and differential size bias, and because they are relatively resistant elements may be reworked following erosion of their host rock (see below). Reworking and bioturbation may produce conodont faunas of mixed age and environmental affinities, and, given the evidence of time-averaging in macrofossil groups (see Behrensmeyer et al. 2000 for a review), it is highly likely that most conodont faunas are significantly time-averaged, possibly representing tens of thousands or even hundreds of thousands of years. This has obvious implications for temporal and spatial resolution of interpretations that draw directly on stratigraphic ordering of fossils (see Barrick and Männik 2005; Dzik 2005; Roopnarine 2005). Reworking is also likely to result in significant element size bias.

Transport of elements, either all the elements of a species or just the more easily entrained components of the skeleton, may result in their removal to different depositional settings. This can ultimately result in their complete loss from the record if those environments are less likely to be collected (lithological sampling bias), are more difficult or impossible to process effectively, or are more likely to be subject to tectonic recycling. Quiet, offshore, deep-water environments are particularly susceptible to these biases.

Sediment type and rate of accumulation

Many of the effects of sedimentation on conodont faunas are mediated by other potential biases. Rapid sedimentation, for example, will tend to remove elements more quickly from predators, scavengers and burrowers, reducing the bias arising from these factors. However, high rates of sediment input will result in fewer elements per unit rock volume that, depending on the downstream effects of compaction and sample size, may result in lower element recovery, which in turn can have a significant impact on interpretation (see Jeppsson 2005). Slow net rates of sedimentation will increase the potential for reworking and time-averaging. Interactions between sediment type, compaction and diagenesis also have a significant effect on fragmentation. Shales, some of which may be low-density, soupy sediment at the time of deposition (see Purnell and Donoghue 1998 for a discussion of black shale density and conodont taphonomy), are subject to higher levels of compaction, and thus higher levels of element fragmentation (von Bitter and Purnell 2005). Carbonate sediments, especially framework-supported lithologies such as grainstones, or other sediments liable to rapid cementation, will be less compacted and elements consequently less fragmented (although the high depositional energy of grainstones will result in winnowed and sorted faunas; e.g. Krumhardt et al. 1996).

Non-preservation of host sediment

The effects of current activity range from light disturbance of elements within natural assemblages through various degrees of winnowing, transport and hydrodynamic sorting, to complete loss or non-deposition of elements and host sediment. Whether or not conodont elements themselves are removed to a different depositional setting,

destroyed or remain as part of a lag deposit will depend on the specific hydrodynamic regime. The net results will vary from time-averaging to loss of record; the downstream effects on interpretation are discussed above.

POST-DEPOSITIONAL BIAS

The various processes that a sedimentary unit undergoes during its incorporation into the stratigraphic record will significantly affect the conodont elements it contains. Compaction, for example, will result in element fragmentation and possible downstream loss (see below), whereas early cementation will reduce fragmentation. Elements are more resistant to the effects of pressure solution than carbonate grains, and this can result in penetration of calcareous fossils by conodont elements. Conodont elements can survive hydrothermal alteration, contact metamorphism and regional metamorphism up to greenschist facies and more (Rejebian *et al.* 1987), but the biases introduced by declining element identifiably increase as elements become more tectonically deformed, recrystallized or covered with mineral encrustations (e.g. Kovács and Árkai 1987; Rejebian *et al.* 1987). Cement mineralogy also exerts a bias that is linked to processing and collection. Rocks cemented with quartz or other minerals that are insoluble in buffered acetic or formic acids are less likely to be collected by conodont workers, leading to significant lithological collecting bias (see below). If collected, such rocks are likely to be processed using more aggressive chemical or mechanical techniques that will tend to increase element loss through dissolution, fragmentation or decreased identifiably (Jeppsson 2005; for illustrations of conodonts recovered using hydrofluoric acid, see Barrick 1987; Orchard 1987).

Loss of rock through erosion or tectonic recycling varies according to tectonic and depositional setting, and sequence architecture. The longest surviving strata are found on stable cratonic areas, continental rift margins and aulacogens (Behrensmeyer *et al.* 2000), but sequences from these areas may be far from complete, containing numerous depositional hiatuses and erosional unconformities. Barrick and Männik (2005) and Lehnert *et al.* (2005) discuss the implications of these factors for analyses of conodont biostratigraphy and evolution.

In most cases loss of a sedimentary unit will result in loss of the elements it contained, but this is not always true. For example, conodont faunas from redeposited clasts or olistoliths have been used to reconstruct otherwise unpreserved inner shelf palaeoenvironments of the Ordovician Cow Head Group of Newfoundland (Pohler *et al.* 1987; Pohler and James 1989), shallow-marine carbonate and flysch sequences from a cryptic Ordovician arc terrane in northern Britain (Armstrong *et al.* 2000),

and a lost Devonian carbonate shelf reconstructed on the basis of polymictic clasts in the Viséan of the Holy Cross Mountains (Belka *et al.* 1996). Lehnert *et al.* (2005) discuss more examples.

Element fragmentation

Several pre-, syn- and post-depositional processes (Text-fig. 1) will result in element fragmentation, as will certain collecting and processing methods (see Jeppsson 2005 for discussion). The downstream affects of fragmentation, particularly after sieving or decanting to separate elements from sediment, are potentially huge, with those elements most susceptible to fragmentation being completely lost, or rendered unidentifiable. At the interpretation stage, this can result in the effective loss (through non-recovery) of species with small or gracile elements (Jeppsson 2005) and in itself, without current sorting, is sufficient to bias the relative abundance of element types recovered (von Bitter and Purnell 2005).

Controlling for bias in the sedimentary record

Although the sedimentary rocks within which conodont elements are entombed were accumulated episodically in response to changes in sea level resulting from a combination of eustatic and local effects, the apparent completeness of a particular sedimentary record is relative and contingent upon the time span and the resolution of the time intervals required (Strauss and Sadler 1989; Sadler and Strauss 1990). The coarser the temporal resolution required the more complete a section will be perceived to be over a given time span. Thus, if a sedimentary section has accumulated over a few million years, it will provide a much better record with respect to 100-ky intervals than to 10- or 1-ky intervals. However, sequences deposited over shorter periods of time are generally more complete because the longer the time span the more likely the sedimentary record is to include significant gaps (Sadler 1981; Schindel 1980).

It is possible to overcome the limitations of individual sections through compilation of numerous stratigraphic sections that represent the time span of interest, using the method of graphic correlation for example (Shaw 1964; Sweet 2005). If gaps are distributed randomly throughout the component sections then it is likely that individual sections will compensate for one another and the completeness of the composite section will increase as more sections are included. Valentine *et al.* (1991) calculated the increasing probabilities of completeness for composite sections by dividing the average sediment accumulation rate for the time span of interest by the average rate for

the resolution interval (rates were based on comparable modern marine environments; Sadler 1981). Thus, for a 1-my resolution interval, a 30-my time span and average accumulation rates for carbonate sediments, the probability that any given interval is represented by some sediment at one site (at the very least) rises from 0·33 in one section to 0·98 for ten independent sections, with probability increasing still further if either the resolution interval or the number of independent sections is increased. However, this improvement in completeness only applies if the gaps within the component sections are randomly distributed within and therefore between the sections.

Despite the veracity of the global record at the given time span and resolution interval, Valentine *et al.* (1991) also showed that the precision of correlation between component sections is much lower. Given that the probability of any 1-my interval being represented by at least some sediment over a time span of 30-my in a marine carbonate sediment setting is 0·33, the likelihood that the same interval is represented in further independent sections drops to less than 0·11 for two sections and $1·53 \times 10^{-5}$ for ten sections. As they argue, this observation should severely limit the application and resolution of biostratigraphic correlation, but this technique is universally applied and 1-my resolution is often achieved and exceeded, particularly with respect to graphically correlated global composite sections (Sweet 2005).

The reason is that the gaps in sedimentary sections are non-independent; they are controlled by regional and eustatic fluctuations in sea level. One consequence is that there are gaps in the record that may never be filled because there are intervals of geological time for which there is no stratigraphic record over large geographical areas (Valentine 2004, p. 159). The conodont record is further impoverished because there are also intervals of geological time for which there is no sedimentary record of the environments in which conodonts lived and died.

So although global composite sections derived from graphic correlation provide the best means of recovering the available record, they will nevertheless include undetected gaps. This has implications for those scientists who attempt to derive the phylogenetic relationships of organisms using stratigraphic range data because we have no means of directly recovering the absolute and sometimes even the relative stratigraphic ranges of taxa (Wickström and Donoghue 2005). Cladistics, on the other hand, because it eschews stratigraphic data in the formulation of phylogenetic hypotheses, can reveal the existence of gaps through post hoc calibration of cladograms to the stratigraphic ranges of their component taxa (Norell 1992; Benton 1995*b*; Donoghue 2001*a*). The logic of this is simple: because sister taxa diverge from their most recent common ancestor at the same time, they should exhibit coincident first appearances in the stratigraphic record. If one member (species A) of a pair appears before the other (species B), the interval between the first recorded appearance of species A and that of B gives a minimum estimate of the unpreserved range of species B. Such gaps are termed 'ghost lineages' (Norell 1992) but ghost ranges can be accounted for not only by a gap in the range of a known taxon, but also by the existence of hitherto undescribed taxa that are more closely related to one of the pair of sister taxa. Wickström and Donoghue (2005) show that it is possible to discriminate between these two possibilities by employing confidence intervals to constrain the expected range of known taxa. Donoghue *et al.* (2003) showed that even existing hypotheses of conodont intrarelationships, which are heavily based on stratigraphic data, indicate that the conodont fossil record is far from complete.

SAMPLING, COLLECTING AND LABORATORY BIAS

Although the potential biases discussed above act and interact in different ways at different times over millions of years, a number of them are only realized as actual biases after a sample has been collected and processed. For these biases, particularly those that increase element fragmentation, different sampling, collecting and laboratory processing can exaggerate or reduce their impact on the collection of conodont elements that results. Much of this is intuitively obvious and has been touched upon in previous discussion: collecting small samples of rock deposited under high rates of sedimentation, for example, will yield few elements; sieving will result in loss of all elements and fragments below the minimum screen size used. Perhaps the dominant factor at this stage, however, is the lithological sampling bias imposed by the preferred method of recovering conodont elements from their host rock; since the 1940s dilute acids have been used to extract elements by dissolution of carbonates (Ellison and Graves 1941). We are aware of no rigorously collected data concerning lithological selection, but estimates based on a straw poll of conodont workers who subscribe to the con-nexus listserver (http://www.conodont.net) indicate that percentages for sample lithologies processed by different laboratories average out at *c.* 80 per cent limestones, *c.* 10–15 per cent dolomites, *c.* 5 per cent shales, and 2 or 3 per cent 'other lithologies'. There is some variation from one laboratory to another, and with different geographical sampling areas, but the data confirm that the vast majority of recent conodont collections are derived from carbonates, with many conodont workers collecting other lithologies only when they have no alternative, or where stratigraphic/ecological coverage demands. This will obviously impose certain biases on

conodont collections in general, especially when coupled with the fact that the volume and area of deposition and preservation of these different lithologies varies through the Phanerozoic (Bluth and Kump 1991). It is also worth noting that lithological sampling bias has changed with time. The work of Hass, active between the 1930s and 1960s, and Huddle, active in the 1930s to mid 1940s, then again in the 1960s and 1970s, for example, included a much higher proportion of shale samples, with the majority of Hass's samples being obtained from shales, either by examination of split surfaces or by disaggregation of rock by boiling or slaking. As acid processing became more routine, shale sampling percentages declined because of the increase in opportunity to process carbonate rocks, so that Huddle's overall black shale percentages probably were more like 50 per cent (J. E. Repetski, pers. comm. 2004).

The biases inherent in sampling, collection and laboratory processing are touched on by a number of authors in this volume, but are dealt with most comprehensively by Jeppsson (2005), who also provides suggestions for monitoring, evaluating and minimizing their biasing effects.

Temporal and spatial collecting bias

Stratigraphic collecting bias and research effort through time. In addition to these intrinsic and operational biases, the conodont fossil record is also subject to cultural biases. If we are to read anything into diversity curves through the stratigraphic range of conodonts we must assume that there has been a consistent degree of research effort expended throughout, or at least that the record has been randomly sampled. However, this does not square easily with the fact that most conodont workers specialize on particular stratigraphic intervals, with factors other than the desire for uniform stratigraphic coverage involved in determining their specialism.

To test for sampling biases in the conodont fossil record we searched the ISI® Science Citation Index (SCI) database (1945–July 2004) using the search string <conodont* and [period name]> for each geological period (including Mississippian and Pennsylvanian in totals for the Carboniferous). Because conodonts only occur in the later parts of the Cambrian, we have excluded this period from our analysis. The SCI by no means captures all publications presenting or using conodont data but we have assumed that its sampling of the palaeontological literature does not vary from period to period, and our data should thus provide a representative sample of the number of publications containing conodont data for each of the periods within the stratigraphic range of conodonts. Such publication counts provide a relatively crude measure of research effort, but they do allow us to explore

the possibility that the record is biased by uneven sampling through time. The results of this search, presented in Text-figure 2A, demonstrate that the number of publications per period varies considerably, with the Ordovician and Devonian having particularly high research productivity. However, even if research productivity were uniform throughout we should not expect equal productivity on a period-by-period basis because of the varying duration of Phanerozoic periods. Rather we should expect longer periods to exhibit the highest research productivity (in terms of total publications), with the number of publications correlated with period duration. The result of a Spearman's Rank Correlation test ($r_s = 0.257$, $P = 0.623$), however, indicates that they are not (we have used the timescale of Gradstein *et al.* 2004 throughout). [The non-parametric Spearman's Rank Correlation is used because n is small, and we have no evidence that our data are normally distributed; analyses were carried out using PAST (Hammer *et al.* 2001).] Plotting publications onto duration (Text-fig. 2B) provides graphic confirmation of this lack of correlation. If sampling is uniform through time, then standardizing research effort per unit time (number of publications divided by period duration) should produce a correlation close to zero, but once again these data do not conform to this expectation ($r_s = -0.429$, $P = 0.396$). This negative correlation is non-significant, but given the limitations of our dataset it is high enough to suggest that there may be a weak negative relationship that better data might reveal. If the correlation were real, it would mean either that longer periods have higher research effort (publications my^{-1}), or that shorter periods have lower effort. Our limited data suggest the latter, but clearly we cannot with any confidence reject the hypothesis that sampling of the conodont record at period level is non-uniform.

However, if we look deeper within the stratigraphic hierarchy for the periods that show the highest absolute and/or standardized research productivity (Ordovician, Silurian, Devonian), a different pattern emerges. The same search strategy was conducted using epoch (for the Ordovician and Silurian) and stage names (for the Devonian) in the search string. We conducted searches for stratigraphic units of unequal rank because some stage names have been in widespread international use for decades while others have been conceived only relatively recently, and we chose to use those stratigraphic names that have been in circulation longest for each period. The use of stratigraphic units of differing rank should not affect the analysis because if the record has been evenly sampled research productivity per unit time should be independent of rank (see below). More importantly, however, in terms of duration there is no clear distinction between the Ordovician–Silurian epochs and Devonian stages. Two of the three shortest intervals are epochs
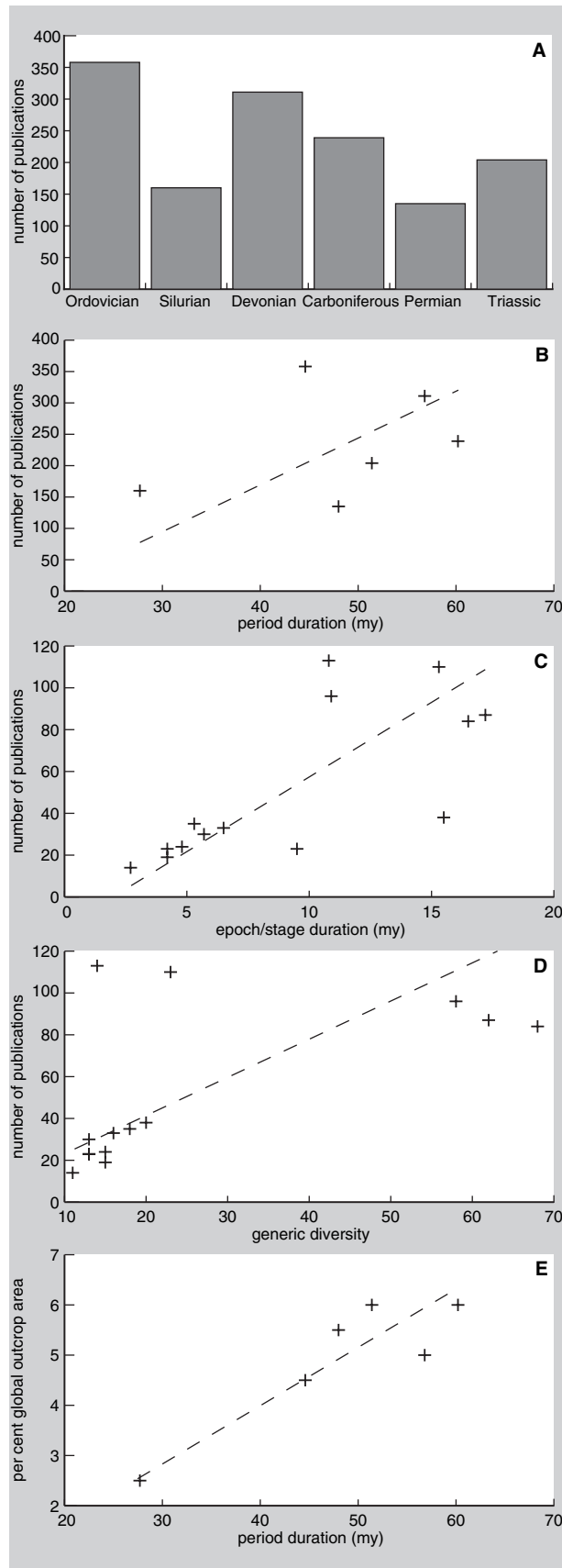
(Přídolí and Ludlow) and the fourth longest interval is a stage. Furthermore, although its reliability is open to question because of the nature of our data, the results of a Welch test (an unequal variance t statistic) suggest that mean stage length (8·11) is not significantly different from mean epoch length (10·33; $t = 0.791$, $P = 0.447$).

The same caveats apply to these data as those for periods, and once again our analysis should be viewed as exploratory in nature. Nevertheless, the stage/epoch data are better than the period data in that n is higher, and analysis reveals a highly significant correlation between raw research productivity and epoch/stage duration ($r_s = 0.798$, $P = 0.0006$). Epoch/stage duration and standardized publication data are not correlated ($r_s = 0.004$, $P = 0.988$). Both these results are what we would expect from uniform sampling through this stratigraphic interval, but there are clearly intervals where publication effort differs markedly from the norm (Text-fig. 2C), and this observation is compatible with a sampling bias of uneven research effort. These intervals cannot simply be ignored, but alternative explanations remain which must be rejected before it can be concluded that sampling of the conodont fossil record is significantly biased.

It is possible that those stratigraphic units exhibiting unusually high and low levels of research productivity are those that exhibit highest and lowest levels of diversity. This relationship has been observed in analyses of the Phanerozoic fossil record as a whole (Raup 1976) and can be interpreted as indicating either that high diversity stimulates high palaeontological interest, or that high levels of activity produce more taxa (Raup 1977; Sheehan 1977); that is, the pattern of diversity is either real, as advocated by Valentine (1969, 1973), or it is an artefact of sampling effort (Raup 1972, 1976). We are not about to try and resolve this ongoing debate (e.g. Benton 1995a, 2003; Peters and Foote 2001, 2002; Smith 2001; Smith *et al.* 2001). Rather, our purpose is to determine whether any of those Ordovician–Devonian epochs/stages identified as exhibiting markedly high or low levels of research productivity coincide with intervals of markedly high or low conodont generic diversity. Raup's (1976) database is clearly better than ours in that it is more heavily researched and, being based on the Zoological Record, attempts to recover data from all

TEXT-FIG. 2. Histogram (A) and bivariate plots of data (B–E) pertaining to analysis of bias in research effort expended on conodonts through geological periods and epochs/stages. Dashed lines indicate the results of RMA regression (calculated with PAST; Hammer *et al.* 2001); they are intended solely as a guide to general trends in the data and cannot be assumed to be significant (for discussion of correlations between variables and significance, see text).

literature, not just from those journals sampled by the SCI. However, Raup's database records dates of description of new taxa, rather than research effort *per se*. It is research effort that we are interested in, and in this respect our data may be a better reflection of the maturity with which the record has been sampled and so better serve our objectives.

As might be expected, we have found a significant correlation between conodont generic diversity (diversity data modified from Aldridge 1988) and absolute research productivity ($r_s = 0.69$, $P = 0.006$) (data shown graphically in Text-fig. 2D; we also obtain a significant correlation if diversity data are detrended using methods similar to Smith 2001). We have tested the hypothesis that one is biasing the other in two ways. Firstly, if inequalities in research productivity are biasing diversity, then standardized productivity (publications my^{-1}) not just raw productivity should be correlated with diversity, but it is not ($r_s = 0.062$, $P = 0.833$; detrended diversity data are also uncorrelated). Although this does not itself support the hypothesis that diversity is biasing research effort, it does not directly test whether intervals with publication effort differing markedly from the norm have unusually high or low diversity, and this leads to our second test. If we take the fifth and ninety-fifth percentiles in the productivity data as cut-off points, this identifies the Frasnian and the Přídolí as intervals of abnormally high and low absolute research productivity, respectively, but this is biased by the short duration of the Přídolí (we have already established a strong correlation between research effort and stage/epoch duration). The extremes of the data for standardized research productivity (my^{-1}) are the Frasnian (high) and the Emsian (low; it is also worth noting that the Llandovery, 2·45 publications my^{-1} is very close to the fifth percentile at 2·42 publications my^{-1}). The generic diversity for the Frasnian and Emsian stages is comparable (13 and 14, respectively), and Llandovery diversity is higher (20), providing no support for a relationship between abnormal research productivity and diversity. A similar pattern emerges if we apply the same percentile-based test to the diversity data. The Early Ordovician (unusually high diversity) and the Přídolí (unusually low) both have research productivity of just over 5 publications my^{-1} (in terms of publications my^{-1}, mean productivity = 5·61, median = 5·14). Thus none of our tests provides support for the hypothesis that conodont research effort, including intervals where it is unusually high or low, is biased by conodont generic diversity.

Another possibility is that peaks and troughs in research effort are an artefact of poor correlation between available rock area or volume for sampling and the temporal duration of stratigraphic units. Although the period-level data are limited, this hypothesis can be tested by looking at the relationship between global outcrop area (period-level data from Blatt and Jones 1975) and period duration. The result (Text-fig. 2E) demonstrates some scatter of these data, and a general trend is evident; the correlation between area and duration is relatively high ($r_s = 0.783$) but with this limited dataset we are unable to reject the null hypothesis of no correlation ($P = 0.066$). There are also no significant correlations between outcrop area and raw or standardized research productivity ($r_s = -0.116$, $P = 0.827$; $r_s = -0.754$, $P = 0.083$, respectively) and between genera and area ($r_s = -0.464$, $P = 0.354$). However, outcrop area decreases with increasing geological age, and the correlation between area and time is significant ($r_s = -0.841$, $P = 0.04$), thus detrended outcrop data (residuals from a least squares regression of area onto geological time) may provide a better means of investigating the potential biasing effects of outcrop area. Neither raw nor standardized research effort are correlated with detrended area ($r_s = 0.6$, $P = 0.208$; $r_s = 0.14$, $P = 0.787$, respectively), but the correlation between detrended diversity data and detrended outcrop area is highly significant ($r_s = 0.9443$, $P = 0.004$). In summary, at period level we can find no evidence to support the hypothesis that decoupling of the availability of rock for sampling from the duration of stratigraphic units might provide an explanation for intervals of extreme research productivity. Our data and analysis are limited, but the relationship between detrended area and detrended diversity data suggests either a sampling bias in recorded conodont diversity, or a relationship between habitable marine settings and conodont diversity. Without a detailed analysis of variation in facies distribution and preservation through time we are unable to test which of these alternative explanations is closer to reality.

We are unaware of any data for outcrop area by stage/epoch for the Palaeozoic, but we have tested the hypothesis using formation counts (data from Peters and Foote 2002), and find that generic diversity through the Ordovician–Devonian interval is not correlated with number of formations ($r_s = 0.304$, $P = 0.290$). The meaning of this result, however, is open to question given the doubts raised by Crampton *et al.* (2003) concerning the validity of formation counts as a proxy for outcrop area in analyses of this kind.

Thus, it appears from the analysis of data for all periods through which conodonts range (excluding the Cambrian) that our sampling of the conodont fossil record is neither uniform nor random, and that outcrop area may have biased our sampling of diversity. Looking at epoch/stage data for the Ordovician–Devonian interval, however, our analysis is consistent with even sampling throughout this part of the record. This is noteworthy. The lack of relationship between research productivity and conodont generic diversity is counterintuitive in that it suggests that more intense research effort has not resulted in more

genera. This could mean that our publication counts provide an inadequate proxy for research effort, and although we have no reason to believe that this is the case, further research into this possibility may be fruitful. Alternatively, the sampling of the Ordovician–Devonian conodont record could have reached a level of maturity where there are few new genera left to discover (as noted above). This would be consistent with other studies that have concluded that the fossil records of taxa with robust skeletons are often well sampled (for recent reviews, see Foote and Sepkoski 1999; Forey *et al.* 2004).

As we have explicitly pointed out, our assumptions and methods of data acquisition mean that our investigation is relatively crude, intended only as a first exploratory step in analysing the potential gross temporal biases in the sampling of the conodont record. But our preliminary results are encouraging. At the stage/epoch level for the Ordovician–Devonian interval we have been unable to detect significant temporal biases in the conodont fossil record, suggesting that the recovered diversity pattern contains a significant biological signal. Given the possible area-related sampling bias for period-level data, however, there is clearly a need for more work, in particular investigating the relationship between diversity and outcrop area at stage/epoch level. Similarly, work using collector curves or other methods (Paul 1982; Wickström and Donoghue 2005) is required to investigate the relationship between research productivity and diversity in more detail.

One factor that we have not investigated and which may have significantly biased our recovered record is the varying availability for sampling of rocks that represent those particular environments within which conodonts lived and died, or those lithofacies from which conodont elements can be recovered by standard laboratory methods (see above). It is possible that intervals of particularly high or low apparent diversity have been influenced by this facies bias. However, it is also likely that cultural biases impinge upon the collection of data. In either instance, the raw data for conodont diversity cannot be taken at face value as a literal record and studied in an uncritical manner; biases must be taken into account. This is of particular concern in the case of the Frasnian (with anomalously high research productivity) and the Llandovery (low research productivity) because the diversity data for both intervals are integral to understanding two of the five greatest mass extinction events in Earth history, the recovery phase from end-Ordovician extinction event(s) in the instance of the Llandovery, and the pre-event conditions for the Frasnian–Famennian extinctions. These potential biases cannot be ignored when considering the nature and magnitude of these events and the intrinsic and extrinsic mechanisms that have been implicated.

Spatial (geographical) collecting biases. Whether our sampling of the conodont fossil record has been even with respect to stratigraphy is only one dimension of the problem of sampling biases; the other is biases with respect to geography, both modern and ancient. It is widely appreciated that there is a geographical bias in the sampling of the fossil record as a whole that is concentrated on north-west Europe, the USA and Russia (Raup 1976). This is because palaeontological science began in these regions and so they have engaged the greater number of palaeontologists for the greatest period of time. Thus, geographical regions that are relatively new to modern palaeontology are those areas in which the most surprising discoveries are being made; it is not by virtue of these regions being special in any way, whether evolutionarily or preservational, it is just that they have been sparsely sampled to date and, by analogy to a collector curve (e.g. Paul 1982; Wickström and Donoghue 2005), we remain on the steep, initial part of the curve and can expect more novel discoveries for some time to come. Hence the remarkable discoveries of fossilized remains of all groups and from all time intervals that have been made in China in recent years (Gee 2001).

The same appears to hold true for the conodont fossil record. The census of conodont-related research publications compiled by Ellison (1988) demonstrates that, although sampling of the North American record began within a couple of decades of their discovery in Europe, it took almost 90 years for the search to spread to other continents, with the first discoveries in Asia in the early 1960s (e.g. China; Jin 1960), and in Antarctica in the 1980s. While some regions have made rapid progress in remedying this situation in the years that have elapsed since those first records, the vast majority remain sparsely sampled, in terms of both time and space (South America, eastern Europe, Asia, Antarctica). This uneven and non-random sampling of the record within the spatial dimension indicates that the few composite standards that exist are considerably less than global and that our perception of the conodont fossil record is biased as a result, both in terms of palaeogeography and in terms of the total stratigraphic ranges of individual taxa that can be observed directly.

BIAS AND BIOLOGY: ELEMENT RELATIVE ABUNDANCES AND SECULAR TRENDS IN APPARATUS ARCHITECTURE

The majority of conodont studies have mapped patterns of stratigraphic distribution, diversity, ecology or phylogeny directly from the fossil record. Until recently, little attention has been paid to the potential biases affecting

the record, with one notable exception: the relative abundance of the different types of isolated elements that make up most conodont collections. This is no coincidence. Almost all aspects of modern conodont palaeontology, including systematics, taxonomy, palaeoecology and palaeobiology, rely to some extent on an understanding of conodonts as skeletal apparatuses, not just as isolated elements. But almost all taxa are found as disarticulated, isolated elements, and the reconstruction of apparatuses is thus a fundamental, underpinning activity of conodont research. A variety of methods of reconstruction have been employed, but all except reconstructions drawn directly from articulated skeletons, rely on co-occurrences of elements as data. Ideally, then, the fossil record should furnish information concerning all elements of a conodont skeleton and their relative abundance in the apparatus. Any biases that may have acted to alter the likelihood of preservation and recovery of one component of the skeleton compared with another are of paramount importance to those engaged in reconstruction.

Although study of conodonts was initiated in the mid-nineteenth century, questions concerning the meaning and significance of the relative abundance of element types only came to the fore in the mid 1960s, since when major efforts have been expended in developing a biologically meaningful taxonomy of conodonts rather that simply assigning a different name to every different part of the skeleton. This has involved the development and refining of techniques for the recognition of groups of elements that originally comprised the skeleton of a single taxon (for a review, see Sweet 1988), and it soon became clear as part of this process that the numbers of different element types observed in the comparatively rare fossils that preserve complete skeletons (natural assemblages) do not match those found in collections of isolated elements. Although interpretations of the number of elements in natural assemblages have varied a little over the years, the basic message has not: the vast majority represent taxa assigned to the Ozarkodinida and contain 15 elements, 2 M, 9 S, and 4 P elements (of which two are P_1, or platform elements) (for a discussion of natural assemblages, apparatus architecture, homology and element notation, see Purnell and Donoghue 1997, 1998; Purnell *et al.* 2000); collections of isolated elements, on the other hand, contain far more P_1 elements than would be expected. In some cases the ratio of P_1 to S + M elements exceeds 25:1, 139 times more P_1 elements than would be expected based on the 0·18:1 ratio of the elements in natural assemblages (for further discussion and examples see von Bitter and Purnell 2005).

Various evolutionary and biological hypotheses have been proposed to explain this. For example, Carls (1977), following Schmidt and Müller (1964) to some extent, concluded that post-mortem sorting was unlikely in many cases and that P_1 elements are overrepresented in collections because they were shed and replaced more frequently than other parts of the apparatus (see also Krejsa *et al.* 1990; Armstrong 2005 for discussion). Merrill and Powell (1980) also favoured a developmental explanation but suggested that the composition of the apparatus varied through life: juveniles bore only ramiform elements (= S and M elements), later stages bore ramiform (S and M) and platform elements (= P_1), adult and gerontic animals bore only platform elements, their ramiform elements having been resorbed. They proposed this as a general model of skeletal development, and suggested (p. 1073) that 'the ''normal'' condition, especially in some environments, increasingly became one of platform-only apparatuses later in the Paleozoic and Mesozoic' thereby implying an hypothesis that changes in element ratios through time reflected heterochronic shifts in apparatus development. Sweet (1985, 1988) developed this idea further, presenting data to support long-term evolutionary trends in apparatus reduction. He suggested (1988, p. 144) that under conditions of limited phosphate availability S and M elements did not mineralize, the apparent patterns in the record thus being explained by most Ordovician and Silurian species (and younger species represented by natural assemblages) having inhabited environments in which phosphate was not a limiting factor, whereas species represented largely or entirely by P elements may have been adapted to phosphate-poor conditions.

Several of these authors, and others such as Ellison (1968) and von Bitter (1972), did consider the possibility that to some extent the apparent overrepresentation of P_1 elements reflects post-mortem processes such as current sorting, but only later was the potential role of element hydrodynamics investigated (Broadhead *et al.* 1990; McGoff 1991). As noted above, these authors were able to demonstrate that element size and shape are correlated with their susceptibility to current entrainment, transport and sorting.

That post-mortem factors influence the elemental composition of conodont collections is now beyond doubt, but hydrodynamic sorting as the source of bias in element relative abundance data is difficult to reconcile with the hypothesis, well known among conodont workers, that there is a long-term trend in P element overrepresentation (Sweet 1985, 1988). This apparent pattern continues to provide compelling support for the view that a biological signal of S and M element loss through time lurks beneath the taphonomic noise (Merrill 2002). Even when more recent evidence that apparatus composition did not vary through ontogeny and that elements were not shed is taken into account (Purnell 1994; Donoghue and Purnell 1999; Armstrong 2005), the pattern cannot simply be ignored.

Text-figure 3A is based on Sweet's well-known plot (Sweet 1985, fig. 9; 1988, fig. 6.7) showing ratios between ramiform (S and M) and pectiniform (P) elements in Ordovician–Triassic conodonts. This is probably the clearest published evidence to support the hypothesis of long-term unidirectional trends in apparatus composition, but does the hypothesis stand up to analysis based on what we now know of conodonts? We would like to consider three questions that have a direct bearing on this problem: (1) What is the evidence for variation in the composition of the conodont skeleton through time? (2) Can the trends be explained by changes in diversity of taxa bearing apparatuses with different pectiniform–ramiform ratios? (3) How do alternative hypotheses of

element homology, especially among taxa assigned to Prioniodinida, affect the pattern?

One of Sweet's (1985) original purposes with his plot (and his preceding fig. 8) was to highlight changes in apparatus composition through time. At that time the degree of stability in apparatus composition was unclear, and Sweet discussed three different types of apparatuses characterized as bimembrate (two element types), tri- and quadrimembrate, and quinque- to septimembrate (see also Barnes *et al.* 1979). Apparatuses bearing only P elements have also been advocated by some authors, mainly because ramiform–pectiniform ratios are low to the point that ramiforms are considered to be absent from collections. If conodont taxa with a variety of different apparatus structures existed, each with a different ratio of ramiform to pectiniform elements, then changes in the relative abundance of taxa could cause the overall pattern of ramiform–pectiniform ratios to change through time. The hypothesis certainly has the potential to explain the pattern, but what is the evidence for variation in skeletal composition among Prioniodontids, Ozarkodinids and Prioniodinids (the taxa upon which the plot is based)? Pectiniform–ramiform ratios for natural assemblages are shown in Text-figure 3B as stars. With one exception they plot at 2·75 because current evidence indicates that the structure of the apparatus in these conodonts was remarkably stable. Natural assemblages are now known for more than 20 taxa, ranging from the Ordovician through to the Triassic, and including both primitive and derived members of Prioniodontida, Ozarkodinida and Prioniodinida. Except for one species, they all bear 2 M,
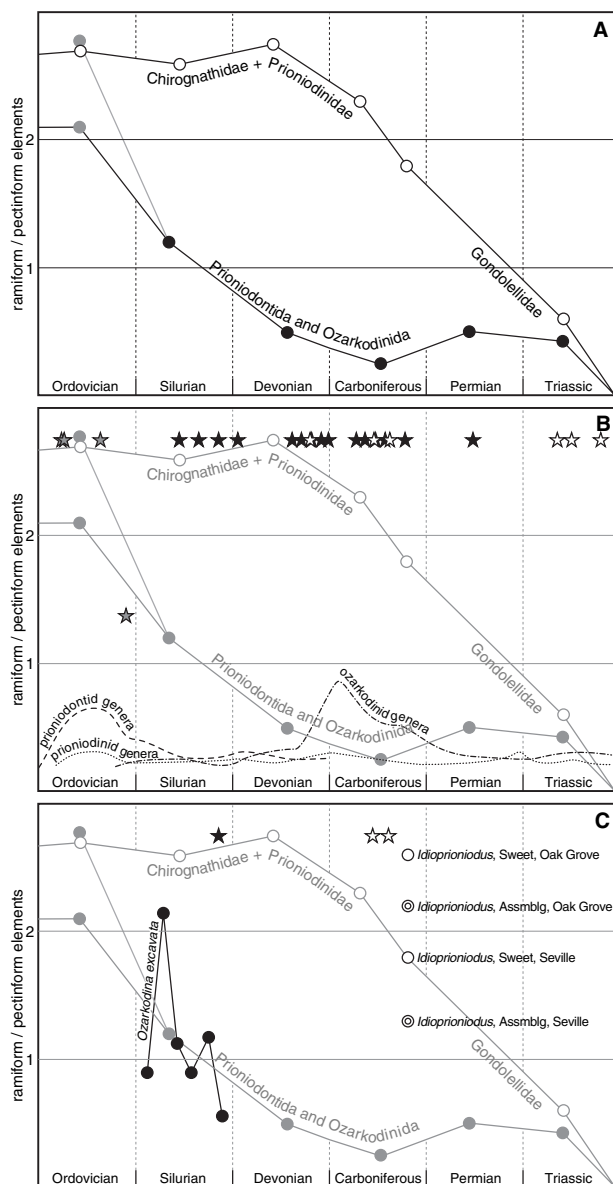
TEXT-FIG. 3. Plot of conodont pectiniform to ramiform ratios through time. A, ratios calculated from collections of isolated elements: grey circles, taxa assigned by Sweet (1988) to Prioniodontida; black, taxa assigned by Sweet to Ozarkodinida; white, taxa assigned by Sweet to Prioniodinida (Gondolellidae in Triassic). See Appendix for sources of data (modified from Sweet 1988, fig. 6.7). B, element ratios in natural assemblages: grey stars, Prioniodontida; black stars, Ozarkodinida; white stars, Prioniodinida. Lower broken lines show relative approximate generic diversity of Prioniodontida, Ozarkodinida and Prioniodinida. See Appendix for sources of data. C, noise in different collections of the same taxon and arising from alternative hypotheses of element homology. Black circles and lines, ratios for *Ozarkodina excavata* calculated in six different collections (see von Bitter and Purnell 2005 for details; points plotted in order, but stratigraphic positions are approximate); black star shows true ratio in natural assemblage. White circles, calculations of element ratios for *Idioprioniodus* (Prioniodinida) based on different data sets (Oak Grove and Seville units of Merrill and King 1971) and alternative hypotheses of element homology (Sweet 1988, and Natural Assemblages; see text for details). White stars shows true ratio in natural assemblages.

9 S and 4 P elements (for more details, see Purnell and Donoghue 1998; Purnell *et al.* 2000). The argument that these taxa, and others, bore a complete apparatus only in certain environments and it is only from these environments that we recover complete natural assemblages (Sweet 1988) can never be fully refuted as it relies on negative evidence, but each discovery of an additional taxon with the 15-element skeletal plan makes the hypothesis weaker. Furthermore, natural assemblages have been found in depositional settings ranging from near abyssal depths to the shallow shelf, from cherts, shales and carbonates; the hypothesis is not strong.

To date, only one taxon provides clear evidence of a different skeletal structure: *Promissum pulchrum*, the giant prioniodontid from the Late Ordovician of South Africa, has 2 M, 9 S and 8 P elements (Aldridge *et al.* 1995). It is likely that some other taxa currently assigned to Prioniodontida also bore more than 4 P elements and some species have been reconstructed as such (e.g. *Pranognathus*: Männik and Aldridge 1989; *Pterospathodus*: Männik 1998; *Coryssognathus*: Miller and Aldridge 1993), but the discovery of Prioniodontids with 15 elements [*Phragmodus*: Repetski *et al.* 1998, and *Oepikodus*: Stewart and Nicoll 2003; *Paracordylodus* (Tolmacheva and Purnell 2002) is probably also a prioniodontid] indicates that the 19-element apparatus may be limited to a few taxa, possibly a single clade within Prioniodontida (*sensu* Aldridge and Smith 1993). Even if the 19-element apparatus were widespread among prioniodontids it could not explain the apparent pattern of pectiniform–ramiform ratios. The ratio for the *Promissum* apparatus is 1:1·375 (or 1:1·833 if P_4 elements are not included among P counts), so periods of high relative generic diversity of prioniodontids (shown as dashed curve on Text-fig. 3B) should correspond to periods of lower pectiniform–ramiform ratios. The opposite is true.

The argument that the pattern of element ratios is influenced by the existence of P-only apparatuses which, if they became more abundant through time would lead to reduced pectiniform–ramiform ratios, is similarly problematic in that, because it relies on negative evidence, complete refutation is impossible. However, other than pectiniform–ramiform ratios there is little if any direct support for the hypothesis. Many taxa for which S and M elements are uncommon seem to have had a standard apparatus, including taxa that have long been held to contain only P elements, such as *Eoplacognathus* (Löfgren and Zhang 2003; see Jeppsson 2005 for further discussion) and *Mestognathus* (Purnell and von Bitter 1993) and contrary to much of the literature, recent work utilizing low-diversity collections from relatively offshore and/or low-energy settings and complete articulated skeletons has demonstrated that even Triassic gondolellids, most of which (following Sweet 1970; Kozur and Mostler

1971) have been reconstructed as having P_1 elements only, had a standard 15-element apparatus (Rieber 1980; Orchard and Rieber 1999; Orchard 2005).

Hypotheses of element homology also have a direct bearing on the problem. Identifying homologous elements in some taxa, almost all members of Ozarkodinida for example, is relatively straightforward. There is a relatively high degree of conservatism in the morphology of homologous elements, different elements in the apparatus exhibit clear morphological differentiation, natural assemblages are comparatively common and apparatus structure is stable over long periods of time. Consequently there is little difference of opinion regarding element homology in ozarkodinids. For other taxa, members of Prioniodinida especially, this is not the case. Until comparatively recently few natural assemblages of prioniodinids were known, and they had failed to yield clear evidence of skeletal architecture. Furthermore, because there is less morphological differentiation within the apparatus it is much more difficult to identify homologous elements in collections of isolated elements. Obviously, this could have a significant impact on calculations of pectiniform–ramiform ratios (or more correctly in this context, ratios of P to S + M elements), and this is illustrated in Text-figure 3C with alternative calculations for *Idioprioniodus*.

Idioprioniodus provides a good example of the problem of homology: sound hypotheses of its apparatus composition were established decades ago (Merrill and Merrill 1974), and these hypotheses have now been confirmed in natural assemblages (Purnell and von Bitter 1996, 2002), but hypotheses of element homology have been far from stable. The significance of this for calculation of ramiform–pectiniform ratios is shown by the difference between the points labelled 'Sweet, Seville' and 'Assmblg, Seville', and those labelled 'Sweet, Oak Grove' and 'Assmblg, Oak Grove' in Text-figure 3C (based on published data for two collections of isolated elements, one from the Oak Grove Member and the other from the Seville Member from the Pennsylvanian of Illinois; Merrill and King 1971). 'Sweet, Seville' and 'Sweet, Oak' are calculations of ratios based on the hypothesis of homology advocated by Sweet (1988); 'Assmblg, Seville' and 'Assmblg, Oak' are calculations based on the same data, but using hypotheses of element homology derived from natural assemblages. In both cases, Sweet's hypothesis significantly overestimated the pectiniform–ramiform ratios in these collections, but places one directly on his curve. The true value for the apparatus is 2·75. Hypotheses of homology can vary between conodont workers, and workers tend to concentrate on one or two geological periods more than others. Differences and uncertainties in hypotheses of homology probably add significantly to the noise in the data for prioniodinid ratios, but it is also possible

that they could contribute towards the trends in element ratios through time.

Differentiating noise from signal in these data is clearly a major problem. This is highlighted by the calculations of pectiniform–ramiform ratios based on data from six Silurian collections containing *Ozarkodina excavata* (Aldridge 1972; Jeppsson 1974; Klapper and Murphy 1974; Rexroad *et al.* 1978; Helfrich 1980; Simpson and Talent 1995). A more sophisticated analysis of element ratios in this species is presented by von Bitter and Purnell (2005), but the plot shows clearly how widely ratios fluctuate in a single species through a single period. The most parsimonious explanation of this is that the signal is dominated by noise (i.e. post-mortem biases) and that collections of isolated elements rarely preserve elements in their original relative abundance.

Perhaps the most obvious test of the pattern of pectiniform–ramiform element ratios would be to repeat Sweet's analysis based on randomly selected published records of element abundance. This is beyond the scope of the present study. Such an analysis may or may not reproduce Sweet's pattern, but given the evidence presented here against there being a long-term trend in apparatus composition within complex conodonts the question should perhaps be rephrased: is there an alternative mechanism capable of explaining trends in calculated ratios in collections of discrete elements? This applies equally to secular trends as outlined by Sweet, and similar apparent ecological, spatial and taxonomic trends in relative ramiform retention (Merrill *et al.* 1991). We propose that there is such a mechanism, and that apparent relative ramiform retention reflects interaction between the biological and post-mortem variables as follows: conodont taxa vary in the relative robustness and relative size of their S, M and P elements (those taxa that have been subject to analysis have similar rates of apparatus growth, but the size differential of S and M elements relative to P elements varies: Purnell 1994; Tolmacheva and Purnell 2002). Taxa that have small and/or fragile S and M elements relative to P elements are less likely to have their S and M elements preserved in collections that contain P elements because S and M elements will be more susceptible to winnowing, current entrainment and removal, and fragmentation (see 'Element fragmentation' above). Such taxa are more likely to have P, M and S elements preserved together in quieter deposition settings, and in lithologies where factors leading to element fragmentation are reduced. It may seem obvious, but it is worth noting here that relative sizes of P, M and S elements in the apparatus of a conodont species can be determined only by measurement of elements in natural assemblages. It is most unlikely that the relative sizes of skeletal components in collections of isolated elements are unaffected by post-mortem processes. If our model is correct, then spatial and secular trends in apparent pectiniform–ramiform ratios within clades should correspond to variation in relative size and robustness of S and M elements relative to P elements.

CONCLUDING DISCUSSION: HOW LESS CAN BE MORE

A complete record of conodont diversity through time was never preserved and can never be recovered. The record we have reflects the interplay of diverse biases, ranging from the differential hydrodynamic effects upon the various element morphologies that constitute apparatuses, through environmental and stratigraphic biases in the sedimentary record, to cultural, operational and interpretational biases imposed by our retrieval and study of rocks and the conodonts they contain. Very few conodont studies have taken these biases into account and even fewer have attempted to control for their influence upon their data. As a result, conclusions drawn from these data are subject to unconstrained artefact to an unknown degree. For instance, studies of conodont evolutionary history through the Phanerozoic (e.g. Aldridge 1988; Sweet 1988) have implicitly assumed that diversity patterns read from the fossil record preserve a strong biological signal. Our preliminary investigation of potential biases provides only limited support for this view, and highlights the need to take secular variation in research effort and outcrop area into account before apparent diversity patterns can be interpreted primarily as the results of evolution and extinction. Our analysis, however, is exploratory in nature, and more work is required before the full effects of these gross biases on sampling *sensu lato* can be evaluated with confidence.

The data upon which most models of conodont palaeo-ecology and biofacies are based are also likely to be biased to some degree. Post-mortem hydrodynamic sorting (Broadhead *et al.* 1990; McGoff 1991) and differential redistribution of elements have affected the final facies distributions of different elements and species in different ways. The degree to which this has influenced apparent associations of elements and species, and perceived environmental ranges, is largely unknown, but, as noted by McGoff (1991), samples containing elements that reflect a narrow range of Reynolds numbers and drag coefficients are very likely to be the product of post-mortem sorting. This applies equally to samples dominated by a single taxon and those containing a more mixed fauna. In either case the sample cannot be used in biofacies analysis (McGoff 1991). A rigorous study of the prevalence of post-mortem sorting would be worthwhile, and has the potential to add significantly to the usefulness of conodonts in palaeoenvironmental analysis. It may be possible, for example, to establish conodont taphofacies

(cf. Speyer and Brett 1986) based on analysis of the size and shape of elements in a sample, attributes that are known to correlate with their relative hydrodynamic properties (Broadhead *et al.* 1990; McGoff 1991).

Hydrodynamic biases also have a bearing on hypotheses that attribute variation in the recovery of pectiniform and ramiform elements from strata of different ages to evolutionary trends in apparatus composition or to changes in differential shedding or resorption of P, S and M elements. We have found no evidence to support these hypotheses, and interpret differences in recovered element abundances as the result, largely, of the interplay between hydrodynamic factors and relative size and fragility of elements within the skeleton. Finally, it is clear from a consideration of biases and the incomplete nature of the stratigraphic record that attempts to reconstruct phylogeny through the assembly of species-level lineages can never lead to a composite tree for all conodonts.

Notwithstanding its imperfections, the conodont fossil record remains among the best of any group of organisms, with clear utility across a range of geological and biological contexts. Attempts to control for biases can be problematic and for some research agenda may prove impossible, but acknowledging the biases that affect the record can actually enrich understanding of it (cf. Behrensmeyer and Kidwell 1985). This, we hope, is clear from our discussions of hydrodynamic sorting, palaeoecology and pectiniform–ramiform ratios, but there are also stratigraphic implications that should not be ignored. Recognizing that the ranges of taxa vary from section to section and from region to region provides an opportunity for closer investigation of the relationship between the spatial and temporal distribution of conodont taxa at a variety of scales. How, for example, have distributions varied in response to extrinsic environmental events? A prerequisite for such studies is the application of more rigorous, quantitative methods of biostratigraphy (e.g. Armstrong 1999). The cause of graphic correlation has been championed on the basis of the conodont fossil record (Shaw 1969) but, with a few exceptions (see Sweet 2005 and references therein), conodont workers have yet to capitalize on the potential and benefits of this technique in resolving rates of sedimentation, detecting otherwise imperceptible hiatuses in sections, and for producing a high-resolution composite chronostratigraphic timescale of global relevance. Confidence intervals, too, provide a basis for assessing the significance of first and last appearances in local sections and in constraining the veracity of apparent bioevents (Paul 1982; Strauss and Sadler 1989; Marshall 1990); protocols for calculating confidence intervals compatible with standard micropalaeontological sampling strategies have been available for some time (Weiss and Marshall 1999).

A range of variables have together conspired to produce what we recover as taxon ranges, element distributions and diversity data. Taking these variables into account will improve our understanding of patterns of conodont palaeobiology, palaeoecology, palaeogeography and phylogeny and their controls while at the same time enhancing the utility of conodonts as geological tools, and highlighting new avenues for research. Above all, the clear message of this collection of papers (Purnell and Donoghue 2005) is that to pay no regard to post-mortem processes and the nature of the conodont fossil record risks overlooking factors that have significantly biased our primary data. Ignorance is not bliss.

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APPENDIX

Data for Text-figure 3

Except as noted in figure caption, isolated element ratio data are taken from the following sources (Sweet, pers. comm. 2002): Ordovician, Prioniodontida: *Phragmodus undatus,* based on whole-collection numbers for the 4-component elements in the large dataset assembled by Kohut (1969), the higher point is based on counts in Bergström and Sweet (1966). Silurian: unpublished material from the Bainbridge Formation (since donated to Hans Peter Schönlaub). Devonian: based on element counts of Gable (1973) and Ramsey (1969). Carboniferous: unpublished Pennsylvanian collections of Sweet. Triassic, Ozarkodinida: based on data for *Hindeodus typicalis* in Sweet (1970; P elements = *Anchignathodus typicalis* and LA element of *Ellisonia teicherti*, S and M elements = remainder of *E. teicherti*). Using the same dataset, calculation of ratios for *Neospathodus cristagalli* (reconstruction of Purnell *et al*. in prep.) gives the same result (P elements = *Neospathodus cristagalli* and *Xaniognathus deflectus*, S and M elements = *Ellisonia gradata*). Triassic, Gondolellidae: based on counts by Sweet in most complete samples in the collections of Hieke (1967). Natural assemblage data are based on the following sources: Prioniodontida – O, *Paracordylodus gracilis* (Tolmacheva and Purnell 2002), *Phragmodus* (Repetski *et al*. 1998), *Oepikodus* (Stewart and Nicoll 2003), *Promissum pulchrum* (Aldridge *et al*. 1995); Ozarkodinida – S, *Ozarkodina steinhornensis* (Nicoll and Rexroad 1987), *Ozarkodina excavata* (von Bitter and Purnell 2005), *Ctenognathodus muchisoni* (von Bitter and Purnell 2004); D, *Criteriognathus* (Mashkova 1972; Purnell and Donoghue 1998), *Palmatolepis* (Lange 1968; Donoghue 2001*a*), *Bispathodus aculeatus* (Purnell and Donoghue 1998), *Polygnathus xylus xylus* (Nicoll 1985), *Polygnathus nodocostatus* (Dzik 1991; illustrated as *Hemilistrona*); C, *Clydagnathus windsorensis* (Aldridge *et al*. 1993; Purnell and Donoghue 1998), *Lochriea commutata* and *Gnathodus bilineatus* (Schmidt and Müller 1964; Norby 1976), *Cavusgnathus unicornis* (pers. obs.), *Adetognathus unicornis* (Purnell and Donoghue 1998); P, *Sweetognathus* (Ritter and Baesemann 1991); Prioniodinida – D, *Hibbardella angulata* (Nicoll 1977), *Prioniodina*? (pers. obs., unpublished cluster from the Gogo Formation); C, *Kladognathus* (Purnell 1993), *Idioprioniodus* (Purnell and von Bitter 1996); ᴦR, *Neogondolella* (Rieber 1980; Orchard and Rieber 1999), *Pseudofurnishius* (Ramovš 1977, 1978), *Misikella* (Mastandrea *et al*. 1997, 1999).