The Reconstruction of Fossil Organisms Using Cluster Analysis

A Case Study from Late Paleozoic Conodonts

Peter H. von Bitter and Glen K. Merrill

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The Reconstruction of Fossil Organisms Using Cluster Analysis: A Case Study from Late Paleozoic Conodonts

Abstract

The reanalysis of the data of others has become increasingly attractive. The reanalyst may, however, have little understanding of the original data, their sources and limitations. Effects of this may include data mistreatment and misinterpretation of analytical results. We present a case study of the work of D. L. Clark and T. R. Carr in which they applied cluster analysis to colleagues' data to reconstruct conodont apparatuses, sclerotized structures borne by small, extinct marine animals. We demonstrate that their inability to support their conclusions is the result of uncritical data modification prior to analysis and overextrapolation and misinterpretation of the results. Among the reasons for the latter was their failure to acknowledge established biological models based on unusually well-preserved specimens and to take into account the extent to which the fossilized parts of plants and animals cluster in dendrograms for ecological as well as anatomical reasons.

We caution against blind analysis of the data of others and against rigid reliance on cluster analysis for the reconstruction of disarticulated fossil plants and animals. Our analysis of their study does not support the following of Clark and Carr's specific claims: (1) species of *Streptognathodus-Idiognathodus* contained only platform elements, and those of *Adetognathus* [*Cavusgnathus*] may have contained only platform elements; (2) the apparatus of *Diplognathodus* included the ramiform elements previously assigned to *Adetognathus* [*Cavusgnathus*] and possibly some of those previously assigned to *Streptognathodus-Idiognathodus*; and (3) the *Hindeodus* apparatus contained the Pb element previously assigned to *Streptognathodus-Idiognathodus*.

INTRODUCTION

The increased availability, and the increasingly user-friendly nature of computers has led to the greater utilization, and testing, of a great scientific resource—the data of others. Mathematically inclined individuals can reexamine published data using new and powerful analytical tools. Although this approach is attractive, it is, nevertheless, full of pitfalls. The analyses are only as good as the data used, the analytical technique applied, and/or the interpretation of the results.

There are several reasons why reanalysis of data may lead to difficulties. One is that the reanalyst commonly has little or no direct knowledge or understanding of the limitations of the material the data are based on and of how that material was collected. This, in turn, may lead to invalid assumptions and misinterpretations, both in the treatment of the data and in the interpretation of analytical results. This paper is a critique of the analytical methods used by Clark and Carr (1982), and all references to them together in this paper pertain to that publication. Their study dealt with the reconstruction, using cluster analysis, of the apparatuses of conodonts. This is a group of small, extinct marine organisms that had a remarkably long evolutionary history of ca. three hundred million years. Conodont apparatuses were generally composed of a number of kinds of paired, phosphatic toothlike elements.

The analytical methods used by Clark and Carr consisted of 12 R-mode cluster analyses, using three coefficients, of the distributional data of conodonts from von Bitter (1972), Baesemann (1973), and Perlmutter (1975). The data of these authors were modified by Clark and Carr prior to analysis and were used in both binary and absolute form. This study will show that Clark and Carr were unable to demonstrate what they claimed because of uncritical data modification and misinterpretation of the results of cluster analysis. We (von Bitter and Merrill, 1985) previously considered their taxonomic interpretations.

The reconstruction from fossil “graveyards” of in-

dividual species, and of the communities to which they belonged, is one of the ongoing challenges in palaeontology. Burials may look chaotic because of the action of various geological forces, and the fossilized parts of organisms may be dismembered and separated. A variety of numerical techniques, including cluster analysis, has been applied to discern structure or order in such burials.

Parts of fossilized animals and plants are associated physically in a sample, or statistically in a cluster on a dendrogram, for random and nonrandom reasons. Among the nonrandom reasons is the association of body parts that came from the same species, a situation we refer to as being caused by anatomical association. An association of fossilized parts in a sample or on a dendrogram may be suspected to have an anatomical cause; however, only a reasonably complete individual, whose fossilized parts are somewhat articulated and not scattered, constitutes proof that disarticulated body or skeletal parts were part of the same species. Such specimens are useful as biological blueprints—in the Conodonts, one kind of reasonably complete specimen is referred to as a natural assemblage (Fig. 1). A second kind of nonrandom association in a sample, one often measured by a high level of clustering in dendrograms, is caused by ecological association. This is an association of more than one species (or their body parts) that lived, and died, together in a community.

In our usage of the names *Adetognathus* [*Cavusgnathus*], we do not consider the second to be a subgenus of the first. Rather, we use this format to list the generic name used by Clark and Carr and to provide in square brackets the generic assignment favoured by us. Similarly, when referring to *Streptognathodus-Idiognathodus*, we follow the usage of Clark and Carr rather than the phylogenetically correct *Idiognathodus-Streptognathodus*. In Table 1 we provide our identifications of the taxonomic categories of Clark and Carr. Table 2 compares the size and format of data matrices before and after modification by them.

FIG. 1. Natural assemblage of conodonts of the *Streptognathodus-Idiognathodus* plexus (A) and of *Cavusgnathus* (B-D) from the Pennsylvanian and Mississippian of North America, respectively.

A. *Streptognathodus-Idiognathodus*, natural assemblage, holotype of *Scottognathus typica* (Rhodes) of Rhodes (1952); the Pb elements are the second element pair from the top. Photographed by R. D. Norby, University of Illinois X-1480, $\times 21$. Magnification calculated from direct measurement of specimen by R. D. Norby.

B. *Cavusgnathus altus* Harris and Hollingsworth, natural assemblage, identification from Norby (1976); photographed by R. D. Norby, Illinois State Geological Survey 62P-401A, $\times 36$. Magnification calculated from direct measurement of specimen by R. D. Norby.

C,D. *Cavusgnathus* cf. *C. unicornis* Youngquist and Miller, natural assemblage, counterparts; identification from Scott (1973); printed from negatives supplied by H. W. Scott, United States National Museum 183567 and 183568, $\times 10$ and $\times 13$, respectively. Magnifications calculated from Scott (1973).

TABLE 1. Our identification of the taxonomic categories of Clark and Carr (1982). Table format conforms to table 2 of Clark and Carr. Data set 1 was based on von Bitter (1972), data set 2 on Baesemann (1973), and data set 3 on Perlmutter (1975).

Element no.	Data set 1	Element no.	Data set 2	Element no.	Data set 3
1	<i>Streptognathodus-Idiognathodus</i> Pa element	1	<i>Streptognathodus-Idiognathodus</i> Pa element	1	<i>Streptognathodus-Idiognathodus</i> Pa element
2	<i>Adetognathus [Cavusgnathus]</i> Pa element	2	<i>Adetognathus [Cavusgnathus]</i> Pa element	2	<i>Adetognathus [Cavusgnathus]</i> Pa element
3	<i>Hindeodus minutus</i> Pa element	3	<i>Hindeodus minutus</i> Pa element	3	<i>Hindeodus minutus</i> Pa element
4	<i>Diplognathodus</i> Pa element	4	<i>Diplognathodus</i> Pa element	4	<i>Diplognathodus</i> Pa element
5	<i>Streptognathodus-Idiognathodus</i> Pb element	5	<i>Streptognathodus-Idiognathodus</i> Pb element	5	<i>Streptognathodus-Idiognathodus</i> Pb element
6	<i>Adetognathus [Cavusgnathus]</i> Pb element	6	<i>Adetognathus [Cavusgnathus]</i> Pb element		
7	<i>Hindeodus minutus</i> Pb element	7	<i>Hindeodus minutus</i> Pb element		
8	<i>Streptognathodus-Idiognathodus</i> M element	8	<i>Streptognathodus-Idiognathodus</i> M element	6	<i>Streptognathodus-Idiognathodus</i> M element
9	<i>Adetognathus [Cavusgnathus]</i> M element	9	<i>Adetognathus [Cavusgnathus]</i> M element		
10	<i>Hindeodus minutus</i> M element	10	<i>Hindeodus minutus</i> M element		
11	<i>Streptognathodus-Idiognathodus</i> Sa element	11	<i>Streptognathodus-Idiognathodus</i> Sa element	7	<i>Streptognathodus-Idiognathodus</i> Sa and Sc elements
12	<i>Adetognathus [Cavusgnathus]</i> Sa element	12	<i>Adetognathus [Cavusgnathus]</i> Sa element		
13	<i>Hindeodus minutus</i> Sa element	13	<i>Hindeodus minutus</i> Sa element	8	<i>Hindeodus minutus</i> Sa element
14	<i>Hindeodus minutus</i> Sb element	14	<i>Hindeodus minutus</i> Sb element		
15	<i>Adetognathus [Cavusgnathus]</i> Sc element	15	<i>Adetognathus [Cavusgnathus]</i> Sc element		
		16	<i>Adetognathus [Cavusgnathus]</i> Sb element		
16	<i>Streptognathodus-Idiognathodus</i> Sc element	17	<i>Streptognathodus-Idiognathodus</i> Sb element		
		18	<i>Streptognathodus-Idiognathodus</i> Sc ₁ element		
		19	<i>Streptognathodus-Idiognathodus</i> Sc ₂ element		
17	<i>Hindeodus minutus</i> Sc element	20	<i>Hindeodus minutus</i> Sc ₁ element		
		21	<i>Hindeodus minutus</i> Sc ₂ element		
18	Unidentified Pb element				
19	Unidentified Pb element				
20	Unidentified M element				
21	Unidentifiable Sc element				
22	Unidentifiable Sa element			9	<i>Hindeodus minutus</i> Pb, Sb, and Sc elements
				10	<i>Hindeodus minutus</i> M element
				11	<i>Ellisonia</i> sp. A Sc element

TABLE 2. Comparison of data matrices before and after modification by Clark and Carr.

	Size of original data matrices	Size of modified data matrices
von Bitter (1972)	79 element types $\times$ 153 samples*	22 element types $\times$ 152 samples
Baeseemann (1973)	45 element types $\times$ 193 samples**	22 element types $\times$ 197 samples**
Perlmutter (1975)	25 element types $\times$ 93 samples	11 element types $\times$ 76 samples***

* Clark and Carr (p. 128) stated this data matrix as having been 78 $\times$ 148; however, see von Bitter (1972:29).

** Baeseemann (1973, tables 1–3) processed 229 samples, of which 193 contained conodonts.

*** Perlmutter (1975, tables 1–6) listed 95 samples, and although he (1975:104) noted that barren samples were not tabulated, samples 4/6 and 10/6 contained no conodonts. Removing these 2 samples and the 17 samples dropped by Clark and Carr (pp. 128–129) leaves 76 rather than the 75 samples given by Clark and Carr (p. 129).

DATA MODIFICATION

We agree with Clark and Carr that the form of data used in an analysis can have a profound effect on the results. The three subsections that follow document instances of their inappropriate modification of data. Our critical assessment of their paper is based on the view that only reasoned and explicit taxonomic, ecological, and analytical methods should be applied to palaeontological data prior to analysis, and that these should be applied consistently.

Data Deletion

Although it may be desirable to clean up data by deleting certain taxonomic categories prior to analysis (see von Bitter, 1972:29), this must be done with sound taxonomic judgement and consistency. The deletion by Clark and Carr of elements of *Aethotaxis*, *Idiopriodontus*, and *Gondolella* from two data sets (von Bitter, 1972; Baeseemann, 1973) was consistent (particularly since Perlmutter [1975] lacked these genera); however, the treatment of other taxa was not. The five element types placed by von Bitter (1972) in *Delotaxis? conflexa* (Ellison)—and reassigned by von Bitter and Merrill (1983) to *Ellisonia conflexa* (Ellison)—were deleted in the modification of his data set, as were the three components of the same apparatus from the data of Baeseemann (1973). The most characteristic element (Pl) of the *E. conflexa* apparatus was deleted from the data of Perlmutter (1975), but the Se element was retained for analysis. Thus, a single element of the *E. conflexa* apparatus was retained in only one of the three data sets analysed. If the elements of this species were deleted from two data sets, then the *E. conflexa* Sc element should also have been dropped from data set 3, or at least an explanation for this inconsistency should have been provided.

The deletion of the ramiform elements that Perlmutter (1975) placed in *Ozarkodina* [= *Diplognathodus*] *expansa* was remarkable. Clark and Carr recognized the similarity of these elements to those of *Adetognathus* [*Cavusgnathus*] and concluded that “*Diplognathodus* spp. were [anatomically] associated with ramiform elements previously assigned to *Adetognathus*” (p. 132). Reassignment of the ramiform elements of Pennsylvanian *Adetognathus* [*Cavusgnathus*] to Permian *Diplognathodus* was based on cluster analysis of data of von Bitter (1972) and Baeseemann (1973), data that included the *Adetognathus* [*Cavusgnathus*] ramiform elements (Table 1, data sets 1 and 2). However, the morphologically similar ramiform elements of *Diplognathodus* were deleted from the data set of Perlmutter (1975) and were, inexplicably, not subjected to the same analyses (Table 1, data set 3).

Related to the treatment of these ramiform elements is the deletion of a number of samples prior to analysis. Clark and Carr (pp. 128–129) stated, “All of the Perlmutter’s (1975) samples that contained conodont elements (except for [those from] sections 6, 7 and 9 which consist solely of *Diplognathodus expansus* elements) were utilized to construct a second data matrix.” Sample 37 from section 9 was deleted, but this sample does contain conodonts other than *Diplognathodus expansus* (Perlmutter, 1975, table 6). It is unclear whether conodonts from samples 3, 9, and 12 in section 10, from which *D. expansus* Sa elements were reported (Perlmutter, 1975, table 4), were retained. Because Clark and Carr apparently deleted the elements they recognized as the ramiform elements of *D. expansus* from their analyses, and because samples from sections 6, 7, and 9 were deleted, it is possible that samples 3, 9, and 12 from section 10 were treated

the same way. All three samples contained *Adetognathus* [*Cavusgnathus*] Pa elements, which might have been significant in deciding whether the ramiform elements in question belong to that genus or to *Diplognathodus*.

The data treatment by Clark and Carr also involved the differential deletion of element categories between analyses of the same data set. For example, the *Idiognathodus* Sc(A₂) element of Clark and Carr (Table 1, data set 2, element 17) is missing from the results of association analysis of the modified data of Baesemann (1973). It is, however, present in the three other analyses of those data (Clark and Carr, figs. 3, 4, 6). Similarly, element category *Ozarkodina* sp. A of Clark and Carr (Table 1, data set 1, element 18) is missing from the analysis using the coefficient of Jaccard of the data of von Bitter (1972) (Clark and Carr, fig. 3), but is present on the dendrograms of the three subsequent analyses of the same data (Clark and Carr, figs. 4–6).

Questionable Taxa

In some cases it may be necessary to delete certain taxonomic categories prior to analysis. These include the taxonomic chaff present in many palaeontological studies—i.e., fragmentary and rare taxa, or those not identified to genus and/or species. Clark and Carr deleted numerous significant conodont elements from the three data sets prior to analysis, but retained taxonomic categories of questionable value. Examples include elements 18 (based on a single Pb element), 19, 21, and 22 from von Bitter's data set (Table 1, data set 1).

Condensing of Data

The Pa elements of 17 species of *Streptognathodus-Idiognathodus* were collapsed into a single category and those of 3 species of *Adetognathus* [*Cavusgnathus*] of von Bitter (1972) into a second category “to focus on the relationships of the Pa elements to their possible ramiform elements” (p. 128). The treatment of the data of Baesemann (1973) was based on a slightly different reasoning: “The various species of *Idiognathodus* and *Adetognathus* [*Cavusgnathus*] were again lumped into two generic entities following the practice of lumping the other elements of the apparatus” (p. 129). Presumably one, or both, of these reasons were also used to collapse these element categories in the data of Perlmutter (1975). These procedures were “justified due to the lumping in all three studies of the non-platform elements of the two entities above into two groups of 4 elements each; (1) *Streptognathodus-*

Idiognathodus ramiform elements, and (2) *Adetognathus* [*Cavusgnathus*] ramiforms” (p. 128).

Unfortunately, Clark and Carr misunderstood the taxonomic treatment of the ramiform elements of *Streptognathodus-Idiognathodus* and *Adetognathus* [*Cavusgnathus*]. The so-called lumping was not that at all. Rather, being aware of, and using, natural-assemblage evidence, the three authors realized that the ramiform elements of *Streptognathodus-Idiognathodus* were present throughout the group and were present within the several species of each genus, according to the then-accepted models. Evidence from natural assemblages was also applied by von Bitter (1972) and Baesemann (1973) to the ramiform elements of *Adetognathus* [*Cavusgnathus*]. This procedure resulted in the establishment of such taxonomic categories as *Streptognathodus-Idiognathodus* Oz(O₁), Ne(N), Hi(A₁), Pl(A₂), and Tr(A₃) elements for these vicariously shared conodonts (von Bitter, 1972; Baesemann, 1973; Perlmutter, 1975).

The lumping of ramiform elements as perceived by Clark and Carr was in error and should not have been used as justification for the condensing of 20 Pa element categories. The condensing of the *Streptognathodus-Idiognathodus* Pa elements is of particular concern. There are differences of opinion and interpretation about the number of distinct species and about the method of differentiating species of these genera (e.g., the taxonomic decisions of Gunnell [1933], Ellison [1941], and Baesemann [1973] differed greatly), but the actions of Clark and Carr were extreme. The ubiquitous distribution of Pa elements of *Streptognathodus-Idiognathodus*, implied by condensing the Pa elements into one category in von Bitter's data set, was never observed or conceived by even the most conservative of the three authors (viz. Baesemann, 1973). To collapse 17 taxonomic categories into 1 was to discard an enormous body of information about the evolution of platform elements, as well as all the data about their differing palaeoecological distributions.

The decision to group all Pa elements of *Adetognathus* [*Cavusgnathus*] into a single category in each of the three data sets is also problematic. Although Clark and Carr's grouping of *Cavusgnathus lautus* and *C. gigantus* is taxonomically sound (these being the sinistral and dextral Pa elements of a single species—see von Bitter, 1972), no such taxonomic justification exists for including *Cavusgnathus merrilli* in element category 2, *Cavusgnathus* (Pa) [element]. *Cavusgnathus merrilli* is morphologically not characteristic of the genus, is remarkably similar to *Neostreptognathodus clinei* of Behnken (1975), and may, unlike *C. lautus* (*sensu* von Bitter, 1972), have regularly lacked ramiform elements (von Bitter, 1972).

CLUSTER ANALYSES

It is difficult to judge the effect that extensive deletion, unequal retention, and large-scale collapsing of data prior to analysis will have on cluster analysis. The data sets of von Bitter (1972), Baesemann (1973), and Perlmutter (1975) were presented as objective representations of the distribution of fossils in the Pennsylvanian and Permian strata of their respective field areas. This level of objectivity was removed when these data were subsequently modified by Clark and Carr.

Binary versus Absolute Data

We share the concern of Clark and Carr about information loss when using binary (presence-absence) rather than absolute, or quantitative, counts in cluster analysis. Coefficients of association that utilize absolute or quantitative data are being proposed and tested (Sepkoski, 1974; Nowlan and Barnes, 1981; Horowitz and Rexroad, 1982). At first glance, absolute data would seem to be superior because they maximize the information content in samples.

Much of the earlier criticism of the use of binary data for the reconstruction of conodont apparatuses was based on the incorrect assumption by some conodont workers that they were attempting to reconstruct a single apparatus for a taxon, and that specimen counts would assist in achieving that goal. Clark and Carr are among those who assumed that there was a constant numerical ratio among elements of an apparatus and only a single apparatus type for a taxon. Realization that variable ratios of elements were probably present within the apparatuses of many species makes absolute data less attractive. Presence-absence data are unaffected by such variations as long as the remains of any one individual that possessed the maximum number of kinds of elements present in the taxon are recovered.

Clark and Carr commented that the use of binary data "equates rare and common elements completely ignoring any numerical relationships among the various morphologic elements," that binary data "equalizes abundant and sparse faunas," and that "this loss of information may be critical for accurate recognition of multielement species" (p. 128). Natural-assemblage models have been used to predict the existence of a particular fixed ratio of platform to ramiform conodonts in a sample; however, ramiform conodonts are, for biological, sedimentological, and methodological reasons, known to be notoriously underrepresented in many faunas (Ellison, 1941; von Bitter, 1972; Carls, 1977; Merrill and Powell, 1980). Any coefficient that corrects for this shortfall in palaeontological data is

useful. Binary coefficients compensate for such underrepresentation. Gill and Tipper (1978) have shown in elegant fashion that presence-absence data are useful approximations of the true distributions of absolute data and that presence-absence methods approximate biological reality.

Ecology and Cluster Analyses

Clark and Carr did not attribute sufficient influence to palaeoecological controls of the element distributions they analysed. Fossil organisms, or their components, are often strongly linked in dendrograms for ecological reasons.

The degree of association indicated by such methods as cluster analysis is the cumulative result of various components of such diverse factors as physical association of elements, ecologic composition and taphonomic effects. The components of such association cannot be easily separated. Our tacit assumption is that the physical association of conodont elements in an apparatus is the dominant component. (p. 128)

In cluster analysis of palaeontological data, the physical association (i.e., anatomical association in our usage) is often not the dominant "component," and in many cases it is ecological association that is being recorded. In the case of conodonts, if the apparatus composition of a species is not constant, then the association measured may be largely owing to ecological rather than to anatomical effects. If $A + b + c + d + e$ is a multielement apparatus (where A represents platform, and $b, c, d,$ and e are ramiform elements) and if B and C are common ecological associates that are platform-only apparatuses, then B and C may have higher association values with A than A does with its $b + c + d + e$ ramiform elements.

There are several instances of failure by Clark and Carr to appreciate the determining ecological forces that may cause well-defined associations in cluster analysis. For example, they observed that in the R-mode dendrograms of von Bitter (1972) (Fig. 2), *Diplognathodus* and *Hindeodus* Pa elements occurred in the same clusters as the Pa and ramiform elements of *Streptognathodus-Idiognathodus* and *Adetognathus* [*Cavusgnathus*], noting specifically that *Hindeodus*, in particular, "is always closely tied to *Streptognathodus-Idiognathodus*."

A difficulty in evaluating the preceding observations is that we are unable to duplicate them (Fig. 2). *Diplognathodus moorei* is part of Group A, a grouping

FIG. 2. Dendrogram of R-mode cluster analysis of the conodont distribution in the Shawnee Group (Upper Pennsylvanian) of northeastern Kansas, using the coefficient of Jaccard, binary data, and weighted pair-group method (WPGM); amended from von Bitter (1972, fig. 18) using our element nomenclature and notation. Element numbers are those of von Bitter (1972).

that includes most or all of the common Pa elements (and nearly all of the ramiform elements) of *Streptognathodus-Idiognathodus*. However, *Diplognathodus edentulus* is in Group D, a cluster that lacks *Streptognathodus-Idiognathodus* ramiform elements. One species of *Diplognathodus* does occur with the Pa and ramiform elements of *Streptognathodus-Idiognathodus*; the other does not. Neither of the two species of *Diplognathodus* of von Bitter (1972) is present in Group C, the cluster that not only contains the most commonly occurring Pa elements of *Adetognathus [Cavusgnathus]*, but also nearly all the ramiform elements of *Adetognathus [Cavusgnathus]*. The *Hindeodus* Pa element is indeed associated with the *Streptognathodus-Idiognathodus* Pa and ramiform elements in Group A. However, except for its association in Group A with *Adetognathus [Cavusgnathus] merrilli*, the *Hindeodus* Pa element is not associated with the Pa elements of *Adetognathus [Cavusgnathus]*, nor with the ramiform elements of *Adetognathodus [Cavusgnathus]*. *Adetognathus [Cavusgnathus] merrilli*, an unusual cavusgnathid (see von Bitter, 1972), is the last to be linked to the group (and then at the very low linkage of approximately 0.23).

Because component elements of several different species were often present in the same cluster of von Bitter's dendrograms, Clark and Carr concluded that his results (Fig. 2) did not clearly support his, or their, interpretations of the apparatus structure of *Diplognathodus* and *Hindeodus* (and by extension those of *Streptognathodus-Idiognathodus* and *Adetognathus [Cavusgnathus]*). The observations on element associations in the R-mode dendrograms of von Bitter were regarded as evidence of "two contradictory interpretations" (p. 128).

We maintain that it is normal for the component elements of different but ecologically associated species to be present in the same cluster of a dendrogram. We suggest that Clark and Carr attributed too great a taxonomic significance to many of the associations they noted and that they disregarded well-documented (von Bitter, 1972; Merrill, 1973; Merrill and von Bitter, 1976; Merrill and Martin, 1976) palaeoecological reasons for these groupings. Thus, the association of the elements of *Diplognathodus* and *Hindeodus* with those of other genera in R-mode cluster analyses of the data of von Bitter (Figs. 2, 3) is most easily and logically explained by ecological associations. *Diplognathodus moorei* was ecologically a member of the *Streptognathodus* biofacies (Group A, Fig. 2) (= *Streptognathodus*

1 biofacies of Merrill and von Bitter, 1976, table 2), and was ecologically associated with *Adetognathus [Cavusgnathus] merrilli*, a cavusgnathid of unknown ramiform apparatus structure. *Diplognathodus edentulus* was a member of the *Lonchodina* biofacies (Group D, Fig. 2) (= *Aethotaxis* biofacies of Merrill and von Bitter, 1976, table 2). Neither species of *Diplognathodus* was ecologically a part of the *Cavusgnathus* biofacies (Group C, Fig. 2), a community characterized on dendrograms (Fig. 2) by the Pa and ramiform elements of the common cavusgnathids (von Bitter, 1972, table 15; see also Merrill and von Bitter, 1976, table 2). *Hindeodus* Pa and ramiform elements were ecologically associated with *Streptognathodus-Idiognathodus* Pa and ramiform elements in Group A (Fig. 2). *Hindeodus* Pa and ramiform elements were not ecologically a part of Group C (Fig. 2).

Conodonts are associated in dendrograms for a variety of ecological and anatomical reasons—a fact recognized by von Bitter (1972:38) when he stated that the "grouping of taxonomic categories in a cluster should have some paleoecological or biological basis." He maintained that it was necessary to apply external evidence such as natural assemblages, previous reconstructions, the existence of symmetry transitions, colour similarity, and stratigraphic distribution to test the significance of the elements in each cluster. Only the application of such criteria allows differentiation between the anatomical and the ecological reasons for the presence of an element in a cluster.

Many of the ecological associations of Pennsylvanian conodonts were documented more than a decade ago (von Bitter, 1972; Merrill, 1973; Merrill and von Bitter, 1976). It does not surprise us that Clark and Carr observed that *Hindeodus* is always closely tied to *Streptognathodus-Idiognathodus* and that "the *Hindeodus* Pa [element] is closely linked to the ozarkodian Pb element of *Streptognathodus-Idiognathodus*" (p. 129). We agree with them; however, we suggest that this association exists for the best of ecological reasons—*Hindeodus minutus* lived together in the same community as the most common Late Pennsylvanian–Early Permian species of *Streptognathodus*, *S. elegantulus*. There is no justification for translating an ecological association into an anatomical one by concluding that "*Hindeodus* spp. consists of the ozarkodian element of *Streptognathodus-Idiognathodus*" (p. 132). There is strong evidence for this element in the apparatus of *Streptognathodus-Idiognathodus* (Fig. 1A).

CONODONT APPARATUS STRUCTURE

The remainder of this paper examines the interpretations of the results of cluster analysis by Clark and Carr and their claims concerning the apparatus structure of specific conodont taxa.

Were *Diplognathodus* Pa and *Adetognathodus* [*Cavusgnathus*] Ramiform Elements Parts of the Same Conodont Apparatus?

A taxonomically important claim by Clark and Carr was that "*Diplognathodus* spp. were [anatomically] associated with the ramiform elements previously assigned to *Adetognathodus* [*Cavusgnathus*] and possibly some of the elements of *Streptognathodus*-*Idiognathodus*" (p. 132).

The groundwork for this suggestion was laid when they observed that, although von Bitter's cluster analyses supported the interpretation that the Pa elements of both *Streptognathodus*-*Idiognathodus* and *Adetognathodus* [*Cavusgnathus*] were associated with a group of four ramiform elements, "the Pa elements of *Hindeodus* and *Diplognathodus* also occur within the same clusters" (p. 128). We suggest that their initial observation is unsupported. Neither of von Bitter's two species of *Diplognathodus* was present in the same cluster (Group C) as that which included nearly all of the

elements of the *Adetognathodus* [*Cavusgnathus*] apparatuses (Fig. 2).

Subsequently, Clark and Carr reinforced their claim through a series of cluster analyses on the three modified data sets using the coefficient of Jaccard and the unweighted pair-group method (UPGM) (Figs. 3-5). They concluded that von Bitter and Baesemann "identified a group of ramiform elements assigned to *Adetognathodus* [*Cavusgnathus*]. Where identified, these elements form a cluster that along with various other elements chain to species group 1 [reference to species group 1 by Clark and Carr is presumably to Group A of von Bitter, 1972, figs. 15-18 and table 13]. The Pa element of *Diplognathodus* is placed among the various ramiform elements" (p. 129). There is no support for this claim in the dendrograms of von Bitter's and Baesemann's material (Figs. 3, 4). The *Adetognathodus* [*Cavusgnathus*] ramiform elements are grouped together and are either separated from the *Diplognathodus* Pa element (Fig. 3) or only join it at a very low level of affinity (Fig. 4). The only elements in Perlmutter's data that might have been candidates for the *Adetognathodus* [*Cavusgnathus*] ramiform elements were removed by Clark and Carr prior to analysis.

The results of similarity analysis using Euclidean

von BITTER (1972)

FIG. 3. Dendrogram of R-mode cluster analysis of the conodont distribution in the Shawnee Group (Upper Pennsylvanian) of northeastern Kansas, using the coefficient of Jaccard, binary data, and unweighted pair-group method (UPGM). Data modified from von Bitter (1972); amended from Clark and Carr (fig. 3) using our identifications (Table 1).

BAESEMANN (1973)

FIG. 4. Dendrogram of R-mode cluster analysis of the conodont distribution in the Kansas City and Lansing groups (Upper Pennsylvanian) of northeastern Kansas, using the coefficient of Jaccard, binary data, and unweighted pair-group method (UPGM). Data modified from Bacsseman (1973); amended from Clark and Carr (fig. 3) using our identifications (Table 1).

PERLMUTTER (1975)

FIG. 5. Dendrogram of R-mode cluster analysis of the conodont distribution in the uppermost Wabaunsec Group (Upper Pennsylvanian) and the Admire and Council Grove groups (Lower Permian) of northeastern Kansas, using the coefficient of Jaccard, binary data, and unweighted pair-group method (UPGM). Data modified from Perlmutter (1975); amended from Clark and Carr (fig. 3) using our identifications (Table 1).

PERLMUTTER (1975)

FIG. 6. Dendrogram of R-mode cluster analysis of the conodont distribution in the uppermost Wabaunsee Group (Upper Pennsylvanian) and the Admire and Council Grove groups (Lower Permian) of northeastern Kansas, using Euclidean distance, binary data, and minimum-variance clustering. Data modified from Perlmutter (1975); amended from Clark and Carr (fig. 4) using our identifications (Table 1).

BAESEMANN (1973)

FIG. 7. Dendrogram of R-mode cluster analysis of the conodont distribution in the Kansas City and Lansing groups (Upper Pennsylvanian) of northeastern Kansas, using Euclidean distance, binary data, and minimum-variance clustering. Data modified from Baesemann (1973); amended from Clark and Carr (fig. 4) using our identifications (Table 1).

von BITTER (1972)

FIG. 8. Dendrogram of R-mode cluster analysis of the conodont distribution in the Shawnee Group (Upper Pennsylvanian) of northeastern Kansas, using Euclidean distance, binary data, and minimum-variance clustering. Data modified from von Bitter (1972); amended from Clark and Carr (fig. 4) using our identifications (Table 1).

distance (Figs. 6–8) were used to claim that “the Pa element of *Diplognathodus* clusters in all three sets with various ramiform elements. In von Bitter’s data set, *Diplognathodus* forms a well defined cluster with the ramiform elements usually assigned to *Adetognathus*” (p. 130). In the case of the analysis of the modified data of Perlmutter (1975), these results (Fig. 6) are meaningless in terms of demonstrating an anatomical relationship between *Diplognathodus* Pa elements and potential ramiform elements. The results of similarity analysis of the modified data of Baesemann (1973) (Fig. 7) do not support Clark and Carr’s view of an anatomical relationship between the elements under discussion, because the *Adetognathus* [*Cavusgnathus*] ramiform elements are separated noticeably from the *Diplognathodus* Pa elements. Finally, their claim that the results of similarity analysis of von Bitter’s modified data (Fig. 8) show a well-defined cluster of *Diplognathodus* Pa and *Adetognathus* [*Cavusgnathus*] ramiform elements is unsupported. The cluster is not well defined, and the *Diplognathodus* Pa element (number 4) is joined to the ramiform elements referred to *Adetognathus* [*Cavusgnathus*] (numbers 6, 9, 12, 15) by us at too low a level of affinity to support the conclusion of an anatomical relationship between the two groups.

As a part of their interpretation of the results of similarity analysis using Euclidean distance on von Bitter’s modified data (Fig. 8), Clark and Carr observed that “a well defined” cluster containing *Diplognathodus* Pa elements and “the ramiform elements usually assigned to *Adetognathus* [*Cavusgnathus*] . . . duplicates the model proposed by Perlmutter (1975) and Kozur (1975) for the multi-element *Diplognathodus* apparatus” (p. 130). Not only is this cluster ill defined, but Kozur and Merrill (*in* Kozur, 1975) failed to provide illustrations or any other supporting data for the claim that species of the genus bore ramiform elements. Therefore, the apparatus described by Kozur and Merrill cannot be examined or tested. That reconstructed by Perlmutter as *Ozarkodina expansa* is correct (von Bitter and Merrill, *in press*); however, it is odd that Clark and Carr would delete key ramiform elements from Perlmutter’s data prior to their analysis and would then use the cluster analyses of von Bitter’s highly modified data to claim that they support the model of Perlmutter.

Despite their own cautions about the use of association analysis, Clark and Carr used the results of such analyses (Figs. 9–11) to conclude that “the *Diplognathodus* Pa [element]. . . is grouped with the ramiform elements of *Adetognathus* [*Cavusgnathus*]”

PERLMUTTER (1975)

FIG. 9. Dendrogram of R-mode cluster analysis of the conodont distribution in the uppermost Wabaunsee Group (Upper Pennsylvanian) and the Admire and Council Grove groups (Lower Permian) of northeastern Kansas, using a monothetic divisive procedure (association analysis) and binary data. Data modified from Perlmutter (1975); amended from Clark and Carr (fig. 5) using our identifications (Table 1).

BAESEMANN (1973)

FIG. 10. Dendrogram of R-mode cluster analysis of the conodont distribution in the Kansas City and Lansing groups (Upper Pennsylvanian) of northeastern Kansas, using a monothetic divisive procedure (association analysis) and binary data. Data modified from Baesemann (1973); amended from Clark and Carr (fig. 5) using our identifications (Table 1).

von BITTER (1972)

FIG. 11. Dendrogram of R-mode cluster analysis of the conodont distribution in the Shawnee Group (Upper Pennsylvanian) of northeastern Kansas, using a monothetic divisive procedure (association analysis) and binary data. Data modified from von Bitter (1972); amended from Clark and Carr (fig. 5) using our identifications (Table 1).

(p. 131). The results of association analysis of the modified data set of Perlmutter (Fig. 9) again cannot bear out their claim because of the missing *Diplognathodus expansus* ramiform elements. The results of association analysis of Baesemann's modified data (Fig. 10) show a degree of linkage between the *Diplognathodus* Pa and *Adetognathus* [*Cavusgnathus*] ramiform elements that is, at best, marginal, and the cluster containing these also includes most of the ramiform components of *Hindeodus* and *Streptognathodus-Idiognathodus*. The results of association analysis of von Bitter's modified data are even less conclusive in their linkage of *Diplognathodus* Pa and *Adetognathus* [*Cavusgnathus*] ramiform elements (Fig. 11).

Finally, Clark and Carr attempted to use cluster analysis of quantitative data to demonstrate a biological relationship between *Diplognathodus* Pa and *Adetognathus* [*Cavusgnathus*] ramiform elements. The results (Figs. 12–14) caused them (p. 132) to observe that “the ramiform elements and *Diplognathodus* Pa [elements] form a tight cluster of rare elements.” Examination of the three dendrograms (Figs. 12–14) does not support their claim. The analysis of the modified data of Perlmutter (Fig. 12) is again inconclusive because of the previously mentioned deletion of key ramiform elements. The analyses of neither von Bitter's nor Baesemann's modified data (Figs. 13, 14, respectively) are grouped closely enough, or at a sufficiently

high level of affinity, to support the conclusion that the ramiform elements of *Adetognathus* [*Cavusgnathus*] and the *Diplognathodus* Pa elements were parts of the same apparatus.

Clark and Carr were unable to support their generalizations concerning an anatomical relationship between the *Diplognathodus* Pa elements and the *Adetognathus* [*Cavusgnathus*] ramiform elements. These general statements include the following: “the Pa element of *Diplognathodus* is usually associated with the ramiform elements of *Adetognathus*”; the converse inference, “*Adetognathus*, whose presumed ramiform elements are associated with *Diplognathodus*”; and the concluding proposition, “*Diplognathodus* spp. were associated with ramiform elements previously assigned to *Adetognathus*” (pp. 131, 132). The dendrograms do not show what Clark and Carr claimed, and the results do not demonstrate an anatomical relationship between *Diplognathodus* and *Adetognathus* [*Cavusgnathus*] ramiform elements.

Did *Adetognathus* [*Cavusgnathus*] Bear Only Platform Elements?

Clark and Carr, having assigned the ramiform elements of *Adetognathus* [*Cavusgnathus*] to *Diplognathodus*, then suggested the corollary that “*Adetognathus*

PERLMUTTER (1975)

FIG. 12. Dendrogram of R-mode cluster analysis of the conodont distribution in the uppermost Wabaunsee Group (Upper Pennsylvanian) and the Admire and Council Grove groups (Lower Permian) of northeastern Kansas, using Euclidean distance, minimum-variance clustering, and quantitative data. Data modified from Perlmutter (1975); amended from Clark and Carr (fig. 6) using our identifications (Table 1).

[*Cavusgnathus*]. . . may be a single element species [correctly, genus],” concluding that “the exact structure associated with *Adetognathus* [*Cavusgnathus*] cannot be determined but it may also have been a species [*sic*] consisting solely of Pa elements” (pp. 131, 132).

We have no difficulty with the concept of Pa-element-only apparatuses (see Merrill and Powell, 1980)—or even with a ramiform-element-only apparatus of *Adetognathus* [*Cavusgnathus*] (see von Bitter and Merrill, 1985)—but Clark and Carr were unable to demonstrate (1) the existence of Pa-element-only apparatuses, or (2) that *Adetognathus* [*Cavusgnathus*] was exclusively platform only. Their concluding proposition regarding a ramiform-element-bearing *Diplognathodus* apparatus was not in itself a demonstration of the existence of Pa-element-only apparatuses of *Adetognathus* [*Cavusgnathus*]. Ramiform-bearing apparatuses of *Cavusgnathus* are well known (Fig. 1B–D). Using ecological and taxonomic evidence, von Bitter and Merrill (1985) demonstrated that not every individual within a species of *Adetognathus* [*Cavusgnathus*] was invariably Pa-element-bearing only. Indeed, we view conodont species as having had variable numbers and kinds of elements in their apparatuses, only some of which would be Pa element only. The ecological and palaeontological evidence required to demonstrate that the ramiform elements of a well-established apparatus, based on natural assemblages, really belonged to another taxon was not presented by Clark and Carr.

A Biological Connection Between *Diplognathodus* Pa and *Streptognathodus-Idiognathodus* Ramiform Elements?

A concluding proposition by Clark and Carr was that “*Diplognathodus* spp. were associated with. . . possibly some of the elements of *Streptognathodus-Idiognathodus*” (p. 132). This was indeed the case—it would be unusual if one or more of the nearly ubiquitous species of the *Streptognathodus-Idiognathodus* group were not associated with species of *Diplognathodus* in Pennsylvanian and Lower Permian rocks. We are assuming from the context of their study, however, that “*Diplognathodus* spp.” refers to *Diplognathodus* Pa elements, that “the elements of *Streptognathodus-Idiognathodus*” refers to *Streptognathodus-Idiognathodus* ramiform elements, and that the association they infer was anatomical rather than ecological.

Examining the results of association analysis, Clark and Carr noted that “the *Diplognathodus* Pa [element]. . . is grouped with the ramiform elements of. . . *Streptognathodus-Idiognathodus*” (p. 131). We suggest that the dendrograms from association analysis (Figs. 9–11) are unconvincing because of the low levels of affinity between elements in a cluster and the lack of separation of distinct clusters (Figs. 9–11). In the analysis of the modified data of Perlmutter (Fig. 9), the *Diplognathodus* Pa element (number 4) is associated with only a single *Streptognathodus-Idiognathodus* ramiform element (number 6). The association analysis of the modified data of Baesemann is slightly more

von BITTER (1972)

FIG. 13. Dendrogram of R-mode cluster analysis of the conodont distribution in the Shawnee Group (Upper Pennsylvanian) of northeastern Kansas, using Euclidean distance, minimum-variance clustering, and quantitative data. Data modified from von Bitter (1972); amended from Clark and Carr (fig. 6) using our identifications (Table 1).

BAESEMANN (1973)

FIG. 14. Dendrogram of R-mode cluster analysis of the conodont distribution in the Kansas City and Lansing groups (Upper Pennsylvanian) of northeastern Kansas, using Euclidean distance, minimum-variance clustering, and quantitative data. Data modified from Baesemann (1973); amended from Clark and Carr (fig. 6) using our identifications (Table 1).

supportive of their inference regarding a biological connection between *Diplognathodus* Pa and *Streptognathodus-Idiognathodus* ramiform elements (Fig. 10). However, the analysis of the modified data of von Bitter totally refutes this possibility (Fig. 11). The *Diplognathodus* Pa element (number 4) is joined to most of the ramiform elements of *Streptognathodus-Idiognathodus* (numbers 5, 8, and 11) at the very lowest level(s) of association.

Clark and Carr used the word “possibly” in their consideration of a biological relationship between *Diplognathodus* Pa and *Streptognathodus-Idiognathodus* ramiform elements (p. 132), but the cluster analyses do not support such an affinity. Their interpretations cannot reasonably be used to challenge the composition of well-established apparatuses, based on natural assemblages (e.g., *Streptognathodus-Idiognathodus* [Rhodes, 1952; von Bitter and Merrill, 1985]) (Fig. 1A).

Streptognathodus-Idiognathodus — Platform-only Apparatuses?

A corollary of Clark and Carr’s view of a biological relationship between *Diplognathodus* Pa and *Streptognathodus-Idiognathodus* ramiform elements is the proposition that “the Pa elements of *Streptognathodus* and *Idiognathodus* were single element species [*sic*] during the Late Pennsylvanian and Early Permian” (p. 132). This was a reformulation of a view previously expressed by Clark (1972) that restricted itself to the apparatus structure of Permian species of *Streptognathodus-Idiognathodus*.

Many natural assemblages and numerous independent apparatus reconstructions have demonstrated that species of *Streptognathodus* and *Idiognathodus* bore an apparatus that included paired Pa and ramiform elements. Merrill and Powell (1980) proposed that in some instances, species of such genera as *Streptognathodus* and *Idiognathodus* may have, for anatomical and/or ecological reasons, had platform-only apparatuses. Thus, the proposition by Clark and Carr was not startling, or new. Their assertion, however, is absolute, is not supported by their cluster analyses, and is contradicted by independent apparatus reconstructions. The view that there were platform-only species of *Streptognathodus* and *Idiognathodus* universally throughout the Late Pennsylvanian and Early Permian is certainly not supported by natural assemblages of these genera (Fig. 1A).

Clark and Carr initially observed that in cluster analyses using Euclidean distance, “the commonly occurring elements in all three studies tend to occur as a cluster consisting of the Pa elements of *Hindeodus*,

Streptognathodus-Idiognathodus and *Adetognathus* [*Cavusgnathus*]” (p. 129) (numbers 3, 1, and 2, respectively, in Figs. 6–8). This observation is true for the analyses of the modified data of Perlmutter (1975) and Baesemann (1973) (Figs. 6 and 7, respectively), but only partially true for that of von Bitter (1972) (Fig. 8). Despite this discrepancy, we agree that Pa elements do commonly group together in cluster analyses. The suggestion that “the group of common [Pa] elements could be attributable to differential representation of the more robust and identifiable elements” (p. 129) is one of several reasonable interpretations.

Clark and Carr went on to use association analysis, noting that it “produced dendrograms. . . that in two cases immediately separates the Pa element of *Streptognathodus-Idiognathodus* from the other elements” (p. 130). This separation indicated to them that “the *Streptognathodus-Idiognathodus* Pa element is either a single element species or it is over-represented in relation to the Pa elements of *Hindeodus* and *Adetognathus*” (pp. 130–131). This was the first suggestion regarding the Pa-element-only interpretation of species of *Streptognathodus-Idiognathodus*, and was followed by the slightly more definite statement, based on the results of their nine analyses (Figs. 3–11) of binary data, that “there is some indication that the Pa element of *Streptognathodus-Idiognathodus* is a single element species [*sic*]” (p. 131). Cluster analysis utilizing quantitative data predictably resulted in dendrograms (Figs. 12–14) in which the most abundantly occurring element, the Pa element of species of *Streptognathodus-Idiognathodus* (number 1), is separated and is the last to join each of the three dendrograms, leading to the suggestion that Pa elements, especially those of *Streptognathodus-Idiognathodus*, were overrepresented (p. 132).

Explanations in the preceding paragraphs involving overrepresentation of *Streptognathodus-Idiognathodus* Pa elements relative to other Pa elements, or differential representation of the more robust and identifiable Pa elements, are likely and normal. *Hindeodus*, *Streptognathodus-Idiognathodus*, and *Adetognathus* [*Cavusgnathus*] Pa elements are usually overrepresented relative to their ramiform elements, and of the three categories, the Pa element of *Streptognathodus-Idiognathodus* predominates in most Pennsylvanian conodont collections (Ellison, 1941; von Bitter, 1972; Baesemann, 1973; Merrill, 1975; Merrill and von Bitter, 1984). Although Clark and Carr found the explanation of overrepresentation of *Streptognathodus-Idiognathodus* Pa elements over those of *Hindeodus* and *Adetognathus* [*Cavusgnathus*] “difficult to accept due to the similarities of the three Pa elements” (p. 131), the distribution and abundance of the Pa elements of

these morphologically dissimilar genera are strongly governed by palaeoecological factors (Merrill and von Bitter, 1976, 1984; Driese, Carr, and Clark, 1984).

Large numbers of platform elements relative to few ramiform elements is a well-documented phenomenon (Ellison, 1941; von Bitter, 1972; Carls, 1977; Merrill and Powell, 1980), one that predictably causes separation of Pa elements (such as those of *Streptognathodus-Idiognathodus*) from their anatomically associated ramiform elements during cluster analysis. Analyses using Euclidean distance, monothetic divisive procedures, and quantitative data appear to be particularly vulnerable to this effect. That differential or overrepresentation of *Streptognathodus-Idiognathodus* Pa elements may have a biological cause is not in dispute (see von Bitter and Merrill, 1980). We also do not disagree with the suggestion by Clark and Carr that the *Streptognathodus-Idiognathodus* Pa element may have been the only element type in the apparatuses of individuals belonging to these genera, other than to modify the absoluteness of that interpretation and add the qualifiers “at some times and in some places.” Cluster analysis is sensitive to and measures the same aspect observable in most abundance charts; that is, platform elements are overrepresented. The separation of Pa elements in dendrograms cannot, by itself, be used to decide whether Pa-element-only apparatuses really existed. This question can only be resolved by empirical external evidence such as recurring natural assemblages consisting of only Pa elements.

The various cluster analyses do not and cannot support the proposition by Clark and Carr that Late Pennsylvanian and Early Permian species of *Streptognathodus-Idiognathodus* invariably bore only Pa elements. Apparently, Clark and Carr lacked natural assemblages and resorted to cluster analysis, a method that cannot differentiate between various causal factors. Their statement was too broadly applied, and it ignored evidence from natural assemblages and previous reconstructions.

Does the *Streptognathodus-Idiognathodus* Pb Element Really Belong to *Hindeodus*?

Finally, we disagree with the concluding proposition based on cluster analysis, that the wrong Pb element was reconstructed into the *Hindeodus* apparatus by von Bitter (1972), Baesemann (1973), Sweet (1976, 1977), Rexroad (1981), Horowitz and Rexroad (1982), and others.

Clark and Carr, while discussing the results of cluster analysis using Euclidean distance (Fig. 6), noted

that “the *Hindeodus* Pa [element] is closely linked to the ozarkodian Pb element of *Streptognathodus-Idiognathodus*” (p. 129). A linkage is suggested in two of the analyses (Figs. 6, 7), but not in that of the modified data of von Bitter (Fig. 8). Almost the entire apparatus of *Hindeodus* is grouped together in one discrete cluster in Figure 8. The Pb, M, and Sc elements of *Streptognathodus-Idiognathodus* are together and are clearly separated from the elements of *Hindeodus*.

The results of association analysis (Figs. 9–11) do appear to show a relationship between the *Hindeodus* Pa element and the *Streptognathodus-Idiognathodus* Pb element, causing Clark and Carr to note that “the *Hindeodus* Pa element . . . is associated with the ozarkodian element (Pb) of *Streptognathodus-Idiognathodus*” (p. 131).

The *Streptognathodus-Idiognathodus* Pb and the *Hindeodus* Pa elements, like other elements of these genera, cluster together on dendrograms for reasons other than that they belong to the same organism. The first, discussed earlier, is that *Hindeodus* Pa and *Streptognathodus-Idiognathodus* Pb elements were generally associated during life (albeit in different genera and species) for ecological, rather than anatomical, reasons. The other is that the *Streptognathodus-Idiognathodus* Pb element, a fairly robust element, is, after the Pa element of such genera as *Streptognathodus-Idiognathodus*, *Adetognathus* [*Cavusgnathus*], and *Hindeodus*, the most commonly preserved (and the most easily identified) element in Pennsylvanian collections. One of the predictable properties of association analysis is that the more common elements group together. The results of Perlmutter’s modified data (Fig. 9) could have been used to infer a biological connection as easily (and as incorrectly) between the *Adetognathus* [*Cavusgnathus*] Pa element and the *Streptognathodus-Idiognathodus* Pb element as between the *Hindeodus* Pa element and *Streptognathodus-Idiognathodus* Pb element.

Thus, there is no support for the view by Clark and Carr that the *Streptognathodus-Idiognathodus* Pb element was a part of the same apparatus as the *Hindeodus* Pa element—a premise previously rebutted on taxonomic grounds by von Bitter and Merrill (1985). There is also no evidence to support Clark and Carr’s generalization that “the ozarkodiniiform Pb element of *Streptognathodus-Idiognathodus* appears associated with the *Hindeodus* Pa [element],” nor for the conclusion that *Hindeodus* spp. contain, among other elements, the Pb element of *Streptognathodus-Idiognathodus* (pp. 131–132). Despite the various claims based on cluster analysis to support these conclusions, well-preserved natural assemblages (Fig. 1A) demonstrate that they are not true.

CONCLUSIONS

Prior to analysing palaeontological data by cluster analysis, considerable care should be taken in the preparation of those data. This is particularly true when analysing other people's data. An analysis can only be as good as the data used.

Data treatment, such as deleting or condensing some taxonomic categories, should be applied consistently (particularly between different data sets), with an understanding of the taxonomic and ecological implications of that treatment. Data should not be over-condensed.

Clusters or groupings in cluster analysis are the result of, among other things, anatomical association (as in the skeletal parts of a species clustering together) or ecological association (as in a grouping of species that commonly lived together in a community). Ecological association may be as important as (or of greater importance than) anatomical association as a causative agent for strong groupings in cluster analysis. Only the application of both ecological and anatomical models can serve to identify the relative weight of the cause(s) of such groupings.

Binary (presence-absence) data compensate for underrepresentation, a common problem in palaeontology. These data are useful approximations of the structure of fossil populations.

Cluster analyses by Clark and Carr do not support their view that the *Diplognathodus* Pa and the *Adetognathus* [*Cavusgnathus*] ramiform elements were part of the same apparatus, nor their suggestion that some or all of the *Streptognathodus-Idiognathodus* ramiform elements were possibly part of the same apparatus as the Pa element of *Diplognathodus*.

Some of the time, species of *Streptognathodus-Idiognathodus* and *Adetognathus* [*Cavusgnathus*] may have contained only paired Pa elements, but cluster analysis is not an effective means of providing evidence either for or against this question. There is, however, much evidence from natural assemblages that these species commonly bore apparatuses complete with ramiform elements.

Cluster analysis does not support the claim that the Pb elements of *Streptognathodus-Idiognathodus* are really those of *Hindeodus*.

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APPENDIX

The Appendix covers three further aspects discussed by Clark and Carr to which we wish to respond.

1) Clark and Carr suggested that von Bitter (1972), Baesemann (1973), and Perlmutter (1975) relied heavily on the Middle Pennsylvanian natural assemblages of Rhodes (1952) as models for apparatus reconstructions.

Not only did most of Rhodes's material come from Upper Pennsylvanian (Missourian) rather than Middle Pennsylvanian rocks, but the three authors cited could not have used the conformity paradigm for reconstructing *Hindeodus*, *Diplognathodus*, and *Ellisonia* (the genera whose apparatus compositions Clark and Carr challenged) since natural assemblages are unknown for species of these genera. Sweet (1970a,b; 1976; 1977), von Bitter (1972), Baesemann (1973), Merrill (1980), Merrill and Powell (1980), Rexroad (1981), and Horowitz and Rexroad (1982) independently reconstructed the apparatuses of *Hindeodus* spp. using a variety of criteria other than natural assemblages. These reconstructions differed from each other only in completeness. Whether species of *Diplognathodus* bore ramiform elements is being established from discrete collections (Perlmutter, 1975; Clark and Carr, 1982; von Bitter and Merrill, 1985, in press), and the element composition of *Ellisonia* spp. was elucidated, again independently and without natural-assemblage blueprints, by Sweet (1970a,b; 1988) and von Bitter and Merrill (1983).

2) Clark and Carr suggested that if the multielement model of *Diplognathodus* and *Hindeodus* was accepted, then it followed that Pa and ramiform elements of these genera should be found in the same stratum.

For anatomical and ecological reasons, ramiform elements did not always accompany their Pa elements. For example, no one who has examined natural assemblages of *Streptognathodus-Idiognathodus* seriously questions that species of these genera commonly bore ramiform elements during the Pennsylvanian. However, Upper Carboniferous strata containing large numbers of these ramiform elements alternate with those that either lack, or contain very few, of these elements (Merrill and Powell, 1980). The most reason-

able conclusion is that most samples consist of mixtures of varying proportions of animals with, and without, ramiform elements. Clark and Carr proposed that younger species of *Idiognathodus* may have possessed platform-only apparatuses. This is correct in part, but probably some had ramiform elements as well. Since the evidence of natural assemblages conflicts with that of alternating occurrences of Pa- and ramiform-dominated samples and with the likelihood of younger Pa-element-only apparatuses, it is likely that for the *Streptognathodus-Idiognathodus* group, the existence of Pa elements in strata does not dictate the presence of other morphological components in the same strata. Ramiform elements of *Diplognathodus* and *Hindeodus* may have been absent some of the time for the same anatomical/ecological reasons (see Merrill and von Bitter, 1984) that caused them to be absent in *Streptognathodus-Idiognathodus*.

3) Clark and Carr noted in their discussion of the relative merits of binary data that "the environment should be equally favorable for all elements of a single organism" (p. 128).

This is not true, and many environments were unfavourable to selected conodont elements. Ramiform underrepresentation is accepted by nearly all conodont workers dealing with late Paleozoic and early Mesozoic conodonts (Ellison, 1941; von Bitter, 1972; Carls, 1977; Merrill and Powell, 1980). In many cases the taxa exhibiting this underrepresentation are the same ones known from natural assemblages (e.g., *Streptognathodus-Idiognathodus*, *Neogondolella*). That these were multielemental in many instances is beyond doubt. Despite this, many collections consist of mixtures of elements best interpreted as being from both multielement and platform-only apparatuses, a condition leading to differing degrees of ramiform-element underrepresentation.

Our studies of Pennsylvanian conodont palaeoecology suggest that these different apparatus types belonged to animals that exhibited different environmental tolerances (von Bitter and Merrill, 1980; Merrill and von Bitter, 1984, fig. 4). The presence, absence, or abundance of a particular element type or group of element types was probably a function of environmental stresses.

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