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MULTICHARACTER CHRONOLOGICAL CLUSTERING IN A SEQUENCE OF FOSSIL STICKLEBACKS

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Abstract.—Chronological clustering of morphotypes, based on five characters, detected morphological discontinuities in a stratigraphic sequence of the fossil stickleback *Gasterosteus doryssus*. Discontinuities that were not detected analyzing individual characters became apparent, and different discontinuities depend on changes in the frequencies of different sets of morphotypes. However, recognition of discontinuities between a group and neighboring groups of samples depended strongly on existing group structure. The results of this analysis generally were consistent with conclusions of a previous study using single characters, which indicated that patterns of chronological variation within the lineage are diverse. Care must be taken in interpreting the results of this chronological-clustering technique because the results depend strongly on criteria for formation of morphotypes, but the technique is useful to detect discontinuities of multicharacter change within biostratigraphic sequences. [*Gasterosteus*; stickleback; gradualism; punctuated equilibria; evolutionary pattern; biostratigraphic variation; chronological clustering.]

Publication of the "punctuated equilibria" model for evolution as viewed in the fossil record (Eldredge and Gould, 1972) greatly stimulated interest among paleontologists in the analysis of sequences of fossils with putative ancestor-descendant relationships. This model also challenged evolutionary biologists to more fully consider the fossil record in the formulation of theory. Renewed interest in biostratigraphic sequences has been manifested in two ways: A great number of sequences with relatively good stratigraphic control have been accumulated since 1972, and new statistical methods have been developed to test the sequences for conformity to particular patterns of change. Patterns of morphological variation within fossil sequences have proven to be diverse (e.g., Gould, 1982; Cope and Skelton, 1985), and a number of statistical methods have been proposed to analyze these sequences. In the contest between proponents of punctuated equilibria and gradualism, the time has passed when it is enough simply to place a plot on the wall, step back, look at it, and decide whether it appears to be gradual or punctuated.

A number of techniques for analysis of biostratigraphic sequences have been presented in recent years. Of course, routine statistical tests for heterogeneity among samples, tests for trends, and tests for association between time and character states can be employed. Bookstein et al. (1978) presented a procedure in which biostratigraphic data are fitted to linear models which form a hierarchy of complexity. The data are tested using successively more general models within a set with the same general topology until the goodness of fit ceases to improve significantly. This technique allows one to classify a sequence as static, gradual or punctuated. Raup and Crick (1981) used two up-and-down runs tests to evaluate the hypothesis that an apparent temporal trend in a fossil sequence is the product of a random process. One of the runs tests assumes that the probability of the value of a character to increase or decrease is independent of the character mean, and the other assumes that it is contingent on the mean. Charlesworth (1984) pointed out that the runs tests used by Raup and Crick (1981) have limited power and applicability to fossil samples, and he developed a statistical test for variation in the rate of change within a biostratigraphic se-

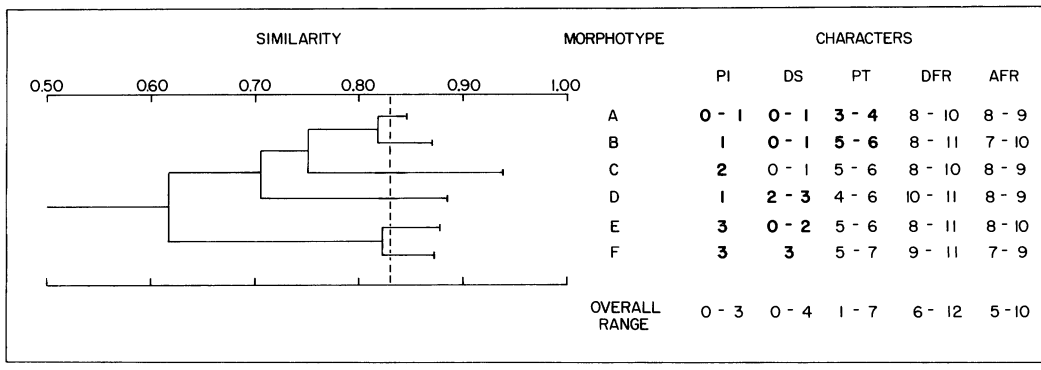
quence. Bell et al. (1985) employed a number of standard statistical techniques to test six characters of a fossil sequence for patterns of temporal variation. They also developed an exploratory technique, termed a "stepwise *G*-test," to estimate how far forward in time one must go in the sequence to detect significant temporal heterogeneity in the composition of samples for single characters. Regardless of the results of such tests, it will be necessary to interpret the results to decide whether some set of results is consistent with gradualism, punctuated equilibria, or some combination of the two models. However, rigorous testing for patterns must be the initial step.

Legendre et al. (1985) developed a chronological-clustering technique to study succession within ecological communities, but noted that it could be applied to sequences of fossils to search for clustering of morphotypes in time. In this study we apply this technique to test for discontinuities in the chronological distribution of multicharacter phenotypes within the sequence of fossil sticklebacks originally studied by Bell et al. (1985). Our results confirm their conclusion that temporal variation within the sequence can be explained by Neo-Darwinian mechanisms, but reveal discontinuities in the data that were not apparent from analysis of single characters.

MATERIALS AND METHODS

We used the original data set from the study of Bell et al. (1985) for the fossil stickleback fish *Gasterosteus doryssus*. Methods used to determine the stratigraphic position of samples, to collect the samples, and to score characters are presented in the original paper. Sample 1 was collected at the lowest horizon in the stratigraphic section, and typically samples were made at approximately 5,000-year intervals and numbered consecutively upward in the section. Although it now appears that the time intervals between samples 7 and 11 were underestimated, the order of samples in the sequence is correct (F. H. Brown, pers. comm.). The present analysis, which uses only the order of samples, is not affected by these errors. Standard length was excluded from this analysis because it is missing from many specimens and depends in part on growth, but the other five characters were employed. These characters are (a) pelvic index, (b) number of dorsal spines, (c) number of pterygiophores preceding the one on which the first dorsal fin ray originates, (d) number of dorsal fin rays, and (e) number of anal fin rays. Except for pelvic structure, all characters are meristic, and the states of each are simply the number of elements in the series. The four states of the pelvic index are *absent* (0, pelvic girdle bilaterally absent), *stereotyped ovoid vestige* (1, single ovoid bone on one or each side), *intermediate vestige* (2, two vestiges on at least one side, with reduced ascending branch and no pelvic spine), and *developed* (3, a complex and robust structure that is the primitive condition for the *Gasterosteus aculeatus* species complex; Nelson, 1971; Bell, 1984). Phenotypic variation of these characters includes a substantial genetic component (Bell, 1984; Bell et al., 1985).

First, one-half of the specimens ($n = 227$) from samples, 1, 7, 10, 21 and 26 of Bell et al. (1985) were used to define multicharacter morphotypes. These samples were chosen because they represented times of extreme variation in most or all of the five characters, as depicted in figure 3 of Bell et al. (1985). Gower's (1971) similarity coefficient (S15 in Legendre and Legendre, 1983) was computed among these individuals, and WPGMA clustering (Sneath and Sokal, 1973) was used to form morphotypes. WPGMA was chosen instead of UPGMA because there was no reason to believe that morphotypes would be equally represented in the 227 specimens; indeed, they were not. Specimens with similarity greater than 0.83 were classified as a single morphotype (Fig. 1), because use of a higher similarity value as the threshold for morphotype recognition would have produced too many morphotypes to be useful in the analysis. The morphotypes were assigned identification letters and examination of the character-state data made



MORPHOTYPE	CHARACTERS				
	PI	DS	PT	DFR	AFR
A	0 - 1	0 - 1	3 - 4	8 - 10	8 - 9
B	1	0 - 1	5 - 6	8 - 11	7 - 10
C	2	0 - 1	5 - 6	8 - 10	8 - 9
D	1	2 - 3	4 - 6	10 - 11	8 - 9
E	3	0 - 2	5 - 6	8 - 11	8 - 10
F	3	3	5 - 7	9 - 11	7 - 9
OVERALL RANGE	0 - 3	0 - 4	1 - 7	6 - 12	5 - 10

FIG. 1. Morphotypes of *Gasterosteus doryssus* used in chronological clustering. Dendrogram of morphotypes generated from Gower's similarity measure and WPGMA clustering (left). Branches extend only to point of furcation within morphotypes, and broken line is threshold above which specimens were treated as single morphotype. Character-state distributions of morphotypes (right). Abbreviations: AFR, number of anal fin rays; DFR, number of dorsal fin rays; DS, number of dorsal spines; PI, pelvic index (see Materials and Methods); PT, number of predorsal pterygiophores. Overall range of character states may not occur among specimens assigned to morphotypes.

it possible to characterize the morphotypes by diagnostic characters. The morphotypes were used in turn to assign the 2,115 specimens to morphotype, 555 of which were rejected because they had missing values in diagnostic characters. Indeed, large numbers of missing values are typical of paleontological data. The remaining 1,560 specimens were assembled in a sample-by-morphotype data table.

A matrix of similarity among samples was computed from Whittaker's (1952) index of association (D09 in Legendre and Legendre, 1983), which was transformed from distance (D) to similarity (S) using $S = 1 - D$. The chronological-clustering technique of Legendre et al. (1985) was used to test the sequence for significant chronological clusters in morphotype composition. Chronological clustering is a time-constrained form of agglomerative clustering in which only neighboring samples, or groups of samples, can cluster. At each step of the intermediate-link linkage agglomerative process (50% connectedness was used throughout), a test of statistical significance is performed to decide whether or not fusion of the groups is warranted. The null hypothesis states that two such groups are an artifact of the clustering procedure and should be fused into a single group. The test is performed by permuting the specimens at random across the group barrier, as described by Legendre et al. (1985); it is a special form of the Mantel test (1967). The criterion for rejection of the null hypothesis was relaxed progressively in three steps ($\alpha = 0.01, 0.05, 0.10$) to test for successively less significant clusters.

If a single sample forms a group that is significantly different from the previous and subsequent groups in the chronological-clustering analysis, it is called a singleton. Singletons within larger groups will tend to obscure group structure because of the time constraint built into the clustering procedure. Thus, the chronological-clustering program allows one to ignore singletons. Such singletons might occur as a result of temporary ecological changes that may have interfered with taphonomic (fossilization) processes, or they may be due to perturbation, displacement, or loss of sediment strata. No singletons were present in our analysis.

To examine properties of the groups formed by chronological clustering, we did: (1) group-expansion tests to determine whether a group can incorporate samples in adjacent groups when group structures of the chronological neighbors are ig-

nored; and (2) a posteriori tests to indicate whether similar sets of morphotype frequencies occur in distant groups of samples. The matrix of Whittaker's distances among samples was also subjected to a principal coordinates analysis (Gower, 1966). The chronological-clustering results were drawn in the space of the first two principal coordinates to help interpret relationships among groups and to evaluate the importance of the discontinuities.

RESULTS

Individuals were clustered on the basis of five morphological characters, and six morphotypes (A to F in Fig. 1) were produced using a similarity threshold of 0.83 as the criterion for morphotype membership. The number of dorsal spines and pelvic-girdle structure were the most important diagnostic characters. The number of pterygiophores was also useful to discriminate between morphotypes A and B, but the two fin-ray characters had little diagnostic importance. The contingency table of morphotypes within samples (Table 1) was used to search for discontinuities in morphotype frequencies.

Figure 2 shows the chronological clusters. The most fundamental break occurs between samples 20 and 21 ($\alpha = 0.01$). This discontinuity reflects a shift from morphotypes A, B and D (reduced spine counts and pelvis) to morphotypes E and F (greater spine and pelvic development). Relaxation of the significance level to 0.05 yields a break between samples 14 and 15, which involves a shift from roughly equal frequencies of morphotypes A and B to dominance by morphotype B. This discontinuity reflects subtle changes in most characters and a consistent difference in number of predorsal pterygiophores. Breaks also were evaluated at $\alpha = 0.10$; although they may not be statistically significant, their recognition will enable a posteriori testing for the recurrence of morphotype group structures along the time series. At $\alpha = 0.10$, breaks occur between samples 4 and 5, 7 and 8, 11 and 12, and 22 and 23. The first three of these discontinuities largely reflect a shift from dominance by morphotype B to dominance by A (4 to 5), back to dominance by B (7 to 8), and then to roughly equal frequencies (11 to 12). There also is a reduction in the frequency of morphotype F between samples 4 and 5. The shift between samples 22 and 23 reflects a transition from strong dominance by morphotypes C, E and F to dominance by B, C and D; morphotypes E and F have more dorsal spines and more strongly developed pelvic structure than do B, C and D.

The chronological clusters obtained at $\alpha = 0.10$ are represented in Figure 3 in the space formed by the first two axes of a principal coordinate analysis. Nonmetric multidimensional scaling, using this two-dimensional ordination as its initial structure, did not improve the structure. To help interpret the clusters, the six morphotype variables are plotted in an approximate

TABLE 1. Distribution of morphotypes among sample pits. Character states that distinguish among morphotypes listed in Table 1. Sample numbers correspond to those used by Bell et al. (1985).

Sample[a]	Morphotypes					
	A	B	C	D	E	F
1	6	31	10	1	1	0
2	13	25	1	0	0	0
3	17	18	1	0	0	0
4*	16	29	0	3	0	7
5	40	18	0	0	0	1
6	40	15	0	0	0	1
7*	56	29	0	0	0	1
8	19	44	0	0	0	0
9	11	19	0	0	0	0
10	11	27	0	7	0	0
11*	20	40	0	2	0	0
12	32	31	0	1	0	0
13	17	23	0	0	0	0
14**	21	25	0	0	0	0
15	15	44	0	0	0	0
16	7	24	0	3	1	0
17	4	28	0	3	0	1
18	17	37	0	0	0	0
19	5	32	1	6	0	2
20***	4	72	1	19	0	0
21	0	1	0	0	19	77
22*	0	1	16	3	80	5
23	0	52	33	13	9	1
24	1	44	10	21	2	3
25	3	29	4	7	1	0
26	7	51	5	6	0	0

[a] Chronological clustering detected discontinuities between samples marked with asterisks and the next sample (*, $\alpha = 0.1$; **, $\alpha = 0.05$; ***, $\alpha = 0.01$).

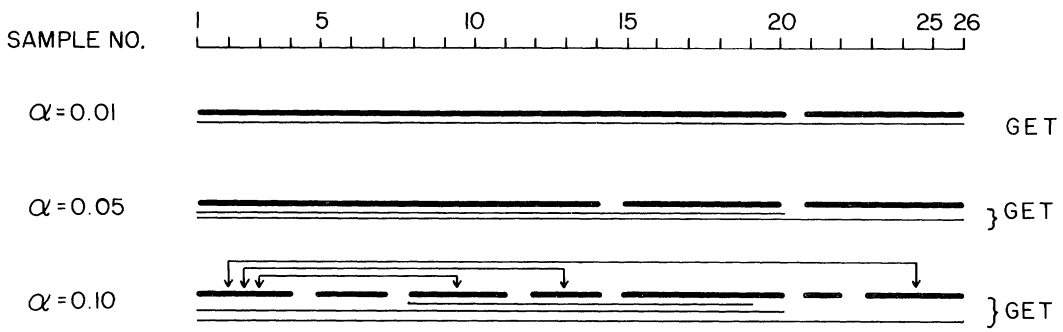


FIG. 2. Results of chronological clustering. Abbreviations and symbols: heavy horizontal lines, clusters of contiguous samples; GET, group expansion tests; double arrows, a posteriori tests with probability of fusion greater than α.

manner, from the results of a correspondence analysis of the morphotype frequency data (Table 1). The correspondence-analysis ordination is quite similar to the principal-coordinate ordination, except for a nonlinear distortion in the right-hand part of the ordination, which leads us to prefer the principal-coordinate plot. While the population had gradually reached (with samples 19 and 20) a position in the morphotype space somewhat different from its past history, the transition to samples 21 and 22 (dominated by morphotypes E and F) represents an abrupt change. In samples 22 to 25, the population returns progressively in morphotype space to the same position that it occupied in samples 19 and 20. The first step, between samples 22 and 23, also represents an abrupt change in morphotype composition. The path from sample 21 to sample 26 is represented by a series of arrows in Figure 3.

Group-expansion tests reveal whether transitions between adjacent groups along the series are abrupt or smooth. The expansions show that the discontinuities are not hermetic; when the clustering structure of all but one group is ignored, that cluster can expand by incorporation of chronologically-adjacent samples. The a posteriori tests performed on groups formed with $\alpha = 0.10$ indicate that three groups that occur later in the section do not have a composition significantly different from group [1–4].

DISCUSSION

First, we consider the implications of the results for the temporal variation in *Gasterosteus doryssus* and then turn to the general utility of the chronological clustering technique of Legendre et al. (1985) for analysis of biostratigraphic sequences. In *G. doryssus*, the analysis detected a major discontinuity between samples 20 and 21 (Fig. 3), which Bell et al. (1985) considered on the basis of dorsal spine number and pelvic structure to represent replacement of a low-spined population by a spiny one. Subsequent field research indicates that this marked discontinuity occurred within about 30 years (Bell, unpubl. data). Considering the speed of this morphological transition and that it involves replacement of advanced character states (for both dorsal spine number and pelvic structure) by the primitive states for the *G. aculeatus* species complex (Nelson, 1971; Bell, 1984), it seems likely that this transition represents replacement of one population by another through immigration. The discontinuity between samples 22 and 23, though of doubtful statistical significance ($P = 0.07$), marks a rapid evolutionary change in pelvic structure. Although the single-character analyses revealed a number of apparently significant differences in phenotype frequencies near this discontinuity, only the frequencies of standard length classes (not used to form our morphotypes;

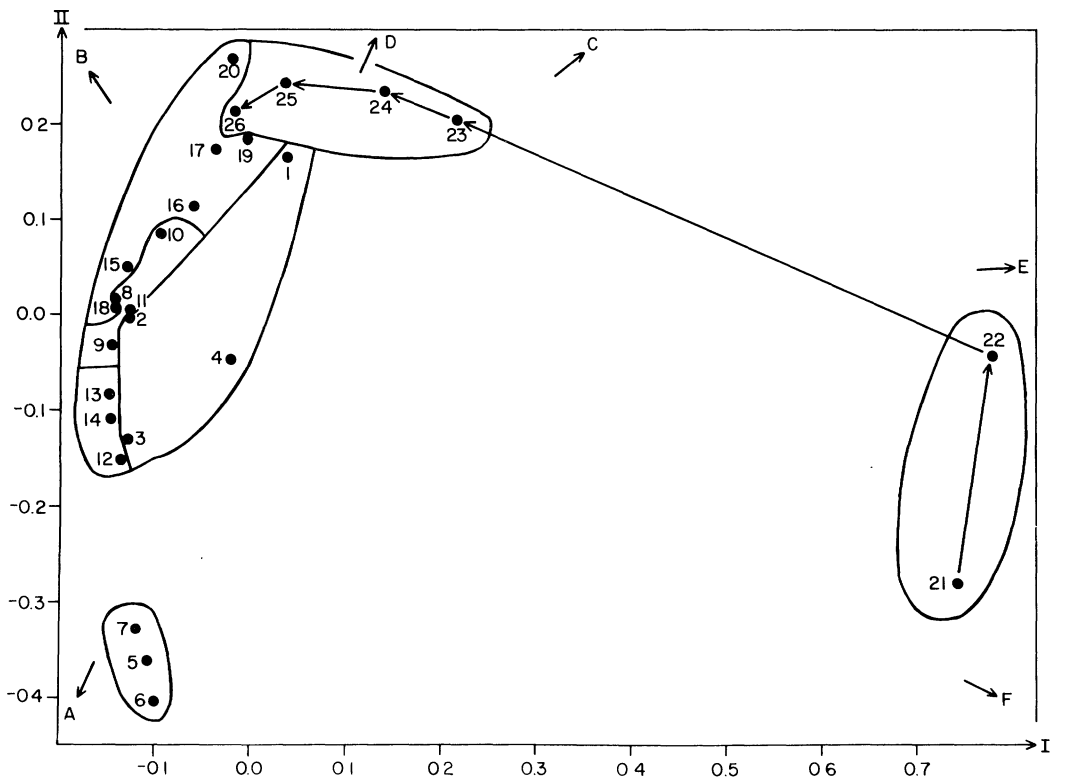


FIG. 3. Principal coordinate analysis of distance matrix among 26 samples (Whittaker's index of association). Axes I and II together explain 55% of variance. Envelopes represent groups obtained by chronological clustering at $\alpha = 0.10$. A to F arrows are approximate directions of six morphotype variables. Time sequence from sample 21 to sample 26 also represented by arrows.

see Bell et al., 1985) and of pelvic structure classes change significantly between samples 22 and 23.

Both the single-character and morphotype change between samples 20 and 26 suggest very rapid evolution. Chronological clustering of morphotypes, however, actually suggests that morphotype structure began to change with samples 19 and 20. These samples are dominated by morphotypes B and, for the first time in the sequence by D. Immigration from adjacent areas within a 30-year period between samples 20 and 21 may have brought in morphotypes E an F of sample 21, with their highly developed pelvic structure. Next there is a transient increase in the frequency of morphotype C in samples 22 and 23, which had been absent or rare ($\leq$1 specimen per sample) since the time of sample 1 (i.e., a period of about 93,000 years; Bell et al., 1985). After sample 22 there is a gradual return to a structure resembling sample 20, while retaining a major proportion of morphotype C (Fig. 3). Persistence of morphotype C reflects slower evolution of pelvic structure compared to dorsal spine number (Bell et al., 1985).

Other discontinuities reflect more subtle morphological transitions, but indicate that morphological change was common within the *G. doryssus* lineage during the sampled time interval. The first four discontinuities (between samples 4 and 5, 7 and 8, 11 and 12, 14 and 15) involve changes in the frequencies of morphotypes A and B, which differ slightly for all characters except dorsal spine number and strongly

for only the number of predorsal pterygiophores. Thus, similarity of these morphotypes is 82% on the dendrogram (Fig. 1), and discontinuities produced by variation in the frequencies of morphotypes A and B reflect qualitatively minor morphological change. In addition, all but the last of these discontinuities result from relatively small changes between adjacent groups in the ratios of morphotypes A and B, which is to be expected when the criterion of significance is relaxed to $\alpha = 0.10$. The morphological discontinuity between samples 14 and 15, detected at the 0.05 significance level, represents a stronger discontinuity than the previous three. The sharpest discontinuity between samples 20 and 21 is excluded here for the moment because it does not appear to reflect in situ evolution. Furthermore, the expansion tests indicate that groups of samples are not separated by sharp discontinuities and can be merged when the structure of neighboring groups is ignored. Thus, the overall pattern has some aspects of punctuation (i.e., a single major discontinuity; Gould, 1982), but some important properties of the sequence do not fit the model well.

It may be more reasonable to view the structure of the morphotype sequence as hierarchical, rather than trying to fit it to gradualism or punctuated equilibria as alternative models. As the criterion of significance is relaxed, additional discontinuities in morphotype frequency of progressively smaller magnitude are detected. Rather than observing a single discontinuity between markedly different morphotypes and complete stasis (i.e., punctuated equilibria) or a progressive pattern of change spread over a large proportion of the phylogeny (gradualism), there may be a hierarchy of discontinuities, such that discontinuities of similar magnitude are separated by even smaller discontinuities. This structure was observed for single characters in the *G. doryssus* sequence, which have significant rank-order correlations with time but still tend to have a stepped pattern of change through time (Bell et al., 1985). The hierarchical distribution of discontinuities also is consistent with the inverse relationship between evolutionary rate and the time interval over which the rate is measured in diverse data sets (Gingerich, 1983). Similarly, Legendre et al. (1985) observed hierarchies of discontinuities within time series of ecological data. It is not inconceivable that there is a cause-and-effect relationship between the hierarchical structure of discontinuities in community structure through time and that within a lineage, though other explanations are possible (e.g., Ginzburg, 1981).

The group-expansion tests also have an interesting implication. The chronological-clustering technique emphasizes discontinuities in the sequence (Legendre et al., 1985), but the group-expansion tests consistently showed that chronological groups are not discrete (Fig. 2). Rather, neighboring samples from adjacent groups can be exchanged between groups when the group structure of all but one group is destroyed. Failure to obtain this result would suggest that the sequence of fossil sticklebacks does not represent a lineage, but rather a succession of invasions by separate, differentiated populations. Absence of singletons (groups consisting of one sample) also indicates that transient appearance of large numbers of specimens from a second population in the depositional environment did not occur, except for group [21–22], which can be considered as a "doubleton." Using information on modern stickleback populations (*G. aculeatus*), paleozoogeographic considerations, and statistical properties of the univariate data, Bell et al. (1985) argued that the biostratigraphic sequence studied here represents a lineage, except that the discontinuity between samples 20 and 21 (beginning the "doubleton") represents a population replacement. While not representing a powerful test of this argument, results of the group expansion tests and absence of singletons are consistent with this interpretation.

The a posteriori tests provide insights that complement results of the group-expansion tests. Not only are groups distinguished by chronological clustering at $\alpha =$

0.10 not discrete, but there are similarities of overall structure between the first group and three subsequent groups (Fig. 2). The most interesting of these similarities is that between the first and last group, also illustrated by Figure 3. Bell et al. (1985) noted that for the single characters, samples 1 and 26 were not significantly heterogeneous for pelvic structure, number of predorsal pterygiophores, numbers of anal fin rays, and standard length. They argued that after replacement of a population with reduced pelvic structure and dorsal spine numbers by a spiny population (i.e., between samples 20 and 21), there was "re-evolution" of reduced pelvic structure and dorsal spine numbers. Results of the a posteriori test appear to reflect this phenomenon.

The findings of this study may be considered from the more general perspective of the utility of chronological clustering for the study of stratigraphic variation within taxa in the fossil record. Although the results of the chronological-clustering technique of Legendre et al. (1985) must be applied and interpreted with some care, it clearly is a valuable tool for analysis of biostratigraphic sequences. The results of chronological clustering are generally consistent with the univariate analyses of Bell et al. (1985), but also reveal discontinuities that were not apparent to them. Chronological clustering suggested discontinuities between samples 11 and 12, and 14 and 15, while for single characters neither of these pairs of samples produced significant heterogeneity (G_H-tests) when combined. Thus, chronological clustering can detect discontinuities caused by minor simultaneous changes in several characters that may not be detectable individually. Most studies of morphological change in fossil sequences have used a single character and, when more than one character has been used, they generally have been analyzed individually. Although discontinuities detected in this analysis of only five characters often can be recognized in the univariate analyses, sometimes they cannot. As the number of characters increases, the importance of minor but synchronized changes of multiple characters should become more important and more difficult to detect from separate analyses of single characters. Availability of this technique will facilitate use of larger numbers of characters and the detection of significant changes that depend on associations among characters within sequences of fossils.

Application of the group-expansion test to the groups distinguished by chronological clustering provides crucial information. If a specific group incorporates samples from adjacent groups when the structure of other groups is ignored, it is reasonable to conclude that the successive groups represent a lineage with ancestor-descendant relationships, despite the discontinuities. If the groups are discrete and do not expand when structure of adjacent groups is ignored, the discontinuities may represent successive invasions of differentiated populations of a morphospecies or of separate species, which may be expected under the model of allopatric speciation. Demonstration that a biostratigraphic sequence represents a single lineage is a serious problem in all empirical work on punctuated equilibria and gradualism (Schaeffer et al., 1972; Gould and Eldredge, 1977; Bell and Haglund, 1982), and any technique that will provide insights (even weak ones) into this problem is important.

The a posteriori tests provide information on the recurrence of groups with similar composition at different times in the section. Recurrence of similar group structures at different times in the section may indicate recurrent evolutionary trends within a single lineage, repeated invasion of a depositional environment by separate populations which then experience similar evolutionary trends, or repeated cycles of appearance in the biostratigraphic sequence of two or more differentiated populations.

Although the techniques of Legendre et al. (1985) provide a valuable means of identifying chronological discontinuities within fossil lineages, caution must be exercised in interpreting the findings, as the results of chronological clustering are no more subtle than the method used to group

specimens into morphotypes (similarity, clustering). Since the morphotypes are formed on the basis of character associations among specimens, they emphasize discrete character complexes and do not take into account the magnitude of the morphological differences among morphotypes. Most of the discontinuities detected in this study at $\alpha = 0.10$ involved changes in the relative frequencies of morphotypes A and B. These morphotypes differ slightly in four of the five characters and have overall similarity of 82% on the dendrogram (Fig. 1). In contrast, morphotypes A and B have only about 62% similarity on the dendrogram to morphotypes E and F. Thus, replacement of all A morphotypes by B morphotypes, for example, would not represent as much morphological change as their replacement by morphotypes E or F. While the technique has been very sensitive to a change involving several characters, the magnitude of change in any one of these characters might not necessarily reflect substantial morphological change. Thus, the definition of character states, as well as the clustering technique used to define morphotypes, may have a profound effect on the magnitude of the morphological change observed at discontinuities using the same value of alpha. Examination of the morphotypes responsible for discontinuities, in addition to further analyses of morphological change at discontinuities recognized by chronological clustering of morphotypes, will generally be necessary.

The detection of discontinuities in the composition of fossil samples, whether based on single or multiple characters, does not in itself tell us whether a pattern of change is punctuated or gradual. However, detection of significant chronological clusters within a sequence of samples serves a number of useful purposes. First, it indicates whether numerous discontinuities have occurred, which might suggest that morphological change was distributed broadly throughout the phylogeny (i.e., gradual, sensu Gould, 1982). Charlesworth's (1984) technique also is sensitive to this property of a biostratigraphic sequence, but can be used only for single characters. Second, it draws our attention to the significant discontinuities, which then can be examined to determine whether a large proportion of morphological change is concentrated within one discontinuity (i.e., punctuated). Finally, examination of phenotype frequency distributions or of the mean phenotypic state in the vicinity of discontinuities between chronological clusters will indicate whether transitions involve a trend in the vicinity of the discontinuity or are truly instantaneous at the level of temporal resolution available for the fossil sequence. The group expansion tests and a technique presented by Kellogg (1983) allow such examinations. Thus, while chronological clustering does not tell us whether a biostratigraphic sequence is punctuated, gradual, or something in between, it draws attention to points in the sequence that warrant further attention to select a model for stratigraphic variation.

Chronological clustering could prove useful for analyzing other kinds of paleontological data, namely sequences of species in the fossil record. Since the method was originally developed to study ecological succession in multispecies assemblages, it is directly applicable to detection of discontinuities in multispecies paleontological communities. For instance, combined with group-expansion tests, chronological clustering could contribute to testing hypotheses about "mass extinctions" in the Phanerozoic (Raup, 1986). Another kind of paleontological data that would lend itself to chronological clustering is stratigraphic distribution of species in local sections or of microfossil species or pollen from deep-sea or lake cores.

The program that performs chronological clustering, group-expansion tests and a posteriori tests among nonadjacent groups is written in the PASCAL language. It is available from P. Legendre.

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