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Patterns and Processes in the History of Life

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Editors

Report of the Dahlem Workshop on
Patterns and Processes in the History of Life
Berlin 1985, June 16–21

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Springer-Verlag
Berlin Heidelberg New York
London Paris Tokyo 1986

136

Copy Editors: K. Geue, J. Lupp

Photographs: E. P. Thonke

With 4 photographs, 36 figures, and 8 tables

ISBN 3-540-15965-7 Springer-Verlag Berlin Heidelberg New York
ISBN 0-387-15965-7 Springer-Verlag New York Berlin Heidelberg

Library of Congress Cataloging-in-Publication Data
Dahlem Workshop on Patterns and Processes in the History of Life
(1985: Berlin, Germany)
Patterns and processes in the history of life.
(Dahlem workshop reports) (Life sciences research report; 36)
Includes indexes.
1. Evolution–Congresses.
2. Paleontology–Congresses.
I. Raup, David M.
II. Jablonski, David.
III. Title.
IV. Series.
V. Series: Life sciences research report; 36
QH359.D34 1985 575 86-26005
ISBN 0-387-15965-7 (U.S.)

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Typesetting, printing and bookbinding: Brühlsche Universitätsdruckerei, Giessen
2131/3020-543210

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Patterns and Processes in the History of Life,
eds. D. M. Raup and D. Jablonski, pp. 47–67. Dahlem Konferenzen 1986
Springer-Verlag Berlin, Heidelberg
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Directions in the History of Life

Group Report

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Introduction

The discussions of this group centered on the oldest topic in evolutionary biology – patterns in the history of life and their causes. We live in an apparently ordered world, and because evolutionary biology developed as a discipline in the context of western intellectual history, it was perhaps inevitable that perceived patterns in the history of life would be interpreted in terms of some of the major hopes and aspirations of Europeans. Thus we see the wide prevalence of ideas relating such concepts as directionality, progress, determinism, and adaptationism to diverse patterns and trends, ranging from the taxonomy of life (Linnaeus) to the Scala Naturae [6, 19]. We now reject simple notions of order such as special creation, foreordination, or that life is just the manifestation of the postulated law-like structure of the universe. But we are still left with the facts that there are perceived patterns and directional trends in the history of life. We must first recognize and define patterns in order to help us detect and identify underlying structure, cause, or both. Patterns demand explanation and careful analysis of them may lead to the identification, recognition, and understanding of underlying processes. In turn, we may generate hypotheses concerning both pattern and process, and attempt tests.

Our job, then, has been to develop an analytical approach to patterns in evolution. Patterns are first detected, then characterized and defined. When we are satisfied that a pattern is real, we seek cause(s). Directionality is especially intriguing, for we have no a priori expectation from current theory that evolution should be directional or progressive.

Patterns in the History of Life

Nineteenth-century biologists perceived patterns in the history of life (e.g., Cope's Rule, Williston's Principle, Dollo's Law) [18]. While these evolutionary laws were based on empiricisms from the fossil record, all were framed using intuitive ideas and non-quantitative approaches. Our group in discussion arranged patterns and directional trends according to levels of organization in tabular form for purposes of discussion (Table 1, a selective list). In analyzing potential trends, problems of hierarchy and genealogy and matters related to scaling arise. We largely restricted our discussion to general patterns in order to avoid narrow discussion of trends that appear to be group- or lineage-specific. We also limited our discussion primarily to patterns and trends that could be detected in the fossil record.

Identification of Patterns

The reality of the trends selected remains controversial, and thus a good deal of our group's discussion centered on recognition of patterns. Considerations of pattern in evolution are biased from the outset if we assume that pattern and directionality will be found. Often our data base is inadequate to demonstrate statistically a trend that we believe that we can see. Both the quantity and the quality of the data base need to be improved, and we especially must make the transition to more quantitative analyses of data. With increased quantification will come opportunities for in-depth examination of patterns, both to test for their reality and to analyze them more specifically.

Table 1. Patterns in the history of life

Patterns at the level of cells and molecules
Accumulation of random changes in evolution (molecular evolutionary clock)
Changes in genome size
Trends in organismal design
Increasing autonomization
Size changes
Changes in organizational complexity
Differentiation and synorganization
Modification of ontogeny and astogeny
Trends in the formation of clades
Unspecialized ancestor, specialized descendants
Early experimentation, later specialization
Irreversibility
Parallel and interactive evolution
Convergence
Trends in diversity
Increase in the occupancy of ecospace
Replacement of taxa through time

Probabilistic and Statistical Approaches

Despite severe problems in applying statistics to paleobiology, attempts should be made to use statistical methods whenever possible. Some statistical approaches are outlined in Table 2. Manipulative experiments are the most powerful, but they may be difficult to design and conduct. Suppose, for example, that a decrease of shell ornamentation were detected that appeared to be correlated with increase in burrowing in bivalves. We hypothe-

Table 2. Statistical approaches to the study of directional trends in evolution

Approach	Amount of observer intervention	Strength of conclusions
Manipulative experiment	High	High
Sample survey	Intermediate	Intermediate
Judgement sample	Low	Low

size that shell ornamentation affects burrowing rate. Ten fossil shells would be selected randomly, plaster casts produced of each, and ornamentation then filed off five randomly selected casts. Burrowing motion of the bivalves could be simulated by burrowing the plaster casts in an appropriate medium using a mechanical arm. Ideally, manipulative experiments of this sort should contain at least two different treatment levels, each of which is separately and independently applied to at least two experimental units for purposes of replication. An example of an approach such as this is the work of Stanley [24].

Nonexperimental approaches can also be used. For example, in a sample survey a researcher specifies a hypothesis concerning Cope's Rule. Ten individuals of a given species of mollusk are selected randomly from each of six (geological) stages and measurements are taken. Subsequent analysis will disclose whether size has increased during the time period selected and if the data are in accord with expectations derived from Cope's Rule.

The least robust approach is a judgment sample test in which, for example, a researcher decides to test Cope's Rule on bivalves and chooses a few families which, in the researcher's opinion, represent the "cleanest" case for the test.

Statisticians have difficulty with concepts such as "natural experiment" or "Gedanken-experiment." The problem is that with repetition the force of the modifier, "natural," is lost – what was originally a correlative study acquires "strength by association" with the concept of the "experiment." In a properly conducted (scientific) experiment, an experimenter applies specific treatments to randomly selected units while others serve as controls. However, natural experiments result from phenomena that are unknown and the "treatments" are applied to the observational units in an uncontrolled way. As a result, there are many possible explanations as to *why* the treatments did or did not cause a difference.

Models of randomness are appropriate in many contexts and often are useful as null hypotheses, but randomness must be judged relative to a defined context. Even if we were to take the philosophical position that no phenomenon is random, all of its causal determinants may never be discovered, leading to the appearance of unpredictable or random behavior. There are many probabilistic models of randomness. The fact that the data in any particular case are consistent with a randomness model does not refute the possibility of a deterministic process, but it might suggest that the forces producing the variation (or presumed pattern) are many, rather small, and operating independently. A number of statistical methods exist

which can be applied to the problems of detection of patterns in the fossil record, from relatively simple correlation analysis to relatively complex time series analysis (Connor, this volume).

Generally, observations close in time or space are independent; closeness is measured relative to the temporal or spatial extent of the processes causing the variation. But most statistical techniques assume that observations are independent, contrary to the situation common in paleobiology. The *consequences* of violating the assumption of independence are severe: for example, in many cases standard errors are underestimated. If possible, statistical techniques which do not assume independence of data points should be used.

Time series methods deal with dependence in data in an explicit way. Paleobiologists should encourage statisticians to work on new time series techniques to deal with the problems peculiar to paleobiology. These problems include differing durations of species and the separation of species in evolutionary time by periods of discretely different duration, as well as missing data.

Some statistical methodologies of value include the following [7, 9, 14, 15]:

Survivorship and Reliability Analysis techniques from the fields of engineering and biostatistics for examining, fitting, and testing the distribution of life lengths. These models deal with *censoring* of data, death due to *competing* risks, and nonparametric estimates of life distributions.

Probabilistic Models and Stochastic Processes. The theories of Markov processes, birth and death processes, epidemics, and branching and diffusion are all potentially useful – in most cases, however, the development of theory has outstripped techniques for applying the models to actual data [2, 3].

Simulation. The output of any simulation depends on the specific choices made for the factor levels and the way the factors are functionally related. The design of experiments can be used in simulation studies to expand the usefulness and generality of the output [5, 11].

Hypotheses of patterns and processes can only be tested by evidence collected in an unbiased way after agreement about what sort of evidence constitutes an appropriate test. Concern with standards of evidence (the nature, quantity, types, repeatability, etc., of appropriate evidence) has been a major preoccupation of ecologists. This has enabled ecology to move from a field dominated by anecdotes and unsupported assertions to one in which theory, models, and hypotheses can be corroborated or rejected by

acquisition of quantitative observations. Paleobiology might benefit from using similar methodologies and analyses. This was not a focus of this workshop, but we suggest the following as a guideline for the future.

Theory is an important guide for collecting evidence, and data are critical in evaluating theories. However, this interdependency among data, hypothesis generation, and hypothesis testing has led to confusion about that which constitutes a "test" of a hypothesis rather than simply the generation of a new hypothesis. To "test" a hypothesis one must first explicitly state the hypothesis and define a group or population to which test inferences will apply. Data can then be collected from the population, but this must be done in a manner such that the probability of sampling any datum for the group is known and nonzero. Hence, the data could conceivably falsify the hypothesis. Decision rules can be established concerning whether the tested hypothesis should be entertained or rejected, given the sampled data. These decision rules embody statements about the probability of errors that may arise in deciding whether or not the tested hypothesis should be rejected. Failure to reject the tested hypothesis does not necessarily constitute its acceptance but should lead to further, more critical tests of the same hypothesis.

In general, conclusions concerning the reality of trends and directions become convincing only with repetition. Although we urge statistical approaches whenever possible, highly subjective elements enter into most paleobiological considerations of patterns, in part due to the limited data sets available. In general, repetition should be attempted at several different levels – using independent cases, independent methods, independent investigators, and by analyzing different subsets of the data. The key element is congruence (i.e., consilience, consistency, coherency) of results, tested statistically.

Recognized Patterns

Despite difficulties with recognition and identification, most biologists and paleontologists would agree that patterns in evolution exist and that there are trends and vectors (which may have both speed and directional components) over evolutionary time. But which patterns, trends, and vectors exist, how pervasive they are, and how they may be explained remain controversial. For example, at the molecular level there is a good correlation of molecular evolution and time, different molecules evolving at different but relatively constant rates depending on their function and complexity [10, 28]. Patterns at the molecular level appear to be time-dependent only for a given

molecule and there is little correlation with change at the organismal level.

There are also putative trends at the level of organismal design (Table 1), but confirmation of these trends is difficult for at least three reasons: the features of interest are often qualitative rather than quantitative traits, the hypothesis of a particular trend has rarely been framed in a manner allowing it to be tested, and the data available usually involve comparisons across clades rather than within clades.

Complexity of structure and autonomization (i.e., the degree of homeostasis or autonomous buffering of environmental variables) are two aspects of organismal design that often are perceived to be closely associated, although they may be quite independent ("complexity" may include such diverse features as shell sculpturing and neuronal connectivity); we will treat them together. Across the spectrum of metazoans and metaphytes, from invertebrates through vertebrates, and algae to seed plants, autonomization and complexity obviously increase, but on lower levels of organization the trends are less clear. The independent evolution of endothermy in vertebrates and insects represents trends towards increasing autonomization and complexity (via the tight integration of nervous and endocrine systems acting on cellular metabolism), presumably driven by the premium on behavioral performance in these animals. All possible combinations of trends of increasing or decreasing complexity and internalization can be found in various clades of metazoans, each presumably driven by the selective factors arising from the ecology of the organisms involved. Note, however, that complexity at the cellular and tissue levels remains approximately constant within phyla, and across most of the metazoan phyla [1].

Although Cope's Rule (a trend of size increase within lineages) generally seems to hold true, there are numerous exceptions ([16, 23]; see LaBarbera, this volume). Aspects of hierarchy and scale often determine the pattern observed. For example, both brachiopods and crinoids reach their maximum size in approximately the middle of their history, and size declines in later times, but this pattern is dictated by size trends within particular classes in each phylum and the true pattern is most likely to be stasis. Stanley [23] has proposed that Cope's Rule arises from an artifact of cladogenesis – most groups arise from small ancestors, and subsequent radiation yields the appearance of a general increase in size. However, data on body sizes of all members of a clade or a series of clades have not been gathered, so whether the pattern of increase in maximum size within a clade results from an increase in mean size or an increase in the variance in body size within a clade remains unknown. A number of selective pressures doubtless underlies size

determination of individuals in populations and species and size trends in clades ([16, 23]; see LaBarbera, this volume).

Another aspect of organismal size change during evolution that deserves mention is that of the two distinct quantum changes in the *limits* to size that can be deduced as having occurred. The first, the evolution of multicellularity, represented an escape from the limits on complexity and size imposed by the unicellular condition; the second, the evolution(s) of an internal fluid transport ("circulatory") system, freed metaphytes and metazoans from the limits imposed by diffusion within the organism or between the organism and the environment [12] and permitted the evolution of complexity mentioned above (in aquatic photoautotrophic plants, size and complexity obviously are not so immediately dependent on the evolution of an internal circulatory system).

Patterns of differentiation and synorganization in organisms are similar to patterns of autonomization and complexity. The evolutionary process has produced the diversity of morphologies seen through the Phanerozoic using a surprisingly small diversity of essentially stereotyped material – the cells and tissues. For example, from the Ordovician through the Recent, the number and diversity of tissue types in vertebrates has remained virtually constant. However, although the "bricks" are stereotyped, the architectural variants show clear trends within groups towards increasing differentiation. Classical examples would include the repeated trend from full metamerism to oligometamerism in polychaete annelids and both tagmatization of body segments and differentiation of endo- and exopodites of the appendages of arthropods.

It may be useful to add the concept of vectors to analyses of trends, for then speed and direction naturally follow as parameters to be measured. If variances in speed and direction are high, we will observe no trend or pattern but only "noise". But if speed is slow or has a high variance while directional variance is low, an evolutionary trend will be seen. Vector analysis will also provide a means of analyzing pattern among clades. A clade can show a directional trend if one group speciates rapidly (high speed) with little variance in direction (in respect to features under study) regardless of what has happened to other groups within the clade. A clade can also show a directional trend if all groups speciate (with or without high variance in speed), but with low to modest directional variance (i.e., there is a group trend or a homogeneity in the clade). It is important to determine if trends perceived are real or if they might have resulted from similar vectors in non-monophyletic groups.

Pattern and Process

Pattern and process are closer conceptually than we have thought, and we quickly learned that it was difficult if not impossible to discuss pattern without respect to processes. Pattern can be understood as process in reduced dimensionality. One might argue that patterns are simplified, less continuous characterizations of process. An additional important implication is that concepts of pattern and process are hierarchically slippable ("heterarchical") [8]. Size increase is a *pattern* with respect to the lower-level process that generates it but is itself a *process* to a higher-order history of transformation. A pattern is a pattern because it characterizes a process.

Table 3 contains several modes of explanation for perceived directional trends in evolution. The first, microevolution and its consequences, is probably the most common explanation for evolutionary trends, but other explanations deserve consideration. The second explanation, the topology of phylogenetic trees, relates to the fact that there has been but one history and one genealogy of life. The matrix of intercorrelated characters is very complex, and this historically based framework of homology and descent gives pattern and order by itself. The third mode, differential origination and extinction, includes what has become known as species selection, a somewhat controversial process that relates to the dynamics of patterns of origination and extinction, which can produce trends [25]. The fourth mode involves internal dynamics at the organismal level – the systems of fabricational, functional, and developmental constraints which characterize highly integrated systems. Constraints serve as boundaries that bias the direction of evolution when they are approached (Wagner and Stearns, both this volume; see [17, 20]). The final point ("artifacts") is not a biological explanation, but as a procedural matter we should probably always try to eliminate first element 5 of Table 3 and then element 2 before seeking other explanations.

Table 3. Modes of explanation for patterns

1.	Consequences of deterministic processes in natural populations (microevolution)
2.	Topology of phylogenetic trees in a random world
3.	Differential origin and extinction of taxa (species selection)
4.	Fabricational, functional, and developmental constraints (or internal organismal dynamics, evolutionary diffusion in a constraint morphospace, and "ratchets" within Markovian processes)
5.	Artifacts

We have chosen one detailed example and a few additional ones which illustrate the interplay between pattern and process in establishment of evolutionary direction. We do this in the full knowledge that presentation of a few examples, even elegant ones, is not sufficient to serve as a general explanation for the appearance of patterns in the evolution of life. We would have liked to discuss relative frequencies of phenomena, but we could not because either the data base is inadequate, the appropriate analyses have not been done, or both. The examples we chose are well studied directional trends which illustrate the interplay of pattern and process.

Evolutionary History of Bivalves: An Example

The evolutionary history of bivalve mollusks outlined by Seilacher [21] illustrates the interplay between two of the possible modes of explanation: microevolution and channeling by a variety of internal and external constraints (Fig. 1). Because of their relatively simple and uniform construc-

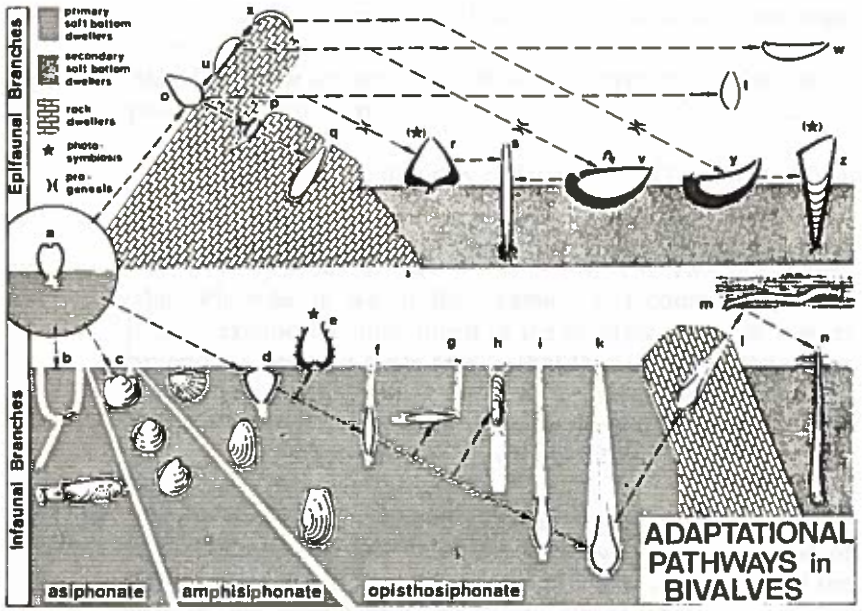

Fig. 1. Evolutionary pathways in the Bivalvia showing several alternative tracks leading from an ancestral, vagile, microphagous soft-bottom dweller (a). See text for explanation

tion, bivalve shells are particularly suited for comparison of evolutionary trends in extant and fossil lineages. As will be seen, "directionality" arises as the outcome of a Markovian progression (Fisher, this volume) in an adaptive landscape. The adaptational pathway is determined by the (a) point of entry into the ecospace (in this case as vagile, microphagous bottom dwellers, Fig. 1 a); (b) nonrandom distribution of adaptive peaks (niches, guilds, "Lebensformtypen") that allow groups to become established along various tracks; (c) constructional and developmental constraints that limit the number of options available at any point; and (d) "racheting" by the irreversibility of most adaptational transformations.

The evolutionary progression can thus be described as sequence of steps. Each step is dependent on the changes that had gone before and in turn provided, retrospectively, the opportunity to improve fitness either by *elaboration* on an adaptive theme or exploitation of a new mode of life made available as an accidental by-product of the immediately preceding changes (*innovation*).

Infaunal branches

Since the transition to filter-feeding in early bivalves removed the necessity for contant mobility, retreat into the sediment was an obvious response to increasing predator pressures. This habitat shift required (a) transformation of the crawling foot into a hydrostatic organ for push-and-pull burrowing, and (b) a ventilation system for continuous flushing of the gills with surface water. Of the three solutions to the ventilation problem (Fig. 1, b: pumping water through a U-shaped dwelling tunnel, *Solemya*; Fig. 1, c: anterior inhalant tube and posterior exhalant siphon, lucinoids; Fig. 1, d: both exhalant and inhalant siphons at posterior and as in all other burrowing bivalves), the third was most successful because it freed the anterior margin for the activity of the foot and allowed shell streamlining without shortening the hinge. Increasingly deeper burrowing proceeded along the following routes:

Fig. 1, d: *Upper tier burrowers*
Elaboration: Establishment of "recovery strategists" with sturdy and highly sculptured shells and the potential to reburrow quickly (cockles, trigoniids, venerids, *Donax*), which allows them to colonize mobile sediments; fusion of ventral mantle edges to keep sediment from intruding into gill chamber.
Innovation: Either return to the surface by the "drag" of photosymbiosis (Fig. 1, e: *Tridacna*, *Corculum*, and several fossil

venerids) followed by reduction of the foot, or deeper burrowing.

Fig. 1, f: *Middle tier burrowers* streamline the shell and extend the fused mantle into long siphons that are completely retractable but remain separate.
Elaboration: Use of the inhalant siphon to sediment-feed by "vacuum-cleaning" the surface. Burrowing in a horizontal position (Fig. 1, g) increases efficiency of movement to new grazing grounds.
Innovation: Razor-clam shape for quick retreat along a vertical tunnel (*Tagelus*, Fig. 1, h) or deeper burrowing.

Fig. 1, i: *Lower tier burrowers* (gape clams), whose united twin siphon is only partly retractable but can be closed during burrowing to transform the mantle cavity into a hydrostatic skeleton. With this to aid in valve-opening, the ligament can be reduced in spite of increasing sediment pressure.
Elaboration: Well protected suspension feeders.
Innovation: Transformation of the foot into a holdfast and transition to mud boring.

Fig. 1, k: *Mud borers* use the versatility of the new opening mechanism to produce a permanent, club-shaped dwelling tube by scraping with the shell edges.
Elaboration: Invasion of muds that are too stiff for conventional burrowing.
Innovation: Transition to mechanical rock boring.

Fig. 1, l: *Rock borers* concentrate action on the anterior part of the shell edge. Pholads, in which the ligament has completely disappeared, expand the attachment of the anterior adductor muscle beyond the primary hinge axis so that they can open the valves around two axes allowing the rows of marginal teeth successively to "chisel" the rock during a single active stroke.
Elaboration: Establishment in a variety of rock types.
Innovation: Transition to wood.

Fig. 1, m: *Wood borers* reduce valve movement to the secondary (dorsoventral) hinge axis and "file" the wood with a regular grid of teeth formed around an angular pedal gape. They also seal the walls of their boreholes with a calcareous lining.
Elaboration: Use of sawdust as an accessory food source via bacterial symbiosis (*Teredo*).

Innovation: Transition to Fig. 1, n, digesting of small wood fragments.

Fig. 1, n: *Tube-inhabiting secondary soft-bottom dwellers* extend the calcareous tube into the sediment, using the flush for piston-boring to substitute for the lost burrowing ability.
Elaboration: Invasion of soft bottoms.
Innovation: None.

Epifaunal branches

The early commitment to a life attached to rocks led to reduction of the foot and either maintenance of the larval byssus throughout life, cementation, or other means of stabilization.

Fig. 1, c: *Edgewise byssal attachment* leads to reduction of the anterior adductor and migration of the posterior one to a more central position.
Elaboration: Broadening of anterior base (*Mytilus*); escape by swimming (*Lima*, Fig. 1, t).
Innovation: Nestling in rock crevices (Fig. 1, p), pleurothetic attachment (Fig. 1, u) or reclining on soft bottom (Fig. 1, r).

Fig. 1, p: *Nestlers* enjoy increased protection, but their growth is limited by the size of available crevices.
Elaboration: Adaptation by size reduction.
Innovation: Active enlargement of crevice by boring (Fig. 1, q).

Fig. 1, q: *Byssate borers* (e.g., *Lithophaga*), lacking the preadaptations of a siphon and a burrowing mechanism, bore mainly by chemical means and are therefore restricted to carbonate rocks.
Elaboration: Life in wave-exposed cliffs or in symbiosis with corals.
Innovation: None.

Fig. 1, r: *Edgewise recliners* invade soft bottoms, stabilizing themselves by byssus-rooting and differential shell weighting.
Elaboration: Size increase; acquisition of photosymbiosis.
Innovation: Transition to Fig. 1, s.

Fig. 1, s: *Endobyssate mud-stickers* are stabilized by the byssus and by mud deposited around them.
Elaboration: Ability to adjust to changes of the level of the sediment surface by byssus displacement, elongation and development of accessory opening mechanisms (e.g., *Pinna*).

Innovation: Return to surface by the evolution of photosymbiosis.

Fig. 1, u: *Pleurothetic byssate rock dwellers* tend to become unequally valved.
Elaboration: Escape by swimming in flat position (Fig. 1, w).
Innovation: Transition to soft bottoms or to rock cementation (Fig. 1, x).

Fig. 1, v: *Pleurothetic recliners* returned to soft bottoms either via swimmers (pectinids, Fig. 1, w) or via reversal of the original attitude (Fig. 1, u).
Elaboration: Weighting the more convex (now lower) valve in a *Gryphaea*-like fashion.
Innovation: Transition to mud-sticking (Fig. 1, s) with accessory opening mechanisms.

Fig. 1, x: *Cemented rock dwellers* become firmly attached with one valve and consequently lose their rigid morphogenetic programs.
Elaboration: Encrustation of various hard substrates (oysters).
Innovation: Transition to soft bottoms via miniaturized (progenetic) shell encrusters by change in larval substrate preference.

Fig. 1, y: *Pleurothetic cemented recliners*, after having outgrown their initial shell substrates, extend growth programs into shapes that increase stabilization by weighting (differential in gryphid forms, Fig. 1, y), flattening, or outriggers, but always in a pleurothetic mode.

Fig. 1, z: *Cemented mud-stickers* either elongate both valves and develop accessory opening mechanisms (similar to Fig. 1, s), or the attached valve grows into a high cone with the other valve modified as a lid.
Elaboration: Dense growth; obstruction of lower shell cavity by septa; return to surface after acquisition of photosymbiosis (in rudists).
Innovation: Transition to reef-building (rudists).

This flow diagram portrays only a small number of anastomoses; "directionality" is imparted only by the necessarily preceding evolutionary steps. Similar diagrams could be established for other clades and at different taxonomic levels [21].

Additional Examples of Interplay of Pattern and Process

There are other examples of long-term trends involving interplay of pattern and process. One of these has been outlined by Niklas (this volume). Another was presented by Vermeij (in preparation) as the hypothesis of escalation. He argues that within a given environment the competitive and defensive capacities of individuals should increase in expression and incidence under the selective pressure of their enemies. Since the latter in turn increase their capacities with respect to the former, escalation occurs; a pervasive directionality results. This is an argument from principles of natural selection and adaptation ("first principles" to Vermeij) for a particular microevolutionary process underlying a particular pattern in particular environments. The generality of the pattern (i.e., its repetition) is unclear, because available data are insufficient to perform the steps necessary to test the hypothesis for different environments.

One can imagine other patterns, including those which involve major changes in organismic design, as having evolved via an extended microevolutionary process. One example might be the trend towards autonomization in the early history of metazoans, but no data are available nor will they ever be (because it is a unique historical event) for adequate testing of hypotheses of the underlying process for this example; furthermore, microevolutionary theory is sufficiently robust to obviate the need for alternative explanations.

Good example exist to illustrate our four main modes of explanation (Table 1) either by themselves or in concert with each other (e.g., [27] on differential species proliferation and its consequences in African antelope). An example of tree topology is the prevalence of hair and feathers among living vertebrates and the increase of feathered and haired species in the Cenozoic. This trend is a simple outcome of the rapid speciation rates of birds and mammals whose remote ancestors had evolved feathers and hair. While feathers and hair, and associated features, may indeed have direct relevance to the general success of these groups, these structures are probably only indirectly related to events at the level of speciation, except in such non feature-specific aspects as coloration. There are also good examples illustrating uncoordinated trends in a given clade and suggestion of hierarchical levels of processes underlying such patterns [26].

However, there are also directional evolutionary trends for which we have no ready explanation: rapid origin of new body plans early in metazoan history (Valentine, this volume); increase in body size in Cenozoic mammals, correlated with reduced reproductive potential (pressures leading to increase in body size must be strong in order to counter fitness loss; LaBarbera, this volume); increasing complexity of lineages resulting from the construction of complex and highly integrated systems (e.g., the mammalian middle ear); different patterns of symmetry.

Explanations for Patterns

Some members of our group strongly prefer multiple explanations and see patterns as resulting from three or four modes of explanation; others are satisfied that microevolutionary explanations, with natural selection as the exclusive driving force, are sufficient to account for all significant patterns and they see no need to invoke alternative explanations. In general, all members of our group avoid both strict reductionist and unitarian views of natural selection as well as the (antagonistic) dualist view of microevolution versus macroevolution, in favor of hierarchical views which span several levels of biological organization (Wagner, this volume; see [4, 13]). Microevolutionary explanations may fail to satisfy because they are seen as oversimplified models of phenotypic evolution that are too local in their effects. We seek a broader kind of explanation, based in the organism but extending to issues relating to the relative rates of origination and extinction of groups, and patterns of replacement and occupation of ecospace, as well as to issues relating to complex interactions at the level of organisms (e.g., developmental constraints), relative constancy of cell and tissue types over vast periods of time, and the uncertain relation between molecular and morphological evolution.

Trends in Diversity

Our discussions dealt only in passing with trends in diversity, for we felt they were discussed more meaningfully in the groups dealing with extinction and ecology. Succession of major evolutionary faunas (Sepkoski, this volume) requires some explanation, but whether there is a pattern is very uncertain. It may be that each event is unique. The opinions of members of our group vary, but there is a subjective impression that there is resilience in the organic world, and only catastrophies such as major extinction events can produce any substantial resetting of evolutionary direction. The unanswered and probably unanswerable question is whether there is any predictability or directionality to the resetting. Replacements of faunas involve changes that may well include directional evolution of ecological and physiological attributes of the organisms. For example, there may by a tendency towards increased physiological homeostasis and efficiency which might be fostered by processes akin to Vermeij's escalation hypothesis. Perhaps Sepkoski's [22] three faunas (Seilacher would prefer "dynasties") can be interpreted in terms of directed replacements in a world in which both interspecies competition for primary food resources and predation pressure

gradually increased. If a Vendian and a Tommotian dynasty are added at the beginning, the pattern may become more visible.

Conclusions and Recommendations for Future Research

Patterns exist in the history of life, as has been known from ancient times, but for the most part they remain intuitional, unquantified, and anecdotal. There are trends, including some fascinating ones, but others (such as Cope's Rule, which was thought to be on a sound footing as a generalization) are not secure (LaBarbera, this volume). We are united in our belief that the fossil record even as presently known contains much more useful information than has been utilized to date. We urge that quantitative, statistically sound, hypothesis-based studies be undertaken of specific trends and of patterns more generally (as in Connor's application of time series statistics to the mass extinction data, this volume). We have failed to get a truly "new" understanding of the issue we addressed in this workshop, possibly because we continue to use the same methods. New methods and new ideas are needed, and extension of such promising approaches as stochastic simulation and statistical analysis will help. Our theories seem to be too general, and the reliable, well analyzed data sets are perhaps too specific (and certainly too few in number). Some believe that new ideas are needed, but if these new ideas include concepts that have not proven to be solidly based or tractable to analysis in the modern living world, much caution is necessary. While there is much to be gained from the fossil record, it is very tempting to go too far and to speculate on unknowable topics.

There is substantial difficulty, given our present knowledge and the state of the fossil record, in recognizing whether or not patterns are present. Close study of the evidence with modern statistical techniques should be pursued. It is possible to fail to detect a pattern that exists if one's procedures lack statistical power. This could occur because the data are highly variable, the alternative hypothesis(es) is indistinguishable from the tested hypothesis (given the data at hand), the sample size is inadequate, or because one slavishly demands significance levels (i.e., $p<0.05$) hallowed by custom rather than by conscious evaluation.

We present a list of suggestions for future training and research of those who wish to study patterns in the history of life.

1. The field is growing more quantitative, and changes in the education of graduate students are necessary. Statistical methods can be borrowed

from other fields to some extent, but we need new kinds of statistical tests. At least some workers in this field must work closely with statisticians and mathematicians to generate new approaches, an endeavor that will require persistence and may entail disappointment.

2. There are differences in approach, and such diversity is good for the field. Some (e.g., Vermeij) argue from first principles of natural selection and adaptation, seeking to pursue specific issues to the point where pattern emerges. Others place their emphasis on patterns being predictable outcomes of processes than can be modeled, and believe that a close and disciplined study will elucidate the underlying processes. Whatever the approach, independent confirmation of findings is essential.

3. Directional patterns in life's history have traditionally been described as secular changes in mean values of the proposed "trait" – size increase, complexity, etc. We need new modes of description as well as explanation to move this subject away from the narrative nineteenth-century "Gesetzmäßigkeiten" to testable ideas. For example, many trends now viewed as only shifts of means may arise as consequences of expansions or contractions of variance about a constant central tendency. Attempts to identify and characterize evolutionary vectors should be undertaken.

4. Attention should be given to questions of relative frequency of events in the fossil record, and documentation is needed both of instances in which there are patterns and trends and of situations in which no pattern emerges. In this context, negative data are just as important as positive data.

5. More ontogenetic information can be gleaned from the fossil record. Careful study of ontogenies within clades can contribute to our understanding of directional trends and the appearance of novel structures. With this foundation, studies of specific problems relating to patterns and trends can be pursued, e.g.: (a) introduction of evolutionary novelty in serially arranged organs; (b) development of polymorphism in colonial organisms, divergent evolution of particular polymorphs and the control of their spatial distribution in the colony; (c) introductions of evolutionary novelties during astogeny of such colonial organisms as bryozoans and graptolites, with special reference to problems of morphogenesis and trophic ecology. What does the succession of ontogenies within a phylectic lineage tell us about evolutionary mechanisms?

6. Careful study of time-controlled, continuous sequences of paleontological data is needed to provide the basis for sound phylogenetic analysis. Parallelism is a heavy constraint on phylogenetic analysis, but a careful study of ontogeny, morphogenesis, fine structure, and functional morphology can in part resolve some of the homeomorphy caused by parallelism.

7. A common, central data base consisting of data gathered with defined standards could be of great importance for the field. It may be impossible to detect and analyze any but the most evident trends without a greatly improved and accessible data base.

8. The search for trends should be made more clade-specific. For example, careful analysis of sizes in all members of a clade is needed in order to determine whether traditional framing of Cope's Rule is appropriate. An analysis of size distributions of all species in a hierarchically nested set of clades would be especially useful.

9. There is need for a microevolutionary model to deal with the evolution of complex functional systems in organisms, because in the absence of such a model the explanatory power of population genetics is unclear.

10. We need operational measures of complexity, preferably quantitative measures. For morphological features, one aspect that might be explored is image processing techniques for computer visualization.

11. We should map Markovian flow diagrams of major taxa as hypotheses for future verification or falsification.

12. It may be that entrenched ideas and cultural biases tied to linguistic issues and intellectual history are at the base of our difficulty in communicating about some of the issues raised. For example, while the English-speaking tradition, dominated by the Neo-Darwinian paradigm, by and large insisted upon external (ecologial) factors and selective pressures upon organisms, the earlier tradition primarily in the continental Western European countries had a different emphasis. Stemming from the "rational morphology" program, it emphasized internal constraints in organisms' evolution. The renewal of interest in functional, constructional, geometrical/topological, and temporal constraints in organism ontogenies together with current progress in developmental genetics may help to reconcile these traditions into a more general synthesis of evolutionary mechanics. More than ever before we need to be clear and precise in our use of words and in developing the concepts associated with these words: we must strive to understand each other.

13. Some phenomena in the history of multicellular organisms may not be understandable in terms of classical and even refined microevolutionary mechanisms; new modes of explanation may be required.

14. We need to explore new and alternative modes of explanation for patterns and trends, especially those which can be detected only with information from the fossil record. The analysis of patterns, trends, directionality, and the like is not of great interest if it involves just the unfolding through time of well understood, classical microevolutionary mechanisms.

We believe that constraints have played important roles in the history of life. We expect that data from large-scale patterns will give new insight into the relationship of order and diversity in the natural world.

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