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CORRELATIVE, EXPERIMENTAL, AND COMPARATIVE EVOLUTIONARY APPROACHES IN ECOMORPHOLOGY

by

P. J. MOTTA and K. M. KOTRSCHAL

(*University of South Florida, Department of Biology, 4202 East Fowler Ave, Tampa, Florida, 33620 U.S.A.; Konrad Lorenz Forschungsstelle für Ethologie, Auingerhof 11, A-4645 Grunau, Austria*)

ABSTRACT

This paper discusses questions, pitfalls, and constraints of ecomorphology, and proposes a step-wise approach to its study. Five broad and overlapping questions in ecomorphology are proposed and examples given. The questions address (1) the covariation between environmental factors and form, (2) performance testing in ecomorphology, (3) the optimization of the form-function faculty and constraints on optimization, (4) the ontogeny of ecomorphological relationships, and (5) direction of evolutionary change in ecomorphological relationships. Ecomorphological relationships are clouded by various factors, including (1) improper selection of morphological or ecological characters, (2) differing and/or improper methods of data analysis, (3) restricting the depth or scale of the analysis, either morphologically or ecologically, (4) lack of a proper null hypothesis against which to test ecomorphological relationships, (5) lack of knowledge of the life history of the species, and (6) lack of knowledge of the constraints acting on the ecomorphological relationship. Two general approaches to character selection, *a priori* and *a posteriori*, are examined. In either approach, character selection may be inappropriate, resulting in faulty conclusions. Historical (evolutionary) and current constraints that act against ecomorphological relationships are briefly listed. Finally, a practical, hierarchical approach to ecomorphology is put forward. The first step seeks correlations between form and environmental factors. Predictions are generated and tested with field and laboratory experiments to determine the biological role and performance of the form-function faculty and its optimal range. Comparative phyletic analysis of either closely or distantly related organisms may then elucidate parallel and divergent, or convergent evolutionary pathways, respectively.

Key words: performance testing, optimization, constraints, convergence, divergence, ontogeny.

INTRODUCTION

Recently there has been renewed interest in the relationship between functional morphology and ecology. This has resulted in a synergistic approach termed ecological morphology or ecomorphology. Defining

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[1] Function is a proximate-level explanation of the mechanical interplay of the parts of an apparatus at the interface with the environment (*e.g.* closing jaw, running) and

ecomorphology, however, proves to be somewhat more difficult. Whereas functional morphology is the study of form and function[1], ecomorphology overlaps functional morphology and emphasizes form in relationship to the biological role(s)[2] of the structure(s) under consideration. Underlying the study of ecomorphology is the premise that a species' morphology is related to its ecology (BLOCK *et al.*, 1991). Ecomorphology attempts to understand the interrelationships between morphological variation among individuals, populations, species and higher taxa, and communities, and the corresponding variation in their ecology (LEISLER & WINKLER, 1985). In more precise terms, BAREL *et al.* (1989) define ecological morphology as the relations between environmental factors and form or, preferably, the explanation of form from environmental demands.

One of the advantages of the ecomorphological hypothesis, therefore, is its predictive power (KARR & JAMES, 1975; MILES & RICKLEFS, 1984; GROSSMAN, 1986; DOUGLAS, 1987). Given that environments constrain morphology and ecology in parallel fashion, we should be able to predict patterns in the ecology of individuals, populations, or species assemblages from their morphological characteristics (WIENS & ROTENBERRY, 1980).

We define ecomorphology as the study of the relationship between environmental factors[3] and form such as to isolate the mutual contribution of one on the other. Our definition differs somewhat from that of BAREL *et al.* (1989) in that it explicitly implies a two-way relationship between environmental factors and form, *i.e.* form might explain environmental factors (*e.g.* an existing form might determine where an animal forages) or vice versa (*e.g.* where or how the animal forages might determine/shape its form).

The purpose of this paper is to discuss the central questions of ecomorphological analyses, recognize common pitfalls, and propose a step-wise, hierarchical approach for ecomorphology. Our goal is to better define and to encourage work in this field because we feel that ecomorphology necessitates an integrative approach, combining such disciplines as morphology, ecology, physiology, animal behaviour,

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with the other parts of an organism. Basically, the function of a feature is its action or how it works (BOCK & VON WAHLERT, 1965). Form is any spatial part of an organism which can be distinguished by the physical properties of its constituent materials (BAREL *et al.*, 1989).

[2] Biological role is how the organism uses the form-function complex in the course of its life history (BOCK & VON WAHLERT, 1965; BOCK, 1980) (*e.g.* feeding, avoiding predators).

[3] Environmental factors are external factors, physical and biotic, which interact in some way with the organism (BOCK & VON WAHLERT, 1965; BOCK, 1980).

evolutionary biology, physics, and engineering. Consequently multiple levels of explanation may result, and are indeed desired. This article reflects our personal views with only sample references primarily from the ichthyological literature.

DISCUSSION

Questions and Goals in Ecomorphology

In accordance with ecomorphology's integrative character, a nested set of five broad overlapping ecomorphological questions and working hypotheses can be put forward, any of which singly or as a group can be addressed in a viable ecomorphological analysis. From these broad questions more specific ones can be generated (for example WIENS & ROTENBERRY, 1980; FINDLEY & BLACK, 1983; LOSOS, 1990a; WIKRAMANAYAKE, 1990; WINEMILLER, 1992). The complex of questions and goals for a step-wise ecomorphological study is summarized below:

1. Is there covariation between environmental factors and form? If so, what are the morphological, ecological, and behavioural patterns?

This is usually the first and most rudimentary question that ecomorphological studies address. If there is no correlation found between form and environmental factors, then one might determine the constraints (see Constraints) on the system. WIKRAMANAYAKE (1990) found that suites of morphological attributes of Sri Lankan stream fishes were correlated with microhabitat and feeding ecology. Body size and shape segregated the fishes by water velocity and depth. The size of the eyes also reflected feeding position and microhabitat depth. Gut length, mouth orientation, and barbels segregated the fishes in morphological space and were correlated with feeding biology. However, GROSSMAN (1986) found little support for the ecomorphological hypothesis as he views it, that morphological specializations of the feeding apparatus limit a species' ability to utilize prey; hence, species with similar morphologies should possess similar diets. Although morphology does play a role in determining diet, his data suggest that behavioural factors may be more important in determining prey utilization. Assuming that an ecomorphological correlation has been found, one can then approach causality and proceed with the following questions.

2. Do differrences in form translate into differences in performance capability (ARNOLD, 1983) resulting in differences in behaviour or ecology?

To approach this question, the effect of morphological variation on performance may be ascertained through experimentation or modelling in the laboratory (*i.e.* the potential niche), and secondly the effect of performance on actual patterns of resource may be determined through field studies (*i.e.* the realized niche) (Wainwright, 1987, 1991). The goal is to detect at least one factor driving ecomorphological correlations.

Based on experimentation, the ability of wrasses (Labridae) to crush hard-shelled prey was estimated. Dietary analysis revealed that the fishes switched from soft to hard prey at the size and crushing ability predicted by measurements of the pharyngeal jaw gape and maximum pharyngeal crushing force. This resulted in a reduction of dietary breadth as fishes specialized on hard-bodied prey (Wainwright, 1987). Here the proximity to optimal foraging studies, such as shell crushing by crabs (Elner & Hughes, 1978), becomes evident. This leads us to question number 3: optimality. Though close, this is not the same as performance, number 2, *e.g.* even though a crab's claw may perform well with a large mussel, intermediate sizes may be optimal in terms of energy gain, notwithstanding eco-ethological parameters such as search and handling time (see Krebs & Davies, 1987).

3. Is the form-function complex[4] optimized with respect to its biological role(s)? If the complex is not optimized, what are the constraints on optimization?

By devising an optimality model (for example, mechanical model) of the form-function complex and comparing it with the organism's form-function complex, the constraints on optimization may be identified. Barel (1983, 1984) found that shape, size, and position of the eye are geometrically closely related to the form of the suspensorium in cichlids. One way for biters to realize a larger adductor mandibulae muscle is by increasing the depth of this muscle. However, this increase may be constrained by constructional demands. This constraint may affect the entire head profile and the size and shape of the eye. Spatial constraints determine to a major extent what combinations of apparatuses (and thus functions) can or cannot be accomodated in certain spaces (Barel, 1983).

4. How do the ecomorphological relationships vary with ontogeny? If they do, how does this affect performance during ontogeny?

The goal of this question is to ascertain ontogenetic changes in ecomorphology and identify the changing constraints. Galis (1991) calculated the maximum possible biting force for juvenile and adult cichlid fish, *Haplochromis piceatus*. Experiments on the piercing forces of natural prey were compared with data on feeding behaviour. The model explains that adult fish can pierce *Chaoborus* larvae and pupae

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[4] A form-function complex is a combination of form and function of a feature. It may be termed the faculty of the feature and may have one or more biological roles (Bock & von Wahlert, 1965; Bock, 1980).

with the pharyngeal teeth, whereas juvenile fish are only able to pierce larvae. The absence of the harder pupae in the diet of juveniles is due to the morphological constraint in the size of the muscles (see also WAINWRIGHT, 1987, 1991; BRANDSTÄTTER & KOTRSCHAL, 1990; KOTRSCHAL *et al.*, 1990, 1991).

5a. What is the phylogeny of the ecomorphological relationship? What was the direction of evolutionary change: does it result from parallel or divergent evolution from a common lineage?

By examination of evolutionary trends in a group of closely related organisms such as co-familials or co-genera, evidence of parallel or divergent evolution in ecomorphological relationships may be found. Losos (1990a, b) constructed a phylogeny of *Anolis* lizards from osteological, karyological, immunological and electrophoretic data from other studies and tested predictions that morphological proportions and maximum sprinting and jumping ability have evolved concordantly among the species. Evolutionary changes in morphology, performance ability, ecology, and behaviour were correlated. Long-legged, heavy-bodied lizards jump farther in nature, jump and display more often, walk less often, and use wide perches that are distant from the nearest available perches. Species with more subdigital lamellae perch lower, use narrower supports, and walk more frequently. The inclusion of performance measurements only partially explained these relationships (see also MOTTA, 1988, 1989).

Or 5b. did the ecomorphological relationship result from convergent evolution?

By examination of evolutionary trends among unrelated or distantly related organisms in comparable environments, evidence of convergent evolution may be revealed. Examining correlations between form and ecobehaviour in 196 species of birds from different families and continents, KARR & JAMES (1975) found several predictable ecomorphological relationships, demonstrating convergence between ecologically similar species of different phylogeny, and divergence between ecologically different species of the same phylogeny (question 5a). Birds with extremely long thin bills and small bodies tend to be hover-gleaners. Birds having relatively long legs tend to occupy the ground substratum. Small birds having long bills tend to be insectivorous. KARR & JAMES were also able to identify one-to-one convergence of species, that is, ecomorphologically equivalent species from different geographic areas.

We emphasize that from these broad questions one can generate numerous, ancillary, more specific questions and hypotheses, for example, WIENS & ROTENBERRY (1980) reiterated seven specific hypotheses including one that small animals exhibit greater dietary specialization than large animals and generalists should also express greater within-population variability in traits than specialists.

Pitfalls for Ecomorphology

Unfortunately many pitfalls and constraints may obscure or affect ecomorphological relationships. These include (1) improper selection of morphological or ecological characters, (2) differing and/or improper methods of data analysis, (3) restricting the depth or scale of the analysis, either morphologically or ecologically, (4) lack of a proper null hypothesis against which to test ecomorphological relationships, (5) lack of knowledge of the life history of the species, and (6) lack of knowledge of the constraints acting on the ecomorphological relationship. We briefly discuss character selection and data analysis, then outline constraints on ecomorphological relationships.

(a) Character selection and data analysis.

One problem lies in the choice of morphological and ecological characters under study and the disparate methodologies of analysing them. MILES & RICKLEFS (1984) caution about interpreting data derived from the mixing of variables such as measurements, ratios of measurements, or measurements having different scales. Although they propose a protocol for ecomorphological analysis, there is as yet no consistency in data analysis.

Two general approaches have resulted: the first which we coin the *a priori* or 'scatter-shot' approach involves making few assumptions about form or function. The researcher chooses a plethora of morphological characters and seeks correlations with a set of ecological parameters (GATZ, 1979). Initial working hypotheses can be achieved or refined by scanning data with hypothesis-free multivariate statistics, such as Principal Component Analysis, which can also be used to reduce the number of variables in a meaningful way (FINDLEY & BLACK, 1983; LEISLER & WINKLER, 1985; KOTRSCHAL & PALZENBERGER, 1990). GOLDSCHMID & KOTRSCHAL (1989) term this the ecological-correlative approach.

In another approach, the researcher uses a subset of morphological characters others have found significant by other qualitative or quantitatium studies (*e.g.* tarsus length in birds, mouth size in fish) (*e.g.* RICKLEFS & TRAVIS, 1980; MOYLE & SENANAYAKE, 1984; MILES *et al.*, 1987). We could call this the *a posteriori* approach or the morphological-correlative approach (GOLDSCHMID & KOTRSCHAL, 1989) because it is most widely used by morphologists. The biological role is generally determined by comparative field studies or laboratory experiments

(KOTRSCHAL & THOMSON, 1986; MOTTA, 1988; KOTRSCHAL, 1989; GOLDSCHMID & KOTRSCHAL, 1989; VAN DEN BERG, 1992).

In either approach, character selection may be skewed with respect to morphology or ecology. For example, a study on fish feeding may include 15-30 morphological characters in the inital analysis and seek correlations only with what the organism feeds on (*i.e.* dietary analysis). However, ecological analysis should, in some cases, include analysis of where an organism feeds, on what, and how it feeds. For example, there appear to be ecomorphological correlates between jaw morphology and how butterflyfishes feed, but not especially with what they feed on (MOTTA, 1988).

Many ecomorphological studies seek mathematical correlations between form and environmental factors without considering the underlying mechanisms (BAREL *et al.*, 1989). For example, BAREL *et al.* describe paedophagous cichlids that utilize egg snatching, snout-engulfing, and ramming as techniques to secure eggs and juvenile prey. The oral feeding apparatus (OFA) of the egg snatcher is similar to that of a bottom-feeding insectivore, whereas that of the snout engulfer corresponds most with the OFA of an ambush-hunting piscivore. Little is known of the OFA of the rammer (BAREL *et al.*, 1989). Correlations between form and what they eat (eggs and larvae) would be quite different from correlations with how they feed (snatching, engulfing, ramming).

Extrapolating characters from one species group to another may not always be sound. FELLEY (1984) tested the usefulness of two types of morphological character sets for predicting habitat use in cyprinids. He chose two sets of morphological characters thought to be related to habitat use, including a set derived from previous studies on functional morphology and morphological-environmental associations in various other taxa, and another based on morphological-environmental relationships revealed by factor analysis for a subgroup of cyprinids. None of the former sets of morphological characters could be used to predict habitat use in cyprinids. The only group that allowed such prediction was among the cyprinid set. He believes that the ecomorphological associations shown for one group of species may not be relevant to other groups. Furthermore, ecological generalizations or explanations developed for one region of the world may not apply in other regions, even if the habitats are apparently similar (WIENS, 1991a).

(b) Constraints on ecomorphological relationships.

In some instances there may be a poor correlation between morphological patterns and ecological patterns within a group of organisms, or ecomorphological patterns ascertained for one group of organisms may not be applicable to another seemingly similar group of organisms (WIENS, 1991b). A variety of behavioural, ecological, physiological, and morphological constraints might prohibit a fit between the morphological and ecological (or ecobehavioural) parameters under consideration, or result in a less than optimal fit.

The constraints on ecomorphological relationships can be historical (evolutionary) or current, although the dichotomy is blurred in many cases. Historical constraints may include multiple selection pressures and hence multiple adaptive peaks, lack of evolutionary time (phyletic inertia), genetic drift, linkage, recombination, epistasis, pleiotropy, developmental limitations (including allometry), lack of suitable elements (the building blocks are not there) or suitable biological materials for a particular function, and evolutionary bottlenecks. Current constraints may include a variety of ecological constraints (*e.g.* environmental instability, resource availability, competition), behavioural constraints (*e.g.* behavioural flexibility), physiological constraints (*e.g.* sensory limitations, nutritional requirements), or morphological constraints. Morphological constraints include constructional constraints (the structural and spatial limitations on combining functionally relevant forms) resulting from multiple biological roles, phenotypic plasticity, architectural constraints, and ontogenetic constraints (in part GOULD & LEWONTIN, 1979; ALBERCH, 1980; LANDE, 1982; MAYR, 1983; BAREL, 1984; BAREL *et al.*, 1989; MAYNARD SMITH *et al.*, 1985; REIF *et al.,* 1985). For an attempt to make these constraints more transparent, see ANTONOVICS & VAN TIENDEREN (1991).

One goal of ecomorphology is to identify such constraints and their contributions to the ecomorphological relationship. At the same time this identifies the contemporary adaptation pressure, which may allow careful inferences to be made about the evolutionary history (GOULD, 1986; GRAFEN, 1988).

Approaches to Ecomorphology

Demands for a 'holistic' approach in functional morphology including experimental and behavioural work were forwarded by DULLEMEIJER (1974), BOCK (1980), GOLDSCHMID & KOTRSCHAL (1989) and others. Constrained by limited manpower and resources, a 'holostic' approach, integrating functional morphology with ecology and behaviour, is frequently not achievable in the average research lab. In the following, we propose a practical, hierarchical approach to ecomorphological analyses.

Almost invariably in the first step, morphological characters or combinations thereof are correlated with environmental factors (our

Question 1) (Goldschmid & Kotrschal, 1989). This approach may provide predictability, but no causal explanation, and it leaves the investigator with uncertainty on performance, optimality, and constraints. Also, predictions derived from ecomorphological correlations in certain environments may not apply to the same organisms under different environmental regimes. For this reason the initial correlative approach provides a working hypothesis on the relationship between a certain morphological structure and its potential use (fig. 1).

In the second step of investigation, these predictions can be tested by field or laboratory experiments to determine the biological role and performance of a form-function faculty (Question 2) and its optimal range. Only then, can general predictions from the ecomorphological relationship be made with any certainty. Cost-efficiency models may indicate the optimal use of structure, and constraints on the system may be identified (Question 3). At this stage, the adaptive value of the structures of interest can be stated. An ontogenetic analysis of the ecomorphological relationship may be performed as well (Question 4).

In the third step, a comparative phylogenetic analysis may allow us to formulate evolutionary hypotheses and scenarios and interpret present-day patterns. It not only guides the selection of species appropriate for comparison, but also suggests likely direction of past evolutionary change (Huey & Bennet, 1986). Two different types of comparisons have been applied with different aims:

1. Most researchers advocate comparing the variation of a structure and its use within closely related taxa, including outgroup comparison with distantly related taxa (Question 5a). It is assumed that the greater the phylogenetic distance among the species being compared, the greater the chance of confounding variables (Lederer, 1984). Therefore, choosing closely related species will reduce the risk that coincidental differences will mask significant patterns (Huey & Bennet, 1986). Findley & Black (1983) explicitly believe and others implicitly assume that ecomorphological relationships may be most detectable in closely related species that have a long history of evolution and radiation in the same region. This kind of comparative approach allows one to propose evolutionary scenarios and hypotheses on the process of adaptation and most readily reveals parallel and divergent evolution (fig. 2).

2. The second approach in evolutionary biology is the comparison of solutions to the same set of ecological questions among and between guilds of relatively unrelated organisms (Question 5b). This can be a powerful indicator of convergent evolution (*e.g.* Karr & James, 1975; Wiens, 1991b). Convergent evolution is the evolution of similar features independently in unrelated taxa, usually from different ante-

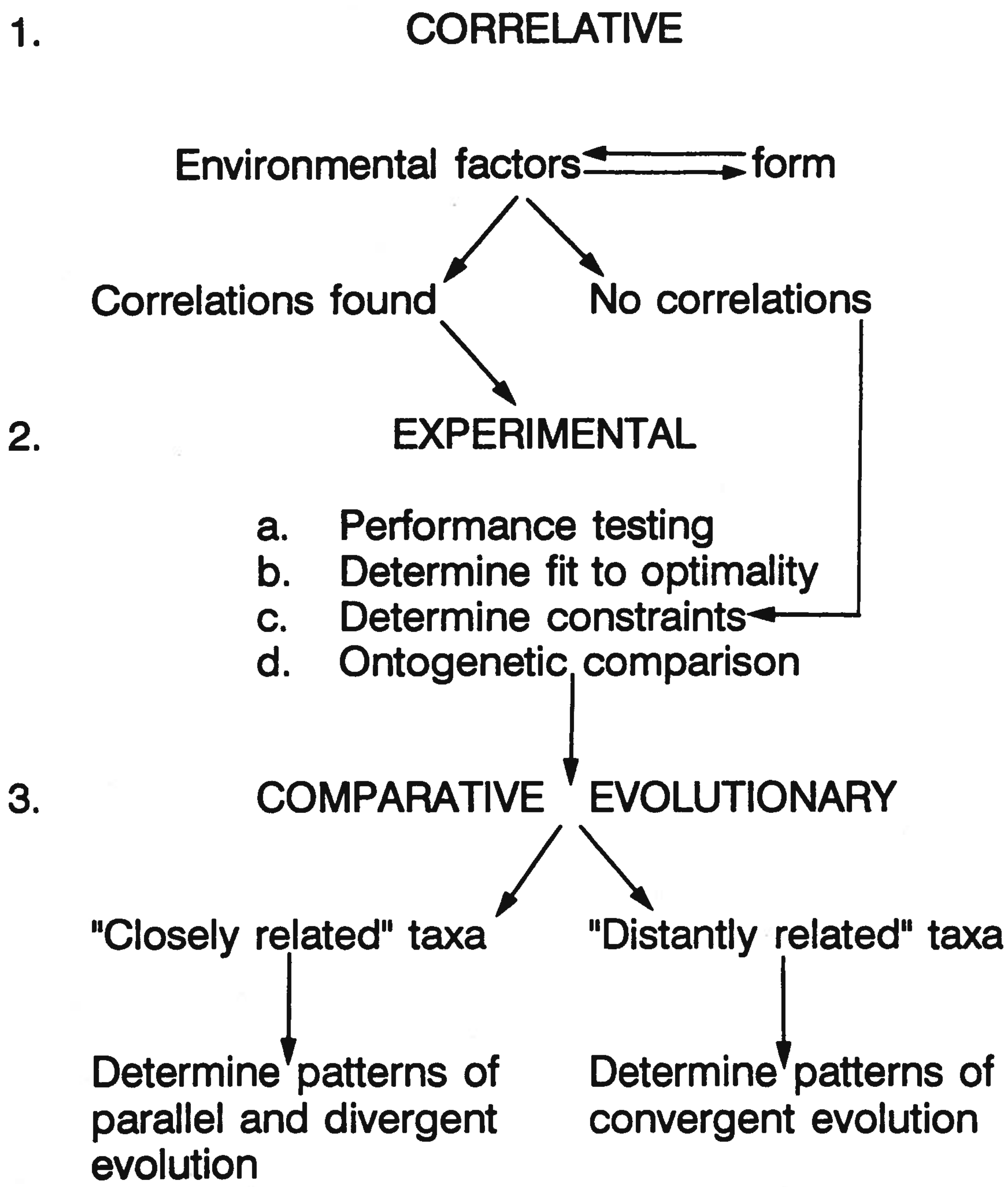

Fig. 1. Flow chart of a step-wise approach to ecomorphology involving correlative, experimental, and comparative evolutionary approaches. If correlations between environmental factors and form are found, then step 2 procedures can determine performance criteria, the fit to optimality models, and ontogenetic changes and constraints of the ecomorphological relationship. If no correlations are found initially, then constraints on the fit between environmental factors and form may be sought. In step 3, comparative evolutionary interpretations might reveal patterns of parallel and divergent evolution among closely related taxa, or patterns of convergence among distantly related taxa. See text for a more thorough explanation.

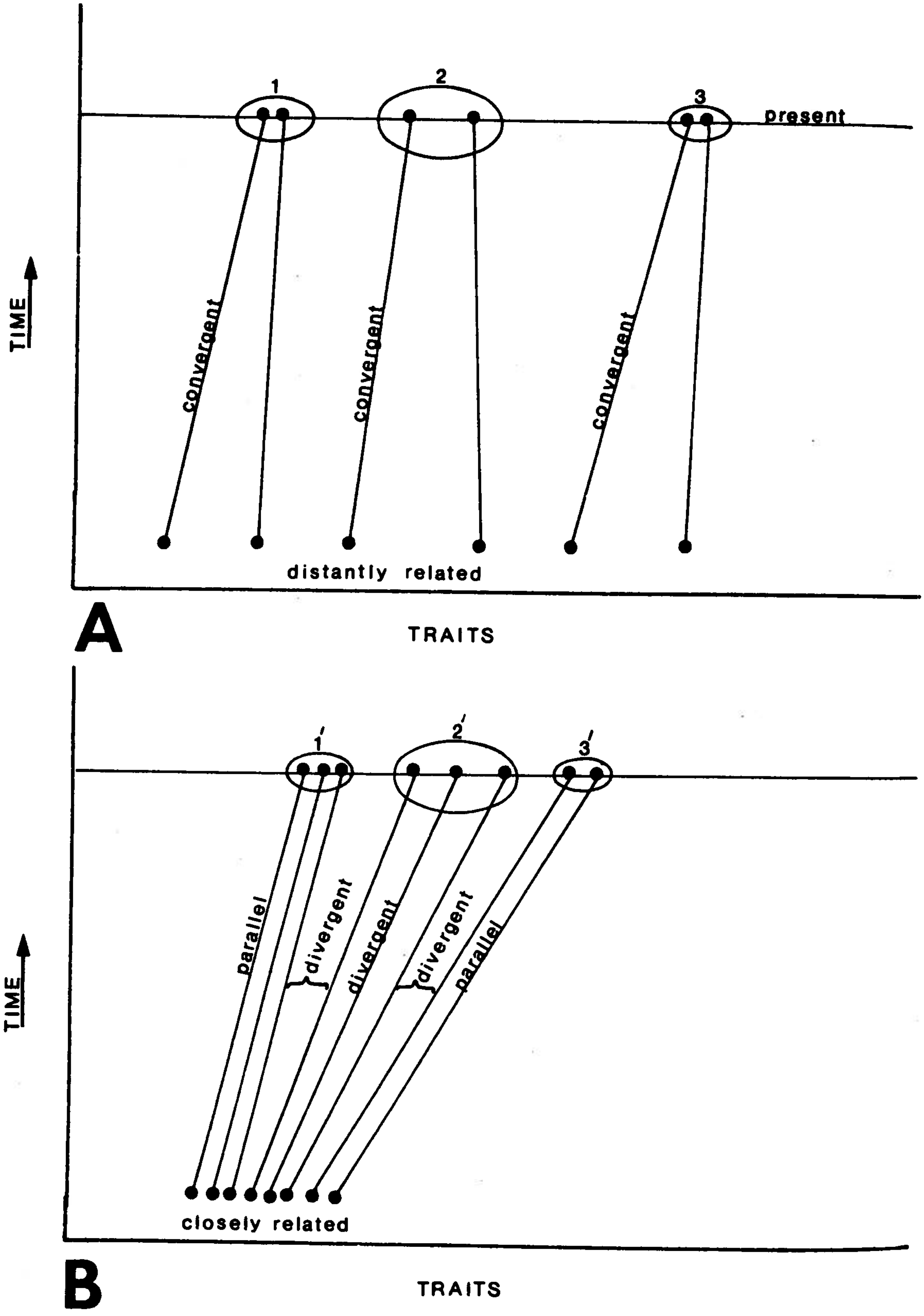

Fig. 2. Two approaches utilized in ecomorphological studies. (A) distantly related organisms are compared and ecomorphological groupings are found. The groups may be tightly clustered in morphospace or ecospace, for example groups 1 and 3, or less closely structured as in 2. Either way, convergent evolution may be demonstrated. (B) Ecomorphological groups are found among a group of closely related organisms. The groups can differ in morphospace and ecospace, being tightly (1') or loosely spaced (2'). Parallel evolution may be demonstrated within ecomorphological groups (groups 1' and 3'), and divergent evolution among (2') and between groups (1' and 2', 2' and 3'). Degree of relatedness can vary and confound the interpretations.

cedent features or by different developmental pathways (Futuyma, 1986). If, for example, a certain tooth morphology such as tricuspid incisor-shaped teeth is found to be associated with browsing on algae, and this morphotype is repeatedly correlated with this foraging mode (*e.g.* blennies, damselfishes, porgies, surgeonfishes, angelfishes, even marine iguanas), is suggests convergent evolution in form. Such arguments may be bolstered by performance testing, indicating that such teeth are indeed efficient at shearing plant material. However, this approach interjects uncontrolled variables, due to lack of common ancestry, that confound the association, and Liem (1990) argues that in aquatic systems, more than terrestrial systems, design might reflect underlying historical factors characteristic of the lineage, rather than functional convergence in response to a common environmental challenge. This is the consequence of the versatility of the aquatic feeding mechanism.

A major problem in either approach is deciding what constitutes 'closely-related' and inferring and testing evolutionary patterns. This cannot be done without knowledge of the phylogenetic relationships, including time since divergence or phenetic or genetic distance. By definition, it appears that convergent evolution cannot occur in a group of closely related organisms. If the grouping of organisms at the base of fig. 2B are spread out (more distantly related), then one can envision convergence as in 2A. Therefore, a period of divergence must precede convergence.

Furthermore, the comparative method involves a comparison of phenotypes across a range of species or higher taxa. Because species are linked by a network of shared ancestry, species may however be similar because these characters have been inherited from a common ancestor (Felsenstein, 1985; Losos, 1990a). Consequently, according to Felsenstein (1985), character states among species are not independent and cannot be treated as such for statistical analysis. The problem of non-independence can be circumvented if adequate information on the phylogeny is known. Many of these problems may be overcome with a cladogram derived from a set of character states differing from the ecomorphological variables under question (or at least being more extensive than the character set under question). In this case analysis of convergence, divergence, and parallelism may be recognized (fig. 3) and statistical analyses performed, as has been utilized and discussed extensively by Losos (1990a).

We have outlined a three-step approach to ecomorphology involving correlative, experimental, and comparative evolutionary approaches. How far along this three-point schedule an ecomorphological analysis is pursued, depends on the questions asked and on the logistics of the

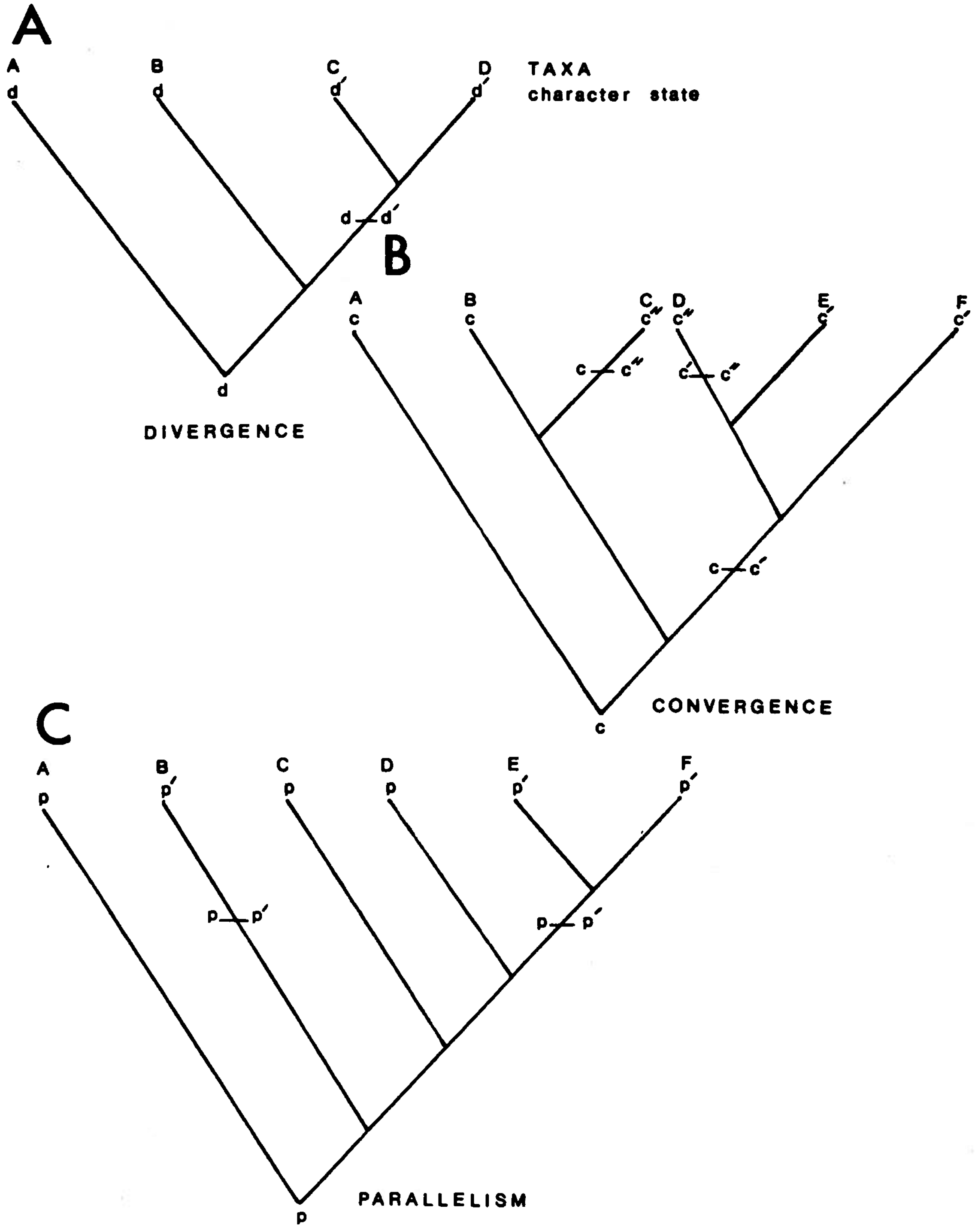

Fig. 3. Three hypothetical cladograms of taxa (A-F) based on parsimony and their common ancestors demonstrating divergence, convergence, and parallelism. The taxa could represent species, or for argument's sake, ecomorphological groupings of organisms sharing the same character states in question. The cladograms may be derived from numerous, for example 50, character traits (not shown here), the majority of which are independent of the traits used for the ecomorphological analysis. The evolution of a few ecomorphological characters (cdp) under investigation are given from the ancestral (pleisiomorphic) to derived (apomorphic) states (indicated by primes). (A) Taxa C and D have diverged from taxa A and B in character state d' as a result of normal descent with modification; (B) assuming character evolution is unordered, taxa C and D have converged in character state c" because of the evolution of similar features (c") from different antecedent features (c and c'); (C) taxa B and E/F demonstrate parallelism in character state p', parallelism being the evolution of similar or identical features independently in related lineages, usually based on similar modifications of the same developmental pathway (Futuyma, 1986).

investigation. Each partial analysis is acceptable as long as one is aware of the inherent limitations and pitfalls.

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