

be misinterpreted to indicate the influence of proximal factors (e.g., strong synecological interactions) if the evolutionary interactions within the community are not investigated within a historical framework.

At the moment, it is impossible to draw any meaningful generalizations about the relative contributions of historical constraints and adaptive change to the evolution of either closely interacting species (coevolutionary studies) or interacting communities (community evolution studies). Traditionally there has been very little interaction between biologists who study these two aspects of coadaptation. We hope we have demonstrated that there is so much common ground between these research programs, at least from a macroevolutionary perspective, that any cross-fertilization will be mutually beneficial. Indeed, some researchers are already discovering the benefits of examining complex systems within a cooperative atmosphere (see, e.g., Futuyma and Slatkin 1983 and Strong et al. 1984).

9 Prospective: Mastering the Possibilities of Historical Ecology

We hope that the analytical results and theoretical discussions from the preceding chapters have established two things about historical ecology as a research program. First, it is **feasible**; both the basic methodologies and some of the pertinent models have been developed and are awaiting application in the ecological and ethological domains. Second, it is **relevant** because *the patterns detected by this method are important components of evolutionary explanations that would not have been discovered without phylogenetic analysis*. We believe that historical ecology has a bright future, not only because so much of the data base is yet to be investigated, but because of the potential for forging connections with other research programs. In this chapter we will summarize the current data base and discuss some new areas of research that may either benefit from, or complement, historical ecological studies.

The Current Data Base

Historical ecology is concerned with uncovering and tracking the trail left by evolutionary change. This trail, although appearing to cut a uniformly straight swath through time, is in reality a complex mosaic of numerous processes. Some of these processes are directional, driving the path forward. Others seem to disrupt this progression and bend the pathway just a little with their oscillations. Some of these processes seem to be initiated by ecological phenomena, others by genealogical (especially developmental) phenomena. Regardless of the manner in which these changes are initiated, they are mediated by ecological considerations. We have concentrated our attention on two major evolutionary processes, **speciation** and **adaptation**, and on two major manifestations of these processes, **diversity** and **ecological interactions**. We have discovered that there is a paucity of rigorous phylogenetic hypotheses from which we can begin historical ecological studies, but from those that are available we can begin to perceive a glimpse of the not-so-obvious in evolution.

The Historical Ecological Perspective on Diversity: Speciation and Extinction Rates

In chapter 4 we discussed how to discriminate among the products of various speciation modes. Having delineated the patterns, we then asked how often each mode occurred and discovered that the majority of cases support an interpretation of vicariant speciation. This implies that most of the diversity component defined by species number is primarily the result of the physical disruption of gene flow by geological and geographic alterations, and not of the direct effects of adaptive changes. Allegorically speaking, speciation provides the bricks with which the evolutionary pathway is constructed, and common ancestry provides the mortar.

If speciation is affected by environmental changes, then we must search for environmental processes that, like speciation, are irreversible. Geological evolution is such a process. Although speciation can occur in the absence of geological changes, such changes will dramatically affect the rates of speciation if the rate of geological partitioning is greater than the rate of population equilibration, determined by mutation rates and gene flow and affected by short-term environmental processes. Cracraft (1982b, 1985a) suggested that the key to understanding speciation rates for any clade is the history of geological change and accompanying vicariant speciation.

Vicariant speciation may also influence our perceptions of the rates and evolutionary roles of extinctions. In every vicariant speciation event, the ancestor giving rise to the allopatric sister species becomes extinct. *If the majority of speciation events are due to vicariance, then the majority of extinctions historically have been by-products of speciation and not the result of irreplaceable losses of evolving lineages.*

Adaptation and Key Innovations

In chapter 5 we established a framework for asking four macroevolutionary questions about the second evolutionary process, adaptation. First, did the character of interest originate in the existing species or in an ancestor and, if it originated in an ancestor, how long ago and in what environmental context? Second, how often has the trait arisen in evolution, that is, is its occurrence unique or is it a repeating evolutionary theme? Third, for any adaptive scenario involving evolutionary changes in traits or the evolutionary accumulation of traits, in what sequence did the component traits appear? Are they historically independent or historically correlated, and if they are correlated, did they arise in the same or in different ancestors? Fourth, how frequent are adaptive changes in phylogeny; do ecological and behavioral changes promote or constrain phylogenetic diversification?

In every case studied so far, ecological and behavioral change is more

conservative than phylogenetic diversification. This complements the discovery that the predominant speciation mode does not require adaptive responses to initiate speciation. It would appear, then, that although the production of biological diversity is the result of both speciation and adaptation processes, the two are not always tightly linked. Whenever adaptive processes, in the form of ecological or behavioral diversification, accompany speciation, they can be interpreted as contributing to the production of diversity. Conversely, whenever such adaptive changes lag behind speciation, as is usually the case, they can be interpreted as constraints, or cohesive influences, on evolutionary change. Hence, the conservative nature of evolutionary diversification in ecological correlates of adaptation plays an important role in maintaining a degree of organization and predictability in the production of diversity.

Coming as it does from a macroevolutionary perspective, the assertion that some adaptive changes function as evolutionary constraints may at first sound counterintuitive. However, if there were no underlying core of historical continuity within and between species, there would be no rationale for a comparative method. We believe that this perspective is consistent with MacArthur's proposal that we should search for evidence of competitive interactions among sympatric congeners. This proposal can be restated in historical ecological terminology: macroevolutionary conservatism in ecological and behavioral evolution leads to the potential for niche overlap in closely related species, so that when congeners are sympatric, we expect to find ecological interactions on a microevolutionary scale. Only if diversification in ecology and behavior are conservative on a macroevolutionary scale would we generally expect to find congeners with enough similarity in ecological and behavior traits to create the initial conditions for such niche overlap, competition, and habitat partitioning.

The Historical Ecological Perspective on Interactions

The conclusion that ecological diversification plays a cohesive role in evolution, based on the study of adaptation and speciation patterns within clades, was reinforced when the evolutionary framework was expanded to include interactions among clades. In chapter 7 we discussed the work of researchers interested in uncovering the extent to which different clades share common histories of speciation. Reconstruction of the speciation patterns for co-occurring groups of organisms revealed a background of phylogenetic association among clade members which often accounted for more than 50% of existing ecological associations. Superimposed upon this phylogenetic framework were independent speciation events accounting for the variation in species composition among biotas that share common historical elements. This research was extended to include the traits characterizing such ecological

associations in chapter 8. Although studies of this particular evolutionary component are rare, the current data base supports an interpretation that ecological and behavioral diversification have been highly conservative phylogenetically in the evolution of biotas; hence, as we discovered in our examination of adaptational change within a clade, this process is a major cohesive force, rather than a diversifying force, in evolution.

Summary of the Current Data Base

The evidence presented in chapters 4, 5, 7, and 8 reveals a substantial degree of phylogenetic influence on both the species composition and species interactions within contemporaneous ecological associations. Geologically mediated speciation patterns (chapter 4) lead to geologically mediated co-speciation patterns (chapter 7). Conservative adaptive responses in phylogeny (chapter 5) herald a conservative interaction structure in ecological associations and biotas (chapter 8). The interchange between speciation and adaptation on all evolutionary levels produces stable assemblages of ecological associations, because the core of resident species exhibiting plesiomorphic interactions will serve as a stabilizing force with respect to each other's evolution and to the addition of colonizers. Paleontological data support the proposal that the structure and composition of ecological associations have always been highly conservative (Boucot 1975a,b, 1978, 1981, 1982, 1983). Hence, the glimpse of the evolution of global diversity that this new research program provides is one of long periods of ecological stability interrupted occasionally by adaptive shifts. At the moment the data base is limited, so these glimpses are but fleeting, tantalizing hints of future discoveries. The answer to this riddle cannot fail to be exciting, whether it is a general proposition that phylogenetic constraint rather than adaptation is the predominant force shaping species associations on the macroevolutionary scale, or the discovery that each system represents a unique outcome of the interplay between the two processes.

Are there any practical advantages for a biologist who adopts the historical ecological viewpoint? If you are a graduate student, should you invest some of your most precious commodity, time, in formulating and examining your particular question within this framework? If you are a graduate adviser, should you encourage students to master the possibilities of this program? Should you even consider leading the way by expanding the scope of your own research? We suggest that the answer to these questions is a resounding "Yes!" Historical ecology expands the spatial and temporal perspective of evolutionary biology, opening doors on more, and more varied, research possibilities. One ambitious project that is well underway is the development of the freshwater fish fauna of North America as a model system for historical ecological studies (see Maiden in press). As a result of this extensive coop-

erative venture, over 40% of the fauna has been analyzed phylogenetically, and a plethora of ecological, behavioral, and distributional data have been collected and examined within that phylogenetic framework. No doubt similar collaborative efforts by other groups of biologists could produce equally substantial results.

One reason for the success of the North American ichthyologists is that robust methods for studying historical effects in ecology and ethology are already available. Because of this, field and experimental biologists can concentrate on the development of the empirical data base without the distractions of constant philosophical and methodological debates. Conversely, because the program is so young, there is room for future methodological fine-tuning and innovation, so theoretically minded biologists can also participate in this time of high productivity and burgeoning ideas. Truly, this is the "best of times" for any scientific discipline! To date, the empirical research supports the hypothesis that persistent historical effects are an important component of evolutionary diversification, so there is reason to believe that embarking on similar quests will produce useful new information. In addition, since relatively few studies have been undertaken, there is little chance of embarking on a project that will not be original. We view historical ecology at this early developmental period as a form of "no-loss" research. No matter what you find, it is interesting because the field is still in its basic discovery phase. For example, what if the current data base and its implications about the importance of phylogenetic constraints on adaptive changes in the evolution of biotas is not representative of evolution in general? Using the implications of the current data base as the null hypothesis for future research, we can determine whether the generalities of today are in fact exceptions to some other general pattern, rather than the pattern itself.

It is important at this point to reemphasize the nonreductionist approach that historical ecology represents. What we seek, and what we think is more representative of the way in which evolution has occurred, are explanations that are constructed somewhat like analysis of variance (ANOVA) studies. That is, rather than asking what single factor (e.g., "history" or "ecology") accounts for the evolution of a given system, we would ask, what has been the relative contribution to, or effect of, a variety of possible processes on the evolution of the system we are studying? This is the reason we encourage closer collaboration between ecologists, ethologists, and systematists to produce an integration of microevolutionary and macroevolutionary data.

Possibilities for Future Research

Conservation

Neither of the authors of this book is a conservation biologist. Like everyone else on this planet, however, we have a vested interest in contributing to

the protection of the global ecosystem. We believe that historical ecological methods can provide information that will complement current conservation/management practices based on theories about the relationship between species number and area size or number. For example, historical biogeographical studies (cospeciation in a geographical context) can identify geographical areas that have been associated with "hot spots" of evolutionary activity in the past, and which might serve as areas of evolutionary potential in the future. Such areas of endemism are interesting because they do not always encompass the greatest number of extant species, nor are they always extremely large or centrally located. As a consequence, if, as is so often the case, a choice must be made about areas requiring protection, historical ecological data can provide information about regions that have been very important in the evolution of biological diversity.

For example, consider the neotropical freshwater stingrays and their associated parasite communities. Historical ecological studies have demonstrated that the ancestors of these organisms moved into the Amazon River at a time in the far distant past when that river flowed into the Pacific Ocean. This component of the South American freshwater fauna is thus the result of a historically unique event that can never be repeated, or recovered, if lost. Now, suppose a decidedly unusual conservationist felt that it was important to preserve the parasites of neotropical freshwater stingrays. How would we rank the six known communities of ray parasites with respect to their importance in the evolution of the fauna (see chapter 8)? The "least important" areas would be (1) the Lake Maracaibo area, because it contains only species that evolved, and currently occur, elsewhere, and (2) the mid-Amazon, because it shelters only a single endemic species. The remaining four areas all have a relatively large number of endemic species. Of these, the community in the delta of the Orinoco River has the highest species number (eleven species), due to the combination of endemics that evolved there plus species that have colonized from elsewhere. Unfortunately, it is likely that the delta of the Orinoco will face increasing pressures for industrial development in the future. The remaining three communities occur in more remote areas, the upper Paraná (six species), the upper Amazon (six species), and the Magdalena (four species). Protecting these areas would protect a high proportion of the species of stingray parasites (sixteen out of twenty-three species), including five of the eleven species of helminths that occur in the Orinoco Delta. If we examine these three areas more closely, we find that four of the six species found in the upper Amazon, three of the six species in the upper Paraná, and three of the four species in the Magdalena are not known to occur anywhere else. Because these areas are less likely to feel the encroachment of human development, they also represent good compromises between the need to protect and the need to develop.

The historical ecological perspective leads us to postulate two general cases in which traditional criteria could be detrimental to long-term conservation efforts. (1) Preserving areas based on current species numbers: If the chosen area encompasses the region of overlap between two biotas, then we may be preserving marginal habitats that have limited the expansion of members of both biotas. Confining organisms to such an area may, in turn, increase the likelihood of competitive interactions that could be detrimental to all species. It has long been postulated that the more closely related the species, the more likely they are to use the same resources (MacArthur 1958, 1972; Root 1967), something the evidence presented in this book corroborates. In undisturbed communities, congeneric species are found together less often than expected by a process of combining groups randomly from a pool of all possible species that have access to the communities (Bowers and Brown 1982). Furthermore, congeners rarely occur together often enough to allow adaptations for competitive exclusion to evolve (Maurer 1985; Graham 1986). Hence, artificially confining sets of closely related species from separate communities that evolved allopatrically could be counterproductive for the survival of any of them. (2) Preserving many small areas: In this scenario, we are asked to choose between many species with small geographic ranges and few species with large ranges. If the species exhibiting small ranges represent the outcome of peripheral isolates allopatric speciation, saving a large number of peripheral isolates areas rather than a few large central areas might destroy the central populations from which all those descendant species came. In both of these general cases, we would be trading evolutionary potential for current diversity, and possibly harming the current diversity in the process.

We are not advocating a blanket conservation policy based on phylogenetic considerations. However, we do believe that history has been a critical missing component in many conservation studies. In fact, the current historical ecological data base suggests some reasons for pessimism about global conservation efforts. Ecological structure in biotas appears to be much more conservative evolutionarily than previously thought, raising questions about the adaptability of ecosystems on time scales relevant to human activities. The greater the phylogenetic constraints on an ecosystem, the more slowly it will be able to respond to perturbations. And if it is not bad enough that current ecological structure is older and more conservative than we thought, paleontological studies indicate that this may be the way it has always been. As a consequence, our concern about the survivability of any given ecosystem should be directly proportional to the degree of phylogenetic constraint on its structure and composition. Those ecosystems that have been around for the longest time and contain the largest number of endemic species would be those least likely to survive human intervention, and thus are the most in need

of immediate conservation. Similarly, those species that have been part of any given biota for the longest periods of time may be those most in need of protection against exploitation and removal.

Integrating Historical Ecology and Functional Morphology

In chapter 5 we discovered that the analysis of adaptive radiations is more complex than comparing the degree of ecological diversification with the degree of speciation in any given clade. Specifically, we suggested that evolutionary diversification in functional morphological attributes might also be involved (see also Coddington 1988). Fortunately, an explicitly phylogenetic approach to the study of functional morphology has been developing, pioneered by George Lauder (e.g., 1981, 1986, 1988, 1989; Schaefer and Lauder 1986; Lauder and Liem 1989).

Lauder's approach is based on the proposal that the realized phenotypic diversity is only a fraction of all possible phenotypic diversity, and attributing the "missing" possibilities solely to the effects of environmental selection overlooks the role for developmental dynamics and phylogenetic constraints in determining the ranges of realized phenotypes. He suggested that, since organisms are historical entities, the intrinsic phylogenetic component of organismal design may impose limitations on the way in which and the degree to which structural modifications can occur in the evolution of a lineage. Lauder (1981) proposed that the relative importance of phylogenetic constraints in the evolution of functional morphology could be assessed by examining (1) emergent structural or functional traits that have general properties within (2) an explicit phylogenetic framework to (3) test hypotheses of phylogenetic constraint by comparing general properties among clades. He further suggested that this mode of study could be integrated with studies of extrinsic (environmental) constraints on form, to generate robust explanations for the range of existing morphotypes.

Food: Lingual feeding in lizards

It has been suggested that the tongue has played a central role in the evolutionary movement from aquatic to terrestrial vertebrates (Bramble and Wake 1985; Hiiemae and Crompton 1985). However, an understanding of the evolution of vertebrate feeding patterns requires more information about the tongue's role than is presently available for many groups. Schwenk and Throckmorton (1989) began the process of producing a solid foundation for a general evolutionary study by focussing their attention on one particular group, the Sauria (lizards). They were primarily interested in examining the initial stages of prey capture and ingestion in these organisms. Independent phylogenetic analysis of the Sauria based on 148 morphological characters

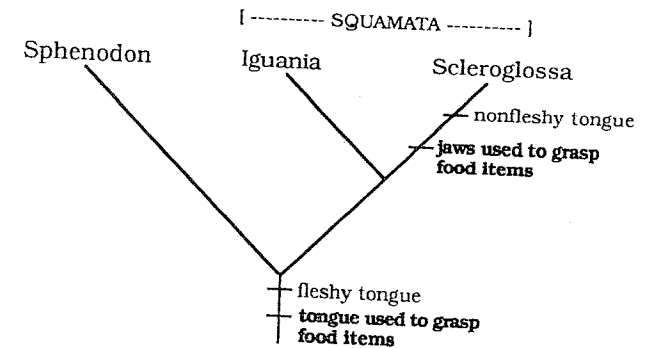


Fig. 9.1. The evolution of feeding modes in squamate lizards. Change in tongue structure and feeding behavior mapped onto a phylogeny for the squamata. (Estes, de Queiroz, and Gauthier 1988; redrawn from Schwenk and Throckmorton 1989.)

(Estes, de Queiroz, and Gauthier 1988) suggests that modern lizards comprise two basal groups, the Iguania and the Scleroglossa. Members of the fleshy-tongued Iguania capture prey items (animal or plant) by combining rapid extensions of the dorsally arched tongue with forward and downward movements of the head to pin the food item to the substrate. Food is thus both grasped and drawn into the mouth by tongue action alone. In contrast to this feeding mode, members of the "nonfleshy"-tongued Scleroglossa grasp and ingest prey items solely through the use of their jaws; the tongue is not involved in these early stages of feeding. Outgroup comparisons with *Sphenodon* (the tuatara of New Zealand) suggest that the condition found in the Iguania is plesiomorphic (fig. 9.1).

This study leads us down a number of interesting pathways. To begin with, although tongue morphology is extremely diverse (i.e., provides important taxonomic characters), there has been only one major change in feeding mode within this group of lizards. The presence of lingual feeding in all members of the Iguania represents the persistence of an ancestral condition, while the appearance of jaw feeding was an evolutionary novelty in the ancestor of the scleroglossans, which has been retained in all members of that group. The shift in feeding mode thus occurred against a background of considerable phylogenetic constraint. Interestingly, the origin of jaw feeding is associated phylogenetically with an alteration in tongue morphology, but this by itself does not establish a causal link between the two. Further research is required to uncover the origin of lingual feeding and the fleshy tongue. If they also arose at the same point in evolution, the hypothesis of a causal link between feeding mode and lingual morphology will be strengthened. Additionally, experimental studies investigating the dynamics of the derived feeding mode, using the plesiomorphic feeding mode as the control, are necessary to estab-

lish a functional connection between shifts in behavior and shifts in morphology. A cascade of new questions will naturally be produced: for example, (1) has there been an adaptive radiation of the scleroglossans and, if so, (2) can the new feeding mode be identified as the "key innovation," (3) do other behavioral modifications accompany this change, (4) have there been shifts in diet correlated with jaw feeding, and (5) what other morphological innovations appear in the ancestor of the scleroglossans? Overall then, this example is exciting because of the number of new questions generated and because it proposes that a relatively simple modification in a morphological pattern may have been responsible for a number of behavioral and ecological evolutionary changes.

Sex: Inner ears and mating calls in frogs

Auditory cues are an integral part of all anuran breeding systems. Both the structure of the male's vocalization and the female's response to the call are extremely species-specific. In fact, of the more than twenty-seven hundred frog species no two species produce identical calls (Blair 1964). These behavioral characters are thus hypothesized to be critical components in the maintenance of reproductive cohesion within a species and reproductive isolation among species. Ryan (1986) examined the hypothesis that changes in the structure of the neuroanatomy of frog ears amplified the divergence of mating-call behaviors, which in turn may have affected the rate of speciation in various lineages. The frog inner ear contains two organs, the amphibian papilla and basilar papilla, which are sensitive to airborne sound waves. Based upon an examination of the amphibian papillae in approximately eighty anuran species, Lewis (1984) divided the organ into four states characterized by an initial increase from one to two sensory patches and a subsequent increase in the complexity of the second patch. This increase in morphological complexity has behavioral consequences; frog species with the best-developed amphibian papillae respond to a wider range of call frequencies than their acoustically more restricted relatives. Ryan mapped the differences in the structure of the inner ear onto a phylogeny for the major frog families (fig. 9.2 depicts the distribution of these traits on the more recent phylogenetic tree for frog families by Duellman and Trueb 1986), using the condition in the sister group to the anurans, the urodeles (salamanders), to establish the plesiomorphic condition.

Ryan discovered that changes in the inner-ear system were highly correlated with frog phylogeny and were highly conservative. Once again, history provides the backdrop to the evolutionary play. Ryan concluded that the morphological structure of the inner ear has influenced speciation rates within the anuran clade by affecting the degree of divergence in detectable mating-call

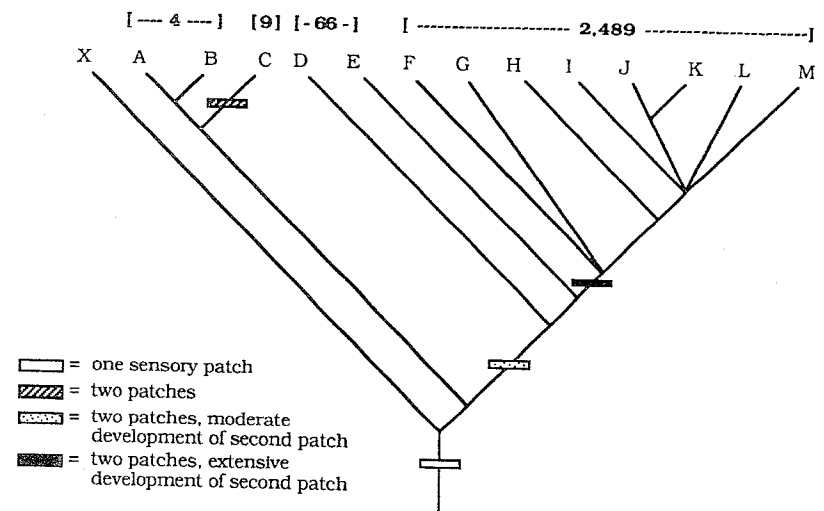


Fig. 9.2. Structure of the amphibian papilla of the inner ear, mapped onto the phylogeny for some of the anuran families. A = Ascaphidae; B = Leiopelmatidae; C = Discoglossidae; D = Pipidae; E = Pelobatidae; F = Leptodactylidae; G = Dendrobatidae; H = Hylidae; I = Bufonidae; J = Ranidae; K = Hyperoliidae; L = Rhacophoridae; M = Microhylidae; X = the outgroup, Urodela. Numbers = number of species associated with each character state. (Redrawn from Duellman and Trueb 1986; Ryan 1986.)

frequencies. Thus, the more frequencies you can detect, the more material is available for potential evolutionary modification and diversification. When the number of species among lineages with different inner-ear character states are examined, the expected trend towards increasing numbers of species associated with increasing complexity of the inner ear is observed. The role of breeding behavior in maintaining reproductive isolation has become a focal point of many behavioral ecological studies. Ryan's study is an important step towards integration of morphological, behavioral, and genetical information into a more complete investigation of this problem. The next step involves the collection of additional data, particularly for the families missing from this initial analysis. Additionally, it will be interesting to examine other potential correlates of speciation rates within the context of phylogeny. For example, Duellman's (1985) study suggests that other reproductive characters may be associated with anuran adaptive radiations (see also the discussion in chapter 5). The six families displaying only one reproductive mode have not undergone widespread speciation, whereas the eight most species-rich families are characterized by either widespread convergent adaptation or a combination of widespread convergence and the appearance of novel parental-care behaviors. In this case, then, the adaptive radiations of various anuran

lineages may be the result of a combination of factors, including a key morphological innovation that was reinforced by a variety of ecological and behavioral innovations.

More food: Evolution of feeding modes in centrarchid fishes

Sunfishes belong to the family Centrarchidae, a group of thirty-two species of fishes endemic to North America. Thirty of the species are foraging generalists. The remaining two species, the pumpkinseed (*Lepomis gibbosus*) and the redear (*L. microlophus*) eat only snails, a dish scorned by all other self-respecting centrarchids except, occasionally, the green sunfish, *L. cyanellus*. The pumpkinseed and redear eat snails in the wild and in the laboratory in a very refined manner. Rather than simply gobbling up snails and swallowing them whole, they crush the snail shells in the pharynx, separate the shell from the body, and eject the shell detritus before swallowing the edible snail body (Lauder 1983a,b). Lauder (1986) suggested that this particular behavioral pattern is an excellent model system for studies in functional morphology and behavioral evolution for four reasons: the behavior is apomorphic and not widespread within the group; there are morphological specializations in the feeding mechanism of species that regularly exhibit the crushing behavior; the motor patterns used in the behavior can be identified experimentally by recording electrical activity in the muscles involved in snail crushing; and the crushing behavior is composed of repetitive crushing phases, and cyclically repeating motor patterns are excellent systems for studying the manner in which behavioral activities are generated by the nervous system.

Lauder's experimental studies (1983a,b) demonstrated that, in terms of muscles, bones, muscle origins, or muscle insertions, the basic musculoskeletal design of the jaw and buccal area of *L. gibbosus* and *L. microlophus* does not differ from that of any other centrarchids. There are, of course, some differences that emerge from closer examination. For example, the two snail eaters have more-robust lower pharyngeal jaws, with larger and more-rounded teeth, and the upper pharyngeal jaw teeth are hypertrophied with respect to the lower jaw teeth. There are two basic chewing patterns. First, when centrarchids are given fishes and worms to eat (the snail eaters will deign to ingest nonsnail prey in the laboratory when faced with the option of missing a free meal), all species except *L. microlophus* exhibit the same rhythmic pattern of alternating activity in the pharyngeal musculature, lasting for as much as a minute, as the prey is transported from the pharynx into the esophagus. Second, when the pumpkinseed, redear, and green sunfishes eat snails, nearly all of the pharyngeal muscles are electrically active simultaneously during the crushing process; no rhythmic alternating pattern is found.

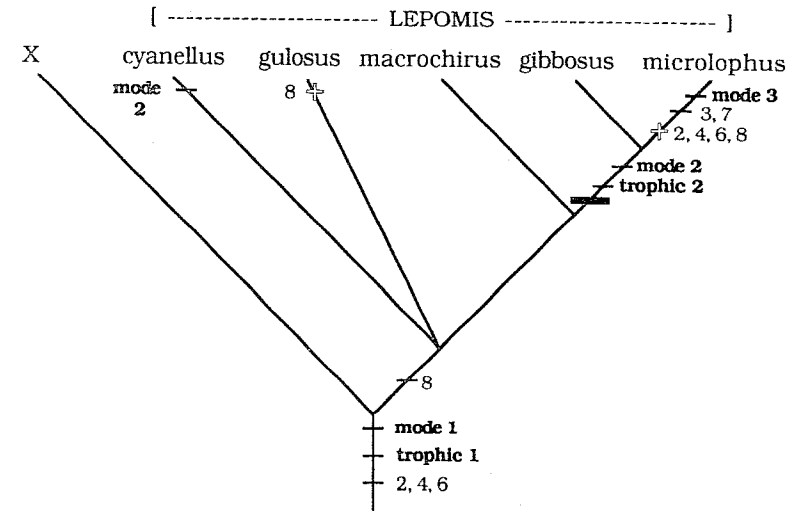


Fig. 9.3. Simplified phylogenetic tree for centrarchid fishes. *X* = outgroups. *Ambloplites*, *Pomoxis*, and *Micropterus*. Numbers = functional characters (patterns of muscle activity involved in chewing food; see Lauder 1986 for descriptions). Mode 1 = only rhythmic pattern of chewing food; mode 2 = rhythmic for soft foods, crushing for snails; mode 3 = only crushing pattern. Trophic 1 = generalist, no snails; trophic 2 = snail specialists. Black bar = three morphological characters that serve as synapomorphies for *L. gibbosus* + *L. microlophus* (hypertrophy of the pharyngohyoideus muscle, hypertrophy of the levator posterior muscle, and expanded tooth areas on the upper and lower pharyngeal jaws). (Redrawn and modified from Lauder 1986.)

different motor pattern, the shell fragments are ejected from the mouth, and the snail is swallowed. This pattern is used by *L. microlophus* regardless of the prey type; unlike *L. gibbosus* and *L. cyanellus*, this species does not modulate its feeding behavior to suit its food.

Lauder's study of the morphological, functional, ecological, and behavioral characteristics involved in sunfish feeding is presented in a simplified form in figure 9.3. The phylogenetic tree suggests that the two "natural" snail eaters (*L. gibbosus* and *L. microlophus*) are sister species and are relatively highly derived members of the genus. Examination of sunfish feeding within this phylogenetic framework reveals that a new chewing pattern has appeared three times over the evolution of this group. Mode 2, the development of the crushing motor pattern, appeared convergently in the green sunfish (*L. cyanellus*) and in the common ancestor of *L. gibbosus* and *L. microlophus*. The suite of characters composing this mode was passed on to its descendants, one of which, *L. microlophus*, became even more specialized through the loss of four plesiomorphic (2, 4, 6, 8), and acquisition of two autapomorphic (3, 7), functional traits. Nevertheless, both the redear and the pumpkinseed continue to display a similar snail-eating behavioral pattern, suggesting that

characters 2, 3, 4, 6, 7, and 8 are not integral components of this feeding preference.

Lepomis cyanellus is the only other sunfish that considers snails to be edible items, although it must be encouraged in this consideration. Initially, this convergent evolution of chewing mode 2 only in the snail-eating sunfishes might be offered as support for a hypothesis that the appearance of feeding mode 2 was involved in the shift to snail eating. However, closer examination reveals that, of the three changes in chewing pattern, only one was associated with a trophic shift. Since chewing pattern and food type are not tightly coupled at any other point on the tree, it appears that the origin of the crushing mode is not, of itself, sufficient to explain that species' change into a snail-eating specialist. The answer to this problem may lie in the three morphological changes that occurred in the ancestor of *L. microlophus* and *L. gibbosus* and have been transmitted to both of its descendants. To approach this from another perspective, it appears that, on their own, the functional changes in chewing pattern (from mode 1 to mode 2) explain the functional **ability** to eat snails, while, in combination with the morphological changes, they explain the trophic **specialization** on snails.

**Integrating the Experimental and Phylogenetic Approaches:
From Pattern to Process**

The long-standing tradition of integrating experimental and evolutionary information, especially in comparative ethology, has been de-emphasized during the "eclipse of history" in ethology and ecology. The advent of historical ecological methods should reemphasize this area of research and help promote an integration of evolutionary patterns and evolutionary processes. We have already discussed examples of this type of study using ecological data (see Huey and Bennett's study of sprinting speed and thermal preferences in skinks in chapter 5 and Gorman's study of freshwater fish communities in chapter 8). In the following paragraphs we will turn our attention to the "*Drosophila*" of ethology, the stickleback fishes.

Gasterosteid fishes: Color and behavior

Sticklebacks and their relatives (family Gasterosteidae) have played a leading role in behavioral ecological research for decades. Within this family, the diminutive three-spined stickleback, *Gasterosteus aculeatus*, has commanded the most attention because breeding males undergo a wondrous transformation from inconspicuous silver-green fishes into flamboyant mosaics of intense flame-scarlet and flashing aquamarine-blue. Needless to say, such a transformation did not go unremarked. The red component of the male's breeding livery is hypothesized to play a role in (1) territory acquisition and

maintenance (intrasexual selection), (2) courtship and mate acquisition (intersexual selection), or (3) paternal care (natural selection). These hypotheses are generally based upon the assumption that the origin and elaboration of male nuptial coloration occurred in an ancestral *G. aculeatus* population. As we have discovered in preceding chapters, however, studies of a single species can, at best, only address questions concerning character maintenance in that species. To investigate character origin and elaboration you need at least two other species, preferably the closest relatives to the test organism, and an outgroup.

Historical ecological methods can provide a useful way to disentangle the potential contributions of various selection pressures in the evolution of sexually dimorphic nuptial coloration in gasterosteids, by generating predictions for experimental investigation. McLennan, Brooks, and McPhail (1988) examined the macroevolutionary relationships among color and various breeding behaviors on a phylogenetic tree for the sticklebacks. They discovered the following associations.

Intersexual selection (fig. 9.4): The initial elaboration of male nuptial coloration is preceded by an increase in the complexity of courtship on the

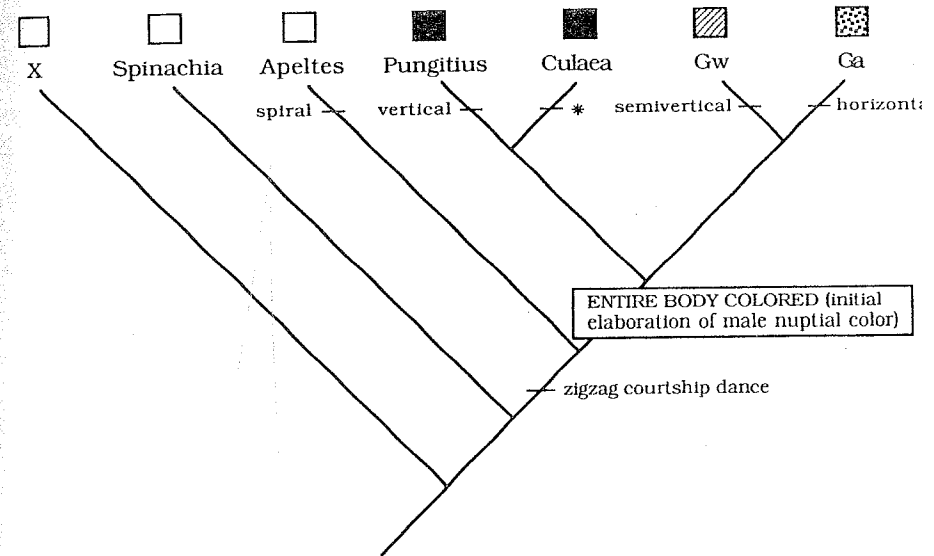


Fig. 9.4. Relationship between diversification of color and courtship in the gasterosteids. X = outgroup; Gw = *Gasterosteus wheatlandi*; Ga = *G. aculeatus*. Nuptial body colors: white box = no color; black box = black body; striped box = gold body; boldly stippled box = red body. The orientation of the zigzag courtship dance is mapped beneath each appropriate species. * indicates that the courtship dance has been replaced by a tail-flagging display in *Culaea inconstans*.

phylogenetic tree. This reinforces the intersexual selection hypothesis because an increase in the intricacy of signal exchange focusses the receiver's attention on the sender and increases the amount of information available in the interaction. This, in turn, creates the potential for the evolution of differential female response (female choice) to variability in a male character. Apparently this potential was realized in the ancestor of the *Pungitius* + *Culaea* + *Gasterosteus* clade, where nuptial coloration underwent an exaggeration (from no color to the entire body) consistent with Fisher's (1930) runaway sexual selection scenario. The phylogenetic tree supports the interpretation that initially color was not necessary in courtship (the outgroup, *Spinachia*, and *Apeltes* do not change color during the breeding season), but that it later became intimately involved with male-female interactions. Once associated, the elaboration of color and courtship are tightly coupled on the tree.

Intrasexual selection (fig. 9.5): Color may play a role in male-male interactions as part of a threat display, allowing an individual to assess the social status, experience, and motivational state of an opponent. Depending on the system employed, the information exchanged during these interactions may contain elements of both truth and bluff. However, once an encounter has escalated past threat, the emphasis should shift away from signals such as

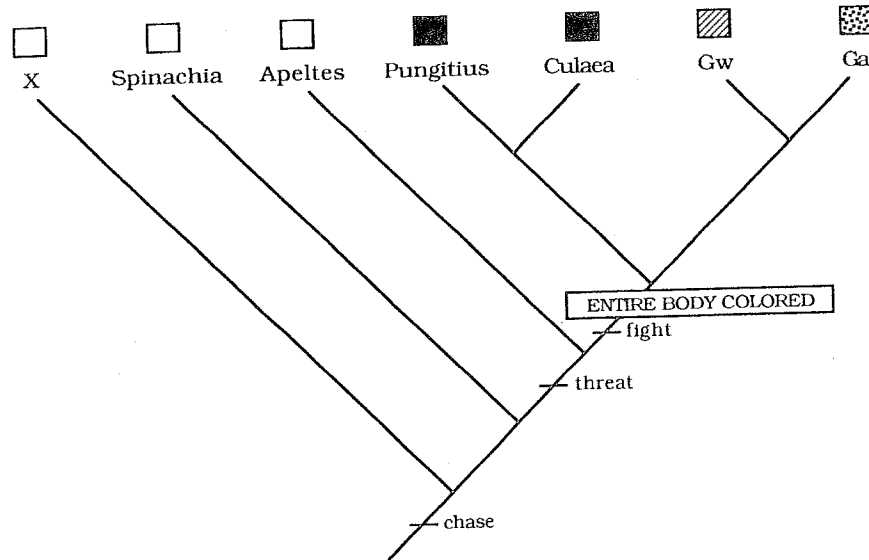


Fig. 9.5. Relationship between diversification of color and aggressive behaviors in the gasterosteids. Behaviors involved in male-male interactions have been mapped onto the tree. X = outgroup; Gw = *Gasterosteus wheatlandi*; Ga = *G. aculeatus*. Nuptial body colors: white box = no color; black box = black body; striped box = gold body; boldly stippled box = red body.

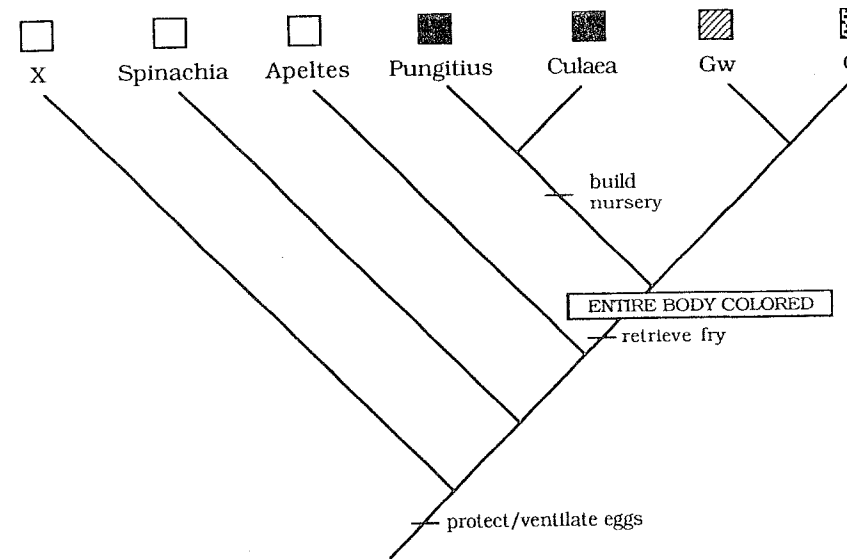


Fig. 9.6. Relationship between diversification of color and parental behaviors in the gasterosteids. Parental-care behaviors have been mapped onto the tree. X = outgroup; Gw = *Gasterosteus wheatlandi*; Ga = *G. aculeatus*. Nuptial body colors: white box = no color; black box = black body; striped box = gold body; boldly stippled box = red body.

color to factors directly involved with fighting performance (stamina, skill strength). Examination of the phylogenetic tree indicates that, contrary to our expectations, color elaboration is initially associated with the appearance of fighting, not threat, behavior. Additionally, once threat and fight behaviors arose, they remained very conservative, whereas color continued to be elaborated. So, macroevolutionary analysis suggests that any subsequent function of color in male-male interactions is secondary to the more direct coupling of color and male-female interactions.

Natural selection (fig. 9.6): The relationship between color and parent care falls between the intra- and intersexual selection patterns. Like courtship, the initial elaboration of color is associated with an increase in parent care (prolonged fry retrieval). This supports the hypothesis that natural selection played a role in the elaboration of the color signal in this ancestor. Past this point in phylogeny, however, changes in color and parental care are not as closely associated as the macroevolutionary relationship between color and courtship.

The macroevolutionary associations between breeding color and behavior uncovered by phylogenetic analysis provide a set of predictions about color changes across the breeding cycle and about female choice based on male color, which can be tested by laboratory studies at the population level.

any of the gasterosteids. These predictions have been examined for that most handsome of fishes, the three-spined stickleback (McLennan and McPhail 1989, 1990).

The breeding cycle of *Gasterosteus aculeatus* can be divided into four behaviorally distinct stages, territory acquisition/nest building, courtship, egg guarding, and fry guarding. Fortunately, the three-spined stickleback is notoriously easy to breed in the laboratory, so McLennan and McPhail (1989) were able to take males through their paces with a maximum amount of cooperation from the fishes. The intensity of red body color was measured on a daily basis from a male's introduction into the test aquarium to the completion of fry guarding (fig. 9.7). Color changes across the breeding cycle of this species were then compared to the changes predicted from the macroevolutionary associations of color and behavior in the family Gasterosteidae.

Intrasexual selection (fig. 9.5): The nesting male in this population tends to be a lightly colored individual, displaying just a hint of flame-orange in the lower jaw and opercular areas (fig. 9.7: nest). He is, in fact, barely distinguishable from a nonterritorial male. Evidence from other microevolutionary studies on populations in Europe (Van Iersel 1953), Japan (Ikeda 1933)

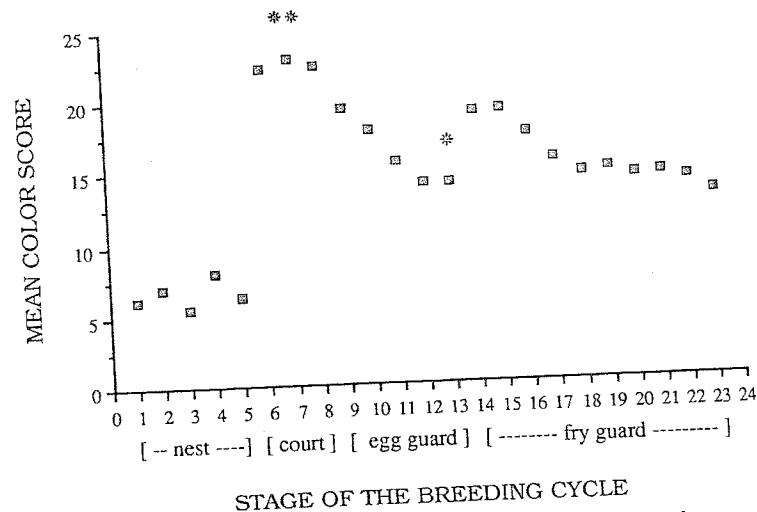


Fig. 9.7. Change in total score (intensity) for red body color of *Gasterosteus aculeatus* males ($N = 19$) across a complete breeding cycle. The breeding cycle is broken into four distinct stages. Days 1–5, nest building/maintenance; days 6–8, courtship; days 9–13, egg guarding; days 14–23, fry guarding. All nests were completed by the end of day 2. Asterisks refer to the results of two Wilcoxon analyses: * = significant difference ($p < 0.01$) between color scores of individuals on day 13 (last day of egg guarding) and day 14 (first day of fry guarding); ** = significant difference ($p < 0.001$) between courtship peak (days 6–8) and fry-guarding peak (days 14–16).

and North America (McPhail 1969) also indicates that the development of full nuptial coloration is not a necessary prerequisite for territory establishment and maintenance. This supports the phylogenetic prediction that intra-sexual selection did not play a major role in the evolutionary elaboration of the nuptial signal in the gasterosteids.

Intersexual selection (fig. 9.4): Courting males are characterized by a peak in both the intensity and the distribution of scarlet across the entire ventral and lateral surfaces of the fish (fig. 9.7: court). Since the correlation between the intensity of red body and blue eye color is also higher at this stage than at any other time in the breeding cycle, the male presents his most intense, widely dispersed, and cohesive mosaic signal during the brief courtship phase. As predicted, the strong association between the evolutionary elaboration of color and courtship behavior in the gasterosteids in general, is mirrored within *G. aculeatus* in particular.

Natural selection (fig. 9.6): The parental male presents a more somber image as a wave of dark gray sweeps forward from the caudal fin, masking all colors except the bright blue of the eyes and intense flame-scarlet in the throat region. A small decrease in mandibular color during egg guarding (fig. 9.7: egg guard) is followed by a surge in intensity to courtship levels coinciding with the appearance of fry and an increase in aggression (fig. 9.7: fry guard). The second peak in overall color is lower than the level achieved during courtship, as color increases in the anterior third of the fish are countered by "losses" in the posterior and middle regions. Nevertheless, this peak suggests some role for color during the initial stages of fry guarding. As predicted by the phylogenetic analysis, color intensity is moderately tied to parental care, falling somewhere between the peaks of courtship and the valleys of territory acquisition.

The phylogenetic predictions based on the macroevolutionary relationships between the elaboration of breeding color and behaviors are thus confirmed in this microevolutionary study of color changes across the breeding cycle of *Gasterosteus aculeatus*. This, in turn, focusses our attention upon the influence of intersexual selection on the elaboration of male nuptial color in these fishes. Researchers have been investigating female mating preferences in the three-spined stickleback for over fifty years (Pelkewijk and Tinbergen 1937; McPhail 1969; Semler 1971). The results of these experiments are unequivocal: when offered a choice between red or nonred (grey or black) males, females overwhelmingly prefer red. Since red is a species-specific character (autapomorphy) for *G. aculeatus*, this research has provided ample evidence for mate recognition; that is, the female's ability to discriminate potential mates (territorial, conspecific males) from nonmates (immature, nonterritorial conspecifics and other gasterosteid males). Now, how does a female discriminate among potential mates, all of whom are red?

As discussed previously, the presence of "entire body" breeding coloration represents the persistence of an ancestral trait in three-spined sticklebacks. The actual event associated with the initial elaboration of the distribution of color occurred in the ancestor of the *Pungitius* + *Culaea* + *Gasterosteus* clade. If, as this rapid elaboration within one species suggests, this event was driven by runaway sexual selection, then it may be possible to document the effects of female choice based upon differences in intensity of body color in *G. aculeatus*. A series of female choice experiments confirmed the phylogenetic predictions: when females were offered the choice of two competing males, they displayed a significant, preferential response for the most intensely colored red male (McLennan and McPhail 1990). The results of this and the preceding experiment thus confirm the macroevolutionary prediction that intersexual selection has been the dominant force shaping the evolution of male nuptial coloration in the Gasterosteidae.

The tradition of studying behavioral evolution by combining phylogenetic and experimental information was developed by Tinbergen and Lorenz many years ago. As discussed in chapter 1, however, this tradition foundered as both ethologists and systematists became deeply enmeshed within their own theoretical revolutions. Historical ecology allows us to reestablish a dialogue between systematics and experimental ethology, to the mutual benefit of both. This section is a tribute to the original ethologists' insights, both because it refines and reemphasizes the power of a phylogenetic/experimental integration, and because it reinforces the fundamental views of stickleback behavior unveiled by Pelkewijk and Tinbergen's elegant experiments in 1937.

Adaptive Changes in Quantitative Traits: Integrating the Statistical and Phylogenetic Approaches

Over the last decade, a renewed interest in the genealogical aspects of evolution has emerged in the form of a new research program that attempts to strengthen our examination of adaptive hypotheses by considering the effects of phylogenetic constraints on quantitative traits (Stearns 1977, 1983; Gittleman 1981; Ridley 1983; Clutton-Brock and Harvey 1984; Cheverud, Dow, and Leutenegger 1985; Pagel and Harvey 1988; Gittleman and Kot 1990). These researchers have repeatedly emphasized the caveat that data from related taxa are not statistically independent, so persistent phylogenetic effects will confound statistical tests of adaptation. Most of the research in this area has centered on the evolution of life-history traits. For example, Stearns (1983) reported phylogenetic constraints on the patterns of covariation in a variety of life-history traits in mammals. Gittleman and Kot (1990) discovered significant positive correlations between (1) body weight and phylogeny within and between genera of carnivores, and (2) modal clutch size

and phylogeny within and between genera for 256 western Palearctic nonpasserines. Other studies along similar lines have been published (Gittleman 1981, 1985, 1986, 1989; Ballinger 1983; Brown 1983; Ridley 1983; Stearns 1983; Bekoff, Daniels, and Gittleman 1984; Fenwick 1984; Cheverud, Dow, and Leutenegger 1985; Dunham and Miles 1985; Felsenstein 1985; Harvey and Clutton-Brock 1985; Stearns and Koella 1986; Huey and Bennett 1987; Kool 1987; Wootton 1987; Dunham, Miles, and Reznick 1988; Pagel and Harvey 1988; Fox 1989; Gittleman and Kot 1990; Faith, in press). Although a variety of different methods were used to identify and quantify phylogenetic effects, all these studies confirmed the presence of phylogenetic influences on quantitative life-history traits that had traditionally been accorded high adaptive significance. As it became apparent that phylogenetic effects may be an important component in the evolution of qualitative *and* quantitative traits, two general approaches began to emerge.

The first of these represents an attempt to examine the evolutionary diversification of quantitative traits *within a phylogenetic context* (e.g., Farris 1970; Felsenstein 1985; Huey 1987; Huey and Bennett 1987; Faith in press). This research involves methods for estimating ancestral states for quantitative traits on phylogenetic trees. Although methods differ somewhat among these authors, all agree on one point: genera, families, and other supraspecific categories do not evolve and have no status within evolutionary theory, even if they represent monophyletic groups. Therefore, the statistical study of "generic constraints" or "familial constraints" becomes an exercise in determining the consistency with which different taxonomists discern groupings, rather than an analysis of evolutionary processes. What are termed "generic-level constraints" that have evolutionary relevance correspond to attributes that originated in the common ancestor of a clade, that is, traits that originated in an ancestral *species*. Since the term "genus" is an arbitrary artifact of a classification scheme, it is likely that the degree of "generic-level constraints" will differ for each "genus," and this, in turn, might lead to mistaken conclusions about the different degrees of adaptive influences operating on different clades (fig. 9.8). Thus, *it is important to use sister-group relationships in making comparisons, rather than making comparisons across levels in a tree, each of which might be construed as coinciding with a particular classification category* (see also Felsenstein 1985).

So, let us consider the hypothetical group of "winged" species depicted in figure 9.9. An intrepid historical ecologist might first approach the problem of the evolutionary modification of the quantitative trait, wing length, in this clade by averaging across accepted taxonomic levels. Upon completion of this analysis the ecologist concludes that wing length increased at the subfamily level and decreased slightly on the generic level. There has therefore been an evolutionary trend towards increasing, followed by decreasing, wing size

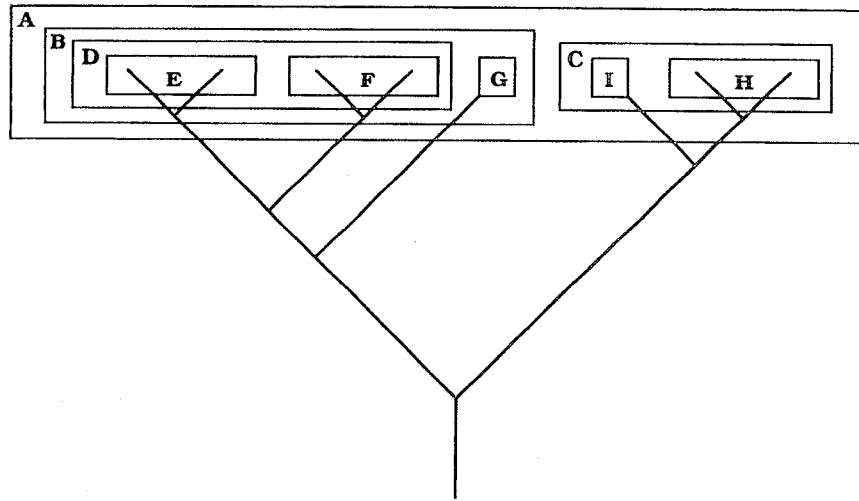


Fig. 9.8. The arbitrary nature of taxonomic levels above the species. Relationships among eight hypothetical species are depicted on a phylogenetic tree. Although the relationships among these species will remain the same, there are potentially six different classification schemes of these relationships at the genus level: (1) one genus (box A); (2) two genera (boxes B and C); (3) three genera (boxes B, I, and H); (4) three genera (boxes C, D, and G); (5) four genera (boxes C, E, F, and G); or (6) five genera (boxes E, F, G, H, and I). Researchers investigating hypotheses of adaptation based upon differences between taxonomic units larger than the species will have to choose from among these schemes; therefore, their explanations will be strongly influenced by the arbitrary and artificial nature of these supraspecific units.

in this group. In addition, it would appear that there has been some degree of evolutionary change associated with each branch on the phylogenetic tree.

During the final preparations for publication our researcher, by chance, attends a seminar concerning the pitfalls of averaging across taxonomic levels. Being of tenacious nature, the ecologist tears up the original analysis and approaches the problem by averaging the values of wing lengths between sister species (fig. 9.10). This leads to the conclusion that there has been a trend towards gradual wing reduction in the monophyletic group A + B + C + D + E, and gradual wing enlargement in the group F + G + H.

Finally, our hypothetical, and weary, historical ecologist decides to investigate wing length from yet another perspective, that of phylogenetic character optimization. This analysis produces results similar to those revealed by sister-group averaging, with some interesting differences (fig. 9.11). There is a trend towards wing reduction in one lineage and wing enlargement in the other, but this trend is superimposed upon a large amount of phylogenetic constraint in wing length within members of the entire clade. Optimization reveals that five was the ancestral wing length and that this length has been

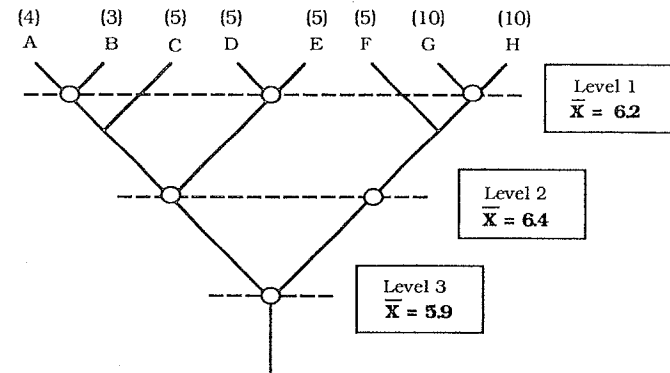


Fig. 9.9. Problems that can arise from averaging across taxonomic levels on a phylogenetic tree. Letters = species. Values for a character—say, wing length—are plotted above each species. The first-level value is arrived at by summing the average wing lengths of species A and B, of species D and E, and of species G and H, then dividing by 3, the number of groups. This might be considered to be a comparison across genera. The second level, perhaps corresponding to a comparison across subfamilies, is even more arbitrary. It is composed of [(the average wing length of species A, B, C, D, and E) + (the average wing length of species F, G, and H)] / 2. Finally, the last-level value represents the average wing length of species A, B, C, D, E, F, and G.

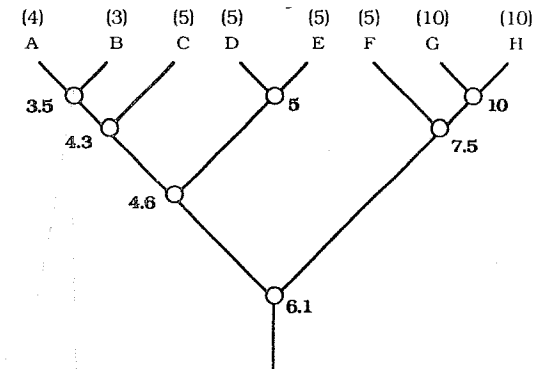


Fig. 9.10. Problems that can arise from averaging between sister groups on a phylogenetic tree. Letters = species. Values for the character wing length are plotted above each species. The differences in wing length demonstrated among members of this clade are postulated to be the result of a gradual progression of evolutionary modifications. Although the existing species demonstrate considerable overlap in wing length, all the ancestors in this group are hypothesized to have displayed different wing lengths.

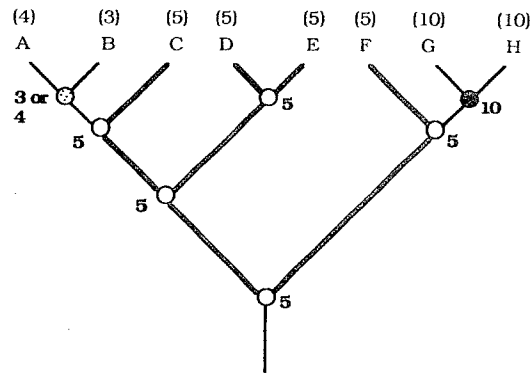


Fig. 9.11. Optimizing the values for a quantitative character on a phylogenetic tree. Letters = species. Values for the character wing length are plotted above each species. This analysis reveals a core of phylogenetic stasis (bold lines) and identifies the areas on the tree where substantial adaptive changes have occurred (in the ancestors of species A + B and species G + H).

retained by 50% of the clade (species C + D + E + F). There was one change from five to ten in the ancestor of species G + H, and two more changes in species A + B. The sequence of change in these latter two species cannot be resolved by optimization analysis alone. In general then, this example demonstrates that taxonomic averaging can potentially produce very misleading results, and sister-group averaging, while being the more preferable of the two methods, may obscure the historical background of adaptive change within a lineage. In this particular case it obscured the high degree of adaptive change in the ancestors of species A + B and species G + H, and overestimated the degree of adaptive change in all other lineages.

The above example uses hypothetical quantitative data that have been reduced to a single (e.g., mean or median) value for each species, which is then treated as a qualitative trait among taxa. We simplified the discussion by allowing many of the mean character values for the species to be the same. What do we do when all the values differ, and none of the character optimization procedures will work? A number of "averaging" methods have been proposed for optimizing quantitative traits (e.g., using median values, Farris 1970; using mean values, Huey and Bennett 1987), but at present there is no generally accepted approach among phylogeneticists (see Felsenstein 1988 for a review of methods). If a new spirit of cooperation and collaboration between ecologists and systematists emerges in the future, it would not surprise us to find that population biologists working on quantitative life-history traits will provide the insights necessary for phylogeneticists to develop general methods for optimizing quantitative traits.

The second general approach to studying phylogenetic effects on tests of

adaptation involves attempts to reduce spurious correlations due to phylogenetic constraints by removing these effects from the data set. Three statistical approaches have been developed to try to achieve this goal: an "independent contrasts" method (Felsenstein 1985; see also Sessions and Larson 1987), the use of nested analysis of variance (ANOVA) and analysis of covariance (ANCOVA; see Pagel and Harvey 1988), and the use of autocorrelation procedures (see Cheverud, Dow, and Leutenegger 1985; Gittleman and Kot 1990). Although we are not qualified to discuss the technical aspects of these statistical approaches, we can emphasize some points of similarity between this research program and historical ecology. Both of these evolutionary investigations require that we identify the phylogenetic components of diversity; therefore, both are subject to the same caveats with respect to phylogenetic analysis (see also Gittleman and Kot 1990; Burghardt and Gittleman 1990): (1) do not confuse similarity with relationship, (2) do not confuse plesiomorphy with apomorphy, (3) do not confuse taxonomy with phylogeny, and (4) do not confuse averaging with optimizing.

Many of the studies we have enumerated above begin with an explicitly historical step; they examine the best current estimates of phylogenetic relationships available. The second step should be an analysis of the sequence of character evolution *on the phylogenetic tree* (remember from chapter 2 that the transformation series for a given character may not correspond exactly to the phylogenetic pattern of diversification of the character). This is rarely done, however, often because explicit phylogenies are not available. As a result, there is no information available about the history of character associations (character associations that show similar correlations among extant species may have originated in a variety of different sequences), nor is there any way to distinguish phylogenetic correlations due to plesiomorphy from those due to apomorphy, or those due to homology from those due to homoplasy. The result is often more phenetic than phylogenetic, with similarity being equated with homology and relationship.

Historical ecologists attempt to identify phylogenetic effects and incorporate them into macroevolutionary explanations. The statistical research program attempts to identify and remove phylogenetic effects so they do not confound microevolutionary tests of adaptation. Ultimately, both programs are interested in producing a more rigorous set of adaptationist hypotheses, and from this a more robust theory of evolution. Fortunately there is enough overlap in these perspectives to promote the establishment of mutually beneficial cross-communication. For example, the first step in both programs is the identification of the phylogenetic constraint. What could be more robust than the simultaneous identification of the same qualities and quantities as the constraints? Communication between programs with different evolutionary viewpoints will enable us to address more empirically questions about the

relationship between microevolution and macroevolution. If we only discover the effects of history in a restricted class of qualitative characters, then we would be justified in assuming that such macroevolutionary patterns were of limited usefulness to discussions of evolutionary mechanisms. On the other hand, if phylogenetic effects are so pronounced even in quantitative life-history traits that they can confound purely microevolutionary studies, they might well be important aspects of evolutionary mechanisms. That is, if such effects are important enough to be partitioned out of some studies, they are important enough to be explained by general evolutionary theory. Every study that has investigated evolution within a historical framework has found evidence of the (often marked) effects of phylogenetic constraints.

How are we to explain the observation that contemporary evolutionary dynamics involve an interaction between constraints and adaptation? The extrapolationist view would suggest that today's constraints are simply yesterday's adaptations. If that is so, there must have been fewer constraints and more adaptation in the past than we now see, forcing us to conclude that phylogenetic effects should become even more pronounced in the future, at the expense of adaptive plasticity. However, it is difficult to reconcile this with the recognition that diversity of adaptations at the macroevolutionary level is conservative relative to phylogeny, while adaptive plasticity within populations of species remains relatively high. The nonextrapolationist view would suggest that evolution in the past comprised an interaction between constraints and adaptation just as it does today.

Our thought experiment with crabs, tide pools, and finches in chapter 1 demonstrated that, in some systems, we will be able to make better predictions by reference to history than to current environments, while in others, the environment will be more informative. Because of this, it is important that researchers do not feel obligated to choose between *either* history *or* adaptation when formulating evolutionary hypotheses. Since phylogenetic diversification is open-ended, *both* adaptations *and* constraints can accumulate over time. We can metaphorically view adaptations as the (ecological) tip of the iceberg of (genealogical) constraint (fig. 9.12). This metaphor gives us an important glimpse of the ecological insights that can be gained from the perspective of both the environment (adaptation) and the organism (constraint). In the next section we will address the question of how we might begin to integrate the metaphor that evolution results from an interaction between constraints and adaptation into general evolutionary theory.

Integrating Historical Ecology with General Evolutionary Theory

Evolutionary theory is experiencing a period of intensive reexamination. Some researchers assert that the synthetic theory of evolution, or neo-

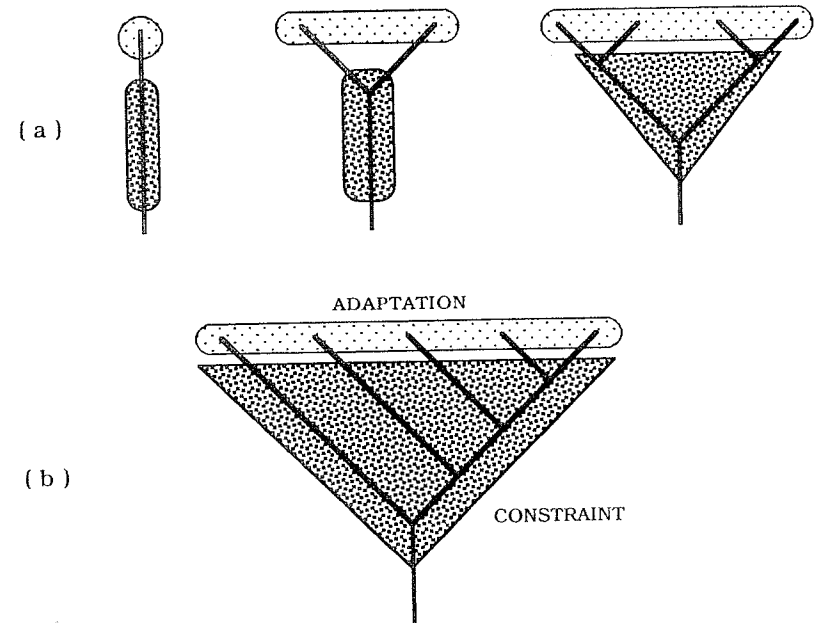


Fig. 9.12. The historical accumulation of adaptation (*light stippling*) and constraint (*dark stippling*) in the phylogenetic diversification of a group of species (*a*). Each species lineage is a mixture of ancestral traits (historical constraints) and adaptive changes. Speciation increases the number of species present, hence increasing both the constrained and the adaptive components of biological diversity. Adaptation is thus metaphorically the tip of the iceberg of constraints (*b*).

Darwinism, is essentially a complete theory (e.g., Stebbins and Ayala 1981; Charlesworth, Lande, and Slatkin 1982; Buss 1987). Others argue that there are gaps in the theory that can only be addressed by integrating traditional principles and research programs with new ideas. This is exemplified by recent texts and articles that promote attempts to “expand” (Gould 1980), “finish” (Eldredge 1985), “extend” (Wicken 1987), or “unify” (Brooks and Wiley 1988; Brooks, Collier, Maurer, Smith, and Wiley 1989) evolutionary biology. The mechanisms of evolutionary constraint are being examined on many levels, from phylogenetic to developmental (Alberch et al. 1979; Lauder 1981, 1986, 1988, 1989; Alberch 1982; Fink 1982; Charlesworth, Lande, and Slatkin 1982; Kauffman 1983; Buss 1987), to genetic (e.g., Kauffman 1974; Zuckerkandl 1976; Dover 1982), to those derived from basic physicochemical laws (e.g., Brooks and Wiley 1986, 1988; Kauffman 1986; Wicken 1987; Brooks, Collier, Maurer, Smith, and Wiley 1989; Weber et al. 1989). We believe that a richer theory, based upon the incorporation of microevolutionary and macroevolutionary information, is emerging from these debates. Historical ecology may play a role in this emergence because it provides us with

a way to integrate the study of macroevolution with the study of microevolution in a nonreductionist manner.

Throughout this book we have concentrated on the reconstruction and interpretation of macroevolutionary patterns without directly addressing the issue of underlying mechanisms. It is now time to ask, Is there any reason to believe that macroevolution is more than just "microevolution writ large"? Like many questions in science, researchers who have an opinion about the answer to this question find themselves in one of two philosophical camps. The "extrapolationists" believe that macroevolutionary patterns simply reflect the accumulation of a series of independent microevolutionary events over time (Eldredge 1985). The patterns may be real, that is, they may give us an accurate picture of part of the past, but they do not indicate the actions of macroevolutionary processes. Schoch (1986) suggested that three predictions could be drawn from this perspective: grades (paraphyletic groups) are real and discrete evolutionary units, speciation patterns are not correlated geographically, and ecology and behavior are better correlated with the local environment than with phylogenetic history. He then suggested that phylogenetic systematic research had largely refuted all three of these predictions, and the evidence presented in this book corroborates his assertion. The current data base thus supports the nonextrapolationist view that "something else" beside microevolutionary processes is going on in evolution.

Two general features of evolution that might conceivably fall under the heading of "something else" have emerged from our considerations of historical ecology. First, evolution results from an interaction of ecological and genealogical phenomena; ecological processes do not "cause" genealogy, nor is genealogy independent of the environment. Second, viewing biological systems on different temporal and spatial scales may produce very different pictures of evolutionary patterns and processes. In the remaining pages we will present a more detailed discussion of these two themes as our contribution to the ongoing study of macroevolutionary processes.

The Two Biological Hierarchies

Environmental and genealogical phenomena are intimately connected; therefore, it is difficult to disentangle "environmental effects" from "genetic (genealogical) effects" in evolutionary studies. This difficulty has prompted some authors to propose that two forms of hierarchically organized systems coexist in biology (Eldredge and Salthe 1984; Salthe 1985; Eldredge 1985, 1986; Brooks 1988b; Brooks and Wiley 1988; Brooks, Collier, Maurer, Smith, and Wiley 1989). The ecological hierarchy is an energy-flow system, manifested by patterns of energy and matter exchange between the organism and its environment. It is the hierarchy of biological classes, such as trophic levels or ecological associations (e.g., herbivore-crop, predator-prey, host-

parasite). Since any plant and any herbivore are sufficient to define an herbivore-crop association, the particular identities of the species involved is unimportant. The genealogical hierarchy is an information-flow system, manifested by genealogical relationships over short (genetic) and long (phylogenetic) time scales. It is the hierarchy of individuals. From the genealogical perspective identity is paramount. It does not matter what each species does so long as its members find resources sufficient for survival and perpetuation.

The relationship between the two hierarchies can be illustrated with the following sports metaphor: the ecological hierarchy establishes the dimensions of the playing field, while the genealogical hierarchy establishes the rules of the game being played. In other words, biological systems obey rules of self-organization transmitted genealogically (historically) and played out within environmentally defined boundaries. However, the genealogical processes that characterize life and evolution are autonomous enough from environmental conditions to be capable of overrunning available required resources and of changing the environment substantially. Because of this, the game may redefine the boundaries of the playing field and may be subsequently constrained by these self-imposed changes. For example, the evolution of photosynthetic prokaryotes from anaerobic ancestors resulted in increased oxygen content in the atmosphere. This increase, in turn, ultimately altered the diversity and distribution of anaerobic organisms, limiting them to relatively rare environments.

The ecological hierarchy is the means by which two different genealogies, or two different generations in one genealogy, can causally influence one another. We believe that this is the reason historical ecology is important to the development of evolutionary theory in general. The conservative nature of ecological diversification uncovered so far by historical ecological methods implies that adaptive processes act as cohesive rather than as diversifying forces in evolution. This, of course, begs the question of just what is the diversifying force. At the moment, the answer to this question remains widely and passionately disputed (see, e.g., Brooks and Wiley 1986, 1988; Brooks, Collier, Maurer, Smith, and Wiley 1989; Weber *et al.* 1989 and references therein).

Spatial and Temporal Scaling Effects

In the preceding chapters we have uncovered numerous examples of the ways in which the effects of temporal and spatial scaling shape our evolutionary perspective. One such example was considered without its temporal implications when we discussed methodology in chapter 2. The designation of plesiomorphic or apomorphic status to character states is a relative, not absolute, statement. All characters begin as evolutionary novelties (autapomor-

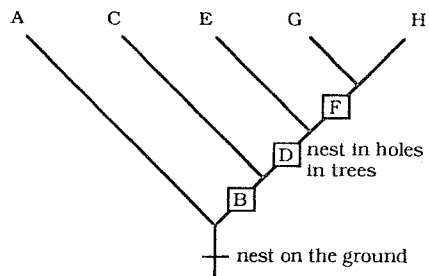


Fig. 9.13. The plesiomorphic or apomorphic status of a character is relative to the temporal scale of the investigation. There has been an evolutionary change from nesting on the ground to nesting in trees in this hypothetical clade of birds. Nesting in tree holes is an autapomorphy for species D, a synapomorphy for species D + E + F, and a plesiomorphy for species D + E + F + G + H.

phies) in a new species. If the species undergoes another speciation event before the character changes again, the character becomes a synapomorphy uniting the descendant sister species. If speciation continues in this lineage while the character remains unchanged, the character will come to be considered plesiomorphic for the group (fig. 9.13). This reemphasizes the basic phylogenetic assertion that only synapomorphies (homologies on an intermediate temporal scale) are useful for reconstructing phylogenetic relationships. Homologies on a small temporal scale (autapomorphies) or homologies on a large temporal scale (plesiomorphies) do not contain information useful to this reconstruction. In a similar vein, the difference between convergent and divergent adaptation is also dependent upon the temporal scale of the investigation. All convergent adaptation is the accumulation of parallel independent episodes of divergent adaptation between sister species (see *Montanoa* example in chapter 5; fig. 9.14).

We have discussed several instances in which the evolution of a particular association or portion of a biota might be explained by reference to a specific model of coevolution or community evolution, whereas the explanation for the evolution of associated clades or of entire biotas would invoke the influences of several such models. This implies that the kind of ecological associations, as well as the kinds of explanations relevant to studies of the evolution of those associations, depends on the temporal and spatial scale chosen by the researcher. The original concern of many evolutionary ecologists was to partition out the effects of different scales by adopting what Wiens (1984) termed a Goldilocks approach. That is, do not choose a scale so large that patterns will be influenced by phylogeny and other historical factors, but also do not choose a scale that is so small that no regularities of interest emerge.

Ricklefs (1987, 1990; see chapter 1) and Brown and Maurer (1989) have recently discussed the significance of scaling effects in explaining the struc-

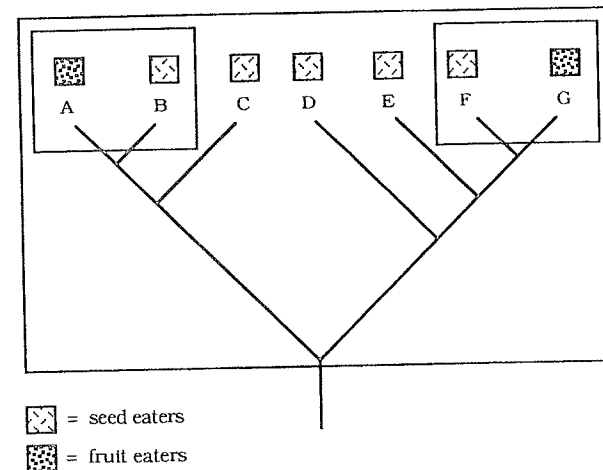


Fig. 9.14. Identification of convergent and divergent adaptation is dependent upon the temporal scale of the investigation. The change from eating seeds to eating fruit represents independent cases of divergent evolution between sister species A + B and sister species F + G. The temporal scale must be increased to include all the members of this clade before the convergent evolution of fruit eating in species A and G can be identified.

ture and evolution of biotas. Their approach differs from the original attitude adopted by evolutionary ecologists by virtue of fact that they wish to take such scaling effects into account and integrate them into ecological studies. On the systematic side, Brooks (1988b) recently suggested that phylogenetic studies in biogeography could be related to the biological relationships between phylogenetic (temporal) and spatial scaling effects. On the smallest spatial scales, biogeographic patterns result from microhabitat distribution and vagility of the organisms being studied. Increasing the power of the spatial telescope increases the number of species involved in the biogeographic tapestry until an intermediate level is reached where particular communities, ecosystems, or biotas form the threads of the pattern. The processes dominating these spatial scale patterns are species-composition phenomena such as immigration-emigration dynamics and biotic expansion and contraction. Finally, the entire tapestry is revealed on large spatial scales where groups of biotas compose the units of study. Since most species occur allopatrically from their closest relatives (see chapter 4), expanding the study area increases the likelihood that the relevant biogeographical patterns will involve groups of phylogenetically related species. Or, to put this another way, increasing the spatial scale chosen for observation of a biological system increases the influence of historical constraints (effects of the temporal scale) on the evolution of observed diversity and distribution patterns. Figure 9.15 presents a

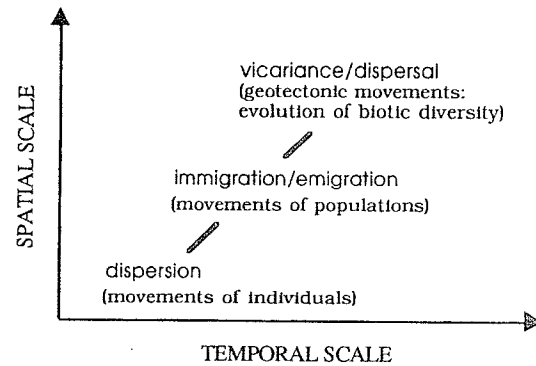


Fig. 9.15. Spatial and temporal scaling effects on biogeographical patterns. On the smallest scales, movements of individuals within populations are revealed, whereas on intermediate scales, movements among populations are important. It is only on the largest spatial and temporal scale that the evolution of biological diversity, resulting from the interaction between biotic dispersal and geographical changes, is observed. (Redrawn and modified from Brooks 1988b.)

heuristic view of biogeography unified by spatial and phylogenetic (temporal) scaling effects (Brooks 1988b). Analogous reasoning about the significance of scaling effects can be applied to studies of coevolution in an ecological context by substituting “hosts” or “other associated species” for “areas.”

Although heuristic, this diagram of the interaction between space and time in evolutionary processes produces two testable predictions: increasing the analytical spatial scale increases the likelihood of finding vicariant components in any patterns of ecological association; and if ecological associations reflect organized patterns of energy use, then the larger the space occupied by an association, the greater the proportion of phylogenetically determined energy-use patterns (Brown and Maurer 1987, 1989).

Both the phylogenetic and geographical scales determine what macroevolutionary regularities you will see. In chapter 4 we discussed a variety of modes of speciation. Every speciation event is the result of a single mode, but the evolution of a clade might well involve a variety of speciation modes. Hence, at the macroevolutionary level, we would ask questions about the relative frequency of modes of speciation. In addition, enlarging the phylogenetic and geographic scale of speciation studies allows us to ask questions about the relative frequency of cospeciation among clades (chapter 7). Similarly, there are a variety of adaptive modes (chapter 5) and models of coevolution (chapter 8), any number of which might be involved in the evolution and coevolution of a diverse group of species. Again, at the macroevolutionary level, we would ask questions about the relative frequency of adaptive changes or of different coevolutionary effects. Finally, individual species occurring in communities may correspond to as many as four different classes

of evolutionary patterns (chapter 8). Communities may differ macroscopically as a result of the differential degree of influence by these various effects (see also Emig 1985).

The preceding discussion highlights the most important aspect of scaling considerations: *there is no objective level of organization, time interval, or spatial interval for biological evolution.* A variety of evolutionary processes operate on all levels and at all scales; however, they do not all play equally important roles at all levels. Therefore, the macroscopic manifestations of evolutionary principles will differ depending on the window of observation (see also Salthe 1985). Gould (1982b) summarized this elegantly in his defense of the hierarchical approach to evolution.

We do not wish to advocate the despairing conclusion that micro- and macroevolution are absolutely separate in principle and that nothing about one illuminates the other. . . . Rather, the same processes of variation and selection operate throughout the hierarchy. But they work differently upon the varying materials (individuals) of ascending levels in a discontinuous hierarchy. . . . Important ties of feedback unite all levels, but new modes emerge at higher levels and reduction to natural selection upon organisms will not render all evolution. Nothing about microevolutionary population genetics, or any other aspect of microevolutionary theory, is wrong or inadequate at its level. Little of it is irrelevant to students of macroevolution. But it is not everything.

We agree with Gould's conclusion that microevolutionary processes, although important, are not the sole forces of evolution. They are currently high-profile processes because they dominate evolution on limited temporal and spatial scales, scales that are the most easily accessible windows of study for organisms with our biological and career life-span constraints. Processes relevant to evolution are either generative (originating or diversifying) in their effects, or conservative (maintaining or cohesive) in their effects. The interplay of diversity-promoting and diversity-limiting processes through time produces historically constrained order. Many processes affect biological systems, at all levels of organization and at all times, but their effects are often manifested on different time scales. Changes occurring on time scales shorter than speciation rates will appear as microevolutionary patterns; those occurring on time scales longer than speciation rates will appear as macroevolutionary patterns. **In this sense, macroevolutionary processes are neither reducible to, nor autonomous from, microevolutionary processes.**

The Hierarchy of Evolution: Looking through Windows of Time

The relationships among various components of evolutionary biology are depicted heuristically in figure 9.16. This figure summarizes our perspective

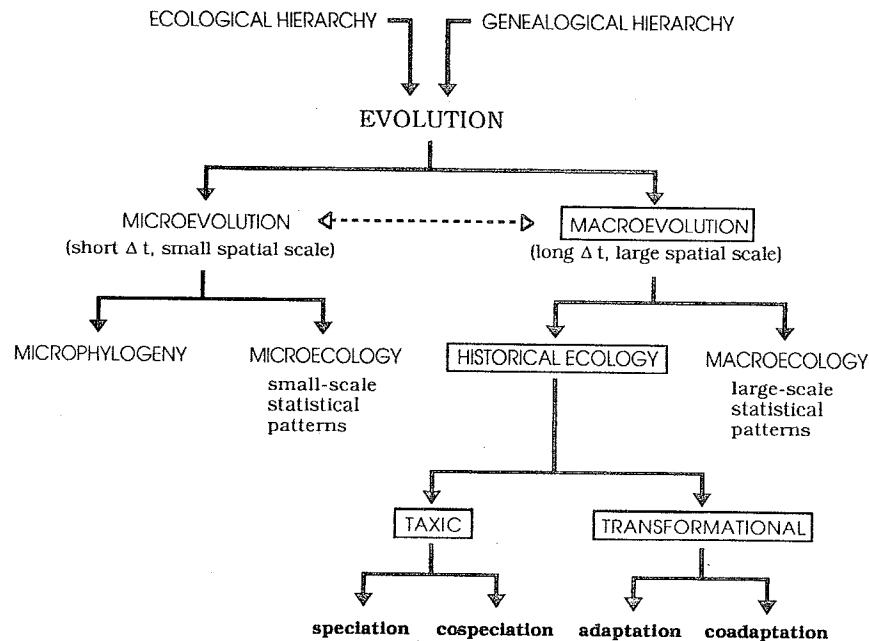


Fig. 9.16. Heuristic flowchart depicting the relationship of historical ecological research to various areas of evolutionary biology.

on the role and place of historical ecology within the evolutionary framework. Microevolutionary research emphasizes short time-scale and small spatial-scale evolutionary processes. It comprises two elements, one dealing with ecological factors, microecology, and the other with genealogical factors, microphylogeny. Microecology incorporates population ecology, ecological aspects of population genetics, and the statistical analysis of phylogenetic constraints on population-level adaptive processes. The results of microecological research are generally presented as statistical patterns on short time scales and small spatial scales. Studies of microphylogeny use historical reconstructions rather than statistical summaries to answer evolutionary questions at the population level. This category therefore includes population genetical studies of speciation and phylogenetic analysis based on population-level information (Avice 1989).

Macroevolutionary research is concerned with long time-scale and large spatial-scale evolutionary patterns and processes. Like microevolution, it incorporates both ecological and genealogical influences; however, the distinction between the two is somewhat blurred at this level. Students of macroecology (Brown and Maurer 1989) are primarily concerned with documenting the **statistical patterns** of spatial and resource allocation of energy use (e.g.,

Maurer and Brown 1988). Students of historical ecology are interested in uncovering the **phylogenetic patterns** of spatial and resource allocation of biological information. There are two classes of research programs within historical ecology. The taxic approach concentrates upon explanations of speciation and extinction rates and patterns. The transformational approach focuses upon adaptive changes in evolution. Investigations at the macroevolutionary level thus highlight the mutually dependent nature of interactions between ecological and genealogical factors.

Evolution is not a process, it is a result. When we document evolutionary change within any group of organisms, what we are really describing is the outcome of an interaction between a variety of processes. Darwin (1872:403) himself detailed the existence of several evolutionary "laws," including growth, the "correlation of parts," reproduction, variability in traits, competition, natural selection, character divergence, and extinction. These processes, in turn, are characterized by both the unique properties of the ecological and genealogical hierarchies and the properties arising from their interactions. Because of this, evolutionary explanations that do not consider all of these components are inherently incomplete.

Modern ecology, ethology, and systematics were founded upon the Darwinian tradition of integrating genealogical and ecological information into explanations of descent with modification. All these disciplines have drifted from this pathway, moving along a star burst of increasingly specialized and independent trajectories. However, evolution is more than the observations, results, and theories of any one discipline. In the past decade, we have finally come to the realization that questions of global diversity and global ecology are the concern of all people, so a reconciliation between these research programs is now critically important. This reconciliation can be accomplished by incorporating historical and nonhistorical, biological and nonbiological processes into our evolutionary perspective. Evolution binds all organisms in both a common hierarchy of life on this planet and a common hierarchy of processes shaping the universe. This "web of existence" is strongly influenced by the irreversible and indelible effects of time. Because of this, the potential of the future is hidden within the constraints of the past in biological systems. Uncovering, understanding, and preserving this potential will be the task of a coalition of evolutionary biologists working on all spatial and temporal scales.