

### Adaptive Radiations

When we examine populations within individual species, we generally discover extensive evidence of changes in gene frequencies correlated with environmental changes over relatively short time scales and relatively small spatial scales. The extrapolationist view of macroevolution is based upon the assumption that this degree of intraspecific adaptive plasticity can be smoothly extended to explain the degree of diversity among species within a clade. Futuyma (1986:32) defined adaptive radiation as "a term used to describe diversification into different ecological niches by species derived from a common ancestor." This concept has played an important role in evolutionary biology, as an explanation for differences in species richness among groups. Such differences are postulated to result from unusually high speciation rates in the more speciose group. Some authors have suggested that there should be an adaptive explanation for all speciation events (Stanley 1979; Stanley et al. 1981). Simpson (1953) believed that adaptive radiations resulted from diversification accelerated by ecological opportunity, such as dispersal into new territory (see peripheral isolates allopatric speciation in chapter 4), extinction of competitors, or adoption of a new way of life (i.e., an adaptive change in ecology or behavior). Other factors, including the adoption of a specialist foraging mode (Eldredge 1976; Eldredge and Cracraft 1980; Vrba 1980, 1984a,b; Cracraft 1984; Novacek 1984; Mitter, Farrel, and Wiegemann 1988), sexual selection and population structure (Spieth 1974; Wilson et al. 1975; Carson and Kaneshiro 1976; Ringo 1977; Templeton 1979; Gilinsky 1981; West-Eberhard 1983; Barton and Charlesworth 1984; Carson and Templeton 1984), or the origin of key ecological innovations in an ancestral species (Cracraft 1982a; Mishler and Churchill 1984; Brooks, O'Grady, and Glen 1985a), have also been postulated to have a positive effect on speciation rates. The consensus view of adaptive radiations today remains one with emphasis on "adaptive" (Futuyma 1986:356):

a lineage may enter an adaptive zone and proliferate either because it was pre-adapted for niches that became available, or because it evolves "key innovations" enabling it to use resources from which it was previously barred.

Nevertheless, some authors have argued that differential rates could emerge naturally from a stochastic model of speciation. (Raup et al. 1973; Raup and Gould 1974; Gould et al. 1977).

Radiations, whether "adaptive" or not, can only be distinguished on the macroevolutionary level of analysis. At the moment, however, there have been relatively few discussions about the patterns that should identify such radiations. Because of this, it is difficult to objectively examine the potential influences of various adaptive, geological, or stochastic factors on changes in

speciation rates. Historical ecology, with its emphasis on macroevolutionary patterns, offers a solution to this problem. Armed with a set of explicit criteria for recognizing an adaptive change, we can search for historical coupling between high speciation rates and one or more of these criteria. Such a discovery would corroborate the hypothesis that a given radiation was, in fact, adaptive.

### Adaptive Radiations in Ecological Preferences

The search for rigorous criteria by which we can document such radiations is a relatively new one. Ross (1972a) used the following ecological criteria when discussing the adaptive radiation of a variety of insect groups: (1) geographic dispersal from the primitive climatic zone to a derived one, and (2) shifts from the plesiomorphic condition to any apomorphic state in ecological life-history traits, behavior, and host preference. Based on the discovery that only approximately one out of every thirty speciation events in these groups was correlated with some form of ecological diversification, Ross concluded that adaptive changes (in any of the above characters) were consistent with, but much less frequent than, phylogenetic diversification. Furthermore, he felt that there were no predictable patterns explaining the shifts that did occur and suggested that ecological diversification in evolution comprised a biological "uncertainty principle." This interpretation was certainly at odds with hypotheses of ecologically driven phylogenetic change.

*Where, and on whom, do parasitic wasps prefer to lay their eggs?*

The Labeninae are a monophyletic group of ichneumonid hymenopterans (parasitic wasps) residing mainly in Australian and neotropical regions. Based upon a phylogenetic analysis of adult morphological characters, Gauld (1983) recognized four monophyletic groups as tribes within the subfamily. He then examined the distribution of two ecological characters on the phylogenetic tree (fig. 5.30).

Members of the tribe Labenini display the plesiomorphic condition for both characters, oviposition through lignified tissue and development of the larvae on coleopteran hosts. The Groteini retain the plesiomorphic oviposition-site preference, but the host chosen by all members has switched from beetles to bees (one group on ground-nesting bees, another on stem nesters). Divergence within the Poecilocryptini has involved switches in both host and oviposition-site preferences. *Poecilocryptus* retains the plesiomorphic oviposition site but attacks gall-forming insects, while species in the anomalous genus *H* retain the plesiomorphic attachment to beetle larvae, but have changed their oviposition site from wood to seeds. Finally, members of the Brachycyrtini display derived conditions in both characters. All species in

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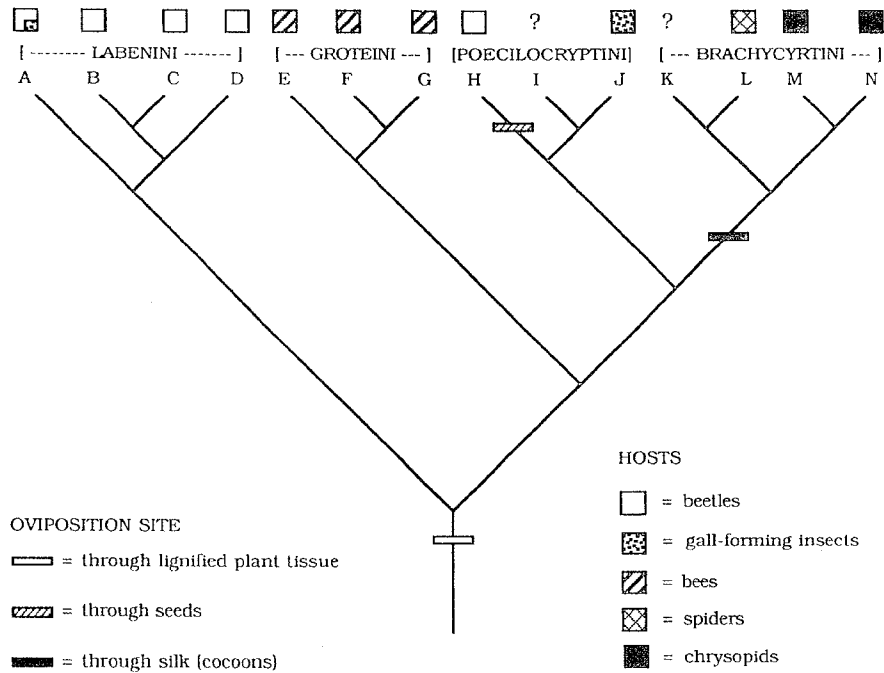


Fig. 5.30. Phylogenetic tree for parasitic wasps of the subfamily Labeninae, with the distribution of oviposition-site-preference and host-preference characters. A = *Labena*; B = *Asperellus*; C = *Certonotus*; D = *Apechoneura*; E = *Labium*; F = *Macrogrotea*; G = *Grotea*; H = genus A; I = genus U; J = *Poecilocryptus*; K = *Pedunculus*; L = *Adelphion*; M = *Habryllia*; N = *Brachycyrtus*. The general types of preferred host, represented in boxes atop the taxa names, have not been optimized onto the tree because data are missing for several genera. (Redrawn and modified from Gauld 1983.)

this tribe oviposit through silk cocoons, with the choice of host varying according to the genus of wasp. *Habryllia* and *Brachycyrtus* are united in their preference for chrysopid cocoons, while some species within the genus *Adelphion* develop in spider egg sacs. The evolutionary divergence of these parasitic wasps thus appears to involve a combination of (1) phylogenetic constraints, indicated by conservative changes in oviposition-site preferences, as only two changes, from lignified tissue to seeds and from lignified tissue to silk, have been documented in the entire subfamily, and (2) potential adaptive radiation of the genera due to switches in host preference. These changes, although quite extensive, are congruent with the phylogeny proposed for the wasps and demonstrate some historical influence on a general "host type" level. For example, all members of the Labenini develop on some type of coleopteran larvae, a pattern that is paralleled in the Groteini (bee larvae) and the *Habryllia* + *Brachycyrtus* clade (chrysopid cocoons).

The preceding study corroborates Ross's observations of a high degree of phylogenetic concordance and conservatism in ecological diversification within, at least, the Insecta. Andersen (1982) reported similar findings in a study of the Gerromorpha, a large group of semiaquatic hemipteran insects. Erwin (1985) extended the line of thinking represented by the above investigations to include yet another group of insects, the incredibly species-rich carabid beetles. Coupling the observed phylogenetic conservatism in ecological traits with a hypothesized high number of peripheral isolates allopatric speciation events in that group, Erwin proposed a macroevolutionary model called the "taxon pulse" to explain their adaptive radiation. Under this model, a group of beetles begins with an ancestral species displaying a certain ecological propensity. As time progresses, the ancestor and its descendants spread over a larger and larger geographical area, with descendant species fulfilling the same or very similar ecological roles in different locations. Subsequent to this first wave of dispersal, a new ecological trait arises in one of the descendant species in one of the localities. The species bearing this novel trait then undergoes widespread dissemination and a new "pulse" of diversity occurs, producing a new set of descendant species, all performing similar functions in different locations. Diverse and highly structured communities of carabid beetles could be formed in many different areas in this manner, with every community containing a member of each of the "pulses." According to this model, the number of "occupied niches" within a community would correspond to the number of pulses represented by the beetles present (see Roughgarden and Pacala 1989 for a similar example using anoline lizard communities on Caribbean islands).

#### Adaptive Radiations in Life Cycle Patterns

Brooks, O'Grady, and Glen (1985a) modified Ross's macroevolutionary criteria of adaptive radiations to include the diversification of life cycle patterns. According to this proposal, any phylogenetic diversification in ecological or behavioral traits, or in developmental characters relevant to the successful completion of the life cycle, were considered evidence of adaptive change. In other words, studies of adaptive radiations should focus on assessing the degree of diversification in ecological and reproductive strategies. A similar proposal was made by Duellman in a study of the diversification of reproductive modes among frogs.

#### Adaptive radiation in a free-living group: reproductive modes in frogs

Duellman (1985) examined frog breeding systems within a phylogenetic context. Based on a combination of oviposition site, parental care, and developmental characters, he identified twenty-nine reproductive modes among

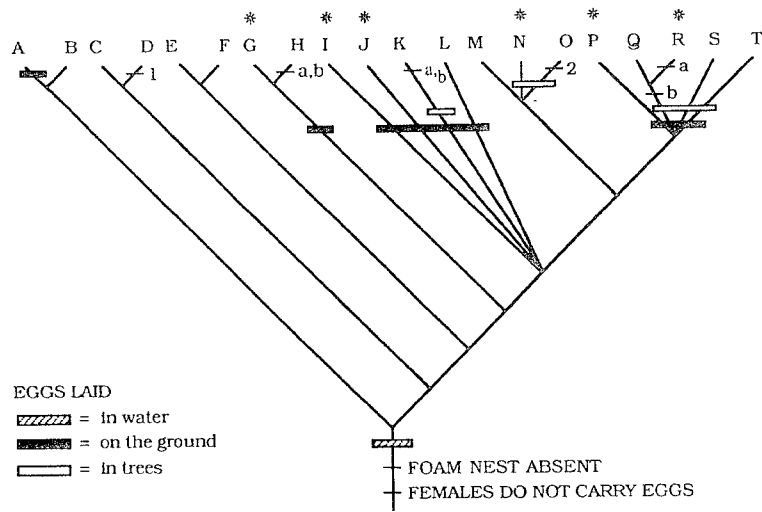


Fig. 5.31. Phylogenetic tree of major anuran family groups, mapping reproductive modes. A = Leiopelmatidae; B = Discoglossidae; C = Rhinophrynidae; D = Pipidae; E = Pelobatidae; F = Pelodytidae; G = Sooglossidae; H = Myobatrachidae; I = Brachycephalidae; J = Rhinodermatidae; K = Leptodactylidae; L = Bufonidae; M = Pseudidae; N = Centrolenidae; O = Hylidae; P = Dendrobatidae; Q = Hyperoliidae; R = Rhacophoridae; S = Microhylidae; T = Ranidae. Two general characters are represented. Type of female egg carrying: 1 = aquatic; 2 = terrestrial. Type of foam nest: a = aquatic; b = terrestrial. \* = no members lay their eggs in water. The plesiomorphic conditions for these characters are mapped on the stem of the tree.

twenty anuran family groups (fig. 5.31). Six of the families are characterized by the possession of only one mode. The rhinophrynids (C), pelodytids (F), and pseudids (M) possess the primitive strategy “deposit eggs free in ponds/feeding tadpoles develop in ponds.” The remaining three families each exhibit a different derived mode associated with the deposition of terrestrial eggs. Eggs of the brachycephalids (I) develop directly into froglets; dendrobatid (P) adults carry their newly hatched, feeding tadpoles to water; and the tadpoles of centrolenids (N) fall out of their arboreal hatching place into (with luck) an underlying pond or stream. The other fourteen families comprise species exhibiting more than one mode.

When the twenty-nine strategies are optimized onto the phylogenetic tree for the frog families (Duellman and Trueb 1986), a consistency index of only 36% is achieved. This indicates a great deal of convergent evolution of reproductive strategies at the family level. However, this convergence is not totally random; it has been played out against a phylogenetic background. As mentioned previously, three of the twenty families display only the plesiomorphic reproductive mode. Interestingly, none of the suprafamilial (nonterminal)

branches on the phylogenetic tree are characterized by any evolutionarily derived reproductive strategy, suggesting that much of the early radiation of frogs occurred in the context of “eggs and tadpoles in ponds/no parental care.” This suggestion is corroborated by the fact that all members of the Pseudidae, one of the most recently derived groups, retain this plesiomorphic reproductive mode, while thirteen of the twenty families contain members displaying this strategy. Subsequent to the radiation of the ancestors of the frog families bearing this initial reproductive strategy, there has been an evolutionary “drive” in several families towards placing the eggs out of water; in fact, six of the families have severed the association between egg laying and water altogether (marked with an asterisk in fig. 5.31). This movement onto land has been coupled with a great amount of divergent and convergent adaptive change. This adaptive radiation is particularly pronounced in the myobatrachids (H) and in seven of the twelve most recently derived frog families, the leptodactylids (K), bufonids (L), hylids (O), hyperoliids (Q), rhacophorids (R), microhylids (S) and ranids (T). However, just to reinforce the background of phylogenetic constraints, the majority of the species in all these families except the Leptodactylidae exhibit the plesiomorphic reproductive mode. Within the leptodactylids, the majority of species outside the genus *Eleutherodactylus* exhibit the plesiomorphic reproductive mode, while within *Eleutherodactylus* there are a variety of derived reproductive modes. Because *Eleutherodactylus* is the most species-rich vertebrate genus, comprising more than half the members of the family Leptodactylidae, we cannot say that most leptodactylids exhibit the plesiomorphic reproductive mode.

Divergent adaptive change is suggested by the appearance of eleven reproductive modes, which are each restricted to members of a single family. Seven of these changes involve the appearance of some form of parental care: two modes in the pipids (involving eggs embedded in the dorsum of the female), three modes in the hylids (the eggs carried by the female), and one mode each in the myobatrachids (the eggs swallowed by the female) and the discoglossids (the eggs carried by the male). The remaining four divergences involve changes in the aquatic oviposition site from ponds to either small basins (hylids) or to water in tree holes or aerial plants (microhylids), the appearance of foam-nest-building behavior in pools (myobatrachids), and the appearance of viviparity (bufonids). Convergent adaptive change is suggested by the independent appearance of twelve reproductive modes in several families. In contrast to the predominance of parental care behaviors within the divergent radiation category, this category is primarily associated with changes from aquatic to terrestrial oviposition site and the concomitant modifications in development. Of these twelve convergences, one (ovoviviparity) is shared between two families; six (various changes in oviposition or foam-nest site/development) are scattered among three different families; one (car-

ying tadpoles to the water) is exhibited by four families; two (changes in oviposition site/development) are found in five different families; one (direct development of terrestrial eggs) is shared among eight families; and one (eggs and tadpoles in streams rather than ponds) is scattered among nine families.

In summary, the distribution of these reproductive modes across the families of frogs supports the interpretation of an interplay between phylogenetic constraints and adaptive radiation in these animals. Six families display only one reproductive mode and have not undergone widespread speciation. At the other end of the spectrum, the eight most species-rich families are characterized by either widespread convergent adaptation (leptodactylids, hyperoliids, rhacophorids, and ranids) or a combination of widespread convergence and the appearance of novel parental-care behaviors (myobatrachids, bufonids, hylids, and microhylids).

*Adaptive radiation in a parasitic group:  
life cycle patterns in digeneans*

Every student who has ever taken a course in parasitology has been left reeling by a seemingly never-ending procession of life cycle descriptions. It seems that every single species of parasitic organism has evolved a unique life cycle pattern that is specifically designed to enhance the chances that the parasite and its offspring will be able to bedevil hosts and students for all of eternity. In the following discussion, we will provide some evidence that the evolution of life cycle patterns in the parasitic flatworms conforms to the major postulates of this chapter. First, these life cycle patterns have been assembled in a historically coherent sequence. Second, the transformations in life cycle patterns, like other aspects of ecological evolution, are more conservative phylogenetically than is morphological diversification. Third, because the life cycles have been assembled piecemeal, rather than arising *de novo*, different components in the evolution of the life cycle patterns are detectable only at particular phylogenetic (temporal) scales. And fourth, in the absence of outgroup comparisons and explicit phylogenetic hypotheses, it is possible to make mistakes about evolutionary transformations (e.g., "simple" does not always mean "primitive"). We also hope to convince you that host-parasite systems are widely represented in this book because they are good general models for studies in evolutionary biology (not because DRB is fixated on life cycles).

Price (1980) stated that no groups of free-living organisms exceed parasitic organisms in the extent of their adaptive radiation. If this is true, parasitic taxa should be good model systems for studying adaptive evolution. Brooks, O'Grady, and Glen (1985a) and Brooks, Bandoni, Macdonald, and O'Grady (1989) presented phylogenetic systematic studies of sixty-three major family

groups of the most handsome of flatworms, the digenetic trematodes, or flukes. Besides being an integral part of every first-year biology laboratory (recall *Fasciola* and *Clonorchis*, the liver flukes), digeneans are one of the most extensively studied parasite groups in existence. Second only in abundance and distribution to the species-rich nematodes, they inhabit a wide range of vertebrates, preferring sites such as the intestine, liver, lungs, or circulatory system of their hosts. The morphological data base for the phylogenetic analysis of the group comprised 180 characters, which supported a phylogenetic tree with a consistency index of 75%. The variety of life cycle patterns exhibited by digeneans has been the focus of discussions about the adaptive radiation of the group. It was generally believed that this diversification, as a reflection of adaptive responses, should be more closely related to the ecology of individual species than to their phylogeny. Brooks, O'Grady, and Glen (1985a) investigated this prediction within a phylogenetic context. They considered five classes of life cycle attributes: developmental changes in invasive larvae that increased the numbers of such colonizing stages; changes in preferences for the first intermediate host, the second intermediate host, and the final host; and changes in the mode of infection of the second intermediate host (a reflection of juvenile colonization ability). The outcome of this investigation is depicted in figure 5.32.

In contrast with the anuran example, derived changes in life cycle characters for the digeneans are not concentrated within family groups. Rather, they appear interspersed throughout the more basal (suprafamilial) branches of the phylogenetic tree. This conforms more closely to Ross's (1972a,b) observations, indicating that diversification in life cycle patterns occurred relatively sporadically during the early evolution of the digeneans. However, there is once again a strong phylogenetic background to this evolutionary change. Only a small proportion (about 28%) of the branchings on the phylogenetic tree are correlated with any diversification in these life cycle characters. The modification of life cycle patterns is therefore more conservative than phylogenetic diversification at the family level. Studies at the genus and species levels indicate that the conservatism in the evolution of life cycle patterns is even more pronounced than the family-level analysis would suggest (Brooks and Overstreet 1978; Brooks 1980b; Brooks and Macdonald 1986; Macdonald and Brooks 1989).

Furthermore, the diversification of digenean life cycle patterns is more closely correlated with phylogeny than were the reproductive modes for frogs (see fig. 5.33). There is a historically coherent sequence of elaboration of life cycles at this level of phylogenetic analysis that explains much of the diversity of digenean life cycle patterns. Interestingly, most of the diversification appears to have been initiated by evolutionary changes in the cercarial stage. The cercaria is a juvenile stage that develops in the molluscan intermediate

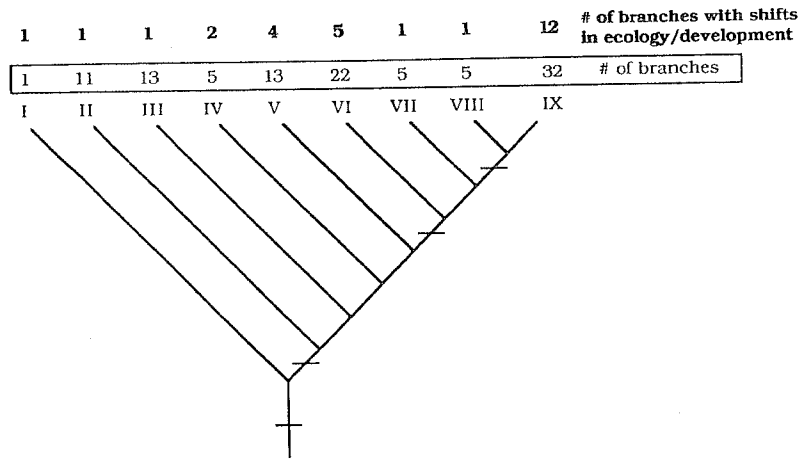


Fig. 5.32. Phylogenetic tree for nine orders of digenetic trematodes. *I* = Heronimiformes (1 family); *II* = Paramphistomatiformes (6 families); *III* = Echinostomatiformes (7 families); *IV* = Haploporiformes (3 families); *V* = Hemiuriformes (7 families); *VI* = Strigeiformes (12 families); *VII* = Opisthorchiiformes (3 families); *VIII* = Lepocreadiiformes (3 families); *IX* = Plagiorchiiformes (23 families). Numbers above each order indicate the number of evolutionary changes in five classes of life cycle traits, discussed in text, and the total number of terminal (family) and nonterminal branches within each order. Slash marks on nonterminal branches of the phylogenetic tree indicate additional points of diversification in life cycle traits for this group. Of the 115 branches on the phylogenetic tree, 32 (28%) are associated with some form of diversification in life cycle patterns. (Brooks, Bandoni, Macdonald, and O'Grady 1989.)

host and becomes infective to the second intermediate host (or sometimes to the final, definitive host). When cercariae began emerging from their molluscan hosts and encysting on vegetation and animal exteriors (most often on the exoskeletons of aquatic arthropods), the range of potential vertebrate hosts was enlarged greatly. No longer would trematodes be restricted to molluscivores. When the cercariae began penetrating particular intermediate hosts and encysting within them, a high degree of specificity in type of second intermediate host emerged, possibly enhancing adaptive modes of speciation. The evolution of cercarial emergence and the evolution of cercarial encystment and penetration therefore had significant adaptive consequences. The general evolutionary trend in the case of the digeneans appears to have been from relatively simple to relatively complex life cycles. Departures from congruence are due primarily to the reappearance of plesiomorphic life cycle patterns in relatively derived groups, generally involving the secondary loss of a host (see Brooks, O'Grady, and Glen 1985a). Overall, the diversification of life cycle patterns for this group of parasitic organisms appears to have been much slower than the evolution of individual species. We can gain additional insights into the evolutionary assemblage of life cycle patterns by examining

the larger clade within which the digeneans are nested. Three plesiomorphic life cycle traits are listed at the base of the phylogenetic tree for the flukes (fig. 5.33): a mollusc first intermediate host, a vertebrate final host, and endoparasitic, rather than ectoparasitic, adults. Where did these traits originate?

The digeneans belong to a larger group, called the Cercomeria (Brooks, 1982, 1989a,b; Brooks, O'Grady, and Glen 1985b), which encompasses the major groups of parasitic flatworms (including flukes and tapeworms). Within this group, the simplest life cycle is displayed by the monogeneans. Adult monogeneans live on the exterior of their vertebrate hosts and transmit their offspring directly to another vertebrate, where they mature and begin the cycle again. Among parasitologists, it has often been considered axiomatic that simple life cycles are more primitive than complex life cycles (cf. fig. 5.33). By that reasoning the one-host/direct-transmission pattern dis-

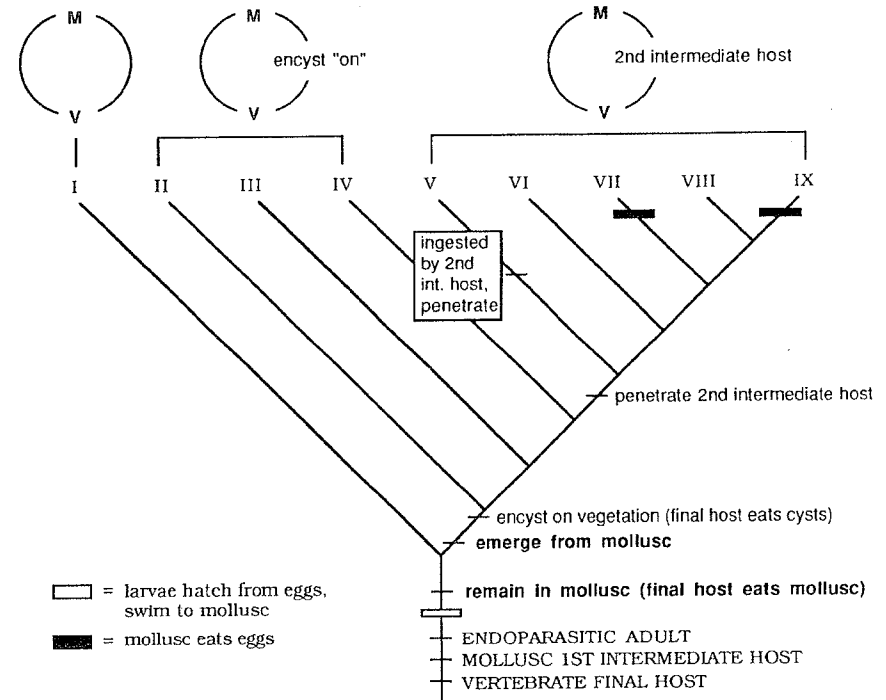


Fig. 5.33. Phylogenetic diversification in life cycle patterns for digenetic trematodes. Summary of the degree that can be explained by ordinal- and supraordinal-level phylogenetic relationships. Orders of digeneans: *I* = Heronimiformes; *II* = Paramphistomatiformes; *III* = Echinostomatiformes; *IV* = Haploporiformes; *V* = Hemiuriformes; *VI* = Strigeiformes; *VII* = Opisthorchiiformes; *VIII* = Lepocreadiiformes; *IX* = Plagiorchiiformes.

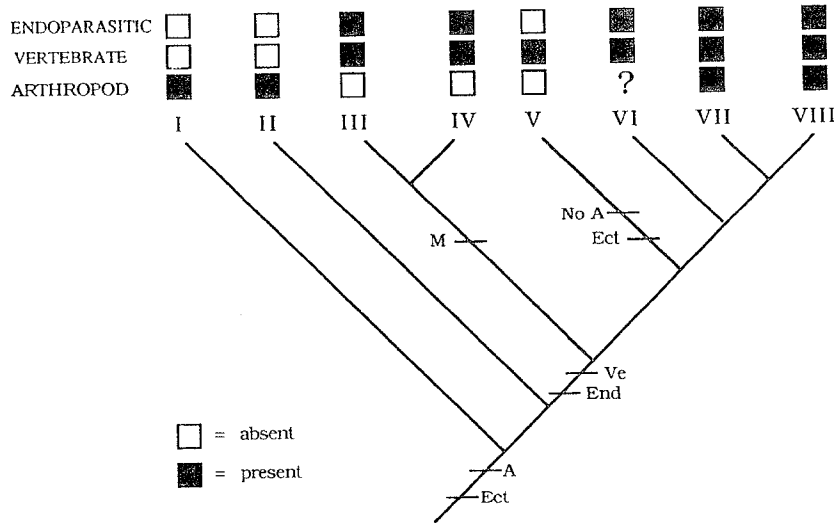


Fig. 5.34. Phylogenetic patterns of diversification of life cycle patterns among major groups of cercomerian platyhelminths. I = Temnocephalidea; II = Udonellidea; III = Aspidobothrea; IV = Digenea; V = Monogenea; VI = Gyrocotylidea; VII = Amphilinidea; VIII = Eucestoda. Boxes above taxa indicate distribution of traits for three components of life cycle patterns. Top row: white boxes = adults ectoparasitic; black boxes = adults endoparasitic. Middle row: white boxes = no vertebrate host; black boxes = vertebrate host. Bottom row: white boxes = arthropod host; black boxes = molluscan host; ? = presence or absence, and type, of invertebrate host unknown. Slash marks on tree, and accompanying abbreviations, summarize phylogenetically the data presented in the boxes. A = arthropod host acquired (primitive one-host ectoparasitic life cycle); V = vertebrate host acquired (primitive two-host endoparasitic life cycle); M = molluscan host acquired in exchange for arthropod host (derived two-host life cycle); No A = arthropod host lost (derived one-host life cycle); Ect = ectoparasitic adult; End = endoparasitic adult.

played by monogeneans would be considered plesiomorphic among flatworms parasitizing vertebrates. According to that hypothesis, the addition of intermediate hosts, and the appearance of endoparasitic modes of life, have been independently derived by the digeneans and the tapeworms from this primitive pattern.

Figure 5.34 suggests an alternative interpretation. To begin with, the plesiomorphic life cycle pattern for all the parasitic flatworms appears to be one in which an arthropod is used as the only host by an ectoparasitic species (see the Temnocephalidea [I] and Udonellidea [II] in fig. 5.34). The pattern became more complicated in the ancestor of the trematodes + cercariforms, as a vertebrate host was added and the adult parasites became endoparasitic. At this level, then, the basal life cycle pattern involves an arthro-

pod intermediate host plus a vertebrate final host, with the adult parasite living endoparasitically in the vertebrate. The current information on life cycle patterns in the gyrocotylids + amphilinids + tapeworms (a group called the Cestodaria) suggests that most of them have retained this primitive life cycle pattern. The trematodes (III + IV) display one variation on this central life cycle theme: in their ancestor, a molluscan host was substituted for an arthropod host. Finally, we come back to the monogeneans. Figure 5.34 suggests that the monogeneans [V] have a highly derived life cycle pattern, in which both the arthropod intermediate host and the endoparasitic life style have been lost. Virtually every discussion of the evolution of life cycle patterns in parasitic flatworms has assumed that the life cycle pattern displayed by monogeneans is primitively simple. The discovery that these flatworms display a *secondarily* simplified life cycle pattern forces parasitologists to rethink long-established assumptions and evolutionary scenarios.

### Adaptive Radiations and Species Richness

We might also consider another perspective on adaptive radiations. It is possible that adaptive changes early in the ancestry of a group might constitute a productive theme that led to unusually high speciation rates and survival (i.e., low extinction rates) in descendant species. The result would be a species-rich clade whose members share a plesiomorphic trait that could explain the group's success. Studies along these lines would concentrate on finding "key innovations" that arose in one lineage and are correlated with an unusually high diversity in that lineage compared with its sister group (Cracraft 1982a,b). This line of research would also help provide a bridge between the taxic and transformational views of macroevolution.

Larson et al. (1981) proposed that speciation rates in clades could be regulated by the appearance of particular key innovations or evolutionary novelties in ancestors that give the descendant species in the clade an advantage over competitors. Traditionally, a key innovation was considered to be any novel feature that characterizes a clade (i.e., any synapomorphy) that is proposed to be correlated with the adaptive radiation of the clade (Mayr 1960; Liem 1973). The possession of this novelty alone was thought to be necessary and sufficient to explain the adaptive radiation of the clade. Liem (1973), for example, suggested that the extensive diversification of cichlid fishes in the African Rift lakes was due to the origin of a lower pharyngeal jaw suspended in a muscular sling in their common ancestor. Lauder (1981; see also Liem and Wake 1985 and Stiassny and Jensen 1987) discussed several reasons for caution in applying this concept for explanations of adaptive radiations. First, each ancestral branch on a phylogenetic tree may be characterized by more than one apomorphic trait. Hence, there is no a priori way to determine which

of those traits would be “the” key innovation (perhaps even a combination of traits could be the innovation). Second, there is rarely strong evidence about the manner in which the trait considered to be the key innovation enhances speciation rates (or reduces the likelihood of extinction) in the clade. And finally, if the key innovation arose only once in evolution, how are we to test whether the putative key innovation confers a competitive advantage in all cases? As we have noted previously, our hypotheses of adaptation are strongest when we can compare convergent acquisition of traits under similar environmental conditions. Once again, historical ecological methods can help set the stage for more detailed studies.

*Why are there so many species of digeneans and so few species of aspidobothreans?*

As we discussed above, the digeneans are the sister group of the aspidobothreans. Both groups share an ancestral life cycle pattern involving a molluscan and a vertebrate host (fig. 5.34). As sister groups, both lineages are the same age, and as monophyletic groups, both are evolutionary units. However, there are fewer than five hundred described species of aspidobothreans and more than five thousand species of digeneans. Why the disparity in species richness? We have already discovered that the radiation of the digeneans was more strongly associated with developmental, rather than ecological or behavioral, diversification (figs. 5.32 and 5.33). In the aspidobothreans, larvae hatch from eggs and develop directly into juveniles in the molluscan host, are then ingested by a mollusc-eating vertebrate, and develop to the adult state. Hence, each embryo potentially can give rise to a single adult. Digeneans are characterized by a series of complex developmental stages in the molluscan host, at least one (and usually two) of which produce a large number of cloned larvae or juveniles (depending on the species and the stage). The reproductive potential of a single digenean embryo may exceed ten thousand adults, in contrast to the single individual produced by each aspidobothrean embryo. Although the changes in the ancestral digenean that are correlated with the high success of digeneans relative to their sister group were developmental rather than ecological (effect macroevolution rather than species selection), they were certainly adaptive and resulted in a markedly greater diversity for the digeneans. Significantly, this radiation was enhanced by further developmental changes within the digeneans themselves (see fig. 5.33).

***A Last Look at Adaptive Radiations***

It is clear that the term “adaptive radiation” means different things to different people. To some, it has been virtually synonymous with speciation. To others, it involves an association between overall diversification and adaptive

changes in ecological and behavioral characters, as well as a high degree of homoplasious phenotypic change. Coddington (1988) expanded the criteria for assessing adaptive evolution to incorporate functional morphological as well as ecological information. His study added the following general criteria to the list of “ways to recognize an adaptive radiation”: (1) the appearance of homoplasy correlated with functional change on a phylogenetic tree, (2) the appearance of predicted homoplasy correlated with predicted functional changes, and (3) the appearance of particular structural change correlated with particular functional change, regardless of homoplasy. Lauder and Liem (1989) suggested an experimental approach to testing hypotheses of this form of adaptive radiation. Their approach examines patterns of structural diversification throughout particular clades, thus equating adaptive radiation more with degree and extent of structural diversification than with speciation rates per se. They also emphasize the importance of having a causal model that predicts what the relationship should be between possession of an innovation and the pattern of structural diversification in a clade, in order to recognize particular synapomorphies as key innovations.

“Adaptive radiation” may also mean different things to different groups of organisms. For example, consider the insects, the frogs, and the digeneans presented in this chapter. In each case, a unique combination of phylogenetic conservatism and adaptive innovation has contributed to the contemporaneous diversity of these organisms. Much of early frog evolution occurred in species bearing the initial reproductive strategy “deposit your fertilized eggs in ponds/leave the tadpoles to fend for themselves.” Diversification in reproductive modes apparently arose subsequent to this *radiation* by the ancestors of the frog families. By contrast, ecological changes appear to have occurred relatively early in the diversification of many insect groups. The evolution of digenean life cycles illustrates yet another pattern, in which episodes of ecological change are sprinkled throughout the phylogenetic tree. Given the new evolutionary insights uncovered from just three studies, what treasure troves are in store for us, buried within the phylogenetic histories of the cichlid fishes in African Rift lakes, the gammarid amphipods in Lake Baikal, the Hawaiian honeycreepers, or the Galapagos finches?

**A Comment on Transformational Aspects of Macroevolution**

The examples we have presented indicate that ecological and behavioral diversification within clades lags behind phylogenetic diversification of clades. Interestingly, this mirrors the information provided in the fossil record (Bakker 1983).

The fossil record of mammals shows that stasis for  $10^5$  or  $10^6$  generations is the rule, not the exception, for species . . . and that in many cases chronic stasis preserved phenotypes probably very far

from the optimal compromise possible within the given habitat. Ever since Darwin, most evolutionary theory has concentrated on providing explanations of why populations should evolve. The fossil record demands more emphasis on explaining why populations do not evolve. . . . Perhaps, as a complement to our Society for the Study of Evolution, we need a Society for the Study of the Prevention of Evolution, to explore explanations of the apparent rarity of major adaptive change.

So, in contrast to the expectations of the extrapolationist view of macroevolution, it would appear that most of the adaptive plasticity exhibited by any given species is not translated into adaptive diversity among species within a clade. This supports the perspective of some researchers that macroevolution is more than just microevolution "writ large." However, it is important to recognize that this interpretation is derived from a limited phylogenetic data base, so at the moment it is simply an observation and not a theory of diversification per se. The generality of this observation can be tested by examining different groups of organisms using the methods described in this chapter. Once a trait has been identified as an "adaptation" at the macroevolutionary level using these methods, there is still work to be done at the microevolutionary level to strengthen the hypothesis that the trait is adaptive. This includes studies of the selective environment, and the character's function and its fitness with respect to that function. These areas of research, beyond the purview of historical ecology, highlight the need for a closer collaboration between micro- and macroevolutionary research programs.

If it is generally true that ecological and behavioral diversification is a conservative feature of **macroevolution**, we should not expect adaptive radiations to be manifested as a one-to-one mapping of species and divergent ecologies on phylogenetic trees. If, as Coddington has suggested and we have tried to show, adaptive radiations result from developmental and functional morphological, as well as ecological, changes within a phylogenetic context, we will need to map information from a variety of sources in order to provide robust explanations for the adaptive radiation of any group. We may also have to rethink our theories about the causal basis of such radiations. Cracraft's perspective on the importance of taxic macroevolutionary phenomena in shaping macroevolutionary patterns of diversity becomes even more important if the transformational aspects of macroevolution discussed in this chapter are cohesive, rather than diversifying, influences in evolution.

### Summary

Biological diversity has been shaped on this planet by countless years of interactions between the evolutionary processes of speciation and

adaptation. It should be clear by now that no one process can be assigned the dominant role in evolution; every clade is a unique combination of historical and environmental influences. Because each species is a unique evolutionary lineage, we cannot predict the exact pathway that clades will travel in the future. However, because each species carries with it the burden of history and, as such, is constrained by the past, we may be able to determine pathways that will not be available for that journey. These constraints can be investigated from both the macroevolutionary perspective of historical ecology (i.e., analysis of origins, elaborations, and associations) and from the microevolutionary perspective of population ecology (i.e., analysis of character maintenance and the effects of constraints on current population structure). Combining the information from both these research programs will produce a more robust theory of evolutionary ecology, and this, in turn, will allow us to make more informed decisions in our attempts to understand and preserve our ecosystem.