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Daniel R. Brooks

University of Toronto, dnlbrooks@gmail.com

Deborah A. McLennan

University of Toronto

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COMPARATIVE STUDY OF ADAPTIVE RADIATIONS WITH
AN EXAMPLE USING PARASITIC FLATWORMS
(PLATYHELMINTHES: CERCOMERIA)

DANIEL R. BROOKS AND DEBORAH A. McLENNAN

Department of Zoology, University of Toronto, Toronto, Ontario M5S 1A1, Canada

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Abstract.—Studies of adaptive radiations require robust phylogenies, estimates of species numbers for monophyletic groups within clades, assessments of the adaptive value of putative key innovations, and estimates of the frequency of speciation modes. Four criteria are necessary to identify an adaptive radiation within the parasitic platyhelminths: (1) a group contains significantly more species than its sister group, (2) species richness is apomorphic, (3) apomorphic traits enhance the potential for adaptively driven modes of speciation (sympatric speciation and speciation by peripheral isolation via host switching), and (4) the frequency of adaptively driven speciation modes is high within the group when compared with data from free-living groups. Only the species-rich Monogenea fulfill all four criteria. The Digenea and Eucestoda also are more species rich than their sister groups, their species richness is derived, and they possess unique characters that increase the potential for host switching to occur. However, because there is not enough information to determine whether the frequency of adaptive modes of speciation is high for those groups, we cannot yet assert that their radiations have been adaptive.

The disproportionate representation of one taxon within an assemblage is widespread throughout nature. For example, passerines dominate all other orders of birds, and teleost fishes dominate the actinopterygians. Some authors have argued that the perception of dominance is nothing more than a taxonomic artifact (Mayr 1969; Raikow 1986, 1988). Others have argued that such patterns can be explained by stochastic speciation and extinction processes (Raup et al. 1973; Raup and Gould 1974; Gould et al. 1977; Raup 1984). Flessa and Levinton (1975; cited in Dial and Marzluff 1989, p. 28) disagreed, concluding that “deterministic processes so pervade the evolution of diversity that stochastic processes must be regarded as secondary in importance” (see also Stanley et al. 1981; Ehrlich and Wilson 1991). Dial and Marzluff (1989) compared patterns of species richness within 85 clades to the patterns predicted by five null models (Poisson distribution, Raup et al.’s [1973] simulation, Anderson and Anderson’s [1975] simulation, simultaneous broken-stick distribution, and canonical lognormal distribution). They discovered that nearly all of the groups were dominated to a significantly greater extent by one taxon than predicted by any of the null models, regardless of the classification scheme used to delineate the clades. On the average, the species-rich group tended to account for 37% (traditional, or evolutionary taxonomic, classification)

to 39% (phylogenetic systematic, or cladistic, classification) of the subunits within each assemblage. The generality of this result across a wide biological spectrum, from plants, through insects, to mammals, prompted their conclusion that "over dominance of an assemblage by one unit is a common and *non random* feature of distributions of taxonomic diversity" (Dial and Marzluff 1989, p. 34).

The strength of Dial and Marzluff's results supports the hypothesis that real biological mechanisms are responsible for differences in species number between clades (Fitzpatrick 1988; Vermeij 1988; Dial and Marzluff 1989). This begs the question of what those mechanisms could be. The answer to this question has traditionally centered around the concept of adaptive radiation. In general, differences among clades have been postulated to result from higher speciation rates in the more species-rich group rather than from high extinction rates in the species-poor groups. 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, 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, 1984b; Cracraft 1984; Novacek 1984; Mitter et al. 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 1982; Mishler and Churchill 1984; Brooks et al. 1985), 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, p. 32): "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."

Because of this focus on adaptation, there has been a tendency to equate species richness with evolutionary success, and this, in turn, has led to the implicit assumption that speciation is equivalent to adaptive radiation. Not all modes of speciation, however, require adaptive changes. Current evidence suggests that modes of allopatric speciation that do not require adaptive changes have played the dominant role in the speciation of many groups (Lynch 1989; Brooks and McLennan 1991). This indicates that speciation and adaptation may be distinct, albeit historically correlated, evolutionary processes. Because of this decoupling, we cannot assume a priori that all radiations are adaptive, and we must search for criteria by which we can distinguish adaptive radiations from radiations (or nonextinctions).

Studies of adaptive radiations must occur within the larger framework of phylogeny because it is necessary to identify "evolutionarily equivalent" groups for comparisons of species richness. Groups of species can be considered evolutionarily equivalent if they are all monophyletic and the same age. There have been a number of criteria proposed by which the relative ages of clades can be as-

sessed, such as stratigraphic, biogeographic, or molecular clock comparisons. Comparison of sister groups is the most objective means possible for making certain we are dealing with evolutionarily equivalent units, since sister groups are, by definition, of equal age (see Mayden 1986 for an extended discussion). The search for correlates of species richness can be made by comparing either species-rich groups with each other or by comparing species-rich groups with their species-poor relatives. We believe that the latter comparison provides the best context for determining whether the species-rich group is characterized by evolutionarily derived traits associated with species richness. Comparisons among species-rich groups alone will not allow us to determine whether any common characters are also common to some of their species-poor sister groups and will not allow us to determine whether any of the characters that are unique to a particular species-rich clade might actually be the key to explaining species richness in that group. In other words, we should begin phylogenetic studies of adaptive radiations by assuming that adaptive radiations, like adaptations, are clade specific. Once a significant database has been assembled, we may ask whether there are any common derived (i.e., convergent) characteristics of species-rich clades.

Merely comparing the species-rich group with its species-poor sister group, however, will not tell us which of the two groups might require special explanation. That is, we can only assume that the species-rich groups require explanation if we always assume that extinction rates are equivalent across taxa. For example, consider the hypothetical family of fish depicted in figure 1. An ichthyologist comparing sister genera D and E might conclude that E was species rich (fig. 1*a*). In light of the larger phylogenetic picture, that conclusion might be premature. The pattern depicted in figure 1*b* corroborates the conclusion; however, the pattern depicted in figure 1*c* indicates that E is not species rich compared with the other members of the family except its sister group. Within the context of species distributions across genera of the family, genus E is not species rich; rather, its sister group, genus D, is species poor. The situation is further complicated when the pattern depicted in figure 1*d* is uncovered. Plotting the number of species per genus against number of genera would produce the typical U-shaped curve (Dial and Marzluff 1989), in which the dominance of genus E would be postulated to represent a rare event. However, because the species-rich group is also the oldest member of a clade composed of relatively depauperate groups, it is impossible to determine whether species richness is plesiomorphic (ancestral) or apomorphic (derived) for the family. To do this, we need to expand the phylogenetic framework to include information about species number in the closest relatives of the ABCDEidae. If the sister group of the ABCDEidae is species poor, then group E might represent a rare event in the family. If the sister group is species rich, then we need to search for explanations about the species-poor clades A, B, C, and D. This is an important distinction because, in the absence of the additional phylogenetic information, a statistical analysis might give an incorrect picture of the evolutionary trends in the family.

Having documented pairs of species-poor and species-rich sister groups nested within a phylogenetic context in which species richness is the derived trait, we

FIG. 1.—Heuristic example demonstrating how the explanation for observed species number is dependent on phylogenetic patterns and the level of the analysis. *a*, A two-taxon statement provides no information about origins of species richness. *b*, Species richness is derived within the family. *c*, Species richness is plesiomorphic (ancestral) within the family. *d*, Pattern that might confound a statistical analysis of diversity because, without expanding the scope of the analysis to include information from outgroups, it is impossible to tell whether species richness is derived or plesiomorphic within the family.

can proceed to ask the question of primary importance in studies of adaptive radiations: What, if anything, is adaptive about the radiation? Some researchers have sought the answer to this question in the concept of “key innovations.” A key innovation was originally defined as any novel feature that characterized a clade (i.e., any synapomorphy) and was therefore correlated with its adaptive radiation (Mayr 1960; Liem 1973). 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. Although intuitively pleasing, the concept as stated falters on closer examination (Lauder 1981; Liem and Wake 1984; Stiassny and Jensen 1987; Lauder and Liem 1989). First, by definition, every branch on a phylogenetic tree is characterized by at least one apomorphic change. Simply asserting that every apomorphy is an adaptation, and therefore potentially responsible for an observed adaptive radiation, is of limited value at best and circular at worst. The question, then, is how to define the term “adaptive” in a manner that allows a hypothesis of adaptation to be falsified. Since the diversification of fixed characters can only be identified from a macroevolutionary perspective, the concept of adaptation must incorporate phylogenetic information, as well as information about the functional superiority of the putative adaptive character. In this article, therefore, we

will follow the position presented by Baum and Larson (1991) that an adaptive character is any derived state that confers a performance advantage to its possessor (see also Arnold 1983; Greene 1986; Coddington 1988) in comparison with its plesiomorphic state.

Second, if the species-rich clade is characterized by more than one apomorphy, there is no *a priori* way to determine which of those traits might be the key innovation (perhaps even a combination of traits could be *the* innovation). This problem is made more complex because there is no theoretical reason to expect that the innovation originated with the ancestor of the species-rich clade. It may have appeared in one of the sister species of the original ancestor, or the clade may be composed of several species-rich subunits, each of which may be characterized by a different key innovation.

The third problem with the concept of a key innovation is that there is rarely strong evidence about the manner in which the innovative trait affects speciation rates in the clade. The null mode for speciation is geographical or vicariant allopatric speciation (Brooks and McLennan 1991), in which speciation rates are determined by rates of geological change leading to physical fragmentation of ancestral species populations (Cracraft 1985). Vicariant speciation is sometimes termed a "nonadaptive" mode of speciation, because specific adaptations are not required for speciation to occur. Key innovations can influence speciation rates directly if they increase the likelihood that species within the clade will participate in other, relatively rapid, modes of speciation, such as allopatric, parapatric, and sympatric speciation by peripheral isolation (sometimes referred to as adaptive modes of speciation: see, e.g., Bush 1982; Diehl and Bush 1989). Vicariance biogeographical methods are a useful way to study this interaction of adaptation and speciation because episodes of adaptive speciation are highlighted against a background of vicariance (Brooks and McLennan 1991).

Key innovations can also influence speciation rates indirectly by decreasing the chance that species will become extinct before they have a chance to be affected by vicariant speciation (Cracraft 1982). Larson et al. (1981), for example, proposed a species-selection argument in which key innovations gave the descendant species in the clade an advantage over competitors. Such lineages would be expected to survive longer and extend over a larger geographical range than other lineages, thus increasing the likelihood of vicariant speciation, which would result in increased species richness. This raises the question of whether there need be anything adaptive about simply surviving long enough to participate in many episodes of vicariant speciation. In general, the probability of bifurcation should increase with increased species longevity; however, the key innovation need not play a role in initiating those bifurcations. For example, long-lived species residing in areas subject to repeated vicariant episodes (hot spots; Cracraft 1982) may show more bifurcations than equally long-lived species inhabiting more stable environments. The problem arises out of the assumption that adaptation is equivalent to speciation. If, as we discussed previously, the two processes are decoupled, then we must incorporate both processes into our definition of a key adaptation. In this article, then, we define a key innovation as any apomorphic character that can be demonstrated to have adaptive value relative to its plesiomorphic

antecedent and can be demonstrated to play a direct role in initiating speciation (and thus increasing speciation rates). Given this definition, characters that simply promote the longevity of a species so that its chances of participating in vicariant speciation are increased are not key innovations.

PARASITES AS MODEL SYSTEMS FOR STUDYING ADAPTIVE RADIATIONS: AN EXAMPLE
USING PARASITIC PLATYHELMINTHS

Evolutionary studies in parasitology are founded on a number of traditional beliefs about parasites. One of those beliefs is that "the most extraordinary adaptive radiations on earth have been among parasitic organisms" (Price 1980, p. 3). To evaluate this statement, we need to ask whether there is any evidence for adaptive radiations in parasite groups. If the answer to this question is yes, we must then ask whether parasites display more instances of adaptive radiation than do their free-living sister groups. At the moment, although several parasite groups have been examined phylogenetically, the database for their free-living relatives is not as extensive. We will, therefore, address only the first question in this article. To do this, we will use the extensive phylogenetic database that has been accumulating for the parasitic platyhelminths over the last two decades. These worms comprise the superclass Cercomeria, which contains some of the most well known medical and veterinary scourges of the parasite world (e.g., liver flukes, schistosomes, and tapeworms). Approximately 1,500 morphological and ultrastructural characters are known, providing resolution at least to family level for all groups within the subclass (for details, see Brooks and McLennan 1993). In addition, there is extensive information about the developmental and ecological aspects of the life-cycle patterns for cercomerians. Consequently, we have used this group to search for adaptive radiations and their explanations.

Identifying the Species-rich Groups

Phylogenetic analysis of 154 morphological and ultrastructural characters produced one tree for the major groups of parasitic platyhelminths with a consistency index of 98.1% (PAUP computer program, branch and bound algorithm, see Swofford 1991; Brooks 1989a, 1989b; Brooks and McLennan 1993; fig. 2a). Unlike many of the groups discussed by Dial and Marzluff (1989), the parasitic platyhelminths are dominated by more than one group: the Digenea (5,000+ species) and Monogenea (5,000+; Schmidt and Roberts [1985] suggested that fewer than half of the monogeneans have been described) and, secondarily, the Eucestoda (2,500+ species). Plotting number of species per group against group produces a slightly modified U-shaped curve. The coefficient of dispersion for these data is substantially greater than one, which indicates that this pattern, like most of the cases discussed by Dial and Marzluff (1989), does not conform to a Poisson distribution. Having determined that the diversity patterns appear to be nonrandom, the next question to answer is whether a high number of species per clade is ancestral or derived within the platyhelminths. One way to do this is by optimizing the relative number of species onto the phylogenetic tree. To be as

FIG. 2.—Phylogenetic tree depicting relationships among the major groups of parasitic platyhelminths. Numbers after each taxon name are the approximate species numbers. A simplified optimization procedure is illustrated. Low represents groups with significantly fewer species than expected if species were equally distributed among all groups; high represents groups with significantly more species than expected if species were equally distributed among all groups. a, Number of species mapped above the branches for the major cercomeridean groups. b, Results of generalizing down the tree. c, Results of predicting up the tree showing that species richness (high) has been independently derived in the Digenea, Monogenean, and Eucestoda.

conservative as possible, we used a χ^2 analysis to identify groups with fewer than expected, and groups with more than expected, numbers of species.

Phylogenetic optimization techniques (Brooks and McLennan 1991; Wiley et al. 1991) are designed to uncover the best-supported (most parsimonious) sequences of evolutionary transformations for a character by reference to a phylogenetic tree (Farris 1970). There are three steps involved in this process. (1) Map the distribution of the character “high” versus “low” number of species above the taxa on the phylogenetic tree (fig. 2a). (2) Generalize down the tree (fig. 2b). Beginning with the two nodes that are farthest from the ingroup node, label the state of the binary character at each node according to the rule, If the two closest nodes or branches either are both “high” or are “high” and “high, low,” label the node “high,” and vice versa. If two closest nodes or branches are “high”

and "low," label the node "high, low." This indicates that the character state is ambiguous at this particular node. (3) Predict back up the tree (fig. 2c): move from the ingroup node up the tree, resolving ambiguity by comparing the value of the ambiguous node with the value of the node directly below it (for details of this method, see Maddison et al. 1984; Brooks and McLennan 1991). In this example, the optimization is unambiguous at the ingroup node (fig. 2b), so we do not require information from outgroups. In addition, the process has been simplified by breaking the species number into two large states rather than leaving it as one multistate character. Because of this, information about the exact transitions in species number among groups is lost during the analysis. This is not important in this case because we are only trying to ascertain whether the species-rich groups represent the plesiomorphic or derived condition within the superfamily.

Optimization procedures will not always resolve the sequences of character evolution unambiguously (see, e.g., Swofford and Maddison 1987; Donoghue 1989); however, in this case the results are unequivocal. The results depicted in figure 2c indicate that the low number of species in five of the eight terminal cercomerian groups represents the ancestral condition in parasitic flatworms. The substantial increase in species number within the digeneans, monogeneans, and cestodes thus represents the derived condition (pattern *a* in fig. 1).

Dial and Marzluff (1989) reported that the median dominance value for their 85 groups was 36%. The three groups displaying the derived species number within the Platyhelminthes greatly exceed this median value when compared with their sister groups: the digeneans (flukes) constitute 99.1% of the known trematode species, monogeneans constitute 66.5% of the cercomeridean species, and the eucestodes (tapeworms) constitute 99.8% of the cestodarian species. It appears, then, that these groups represent cases of radiation within the Cercomeria. Given this, is there any evidence that these radiations are adaptive?

Setting the Stage: Comparisons of Life-Cycle Patterns

The association between vertebrates and cercomerideans began a long time ago, possibly very shortly after the first (agnathan) vertebrates evolved, but almost certainly early in the evolution of the placoderms. The stem diversification of the Trematoda, the Monogenea, and the Cestodaria (gyrocotylideans, amphilinideans, and eucestodes) occurred in association with placoderm groups prior to the divergence of chondrichthyans from the rest of the gnathostomous vertebrates (actinopterygians, sarcopterygians, and tetrapods). Subsequent to that early diversification, the divergence of the aspidobothreans from the digeneans, the gyrocotylideans from the cestoids (amphilinideans plus eucestodes), and possibly various groups of monogeneans from each other are all correlated with the divergence of the chondrichthyans from the ostracoderm ancestor, giving rise to the rest of the gnathostomous vertebrates. Hence, there is evidence of long-standing conservative association with particular vertebrate host groups (Brooks 1989b).

Figure 3 depicts the evolution of life-cycle characteristics on the phylogenetic tree for the Cercomeria. The plesiomorphic life-cycle pattern for all the parasitic

FIG. 3.—Phylogenetic patterns of life-cycle diversification among major groups of cercomerian platyhelminths.

flatworms appears to be one in which an arthropod is used as the only host by an ectoparasitic species (the Temnocephalidea and Udonellidea). The pattern became more complicated in the ancestor of the cercomerideans as a vertebrate host was added and the adult parasites became endoparasitic (this presumably arose as a result of predation by early vertebrates on crustaceans). At this level, then, the basal life-cycle pattern involves an arthropod 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 Cestodaria, including the species-rich Eucestoda, suggests that most of them have retained this primitive life-cycle pattern. The Trematoda, including the species-rich Digenea, display one variation on this central life-cycle theme; in their ancestor, a molluscan host was substituted for an arthropod host. Finally, the Monogenea have a secondarily simplified life-cycle pattern, in which both the arthropod intermediate host and the endoparasitic lifestyle have been lost. Thus, each of the three species-rich clades exhibits a different phylogenetic background with respect to its basic life-cycle pattern.

Types of Apomorphic Changes among Cercomerian Groups

Dial and Marzluff (1989) suggested that life-history traits might play an important role in speciation rates. This perspective is not new to parasitologists, who have traditionally searched among life-cycle patterns for evidence of key innovations (see, e.g., Seurat 1920; Baer 1950; Chabaud 1954, 1955, 1965, 1982; Anderson 1957, 1958, 1982, 1984; Osche 1958; Combes 1972; Freeman 1973; Cable 1974; Odening 1974a, 1974b; Euzet and Combes 1980; Price 1980; Moore 1981; Sprent 1982; Durette-Desset 1985). Rogers (1962) suggested that adaptive radiation of parasite groups was marked by the evolution of key adaptations that increase the chances of transmitting offspring from generation to generation. We

used Rogers's perspective to establish six categories of potential key innovations in parasite groups: (1) adult morphology pertaining to reproductive activities, (2) adult morphology not pertaining to reproductive activities (predominantly traits having to do with maintaining location within a host and feeding), (3) modification of ontogenetic stages, (4) origin of new ontogenetic stages, (5) loss of old ontogenetic stages, and (6) changes in ecological characteristics. To determine whether any members of these character categories have been key innovations, we must compare sister groups within the Cercomeridea, searching for the synapomorphies that (a) are correlated with species richness, (b) confer a fitness advantage when compared with the ancestral condition, and (c) may have been associated with an increase in adaptive modes of speciation in the species-rich clade.

Correlates of Species Richness among Cercomerian Sister Groups

Table 1 depicts the distribution of synapomorphies among the character categories for the sister groups within the Cercomeria that demonstrate differential species richness. There is no significant difference between species-rich groups and their sister groups in the origin of adult reproductive and nonreproductive characters; the patterns depicted for each sister-group pairing represent a unique mosaic of conservative and derived characters. We will begin our search for key innovations within the character categories that exhibit apomorphic changes in the species-rich groups and not in the species-poor groups. For example, apomorphies based on modifications of larval characters typify the Digenea and Eucestoda. Changes in larval characters are absent from their respective sister groups. The monogeneans, on the other hand, are characterized by changes in ecological characters that are not matched in their cestodarian sister group. As mentioned earlier, however, there is no a priori way to determine which, if any, of the apomorphies displayed by each species-rich group is *the* innovation, so it is possible that the key innovation will reside in a character category that does not differ in the absolute number of synapomorphic changes demonstrated by a species-rich group and its sister group.

The Monogenea.—The most obvious difference between the species-rich Monogenea and their sister group, the Cestodaria, is the appearance of two novel ecological traits in the monogeneans (table 1). Monogeneans have lost the arthropod intermediate host that is plesiomorphic for the Cercomeridea, which has resulted in a direct life cycle using only a vertebrate host, and they are ectoparasitic on the host. A role for ectoparasitism and a direct life cycle as key innovations, on their own, can be ruled out because the species-poor groups Temnocephalidea and Udonellidea possess these characters. Temnocephalideans and udonellideans, however, display the characters in the plesiomorphic context of an arthropod host, while the monogeneans display the characters in the apomorphic context of a vertebrate host (fig. 3) (this is the reason we consider ectoparasitism to be apomorphic within the Monogenea, derived from endoparasitism in a vertebrate, rather than plesiomorphic, with endoparasitism derived independently in the common ancestor of the Trematoda and the Cestodaria). Kearns (1986) discussed studies demonstrating that the transmission of monogeneans, either via the free-swimming oncomiracidium or by direct transfer from host to host, was

TABLE 1

IDENTIFYING CORRELATES OF SPECIES RICHNESS IN MAJOR PARASITIC PLATYHELMINTH GROUPS

CHARACTER CATEGORY	TAXA					
	Digenea (5,000+ spp.)	Aspidobothrea (50+ spp.)	Monogenea (5,000+ spp.)	Cestodaria (2,518+ spp.)	Eucestoda (2,500+ spp.)	Amphiliinidea (8 spp.)
Adult reproductive	2	1	6	6	3	5
Adult nonreproductive	0	4	5	7	2	2
Development (modification)	13	0	4	4	8	0
Development (origin of stages)	3	0	1	0	2	0
Development (loss of stages)	0	0	0	0	0	0
Ecological	0	0	2	0	0	1

NOTE.—The total number of character changes (apomorphies) associated with the origin of each group is listed according to character category. For example, the Digenea are distinguished by the presence of 18 autapomorphies: three origins of new developmental stages, 13 modifications of developmental stages, and two changes in adult reproductive characters.

enhanced by various aspects of the host's behavior (e.g., concentrations of host populations during spawning or during parental care). It appears, then, that, if there is a fitness advantage conferred by these two ecological changes, it occurs because the monogeneans inhibit a derived host type relative to other parasitic platyhelminths having direct (single-host) life cycles.

The putative key innovation displayed by the monogeneans is thus a suite of traits, involving a complex interaction among three characters, vertebrate host (plesiomorphic for the monogeneans), ectoparasitism (apomorphic for the monogeneans), and direct life cycle (apomorphic for the monogeneans). There is currently little information available about the adaptive value, if any, of ectoparasitism over endoparasitism, so its potential role as a key adaptation or as part of a key adaptive complex cannot be evaluated. The direct life cycles in monogeneans result from the deletion of the arthropod intermediate host. Three different heterochronic changes (acceleration, postdisplacement, or progenesis) can result in precocial sexual maturation, leading to deletion of an intermediate host (Brooks and McLennan 1993). Thus, the characterization "direct life cycle" for the monogeneans may be better considered a description of the ecological effect of precocious sexual maturation. If so, it is the change in the developmental rate, not the loss of the arthropod host with subsequent reduction to a direct life cycle, that should be considered the putative key innovation. Heterochronic changes in maturation rate originating in the ancestor of the monogeneans continued to play a role in character change throughout the evolutionary diversification of the group, leading ultimately to the appearance of a variety of autoinfective strategies, including reinfection of a host by a nonswimming oncomiracidium, ovoviviparity, and viviparity.

Studies have demonstrated that autoinfection has a positive effect on the reproductive success of the bearer (see Tinsley 1983; Kearn 1986 and references

therein). First, delaying hatching until embryos are well developed decreases the hazards of development in the external environment. This hazard is a substantial one. Wilson et al. (1982) estimated that, of 100,000 *Fasciola hepatica* eggs deposited in a pasture from the middle of winter to the end of summer, only 17 would hatch. Second, remaining on the same host (resource patch) decreases the riskiness involved in parasite transfer involving a free-swimming but short-lived larva (Llewellyn 1968, 1981). Tinsley (1982, 1983) compared the reproductive success of two species of monogeneans, *Polystoma integerrimum* and *Pseudodiplorchis americanus*. *Polystoma integerrimum* displays the ancestral monogenean life cycle "deposit eggs in the environment, ciliated oncomiracidia hatch and swim to vertebrate host." *Pseudodiplorchis americanus* displays the derived strategy of ovoviviparity. Tinsley compared a number of variables, including details of the life cycle, number of eggs and fully developed larvae produced, metabolic demands of reproduction, and prevalence and intensity of each species in its host. He concluded that, if he assumed no mortality, a single adult *P. americanus* could potentially produce 3.9×10^9 adults after 4 yr, compared with a production of 2.5×10^3 adults for *P. integerrimum*. An enormous increase in fecundity is obviously associated with ovoviviparity when compared with the plesiomorphic condition. We can conclude, therefore, that the origin of a change in development in the context of a derived (vertebrate) definitive host is adaptive within the monogeneans.

Is the association between the monogenean radiation and the developmental change more than just a spurious correlation? From a theoretical perspective, the answer to this is yes, because the subsequent changes in life-history characteristics have a direct effect on deme structure. Parasite demes have a tendency to be ephemeral. In the vast majority of cases, they must be reassembled each generation by the relatively random immigration of larvae, juveniles, or both, usually from a much larger gene pool (the parasite species population occurring in multiple hosts) than that represented by the members of the original deme. Parasites that autoinfect their individual host and inhabit long-lived hosts can produce more than one generation on or in the same host organism. This reduces the ephemerality of the deme structure, increasing the potential that differences appearing within a deme could be maintained by inbreeding. Tinsley (1983, p. 174) hypothesized that such inbreeding could "promote rapid increase in gene frequency and potential fixing of beneficial variation, and enable tracking of host and other environmental variations." The monogeneans are thus characterized by the appearance of an adaptive reproductive strategy that increases the opportunity for sympatric speciation to occur. In addition, the ability to produce a viable deme from one pregnant individual increases the likelihood that speciation by peripheral isolation via host switching will occur.

Have adaptive modes of speciation occurred frequently in the monogeneans? On the basis of an analysis of 66 documented cases of vertebrate speciation, Lynch (1989) suggested that 21% of the speciation events were due to possibly adaptive modes of speciation (allopatric speciation by peripheral isolation and sympatric speciation). Phylogenetic analyses of speciation in monogeneans has revealed that, depending on the group, the combined frequency of speciation by

peripheral isolation and sympatric speciation ranged from 22% to 100% (Brooks and McLennan 1991, 1993 and references therein). The median value of 56% is much higher than the value reported in Lynch's study, supporting the conclusion that monogeneans exhibit a high rate of speciation modes that might be adaptively driven. The hypothesis that the evolution of direct life cycles and autoinfection influence the rates of adaptively driven speciation is supported by an additional piece of evidence. Within the monogeneans, one of the most species-rich groups, the gyrodactylids, displays the extreme condition of this developmental trend, viviparity.

Overall, then, the monogeneans display the key adaptive complex "change in developmental rate of sexual maturity leading to the appearance of a direct life cycle and a variety of autoinfective strategies within the context of a derived definitive host." This change has a positive effect on the fitness of its bearers and enhances the potential for sympatric speciation and speciation by peripheral isolation (host switching) to occur. It is not surprising that adaptively driven modes of speciation occur more often in the monogeneans than do levels detected for a variety of free-living groups. This, we believe, is a strong example of an adaptive radiation. Of course, the story does not stop here. Tinsley (1983) discussed a variety of novel characters that further enhanced the adaptive advantage of delayed development (e.g., uterine elongation). We cannot assess the putative adaptive values of these characters, nor can we examine their effects, if any, on speciation rates until detailed phylogenies are available for the monogenean families. Nevertheless, this highlights the important and often-overlooked fact that key innovations, be they characters or complexes of characters, are themselves subject to evolutionary change. It is therefore important to trace the diversification of the innovation, in terms of both changes in the character itself and changes in other characters that may enhance or decrease the adaptive value of the innovation.

The Eucestoda.—Unlike monogeneans, eucestodes originated within the plesiomorphic ecological context for the Cercomeridea (i.e., arthropod intermediate host, vertebrate definitive host). The major difference between the tapeworms and the amphilinids lies in modifications to larval stages (table 1). Although most of these modifications appear relatively minor on an intuitive level (see Raikow 1986 for a similar discussion of passerine evolution), there is not enough information available to test hypotheses about their adaptive significance (Fitzpatrick 1988). The major correlate of the eucestode radiation for which any experimental data have been collected is the proliferation of adult reproductive structures (proglottids). The increase in sexual reproductive output for the tapeworms is dramatic. The average daily reproductive output of 100 eggs per worm in the Monogenea, and even the exceptional output of 24,000 eggs per worm in some of the larger digeneans (Tinsley 1983) pales in comparison with the 720,000 eggs expelled per day by the human beef tapeworm, *Taenia saginata* (Crompton and Joyner 1980). The lifetime fecundity of a tapeworm is much greater than the lifetime fecundity of an amphilinid (sister group bearing the plesiomorphic condition "lack of proglottids"), so the appearance of this new reproductive strategy can be assigned an adaptive status.

The proliferation of dispersal stages created by the new strategy increases the likelihood that a larva will find a suitable host, decreasing the chance that a given population will become extinct (Moore 1981 and references therein). This, in turn, has an indirect effect on speciation because it allows a species to persist long enough to encounter a variety of speciation-causing factors. These factors, however, need not fall into the domain of adaptively driven speciation; it is equally likely that they will have something to do with the long-term survival and geographical spread of species, increasing the likelihood of vicariant speciation. So, although the persistence of an individual's genealogical lineage is adaptive from that individual's perspective, this does not necessarily lead to an enhanced potential for adaptive speciation modes.

Proliferation of dispersal stages should have a more direct effect on speciation by increasing the probability that allopatric speciation by peripheral isolation via host switching will occur. This hypothesis can be tested by comparing the frequency of host switching between the Eucestoda and its sister group, the Amphiliniidea. At the moment, only one study of speciation within a phylogenetic framework is available for the tapeworms, so the hypothesis cannot be tested rigorously. Nevertheless, the data are tantalizing; 13% host switching in the amphilinids (two of 15 speciation events: Bandoni and Brooks 1987*a*) versus 40% in the tapeworm group (six of 15 speciation events: Hoberg 1986). Preliminary studies with other tapeworm groups also indicate that host switching has been widespread throughout the group (Moore and Brooks 1987). It is difficult to determine whether these results are more reflective of rampant host switching or of poorly resolved parasite phylogenies, though, because the analysis produced multiple trees with a low-consistency index.

Circumstantial support for the direct effect of an increase in dispersal stages on speciation rates is also found by investigating groups within the Eucestoda that have secondarily lost their segmentation, reverting to the plesiomorphic state "one set of reproductive organs/adult." One such group is the Caryophylliidea, monozoic tapeworms inhabiting the intestines of freshwater fish (predominantly ostariophysans) and most closely related to the species-rich diphyllbothriid pseudophyllideans (Brooks et al. 1991). Caryophyllideans are widespread, parasitize a species-rich host group, and are presumably quite old (Mackiewicz 1981); however, they have not enjoyed high speciation rates (approximately 111 known species). Mackiewicz (1981) attributed this to their low reproductive potential relative to that of polyzoic cestodes and characterized them as an evolutionary dead end. Another example is found in the order Aporidea, parasites in the intestines of ducks and swans, that are most closely related to the species-rich cyclophyllideans. Although not closely related to caryophyllideans, aporideans share two common traits with those tapeworms, low species number (fewer than six species in the order) and the monozoic lifestyle.

In summary, the appearance of segmentation in the ancestor of the Eucestoda is associated with increased fecundity (and thus presumably also increased potential for speciation by host switching) and an increase in the frequency of that speciation mode compared with its frequency in the amphilinideans and in free-living groups. Within the Eucestoda, the ability to produce replicated sets of

reproductive organs has been independently lost at least twice in the Caryophyllidea and the Aporidea. Both of these groups are species poor relative to their sister groups. To provide stronger support for the hypothesis that the character "polyzoic body" is a key innovation, we need better estimates of the role that speciation by peripheral isolation has played in tapeworm diversification. If it has been widespread throughout the group, or if it is always associated with species-rich clades within the Eucestoda (e.g., the two most species-rich groups within the Eucestoda, the Tetraphyllidea and the Cyclophyllidea, originated following a host switch; see Brooks et al. 1991), then we can assign the new reproductive strategy the role of a key innovation. At the moment, we can only conclude that the hypothesis is interesting but requires substantial input from speciation studies within a phylogenetic framework before it can be corroborated or discarded.

The Digenea.—Like the eucestodes, the digeneans display an apomorphic increase in the number of dispersing larvae. Unlike the tapeworms, in which the larvae are products of sexual amplification, digeneans exhibit a strategy that is characterized by the origin of a completely new dispersal stage, the cercaria, and the origin of at least one, and generally two, phases of asexual amplification of larval stages between the miracidium and cercaria (the sporocyst and redia). Consequently, a single miracidium can produce 1,000 or more infective cercariae. This is another example of a putative key innovation that is really an innovation complex, the origin of a new free-swimming dispersal stage and of asexual reproductive phases intercalated in ontogeny.

The cercarial stage has also been perceived as an adaptation for enhancing the probability of infection, in this case not by amplifying the numbers of infective larvae but by dispersing those larvae spatially to the greatest extent possible, thereby increasing the likelihood of contacting a suitable host. We can evaluate that hypothesis by examining relative species richness among groups within the Digenea whose cercariae are not free-swimming. Some of those groups are species poor (Heronimidae, Troglorematidae, perhaps the Ptychogonimidae), some exhibit moderate species richness (Gymnophallidae, Brachylaimidae), and others are quite species rich (the Opcoelidae, Zoogonidae, and Lissorchiidae, which constitute the superfamily Opcoeloidea, and the Dicrocoeliidae). If the cercarial stage has adaptive significance in the evolutionary radiation of the Digenea, therefore, it is not spatial dispersion by swimming.

Alternatively, it has been postulated that the significance of the cercarial stage is tied to the evolutionary diversification of cercarial behaviors that opened up a broad spectrum of definitive hosts to infection by digeneans. The evolutionary diversification of cercarial behaviors cannot be assigned an adaptive status without a demonstration that each apomorphic change in cercarial behavior (e.g., from encysting on vegetation to encysting in a fish) conferred a fitness advantage to its bearers over organisms displaying the plesiomorphic behavior (Coddington 1988). We expect that this will be difficult to demonstrate because changes in cercarial behavior often result in the infection of new types of second intermediate hosts, which are eaten by new types of vertebrate definitive hosts. Although the origin of these novel behaviors could theoretically decrease competition for the plesiomorphic host resource, this would represent adaptive change only if the

plesiomorphic host were a limiting resource. Given that the plesiomorphic cercarial behavior is encystment on vegetation, on exoskeletons of mollusks and arthropods, and in the open, it is difficult for us to conceive that the plesiomorphic resource was ever limiting.

The origin of asexual amplification is clearly an adaptation, because it increases the reproductive output of each adult. This amplification should always have an indirect effect on speciation because, as discussed for the Eucestoda, it decreases the probability of population extinction, thereby increasing the chances for geographical spread and subsequent vicariance. It may also have a more direct effect on speciation by increasing the probability of speciation by peripheral isolation via host switching. Like the eucestodes, however, we do not have enough information on the actual role that adaptive modes of speciation have played in the diversification of the Digenea, so we cannot yet determine whether their species richness is due to longevity or to accelerated speciation rates.

In summary, then, although the digeneans have experienced an evolutionary radiation, there is little concrete evidence that the radiation has been adaptive. Asexual amplification would increase the chances for speciation by host switching. If this has been the case, then the digeneans should show a significantly higher frequency of speciation by peripheral isolation than the aspidobothreans, their sister group. Asexual amplification has arisen independently in another parasite group, the species-rich Taeniidae within the Eucestoda. Unfortunately, since many taeniids are not capable of asexual propagation (Moore 1981), and since there is no estimate of phylogenetic relationships within the group, we cannot determine whether asexual propagation is correlated with the taeniids' species richness. This will prove an interesting area for future research.

COMPARISONS AMONG SPECIES-RICH GROUPS: EVIDENCE FROM CONVERGENT CHARACTERS

One of the major problems encountered in studies of adaptive radiations is that, in many cases, such radiations may represent historically unique events. From a statistical perspective, a strong test of an adaptive radiation hypothesis is provided by the discovery of a convergent, adaptive trait correlated with species richness in more than one group (Coddington 1988). Although nature is rarely so obliging, one example exists in the parasitic platyhelminths.

Three species-rich groups, the Cyclophyllidea, within the Eucestoda (representing virtually all of the tapeworms inhabiting terrestrial vertebrates and the majority of tapeworms occurring in birds and mammals), and the Opisthorchiformes and the Plagiorchiformes (the most species-rich group), within the Digenea, share the derived condition "larvae remain in the egg (extended intrauterine development) until ingested by the first intermediate host (delayed hatching)." This character has arisen independently in all of these lineages. Once again, we have evidence of a change in development, in this case an increase in the duration of intrauterine development, associated with the radiation of a group. These developmental changes have allowed the Cyclophyllidea to exploit a previously untapped resource—terrestrial arthropods and vertebrates. If we consider the movement into this new habitat as the "selective regime" (sensu Baum and Lar-

son 1991), then the retention of the infective larval stage within the eggs until ingestion by the intermediate host provides a substantial performance benefit over the plesiomorphic condition of hatching in water and swimming in search of that host.

Several theories about the adaptive value of this strategy in the digeneans have been proposed, including avoiding the hazards of development in the external environment, promoting invasion of the intermediate host at the earliest opportunity, and providing protection for the embryo during the passage through the digestive system of the definitive host and through any unsuitable host that eats the eggs (Tinsley 1983). We now have three independent tests of the hypothesized adaptive value of this developmental change and of its involvement in the radiation of the groups that possess it. Indeed, when we also consider the basic biology of metacercarial stages in digeneans, the plerocercoid (and derivative) stage in eucestodes, dauerlarvae in nematodes, and cystacanths in acanthocephalans, this would seem to be a graphic example that "an important adaptation to parasitism is the suspension of development in the infective stage" (Rogers 1962, p. 253). These conclusions will be strengthened by the demonstration that adaptively driven modes of speciation are widespread within these three groups.

Species-poor Groups

We now turn to the three cercomeridean taxa that are the species-poor representatives of the Cercomeridea. Simpson (1944) was among the first modern evolutionary biologists to consider general explanations for groups of low species richness. He considered all such groups relicts of one form or another and postulated that different processes could produce different kinds of relictual groups. We will be concerned with two major types of relicts. Phylogenetic relicts are "living fossils"—members of groups that have existed for a long time without speciating very much. Such low speciation rates could result from phylogenetic or developmental constraints on phenotypic diversification or from unusually pronounced ecological specialization (i.e., ecological constraints due to the effects of strong, long-term stabilizing selection from the specialized habitat). Numerical relicts, by contrast, are the surviving members of groups that were once more species rich whose ranks have been depleted by extinction.

Brooks and Bandoni (1988) suggested that a combination of phylogenetic, biogeographical, and ecological information could be used to distinguish between phylogenetic and numerical relicts among parasites for which there is rarely any fossil record to provide an empirical estimate of past species richness. Establishing a group's relictual status first requires methods for determining that the group is old enough to be highly diverse, something that is established if the species-poor group's sister group is unusually species rich. Brooks and Bandoni further suggested that phylogenetic relicts should be ecologically conservative, whereas numerical relicts should be ecologically diverse. Among living groups, crocodilians (Crocodylia) are the sister group of the species-rich clade, the birds (Aves). The approximately 22 species of living crocodilians inhabit a variety of estuarine to freshwater habitats throughout the tropical and subtropical regions of the world. They prey on a wide variety of vertebrates and some invertebrates. The

fossil record indicates that crocodilians were once a species-rich group, including many fully marine species; in addition, the earliest known crocodilian fossils suggest a terrestrial origin for the group. Hence, the current diversity of crocodilians represents only a fraction of the species number and ecological diversity once encompassed by the group, so we considered crocodilians to be numerical relicts. The helminth parasite fauna of crocodilians also appears to comprise numerical relicts (Brooks and McLennan 1993).

Now, consider the ratfish (chimaeroids), the sister group of sharks, skates, and stingrays (elasmobranchs). There are 25 species of ratfish, compared with approximately 625 species of elasmobranchs. Ratfish occur worldwide in mid- to deep water marine habitats and forage on benthic invertebrates. The fossil record indicates that ratfish have been in existence for a considerable period of time but have never been highly diverse. Both the fossil evidence and the ecological homogeneity of contemporaneous species suggest that ratfish are phylogenetic relicts. There are at least two types of phylogenetic relicts in parasite-host systems. The first type involves cases in which the hosts have become highly diverse while the parasites have not diversified. In the second type, neither of the associated groups ever became very diverse.

The Aspidobothrea.—Aspidobothreans are an example of a group that did not become as diverse as its host group. Phylogenetic analysis (Brooks et al. 1989) and comparison with the phylogenetic relationships of their vertebrate hosts indicate that aspidobothreans have been around at least as long as the common ancestor of chondrichthyans and the rest of the gnathostome vertebrates. Both aspidobothreans and digeneans share an ancestral life-cycle pattern involving a molluscan and a vertebrate host (fig. 3). One obvious difference between the groups is species richness; there are fewer than 50 described species of aspidobothreans and more than 5,000 species of digeneans. Why this disparity?

In the aspidobothreans, larvae hatch from eggs and develop directly into juveniles in the molluscan host and are then ingested by a molluscan-eating vertebrate and develop to the adult state. Hence, each embryo can potentially give rise to only a single adult. As we discussed above, 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). It would appear, then, that the life-cycle characters possessed by aspidobothreans have allowed them to persist over a very long period of time but have not created the potential for increasing speciation rates. In this regard, they are similar to acanthocephalans, another group of helminth parasites with an apparently long history and a relatively low diversity.

The Amphilinidea and the Gyrocotylidea.—Like the aspidobothreans, amphilinideans (see Bandoni and Brooks 1987a for phylogenetic, biogeographical, and coevolutionary analysis of the group) do not inhabit hosts that are themselves phylogenetic relicts; therefore, they are an example of a parasite group that has not become as diverse as its host group. Amphilinideans display an ecological synapomorphy. Rather than inhabiting the intestine (plesiomorphic for the Cercomeridea, see fig. 3), all species occur as adults in the body cavity of their, primarily freshwater actinopterygian, hosts. Perhaps living in the body cavity of

fishes has kept amphilinidean diversity low, since amphilinideans are relatively large and thus restricted to relatively large hosts. In addition, amphilinidean eggs cannot reach the outside environment from the body cavity of all fishes, which further restricts their range of suitable hosts.

The gyrocotylideans (see Bandoni and Brooks 1987*b* for phylogenetic, biogeographical, and coevolutionary analysis of the group), on the other hand, are prime candidates for the second type of phylogenetic relict. They are ecologically conservative, being restricted as adults entirely to the spiral intestines of chimaeroid fishes, and are found in association with hosts that are themselves phylogenetic relicts. Like their hosts, the gyrocotylideans are less species rich than their sister group (in this case the amphilinideans plus the tapeworms). This suggests the possibility that the interaction between developmental conservatism and a conservative and highly specialized ecology limited diversity.

SUMMARY

The concept of adaptive radiation has come to mean many different things. To some researchers, 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. And to still other researchers, speciation has dropped out of the picture and the term has become associated with character diversification. Recognizing that this diversification of definitions has weakened our ability to test the concept, several authors have begun to build a more rigorous framework for defining and testing hypotheses of adaptive radiation (Lauder 1981; Liem and Wake 1985; Mayden 1986; Stiassny and Jensen 1987; Coddington 1988; Lauder and Liem 1989; Baum and Larson 1991; Brooks and McLennan 1991). We suggest that, for each putative case of an adaptive radiation, it must be demonstrated that (1) the group in question contains more species than its sister group, (2) species richness is a derived characteristic within the larger clade, (3) an apomorphic character present in the more species-rich group enhances the potential that adaptively driven speciation (i.e., sympatric speciation or speciation by peripheral isolation) will occur, and (4) adaptively driven speciation modes played the dominant role in the speciation of the more species-rich group. This latter point is extremely important because, if speciation has been driven primarily by vicariance, then we only have evidence for a radiation, that is, that whatever innovations have occurred in the ancestry of the group, the result has been only the persistence of the group long enough to participate in additional episodes of vicariance. In such cases, the presence of adaptive characters is not causally involved with any increase in speciation rates even though it is correlated with an evolutionary radiation.

Parasitic organisms are thought to be paradigm examples of adaptive evolution (Price 1980) and thus, by extension, good model systems for phylogenetic studies of adaptive radiations. Among parasites, the eight major groups of parasitic platyhelminths (Cercomeria) are well suited for such studies because their phylogenetic relationships are supported by an extensive database and because they

exhibit a rich mosaic of evolutionary diversification in reproductive, developmental, and ecological characteristics. Our analysis of these groups has demonstrated that a strong postulate of adaptive radiation can be advanced only for the Monogenea, which satisfy all four of the above criteria. The Digenea and the Eucestoda satisfy the first three criteria, but we do not at present have enough information about the frequency of adaptive modes of speciation to differentiate a radiation from an adaptive radiation for these groups. The remaining five groups are species poor. Given the paucity of comparable phylogenetic analyses for the free-living sister groups of the Cercomeria, or indeed for free-living groups in general, it is difficult to assess whether the cercomerians support Price's (1980) contention that parasites exhibit high rates of adaptive radiation. As a point of departure for future discussions, we note that the groups analyzed by Dial and Marzluff (1989) were generally dominated by one species-rich taxon. In the case of the Cercomeria, the group is characterized by three separate species-rich clades, which indicates that these parasitic flatworms have at least undergone extensive radiation.

Species richness is associated with different phenomena in the Monogenea, Digenea, and Eucestoda, including apomorphic changes in the developmental rate of maturation, the production or amplification of dispersing larval or juvenile stages, and the amplification of sexual reproductive output, respectively. Species poverty in the other groups appears to be associated with ecological specialization or specialization on relictual hosts. While these characteristics have allowed the groups to persist over a very long period of time, they have not resulted in increased rates of any speciation modes, including vicariant speciation. It is far too simplistic to suggest that species-poor groups have not speciated because they did not evolve the synapomorphies of the species-rich clades. It is more interesting to search for explanations for species poverty by examining characteristics of the groups themselves, because synapomorphies need not explain only species richness. For example, the Amphilinidea exhibit an ecological apomorphy that has restricted the range of suitable hosts.

Biologists interested in studying adaptive radiations find themselves in one of two frustrating positions. Some researchers have a plethora of information about the functional significance of certain characters and the number of species within traditionally classified groups but little or no information about the phylogenetic relationships and the frequency of speciation modes within the group. Other researchers have accumulated data about phylogenetic relationships and speciation modes but have no information about the functional significance, if any, of the traits within their groups. The solution would be simple if both groups of researchers were working on the same groups of organisms, but this is rarely the case. It is clear that the study of adaptive radiations is fraught with difficulties, but these difficulties are not insurmountable. Theoretical discussions have been intensifying over the last decade. What is required now is a collaborative interaction among systematists and ecologists to begin providing rigorous empirical tests of the hypothesis that adaptive radiation has played a role in the diversification of life on this planet.

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