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At the interface of phylogenetics and ecology: the case of chemical defenses in *Cicindela*

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The evolutionary ecology of chemical defenses in the tiger beetle genus *Cicindela* has been investigated by Pearson *et al.* (Am. Nat. 132, 404–416, 1988), but not without controversy. We re-evaluate some of the conclusions of this paper and the controversial discussions that followed. Problems with the quality and the interpretation of the data, some of which have been identified by previous authors, are seen in two main areas. First, the historical (phylogenetic) analysis relied on the use of a traditional ("Linnean") classification of the genus *Cicindela* to infer relationships among taxa. This is insufficient to study transformation of characters involved in defensive strategies such as benzaldehyde production, habitat type, and body coloration. Also, it precludes any studies of covariation and association among these characters during the evolution of *Cicindela*. Second, the types of ecological data that have been used to make inferences about the evolution of defensive strategies are problematic. In particular, the use of "habitat type" may not be appropriate because the various character states have not been specified in the context of predation, and because the habitat type is of questionable relevance to other traits involved in predator defense and escape. We also question previous approaches which used Pearson *et al.*'s (1988) data to construe chemical defenses as adaptations to particular environmental conditions. We argue that the first problem can be overcome with specific knowledge of phylogenetic relationships of the taxa under study, while resolution of the second problem requires identifying characters that are more relevant to the selective regime experienced by tiger beetles. We conclude that integrating ecological and phylogenetic data in cicindelid and carabid studies will yield stronger evidence for the patterns and processes underlying character change in these groups.

1. Introduction

It is now commonplace to incorporate information on the phylogenetic history of taxa into ecological studies, and to use 'comparative methods' for the examination of character state distribution in groups of organisms. The kinds of inferences that may be drawn from these studies and the best approach to obtain those inferences are unresolved debates in evolutionary biology (Brooks & McLennan 1991, Pagel 1994, Wenzel & Carpenter 1994, Harvey *et al.* 1995, Westoby *et al.* 1995). Many have argued that explicit hypothesis testing within a phylogenetic context can yield strong inferences about the causal factors affecting the evolution of traits, including those characterizing ecological interactions (Lauder 1981, Greene 1986, Coddington 1988, 1994, Baum & Larson 1991). At a time when the synthesis of ecological and phylogenetic approaches is imminent, it seems important to assess the potential of this development for research in the Carabidae and the related Cicindelidae.

Most research on carabids has been pursued on one of two main lines of investigation, ecology and systematics. Work in ecology benefited greatly from the seminal works of Lindroth (1949) and Thiele (1977) as well as biogeographic approaches by Darlington (1943) and others. At the same time, a tremendous body of literature on the systematics of many groups has accumulated (Lawrence *et al.* 1995). Yet, it appears that ecological studies and phylogenetic research in the Carabidae are largely carried out in isolation from each other. The work of Pearson and colleagues in the related Cicindelidae (e.g. Pearson & Mury 1979, Pearson *et al.* 1988, Pearson & Juliano 1994) has been a notable exception. These authors made an effort to incorporate an historical perspective in ecological research by assessing behavioral and ecological data sets in the context of presumed relationships among taxa at a time when comparative methods were just beginning to be developed (Felsenstein 1985, Greene 1986). Not surprisingly, their approach stimulated controversy on the way in which ecological and historical analyses should be combined in cicindelids (e.g. Mooi *et al.* 1989, Altaba 1991).

Tiger beetles are model organisms for ecological study because their life history parameters lend themselves to observation in the field and in the laboratory. Most species can be distinguished by their narrow habitat associations, distinct seasonal cycles with larval or adult overwintering, and numerous morphological and behavioral differences presumed to be correlated to their life style. Consequently, cicindelids have been used to address questions in a wide range of fields, including biogeography and phylogeography (Pearson & Ghorpade 1989, Vogler & DeSalle 1993), community ecology (Knisley 1984, Knisley 1987, Mury-Meyer 1987, Schultz & Hadley 1987, Pearson & Juliano 1994), conservation biology (Pearson & Cassola 1992, Vogler & DeSalle 1994), and population differentiation (Vogler *et al.* 1993). As we will argue below, studies in all of these areas will benefit greatly from incorporation of a phylogenetic perspective into ecological analyses.

The classification of cicindelids currently in use by most taxonomists was established by Rivalier in a series of papers for the world fauna of Cicindela (1950–1963) (e.g. Rivalier 1950, Rivalier 1963) and for the Cicindelidae (Rivalier 1971), but it was not primarily intended to reflect phylogenetic relationships. By grouping taxa into subgenera and species groups, an implicit statement of relationships was made without the aid of character based analysis. Subsequently, this situation was improved upon for some groups of *Cicindela*, in particular for the Australian (Freitag 1979) and South American (Freitag & Barnes 1989) taxa. However, Pearson *et al.*'s (1988) historical approach in the study of morphological and behavioral traits in North American and Indian *Cicindela* entirely relied on such non-evolutionary groupings.

In this paper, we address several issues raised by a study of chemical defenses in the genus *Cicindela* by Pearson *et al.* (1988), because they exemplify the difficulties that must be addressed in any study at the interface of ecology and systematics. First, we will examine the method of analyzing and interpreting variation in chemical defenses, as found in the paper of Pearson *et al.* (1988) and in subsequent controversial discussions. Next, we will evaluate prior assumptions made regarding character state transformations and character definition. Finally, we will illustrate a methodology of hypothesis formation and testing that is based on a phylogenetic approach to character evolution and analysis. Issues related to other aspects of tiger beetle defensive strategies, including the evolution of bright coloration, will be addressed elsewhere.

2. The evolution of chemical defense in tiger beetles

Many tiger beetles employ organic compounds to deter predators. The dominant compound of cicindelid defensive secretions is benzaldehyde, a constituent found in no other group of insects (Blum *et al.* 1981). Experimental evidence for the efficacy of this defensive compound comes from Pearson's (1985) studies of robber flies presented with paper models; benzaldehyde significantly reduced attack of models, when compared to untreated models. Pearson *et al.* (1988) assayed for the presence of benzaldehyde in some 80 *Cicindela* species from North America and India and in several outgroup taxa. Most outgroup taxa and 46% of the *Cicindela* species sampled were shown to produce more than trace amounts of benzaldehyde, while 40% and 14% of the *Cicindela* showed trace or no evidence of benzaldehyde production, respectively.

In the analysis of their data, Pearson *et al.* (1988) formulated two competing hypothesis with regard to the evolution of chemical defenses in *Cicindela*: —1. "similar (defensive) compounds occur among systematically similar species regardless of habitat and associated ecological differences"; and — 2. "similar compounds occur among ecologically similar species regardless of systematic affinities". The two data sets used to test these hypotheses, taxonomic affinities of species and classifications of the habitat in which species are found, were based on limited available information: taxonomic affinities were taken directly from the subgenus and species group designations of Rivalier (1954, 1963); habitat types were defined by Pearson *et al.* (1988) to describe the general physical aspect of each species' habitat.

A chi square test was used to examine the association of both parameters, systematic affinities and habitat type, with the presence of benzaldehyde. Whereas systematic affinity was significantly associated with benzaldehyde production, only a single habitat type was found significantly associated with the character. This resulted in the general conclusion by these authors that "historical factors are closely tied to predictable patterns of benzaldehyde presence", whereas "ecological factors alone have only limited predictive power". In a separate test, Pearson *et al.* (1988) found a significant association between the absence of benzaldehyde and the presence of one or more characters they thought might reduce predation through other means, including bright coloration, small size, and aggregating behavior.

Pearson *et al.* (1988) concluded that there was strong evidence of an historical effect in the evolution of benzaldehyde and little evidence of an ecological effect, thus supporting their first and rejecting their second hypothesis. In subsequent discussions, the conclusions of Pearson *et al.* (1988) were strongly endorsed by Mooi *et al.* (1989), but firmly rejected by Altaba (1991). Therefore, we will revisit the question about the evolution of chemical defenses in *Cicindela*, using a strictly phylogenetic approach. Our discussion follows the line of investigation established by Pearson *et al.* (1988), focusing first on the evidence used to evaluate historical effects, and then addressing the evidence used to study ecological effects.

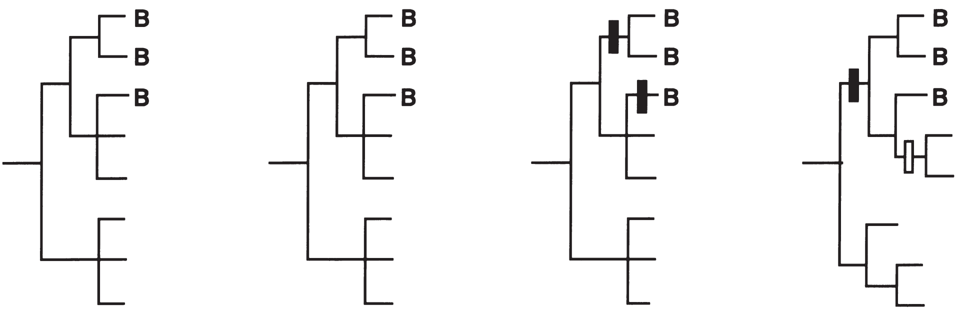
3. Using appropriate phylogenetic data

3.1. Linnean taxonomy

Pearson *et al.*'s (1988) conclusion that there was strong evidence of an historical effect on benzaldehyde evolution critically depends on their acceptance of the traditional classification scheme for the genus *Cicindela* as proposed by Rivalier (1954). This author established only two levels of hierarchy within the genus *Cicindela* (*s. l.*), subgenera and species groups, and made no further attempt to determine relationships within or among each of these groupings. Pearson *et al.* (1988) treated both of the hierarchical levels as groupings of equal rank, using each of them as an independent entity in their analysis of benzaldehyde production (Fig. 1). Because most of these groupings of closely related species are conserved for the state of benzaldehyde production, accepting these groupings as evolutionary entities means also to accept Pearson *et al.*'s (1988) basic conclusions of historical conservatism in benzaldehyde production.

In a re-evaluation of these data, Mooi *et al.* (1989) represented Rivalier's classification in the form of a phylogenetic (albeit highly unresolved) tree. In their estimation, the classification "contain[ed] sufficient hierarchical information and phylogenetic resolution to make the desired comparisons" (p. 191). Despite presenting an hypothesis of relationships, Mooi *et al.* (1989) did not consistently make use of this information in their analysis. In fact, they treated each species as an independent data point (e.g., when stating that 16% of *Cicindela* species unambiguously lack benzaldehyde) (Fig. 1), a procedure that is clearly inappropriate for the stated purpose of testing character associations (Felsenstein 1985).

In a dissenting conclusion, Altaba (1991) attempted to reconstruct the character states for ben-



Pearson et al. (1988)
Fraction of taxa consistent within each group:
2 out of 2
2 out of 3
3 out of 3

Mooi et al. (1989)
Total number of taxa producing benzaldehyde:
3 out of 8

Altaba (1991)
Optimization of benzaldehyde production:
2 forward changes

resolved phylogeny
Optimization of benzaldehyde production:
1 forward change, 1 reversal

Fig. 1. Schematic representation of previous approaches to analyzing historical associations of benzaldehyde production. A hypothetical cladogram represents the traditional classification of *Cicindela,* with two hierarchical levels equivalent to the species groups and subgenera of Rivalier (1950) and 8 terminal taxa. Taxa producing benzaldehyde are labeled with "B". Hash marks denote character state changes for benzaldehyde (filled hash marks, forward changes; open hash marks, reversals). The approaches of three previous studies to associate benzaldehyde production with the "phylogeny" are compared. Also shown is one possibility to resolve the polytomies of the traditional classification, with character state changes mapped. Assuming that the ancestral condition is absence of benzaldehyde, one (of the two) most parsimonious optimization of benzaldehyde production includes one forward change and one reversal.

zaldehyde based on outgroup criteria (Fig. 1), in order to infer the direction of character state changes during the evolution of *Cicindela*. This approach avoided the use of questionable statistical associations of the species groups with the character state of benzaldehyde. It also avoided the problem of giving equal rank to taxa for which no information of hierarchic position or monophyly is available. While we strongly favor his methodology, we believe that the phylogenetic data were not sufficient for his approach. In particular, it is unclear how he optimized character states on the unresolved phylogenetic hypothesis, especially given the large number of polytomies containing numerous terminals.

3.2. Character polarity

The direction of character state change is essential to hypothesis formation in integrating analyses of phylogeny and ecology. In fact, determining the ancestral state for benzaldehyde production was an important part of the scenario that Mooi *et al.* (1989) developed to interpret the distribution of benzaldehyde production among taxa. However, their claim that the presence of benzaldehyde is the ancestral state for the genus was not justified. The phylogenetic data currently available are not sufficient to draw any conclusions on polarity in this character (also see Altaba 1991). Mooi *et al.* (1989) argued that a larger number of taxa (seven of eight) in the outgroup, as well as those in the ingroup ("in most of the members of the genus *Cicindela*"), produced benzaldehyde. This "strongly suggests the occurrence of benzaldehyde is primitive for the genus" (p. 193/194). The proposition that the character state most widely distributed is plesiomorphic ("the commonality principle") is a weak one indeed and ignores basic principles of phylogenetic reconstruction (Watrous & Wheeler 1981, Nixon & Carpenter 1993). In conclusion, it is clear that accepting the "Linnean" taxonomy as a surrogate for a nested hierarchy is fraught with difficulties and can result in the formation of evolutionary hypotheses without proper evidence.

4. Identifying appropriate ecological factors

The intention of Pearson *et al.* (1988) was to evaluate the correlation of "ecological factors" with the evolution of defensive compounds and to separate these from historical factors. The analysis lacked, however, the necessary phylogenetic perspective required to conduct such an evaluation. As in any analysis of character evolution, the analysis of ecological associations requires two steps. First, the characters of interest must be defined in terms of their character states and the transformation among these states. Second, the character transformation must be tested with a phylogenetic hypothesis for the organisms under study. We address the first step here, leaving the second step for future analysis .

4.1. "Habitat type" as a phylogenetic character

As is the case for many carabids and their relatives, most species of *Cicindela* can be distinguished based on their association with a narrowly defined type of habitat. These habitat types can be classified by their physical aspects and appear to be similar in many parts of the world (Pearson & Juliano 1994). Also, there is little variation in habitat specificity throughout the geographical range of a species (Schultz 1989). Therefore, it is tempting to use information on habitat type as a proper phylogenetic character (Vogler *et al.* 1993, Pearson & Juliano 1994). It is evident, however, that a particular "habitat type" can be more precisely described by its physical properties, such as soil type, humidity, soil particle size, vegetation cover, climatic conditions etc. Additionally, in cicindelids all these properties appear to affect both larval and adult survivorship, and therefore the fitness of individuals in a given habitat (Knisley 1984, Pearson & Knisley 1985, Knisley 1987, Mury-Meyer 1987, Schultz & Hadley 1987). Thus, habitat type represents a grossly oversimplified, but convenient surrogate for a complete description of the environment experienced by cicindelids.

Is it possible, then, to use habitat type as a character that can be optimized on a phylogeny to assess its transformation during the history of a lineage? And, if so, can this character transformation be used to test whether a particular defensive strategy is "correlated with ecology", i.e., if there are associated character state changes in the defensive strategy? As with many ecological and behavioral characters (Miller & Wenzel 1995), the character of habitat type suffers from the problem that common descent of the character states cannot be established easily. The habitat association of a certain species, as the grand sum of complex ecological interactions of organisms with their biotic and abiotic environment, is based on factors that cannot be observed easily. Also, the factors that determine the habitat associations may be different for separate colonizations of a certain habitat type. Therefore, the occurrence of taxa in a particular habitat type may have multiple evolutionary origins and causes in a lineage and, thus, the test of associations with other parameters (such as the evolution of benzaldehyde) may not necessarily reflect the same kind of interdependence.

In addition, the homology assessment for a character such as "habitat type" is likely to be dependent on the ecological context (Miller & Wenzel 1995). Even if we ignore the problem of the definition of character states and presume that habitat type can be established as a character using overall resemblance in physical appearance, the evolution of chemical defenses may have to be viewed in a different context of ecological interactions. This is because those parameters that determine habitat associations may not be the same as those involved in predator escape and defense. Whereas these may be the same in some cases (e.g. physical aspects of the habitat such as vegetation cover that affect interactions with predators as well), others (e.g. the occurrence of particular predators) may be completely different. It is obvious, therefore, that the evolution of "habitat type" is different with respect to habitat requirements and the predator environment. Thus, general statements about the "correlation with ecology" have to be evaluated very carefully, and are, in our opinion, only possible when the ecological context has been defined in very specific terms.

4.2. "Habitat type" and adaptation

The exact definition of habitat as a phylogenetic character may appear a rather esoteric exercise without an explicit purpose to apply this information. We have to be equally explicit, therefore, about what can be learned from the delineation of habitat type as a phylogenetic character and its character state transformations. The previous papers on the issue vary in the extent to which this problem is discussed. In the initial interpretation of the data, Pearson *et al.* (1988) made only a modest claim about the purpose of the study; focusing on the assumption of many ecologists of the time which mostly ignored the phylogenetic conservatism of ecological parameters. However, it is clear that by limiting the discussion ton the issue of ecological *versus* historical associations, they avoided one of the most interesting, but highly problematic questions: is "habitat type" the factor that represents the selective regime causing changes in a particular defensive strategy, such as benzaldehyde production? While the issue was avoided in the original presentation, Altaba (1991) followed with his reappraisal and stated insightfully that "the dichotomy of history versus ecology is only valid if the latter denotes current selective pressures not accountable for traits inherited from ancestral populations", thus raising the issue of adaptation. The evidence considered necessary to infer adaptation is probably one of the most controversial issues in comparative biology and has recently received discussions from many angles (Coddington 1994). In the context of this debate, the data set on defensive compounds in *Cicindela* gains new relevance. We will discuss this issue in greater detail, as it is important to analyzing the evolution of chemical defenses of tiger beetles, in particular, and in discussing the application of comparative methodology to studies of carabids and cicindelids, in general.

The dichotomy of ecology and history in the discussion of adaptive traits is based on the assumption that both factors are somehow mutually exclusive. More specifically, historical factors are assumed to represent the accumulated "phylogenetic constraints" of a lineage, whereas ecological factors represent the current selective pressures acting on existing taxa. Thus, "it is important to distinguish characters that are inherited through phylogeny from those that are directly linked to an individual's fitness" (Altaba 1991, p. 104). This view, and similar propositions in the more recent ecological literature such as "phylogenetic correction" (Westoby *et al.* 1995), identify the variation correlated with phylogeny as a confounding parameter which needs to be eliminated from the data before assessing the adaptive significance of traits. The purpose of phylogenetic reconstruction, according to this perspective, is to provide the data base for this correction.

This approach of evaluating the historical and ecological information does not seem appropriate to us. Information relating to the history of a trait and to the adaptive significance of a trait are of different kinds. Whereas the latter pertains to the biological function of the trait, the function is not necessarily correlated with a particular history of this trait. An adaptation may have occurred early in the evolution of a clade, and still be adaptive. It could have evolved very recently, in the extreme case being an apomorphy. It even may have originated for a biological role that is different from its current function (exaptations *sensu* Gould & Vrba 1992). In turn, the current function of this trait says nothing about its history. If a good case for the adaptive significance of a trait exists (as there is evidence from Pearson's study with paper models to demonstrate the deterrent effect of benzaldehyde), this information does not mean it has evolved in the particular species or population where its adaptive significance can be demonstrated. Thus, the dichotomy of ecological and historical factors is not meaningful to distinguish between traits that are adaptive (i.e. contribute to fitness) and those that are merely conserved as a result of the phylogenetic history. In fact, adaptive traits may very well be conserved because of the phylogenetic background. This phenomenon may be particularly prevalent among closely related taxa that share most of their traits and tend to experience similar selective environments. Therefore they may also share a large number of their adaptations. In conclusion, the optimization of characters onto a phylogenetic hypothesis may be used to reconstruct the evolution of any character including those that are presumed to be adaptations. The approach can merely provide support consistent with a hypothesis of adaptation but cannot usually be taken as proof of it. Strong evidence for adaptation must come from a synthesis of phylogenetic analyses of character transformation in a lineage in combination with ecological experiments in relevant taxa (Leroi *et al.* 1994).

5. The phylogenetic approach

Weaknesses have been demonstrated in Pearson *et al.*'s (1988) approach of evaluating the effects of ecology and history on the distribution of benzaldehyde production among cicindelids (Mooi *et al.* 1989, Altaba 1991, this analysis). Yet, we feel that a phylogenetic approach to studies in ecology has tremendous potential to enhance the understanding of the evolution of complex character suites, including the multiple defensive strategies of tiger beetles. In fact, the phylogenetic context is critically important to formulating specific hypotheses in the study of many ecological traits. We maintain that the primary reason for the failure in previous analyses was the lack of a well supported hypothesis of relationships among *Cicindela* species.

In general, Pearson *et al.* (1988) were interested in detecting the effects of ecological and historical factors on benzaldehyde production. As pointed out before, the more interesting question concerns the selective factors in the evolution of benzaldehyde defenses. Altaba (1991) made an attempt to invoke a role of selection in the evolution of benzaldehyde defense. According to his argument, robber flies are the primary targets of benzaldehyde defenses, and these predators are found primarily in wet habitats. If benzaldehyde production is an adaptation to the presence of robber flies, then wet habitat and the presence of benzaldehyde should be associated. Altaba's (1991) finding of a significant association between the character states would be necessary, but not sufficient, to argue that some aspect of the habitat is a causal factor determining changes in benzaldehyde production. An additional condition would be a direction of character change that is consistent with the hypothesized selection regime (Greene 1986, Baum & Larson 1991, Coddington 1988).

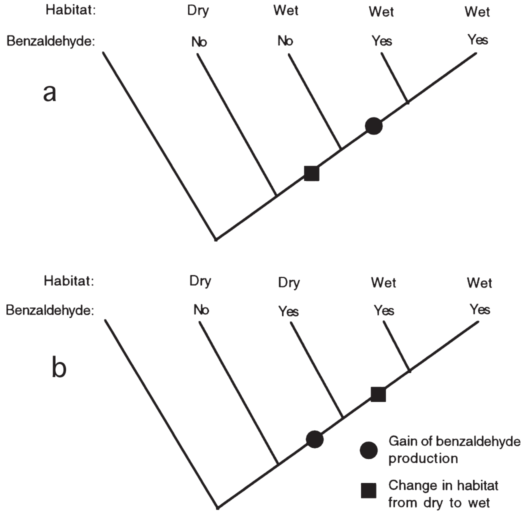


Fig. 2. Hypothetical cladogram and character variation for a putative selective regime (robber flies in wet habitat) and a putative adaptation (benzaldehyde production). Only the character distribution in the upper panel (a) is consistent with the hypothesis of adaptation in this trait.

At this point, a phylogenetic hypothesis for the taxa included in the Pearson *et al.* (1988) analysis is not available for this test, and we are limited to a hypothetical analysis of this problem. For this purpose, we have coded the two characters of interest, benzaldehyde and habitat water availability, as binary characters (benzaldehyde present or absent, habitat wet or dry). [It is clear that both of these characters should be defined in more precise terms: e.g., recent assays have demonstrated that there is continuous variation in benzaldehyde production, and that other compounds may be important in predator deterrence (Kelley & Schilling, in preparation). Similarly, the character of water availability is not an overall aspect of the habitat, such as "sand dune" or "moist forest floor", but a factor that can be defined more specifically, e. g., with respect to moisture content of the soil]. To support the conclusion that benzaldehyde production evolved as adaptation to, e.g., the presence of robber flies (or some other factor) in wet habitats, it now must be shown that the origin of benzaldehyde production occurred in a species living in a wet habitat. Thus, the pattern of character state change shown in Fig. 2a (change in habitat from dry to wet precedes the gain of benzaldehyde production) is consistent with this hypothesis. Alternative orders of change, for example in the case where benzaldehyde production originates in a lineage in dry habitat (Fig. 2b), are inconsistent with the proposed hypothesis. The hypothesized sequence of change could not be distinguished, however, from a pattern of simultaneous character change in benzaldehyde production and habitat wetness (Baum & Larson 1991), or if relevant species had not been sampled in the analysis (Miller & Wenzel 1995). Finally, it is important to note that finding of character state associations and patterns of character state change consistent with an hypothesis are not conclusive as evidence of adaptation (Leroi *et al.* 1994). Demonstration of adaptation requires additional studies that show the fitness advantage of the trait, similar to the approach taken in Pearson's

(1985) study of robber fly deterrence by benzaldehyde.

Assuming, however, the sequence of habitat and benzaldehyde evolution has been established, the distribution of character change can be further scrutinized. For example, the distribution of character state combinations in the genus *Cicindela* suggests that benzaldehyde production also may have been lost in some lineages (Pearson *et al.* 1988, Altaba 1991). Such a loss in benzaldehyde production should have been preceded by a change of habitat type to a drier condition, perhaps one in which (for example) robber flies are less abundant. If this is not confirmed by the data, alternative causal explanation can be considered. One of them would be, as proposed previously (Pearson *et al.* 1988), that there is selection for the loss of benzaldehyde because of the high energy expenses for its production. It is also possible that alternative defensive strategies such as cryptic body coloration become relatively more important in these taxa. Refined hypotheses of this kind, however, are only possible with information on the phylogenetic context in hand.

6. Conclusion

There is no doubt that the integration of phylogenetic and ecological approaches will have far-reaching consequences for Carabidology. Pearson *et al.*'s (1988) study was the first to explicitly investigate a historical association of ecological traits, but other researchers, too, have suggested that many traits of interest in ground beetles are shared with related taxa. As recent reviews show (e.g. DeQueiroz & Wimberger 1993, Miller & Wenzel 1995), there is ample evidence for phylogenetic conservation of ecological, behavioral and physiological traits in most groups of insects. Prerequisite for the study of phylogenetic associations of traits and their sequence of character states is the availability of information on hierarchical relationships. We are confident that the recent development in DNA sequencing techniques will provide the needed data to establish strong phylogenetic hypotheses for many of those carabids most often the focus of ecological studies. Several such molecular analyses are now under way.

Well supported phylogenetic hypotheses of relationships will change the analysis and interpretation of ecological data obtained for carabids. For example, the complex traits that determine presence or absence of taxa in pitfall traps can be dissected into specific pieces of information regarding habitat associations, seasonality, dispersal activity and other ecological and behavioral traits. Phylogenetic information also will enhance the design of field and laboratory experiments by helping the researcher to select appropriate taxa for such studies, and determining the correct taxonomic level for comparative ecological analyses. Finally, and perhaps most important, this phylogenetic integration can be used by researchers to rephrase anecdotal arguments of adaptation as hypotheses that are amenable to rigorous testing.

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