

Historical Perspectives, Ecology, and Tiger Beetles: An Alternative Discussion

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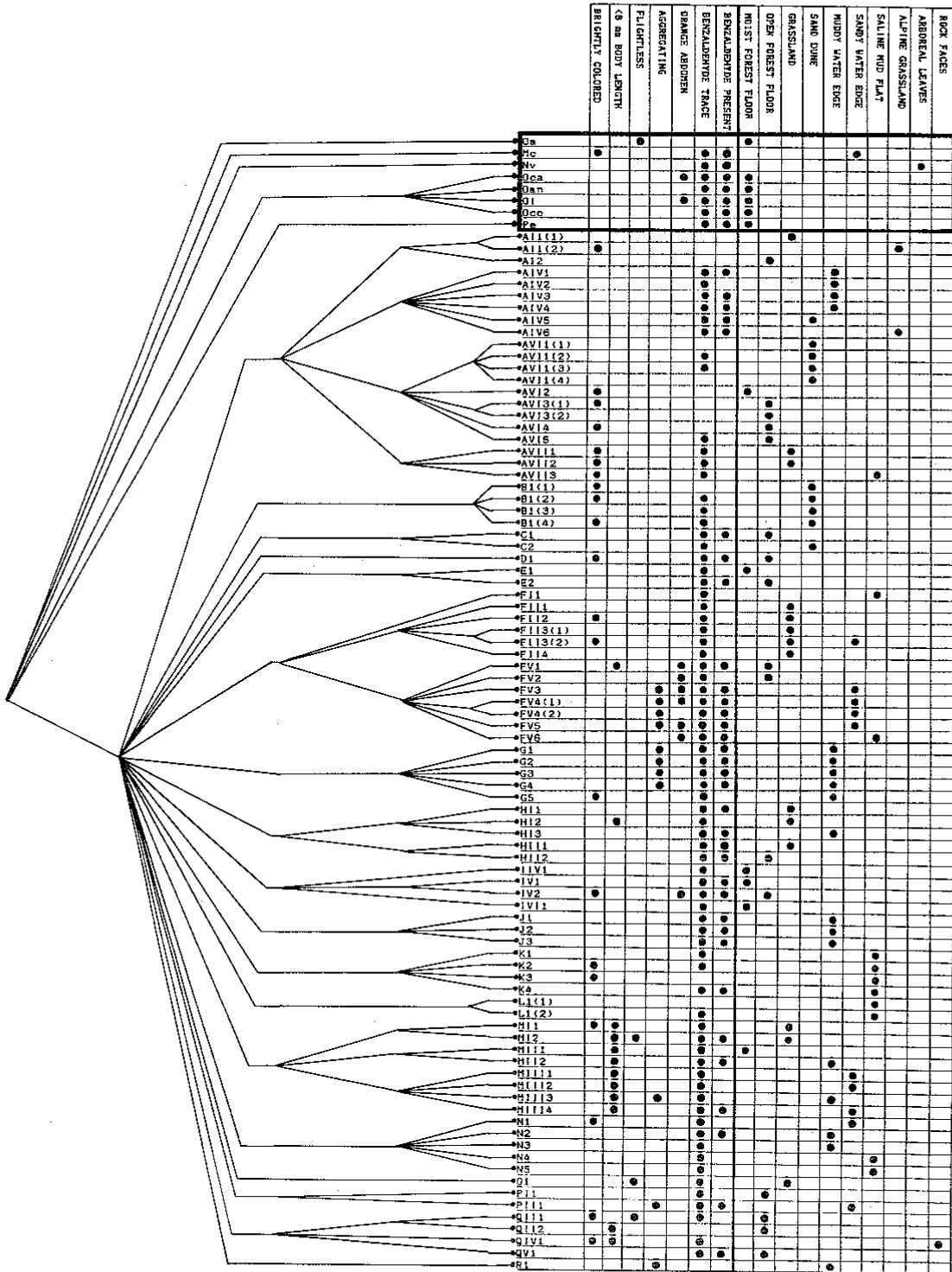
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In a recent work entitled "Historical perspective and the interpretation of ecological patterns: Defensive compounds of tiger beetles (Coleoptera: Cicindelidae)," Pearson et al. (1988) present a valuable data set with which they explore the relationship between evolutionary history and ecology. They showed statistically that in tiger beetles, the presence of benzaldehyde is non-randomly correlated with systematic relatedness (historical factors), regardless of ecological factors, and that these historical factors were "likely to be generally important in interpreting ecological data, either as alternative or interactive processes." We would like to take this argument further and demonstrate that, in

the study by Pearson et al., history is not merely a factor, but is the sole determinant of benzaldehyde distribution. We hope to show that a slightly different and more promising synthesis of phylogenetic and ecological approaches can be taken from the same data and assumptions.

We follow Pearson et al. in assuming that the classification given in their Appendix A approximates evolutionary relationships. Our review of the literature indicates that this classification contains sufficient hierarchical information and phylogenetic resolution to make the desired comparisons. Figure 1 presents a tree that faithfully reconstructs the hierarchies inherent in this classification. The habitat,



behavioral, and morphological characters listed in Pearson et al.'s Appendix A have been superimposed on the tree in the form of a data matrix, and the occurrence of benzaldehyde in the various taxa can also be mapped onto the phylogeny (Fig. 1). We chose to map the occurrence of "trace" quantities of benzaldehyde as well, so that all taxa in which benzaldehyde is present are redundantly coded for trace amounts. This takes into account the fact that the character "benzaldehyde trace" is subsumed by "benzaldehyde present."

The two "alternative predictions" presented by Pearson et al. can now be restated in a phylogenetic context:

1) *The distribution of benzaldehyde is more compatible with phylogeny than with habitat preference.* That is to say, habitat preference exhibits more incongruencies with the phylogeny than does benzaldehyde distribution when these characters are mapped onto the phylogeny.

2) *The distribution of benzaldehyde is more compatible with habitat preference than with phylogeny.* That is, benzaldehyde distribution exhibits more incongruencies with the phylogeny than does habitat preference.

Having presented the analysis in a way

that *neither adds new data nor relies on new assumptions*, what follows can be regarded as an alternative discussion to that of Pearson et al. that presents some of their premises and conclusions in a more explicit way. Figure 1 shows that the benzaldehyde data are more congruent with the phylogeny than the habitat data, upholding prediction 1. There are numerous examples of taxa that share a habitat preference, but do not share most recent common ancestry. For tiger beetles at least, habitat preference appears to have little predictive value in defining the groups indicated by the classification. This is not surprising, as members of monophyletic groups often live in widely varying habitats.

The distribution of benzaldehyde amongst the *Cicindela* subgroups is slightly more complicated. A hypothesis of the evolutionary polarity of benzaldehyde occurrence in the genus *Cicindela* is germane to a discussion of the relationship between tiger beetle phylogeny and ecology. Figure 1 shows that benzaldehyde is present not only in most of the genera and species sharing recent ancestry with *Cicindela* (the "outgroups" of *Cicindela*), but also in most of the members of the genus *Cicindela* itself.

FIG. 1. Character matrix and phylogeny constructed from the classification in Appendix A of Pearson et al. (1988). Large dots in matrix indicate presence of feature. Habitat characters are listed above the heavy horizontal line, benzaldehyde distribution and morphological characters below the heavy line. Taxa in box constitute the outgroup to the genus *Cicindela*. For the genus *Cicindela*, the first letter of each code refers to the species group, roman numeral to subgroups, arabic numeral to species, and numeral in parentheses to subspecies as listed in Appendix A of Pearson et al. (1988). Codes: Oa = *Omus audouini*, Mc = *Megacephala carolina*, Nv = *Neocollyris variitarsus*, Oca = *Odontocheila cayennensis*, Oan = *O. annulicornis*, Ol = *O. luridipes*, Oco = *O. confusa*, Pe = *Pentacomia egregia*, AI1(1) = *Cicindela longilabris longilabris*, AI1(2) = *C. longilabris ostenta*, AI2 = *C. nebraskana*, AIV1 = *C. hirticollis*, AIV2 = *C. duodecimguttata*, AIV3 = *C. repanda*, AIV4 = *C. oregona*, AIV5 = *C. depressula*, AIV6 = *C. limbata*, AVI1(1) = *C. formosa formosa*, AVI1(2) = *C. formosa manitoba*, AVI1(3) = *C. formosa generosa*, AVI1(4) = *C. formosa pigmentosignata*, AVI2 = *C. sexguttata*, AVI3(1) = *C. patruela patruela*, AVI3(2) = *C. patruela consentanea*, AVI4 = *C. splendida*, AVI5 = *C. purpurea*, AVI11 = *C. pulchra*, AVI12 = *C. pimeriana*, AVI13 = *C. fulgida*, B1(1) = *C. scutellaris scutellaris*, B1(2) = *C. scutellaris lecontei*, B1(3) = *C. scutellaris rugifrons*, B1(4) = *C. scutellaris rugifrons*, C1 = *C. tranquebarica*, C2 = *C. lengi*, D1 = *C. aurofasciata*, E1 = *C. andrewesi*, E2 = *C. calligramma*, F11 = *C. willistoni*, F111 = *C. nigrocoerulea*, F112 = *C. horni*, F113(1) = *C. punctulata punctulata*, F113(2) = *C. punctulata chihuahuae*, F114 = *C. obsoleta*, FV1 = *C. abdominalis*, FV2 = *C. rufiventris*, FV3 = *C. sedecimpunctata*, FV4(1) = *C. ocellata ocellata*, FV4(2) = *C. ocellata rectilatera*, FV5 = *C. haemorrhagica*, FV6 = *C. schauppi*, G1 = *C. sumatrensis*, G2 = *C. fowleri*, G3 = *C. angulata*, G4 = *C. cardoni*, G5 = *C. chloris*, H11 = *C. catena*, H12 = *C. striatifrons*, H13 = *C. cancellata*, H111 = *C. multiguttata*, H112 = *C. striolata*, H113 = *C. fabriciana*, IV1 = *C. assamensis*, IV2 = *C. bicolor*, IV11 = *C. hamiltoniana*, J1 = *C. virgula*, J2 = *C. intermedia*, J3 = *C. dupontii*, K1 = *C. pamphila*, K2 = *C. circumpicta*, K3 = *C. fulgoris*, K4 = *C. severa*, L1(1) = *C. togata togata*, L1(2) = *C. togata globicollis*, M11 = *C. lemniscata*, M12 = *C. celeripes*, M111 = *C. severini*, M112 = *C. bigemina*, M113 = *C. minuta*, M114 = *C. erudita*, M115 = *C. venosa*, M116 = *C. grammophora*, N1 = *C. marutha*, N2 = *C. macra*, N3 = *C. cuprascens*, N4 = *C. hamata*, N5 = *C. nevadica*, O1 = *C. belfragei*, P11 = *C. fastidiosa*, P111 = *C. melancholica*, Q111 = *C. westermanni*, Q112 = *C. dasiodes*, Q113 = *C. rugosiceps*, Q114 = *C. motschulskyana*, R1 = *C. biramosa*.

Regardless of how the precise relationships at the base of the phylogeny are eventually resolved, this strongly suggests that the occurrence of benzaldehyde in *Cicindela* is primitive for the genus (present in the common ancestor of the genus), and that any taxa that lack the compound have secondarily lost the ability to produce it. This means that the presence of benzaldehyde cannot be used to define monophyletic groups (clades) within *Cicindela*. Thus the most important historical aspect of benzaldehyde distribution within *Cicindela* is not the production of the compound, but its absence.

This observation raises questions about the nature of the characters "benzaldehyde present" and "benzaldehyde absent." When the distribution of the state "benzaldehyde trace" is examined (see Fig. 1), only 14 of the 87 taxa (about 16%) in *Cicindela* unambiguously lack the compound. Therefore, there is a suggestion that the potential to produce the compound is present in up to 84% of the taxa in the genus as well as in most outgroup taxa. The absence of this potential can be construed as a shared, derived trait (synapomorphy) that groups (albeit with some incongruence) those taxa in which benzaldehyde was undetected. Further study might show the benzaldehyde metabolic pathway to be a better phylogenetic character (in the sense that confidence in homology of the character is greater) than simple presence, absence, or trace of the compound. However, the possibility exists that benzaldehyde is the product of independently evolved pathways in different species. Because we have no evidence of this, we have assumed that the ability to produce benzaldehyde is homologous.

The phylogeny suggests a test of the hypothesis that benzaldehyde is absent in some taxa because of the high energy expenses incurred in its production. If it is relatively simple to "turn off the benzaldehyde tap," and if it is indeed advantageous to do so to reduce energy expenses, then repeated, independent loss of benzaldehyde would be more likely than repeated, independent gain. The test de-

pends on the ability to infer that the production of benzaldehyde, however slight, is primitive for the entire genus *Cicindela*. The phylogenetic hypothesis has allowed us to make this inference.

Loss of the ability to produce benzaldehyde raises several ecological questions. Using the phylogeny, an explicit hypothesis relating the history of the taxa to ecological factors can be produced. For example, if the major predators of tiger beetles are absent from the habitats in which are found taxa with no more than trace amounts of benzaldehyde, then we can pose at least three questions:

1) Is there a correlation between the absence of benzaldehyde and the absence of robber flies?

2) Is there a correlation between the complete absence of robber flies and the habitats in which we find benzaldehydeless tiger beetles?

3) Do any other characters exhibit correlations with predators? There are presently no data with which to explore 1) and 2), but these should not be difficult to obtain. It would be of interest to map the ranges of *Cicindela* taxa with those of major predators in order to determine if robber flies actually occur everywhere that tiger beetles do. If they do not, might we expect a concomitant drop in the production of benzaldehyde? Or do other predators fill the robber fly role? As for question 3, it is possible in a phylogenetic context to test for correlations between behaviors and morphologies that could compensate for the absence of benzaldehyde in some taxa. Different predators may trigger different strategies of defense. For example, loss of benzaldehyde production might be correlated with the presence of such features as aggregating behavior, an aposematic abdomen, or other bright coloration. It is of interest to note that of the 37 *Cicindela* taxa with these non-chemical antipredator strategies, only 13 also produce benzaldehyde in more than trace amounts. In addition, 19 of the 21 brightly colored *Cicindela* taxa produce no more than trace amounts of benzaldehyde. A conservative estimate from the phylogeny suggests that

the latter situation could have evolved independently at least a dozen times, attesting to the potential importance of a "compensatory effect." The phylogenetic significance of these sorts of findings can only be determined when the features are mapped onto a phylogeny, clearly pinpointing areas for further investigation.

Leaving the alternative discussion and returning now to Pearson et al.'s invocation of "historical factors" to explain "some of the exceptions to patterns of benzaldehyde presence or absence," it is clear that history cannot be considered a factor in the same sense that habitats, morphology, predators, or behaviors can. History runs through all of the character distributions because changes in these characters are actually historical events that occur in the evolution of the taxa in question. The events are embedded in, and actually comprise that history.

Because of its potential and novelty, Pearson et al.'s approach is an important contribution to the integration of ecological and phylogenetic approaches. However, we would emphasize that phylogenetic analyses are of primary importance

in studies of this type, and that a fully corroborated phylogeny for the tiger beetles is urgently needed to expand upon and make explicit the themes hinted at in Pearson et al.'s treatment, and in the alternative discussion presented here. We strongly endorse the policy that "historical perspective should be an integral part of every ecologist's hypothesis formation," but add that the panorama from this perspective is greatly enhanced when viewed from the top of a tree.

ACKNOWLEDGMENT

We thank David Pearson and his colleagues for sending a pre-print of their paper on tiger beetle defensive compounds to our phylogenetics discussion group. Their paper was a focal point for the evolution of several ideas that eventually became incorporated into this alternative discussion.

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Received 11 November 1988; accepted 27 January 1989