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THE PHYLOGENETIC STUDY OF ADAPTIVE ZONES:  
HAS PHYTOPHAGY PROMOTED INSECT DIVERSIFICATION?

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Differential diversification rates are a fundamental problem in macroevolution. In Simpson's (1953) influential view, diversification is accelerated by ecological opportunity, such as dispersal into newly opened territory, extinction of competitors, or adoption of a new way of life ("adaptive zone"). As summarized by Futuyma, "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" (1986, p. 356).

The adaptive-zone concept is widely invoked to explain the histories of particular groups (Hecht 1963; Tevesz and McCall 1976; Foote 1977; Berenbaum 1983). It figures prominently in theories of community evolution (Ehrlich and Raven 1964; Zwölfer 1978) and in the "syncretistic" theory of classification (Simpson 1961; Mayr 1969). It is part of the common lore of biology. Most entomology texts, for example, contain an assertion like the following: "[The ability to fly] is perhaps one of the most important reasons for [insects'] tremendous success relative to the rest of the animal kingdom. Flight has enabled insects to take advantage of environmental situations virtually untouchable by their non-flying rivals." (Romoser 1973, p. 161.)

Prima facie adaptive-zone arguments, however, are probably not well justified. First, much of the apparent variability in evolutionary rates may be consistent with simple stochastic models of phylogenesis (Raup et al. 1973; Raup and Gould 1974; Gould et al. 1977; but see Stanley 1979; Stanley et al. 1981). For example, all degrees of relative diversity between sister groups are equally likely under one model of random speciation and extinction (Farris 1976). Although the standing of such "null" models is doubtful (Hoffman 1983), they suggest caution about facile ecological explanations of differential diversity.

Second, there are deterministic alternatives (not mutually exclusive) to the adaptive-zone hypothesis. One hypothesis holds that rapid diversification (and extinction) is associated with stenotopy, since ecological generalists are relatively insensitive to geographic and temporal environmental variation and hence less susceptible to isolation and differential selection that might foster speciation

(Eldredge 1976; Eldredge and Cracraft 1980; Vrba 1980, 1984; Cracraft 1984; Novacek 1984; but see Flessa et al. 1975). Vrba (1984) provided a possible example in the antelopes. Diversification rate may also be affected by breeding system and population structure, independent of ecological role (Wilson et al. 1975; Gilinsky 1981; West-Eberhard 1983). Thus, some authors have invoked founder effects and/or sexual selection, rather than ecological opportunity per se, to account for the spectacular diversification of drosophilid flies in the Hawaiian Islands (Spieth 1974; Carson and Kaneshiro 1976; Ringo 1977; Templeton 1979; Barton and Charlesworth 1984).

Finally, adaptive-zone hypotheses have generally been derived a posteriori, invoking simply the unique ecological features of a diverse group (Cracraft 1982). As Gould and Calloway suggested, in doubting that superior adaptation was responsible for the Mesozoic "replacement" of brachiopods by lamellibranchs: "We all know, in our heart of hearts, that we could have devised equally compelling reasons for [group] B's success over [group] A had this, rather than A's triumph, been the actual outcome" (1980, p. 384).

In testing the adaptive-zone hypothesis, we may, by analogy to the study of individual adaptation (Lewontin 1978), distinguish functional from comparative approaches. Taking the first of these, one might attempt to show for a particular diverse group how its diversification makes use of ecological opportunity. For example, the hypothesis that the rodents have diversified rapidly (in part) *because* of the diverse resources made available by their "key adaptation," gnawing, gains credence from the striking diversity of trophic uses to which that ability has been put (Simpson 1961).

Single-case adaptive-zone studies, however, are not likely to be definitive. The existence of ecological differentiation is neither necessary nor sufficient evidence for an effect of ecological opportunity on diversification rate. It is hard to rule out all the potentially confounding influences on any one lineage, which may include such singular events as sudden widespread extinctions (Gould and Calloway 1980). Moreover, an association of species diversity with ecological opportunity has several possible mechanisms (Echelle and Kornfield 1984). It could reflect increased speciation rate resulting from diversifying selection in new niches; decreased extinction from competitive exclusion among new reproductive isolates whose niche differences were incidental to speciation; or simply increased speciation opportunity resulting from expanded species' ranges, with no requirement for niche differentiation.

To test the adaptive-zone hypothesis in its broad sense, as distinct from a particular diversification model, we must ask whether adaptive shifts are repeatedly associated with accelerated diversification across many independent groups. To pursue this correlative approach, we must avoid the charge of circularity by specifying a priori what constitutes an adaptive shift. One way to do this is by equating adaptive zones to broad resource or habitat categories, such as grazing versus browsing among herbivorous mammals, or phytophagy versus parasitism or predation among insects. Adaptive zones so defined are likely to have been invaded independently by different lineages, permitting replicated tests of their influence on diversification.

Second, we require a means of comparing diversification rates among lineages. One approach is to map resource use most parsimoniously on a cladogram (Farris 1970; Fitch 1971) in order to identify the lineages in which adaptive shifts have occurred. By definition, the sister group(s) (Hennig 1966) of such a lineage is (are) the same age. Any difference in diversity between sister groups, therefore, reflects different rates of diversification (origination minus extinction; Stanley 1979). The adaptive-zone hypothesis can be taken to predict that, when one of two sister groups remains in the adaptive zone of their common ancestor, the group that has undergone the adaptive shift will be consistently the more diverse. Since sister groups have had identical histories up to the time of their divergence, they should provide the closest possible phylogenetic control for other effects on evolutionary rate. In statistical terms, the design is a paired comparison. The test is conservative because the adaptive shift may postdate the divergence of the sister groups.

Sister-group comparisons of evolutionary rates have been advocated by several authors (Hennig 1966; Cracraft 1982; Eldredge 1982; Novacek and Norell 1982; Mitter and Brooks 1983; Larson 1985), but the practical complications have not been thoroughly explored. Here we apply this approach to one type of ecological shift, the origin of phytophagy among insects. We take "diversity" to mean number of species. Similar logic could, of course, be applied to other aspects of morphological or taxonomic diversity.

#### PHYTOPHAGY IN THE INSECTS AS A TEST CASE

Amplifying an argument of Southwood (1973), Strong et al. (1984) pointed out that half the total number of insect species feed on vascular plants, but these phytophages are essentially restricted to just 9 of the 30 extant orders (Kristensen 1981). Habits such as saprophagy and predation, by contrast, occur in nearly all orders. Strong et al. proposed that "life on higher plants presents a formidable evolutionary hurdle that most groups of insects have conspicuously failed to overcome. Once the hurdle is cleared, however, radiation may be dramatic." (1984, p. 15.) A variety of similar hypotheses linking insect and plant diversification has been proposed (Ehrlich and Raven 1964; Zwölfer 1978; Narchuk 1979; Price 1980).

Southwood (1973) envisioned three evolutionary barriers to phytophagy. The risk of desiccation is greater for exposed phytophagous feeding than for the primitive hexapod habit of concealed, detritivorous feeding. Attachment to the host is a second problem. Finally, living plants are often markedly less nutritious and palatable than other insect foods, since they are both low in nitrogen and "unbalanced" in amino acid composition and, moreover, protected by a variety of chemical and mechanical properties (Denno and McClure 1983; Strong et al. 1984).

Once the insects have circumvented these barriers, phytophage diversification may be promoted by the biomass and the great variety of resources offered by host-plant species and plant parts and by the probable absence of interspecific competition among phytophages (Strong et al. 1984). Like other authors (Ehrlich

and Raven 1964), Strong et al. suggested that insect and plant diversification are mutually reinforcing. Zwölfer (1978) also stressed the diversifying pressures on phytophages exerted by parasitoids.

We have reexamined Southwood's (1973) postulate that the origin of phytophagy has accelerated insect radiation, by cataloguing the independent origins of higher-plant feeding in the Hexapoda and by comparing sister-group diversities for as many of these as current taxonomic evidence allows.

#### METHODS

We have attempted to identify all of the known higher-plant-feeding insect groups (see the Appendix), beginning from the compilations by Southwood (1973) and Strong et al. (1984). We have undoubtedly omitted some groups, and will be grateful for other examples.

The first methodological problem is to define "higher-plant feeding," because insects use higher plants as food in many ways (Southwood 1973). We have followed as closely as possible Strong et al.'s definition of phytophagy, "feeding on the living tissues of higher plants" (1984, p. 3), which excludes algal and other non-tracheophyte feeders, wood borers, nectar feeders, and species that use dead plants and leaf litter as food. Insects feeding on developing seeds are included, but those that take only shed seeds are excluded. Pollen feeding is also excluded, even though it is often hypothesized to be transitional to phytophagy in the strict sense (Malyshev 1968). Strong et al. did not explicitly categorize holometabolous insects, in which only the adult stage takes plant food (e.g., the meloid beetles). Such species depend much less on plants for growth and reproduction than do species whose larvae eat plants; we catalogue them below, but we exclude them from the strict definition of phytophagy.

This definition of phytophagy is somewhat arbitrary (Strong et al. 1984) because the variation among insect diets is too complex to be fully rendered by any discrete classification (see the Appendix). Nevertheless, this definition is largely independent of insect taxonomy and clearly corresponds to a major ecological difference from most other feeding habits.

We encountered several methodological problems in constructing sister-group comparisons. First, many phytophagous lineages have given rise secondarily to species with other habits. For example, the Hymenoptera (see below; fig. 1) include both primitively phytophagous and derived, enormously diverse parasitic forms. We have counted the diversity of only the phytophages in such groups, because these represent the degree of radiation in the phytophagous adaptive zone since it was invaded.

As the hymenopteran example illustrates, the adaptive-zone hypothesis in its usual formulation, adopted here, would not predict that phytophagous groups should always diversify faster than their sister groups. Rather, it says only that the origination of phytophagy (like other novel ways of life) should speed diversification with respect to sister lineages retaining more-primitive habits, because it results in a kind of ecological release. Thus, the great diversity of parasitic Hymenoptera as compared to the primitively phytophagous sawflies

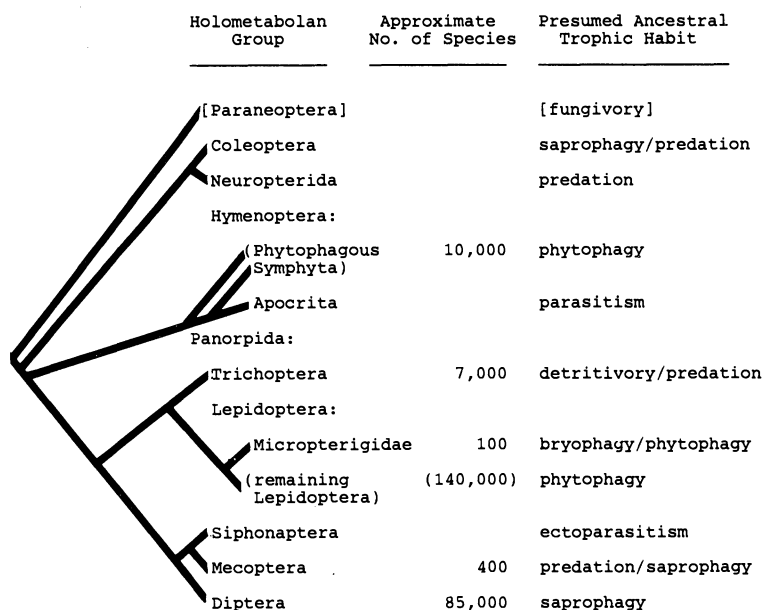


FIG. 1.—Partial phylogeny of the Holometabola, showing relationships of some phytophagous groups. Sources for relationships, diversities, and feeding habits in the table and the Appendix.

offers no evidence against the proposition being tested; indeed, it supports the more general adaptive-zone hypothesis. It might be hypothesized, however, that phytophagy always offers greater ecological opportunity than other adaptive zones (Strong et al. 1984), regardless of its novelty to a lineage. In that case, all sister-group comparisons involving phytophages should be counted. We have found insufficient evidence about secondarily non-phytophagous groups to distinguish these alternatives.

A second problem arises when the primitively non-phytophagous sister group of a phytophagous clade includes a phytophagous component. The comparisons of these two phytophage lineages with their sister groups will not be entirely independent, because the sister group of the younger phytophages will be included in that of the older. For example, the primitively phytophagous Hymenoptera are compared below with their primitively saprophagous probable sister group, the panorpoid orders (fig. 1). The panorpoids themselves contain several derived phytophagous groups, such as the Lepidoptera. The sister groups with which these phytophages might individually be compared also form part of the basal saprophagous element of Panorpidia, whose diversity it is logical to compare with that of phytophagous Hymenoptera.

Our approach to such interdependent comparisons has been to determine first whether exclusion of the sister groups of the younger phytophage groups (e.g., Trichoptera, in the case of Lepidoptera) would affect the conclusion regarding the older phytophage group (Hymenoptera, in this example). If not (as in this and all

other cases we encountered), then both comparisons can safely be used. If the reverse were true, one might reasonably include either comparison, perhaps randomly chosen, but not both.

Two final complications can arise when the relationships of phytophagous groups are incompletely resolved. Some well-defined, predominantly phytophagous clades contain a few taxa of more-primitive habits but unknown systematic position, for example, the exceptional saprophages in the chloropine-oscinelline clade of chloropid flies. A comparison of such clades with their sister groups may be biased against the adaptive-zone hypothesis, if their non-phytophagous members are in fact primitive, since phytophagy would then have originated after the clade had diverged from its sister group. We have excluded even predominantly phytophagous clades (e.g., the cecidomyiine flies), however, when there is evidence that they harbor multiple, currently unclarified origins of phytophagy.

In other cases, the sister group of a phytophagous clade has been only approximately established. For example, the affinities of the enormous phytophagous beetle group *Phytophaga* (*Chrysomeloidea* plus *Curculionoidea*) lie clearly with the *Cucujoidea*, but whether the exact phytophagan sister group is the cucujoids as a whole or some subgroup thereof is not certain. In this case, however, the answer does not bear on Southwood's (1973) postulate, because the *Phytophaga* are far more diverse than the entire *Cucujoidea*. We have included such comparisons in our tally because in all similar instances we have so far encountered (table 1), all defensible resolutions of the phylogeny yield the same answer about relative diversification rates. Bias might be introduced, however, if they did not; this and other possible artifacts are treated in the Discussion.

A review of the trophic habits and phylogenetic relationships of all phytophagous insect groups known to us, with a defense of the inclusion or exclusion of each from the final tally of sister-group comparisons (the table), is given in the Appendix. Our treatment of inter-ordinal phylogeny follows Kristensen (1981). Estimates of intra-ordinal relationships were based on our evaluation of the recent literature, in consultation with specialists (see the Acknowledgments). To maximize the number of comparisons, we have used some groups whose taxonomic relationships (e.g., languriid beetles), ancestral feeding habits (e.g., agromyzid flies), or trophic advancement with respect to the sister group (trichophoran bugs) is only provisionally established. Because these hypotheses are independent of our investigation, their provisional acceptance here should introduce no bias.

#### RESULTS

In 11 of the 13 sister-group comparisons extractable from our review of insect phytophagy (see the Appendix), the phytophagous lineage is more diverse than its presumed sister group, by at least twofold (table; one-tailed sign test,  $P = 0.01$ ). Several additional cases will, on further taxonomic resolution, almost surely support this trend (e.g., psilid flies and several lineages of cecidomyiid flies; acridoid grasshoppers; trachyine buprestid beetles). *Cylindrotomine* flies, on the other hand, may be another contrary example.

TABLE 1

SUMMARY OF SISTER-GROUP DIVERSITY COMPARISONS ON INDEPENDENT PHYTOPHAGOUS LINEAGES

PRIMITIVELY PHYTOPHAGOUS LINEAGE		SISTER GROUP		
Taxon	Approximate No. of Species (phytophages only)	Taxon	Approximate No. of Species (excluding phytophages)	SIGN OF DIFFERENCE IN DIVERSITY*
<b>HEMIPTERA</b>				
Tingidae	1,800 <sup>1</sup>	Joppeicidae	1 <sup>2</sup>	
(? + Thaumastocoridae)	<u>15<sup>1</sup></u>			
	≤1,815			+
Miridae	10,000 <sup>1</sup>	Isometopidae	60 <sup>3</sup>	+
Trichophora	>5,000 <sup>4</sup>	Aradidae	1,000 <sup>1</sup>	+
<b>COLEOPTERA</b>				
Elateridae	9,000 <sup>5</sup>	Cerophytidae and/or	7 <sup>5</sup>	
+ Cebriionidae	<u>170<sup>5</sup></u>	Eucnemidae and/or	1,200 <sup>5</sup>	
	9,170	Throscidae	<u>190<sup>5</sup></u>	
			≤1,397	+
Scarabaeidae <i>sensu lato</i> , minus Geotrupinae, Aphodiinae, and Scarabaeinae	14,000 <sup>6</sup>	Geotrupinae or Aphodiinae/Scarabaeinae	400 <sup>7</sup> 3,200 <sup>6</sup>	+
Languriinae	410 <sup>8</sup>	Lobarinae + Erotylidae	200 <sup>8</sup> <u>1,500<sup>8</sup></u>	
			1,750	-
Epilachninae	700 <sup>9</sup>	Coccinellini	250 <sup>9</sup>	+
Phytophaga	130,000 <sup>5</sup>	non-phytophagous Cucujoidea	≤10,000 <sup>5</sup>	+
<b>HYMENOPTERA (Symphyta only)</b>	10,000 <sup>10</sup>	Panorpida	80,000 <sup>4</sup>	-
<b>LEPIDOPTERA</b>	140,000 <sup>11</sup>	<i>Trichoptera</i>	7,000 <sup>12</sup>	+
<b>DIPTERA</b>				
Chloropidae				
Oscinellinae	1,350 <sup>13</sup>	Siphonellopsinae	80 <sup>13</sup>	
+ Chloropinae	<u>860<sup>13</sup></u>			
	2,210			+
Tephritidae <i>sensu stricto</i>	4,000 <sup>14</sup>	all or part of non-phytophagous Tephritidae <i>sensu lato</i>	1,733 <sup>14</sup>	+
Agromyzidae	2,000 <sup>15</sup>	Clusiidae	200 <sup>14</sup>	+

NOTE.—Summary: the number of positive differences, 11; the number of negative differences, 2; sign test, one-tailed,  $P = 0.011$ .

SOURCES.—1, Slater 1982; 2, Davis and Usinger 1970; 3, Wheeler and Henry 1978; 4, Richards and Davies 1977; 5, Lawrence 1982; 6, Britton 1970; 7, Boucomont 1912; 8, Schenkling 1930–1934; 9, Sasaji 1968; 10, Smith 1979; 11, Nielsen 1985; 12, Wiggins 1982; 13, H. Anderson 1977; 14, Bickel 1982; 15, Spencer and Steyskal 1986.

\* The phytophagous lineage minus the sister group.

DISCUSSION

Although narrowly defined higher-plant feeding is confined to only nine orders, it has probably arisen at least 50 times among just the extant forms with known habits. However, since even approximate delimitations and sister-group comparisons are currently possible for only a small fraction of known phytophagous lineages, we regard our present findings as preliminary. With additional phylogenetic and life history work, the association of phytophagy with diversification

rate should be testable with some precision, given the potential number of independent comparisons.

Our small final tally represents a complex set of judgments about often fragmentary evidence (see the Appendix), and it is potentially subject to a number of artifacts. Moreover, even if the trend suggested by our compilation is real, we cannot conclusively rule out explanations other than ecological opportunity. We claim only that Southwood's (1973) postulate has survived an initial attempt at phylogenetic quantification. The complications encountered, however, are worth considering because they may be general to sister-group analysis of diversification rates.

The possible artifacts in our tally include those affecting the scorings of comparisons included and those affecting the representativeness of our sample of phytophagous clades. Errors in scoring might result from including "predominantly phytophagous" clades that contain trophic exceptions of unknown systematic position. These could conceivably harbor multiple independent origins of phytophagy, with different diversities in relation to their sister groups. Although we have excluded any comparisons in which this seemed likely, clades containing undetected multiple origins of phytophagy should still provide valid comparisons, albeit weaker ones, when compared with their primitively non-phytophagous sister groups.

One source of possible sampling bias is our use of incompletely resolved relationships. We have included such comparisons when the plausible sister groups for a phytophage lineage have been narrowed to just a few possibilities, all of which yield the same conclusion about relative diversification rates. This criterion could bias the sample toward either exceptionally diverse or exceptionally depauperate phytophagous groups. However, we are not aware of any phytophage lineage with relationships as well understood as those included in our tally, whose implications for the postulate under test are ambiguous. This potential artifact should be detectable in the future by phylogenetic study of groups excluded here because of insufficient taxonomic resolution.

Bias could arise if the habits and relationships of large phytophagous groups were better known than those of small ones. For example, a small, entirely phytophagous taxon might be undetected as such because we had no information on its habits. Since the sister groups of phytophagous clades are equally subject to this effect, it is not a likely source of bias. The probability that a clade's sister group is known appears to be primarily a function not of its diversity, but of the availability of character evidence. Indeed, some of the largest phytophagous groups are of uncertain placement, in part because their very diversity makes them hard to characterize.

Although we doubt that our sample is biased toward large phytophagous groups for any given age, it is almost certainly slanted toward relatively old ones. Most of our comparisons involve groups of family rank or higher, even though most phytophagous groups are of lower rank. Phylogenetic relationships among higher taxa appear to be understood more often than those among their subordinate taxa. This effect should not bias the results toward a positive association of phytophagy

with diversification rate so long as phytophagous clades have been sampled from the same size distribution as their sister groups. The age at which the adaptive-zone effect will be most manifest is itself a question of interest, but it cannot be addressed with the available data.

Assuming that our results do not have an artifactual basis, as we have argued, they may have several explanations. If both new characters and reproductive isolation arise only in peripheral isolates and, further, if only such new species were capable of further speciation, an asymmetrical phylogeny would result in which the sister group of each species (except the most recent) would be both more derived and more diverse. Any new feature would thus appear associated with an increased diversification rate. Although a similar model has been posed for the relationship between speciation and biogeography (Hennig 1966; Stanley 1979), as in unidirectional colonization of an archipelago, it is doubtful that such localized and extreme effects can be extrapolated to large, now widespread groups.

Phytophagy per se could increase the diversification rate in several ways. The resource base available to primary consumers is larger than that available to higher trophic levels, and this could enhance diversity by itself (Brown and Gibson 1983; Strong et al. 1984; Glazier 1987). Alternatively, as the adaptive-zone argument proposes, diversification may follow from ecological release associated with adaptive shift per se. These alternatives might be distinguished by extending our form of analysis to higher trophic levels. An analysis of parasitism among insects (Askew 1971) would be an illuminating comparison.

If the acceleration of phytophage diversification is a consequence of access to diverse new niches, shifts of phytophagous lineages to new groups of hosts, defined according to taxonomy, chemistry, or ecology, should also enhance diversity (Ehrlich and Raven 1964; Mitter and Brooks 1983). No such effect is predicted by an alternative (but complementary) hypothesis, that phytophages speciate rapidly because their hosts impose a fragmented population structure and diversifying selection (Bush 1975; Zwölfer 1978; but see Futuyma and Mayer 1980; Mitter and Futuyma 1983). Several authors have described cases in which shifts of phytophagous insect lineages to new hosts may have occasioned adaptive radiation (Zwölfer 1978; Berenbaum 1983; but see Thompson 1986), but no explicit phylogenetic analyses of these cases exist.

Even if the practical problems can be solved, our approach to the question of adaptive zones will necessarily have limitations. First, it cannot distinguish among possible mechanisms for radiation resulting from adaptive shift. It does, however, constitute necessary evidence for the adaptive-zone hypothesis in its broad, macroevolutionary sense, as invoked by diversification models based on resource use (Hoffman 1983).

Second, the requirement for sets of equivalent adaptive zones, while making these zones independent of particular (diverse) groups, risks arbitrary definitions because no two invasions of the "same" zone are identical in detail. But arbitrary adaptive zones should make the ecological-shift effect harder to detect. The objection loses force when, as in this case, a strong trend emerges.

Finally, affording equal weight to each sister-group comparison ignores the subtleties of Simpson's (1953) original argument. For example, it does not distinguish between early and late stages of an adaptive radiation (Sepkoski 1978) or between initial and subsequent invasions of the same adaptive zone (Ehrlich and Raven 1964). Given a sufficient diversity of comparisons, particularly with some fossil dates, it should be possible to take account of these complexities. At the same time, focusing on a representative sample of adaptive shifts, not just on "successful" radiations, should tell us how much special pleading the adaptive-zone hypothesis requires.

#### SUMMARY

Simpson's postulate that rapid diversification follows entrance into a new "adaptive zone" is frequently invoked a posteriori for groups of unusual diversity. The postulate can be tested more rigorously by defining an adaptive zone according to ecological criteria, independent of particular groups of organisms. The adaptive-zone hypothesis predicts that if multiple lineages have invaded a new adaptive zone, they should be consistently more diverse than their (equally old) sister groups, when the latter retain the more primitive way of life.

Higher-plant feeding among insects is an independently defined, repeatedly invaded adaptive zone, to which a profound acceleration of diversification rate has been attributed. We have quantified the evidence for this hypothesis by comparing sister groups and species diversity of as many phytophagous insect groups as current taxonomic evidence allows. A sign test showed significant association of diversification rate with the adoption of phytophagy. The possible artifactual bases for this trend are discussed and provisionally rejected. We discuss several possible biological explanations for the association, including models of phylogenesis either dependent on or independent of ecological role.

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## APPENDIX

## HIGHER-PLANT-FEEDING HEXAPOD GROUPS AND THEIR RELATIONSHIPS

The trophic habits, phylogeny, and species diversities of the phytophagous insect groups known to us are reviewed below, in approximate phylogenetic sequence (Kristensen 1981). At first mention, the names are set in capital letters of those few taxa for which sufficient ecological and phylogenetic information exists for inclusion in our tally of sister-group comparisons (the table), according to the criteria developed in the text.

## ENTOGNATHA

Some sminthurid collembolans (*Bourletiella* spp. and *Sminthurus* spp.) are phytophagous, but the habits of the family are too poorly known (Christiansen 1964; W. Richards 1968) to trace the origins of phytophagy.

## LOWER NEOPTERA

Phasmida (2500+ spp.), including timemas, are entirely phytophagous (Key 1970), but their phylogenetic position, like that of other neopteran groups, is obscure (Kristensen 1981).

Among Orthoptera (sensu stricto), the Caelifera comprises the entirely phytophagous 10,000+ species of Acridoidea (Key 1970) and the 1000+ species of algal- and detritus-feeding Tetrigoidea and Tridactyloidea (Gangwere 1961, 1967; Key 1970). Phylogenetic relationships within the Caelifera are little understood, and phytophagy may not be primitive. The Acridoidea contains more than half the species of Orthoptera (Key 1970).

Most groups of Ensifera (sister group of Caelifera) are omnivores and are not regarded here as phytophages (Southwood 1973). The Phaneropterinae, largest subfamily of tetrigoniids, and a few other groups are true foliage feeders (Gangwere 1961, 1967). Phylogenetic relationships within the Ensifera are little understood.

## PARANEOPTERA

Phytophagy in the Acercaria (fig. A1; Kristensen 1981) is restricted to the Condylognatha, which comprises the sister groups Thysanoptera and Hemiptera.

Thysanoptera are predominantly phytophagous; many species live in and feed on flowers (Lewis 1973; Southwood 1973; Ananthakrishnan 1979). A few groups feed on fungi (Mound and Palmer 1983), and some are predators. Thysanopteran phylogeny is uncertain, and phytophagy may have arisen more than once (fig. A1). In one view (Stannard 1957, 1968; modified in Ananthakrishnan 1979), the thrips are parsimoniously treated as primitively phytophagous, with fungus feeding derived independently in Merothripidae, Uzelothripidae, and Phlaeothripinae. (This assumes, on no definitive evidence, that the Aeolothripidae are primitively flower feeding and that the predatory forms are derived.) Mound et al. (1980), however, offered two alternative phylogenies (apart from the possibility that phlaeothripines are the oldest thysanopterans), both differing from Stannard's in the placement of *Uzelothrips* and in treating the aeolothripids and merothripids as sister groups and in rejecting assignment of *Uzelothrips scabrosus* Hood to the Thripidae. Under neither of Mound et al.'s proposals can either the primitive habit of the order or the number of origins of phytophagy be determined without reference to higher-level relationships in the Acercaria (see below).

The primitive habits of Hemiptera (including Homoptera) are uncertain (fig. A1). The suborder Heteroptera (true bugs) is most parsimoniously regarded as originally predaceous (but see Cobben 1978, 1979; Sweet 1979). The apparent sister group of the heteropterans, Coleorrhyncha (20 spp.; Kristensen 1975), may feed on bryophytes (Southwood 1973). The apparently monophyletic homopteran groups Auchenorrhyncha ( $\approx 20,000$  spp.; Richards

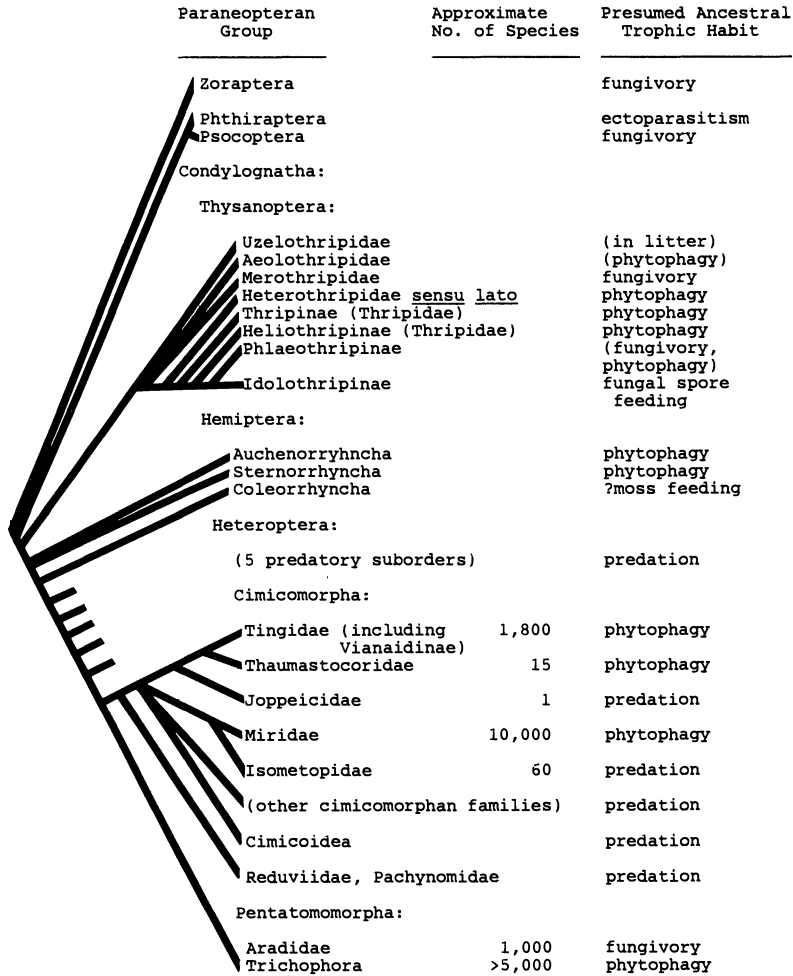


FIG. A1.—Partial phylogeny of the Paraneoptera, showing placement of some phytophagous groups. Sources for relationships, diversities, and feeding habits in the table and the Appendix text.

and Davies 1977) and Sternorrhyncha ( $\approx 12,000$  spp.; Woodward et al. 1970), which together are more diverse than the rest of the Acercaria combined, are entirely phytophagous, but their relationships to each other and to the Heteroptera plus Coleorrhyncha are unknown (Kristensen 1981). Hence, the early origins of true phytophagy in Condylognatha are too uncertain for inclusion in our tally.

Following the cimicomorphan heteropteran relationships (fig. A1) of Kerzhner (1981) as modified by Schuh (1986), phytophagy in the Cimicomorpha is most parsimoniously interpreted as having arisen from predation independently in Miridae and in the group TINGIDAE ( $\approx 1800$  spp.; Slater 1982) plus THAUMASTOCORIDAE (15 spp.; Slater 1982). The probable sister group of the tingid-thaumastocorid lineage is the predaceous species *Joppeicus paradoxus* (see Davis and Usinger 1970). The thaumastocorids may not actually be closely related to the tingids (Schuh, pers. comm.); their deletion from the diversity comparison would not affect the conclusion.

The apparently predaceous family Isometopidae (about 60 spp.; Wheeler and Henry 1978) is the probable sister group of the MIRIDAE *sensu stricto* (Schuh 1976, 1986; Wheeler and Henry 1978). The mirids, by far the largest heteropteran family (10,000 spp.; Slater 1982), are largely phytophagous, though whether they are primitively so awaits study of the monotypic, cladistically basal subfamily Cylapinae (Schuh 1976). We have therefore included the isometopid-mirid comparison in our tally. It must be pointed out, however, that most phytophagous mirids are probably also facultative predators (Leston 1961; Southwood 1973), and several derived groups show distinctly different habits, including obligate predation. Further phylogenetic analysis of this family should allow more-detailed study of the evolutionary consequences of trophic habits.

The remaining heteropteran phytophages belong to the TRICHOPIPHORA (Schuh 1986). The nearest relatives of trichophorans (Leston et al. 1954; Usinger and Matsuda 1959; Schuh 1986) are probably the fungivorous Aradidae (1000 spp.; Richards and Davies 1977; Slater 1982). The Trichophora includes 5000 or more plant feeders (Richards and Davies 1977); there are also several groups of predators (e.g., asopine pentatomids), and most lygaeoids feed on seeds, many on shed seeds. We have assumed that concealed fungus feeding preceded phytophagy, a frequent progression among other insects. This comparison is provisional, however, because given only these two groups one could not rule out the opposite sequence.

#### HOLOMETABOLA: COLEOPTERA

Phytophagy appears to have arisen independently in four holometabolan orders, the Coleoptera, Hymenoptera, Lepidoptera, and Diptera (fig. 1).

Adults of many coleopteran species feed on pollen or take fallen seeds, but phytophagy in the narrow sense appears restricted to the Staphyliniformia, Elateriformia, Scarabaeiformia, and Cucujiformia (fig. A2; Crowson 1981). The primitive habit in Coleoptera is probably saprophagy or fungivory (Hamilton 1978; Crowson 1981); predation is also widespread in largely saprophagous lineages (Crowson 1981). Our estimate of phylogeny follows Crowson (1955, 1981) except as otherwise specified.

Within the Staphyliniformia, phytophagy appears restricted to the silphid genus *Aclypea* (R. Anderson and Peck 1984), whose sister group is not known.

Within the Elateriformia, phytophagy in the narrow sense is restricted to the ELATEROIDEA and Buprestoidea. Except for the small subfamily Pyrophorinae, whose members are largely predatory, most elaterid larvae feed on plant roots. Relationships within the family are poorly known, but predation is probably secondary, since the probable sister group CEBRIONIDAE (Crowson 1955) also has root-feeding larvae. The sister group of the elaterid-cebrionid lineage is possibly the Throscidae (= Trixagidae, about 190 spp.; Crowson 1955; Britton 1970); these three families bear an apparent sister-group relationship to the Cerophytidae (7 spp.) and to the 1200 species of the Eucnemidae (Lawrence 1982). The throscids, cerophytids, and eucnemids all live in rotting wood (Arnett 1968). Since all resolutions of this set of families yield the same conclusion for diversification rates, we include the elaterid-cebrionid phytophages in our tally.

Most buprestid larvae are borers in living or freshly killed wood, and they are thus not phytophagous in the strict sense. The largest, apparently monophyletic subfamily Trachyinae consists of leaf miners, apparently derived from agriline twig miners (Fisher 1922; Cobos 1979). This subfamily is excluded from our tally, however, because relationships within the apparently paraphyletic Agrilinae are little known. The buprestids illustrate the somewhat arbitrary definition of phytophagy adopted here, since their various plant-attacking habits grade into each other. The Buprestidae are two orders of magnitude more diverse than their nearest relatives, the Dryopoidea (or some subset thereof; Kasap and Crowson 1975). The dryopoids are aquatic or semiaquatic algal and detritus feeders (Dillon and Dillon 1972).

Phytophagy in the Scarabaeiformia is restricted to the SCARABAEIDAE broadly defined (Howden 1982). The majority (>70%) of the nearly 25,000 scarab species (Lawrence 1982)

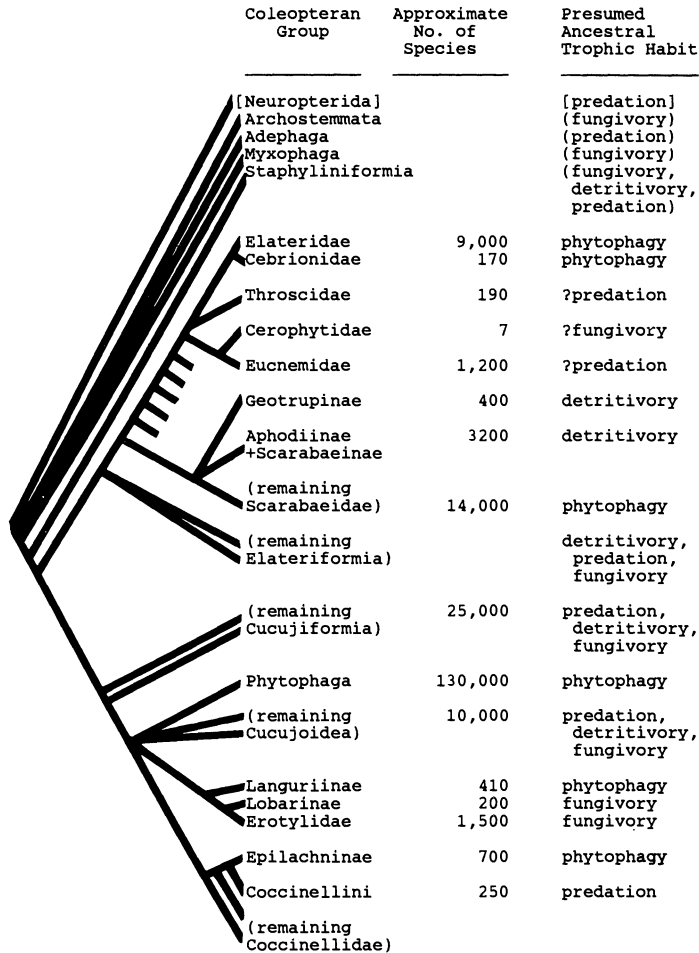


FIG. A2.—Partial phylogeny of the Coleoptera, showing relationships of some phytophagous groups. Sources for relationships, diversities, and feeding habits in the table and the Appendix text.

belong to a largely phytophagous clade including the subfamilies Dynastinae, Rutelinae, Cetoniinae, and Melolonthinae; larvae in these groups feed on roots of angiosperms, and adults feed on the foliage. The probable sister group of this assemblage is either the aphodiine-scarabaeine clade (3200 spp.; Britton 1970) or the geotrupines ( $\approx 400$  spp.; Boucomont 1912). Most of these are saprophagous, although members of the monotypic geotrupine tribe Lethrini provision larval cells with fresh vegetation (Howden 1955), and root feeding appears to have evolved independently in the aphodiines (Howden 1982). The phytophagous clade is far more diverse than any candidate sister group.

Within the Cucujiformia are several phytophagous clades.

Among the otherwise fungivorous or saprophagous Languriidae, members of the derived subfamily LANGURIINAE (410 spp.; Schenkling 1931–1934), so far as they are known, bore into the stems of herbs. The apparent sister group of the Languriinae is the subfamily Lobarinae, the tribe Pharaxonothini of which appears to be the nearest relative of Eroty-

lidae, whose members are strictly fungivorous (1500 spp.; Schenkling 1931–1934; Gupta and Crowson 1971). We have therefore compared the Languriinae with the lobarinerothyrid clade, though we do not know the habits of the small, most primitive languriines (tribe Thallisellini), which are characterized by peculiar mouthparts (Gupta and Crowson 1971).

Many Mordellidae (about 1200 spp.; Lawrence 1982) feed on flowers as adults and mine stems or leaves as larvae; many others have predatory or parasitic larvae (Richards and Davies 1977). Relationships are obscure within the family; these beetles may not be primitively or even predominantly phytophagous.

Meloidae (3000 spp.; Lawrence 1982) are parasitic as larvae, but the adults feed on foliage. As discussed earlier, taxa whose early stages are not phytophagous are excluded under our strict definition of phytophagy. The phylogenetic position of this family is unclear. Crowson initially placed it doubtfully near the Rhipiphoridae but later moved it to a distant set of cucujiform families (1955, 1981).

The larvae of *Byturus* attack developing rosaceous fruits, but the habits of the remaining Byturidae (about 300 spp. in about a dozen genera) are little known (Barber 1942). According to Crowson (1955), the byturids are most closely related to the fungivorous Biphyllidae (200 spp.; Lawrence 1982).

Most species of Nitidulidae are saprophagous, but two of six subfamilies (Cateretinae and Meligethinae) are characterized by phytophagy: the larvae feed on developing flowers, and the adults on pollen. The relationships among the subfamilies, however, have not been studied, and the placement of the family is obscure (Crowson 1981).

Tenebrionidae (18,000 spp.; Lawrence 1982) are mostly fungivores or detritivores, but a few (relationships unknown) have root-feeding larvae, and the adults of the lagriine genus *Lagria* are reported to feed on foliage.

Among the otherwise predaceous Coccinellidae, EPILACHNINAE are strictly phytophagous as both larvae and adults. We have compared the Epilachninae (700 spp.) with its apparent sister group, the tribe Coccinellini (250 spp.; Sasaji 1968); the nominate subfamily is paraphyletic.

The feeding habits of the very diverse PHYTOPHAGA (Chrysomeloidea plus Curculionoidea; 130,000 spp.; Lawrence 1982) range from root, wood, or seed boring to leaf mining to exposed feeding on foliage, but phytophagy in the strict sense is predominant and apparently ancestral. The major exception is the Cerambycidae (30,000 spp.; Lawrence 1982), which resembles the Buprestidae in that its members were originally wood borers; attacking live plants and folivory are restricted to the advanced supertribe Phytoeciides. The sister group of the Phytophaga is either the Cucujoidea (about 10,000 spp.; Lawrence 1982) or some subset thereof (Crowson 1955, 1981); Phytophaga are considerably more diverse than any candidate sister group. Cucujoids are primitively saprophagous or fungivorous (Lawrence and Newton 1982), though some are also predatory, and one group, the Epilachninae, is phytophagous but not related to the Phytophaga (see above).

#### HOLOMETABOLA: HYMENOPTERA

SYMPHYTA (10,000 spp.; Smith 1979) are entirely phytophagous in the broad sense (though some are wood borers) except for the small parasitic family Orussidae (Smith 1979). Sawflies are generally agreed to be paraphyletic, and the Siricoidea is the probable sister group of the Apocrita (Gibson 1985). Phytophagy may thus be taken as the primitive hymenopteran habit, from which parasitism arose in the ancestral Apocrita. The probable sister group of the Hymenoptera (Kristensen 1981) is the Panorpida (fig. 1), which seems likely to have been primitively detritivorous and/or fungivorous given the predominance of these habits among the Mecoptera, primitive Diptera, and Trichoptera. We have compared the symphytan Hymenoptera (excluding Orussidae) with the Panorpida (excluding Lepidoptera and other phytophagous groups); Panorpida are several times more diverse. The same conclusion holds if the Hymenoptera is instead the sister group of the remaining Holometabola (Kristensen 1981).

Strict phytophagy has re-evolved in several groups of Apocrita, including the cynipid gall wasps, the agaonid fig wasps, and scattered members of chalcidoid families such as Encyrtidae, Eurytomidae, Pteromalidae, and Torymidae (Riek 1970; Krombein et al. 1979), but sister groups are known for none of these. Bees (Apoidea), as pollen feeders, are not phytophagous in the strict sense, but they are several times more diverse than any of their likely sister groups among the generally predatory sphecoids (Michener 1970). The pollen-provisioning masarine vespids, in contrast, are much less diverse than their predatory sister group, Gayellinae (Carpenter 1982).

PANORPIDA: LEPIDOPTERA

Within the panorpoids, phytophagy has arisen independently in Lepidoptera and Diptera.

Whether primitive LEPIDOPTERA (140,000 spp.; Nielsen 1985) fed on higher plants is not certain. The larval biology of the oldest group, Micropterigidae (Kristensen and Nielsen 1979), has been little studied, but some species feed on bryophytes (Powell 1980; Tuskes and Smith 1984), and others include angiosperms in their diet (Lorenz 1961; Luff 1964). With a few secondary exceptions, all remaining Lepidoptera feed on higher plants (Powell 1980). Whether we compare the micropterigids with the remainder of the Lepidoptera, or that order as a whole with its sister group, the Trichoptera, we obtain the same conclusion.

PANORPIDA: DIPTERA

Although most flies are saprophages, feeding on higher plants has probably arisen more often in the Diptera than in any other insect order, and it now occurs in at least 20 families (Narchuk 1979). Phytophagous fly larvae frequently mine leaves, fruits, or roots, but they seldom feed on exposed foliage (Southwood 1973). Few fly families are trophically homogeneous, and phylogenetic relationships within (and indeed among) most fly families are little understood. We have therefore been able to extract only three provisional sister-group comparisons from this order. Except as indicated, we have relied on Steyskal's (1974) synthesis of recent views on dipteran phylogeny.

Among the nematocerans, Tipulidae are mostly aquatic or terrestrial detritivores, but some members of all three subfamilies feed on the foliage of mosses or higher plants. This is especially characteristic of the small, possibly relict subfamily Cylindrotominae (especially *Cylindrotoma*; Alexander and Byers 1981; Pritchard 1983). One Hawaiian tipulid (*Limonia kauaiensis*) is unique in having leaf-mining larvae (Hardy 1960). Neither feeding habits nor relationships in this family are known well enough for us to include tipulid phytophages in our tally. The soil-inhabiting bibionids have sometimes been reported to damage the roots of higher plants, but their habits and relationships have been little studied; they may not feed on live tissue (Colless and McAlpine 1970).

Cecidomyiidae exhibit a great diversity of feeding habits, including parasitism, predation, saprophagy, mycophagy, and phytophagy in the strict sense. The probable sister group, Sciaridae (Matuszewski 1982), is mycetophagous, as are the primitive cecidomyiid subfamilies Lestremiinae (194 spp.) and Porricondylinae (278 spp.; Skuhravá 1986, cited in Roskam 1985). Cecidomyiinae (1800 spp.) are predominantly phytophagous, but evidence suggests several independent origins of this habit (Roskam 1985; Gagné 1986). Although the current lack of phylogenetic resolution for these clades precludes their inclusion in our tally, they are almost certainly larger than their respective mycetophagous sister groups (Narchuk 1979; Roskam 1985; Gagné 1986).

Among the orthorrhaphous brachycerans, narrowly defined phytophagy seems restricted to the dolichopodid genus *Thrypticus* (Robinson and Vockeroth 1981; relationships not established), whose larvae mine grass stems.

Phytophagy has multiple origins in the Muscomorpha. Most larval Syrphidae are saprophages; some are predaceous; and both fungus feeding and live-stem and root mining are common in *Cheilisia* (>250 spp. worldwide; relationships unknown; Wirth et al. 1965). Larvae of isolated species in such genera as *Lampetia*, *Eumerus*, *Merodon*, and *Portevinia*

are reported to damage bulbs (Stubbs and Chandler 1978), but they may be feeding only on already rotting tissue or associated fungi (Wirth et al. 1965).

Psilidae ( $\approx 100$  spp.; Richards and Davies 1977) mine live stems and roots (Shewell 1965; Hennig 1973). We have excluded them from our tally because of divergent opinions about their relationships, although they are more diverse than any suggested sister group. Griffiths (1972) placed the psilids in the Nothyboidea, along with the much smaller families Nothybidae, Teratomyzidae, and Periscelididae, but he left relationships within this group unresolved. The periscelidids have been found in fermenting sap and the leaf mines of weevils (Hennig 1973); the habits of the other two families appear to be unstudied. McAlpine (1977), in contrast, placed the Psilidae as a relative of the Strongylophthalmyiidae ( $\approx 25$  spp.), regarding these together as the sister group of the Tanypezidae (20 + spp.). Tanypezidae have been characterized as saprophagous (Hennig 1973); the habits of *Strongylophthalmyia* appear unknown.

Among the Muscoidea, phytophagy has had multiple origins from saprophagy. One muscid genus of unknown affinities, *Atherigona*, is reported to include 32 leaf- and stem-mining species (Skidmore 1985). The anthomyiid genus *Pegomyia* (Griffiths 1982), whose coprophagous sister group is *Emmesomyia* (9 spp.), contains mycetophages and various phytophages, such as the leaf-mining nominate subgenus (95 spp.); the relationships among these are not clear. Other primarily phytophagous anthomyiids include *Delia*, *Heterostyloides*, *Phorbia*, and *Chirosia* (Griffiths, pers. comm.). The Scatophagidae also includes several genera (affinities unknown) of leaf miners.

The Drosophiloidea (Griffiths 1972) includes at least two phytophagous groups of unknown relationships. Ephydriidae are mainly aquatic detritivores, but several genera, such as *Hydrellia*, *Lemnaphila*, and *Clanoneurum*, are leaf miners (Deonier 1971; Foote 1977). The drosophilid genus *Scaptomyza* also includes some leaf miners.

Among Diopsidae (Griffiths 1972), *Diopsis macrophthalma*, a pest of rice in Africa, is the only known obligate phytophage. Other Diopsidae may be saprophagous, predaceous, or facultatively phytophagous (Feijen 1984).

Anthomyzoidea (Griffiths 1972), 10 families of unresolved relationships, include Opomyzidae, which appear to be grass-stem miners (Vockerth 1965). Larvae of Anthomyzidae have also been found in the stems of plants, but whether they are phytophagous, saprophagous, or mycetophagous is not clear (Sabrosky 1965; Hennig 1973).

Within his "Tephritoinea," which differs from the "tephritid-type ovipositor" group of McAlpine (1977) mainly in excluding the psilids, Griffiths (1972, pers. comm.) recognizes a "family group" consisting of Chloropidae (2000+ spp.), Acartophthalmidae ( $\approx 10$  spp., habits unknown), and Milichiidae ( $\approx 300$  spp., apparently saprophagous). Within Chloropidae, we have compared the probable sister groups Siphonellopsinae (80 spp., wholly saprophagous) and OSCINELLINAE (1350 spp.) plus CHLOROPINAE (860 spp.; H. Anderson 1977). The latter clade appears largely phytophagous (see, e.g., Richard and Davies 1977), mining in the stems of monocots; it is not clear why H. Anderson (1977) ascribed phytophagy to the chloropid ground plan. This comparison is provisional, because other habits have been reported for the poorly studied oscinellines-chloropines, including predation, parasitism, and saprophagy (H. Anderson 1977; Spencer 1986). Some evidence indicates that even the phytophagous chloropids eat only bacteria, which they introduce into healthy plant tissue after scarifying it with their mouth hooks (Tschirnhaus 1981; Spencer 1986).

The TEPHRITIDAE narrowly defined (McAlpine 1977) consists exclusively of phytophagous flies that attack fruits, bore in stems, mine leaves, or form galls. In a larger concept of the family, these flies were included by Griffiths (1972) together with the broadly defined Otitidae (see, e.g., Richards and Davies 1977), subsuming, for example, Platystomatidae ( $\approx 1000$  spp.), Pyrgotidae ( $\approx 300$  spp.), and Tachiniscidae (4 spp.). The otitids in this sense are largely saprophagous, though a few species (e.g., *Tritoxa flexa* and *Tetanops myopaeformis*; Steyskal 1965) attack living plants, and Pyrgotinae parasitize scarab beetles. The exact phylogenetic position of the narrowly defined Tephritidae is not certain (but see McAlpine 1977). We have included this group in our tally, however, because none of its possible sister groups within the broadly defined Tephritidae is more than half as diverse.

Griffiths' (1972) Agromyzoinea includes the sister groups Clusiidae and AGROMYZIDAE. Clusiidae, found as larvae under the bark of trees, are inferred on the basis of their larval morphology to ingest liquid food; the group comprises about 200 species (Hennig 1973). The larvae of most Agromyzidae (2000 spp.; Spencer and Steyskal 1986) are leaf miners, though the cambium-feeding *Phytobia* may represent the primitive habit (Nowakowski 1962).

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