# ESCALATION OF PLANT DEFENSE: DO LATEX AND RESIN CANALS SPUR PLANT DIVERSIFICATION?

Brian D. Farrell, David E. Dussourd,* and Charles Mitter

Department of Entomology, University of Maryland, College Park, Maryland 20742

*Abstract.*—Ehrlich and Raven's postulate that rapid diversification follows innovation in plant defense has often been invoked a posteriori for plant lineages of unusual diversity and chemical distinctiveness. The postulate can be more rigorously tested by defining a novel class of defense using chemical and/or anatomical criteria, independent of taxonomic lineage. If multiple plant lineages have evolved the new defense type, then according to the postulate they should be consistently more diverse than their sister groups (of equal age, by definition) when the latter retain the primitive defensive repertoire. Secretory canals are an independently defined, repeatedly evolved feature that functions to protect plants from herbivores and pathogens. The canals might therefore be expected to allow plant radiation in an adaptive zone of reduced herbivory and disease. We have quantified the evidence for this hypothesis by comparing the diversities of lineages that have independently evolved canal systems with their sister groups for as many plant lineages as current taxonomic evidence allows. A sign test showed that canal-bearing lineages have consistently higher diversities than their sister groups ($P = .0021$). Explanations for this result, other than selective advantage conferred by secretory canals, are examined and provisionally rejected.

The dependence of evolutionary rates on ecological opportunity is a major theme of the "modern synthesis" (Mayr 1942; Simpson 1944; Rensch 1959; Vermeij 1987). Ehrlich and Raven (1964) extended this concept to sets of interacting species, specifically species-rich plant taxa and their diverse insect herbivores. They hypothesized that plant lineages diversify at a greater rate when the lineages are temporarily freed from herbivores via the origin of a novel defense. In turn, eventual circumvention of this defense allows some herbivore lineages to radiate onto an underused resource. Thus, the major radiations of herbivorous insects and plants might reflect the historical sequence of adaptive zones that each has presented to the other.

While many species-rich plant taxa have distinctive (and presumably defensive) secondary chemistries, the hypothesis that these compounds foster diversification (Ehrlich and Raven 1964; Cronquist 1977) has scarcely been tested. The most rigorous attempt to specify and evaluate the predictions of Ehrlich and Raven's proposal, which we term the "escalation/diversification hypothesis" after Berenbaum and Feeny (1981) and Vermeij (1987), is Berenbaum's (1983) essay on coumarin evolution.

Berenbaum proposed an evolutionary sequence among coumarin types, proceeding from simple forms found in the Umbelliferae and many other plant families to increasingly complex structures of ever-more restricted taxonomic distribution. Each step of the sequence, which was postulated to have occurred in multiple independent lineages, purportedly reduced attack by plant enemies, thereby facilitating plant diversification. In support of this scenario, Berenbaum documented that groups of umbellifer genera, characterized by coumarins of increasing advancement, showed increasing mean numbers of species per genus (Berenbaum 1983).

While it is intuitively appealing, Berenbaum's hypothesis has not yet been corroborated. There is no direct phylogenetic evidence for the postulated evolutionary sequence of coumarin profiles (Miller 1987), nor is there compelling evidence that herbivores adapted to the widespread, simple coumarin types are excluded from plants bearing more advanced coumarins (Thompson 1986).

Moreover, the proposition that coumarin advancements have driven umbellifer diversification contains a fundamental problem common to adaptive-zone hypotheses (Mitter et al. 1988). The umbellifer genera bearing similar coumarin profiles are probably related (e.g., the genera bearing angular furanocoumarins are classified in adjacent tribes; Nielsen 1971) and may thus represent single origins of each coumarin type. Whether the high diversity of these umbellifer genera can be attributed specifically to the protective properties of the furanocoumarins is therefore difficult to determine. Any one "successful" group is likely to have several distinguishing features in addition to a singular history of biogeography and extinction (Gould and Calloway 1980). The success of the early angiosperms, for example, has been ascribed as plausibly to their carpellate protection of the ovules as to their acquisition of isoquinoline alkaloids (Ehrlich and Raven 1964).

However, if an adaptation opening a new adaptive zone has evolved in multiple lineages, its effects on diversification can be tested repeatedly. The multiple independent origins control for confounding factors influencing the phylogeny of any single group (Mitter et al. 1988). To identify the lineages in which the "key innovation" has arisen, its distribution is mapped on cladograms (Farris 1970; Fitch 1971). Each lineage bearing the innovation is equal, by definition, in age to its sister group. Differences in diversity (measured here by number of species) between such lineages and their sister groups, therefore, reflect different rates of diversification (origination minus extinction; Stanley 1979). The adaptive-zone hypothesis can be taken to predict that lineages entering the new adaptive zone should be consistently more diverse than their sister groups when the latter remain in the ancestral adaptive zone. The practicality of this approach was demonstrated by Mitter et al. (1988), who showed that insect phytophagy, derived repeatedly from older habits such as saprophagy (Southwood 1973; Strong et al. 1984), has significantly accelerated insect diversification. (This finding is consistent with the hypothesis that insects and plants enhance each others' radiation [Ehrlich and Raven 1964; Zwölfer 1978], although it has noncoevolutionary explanations as well.)

While the multiple independent comparisons seem essential for rigorously testing diversification hypotheses, this requirement raises a dilemma of sample size.

It is hard to statistically demonstrate an effect on diversification when adaptations (such as angular furanocoumarins) have arisen only a few times at most. To apply the multiple-comparisons approach, it may first be necessary to combine such features in groups of structurally or functionally similar adaptations, in effect testing broader adaptive-zone hypotheses. For example, multiple comparisons would certainly be available (Berenbaum 1983) to test the hypothesis that "advances" in coumarin chemistry enhance diversification. In turn, if such relatively broad hypotheses could be corroborated, we could be more confident in ascribing the enhanced diversity of individual taxa to escalated defense, especially if experimental evidence documents a defensive function.

We have sought to evaluate the utility of a multiple-comparisons approach to the escalation/diversification hypothesis with a test case involving a broadly defined plant defense: secretory canals bearing latex or resin. The multiple origins of these canals permit a replicated statistical test of their effects on plant diversification. Given the evidence outlined below for a protective role for secretory canals, we predicted that canal-bearing clades would consistently be more diverse than their sister groups.

THE LATEX AND RESIN CANAL ADAPTIVE ZONE

Plants store a variety of fluids, including latexes, resins, gums, and mucilages, within secretory cells, cavities, and canals (Esau 1965; Fahn 1979; Metcalfe and Chalk 1983). We restrict our analysis to secretory canals containing latex or resin because direct evidence (summarized below) on their defensive properties is available for multiple plant lineages. We argue that these canals are so functionally similar that they can be considered to constitute a single defensive syndrome, despite differences in anatomy. Latex is typically contained within living cells (laticifers), while canal-borne resins are sequestered within intercellular spaces. Both structures often ramify extensively, forming a complex network of tubes throughout the plant (Esau 1965; Fahn 1979; Metcalfe and Chalk 1983). In most species, damage to the canals elicits an abrupt release of secretion. It is this response that we believe to be the critical feature of the latex and resin canal adaptive zone.

A variety of nondefensive functions have been proposed for latex or resin canals, including conduction and storage of food (Gaucher 1900; Haberlandt 1914; Maksymowych and Ledbetter 1987), regulation of water balance (Parkin 1900; Sen and Chawan 1972), and storage of nonfunctional by-products of cellular metabolism (Esau 1965; Olson et al. 1967; Biesboer and Mahlberg 1978). Yet, after a century of investigation and debate, compelling evidence for these functions is lacking (Esau 1965; Fahn 1979; Metcalfe and Chalk 1983; Rudall 1987).

In contrast, a defensive role for latex and resin canals is supported by many lines of evidence. Plants with canal systems artificially disrupted by drainage of canals or severance of leaf veins or stems suffer greater herbivory than plants with intact canals (Kniep 1905; Harris 1960; Stradling 1978; Dussourd and Eisner 1987). Similarly, plant varieties or individuals with reduced canal systems (or low titers of canal-borne chemicals) are more vulnerable to herbivore attack than are

plants with well-developed canals (Harris 1960; Joel 1980; Cates and Alexander 1982; Langenheim 1990). Tests with whole latex or resin have documented a direct role for the secretions in deterring feeding or reducing growth in diverse herbivores (Kniep 1905; Jantz and Rudinsky 1965; Langenheim et al. 1980; Dussourd and Eisner 1987).

Canal-borne secretions are often viscous and frequently become sticky on exposure to air. Insects attempting to bite or bore into plants with intact canals may be immobilized by sticky latex (Stradling 1978; Dillon et al. 1983; D. E. Dussourd, unpublished data) or, in the case of bark beetles, "pitched out" of the plant or entombed in resin (Rudinsky 1966).

Besides adhesives, many latex and resin canals contain secondary metabolites known to be toxic or deterrent to animals. These include cardiac glycosides in *Asclepias* latex (Asclepiadaceae; Seiber et al. 1982; Nishio et al. 1983); diterpenes (Evans and Schmidt 1976; Noack et al. 1980) and nonprotein amino acids (Haupt 1976) in *Euphorbia* latex (Euphorbiaceae); morphine, berberine, and other alkaloids in *Papaver* and *Chelidonium* latex (Papaveraceae; Roberts 1987; Matile 1976); coumarins in *Heracleum* and *Ferula* resin (Apiaceae; Camm et al. 1976; Valle et al. 1987); catechols in *Rhus* resin (Anacardiaceae; Dawson 1954); sesquiterpene lactones in *Cichorium* latex (Asteraceae; Rees and Harborne 1985); and monoterpenes and resin acids in conifer resin (Coniferae; Farentino et al. 1981; Schuh and Benjamin 1984; Everaerts et al. 1988). The widespread use of latexes from several plant families as fish and arrow poisons attests to their frequent toxicity (Blohm 1962; Shaw et al. 1963; Rizk 1987). In some cases, canal-borne chemicals may deter herbivores not through direct toxic effects but by inhibiting symbiotic microorganisms involved in digestion (Longhurst et al. 1968).

Latexes and resins may also protect plants from pathogens by sanitizing and sealing wounds. Isolated whole resin or latex has been reported to inhibit viruses (Rafiq et al. 1985) and fungi (Cobb et al. 1968; Abdalla and Omer 1981; Arrhenius and Langenheim 1983; McDowell et al. 1988). Monoterpenes and alkanes in the resin of conifers are toxic to symbiotic fungi transmitted by bark beetles (Cobb et al. 1968) while a sesquiterpenoid, caryophyllene epoxide from legume resin has been shown to inhibit a leaf fungus (Arrhenius and Langenheim 1983) as well as fungi cultivated by leaf-cutting ants (Howard et al. 1988). Bacteriolytic and proteolytic enzymes (Smith et al. 1955; Shukla and Krishna Murti 1971), furanocoumarins (Camm et al. 1976), vanillic acid (Balansard et al. 1980), aliphatic ketones (McDowell et al. 1988), and resin acids (Hartman et al. 1981) in various latexes and resins may similarly confer protection against pathogens.

In addition to these protective roles, latex and resin canals may also benefit plants by isolating chemical defenses from sensitive tissues (McKey 1979). It is important to note, however, that canal systems not only store defensive chemicals (including both adhesives and toxins) but also augment that defense (Nelson et al. 1981; Dussourd 1986). In milkweeds, for example, latex is contained under pressure within a small number of cells (e.g., 16 in *Asclepias syriaca;* Chauveaud 1891) that elongate and branch throughout the plant (Blaser 1945; Wilson and Mahlberg 1980). The amount of latex at any location in the plant is small compared with the total volume within the entire canal system. When a laticifer is

ruptured, latex flows to the site of damage immediately upon injury. A herbivore biting into a milkweed leaf is thus quickly confronted with a high-concentration latex barrier to further feeding.

Further evidence for a defensive role for latex and resin canals and for the functional similarity of these canal systems is provided by the herbivores themselves. Leaf-feeding insects from 11 families in three orders exhibit convergent behavioral counteradaptations to the secretory canals of host plants, which include at least nine plant families (Dussourd and Eisner 1987 and references cited therein; Dussourd and Denno 1991). The insects disrupt canals either by severing veins or by cutting trenches, then feed distal to the cuts. In each case, the behaviors reduce the subsequent outflow of secretion during feeding. Sawflies on pine likewise damage resin canals in the needles before ovipositing beyond their punctures (M. Wagner, personal communication).

A different solution to canalicular defenses has arisen in the bark beetles. Bark beetles overwhelm resin ducts in conifers by attacking en masse and by inoculating trees with pathogenic fungi (Birch 1984; Rhoades 1985). The number of beetles boring into a host directly influences the success of an attack (Cates and Alexander 1982). Group feeding by other herbivorous insects on canal-bearing plants may similarly aid in overcoming secretory responses (Dussourd and Denno 1991).

The functional similarity of diverse secretory canals is further suggested by the host ranges of behaviorally adapted insects, some of which attack phylogenetically, morphologically, and chemically diverse plants united only by their possession of secretory canals. Related genera and some individual species in the sphingid tribe Dilophonotini, for example, feed on Apocynaceae/Asclepiadaceae, Caricaceae, Euphorbiaceae, and Moraceae, distantly related plant families with variable laticifer systems (Hodges 1971; Winder 1976). Similarly, butterflies in the genus *Lycorea* (Danainae) feed on Asclepiadaceae, Caricaceae, and Moraceae (Ackery and Vane-Wright 1984), while phloem-feeding bark beetles specialize on diverse laticiferous and resinous plants (Wood 1982; Atkinson and Equihua 1986; Atkinson and Equihua-Martinez 1986).

In summary, we propose that latex and resin canals (morphological structures and associated secretions) constitute a repeatedly evolved defensive adaptive zone. Their effectiveness against enemies, achieved in similar fashion across unrelated plant groups, has been documented for many plant species. The canal systems thus provide the basis for a replicated test of the postulate that novel defenses promote plant diversification.

## METHODS

Our test requires that we locate all plant lineages that have independently evolved latex or resin canals, identify their sister groups, and compare the diversities of the paired lineages. To locate plant groups with latex and resin canals, we surveyed botanical reviews by Metcalfe and Chalk (1983), Esau (1965), Fahn (1979), and Cronquist (1981), together with detailed studies of the systematic distribution of canals (e.g., French 1988) where available. In a few groups, delineation of canal-bearing clades is difficult since canals intergrade with intermediate

TABLE 1

COMPARISON OF DIVERSITIES OF LINEAGES BEARING LATEX AND RESIN CANALS WITH SISTER GROUPS

| Canal-bearing Taxon | No. of Species | Sister Group(s) | No. of Sister Group Species | Sign of Diversity Difference* | Age† |
|---|---|---|---|---|---|
| Pteridophyta (Marsileaceae (Regnellidium)[1] | 1 | Marsilea or Pilularia | 60 6 | − | 45 |
| Gnetales (Gnetaceae, Gnetum)[1] | 30 | Welwitschia | 1 | + | 160 |
| Coniferae (Pinaceae [250] + Cupressaceae [130] + Taxodiaceae [16] + Araucariaceae [38] + Podocarpaceae [125])[1] | 559 | Ginkgoaceae | 1 | + | 180 |
| Urticales (Urticaceae [700] + Moraceae [1,000] + Cannabaceae [3])[2] | 1,703 | Ulmaceae | 150 | + | 93 |
| Caryophyllales (Cactaceae, Mammillaria, sect. Mammillaria [110] + sect. Subhydrochylus [22])[5] | 132 | Ancistrocladae or Leptocladae | 35 6 | + | ? |
| Theales (Dipterocarpaceae, Dipterocarpoidea)[1] | 400 | Monotoidea | 35 | + | 60 |
| Ebenales (Sapotaceae)[2] | 800 | Ebenaceae | 450 | + | 67 |
| Celastrales (Hippocrateaceae, Hippocratea)[1] | 100 | Celastraceae (Lophopetalum) | 4 | + | ? |

886

| | | | | * | † |
|---|---|---|---|---|---|
| Hippocrateaceae (Salacia) | 200 | Celastraceae (Glyptopetalum + Crocoxylon + Elaeodendron or part thereof) | 27<br>17<br>2 | + | ? |
| Euphorbiales (Euphorbiaceae, Crotonoideae [2,000] + Euphorbioideae [2,500])[4] | 4,500 | Phyllanthoideae or Oldenfieldioideae | 2,000<br>100 | + | 73 |
| Gentianales (Apocynaceae [2,000] + Asclepiadaceae [2,000])[2] | 4,000 | Gentianaceae and/or Loganiaceae | 900<br>600 | + | 60 |
| Asterales (Asteraceae [20,000] + Campanulaceae [2,000])[2] | 22,000 | Calyceraceae | 60 | + | 30 |
| Arales (Araceae, Philodendroideae [961] + Colocasioideae [39] + Aroideae [351])[3] | 1,350 | Pothoideae in part | ≤995 | + | 10 |
| Alismatiflorae[3] (Alismataceae [90] + Limnocharitaceae [11])[3] | 101 | Butomaceae | 1 | + | 10 |
| Aponogetonaceae | 40 | Alismatiflorae (−[Alismataceae + Limnocharitaceae]) | 61 | − | 10 |
| Zingiberales (Musaceae)[3] | 42 | Remaining Zingiberales | 1,800 | − | 20 |

SOURCE.—[1]Willis (1973), [2]Cronquist (1981), [3]Dahlgren et al. (1985), [4]Webster (1987), [5]Hunt (1979).

NOTE.—Number of positive differences, 13; number of negative differences, 3; one-tailed sign test, $P = .0106$. Number of species in brackets.

* Canal-bearing lineage minus sister group.

† First fossil appearance of any taxon in comparison (in millions of years; Grayum 1984; Johnson 1984; Muller 1984).

887

structures with various degrees of morphological specialization (Esau 1965). To avoid bias, we have followed the literature in delimiting canal-bearing groups and also excluded groups (e.g., the resinous Caesalpiniaceae; see Appendix) in which previous authors have drawn no clear demarcation.

Our estimates of the sister groups of canal-bearing clades are based on our reading of the primary systematic literature and on consultation with specialists (see Acknowledgments). Recent cladistic studies received the greatest weight. Canal-bearing groups are included in our tally of comparisons (table 1) only if the literature provides (1) a clear argument for, and no strong evidence against, monophyly in the sense of Hennig (1966) (which does not necessarily require the author's treatment to have been explicitly cladistic), (2) evidence that canals arose in the group's common ancestor, and (3) evidence to identify either a definite sister group or a set of closely related possible sister groups.

A few of the comparisons meeting our criteria, while reflecting the existing evidence, are clearly provisional (e.g., the contrast of Asteraceae plus Campanulaceae to Calyceraceae; Bremer 1987). Deletion of such cases (see Appendix) would not change our finding. Plant phylogeny is the subject of intense current research, and all of the phylogeny estimates we accept should be regarded as possibly erroneous. We stress, however, that such taxonomic error should be random with respect to the escalation/diversification hypothesis, making a significant effect harder to detect. A review of all canal-bearing plant groups known to us, with a defense of their inclusion or exclusion from the final tally of diversity comparisons (table 1), is provided in the Appendix.

Several complexities arise in the application of the above criteria for identifying canal-bearing lineages and sister groups. In a few canalicular clades, secretory canals have been lost in some members (e.g., the Cecropiaceae in the Urticales). We have counted only the number of species bearing canals in such groups since these represent the degree of radiation in the secretory canal adaptive zone. The secondary loss of canals provides an alternative test for the effects of canals on diversification; however, at this point, the examples are too few and the taxonomic information insufficient for a statistical comparison.

A second problem arises when the sister group of a canalicular clade contains a derived canal-bearing component. The sister-group comparisons of the two canalicular lineages will not be statistically independent because the sister group of the younger lineage will be included in that of the older. For example, according to Dahlgren and Bremer (1985), the sister group of the primitively laticiferous Aponogetonaceae lies in the primitively noncanalicular higher Alismatiflorae (= Alismatales + Najadales; fig. 1). However, the Alismatiflorae itself contains the derived laticiferous group comprising the Alismataceae plus Limnocharitaceae. Our approach to such interdependent comparisons (Mitter et al. 1988) has been to determine whether exclusion of the sister group of the younger laticiferous clade (Butomaceae in the case of Alismataceae plus Limnocharitaceae) would affect the conclusion regarding the older laticiferous clade (Aponogetonaceae, in this example). If not (as in this and all other cases we encountered), then both comparisons can be safely used. If it did alter the result, then one might reasonably include either comparison, perhaps randomly chosen, but not both.

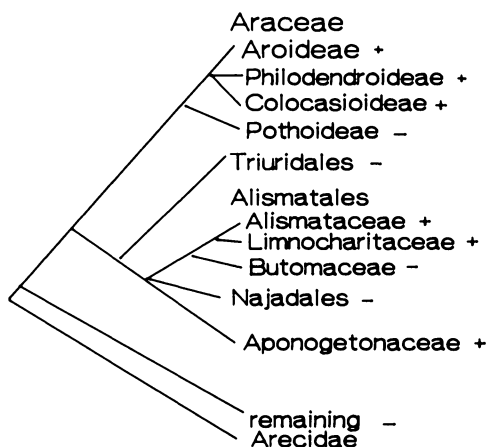In other cases, the sister group of a canal-bearing clade has only been approxi-

FIG. 1.—Relationships among laticiferous groups in the monocotyledonous subclass Areci-
dae (Stant 1967; Argue 1976; Grayum 1984; Dahlgren and Bremer 1985; Dahlgren et al. 1985).
Presence ( + ) or absence ( − ) of laticifers is indicated for each taxon (Metcalfe and Chalk
1983; Grayum 1984; French 1988). The three apparently independent origins of laticifers are
in the Araceae, Aponogetonaceae, and Alismataceae/Limnocharitaceae.

mately established (criterion 3 above). For example, the affinities of the laticifer-
ous Aponogetonaceae clearly lie with the Najadales and Alismatales sensu stricto
(fig. 1), but whether the exact sister group is one of these orders alone or both
together is uncertain (Dahlgren and Bremer 1985). The answer does not matter
to our test, however, since the Aponogetonaceae is less diverse than either order.
We have included such comparisons in our tally (table 1) when all defensible
resolutions of the phylogeny yield the same answer about relative diversification
rates (as in this and all similar instances we have encountered).

RESULTS

In 13 of 16 sister-group comparisons extractable from our review of plant rela-
tionships, the lineage with secretory canals is more diverse than its presumed
sister group, sometimes by two or more orders of magnitude (table 1; $P$ = .0106,
one-tailed sign test). These 16 canalicular clades include 11 groups bearing la-
tex canals, two with resin canals, and three that produce both latex and resin
canals. Several additional cases will, on further taxonomic resolution, almost
surely support our result (e.g., Apiales, Anacardiaceae, Burseraceae, Detariae/
Amherstiae, Primulales, *Allium*). One possible contrary example (*Cyclanthus*)
was also encountered.

DISCUSSION

Canal systems containing latex or resin appear to have originated at least 40
times. Future work on plant phylogeny will therefore permit many more sister-
group comparisons than the 16 identified here and will probably also modify some

of our current contrasts. Our results should therefore be viewed as provisional. Nevertheless, the consistently greater diversity of canal-bearing lineages in our sample appears to provide strong support for the escalation/diversification hypothesis and therefore requires consideration of alternative explanations.

We have previously argued that an association of the kind reported here is unlikely to represent either statistical artifact or an intrinsic asymmetry of phylogenies (Mitter et al. 1988). Two recent studies provide evidence that adaptive novelty or phylogenetic advancement is not inevitably associated with increased diversity. In an analysis similar in design and sample size to this one, insect lineages evolving parasitism sensu stricto, unlike insect phytophages (Mitter et al. 1988), showed no trend in diversity with respect to their sister groups (B. Wiegmann, C. Mitter, and B. Farrell, unpublished manuscript). Herrera (1989), using an approach similar in spirit though not based explicitly on sister groups, likewise found no relation between the development of biotic dispersal syndromes and diversification of angiosperm groups.

It might be argued that our present result is an artifact of geography: laticiferous and resinous plants are especially prevalent in the tropics, and most groups of organisms are more diverse in the tropics than elsewhere. However, in all of our contrasts involving tropical canal-bearing groups, the sister group is also substantially or entirely tropical. Furthermore, the canalicular clades that are primarily temperate are all more diverse than their respective sister groups, whether temperate or tropical.

Canal systems might promote diversification either directly, through genetic correlation with traits affecting the breeding structure and thus the probability of speciation, or indirectly, by conferring increased individual fitness. No evidence exists for the former correlations. In contrast, as we described previously, a large and growing body of experimental data indicates that canal systems confer protection from herbivores and pathogens.

While enhanced individual resistance to enemies thus seems the most plausible explanation for the increased diversification rates of canal-bearing groups, this hypothesis requires much additional corroboration. Improved adaptation itself is hard to document, and its effect on diversification is likely to be indirect and difficult to demonstrate rigorously (Vermeij 1987, 1988; Lidgard and Jackson 1989). There are several possible mechanisms by which increased individual adaptedness could affect diversification rate. Plants with lower rates of herbivory and disease might tend to attain larger ecological and geographic ranges, yielding increased opportunity for speciation (Vermeij 1987), or they might simply have higher population densities on average, which could lower the risk of extinction (Futuyma 1986).

A first step toward distinguishing among these alternatives is to determine whether there *are* any population- or species-level correlates of secretory canal possession (Jablonski 1987). Preliminary evidence for such correlates comes from data on the distribution and abundance of trees in four lowland habitats in Manu National Park, Peru, collected by the BIOLAT Program of the Smithsonian Institution (B. Farrell and C. Mitter, unpublished manuscript). Mean local abundances and habitat breadths were found to be consistently higher in species of seven canal-bearing plant taxa compared with their sympatric near relatives. Recent

inventories of other Amazonian forests also report high abundances of laticiferous and resinous trees, ranging from about 20% to 35% of the total number of individuals (Prance et al. 1976; Boom 1986; Farrell and Erwin 1988).

Attempts to correlate current population properties with long-term diversification rates rely on an important assumption: that fitness differentials, which were responsible for the origin of an adaptation and the initial proliferation of the lineage bearing it, continue to exist. A detailed fossil record preserving the demography of a predator-prey interaction, as exists for some marine bivalves and their drilling predators (Vermeij 1987), could allow direct study of past selection. Such evidence is essentially unobtainable for terrestrial plant/herbivore interactions. However, temporal trends in relative diversities could in principle provide an indirect test of changing selection pressures (Simpson 1944). Thus, if the fitness advantage of a canal-bearing clade with respect to its sister group eventually declines because of counteradaptation by enemies (Ehrlich and Raven 1964), the relative diversity of that clade should eventually decline also. If so, we might expect the oldest sister-group pairs in our tabulation to differ least in diversity. Conversely, if enemies adapted to earlier canal-bearing plant clades can easily shift to newly evolved ones, the canal "adaptive zone" may become "filled" over geological time, impeding the diversification of later-arising canal bearers (Simpson 1944; Ehrlich and Raven 1964). While the results of a detailed analysis will be presented elsewhere (B. Farrell and C. Mitter, unpublished manuscript), inspection of the diversities (table 1) of canal-bearing clades (alone or divided by the diversity of their respective sister group) shows no apparent trend with respect to age of origin, suggesting that the selective advantages of canals may persist through time.

In conclusion, we have argued that latex and resin canals are so functionally homogeneous as to constitute a recognizable syndrome. Despite the potential complexity of their defensive action, often involving chemical and mechanical components, both structures are similar in their delivery of sequestered substances to sites of injury. As such, they offer a test case for the general hypothesis that adaptive innovation, specifically plant defense, confers evolutionary success. Our analysis documents the greater diversity of canal-bearing clades across plant groups of diverse habitat, growth form, and chemistry. No explanation for our result seems plausible other than improved defense, although additional corroboration for this postulate, including illumination of the diversifying mechanism, will be essential. The clearest potential limitation of the multiple-comparison approach is that adaptations defined broadly enough to provide statistical replication risk artificiality. When a strong pattern emerges, however, as in our analysis, this objection is weak. In providing statistical support for a broad version of the escalation/diversification hypothesis, our result lends force to subsequent studies of more narrowly defined and less frequently evolved plant defenses.

## APPENDIX

### RELATIONSHIPS OF PLANT GROUPS BEARING LATEX AND RESIN CANALS

The phylogeny and species diversity of plant groups with latex or resin canals are reviewed below, together with justification of the inclusion or exclusion of each group from our tally of diversity comparisons (table 1). Plant taxa are presented in approximate phylogenetic sequence after Cronquist (1981). However, we stress that *all* estimates of sister-group relationships used in our tally (table 1) are based on the primary literature with emphasis on the most recent cladistic studies and not on any of the more general angiosperm classifications (e.g., Thorne 1976; Taktajahn 1980; Cronquist 1981). These latter references typically provide insufficient resolution and character discussions for comparisons at low taxonomic levels. Furthermore, they often characterize families as "laticiferous" or "resinous," when (often more recent) evidence shows that only a subgroup has in fact evolved canals bearing latex or resin (e.g., Euphorbiaceae; see below). We evaluated canal-bearing taxa according to criteria outlined in Methods (see text). Below, we underline the names of the few taxa for which sufficient biological and phylogenetic information exists for inclusion in our tally. To keep the Appendix within a reasonable length, we have omitted details on the history of each group's taxonomic placement.

### PTERIDOPHYTA

The aquatic, marsiliaceous genus Regnellidium is apparently the only fern bearing laticifers (Metcalfe 1967). Recent cladistic study (Johnson 1984) indicates its sister group to be either *Marsilea* or *Pilularia*, both of which are more diverse than Regnellidium.

### CONIFERAE

The six families constituting the Coniferae possess resin ducts containing mono-, di-, or sesquiterpenes. These structures apparently have been lost secondarily in the 20 species of Taxaceae (DeBary 1884; Young and Watson 1969; Bierhorst 1971), which we therefore exclude from our tally. In the secondary tissues of a few relatively derived genera (*Abies, Cedrus, Pseudolarix,* and *Tsuga*), resin "cysts" and sometimes canals are produced primarily in response to injury (Bannan 1936; Bierhorst 1971; Fahn et al. 1979; Ferrell 1983). However, canals are present in the primary tissues of these groups (Hanes 1927). Recent cladistic studies indicate that the sister group to the Coniferae (559 species) is the monotypic family Ginkgoaceae (Crane 1985; Doyle and Donoghue 1986), which possesses isolated resin cells (DeBary 1884; Bierhorst 1971; Doyle and Donoghue 1986).

### GNETALES

The sister group of the laticiferous genus Gnetum (30 species) appears to be *Welwitschia* (1 or 2 species; Willis 1973; Behnke and Herrmann 1978; Doyle and Donoghue 1986).

MAGNOLIOPSIDA

Within the "primitive" subclass Magnoliidae, laticifers have possibly arisen twice: in the putative common ancestor of the nymphaealean families and in the Papaverales (Metcalfe and Chalk 1983). We have excluded these groups because their phylogenetic positions are problematic, although the nymphaealean clade and the Papaverales may be sister groups (Dahlgren and Bremer 1985). The Eucommiaceae also bear laticifers, but their assignment even to subclass is unclear (Cronquist 1981).

The subclass Hamamelidae also contains several apparent origins of secretory canals. The subfamily Altingioideae of Hamamelidaceae contains two genera, *Liquidambar* and *Altingia,* that produce resin canals (Metcalfe and Chalk 1983). However, relationships within the Hamamelidaceae are obscure (Cronquist 1981). The hamamelid order Urticales contains an apparent monophyletic group comprising the latex and resin canal-bearing families Moraceae, Urticaceae, Cannabaceae, and Cecropiaceae (totaling 1,979 species; Berg 1977). Their sister group appears to be the Ulmaceae (150 species; Bechtel 1921; Tippo 1938; Berg 1977). One should note, however, that concepts of relationships within the Hamamelidae are currently in flux (Humphries 1989); thus this comparison may need to be recalculated if taxonomic assignments change. Laticifers have been lost in the family Cecropiaceae, which is apparently derived from part of the Moraceae. In addition, some of the Ulmaceae possess canals containing mucilage. There is as yet no evidence that these canals serve a protective function. However, should mucilage prove to be defensive, this comparison and the comparison within the Dipterocarpaceae described below may need to be reexamined.

Among the Caryophyllidae, the cactus genus *Mammillaria* contains a laticiferous group comprising sections Subhydrochylus + Mammillaria (132 species; Hunt 1971, 1979; Wittler and Mauseth 1984) whose closest affinities appear to be with sections Ancistrocladae (35 species) or Leptocladae (6 species). The relationships of the other laticiferous genera of Cactaceae, *Coryphantha* and *Leuchtenbergia* (Metcalfe and Chalk 1983), are unclear.

The subclass Dilleniidae contains several independent origins of latex and resin canals. In the Theales, the dipterocarp subfamily Dipterocarpoidea (400 species) possesses resin canals, which its apparent sister group Monotoideae (35 species) lacks (though Monotoidea have been reported to possess mucilage canals; Bancroft 1938; Metcalfe and Chalk 1983). The relationships of the laticiferous Clusiaceae (which includes the Hypericaceae, totaling 1,200 species) are obscure. In the Violales, the affinities of the laticiferous family Caricaceae are enigmatic. The flacourtiaceous genus *Plagiopteron* is laticiferous but also of uncertain position. In the Ebenales, the laticiferous Sapotaceae (800 species) appears to be the sister group to the Ebenaceae (450 species; Lam 1939). The Styracaceae contains some species with resin canals, but relationships within this family are poorly known (Cronquist 1981). Latex or resin canals are probably primitive within the large order Primulales (2,000 species) and apparently lost in the most derived sections of the Primulaceae (Cronquist 1981). The relationships of this group have not been traced.

Within the extremely diverse Rosidae, the Caesalpiniaceae contains the monophyletic group comprising the resinous tribes Detariae and Amherstiae (726 species; Cowan and Polhill 1981a, 1981b), which together are the sister group to the *Sclerobium* group (62 species; Polhill and Vidal 1981). We have excluded this comparison from our tally because the distribution of canals sensu stricto within the Detariae and Amherstiae is not known. Some plants such as *Hymenaea* (the apparent source of Dominican amber) bear resin pockets, whereas others such as *Copaifera* (the source of African amber) sometimes produce both pockets and canals (Langenheim 1973). This case, which would corroborate our result if included, illustrates the difficulty in defining a defensive syndrome since resins in both canals and pockets undoubtedly function in defense (Langenheim et al. 1980, 1986; Arrhenius and Langenheim 1983). The pockets, like canals, are capable of emitting substantial quantities of resin when injured (Langenheim 1969). Laticifers have also been discovered in some species of *Mimosa* (Metcalfe and Chalk 1983), but their sister group(s) is unknown.

Some members of the santalalean family Olacaceae bear resin canals and/or laticifers (Cronquist 1981; Metcalfe and Chalk 1983), but relationships within the family are obscure.

The Celastrales harbor several families with secretory canals. The Hippocrateaceae consists of two laticiferous genera, each apparently derived independently from different parts of the Celastraceae (Robson 1965). Robson presents evidence that the affinities of the genus Hippocratea (100 species) are with the celastracean genus Lophopetalum (4 species), while the hippocrateaceous genus Salacia (200 species) is derived from the celastracean group Glyptopetalum + Crocoxylon + Elaeodendron (46 species total) or some subset thereof. The large laticiferous family Icacinaceae, though allied to the other celastralean families, is of unknown position (Cronquist 1981). Also currently placed in the Celastrales but of uncertain affinities (even as to subclass) is the laticiferous genus Peripterygium in the Cardiopteridaceae (Metcalfe and Chalk 1983).

Within the Euphorbiaceae, recent cladistic study (Webster 1987) identifies an origin of laticifers in the clade comprised of the advanced subfamilies Crotonoideae + Euphorbioideae (total 4,500 species not including the species of Acalyphoideae in which the laticifers have apparently been secondarily lost). The sister group of this clade appears to lie within the cladistically basal, paraphyletic Phyllanthoideae or Oldenfieldioideae (Webster 1987).

The relationships of the resin canal–bearing Anacardiaceae (including the Julianaceae) to other Sapindales are obscure, although they may be related to the likewise resin canal–bearing (and also uncertainly placed) Burseraceae (Cronquist 1981). The Sapindales in turn might be paraphyletic with respect to the Apiales, which comprises two families with resin canals, the Apiaceae and Araliaceae. However, the Apiales have been alternatively grouped with the Cornales (Rodriguez 1971). Within the Cornales, an origin of laticifers has been reported in the family Alangiaceae, whose relationships have not been elucidated (Cronquist 1981).

Laticifers have arisen several times within the subclass Asteridae. The Apocynaceae + Asclepiadaceae (totaling 4,000 species) form a monophyletic laticiferous group (Woodson 1941) whose affinities are probably with the Loganiaceae (600 species), Gentianaceae (900 species), or some subset thereof (Moore 1947; Tournay and Lawalree 1952; Wanntorp 1988). The Convolvulaceae (1,500 species) forms a uniformly laticiferous group with the Dichondraceae and the monotypic Madagascan Humbertiaceae (Cronquist 1981). The affinities of this diverse clade are controversial and may lie with the Solanaceae, Nolanaceae, other Polemoniales, or Gentianales (D'Arcy 1979; Mesa 1986).

In the most comprehensive cladistic study to date of Asterales, the Asteraceae + Campanulaceae appears to form a monophyletic group (Bremer 1987; 22,000 species total) in which a primitive laticiferous condition has given rise one or more times to clades bearing resin canals. The sister group to this enormous assemblage is most likely the Calyceraceae (60 species; Bremer 1987). Other proposed sister groups (reviewed in Bremer 1987; see also Cronquist 1981) would yield the same conclusion concerning relative diversity.

## LILIOPSIDA

The arecid order Cyclanthales contains an origin of laticifers. Some populations of Cyclanthus bipartitus have recently been reported to contain latex canals (Wilder and Harris 1982). Whether this represents a derived condition of (or within) this highly divergent species or the family Cyclanthaceae remains unclear (Hammel and Wilder 1989; Wilder 1989).

The Araceae (fig. 1) contains the canal-bearing (mostly laticifers, some resin canals) group comprising the subfamilies Aroideae + Philodendroideae + Colocasioideae (1,350 species; French 1987, 1988) whose nearest relatives apparently lie within the Pothoideae (totaling 995 species; Grayum 1984; however, see Grayum 1990 for a review suggestive of two possible origins of secretory canals in the Araceae). Recent cladistic studies reveal an independent origin of laticifers in the common ancestor of the families Alismataceae + Limnocharitaceae (totaling 101 species; Stant 1967; Argue 1976; Dahlgren et al. 1985). The apparent sister group to this clade is the monotypic Butomaceae (1 species). The laticifer-

ous Aponogetonaceae (40 species) is probably the sister group of either the primitively nonlaticiferous Alismatales or Najadales or these together (Dahlgren and Bremer 1985). The sign of this comparison (see table 1) is the same under all three possibilities and is unaffected by subtraction of the laticiferous species from the Alismatales (leaving 61 species total; Dahlgren and Bremer 1985).

In the Zingiberidae, the laticiferous family Musaceae (42 species) appears to be the remaining Zingiberales (in 1,800 species; Kress 1990).

Within the Liliidae, the liliaceous genus *Allium* (450 species) contains latex canals. Intergeneric relationships within the Liliaceae are poorly known, although A. Cronquist (personal communication) suggests that *Nothoscordum* (35 species) might be sister group to *Allium*.

LITERATURE CITED

Abdalla, M. H., and F. Omer. 1981. Studies on the rhizosphere mycoflora of *Euphorbia granulata* Forsk. and *E. heterophylla* L. Mycopathologia 73:9–15.

Ackery, P. R., and R. I. Vane-Wright. 1984. Milkweed butterflies: their cladistics and biology. Cornell University Press, Ithaca, N.Y.

Argue, C. L. 1976. Pollen studies in the Alismataceae with special reference to taxonomy. Pollen and Spores 18:161–201.

Arrhenius, S. P., and J. H. Langenheim. 1983. Inhibitory effects of *Hymenaea* and *Copaifera* leaf resins on the leaf fungus, *Pestalotia subcuticularis*. Biochemical Systematics and Ecology 11:361–366.

Atkinson, T. H., and A. Equihua. 1986. Biology of the Scolytidae and Platypodidae (Coleoptera) in a tropical deciduous forest at Chamela, Jalisco, Mexico. Florida Entomologist 69:303–310.

Atkinson, T. H., and A. Equihua-Martinez. 1986. Biology of bark and ambrosia beetles (Coleoptera: Scolytidae and Platypodidae) of a tropical rain forest in southeastern Mexico with an annotated checklist of species. Annals of the Entomological Society of America 79:414–423.

Balansard, G., D. Zamble, G. Dumenil, and A. Cremieux. 1980. Mise en evidence des proprietes antimicrobiennes du latex obtenu par incision du tronc de *Alafia multiflora* Stapf. identification de l'acide vanillique. Plantes Medicinales et Phytotherapie 14:99–104.

Bancroft, H. 1938. The wood anatomy of representative members of the Monotoideae. American Journal of Botany 22:717–739.

Bannan, M. W. 1936. Vertical resin ducts in the secondary wood of the Abietineae. New Phytologist 35:11–46.

Bechtel, A. R. 1921. The floral anatomy of the Urticales. American Journal of Botany 8:386–410.

Behnke, H. D., and S. Herrmann. 1978. Fine structure and development of laticifers in *Gnetum gnemon* L. Protoplasma 95:371–384.

Berenbaum, M. 1983. Coumarins and caterpillars: a case for coevolution. Evolution 37:163–179.

Berenbaum, M., and P. P. Feeny. 1981. Toxicity of furanocoumarins to swallowtail butterflies: escalation in a coevolutionary arms race? Science (Washington, D.C.) 212:927–929.

Berg, C. C. 1977. Urticales, their differentiation and systematic position. Pages 349–374 *in* E. Kubitski, ed. Flowering plants, evolution and classification of higher categories. Plant systematics and evolution. Suppl. 1. Springer, Vienna.

Bierhorst, D. W. 1971. Morphology of vascular plants. Macmillan, New York.

Biesboer, D. D., and P. G. Mahlberg. 1978. Accumulation of nonutilizable starch in laticifers of *Euphorbia heterophylla* and *E. myrsinites*. Planta 143:5–10.

Birch, M. C. 1984. Aggregation in bark-beetles. Pages 331–346 *in* W. J. Bell and R. T. Carde, eds. Chemical ecology of insects. Sinauer, Sunderland, Mass.

Blaser, H. W. 1945. Anatomy of *Cryptostegia grandiflora* with special reference to the latex system. American Journal of Botany 32:135–141.

Blohm, H. 1962. Poisonous plants of Venezuela. Harvard University Press, Cambridge, Mass.

Boom, B. M. 1986. A forest inventory in Amazonian Bolivia. Biotropica 18:287–294.

Bremer, K. 1987. Tribal interrelationships of the Asteraceae. Cladistics 3:210–253.

THE AMERICAN NATURALIST

Camm, E. L., C. Wat, and G. H. N. Towers. 1976. An assessment of the roles of furanocoumarins in *Heracleum lanatum*. Canadian Journal of Botany 54:2562–2566.

Cates, R. G., and H. Alexander. 1982. Host resistance and susceptibility. Pages 212–263 *in* J. B. Mitton and K. B. Sturgeon, eds. Bark beetles in North American conifers. University of Texas Press, Austin.

Chauveaud, G. 1891. Recherches embryogeniques sur l'appareil laticifère des Euphorbiacées, Urticacées, Apocynées, et Asclépiadées. Annales des Sciences Naturelles: Botanique 14:1–161.

Cobb, F. W., M. Krstic, E. Zavarin, and H. W. Barber. 1968. Inhibitory effects of volatile oleoresin components on *Fomes annosus* and four *Ceratocystis* species. Phytopathology 58:1327–1335.

Cowan, R. S., and R. M. Polhill. 1981*a*. Tribe 4. Detarieae. Pages 117–134 *in* R. M. Polhill and P. R. Raven, eds. Advances in legume systematics. Pt. 1. Crown, London.

———. 1981*b*. Tribe 5. Amherstieae. Pages 135–142 *in* R. M. Polhill and P. R. Raven, eds. Advances in legume systematics. Pt. 1. Crown, London.

Crane, P. R. 1985. Phylogenetic relationships in seed plants. Cladistics 1:329–348.

Cronquist, A. 1977. On the taxonomic significance of some secondary metabolites in angiosperms. Plant Systematics and Evolution 1(suppl.):179–189.

———. 1981. An integrated system of classification of flowering plants. Columbia University Press, New York.

Dahlgren, R., and K. Bremer. 1985. Major clades of the angiosperms. Cladistics 1:349–368.

Dahlgren, R. M. T., H. T. Clifford, and P. T. Yeo. 1985. The families of the monocotyledons. Springer, New York.

D'Arcy, W. G. 1979. Classification of the Solanaceae. Pages 3–47 *in* J. G. Hawkes, R. N. Lester, and A. D. Skelding, eds. The biology and taxonomy of the Solanaceae. Linnean Society Symposium Series 7. Academic Press, London.

Dawson, C. R. 1954. The toxic principle of poison ivy and related plants. Records of Chemical Progress 15:39–53.

DeBary, A. 1884. Comparative anatomy of the phanerogams and ferns. Clarendon, Oxford.

Dillon, P. M., S. Lowrie, and D. McKey. 1983. Disarming the "evil woman": petiole constriction by a sphingid larva circumvents mechanical defenses of its host plant, *Cnidoscolus urens* (Euphorbiaceae). Biotropica 15:112–116.

Doyle, J. A., and M. J. Donoghue. 1986. Relationships of angiosperms and Gnetales: a numerical cladistic analysis. Pages 177–198 *in* B. A. Thomas and R. A. Spicer, eds. Systematic and taxonomic approaches in paleobotany. Oxford University Press, Oxford.

Dussourd, D. E. 1986. Adaptations of insect herbivores to plant defenses. Ph.D. diss. Cornell University, Ithaca, N.Y.

Dussourd, D. E., and R. F. Denno. 1991. Deactivation of plant defense: correspondence between insect behavior and secretory canal architecture. Ecology 72:1383–1396.

Dussourd, D. E., and T. Eisner. 1987. Vein-cutting behavior: insect counterploy to the latex defense of plants. Science (Washington, D.C.) 237:898–901.

Ehrlich, P. R., and P. H. Raven. 1964. Butterflies and plants: a study in coevolution. Evolution 18:586–608.

Esau, K. 1965. Plant anatomy. Wiley, New York.

Evans, F. J., and R. J. Schmidt. 1976. Two new toxins from the latex of *Euphorbia poisonii*. Phytochemistry 15:333–335.

Everaerts, C., J. Gregoire, and J. Merlin. 1988. The toxicity of Norway spruce monoterpenes to two bark beetle species and their associates. Pages 335–344 *in* W. J. Mattson, J. Levieux, and C. Bernard-Dagan, eds. Mechanisms of woody plant defenses against insects: search for pattern. Springer, New York.

Fahn, A. 1979. Secretory tissues in plants. Academic Press, New York.

Fahn, A., E. Werker, and P. Ben-tzur. 1979. Seasonal effects of wounding and growth substances on development of traumatic resin ducts in *Cedrus libani*. New Phytologist 82:537–544.

Farentino, R. C., P. J. Capretta, R. E. Kepner, and V. M. Littlefield. 1981. Selective herbivory in tassel-eared squirrels: role of monoterpenes in ponderosa pine chosen as feeding trees. Science (Washington, D.C.) 213:1273–1275.

Farrell, B. D., and T. L. Erwin. 1988. Leaf-beetle community structure in a rainforest canopy. Pages 73–90 *in* P. Jolivet, E. Petitpierre, and T. Hsiao, eds. The biology of the Chrysomelidae. Kluwer Academic, The Hague.

Farris, J. S. 1970. Methods for computing Wagner trees. Systematic Zoology 19:83–92.

Ferrell, G. T. 1983. Host resistance to the fir engraver, *Scolytus ventralis* (Coleoptera: Scolytidae): frequencies of attacks contacting cortical resin blisters and canals of *Abies concolor*. Canadian Entomologist 115:1421–1428.

Fitch, W. 1971. Towards defining the course of evolution: minimum change for a specific tree topology. Systematic Zoology 20:406–416.

French, J. C. 1987. Systematic survey of resin canals in roots of Araceae. Botanical Gazette 148: 360–371.

———. 1988. Systematic occurrence of anastomosing laticifers in Araceae. Botanical Gazette 149: 71–81.

Futuyma, D. J. 1986. Evolutionary biology. Sinauer, Sunderland, Mass.

Gaucher, M. L. 1900. Du role des laticiferes. Annales des Sciences Naturelles Botanique 12:241–260.

Gould, S. J., and C. B. Calloway. 1980. Clams and brachiopods: ships that pass in the night. Paleobiology 6:383–396.

Grayum, M. 1984. Palynology and phylogeny of the Araceae. Ph.D. diss. University of Massachusetts, Amherst.

———. 1990. Evolution and phylogeny of the Araceae. Annals of the Missouri Botanical Garden 77:628–697.

Haberlandt, G. 1914. Physiological plant anatomy. Macmillan, London.

Hammel, B. E., and G. J. Wilder. 1989. *Dianthoveus:* a new genus of Cyclanthaceae. Annals of the Missouri Botanical Garden 76:112–123.

Hanes, C. S. 1927. Resin canals in seedling conifers. Journal of the Linnean Society of London, Botany 47:613–636.

Harris, P. 1960. Production of pine resin and its effect on survival of *Rhyacionia buoliana* (Schiff.) (Lepidoptera: Olethreutidae). Canadian Journal of Zoology 38:121–130.

Hartmann, E., B. Renz, and J. A. Jung. 1981. Untersuchungen über Bakterien- und Pilzhemmstoffe in höheren Pflanzen. Phytopathology 101:31–42.

Haupt, I. 1976. Separation of the sites of synthesis and accumulation of 3,4-dihydroxyphenylalanine in *Euphorbia lathyris* L. Nova Acta Leopoldina Supplementum 7:129–132.

Hennig, W. 1966. Phylogenetic systematics. University of Illinois Press, Urbana.

Herrera, C. M. 1989. Seed dispersal by animals: a role in angiosperm diversification? American Naturalist 133:309–322.

Hodges, R. W. 1971. Sphingoidea. Fasc. 21. The moths of America north of Mexico. Classey, Middlesex.

Howard, J. J., J. Cazin, and D. Wiemer. 1988. Toxicity of terpenoid deterrents to the leafcutting ant *Atta cephalotes* and its mutualistic fungus. Journal of Chemical Ecology 14:59–69.

Humphries, C. 1989. Patterns before process. Nature 333:300–301.

Hunt, D. R. 1971. Schumann and Buxbaum reconciled. Cactus and Succulent Journal 33:53–72.

———. 1979. Recent *Mammillaria* discoveries. Cactus and Succulent Journal 41:95–110.

Jablonski, D. 1987. Heritability at the species level: analysis of geographic ranges of Cretaceous mollusks. Science 238:360–363.

Jantz, O. K., and J. A. Rudinsky. 1965. Laboratory and field methods for assaying olfactory responses of the Douglas-fir beetle, *Dendroctonus pseudotsugae* Hopkins. Canadian Entomologist 97: 935–941.

Joel, D. M. 1980. Resin ducts in the mango fruit: a defense system. Journal of Experimental Botany 31:1707–1718.

Johnson, D. A. 1984. Revision and phylogeny of *Marsilea*. Ph.D. diss. University of Massachusetts, Amherst.

Kniep, H. 1905. Über die Bedeutung des Milchsafts der Pflanzen. Flora oder Allgemeine Botanische Zeitung (Jena) 94:129–205.

Kress, W. J. 1990. The phylogeny and classification of the Zingiberales. Annals of the Missouri Botanical Garden 77:698–721.

Lam, H. J. 1939. On the system of the Sapotaceae, with some remarks on taxonomical methods. Recueil des Travaux Botaniques Neerlandais 36:509–525.

Langenheim, J. H. 1969. Amber: a botanical inquiry. Science (Washington, D.C.) 163:1157–1169.

———. 1973. Leguminous resin-producing trees in Africa and South America. Pages 89–104 in B. T. Meggers, E. S. Ayensu, and W. D. Duckworth, eds. Tropical forest ecosystems in Africa and South America: a comparative review. Smithsonian Institution, Washington, D.C.

———. 1990. Plant resins. American Scientist 78:16–24.

Langenheim, J. H., C. E. Foster, and R. B. McGinley. 1980. Inhibitory effects of different quantitative compositions of *Hymenaea* leaf resins on a generalist herbivore *Spodoptera exigua*. Biochemical Systematics and Ecology 8:385–396.

Langenheim, J. H., C. L. Convis, C. A. Macedo, and W. H. Stubblevine. 1986. *Hymenaea* and *Copaifera* leaf sesquiterpenes in relation to lepidopteran herbivory in southeastern Brazil. Biochemical Systematics and Ecology 14:41–49.

Lidgard, S., and J. B. C. Jackson. 1989. Growth in encrusting cheilostome bryozoans. I. Evolutionary trends. Paleobiology 15:255–282.

Longhurst, W. M., H. K. Oh, M. B. Jones, and R. E. Kepner. 1968. A basis for the palatability of deer forage plants. North American Wildlife Natural Resources Conference Transaction 33:181–189.

Maksymowych, R., and M. C. Ledbetter. 1987. Fine structure of epithelial canal cells in petioles of *Xanthium pensylvanicum*. American Journal of Botany 74:65–73.

Matile, P. 1976. Localization of alkaloids and mechanism of their accumulation in vacuoles of *Chelidonium majus* laticifers. Nova Acta Leopoldina Supplementum 7:139–156.

Mayr, E. 1942. Systematics and the origin of species. Columbia University Press, New York.

McDowell, P. G., W. Lwande, S. G. Deans, and P. G. Waterman. 1988. Volatile resin exudate from stem bark of *Commiphora rostrata:* potential role in plant defense. Phytochemistry 27:2519–2521.

McKey, D. 1979. The distribution of secondary compounds within plants. Pages 55–133 in G. A. Rosenthal and D. H. Janzen, eds. Herbivores: their interaction with secondary plant metabolites. Academic Press, New York.

Mesa, A. 1986. The classification of the Nolanaceae. Pages 86–90 in W. G. D'Arcy, ed. Solanaceae, biology and systematics. Columbia University Press, New York.

Metcalfe, C. R. 1967. Distribution of latex in the plant kingdom. Economic Botany 21:115–125.

Metcalfe, C. R., and L. Chalk. 1983. Anatomy of the Dicotyledons. Vol. 2. Clarendon, Oxford.

Miller, J. S. 1987. Host-plant relationships in the Papilionidae (Lepidoptera): parallel cladogenesis or colonization? Cladistics 3:105–120.

Mitter, C., B. Farrell, and B. Wiegmann. 1988. The phylogenetic study of adaptive zones: has phytophagy promoted insect diversification? American Naturalist 132:107–128.

Moore, R. J. 1947. Cytotaxonomic studies in the Loganiaceae. I. Chromosome numbers and phylogeny in the Loganiaceae. American Journal of Botany 34:527–538.

Muller, J. 1984. Significance of fossil pollen for angiosperm history. Annals of the Missouri Botanical Garden 71:419–443.

Nelson, C. J., J. N. Seiber, and L. P. Brower. 1981. Seasonal and intraplant variation of cardenolide content in the California milkweed, *Asclepias eriocarpa*, and implications for plant defense. Journal of Chemical Ecology 7:981–1010.

Nielsen, B. E. 1971. Coumarin patterns in the Umbelliferae. Pages 325–336 in V. H. Heywood, ed. The biology and chemistry of the Umbelliferae. Academic Press, London.

Nishio, S., M. S. Blum, and S. Takahashi. 1983. Intraplant distribution of cardenolides in *Asclepias humistrata* (Asclepiadaceae) with additional notes on their fates in *Tetraopes melanurus* (Coleoptera: Cerambycidae) and *Rhyssomatus lineaticollis* (Coleoptera: Curculionidae). Memoirs of the College of Agriculture Kyoto University 122:43–52.

Noack, E. A., A. E. G. Crea, and G. Falsone. 1980. Inhibition of mitochondrial oxidative phosphorylation by 4-deoxyphorbol triester, a poisonous constituent of the latex sap of *Euphorbia biglandulosa* Desf. Toxicon 18:165–174.

Olson, K. C., T. W. Tibbits, and B. E. Struckmeyer. 1967. Morphology and significance of laticifer rupture in lettuce tipburn. Proceedings of the American Society for Horticultural Science 91:377–385.

Parkin, J. 1900. Observations on latex and its functions. Annals of Botany (London) 14:193–214.

Polhill, R. M., and J. E. Vidal. 1981. Tribe 1. Caesalpinieae. Pages 81–96 in R. M. Polhill and P. R. Raven, eds. Advances in legume systematics. Pt. 1. Crown, London.

Prance, G. T., W. A. Rodriguez, and M. F. DaSilva. 1976. Inventario florestal de um hectare de mata de terra firme km 30 da estrada Manaus-Itacoatiara. Acta Amazonica. 6:9–35.

Rafiq, M., A. Jabri, K. A. Siddiqui, T. A. Khan, S. I. Husain, and K. Mahmood. 1985. Inhibitory effect of latex on lesions caused by some plant viruses. Indian Botanical Reporter 4:213–214.

Rees, S. B., and J. B. Harborne. 1985. The role of sesquiterpene lactones and phenolics in the chemical defense of the chicory plant. Phytochemistry 24:2225–2231.

Rensch, B. 1959. Evolution above the species level. Columbia University Press, New York.

Rhoades, D. F. 1985. Offensive-defensive interactions between herbivores and plants: their relevance in herbivore population dynamics and ecological theory. American Naturalist 125:205–238.

Rizk, A. M. 1987. The chemical constituents and economic plants of the Euphorbiaceae. Botanical Journal of the Linnean Society 94:293–326.

Roberts, M. F. 1987. Papaver latex and alkaloid storage vacuoles. Pages 513–528 in B. Marin, ed. Plant vacuoles: their importance in solute compartmentation in cells and their applications in plant biotechnology. Plenum, New York.

Robson, N. 1965. Taxonomic and nomenclatural notes on Celastraceae. Boletim da Sociedade Broteriana, Ser. 2, 39:5–55.

Rodriguez, R. L. 1971. The relationships of the Umbellales. Pages 63–92 in V. H. Heywood, ed. The biology and chemistry of the Umbelliferae. Academic Press, London.

Rudall, P. J. 1987. Laticifers in Euphorbiaceae—a conspectus. Botanical Journal of the Linnean Society 94:143–163.

Rudinsky, J. A. 1966. Host selection and invasion by the Douglas-fir beetle, Dendroctonus pseudotsugae Hopkins, in coastal Douglas-fir forests. Canadian Entomologist 98:98–111.

Schuh, B. A., and D. M. Benjamin. 1984. Evaluation of commercial resin acids as feeding deterrents against Neodiprion dubiosus, N. lecontei, and N. rugifrons (Hymenoptera: Diprionidae). Journal of Economic Entomology 77:802–805.

Seiber, J. N., C. J. Nelson, and S. M. Lee. 1982. Cardenolides in the latex and leaves of seven Asclepias species and Calotropis procera. Phytochemistry 21:2343–2348.

Sen, D. N., and D. D. Chawan. 1972. Leafless Euphorbia on Rajasthan (India) rocks. Vegetatio 24:193–214.

Shaw, E. M., P. L. Woolley, and F. A. Rae. 1963. Bushman arrow poisons. Cimbebasia 7:1–41.

Shukla, O. P., and C. R. Krishna Murti. 1971. The biochemistry of plant latex. Journal of Scientific and Industrial Research (India) 30:640–662.

Simpson, G. G. 1944. Tempo and mode in evolution. Columbia University Press, New York.

Smith, E. L., J. R. Kimmel, D. M. Brown, and E. O. P. Thompson. 1955. Isolation and properties of a crystalline mercury derivative of a lysozyme from papaya latex. Journal of Biological Chemistry 215:67–89.

Southwood, T. R. E. 1973. The insect/plant relationship—an evolutionary perspective. Pages 3–30 in H. F. van Emden, ed. Insect/plant relationships. Blackwell Scientific, London.

Stanley, S. M. 1979. Macroevolution, pattern and process. W. H. Freeman, San Francisco.

Stant, M. Y. 1967. Anatomy of the Butomaceae. Botanical Journal of the Linnean Society 60:31–60.

Stradling, D. J. 1978. The influence of size on foraging in the ant, Atta cephalotes, and the effect of some plant defense mechanisms. Journal of Animal Ecology 47:173–188.

Strong, D. R., J. H. Lawton, and T. R. E. Southwood. 1984. Insects on plants. Harvard University Press, Cambridge, Mass.

Taktajahn, A. 1980. Outline of the classification of flowering plants (Magnoliophyta). Botanical Review 46:225–359.

Thompson, J. N. 1986. Patterns in coevolution. Pages 119–143 in A. R. Stone and D. L. Hawksworth, eds. Coevolution and systematics. Systematics Association Special Vol. 32. Clarendon, Oxford.

Thorne, R. F. 1976. A phylogenetic classification of the Angiospermae. Pages 35–106 in M. H. Hecht, W. C. Steere, and B. Wallace, eds. Evolutionary biology. Vol. 9. Plenum, New York.

Tippo, O. 1938. Comparative anatomy of the Moraceae and their presumed allies. Botanical Gazette 100:1–99.

Tournay, R., and A. Lavalree. 1952. Une classification nouvelle des familles appartenant aux ordres des Lugustrales et des Contortées. Bulletin de la Societe Botanique de France 99:262–263.

Valle, M. G., G. Appendino, G. M. Nano, and V. Picci. 1987. Prenylated coumarins and sesquiterpenoids from *Ferula communis*. Phytochemistry 26:253–256.

Vermeij, G. J. 1987. Evolution and escalation: an ecological history of life. Princeton University Press, Princeton, N.J.

———. 1988. The evolutionary success of passerines: a question of semantics? Systematic Zoology 37:69–71.

Wanntorp, H. E. 1988. The genus *Microloma* (Asclepiadaceae). Opera Botanica 98:1–69.

Webster, G. L. 1987. The saga of the spurges: a review of classification and relationships in the Euphorbiales. Botanical Journal of the Linnean Society 94:3–46.

Wilder, G. J. 1989. Morphology of *Dianthoveus cremnophilus* (Cyclanthaceae). Canadian Journal of Botany 67:2450–2464.

Wilder, G. J., and D. H. Harris. 1982. Laticifers in *Cyclanthus bipartitus* Poit. (Cyclanthaceae). Botanical Gazette 143:84–93.

Willis, J. C. 1973. A dictionary of the flowering plants and ferns. Cambridge University Press, Cambridge.

Wilson, K. J., and P. G. Mahlberg. 1980. Ultrastructure of developing and mature nonarticulated laticifers in the milkweed *Asclepias syriaca* L. (Asclepiadaceae). American Journal of Botany 67:1160–1170.

Winder, J. A. 1976. Ecology and control of *Erinnyis ello* and *E. alope*, important insect pests in the New World. PANS (Pest Articles and News Summaries) 22:449–466.

Wittler, G. H., and J. D. Mauseth. 1984. Schizogeny and ultrastructure of developing latex ducts in *Mammillaria guerreronis* (Cactaceae). American Journal of Botany 71:1128–1138.

Wood, S. L. 1982. The bark and ambrosia beetles (Coleoptera: Scolytidae) of North and Central America, a taxonomic monograph. Great Basin Naturalist Memoirs 6. Brigham Young University Press, Provo, Utah.

Woodson, R. E. 1941. The North American Asclepiadaceae. I. Perspective of the genera. Annals of the Missouri Botanical Garden 28:193–244.

Young, D. R., and L. Watson. 1969. Softwood structure and the classification of conifers. New Phytologist 68:427–432.

Zwölfer, H. 1978. Mechanismen und Ergebnisse der Co-evolution von phytophagen und entomophagen Insekten und höheren Pflanzen. Sonderbände des Naturwissenschaftlichen Vereins in Hamburg 2:7–50.