Diversification of Carnivorous Parasitic Insects: Extraordinary Radiation or Specialized Dead End?

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American Naturalist, Volume 142, Issue 5 (Nov., 1993), 737-754.

Vol. 142, No. 5 The American Naturalist November 1993

DIVERSIFICATION OF CARNIVOROUS PARASITIC INSECTS: EXTRAORDINARY RADIATION OR SPECIALIZED DEAD END?

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Submitted May 21, 1992; Revised October 27, 1992; Accepted November 9, 1992

Abstract.—The spectacular diversity of insects has often been attributed to accelerated radiation of groups acquiring specialized trophic habits. In accord with this hypothesis, a previous study demonstrated consistently greater diversification in clades attacking higher plants, as contrasted to their predaceous or saprophagous sister groups. Faster diversification of phytophagous insects could represent radiation in an unsaturated adaptive zone or result from the population fragmentation and diversifying selection imposed by ecological specialization per se. The latter effect underlies the hypothesis that rapid diversification characterizes "parasitic" insects in a broad sense including most phytophages, contrasting with the classical view of parasitic specialization as an evolutionary "dead end." To test these hypotheses, we catalogued the origins and effect on diversification of animal parasitism by insects. Of 15 carnivorous parasitic insect clades with estimated relationships, six were more diverse than their predaceous or saprophagous sister groups, and nine less diverse (Wilcoxon $T = 28$, $P < .10$). The parasitic lifestyle in the broad sense is by itself unlikely to be a dominant explanation of variable insect diversification rate, while the hypothesis that parasitism in the strict sense is an evolutionary dead end remains plausible. Carnivorous parasitism and phytophagy have significantly different effects on diversification. We found no evidence for ascribing either this difference or the heterogeneity of rates among carnivorous parasite clades to clade age, mode of parasitism, diversity of host clade, or host specificity. Greater diversification by phytophages than by other trophic levels might reflect simply greater average abundance of the resource used by primary consumers.

The spectacular radiation of the Insecta poses the problem of differential diversification rates in acute form. Many hypotheses for insect diversity have invoked some form of ecological specialization, particularly with respect to trophic habits (see, e.g., Ehrlich and Raven 1964; Southwood 1973; Zwölfer 1978). However, these hypotheses have rarely been explicitly tested (Mitter et al. 1988).

In this article we examine the potential contribution to insect diversification of one extreme form of trophic specialization, the adoption of parasitism. By "parasite" we mean " 'an organism living in or on another living organism, obtaining from it part or all of its organic nutriment, commonly exhibiting some degree of adaptive structural modification, and causing some degree of real damage.' This contrasts with the more generalized grazers, browsers, and predators that feed on many organisms during their lifetime and with saprophages that feed on dead

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Am. Nat. 1993. Vol. 142, pp. 737–754.

organic matter'' (Price 1980*a,* p. 4; taken in part from *Webster's Third International Dictionary*). Other published definitions (Noble and Noble 1964; Askew 1971) differ only in the degree to which the relationship of parasite to host is obligatory.

Opposing views have been offered on the macroevolutionary consequences of parasitism. Some authors have postulated that parasites should have unusually high rates of diversification; for example, Price (1980*a,* p. 14) argues that ''no group of organisms on earth can surpass the parasites in their potential for . . . adaptive radiation.'' There are several grounds for such a prediction. Under the classical view (Simpson 1953), parasitism can be regarded as a new ''adaptive zone,'' invasion of which might promote radiation by temporarily freeing a lineage from competition or predation. The diversity of available niches and of parasite species might be further amplified by coevolution between parasites and their hosts (Ehrlich and Raven 1964; Thompson 1982, 1987).

It has also been argued that rapid diversification is a population-genetic consequence of ecological specialization per se, of which parasitism is an extreme example (Stanley 1979; Price 1980*a;* Vrba 1980; reviews in Futuyma and Moreno 1988; Eldredge 1989). Parasites are typically modified and intimately dependent for survival on only one or a few types of hosts, which often constitute both food and habitat for the much smaller parasite. They should thus be highly subject to diversifying selection arising from variation within and among host species. Moreover, because mating is often confined to the patchily distributed hosts, gene flow among local parasite populations may be low, which further promotes divergence and speciation. Finally, ecological specialization may favor diversification by reducing competition between incipient species; this is the sense of Mayr's (1976, p. 21) assertion that ''extreme specialization is characteristic in insects and explains their prodigious rate of speciation.''

A strongly contrasting older view (Huxley 1942; Rensch 1960) holds that extreme ecological specialization such as that which parasites exhibit is a dead end, which limits the potential for further evolution and raises the probability of extinction. This postulate has been much debated (reviews in Mayr 1963; Futuyma and Moreno 1988; Moran 1988) but has seemed especially plausible for parasites, with their frequent, perhaps irreversible loss of complex morphological features; ''parasites . . . are worthy examples of the inexorable march of evolution into blind alleys'' (Noble and Noble 1964, p. 686; cited in Price 1980*a*).

To test these opposing predictions about parasite diversification, we use the method of multiple sister-group comparisons (Mitter et al. 1988; Farrell et al. 1991) (see Methods). By this approach, we previously found evidence for elevated diversification in phytophagous insects, which have sometimes been considered parasites in the broad sense (Price 1980*a*). We now examine the effect on insect diversification of parasitism in a stricter, more traditional sense, that is, parasitism of animals. Consistently higher diversity in carnivorous parasite lineages as contrasted to their sister groups is expected if diversification is promoted either by ecological specialization per se, exemplified by parasitism, or by entry into the novel, unsaturated adaptive zone that such parasitism may constitute. We contrast these predictions to the null hypothesis of no relationship and to the opposing prediction that specialization for carnivorous parasitism is an evolutionary dead end, resulting in reduced diversification. Finally, we contrast these results to those of our earlier study, testing the prediction that carnivorous parasites should radiate even faster than phytophages because more host species are potentially available to them (Price 1980*a*).

METHODS

In outline, our test consists of cataloging the insect lineages in which parasitism of animals has arisen, identifying the sister groups of these, and comparing the diversities of the paired lineages. Because sister groups are equal in age by definition (but see below for possible complications), differences between them in diversity, measured here as the number of species, reflect different rates of net diversification (speciation minus extinction; Stanley 1979).

Identification of Parasitic Groups

To avoid bias in identifying animal-parasitic insect groups, we have followed Price (1980*a*) as closely as possible, excluding as he does Diptera that are intermittently blood feeding as adults, mutualists, inquilines, and social parasites. As Price points out, any definition of parasitism must be somewhat arbitrary, because there is a continuum of degree and kind of dependence on the host. However, this arbitrariness should have little effect on our results, given our pairwise design: in all of our comparisons, the clade taken as parasitic fits the definition to a much greater degree than does its sister group. On this logic, and to maximize the number of comparisons, we also followed Price (1980*a*) and tradition in treating as parasites several groups that may not entirely match the above definition. For example, the bedbugs and relatives (Hemiptera: Cimicidae) are completely dependent on bird or mammal blood meals for both growth and reproduction (Askew 1971), and their morphology, physiology, and life history are highly specialized for an ectoparasitic life. Unlike most ectoparasites, cimicids often leave the host when not feeding. However, they are unquestionably more parasitelike than their nearest relatives (Ford 1979; Schuh and Stŷs 1991) among the Anthocoridae. Similar arguments apply to the fleas (Siphonaptera).

Sister-Group Comparisons

To identify as many animal-parasitic insect lineages as possible we searched the literature, beginning from the compilations in Askew (1971) and Price (1980*a*). Our estimates of the sister groups of those lineages are based on our reading of the primary systematic literature in consultation with specialists (see Acknowledgments). Recent cladistic studies received the greatest weight. For insect relationships above the order level, we follow Kristensen (1981, 1991). Animal-parasitic groups are included in our tally of comparisons (table 1) only if the literature provides a clear argument for, and no strong evidence against, monophyly in the sense of Hennig (1966), evidence that parasitism arose in the group's common ancestor, and evidence to identify either a definite sister group or a set

TABLE 1

Summary of Sister-Group Diversity Comparisons on Independent Carnivorous Parasitic Lineages, Their Ages, and Principal Host Groups

Primitively Parasitic Lineage		Sister Group				
Taxon	Approximate No. of Species (Parasites Only)	Taxon	Approximate No. of Species (Excluding Parasites)	Sign of Difference in Diversity	Parasite Group Age (my)	Hosts
Comparisons of carnivorous parasite clades to primitively predaceous or saprophagous clades:						
Dermaptera:						
Hemimeridae	11[a]	Forficulina	1,484			
		−Arixeniina	5			
			1,479[a]	−*†‡	150[q]	Muridae (rodents)
Arixeniina	5[a]	Labiidae	380[a]	−*†‡	150[q]	Bats
Phthiraptera	3,080[b]	Psocoptera	2,580[c]	+*†‡	150[q]	Mammals + birds
Hemiptera:						
Cimicidae	89[b]	Xylocorini + Almeidini	55[d]	+*†‡	150[q]	Mammals + birds
Neuroptera:						
Mantispinae	320[e]	Calomantispinae	10[e]	+*†‡	60[s]	Spider eggs
Coleoptera:						
Leiodidae:						
Platypsyllinae	13[f]	Cholevinae	621[g]	−*†‡	?	Rodents
Strepsiptera	4,000[h]	Coleoptera	600,000[i]	−*†‡	55[aa]	Insects
Siphonaptera	1,740[j]	Mecoptera	470[k]	+*†‡	250[q]	Mammals + birds
Diptera:						
Nemestrinoidea	700[l]	Asiloidea	7,000			
		+ Empidoidea	9,000			
		+ Cyclorrhapha	80,000			
			96,000[l]	−*†‡	150[q]	Spiders, beetles, grasshoppers
Bombyliidae	4,000[l]	Asiloidea (*in part*)	7,000[l]	−*†‡	50[r]	Insects
Pipunculidae	400[m]	Syrphidae	5,000[l]	−*†‡	35[u]	Homoptera
Conopidae	800[l]	Tephritoidea − phytophages and parasites	3,021[l]	−*	35[v]	Aculeate Hymenoptera
		Tephritoidea including phytophages	7,201[l]	−‡		

Sarcophagidae:						
Blaesoxipha (in part)	184[n]	*Blaesoxipha gigantotheca* species group	9[n]	+ *†‡	<30[w]	Millipedes, Orthoptera
Tachinidae	6,000[l]	Nonparasitic Sarcophagidae	3,200[l]	+ *†‡	<30[z]	Insects
Hippoboscoidea	685[l]	Muscoidea + Oestroidea (in part)	7,350[l,m]	− *†‡	25[t]	Mammals + birds
Comparisons of carnivorous parasite clades to primitively phytophagous clades:						
Coleoptera:						
Rhipiphoridae	400[i]	Mordellidae	1,200[i]	− †‡	170[y]	Insects
Diptera:						
Pyrgotidae + Tachiniscidae	334[l]	Tephritidae	4,000[l]	− †‡	<30?	Scarabaeidae
Hymenoptera:						
Parasitic:						
Apocrita-Torymidae	100,000[o]	Cephoidea (or any nonparasitic siricoid sister group)	102[o]	+ †‡	150[x]	Insects
Torymidae-Megastigminae	707[p]	Megastigminae	131[p]	+ †	?	Insects

Note.—Summary: * Comparisons included in test of ecological specialization hypothesis, carnivorous parasites vs. nonparasitic sister group: the number of positive differences = 6, negative differences = 9; two-tailed sign test, $P = .304$; Wilcoxon $T = 28$, $P = .074$. † Comparisons included in test of adaptive zone hypothesis, all cases in which carnivorous parasitism is the more derived habit: the number of positive differences = 8, negative differences = 10; two-tailed sign test, $P = .407$; Wilcoxon $T = 54$, $P = .177$. ‡ Comparisons included in test of carnivorous parasite increased diversification hypothesis, carnivorous parasitism vs. any other habit: the number of positive differences = 7, negative differences = 11; two-tailed sign test, $P = .240$; Wilcoxon $T = 46$, $P = .089$. Sources for species diversities: a, Brown 1982*a;* b, Marshall 1981; c, Smithers 1982; d, Ford 1979; e, J. Oswald, personal communication; f, Newton 1990; g, Jeannel 1911, 1936; h, Brown 1982*b;* i, Lawrence 1982; j, Smit 1982; k, Brown 1982*c;* l, Bickel 1982; m, Ferrar 1987; n, T. Pape, personal communication; o, Brown 1982*d;* p, E. Grissell, personal communication. Sources for age estimates: q, Hennig 1981; r, Larsson 1978; s, Schluter 1986; t, Maa and Peterson 1987; u, Hardy 1987; v, Smith and Peterson 1987; w, Shewell 1987; x, Rasnitsyn 1980; y, Crowson 1981; z, Rohdendorf 1991; aa, Kinzelbach and Lutz 1985. Sources for phylogenies: Popham 1985; Lyal 1985; Schuh and Stŷs 1991; Lambkin 1986; Peck 1990; Selander 1957; Kinzelbach 1971; Kristensen 1981; Woodley 1989; McAlpine 1989; Pape 1992; Rasnitsyn 1980; Gibson 1985; E. Grissell, personal communication.

of closely related possible sister groups, choice among which does not affect the outcome of the diversity comparison.

A detailed review of the habits, hosts, species diversities, and relationships of all carnivorous parasitic insect groups known to us and our reasons for including or excluding each from the final tally of comparisons (table 1) is available upon request from the authors; it is too large to include here. Many parasitic groups were excluded because of the lack of evidence on their relationships. Examples include lineages within phorid, muscid, calliphorid, and chloropid flies. Other taxa were excluded because conflicting current views on their sister groups lead to different conclusions about the sign of diversity differences. Examples include the dipteran families Cryptochaetidae (Griffiths 1972; McAlpine 1989), Rhinophoridae, and Oestridae (McAlpine 1989; Pape 1992) and the heteropteran bat-ectoparasitic family Polyctenidae (Schuh and Stŷs 1991). In contrast, although two competing arrangements of the oestroid Diptera have been proposed (McAlpine 1989; Pape 1992), the parasitic clade containing the Tachinidae is much more diverse than its nonparasitic sister group under either hypothesis, which thus allows its inclusion in our tally. Similarly, the apocritan Hymenoptera are included (probably at least 100,000 parasitic species [Brown 1982*d*], although estimates vary), as they are clearly more diverse than any of the several sawfly sister groups that have been suggested for them (Rasnitsyn 1980; Gibson 1985).

Insect diversity and phylogeny are the subject of intense current research, and all of the phylogeny as well as diversity estimates we accept should be regarded as possibly erroneous. However, such taxonomic error should be random with respect to the hypotheses under test, and previous studies (Mitter et al. 1988; Dial and Marzluff 1989; Farrell et al. 1991; Marzluff and Dial 1991) have shown that comparisons of the kind and number undertaken here are capable of detecting patterns of diversification rate if they exist. As we have previously detailed (Mitter et al. 1988; Farrell et al. 1991), comparisons of extant diversity between sister groups present several limitations and complexities. First, within the sister group bearing the more derived trophic habit, the habit itself may have arisen after the split between sister groups, species with earlier habits having gone extinct. Diversification rate in the new adaptive zone may therefore be underestimated. Given previous findings of strong association between extant diversity and other "key innovations" (Mitter et al. 1988; Farrell et al. 1991), we doubt that this bias is strong, but its importance will only be quantifiable when better estimates become available of divergence times among extant species. That the early members of some parasite clades had different habits from the extant species is suggested by the fact that several clades parasitizing birds or mammals appear to be older than their present-day hosts (table 1). For example, fleas (Siphonaptera) probably arose in the late Paleozoic (Hennig 1981; Kukalova-Peck 1991), roughly the time of appearance of the first amniotes; it has been speculated that early fleas parasitized reptiles (Kukalova-Peck 1991).

A second difficulty is ensuring independence of comparisons when the taxonomic distribution of habits is complex. If one potential sister-group comparison is embedded inside another, it is only legitimate to include both when removal of the lower-level pair from the broader comparison leaves the result of the latter unchanged. Thus, the comparison of phytophagous versus parasitoid lineages within the hymenopteran family Torymidae can be regarded as independent of that between the suborder Apocrita and its sister group, even though torymids are apocritans, because the latter are orders of magnitude more diverse than their sister group whether or not torymids are excluded from the species count. Secondary nonparasites within parasitic clades, such as the only intermittently blood-feeding glossinid flies, derived within the ectoparasitic Hippoboscoidae (McAlpine 1989), must also be excluded so that the diversity estimate reflects only that of the parasites.

Three different sets of sister-group comparisons were conducted, corresponding to the three hypotheses distinguished earlier (table 1). To determine whether carnivorous parasites might diversify rapidly because of their characteristic ecological specialization, we contrasted carnivorous parasites only to nonparasitic, presumably less ecologically specialized relatives ($N = 15$). Sister-group comparisons of carnivorous parasites to phytophagous clades were excluded from this test because most phytophages could also be considered ecologically specialized and parasitic under the definition given earlier (Price 1980*a*). However, comparisons of carnivorous and phytophagous sister groups in which phytophagy is the primitive habit *are* included for testing the broader hypothesis that entry into a new adaptive zone per se, in this case parasitism of animals, promotes diversification ($N = 18$). Finally, to test the hypothesis that diversification rates are higher in carnivorous parasites than in either nonparasites or phytophages, all comparisons of carnivorous parasitism to other habits are included ($N = 18$).

Trends in relative diversity of parasitic lineages with respect to their nonparasitic sister groups were evaluated with both a sign test and the Wilcoxon signed-ranks test. The Wilcoxon test was performed on the logarithms of species diversities, which are proportional to net diversification rates (Stanley 1979) when time is held constant. Since both elevated and depressed relative diversities of parasitic groups have been predicted, the tests are two-tailed. To determine whether carnivorous parasitism and phytophagy have different effects on diversification as contrasted to entirely nonparasitic habits, we compared the proportions of positive and negative diversity differences between sister groups in this study and in our previous study of insect phytophages (Mitter et al. 1988), using a 2×2 contingency table.

Following the initial diversity comparisons, we undertook a preliminary search for possible sources of the variable relative diversities (with respect to their sister groups) of parasite and phytophage clades. To test whether those differences might be a function of geological time, we compiled approximate ages for each sister-group pair in this study, as well as the phytophage/sister-group comparisons identified previously (Mitter et al. 1988). Sources for these estimates, which are rough minima based on the oldest fossil attributable to either sister group (Hennig 1966), are given in table 1. The analysis employed the three distinct categories into which the estimates seemed to fall, corresponding roughly to the Upper Paleozoic, Lower Mesozoic, and Lower Tertiary.

To test the postulate of Price (1980*a*) and others that diversification should be related to host specificity, we estimated the latter by compiling information on numbers of host species used from taxonomic monographs (sources in table 2), beginning with the data from Britain used by Price (1980*a*) but for most groups covering several other regions as well. We regressed differences in log diversity between carnivorous parasite clades and their sister groups on host specificity quantified as the fraction of species known from just a single host species (Price 1980*a*). The use of broader criteria (two or fewer hosts, three or fewer hosts) had no effect on the conclusions.

Finally, to explore whether these univariate analyses might be obscuring interactions among multiple influences on relative diversity, age, vertebrate versus invertebrate parasitism, and host specificity were included in a multiple regression performed using SYSTAT version 5.0. The dependent variable, as in the preceding test, was the signed difference in the logarithm of species diversity between sister groups. Age classes A and B (table 3) were combined because the former included only one comparison.

RESULTS

Of the approximately 65 insect groups we identified as parasitizing animals, there was sufficient phylogenetic information for 19 to support inclusion in our tally of comparisons (table 1). When attention is restricted to comparison of carnivorous parasitic to less specialized nonparasitic lineages, the parasitic group is more diverse in six cases and less so in nine (see asterisked note in table 1). Under a sign test, we cannot reject the null hypothesis of no effect on diversification ($P = .304$). Under the Wilcoxon test, which should be more powerful (Conover 1971), there is a stronger suggestion ($P = .074$) of a negative effect. The results are similar when the sample is broadened to include all contrasts in which carnivorous parasitism is a new adaptive zone as contrasted to the habits of the sister group, whether these be phytophagous, saprophagous, or predaceous (see daggered note in table 1; 8+, 10−, sign test, $P = .407$; Wilcoxon $T = 54$, $P = .177$), or to all comparisons of carnivorous parasite clades with any other trophic habit (see note designated by double dagger [‡] in table 1; 7+, 11−, sign test, $P = .240$; Wilcoxon $T = 46$, $P = .089$).

A χ^2 test for difference in proportions shows that the phytophagous insect groups cataloged previously (Mitter et al. 1988) are more diverse than their predaceous or saprophagous sister groups significantly more often than are the animal-parasitic groups compiled in this study (table 4: $\chi^2 = 5.81$, df = 1, $P = .016$), though it should be noted that no trend was apparent among the few direct comparisons between carnivorous and phytophagous parasites. Also, χ^2 tests show that relative diversity of parasitic clades as compared to the sister group is not a function of clade age (table 3: $\chi^2 = 1.16$, df = 2, $P = .559$) or, for carnivorous parasites, of attacking vertebrate versus invertebrate hosts ($\chi^2 = 0.076$, df = 1, $P = .783$). Regression analysis suggested that relative diversification rates of parasite clades are, if anything, negatively related to host specificity ($y = -1.98x + 39.85$, $R^2 = 0.19$, $.20 > P > .10$). The multiple regression yielded results qualitatively similar to the univariate tests. Neither the partial regression coefficients for clade age ($t = 1.3$, $P = .2$), vertebrate versus invertebrate hosts

TABLE 2

Distributions (in percentages) of Numbers of Host Species Used by Species in Carnivorous Parasite Clades of Table 1 (data unavailable for tachinidae)

No. of Host							SIP								
Species Used	HEM	PTH	CIM	MAN	PLA	STR	P	H	L	NEM	BOM	PIP	CON	BLA	HIP
1	27	64	36	8	31	23	35	37	30	60	60	60	45	34	45
2	27	17	28	8	0	9	20	20	20	11	10	12	14	8	20
3	19	6	7	8	0	19	11	9	9	5	4	7	4	11	14
4	9	3	5	0	8	5	6	5	6	4	1	8	9	7	7
5	0	3	1	8	0	10	6	5	5	2	4	5	4	3	4
6	9	1	3	18	0	10	1	6	5	2	3	0	4	1	2
7		1	0	0	8	2	1	2	5	0	3	1		1	2
8		1	4	0	0	0	2	3	6	0	1	1		3	2
9		1	0	0	8	2	1	3	5	2	3	1			<1
10–19		2	1	8	8	10	9	9	9	2	1	2		14	1
20–29		<1		8	0	2	3	<1						6	2
30–39						2	1	<1						3	<1
40–49		<1					1							1	0
50–59		<1					3								<1
60–69						2									0
70–79															0
80–89															2
?	9		15	34	39	4				12	10	3	20	8	
N	11	544	73	12	13	57	114	399	150	57	138	91	22	73	192

Note.—?, number of species sampled for which hosts are recorded at genus level or above only. Sources: HEM, Hemimeridae (Nakata and Maa 1974); PTH, Pthiraptera (Emerson and Price 1981; Kim et al. 1986); CIM Cimicidae (Usinger 1966; Ueshima 1968); MAN, Mantispinae (Eason et al. 1967; Austin 1985; New 1986; Hoffman and Brushwein 1989; Rice and Peck 1991); PLA, Platypsyllinae (Buckle 1976; Peck 1982; Newton 1990); STR, Strepsiptera (Kinzelbach 1978; Waloff and Jervis 1987); SIP, Siphonaptera: P, Pulicidae, H, Hystrichopsyllidae, L, Leptopsyllidae (Hopkins and Rothschild 1953–1971, cited in Price 1980*b*); NEM, Nemestrinoidea (Schlinger 1987); BOM, Bombyliidae (Hull 1973); PIP, Pipunculidae (Waloff and Jervis 1987); CON, Conopidae (Smith 1959; Freeman 1966); BLA, *Blaesoxipha* (T. Pape, personal communication); HIP, Hippoboscoidea (Bequeart 1956; Wenzel et al. 1966; Guimãeres 1972; Wenzel 1976; Price 1980*a*).

TABLE 3

AGE CLASS DISTRIBUTION OF CARNIVOROUS PARASITE AND PHYTOPHAGE CLADES AS A FUNCTION OF RELATIVE DIVERSITY

SIGN OF DIVERSITY COMPARISON	PALEONTOLOGICAL AGE CLASS A	B	C	TOTAL
+	1	12	5	18
−	0	7	5	12
Total	1	19	10	30

NOTE.—Age classes are A, 250 my and older; B, 250–50 my; C, <50 my; see tables 1 and 5. $\chi^2 = 1.16$; df = 2; $P = .559$, NS.

TABLE 4

PROPORTIONS OF CARNIVOROUS AND PHYTOPHAGOUS PARASITIC CLADES MORE DIVERSE THAN THEIR NONPARASITIC SISTER GROUPS

TYPE OF PARASITISM	SIGN OF DIVERSITY COMPARISON* +	−	TOTALS
Phytophagous†	11	2	13
Carnivorous‡	6	9	15
Total	17	11	28

NOTE.—Results of χ^2 test for difference in proportions: $\chi^2 = 5.81$, df = 1, $P = .016$.

* Parasite clade minus sister group.

† From Mitter et al. (1988); see table 5.

‡ From table 1.

($t = 0.02$, $P = .983$), or host specificity ($t = 1.9$, $P = .09$) nor the overall model ($F = 1.5$, $P = .3$) was significant.

DISCUSSION

Carnivorous parasitism appears to have originated more than 60 times among insects. Future phylogenetic work should therefore permit many more sister-group comparisons than the 19 identified so far, and such work may also modify some of our current contrasts.

While our results should thus be taken as provisional, several conclusions emerging from them seem unlikely to change. The postulate that carnivorous parasitic insects typically diversify rapidly in comparison to predators and saprophages, more so even than phytophagous insects, cannot be supported. There is a stronger suggestion (though not statistically significant) of the contrary effect, that specialization for carnivorous parasitism retards subsequent diversification.

There is no typical macroevolutionary behavior exhibited by parasitic insects in the broad sense (Price 1980*a*): carnivorous parasitism and phytophagy have significantly different effects on diversification. (The possible conservatism of the test mentioned earlier applies equally to both studies.) A corollary is that, while there surely is some explanation (Slowinski and Guyer 1989) for the spectacular diversity of a few carnivorous parasitic groups, such as parasitic Hymenoptera, to date there is no evidence that parasitism itself is the cause.

One general implication of these findings concerns the ''geometry'' of macroevolution. It has been suggested that shift to a new adaptive zone, with its attendant specialization in the phylogenetic sense, is inevitably associated with elevated diversity, which reflects an intrinsic property of either phylogenesis or classificatory practice (Hennig 1966; Stanley 1979; discussion in Mitter et al. 1988). Our results argue against such an effect. Carnivorous parasitism seems to define fully as distinct and novel an adaptive zone, as does either phytophagy among insects (Mitter et al. 1988) or secretory canal possession among plants (Farrell et al. 1991), both of which are significantly associated with diversification rate. The evolutionary barriers to living and feeding on animals are analogous to those to higher-plant feeding (Southwood 1973), and carnivorous parasitism is restricted, like phytophagy, to a minority of insect orders. Parasites require special adaptations for locating and identifying the host; for synchronizing their life histories with those of their hosts; for living, feeding, and reproducing in or on the host; and for resisting host defenses (Marshall 1976; Vinson 1976, 1984; Waage 1979; Vinson and Iwantsch 1980). Moreover, carnivorous parasites are typically highly derived morphologically, even more so, we suspect, than phytophages. Yet such parasites are *less* diverse, if anything, than their less modified sister groups. This result is paralleled by that of Herrera (1989), who, using a similar approach, found no support for the hypothesized relationship of angiosperm diversification to the repeated origin of biotic dispersal syndromes (but see Erikkson and Bremer 1991). The lack of an inevitable association of phylogenetic advancement with diversity lends force to the search for specific explanations when diversification and particular evolutionary innovations are related.

A second implication of our finding concerns the hypothesis that ecological specialization promotes rapid diversification. Like phytophages, carnivorous parasites typically have narrow host ranges and, as Price (1980*a*) argues, seem clearly to be more ecologically specialized than their nonparasitic relatives. If specialization per se were the principal explanation of elevated diversity for phytophages, and for insects generally, such diversity should especially have characterized the relatively stenotopic carnivorous parasites. Our studies of carnivorous and phytophagous parasites, apparently the only statistically replicated sister-group tests of the specialization-diversification postulate (but see Futuyma and Moreno 1988 and references therein), suggest that, in insects, this hypothesis lacks broad explanatory power. It is possible that this effect would be detectable in more restricted comparisons (but see below).

Why do carnivorous parasitism and phytophagy have such different macroevolutionary consequences? It might be argued that the carnivorous parasite adaptive zone subsumes so broad an array of life histories—internal and external

TABLE 5

SUMMARY OF RELATIVE DIVERSITY (WITH RESPECT TO SISTER GROUP) AND ESTIMATED AGE FOR PHYTOPHAGOUS INSECT LINEAGES TABULATED BY MITTER ET AL. (1988)

Herbivore Lineage	Relative Diversity	Age Class*	Herbivore Group Age (my)
Tingidae	+	B	200
Miridae	+	B	200
Trichophoran Heteroptera	+	B	200
Elateridae + Cebrionidae	+	B	200
Scarabaeidae (in part)	+	B	200
Languriinae	−	B?	200?
Epilachninae	+	B?	200?
Phytophaga	+	B	170
Symphyta	−	B	200
Lepidoptera	+	B	200
Chloropidae (in part)	+	C	<50
Tephritidae s.s.	+	C	<50
Agromyzidae	+	C	<50

* B, 250–50 my; C, <50 my. (From Hennig 1981.)

feeders, with and without free-living stages, on hosts ranging from mammals to arthropods—that to have expected any consistent trend in diversification rate was naive. Strongly disfavoring this view is the consistently elevated diversity of phytophages, which are arguably no less ecologically heterogeneous. Nonetheless, we made a preliminary search for sources of heterogeneity within the carnivorous parasites, as well as between these and phytophages.

One potential source of variation in relative diversity between sister groups is simply age (Price 1980*a*). Some time is undoubtedly required before any deterministic difference in diversification rates between sister groups becomes manifest. A constant trend might thus only be apparent in older comparisons. This effect might even explain the difference between the phytophage and carnivorous parasite results, if for some reason phytophagous groups were on the average older. The available age estimates, certainly imprecise, provide little evidence for such an effect. The age distributions of relatively diverse and relatively species-poor carnivorous parasite clades are statistically indistinguishable from each other and from that of phytophages (tables 3 and 5).

The most obvious ecological distinction within the carnivorous parasites in our sample is that about half the groups attack birds or mammals, while the rest mostly attack insects or other arthropods (table 1). Greater relative diversity might be expected for the arthropod parasites. Price (1980*a*) predicted that parasite diversification should depend most strongly on (among several factors) the diversity of hosts available. He pointed to the much greater number of host species available to parasites of insects than of mammals or birds and suggested that this effect on diversity would overshadow that of host specificity (p. 125). This taxonomic distinction is paralleled in our sample (though not always in general) by feeding mode: the groups attacking invertebrate hosts are mostly internal feeders, whereas those attacking vertebrates are all ectoparasites. However, the vertebrate—and invertebrate—attacking lineages in our sample have essentially identical distributions of diversities with respect to their sister groups.

Price (1980*a*) and others (Noble and Noble 1964; Waage 1979; Askew and Shaw 1986; Gauld 1988) have also argued that diversification rate should increase with parasite host specificity. Our provisional estimates of host specificity provide no evidence for this hypothesis. Thus, a number of highly host-specific lineages, such as Phthiraptera and pipunculid, bombyliid, and conopid flies, show little or no elevation in diversity, whereas some of the highest relative diversities are seen in relatively euryphagous parasites such as Siphonaptera and Mantispidae. (It is conceivable, if unlikely, that this analysis could be complicated by a tendency for better-studied groups to have both greater numbers of described species and larger documented host ranges.)

The exploratory analyses just presented must be viewed with caution, given the coarseness of the age and host specificity estimates and the small sample size. They serve only to show that the contributions to parasites' variable relative diversities of clade age, diversity of available hosts, and host specificity are not immediately apparent. Detailed studies, based on many more comparisons, will be needed to test fully the phylogenetic predictions of these as well as related hypotheses, invoking host geographical range (Lawton and Price 1979; Hawkins 1990), mobility (Waage 1979; Price 1980*a*), size and complexity (Price 1977, 1980*a;* Hawkins and Lawton 1987; Hawkins 1988), nutritive value (Waage 1979), and degree of trophic specialization (Price 1980*a;* Lawton 1986; Hawkins 1988, 1990). Origin of novel strategies within parasitic lineages, such as the repeated evolution of koinobionts from idiobionts among the Hymenoptera (Askew and Shaw 1986), might also promote adaptive radiation. While many of these factors have been correlated with parasite community diversity, it is important to recognize that ecological diversity bears no simple relationship to diversification rate of lineages. For example, correlations between host taxon diversity and number of parasite species hosted (Price 1980*a*) could reflect more frequent independent colonization of, rather than increased diversification of parasites restricted to, those hosts. In addition, the diversification hypotheses themselves need refinement. Diversity of hosts available, for example, is difficult to define, apart from the diversity already colonized, which in turn depends on parasite diversity. Thus, do the nemestrinoid flies, which are so far known only from spiders, beetles, and grasshoppers but contain only 700 species, have fewer available hosts than the apocritan Hymenoptera, which use many more host groups but are also 20 times as diverse?

One final explanation for the greater evolutionary success of phytophagous than of carnivorous insect parasites may be more plausible than any of the hypotheses just reviewed. Price (1980*a*, p. 126) argues that many resources that could potentially support parasite specialization and diversification are too rare to do so. Although the number and nutritive quality of host species available may be smaller for phytophages than for carnivorous parasites, the trophic pyramids of biomass and productivity typical in terrestrial ecosystems (Lindeman 1942; Odum 1957; Smith 1980) suggest that the average abundance of a typical resource is likely to be much greater for primary than for secondary or higher-level consumers. Similar broad correlations of taxonomic diversity with trophic level (although uncorrected for phylogenetic interdependence) have been interpreted by Glazer (1987) to suggest a connection among energy demand, available energy, and speciation/extinction rates (see also Marzluff and Dial 1991).

In sum, carnivorous parasitism, unlike phytophagy, is not consistently associated with accelerated diversification of insect lineages. While some carnivorous parasites have undoubtedly undergone significant adaptive radiation, there is little evidence that the success of these groups is the result of their trophic specialization or that they represent a general pattern among parasitic insects sensu lato. Indeed, there is some suggestion that carnivorous parasitism may even dampen diversification, concordant with the view that extreme specialization reduces evolutionary potential. Differences in the quantity and availability of resources may account for the significantly different macroevolutionary consequences of carnivorous as opposed to phytophagous parasitism.

ACKNOWLEDGMENTS

The authors wish to acknowledge the generous contribution of insight and information on parasites by many colleagues, especially but not exclusively B. Brown, E. Grissell, A. F. Newton, Jr., J. Oswald, T. Pape, K. Rognes, F. Ronquist, C. W. Sabrosky, R. T. Schuh, F. C. Thompson, D. M. Wood, N. E. Woodley, and D. Yeates. Critique of earlier drafts by D. Futuyma, P. Price, the editor, and two anonymous reviewers has greatly improved the manuscript; the remaining faults are ours. This work was supported in part by grants from the U.S. Department of Agriculture (90-37250-5482 NRIGCP), the Maryland Agricultural Experiment Station, and the Smithsonian Institution. This is contribution number 8676, Scientific Article A6473, from the Maryland Agricultural Experiment Station.

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Editor: Mark D. Rausher