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Flowers and Insect Evolution

Brian D. Farrell (*1*) provides a clear illustration of the utility of phylogenetic reasoning in evaluating the evolutionary history of ecological or behavioral traits, or both. With the use of morphological and molecular evidence, Farrell demonstrated that phytophagous beetle lineages feeding on angiosperms had considerably higher rates of diversification than their gymnosperm-feeding sister taxa (table 1 in the report). These results support Ehrlich and Raven's hypothesis that insect diversity is intimately tied to the rise and diversification of the angiosperms in the Cretaceous (*2*). Farrell argues that the pattern he observed in beetles is of broad significance and should be reflected in other lineages of insects showing close ecological associations with angiosperms.

Bees [Series Apiformes, Superfamily Apoidea (*3*)] provide support for this hypothesis, but have often been overlooked in this context (*4*), because, instead of feeding internally or externally on plant vascular tissues, they consume angiosperm pollen and provide a direct benefit to plants through their activities. Like many beetle lineages, bees form a speciose group, and, like beetles, many species of bees have intimate and often specialized (oligolectic) ecological associations with specific plant genera or species (*5*). Like angiosperm-feeding beetles, bees may have arisen in the early Cretaceous (*6*), and diversified along with the early angiosperms.

Recent phylogenetic evidence indicates that bees form a monophyletic lineage that has arisen from within the spheciform wasps [Series Spheciformes, Superfamily Apoidea (*3*), or "hunting wasps"], thus rendering the hunting wasps paraphyletic (*7, 8*). However the precise position of the bees within the Spheciformes is unclear. Recent studies indicate that bees either arise basally within this lineage as sister to all Spheciformes except the families Sphecidae and Ampulicidae (including ~7000 species) (*7*), or as sister to the family Philanthidae (including ~1100 species) (*8*). The vast majority of hunting wasps are predatory on insects and other arthropods (*9*). Association with angiosperms in this case has led to enhanced rates of speciation: bees include ~20,000 species, or 3 to 18 times the number of species included in their putative sister clade.

However, not all aculeate Hymenoptera support Farrell's hypothesis. The vespid subfamily Masarinae includes angiosperm-associated wasps [also called pollen wasps (*10*)], which are ecologically very similar to bees, despite their independent origin. Like bees, masarines arose in the Cretaceous (*11*) from within a lineage of predatory wasps (the fam-

ily Vespidae). Masarine wasps include ~300 species (*10*) and form the sister group to a clade of over 3500 species of predatory solitary and social wasps (*12*). In this case the angiosperm-associated lineage shows lower diversity than its non-herbivorous sister clade.

Phylogenetic reasoning of this kind can provide an extremely powerful tool for assessing the implications of angiosperm associations in insects. However, before fully accepting the hypothesis that angiosperms have had a direct impact on insect diversity, we should seek additional evidence from other speciose phytophagous insect orders, including Hemiptera, Thysanoptera, Orthoptera, Phasmida, Lepidoptera, and Hymenoptera (especially sawflies, bees, and pollen wasps). Finally, we should distinguish between herbivores that feed on plant vascular tissues and pollenivores, and ask whether these two groups exhibit similar patterns of coevolution with angiosperms.

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- The one exception to this rule is *Krombeinictus nordena*, a bizarre crabronine that feeds pollen, rather than paralyzed arthropods, to its offspring [K. V. Krombein and B. B. Norden, *Asian Nat. Hist.* **2**, 145 (1997); *Proc. Entomol. Soc. Wash.* **99**, 42 (1997)].
- S. K. Gess, *The Pollen Wasps* (Harvard Univ. Press, Cambridge, MA, 1996).
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- J. M. Carpenter, in *The Social Biology of Wasps*, K. G. Ross and R. W. Mathews, Eds. (Cornell Univ. Press, Ithaca, NY, 1991). The subfamily relationships within the Vespidae are as follows: (Masarinae + (Eumeninae + (Stenogastrinae + (Polistinae + (Vespinae)))).

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In 1995, I authored a paper (*1*) dealing with the question of why there are so many weevils. Given that the beetle family Curculionidae (weevils) is arguably the most diverse family of organisms known, with about 50,000 described species (*2*), an explanation for weevil megadiversity should help address the fundamental question of what determines taxonomic diversity. I proposed (*1*) two theses to explain the evolution of this megadiversity: (i) an association of the ancestors of Curculionidae with ancestors of angiosperms (before the origin of the latter and thus setting the stage for an adaptive radiation) and (ii) the development of a "key innovation," this being the use of the snout (or rostrum) by adult female weevils in the preparation and excavation of oviposition sites.

Farrell (*3*) comes to a similar conclusion in recognizing the association of primitive lineages of Curculionoidea with primitive lineages of plants as an important precursor for the evolution of weevil megadiversity; however, this is only part of what I think is a much more complex evolutionary picture.

Evidence indicates morphological and behavioral changes play an important role in the evolution of diversity. As examples, consider the evolution of wings and flight by bats (*4*); and, the evolution of special modifications in the jaws of cichlid fish (*5*). Similarly, for the weevils, one such structural change, or a "key innovation," is the key that unlocked the door to diversification. Other adult beetles do not have an ovipositor that is capable of placing eggs in close proximity to (if not within) the food source where the eggs would also likely be less prone to desiccation or parasitism. On the other hand, weevils have an "ovipositor," in a sense, located at the other end of the body. Use of the snout in the excavation and preparation of oviposition sites by adult female curculionids fulfills the role of an ovipositor, and appears to have been an important, if not integral, factor in their success. Primitive Curculionoidea such as Nemomychidae and Anthribidae (*6*) do not use the snout in oviposition site preparation, but the sister clade consisting of Oxycoryninae-Allocoryninae, Belinae, Atteblabinae-Rhynchitinae, Apioninae, and Curculionidae-Rhynchophorinae do use the snout in this manner. Not coincidentally, this latter clade comprises the bulk of curculionoid diversity (*7*). My contention is that the use of the rostrum as an "ovipositor" serves as a "key innovation" facilitating the use of angiosperm plants as food sources by weevils. Use of the rostrum in this manner circumvented barriers to the plant feeding way of life faced by most other insects; specifically, desiccation of the immature stages while associated with the plant host, initiation and maintenance of attachment to the plant host, and presence of plant host structural defenses (*8*). Furthermore, angiosperm evolution is characterized by increasing complexity in structure

and chemistry, and different (and more complex) life history traits, growth habits, and habitat associations (especially with arid lands). As these features evolved, weevils (with their snouts) were able to adapt to and track these changes, whereas other contemporaneous beetles were not. It is not enough to say only that weevils developed an early association with angiosperms; some characteristic must have allowed them to make better use of angiosperms as food sources than their competitors—their snouts!

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References and Notes

1. R. S. Anderson, *Mem. Ent. Soc. Wash.* **14**, 103 (1995).
2. On the basis of known but undescribed species in museum collections, the figure of 50,000 is likely an underestimate by at least an order of magnitude.
3. B. D. Farrell, *Science* **281**, 555 (1998).
4. J. E. Hill and J. D. Smith, *Bats. A Natural History* (British Museum of Natural History, London, 1984).
5. K. F. Liem, *Syst. Zool.* **22**, 425 (1973).
6. The primitive curculionoid family the Anthribidae (fungus weevils), considered the sister group to the Curculionoidea (excluding the most primitive family, the Nemonychidae), were not included by Farrell in his analyses.
7. Whereas certain primitive Curculionoidea are associated with angiosperms (for example, Attelabinae-Rhynchitinae), they do not feed on living plant tissues but rather many likely feed on fungi colonizing the dead or dying plant parts (in some instances, actually killed by the adult female weevil) where the eggs are laid and larvae feed.
8. T. R. E. Southwood, *Symp. R. Entomol. Soc. Lond.* **6**, 3 (1973).

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Response: I fully agree with Danforth and Ascher that the angiosperm-based explanation for beetle diversity implies an extension to other herbivorous insect groups. While phytophagous beetles are among the better known examples of generally elevated herbivore diversity [across some 13 documented origins of plant-feeding among the insect orders (1)], the also well-studied symphytan Hymenoptera and Lepidoptera show similar histories. Like the Curculionoidea and Chrysomeloidea, these two orders each contain apparently primitive, early Mesozoic, species-poor families (the Xyelidae sawflies and Agathiphagidae moths, respectively) today affiliated with conifer strobili, while their species-rich relatives are external and internal

angiosperm-feeders (2). The other insect herbivore groups are also largely species-rich angiosperm-feeders, but limited information on phylogenetic relations and natural history preclude ascribing their diversity to the rise of flowering plants, per se, rather than simply to herbivory (1).

Danforth and Ascher extend the angiosperm-herbivory hypothesis to include pollen-feeders, and offer evidence that flowering plant mutualists may not show a uniform response to the rise of angiosperms. It is possible that pollinators were more generally influential in the proliferation of flowering plants (indirectly favoring herbivores) than the reverse. Masarine wasps, however, could also be exceptional departures from an overall pattern of elevated pollinator diversity.

As Danforth and Ascher suggest, some differences between pollinators and herbivores might be important. Apart from their beneficial rather than antagonistic relationship with flowering plants, the pollen-feeding bees and masarine wasps apparently arose from immediate ancestors that were carnivores rather than gymnosperm-associated herbivores as in these beetles (and apparently as in the Symphyta and Lepidoptera). The additional requirement of suitable nest sites by these bees and wasps, a feature inherited from their carnivore ancestors, might also constrain their evolutionary opportunities. It seems premature to conclude that bee association with angiosperms “has led to enhanced rates of speciation . . .,” especially in light of the counter-example offered, until cladistic studies of a representative set of angiosperm pollinators (for example, including syrphid flower flies and bombyliid bee flies) are completed. Parasitic insects were also thought, until recently, to generally undergo radiations comparable to herbivores (3).

Anderson suggests that the uniquely ovipositional curculionoid rostrum—a trait that antedates use of angiosperms in weevils though not in other beetle groups—is actually responsible for weevil diversity. Anderson states that the location of the weevil mandibles at the tip of an elongated, ovipositor-like rostrum permits use of plant resources not open to other beetles. Although many beetles use the mandibles to modify host plants for larvae (4) and many weevils lack an elongated rostrum (5), the most serious difficulty for the ovipositional rostrum hypothesis lies in

the absence of this structure in the weevil sister group, the Chrysomeloidea. The 50,000+ species of chrysomeloids collectively use an array of plant parts similar to that used by weevils, including stems, seeds (6), flowers, and roots. Chrysomeloid beetles and such other herbivorous insects as flies and moths use these larval resources without the aid of a rostrum or other heavily sclerotized ovipositor. Indeed, there may be few plant species—and probably no plant tissues—used exclusively by weevils, although there may be many plant species for which particular tissues are used by only a single herbivore group in any particular place. Indeed, it is doubtful whether any single key morphological feature enabled the many radiations of plant-feeders in the beetles and other insect groups. The consistent success of angiosperm herbivores across their numerous, independent origins in insects may lie in the disparate, often lineage-specific ways in which they use these plants as hosts.

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2. I. A. Gauld and B. Bolton, Eds., *The Hymenoptera* (Oxford Univ. Press, Oxford, 1988); J. Powell, C. Mitter, B. D. Farrell, in *Handbook for Zoology*, N. Kristensen, Ed. (in press).
3. B. M. Wiegmann, C. Mitter, B. D. Farrell, *Am. Nat.* **142**, 737 (1993).
4. For example, the Cerambycidae often modify stems with mandibles before ovipositing inside, sometimes cutting trenches to kill the stem distally [E. G. Linsley, *The Cerambycidae of North America: Part I. Introduction* (University of California, Berkeley, CA, 1961), p. 3].
5. G. Kuschel [*GeoJournal* **7.6**, 501 (1983)] points out the sexual dimorphism in rostrum length (implying use for oviposition) in the most primitive, conifer-associated weevil family Nemonychidae. Use of the rostrum for oviposition may therefore be the ancestral condition in the Curculionoidea, much reduced or lost in more derived taxa such as the Entiminae (12,200 species) and related subfamilies, and the Scolytidae/Platypodidae (7000 species) which respectively feed on roots or under bark; R. T. Thompson, *J. Nat. Hist.* **26**, 835 (1992).
6. The chrysomelid lineage informally known as the Bruchidae specialize on seeds of palms, legumes, and other angiosperm groups used by weevils. The eggs are placed on the seed surface and the larvae tunnel into the endosperm.

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