# Species richness: **Does flower power explain beetle-mania?**

Timothy G. Barraclough*, Maxwell V.L. Barclay† and Alfried P. Vogler*†

**The huge species richness of beetles has been attributed to their colonisation of flowering plants, but a vegetarian diet may not be the sole secret of the beetles' success.**

Addresses: *Department of Biology and NERC Centre for Population Biology, Imperial College at Silwood Park, Ascot, Berkshire, SL5 7PY, UK. †Department of Entomology, Natural History Museum, Cromwell Road, London SW7 5BD, UK.

Current Biology 1998, 8:R843–R845
http://biomednet.com/elecref/09609822008R0843



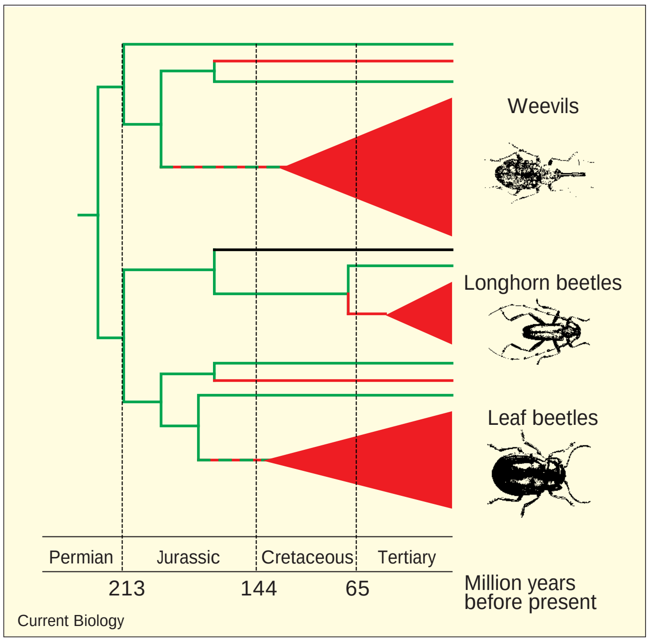
With well over 300,000 known species, the incredible diversity of beetles has long puzzled and astounded biologists. It even provoked one of evolutionary biology's most famous aphorisms; when the great British biologist J.B.S. Haldane was asked by a group of theologians what insights his studies of creation had given him into the nature of the Creator, he is said to have replied "An inordinate fondness for Beetles" [1]. Indeed, one of every five known animal species on Earth is a beetle [2], and no doubt thousands more still await discovery. Beetles form by far the largest order — Coleoptera — of insects, and the insects comprise over half of all described organisms. For biologists trying to explain why some lineages evolve more species than others and, ultimately, to discover the forces that drive the origin of species itself, the beetles are an invaluable test-case.

In a recent paper, Farrell [3] claims to have found an explanation for the diversity of Coleoptera. He ascribes their success to the rise of the angiosperms, or flowering plants. Plant association has long been linked to the success of some beetles [4,5], and insects as a whole [6]. In present-day ecosystems, a huge proportion of insect species are found in those few orders that have made the transition to feeding on living plants. The origins and radiations of some beetle and plant groups are broadly contemporaneous in the fossil record, and around half of modern beetle species are directly dependent on plant tissues. Hence, the origin of plant feeding within beetles may be a significant factor in attempts to explain their extreme species richness.

Farrell [3] has combined data from the fossil record and morphological analyses with newly generated DNA sequences, in a phylogenetic study of the evolution of plant–insect interactions in what is perhaps the most prolific of all beetle radiations, the Phytophaga (Figure 1). This comparatively recent group includes the leaf beetles (Chrysomelidae), longhorn beetles (Cerambycidae) and weevils (Curculionoidea), together making up over one-third of all beetles. As the name suggests, the Phytophaga are primarily herbivorous. Most species feed on flowering plants, though a number are associated with older plant groups, such as conifers and cycads. The larvae of Cerambycidae predominantly develop in dead or dying woody tissue, though some attack healthy wood and a few even herbaceous plants.

Tracing feeding style and host plant affiliations onto a phylogenetic tree of the Phytophaga revealed two things (Figure 1). First, early lineages originally fed on conifers and cycads, dominant plant groups in the past, and from these ancestors a few beetle lineages made the transition to flowering plants. The phylogeny supports previous suggestions [4,5] that some elements of the ancient fauna persisted, and these are the principal present-day herbivores of monkey puzzle trees (*Araucaria*) and cycads. Second, and more importantly, those lineages that still live on ancient plant groups are less species-rich than their

**Figure 1**




The radiation of the Phytophaga, simplified from [3]. Green branches represent lineages feeding on conifers and/or cycads, red branches those feeding on flowering plants, and the black branch represents a non-herbivorous lineage. The widths of terminal branches are proportional to species richness, with most species found in one of three massive radiations associated with the origin of flowering plant feeding.

angiosperm-feeding sister groups, just what is to be expected if the angiosperm radiation in some way promoted the radiation of these beetles. Farrell's conclusion [3] is that, without the radiation of the angiosperms, the Phytophaga would have remained a species-poor and ecologically homogeneous group, similar to the present-day remnant fauna of gymnosperms and cycads, and beetles as a whole would have been species-poorer for it.

Farrell's work [3] attests to the power of phylogenetic analysis in testing evolutionary hypotheses, in particular those attempting to explain species richness. The molecular revolution has provided large amounts of new data for reconstructing phylogenetic relationships among organisms, from which we can identify events in the history of lineages leading to increases in species numbers [7,8]. Only now are the molecular trees necessary for tests of this kind becoming available, especially in the Coleoptera. Even in Farrell's study, however, the tree is not purely molecular, but is strongly dependent on existing morphological studies [9,10].

The broad conclusion that angiosperm-feeding explains the high species richness of beetles raises some additional questions not addressed by Farrell's data. First, why did angiosperms and their associated beetles proliferate to such an extent? Did diversity in one of the partners trigger the diversity of the other and *vice versa*? This has been debated since Ehrlich and Raven [6] first proposed their theory of co-evolution. The intricate 'arms race' between herbivores attacking plants — the production of defensive secondary metabolites by plants in response to attack, and the subsequent overcoming of these defences by certain herbivores — could result in the ever-increasing diversification of both groups. This possibility remains controversial, as there is little evidence that the evolution of plants is much affected by the presence of their herbivore community [11], and it remains unclear why adaptive breakthroughs by one of the partners would result in higher species numbers (rather than in higher abundance) [12].

If co-evolutionary interaction is not the answer, what else might have promoted species richness? The great variety of forms exhibited by flowering plants provides a large number of opportunities for specialisation by insect herbivores. Furthermore, flowering plants are the dominant producers, in terms of both numbers and biomass, in present-day terrestrial ecosystems, particularly in the tropics. They may simply offer a larger resource, so we would expect more beetles to live on them. Considering the vast availability of resource they provide, it is initially surprising that only a few groups of insect have made the transition to herbivory, and fewer still as successfully as beetles. However, plant surfaces represent a harsh, exposed environment for many insects, and their mechanical and chemical defences make plants indigestible food for most species. Beetles seem to have the level of evolutionary plasticity and adaptability required to make this transition. In weevils (Curculionoidea), the transition might have been facilitated by evolution of the rostrum, a characteristic 'beak-like' extension of the head used in feeding and oviposition. It has been suggested that this is the key innovation explaining their success [5]. The rostrum is extremely adaptable and has allowed weevils to exploit plant tissue in ways not possible to other groups. Indeed, the entire Phytophaga were enormously flexible when it came to using the angiosperms as a food source, employing a vast repertoire of behavioural and ecological strategies and utilising virtually every part of living and dead tissue, including roots, seeds, leaves, stems and fruits.

So, does angiosperm feeding explain nature's inordinate fondness for beetles? Farrell [3] argues that it explains the radiation of nearly half of all beetle species, without which beetles would be equivalent to other "large, young, and non-herbivorous insect orders". But the obvious corollary is that half of beetle species are non-herbivorous, and without them beetles would also be equivalent to other large insect orders. Herbivory is certainly associated with a massive radiation within this group, but some non-herbivorous groups of beetles, such as the presumed sister group to Phytophaga, the largely carnivorous or fungivorous Cucujoidea — with roughly 50,000 species — or the mostly predatory, and comparatively under-described Staphylinoidea — with more than 50,000 species known so far — are also massively species-rich.

"Inordinate fondness" thus seems to be found scattered throughout the tree of beetles, interspersed with many lineages that are poorer in species numbers — in fact, pockets of such 'fondness' might be a feature of the holometabolan insects as a whole, rather than just restricted to Coleoptera. Farrell's results [3] clearly show an effect of angiosperm feeding on the species richness of Phytophagan lineages, but it seems unlikely that the huge diversity of beetles is solely a function of their relationship with plants. Beetles appear to have the plasticity and adaptability to seize ecological opportunities wherever they occur.

Farrell's study [3] is the first to bring together palaeontology, morphology and molecular systematics in an attempt to discover why there are so many species of beetle. Although the puzzle of beetle, and indeed insect, diversity is still far from solved, it is multidisciplinary phylogenetic studies of this kind that provide our best hope of finding the answers. Further work is required to identify systematically where the major radiations occurred within the family trees of beetles and their holometabolan relatives, and to determine what features, if any, can be associated with them. Such research will address some of the most important ecological, systematic and evolutionary questions of the second half of this century. Why are some lineages species-rich while others are not? How important is co-evolution, and how can it be quantified? How were groups less glamorous, but ultimately more important, than the dinosaurs affected by the turmoil of biotic change that accompanied the transition to the modern natural world? The Creator's inordinate fondness for beetles has provided evolutionary biologists with an ideal study system to address these problems.

**Acknowledgements**

The authors' work on beetle diversification is funded by the Leverhulme Trust, and NERC. The authors would like to thank Chris Lyal, Ignacio Ribera and Peter Hammond for their helpful comments on the manuscript.

**References**

1. Hutchinson GE: Homage to Santa Rosalia or Why are there so many different kinds of animals. *Am Nat* 1959, 93:145.
2. Hammond PM: Species inventory. In *Global Biodiversity: Status of the Earth's Lving Resources.* Edited by Groombridge B, London: Chapman & Hall; 1992:17-39.
3. Farrell BD: "Inordinate fondness" explained: why are there so many beetles? *Science* 1998, 281:555-559.
4. Crowson RA: The evolutionary history of the Coleoptera, as documented by fossil and comparative evidence. *Atti del X congresso nationale Italiano do Entomologia* 1975:44-90.
5. Anderson RS: An evolutionary perspective on diversity in Curculionoidea. *Memoir Entomol Soc Wash* 1995, 14:103-114.
6. Ehrlich PR, Raven PH: Butterflies and plants, a study in coevolution. *Evolution* 1964, 18:586-608.
7. Sanderson MJ, Donoghue MJ: Reconstructing shifts in diversification rates on phylogenetic trees. *Trends Ecol Evol* 1996, 11:15-20.
8. Barraclough TG, Vogler AP, Harvey PH: Revealing the factors that promote speciation. *Phil Trans R Soc Lond [Biol]* 1998, B353:241-249.
9. Kuschel G: A phylogenetic classification of Curculionoidea to family and subfamily level. *Memoir Entomol Soc Wash* 1995, 14:5-33.
10. Reid CAM: A cladistic analysis of subfamilial relationships in the Chrysomelidae sensu lato (Chrysomeloidea). In *Biology, Phylogeny and Classification of Coleoptera: Papers Celebrating the 80th Birthday of Roy A.Crowson Vol II.* Edited by Pakaluk J, Slipinski SA. Warszawa: Muzeum i Instytut Zoologii PAN; 1995: 559-631.
11. Schoonhoven LM, Jermy T, van Loon JJA: *Insect Plant Biol*. Chapman and Hall, London; 1998.
12. Vogler, AP, Goldstein PZ: Adaptation, cladogenesis, and the evolution of habitat association in North American tiger beetles: a phylogenetic perspective. In *Molecular Evolution and Adaptive Radiation.* Edited by Givnish T, Systma, K. Cambridge: Cambridge University Press; 1997:353-373.