Journal Club

Law of the unspecialized: broken?

Specialization has posed crucial problems for evolutionary biologists: What are the benefits of specialization? Is specialization an evolutionary dead end? Theory has long predicted that specialization is favored because of tradeoffs in fitness when organisms utilize different resources. These microevolutionary benefits are thought to be offset by a reduction in macroevolutionary diversification. Again, theory has suggested that the narrow ecology of specialists will result in fewer opportunities for speciation, and, therefore, lower levels of diversification than in less specialized clades. This suggestion dates back to E. Cope in 1896, who coined the idea 'law of the unspecialized'. However, specialization as an evolutionary dead end appears inconsistent with the existence of diverse and highly specialized clades. For example, it is estimated that 80% of phytophagous insects, one of the most diverse groups of organisms, are specialized. Why is this group of specialists so diverse? There are now several phylogenies of groups with more and less specialized clades, and a new study by Termonia *et al.*[1] 'ups the ante' by combining knowledge of the mechanistic basis of specialization in Chrysomelina beetles with a phylogenetic analysis of diversification.

In response to harassment, Chrysomelina beetles produce defensive secretions that are repulsive to predators. The type of defensive secretion produced defines three different types of beetles: those that synthesize their own defense chemicals; those that are fully reliant on their host plant for such chemicals; and an intermediate group that are only partially dependent on the host plant for their chemical defense. Termonia *et al.*'s phylogenetic analysis reveals that this partially dependent strategy is the most derived of the three, and is descended from the more specialized group, which relies fully on the host plant for defense. In addition to specialization not being a dead end in this system, the authors show that the derived defense strategy has allowed for beetles to move to host plants that are both chemically and phylogenetically distinct.

This paper[1] is part of a new generation of studies that link chemical ecology to evolutionary biology. Conventional wisdom has been that specialization of herbivores is an evolutionary response to plant defenses.

Maurice Leponce and Jacques Pasteels.

However, for the Chrysomelina beetles, specialization is apparently a response to avoid predation. Although it is not clear how frequently specialization in herbivorous insects is driven by predators, host-plant chemistry plays a prominent role in both plant defense and predator avoidance. This still begs the question: why are specialized clades of phytophagous insects so diverse? Does the type of resource used by such insects (i.e. hosts that are defended by chemicals or hosts that provide insect defense) and the spatial scale over which these resources occur delimit opportunities for reproductive isolation? If so, the law of the unspecialized will fail whenever novel specializations promote reproductive isolation. Well-described cases of incipient sympatric speciation (e.g. sticklebacks *Gasterosteus* spp. and Apple maggot fly *Rhagoletis* spp.) and the maintenance of species boundaries in sympatry (columbine *Aquilegia* spp. and monkey flower *Mimulus* spp.) occurring as a result of the evolution of novel specializations for resource use support this view.

1 Termonia, A. *et al.* (2001) Feeding specialization and host-derived chemical defense in Chrysomeline leaf beetles did not lead to an evolutionary dead end. *Proc. Natl. Acad. Sci. U. S. A.* 98, 3909–3914

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Rearguard action: why do some butterflies have false heads?

Most readers of *TREE* will know that some butterfly species have developed colour patterns that make them look as though they have another head at the posterior end of their body. This phenomenon is a classic example used in adaptive coloration lectures. The standard explanation for the false head is that it confers an anti-predatory advantage to the butterfly. It is suggested that this has developed because predators preferentially attack the head of butterflies, as this is a particularly vulnerable part of the body. The false head acts to increase the chance that an attack is directed to the less vulnerable posterior, providing the butterfly with an increased chance of surviving an attack.

This explanation has now been challenged by Cordero[1], who argues that the 'vulnerable head' hypothesis has not been subjected to critical examination that would allow testing between this standard hypothesis and plausible alternatives. The author goes on to introduce just such an alternative. Under the new hypothesis, predators preferentially target the posterior end of butterflies, because butterflies are more able to detect and react to impending attacks on their head, as this is where their eyes are. Under this alternative hypothesis, the false head acts to increase the likelihood that an attack will be directed to the real head.

Cordero argues that it should be possible to differentiate between these two hypotheses empirically. The first hypothesis suggests that attacks directed to the head are more successful than are those directed to the rear, whereas the alternative hypothesis predicts the opposite. In addition, the standard hypothesis predicts that evolution of a false head will induce a shift in attacks toward the rear, whereas the alternative hypothesis predicts the opposite. Cordero suggests that experiments could be performed on butterfly species without false heads (but that are related to species with false heads) in which artificial heads are experimentally added, or in species with the false heads experimentally removed.

We feel that such manipulations would be technically challenging, and the experiments difficult to design if manipulations are not to affect prey behaviour, and the target part of the body of a butterfly in a given attack is to be definitively identified. We suggest that an effective way to explore how adding a false head affects predator attack targets would be to use a predatory bird trained to peck at computer-generated images on a touch-sensitive screen. This technique is already well established in the study of prey visual detection by predators (e.g. Ref. 2) and might well lead to exciting and rapid advances in a system previously (but perhaps prematurely) considered to be well understood.

1 Cordero, C. (2001) A different look at the false head in butterflies. *Ecol. Entomol.* 26, 106–108
2 Dukas, R. and Kamil, A.C. (2001) Limited attention: the constraint underlying search image. *Behav. Ecol.* 12, 192–199

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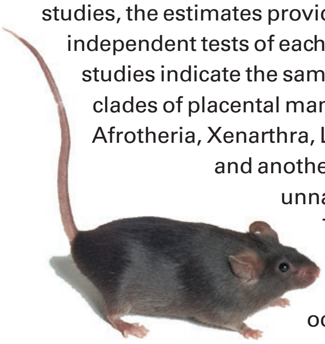
Making sense of mammals

The higher level relationships of eutherian mammals have long been a phylogenetic puzzle, the main reason being a temporal inconsistency: although most of the major lineages ('orders') of placental mammals originated well before the Cretaceous–Tertiary (K–T) boundary, they only diversified in a massive adaptive radiation after this event. Therefore, much of the early evolutionary history is difficult for morphological studies to address and often only the adaptive radiation is reflected as unresolved relationships at the base of the tree. Molecular studies hold more promise at seeing past the K–T boundary, but this promise has been largely unfulfilled owing to limited data. Comparatively few, distantly related eutherian species have been sampled for only a few molecular markers, a scenario for which accurate phylogenetic estimation is known to be difficult. Now, three research groups[1–3] using two different approaches have attempted to address these limitations to present the first comprehensive mammalian trees. The results show a surprising degree of concordance.

Madsen *et al.*[1] and Murphy *et al.*[2] independently constructed two of the largest molecular data sets yet assembled for any phylogenetic study (8655 bp for 26 species and 9779 bp for 64 species, respectively). Moreover, because the sequence data do not overlap between the studies, the estimates provide independent tests of each other. Both studies indicate the same four major clades of placental mammals: Afrotheria, Xenarthra, Laurasiatheria and another large as yet unnamed group. Two other unexpected results occur. First is the grouping of rodents plus rabbits and pikas as Glires, a result previously supported primarily by morphological studies. Second is the grouping of elephants, sirenians, aardvark, elephant shrews and Old World insectivores (together, the Afrotheria), a cluster with no morphological support.



Liu *et al.*[3] take another approach by combining 430 morphological and molecular estimates of eutherian phylogeny to form a comprehensive family-level supertree. In spite of large differences between the molecular and morphological supertrees, the combined data reveal the same four major eutherian clades as Refs 1 and 2, with only two exceptions (slightly altered placements for Old World insectivores, and Primates, Dermoptera, plus Scandentia).

The phylogenetic picture for mammals is still far from complete. Differences between all three studies still exist, especially within the four major clades. However, the root of the placental tree is more agreed upon – and better resolved – than ever before. With continued sequencing efforts and data accumulation, agreement should increase up towards the tips of the mammal tree. Molecular evidence has done much to, and will continue to, foster this growth. However, as pointed out by Liu *et al.*[3], the importance of additional morphological data cannot be ignored. Together, only the use of as much information as possible, from all data sources, will allow us to finally put all mammals in their place.

1 Madsen, O. *et al.* (2001) Parallel adaptive radiations in two major clades of placental mammals. *Nature*, 409, 610–614
2 Murphy, W.J. *et al.* (2001) Molecular phylogenetics and the origins of placental mammals. *Nature*, 409, 614–618
3 Liu, F-G.R. *et al.* (2001) Molecular and morphological supertrees for eutherian (placental) mammals. *Science*, 291, 1786–1789

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Oops, they're doin' it again…The Permian–Triassic Extinction

The Permian–Triassic (P–T) extinction (approximately 251 million years ago) was the largest in the history of the Earth, with ~90% of marine species, nearly 70% of terrestrial vertebrates, and many plants disappearing. However, in spite of being larger than its flashier cousin, the Cretaceous–Tertiary (K–T) extinction – when dinosaurs bit the big one – the P–T event has not received as much press. During the 1980s, a debate raged about the cause of the K–T extinction. Opinion polarized between two camps: those who attributed all extinctions to a single environmental catastrophe caused by an asteroid impact, and those who believed that Earth-based phenomena such as sea-level, climate change and volcanism were to blame. This polarization obscured the probably complex link between Earth-based and

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