

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

Graeme D. Ruxton

G.Ruxton@bio.gla.ac.uk

Stuart Humphries

S.Humphries@bio.gla.ac.uk

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

Olaf Bininda-Emonds

bininda@rulsfb.leidenuniv.nl

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



extraterrestrial events and, eventually, the issue dropped from the scientific radar screen. We are moving on to bigger extinctions.

Two new papers have recently set up a similar dichotomy at the P–T boundary. Hotinski *et al.*¹ explored the hypothesis that world-wide anoxia in the deep ocean contributed to P–T extinctions. The idea is not a new one. Pyrite-rich black shales common in the late Permian and early Triassic hinted at changes in deep-ocean chemistry. Excursions in the isotope ratios of carbon, sulfur and strontium suggested major rearrangements in ocean circulation. This new work combined models of marine circulation with the additional feedback between nutrient availability and marine primary productivity¹. The modification was essential because the accumulation of black shales requires both anoxia (which implies reduced upwelling) and high marine productivity (which requires an adequate nutrient supply). The authors found that warming at the Poles during the latest Permian could slow upwelling sufficiently to generate wide spread marine anoxia. However, the mechanism required a higher marine nutrient inventory than is typical of the modern ocean¹.

In counterpoint, Becker *et al.*² reported the discovery of interstellar helium trapped in fullerenes found at P–T boundary sites in China and Japan. The paper, which was widely covered in the popular press, determined that the isotopic composition of trapped helium was similar to that found in other extraterrestrial bodies, and was different from helium native to Earth. This observation, coupled with the particular cocktail of noble gasses inside the fullerenes, suggested that they formed in a star or interstellar cloud and were transported to Earth by the impact of large (approximately 9 km) comet or asteroid². Therefore, they concluded that ‘such an event could have caused the severe end-Permian mass extinction’².

The stage seems to be set for another polarizing debate.

1 Hotinski, R.M. *et al.* (2001) Ocean stagnation and end-Permian anoxia. *Geology* 29, 7–10

2 Becker, L. *et al.* (2001) Impact event at the Permian–Triassic boundary: evidence from extraterrestrial noble gases in fullerenes. *Science* 291, 1530–1533

Nan Crystal Arens

nanarens@socrates.berkeley.edu

Beware of trojans bearing fish

Neither academic biologists nor politicians have been particularly well poised to confront a difficult question increasingly posed by the public: ‘Are genetically modified organisms harmful or benign?’. The answer ‘it depends’ satisfies neither the desire of academics for general theory allowing replicable predictions, nor the need of politicians for clear-cut, popular stances addressing public concerns – nor does it result in effective regulatory action. Because the necessary case-by-case examination of each genetically modified organism (GMO) is difficult, and the proper methodology has been unclear, a data vacuum has been left that extremists on both sides have been free to fill with fear mongering or hand waving, according to their biases.



Muir and Howard’s¹ new study of the potential effects of the escape of GM fish into wild stocks provides the rare detailed perspective that has been so needed. In response to the commercial creation of numerous species of growth-enhanced transgenic fish for potential use in aquaculture, the authors developed a stage-based population genetic model. They explored the hypothetical introduction of 60 transgenic fish into a panmictic wild-type population of 60 000 individuals using recurrence equations that included juvenile and adult viability, age at sexual maturity, female fecundity, male fertility and mating advantage. They then derived actual estimates of these parameters to test their model, by creating a model GMO – a Japanese medaka *Oryzias latipes* containing a human/salmon growth hormone construct – on which they conducted a series of comparative fitness experiments. They thus could explore changes in transgene frequency under multiple realistic scenarios, as well as identify parameters most influential in the spread of the transgene.

Contrary to the common notion that viability has the greatest influence in

transgene spread (and thus that transgenics, which often have reduced viability, present no threat), the authors found that age at sexual maturity was by far the most influential fitness component, giving early-maturing transgenic fish the advantage. Disturbingly, there appears to be a large area of realistic parameter space in which transgenic males might be large enough to dominate matings, but reduced enough in their juvenile survival that their introduction into a wild population could drive it extinct. This interaction allows transgenic fish to become ‘Trojan horses’ of sorts: they are more attractive to mates but eventually doom the population that they enter.

Most sobering, however, might be the empirical demonstration by this study of a phenomenon currently under renewed scrutiny by quantitative geneticists: epistasis. The effect of the genetic insert varied enormously, even in a constant environment and among strains derived from a single founding fish. Growth in second-generation transgenic medakas ranged from –4% to 76% relative to wild-type controls, reflecting the large impact of the exact genetic background on transgene expression, and underscoring the need for extensive testing within each new GM strain.

Thus, although the authors provide no easy answers, they take the crucial step of mapping the road to real regulatory solutions by providing a clear methodological framework. These experiments demonstrate that the rather arbitrary measures used in the past to assess GM fish (swimming speed, predator avoidance, gill size, etc.) could be replaced profitably with interacting fitness-component models and fitness experiments. Although much remains to be explored (e.g. more realistic population structures incorporating genetic drift), this model provides a framework in which GM fish could conceivably be either approved (e.g. if performance relative to wild-type counterparts is much worse in all six fitness parameters) or unmasked as potentially Trojans.

1 Muir, W.M. and Howard, R.D. (2001) Fitness components and ecological risk of transgenic release: a model using Japanese medaka (*Oryzias latipes*). *Am. Nat.* 158, 1–16

Kathryn M. Rodríguez-Clark

kate@sigmaxi.org

Jon Paul Rodríguez

jonpaul@ivic.vc