

presentations ranged from the use of the production and molecular biology of mutant fish and amphibians to examine the interaction of the environment and the development of physiological functions during ontogeny, through the ontogeny of biochemical and pharmacological controls in the respiratory and cardiovascular systems of invertebrates and vertebrates, to the effect of the environment on the timing and nature of physiological regulations and functions and the implications for life history and fitness in crustaceans and fish.

Throughout, it was gratifying to see mechanisms and patterns in, and the ecological/evolutionary significance of, the development of function being treated as equally important. Discussion scaled the hierarchical levels involved, and targeted investment of time and energy in multidisciplinary approaches to study would pay dividends in terms of understanding physiological mechanisms and, in particular, their ecological and evolutionary significance.

In this regard, the workshop was extremely timely as it comes at a point when a 'developmental' approach is invigorating research in ecology (e.g. study of the relationship between developmental stability and fitness⁸) and evolution (e.g. study of the developmental evolution of metazoan body patterns and developmental regulations⁹). The signs from the workshop are that the 'developmental dimension' has the possibility of invigorating ecological physiology too. From an ecological perspective the lowest meaningful level of physiological variation is that of the individual. While such variation is quite profound, it is also extremely difficult to handle, with one of the cardinal obstacles centring on the fact that it is not possible to replicate the in-

dividual. However, variation in the development of physiological functions and regulations within the individual may be particularly critical to comparisons at higher levels, and in particular to an understanding of population variation; at any one point in time, a real population may be composed of individuals of different ages and different developmental stages.

While the workshop highlighted physiological variation at the level of the individual, in some sense this may merely represent the tip of the iceberg of the importance of physiological variation. This importance has often been highlighted in the past by many of the chief proponents of ecological physiology^{1,10-12} but understanding is arguably patchy at best.

Given the unevenness of the investigation of the different potential levels of physiological variation, it is not possible at the present time to distinguish exactly how this variation is distributed amongst these levels. Just as the proportion of variance in other traits (e.g. body size) which is explained at different taxonomic levels has been explored in the context of the comparative method¹³, it would seem highly desirable to understand at which of the levels of individual, population, species and assemblage most variation in physiological traits occurs. Perhaps only then will it be possible to determine the significance of physiological variation to many basic issues current in ecology and related disciplines, such as the mechanisms underpinning geographic scale patterns in assemblage structure (macroecology), how these patterns respond to environmental changes (global environment change) and how assemblages might best be managed to ensure persistence in the face of environmental changes (conservation biology).

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The diversity of speciation

The origin of species remains one of the least well understood and most important questions in evolutionary biology. We know that biological diversity is generated by populations differentiating and is consolidated by speciation. But the historical nature of these processes has left us with only a sketchy idea of the driving forces behind them. A recent discussion meeting held at The Royal Society in London brought together an international field of speciation luminaries under the title 'Evolution of biological diversity: from population differentiation to speciation'. The meeting* was co-organized by Anne Magurran (University of St Andrews, UK) and Robert May (Oxford University, UK).

As May pointed out in his introduction, the intention was not to provide a synopsis of the field; nevertheless, over 2 days the 14 speakers and 300+ participants left few areas untouched.

To study the generation of biodiversity we need some way to quantify it. Genetic diversity, which many would consider to be the bottom line, is difficult to measure. Practising ecologists use species as units of ecological diversity, creating a debate about whether conservation efforts should be based on the preservation of genes or species. By surveying databases of allozyme variation (used as a rough guide to genetic variation) Roger Butlin (University of Leeds, UK) showed that species vary

widely in their genetic variability and in how much they differ genetically from other species, so they cannot be considered equivalent reservoirs of diversity. Furthermore, allozyme variation is a poor predictor of genetic variation within populations and of prezygotic isolation (where factors such as variation in mating signals mean that potentially hybridizing populations fail to mate with one another). This suggests that genetic differentiation alone does not inevitably lead to speciation. Other processes, such as adaptation and sexual selection, must be crucial in the initial establishment of barriers to gene flow.

This issue was taken up by Jerry Coyne (University of Chicago, IL, USA). Species are defined in terms of their genetic isolation from other species. Isolation can result from prezygotic or postzygotic barriers (where even if fertilization occurs, genetic incompatibilities render any offspring

produced inviable or infertile). Coyne's work on *Drosophila* reveals rapid evolution of prezygotic isolation independent of postzygotic barriers. This pattern is supported by work presented by Roger Butlin, which shows that traits associated with mate recognition in populations of the grasshopper *Chorthippus parallelus* are not correlated with the pattern of genetic divergence within the species. Coyne suggested that more attention should be devoted to identifying the single trait which first breaks down gene flow between incipient species and to identifying its genetic basis. Of the 37 studies in which genes involved in speciation have been identified, the majority are of postzygotic isolating factors. They are also a rather taxonomically biased sample: 27 are on *Drosophila* and another 5 are on species of *Mimulus* (monkey flowers). Clearly, studies of other species are needed to provide comparisons between taxa and life histories allowing us to identify general patterns.

It is clear that the evolution of prezygotic isolation is central to speciation, but what drives these processes? David Wilson (Binghamton University, NY, USA) pointed out that there had been a paradigm shift from regarding speciation as a result of random changes in populations to the view that it results from populations adapting to different environments. His work on pumpkinseed sunfish (*Lepomis gibbosus*) suggests that natural selection may also explain differences between individuals within a single population. Even within a single lake, fish may be partitioned according to factors such as habitat preference and their ability to tolerate predation. Study of these factors is complicated by the observation that only certain traits tend to differ between divergent groups whereas others vary continuously between them.

Susan Foster (Clark University, Worcester, MA, USA), suggested an alternative approach, exemplified by her work on the 3 spined stickleback (*Gasterosteus aculeatus*). Foster compared fitness associated differences between individuals within a population of one species with the pattern of differences in phenotype between populations or between related species. This reveals similar patterns, indicating that the factors driving divergence within a population or species are similar to those acting between species.

As well as natural selection, speciation may be driven by divergence resulting from female preference for male traits – sexual selection. Trevor Price (University of California at San Diego, USA) reviewed studies from the bird literature, concluding that sexual selection is likely to be most important where ecological differentiation

between incipient species is minimal. However, because hybridization will act against differentiation he suggested that the final stages of speciation may require reinforcement – selection for avoidance of hybridization.

The possibility that persistent outbreeding might retard speciation was echoed by Anne Magurran. Study of Trinidadian guppies transplanted between pools has shown that they are able to adapt very rapidly to changes in their environment. Despite this capacity, genetically divergent populations from separate river drainages, are still able to interbreed. Magurran suggests that the reason this apparent prime candidate for speciation has remained a single species is that sneaky matings in which a male manages to inseminate a female without going through courtship account for at least 15% of all fertilizations. Courtship provides the opportunity for mate choice, whereas sneaky matings are difficult to avoid, mainly because females are subject to an attempted copulation around once a minute.

The possibility that male promiscuity will break down divergence between incipient species was modelled formally by Geoff Parker (University of Liverpool, UK). His game-theoretical approach seeks to identify conditions under which it will benefit males to attempt to outbreed and for females to accept or reject such attempts. There is likely to be a fundamental asymmetry between the sexes since the costs of matings to males are likely to be very small, whereas a mated female may require a long regeneration time for production of offspring before she can breed again. A male mating with a genetically divergent female who produces lower fitness offspring, has typically invested little and still gains some offspring, whereas the female uses precious time and resources which could be spent producing fitter offspring. It seems likely that in the guppy although females are under strong selection to avoid sneaky matings they are unable to do so. This suggests that groups in which females find it difficult to reject matings may be less speciose than those where females are more in control.

The final talks of the meeting provided a long-term perspective on patterns of speciation. Stephen Gould (Harvard University, Cambridge, MA, USA) defended his belief that selection between species has dominated the evolution of biodiversity, suggesting that our focus on the individual as the unit of selection results from our own status as individuals. He conceded that the best argument against species selection is that the rate of extinction of species relative to that of individuals is so low that individual selection will be more important, but contended

that this is only the case if species really change. His interpretation of the fossil record is that species don't tend to change, leaving the door open for species selection. The debate over this contentious issue, as much of Gould's talk, centred on somewhat semantic questions such as whether species are individuals. However, as James Mallet (University College London, UK) pointed out, even if you don't believe species are individuals there remains a question as to whether species selection is an important macroevolutionary process.

What was clear, is that there is much for biologists to learn from the fossil record. Simon Conway-Morris (University of Cambridge, UK) described several major discrepancies between estimates of the origination of species from molecular and fossil evidence. Similarly, reassessment of the major adaptive radiations such as the Cambrian explosion suggest that they might have been more protracted than has hitherto been thought. Jack Sepkoski (University of Chicago, IL, USA) pointed out that since 99% of species ever in existence are now extinct, current biodiversity represents only a small surfeit of speciation over extinction. A rough calculation suggests that over the history of life on earth, three species are produced every year, and nearly the same number go extinct. However, there are enormous unexplained variations in the rate of speciation over time and between taxa, although rates within taxa are highly conserved, again for reasons we don't understand. The fossil record suggests that following major perturbations in the past, such as the major extinctions, speciation rates have increased, but only after unexplained delays of millions of years.

The message the meeting brought home most clearly was that we must use approaches at all levels, from within populations, to between species, right up to the grand march of the fossil record. Emerging molecular techniques are already allowing examination of the genetic bases of adaptation and speciation as well as providing essential information about historical patterns. The increased dialogue between genetics, behavioural ecology, ecology and palaeontology fostered by this meeting can only help in furthering our understanding of the evolution of biodiversity.

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*The proceedings of the meeting will be published in 1998 in *Philos. Trans. R. Soc. London Ser. B*, 353.