A duet on speciation

A synthesis of ideas about how species arise hits the right note.

Speciation
by Jerry A. Coyne & H. Allen Orr
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Identifying and understanding the processes that lead to the origin of species is one of the fundamental problems of evolution. Solving it requires not only field studies, comparative analyses and lab work, but also a scholarly knowledge of previous work. *Speciation*, a joyous duet by two of the field's leading soloists, Jerry Coyne and Allen Orr, should help. This treasure trove of knowledge, which provides ample food for thought, succinctly outlines hypotheses and proposes research programmes to test them.

The literature on speciation spans more than a century and a half, and includes contributions from experimenters, innovative thinkers and theoreticians. A vast jungle of empirical data has accumulated, but every single tree must still be inspected carefully to develop a comprehensive picture of the entire forest. The empirical evidence must then be analysed rigorously to see how it fits with alternative models, to distinguish between competing hypotheses. Coyne and Orr have succeeded in this task.

But why, almost 150 years after the publication of Darwin's *On the Origin of Species*, is there still so much left to say and do? Surprisingly, Darwin did not directly address the question of the origin of species in his published writings. For him, the origin of adaptations to new ecological challenges within species and the origin of the species themselves seemed almost the same thing. Arguably, the processes that result in the divergence of lineages to form new species are different from the mechanisms of the longer, and often more pronounced, divergence that occurs afterwards. It is generally accepted that the processes differ in timescale: whether species arise rapidly (for example through polyploidation, as in some plants) or more gradually, the splitting of lineages is generally much faster than the subsequent divergence within a species. But are the processes through which divergence occurs during and after speciation fundamentally different? Coyne and Orr would probably say yes; others might disagree.

The study of speciation depends on the 'species problem' — knowing what constitutes a species. How objective are the criteria that we use to assign individuals and populations to units that we call species, and do they affect the study of the processes of speciation? Darwin largely ignored this issue as well and, at least in *On the Origin of Species*, seemed to treat species as if they are not even real in the philosophical sense. To him, species were convenient constructs — groupings of sets of individuals that resemble each other, but which are not distinct, being just artificially united fluctuating forms that overlap with other potential species. To overstate the dilemma, Darwin neither believed in species nor did he write about how new species arise. He left these really hard nuts for subsequent generations of evolutionary biologists to crack.

Going separate ways: divergence and speciation in the herring family.

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Ernst Mayr, the centenarian doyen of evolutionary biology, contends that the species problem can be reduced to a simple choice between species as realities of nature or as theoretical constructs of the human mind. There are many alternative definitions of species, each emphasizing some cause or biological feature of species, and/or basing its definition on a particular analytical or empirical approach or data set in an attempt to capture the essence of what makes a group of individuals a species. (Thankfully, these are discussed in the appendix of the book.) Some researchers have even advocated abolishing the notion of species altogether.

Can we even begin to answer questions about speciation without knowing what species are? Having grown impatient over what they feel are pointless philosophical or (worse) semantic debates over the species problem, Coyne and Orr advocate the collection of more data on speciation and fewer debates on what species are. They conclude that it doesn't really matter to which particular species concept one subscribes.

I have painted a picture that is bleaker than it really is. Most biologists since Darwin have believed that species are real. The biological species concept (BSC) proposed by Mayr and Theodosius Dobzhansky is the most prominent and widely accepted one. It defines species as "groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups". Thus, new species arise when reproductive isolation separates formerly interbreeding populations.

Like most researchers, Coyne and Orr feel that the study of speciation is helped, or even only becomes possible, by accepting the BSC and focusing on the study of reproductive isolation. They want to know where, how and when reproductive isolation comes about, and how it can be measured. However, some researchers believe that accepting the BSC stifles the study of speciation by limiting it to the study of the origin of reproductive isolation. The concept's dependence on reproductive isolation among sexually reproducing organisms, for example, means it cannot easily be applied to bacteria and organisms that reproduce clonally.

Geographic mechanisms of speciation, in which formerly interbreeding populations are prevented from doing so by geographic barriers, are generally thought to be the most common way for new species to arise, and this idea receives much empirical support. A non-adaptive by-product of isolation is that, over many generations, genomes or gene frequencies drift apart. This then prevents interbreeding and the homogenizing flow of genes from one species to the other when they come into contact again.

It was Mayr who laid the foundations for much of the current research on the origin of species, in particular for the BSC and for most geography-based hypotheses of speciation. Coyne and Orr could be accused of being ‘admayrers’, but that’s not the worst thing one can be called, in my opinion. Unlike Mayr in his early work, the authors admit, albeit with palpable hesitation, that speciation can also occur without geographic isolation, in overlapping or ‘sympatric’ areas. Sympatric speciation, which for decades had all the caché of a four-letter word, is increasingly seen to be responsible for the origin of at least a minority of species.

Coyne and Orr also give renewed credence to models of speciation that emphasize a role for sexual or natural selection, rather than viewing the origin of species as little more than a by-product of isolation. One currently popular model, ecological speciation, de-emphasizes geographical settings and reaffirms the importance of local adaptations and natural selection in bringing about speciation. Reproductive isolation may be brought about by ecological processes, such as habitat fragmentation or the uneven distribution of resources. In such cases, interbreeding is prevented between populations that are limited — by behavioural, physiological and morphological adaptations — to a very particular set of prey items, for example, or a particular tree species that they need to build their nests. The absence of the homogenizing effect of gene flow between individuals, not through geography but by the divergence of adapted and ecologically important traits, possibly even in the same environment, then leads to reproductive isolation. In this way, natural selection can play a prominent role in speciation.

The most recent work, largely done on fish models, includes modern genomic approaches, such as the analysis of quantitative trait loci. It concludes that reproductive isolation and speciation may be a by-product of ecological differences and disruptive selection on a surprisingly small number of phenotypic traits, which are controlled by an equally small number of underlying genes. A role for selection can also be inferred from molecular genetic data on hybrid incompatibilities from models such as the fruitfly. These have yielded a few candidate ‘speciation genes’, which also show signs of natural selection having been at work.

Performing this demanding duet in masterly harmony, Coyne and Orr present an authoritative treatise on one of the most long-running debates in evolutionary biology. *Speciation* is an impressively up-to-date and enlightening synthesis — and an entertaining read. It deserves to join Darwin’s *On the Origin of Species*, and Mayr’s *Systematics and the Origin of Species* on the bookshelf of anyone who is interested in evolution. ■

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Grabbing a bite: the main role of teeth is to break down large items of food into smaller ones.

Something to chew on

Dental Functional Morphology: How Teeth Work
by Peter W. Lucas
Cambridge University Press: 2004. 372 pp. $130, £75

Daniel E. Lieberman

Science has made substantial progress since Aristotle wrote (apparently without doing much research) that women have fewer teeth than men. The sheer volume of published research on teeth since may lead some to conclude that we have over-compensated for Aristotle’s ignorance. Yet teeth merit all this attention because of their tremendous biological importance — not to mention the dreadful pain they can cause. Dental development and function are the focus of much clinical attention. And for evolutionary biologists, teeth are invaluable sources of information about taxonomy, phylogeny and many other aspects of animal biology.

There are already many excellent texts on dental function and development within the context of craniofacial development and clinical dentistry, as well as several good reviews of dental variation and evolution among vertebrates. But *Dental Functional Morphology* provides a fresh perspective on dental function. Peter Lucas’s basic argument is that because the primary function of teeth is to reduce the size of food particles, dental morphology must be analysed in the context of how teeth fracture food, and how foods resist this. So the book reviews in detail many of the key mechanical properties of food, such as toughness and elasticity, which influence how teeth initially deform food items and generate cracks in them to break down large particles. Lucas then considers how variations in tooth size and shape influence this. He also includes more general reviews of dental and oral anatomy, and provides an excellent summary of the processes of chewing and oral transport, viewed from the perspective of the mechanical properties of food, such as particle size and stickiness.

This food’s-eye view leads to numerous insights and interesting ideas, such as Lucas’s theory of fracture scaling. Bigger animals have bigger teeth, whose surface areas might be predicted to scale with body mass to the power of 0.67 (because tooth area increases to the power of two, and body mass increases to the power of three, yielding a scaling ratio of 2/3). Yet tooth surface area in mammals typically scales to the power of 0.61. Why this is so remains elusive, but Lucas argues that fracture mechanics plays a role.

The argument is complex, but boils down to the observation that once a crack is initiated in an object, little additional energy is needed to finish the job, regardless of its size. Bigger foods fracture at relatively low stress, which has several implications. One is that bigger animals (assuming that they chew bigger food) need relatively less muscle force (as quantified by muscle cross-sectional area), so this should only increase to the power of 0.5 relative to body mass, although this has yet to be tested. If tooth surface area does not increase relative to bite force, then tooth surface area should also scale to 0.5 relative to body mass. But teeth scale to the power of 0.61, so other factors must also influence tooth size, including other complex aspects of food mechanics also reviewed by Lucas. We can look forward to efforts to test this hypothesis and explore its implications.

Lucas does not consider in detail how dental function relates to tooth development and microstructure, or to the neuromuscular control of chewing. But readers interested in such topics as evolution, diet and ecology will enjoy his many other ideas about how vertebrate teeth work. The final chapter focuses mainly on mammals, creatively integrating