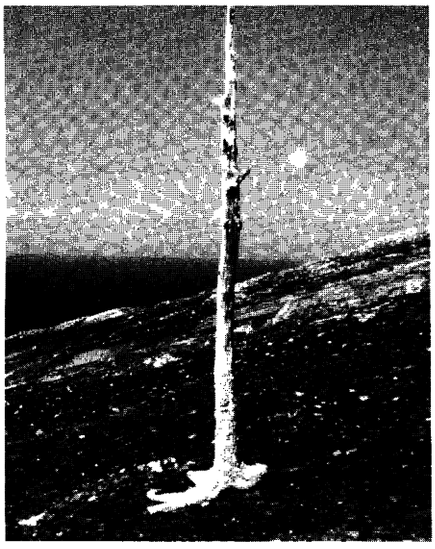

"Devastation caused by introduced rabbits on Round Island," Mauritius. "Goats, sheep, and rabbits are capable of causing severe damage to habitats. . . . On oceanic islands where these herbivores have destroyed the native habitat, complete reptilian or avian communities have been affected." [From *The Balance of Nature*; photograph from Ian Atkinson]

contentious issue. Some would argue that the only purpose of general models, at least in ecology, is to point out the kinds of possible ways in which nature could work. When it comes to determining how nature actually does work and managing nature at these high levels of biological organization (communities and ecosystems), empiricism, they would argue, is a more practical and fruitful guide.

On the other hand, recent experience provides at least one counter-example. Usually, even in ecological management, we must begin to answer a question with a guess. The nature of government is that we, as scientists, usually are not called in until there is some urgency. We must guess before the facts are all in. Later, we can refine our guesses by collecting more data and making our models more specific and detailed. The case of the federally listed and endangered northern spotted owl is a prime example. Russell Lande presented a very general model in *American Naturalist* in 1987. This model, really not owl-specific at all, predicted an extinction threshold such that, if habitat abundance was fragmented and reduced below it, the young searching for suitable territories amid a matrix of unusable habitat would likely die. Extinction of the metapopulation would be almost guaranteed, even though the available habitat might be sufficient to support many individuals.

Lande, the U.S. Forest Service, and other state and government agencies were guided in part by this model in creating a new management plan (published in 1990). This new plan carefully avoids the habitat fragmentation and consequential risk of extinction inherent in the previous policy.

The message is that general and qualitative models will still play a role in understanding important issues in ecology and conservation for some time to come. If you want to hone your intuition about big problems in ecology, Pimm's book is a great place to start. Though the book is not mathematical, Pimm has the professor's ability to distill the workings of complicated models into verbal descriptions that provide the essence, if not the grit. He provides profuse illustrations to explain and develop his points. This will be a entertaining and provocative book for graduate seminars.

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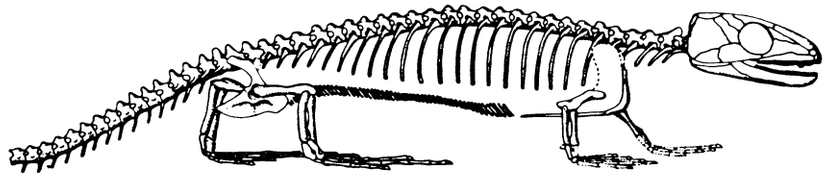
Vertebrate Transitions

Origins of the Higher Groups of Tetrapods. Controversy and Consensus. HANS-PETER SCHULTZE and LINDA TRUEB, Eds. Comstock (Cornell University Press), Ithaca, NY 1992. xii, 724 pp., illus. $95.

Representatives of the major groups of living vertebrates are profoundly distinct from each other, and this fact is traditionally recognized by according these groups the rank of class in the Linnaean taxonomic hierarchy. With the general acceptance of evolutionary thinking in biology during the second half of the 19th century, attention focused on the search for genealogical links between the various classes of tetrapods and between tetrapods and "fishes." Traditionally, paleontologists have sought to identify ancestral groups or even to trace actual ancestor-descendant sequences in the fossil record. In the late 1960s and 1970s, this approach was supplemented by explanatory scenarios for evolutionary transitions in functional terms. More recently, biologists have returned to analyzing the interrelationships of vertebrates, drawing on both morphological and molecular data. The paleontological community has generally been perceived as being rather slow to climb aboard the bandwagon of modern phylogenetic analysis, and some biologists have even come to dismiss fossils as unimportant for phylogenetic inferences. Various recent studies, however, have elegantly demonstrated that phylogenetic relationships are best inferred from simultaneous consideration of both extant and fossil vertebrates.

The present volume comprises a broad spectrum of papers by an international group of experts on the evolutionary transition from aquatic sarcopterygians to tetrapods and the origins of the major taxa of tetrapods. It grew out of a series of seminars presented at the University of Kansas in the spring of 1985; a number of chapters were subsequently added to expand the coverage.

The first five chapters present competing hypotheses concerning the interrelationships of sarcopterygian "fishes" and tetrapods. Among living vertebrates, tetrapods are most closely related to lungfishes, but the picture is much less clear once Paleozoic sarcopterygian "fishes" are also considered. Although the latter are among the most thoroughly studied of all fossil vertebrates, there is still no consensus concerning the relationships of the various major taxa of aquatic sarcopterygians to tetrapods. Chang presents a novel hypothesis of a sister-group relationship between a monophyletic grouping including all aquatic sarcopterygians and tetrapods. This phylogenetic scheme is rendered unlikely by the many derived similarities shared between tetrapods and less inclusive groupings of aquatic sarcopterygians and is rejected by other authors in this section of the volume. Schultze and Vorobyeva provide much new anatomical information on the Devonian Panderichthyidae, based mostly on excellently preserved fossils from Latvia, and argue that panderichthyids are most closely related to tetrapods. Panchen discusses the enigmatic Lower Carboniferous taxon *Crassigyrinus*, which he considers related to anthracosaurian amphibians even though several characters place this taxon close to the base of tetrapod phylogeny. Rather than attempting to examine this problem in an explicitly cladistic fashion, he opts to deliver



"Skeleton of the earliest known reptile, *Hylonomus lyelli*, from the Westphalian B of Joggins, Nova Scotia. Approximately two-thirds natural size." [From R. L. Carroll's chapter in *Origins of the Higher Groups of Tetrapods*]

a polemic against current approaches to phylogeny reconstruction. In their excellent summary chapter, Forey, Gardiner, and Patterson summarize the conflicting views in the preceding contributions and examine them using numerical cladistic methodology. They favor a hypothesis that tetrapods are most closely related to a grouping comprising coelacanths and lungfishes plus the Early Devonian *Diabolepis*.

The second section of the book is concerned primarily with the origin of the three major groups of living amphibians, which are commonly and conveniently grouped together as Lissamphibia. The review by Bolt on the relationships of modern groups to certain Paleozoic taxa and the thorough phylogenetic analysis of living and fossil amphibians by Trueb and Cloutier both present a convincing case for the monophyly of lissamphibians and their sister-group relationship to the mostly late Paleozoic Dissorophoidea.

The third section discusses the origin and interrelationships of reptiles. The review of diapsid interrelationships by Carroll and Currie supports recent phylogenetic hypotheses and emphasizes persistent problems (such as the affinities of the various taxa of aquatic diapsids) that appear to be due to pervasive homoplasy.

The chapters devoted to *Archaeopteryx* and the origin of birds (section 4) offer little new information and insight, and several of the phylogenetic discussions display a lack of analytical rigor. Witmer provides a valuable historical review of the problem. Ostrom restates his (cladistically now well-supported) hypothesis that birds are most closely related to theropod dinosaurs. Martin criticizes many of Ostrom's arguments and instead postulates derivation of birds from a crocodile-like ancestor. Tarsitano's chapter presents a curious mixture of cladistics, evolutionary scenarios, and intuition. He rejects Ostrom's hypothesis and attempts to relate birds to forms similar to the poorly known Late Triassic *Megalancosaurus* (which is probably not an archosaur).

The final section deals with the Synapsida and the origin of mammals. Hopson's excellent, even-handed review of synapsid interrelationships reiterates the traditional view that parallel evolution is indeed a pervasive phenomenon during the evolutionary history of this group (and presumably other major taxa as well), rather than (as has frequently been alleged) the result of unparsimonious phylogenetic inferences.

Although it is encouraging that the majority of contributors at least use some form of cladistic analysis, their detailed methodological approaches vary considerably. Unfortunately, many chapters lack matrices for character distribution, which hinders evaluation of the arguments advanced by the various authors.

This volume contains many new data and insights and is an important reference work for any advanced student of vertebrate evolution. It will figure prominently in paleontological debates for years to come and succeeds well in highlighting areas of continuing controversy. The book also underscores the intriguing fact that, after almost two hundred years of intensive scientific study, there is still little consensus concerning the higher-level interrelationships among tetrapods and their aquatic sarcopterygian sister taxa.

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Themes in Ethology

The Tinbergen Legacy. M. S. DAWKINS, T. R. HALLIDAY, and R. DAWKINS, Eds. Chapman and Hall (Routledge, Chapman and Hall), New York, 1992. xii, 146 pp., illus. $57.50. From a conference, Oxford, U.K., March 1990.

Niko Tinbergen was the single most important individual in the development of modern ethology. He combined the separate strengths of the two ethologists who shared the Nobel Prize with him: Like Karl von Frisch, he had experimental finesse that set the standard for tricking animals into revealing their secrets through their behavioral responses; no one has ever surpassed Tinbergen's adroit use of models to dissect the innately recognized cues that trigger behavior. Like Konrad Lorenz, he insisted that animals be studied under natural or (when sufficiently understood) semi-natural conditions, setting another important standard for the field; his demonstration that evolutionary hypotheses could at least sometimes be tested added an essential empirical element to a discipline in which the formulation of just-so stories was (and remains) a debilitating temptation. Moreover, Tinbergen was the most effective communicator of the three; though Lorenz's *King Solomon's Ring* is in a class by itself, Tinbergen's *The Study of Instinct*, *The Animal in Its World*, *Curious Naturalists*, and *The Herring Gull's World* have had an enormous impact on young ethologists, particularly in the English-speaking world. In *The Tinbergen Legacy*, which consists of eight papers presented at a one-day conference in Oxford in 1990, the contributors attempt to capture the unique contributions of Niko Tinbergen.

Gerard Baerends, one of Tinbergen's early Dutch collaborators, offers a thumbnail biography, with special attention to the cultural milieu of the prewar Netherlands. I hope Baerends will expand this all too brief and telegraphic account into a book some day. Nicholas Davies focuses on the development of behavioral ecology from Tinbergen's early tests on the evolutionary purpose of behavior. Davies points out that Tinbergen's concentration on species-typical behavior led him largely to ignore individual differences and thus the various strategies that various individuals in a population adopt. In some species, animals measure the relevant variables and then opt for the preprogrammed alternative that has the most favorable cost-benefit ratio. Davies nicely balances his chapter by taking behavioral ecologists to task for ignoring the mechanistic bases of behavior, a factor that Tinbergen consistently emphasized.

Robert Hinde considers Tinbergen's special interest in human ethology. This was one of Tinbergen's less successful endeavors, and Hinde loyally attempts to gloss over the remarkable and uncharacteristic error Tinbergen made in assuming that autism is primarily a cultural phenomenon rather than mainly the consequence of genetic predispositions. Perhaps the best chapter is the one on motivation by Felicity Huntingford; it clearly and accurately summarizes Tinbergen's pioneering work and then looks honestly at the status of his ideas in modern ethological thought.

John Krebs's chapter on communication offers a brief view of Tinbergen's and (mostly) Lorenz's ideas on the evolution of communication and then presents at some length Krebs's by now familiar view that communication is inevitably dishonest and deceptive (excluding, one must suppose, book chapters). This is one of only two papers that cite their authors' work more often than Tinbergen's. Juan Delius chose as his topic the nature of culture, a subject on which Tinbergen had little to say. This is the only chapter that deals with learning, an important component of the Tinbergen legacy, and it doesn't really capture the essence of Tinbergen's contribution to the modern realization that much learning is species-specific and innately directed.

Michael Robinson's topic is the use of species comparisons in understanding behavior, a technique whose immense potential was clearly demonstrated in Tinbergen's work on gulls. Like Krebs's chapter, however, this one is more about the author's work than Tinbergen's or its legacy. The book ends with a curious chapter on Tinbergen's use of photography. The films that Tinbergen helped make (especially "Signals for Survival") are unsurpassed in communi-