Phylogeny and Coevolution

Coevolution and Systematics. A. R. STONE and D. L. HAWKSWORTH, Eds. Clarendon (Oxford University Press), New York, 1986. xii, 147 pp., illus. $39.95. Systematics Association Special Volume no. 32. From a symposium, Brighton, U.K., July 1985.

With the development of increasingly rigorous methods and new kinds of data for inferring genealogical relationships among species, systematics is emerging from a period of eclipse to take its rightful place as an essential, integral party to evolutionary studies. There is increasing recognition that the study of both adaptive and nonadaptive traits cannot be divorced from the historical analysis that systematics includes among its subjects. Among the topics on which systematic analyses should make especially critical contributions is the coevolution of ecologically interacting species. As J. N. Thompson points out in this volume, coevolution includes two phenomena: coadaptation, the reciprocal adaptation of taxa to each other, and cospeciation, the joint speciation of associated taxa such as hosts and their parasites.

In principle, systematics should contribute to answering several kinds of questions about coevolution. For example, Ehrlich and Raven postulated in 1964 that adaptive radiation (hence, species diversity) of hosts may be stimulated by escape from parasitism via the evolution of novel defenses and that parasites (or herbivorous insects) may diversify when a lineage becomes adapted to a host group that had escaped exploitation. As Thompson shows by an analysis of a controversial case in plants and insects, this hypothesis can be tested only by an adequate diagnosis of species and monophyletic groups.

If cospeciation is general, the phylogenies of hosts and their parasites should be topologically congruent, in the absence of extinction of parasite lineages and of lateral transfer of parasites between host lineages. The supposition that parasite phylogenies mirror host phylogenies has been christened "Fahrenholz's rule" by parasitologists and has long been used as a guide to classification in parasitology. This rule is examined in this volume both by workers who do not use explicitly cladistic methods to infer phylogeny (V. F. Eastop on aphid-plant associations and I. Beveridge on the helminths of Australian marsupials) and by several workers who do (C. J. Humphries *et al.* on associations of moths, scale insects, and fungi with southern beeches, *Nothofagus*, and C. H. C. Lyal on trichodectid lice of mammals). It will be necessary to read these authors' primary publications to evaluate their methods, which in some cases are not specified and in others may evoke skepticism. Lyal, for example, uses manual methods, which are notoriously inexact, to determine relationships among 351 taxa of lice on the basis of only 187 characters. Humphries *et al.* report 190 equally parsimonious trees for 17 species of *Nothofagus*, which leads one to wonder if the shortest trees were indeed found. (Incidentally, their important figure 4.6, on the *Nothofagus* relationships implied by the moth phylogeny, is in error.) These essays also illustrate the need for explicit methods of finding, and testing the significance of, points of incongruence between phylogenies.

With these caveats, the message nonetheless emerges that the phylogenies of hosts and parasites show little congruence at any taxonomic level. Cospeciation is far from universal, and host lineages seem often to have lost their parasites. In every case, sister groups of parasites often occupy unrelated hosts (for example, rodents and marsupials), so lateral transfer has been a major feature of parasite evolution. As the population biologists (J. A. Barrett, J. E. Parlevliet, J. N. Thompson) note, genetic variation in many groups of parasites enables ready transfer to new hosts; moreover, strict cospeciation would be expected only if evolution in one partner caused reproductive isolation in the other or if populations of both hosts and parasites acquired reproductive isolation at similar rates.

Perhaps because long-term associations are so frequently confounded by transfers to unrelated hosts, it is hard to demonstrate progressive coadaptation between associated lineages—which systematics should in principle be able to document from character analysis. This topic is not treated explicitly in the volume; still, as Eastop says, it is hard to show that the macroevolution of either hosts or associates has been affected by their interaction, even though adaptation of individual species to their hosts is clear.

This volume, informative as it is, only sketches what has been done and what we may hope for. That Fahrenholz's rule is more evident in the breach than the observance points to the role that systematics may play in documenting the history of host

transfers and opens a world of questions about the factors governing host shifts that remain to be explored. Abundant though host transfers may be, there is yet a strong phylogenetic component in parasite-host associations that any study of parasite ecology and evolution must take into account.

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High Energy Cosmic Photons

Gamma-Ray Astronomy. POOLLA V. RAMANA MURTHY and ARNOLD W. WOLFENDALE. Cambridge University Press, New York, 1986. x, 248 pp., illus. $49.50. Cambridge Astrophysics Series.

Like modern cosmology, gamma-ray astronomy depends on the marriage of high energy physics and astronomy. The offspring of such unions can be dramatic new insights and revelations. However, the field of gamma-ray astronomy has been slow to come of age. As full of promise as a Kentucky foal in spring, patiently nurtured by a few pioneering researchers through difficult technical and budgetary periods, this area of research offers much promise for a future generation of astronomers. Ramana Murthy and Wolfendale's up-to-date monograph on the subject can provide a useful function by helping to educate the future investigators.

Despite the paucity of cosmic photons of gamma-ray energies and the subsequent difficulty and expense of detecting them, there has been theoretical interest in the subject for almost four decades. The astronomy of the highest energy region of the electromagnetic spectrum can provide fundamental information that is unavailable to other branches of astronomy (except perhaps the less developed and more difficult field of neutrino astronomy). The questions that can be addressed by gamma-ray observers and theorists relate to the origin of cosmic rays and the highest energy physics of astronomical sources of violent activity such as quasars, pulsars, supernovas, black holes, and x-ray binary stellar systems. Owing to the strong penetrating power of gamma rays, their astronomy can also tell us about the structure of the Galaxy. Reaching us from a distant past, gamma rays from redshifts beyond those accessible in other parts of the electromagnetic spectrum (excepting the primordial cosmic microwave background radiation) will enable us to probe the nature of the young universe and the violent astronomical objects that populated it. Studies of the cosmic background gamma radiation may also help to determine whether antimatter plays a large-scale role in the makeup of our universe.

Ramana Murthy of the Tata Institute of Fundamental Research in Bombay, India, has been involved in experiments using the earth's atmosphere to detect very high energy cosmic gamma rays. Wolfendale of the University of Durham, United Kingdom, has long been interested in the interpretative and theoretical aspects of high energy astrophysics and gamma-ray astronomy. Their book provides an introductory survey of gamma-ray astronomy for students with backgrounds in basic physics. It can be integrated into a graduate-level course in high energy astrophysics.

The book is divided into relatively self-contained chapters that delineate the major subfields of gamma-ray astronomy: gamma-ray spectral line astronomy, "gamma-ray bursts," medium energy (30 MeV to 5 GeV) astronomy, and ultrahigh energy gamma-ray astronomy, which uses the techniques of detecting atmospheric air showers produced by incoming cosmic photons having energies greater than about 1000 GeV. The last two topics are the special interests of Wolfendale and Ramana Murthy, respectively. A brief, rather sketchy introduction outlining the basic physical processes that are responsible for the production of astronomical gamma rays is provided. For a deeper theoretical background, some readers will find it useful to consult the previously published books to which the authors refer (*Cosmic Gamma Rays* by F. W. Stecker, Mono, Baltimore, 1971; *Gamma-Ray Astronomy* by E. L. Chupp, Reidel, Dordrecht, Holland, 1976).

In the other four chapters of the book, the material is presented in a form reminiscent of traditional review articles, with extensive reference to the published literature. In this manner, the authors survey the entire subject of extra–solar-system gamma-ray astronomy. However, the interpretative material in the chapter on medium energy gamma rays is heavily weighted with the work of the Durham University group on this subject. Because there has been a rather lively controversy involving other researchers about the interpretation of the Galactic gamma-ray flux, and because of the implications of this discussion for the origin of cosmic rays, it would have been useful to bring in more of the recent theoretical work of the other groups involved in the debate.

The introduction to the techniques of air-shower detection of ultrahigh energy gamma rays and the accompanying discussion of the Cygnus X-3 binary system are timely, given the recent excitement over this mysterious source. The gamma-ray results imply that this source, by itself, could supply a significant fraction of the high energy cosmic rays in the Galaxy. In addition, reports of unexpected fluxes of high energy muons coming from Cygnus X-3 have caused it to become a subject of much speculation and the plaything of theoretical astrophysicists and particle physicists alike.

A significant fraction of the volume is devoted to a review of gamma-ray bursts, a phenomenon about which we have a plethora of observational information and no real understanding. This again reflects the state of the art in a field that has begun to yield important results and that, though still in its infancy, has great potential.

One of the earliest scheduled scientific missions of a renewed space shuttle program will be the launching of the next generation of gamma-ray telescopes aboard the Gamma Ray Observatory. This event should occur within the next few years. Experimental activity on the "ultrahigh energy air-shower" end of the spectrum is brisk. An exciting future awaits. Students interested in finding out more about gamma-ray astronomy can get a taste of where we are at present from reading this book.

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Ancient Soils

Paleosols. Their Recognition and Interpretation. V. PAUL WRIGHT, Ed. Princeton University Press, Princeton, NJ, 1987. xiv, 315 pp., illus. $42.

Quaternary paleosols have been widely recognized, studied intensively, and used for stratigraphic correlations and to interpret paleoclimates. This collection of papers is an admirable attempt to draw attention to pre-Quaternary paleosols, detailed study of which has been much less common. Several of the papers are particularly notable.

The introduction provides a concise overview not only of the contents of the book but of ancient paleosols in general. It convinced me that pre-Quaternary paleosols are much more abundant than I had believed and that careful study of them can yield valuable information.

In chapter 1, Retallack presents a thought-provoking account of the fossil record of soils. Several lines of circumstantial evidence for the early development of life in soils are presented. The reasons for preferring a "primordial sludge" to a "primordial