

Avian arrangements

Jared M. Diamond

Phylogeny and Classification of Birds: A Study in Molecular Evolution. By Charles G. Sibley and Jon E. Ahlquist. Yale University Press: 1990. Pp. 976. Hbk \$100, £60.

Distribution and Taxonomy of Birds of the World. By Charles G. Sibley and Burt L. Monroe, Jr. Yale University Press: 1990. Pp. 1111. Hbk \$125, £75.

"I'm sick of hearing about that stuff. I no longer pay attention to anything those guys write."

"Why would anyone want to do something so boring as all that bird taxonomy?"

"Their results are the Revealed Truth, and you better believe it."

As these divergent opinions of three scientist friends of mine illustrate, taxonomy is a field noted for controversy. The opinions all refer to the same study, now summarized in two books, that used molecular methods to revolutionize taxonomy. These books make clear why taxonomy, though often despised as the most mundane science, inspired crucial insights in Darwin and continues to offer crucial new insights today.

As background, recall that the morphological criteria traditionally used in taxonomy are imperfect because they are subject to natural selection. Hence legacies of close relationship are often mimicked by adaptive convergence (for example, of whales and sharks) and obscured by adaptive divergence (for example, of New World vultures from storks). The same problems affect amino-acid sequences as taxonomic characters. DNA has the advantage that most DNA seems to be nearly neutral selectively and seems not to code for detectable proteins.

DNA-based taxonomic studies use two alternative methods: sequencing of short DNA segments, or single-copy DNA hybridization. The latter method involves measuring the difference between two entire genomes by the observed lowering of mixed melting point (about 1°C for a base-pair mismatch of one per cent). Theoretically, both methods should converge on the same answer with increasing length of the sequenced segment. This expectation is confirmed by multispecies comparisons of hominoid globin DNA sequences. But single-copy DNA hybridization has decisive practical advantages, because (in Roy Britten's words) it "is quicker than DNA sequencing and the results are more conclusive since the whole genome is averaged."

To date, by far the most extensive application of DNA hybridization to taxonomic problems has been the study of bird classification by Charles Sibley and Jon Ahlquist. From 1974 to 1986 they collected specimens from thousands of individual birds belonging to 1,700 of the world's 9,672 bird species, and they measured melting curves of 26,554 bird DNA hybrids. Birds have the advantage that, on the one hand, they have been intensively studied and almost all ex-

tant species have been described; and that, on the other hand, the severe aerodynamic constraints imposed by flight make traditional morphological criteria especially equivocal. This massive study is the basis of the two correspondingly massive books under review.

Phylogeny and Classification of Birds by Sibley and Ahlquist presents the immediate results of the study itself, and much more. Nearly half the text consists of excellent detailed accounts of general subjects that will interest many biologists who care not a whit about birds. These subjects include the organization of DNA, the (debated) selective neutrality of most mutations, practical details of DNA hybridization, problems in deducing relationships by any method, differing philosophies of taxonomy, the tempo of evolution, and the mutual insights derived from the knowledge of Earth history and of taxonomy. The rest of the book consists of the results for each group of birds, buttressed by detailed presentations of the data (nearly 400 sets of melting curves and phylogenetic trees).

Distribution and Taxonomy of Birds of the World by Sibley and Burt Monroe then goes through the world's 9,672 bird species, summarizing for each species its geographical distribution, preferred habitat, relationships, and classification based on the Sibley/Ahlquist conclusions. The classification is according to W. Hennig's cladistic principles: it reflects only the inferred branching pattern of phylogeny; taxonomic rank reflects only the inferred time of divergence; sister groups have coordinate rank; and degree of adaptive differences is not a consideration. The previous reference work most nearly similar in content, the 16-volume *Check-List of the Birds of the World* (Harvard Museum of Comparative Zoology, 1931-87) by James Peters and his successors, instead does consider degree of adaptive differences. Peters' set has the advantage of being far longer and more detailed because its unit is the subspecies, whereas Sibley's and Monroe's unit is the species. Peters' set has the disadvantage of having been written by many authors over the course of 56 years, resulting in somewhat varying standards and much now out-of-date material. Sibley's and Monroe's volume has the advantage of uniform standards, uniformly modern information, a large set of maps and gazetteer, and consistent evaluation for every species of its association in superspecies and its division into subspecies

groups. Every student of bird taxonomy will surely want to own both Peters and the new book by Sibley and Monroe, though students with limited budgets may have to content themselves with Sibley and Monroe alone.

Let us return to the criticism; "Why would anyone want to do something so boring as all that bird taxonomy?" Among the answers implicit in these volumes, here are three examples.

First, with true relationships established by non-morphological criteria, morphological evidence can now be used independently to study evolutionary convergence and divergence. The enormous richness of examples in these volumes will occupy evolutionary biologists for a long time. For instance, Sibley and Ahlquist discovered a marsupial-like radiation involving most Australian songbirds, a radiation that was previously unrecognized because those songbirds so closely resembled their unrelated Eurasian ecological equivalents, and because Australian songbirds are not united by any visible shared feature of morphology like the marsupial pouch. Storks and New World vultures prove to be closely related but strikingly divergent in adaptive characters, the former being convergent on herons, the latter on Old World vultures. Lest anyone fear that Sibley and Ahlquist have solved all problems of bird taxonomy, hundreds of major ones remain, involving relationships within families as well as between higher groupings. For instance, with more information the radiations of parrots and pigeons may come to tell tales as fascinating as the radiation of Australian songbirds.

Second, the effect (if any) of generation time on rates of evolution has been much debated. Sibley's and Ahlquist's results show clearly that demographic parameters have large effects on the rate of accumulation of selectively neutral mutations: the rate is higher in species with shorter generation times or with younger ages at first breeding. Because these two variables tend to be linked, it is still uncertain which variable is responsible. That issue, and the problem of the underlying mechanism, now become questions of great interest ripe for attack.

As a final example, all scientists face the dilemma of reconciling their desire for the truth with their personal egos and their instinctive defensive reactions to personal criticism. That dilemma is acute in cladistic taxonomy, a field notorious for its prevailing standard of vicious personal criticism, but the Sibley/Ahlquist study has attracted criticism notable for its viciousness even by the standards of taxonomists. It is thus all the more impressive that Sibley and Ahlquist in their book are conspicuously fair in presenting both the limitations and the advantages of their own and other results. In many places they cite and correct erroneous conclusions that they (as well as others) reached previously, and they trace how they became misled in each case. Their presentation can

serve as a model of how to handle criticisms and errors.

Who should buy which book? Anyone studying birds will want both books. They are long, crammed with information, and a bargain for the price. Anyone concerned with relationships within a group other than birds will at least want to study Sibley and Monroe, as a model of what taxonomy can achieve. The Sibley and Ahlquist book is for anyone in molecular evolution and evolutionary biology, for many other types of biologists, and for anyone (including historians) interested in how to do and present landmark science. □

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Classical agriculture

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The Ecology of the Ancient Greek World. By Robert Sallares. Duckworth/Cornell University Press: 1991. Pp.588. £42, \$84.

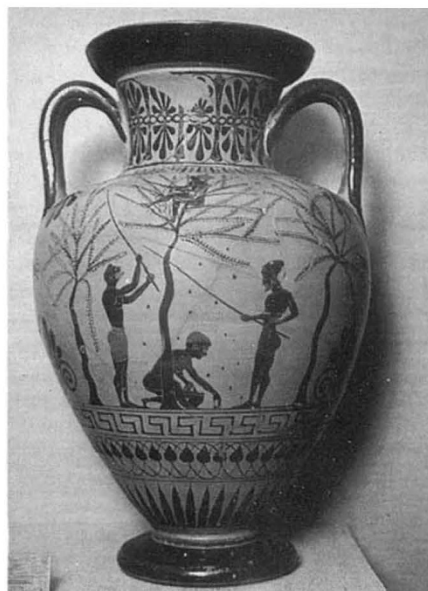
UNLIKE prehistorians, who readily pillage the natural sciences for insights into the material record of the human past, ancient historians prefer the more familiar and superficially more tangible testimony of ancient texts. In *The Ecology of the Ancient Greek World*, Robert Sallares aims to cast some much-needed, multidisciplinary light on this dim recess of academia by writing "the first comprehensive ecological history of the ancient Greek world".

That Sallares transcends contemporary disciplinary parochialism is beyond dispute — detailed philological and historiographical argument competes for space with wide-ranging forays into archaeology, anthropology and evolutionary biology and ecology. With 800 footnotes and 2,000 bibliographic entries, *The Ecology of the Ancient Greek World* is unquestionably a serious work of scholarship, but never dull. Sallares has opinions on the irrationality of vegetarianism, the evolution of concealed ovulation in humans and the evolutionary prospects for AIDS. He explains the nature of causality and, in a scathing but witty assault on the traditional classical scholar, advocates comparative research as the historian's equivalent of the experimental method in science. He dismisses M. Finley, G. de Ste. Croix, M. Weber, K. Marx and F. Braudel on early Mediterranean towns, repeatedly admonishes 'New Archaeologists' for invasion-phobia, effectively demolishes E. Boserup's model of agricultural development and, at rather greater length, rewrites the evolutionary history of wheat. The historian is brought up to date on the extinction of dinosaurs, history of

bubonic plague and Dutch elm disease; ecologists should enjoy the pioneering work of Hegesandros on island biogeography.

Sallares defines ecology somewhat narrowly as the study of "the distribution and abundance of populations of living organisms in relation to their environment" and of "rates of flow of energy between different levels of food chains". Accordingly, the core of the book deals at length with the demographic and agricultural history of Greece during the first millennium BC. Recent evidence from intensive archaeological surveys, which has revealed drastic and widespread fluctuations in site numbers is taken to indicate equally drastic fluctuations in human population density. The problems of variable 'visibility' of different chronological horizons and of evident alternation between nucleated and dispersed settlement are acknowledged but then ignored — Sallares is, throughout, least convincing in his handling of archaeological evidence.

More particularly, he follows A. Snodgrass in arguing that increasing numbers of burials during the early first millennium BC mark a steep rise in population; he perceptively criticizes but fails to refute T. Morris' suggestion that this trend reflects archaeologically visible burial of an increasing proportion of the population. A lengthy digression on skeletal evidence for the age and sex structure of the population is far too inconclusive to clarify changes in population size. More intriguing is the proposition that early Greek society in the first millennium BC was characterized by a system of age-class organ-



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Images of nature — vase depicting olive harvester from the fourth century BC.

ization, which served to restrain population growth by delaying marriage for males (delayed marriage for females would have been more effective). Sallares seems to demolish his own case, however, by arguing that in Attica the age-class system was falling into disuse at a time when population growth was

slowing down.

On agriculture, Sallares makes perceptive comments on the ecological and economic context of recent farming practices, and on the dangers of uncritical extrapolation from present to past. Ultimately, however, his arguments on the nature and scale of classical land use are sloppy, failing to draw a clear distinction between what was ecologically or technologically possible, what would have been economically viable or 'rational' and what may be implied by scarce historical and archaeological evidence. The unorthodox claim that classical Athens was basically self-sufficient in staple grains is probably correct, but hardly substantiated. Even more unjustified is the assertion that the steep rise in human population during the first millennium BC was made possible by significant improvements in agriculture. Sallares justly criticizes the traditional emphasis on improvements in agricultural technology, but his claim that the displacement of glume wheats by free-threshing wheats reflects the improved productivity of the latter is quite unsubstantiated. Even if classical archaeologists bothered to collect charred crop remains, grain size is affected by interannual and local variation in growing conditions, by crop-cleaning methods and by charring regime, and is only indirectly related to area yield. Given that naked wheats had remained in cultivation on a small scale for millennia throughout Europe, their ultimate displacement of the more storable but troublesome glume wheats surely reflects a shift of emphasis in risk-buffering behaviour from local self-sufficiency and storage to regional integration and exchange. Furthermore, the assumption that classical civilization was underpinned by surplus resulting from higher-yielding crops reflects the same misplaced faith in progress which Sallares effectively condemns in earlier works. In fact, in an area of high agricultural risk such as southern Greece, a 'normal surplus' will have been an inevitable by-product of any viable farming economy and an investigation of changes in access to land, labour and produce would probably have been far more illuminating.

Despite these criticisms, *The Ecology of the Ancient Greek World* is informative and thought-provoking. Sallares' inability to leave any intellectual stone unturned does nothing for the clarity of his argument, but it also makes him eminently readable and his evident enthusiasm for history and ecology is very engaging. This unusual book, with its blend of references to scientific papers from the first millennium BC and 1980s AD, will interest a wide readership. For ancient historians, to whom it is primarily addressed, it should be compulsory reading and those not yet beyond redemption will learn much from the experience. □

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