REVIEWS

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The Shape of Things that Come.

Sexual Selection and Animal Genitalia.—William G. Eberhard. 1985. Harvard University Press. xii + 244 pp. $25.00.

It is fashionable, these days, to point out that the agenda and interests of science are often influenced by its cultural milieu. Whether true or not, it was difficult to read this book without noting a correlation between the way humans view their own sex roles and gender differences, and the way they apparently view those of other species. For example, our culture made women passive and put them on pedestals for centuries, and the biology of that era duly explained genitalia as male keys evolved to open female locks—sex as ritual mystery. More recently, Simone de Beauvoir, Betty Freidan, and other writers initiated our current era of confusion by suggesting that gender roles and differences resulted from a struggle for power—sex as war. Some 10 years later, R. D. Alexander and others suggest that genitalia are the result of an arms race, a "mechanical conflict of interest." Males have "snippers, levers, and syringes" (Lloyd, 1979, cited in Eberhard), and females build labyrinthine armored catacombs to defend themselves. Wing (1982, cited in Eberhard) bleakly suggests that male genitalia have evolved to damage female genitalia so that they can't copulate with other males. However, the influence of culture seems to go only one way. Although biologists have offered pleiotropy as a kind of nihilistic explanation of genitalic diversity, their fellow humans apparently remain uninterested in so apathetic an explanation.

Against, or perhaps because of, this diverse background, Eberhard proposes a new explanation: the diversity of male genitalic morphology is an epiphenomenon of female choice for stimulation or fit during copulation, because mothers want their sons to be the best possible stimulators. One wonders if this is the feminist response?

Macroscopic implications aside, Eberhard thus initiates discussion of a subject about which taxonomists probably know most, and one which, as he points out, they have ignored. I found Eberhard's fundamental empirical claim the most interesting part of the book: for male genitalia to be such good "species" characters, during speciation male genitalia must evolve more rapidly and more divergently than any other part of the organism. All the arguments in the book vividly depend upon this generalization; how true is it? Eberhard clearly has a unique and encyclopaedic knowledge of the genitalia of animal phyla, and he compares acanthocephalans and primates with ease. His evidence is the primary alpha taxonomic literature, which he collates into dozens of well-referenced tables. The correlation (positive and negative) between species-specific male genitalia and the use of intromittent organs by males to inseminate females is overwhelming. I agree that it is, and that any fact so large and so all-encompassing should have been recognized long ago. That it has been missed for so long only adds to Eberhard's credit in discerning and describing it. A second fascinating insight, in retrospect also long overdue, is his three-part taxonomy of sex: copulation, insemination, and fertilization. He shows that, particularly from the female point of view, they are distinct and often uncoupled events. No doubt the distinctions will clarify much sociobiological debate.

Still, taxonomists must wonder if the reasons we use male genitalic characters to discriminate species are not more prosaic. Such characters are traditional (thus facilitating comparison with older work), they are simple to see (being extroverted), they are cheap

to examine (light microscopy suffices), they persist in museums (being morphology), and, most obviously, taxonomists, as visual creatures in museums, are well suited to perceive them. There is a big difference between characters that suffice to distinguish species to taxonomists, and characters that uniquely or most clearly distinguish species. Eberhard, I think, ultimately has to make the latter claim, but I am not sure that it will hold up as well as it does on first glance. Species of frogs, fireflies, grasshoppers, and microtine rodents were first recognized by features other than genitalia, and without doubt many taxa still go unrecognized because their unique features don't survive the transition to a museum specimen. In any case, Eberhard is perhaps not quite as careful as he needs to be on this point. From the ability of taxonomists "to find greater differences between related species in genitalia than in other structures," he infers that "relative to the other structures the genitalia have diverged rapidly." I'm not sure that follows, and I think most field biologists, ethologists, and molecular geneticists, who examine closely related species in detail, would agree.

Eberhard commendably makes his philosophical prejudices explicit. In particular, he announces that we should prefer a weaker explanation of the total phenomenon to a series of ad hoc explanations that each apply to limited number of cases. Male-male competition, for example, could explain genitalic evolution in damselflies (males displace the sperm left in females by previous copulations and thus compete directly in space, but not in time, for preferred insemination sites in the female). Eberhard rejects that hypothesis in part because it explains only these sorts of cases, and not the myriad others. This philosophical program, of course, is difficult to contain. How weak can the general argument get, and still be preferred over an argument derived from, for example, the natural history of a monophyletic taxon, thus constituting a unique explanation for the evolution of a unique genitalic morphology? A well-substantiated unique explanation for a unique event might be preferred to a weaker general explanation, because the former would naturally be more testable because more closely dependent on the facts of the case. Often the competing explanations are not exclusive, but when they are, how do we choose between generality and a better fit to the data?

Eberhard uses a falsificationist approach to evaluate the various competing hypotheses. He considers six hypotheses to explain male genitalic diversity (lock and key, species recognition, pleiotropy, mechanical conflict of interest, male-male competition, female choice) and devotes several chapters to their explication and test. He gives each hypothesis its due, evaluating its predictions, and the fit of the evidence to them. By the end of the book he has marshalled thirteen points that separately or together refute all hypotheses except that of female choice. For example, males of geographically isolated taxa have species-specific genitalia, which is not predicted by either of the species recognition hypotheses. Females, in general, do not have anti-clasper devices, and the species-specific morphology of the males does not seem well suited to manipulate females against their will, which the conflict of interest hypothesis would predict. Pleiotropy fails to explain why male, and not female, morphology should diversify, and also fails to explain why species-specificity in primary genitalia is lost when a taxon switches to the use of secondary male genitalia (which are almost always species-specific themselves). For various reasons only the hypothesis of female choice survives all tests. Although almost all the data Eberhard considers were gathered for other purposes, he is able to extract enough information to make his arguments convincing. To his credit, Eberhard also deduces a series of specific predictions from the female choice hypothesis, which should make first-hand tests straightforward.

Two additional topics raised in the book seem interesting in a cladistic context. One is that male genitalia are not usually homologous as genitalia. Genitalia is thus a term defined by function, and hence there can be no historically objective definition of the set. Eberhard includes any male structure that is inserted in the female or that holds

her near her gonopore. He is dissatisfied with so arbitrary a definition, chiefly because it excludes other parts of the male body that occasionally are modified for sexual purposes (antennae, legs, jaws, wings, eyes, heads, palps, tarsi, horns, gills, etc.). On the other hand, the female choice hypothesis predicts that sexual selection will not on any part of the phenotype affected by female choice, and clearly, many portions of the body have qualified. Because the book is fundamentally about convergence, and because convergence is usually about the result of selection, Eberhard might have been better off subsuming genitalia under a general class including any aspect of an organism's biology that has undergone sexual selection. He then could have investigated whether such features, once identified, were species-specific. Because his hypothesis basically invokes disparate evolutionary rates due to intense selection to explain species-specificity, it must predict that all sexually selected characters are species-specific, not just genitalia. As it was, he proceeded the other way around, and puts off the subject of what genitalia are until the end of the book. Once there, he does aptly connect his discussion to the evolution of sexually selected signals in general, but only on the last page. This definitional problem may also have caused him to omit an additional argument for his hypothesis. Convergent morphologies that are the result of natural selection generally look the same. However, despite so many instances of independent convergences (genitalia) over such a wide array of taxa, no male genitalia, at least that I am aware of, have converged to resemble each other strongly. One could argue that this is strong evidence that they evolve under sexual as opposed to natural selection.

Perhaps because the reader is likely to read the book with the commonplace notion of genitalia in mind, many unexplained aspects of genitalic evolution seem to go untreated. Within sets of homologous genitalia, for example, much morphological structure is conserved. I would have liked to have known why, after at least a half-million speciation events subjected to relentless, diversifying, intense, sexual selection in beetles, coleopterists still homologize the parts of male genitalia, and show that they are of use in inferring phylogeny. Eberhard may have explained why genitalia are different, but it makes me all the more curious as to why they are so alike.

That brings up a final point that I would like to see the author address—his view of speciation theory. One can well understand why he does not attempt to define the species category. Sooner or later, even ardent neo-Darwinists must accept that the ability to produce fertile offspring is a primitive trait, and thus, not being evidence of monophyly, has no place in a definition of any taxonomic category whatever. With that gone, much of the objectivity of the units that Eberhard wants to compare (he is interested only in intraspecific selection) disappear. If "species" are then the minimum sets of animals that share congruent synapomorphies, it is suddenly unclear how well that correlates with specific genitalic morphologies.

I hardly need add that the book is copiously illustrated, but it is also well-written, and interesting to read. I hope it is not only my cultural milieu that made me think so.—**Jonathan A. Coddington, Department of Entomology, National Museum of Natural History, Smithsonian Institution, Washington, DC 20560.**
