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MICROBIAL MUDDLES

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Source: BioScience, 53(10) : 1008-1013

Published By: American Institute of Biological Sciences

URL: https://doi.org/10.1641/0006-3568(2003)053[1008:MM]2.0.CO;2

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Searching for Scales in Fisheries

Hierarchical Perspectives on Marine Complexities: Searching for Systems in the Gulf of Maine. Spencer Apollonio. Columbia University Press, New York, 2002. 229 pp. $29.50 (ISBN 0231124899 paper).

The outlook for fisheries in many marine and freshwater ecosystems is grim. Human-induced changes to ecosystems and the growing demand of a global market have caused widespread reductions in fish populations, leading to dramatic closures and, in many places, the loss of a way of life for fishing communities. In closed fisheries, managers and fishers watch with trepidation to see whether fish stocks will recover. It is in this context that Spencer Apollonio, a marine ecologist and veteran of New England fisheries agencies and commissions, explores the notion that current conservation and management practices are failing and that better options exist.

As a resident of Maine with an avid interest in the ecology and nautical history of this region, Apollonio has chosen to write about his backyard—the Gulf of Maine, a unique geological and ecological component of the North Atlantic coast. This system has a long and complex relationship with the fishers that use it. Apollonio points out that in the 17th century this system was teeming with groundfish, such as Atlantic cod *(Gadus morhua),* and marine mammals, including whales and seals. Centuries of fishing and, in particular, the technological leaps of the 20th century have reduced these populations to a fraction of their previous abundance.

Although it might be argued that the populations within the Gulf of Maine have declined for lack of regulation and enforcement, I am sure that agencies have expended much effort to stem the tide of overfishing. Traditional fisheries management applied to this ecosystem and others has been practiced only for about a half-century, focusing on population dynamics, relying on deterministic models, and typically assuming that populations are in equilibrium with environmental and fishing effects. Although these management approaches are still taught in many fisheries programs, regularly applied by fisheries agencies, and even mandated by the federal government, they have been widely criticized from within the discipline and beyond. However, they are deeply engrained in fisheries science, primarily because of an adherence to tradition and, probably more typically, a lack of robust alternatives.

Apollonio believes that much deeper mechanisms, not captured by contemporary fisheries management, are at work. Simply reducing exploitation or closing the fishery to rebuild stocks will often fail, because the ecosystem and its resident populations have undergone fundamental structural and functional changes as a function of industrial fishing. Many natural resource managers suspect that this is true and endorse a switch to holistic ecosystem management to better predict fisheries responses and develop policies. Unfortunately, a clear definition of "ecosystem management" in this context is elusive.

I was delighted when Apollonio proposed an alternative to the traditional approaches and provided a framework by which ecosystem management of exploited fisheries can be formally defined and adopted in decisionmaking. He invokes hierarchy theory, a concept currently in vogue in the ecological sciences. In the mid-20th century, when quantitative techniques were being folded into fisheries management, concepts such as hierarchy theory were being developed in other disciplines to address growing concerns about reductionism in science. Complex biological systems, including ecological systems, are typically hierarchical in nature, with higher levels constraining and ordering lower ones. Ecosystems have emergent properties that are often simpler to describe and understand than their component parts. Hence, ecologists may use a hierarchical approach to find appropriate and manageable organizational scales for predicting how ecosystems work.

This theory, if found to be sufficiently general in its application, has compelling implications for the management of the Gulf of Maine and other complex ecosystems. After introducing hierarchical concepts early in the book, Apollonio describes the Gulf of Maine geology and ecology in great detail, promising to show later how hierarchy theory may be used to simplify and order our grasp of this complex system. I appreciated this primer, finding it critical for the lessons to follow. Relative to other comparable coastal systems, the Gulf of Maine ecosystem is a geologic youngster. Invoking succession spanning the centuries since the last glaciation, Apollonio argues that this ecosystem may have had less time to accumulate species with complex behavior and life histories and thus contains relatively few high-level hierarchical components to constrain and stabilize it. He believes that these constraining factors are stable, long-lived species that integrate the natural variability within ecosystems and typically are highly sought by humans (e.g., marine mammals, sharks, cod). In other words, the geologically young Gulf of Maine is susceptible to the loss of important higher hierarchical levels. And the decline of the historically abundant marine mammals that dominated the ecosystem in centuries past likely compromises the Gulf of Maine's ecological stability and inherent predictability.

These are powerful ideas that, in my view, have much validity. Apollonio is suggesting that ecosystems have emergent characteristics that may be categorized and scaled to guide policy: It is important to protect those species that constrain and therefore stabilize the ecosystem. Rather than developing ever

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more complex, mechanistic models, managers may arrive at strategies by understanding the relatively simple hierarchical properties of ecosystems, without the requisite bother of teasing apart complex, messy internal dynamics. From an economic standpoint, this is highly desirable and may be used to streamline the decisionmaking process by rapidly finding the relevant management scale.

The catch lies in the biological sophistication with which researchers and resource managers must approach ecosystems and their component parts. Apollonio spends a good portion of the book describing the complexity of the Gulf of Maine before applying hierarchical concepts. How far might he have gone without this depth of understanding? I am sure he is not implying that mechanistic research should be halted in exploited ecosystems. In fact, the hierarchical approach seems to be a fine way of directing limited research dollars toward the most relevant questions in exploited systems. But I do think that the allure of hierarchy theory may mislead policymakers into believing that relatively simple assumptions about the role of species in ecosystems can be substituted for more costly research efforts. A balance between mechanistic and holistic approaches must be struck, lest the pendulum swing too far toward broad speculation about how natural systems work.

In my attempts to train students in fisheries science, I continually strive for new approaches that allow these future generations of researchers and managers to engage the mounting challenges posed by the world's commercial and recreational fisheries. Although Apollonio provides many clear examples from an ecosystem perspective, his few attempts to demonstrate parallel applications of hierarchy theory to the human component of fisheries and thus provide guidance for resource managers are less developed and less compelling. Managers and conservationists are a practical lot, often beleaguered by too many responsibilities and a daunting mandate. Although the ideas encompassed by hierarchy theory are enticing, tangible tools are desperately needed. At the end of the book, Apollonio acknowledges this shortcoming, recognizing that the concepts set forth are simply the raw material from which specific tools have yet to be crafted. My hope is that this can be achieved before time runs out.

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SIX LEGS OF ONE, HALF A DOZEN OF THE OTHER

Physiological Systems in Insects. Marc J. Klowden. Academic Press, San Diego, 2002. 415 pp., illus. $59.95 (ISBN 0124162649 paper).

Insect Physiology and Biochemistry. James L. Nation. CRC Press, Boca Raton, FL, 2002. 485 pp., illus. $109.95 (ISBN 0849311810 cloth).

The two new textbooks in insect physiology by Marc Klowden and James Nation are welcome and timely contributions to this important field. The dominant book in insect physiology during most of the 20th century was *The Principles of Insect Physiology,* by the late, great Sir Vincent Wigglesworth. It has been a long time since the seventh edition came out in 1972, but the charm of the prose and the breadth and depth of the scholarship made Wigglesworth's book a tough act to follow. Although well-written and authoritative multivolume series in insect physiology appeared in 1974 (edited by Rockstein, reprinted in 1984) and 1985 (edited by Kerkut and Gilbert), instructors have been in need of a single-volume textbook in this area that would have the uniformity that results from a single author and a length appropriate for a single-semester course. Chapman (1998) provides an extremely valuable reference used in university courses across the country, but his book is almost twice as long as those of Klowden and Nation; it works particularly well as a textbook for two-semester courses that cover both insect morphology and physiology.

Both Klowden's and Nation's books are intended to be used as textbooks and were written by faculty members who teach insect physiology. Marc J. Klowden is a professor at the University of Idaho who teaches insect physiology as a cooperative course between the University of Idaho and Washington State University. James L. Nation is a professor at the University of Florida who teaches insect physiology and biochemistry. Klowden notes in the preface that his textbook is intended for teaching students who use insects in their research and therefore need to understand how insects function, but who may not intend to become insect physiologists themselves. Similarly, Nation's intended audience consists of graduate students in entomology or nematology, who may have primary interests in biocontrol, toxicology, or integrated pest management rather than in physiology or biochemistry. This tough audience—students who need the material but may not be predisposed toward it—has presumably shaped both books in a positive way. Both authors do an outstanding job of making the relevance of the information clear. Both books are enjoyable to read and are jargon free while introducing readers to the necessary technical terms (highlighted in bold in both books, as in "each ovary consists of one to many **ovarioles**").

Some aspects of the books' overall format are similar. Both books have extensive references at the end of each chapter that include older references but concentrate on those that are most recent (in the last 15 years). Neither has an overall list of references at the end of the book. Both have good indexes, and Klowden has a glossary. Both are well illustrated.

There are differences in style between the two textbooks that may influence the choice of which to use for a course. Nation's book is numerically subdivided

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(e.g., chapter 5 is "Hormones and Development," section 5.5 is "The Prothoracic Glands and Ecdysteroids," and subsection 5.5.1 is "Biosynthesis of Ecdysone"), which makes it easier to find information but slightly more difficult to read straight through. Nation's book is longer, has more factual information, and is somewhat more inclined to detail. For example, in discussion of the composition of the hemolymph, Nation supplies four different recipes for insect saline (pp. 320–321). On the topic of sensory receptors, Nation supplies a table that lists the nine different types of sensilla (table 10.1; sensilla trichoidea, sensilla chaetica, etc.).

Whether more details help to reinforce concepts or distract the reader from them is a subjective call that partially dictates textbook preferences; both faculty members and students differ in whether they are more inductive or deductive learners. In different classes there will be different expectations of what level of detail is appropriate or relevant, and therefore either Klowden or Nation could be an excellent choice, depending on the circumstances. Klowden's book does a remarkable job of identifying the major important physiological principles in a compact but not superficial way, and it would probably be easier for advanced undergraduate students to read it and absorb the material. Either book could work very well at the graduate level.

With regard to differences in content, both books provide excellent coverage of the major physiological functions of insects, although there are small differences in some topics. Nation has an appendix on the relationships between the major groups of arthropods, while Klowden does not cover that topic. Nation's appendix also provides a quick overview of the insect body plan, while Klowden provides that introductory material in the relevant chapters (e.g., mouthparts are covered in the chapter that deals with feeding and metabolism). Klowden covers topics in thermal biology not covered by Nation, such as thermoregulation (countercurrent heat exchange, shivering) and cold hardiness (freeze tolerance) in the circulatory system chapter. Nation spends a greater proportion of his book on the topics of nutrition, digestion, neurobiology, and sensory systems.

So which book should you choose for your course in insect physiology? Pick either to use in your classroom—you can't go wrong.

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ETHICAL ENVIRONMENTAL FUTURES

Searching for Sustainability: Interdisciplinary Essays in the Philosophy of Conservation Biology. Bryan G. Norton. Cambridge University Press, New York, 2003. 554 pp., illus. $30.00 (ISBN 052100778X paper).

Searching for Sustainability: Interdisciplinary Essays in the Philosophy of Conservation Biology examines the quest for sustainability from a variety of disciplinary viewpoints beyond conservation biology. It is a pluralistic and problem-oriented book. Most important, the author—who is a professor of philosophy, science, and technology at the School of Public Policy, Georgia Institute of Technology—emphasizes environmental ethics in a transdisciplinary framework.

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The author's two complementary, though not easily integrated, goals are (1) to understand sustainability as a policy goal independent of multidisciplinary perspective and (2) to show how philosophical discourse and argumentation, carried on within scientific and management contexts, can result in new insights and how changes in philosophical views have been achieved.

The use of the phrase "searching for sustainability" in the title is an excellent reminder that, at present, humankind has only an aspiration to live sustainably. Not only is the question of how to attain sustainability perplexing, but, even if this desirable state is achieved, several generations will be needed to confirm that sustainability has been reached. The author affirms that the most effective conservation ethic represents a concern that humankind leave a habitable planet for posterity. Most discussions on sustainability, however, focus on using technology to alter natural systems so as to serve humankind's unexamined demands. Suggestions rarely include altering human society's "needs" in order to develop a harmonious relationship with natural systems.

The book is composed of 27 papers, divided by category into six main sections. Despite this compartmentalization, transition from one concept to another is remarkably smooth. A number of authors (e.g., Thoreau) appear frequently in various sections; however, redundancy is remarkably low, and use of an author's writings more than once serves to link the various components.

Without meaning to criticize the sequencing of the components of the book, I suggest that paper 10 in section III be read first. This analysis of the Brundtland Report, *Our Common Future* (WCED 1987)—arguably the most influential work on sustainable development—will be beneficial to any reader not familiar with the literature on sustainability and its complexities. Along the same lines, paper 26 should be read by anyone with even a modest interest in sustainability; it states the issues concisely and objectively. Also intriguing is Thoreau's portrait of materialistic consumerism as an immature developmental stage of the person (p. 32).

Even though I had some initial reservations on this pivotal issue, I am inclined to agree with Norton's statement in paper 11: "It would be an ideal outcome if the various disciplines—economics, ecology, philosophy, environmental health, and environmental chemistry, to mention some prominent ones—could speak about social values in a common evaluational vernacular." Norton believes that a clearly articulable difference between economists and most environmentalists exists, and also between economists and members of other disciplines, because of the difference in perspective of the array of disciplines. Environmentalists, he argues, are moralists; they believe that human beings have an obligation to protect the environment for its own sake. Economists, on the other hand, believe no such obligations exist.

A major deficiency of the book is its failure to emphasize humankind's dependence on the planet's ecological life support system, which provides such services as maintaining the atmospheric gas balance so that it benefits humans. Norton discusses ecosystem services, but he places little emphasis on their aggregate function as a life support system. The subsection on biodiversity and resources would have provided a superb opportunity to cover this topic. I would like to have seen the author's evaluation of such volumes as *The Ecology of Commerce* (Hawken 1993) and *Natural Capitalism* (Hawken et al. 1999). Industrial ecology (e.g., Tibbs's article "Industrial Ecology" [1992], Socolow and colleagues' *Industrial Ecology and Global Change* [1994]) also deserved attention, since it advocates the hybridization of two systems often viewed as polar opposites.

I am happy to add this book to my library, and I expect to use it frequently. The notes are very helpful and the references exceptionally broad. The goal of providing principles that combine individual experience and a participatory ecosystem process is admirable. Finally, the book is a "good read": Even though the scope of this volume is great, it is remarkably easy to read and refreshingly free of disciplinary jargon. I recommend it to anyone wishing to gain a multidisciplinary perspective on the problem of sustainable development and its possible solutions.

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MICROBIAL MUDDLES

Acquiring Genomes: A Theory of the Origins of Species. Lynn Margulis and Dorion Sagan. Basic Books, New York, 2002. 240 pp., illus. $28.00 (ISBN 0465043917 cloth).

Over 40 years ago DNA was discovered in chloroplasts and mitochondria. This led Hans Ris, a former supervisor of Lynn Margulis, to revive the 1905 theory of the Russian Konstantin Mereschkowsky that chloroplasts originated by enslavement of formerly free-living cyanobacteria by a nonphotosynthetic protozoan host. Mereschkowsky invented the term *symbiogenesis* for such permanent mergers of phylogenetically disparate organisms into a single chimeric one. His idea of chloroplast symbio-

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genesis and Ivan Wallin's later advocacy of a similar bacterial origin of mitochondria are accepted by all serious scientists, making mainstream the idea that symbiogenesis occasionally plays a key role in evolution.

When Ris, an excellent electron microscopist, revived the symbiogenetic theory, the close resemblance in membrane organization of chloroplasts and cyanobacteria impressed him as much as that of their DNA. He realized that symbiogenesis was a way of acquiring not only foreign genomes but also foreign membranes. My own contributions to the understanding of symbiogenesis over the past 23 years have emphasized the importance of both genomes and novel membranes, which I call genetic membranes, because, like DNA, they never arise de novo and they do have key genetic roles.

Lynn Margulis seems never to have appreciated or accurately discussed the central roles of membranes in symbiogenesis in her numerous popular writings on the subject. Now a Distinguished Professor at the University of Massachusetts–Amherst, she and her science journalist son Dorion Sagan have written another popular book overemphasizing genome acquisition and ignoring that of membranes. The authors incorrectly claim that only characters encoded by genes can be transmitted transgenerationally, which ignores membrane heredity. Their book purports to be a new theory of the origin of species. The authors rightly stress that the biological species concept does not apply to bacteria, but they wrongly call the concept new—this was recognized explicitly all along by its originator, Ernst Mayr, who wrote a tactful foreword to *Acquiring Genomes,* gently indicating that their central thesis about eukaryote speciation is overstated. I consider it totally mistaken. Mayr notes that average readers will learn much they did not know before about the fascination of microbes, a fascination I share with the authors. Sadly, however, they will also be misled about the role of symbiogenesis in evolution and what is now understood about the mechanisms and history of cell evolution.

The authors assert that all eukaryotes (nucleated organisms, e.g., protozoa, plants, animals, fungi) form new species only by symbiogenesis and that random mutation is relatively unimportant. They even present a new definition of species that necessarily would make their claim true. They say that species are different only if they are chimeras of a different set of symbiogenetic partners. As I interpret symbiogenesis and the established picture of cell evolution, this would mean that all animals belong to the same species—the same species as all fungi and most nonphotosynthetic protozoa—because their cells were formed by the symbiogenetic merger of the same protoeukaryote host and α-proteobacterium to form the first true eukaryote, no symbiogenesis having occurred in them subsequently. Plants belong to a different species because they also enslaved a cyanobacterium, but are all just one species, according to the authors' curious definition.

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Apart from the origins of mitochondria and chloroplasts, symbiogenesis has occurred on only about four other occasions in the history of life, none even mentioned by the authors. The two most important are (1) the enslavement of a red alga to make chromalveolates (e.g., brown seaweeds, diatoms, dinoflagellates, a host of other chromophyte algae, malaria parasites and their sporozoan relatives, and pseudofungi); and (2) the enslavement of a green alga to form euglenoid and chlorarachnean algae (Cavalier-Smith 2003). The other, more trivial symbiogenetic events were replacements by a few dinoflagellates of their own chloroplasts by foreign ones. The authors devote only about two sentences to the symbiogenetic origins of mitochondria and chloroplasts, all the book has to offer on the well-established cases of symbiogenesis.

What constitutes the rest of the book? Four things: repeated diatribes against evolutionary biologists and the established idea that mutation is fundamentally important in evolution; readable descriptions for the layman of many fascinating cases of symbiosis involving microbes; one-sided summaries of Margulis's current idiosyncratic view of cell evolution, which ignores most phylogenetic evidence and anyone else's criticisms or sounder interpretations; and peremptory attacks on many standard biological concepts (e.g., genes, competition, mutualism). The authors imply that 10 million to 30 million species of eukaryotes evolved by symbiogenesis, yet evidence exists for only about six symbiogenetic events in the whole history of life.

They do this by ignoring the careful distinction I made in 1985 (Cavalier-Smith and Lee 1985) between an obligate intracellular symbiont and a true organelle of symbiogenetic origin. I pointed out that integration of foreign genomes into the host nucleus can occur only after the host evolves novel, generalized protein-targeting machinery that can place many products of transferred genes back into the former symbiont. I used the presence or absence of such machinery—e.g., the protein-import machinery of mitochondria and chloroplasts—to establish a clear-cut boundary between a symbiont that lacks it and a symbiogenetic organelle that has it. This provides objective demarcation between symbiosis, which is very common, and symbiogenesis, which is exceedingly rare. Nobody disputes that intracellular symbionts are widespread in eukaryotes and often of great physiological and evolutionary importance, as are other types of symbiosis. But acquiring a symbiont is not symbiogenesis. It is simply symbiosis. The authors never so much as mention the central role of novel protein-targeting in symbiogenesis.

They vaguely define *symbiogenesis* as "symbiosis that leads to evolutionary change." Probably all symbiosis leads to evolutionary change. The authors' failure to distinguish symbiogenesis from symbiosis ignores the fact that Mereschkowsky's symbiogenesis meant permanent merger of two organisms into one. Lichens comprise two separate organisms; the fungus temporarily enslaves the alga/cyanobacterium—neither cells nor genomes are merged. The same is true of all the other examples Margulis and Sagan cite, despite their frequent, unsubstantiated claims to the contrary. Consider two examples of tendentious misrepresentation: the sea slugs that harbor chloroplasts temporarily for photosynthesis or cnidarian nematocysts for defense. The former lack even the nuclear genomes of the algae from which they came and have to be replaced periodically. Nematocysts are organelles without genomes, not cells (contrary to the authors' assertion); they also lack the nucleus and the rest of the cell from which they were stolen (Greenwood and Mariscal 1984). Yet the authors say the slugs "flaunt their stolen genomes" even though the slugs have no stolen genomes to flaunt! Algal or cnidarian genomes are not integrated into the slug.

The authors assert that symbionts "often fuse their genomes" and "many such fusions have been documented in all five kingdoms of life" (p. 90). This is false. The latter claim is peculiar, as the authors spend much space arguing that bacteria never undergo cellular symbiogenesis (there is one putative case, not mentioned). At present, there is clear evidence for fusion of cellular genomes for only one of their five kingdoms, the so-called Protoctista, which no serious biologists accept as a sensible group, because it is undoubtedly polyphyletic. In the next paragraph, the authors imply, without actually asserting it, that corals, giant clams, tubeworms, termites, and cows are all examples of such genome fusion. Again, these are simply symbioses. By juxtaposing wild claims with irrelevant examples that fail to support them but nonetheless lose the reader in fascinating symbiotic detail—chattily written in the fashionable mode of pop-science journalism—the authors may make the nonexpert think there is something in their central thesis, despite its lack of empirical evidence or rationally argued theory. They repeatedly confuse a symbiotic consortium of different species of organisms with a single organism by misusing the term "individual" for it.

The authors' viewpoint is illogical and superficial. In one place they argue that bacteria have no species (reasonable), in another that they constitute only one species (unreasonable). That would make cyanobacteria and proteobacteria the same species and talking about the separate symbiogenetic origin of mitochondria and chloroplasts problematic. If there were only one bacterial species, how could you make 10 million to 30 million different eukaryote species merely by mixing and matching that one species in the absence of mutation? Even if we were to equate symbiogenesis with the acquisition of a novel symbiont, as the authors often seem to do, there would be immensely fewer such acquisitions than recognized morphological species. Except for the six established cases of symbiogenesis, all differences between eukaryotic species or bacterial strains have arisen by mutation, plus occasional lateral transfer of individual genes or small gene clusters, not by the symbiogenetic merger of genomes. Mutation is the greatest innovator by far. Even lateral gene transfer is less innovative and less frequent than widely supposed. Unsurprisingly, the authors uncritically repeat early claims that the human genome has laterally transferred genes of bacterial origin, though that idea has

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been refuted by W. Ford Doolittle and others (Andersson et al. 2001).

The chapter on eukaryogenesis adopts as true, without acknowledgment, my 1983 theory (Cavalier-Smith 1983a, 1983b) that the amitochondrial Archamoebae were the first eukaryotes, which I gave up over five years ago because it is thoroughly refuted by phylogenetic evidence that the authors ignore (Roger 1999). Their so-called phylum Archaeprotista is polyphyletic: Archamoebae and metamonad flagellates independently lost mitochondria and are no closer phylogenetically than are animals and plants. They ignore compelling evidence that the first eukaryote was aerobic and had mitochondria. Instead, they espouse the unwarranted theory of a second symbiogenesis prior to the origin of mitochondria and link it to Margulis's long-standing, but long-refuted, idea of the symbiogenetic origin of cilia from spirochaetes.

Some minor irritations: Charles Darwin did not "consistently fail to credit" his grandfather; it is untrue that ctenophores have "stinging cells"; the "40-volume" work on 50 phyla of animals, published in 1940 by "Libby" [properly *Libbie*] Hyman actually had only six volumes (the first recognised only 20 nonprotozoan animal phyla, and other volumes were published decades later); and statements about Cnidaria or Coelenterata are garbled.

Acquiring Genomes is an impressively undiscriminating collage of interesting fact, occasional error, sloppy reasoning, didactic pop biology, and sensible and stupid ideas (among which are the suggestions that nematocysts evolved from microsporidia and that animal larvae evolve by hybridization between phyla). Overall, this book is too confused to recommend to other biologists or even to general readers, for whom it seems intended.

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