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Reviews

Evolution's witness: How eyes evolved by I R Schwab; Oxford University Press, 2012, 328 pages, £45.00 cloth (US $75.00) ISBN 9780195369748

Evolution has become a central motif and a powerful explanatory tool throughout vision science. Increasingly, over the last 20 years or so, researchers who study low-level and high-level systems in the visual stream have framed their analyses in an adaptive context. However, the evolution of eyes — and especially of visual systems—is at best only partially understood, and our understanding of how eyes evolved has itself undergone revision in light of new evidence. So Ivan Schwab's landmark new book, *Evolution's Witness: How Eyes Evolved*, which charts the development of eyes in all major taxa, comes at a propitious time.

The book uses the conceit of the eye as a visual "witness" to tell the story of how different life forms developed their respective light-sensitive organs. Schwab traces the arc of eye evolution as it is instantiated in progressively more complex creatures over geologic time. The story is told through fossil evidence where available, but mostly relies on examinations of extant descendents of ancient life forms, such as the tuatara or limulus, though Schwab helpfully reminds the reader that modern descendents have evolved to some extent over time as well. The book focuses on basal groups as well as oddballs within a given clade possessing particularly bizarre or elaborated eyes, such as the well-known four-eyed anableps and the less famous flyingfish, which has a unique "three-windowed" cornea that may promote visual functions in and out of water.

Schwab helpfully defines what he means by eye early on, calling it a "structure that can compare the amount of light coming from different directions" (page xvi), though he begins his story with simpler light-detecting structures, which he suggests also serve as a kind of visual witness. This approach is illuminating since he argues that early metazoan eyes may have formed through cooptation of simpler light-detecting entities in protists.

Chapters are delineated into periods of geologic time, and are helpfully color-coded according to a geologic timeline on the inside cover of the book. Schwab's writing is clear, powerful, and at times playful, as when he refers to the "prebiotic bouillabaisse" (page 3) or calls eukaryotes "nucleated kleptomaniacs" (page 12). Schwab also maintains a nice blog for the book (http://www.evolutionswitness.com), which reports on emerging findings related to some of the eye types discussed in the book.

The book presents a highly engaging treatment of comparative anatomy to demonstrate historical variation, and it vividly situates anatomy and physiology within ecology and function. One discovers that fish and other sea creatures in particular show fascinating influences of ecology. For example, whereas ray-finned fish are emmetropic for near vision, sharks are emmetropic for far vision, which accords with sharks' niche as long-distance hunters. We learn also that billed fish such as marlin have biochemical "heaters" in their huge extraocular muscles, which warm the retina when the fish is in deep, near-freezing water. This warming makes visual neurons function more efficiently, allowing these fish to be highly effective visually guided predators at greater depths.

One of the book's main themes centers on the genetic toolkit required for building organs that see. By tracing the rise of metazoa, chordata, and the like, Schwab paints an original and vivid picture of the eye's genetic blueprint. For example, he notes that *Trichoplax adhaerens*, a very simple metazoan with no eyes, has an incomplete version of Pax6, a gene which is critical to eye formation in animals. Cnidarians, which are somewhat more elaborated descendents of the earliest metazoans, have a more complete version of the same gene. Schwab shows, in lucid language, the importance of this gene—both for eyes and other fundamental structures—and its complex interactions with other genes. One is struck by the highly detailed understanding of eye evolution that is now possible (and so ably described by Schwab) thanks to advances in genetics. It is particularly remarkable how much new knowledge has been added since Gordon Walls' 1942 landmark, *The Vertebrate Eye and Its Adaptive Radiations*, which was itself a major advance in the systematic understanding of the evolution of vision.

Evolution's Witness can serve a variety of uses. For the scholar of vision, it is a comprehensive reference but also a source of inspiration and ideas for new ways to study myriad aspects of vision.

For the instructor, it would function well as a textbook in a seminar, since it is laid out in a didactic and accessible way, with clear and engaging writing. With its sumptuous illustration, it would make a great coffee-table book for anyone with an interest in biology. The book is also an implicit riposte to the fallacy that eyes are too complex to have evolved by natural selection, so it will also be useful for those engaged in countering creationist agendas.

The book has helpful appendices on detailed anatomical matters that are discussed at many points in the book. It might have made sense to begin the book with this material as a way to prepare the reader. I think Schwab's telling of the evolutionary history is compelling enough that the typical reader could be convinced to wade through some technical bits to get to the good stuff. Moreover, to grasp the profundity of the historical arc, one requires a fairly specialized understanding of anatomy and its terms.

Any other shortcomings are also minor. Lineages and clades can at times be difficult to keep straight; so a cladogram at the beginning or end of each chapter, or a perhaps large fold-out diagram in the appendix, might have been helpful. Also, a decision was clearly made not to weigh down the text with in-line references (a bibliography for each chapter is found at the end of the book). This makes it somewhat more difficult for specialists to track down sources for some findings. However, this choice does facilitate that rare joy of reading a scholarly text purely out of pleasure. An ambitious book such as this one must involve tradeoffs in presentation, and Schwab's judicious choices have in the end produced a work that Russell Fernald's foreword rightly predicts "will be hard to put down."

While *Evolution's Witness* may spur a wealth of new investigations of eye evolution, one can hope that this book also serves as a foundation for a grander project to organize and map the evolution not just of eyes but of entire visual systems. Indeed, the presence of anatomical components in the eye does not necessarily mean the brain can exploit their outputs for perception. For example, having four cone classes may be beneficial for perception in birds, but it does not seem to give much advantage for humans with anomalous trichromacy, perhaps because upstream neural machinery in humans cannot make use of this information. Moreover, different species may process signals arising from homologous eye components in a variety of ways. The challenges of tracing the history of visual systems are similar to those faced in the study of eyes: neither the brain nor the vertebrate eye fossilizes. Inference in comparative neurology is useful, but less is known about the diversity of visual systems than of eyes at present. Schwab's outstanding use of evidence from "the geography of the fossil record, slender glimpses of likely scenarios, and now, by DNA sequence comparisons" (page xi) serves as a model that one can hope will inspire a systematic project to map visual system evolution (by some brave soul!).

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