

Quirks of Human Anatomy: An Evo-Devo Look at the Human Body. By Lewis I. Held, Jr. 2009. Cambridge University Press.

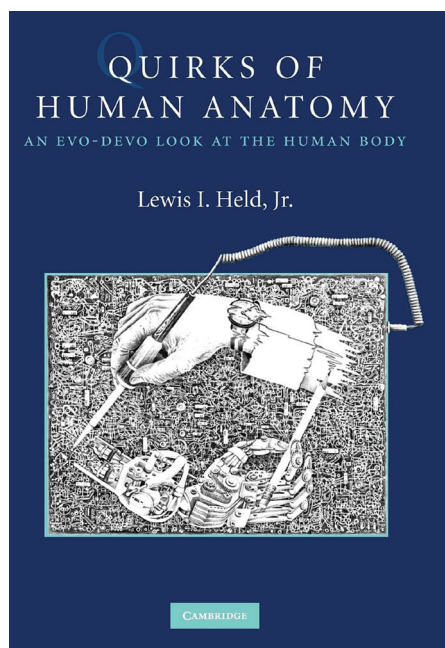
How the Snake Lost Its Legs: Curious Tales from the Frontier of Evo-Devo. By Lewis I. Held, Jr. 2014. Cambridge University Press.

Deep Homology? Uncanny Similarities of Humans and Flies Uncovered by Evo-Devo. By Lewis I. Held, Jr. 2017. Cambridge University Press.

Animal Anomalies: What Abnormal Anatomies Reveal about Normal Development. By Lewis I. Held, Jr. 2021. Cambridge University Press.

I first ran into Lewis I. Held, Jr., associate professor of developmental genetics at Texas Tech, when *Quirks of Human Anatomy: An Evo-Devo Look at the Human Body* appeared during my last few years of classroom teaching. For a couple of decades, I had taken my tenth graders through a seven-week unit on human development, just before we studied the Darwinian revolution, followed by genetics to close out the year. We tracked the first seven weeks of development in real time from fertilization on the first day of the term – talking about all aspects of reproductive anatomy, egg development, and meiosis – then each day marking the new anatomy, location, and size of the embryo from its first mitosis through the differentiation of cell types and tissues and the development of the major body systems. This was primarily old-fashioned descriptive embryology, but I was always on the lookout for new ways to help kids raise questions about how cells diversify which would lead into deeper questions about evolution and genetics. New insights were revolutionizing how all these structures and processes could be understood, under the new heading of “evo-devo,” evolutionary developmental biology, introduced in the early 1990s.

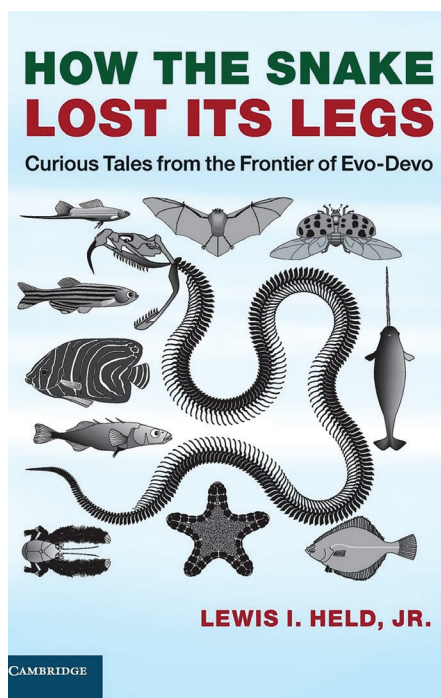
Suddenly here in my hands was *Quirks of Human Anatomy*, highlighting human developmental anatomy from the point of view of this new knowledge of the interaction of genes and the environment, with all the connections to evolution of other animals laid out for further study. The book's illustrations were stunning, clear, and detailed; the text was somehow conversational, entertaining, and challenging. The citations were organized beautifully and simply – a long alphabetic list in the back of the book, with each reference numbered in sequence, so that all that was necessary in



the text was a bracketed number, from [1] (Aamodt and Wang, 2008, *Welcome to Your Brain: Why You Lose Your Car Keys but Never Forget How to Drive, and Other Puzzles of Everyday Life*) to [2924] (Zuzarte-Luis and Hurlle, 2005, Programmed cell death in the embryonic vertebrate limb, from *Seminars in Cell and Developmental Biology*). In this rich wonderland of references, I was delighted to find the great mathematician and writer Lewis Carroll, occupying [380], only two integers away from the great evo-devo exponent and science writer Sean B. Carroll, holding down [382] through [393]. I read and re-read passages from *Quirks of Human Anatomy* and sharpened up my introductions to evo-devo topics, in awe of what I began to realize must be Lewis I. Held's extraordinary, vast, organized teaching files.

What I didn't realize at the time was that Held was in the midst of an ambitious project he'd begun a few years earlier, publishing *Imaginal Discs: The Genetic and Cellular Logic of Pattern Formation* with Cambridge University Press in 2002. I've not read that volume, being far more qualified to understand vertebrate biology, but I now see the logic of what Held has been up to.

In 2014, he published *How the Snake Lost Its Legs: Curious Tales from the Frontier of Evo-Devo*, which is designed to be a smorgasbord of developmental phenomena with titles echoing Rudyard Kipling throughout. Five chapters deal with bilaterians, flies, butterflies, snakes, and cheetahs, each of them addressing a handful of interesting questions. Then his chapter 6, “An evo-devo bestiary,”



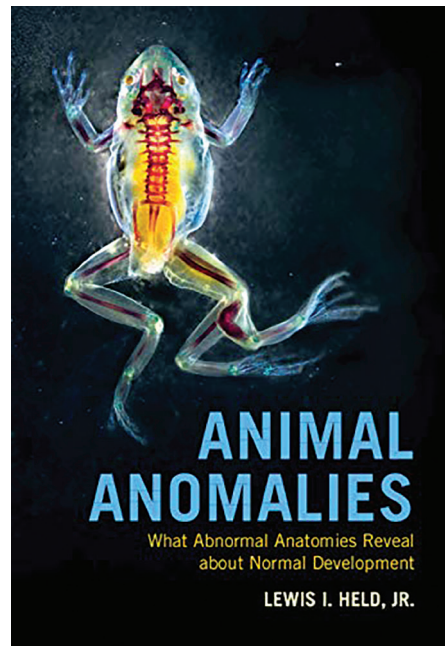
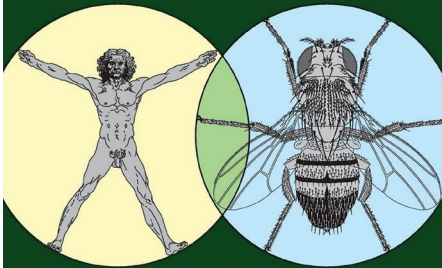
pulls out all the stops: 50 “How the X got its Z” stories, from “How the ant lost its wings” to “How the zebu got its dewlap.” (There are also two Why questions salted in this mix: “Why the centipede has odd segments?” and “Why the quoll kills its babies?”) Just like *Quirks of Human Anatomy*, this book is filled with superb diagrams and illustrations. There's a seven-page glossary of 36 important evo-devo terms. And 2526 citations!

Held wasn't done. His *Deep Homology? Uncanny Similarities of Humans and Flies Uncovered by Evo-Devo* was added to the series in 2017. This offering zeroes in on the astounding discoveries of developmental and genetic mechanisms in these two distantly related bilaterians. The organization of major topics is simple: body axes, nervous system, vision, touch and hearing, smell and taste, limbs, and heart. Under each heading, Held offers half a dozen summaries of research on important systems, and the similarities between humans and flies are usually jaw dropping. As his title implies with its question mark, however, he does not simply claim that there are deep, homologous, evolutionary roots in all these cases. A good example is *Pax6*, a gene that plays a significant role in eye development in arthropods, mammals, and mollusks! The term *deep homology* was apparently invented to establish a better vocabulary for discussing such phenomena. Held follows his *Pax6* section immediately with one that deals with counterexamples and arguments: creatures in which *Pax6* is *not* necessary for

DEEP HOMOLOGY?

Uncanny Similarities of Humans and Flies Uncovered by Evo-Devo

LEWIS I. HELD, JR.



eye development, roles that *Pax6* plays in the development of *other* structures (e.g., mouse nasal and pancreatic islet development), evidence that *Pax6* may be a more general inducer of *cell types* rather than “final” structures. As usual in Held’s universe, detailed, engaging, information-rich diagrams abound, accompanied by 2560 citations.

Rounding out this quartet, which by this point almost begins to feel like *Harry Potter and the Hopeful Monster*, in 2021 Held published *Animal Anomalies: What Abnormal Anatomies Reveal about Normal Development*. This most recent work is divided into sections on frogs, flies, dogs, and cats. Each of these offers two “GPs,” General Principles. GPs sound like this:

GP-1: Inductive signaling can enhance precision.

GP-5: Cells obey local rules with no global blueprint.

GP-21: Temperature acts as a toggle in some species.

A similarly numbered “Tangent” in turn accompanies each of these GPs, for example, Tangent 21, Turtle sex. Many more organisms than the section-heading four, including humans, are described and cited in each of these discussions.

As in all Held’s books, the diagrams are detailed and fascinating, but outstanding in *Animal Anomalies* are the photographs. We are all so used to the way the world “should” look, we can’t help but be stopped in our tracks when confronted with something so

unexpected as, for instance, an otherwise healthy frog who, mouth open, shows us its eyes looking out from the roof of its mouth. This, the first example of anomalous development in the book, demonstrates both the precision of the signaling cascade that results in the formation of complete eyes, and the error of orientation of that cascade that can initiate the process of retinal growth and eye development into the palatal skin rather than the upper epidermis. (Held points out that such frogs are so rare that no experimental program has yet been developed to probe this condition, and he’s unaware of even any offspring that might demonstrate its heritability.) *Animal Anomalies* is a breathtaking sweep of “things gone wrong,” that all illuminate some of the critical steps in normal animal development. *Animal Anomalies* is the lightweight in the References department, a measly 1441.

Having raved about the content and usefulness of these books, here’s a microcosm of Held’s approach and style from p. 128 of *Quirks*, complete with embedded references:

In all likelihood, therefore, our appendix finds itself in the same evolutionary purgatory as kiwi wings [915] and manatee fingernails [559, 1052]. Both of those outmoded structures are on their way to outright elimination [626], but they are not there yet [2802], and in the meantime they look ridiculous. The larger lesson is that *Homo sapiens*, like most species, is just one still frame in an epic movie of anatomical

ebb and flow that is playing itself out at a glacially slow pace on a geological timescale [268]... If *Hoxd12* is artificially turned on [where small and large intestines meet] then the appendix fails to grow out [2895]. Mutations of this sort might be responsible for ... cases of appendicular agenesis in humans [1767].

This passage, which concludes a brief section on the human appendix, is typical in its sharp focus and targeted references, yet casual language. Comparable “vestigial” structures found in kiwis and manatees introduce the passage, while the connection with contemporary evo-devo research closes it out. The third sentence is a sweeping view of evolution and the impermanence of species. The references are eclectic and, as a result, of great use to any teacher or professor in an introductory course. We are directed to, in turn: a major contemporary ornithology textbook; Darwin’s *On the Origin of Species*; a *National Geographic* article; a recent article in *Science*; an 1895 human anatomy classic; a recent article in *Evolution*; a recent article in *Development*; a recent article in the *Bombay Hospital Journal*.

It’s probably clear by now that I am a major fan of Lewis I. Held’s evo-devo books. In each I’ve encountered material that pushes me to, and sometimes over, the edge of my own understanding – but to me, that’s what education is all about. Reading them and using them in my classes, I felt privileged to benefit from the insights of a scholar seriously devoted to his own teaching. Indeed, his Texas Tech website notes that he has received several teaching awards in his career. I came across the following on page xi of his introduction to *Quirks of Human Evolution*:

The impetus for this project was seeing my father’s delight whenever I shared my tales of life’s curiosities, which I’ve collected ever since I fell in love with the idea of evolution in college. He was not a scientist, so I had to explain esoteric concepts in plain English...

I think that explains a lot.
All books in the series:



Mark Terry,
biology teacher (retired)
Northwest School
Seattle, WA
epatas@comcast.net



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Unionville High School, Kennett Square, PA
University Christian High School, Hickory, NC
Ursuline Academy, Dedham, MA
Vincennes University, Vincennes, IN
Visitation Academy - Saint Louis, St. Louis, MO
Westdale Secondary School, Hamilton, Ontario
Western Piedmont Community College, Morganton, NC
West Mifflin Area High School, West Mifflin, PA
Wheeling Park High School, Wheeling, WV
Worthington Christian High School, Worthington, OH

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