How the Snake Lost its Legs

Curious Tales from the Frontier of Evo-Devo

How did the zebra really get its stripes, and the giraffe its long neck? What is the science behind camel humps, leopard spots, and other animal oddities? Such questions have fascinated us for centuries, but the expanding field of evo-devo (evolutionary developmental biology) is now providing, for the first time, a wealth of insights and answers.

Taking inspiration from Kipling's *Just So Stories*, this book weaves emerging insights from evo-devo into a narrative that provides startling explanations for the origin and evolution of traits across the animal kingdom. The author's unique and engaging style makes this narrative both enlightening and entertaining, guiding students and researchers through even complex concepts and encouraging a fuller understanding of the latest developments in the field. The first five chapters cover the first bilaterally symmetric animals, flies, butterflies, snakes, and cheetahs. A final chapter surveys recent results about a menagerie of other animals.

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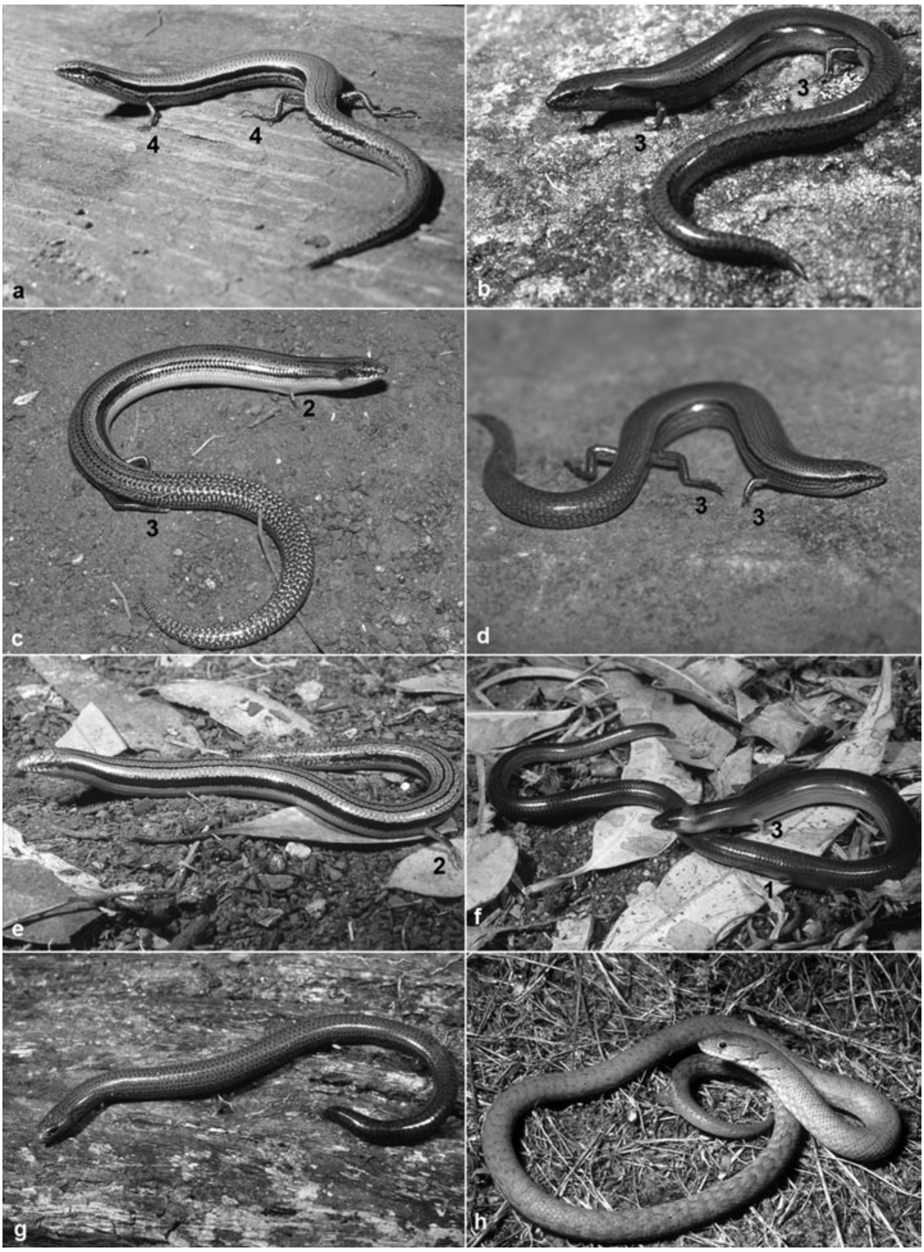

Frontispiece Legless or partially legless lizards, some of which resemble snakes to a remarkable extent. Numbers next to legs in each panel (and in parentheses in this legend) are the number of digits per foreleg or hindleg respectively if present. (a) *Lerista dorsalis* (4+4). (b) *Hemiergis decresiensis* (3+3). (c) *Lerista desertorum* (2+3). (d) *Lerista timida* (3+3). (e) *Lerista edwardsae* (0+2). (f) *Anomalopus verreauxii* (3+1). (g) *Ophioscincus truncatus* (0+0). (h) *Pygopus lepidopodus* (0+0). Leg loss is common among lizards and may have occurred for the same reason as leg loss in snakes. All photographs were taken by Mark Hutchinson, South Australia Museum, Adelaide, and are used by permission. *For color plate see color section*.

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Preface

The most famous accounts of animal origins in Western literature are those of Rudyard Kipling (1865–1936). His *Just So Stories* (1902) offered fabulous tales about how the leopard got its spots, how the elephant got its trunk, and so forth. It remains one of the most popular children's books of all time.

Fables certainly make good bedtime stories, but they are poor substitutes for real understanding. The foundations for modern biology were forged by Charles Darwin (1809–1882) in his *Origin of Species* (1859). Ever since, scientists have been amassing facts about how animal traits arose. Initially, the data came from fossils, embryos, and anatomy. Then, in the first half of the twentieth century, genetics merged with evolution to reveal the causes behind the changes [1420].

Development flirted with evolution for more than a century [46] before their union was consummated around the time of Stephen Jay Gould's *Ontogeny and Phylogeny* (1977) [828,2311]. Their scion was named "evo-devo" [1559]. Evo-devo initially relied on only a few model organisms [2088], including the fly, the worm, and the mouse. The genetic circuitry of these animals turned out to be surprisingly universal, despite their superficial differences [955].

In 1998 the first animal genome was sequenced – the nematode *Caenorhabditis elegans* [1] – followed in 2000 by flies and humans [81], and more genomes have been added at an increasing pace with each passing year [317]. As pieces of the evo-devo puzzle have come together, various authors have attempted to convey the "big picture" to the general public [1488]. Most notable are Sean Carroll's *Endless Forms Most Beautiful* [339] and his more advanced *From DNA to Diversity* [344]. Sean's books would make good primers for anyone who is not already well versed in genetics.

The genome of each species can be thought of as a kind of cookbook for concocting an adult anatomy, starting in most cases with a single fertilized egg. It is also a history book, because it retains remnants of recipes that were previously used by the organism's ancestors. If we could read all those recipes, then we could decipher development and retrace evolution. Decoding DNA beyond the protein level is hard, however, Because genes interact in complex ways [116].

How the Snake Lost its Legs was written at the behest of Martin Griffiths, Life Sciences Commissioning Editor at Cambridge University Press. Originally, he had in mind a book along the lines of Wallace Arthur's majestic *Evolution: A Developmental Approach* (2011) [75]. When I balked at the idea of writing a textbook per se, Martin relented, and we agreed on a more casual format where readers could sample whatever topics caught their fancy. My aim was to blend Darwin's rigor with Kipling's whimsy into a book that could amuse the darling child in all of us. The final product is hence an homage to both *Just So Stories* and *Origin of Species*. It celebrates animal oddities through facts rather than fables.

Truth can be stranger than fiction, and evo-devo is a case in point. Evo-devo defies our intuition in the same way that magicians amaze children by appearing to turn one thing into another.

Once upon a time, for example, snakes really did walk like lizards [2395], whales really did waddle like hippos [1790], and dolphins may have pranced like antelopes [2195], given how they swim as if they were galloping [505]. Relics of these marvels can be seen in their respective embryos, and traces of these transitions can be gleaned from their respective genomes [503]. Researchers around the world have been excavating such insights at an increasing pace, and the impetus to share them with the wider world outside our ivory towers has become almost irresistible. Hence this book.

Chapter 1 introduces concepts that readers will need in order to navigate the rest of the book. It traces key genes and cellular signals back to the common ancestor of all bilaterally symmetric animals. Chapter 2 provides a primer on gene circuitry using the animal whose genetics we know the best – the fruit fly [965]. Chapter 3 examines how some of these circuits arose during evolution and were co-opted for other duties in a related insect – the butterfly. Chapter 4 focuses on one of the strangest animals that has ever lived – the snake, whose quirks reveal its history and thereby allow us to see how natural selection shapes anatomy. Chapter 5 considers animal coat patterns in general, using the cheetah as a handy case study. Finally, Chapter 6 is a potpourri of recent discoveries about a zoo-full of animals that stretches from A to Z. Every chapter is packed with unsolved mysteries that could furnish offbeat topics for term papers, thesis projects, or journal clubs.

Scott Gilbert [783] and others [994,1473,1602,2377] have advocated using evo-devo to teach about evolution in general. With this goal in mind, I have cited all sources (numbers in brackets) as links to the literature. Only by consulting original articles can students appreciate the richness of data, the nuances of arguments, or the thrill of discoveries. The References section offers instructors a reservoir that they can tap for tidbits to spice up their lectures. Two outstanding "must reads" concern snakes, elephants, and manatees in one case [886] and tigers, cream horses, and silver chickens in the other [2470].

To enhance its didactic utility, I have punctuated the narrative with take-home lessons. To ensure accessibility, I have culled as much jargon as possible, compiled a glossary (albeit a spartan one), used a case-study approach, and perforated the book with "rabbit-holes." Readers can enter this Wonderland by studying the schematics, browsing the bestiary (Chapter 6), sampling the glossary, or just looking at the pictures. Like Alice, readers can then explore whatever piques their curiosity.

Because so many key genes were discovered and characterized in flies [761], the conventions of fly nomenclature will be followed here. Thus, gene names are italicized and can begin with either a capital (due to the first mutant allele being dominant; e.g., *Serrate*) or a lower-case letter (recessive; e.g., *engrailed*). Protein names are in roman type and always capitalized (e.g., Serrate or Engrailed). Key concepts are set in **boldface** and are defined in the Glossary. Quotes are set apart from narrative text as indented, blocked paragraphs in smaller, non-serif typeface. The abbreviation "MY" denotes millions of years, and the slang term "app" means an application, as in computer software.

Reconstructing past events can be as tricky as solving a Sherlock Holmes mystery [823] because there is some margin of error in every inference [171]. Authors must assemble the evidence for their arguments as methodically as a lawyer [1330], and readers must weigh the soundness of all theories as carefully as a juror [1529]. Some lessons can be learned from cases where lovely ideas were subsequently overturned in various investigations of fish [247], stick insects [2231], insect wings [1106], turtles [1343], treehoppers [1474], leopards [1687], and acoel flatworms [1408]. The benchmarks listed below may also offer some helpful guidance in this regard.

Plausibility is the first criterion that any evo-devo scenario must meet [1278], but it cannot be the last [1097], lest we run the risk of believing stories that seem valid only because alternatives have not been adequately assessed [778]. Too often we assume that a structure must have served the same function in the past as it serves today [1340]. In fact, structures need not have served any function at all when they first arose [853].

Testability is the second hurdle that any proposal must meet [186], and every attempt will be made to frame hypotheses so that they can be easily tested. Indeed, this venue is where the evo-devo approach has proven to be so valuable [1106]. The field has matured to the point where we can now manipulate the genes that we think caused specific changes in evolution to see whether we can re-create those events in the laboratory [1073,2291].

Ultimately, fidelity to phylogeny is the best way to be sure that the trends we deduce are real [824]. Evolutionary trees furnish a framework within which developmental deviations can be plotted [1907], and the more robust the trees the better [95]. Only by knowing the historical sequence of species (A begat B begat C), for instance, can we show that a certain structure was lost (by B) and regained (by C) [1193].

Kipling's iconic rubric of "how the [blank] got its [blank]" is retained here despite there being no such thing as *the* leopard or *the* zebra. Indeed, there are *many* kinds of leopards and *several* species of zebras. The old notion of Platonic types was disproven in 1859 and supplanted by the Darwinian concept of variations as the raw material for evolution [1418]. There is no need to re-fight that war.

Another shorthand that needs to be clarified concerns genes. When I refer to "cuticle-stiffening genes" for beetle elytra in Chapter 6, for example, I do not mean that the genes themselves have stiffening properties, but rather that the expression of such genes leads to hardening via agents such as enzymes. Genes alone do not cause form! Likewise, when I say in Chapter 4 that "snakes were inventive" in solving an anatomical problem, I am not implying some sort of serpentine Sanhedrin that met to plot an adaptive strategy, though I am a big fan of Gary Larson's *Far Side* cartoons [1252].

The final delusion that must be dispelled is that evo-devo is only about animals. Plants offer enchanting stories as well [506,2505], but including them would have diluted the Kipling conceit.

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chapters were vetted by scholars familiar with topics in Chapter 1 (Richard Campbell, John Gerhart, Thurston Lacalli, and Chris Lowe), Chapter 2 (Joel Atallah, Richard Campbell, Jean-Baptiste Coutelis, Charles Géminard, Artyom Kopp, Stéphane Noselli, and Astrid Petzoldt), Chapter 3 (Vernon French, Ullasa Kodandaramaiah, Fred Nijhout, Jeff Oliver, and Antónia Monteiro), Chapter 4 (Martin Cohn, Jonathan Cooke, Mark Hutchinson, André Pires da Silva, Kurt Schwenk, Oscar Tarazona, John Wiens, and Joost Woltering), Chapter 5 (Jonathan Bard, Jonathan Cooke, and James Murray), and Chapter 6 (Peter Bryant, Richard Campbell, Bonnie Dalzell, and Adam Wilkins).

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