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978-0-521-73233-8 - Quirks of Human Anatomy: An Evo-Devo Look at the Human Body

Lewis I. Held

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QUIRKS OF HUMAN ANATOMY

An Evo-Devo Look at the Human Body

With the emergence of the new field of evolutionary–developmental biology, we are witnessing a renaissance of Darwin's insights 150 years after his *Origin of Species*. Thus far, the exciting findings from “evo-devo” have only been trickling into college courses and into the domain of nonspecialists. With its focus on the human organism, *Quirks of Human Anatomy* opens the floodgates by stating the arguments of evo-devo in plain English and by offering a cornucopia of interesting case studies and examples. Its didactic value is enhanced by 24 schematic diagrams that integrate a host of disparate observations, by its Socratic question-and-answer format, and by its unprecedented compilation of the literature. By framing the “hows” of development in terms of the “whys” of evolution, it lets readers probe the deepest questions of biology. Readers will find the book not only educational but also enjoyable, as it revels in the fun of scientific exploration.

Lewis I. Held, Jr., earned his B.S. in life sciences from the Massachusetts Institute of Technology in 1973. On completion of his Ph.D. in molecular biology from the University of California, Berkeley, in 1977, he became a Postdoctoral Fellow at the Developmental Biology Center at the University of California, Irvine, from 1977 to 1980. Following a 6-year period as an Assistant Professional Research Biologist at the University of California, Irvine, he joined Texas Tech University as an Associate Professor of Biology in 1987. He was awarded the President's Excellence in Teaching Medal from Texas Tech University in 1995 and is the author of *Models for Embryonic Periodicity* and *Imaginal Discs: The Genetic and Cellular Logic of Pattern Formation*.

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Preface

Once upon a time, we thought we were created in the image of a perfect deity. Then came Darwin. In the very first chapter of his *Descent of Man* (1871), he took pains to point out the many flaws in our anatomy, including our useless—but dangerous—appendix, our pathetic covering of body hair, and the silly little muscles that let us wiggle our ears. Each of these odd traits is an anachronism inherited from our nonhuman ancestors.

Of course, the very idea that we had nonhuman ancestors was implicit in Darwin’s earlier *Origin of Species* (1859). That book shook the world. The present book has a much humbler aim: to honor the 150th anniversary of *Origin* and, coincidentally, the 200th birthday of the man himself (b. 12 February 1809).

In Chapter 13 of *Origin*, Darwin asserted that the evidence from embryology alone was strong enough to convince him of the principle of common descent. Having taught embryology myself for more than 20 years, I know what he meant. Human embryos make many structures we don’t need, and we destroy others after we’ve gone to the trouble of making them. No engineer in his right mind would ever allow such idiocy. Only in the light of evolution do these processes make sense [1265], and only in the language of genetics can we comprehend their tortuous logic [2496]. Unfortunately, genetics blossomed only after Darwin died (19 April 1882). In Chapter 5 of *Origin*, he lamented his failure to trace the causes of heritability.

Our ignorance of the laws of variation is profound. Not in one case out of a hundred can we pretend to assign any reason why this or that part differs, more or less, from the same part in the parents. But whenever we have the means of instituting a comparison, the same laws appear to have acted in producing the lesser differences between varieties of the same species, and the greater differences between species of the same genus. [559] (p. 167)

Quirks of Human Anatomy examines one of Darwin's favorite topics (oddities) [965] through the lens of his most incisive approach (embryology) to investigate one of the last remaining riddles from his research—namely, how genetic circuitry has facilitated or frustrated anatomical evolution. This puzzle may now be solvable because we've recently learned so much about genomic logic [896,1413,1822]. What better way to celebrate Darwin's life than to revisit his intellectual playground with fresh eyes and new tools to dig for the treasures that eluded him?

Darwin explored everything that caught his fancy, from barnacles to orchids to earthworms. He was often astonished by what he found, and those surprises led him to wonder why nature should so often defy his intuition. To honor his inquisitive spirit, I have approached this subject as if I were an alien seeing humans for the first time. Hence, *Quirks* is full of childlike questions.

This book is mainly intended for college classes in which students are able and willing to do independent scholarly research—for example, capstone courses, honors tutorials, graduate seminars, and journal clubs. For that reason, I have thoroughly documented all statements. The in-text citations (numbers in brackets) provide essential links to published work, including articles too arcane to be located easily through Internet searches. Strings of such citations can serve as ready-made reading lists for discussions or term papers. The References section may seem excessive to some, but not to teachers devising assignments or to researchers compiling their own bibliography databases. Didactically, one of the best papers for a class to study is Pinker and Bloom's "Natural Language and Natural Selection" (plus commentaries) [2038], but any article in the journal *Behavioral and Brain Sciences* will serve to illustrate the fine art of Talmudic debate. Debatable topics are listed under "puzzles" in the Index and posted on Tom Brody's *Interactive Fly* Web site.

Jargon has been purged here wherever possible, and concepts have been simplified wherever feasible. The intent has been to make the material accessible and digestible. Even so, readers may find the text tough going unless they have (1) a familiarity with molecular genetics (*e.g.*, [1167]), (2) an acquaintance with developmental biology (*e.g.*, [908]), and (3) some prior exposure to basic evolutionary concepts (*e.g.*, [815,1336]).

Given its brevity, *Quirks* can only offer a taste of the many discoveries gushing from the new field of "evo-devo" (evolutionary–developmental biology) [1057,1763]. More riddles can be found in (1) Neil Shubin's popular *Your Inner Fish* [2384], (2) the blogs of Olivia Judson (*Wild Side*) and P. Z. Myers (*Pharyngula*), and (3) two timeless classics: *Natural Selection* by George Williams [2824] and *The Human Machine* by R. McNeill Alexander [50] (*cf.* [2599]). Several new

books specifically probe the evo-devo of the brain: David Bainbridge's *Beyond the Zonules of Zinn* [120], David Linden's *The Accidental Mind* [1555], Gary Marcus's *Kludge: The Haphazard Construction of the Human Mind* [1643], and Aamodt and Wang's *Welcome to Your Brain* [1].

For a fuller treatment of the “evo” side of human anatomy, see John Langdon's recent *The Human Strategy* [1488] or Wiedersheim's 1895 classic *Structure of Man* [2802]. Regarding the “devo” side, start with Scott Gilbert's splendid *Developmental Biology* [908] or the new edition of *Larsen's Human Embryology* [2311]. Congenital anomalies are usefully annotated in Leslie Arey's old embryology text [91], and exotic curiosities are discussed in Armand Leroi's clever *Mutants* [1524]. For more on genetic gadgetry, try Sean Carroll's *Endless Forms Most Beautiful* [386] or his more advanced *From DNA to Diversity* [392]. Darwin's *Origin* was ably “updated” in *Darwin's Ghost* by Steve Jones [1313]. For definitions, see Hall and Olson's *Keywords and Concepts in Evolutionary Developmental Biology* [1061].

Finally, there is no richer repository of evo-devo narratives than the erudite essays of the late Stephen Jay Gould, who is widely credited with reviving the field via his seminal *Ontogeny and Phylogeny* [2814]. Gould often extolled the merits of using quirks as convenient windows into the evolutionary past (bold-face added):

This common claim for organic optimality cannot be reconciled with a theme that I regard as the primary message of history—the lesson of the panda's thumb and the flamingo's smile: the **quirky** hold of history lies recorded in oddities and imperfections that reveal pathways of descent. [968]

Evo-devo offers more visual appeal than the dry mathematics of population genetics, so it may turn out to be a better way to teach students about evolution in general [906,1160]. With this potential application in mind, I've relied on drawings (*vs.* verbiage) wherever possible. Many of the schematics distill so much data that their legends became overly lengthy. “Reflection” boxes were created to absorb the discursive overflow. They should be consulted whenever readers want more information about the contents or implications of particular figures.

The purpose of this book is not so much to survey what we know as to chart the *boundary* of the known so that we can stroll along that shore, peer into the mists of the unknown, and ponder how we came to be. Contemplation has virtually vanished from the crowded curricula of colleges these days, but that is the dreamy realm where connections are discernable and initiatives are imaginable. It is there where the genies await the right supplicant asking the right

question in the right way, and it is there where starry-eyed students may succeed while those of us who teach them the calcified corpus of trite old facts have failed. Reflection boxes are designed to nurture new insights, just as a tour guide might linger by certain paintings to muse about the intentions of the artists. If readers get nothing more than the faint sense of deep secrets beckoning them like buried treasure, then this book will have met its goal.

A handy icon in many of my figures is da Vinci's *Vitruvian Man*, which he drew *ca.* 1492. The choice seems apt, Leonardo was a pioneering anatomist [551]. I have omitted the square and circle that Leonardo used to frame his man (as per the dictates of Vitruvius in *De architectura* 3.1.3 [2696]) because that ideal geometry implies a Platonic perfection that Darwin later disproved [370]. Give Leonardo this much, however: certain aspects of our anatomy *are* astounding from an engineering standpoint. Our two legs, for example, attain equal lengths despite growing independently for decades [106], even though any slight asymmetry at the outset should be amplified greatly by the end [747,2844]. The precision of symmetric growth is as enigmatic mechanistically as it is elegant morphologically [498,1044,1497], although recent evo-devo findings have begun to demystify how we achieve this feat [537,668,2682].

A *symbolic* icon used here is the fishing pole. Indeed, it embodies the book's main theme: evolution is like a fishing expedition in which genes "hook" other genes in abiding causal linkages. The utility of the metaphor is its focus on frivolity [2206]: the genes that have been snared over the eons could not have been predicted in advance and make little sense in hindsight [1606]. The accrual of such arbitrary links, layer upon layer, has culminated in the baroque complexity of our genomic circuitry [1605]. Impressive as the functioning of our genome may be in the aggregate, it is a crazy cobweb in its sundry details, not a coherent tapestry [571].

The challenges that await the next generation of evo-devo researchers are to (1) disentangle this web, (2) decipher its logic, and (3) deduce how it makes the many quirky traits that distinguish our species [390,1823]. (*N.B.*: The hominid lineage that led to us after it diverged from chimps and gorillas is termed the *hominin* subfamily [386,1488], a term used in later chapters.)

Darwin disabused us of the conceit that our outer shell is indicative of our inner workings. What matters for evolution is not beauty but function, and much of our anatomy works adequately but awkwardly—as if it were cobbled together with duct tape and baling wire. (Our clumsy knee comes to mind [10].) With armloads of such evidence, Darwin demoted us from Leonardo's pedestal, but please give him this much: he left our aesthetic appreciation intact—albeit altered [594,2016]. The beauty we now admire is not in our anatomy but in the antiquity of its parts and in the epic stories they have to tell [2384]. Our parts

have played many roles over the eons, like versatile actors in an itinerant repertory troupe [595,2384,2802]. In Darwin’s own words,

Thus throughout nature almost every part of each living being has probably served, in a slightly modified condition, for diverse purposes, and has acted in the living machinery of many ancient and distinct specific forms. [563] (p. 284)

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—an approach that I tried to use here, albeit with limited success.

My mother, brother, and sister, all of whom are accomplished artists, provided encouragement during the writing process. I, in contrast, could never have attempted to draw the figures in this book without Adobe Illustrator as my crutch! George and Ann Asquith served as coach and cheerleader, respectively, and Sam Braudt shared books, blogs, and wisdom. Chris Curcio was my ardent advocate and supportive editor at Cambridge University Press.

Larry Blanton, Richard Campbell, John (Trey) Fondon, Joseph Frankel, and Jeff Thomas read the entire manuscript and improved it greatly. Drafts of chapters were critiqued by generous colleagues, including Robert Bradley, Sam Braudt, Jim Carr, Tom Cline, Jason Cooper, Barry Davis, Mark Hamrick, James Hutson, Thurston Lacalli, David Moury, Robert Paine, Julie Rosenheimer, Kent Rylander, and David Weisblat. For the record, Trey rejects my favoritism of *cis*-regulation, described in Chapter 4 (*cf.* [792,1598]); Tom disputes my portrayal of *dsx* as a switch in Chapter 5; and Sam disdains my reluctance to define cognition in Chapter 7 (*cf.* [1504]). Long ago, to celebrate my first articles, Barry (a college chum) gave me *The Encyclopædia of Ignorance: Everything You Ever Wanted to Know about the Unknown* (1977, Pocket Books, New York). That book’s focus on what we *don’t* know gave me the prism that I needed to see anatomy anew.

Citations of Aristotle’s *Parts of Animals* are encoded in standard format as “{PoA: Book #: Part #: Page # of Bekker’s 1831 edition: column # a or b: Line #}” sensu Barnes [137]. Darwin revered Aristotle. In an 1882 letter to William Ogle [565], who translated *Parts of Animals*, he wrote: “From quotations which I had seen, I had a high notion of Aristotle’s merits, but I had not the most remote notion what a wonderful man he was. Linnaeus and Cuvier have been my two gods, though in very different ways, but they were mere schoolboys to old Aristotle.” To many of us who admire Darwin, he eclipsed even Aristotle in his powers of observation, deduction, and exposition.

If Darwin were alive today, he would be thrilled to see how much his ideas have helped us to interpret the flood of findings from the goldmines of comparative genomics [358,604,1194,1628]. His noble legacy of innocent inquiry lives on today in countless laboratories around the world [1964]. Rank-and-file researchers who have drawn inspiration from the well of his insights owe it to him—especially during this jubilant commemorative year—to let at least a little of evolution’s grandeur shine out from our ivory towers. Hence this book.

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