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BOOK REVIEW

STRAUSFELD N.J. 2012: ARTHROPOD BRAINS. EVOLUTION, FUNCTIONAL ELEGANCE, AND HISTORICAL SIGNIFICANCE. The Belknap Press of Harvard University Press, Cambridge and London, xvi + 830 pp., 175 color illustrations, 24 halftones, glossary, extensive notes. ISBN 978-0-674-04633-7, hardbound. Price USD 65.00.

Students of arthropod behavior know instinctively that their study animals have complex brains for how else could a male salticid dance so exuberantly in front of a conspecific female, an orb weaver spin such an intricate and effective web, or a minute trichogrammatid wasp measure the surface area of a host egg prior to depositing her own. But most behaviorists would admit to knowing little about the brains of their subjects because their theories and methods have proved effective in the absence of such knowledge and because such can be attained only by use of sophisticated methods totally foreign to their experience. In this magnificent volume, Nicholas Strausfeld makes brain structure in arthropods accessible for numerous representatives of each class in exquisite detail and within historical and evolutionary contexts.

The book contains 12 chapters. The first three (pp. 1–124) (*The Polymath of Rennes*, *Discoveries and Losses*, and *Ramón y Cajal's Hunting Case Watch*) summarize the lives, times and discoveries of the principal pioneers of arthropod neuroanatomy from Jan Swammerdam in the 17th century to Ramón y Cajal and Sánchez y Sánchez in the early 20th and is rich in fascinating anecdotes: Who'd guess, for example, that Fridtjof Nansen, a Norwegian best known for his polar explorations, diplomacy and Nobel Peace Prize (1922, for work on behalf of displaced victims of WWI), was among the first (1885) to assert that neurons in bilaterians were discontinuous elements based on his study of diverse marine invertebrates? Chapters 4–7 (pp. 125–352) (*Beneath the Faceted Eye*, *In the Air and Underwater: The Olfactory Brain*, *The Mushroom Body Enigma*, and *The Brain within the Brain*) detail neuropil organization, "wiring" and function, respectively, of the optic and olfactory lobes, the mushroom bodies and the central brain areas (protocerebral bridge, central body, etc.) of numerous arthropod species but with emphasis on insects and crustaceans while Chapter 8 (pp. 353–400) (*Eight Legs and More: Chelicerates, Myriapods, and Some Distant Relatives*), does the same for flat worms, annelids, velvet worms, tardigrades, centipedes, millipedes, and a host of chelicerates. These descriptions reveal both the underlying similarity in brain organisation throughout the Phylum and the remarkable variation in relative size, architecture and function of their principal neuropils and interconnections depending on species, microhabitat and life style.

The final third of the book, Chapters 9–12 (pp. 401–594) (*Reiterations, Appendages, and the Ancient Brain*, *Philosophical Anatomy, Swedish Pioneers and Neuronal Systematics*, *Convergence or Common Descent?*, and *The Origin of Insects*), synthesizes information in chapters 4–7 with that on the role of gene networks in specifying pattern during segment, appendage and brain development in annelid, arthropod and vertebrate embryos and in relation to the structure of fossil arthropods from Middle and Upper Cambrian Lagerstätten of the Chenjiang (China), Sirius Passet (Greenland), and Burgess Shale (Canada) fossil sites. In Chapter 10 Strausfeld summarizes the methods devised to infer evolutionary relationships between taxa, particularly the use of neural characters begun by pioneer Swedish neuroanatomists such as Nils Holmgren and Bertil Hanström (he provides 12 cladograms illustrating the evolution of brain structures throughout the Phylum). In addition, in Chaper 9 he weaves ingenious and detailed scenarios to answer age-old questions about arthropod evolution such as: How many segments has the insect head? Are the cephalic/cephalothoracic segments and their appendages homologous across the Phylum? Is the vertebrate body plan an inverted arthropod (lobster) body plan as postulated by E. Geoffroy St.-Hilaire in 1822? Are the principal components of arthropod brains homologous with those of vertebrate brains in their structure, development and function? Does a labral segment exist or did the labrum evolve from ancestral, paired, frontal appendages prominent in many Cambrian fossil arthropods and in extant onychophorans? What does presence of the recently described labral-apical cerebral complex in the brains of insects (Fig. 9.12) and malacostracans tell us about brain evolution in arthropods? Is the arthropod eye derived from an ancestral appendage? Did arthropods share a common ancestor with annelids or vertebrates? Did insects share a common ancestor with myriapods, or with malacostracan or branchiopod crustaceans? Did the four optic neuropils (lamina, medulla, lobula, lobula plate) and their linking chiasmata in the optic lobes of most neopteran insects and malacostracans descend from a similarly complex lobe in a common ancestor (a possibility bolstered by the recent reconstruction of the brain of the Cambrian fossil *Fauxianhuia protensa* by Ma et al., 2012) or did they evolve by addition of neuropils to a more simple optic lobe of an ancestor having only 2 neuropils (lamina, visual tectum) linked by uncrossed projections as in scutigeromorph centipedes and some branchiopod crustaceans?

Throughout, the text is in lucid and graceful English interspersed with whimsical asides, recollections of collecting trips with his wife Camilla to localities all over the world, notes about the personality quirks, intellectual fisticuffs between and tribulations of early workers and many reflections on what's wrong with modern biology (e.g., why do we focus so much on model organisms?).

The book is a model of the printer's art. It is strongly bound between black covers, is beautifully printed on glossy paper (probably the reason it weighs in at 2.9 kg!), is imaginatively organized, and is illustrated with hundreds of spectacular color photomicrographs (including those imaged by Strausfeld himself of slides prepared by pioneer investigators in the late 19th and early 20th centuries). Many plates include lithographs of Golgi preparations reprinted from the classic papers that are every bit as elegant and accurate as the information-packed images produced to-day using confocal microscopy and preparations multiply and colorfully labeled with tagged antibodies to specific neuronal, synaptic, and glial proteins and to various neuropeptides. Others include his splendid photos of living study animals in their terrestrial and aquatic microhabitats, of Cambrian fossils, or portraits of past and present contributors surrounded by examples of their work.

Most informative for both neophyte and adept are his and his colleagues' beautifully executed, multiply colored, camera lucida drawings showing the complex projections, branches and interconnections of individual neurons and his numerous, artistically drafted explanatory diagrams. Brain diagrams from representatives of each class are compared to those of two well studied "standard arthropods", the American cockroach, *Periplaneta americana*, and the grass shrimp, *Palaemonetes pugio* (Fig. 4.1). The principal neuropils in each of these brains are rendered in different colors used elsewhere to indicate homologous neuropils in the brains of other arthropods and, in one instance, the stem cells (neuroblasts) giving rise to them in the head of a cockroach embryo (Fig. 9.5). Complex wiring diagrams summarize the projection patterns, arbors and synapses of specific neurons in each brain network in graphical format with each neuronal type – again, specifically colored; these greatly assist one in interpreting adjacent photomicrographs of the same areas. Figure 12.4 summarizes the ground pattern, chiasma formation and axonal growth patterns in representative branchiopod and malacostracan optic lobes during postembryogenesis showing them to develop in ways practically identical to those occurring in the lobes of neopteran insects (e.g., Nordlander & Edwards, 1969). Last but not least, his intricate hypothetical diagrams in Chapter 9 illustrate his answers to some of the evolutionary questions posed above. Unlike those in most science books, the illustrations are captioned with short narratives interesting in their own right and understandable without reference to the text.

The book lacks a reference list and, instead, ends with extensive notes (pp. 607–790) for each chapter keyed to numbers printed in superscript in the text. This facilitates reading but makes it difficult to quickly identify the source of particular discoveries because the references are not listed alphabetically. However, most notes do provide these sources and also contain additional information pertinent to each topic (the names of the principal authors he cites are included in the index).

The volume is obviously a labor of love and must have required much of his career to envision, write and illustrate. As well as being an outstanding neuroanatomist, its pages show its author to be a passionate naturalist, writer, artist and historian with a deep understanding of developmental and evolutionary biology and paleontology. Reading it would provide a solid platform for a graduate student to launch a career in arthropod neuroscience.

Strausfeld, FRS, is Regents Professor in the Department of Neuroscience, Professor of Ecology and Evolutionary Biology, Adjunct Professor of Art, and Director, Center for Insect Science, University of Arizona, Tucson. He is well known for his previous masterpiece, *Atlas of an Insect Brain* (Springer, 1976) and for his countless papers on arthropod neuroanatomy.

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