

BOOK REVIEWS

Comparative Terminology

Homology. The Hierarchical Basis of Comparative Biology. BRIAN K. HALL, Ed. Academic Press, San Diego, CA, 1994. xvi, 483 pp., illus. \$54.95 or £42.

The title of this book makes a strong claim: homology is the hierarchical basis of comparative biology. I assert that the claim is too modest. Homology is the central concept for *all* of biology. Whenever we say that a mammalian hormone is the "same" hormone as a fish hormone, that a human gene sequence is the "same" as a sequence in a chimp or a mouse, that a HOX gene is the "same" in a mouse, a fruit fly, a frog, and a human—even when we argue that discoveries about a roundworm, a fruit fly, a frog, a mouse, or a chimp have relevance to the human condition—we have made a bold and direct statement about homology. The aggressive confidence of modern biomedical science implies that we know what we are talking about. But a deeper reflection shows that this confidence is based more on hope than on certainty. This fine book brings together a selection of outstanding comparative biologists, all of whom have struggled to formulate a philosophical foundation for homology that has sufficient generality that it can serve all of biology.

Homology is a pre-Darwinian concept. In fact, the most influential thinking concerning it dates to the 1830s and workers such as von Baer, Geoffroy Saint-Hilaire, and above all, Richard Owen. The last of these achieved an intellectual dominance that continues to this day, and it is the 150th anniversary of his famous paper on homology that this book commemorates. Owen's definition of a homologue as "the same organ in different animals under every variety of form and function" is the conceptual foundation for comparative biology today. "Sameness" and its vagaries are what it is all about.

Hall, a developmental biologist, has made important empirical contributions, and he also has a scholarly approach to the history of ideas in biology. For the present work he has selected 14 authors who represent different traditions and perspectives. The good news is that everyone has taken seriously the task of struggling to define, or at least exemplify, "homology" and has

produced a chapter that is up-to-date (every chapter contains 1993 citations, an indication of the level of interest in the topic) and well worth reading. The bad news is that there is no consensus on even the definition of homology, although everyone admits that it has to do with "sameness" and common ancestry.

The central issue is whether or not homology is something decided a priori, on the basis of such considerations as relative position and connections (both formulated by Owen and Geoffroy Saint-Hilaire over 150 years ago, and supported here by several authors), development, or simple similarity, or decided only a posteriori, as "products of a method of analysis" (Nelson, in an intellectually challenging chapter), "always and only an hypothesis of similarity due to common ancestry, to be tested by congruence, i.e., in relation to all other characters known" (Rieppel, in an aggressively written and stimulating chapter). The debate almost, but not quite, places authors in two general camps—those who are concerned with the biological foundations of "sameness" and those phylogeneticists (followers of the great German thinker Willi Hennig) for whom homology is never more than a hypothesis and at most is a shared, derived feature of two or more taxa, termed a synapomorphy (and always tentative).

Hennig was on a more constructive and heuristic path than some of his revisionist followers. With his characteristic clarity, Hennig observed that it matters little for the concept of "truth" that we cannot recognize truth and that science is restricted to erecting hypotheses concerning it. He noted that an organ could be recognized as a homologue of an organ in another taxon but that a transformation series, such as organ-reduced organ-lost organ, would result in "lost organ" being a synapomorphy of a group of taxa, with nothing left to homologize. Cladistic methodology thus both goes beyond and falls short of homology.

Readers of the present volume will benefit enormously from the first chapter by Hall, a 17-page guide to that which follows. It is a quick, readable, intellectually solid overview of the entire book. Hall has also made an effort to cross-reference the chapters in the book, so that the alternative

viewpoints can be checked if one selects only a chapter here and there.

Authors highlight the controversy that lay dormant for many years but has sprung back to life in the past few years. For example, Wagner titles a section "Why is structural identity more fundamental for the homology concept than common ancestry?," and Rieppel counters that "homology is a logical relation, not a relation of material identity." There are treatments by structuralist developmental biologists (Goodwin, Sattler), by molecular systematists (Hillis), by functional morphologists (Lauder), by morphometricians (Bookstein, who is the only author to deny homology an important role in his research), by behaviorists (Greene), by paleontologists (Shubin, Panchen), and by phylogeneticists (Donoghue and Sanderson). In these papers there is an enormous amount of self-citation and repetition of previous publications by the authors. New data and analyses are scarce and are presented mainly by Greene and by Donoghue and Sanderson. Roth presents her much-cited views in a new perspective, and Shubin's contribution is a very sensible, worked-out example combining paleontology, phylogeny, and development.

Several authors (Nelson, Goodwin, and, especially, Hillis) address the thorny issues surrounding molecular homology. Nelson points out that the exact meaning of orthology and paralogy is not apparent until the information of a gene tree is considered in relation to an ordinary tree of taxa, a proposition that is crystal clear to a phylogeneticist and is a manifestation of the need for "tree thinking" in comparative biology but that will doubtless present problems for some molecular biologists. Hillis, too, addresses difficulties with molecular-based concepts of homology, and both he and Sattler discuss the possibility of "partial homology," a proposition explicitly denied by Donoghue and Sanderson. Curiously, Hillis fails to cite the attempt by molecular biologists themselves to deal with the homology issue (Reeck *et al.*, *Cell* 50, 667 [1987]).

While I benefitted from reading the book, I found no reason to change my personal definition of homology (which is not worth repeating, since I cannot even convince students in my own lab of the correctness of my position!). My conviction is that evolutionary biologists are making ancient words serve too many masters. We take pre-Darwinian terms like "species," "adaptation," and "homology" and try to give them exact modern meanings, but technical meanings require technical terms, and it is time to abandon idealism in favor of pragmatism and utility. It is sufficient to "know" that homology, like truth, exists,

and to proceed to use, or coin, more appropriate terms for specifying what we mean in a modern scientific context.

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A Patch of the Tropics

La Selva. Ecology and Natural History of a Neotropical Rain Forest. LUCINDA A. McDADE, KAMALJIT S. BAWA, HENRY A. HESPENHEIDE, and GARY S. HARTSHORN, Eds. University of Chicago Press, Chicago, IL, 1994. x, 486 pp., illus. \$90 or £71.95; paper, \$28.95 or £23.25.

In 1970, when I began a study of the population ecology of tropical rodents, getting to Finca La Selva from San Jose, Costa Rica, involved a tedious four-hour drive along a mountain road followed by a pleasant 15-minute boat ride up the Rio Puerto Viejo. The field site, recently purchased by the Organization for Tropical Studies (OTS), consisted of about 580 hectares of primary lowland rain forest and a single two-story field station that provided plenty of room for a handful of scientists studying hummingbirds, tree demography, and leaf-litter invertebrates.

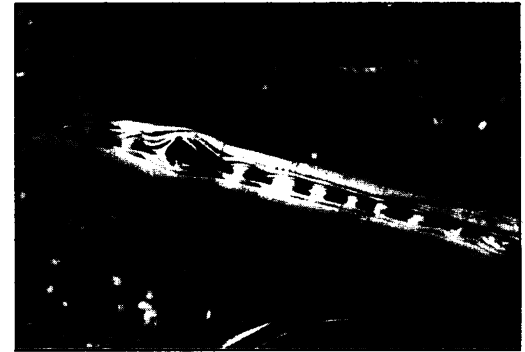
Today, only the forest remains the same at La Selva. The La Selva biological station now encompasses about 1500 hectares, including large tracts of early successional pastures and second-growth forest where manipulative studies can be conducted. The phys-

ical plant has expanded enormously and now includes air-conditioned laboratories in which increasingly sophisticated research is being conducted. A paved road now brings hundreds of scientists and visitors to La Selva's doorstep, and communication with the rest of the world is easy. Whereas about 12 papers, dealing mostly with systematics and species and community ecology, from La Selva were being published annually in 1970, now about 80 papers covering a much wider array of topics are published annually by La Selva researchers.

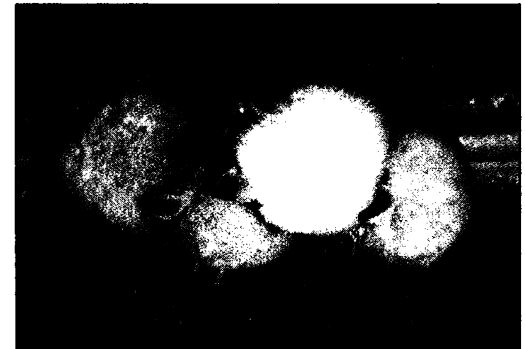
This volume summarizes what is currently known about the biology of the La Selva flora and fauna, which, along with Barro Colorado Island, Panama, and Los Tuxtlas, Mexico, is one of the most intensively studied patches of lowland tropical forest in the northern neotropics. The book contains 26 chapters written primarily by North American scientists and eight appendixes describing how OTS administers the field station and listing the flora and fauna. The chapters are placed in five sections dealing with the abiotic environment and ecosystem processes, the plant community, the animal community, plant-animal interactions, and the human environment around La Selva. The editors instructed the authors to set their chapters in as broad a context as possible while reviewing the La Selva data. Most successfully met this challenge. As a result, the book could serve as a textbook in tropical ecology. It contains very thorough reviews of many areas of tropical ecology, especially those dealing with plant-animal

interactions, and is full of ideas and suggestions for future research. Graduate students will find a wealth of potential research projects in these chapters.

Two issues of special concern emerge from many chapters. The first is how limited is our knowledge of the natural history of most species of plants and animals at La Selva and elsewhere in the tropics. Despite hundreds of person-years spent working at La Selva, we have detailed knowledge about the lives of only one species of frog, one lizard, one bird, and one rodent among the vertebrates, an especially well-



"The strikingly braided stem of the 'monkey-ladder' vine (*Bauhinia guianensis*, Caesalpinoideae) makes it easily recognizable vegetatively; other morphologically distinguishable lianas at La Selva remain unidentified for lack of reproductive material." [From D. A. Clark's paper in *La Selva*; R. Marquis]



"A colony of four white bats, *Ectophylla alba*, roosting in a tent cut from a *Heliconia* leaf. The bats typically hang curled in tight clusters from the midrib. Details of the cut side veins and interconnected tissues may be seen along the midrib of the leaf. The holes in the leaf were made by the bats' claws. Tents such as this one may be used for several weeks. *Ectophylla* roosts only under leaves that it modifies as tents." [From R. Timm's paper in *La Selva*; Barbara L. Clauson]



"Researchers C. Pringle (right) and F. Triska (left) at work on stream insects in a tributary of the Rio Santo Domingo at ca. 2000 m elevations in Braulio Carrillo National Park behind La Selva. In the tropics, roots that grow into the flowing water of streams can provide important habitats for many benthic organisms." [From *La Selva*; G. Dimijian]

studied group at this field station. Several authors go against current ecological fashion and make a strong plea for more natural history studies. According to Philip de Vries, "Natural history" is twentieth-century organismal biology and continues to provide the new data to be used by present and future biologists. Meaningful comparisons of species diversity, seasonality, unpalatability, or mutualisms depend on knowing, not guessing, what species occur where and when and what they do for a living."

In a final synthesis chapter, Gordon Orians highlights the second major concern: the importance of a "comparative tropical ecology." He points out that answering questions about the adaptations of tropical organisms and factors that produce and maintain high species diversity, the hallmark of most tropical ecosystems, requires detailed knowledge about the biology of different floras and fauna, knowledge that for the most part does not yet exist. To this end,