

Caddisflies, the Underwater Architects

Glenn B. Wiggins
University of Toronto Press
2005; 292 pp.
Price: \$125, hardcover
ICBN: 0-8020-3714-3

Caddisflies, or Trichoptera, are usually considered among the “minor orders” in general entomology textbooks or popular publications on insects. In the printed edition of *Zoological Record*, they are included in the volume “Other Orders.” The same is seen in the many pie charts meant to visually display the distribution of known diversity among the insect orders; in these representations, caddisflies are afforded only a tiny slice. As such, when compared with the overwhelming diversity seen in certain subgroups of Coleoptera, Diptera, Lepidoptera, and Hymenoptera, the diversity and importance of Trichoptera are often overlooked or underappreciated. Adding to their status are the secretive, crepuscular habits of the small, somber adults and the aquatic habitat of the immature stages—characteristics that render their collection and observation unfavorable to all but the specialists.

With almost 12,000 described species, Trichoptera ranks as the seventh largest order of insects (closely behind the Orthoptera) and is larger than many other more “popular” groups of arthropods and even vertebrates. The importance of caddisflies in the trophic dynamics and energy flow of freshwater ecosystems is a direct reflection of their biological diversity and abundance. Furthermore, biological indices and other metrics incorporating relative abundance and diversity of larval Trichoptera have long been used by state and federal agencies to assess and monitor water quality. The use of silk by larvae to construct intricate portable cases as protection from predators, to weave delicate nets to capture prey, or to filter food has given this “minor” order a prominent role in the study of insect behavior. It is this feature, the architectural habits of caddisfly larvae, that is the subject of a wonderful new book by Glenn B. Wiggins.

Wiggins long ago established himself as one of the world’s pre-eminent trichopterologists. His 1977 book, *Larvae of the North American Caddisfly Genera (Trichoptera)*, also published by the University of Toronto Press and now in its 2nd edition (1996), was a masterpiece of scientific inquiry and scholarship; it was the seminal piece of literature that started and continues to inspire my career in caddisfly systematics. His new work, *Caddisflies, the Underwater Architects*, will certainly have a similar effect on current and future students of the group.

The book begins with an introduction that contains an inspiring, almost romantically written account of water, its unique qualities, its importance to life on Earth, and as habitat for Trichoptera. The remainder of the book is divided into three sections: Caddisflies in Ecosystems, the Families of Caddisflies, and Supplementary Information.

In Part I, Caddisflies in Ecosystems, Wiggins presents chapters on Architecture and Biology, Caddisflies in Freshwater Communities,

Architecture of Pupation by Caddisflies, Evolution of Caddisflies and Their Architecture, Biogeography of Caddisflies, and an Epilogue, which provides the bulk of the scientific content of the book. These chapters are rich in content and are an encyclopedic source of information about all aspect of larval biology. The accounts of the different ways caddis larvae use silk to construct portable cases or fixed retreats with their accompanying capture nets are fascinating. Wiggins also provides a detailed review of the habitat and trophic diversity of larvae, which is couched in terms of modern stream ecological theory, including the River Continuum Concept.

Much of this information is from Wiggins’ own published research and observations, including his pioneering studies of caddisflies in temporary vernal pools and of pupation behavior (allotted an entire chapter), but he has taken the time to reinterpret his hypotheses on the basis of newly published information. For example, he presents evidence from newly published morphological as well as molecular phylogenetic analyses on the evolution of caddisflies and their construction behaviors. He rightly points out that an understanding of the relationships of the four families of the suborder Spicopalpia, cocoon-makers (itself equivocally monophyletic), and of the taxa with the strongly supported monophyletic suborders Annulipalpia, retreat-makers, and Integripalpia, case-makers, is key to understanding the basal radiation of the order and its biological attributes.

Wiggins’ comparison of previous phylogenetic analyses and their conclusions, however, is confounded by the different datasets (weighted toward adult, larval, behavioral, or molecular characters) and methods of analysis (Hennigian argumentation, compatibility analysis, equally weighted parsimony, noncladistic methods, etc.) used in the published phylogenies. Until a large dataset (in terms of characters and sampled taxa) is accumulated and analyzed by currently accepted modern methods, a firm understanding of caddisfly evolution remains a goal. As in his treatment of caddisfly evolution, I found most of his discussions to include new findings from the recent literature; a rare exception is the omission of recent important contributions by Stuart and Currie on caddisfly case making behavior and its use in phylogeny reconstruction.

Part II is a survey of the larvae of all 45 currently recognized families of Trichoptera. Each North American family is discussed, more or less comprehensively, in terms of its diagnostic characters, construction behavior, biology, and distribution, along with closing comments about its fossil history, taxonomy, or other interesting features. This section is fascinating reading for those enchanted by the morphological and behavioral diversity among organisms. The illustrations accompanying the section are outstanding (among the best in entomology, in my opinion) and were largely excerpted from the author’s previous works.

This section, however, is disappointing, given the comprehensive nature of the previous sections, in that it superficially treats the non-North American fauna. Those families not occurring in North America, except for a few extralimital families previously researched by the author (e.g., Phryganopsychidae, Limnacentropodidae) are treated only briefly and without accompanying illustrations, even though sufficient information exists about their biology and

behavior. This is especially true of those families endemic to the southern continents. Granted, although Wiggins states his intent in the objectives of the book to treat comprehensively only this restricted fauna, where his expertise is rooted, he misses a golden opportunity: no such treatment, to the extent and skill that Wiggins provides for the North American fauna, exists for the world fauna. Similarly, the excellent keys he has provided to the larvae, adults, and pupae of the North American fauna have no equivalent for the world fauna. As such, as an identification resource, the book will be much less useful to non-North Americans, although it will be of use to inhabitants of the northern hemisphere, where the same families by and large occur.

The quality of the illustrations, diagrams, and charts, all in black and white except for a single color frontispiece, are excellent throughout the work. The detailed illustrations of caddisfly larvae and their wonderful cases will enthrall the viewer. The quality of the paper, printing, and binding are excellent. At \$125, the cost may appear high, but given the physical quality of the work and its outstanding scholarship, it is worth the price.

Glenn Wiggins obviously has deep affection for caddisflies. His devotion to the study of Trichoptera has been expressed in this work and in the quality of his entire body of research. Here and elsewhere, he has given this “minor” order the recognition that it deserves.

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The Botanist and the Vintner: How Wine Was Saved for the World

Christy Campbell
Algonquin Books of Chapel Hill, NC,
2005, 320pp.
Price: \$24.95, hardcover
ISBN: 1-56512-460-X

From the title, one might not suppose that this is a story centered on an insect, but the original 2004 British title *Phylloxera* would be instantly recognized by entomologists. The book is a fascinating popular history of the invasion of the grape phylloxera [*Daktulosphaira vitifoliae* (Fitch), Hemiptera: Phylloxeridae] to France, the catastrophic consequences for the vines, and the chaotic but ultimately successful recovery of the French wine industry in the late 19th century. The author, a British journalist and defense correspondent, has clearly immersed himself in the research. On the whole, the result of his research is a finely crafted book that is well worth reading.

Most Americans, perhaps even most American entomologists, are more familiar with the Irish potato famine than with the calamitous impacts of the phylloxera that was introduced into Europe in 1865, some 20 years before the potato famine. Not only was the vine (France's cultural icon) devastated, but a huge portion of the European population and economy was upended. Many peasants lost their land, and Campbell quotes estimated losses in France alone that equate to about \$8 to 25 billion today. The successful “reconstitution” of French vineyards later resulted in another economic

crisis of oversupply, accompanied by further social displacement and tumult.

The cryptic and complex life cycle of the grape phylloxera, and the fact that its origin was then unknown, vastly complicated the response to its introduction. By the time the vines were dead, the tiny root-inhabiting life stages were usually gone, having moved to still-living vines nearby. Unbeknownst at the time, it was these root-feeders that were damaging the susceptible European *Vitis vinifera* vines, in contrast to the importance of aerial galling populations on American grape species. We now know that the alates arising from the root populations, their nonfeeding sexual offspring, and the winter eggs that hatch into stem or root-dwelling stem mothers, are merely a curiosity and not important to grape production in Europe. Granett et al. (2001) provide a nice review of the complex biology of this pest.

There was no shortage of other heroes, villains, mystery, and political intrigue during this crisis. A stupendous reward of Fr. 300,000 was offered for a cure of the phylloxera. Even though the problem was cured, no one was ever awarded the prize. The central character of the book, Montpellier botanist Jules-Émile Planchon, had the best claim. He steadfastly and scientifically pursued the problem. On an investigative foray in the United States with C. V. Riley, he established that the American and European insects were identical. Planchon came to champion resistant rootstock, the eventual solution, but he died suddenly before his claim could be lodged. Our own ESA has some significant artifacts from this convoluted case, including a bronze statue awarded to C. V. Riley in 1892 by French winemakers, and also Riley's French Legion of Honor medal for service to the grape industry.

The book illuminates the interplay between science and ignorance, superstition, and chicanery. The chief consequence of the staggering government prize was to heighten the mania surrounding phylloxera, and to encourage ever more bizarre proposed remedies to the insect, which included snail slime and human urine. French nationalism also complicated the situation. The central debate in France during this time was between chemical control and host plant resistance, the solutions advocated by the French elite and the so-called Americanists, respectively. Neither approach was cheap, yet planting American-based resistant rootstocks that were grafted with *vinifera* scions was the sustainable response. The verdict of the people was clear; “peasants were voting with their grafting knives.”

Although the book is a compelling read, some aspects could have been improved. First, the author's lack of scientific perspective causes him to overlook the important and long-lasting contribution involving soil fumigation, which not only protected particularly valuable vineyards until resistant rootstock could be established, but more importantly inaugurated large-scale agricultural experimentation focused on factors affecting the productivity of soils (Wilhelm 1966). Another problem with the book is that, although it provides a timeline and several maps showing the phylloxera invasion into France, I found myself not infrequently disoriented in time and especially in space. This is because many French regions, towns, and wine-growing areas mentioned in the text are not shown on the maps. Perhaps the British familiarity with France accounts for this oversight.

The phylloxera history illustrates several principles that are important even now. One is that it is difficult to study the subterranean, and our knowledge of underground fauna lags behind that of more accessible taxa. Second, quarantine is always fraught with human issues such as education and enforcement; and these problems are aggravated by problems of detection, particularly for cryptic pests. Also, chemical control alone will not eradicate all but the most restricted and obvious pest invasions. The most important lesson, though, is that science with important practical implications is ipso facto political, and those whom we now call “stakeholders” must

be engaged and convinced of the wisdom and fairness of activities that affect them, preferably by the scientists themselves.

Biological problems are never as simple as they seem. In the big picture, grape phylloxera was an invasive pest exploiting susceptible hosts in Europe, and the solution was to import resistant American rootstock. To the author's credit, he goes into considerable detail about the complexities of this approach, and more than this, he highlights the continuing challenges in California and other wine-growing regions to remind us that no pest problem is ever finally solved, as long as the insect continues to evolve.

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My thanks to Joel Grossman for the Wilhelm reference.



Butterflies of the East Coast: An Observer's Guide

Rich Cech and Guy Tudor
Princeton University Press, Princeton, NJ
2005; 360 pp.
Price: \$49.50, hardcover
ISBN: 0-691-09055-6

This is the latest in a genre of publications targeted to the amateur naturalist who has an interest in observation and “nonconsumptive” study of butterflies. The book is arranged into two parts, beginning with an introductory section that provides ecological, morphological, habitat, and life history information. At the end of the introduction, there is a guide to the use of the “Species Accounts” section, with a key to abbreviations, a key to the color-coding of distributional maps, and an illustration of terms used to describe morphological features and wing patterns necessary for identification. The “Species Accounts” portion is divided into sections by common family names and further divided by subfamily group. Each family section begins with a brief account of the ecology and characteristics of the family and also includes introductory material for each subfamily as appropriate. Latin names for families and subfamilies are given.

Accounts for each species occupy an entire page, headed with the common name and binomial Latin names, although the naming authority is not provided. High-quality photographs from nature, a distributional map, and a photograph of a typical host plant, or in some cases, of a habitat, are provided. In a few instances, photographs of pinned museum specimens are used to fully illustrate the species. A short account of status, ecology, and conservation status appears adjacent to a distributional map of each species. This is followed by brief notes on dorsal and ventral characteristics for identification, habitat, hostplants, occurrence, and a very short general statement on ecological strategy in relation to hostplant and environment. A full-size indication of average wingspan is given at the bottom of each page with measurements in decimal inches. The one-page-per-species format makes for efficient use of this book, without requiring the reader to page between text on one place and

figures on another. There is no need to refer to a set of “standard species” for size references, as is necessary with the series of publications for butterfly observers by Jeffrey Glassberg. The volume finishes with a list of sources and an index arranged by scientific and common names of butterflies and host plants.

A few small nuggets are hidden within the pages of this work in the form of single-page accounts of unique or critical aspects of the ecology, life history, or taxonomy of a particular species or species group. The authors do not list these little treasures in the contents page and refer to them only indirectly in the index, thus leaving the reader to discover them by chance. Upon encountering the first such entry, I was drawn immediately to prospect through the rest of the book, marking and reading each of the other 10 as I found them.

Although the book is limited in geographical scope to the eastern seaboard, many of the species covered are found farther west. This well-done volume will appeal to the amateur and professional alike.

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Invasive Arthropods in Agriculture

G. J. Hallman and C. P. Schwalbe, Editors
Science Publishers, Enfield, NH
2002, 447 pp.
Price: \$99.50, hardcover
ISBN: 1-57808-172-6

U.S. agriculture is crawling with pests and diseases introduced from other countries. Approximately 500 nonnative arthropods are serious pests in crops. Billions of dollars are lost annually, in part, from lost crop production and greater management expenses that often follow pest invasion. By recognizing the risks posed by exotic arthropods, nations may wisely stiffen regulation of international trade to limit new arrivals, but political expressions of concern about invasive species can be mere ploys to change the balance of trade between nations. Beyond trade, awareness of the impacts of invasive species on managed and unmanaged ecosystems continues to grow. Within this context, editors Hallman and Schwalbe depict past, present, and future challenges posed by exotic species in *Invasive Arthropods in Agriculture*.

The text provides unique insights on the invasive species problem from the perspective of regulatory entomology, where laws, rules, and regulations provide additional tools for the integrated management of introduced pests. In this case, management includes efforts to prevent new arrivals, detect recent introductions, eradicate highly threatening species, and implement areawide pest control programs, especially classical biological control.

The text emphasizes challenges faced by the U.S. Department of Agriculture, Animal and Plant Health Inspection Service (USDA, APHIS). This agency strives to “protect the health and value of American agriculture and natural resources” by “safeguard[ing] the health of animals, plants, and ecosystems in the United States; and [facilitating] safe agricultural trade” (USDA 2005). APHIS receives its authority from federal statute (e.g., Plant Protection Act of 2000) but it must work within bounds established by international agreements (e.g., the World Trade Organization [WTO] Agreement on the Application of Sanitary and Phytosanitary Measures).

To achieve its mission, APHIS collaborates with numerous partners within and outside the federal government. The USDA Agricultural Research Service (ARS) provides many key collaborators, especially for the development of quarantine treatments and new pest detection methods. APHIS also works with university and federal scientists to refine methods for pest risk assessment (the process used to evaluate the probability and consequence of establishment by new pests) and improve biological control practices. Hallman (from ARS) and Schwalbe (from APHIS) draw from this pool of scientists and regulatory officials to demonstrate how responses to invasive species have changed and are likely to evolve in the future.

Contributions from 28 authors are loosely organized around four general topics. Chapters 1–6 and 9 deal with the “socio-political facets” of arthropod invasion, including the history and status of current regulations governing invasive species, costs associated with exotic pests, and factors predisposing agricultural systems to invasion. Chapters 7, 8, and 11 address pest risk assessment. Chapters 10, 12–14, and 16 describe new methods for quarantine, eradication, and control. Chapters 15, 17, and 18 focus specifically on classical biological control, a special case in which arthropod invasion can have tremendous advantages, if carefully planned and executed, or disastrous consequences, if not. The final chapter, 19, concludes with thoughts on the future of regulatory entomology.

In many agricultural systems, low genetic diversity among crop plants, high resource input, and high degrees of disturbance create simplified ecosystems that seem prone to invasion. The purported relationship between species diversity and ecosystem stability provides the theoretical underpinnings of this argument. Recommendations for greater agricultural biodiversity would have been stronger had an alternative explanation been addressed. For example, not mentioned in the text is Simberloff (2000) who dismisses the diversity–stability

relationship and suggests that a greater frequency and density of new arrivals accounts for the larger number of successful invasions in agricultural systems than in other ecosystems.

Preventing new introductions is recognized as the ideal method to combat the invasive species problem, though this was not always the case. From the 1700s through the establishment of the Department of Agriculture in 1862, introduction of potentially valuable foreign plants was encouraged. With these plants came new pests. The Insect Pest Act of 1905 and the Plant Quarantine Act of 1912 marked the start of a growing awareness about the invasive species problem and an appreciation for stronger regulatory responses. The historical account in the book is outstanding. Domestic regulations are placed into an international context with a clear, thorough explanation of current WTO rules governing regulatory responses to exotic species moved in international trade. Beyond trade, exotic species may arrive in the United States through a mind-boggling diversity of pathways (e.g., living beetles adorned with rhinestones brought as living jewelry!). These pathways are thoroughly discussed.

Three particularly valuable chapters discuss a suite of tools for pest risk assessment (e.g., phenology models, CLIMEX, GARP analysis, process-oriented simulation models). Better predictions of where exotic species might become established and which systems might be affected will be essential to determine when and what regulatory actions are appropriate.

The discussion of costs associated with introduced species is disappointing. This chapter is almost identical to a paper first published in *BioScience* (Pimentel et al. 2000), but it is limited to excerpts relevant to arthropods and mollusks. The chapter provides no new information. Interested readers would be better served to review the original, which is the source for the widely quoted \$137 billion annual impact from all nonindigenous species in the United States.

The text is particularly suited to those who are interested in but unfamiliar with regulatory entomology and could be the basis for an interesting graduate-level colloquium. Elements of the book will also appeal to anyone interested in historical entomology. A notable, but hardly fatal, shortcoming of the book is a lack of contribution from the USDA Forest Service. The Forest Service has been a partner with APHIS, for example, to slow the spread of gypsy moth [*Lymtria dispar* (L.)] and to evaluate the previously underappreciated risks posed by solid wood packing materials. Some perspectives from this organization would have been an interesting complement to a diverse group of authors who share the common goal of preventing damage from invasive arthropods.

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