Biology of Snail-Killing Sciomyzidae Flies

Written for academic researchers and graduate students in entomology, this is the first comprehensive analysis of sciomyzid flies.

Sciomyzid flies are important as prime candidates for the biological control of snails and slugs that help transmit diseases such as schistosomiasis or are important agricultural pests. They also can serve as a paradigm for the study of the evolution of feeding behavior in predatory insects. Starting with analyses of malacophagy in general and then in Diptera specifically, all important aspects of the Sciomyzidae are discussed, including behavior, ecology, life cycles, morphology, and identification. New behavioral and morphological classifications and hypotheses are proposed on the basis of unpublished information and a complete analysis of the extensive literature. Also included are keys to adults, larvae, and puparia and a checklist of world species, with information on geographical range and the location of type specimens. The accompanying DVD includes Clifford O. Berg's classic film on the biology of Sciomyzidae and biological control of snails.

Lloyd Vernon Knutson is an emeritus of the US Department of Agriculture's Systematic Entomology Laboratory at the Smithsonian Institution and is a Cooperating Entomologist of the Centro Nazionale per lo Studio e la Conservazione della Biodiversitá Forestale, Verona, Italy. He has studied the Sciomyzidae for more than 40 years and has published more than 100 papers on various aspects of their biology.

Jean-Claude Vala is Professor of Biology, Laboratoire de Biologie des Ligneux et des Grandes Cultures, at the University of Orléans, France. His more than 60 published works on the Sciomyzidae over the past 30 years cover field collections, life cycles, biology, classification, scanning microscopy of immature stages, and ecological adaptations relating morphology with larval habitats.

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CAMBRIDGE
UNIVERSITY PRESS

CAMBRIDGE UNIVERSITY PRESS
Cambridge, New York, Melbourne, Madrid, Cape Town,
Singapore, São Paulo, Delhi, Tokyo, Mexico City

Cambridge University Press
The Edinburgh Building, Cambridge CB2 8RU, UK

Published in the United States of America by
Cambridge University Press, New York

www.cambridge.org
Information on this title: www.cambridge.org/9780521867856

First published 2011

Printed in the United Kingdom at the University Press, Cambridge

A catalog record for this publication is available from the British Library

Library of Congress Cataloging-in-Publication Data

Biology of Snail-killing Sciomyzidae Flies / by Lloyd Vernon Knutson, Jean-Claude Vala.
p. cm.
ISBN 978-0-521-86785-6 (Hardback)
1. Sciomyzidae. 2. Snails–Biological control. 3. Snails as pests. I. Knutson, Lloyd,
II. Vala, Jean-Claude. III. Title.
QL537.S365B565 2010
595.77′4–dc22

2010016388

ISBN 978-0-521-86785-6 Hardback

This book is dedicated in remembrance of Clifford O. Berg, the pioneer of research on the natural history of Sciomyzidae.

Clifford O. Berg searching for sciomyzid larvae with a surface net of his design in Australia in 1961.

Clifford O. Berg, 1964. From Clarke (1987).

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Foreword by Benjamin A. Foote

When I first arrived at Cornell University in the fall of 1950 to begin doctoral studies on the biology of snail-killing flies, little did I realize the pleasure awaiting me in the coming years. There was, of course, the continuing excitement of encountering new species and unraveling previously unknown life histories, but even more exciting was developing interactions with many dedicated dipterists, such as Lloyd Knutson and Jean-Claude Vala. The mentor of our group of young fly-chasers at Cornell was Clifford O. Berg, who had discovered, apparently almost by chance, the remarkable association between the larvae of Sciomyzidae and their gastropod prey. One of the early members of this group was Lloyd Knutson, who would go on to enjoy a prominent career with the US Department of Agriculture entomology staff at the United States National Museum in Washington, DC, and later in Europe. Lloyd's doctoral dissertation dealt with the life histories of many European species of the family, and he has continued to explore the mysteries of the Sciomyzidae to the present day. During his European ventures, Lloyd met in 1980 another active worker on the family, Jean-Claude Vala of France. These colleagues developed a highly productive collaboration that has continued to the present day and which has now resulted in the publication of this remarkable discourse on the family Sciomyzidae.

The Sciomyzidae is a moderate-sized family of 539 species scattered through all of the world's biogeographical regions. Its alpha taxonomy is in good shape as a result of the efforts of George Steyskal, Jean Verbeke, Rudolf Rozkošný, Robert Orth, Ted Fisher, and many other dedicated taxonomists. This publication builds on that earlier taxonomic work but focuses on the natural history of the Sciomyzidae.

The information presented in this volume brings together observations published in some 3000 research papers, including over 400 published in the last 20 years or so. As such, it allows workers interested in malacophagy, in general, and in the family Sciomyzidae, in particular, ready access to a large and diverse literature. Particular attention is given to larval feeding habits, life cycles, host and prey relationships, phenology and development, morphology of all life stages, biological control of agriculturally and medically important gastropods, systematic and evolutionary topics, and collecting and rearing methods. The authors point out areas where further research is needed and emphasize topics such as phylogenetic sequencing studies, where meaningful work is just now being initiated. Particularly valuable is the large number of figures and tables that summarize data collected from many sources, so workers can quickly acquire information in their area of interest. I am particularly impressed by the useful and workable keys to genera of adults, puparia, and larvae. Compiling such is a remarkable feat in itself.

It is notable that a family that was practically unknown biologically up to the early 1950s is now generally considered to be one of the best-known families of acalyptrate Diptera, with 240 of 541 (38%) recognized species having known larval feeding habits. Biological information is now available for 41 of the 61 genera. This is truly a significant accomplishment, particularly when it is recognized that the family has not generally been considered economically important. This book is a testament to those many dedicated individuals who laboriously worked out life cycles, described larval feeding habits, explored ecological relationships, and described and illustrated the structures of the eggs, larvae, and puparia.

All authors of scientific treatises hope that their contributions will stimulate interest in the subject and encourage workers to develop new insights and approaches. This volume certainly will fulfill those goals!

Benjamin A. Foote, Professor Emeritus,
Kent State University, Kent, Ohio, USA

Foreword by Rudolf Rozkošný

Study of Sciomyzidae became a great challenge and an opportunity for science beginning in the 1950s. New fields of basic research as well as practical applications began early after proposal of the hypothesis of the general malacophagy of the Sciomyzidae, formulated with remarkable insight by Clifford O. Berg. His hypothesis was based on his rearing of malacophagous sciomyzid larvae in Alaska. Berg well realized the opportunity for further theoretical studies of relationships between flies and molluscs and the potential value of malacophagous larvae as biocontrol agents of undesirable species of snails and slugs. He created very favorable conditions for a new scientific school at Cornell University in Ithaca, New York. Theses of his first postgraduate students were oriented especially to autoecological, phenological, and behavioral studies of individual species and genera of Sciomyzidae from different parts of the world. Berg and his students launched generalizations concerning the range of intimate relations among snail-killing flies and their prey and hosts and in the surprisingly different phenological manifestations within the family Sciomyzidae.

During the following 50 years an array of students at Cornell, Avignon, and other places published results of their studies, frequently in collaboration with colleagues from various parts of the world. Biological information is available for 203 of the known 539 species. This proportion is unusual among the acalyptrate flies, even when families of economic importance are considered.

The present monograph is a panoramic review of achievements in all branches of the science of Sciomyzidae. It includes chapters on the nature of malacophagy, an overview on natural enemies of Mollusca, and parts dealing with biological properties of, and relations among the species of the family (feeding habits and preferences, competition, phenology, reproduction, development and life cycles, ecology, morphology, physiology, behavior, population dynamics, genetics, systematics, biogeography, evolution, and biological control). History of research, notes on methodology, and a world checklist of Sciomyzidae complete this outstanding source of information. The authors present analytical evaluations of the huge amount of information available. They advance synthetic hypotheses in which they both participated recently. I mention especially, a new proposal of behavioral groups and trophic guilds, basic ideas about the evolution of the family, and an improved analysis of phenological types. They combine their deep and broad theoretical knowledge with personal experience in laboratory and field experiments performed not only in the temperate zone, but also in subtropical and tropical areas, with great success.

Sciomyzid larvae feed as aquatic predators of snails, pea mussels, and oligochaetes or as terrestrial parasitoids (and/or predators) of hygrophilous and terrestrial snails; a few attack slugs or consume snail eggs. The Sciomyzidae have colonized a great variety of ecosystems from various types of chiefly stagnant waters, moist habitats of semi-aquatic types, mesophytic woods, and even some xerothermic sites. The larval morphology shows differences in relation to those feeding habits. Larvae of Sciomyzini live chiefly as parasitoids in exposed aquatic, hygrophilous and terrestrial snails whereas larvae of Tetanocerini mainly include overt predators of aquatic molluscs and oligochaetes or terrestrial snails and slugs. Mature larvae of some *Tetanocera* spp. are able to immobilize their prey by injection of a neurotoxin produced in their salivary glands.

The methods used in the research have been as diverse as the investigated phenomena have been rich. Methods of rearing the larvae and laboratory and field experiments are elaborated in detail. Microstructures of eggs, larvae, and adults were studied by scanning electron microscopy. Crucial phases of the development of a few species were followed by video photography. Molecular analyses of DNA sequences as a tool for assessment of phylogenetic relationships are reviewed.

I had the good fortune to participate in the development of the modern study of Sciomyzidae, at least in the main contours, almost from the beginning. I was in correspondence with Clifford Berg from the 1960s and later with

Lloyd Knutson. Professor Berg offered me a one-year stay at Cornell University, but the occupation of what was then Czechoslovakia in 1968 interrupted such educational programs for many years. I met Lloyd Knutson during his first visit to Czechoslovakia in 1970. We discussed Sciomyzidae until the late hours. From that date until today, we have regularly exchanged information and have prepared a series of joint publications. Jean-Claude Vala and I initiated contact in the early 1980s when he started his studies on Mediterranean sciomyzids and began to prepare his Ph.D. thesis. In 1985, he invited me to participate in the defense of his dissertation, but I had to abandon my participation owing to duties at my university. Nevertheless, I have followed his scientific career during the subsequent years and met him when he visited Masaryk University in Brno in 2001. We discussed especially his new discoveries in feeding habits of some species attacking oligochaetes and new microstructures and sensilla on the body surface of larvae. We met at the Fifth International Congress of Dipterology in Brisbane, Australia, where Jean-Claude presented stunning new data on non-malacophagous larvae of Sciomyzidae.

So, my dear friends, it is really a pleasure to assist at the birth of your fascinating book. I am convinced that it will become a much-frequented source of updated information on all aspects of Sciomyzidae, not only for specialists and other dipterists, but also for professional as well as amateur researchers in different branches of biology.

Rudolf Rozkošný, Professor Emeritus,
Masaryk University, Brno, Czech Republic

Preface

We provide here the first review and analysis of the vast amount of information on this intensively studied group of flies, information gained over the past two and a half centuries that is widely scattered in publications in 16 languages, often in obscure journals, some critical studies being in as yet unpublished reports. We have crafted this work from the perspective of our own research on most aspects of Sciomyzidae during the past 4 + and 2 + decades, respectively, in North, Central, and South America, Western Europe, the Middle East, and Africa. We have sought to be comprehensive, not over-emphasizing archival detail but presenting enough appropriate detail when it is necessary to develop a conclusion, a hypothesis, a scenario, the germ of an idea, or a question. Often this has meant combining or relating significant bits of information from many studies, i.e., "bricks" that were not the main subject of a study but which resulted because the species under study provided the opportunity, and the observations then were included as related information. Mining the literature for such gems, unearthing buried bricks as it were, and relating them has been surprisingly rewarding prospecting.

We arrange the data, the "bricks" of Henri Poincaré (1902) and Marston Bates (1949), by subject, i.e., behavioral, ecological, and morphological, etc., not by species, life style, etc. While our approach has the advantage of enabling generalizations, it has the disadvantage of sometimes separating more or less related data gained on biological features of species x, at time y, at place z. A few species (*Ilione albiseta*, *Salticella fasciata*, *Sciomyza varia*, *Sepedon fuscipennis*, *S. sphegea*, *S. spinipes*, and *Tetanocera ferruginea*) have been particularly well studied. Thus it is useful to relate the discussions of these species under the various chapters, developing, so to speak, the architecture of these key species. But for many specific aspects, other species have been better studied. Relating data on those species to data on key species will be instructive. For these purposes, the text is extensively cross-referenced. The reader is encouraged to re-arrange the "bricks" to arrive at more sound generalizations, more pleasing edifices, than we present.

We allude to, ask questions about, and perhaps provide some mortar concerning mechanisms that might be responsible for the diversity of behavioral attributes and morphological features of Sciomyzidae. We are inclined to agree with Huston's (1994) conclusion in regard to the study of biological diversity in general: "The important question . . . is not which explanation for species diversity is correct, since virtually every explanation that has been proposed is important under some circumstances. The critical questions are which of the many potential explanations apply to a specific diversity pattern, whether any particular mechanism is the dominant explanation for a specific pattern . . . and whether there are any general rules about which mechanisms are likely to be important under particular environmental conditions, among specific groups of organisms, or at particular spatial and temporal scales." However, our essentially natural history approach to the study of Sciomyzidae, and some of our conclusions, e.g., the probable lack of competition within and among sciomyzids in nature, lead us to identify more with the autoecological than the demographic paradigm of ecological theory as distinguished by Hengeveld & Walter (1999).

We place special emphasis on ordering and arranging certain information (e.g., feeding behavior, feeding sites, phenology) to make the data easier to grasp, to provide food for thought, and to encourage further analysis and research. We do this at the risk of creating categories of the mind when they may not exist in nature, but with the pardoning admonition of one of our (LK's) instructors at Cornell in 1959, the late Howard E. Evans: "Look out the window – what do you see? Order, not chaos. Nature is ordered, not chaotic" (paraphrased from a 49-year-old recollection). We take the reader from an overview of malacophagy in general, through the major aspects of the biology of Sciomyzidae, building to sections on their potential use as an example of the evolution of behavior in parasitoid and predaceous insects, and finally to their use as economically sound and environmentally safe biocontrol agents. We attempt to relate the biology of Sciomyzidae to

some major questions in behavior, ecology, and evolution, most for the first time.

Some say that a deficiency of modern science is a failure to respect, to make use of, "old" science. In fact, many critical theories, principles, etc. on which "new" science is based rely upon experiments and observations that were made only once and the results of which are questionable. This may be true of even pedestrian analyses such as ours on the Sciomyzidae. As we have plodded through a sizeable literature we have made extensive use of figures and tables published over the past century. Those were presented in various languages and formats. We have translated all of them into English and present them in a uniform format.

In the rich literature on the natural history of animals, there are relatively few treatises on flies, although these ubiquitous creatures make up perhaps as much as 10% of all described animal species. Most of the comprehensive books on flies concern those of pest/biocontrol importance (mosquitoes, black flies, house flies, tsetse flies, horse flies, tephritid flies), environmental significance (chironomid gnats), as genetic research subjects (drosophilids), or some such combination (coffin flies). One of the values of this book may be in providing some indications of subjects worthy of broader treatment in further comprehensive summaries of Diptera biology, morphology, etc. In reading recent manuals and handbooks on Diptera, we have seen little mention of many "unusual" features of some Sciomyzidae – feeding on aquatic oligochaetes, clams, snail eggs and slugs; hydrostatic sperm pump; loss of ptilinum and palpi; calcareous septum produced in snail shells by pupariating larvae, etc. – that may not be, in fact, so unusual among Diptera but which are better known in the Sciomyzidae. Study of such features in related families and other Diptera may be useful.

Much of this book is eighteenth-century biology from a twenty-first-century perspective. For that we make no excuse and hope that our effort may inform, instruct, and perhaps even incite further research on the biodiversity of flies and lesser organisms. We have included detail on some field study and laboratory experimental methods and methods of analysis to aid in their use in other studies.

You are invited to visit the Sciomyzidae website (www.sciomyzidae.info), which includes a nearly complete bibliography, directory of researchers, list of current research projects, needed research, lists of desiderata of material for research, and other resources useful to the dipterist.

L. V. Knutson,
Gaeta, Italy
J-C. Vala,
Orléans, France

Avant propos

It is indeed wonderful to consider, that there should be a sort of learned men who are wholly employed in gathering together the refuse of nature, if I may call it so, and hoarding up in their chests and cabinets such treasures as others industriously avoid the sight of. Addison (1770) cited in Stearn (1981).

There are no principles too deep, no speculations too lofty to find application in such creatures as flies. Williston (1896).

The flies, poor things, were a mine of observation. Levi (in Horvitz 2000).

On fait la science avec des faits comme une maison avec des pierres; mais une accumulation de faits n'est pas plus une science qu'un tas de pierres n'est une maison. Science is built of facts the way a house is built of stones; but an accumulation of facts is no more science than a pile of stones is a house. Poincaré (1902).

Facts form the raw material of science – the bricks from which our model of the universe must be built – and we are rightly taught to search for sound and solid facts, for strong and heavy bricks that will serve us well in building foundations, for clean and polished bricks that will fit neatly into ornamental towers. But while accumulating the bricks may be a contribution to science, we must take care that the pile does not become a hopelessly discouraging jumble. For science itself is not brick-making – it is, at the workaday technical level, bricklaying; and at the creative and artistic level, architecture, the designing of an edifice that will utilize all the bricks to the very best advantage.

The metaphor, of course, cannot be carried too far. The bricklayers and the architects of science are always acquiring strange, new, and beautiful bricks that make it necessary to tear their careful building down and start over. It is an unending, dreamlike game that seems to be limitless – the model of the universe will never be done, nor does any part of it seem to have a comfortable or dependable permanence. But still the bricks, as bricks, cannot be left in a jumbled pile, and we have the task of organizing them into some sort of a pattern, however transient. Bates (1949).

. . . flies are a topic like drains, not to be discussed in polite society, to be left to those strange people who cultivate a professional interest in them. It is a pity. Oldroyd (1964).

About the authors

LLOYD VERNON KNUTSON was awarded a Ph.D. in Entomology from Cornell University in 1963, his thesis research under Professor C. O. Berg being on the biology and immature stages of European Sciomyzidae. He was a National Science Foundation (NSF) supported Research Associate with Professor Berg during 1963–1968, much of the time spent in Europe conducting field and laboratory studies of Sciomyzidae. From 1969 to 1973 he worked with the US Department of Agriculture, Systematic Entomology Laboratory, at the Smithsonian Institution, in which position he was responsible for taxonomic research on Sciomyzidae and other Diptera. He was appointed Chairman of the USDA Insect Identification and Beneficial Insect Introduction Institute at Beltsville, Maryland, in 1973, where he served for 15 years, with one year on leave to the Ecology Program, Smithsonian Institution, and one year on leave as Director, Systematic Biology Program, NSF, Washington, DC. In 1988 he became Director of the USDA Biological Control of Weeds Laboratory in Rome, Italy, and in 1991 as Director of the USDA European Biological Control Laboratory when he was responsible for combining the USDA Rome, Italy, and Paris laboratories in Montpellier, France. He retired in 1997 in southern France and moved to Italy in 2002. He served as President of the Entomological Society of America (ESA) from 1989 to 1990. He is an Honorary Member of ESA as well as an Honorary Foreign Member of the Russian Entomological Society. He has conducted field work on Sciomyzidae in North, Central, and South America, in Europe from Crete to Finnish Lapland, and in Ghana, Iran, Israel, Nigeria, and Pakistan. He has published 92 papers on various aspects of Sciomyzidae, many of which have been in collaboration with colleagues throughout the world. Knutson has been a Cooperating Entomologist, Centro Nazionale per lo Studio a la Conservazione della Biodiversitá Forestale, Verona, Italy, since 2007.

JEAN-CLAUDE VALA studied relationships between aquatic snails and digenetic Trematoda larvae and between fish and monogenetic Trematoda under Professor Louis Euzet at Montpellier University, France, from 1971 to 1973. From 1973 to 1977 he taught parasitology in the Faculty of Sciences of Oran, Algeria. In 1977, he moved to the Faculty of Sciences of Avignon, France, where he taught courses in zoology (systematics, reproduction, physiology, ecology, and entomology). He was awarded a Ph.D. in Entomology from Montpellier University in 1985, his thesis being on the systematics, biology, and population dynamics of the Sciomyzidae of France. He has published 63 papers on Sciomyzidae, covering field collections, life cycles, biology, scanning microscopy of immature stages – particularly on sensilla – and ecological adaptations relating morphology with larval habitats. His graduate students on Sciomyzidae – Claire Haab, Mohamed Ghamizi, Sylvie Manguin, and Ghélus Gbedjissi – and colleagues Christine Brunel, Christine Caillet, Charles Gasc, and Jean-Marie Reidenbach conducted research with him on various aspects of larval feeding, behavior, phenology, and morphology of Sciomyzidae and elucidated several life cycles. He has conducted field work in France, Algeria, and Bénin. In addition to Sciomyzidae, he conducts research on the systematics of Tabanidae and the biology of Chironomidae, pests of rice in southern France. In 1989 his "Diptera Sciomyzidae Euroméditerranéens" was published in the *Faune de France*. From 1998 to 2000 he was the Director of the Department of Biology, Avignon University. Since then, he has been Professor of Biology, Laboratoire de Biologie des Ligneux et des

Grandes Cultures, Orléans University, France where he continues research on many aspects of sciomyzid biology. With his colleague Xavier Pineau, he also studies relationships between cultivated fields and their immediate environment and the colonization and establishment of insects in different types of fallow lands. The work is focused primarily on the biodiversity of Carabidae living on the soil as bio-indicators of degradations of biotopes. From 2006, with his colleagues in plant–insect relationships, he has participated in the project on an emergent pest, the woolly poplar aphid *Phloeomyzus passerini* (Signoret).

JEAN-CLAUDE particularly wishes to thank Professor Louis Euzet, University of Montpellier, and Professor Claude Combes, University of Perpignan and Académie des Sciences de Paris, who were his early mentors in scientific investigation and for their continued rigorous advice.

Acknowledgments

We acknowledge our longstanding colleagues Ben Foote and Rudolf Rozkošný for diverse and important advice, encouragement, and assistance over the past five decades. The classification of behavioral groups was developed in extensive communication with J. K. Barnes. For permission to use published figures and tables and to quote from their publications we thank the authors and publishers as noted in the text, legends and references. For the use of unpublished data we thank J. Abercrombie, S. L. Arnold, J. Bouniard, A. D. Bratt, C. Caillet, E. Colonnelli, J. B. Coupland, J. C. Deeming, K. Durga Prasad, L. G. Gbedjissi, M. Ghamizi, K. D. Ghorpadé, C. Haab, J. B. Keiper, R. J. Mc Donnell, T. Pape, J. B. Peacock, M. C. D. Speight, N. Vikhrev, and P. Withers. For the use of unpublished photos and figures we thank J. K. Barnes, J. Ebel, B. A. Foote, C. Gasc, C. and H. W. Hoffeins, S. A. Marshall, R. E. Orth, M. Thomas, and the late J. W. Stephenson.

We thank Marty Schlabach, A. R. Mann Library, Cornell University and staff of the Division of Rare and Manuscript Collections for recovering Professor C. O. Berg's classic film from the Cornell University Archives and preparing the DVD, and E. Brown for permission to reproduce it herein.

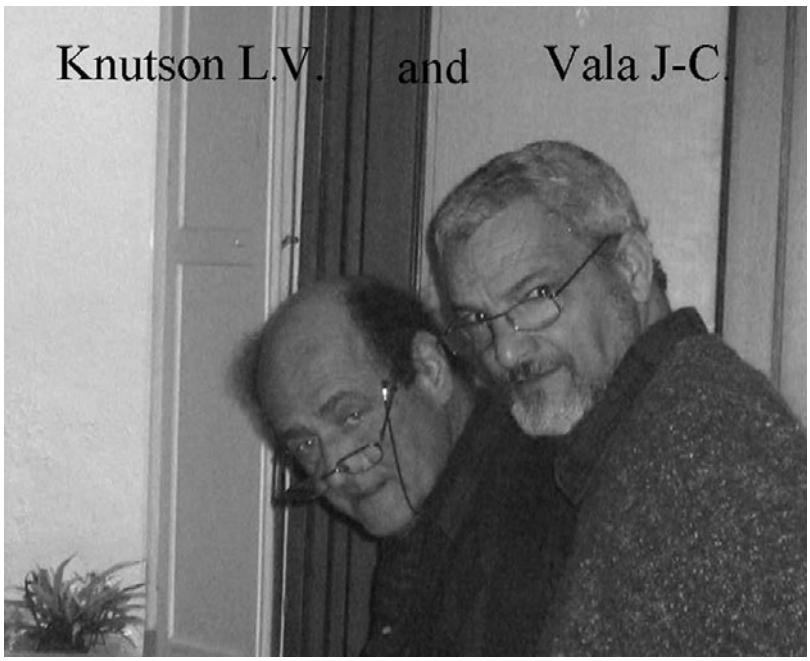
For checking names and classification of Mollusca, we thank C. Audibert, G. Manganelli, B. Métivier, and J-P. Pointier. For checking many names of insects in Index 2, we thank A. Freidberg, D. G. Furth, T. J. Henry, R. R. Kula, A. L. Norrbom, and N. E. Woodley. For obtaining literature references, we thank E. G. Chapman, H. V. Danks, C. Daugeron, E. Delfosse, J. Ebel, P. A. Espenshade, J. Guglielmi, the late M. Leclercq, M. Martinez, P. Mason, R. J. Mc Donnell, B. Merz, L. Munari, W. L. Murphy, D. Rodriguez, M. Schlabach, M. Sueyoshi, M. and C. Tauber, F. C. Thompson, H. Ulrich, and C. D. Williams. For assistance with translations we thank Agriculture Canada, M. Fargier, R. J. Gagné, L. W. Murphy, C. Sarré, R. Rozkošný, H. Ulrich, and J. Zuska.

Special thanks to the reviewers of parts of this manuscript: J. K. Barnes, D. A. Barraclough, E. G. Chapman, E. Colonnelli, R. H. L. Disney, B. A. Foote, A. Freidberg, M. Ghamizi, K. D. Ghorpadé, M. J. Gormally, K. C. Kim, S. A. Marshall, R. J. Mc Donnell, R. Meier, R. M. Miller, S. E. Neff, A. L. Norrbom, R. E. Orth, L. Papp, R. B. Root, R. Rozkošný, J. Sheahan, M. C. D. Speight, M. and C. Tauber, H. Ulrich, and C. D. Williams. We especially thank W. L. Murphy for an impeccable review of much of our final draft. Special thanks to the Cambridge University Press editorial team, D. Lewis, Commissioning Editor – Life Sciences, and his associates A. Evans, J. M. Jackson, A. Jones, L. Talbot, and L. Bennun, excellent copyeditor. We thank W. Cooper, former Editor for our initial contact with Cambridge University Press.

We greatly appreciate the gracious hospitality, assistance, and friendship of the literally hundreds of persons who have expedited our studies over the past, combined 80 decades.

Mara and Martine, thank you for your love, your care, and your patience over all these years of work.

Finally, we thank "our" flies, the Sciomyzidae.



"*Cela est bien dit répondit Candide, mais il faut cultiver notre jardian . . .*" [That is well said, answered Candide, but we must cultivate our garden . . .] Voltaire (1759).