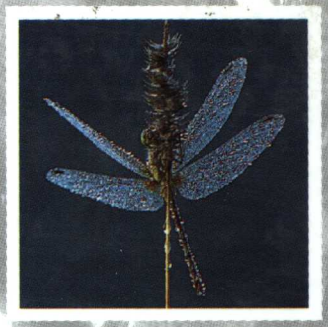
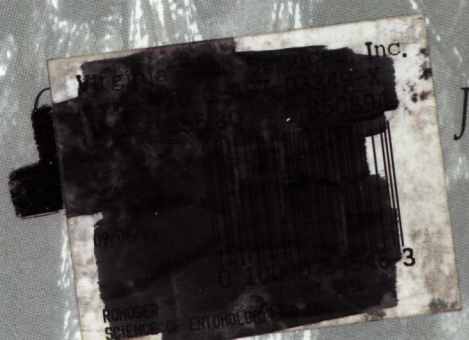
3rd Edition



THE SCIENCE OF

ENTOMOLOGY

William S. Romoser / John G[illegible] Jr.



3rd Edition

THE SCIENCE OF ENTOMOLOGY

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Preface

The magnitude of the role played by insects in the scheme of life is undisputed. In adaptive diversity and number of species, they are among the most successful of all organisms. The relatively few that cause problems have taxed our ingenuity to its fullest throughout history, and the battle will probably never be over. Thus the science of entomology is a vital applied science as well as one of the major areas of basic biology. In keeping with this fact, we have treated entomology from both basic and applied points of view.

Our objective in the third edition of this text has been to continue to provide a broad, balanced introduction to the topic of entomology for use in a one-quarter or one-semester general course. At the same time, we hope professional entomologists will find it useful as an up-to-date review and source of literature references.

The discussion of the literature of entomology has been retained in the introductory chapter from earlier editions with the hope that the student will be encouraged to make full use of the vast amount of information available. The remainder of the text is developed around four topics: structure and function spanning the cellular to organismal levels of biological organization (Part One); insects in an environmental context (Part Two); unity and diversity as reflected in insect systematics and as the result of organic evolution (Part Three); and finally, applied entomology (Part Four).

Substantial changes have been made throughout the book. All chapters have been updated and/or expanded; a new chapter on insects and plants has been added; a new chapter on integrated pest management in agroecosystems has been added; the coverage of the orders of Insecta has been increased; the glossary has been expanded to include new terms; new illustrations have been added, and a few old ones omitted; and the number of literature citations has been increased.

Part One, "Structure and Function," begins with a discussion of the diverse roles played by the integumentary system and subsequently elaborates on the structure and function of the insect skeleton. This is followed by discussions of the nervous, glandular, and muscular systems, and then the alimentary and remaining systems. The placement of the control and effector systems first facilitates discussions of regulation of the alimentary and remaining systems. Because the chapter on reproduction and morphogenesis stresses anatomy and physiology, it follows the chapters on anatomy and physiology. The chapters dealing with sensory mechanisms, locomotion, behavior, follow in a continuous and logical sequence.

Part Two, "Insects and Their Environment," begins with a discussion of insect populations and how these populations are influenced by, and react to, the physical, chemical, and biological factors in their environment. A separate chapter is devoted to the relationships between insects and plants.

Part Three, "Unity and Diversity," begins with a discussion of basic systematics, a topic that is all too often neglected in this day and age of molecular biology, and yet a topic that provides a foundation for the rest of biological science. The remainder of the first chapter in this section of the book centers around the origin and evolution of insects. The following two chapters provide an overview of the orders and selected major families in the class Insecta. We have tried to show how the various groups relate to one another, as well as provide information regarding their biology and medical, economic, and ecological significance.

Three chapters are included in Part Four, "Applied Entomology." In chapter 14, the many ways insects are beneficial and are harmful are discussed. In chapter 15, the various methods available to control insects are considered. In chapter 16, we use the topic of integrated pest management in agroecosystems to illustrate approaches

to insect control that are designed to be compatible with the need to minimize environmental damage.

We have arranged the topics in the sequence we think most appropriate for dealing with the various aspects of entomology. However, each chapter can be read and understood with minimal reference to other chapters. Thus, this text should be amenable to any organizational framework a given instructor may choose to follow. A reference list for each chapter, consisting mainly of major review papers, monographs, and specialized textbooks is given at the end of the book.

In addition to those persons who contributed to the first and second editions, we wish to express our sincere appreciation to the following individuals who have played important roles in the development of this edition. "Guest authors" Lance A. Durden (Institute of Arthropodology and Parasitology; Georgia Southern University), Bruce A. McPheron (Pennsylvania State University), Dave Ferro (University of Massachusetts), Patrice Morrow (University of Minnesota), and Margaret Lowman (Williams College), have greatly enriched the text by providing insightful revisions of chapters from the last edition or by writing new chapters. Although, unfortunately, in most cases their identities to us remain pleasant voices over the phone, the senior editorial staff at Wm. C. Brown—Kevin Kane, Carol Mills, and Michelle Campbell—have been delightful to work with and extraordinary in their patience and guidance in developing this text from the untidy first draft to the finished product. We also wish to thank the following Wm. C. Brown editorial staff members for their contributions to our project: Shirley Lanners, Connie Gibbs, Kathy Huinker, Kristyn Kalnes, and Vicki Krug. Copy editor Lynn Brown and her staff at Brown Editorial Service have done a diligent job of policing our grammatical blunders, run-on sentences, and various other unintentional assaults on the English language.

We also wish to thank our professional colleagues whose constructive comments have proven very helpful in producing an accurate, up-to-date text. These colleagues are as follows:

Chih-Ming Yin
University of Massachusetts, Amherst

Donald G. Cochran
Virginia Polytechnic Institute and State University

Robin Leech
Northern Alberta Institute of Technology/University of Alberta

Hal C. Reed
Oral Roberts University

A. G. Scarbrough
Towson State University

We offer a special thank you to Roger Meola, Texas A & M University, who has provided encouragement and advice throughout the life of this text.

As with past editions, the development of this third edition has been a challenging, demanding, at times frustrating, but ultimately very rewarding, experience. We are enthusiastic about our field; we are pleased to have an opportunity to share it with you; and we wish you well in your entomological quest.

W. S. R.
J. G. S.

BRIEF Contents

EXPANDED Contents

CHAPTER 1

Introduction

Insects are arthropods, the largest group in the Animal Kingdom. Arthropods are characterized by a segmented body that bears a varied number of paired and segmented appendages; bilateral symmetry; an exoskeleton that contains the nitrogenous polysaccharide, chitin; and various internal features, such as an open circulatory system, Malpighian tubules (generally), and in most a system of ventilatory tubules (the tracheae and tracheoles).

Insects can be differentiated from the vast majority of other arthropods by several rather distinct traits. Among these are three well-defined body regions: a head, a thorax, and an abdomen; three pairs of legs in the adult stage; commonly one or two pairs of wings; a single pair of segmented antennae on the head; and several less obvious but equally distinctive characteristics. The name *Hexapoda* (six legs) is commonly applied to insects. However, the name *Insecta* is preferable, because there is some question as to whether all arthropods with six legs in the adult stage actually belong in the same class (Sharov 1966). Insecta literally means "in-cut," which describes the segmented appearance of the members of this class. The arthropods will be discussed in more detail when we consider the evolution of insects.

Significance of Insects

Insects as a group are highly successful organisms. Their significance can be looked upon from two standpoints: their tremendous success relative to organisms other than human beings and their extreme importance from the human point of view.

One useful measure of the success of insects is the number of extant (as opposed to extinct) species. Insects probably outnumber all the other species of animals and all the species of plants combined. Estimates based on the current rates of description of new species of insects run from one to several million, and several large groups have hardly been studied. Arnett (1985) estimates the number of described insect species in the world to be 751,012 and points out the sad fact that we may never know the actual number due to the rapid destruction of habitat worldwide. Studies of tropical insect fauna lead to widely divergent estimates of the total world insect fauna (described plus undescribed) ranging from somewhere between 5 and 10 million (Gaston 1991) to 30 million or more (Erwin 1982, 1988).

Other important criteria for success include the span of geologic time traversed by a group of organisms and their adaptability to various environmental situations. Insects are thought to have arisen in the Devonian era, approximately 400 million years ago. Mammals as a group are approximately 230 million years old; modern humans arose perhaps 1 million years ago. In this sense, insects have not invaded the human world; we have invaded theirs! The adaptability of the basic insectan plan has been phenomenal. Insects can be found in nearly every conceivable terrestrial habitat. As you proceed with your study of insects, you will come to realize the seemingly unlimited adaptability of insects and gain insight as to how they have reached their position of success.

From earliest times people have seen certain insect species as arch enemies. Although the pest species make up a very small proportion of the total number of insect species, members of this group are chronic troublemakers, destroying annually millions of dollars worth of agricultural crops, fruits, shade trees and ornamental plants, stored products of various sorts, household items, and other valuable material goods (Davidson and Lyon 1987). Pest species act as vectors of the causative agents of human and domestic animal and wildlife diseases, and their direct attacks cause irritation, blood loss, and sometimes death (Harwood and James 1979, Kettle 1984).

However, there are two sides to the picture. Insects provide many highly valued goods and services. Such insect products as honey and beeswax, silk, shellac, and cochineal are used for a variety of applications, ranging from sweetening biscuits to constituting one of the basic components of many cosmetics. In addition, there are many indirect benefits of insect activities, such as plant pollination and involvement in nutrient cycling.

Although there is much that can be said both for and against insects as they relate to humans, the vast majority of insects are neutral, neither bestowing benefit nor causing harm.

The Science of Entomology

Entomology is a specialized field within the biological sciences, because it is concerned with "living" systems. The biological sciences can be divided into basic divisions, such as morphology, physiology, genetics, and ecology, and into taxonomic divisions, such as ornithology, mycology, and bacteriology. Entomology, as the study of a very specific group of organisms, is a taxonomic division. Therefore, we can approach the science of entomology by considering the "basic" divisions as they apply to insects: insect morphology, physiology, ecology, and so on.

The study of insects has played and continues to play a major role in the development of biology. This is evident upon examination of a current general biology text. Among the entomological topics, one might find the following:

> Redi's experiments with maggots and spontaneous generation; coevolution of plants and pollinating insects; the mechanisms of sex determination in insects; mutations in *Drosophila;* linkage groups, sex-linkage, chromosomal mapping, and induced mutations in *Drosophila;* chromosomal puffs in *Drosophila* and their induction by ecdysone; pheromones; behavioral genetics of cricket singing; spatial orientation of the digger wasp; migration of the monarch butterfly; circadian rhythms and adult emergence in *Drosophila pseudoobscura;* several other behavioral examples using insects (including behavior of the honey bee); termite–protozoan mutualism; temperature control in termite mounds and beehives; bees and orchids; ants and acacias; fig wasps and figs; industrial melanism; specialization in the *Drosophila willistoni* complex; pesticide problems. . . .

Further evidence for the major role played by entomology in the development of biology is that Nobel Prizes have been awarded to several scientists who studied insects, e.g., Karl von Frisch, Niko Tinbergen, and Konrad Lorenz.

For an excellent introduction to entomology as a science, see Wigglesworth (1976).

Entomological Information

A serious study of entomology requires a knowledge of resources available that help entomologists to acquire information about insects. The oldest and still one of the most important means is by word of mouth. This is the method employed in the classroom, at scientific meetings, conferences, and so on. Perhaps its most valuable aspect is the opportunity for a two-way exchange of information. Ideally, in this situation the lines of communication are wide open and a minimal amount of ambiguity should be the result. Another, equally important—in fact, essential—means of acquiring scientific information is consultation of the literature. The advantage of this method is that one can go back in time as far as one wishes, but the two-way exchange of information is impossible if the author of a piece of recorded work is no longer living. Both these means of acquiring information should be considered to be prerequisites for a third means—personal investigation. This method is, of course, the source of new information. All three means are essential to the existence of science, and certainly no one method could take precedence over the other two. However, let us delve further into the use of entomological literature.

The literature of entomology consists of a wide variety of publications ranging from rather popularized accounts intended for the layperson to highly technical treatises on very specific aspects of the science. The information available on insects is vast and is growing so rapidly that no one person can stay abreast of and learn more than comparatively small portions of it. There is also a great deal of specialization, the concentration of effort on a single topic or a group of closely related topics. Thus, among entomologists there are, for example, insect physiologists, ecologists, morphologists, systematists, toxicologists, and economic entomologists. Generally, the specialization goes even further; someone in one of the preceding groups may concentrate on a particular insect species or group of insects, or on a specific topic, or both. For example, there are specialists in the systematics of a particular family of beetles or in mosquito physiology.

The tremendous number of entomological publications makes a comprehensive review inappropriate within the context of this book. However, a brief discussion of some of the different types of entomological literature may be helpful. More extensive treatments of the literature of entomology and zoology in general can be found in Smith, Reid, and Luchsinger (1980), Chamberlin (1952), and Blackwelder (1967). The recent compendium by Gilbert and Hamilton (1990) deserves special mention.

Publications pertinent to entomology (for that matter, the entire field of zoology) can be divided into two basic groups. The first group includes all those publications, irrespective of type, that contain the actual information about animals (insects). This group presents the products of zoological (entomological) research. The second group

includes all the publications that attempt to coordinate the vast information contained in the first group, making it more readily available to investigators. Examples of publications from each of these groups are presented. This method of classification, as with most, is certainly not without exception, as will be shown.

Publications That Contain the Actual Information about Entomology

Textbooks

A textbook is generally designed to give the reader an understanding of the basic principles involved in a given subject. A textbook may be quite general in scope, presenting a survey or overview of an entire field—for example, a general entomology textbook such as the one you are reading or any of several others, including Borror, Triplehorn, and Johnson (1989), C.S.I.R.O. (1991), Richards and Davies (1977, 1978) and Evans (1984). Other textbooks deal with a particular area within the field. For example, there are texts devoted to insect physiology—Chapman (1982), Blum (1985), and Wigglesworth (1972); insect ecology—Price (1984); insect behavior—Matthews and Matthews (1978), Atkins (1980); medical entomology—Harwood and James (1979), Kettle (1984); or economic entomology—Davidson and Lyon (1987). Books of this type treat a subject in more depth than the general text and are more likely to be used in advanced courses.

Monographs

A monograph is limited in scope, dealing with only a very small area within a science. However, monographs are usually comprehensive in their coverage of pertinent literature and handling of subject matter. Excellent examples are Dethier's superb *The Hungry Fly* (1976) and the 1990 Pulitzer Prize-winning book, *The Ants* by Hölldobler and Wilson.

Symposia

Symposia proceedings are published collections of the presentations of several specialists in a given area who have met to consider a specific aspect of science. A recent example, which deals in great depth with a particular group of mosquito-borne viruses, is *California Serogroup Viruses* (Calisher and Thompson 1983) which is the published proceedings of an international symposium.

Lectures

A lecture is an oral discourse presented to an audience or class, particularly for instructional purposes. Good examples of entomological lectures are the talks presented by outstanding scientists to the general sessions usually held several times during each annual meeting of the various entomological societies throughout the world. These talks are commonly published in bulletins issued periodically by these societies.

Essays

Essays are analytical or interpretative expositions that usually deal with a given topic from a rather personal or limited point of view. A well-known example is the book *Silent Spring* by Rachel Carson.

Reference Works

Reference books generally attempt to offer comprehensive coverage of a specific area and are designed to be consulted as needed rather than read and digested in their entirety. This category may seem rather arbitrary, since any piece of literature that is consulted can be classified as a reference, and rigorously documented and highly technical entomological texts, such as Richards and Davies (1977, 1978) and *The Insects of Australia* (C.S.I.R.O. 1991), can equally well be viewed as reference works. An especially valuable recent reference work is the thirteen-volume set entitled *Comprehensive Insect Physiology, Biochemistry, and Pharmacology* (Kerkut and Gilbert 1985).

Pamphlets

Pamphlets are usually rather brief writings on a specific topic, commonly geared to the persons who put many of the findings of entomological research into practice: farmers, exterminators, and so on. Examples of pamphlets are the *Farmer's Bulletins* published by the U.S. Department of Agriculture, which pertain to the biology and control of economically important species of insects.

Reports

From time to time, groups of experts are called together to investigate or to discuss an issue or problem of particular significance. For example, the World Health Organization (WHO) periodically sponsors meetings of expert committees on various problems pertaining to international health matters, including topics such as malaria and similar diseases with which insects are involved. These committees usually submit reports describing the problems discussed and the conclusions reached in the course of the meeting.

Series

Serial publications are issued periodically (sometimes at irregular intervals) and have a certain unity of subject matter; that is, a particular series deals, volume after volume, with more or less the same general subject matter. Series are published by most professional societies and many private and governmental concerns in the form of journals, bulletins, miscellaneous publications, yearbooks, and so on. Hammack (1970) and more recently

Gilbert and Hamilton (1990) provide useful and comprehensive descriptions of the serial literature pertinent to entomology. Some examples of entomological journals are *Annals of the Entomological Society of America, Journal of Economic Entomology, Environmental Entomology, Journal of Insect Physiology, Systematic Entomology, Ecological Entomology, Physiological Entomology, Psyche, Journal of Insect Behavior, Boletín de La Asociacion Española de la Entomologia, Canadian Entomologist, Deutsche Entomologische Zeitschrift (Berliner Entomologische Zeitschrift), Bulletin de La Société Entomologique de La France.*

Publications That Attempt to Coordinate the Literature

From the time scientists realized the fantastic rate of growth of the literature of science, many very useful attempts to coordinate and integrate the works in various areas have been made. In this section we want to discuss briefly some of the more common publications in this category. Most of these publications are quite expensive and are seldom purchased by an individual.

Bibliographies

A bibliography is to the literature of science as an index is to a book, the basic difference being that a bibliography lists only publications of various sorts on a single topic, instead of the subjects, authors, and so on, that are found in the index of a single book. Bibliographies appear in different forms. For example, one form is a list of pertinent references at the end of a chapter of a book or a scientific paper. Another type of bibliography is issued periodically and lists current publications in a particular field. Important examples of this type are *Zoological Record, Bioresearch Index, Bibliography of Agriculture, Cumulated Index Medicus,* and *Current Contents.* The *Zoological Record* has a very broad coverage, both foreign and domestic, and is arranged according to taxonomic groups and by subjects. The section on insects is quite extensive and contains references to papers of interest to most entomologists, not just taxonomists. *Bioresearch Index* is a monthly publication that furnishes bibliographies from various journals and contains citations of research papers. The *Bibliography of Agriculture,* a monthly publication, generally contains a large number of references to entomological papers. The last issue of each year is a cumulative subject index. *Cumulated Index Medicus* is issued four times yearly, covers much of the foreign and domestic medical literature, and may contain references of interest, particularly to medical entomologists. *Current Contents* reprints the tables of contents of many journals, several entomologically oriented ones included. It is issued weekly and is probably one of the best ways to keep abreast of the most current literature. This is especially important when one is working in a very active area in which a number of researchers are publishing extensively and often. The recent availability of current contents on computer diskettes has greatly enhanced the process of using this publication.

Abstracting Journals

Abstracting journals contain brief descriptions or abstracts of the results reported in the journals that fall within their scope. Abstracts are extremely useful because they give an investigator a better idea of the content of a given reference than does a mere title listing, although they do serve also as bibliographies. This kind of information helps one decide whether or not to consult the actual references and compensates somewhat for the fact that some publications are extremely difficult to obtain or translate from a foreign language. Abstracting journals are usually extensively cross-indexed, which makes them efficient to use. One of the most significant examples of this type of publication is *Biological Abstracts.* This bimonthly publication is comprehensive in its coverage of the literature of both theoretical and applied biology. In addition to the volumes containing the abstracts, a semimonthly publication, *B.A.S.I.C.,* provides an elaborate computerized subject index to the issues of *Biological Abstracts.* A cumulative subject index based on all the issues of *B.A.S.I.C.* is published semiannually. Since January 1970 the abstracts and citations of research papers pertaining to insects and arachnids in *Biological Abstracts* and *Bioresearch Index* have been compiled into a separate publication, *Abstracts of Entomology.* One issue of this publication corresponds to two issues of *Biological Abstracts* and one issue of *Bioresearch Index.*

Other abstracting journals that specialize in covering entomological literature are *Entomology Abstracts* and *Review of Applied Entomology. Entomology Abstracts* is published monthly and covers a wide variety of entomological topics. *Review of Applied Entomology* is published in two series: Series A, Agricultural, and Series B, Medical and Veterinary. It is well indexed, both by subject and author, and contains abstracts covering a wide variety of entomological topics. Other periodical publications that are at least partly abstracting journals are *Biologisches Zentralblatt, Physiological Abstracts, Tropical Diseases Bulletin, Apicultural Abstracts,* and several others from various countries.

Another very useful monthly publication is *Dissertation Abstracts.* This contains abstracts of all dissertations (i.e., the printed results of doctoral student research) by contributing institutions in the United States and Canada. It is arranged by the type of subject matter. These abstracts are useful since there is commonly a significant period of time between the writing of a dissertation and the publication of a research paper or papers based on it. If one decides on the basis of a given abstract that more information is necessary, he or she may

readily obtain, for a fee, a microfilm or printed copy of an entire dissertation. In a similar vein, *Dissertation Abstracts* publishes abstracts from contributing worldwide institutions.

Review Journals

Review journals contain papers that discuss the literature on a rather specific topic in a given field. Review papers not only bring together information from the pertinent literature on a given topic but also commonly contain useful syntheses of information that may not occur in any other type of publication. In this sense they may be classed in either of the two rather arbitrary categories we have used to discuss entomological literature. Two very important review journals in the field of entomology are the *Annual Review of Entomology* and *Advances in Insect Physiology*. Other review journals that may contain reviews of entomological interest are the *Annual Review of Ecology and Systematics, Annual Review of Physiology, Annual Review of Phytopathology,* and the *Annual Review of Medicine*. In addition, review papers may appear in journals, bulletins, and so on, which contain other types of articles.

Taxonomic Indexes and Catalogs

Taxonomic indexes include literature references to such items as the original description of a given genus or species and revisions of genera. These publications are quite useful for tracing the taxonomic literature pertinent to a given group and for determining the systematic position of a given genus or species. Especially important indexes are *Nomenclator Zoologicus* edited by A. A. Neave, *Zoological Record,* and *Biological Abstracts*. *Nomenclator Zoologicus* lists the names of genera and subgenera of all zoological groups from 1758, the year of the publication of the 10th edition of Carl Linne's (Linnaeus) *Systema Naturae,* to 1950. *Zoological Record* contains the names of all new genera described each year and pertinent literature references from 1864. *Biological Abstracts,* in the section "Systematic Zoology," provides references to the original descriptions of genera and subgenera of animals since 1935. Smith (1958) points out that "Neave's *Nomenclator Zoologicus* and *Biological Abstracts* serve admirably as a complete generic index from 1758 to the present." He further suggests that ". . . for names published since the most recent issues of *Biological Abstracts,* journals in which new genera of the various groups might be expected to occur must be consulted."

For species indexes and catalogs similar to the generic ones just described, one must refer to one or more of several currently available. Sherborn's *Index Animalium* is the only general species index available and covers all the specific names proposed for animals from 1758 through 1800. Smith, Reid, and Luchsinger (1980), Chamberlin (1952) and Blackwelder (1967) each contain lists of catalogs for various insectan and other groups.

Science Citation Index

The Science Citation Index is published by the organization that publishes *Current Contents* and is composed of two sets of indexes, a citation index and a source index, both of which are cumulative. Its objective is to list and index the current and past research papers that cite a given reference. It enables an investigator to begin with a given reference and find other references that have cited the "starting reference." Because both the "starting reference" and "citing reference" are likely to pertain to the same or very closely related topics, one is able to proceed forward or backward in time, using "citing references" as "starting references" in a cyclical manner and by doing so accumulate references on a given topic.

Union List of Serials and New Serial Titles

Most libraries do not have complete sets of all journals useful in entomology or any other science. However, they generally have agreements with other libraries, whereby volumes can be borrowed or copies of particular papers can be obtained, that is, interlibrary loans. *The Union List of Serials in Libraries of the U.S. and Canada* and *New Serial Titles* are listings of all journals and of the major libraries that house these journals. Thus, by consulting these lists, one may determine which libraries have the journal he or she is seeking. Both lists are indexed by journal name and by subject.

Books In and Out of Print

Books in Print is an annual listing of books currently available on the commercial market. This list is composed of four volumes: Volumes 1 and 2, titles; and Volumes 3 and 4, authors plus author and title indexes. Out-of-print books may be found by consulting the *A. B. Bookman's Weekly,* various companies that specialize in such books, and major libraries. Facsimiles of out-of-print books are available from University Microfilms International in Ann Arbor, Michigan.

Databases

In recent years the computer has come to play an important role in the management of scientific literature. Several major databases, such as computer-accessible indexes and bibliographies, are maintained and can be tapped for literature searches. Among the databases useful in entomology are AGRICOLA which includes, among others, citations from the *Bibliography of Agriculture,* Bioscience Information Service (BIOSIS), which includes citations from *Biological Abstracts* and *Bioresearch Index,* and Medical Literature Analysis and Retrieval System (MEDLARS), which includes citations from *Cumulated Index Medicus*. These databases are