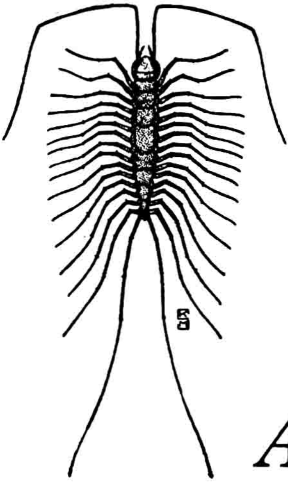
HERBERT H. ROSS

A Textbook of ENTOMOLOGY



A TEXTBOOK OF ENTOMOLOGY

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Preface to the Second Edition

THE number of new ideas propounded in entomology during the last decade is both surprising and gratifying. Many of these ideas have a direct influence on the orientation of the beginning student, and these I have attempted to incorporate into the revised edition.

I want to take this opportunity to express deep gratitude to the host of colleagues who have contributed suggestions, criticisms, illustrations, or other material pertinent to revising this book. Their help has been of inestimable value. Limitations of time and space have made it impossible to follow all the good suggestions that were tendered, yet consideration of them frequently led to changed emphasis or a new approach to a problem.

HERBERT H. ROSS

Illinois Natural History Survey,
Urbana, Illinois, 1956

Preface to the First Edition

IT seems to me that there has been an increasing need for an introductory textbook that would bring under one cover the fundamental aspects of entomology, organized so as to give students a general idea of the entire field. This book has been written with this aim in mind.

Much detailed information has been purposely omitted in the hope that the basic principles would not be obscured. It is thought that this would serve better the needs of both entomological students desirous of specializing later in certain fields and students in other branches of biology desiring a general understanding of entomology for background information.

Too often entomology has been presented with no explanation as to its development. The chapter on the growth of entomology has been designed to outline the development of the science in terms of basic causes rather than to present a long list of dates and names. Another field often neglected is the rich one of paleontology. In the presentation of the chapter on geological history no attempt has been made to achieve completeness taxonomically, but rather to give a picture of the dynamic rise of insects in relation to the forces surrounding them.

In the interest of simplicity, physiology has been segregated as a separate chapter, following a treatment of external and internal anatomy. In this way it has been possible to organize physiology by function, rather than structure, since the former is much easier for students to follow. A word of caution is in place regarding the keys to orders and families. These are designed to accommodate only common members of common families and hence are far from complete. They are intended primarily to aid beginning students in realizing the type of differences used in delimiting orders and families and to give them practice in the actual manipulation of keys.

I am greatly indebted to many persons who have discussed choice of material and organization of the contents or have read portions of the manuscript and made criticisms of value. Of especial help in this capacity have been the late T. H. Frison, and W. V. Balduf, B. D. Burks, G. C. Decker, D. M. DeLong, W. P. Hayes, Harlow B. Mills, C. O. Mohr, M. W. Sanderson, Kathryn M. Sommerman, Roger C. Smith, F. R. Steggerda, and H. J. VanCleave. I wish also to express my thanks to my wife, Jean, for unstinting help in many ways with the preparation of this book.

I am extremely grateful to many organizations and to the following persons who have loaned illustrations for this book: P. N. Annand, B. D. Burks, F. M. Carpenter, Geo. A. Dean, Carl Dunbar, E. O. Essig, Mrs. W. P. Flint, R. C. Froeschner, B. B. Fulton, Robert Glenn, A. S. Hoyt, Ray Hutson, Dwight Isely, L. B. Jameson, G. F. Knowlton, Mary Lyon, Mary S. MacDougall, Robert Matheson, C. L. Metcalf, C. E. Mickel, Albert Miller, H. B. Mills, Marjorie Mitchell, J. D. Mizelle, C. O. Mohr, C. T. Parsons, Victor Reynolds, A. G. Richards, Jr., S. A. Rohwer, M. W. Sanderson, W. T. Shoener, R. C. Smith, R. E. Snodgrass, Kathryn M. Sommerman, Taylor Starck, L. H. Townsend, J. S. Wade, W. H. Wellhouse, V. B. Wigglesworth. I wish to express my sincere thanks to them for permission to use their material.

HERBERT H. ROSS

Illinois Natural History Survey,
Urbana, Illinois
February, 1948

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CHAPTER 1

Growth of North American Entomology

MAN has always had his troubles with insects. When he first emerged as man he already had fleas and lice and was fed on by mosquitoes and pestered by flies. In those early days, when human populations were scattered and sparse, man's struggle was on a primitive plane—to find natural food from day to day and to escape the onslaughts of predatory animals. At this period it is doubtful if insects and insect-borne diseases were nearly as important deterrents to man as were other inimical factors of the environment. In fact, on the average, insects were probably of great help, because termites, grasshoppers, grubs, and the like could be found and eaten when other foods were not obtainable.

From primeval conditions man's progress has been based essentially on changing various factors of his environment and making it better suited for his own survival and increase. But every change that benefited man also benefited a host of insects. Gradually, as the more stark enemies of primeval life, such as the leopard and tiger, ceased to be a great threat to primitive man, insects became increasingly important as a challenge to his success.

In the first place, increase in human populations allowed a great increase of such insect ectoparasites as lice and fleas. This was due to the ready accessibility of additional host individuals for the insects and, therefore, better opportunities for dissemination and chances for reproduction. The same factors favored the increase and spread of pestilence, including insect-borne diseases. When large cities arose, they were repeatedly swept by outbreaks of these maladies, in the same way that Imperial Rome was decimated by bubonic plague in the second century A.D.

Insects became a real factor with food as with health. When man began to store food, it was attacked by a host of insects which before had been of no significance in the human environment. In the tremendous food-storage organization of today, insects destroy thousands of tons of food annually in spite of widespread and expensive control programs.

When populations outstripped the food-producing capacity of natural surroundings, man domesticated animals. The concentration of these allowed an increase of their ectoparasites and diseases, thus partially nullifying the effort to enlarge the food supply. The cultivation of crops brought about the greatest change with regard to insects. Agriculture congregated plant hosts so that their insect attackers could build up extensive populations on them. The Egyptian writer in the time of Rameses II (1400 B.C.) commiserates with the peasant that "Worms have destroyed half of the wheat, and the hippopotami have eaten the rest; there are swarms of rats in the fields, and the grasshoppers alight there." In the more recent period of crop improvement, new varieties of plants developed for increased yield have frequently been more attractive to certain insects than original wild hosts, with a resultant influx of destructive forms to the cultivated crops.

This situation has been made more serious by man's development of transportation between all parts of the world. Insects of many species have been carried to continents new to them, where they have found favorable climates, succulent acceptable cultivated hosts, and a freedom from the natural enemies which had kept their numbers in check in their original homes. Sometimes the result has been disastrous, as, for example, the entry of the European corn borer and the Japanese beetle into North America. These two species are of little economic importance in their native range, but in the United States they have caused losses to crops in the magnitude of millions of dollars per year.

North America has been especially hard-hit by losses due to insects. This is the result of the cultivation here in recent centuries of many crops not indigenous to the area, to introduction of many new pests, and to changes wrought by agriculture that have favored many endemic insect species. Losses of crops, stored products, domestic products, and other commodities were estimated in 1951 at $10,200,000,000 for the United States alone. In addition there is to be considered illness and deaths due to insect-borne diseases, and secondary infections, sickness, and discomfort that result directly from insect bites. This was estimated as a cash loss of about $5,000,000,000. On the basis of these figures, insect damage in this country totals an estimated annual sum of $15,200,000,000.

A review of insect damage gives the entire group a sinister aspect. But the adage, "There is some good in everything," finds a real place even among this group of apparent despoilers. Many kinds of insects are definitely beneficial. The most conspicuous example is the honey bee, which not only produces a marketable crop of high cash value, but also pollinates many valuable plant species. Many crops, including most of our fruits and legumes, are dependent for pollination on a large number of insect groups such as bees, moths, flies, and beetles. Without these insects we would have no apples, pears, peas, beans, and seeds of other insect-pollinated plants.

Another group of economic insects on the beneficial side of the ledger embraces a large assemblage of parasitic insects whose hosts are other insects. These include ichneumon flies, parasitic wasps, parasitic flies, and many predaceous kinds such as the ladybird beetles. The adults or larvae of these species prey on or parasitize many important insect pests. In some cases they can be used as an efficient control method. The vedalia ladybird beetle, for example, is one of the chief means of combating the cottony cushion scale, an insect destructive to citrus orchards in California.

Man's efforts to combat destructive insects and control beneficial ones form a field of activity called applied entomology. It is comparable in many ways to the field of medicine that has arisen out of the challenge to combat sickness and disease. In North America, applied entomology involves a financial outlay of considerable proportions. Over four thousand persons are employed primarily in the investigation of economic species and the development of control measures. Many firms make a specialty of manufacturing insecticides or apparatus for their application. In the United States alone $400,000,000 worth of insecticides are used annually. It must be remembered that the losses of $15,200,000,000 from insects were in addition to this control program, so that the total annual insect bill (exclusive of labor for applying insecticides) in the United States is in the neighborhood of $15,600,000,000.

It is difficult to visualize a loss in the magnitude of billions of dollars. Let us put it another way. In 1952 each person in the United States, on the average, paid out about $100 to insects. This means $400 for a family of four. Some of this sum was spent for insecticides, some for replacing damaged goods, but most of it was disguised as increased cost of commodities of plant or animal origin, such as lumber, clothing, and food.

Entomology, the study of insects, has developed into a very large division of the animal sciences, owing to the proportions and importance of the applied field. For, whereas the primary objective of applied entomology is the reduction of insect damage, it has long been evident that a wide knowledge of fundamental information is necessary as a foundation for effective control. For this reason there has been an appreciation of basic entomological research in many directions. Some phases seemed of little importance when first started and yet later proved of inestimable value in control problems.

BEGINNINGS OF MODERN BIOLOGY

Because of their tremendous abundance, it might seem that insects would have been used a great deal in the early investigations in fundamental biology. The small size of the average insect, however, mitigated against this. Extremely delicate methods of dissection must be used to study anatomy and physiology, and powerful microscopic equipment is necessary for taxonomic studies of almost any insect group. To a large extent, therefore, the fundamentals of biology were based on observations of larger animals. The early development of entomology was a process of transposing to insect studies principles discovered in related fields. To gain a better appreciation of the growth of entomology in the New World, it is instructive to review the origin and evolution of its parent, modern biology, which arose in the European theater of the Old World.

At the time of the discovery of America by the Spaniards, the progress of world science was barricaded by the "age of authority." In the literature of the times were heated arguments over such matters as the number of teeth in a horse; learned authors were quoted, but apparently no one thought to examine a horse and actually count its teeth.

The subsequent sixteenth and seventeenth centuries, which saw the exploration and early colonization of the Americas, witnessed also the overthrow of authority and the return of observation and experiment in science. Both the explorations and scientific advance had their roots in the same fundamental causes, that in these centuries following the Renaissance men developed again the desire to look and think for themselves.

In the field of the biological sciences, Vesalius' work on human anatomy (1543) rejuvenated observation, and Harvey's proof of arterial and venous circulation of blood (1628) introduced experiment. Together, as Locy says, "they stand at the beginning of biological science after the Renaissance." Introduction of the microscope in the seventeenth century led to the microanatomical works of Malpighi and Swammerdam, and to discoveries of microorganisms with which Leeuwenhoek astonished the scientific world.

During this latter period entomology really started to develop. In fact, 1667 and 1668 may be considered almost its birth date, for in 1667 Redi used insects in demonstrations to test the theory of spontaneous creation. He exposed meat in jars, some covered by parchment, others by fine-wire screen, and some not covered. The meat spoiled and attracted flies. These laid eggs in the exposed meat, resulting in a crop of maggots. Of the two covered jars, no eggs were laid on that covered by parchment, but the flies were attracted to the screen-covered one and laid eggs on the screen, since they could not reach the meat itself. Redi observed in this instance that, when the eggs hatched, maggots appeared on the screen instead of on the meat. He concluded, therefore, that maggots in meat resulted from the eggs of insects, and not from spontaneous generation, as was previously supposed.

In 1668 Malpighi published anatomical studies of the silkworm, and Swammerdam published his first insect studies. These men produced the first accurate studies of insect anatomy, preparing skilled illustrations showing details of minute structures and organs, fig. 1. These model works were the inspiration for later work in insect anatomy.

Another important phase of the biological sciences paralleled these advances. As people began to observe nature, interest awakened in natural history, and books on the subject appeared. Early treatises by Wotton (1552) and Gesner (1551–1556) were elemental and general, and were characterized by a lack of discrimination between different kinds of related animals. Imaginary animals of folklore were even given consideration as if they actually existed. Later works by Ray at the end of the seventeenth century were on a sounder basis and introduced a clear species concept of living organisms essentially similar to that understood today. Natural-history museums, fig. 2, came into being, stimulated by the many bizarre and unfamiliar objects brought back to Europe by travelers and mariners. Many of these museums were operated as hobbies by wealthy persons and were the forerunners of the extensive private collections which later played an important role in the development of taxonomy.

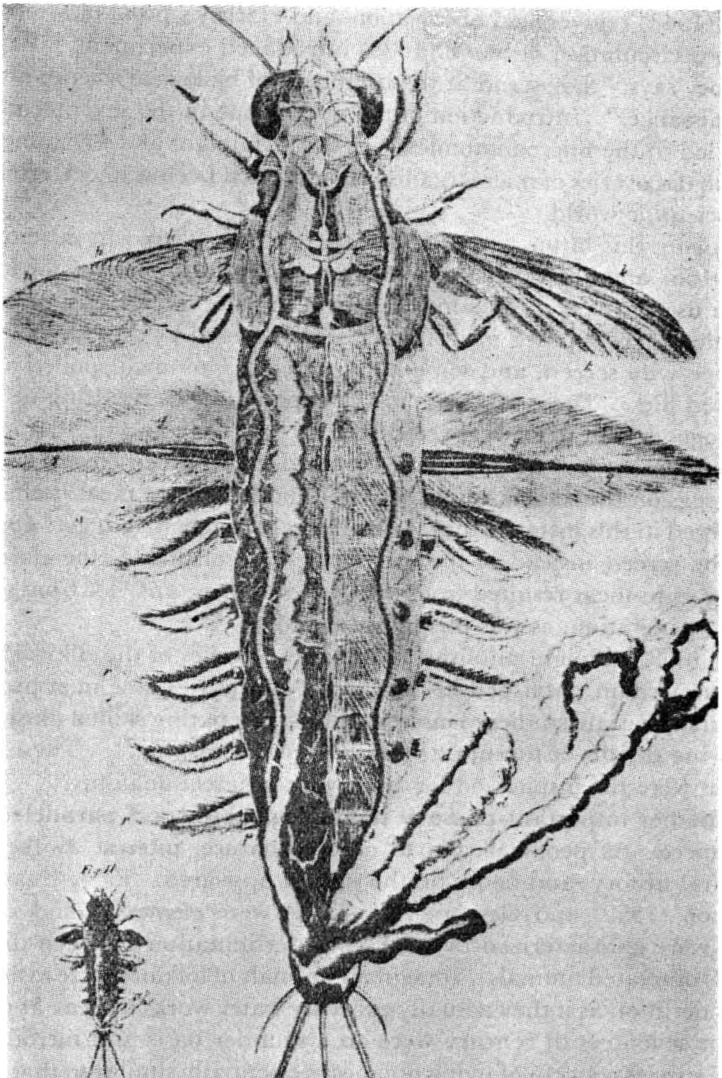

Fig. 1. Anatomy of a mayfly nymph, dissected and drawn by Swammerdam. One of the very early studies of insects, published about 1675. (From Essig, College entomology, by permission of The Macmillan Co.)

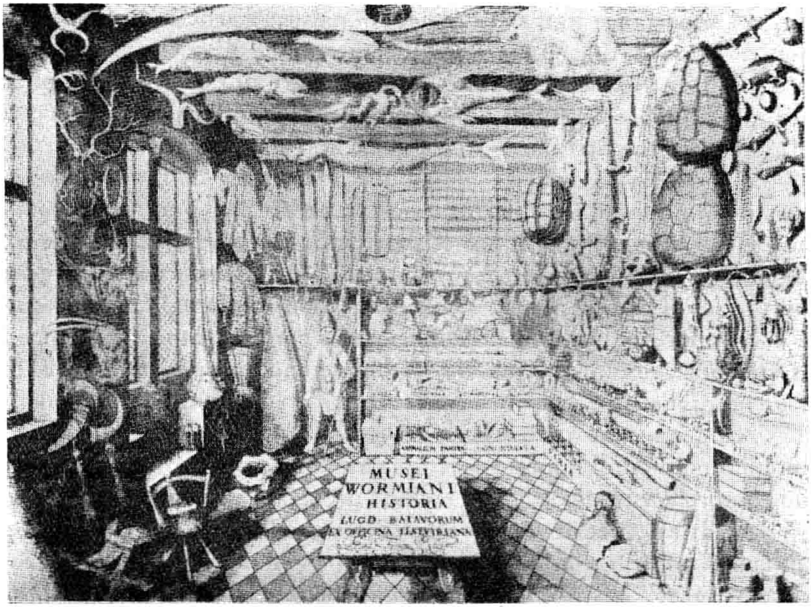

Fig. 2. The famous museum of Olaus Worm, illustrated by its Swedish founder as it appeared in 1655. (Reproduction loaned by Waldo Shumway)

PROGRESS IN THE EIGHTEENTH CENTURY

Historians picture in the eighteenth century the climax of the revolt against authority, in which despotism and ecclesiasticism were to some extent replaced by the individual asserting his right to be an end in himself. Historical expression of this tide of feeling is found in the American Revolution and the French Revolution. In the United States further expression is found in the rise of universality and state control of education.

In this same century, undoubtedly manifesting the same individualistic trend, the biological sciences in Europe progressed to a new peak. Entomology especially attracted a large number of talented workers. Lyonet, a Hollander, contributed anatomical work of the finest detail, his first and best publication describing the anatomy of the larva of the willow moth (1750). More important in this period from the standpoint of arousing widespread public interest were the voluminous works of the German, Roesel; the Frenchman, Réaumur; and the Swede, DeGeer. All three of these authors published detailed well-illustrated observations on many insects, their life histories, habits, and characteristics.

About the middle of the eighteenth century occurred a movement of extreme importance to the entire field of natural science. It has already been mentioned that John Ray introduced the first clear concept of species. But the names for these species were phrases or descriptions (in Latin), often several lines long, cumbersome, and inconsistently used. In most cases the first name was a noun and corresponded to our present-day usage of a generic name; the remainder of the phrase was adjectival and modified this "generic" name, fig. 3. Various authors in this period began the practice of shortening the adjectival phrase to a single particularly descriptive word, the two then constituting the genus and species of present usage. This is known as binomial nomenclature. In this period the naturalist Linnaeus was coming into prominence as a systematist, organizing the known plants and animals into one of the first comprehensive classifications. In 1758 the tenth edition of his work "Systema Naturae" was published. In this, for the first time, the binomial method of names was employed uniformly throughout a large and comprehensive book. The method proved so successful that workers in all fields adopted it almost immediately. In fact, so profound was Linnaeus' influence on later workers that the tenth edition of his "Systema Naturae" has been designated as the official beginning point for zoological nomenclature. Although Latin is no longer the standard language of science, as it was until the end of the seventeenth century, the Latin names have been preserved and are used for scientific names throughout the world.

The stabilization of binomial nomenclature was of tremendous scientific advantage in two ways. First, it gave an easily designated and unambiguous "handle" to species, so that workers in different fields and different countries were able to know better the identity of the species with which others were working. This was of prime importance for integrating advances in comparative anatomy, physiology, and other fields of biology. Second, it provided a system of names which could be expanded indefinitely in a simple manner to accommodate additional genera and species. How necessary to future progress was such a simple method is seen at once by this tabulation: For the entire world Linnaeus recognized about 4500 species of animals, including 2000 species of insects; today over a million and a quarter species of animals are recognized, and of these roughly 900,000 are insects.

Thus taxonomists after Linnaeus were presented with an open invitation to describe and name the myriad of species occurring in all parts of the world. Much of the early work was superficial and has been criticized by many, but it furnished the basis for analyses which led to

(136)

Papilio media, alis pronis, præſertim interioribus, maculis oblongis argenteis perbellè depictis.

SUpina facies intenſiùs & lucidiùs rufa eſt, nervis in alis exteriori-bus nigris, maculis etiam prope extimum latus majuſculis nigris: interiores alæ ad imum marginem circulos obtinent nigros 4 vel 5 in linea marginis parallela.

Papilio pulla maculis rubris, è rubro albicantibus, & circellis luteis depictis.

ALÆ exteriores ſuperiùs ad extimum latus duas habent maculas oblongas rubras. Non longe ab extimo angulo area lata obliquè tranſverſa, alba rubro diluta; juxta quem circellus niger cum puncto luteo in medio. Interiores alas duo velut ocelli linea lutea pupillam nigram cingente, majore ad exterius alæ latus, minore ad interius. Lineæ nigræ & albicantes alam terminant. Maculæ eædem in pronis quæ in ſupinis alis cernuntur. Color autem non pullùs eſt, ſed rufus, aut fulvus intenſior. Alæ interiores lineam albicantes obliquè tranſverſam ab exteriore latere ad interius deſcendentem obtinent.

Papilio parva nigra duplici in alis exterioribus macula alba inſignis.

E Maculis albis una ad exterius alæ latus, altera ad interius ſita eſt. In prono latere plures maculæ albæ in linea ad alás tranſverſa cernuntur.

Phalæna robuſta rubro & obſcurè citrino & albo coloribus pulchrè depicta.

DOrſum ſeu thorax ſupina de utroque colore participat, ſed de rubro magis. Abdomen ſupinum citrinum lineâ rubrâ mediam ſecundùm longitudinem percurrente. Pronum corpus totum rubet. Alæ ſupinæ exteriores ab exortu lineam habent albam ad marginem deorſum deductam: citrinum colorem rubræ lineæ tranſverſæ diſtinguunt. Alæ interiores parvæ, tum exteriores, tum interiores, circa margines præcipuè latè rubent.

Fig. 3. Part of a page from John Ray's Historia insectorum, published in 1710. Note Ray's use of the words *Papilio* and *Phalaena* in a manner comparable to present-day generic names; a short phrase follows, the forerunner of the species name. (Courtesy of the University of Illinois Library)

the formation of the theory of evolution and to the organization of such fields as ecology and limnology.

The field of insect taxonomy in particular had been handicapped under the old system. After Linnaeus' work it began to emerge as a specialized subject. The first outstanding insect taxonomist was Fabricius, a Danish student of Linnaeus. Fabricius' first work, "Systema Entomologica," appeared in 1775; others followed from 1782 to 1804. Fabricius treated the entire insect fauna of the world. By the end of his career it became apparent that this was too large a unit for intensive study by one person. As a result, many workers of the early nineteenth century following Fabricius studied either only one of the larger insect groups or the fauna of only one country.

Fig. 4. Carolus Linnaeus (1707–1778) at the age of forty. (After Shull)

The works of Réaumur, Linnaeus, DeGeer, and Fabricius stimulated a tremendous development of taxonomic study of insects among European entomologists. They also served as the most important basis for the beginning of entomology in North America.

DEVELOPMENT OF NORTH AMERICAN ENTOMOLOGY

American entomology came into existence about the beginning of the nineteenth century. For the first two thirds of the century development was slow, witnessing the appearance of scattered pioneer works such as form the backbone of further progress in any scientific movement. But after the Civil War many factors contributed to a hastening of the tempo in entomology in the United States. The resultant demand for entomological investigation found eager and able enthusiasts available, with the result that by the end of the century American entomology had blossomed into a well-balanced science of wide practical and theoretical scope.

Prenineteenth Century Work

Prior to the nineteenth century only small fragments were known about North American insects. Naturalist Mark Catesby (1679–1749) was possibly the first to illustrate North American insects in his book, "A Natural History of Carolina, Florida and the Bahama Islands, containing figures of the Birds, Beasts, Fishes, Insects and Plants." Fabricius named some species, relying on specimens sent to him by various collectors or specimens which had been acquired by private collections in Europe. John Abbott, an Englishman who settled in Georgia, collected much material for European collectors in the period about 1780 and prepared many drawings of insects. The economic losses occasioned by insects were noticed with grave concern by Thomas Jefferson in 1782. He was particularly aware of the damage caused in stored grain and gave a few remarks on the problems of control, pointing out a need for further study. But until a few years before 1800 no concerted effort was evident by residents of the United States to investigate the native insect fauna.

Pioneering Period, Roughly 1800–1866

Work on American insects by American workers began about the turn of the nineteenth century. One of the first workers was W. D. Peck, who published many articles on the injurious insects of the New England states. These articles appeared from 1795 to 1819 in various agricultural journals. The pioneer work on North American entomology was "A Catalogue of Insects of Pennsylvania," published in 1806 by F. V. Melsheimer. The chief value of this little 60-page book was its stimulating effect. Its author, his collection, and his association with later workers were a real aid in opening up the subject. His insect collection, incidentally, was the first comprehensive one to be built up in North America and was ultimately purchased many years later by the Harvard Museum of Comparative Zoology.

In 1812 a group of enthusiastic naturalists organized the Academy of Natural Sciences of Philadelphia. This nucleus of scientists was the