# INSECTS IN Perspective

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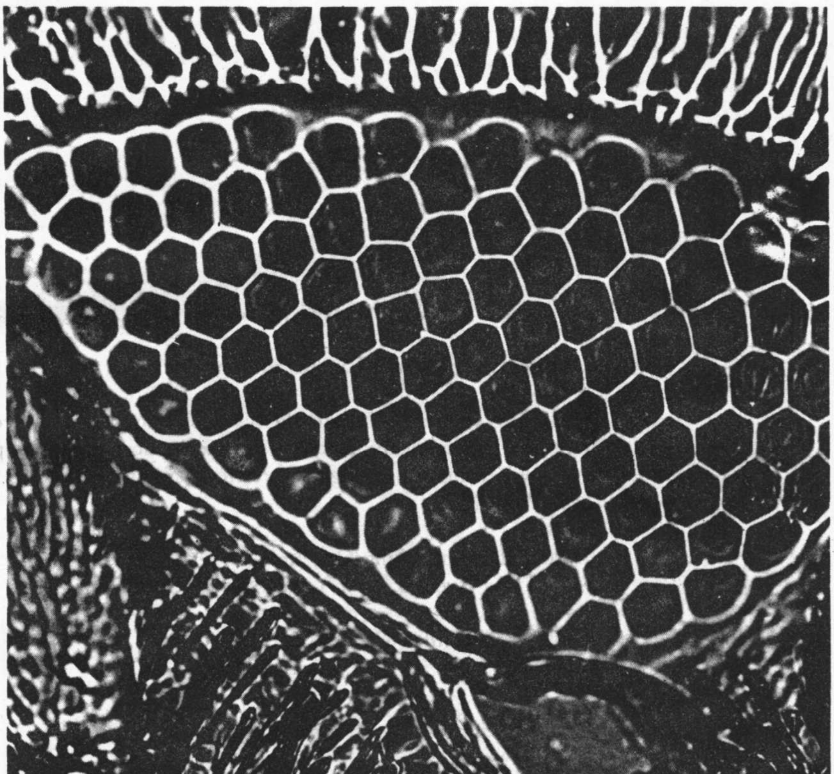

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In memory of JOHN A. CHAPMAN
who first introduced me to the fascinating world of insects
and thereby provided me with countless hours of enjoyment.



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# Preface

I have never met an entomologist who did not thoroughly enjoy his occupation. The reason for this, I believe, lies in the fact that the study of insects presents a constant challenge and repeatedly rewards the investigator with the discovery of something he did not know before. Even though hundreds of thousands of insect species have been described over the centuries and a huge body of knowledge has already been amassed about them, new and exciting discoveries are being made every day.

The field of entomology is so dynamic that teaching even an introductory course presents a real challenge. The field is so broad and so many other disciplines come to bear on the study of insects that presenting a balanced overview can be difficult. If one is not careful, it is easy to become so involved with the basic information about morphology and classification that many of the really interesting aspects of insect biology are given little or no attention. The authors of introductory texts face a similar problem in that by the time they have discussed the structure, function, classification, and identification of insects, there is little space left within a book of reasonable length to devote to other aspects.

I faced this problem too, and decided there was no reason to publish another introductory book about insects unless it was rather different from the others available. Over the years I have found that students rarely request additional reading in support of laboratory exercises, probably because it is relatively easy to provide the resources necessary for a good laboratory learning experience. However, students often ask for reading material that expands on what I have covered in lecture.

My reason for writing this book, therefore, was to provide some up-to-date background reading for a broad range of lecture topics. From the outset, I prepared chapters and distributed them as background reading to students in classes of both majors and nonmajors in entomology. The comments have been very favorable, and I am confident that this text can serve satisfactorily in introductory entomology courses as well as courses about insects taken by nonmajors who wish to expand their general education through courses in the life sciences. I am hopeful that professional entomologists will find it interesting reading as well.

I have tried to organize the chapters into a logical sequence, but I have also tried to keep each chapter sufficiently self-contained that an instructor can develop his own arrangement of lectures. For this reason I have provided a bibliography at the end of each chapter rather than a single list of references at the end of the book.

My over-all objective, of course, has been to present a balanced view of the biology of insects, and thereby stimulate the reader's interest in these fascinating creatures. In Part I, I have tried to show how the development of entomology paralleled and perhaps influenced the development of science in general, to show the relationship of insects within the animal kingdom, and to illustrate how the evolution of insects has led to such a great diversity of kinds. Although it was never my intent to provide an aid to insect identification, the orders are presented in an appendix in the hope that the discussion of insect groups with which students are unfamiliar will be more meaningful. In Part II my objective was to cover the important aspects of structure and function while avoiding, as much as possible, tedious descriptions of anatomy. Consequently, I chose a process orientation and concentrated on the adaptive breakthroughs that have clearly played a major role in the insect success story. Part III is devoted to behavior, an aspect of insect biology so often treated inadequately in general texts. Once again, I based this discussion on a selected list of processes of both biological and practical importance. Finally, in Part IV I have examined the relationships of insects with other organisms and their environment. This is where both the beneficial and harmful roles of insects are reviewed, preparatory to a consideration of how we can reduce pest problems without damaging our natural heritage.

I am indebted to many people who have provided assistance and encouragement throughout this project, as well as to all the entomologists who made the basic discoveries that form the foundation of any book about insects. I am especially grateful to Woody Chapman, Biology Editor for Macmillan Publishing Co., Inc., who guided the project from conception to production, and to John A. Davidson and Fred Delcomyn, who offered valuable criticism of the entire manuscript.

I also thank T. J. Cohn, G. W. Cox, E. Huffman, R. E. Monroe, and C. E. Norland, who freely gave of their time for discussion and commented on selected chapters as I progressed. I am grateful for the assistance and corrections that they and others provided; the errors that remain are solely my responsibility.

I thank the following for generously allowing me to use original material or for providing one or more photographs: Max Badgley, Canadian Forestry Service, Thomas Eisner, W. G. Evans, L. A. Falcon, E. F. Knipling, Jason Lillegraven, Daniel Mahr, Neil Marshall, M. L. McManus, Gary Pitman, William Stephen, Vern Stern, United States Department of Agriculture, University of California, E. O. Wilson, and W. G. Wellington.

M. D. A.

# Contents

# Introduction

New discoveries of ancient humanoid remains have resulted in an ever earlier estimate of our origin. Some anthropologists now believe that man or his immediate ancestors have walked the face of the earth for perhaps two million years, or twice as long as was considered possible just a few years ago. But even if these new estimates are accurate, we are relative newcomers in the eyes of the insects. The insects as a group have their origin somewhere in the order of 350 million years ago, when the climate of the earth was generally warm and humid and a vegetation of giant horsetails, ferns, and club mosses extended northward into Norway and Sweden. The remains of winged insects do not appear in the fossil record until about 80 million years later. By that time, many of the orders in existence were indistinguishable from present day forms. Some orders did not really proliferate until much later when the flowering plants evolved, and others, such as the lice, did not appear until warm-blooded animals were available as hosts. But even the most recently evolved orders of insects have been here for at least as long as man.

By the time man came on the scene and was present in sufficient numbers to spread out from the cradle of his origin, the insects were already a highly integrated part of every terrestrial and fresh-water ecosystem. In fact, the insects had already had a profound influence on all of these systems and on the evolution of many of their plant and animal components. Man, then, was an outsider trying to break in, and to do so, he had to find his place among all of the long-time relationships that already existed as part of his environment.

Undoubtedly from the very beginning, insects that were ectoparasitic, such as the blood-feeding lice and flies, simply adopted man as another animal host and source of food. Many such insects had already established themselves as vectors of disease-causing organisms such as protozoans (sporozoans, trypanosomes) and filarial worms. Therefore, we can safely assume that primitive man was infected by insect-borne pathogens. Parasitologists have postulated that man's serious reaction to sleeping sickness, caused by a tsetse fly-transmitted trypanosome, is indicative of his recent relationship as a host for this protozoan parasite. Animals such as native cattle that become infected by these organisms apparently do not display the same severity of symptoms because they have had time to evolve a more tolerant relationship with them.

Humanoids with the simplest of life styles would have been producers of waste in the form of food scraps, excrement, and corpses, which would have been fed upon by many forms of insect scavengers and carrion feeders. In some cases, these early associations have persisted. Some species of insects, such as the house fly, have become so intimately associated with man-produced waste that they are only found in areas inhabited by man.

We do not know for certain how long man spent as a more or less free-living animal, but archeological evidence indicates that early in our existence we lived in family groups or small bands that had at least temporary home ranges with a living place such as a cave at its center. These earliest of dwellings provided the basis for some additional relationships between the insects and ourselves. Caves were the natural nesting and resting places for other animals as well as for man. Parasitic and scavenging insects, such as fleas, lice, and cockroaches, probably found man and his leavings just as much to their liking as they did the other cave occupants and their leavings.

As time went on, primitive man gradually changed from being strictly a hunter and gatherer to a storer of small surpluses and a possessor of some simple belongings such as hides used for clothing and sleeping pads. We need not stretch our imagination to visualize how insects such as booklice (Psocoptera) and small beetles (Coleoptera) that are common to bird nests might simply have moved to small caches of grain or other food placed in trees to keep the foodstuffs out of reach of ground-dwelling animals. Nor is it difficult to imagine how insects that fed on the skin and hair of carcasses would have become inhabitants of the hides used by man. As man moved about, carrying his simple possessions with him, he began to transport these new insect associates from place to place. From that time onward, man has had a continuous relationship with fleas, bedbugs, roaches, dermestid beetles, and other food pests that infest cereals and dried fruits.

Some time later, man began to devote less time to hunting and wandering in search of food and more time to the cultivation of food plants and the domestication of animals. This led to a new way of life which involved the settlement of tribes in villages adjacent to crop-growing areas. Rather than living in available caves, these early farmers began to build simple living structures from whatever material resources were available. The cultivation of food led to larger surpluses that had to be stored. The reduced need to hunt and gather provided more time to engage in the development of tools and in the manufacture of personal possessions. During this time, referred to as the Neolithic period, which flourished some 10,000 to 15,000 years ago, man's association with the insects expanded still further. The household pests brought from the caves flourished in the villages. The storage pests that had transferred from animal caches, as well as those which normally fed inside the seeds of plants now under cultivation, were provided with a continuous place in which to feed and reproduce. The cultivation of native plants provided conditions, not unlike modern monocultures, which were ideal for the build-up of larger populations of indigenous plant-feeding insects of great variety. Some of the wood used to build houses was almost certainly infested with termites and other wood borers that are now structural pests of some concern. On the other hand, the abundance of the harvest from these early farms was made possible by the beneficial insects that year after year pollinated the crop plants and improved the structure of the soil.

We need also to consider the impact of the early aggregation of larger numbers of people in villages and of the confinement of herds of domesticated animals. Both of those activities would have affected the populations of ectoparasites and blood-feeding insects by providing them with readily available hosts. The concentration of natural odors and the attractant chemicals present in accumulations of their urine and excrement made these corralled animals easy to locate. In addition, the creation of village watering holes and water impoundments for irrigation provided breeding sites for aquatic insects such as mosquitoes that transmit disease-causing organisms.

By about 5,000 B.C., people had begun to live and work in larger cities. Many of these cities were dependent upon the agricultural production of the surrounding countryside. A predictable outcome of this was an increased concern about insect problems in relation to the crops, as well as about the insect pests directly associated with urbanization. There was considerable commerce, which facilitated the transport of storage pests, livestock pests, and crop pests from place to place. Urbanization itself concentrated the production of human waste and increased the incidence of flies, lice, and the rodent reservoirs of insect-borne diseases such as typhus, typhoid, bubonic plague, and dysentary.

Clearly then, the ascent of man, which began long after the insects had established all of their fundamental ecological relationships, made inevitable a complex set of interactions that could only grow in both their beneficial and detrimental consequences as man altered his way of life. Perhaps we should not be surprised, therefore, that some of the very first elements of science, including the work of Aristotle and others, involved the observation of insects and insect-related problems. The relationship between man and the insects, as recent as it is, has provided the source of much concern, fascination, and delight. In the following pages, I hope to reveal some of the reasons for this wide range of attitudes.

# I

# Some Generalizations

# A little history

# 1

Entomology is the scientific study of insects and therefore contributes to the body of knowledge we refer to as science. This body of knowledge has been accumulated over a long period of time and has been influenced by the sociological and philosophical changes that have transpired. It is impossible therefore to separate the history of entomology from the history of science or the history of science from history in general. What follows then is merely an identification of some of the landmark events in the development of science in general and of entomology in particular.

In the early stages of human development, man was simply a part of natural history, another animal living in concert with all the other components of his environment. As a hunter and gatherer, and a little later, as a crude horticulturist, man had to learn certain fundamentals about the plants and animals he relied upon for food and shelter and about their relations with each other and the passing seasons. He gained the information he needed for survival through observation and trial and error, but made no attempt to gain experimental proof of cause-and-effect relationships. At first, most observed events were given supernatural explanations, and the observations and explanations were then passed from generation to generation by way of simple stories that often became more fiction than fact. Later, as man learned the cycles of plants and seeds and applied his knowledge to the cultivation of crops, he became, in a sense, a scientist, with a rather extensive understanding of nature and a basic curiosity about the weather and the influence of the passing seasons.

Man's technological advancement proceeded at different rates in different regions in relation to the climate, ecological diversity, and availability of material resources. The real scientific revolution did not occur until just a few hundred years before the birth of Christ. By this time, many of the fundamental technological advances connected with agriculture and construction had been made, and the earlier time-consuming activities related to the provision of food, shelter, and protection had been simplified considerably. The major problems of the day were war and pestilence, so it is not surprising that some of the earliest detailed "scientific" observations were concerned with insect pests and diseases. Large cities were repeatedly swept by maladies, sometimes unknowingly transmitted by insects. Crops were ravaged by insect pests, and the grains and fruits in storage vaults were decimated by insects and rodents.

The writings of some of the earliest scientists dwelt heavily upon the insects. Theophrastus (ca. 380–287 B.C.) catalogued many plant diseases and insect pests of crop plants. Aristotle (384–322 B.C.), considered the "Father of Zoology," established the basis for the scientific study of insects. He was a careful observer of natural phenomena who by the application of *deductive reasoning* (reasoning from the general to the particular) was able to gain considerable insight into the functioning of natural events. For example, he realized that insects had different stages in their life history and underwent metamorphosis, although he was not clear as to the interrelationships of all the stages, and thought that pupae were eggs.

A little later, the Roman authors, led by Pliny (A.D. 23–79), became the first true encyclopaedists and recorded voluminous information on agriculture, engineering, architecture, crop pests, and veterinary problems. Book eleven of *Historia Naturales* (A.D. 77) by Pliny was devoted entirely to insects.

Following the partition of the Roman Empire in 395, the West Roman Empire fell into chaos and the ancient scientific tradition was largely lost to western Europe. Such manuscripts and knowledge that survived were managed by the monastic schools, but the works of Aristotle and Theophrastus were lost. Fortunately, the East Roman Empire of Byzantium gathered the manuscripts of the ancients into its libraries where they were translated and copied. These formed the basis for the development of Arabic science over the next several hundred years.

In the West, scientific progress was almost nonexistent throughout the Medieval period. The church diverted the best minds from science to theological writing, and the divinity became the predominant theme of art, music, and literature. Throughout this entire period there were only a few significant works dealing with natural history. Insects were mentioned only in the encyclopaedic *Origines sive Etymologiae* by Isidorus of Seville (ca. 560–636) and in *De Universo* by Rhabanus Maurus (776–856) until late in the period when Albertus Magnus (1193–1280) re-established a link with the ancients by paraphrasing Aristotle in his *De Animalibus* (1255–1270). The last great Western work of the Middle Ages that treated entomological subject matter, and perhaps the most influential in that it appeared just prior to the Renaissance, was the *Ruralium Commodorum* (1304–1309), in which Petrus Crescenti of Italy discussed many insect pests and their control.

The Renaissance (1400–1600) was a period of intellectual awakening that encompassed a rediscovery of the Greek and Roman contributions to science, which had been retained largely in institutions of the Eastern Roman Empire and referred to extensively during the rise of Islam. The voyages that returned to Europe from the East brought new knowledge along with the old, and established a new sense of inquiry. Scientists again began to question freely the authority of the church and to lean less heavily on the discoveries and methods of Aristotle, Pliny, and the Scriptures. By the end of the Renaissance, the Modern Scientific Revolution had begun, stimulated in part by the development of a new scientific method that stressed *inductive reasoning* (reasoning from specific questions to general concepts), brought into prominence by Francis Bacon and Galileo. The scientific method made investigation more rigorous because it was based on the assumption that all of the components of the universe interact in a predictable way, and therefore it should be possible to develop an understanding of the laws governing these interactions. Scientists believed that such an understanding would make possible the prediction of certain events that in turn would be useful in the development of ways to modify or control them. (The basic steps in the application of the modern scientific method are described in the accompanying box.)

Every scientific investigation begins with the observation and description of a set of occurrences from which a pattern is established that permits or suggests the formulation of a specific hypothesis. The early advancement of science was therefore limited to the range of objects and phenomena that could be observed with the unassisted senses. In order to investigate the heavens and the microscopic world, technological advancements that would

**The Scientific Method**

The modern approach to scientific discovery involves the adherence to a sequence of logical steps. Each investigation begins with the organization of observed occurrences into a conceptual model. Such a model consists of a description of a process, based on experience, insight, and logic. The conceptual model forms the basis for one or more questions, which are phrased as either a positive statement called a *hypothesis* or a negative statement called a *null-hypothesis.*

An experiment is then designed to test the validity of the hypothesis or null-hypothesis. This involves the establishment of a set of tests in which the effect of treatments or conditions under investigation can be demonstrated clearly. This involves a comparison of treated groups with untreated (control) groups. The experiment must be replicated sufficiently to reduce the influence of anomalies as a result of drawing the samples from a narrow portion of the range of natural variation.

The data obtained from the experiment must then be analyzed statistically to demonstrate that the treatments resulted in effects that were different from those obtained from the controls owing to something other than chance.

The analyzed data must then be interpreted relative to the original hypothesis or null-hypothesis. If the data analysis supports the rejection of the null-hypothesis or the retention of the hypothesis, they stand as factual until such time as refuted by further experimentation. These facts are then incorporated into the formulation of more complete conceptual models that in turn lead to new hypotheses and further experimentation.

increase the power of critical observation were needed. The need for such improvements was obviously recognized, as indicated by the almost simultaneous invention of the microscope and the telescope by the Janssens (father and son) and by Galileo. The use of these magnifying devices ushered in the age of microscopy that led to the devlopment of a basic understanding of plant anatomy (Grew and Malpighi), insect anatomy (Malpighi and Swammerdam), and microbiology (Leeuwenhock).

Typical of the progress made during this period as a result of applying the scientific method and the new tools of science were the disproof by Francesco Redi (1626–1697) of the spontaneous generation of maggots from spoiled meat and his description of ectoparasitic lice. At about the same time, John Ray (1627–1705), a botanist with a basic interest in insects, published the first descriptions of insect life histories, including an accurate account of caterpillar metamorphosis. He also made observations on the parasitism of caterpillars, and in one of his articles stated:

> I shut up ten or so of these in a wooden box at the end of August 1658. They fed for a few days, and fixed themselves to the sides or lid of the box. Seven of them proved to be viviparous or vermiparous: from their backs and sides very many, from thirty to sixty apiece, wormlike animalcules broke out; they were white, glabrous, footless, and under the microscope transparent. As soon as they were born they began to spin silken cocoons, finished them in a couple of hours, and in early October came out as

Jan Swammerdam (1637–1680), the most famous of the early insect anatomists.

flies, black all over with reddish legs and long antennae, and about the size of a small ant. The three or four caterpillars which did not produce maggots after a long interval changed into angular and humped chrysalids which came out in mid-April as white butterflies.

He later wrote in his *Historia Insectorum*, 1710:

Whence these maggots arise is a great problem. I think that the ichneumon wasps prick these caterpillars with the hollow tube of their ovipositor and insert eggs into

Francesco Redi (1626–1698) contributed to the disproof of spontaneous generation through his study of maggots in spoiled meat.

their bodies: the maggots are hatched by the warmth of them, and feed there until they are full grown; then they gnaw through the skin, come out, and spin their cocoons.

The adoption of the scientific method and the use of the microscope opened the floodgates to an ever-increasing flow of information about the natural world in general and the insects in particular. This great expansion of knowledge, combined with the growing lists of plants and animals described at home and abroad, created the need for a refined system for organizing what was known. The development of such a system became the main thrust of many biologists during the eighteenth century. René Antoine Ferchault de Réaumur (1683–1757) produced the first entirely original compendium of entomology since Aristotle. Through his six-volume *Mémoires pour server a l'histoire des insects* (1734–1742), he initiated modern entomology and produced the first well-illustrated classification. Réaumur also introduced behavior and ecology, and provided the first scientific rationale for insect control. At about the same time, a Swedish physician and botanist, Carl von Linné, later called Linnaeus (1707–1778), introduced the binomial system of nomenclature which reduced lengthy Latin descriptions to a two-part name. Linnaeus was clearly a superb observer with a sophisticated understanding of the natural world even though he subscribed to the popular belief of special creation. His ability to select strong diagnostic characters as the basis for classification, his strict adherence to the system he proposed, and his recognition as an authoritative scientist led to widespread acceptance of his work that culminated in the publication of *Systema Naturae*, 10th edition, in 1758.

After the publication of *Systema Naturae*, taxonomy was no longer cumbersome and rapidly gained popularity, particularly among the professional

René Antoine Ferchault de Réaumur (1683–1757) is considered to have laid the foundations of modern entomology.