Radiation, Radioactivity, and Insects

BY
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FOREWORD

This monograph is one in a series developed through the cooperative efforts of the American Institute of Biological Sciences and the U. S. Atomic Energy Commission's Division of Technical Information. The goal in this undertaking has been to direct attention to biologists' increasing utilization of radiation and radioisotopes. Their importance as tools for studying living systems cannot be overestimated. Indeed, their application by biologists has an added significance, representing as it does the new, closer association between the physical and biological sciences.

The association places stringent demands on both disciplines: Each must seek to understand the methods, systems, and philosophies of the other science if radiation biology is to fulfill its promise of great contributions to our knowledge of both the normal and the abnormal organism. Hopefully, the information contained in each publication will guide students and scientists to areas where further research is indicated.

The American Institute of Biological Sciences is most pleased to have had a part in developing this Monograph Series.

JOHN R. OLIVE
Executive Director
American Institute of Biological Sciences

October, 1963

PREFACE

This book is intended for two audiences. One is made up of entomologists and other biologists who want to know the way in which research with radiation and radioisotopes has advanced our understanding of insects, and what entomological problems of their own could be profitably attacked with such techniques. For members of this audience, an appendix has been added which gives a brief introduction to concepts, techniques, and units of measure, so that even if they have no contact with work that uses radiation or radioactivity the book should be comprehensible.

The second audience comprises those knowledgeable in work with irradiation and radioisotopes who would like a comprehensive account of what has been done with insects, and perhaps would like to know for what kinds of problems the insect is a suitable organism. For this second audience, Chapter 1 was written as an introduction to the special features of insects—structural, functional, and behavioral. Insects sometimes are used because they are convenient to rear and treat in large numbers, as in genetic studies on *Drosophila*, and sometimes as organisms with adaptations of special interest, as in cases where metamorphosis can be accurately induced by giving a blood meal.

In view of the fact we are writing for two audiences, we have tried to use language that any scientist would understand, and we have in mind the undergraduate science student as representative of the minimum level of training we anticipate in our readers.

We have seldom attempted to insert material published after the appropriate chapter was written because of the patchwork consequences of such attempts. We have not discussed the genetic effects of radiation upon insects, because this will form a large portion of another monograph in this series concerned with genetic effects on organisms in general. With these exceptions, the book is intended to give a rather complete account of both the academic and utilitarian radiation work that has been applied to insects; and also of the diverse uses of radioisotopes in entomology, both for labeling of insects and for elucidation of biochemical, physiological, and toxicological mechanisms.

The insect names used are those approved by the Entomological Society of America. This has often led us to use names different from those used by the original authors. The reader should therefore not be puzzled if we tell him that Smith worked with *Bracon hebetor*, although Smith himself talks of *Habrobracon juglandis*. All such synonyms are given in the glossary, along with the brief names which we have generally used for much-discussed organisms, such as *Drosophila* for *Drosophila melanogaster*. However, when an insect is first mentioned in any chapter, its full name is given. Occasionally the full name will also appear in a table, when consistency within the table demands it. Our taxonomic adviser, Dr. W. L. Brown of Cornell University, has suggested that we omit the parenthetical mention of authorities for insect names, except in the glossary where there occur a few cases in which confusion is possible.

We acknowledge our indebtedness to the extensive bibliography of Mr. H. Custodio (Philippine Bureau of Plant Industry) in his M.S. thesis from Cornell (1961) entitled "A review of the literature on the use of radioisotopes in entomological research and radiation effects for pest control."

Our reviewers were Dr. L. E. Chadwick (University of Illinois) and Dr. P. A. Dahm (Iowa State University), to whom we are extremely grateful for the scrupulousness of their review and the helpfulness of their suggestions. Since final decisions were left to us, they are in no way responsible for errors or omissions.

R. D. O'Brien
L. S. Wolfe

October, 1963

GLOSSARY

CoA	Coenzyme A
IDP	Inosine diphosphate
ITP	Inosine triphosphate
NAD	Nicotine-adenine dinucleotide (formerly DPN)
$NADH_2$	Reduced form of NAD (formerly DPNH)
NADP	Nicotine-adenine dinucleotide phosphate (formerly TPN)
Aedes	*Aedes aegypti* (L): yellow fever mosquito
Anagasta	*Anagasta* (= *Ephestia*) *kühniella* (Zell): Mediterranean flour moth
Blatella	*Blatella germanica* (L): German cockroach
Bracon	*Bracon hebetor*, Say [= *Habrobracon juglandis* (Auct.)]: a parasitic wasp
Bombyx	*Bombyx mori* (L): a silkworm
Calliphora	*Calliphora erythrocephala* (Meig.): blow fly
Callitroga	*Callitroga hominovorax* (Coq.): screw-worm fly
Chortophaga	*Chortophaga viridifasciata* (De G.): green meadow locust
Culex	*Culex tarsalis* Coq: a mosquito
Dahlbominus	*Dahlbominus fuscipennis* (Zetterstedt): a parasitic hymenopteron
Dermestes	*Dermestes maculatus* (= *vulpinus*) De G.: hide beetle
Drosophila	*Drosophila melanogaster* (Meig.): domestic fruit fly
Galleria	*Galleria mellonella* (L.): greater wax moth
Hyalophora	*Hyalophora* (= *Platysamia*) *cecropia* (L.): cecropia moth
Leptinotarsa	*Leptinotarsa decemlineata* (Say): Colorado potato beetle
Locusta	*Locusta migratoria* L.: migratory locust
Melanoplus	*Melanoplus differentialis* (Thos.): differential grasshopper
Metatetranychus	*Metatetranychus ulmi* (Koch): European red mite
Musca	*Musca domestica* L.: house fly
Myzus	*Myzus persicae* (Sulz.): green peach aphid
Oncopeltus	*Oncopeltus fasciatus* (Dall.): large milkweed bug
Periplaneta	*Periplaneta americana* (L.): American cockroach
Phoenicia	*Phoenicia* (= Lucilia) *sericata* (Meig.): a green bottle fly
Phormia	*Phormia regina* (Meig.): black blow fly
Rhodnius	*Rhodnius prolixus* (Ståhl): an assassin bug
Schistocerca	*Schistocerca gregaria* (Forskål): desert locust
Sitophilus	*Sitophilus granarius* (L.) (= *Calandra granaria*): granary weevil
Tenebrio	*Tenebrio molitor* (L.): yellow mealworm
Tribolium	*Tribolium confusum* Duv.: confused flour beetle

TERMS USED FOR RADIATION AND RADIOACTIVITY

Alpha (α) particle. A particle emitted from a few radioisotopes—e.g., promethium^{147}. It consists of two protons and two neutrons and is identical with the helium nucleus. It has extremely low penetrating power.

Beta (β) particle. A particle emitted from numerous radioisotopes—e.g., C^{14}. It is an electron. Its penetrating power depends on its energy (which in turn depends on its source) and is usually low.

Curie (c). A quantity of radioactivity, measured by the number of disintegrations in a given time. One curie produces 2.22×10^{12} disintegrations per minute.

Gamma (γ) ray. An electromagnetic radiation emitted from certain radioisotopes—e.g., I^{131}. A relatively deeply penetrating emanation.

Kilovolt (kvp). The crest value of the electrical potential wave in a cathode ray tube used to generate x-rays.

Millicurie (mc). One thousandth of a curie.

Million electron volts (Mev). A unit of energy commonly applied to α, β, γ, and X radiations. For any given radiation, high Mev implies high penetration.

Rad. See "roentgen."

Rep. See "roentgen."

Roentgen (r). An exposure dose of x or γ rays. One roentgen will deposit 83.8 ergs of energy in 1 g of dry air at standard conditions. As essentially equivalent unit, though now historical, is the rep. "roentgen equivalent physical", which is an energy deposition ϕ of 93 ergs in 1 g of soft tissue. Another unit, applied to all radiation is the rad, "radiation absorbed dose." The rad, by definition, is the amount of radiation which will deposit 100 ergs per gram in any material.

CONTENTS

CHAPTER 1

Insects

Before specific aspects of the effect of radiation on insects and the use of radioisotopes in entomology are considered, a few general remarks on some of the distinctive features of the anatomy and physiology of insects will be given to orient readers who are not entomologists.

1. Importance and Dominance of Insects in the Animal Kingdom

The phylum Arthropoda is unequaled in the animal kingdom in the number and variety of species it contains and in the diversity of life histories and behavior. It contains 80% of all animal species. The class Insecta is the largest and most successful group of arthropods, and this has been so since Carboniferous times, long before the emergence of man. Insects are small, highly organized, essentially land arthropods in which the body is divided into three parts: head, with the mouthparts and principal sense organs; thorax, with locomotor organs, legs, and wings; and abdomen, with the digestive, reproductive, and excretory organs. Most insects have six legs and are often classified as Hexapoda.

Almost a million species of insects have been described, and several times this number probably await classification. Estimates of total numbers of individuals soon reach incomprehensible figures. Many honey beehives contain 40 to 50 thousand individuals, and ant colonies contain about half a million. On a single tomato plant, 24,688 aphids have been counted. An acre of agricultural land may contain roughly 4 million insects. One square yard of river bed in a rill section at the outlet of lakes in the forests of the southern margin of the Canadian shield is capable of producing half a million black flies. Put another way, despite their small size the combined bulk of insects is about equal to that of all other land animals.

To the layman, insects are either pests such as cockroaches, bedbugs, houseflies, biting flies, ants, wasps, etc., or often beautiful creatures such as dragonflies, butterflies, moths, and beetles. However, the majority of insects are of minute size, scarcely visible to the naked eye. Myriads of microscopic soil collembolans may appear like black soot on the surface of irrigation ditches following heavy rain. The actual number of pest insect species is surprisingly small; certainly no greater than 10,000, only 500 of which are of major importance. Again, these pest insects primarily affect agricultural crops and produce; less than a hundred species are involved in disease transmission in man. In spite of this, the amount of damage caused to crops, products, livestock, and health by insects annually in the United States alone is in the billions of dollars. The appearance in Europe of the grape phylloxera, *Phylloxera vitifoliae*, brought from North America in 1863, had by 1870 cost France alone 10,000 million francs, twice the indemnity exacted from France by Bismarck in the Prussian War. In 1955 Kenya was invaded by a moderate-sized swarm of desert locusts estimated to contain 1500 million insects spread over eight square miles. Each locust eats about its own weight in green vegetation daily, and, since this swarm weighed about 3000 tons, the resulting denudation of the land was catastrophic. It is difficult to exaggerate the economic consequences to man of a handful of the major pest insects.

Not only are insects unique in the great variety of species but also in the number of forms within individual species. Many larvae and pupal forms bear no obvious resemblance to adult forms. An important part of the systematist's and field naturalist's work is involved in connecting the great variety of described larval forms to the correct adult forms. Certain aphids have amazingly complex life histories, and one species, *Phylloxera quercus*, is known to have 21 forms.

All stages in the evolution of animal behavior are found in insects, and this is closely associated with form differentiation or polymorphism. Three broad levels in this process can be seen. In the first level are those insects that behave individualistically and often sustain a heavy loss of their numbers because of it; in the second level, care of the young by the mother has developed; and in the third level, the young offspring, usually female, assist and cooperate with others to form the family-like society characteristic of the social insects such as termites, wasps, bees, and ants. In the most advanced form of insect society the female is the most important member, and the only function of the males is fertilization. Further, the workers dominate and operate the society. The queen becomes the egg producer and also the means by which organization is maintained. This is achieved through the elaboration of chemical substances, called pheromones, which are disseminated throughout the colony and inhibit ovary development and queen rearing. Queen substance secreted by the mandibular glands of the queen bee contains such a material, which has been characterized chemically as 9-oxodec-2-enoic acid. The efficiency of insect communities such as those of ants and bees is due in large measure to the following factors: (1) the division of labor between the queen and workers and among the workers; (2) the attraction workers have for each other and the attraction of the queen for the workers; (3) the development of a method of communication between workers to enable detailed information about food sources and other important matters to be given to all; (4) the development of a method of distinguishing members of one's own colony from intruders and the establishment of a system of nest defenses; and (5) the development of a control system of ovary development and queen rearing which enables replacement of an unsatisfactory queen by a new young one and which, during favorable conditions, leads to reproduction and swarming. The behavior patterns in these remarkable, truly cooperative societies are in many ways in a more advanced stage of behavioral evolution than human societies.

The identification of chemical factors which control insect behavior is a rapidly advancing and exciting field. It has been known for many years that in certain insects sex attraction is elicited by characteristic odors produced by the female. For example, the virgin female American cockroach, *Periplaneta americana,* emits a powerful attractant which causes intense excitement and characteristic wing-raising behavior in the males. The substance causing this activity has now been chemically characterized as 2,2-dimethyl-3-isopropylidenecyclopropyl propionate.[1] A response is elicited from males by amounts below 10^{-14} μg. The gregarious male desert locust, *Schistocerca gregaria,* which is bright yellow in color when mature, secretes a volatile, fat-soluble substance from the surface of its cuticle. This substance is transmitted to young locusts by olfaction through the antennae or by body contact under crowded conditions and accelerates their maturation. The presence of this substance is indicated by a characteristic vibration reaction of the antennae, palpi, and hind femora in the immature locusts.[2]

The evolution and diversification of insects has been very extensive. This is due to their great fecundity, rapid development, and small size, which enable large populations to build up in any one year and to colonize a great number of microenvironments. Adaptations have arisen for survival in every type of environment on this planet, from the arctic wastes of Ellesmere Island to the extraordinary aridity of the Arizona and Atacama deserts. Two factors account for the success of insects. The first is the development of wings, which permits entry to a great variety of new environments. This great evolutionary innovation necessitated considerable advances in the development of sense organs, particularly those for vision and olfaction. The nervous system, in a parallel fashion, became progressively more elaborate, with more and more concentration toward the anterior end (cephalic dominance). However, the so-called brain which is thus formed does not exert as comprehensive a control as does the vertebrate brain; for instance, many insects can survive and perform complex activities after decapitation. The conservatism in the number of neurones required for these reactions at first sight appears remarkable. But insect behavior is predominantly based on habituation and stereotyped instinctive patterns and lacks the modifiability based on the experiential memory and learning of mammals.

The second factor in insect evolution upon which their success to a large measure depends is the development of complete metamorphosis. By this is meant the splitting up and specialization of the life history of the insect into three periods: (1) the larval period of feeding and growth; (2) the prepupal and pupal period of differentiation; and (3) the adult or imaginal period of mating, migration, and reproduction. The three great but antagonistic phases of development—growth, differentiation, and reproduction—are completely separated. The larva, pupa, and adult differ completely in form and thus may utilize a variety of environments appropriate for each stage. Each form has been subject independently to adaptive changes. The evolution of complete metamorphosis is intimately associated with the development of wings which are restricted to the adult stage of intense locomotory and reproductive activity. An indication of the value of metamorphosis is seen when the number of species of insects with complete metamorphosis is compared with those without metamorphosis or with an incomplete one. Eighty-five per cent of all insect species have complete metamorphosis, about 13% have incomplete metamorphosis, and the remaining 2% show no true metamorphosis.

2. Classification of Insects

The classification of insects into subclasses is based on either structural or functional principles. On a structural basis the subclasses are termed (1) Apterygota, primitive wingless insects; (2) Exopterygota, insects in which the wings develop as external wing pads; and (3) Endopterygota, insects in which the wings develop internally in peripodal sacs. On a functional basis the following subclasses are recognized: (1) Ametabola, insects without metamorphosis; (2) Prometabola, insects which pass through four stages of development, egg, aquatic nymph, subimago (sexually immature winged form), and imago (adult); (3) Hemimetabola, insects which pass through a partial metamorphosis from an immature, nymphal stage to adult but with no subimago or true pupa; (4) Holometabola, insects with a complete and exceedingly complex metamorphosis from larva through prepupal and pupal forms to the adult. Table 1.1 lists the orders of insects, common names, and the approximate number of species within each order. Most insects are given generic and specific names only, although some insects which show many geographical variations are named trinomially.

TABLE 1.1

SIMPLE CLASSIFICATION OF INSECTS INTO MAJOR GROUPS

Subclasses	Orders	Vernacular names	Approximate no. of species
Ametabola	Collembola	spring-tails	1,250
	Diplura	two-pronged bristletails	—
	Thysanura	three-pronged bristletails	325
	Protura	—(minute soil insects with primitive abdomen)	62
Prometabola	Ephemeroptera	May flies	1,270
Hemimetabola	Odonata	dragonflies, damselflies (demoiselles)	5,000
	Orthoptera	cockroaches, grasshoppers, crickets, katydids, mantids, etc.	21,000
	Plectoptera	stone-flies	1,260
	Dermaptera	earwigs	1,050
	Isoptera	termites	16,000
	Zoraptera	—(minute colonial insects frequently associated with termite nests)	12
	Embioptera	—(small semisocial insects living in silken tunnels)	100
	Corrodentia	psocids, book lice	875
	Mallophaga	biting lice	2,500
	Thysanoptera	thrips	2,500
	Hemiptera	cicadas, leaf hoppers, aphids, scale insects, water and plant bugs, bed bugs, stink bugs, etc.	57,500
	Anoplura	sucking lice	280
Holometabola	Coleoptera	beetles	250,000
	Strepsiptera	stylops	200
	Neuroptera	ant lions, alder flies, lace-wings, mantispids, etc.	4,350
	Mecoptera	scorpion-flies	310
	Trichoptera	caddis flies	3,600
	Lepidoptera	moths and butterflies	120,000
	Diptera	true flies, mosquitoes, midges, gnats, warble flies, etc.	78,000
	Siphonaptera	fleas	900
	Hymenoptera	sawflies, wasps, bees, ants, ichneumon flies	280,000

3. Anatomy

The anatomical design of insects is very different from that of chordates. Basically, they are bilaterally symmetrical, segmented animals, covered by an exoskeleton and with a dorsal heart and ventral nervous system. In the evolution of insects, the body segments and exoskeleton have been modified

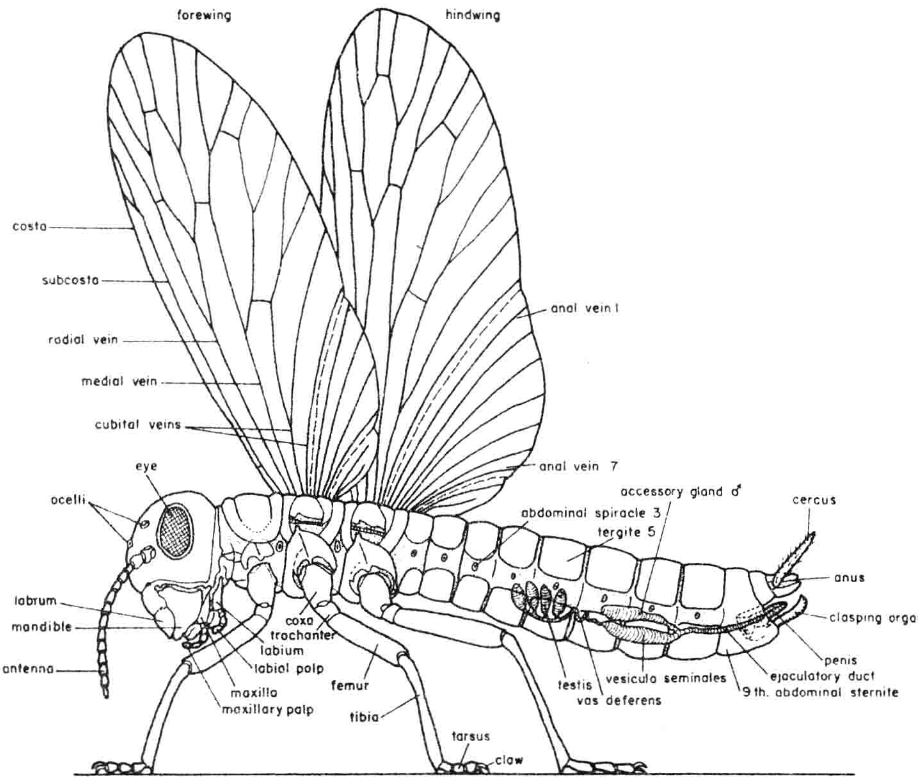

FIG. 1.1. Basic plan of the external anatomy of an insect, showing male reproductive system. (Adapted from H. Weber, *Grundriss der Insektenkunde*, Gustav Fischer, Stuttgart, 1949.)

in many ways. The ancestors of insects are believed to have had segmented bodies with a pair of appendages to each segment. Modern insects have discarded most of these appendages and have modified three thoracic pairs for locomotion, some anterior ones to serve as mouthparts, and the terminal abdominal segments as external sexual organs. The insect head superficially appears unsegmented. However, a careful study of the development of the head of primitive insects reveals its segmented nature. Typically, each body

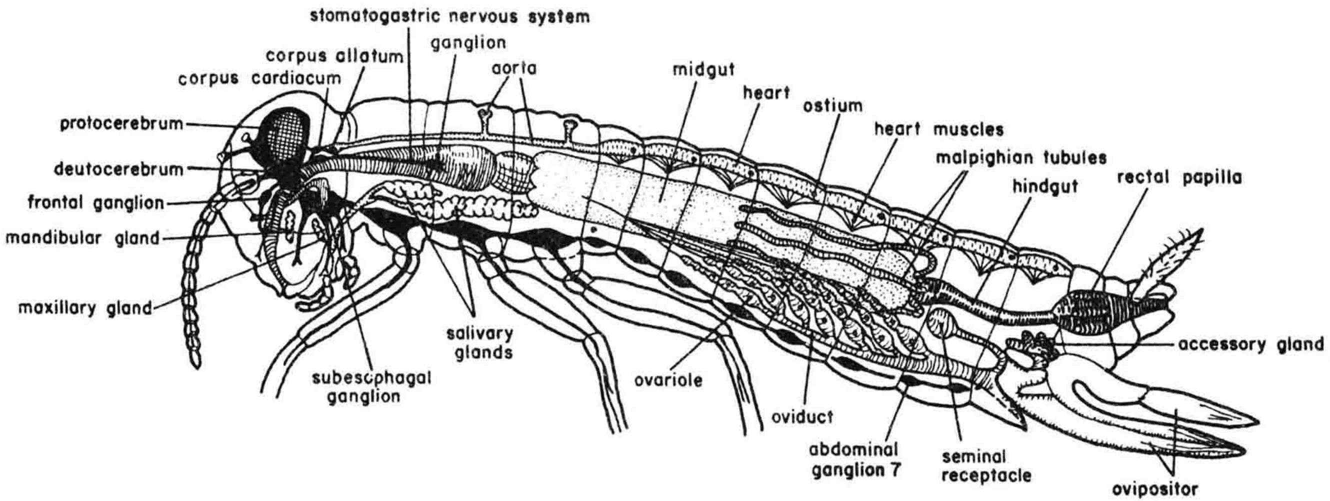

FIG. 1.2. Basic plan of the internal anatomy of an insect, showing female reproductive system. (Adapted from H. Weber, *Grundriss der Insektenkunde*, Gustav Fischer, Stuttgart, 1949.)