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ENTOMOLOGY

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ENTOMOLOGY

WITH SPECIAL REFERENCE TO
ITS ECOLOGICAL ASPECTS

BY
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THIRD REVISED EDITION
WITH FIVE PLATES AND 308 TEXT-FIGURES

LONDON
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1923

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PREFACE

This book gives a comprehensive and concise account of insects. Though planned primarily for the student, it is intended also for the general reader.

The book was written in an effort to meet the growing demand for a biological treatment of entomology.

The existence of several excellent works on the classification of insects (notably Comstock's Manual, Kellogg's American Insects and Sharp's Insects) has enabled the author to omit the multitudinous details of classification and to introduce much material that hitherto has not appeared in text-books.

As a rule, only the commonest kinds of insects are referred to in the text, in order that the reader may easily use the text as a guide to personal observation.

All the illustrations have been prepared by the author, and such as have been copied from other works are duly credited.

To Dr. S. A. Forbes the author is especially indebted for the use of literature, specimens and drawings belonging to the Illinois State Laboratory of Natural History.

Permission to copy several illustrations from Government publications was received from Dr. L. O. Howard, Chief of the Bureau of Entomology; Dr. C. Hart Merriam, Chief of the Division of Biological Survey, and Dr. Charles D. Walcott, Director of the U. S. Geological Survey. Several desired books were obtained from F. M. Webster, of the Bureau of Entomology.

Acknowledgments for the use of figures are due also to Dr. E. P. Felt, State Entomologist of New York; Dr. E. A. Birge, Director of the Wisconsin Geological and Natural History Survey; Prof. E. L. Mark and Prof. Roland Thaxter, of Harvard University; Prof. J. H. Comstock of Cornell University; Prof. C. W. Woodworth of the University of California; Prof. G. Macloskie of Princeton University; Prof. W. A. Locy of Northwestern University; Prof. J. G. Needham of Cornell University; Dr. George Dimmock of Springfield, Mass.; Dr. Howard Ayers of Cincinnati, Ohio; Dr. W. M. Wheeler of the American Museum of Natural History, New York City; Dr. W. L. Tower of the University of Chicago; Dr. A. G. Mayer, Director of the Marine Biological Laboratory, Tortugas, Fla.; James H. Emerton of Boston, Mass.; Dr. and

Mrs. G. W. Peckham of Milwaukee, Wis.; Dr. William Trelease, Director of the Missouri Botanical Garden; Dr. Henry Skinner, as editor of "Entomological News;" and the editors of "The American Naturalist."

Acknowledgments are further due to the Boston Society of Natural History, the American Philosophical Society and the Academy of Science of St. Louis.

Courteous permission to use certain figures was given also by The Macmillan Co.; Henry Holt & Co.; Ginn & Co.; Prof. Carl Chun of Leipzig; F. Dümmler of Berlin, publisher of Kolbe's Einführung; and Gustav Fischer of Jena, publisher of Hertwig's Lehrbuch and Lang's Lehrbuch.

The first edition, which was translated into Japanese by Professors Miyake and Uchida, has had a large sale in Japan.

The second edition contained much new matter, particularly a chapter on the transmission of diseases by insects.

This third edition has been brought up to date by the addition of a great deal of new material, including a few new illustrations. Some two hundred and fifty titles have been added to the bibliography but, to accommodate these, it was necessary to discontinue other titles of less importance.

A new chapter, on insect ecology, is given. This ought to prove useful, as the literature of the subject is scattered, and there has been no similar comprehensive treatment of ecology from the viewpoint of the entomologist.

In the preparation of this chapter the author has been fortunate in having the expert advice of Professor V. E. Shelford, of the University of Illinois; who is not responsible, however, for any possible shortcomings in the chapter.

The following scientific men also have gladly assisted by giving desired information:—Dr. L. O. Howard, chief of the Bureau of Entomology; Mr. A. F. Burgess, of the Bureau of Entomology; Prof. J. H. Comstock, Cornell University; Prof. A. F. Shull, University of Michigan; Mr. Nathan Banks, Museum of Comparative Zoölogy, Cambridge, Mass.; Mr. Charles Macnamara, Arnprior, Ontario, Canada; Professor A. O. Weese, University of New Mexico; Dr. C. P. Alexander, Mr. W. P. Flint and Dr. H. Yuasa, of the Illinois State Natural History Survey; Professor A. D. MacGillivray and Dr. R. D. Glasgow, of the University of Illinois.

Permission to use the map for Plate V. was courteously given by Dr. B. E. Livingston and the Carnegie Institution of Washington.

CONTENTS

CHAPTER	PAGE
I. CLASSIFICATION.....	I
II. ANATOMY AND PHYSIOLOGY.....	27
III. DEVELOPMENT.....	129
IV. ADAPTATIONS OF AQUATIC INSECTS.....	165
V. COLOR AND COLORATION.....	172
VI. ADAPTIVE COLORATION.....	194
VII. INSECTS IN RELATION TO PLANTS.....	212
VIII. INSECTS IN RELATION TO OTHER ANIMALS.....	233
IX. TRANSMISSION OF DISEASES BY INSECTS.....	248
X. INTERRELATIONS OF INSECTS.....	270
XI. INSECT BEHAVIOR.....	302
XII. DISTRIBUTION.....	322
XIII. INSECT ECOLOGY.....	348
XIV. INSECTS IN RELATION TO MAN.....	410
LITERATURE.....	430
INDEX.....	479

ENTOMOLOGY

CHAPTER I CLASSIFICATION

At the outset it is essential to know where insects stand in relation to other animals.

Arthropoda.—Comparing an insect, a centipede and a crayfish with one another, they are found to have certain fundamental characters in common. All are bilaterally symmetrical, are composed of a linear series of rings, or segments, bearing paired, jointed appendages, and have an external skeleton, consisting largely of a peculiar substance known as chitin.

If the necessary dissections are made, it can be seen that in each of these types the alimentary canal is axial in position; above it extends

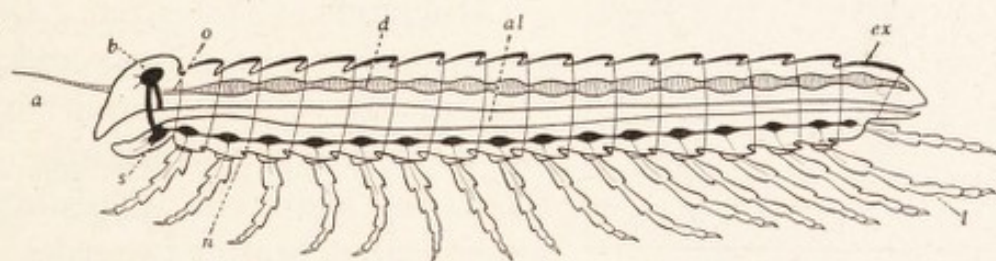


FIG. 1.—Diagram to express the fundamental structure of an arthropod. *a*, antenna; *al*, alimentary canal; *b*, brain; *d*, dorsal vessel; *ex*, exoskeleton; *l*, limb; *n*, nerve chain; *s*, subcesophageal ganglion.—After SCHMEIL.

the dorsal blood vessel and below lies the ventral ladder-like series of segmental ganglia and paired nerve cords, or commissures; between the commissures that connect the brain and the subcesophageal ganglion passes the œsophagus. These relations appear in Figs. 1 and 165. Furthermore, the sexes are almost invariably separate and the primary sexual organs consist of a single pair.

No animals but arthropods have all these characters, though the segmented worms, or annelids, have some of them—for example the segmentation, dorsal heart and ventral nervous chain. On account of these correspondences and for other weighty reasons it is believed that

arthropods have descended from annelid-like ancestors. Annelids, however, as contrasted with arthropods, have segments that are essentially alike, have no external skeleton and never have paired limbs that are jointed.

Classes of Arthropoda.—Excluding the king-crab, trilobites and a

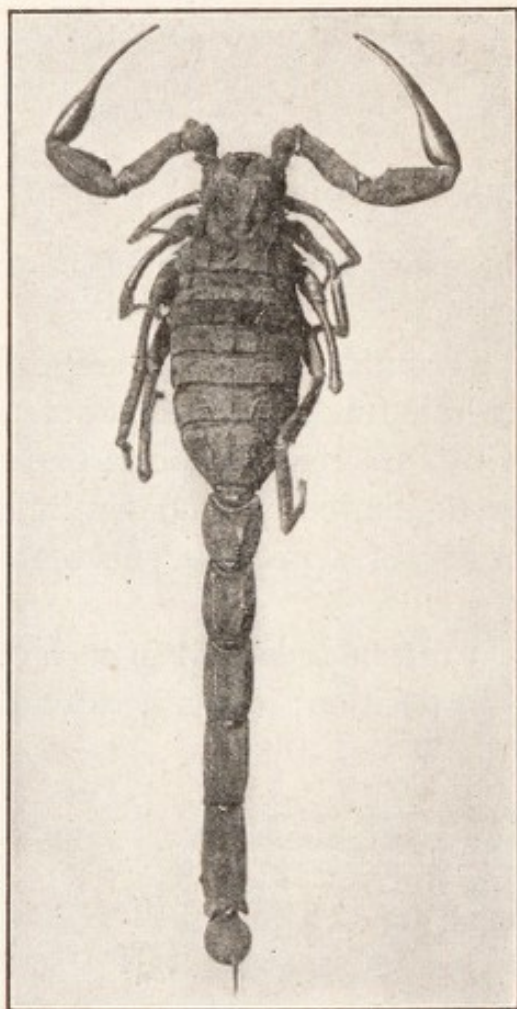


FIG. 2.—A scorpion, *Buthus*. Natural size.

few other forms that have no immediate entomological importance, the remaining arthropods fall into nine classes, which are characterized as follows:

Crustacea.—Aquatic, as a rule. Head and thorax often united into a cephalothorax. Numerous paired appendages, typically biramous (Y-shaped); abdominal limbs often present. Two pairs of antennæ. Respiration branchial (by means of gills) or cutaneous (directly through the skin). The exoskeleton contains carbonate and phosphate of lime in addition to chitin. Example, crayfish.

Arachnida.—Terrestrial. Usually two regions, cephalothorax and abdomen; though various Acarina have but one and Solpugida have all three—head, thorax and abdomen. Cephalothorax unsegmented, bearing two pairs of oral appendages and four pairs of legs. Eyes simple. Abdomen segmented or

not, limbless. Respiration tracheal, by means of book-leaf tracheæ, tubular tracheæ, or both; stigmata almost always abdominal, at most four pairs. Heart abdominal in position. Example, *Buthus* (Fig. 2).

Onychophora.—Terrestrial. Vermiform (worm-like), unsegmented externally. One pair of ringed antennæ, a pair of jaws and a pair of oral slime papillæ. Legs numerous, paired, imperfectly segmented. Respiration by means of short tubular tracheæ, the stigmata of which are scattered over the surface of the body, or arranged in rows. Genital opening posterior. Numerous nephridia (excretory) are present, arranged segmentally in pairs. Two separate longitudinal nerve cords,

connected by transverse commissures. Integument delicate. Some fifty species are known. Example, *Peripatus* (Fig. 3).

Diplopoda.—Terrestrial. Two regions, head and body. Body usually cylindrical, with numerous segments, most of which are double and bear two pairs of short limbs, which are inserted near the median ventral line. Eyes simple, antennæ short, usually seven-segmented,



FIG. 3.—*Peripatus capensis*. Natural size.—After MOSELEY.

mouth parts consisting of a pair of mandibles and a compound plate, or gnathochilarium. Genital openings separate, anterior in position (on the second segment of the body). Example, *Spirobolus* (Fig. 4).

Pauropoda.—Terrestrial. Two regions, head and body. Body elongate, twelve-segmented, with nine pairs of functional legs; each of the first five apparent terga consists morphologically of two united terga. Eyes absent, but a pair of eye-like spots may be present. Antennæ characteristic; with four proximal segments and a pair of distal branches bearing three filaments in all. Mouth parts represented by mandibles, maxillæ (?) and labium (?). A single genital opening (female) or a pair of openings (male) on the third body segment. Minute arthropods, at most about one millimeter in length. Example, *Pauropus*.

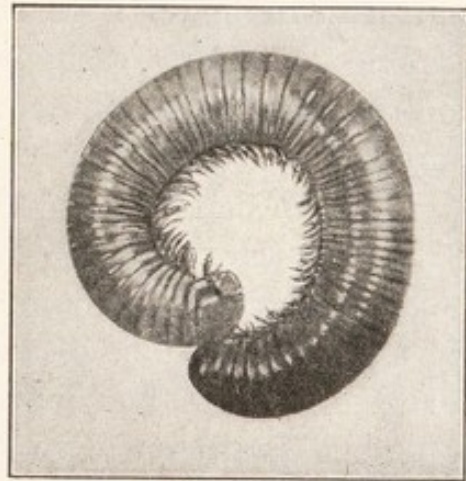


FIG. 4.—A diplopod, *Spirobolus marginatus*. Natural size.

Chilopoda.—Terrestrial. Two regions, head and body. Body long and flattened, with numerous segments, each of which bears a pair of long six- or seven-segmented limbs, which are not inserted near the median line. Eyes simple and numerous (agglomerate in *Scutigera*) antennæ long, many-segmented. A pair of mandibles and two pairs of maxillæ. A single genital opening, on the preanal segment. Example, *Scolopendra* (Fig. 5).

Symphyla.—Terrestrial. Two regions, head and body. Head prognathous, with a Y-shaped epicranial suture. Eyes few. Antennæ long, multiarticulate. Four pairs of mouth parts; mandibles two-

segmented. Body elongate, with fifteen distinct terga, and eleven or twelve pairs of legs. Cerci well developed. Genital opening in the third body segment. One pair of spiracles, opening on the head, under the antennæ. Small arthropods not more than five or six millimeters in length. Example, *Scolopendrella* (Fig. 6).

Myrientomata.—Terrestrial. Three regions: head, thorax and abdomen. Head small, conical, prognathous. One pair of eye-like spots. Antennæ absent. Mouth parts suctorial. Mandibles and maxillæ attenuate, styliform, protrusible and retractile. Labium attenuate. Body strongly elongate, fusiform, narrowing posteriorly, fifteen-segmented in adults. Thorax distinct from abdomen; prothorax shorter than meso- or metathorax. Three pairs of thoracic legs, and a pair of vestigial legs on each of the first three abdominal segments. Last four abdominal segments more or less retractile. Cerci absent. Genital opening posterior. Male genitalia elongate, retractile, distally bilobed, with a pair of slender, forceps-like appendages. Female appendage short, with short forceps. Minute delicate arthropods, seldom more than one millimeter in length. Example, *Acerentomon* (Fig. 8.)

A single order, Protura, discovered and named by Silvestri, and consisting of two families: Acerentomidæ, without a tracheal system, and Eosentomidæ, with simple tracheæ and two pairs of thoracic spiracles. Protura, easily overlooked on account of their small size, are doubtless widely distributed. At present twelve species are known from Europe and twelve from the United States, all but one of our species having been described by Dr. H. E. Ewing.

Insecta (Hexapoda).—Primarily terrestrial. Three distinct regions—head, thorax and abdomen. Head with a pair of compound eyes in most adults, one pair of antennæ and typically three pairs of mouth parts—mandibles, maxillæ and labium—besides which a hypopharynx, or tongue, is present. In Apterygota a fourth pair of mouth parts is associated with the hypopharynx. Thorax with a pair of legs on each of its three segments and usually a pair of wings on each of the posterior two segments; though there may be only one pair of wings (as in Diptera, male Coccidæ and male Strepsiptera); the prothorax never bears wings. Abdomen typically with eleven segments and without legs, excepting in some larvæ (as those of Lepidoptera, Tenthredinidæ and Panorpidæ). Stigmata paired and segmentally arranged. A metamorphosis (direct or indirect) occurs except in Thysanura and Collembola.

Relationships.—The interrelationships of the classes of Arthropoda form an obscure and highly debatable subject.

Crustacea and Insecta agree in so many morphological details that their resemblances can no longer be dismissed as results of a vague "parallelism," or "convergence" of development, but are inexplicable except in terms of community of origin, as Carpenter has insisted.

Arachnida are extremely unlike other arthropods but find their nearest allies among Crustacea, particularly the fossil forms known as trilobites.

Onychophora, as represented by *Peripatus*, are often spoken of as bridging the gulf that separates Insecta, Chilopoda and Diplopoda from Annelida. *Peripatus* indeed resembles the chætopod annelids in its segmentally arranged nephridia, dermomuscular tube, coxal glands and soft integument, and resembles the three other classes in its tracheæ, dorsal vessel with paired ostia, lacunar circulation, mouth parts and salivary glands. These resemblances are by no means close, however, and *Peripatus* does not form a direct link between the other tracheate arthropods and the annelid stock, but is best regarded as an offshoot from the base of the arthropodan stem.

In speaking of annelid ancestors, none of the recent annelids are meant, of course, but reference is made to the primordial stock from which recent annelids themselves have been derived.

Though Diplopoda and Chilopoda have long been grouped together under the name Myriopoda, they really have so little in common, beyond the numerous limb-bearing segments and the characters that are possessed by all tracheate arthropods, that their differences entitle them to rank as separate classes. Chilopoda as a whole are more nearly related to Insecta than are Diplopoda, as regards segmentation, mouth parts, tracheæ, genital openings and other characters.

Scolopendrella, now placed in a class by itself, Symphyla, presents a remarkable combination of diplopodan and insectean characters. *Scolopendrella* (Fig. 6) and the thysanuran *Campodea* have the same

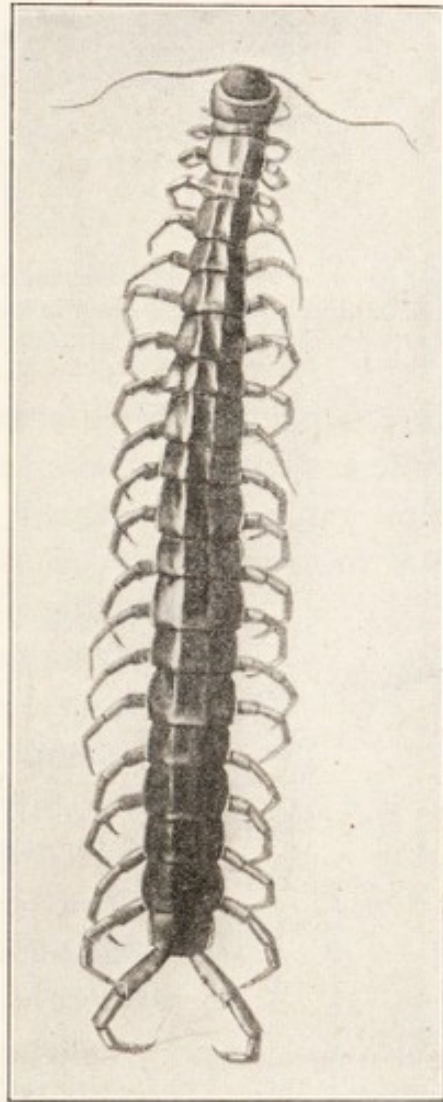


FIG. 5.—A centipede, *Scolopendra heros*. About two-thirds the maximum length.

kind of head, with long moniliform antennæ, and agree in the general structure of the mouth parts; the number of body segments is nearly the same, the legs and claws are essentially alike, and cerci and paired abdominal stylets are present in the two genera, not to mention the

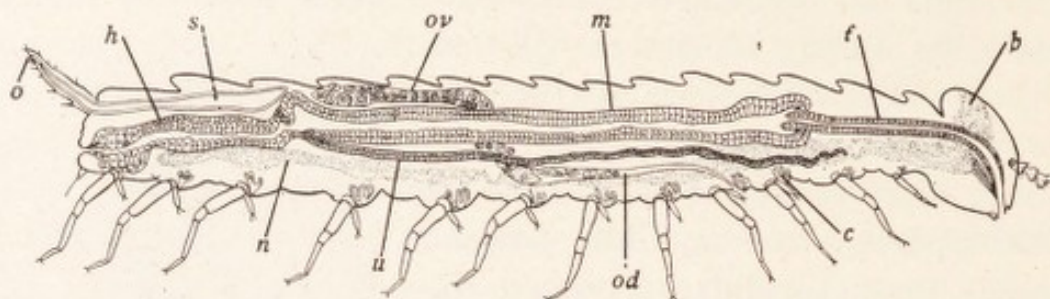


FIG. 6.—Section of *Scolopendrella immaculata*. *b*, brain; *c*, coxal gland; *f*, fore intestine; *h*, hind intestine; *m*, mid-intestine; *n*, nerve chain; *o*, opening of silk gland; *od*, oviduct; *ov*, ovary; *s*, silk gland; *u*, urinary tube.—After PACKARD.

correspondences of internal organization. Indeed, it is highly probable, as Packard maintained, that the most primitive insects, Thysanura (and consequently all other insects), originated from a form much like *Scolopendrella*. A singular thysanuran, *Anajapyx vesiculosus* (Fig. 7) was discovered by Silvestri, who regarded it as being in many respects the most primitive insect known, combining as it does characters of Symphyla, Diplopoda and *Campodea*.



FIG. 7.—*Anajapyx vesiculosus*. Length, 2 mm.—After SILVESTRI.

Silvestri discovered also a peculiar arthropod, *Acerentomon doderoi* (Fig. 8) for which he made a new order—*Protura*. Berlese added two genera to this order, namely, *Eosentomon* and *Acerentulus*; and according to good authority *Protapteron indicum* Schepotieff belongs to the former genus. Silvestri, followed by Börner, put *Protura* among Apterygota; but Berlese, who grouped these forms under the name of *Myrientomata*, found that they had myriopodan as well as insectean affinities; and Rimsky-Korsakow argued that *Myrientomata* cannot be rightly regarded as insects, but logically constitute a class by themselves; and that this class does not form a direct link between myriopods and insects, but that all these groups came from the same ancestral stock. *Protura* have actually little in common with insects; the peculiar structure of the mouth parts and genitalia excluding them from the group Apterygota.

The following diagram (Fig. 9) expresses very crudely one view as to the annelid origin of the chief classes of Arthropoda.

The naturalness of the phylum Arthropoda was questioned by Kingsley and Packard. The latter author divided Arthropoda into five independent phyla, holding that "there was no common ancestor of the Arthropoda as a whole, and that the group is a polyphyletic one." This iconoclastic view, however, by emphasizing unduly the structural differences among arthropods, tends to conceal the many deep-seated resemblances that exist between the classes of Arthropoda.

Carpenter, in a most sagacious summary of the whole subject of arthropod relationships, brought together no little evidence in favor of a revised form of the old Müllerian theory of crustacean origins. He traced all the classes of Arthropoda back to common arthropodan ancestors with a definite number of segments and distinctly crustacean in character; then traced these primitive arthropods back to forms like the nauplius larva of Crustacea, and these in turn to a hypothetical form like the trochosphere larva of recent polychæte annelids.

Orders of Insects.—Linnaeus arranged insects in seven orders, namely, Coleoptera, Hemiptera, Lepidoptera, Neuroptera, Hymenoptera, Diptera and Aptera. The wingless insects termed Aptera were soon found to belong to diverse orders and the name has become so ambiguous as to meet with little approval.

From the Linnæan group Hemiptera, the Orthoptera were set apart the old order Neuroptera a heterogeneous and unnatural group, was split into several distinct orders, and many other changes in the classification were necessary.

Without entering any further into the history of the subject, it is sufficient to say that increasing discrimination on the part of entomologists has been followed by a gradual increase in the number of orders.

Naturally, the systems of classification have grown and changed considerably, keeping pace with increasing knowledge.

Brauer (1885) made such important contributions to the subject that his system, modified more or less by Packard, Comstock and others, has been followed for almost forty years.

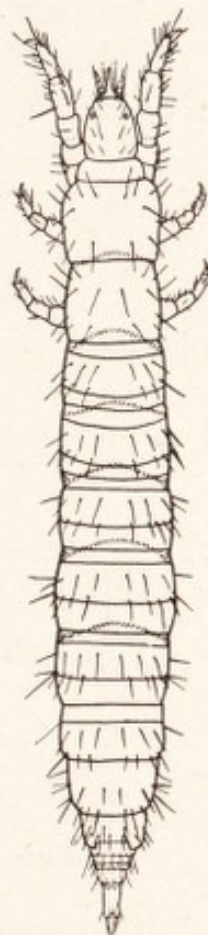


FIG. 8.—*Acerentomon doderói*. Length, 1.28 mm.—After SILVESTRI.

Handlirsch has made the most exhaustive investigation of the phylogeny of the major groups of insects. His revolutionary system, which is based upon fossil as well as recent forms, is of the kind to which one applies the term "epoch-making," but is unfortunately so erratic and fantastic in some respects that it has not been generally adopted.

As the orders of insects have evolved from one another in many different directions, like the branches of a tree, their natural relationships can not be expressed correctly in any linear sequence, like that of this book. Here the orders are listed approximately according to the degree of specialization, beginning with the most primitive insects;

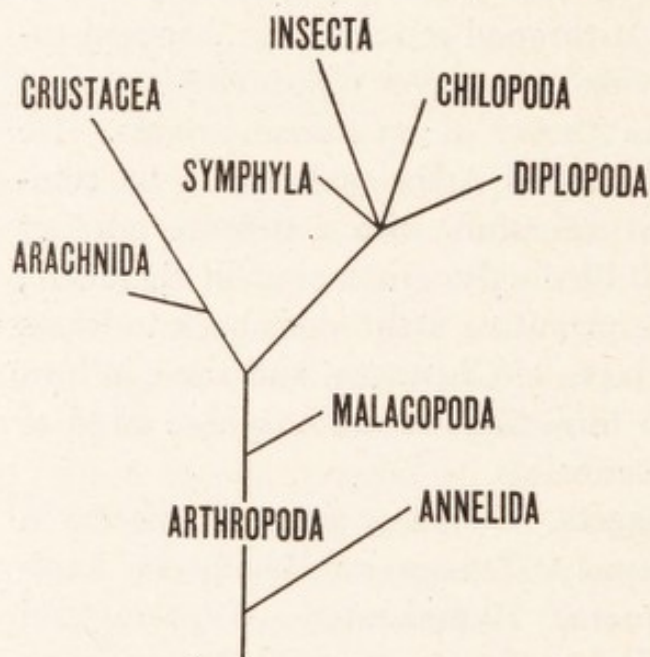


FIG. 9.—Diagram to indicate the origin of classes of Arthropoda.

and the attempt is made to group together orders that are nearly related to one another.

In the course of the following synopsis of the orders of insects it is necessary to use some terms, as *metamorphosis* and *thysanuriform*, in anticipation of their subsequent definition.

1. Thysanura.—No metamorphosis. Eyes aggregate, compound or absent. Antennæ long, filiform, multiarticulate. Mouth parts mandibulate, either free (*ectognathous*) or enclosed in the head (*entognathous*). Wings invariably absent. Thoracic segments simple and similar; prothorax well developed. Abdomen usually elongate, with ten evident segments and often traces of an eleventh segment; with two to eight pairs of rudimentary limbs, or styli, often accompanied by eversible ventral sacs. Cerci usually long, filiform, multiarticulate, with frequently a similar median pseudocercus; but sometimes with

few segments (*Anajapyx*) or represented by a pair of forceps (*Japyx*). Integument thin; scales present or absent. Active and terrestrial, "bristletails." Examples, *Campodea* (Fig. 10), *Japyx*, *Machilis*, *Lepisma* (Fig. 11), *Anajapyx* (Fig. 7). Some three hundred species are known.

2. Collembola.—No metamorphosis. Eyes ocelliform, not more than eight on each side, often fewer in number or absent. Antennæ short, of four segments in most genera; five or six in a few genera. Mouth parts entognathous and typically mandibulate, with occasional secondary suctorial modifications. Wings invariably absent. Tho-

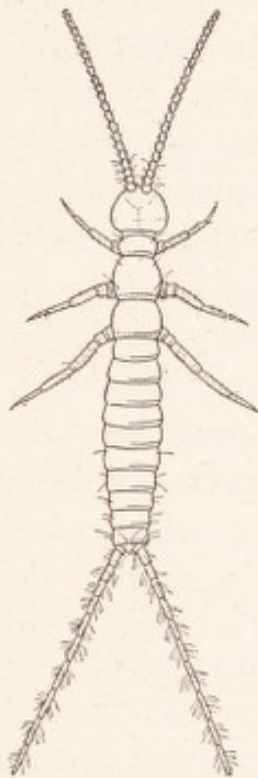


FIG. 10.—*Campodea*. Length, 3 mm.

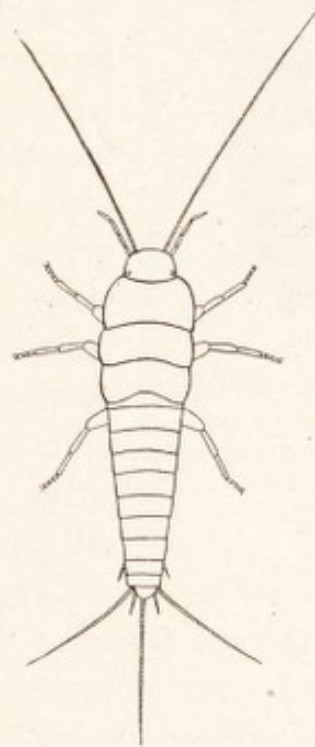


FIG. 11.—*Lepisma*. Length, 10 mm.

racic segments simple and similar, or prothorax reduced. Body cylindrical or globular. Ventral tube and furcula usually present, sometimes rudimentary. Integument delicate; scales present in some genera. Small or minute terrestrial insects, "springtails." Examples, *Achorutes* (Fig. 12), *Sminthurus* (Fig. 13). About nine hundred species have been described.

Under the term *Apterygota* the Thysanura and Collembola, as primitively wingless insects, are conveniently distinguished from all other insects, or *Pterygota*.

3. Orthoptera.—Metamorphosis direct. Eyes well developed. Antennæ usually filamentous, shorter or much longer than the body, multiarticulate. Mouth parts mandibulate. Pronotum usually large

(small in Phasmidæ). Wings two pairs as a rule, though not infrequently reduced or absent. Fore wings coriaceous (leathery, forming *tegmina*); hind pair membranous, ample, closely reticulate, plicate

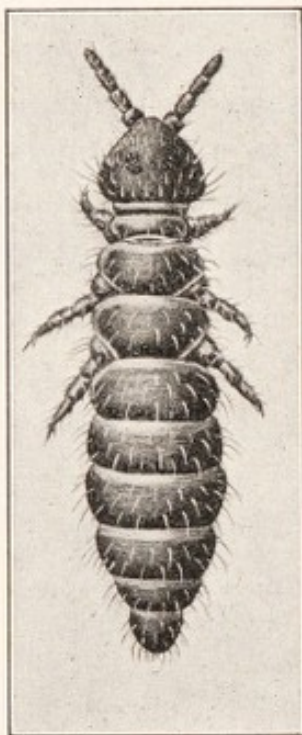


FIG. 12.—The snow flea, *Achorutes nivicola*. Length, 2 mm.

along the numerous radiating principal veins. Abdomen with ten evident segments and traces of eleven or twelve. Cerci one- to eight-segmented. Terrestrial and mostly phytophagous. Seven families: Blattidæ, Mantidæ, Gryllidæ, Grylloblattidæ, Tettigoniidæ (formerly Locustidæ), Locustidæ (formerly Acridiidæ, Fig. 14), Phasmidæ (Fig. 243). More than ten thousand species are known.

4. Dermaptera.—Metamorphosis direct. Eyes faceted, reduced, or absent. Antennæ long, filiform, with ten to fifty segments in adults. Mouth parts mandibulate, prognathous; lingua and superlinguæ well developed; labium split to the mentum; paraglossa united with glossa of same side. Prothorax large. Thoracic segments distinct. Tarsi three-segmented. Elytra short, scale-like, meeting in a straight line. Wings projecting from under the elytra, ear-shaped, with many radiating principal veins, folding plicately, also twice transversely.

Abdomen with eleven segments, the tergites and sternites strongly and complexly imbricate laterally, with a terminal pair of forceps (cerci). Wingless species numerous. Some four hundred species are at present known.

Three suborders, each represented by one family: Arixeniidæ (one species); Hemimeridæ, containing a single African species (Fig. 15), which is flattened, eyeless, wingless, with long unsegmented cerci, viviparous, and parasitic on the rat; and Forficulidæ, formerly a family of Orthoptera.



FIG. 13.—*Sminthurus hortensis*. Length, 1.2 mm.

5. Platyptera.—Metamorphosis direct. Mouth parts mandibulate. Wings, if present, two pairs, delicate, membranous, equal or hind pair smaller, and with the principal veins few and simple. Abdomen with usually ten evident segments and often traces of an eleventh. Integument usually thin. Nymphs thysanuriform. Five suborders.

Suborder Isoptera.—Eyes faceted, vestigial or absent. Antennæ long and filamentous or short and moniliform, nine- to thirty-one-

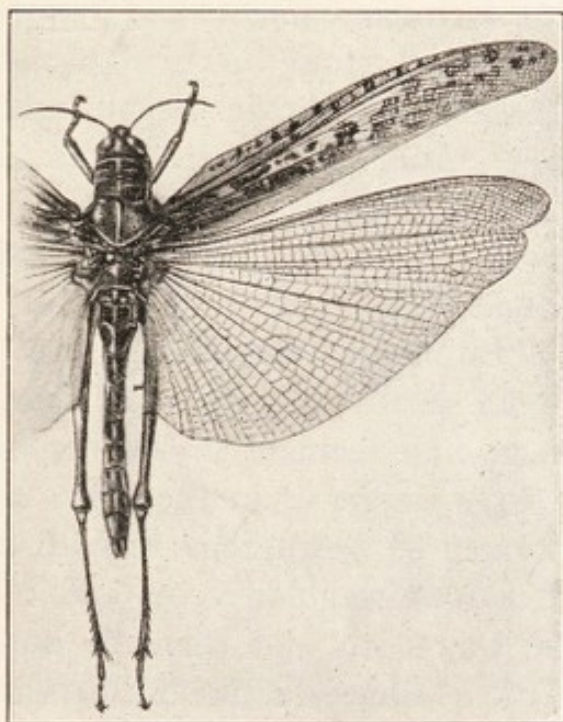


FIG. 14.—*Schistocerca americana*. Slightly reduced.



FIG. 15.—*Hemimerus talpoides*. Length, 11.5 mm.—After HANSEN.

segmented. Mouth parts prognathous or hypognathous.¹ Thoracic segments simple, similar and equal; prothorax large, free. Tarsi four- or five-segmented. Alate or apterous. Wings elongate, similar, equal, membranous, delicate, with few veins, sometimes with an indefinite reticulation, with a characteristic basal suture along which the wing breaks off; hind wings not folded. Abdomen elongate, with ten segments and a pair of short two- to six-segmented cerci. Integument weak. Social in habit and polymorphic; known as white ants. Example, *Termes* (Fig. 280) About one thousand described species.

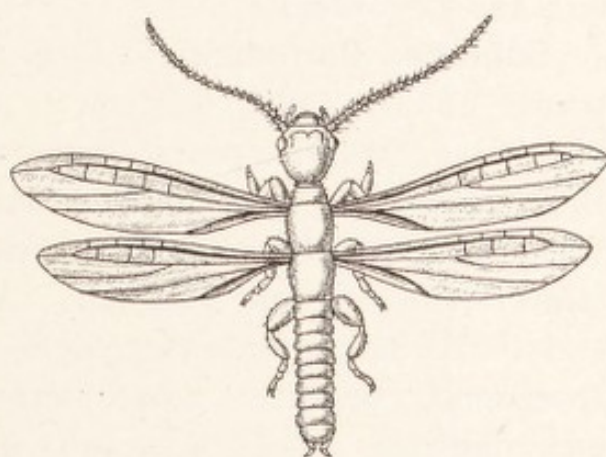


FIG. 16.—*Oligotoma michaeli*. Length 10.5 mm.—After McLACHLAN.

Suborder Embioptera.—Eyes faceted. Antennæ with fifteen to thirty-one or more segments. Mouth parts prognathous; with a labial

¹ *Prognathous*, directed forward, *hypognathous*, directed downward.

spinneret. Thorax elongate; prothorax small. Tarsi three-segmented. Wings (sometimes absent) two pairs, elongate, similar, equal, membranous, delicate, with few and feebly developed longitudinal and cross veins; not folded. Abdomen elongate, with ten segments and frequently an eleventh tergite, and a pair of short stout biarticulate cerci.



FIG. 17.—*Psocus venosus*. Length, 5 mm.

Integument delicate. Feeble insects, not social in habit. Examples, *Embia*, *Oligotoma* (Fig. 16). Some twenty species, all from warm climates.

Suborder Zoraptera.—Eyes vestigial or absent. Antennæ moniliform, nine-segmented. Thorax long, as long as the abdomen; prothorax large, larger than the meso- and metathorax combined. Tarsi two-segmented. Apterous, or with two pairs of wings; the fore wings with a few irregular veins and cells. Abdomen with ten evident segments; the tenth and eleventh united dorsally. Cerci short, one-segmented. Minute, active forms (little more than two millimeters in length), terrestrial, predaceous. One genus, *Zorotypus*, represented by three Oriental species (Africa, Ceylon, Java), one species from Costa Rica and two from the United States.

These insects are most nearly related to Isoptera and Corrodentia.

Suborder Corrodentia.—Eyes faceted. Antennæ filiform, with thirteen to fifty or more segments. Mouth parts hypognathous. Prothorax reduced. Tarsi two- or three-segmented. Wings present, rudimentary or absent; fore pair the larger; veins few and irregular. Abdomen short and stout, with nine or ten segments. Cerci absent. Integument delicate. Small terrestrial insects, including the book lice and other psocids.

Example, *Psocus* (Fig. 17). More than two hundred species are known.

Suborder Mallophaga.—Small wingless flattened insects of parasitic habit. Head large. Eyes of a few isolated ocelli, or vestigial, or absent. Antennæ three- to five-segmented. Mouth parts prognathous. Prothorax distinct; mesothorax often, and metathorax usually, trans-

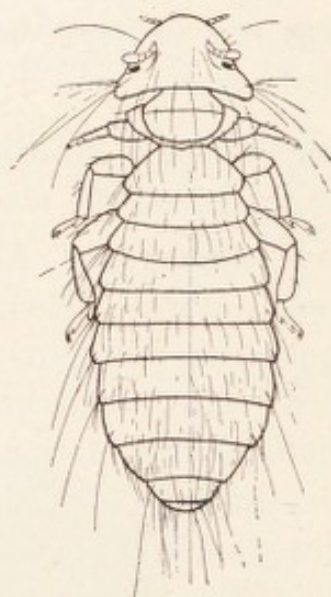


FIG. 18.—A chicken louse, *Menopon*. Length, 2 mm.

ferred to the abdominal region. Tarsi one- or two-segmented. Abdomen usually short and broad, eight- to ten-segmented. Cerci absent.

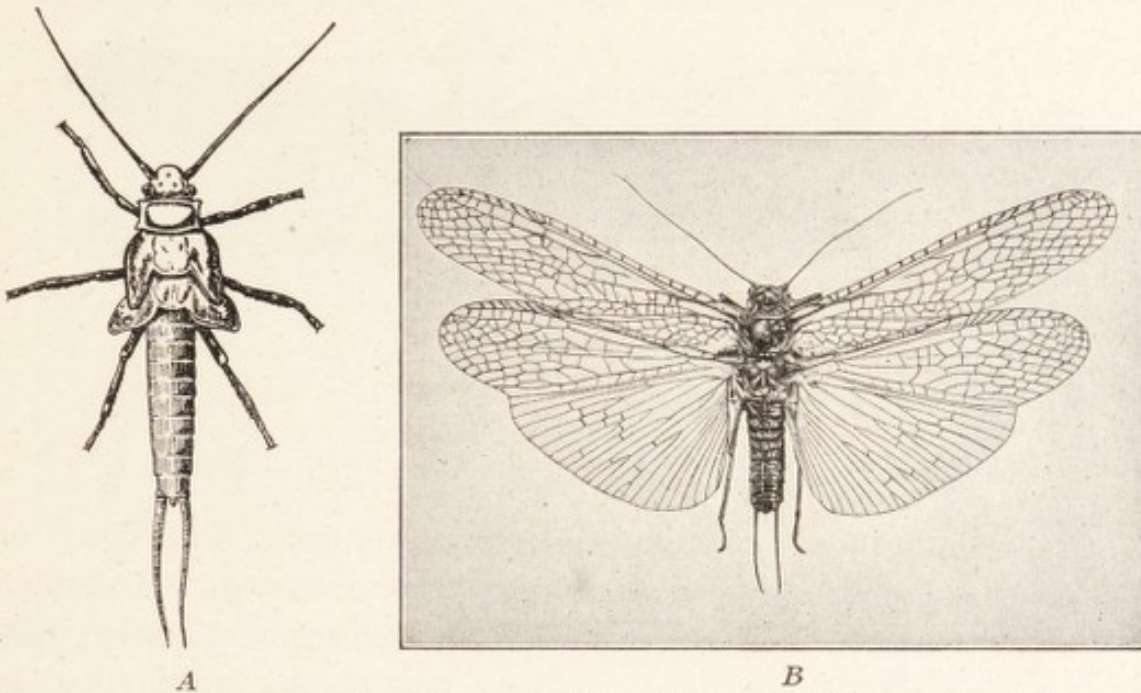


FIG. 19.—*Pteronarcys regalis*. A, nymph (after NEWPORT); B, imago. Slightly reduced.

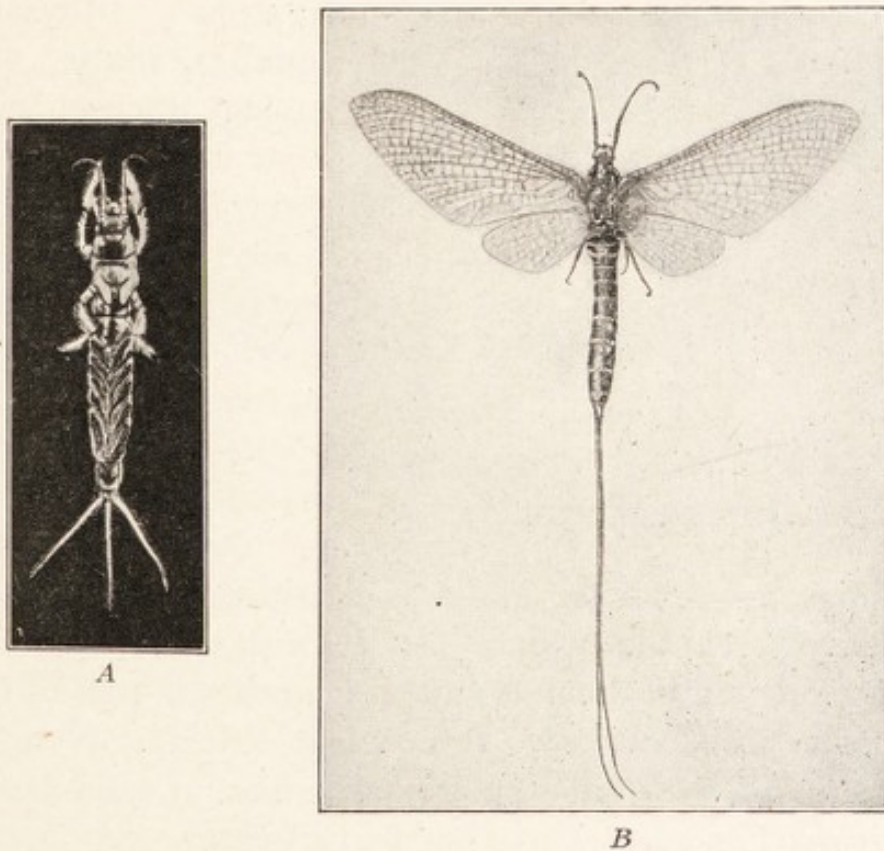


FIG. 20.—*Hexagenia variabilis*. A, nymph; B, imago. Natural size.

Biting lice, or bird lice, parasitic on birds and a few mammals, feeding on feathers, hair or skin. Example, *Menopon* (Fig. 18). More than fifteen hundred species have been described.

6. **Plecoptera**.—Metamorphosis direct. Antennæ filiform, long, multiarticulate. Mouth parts mandibulate. Prothorax large. Wings

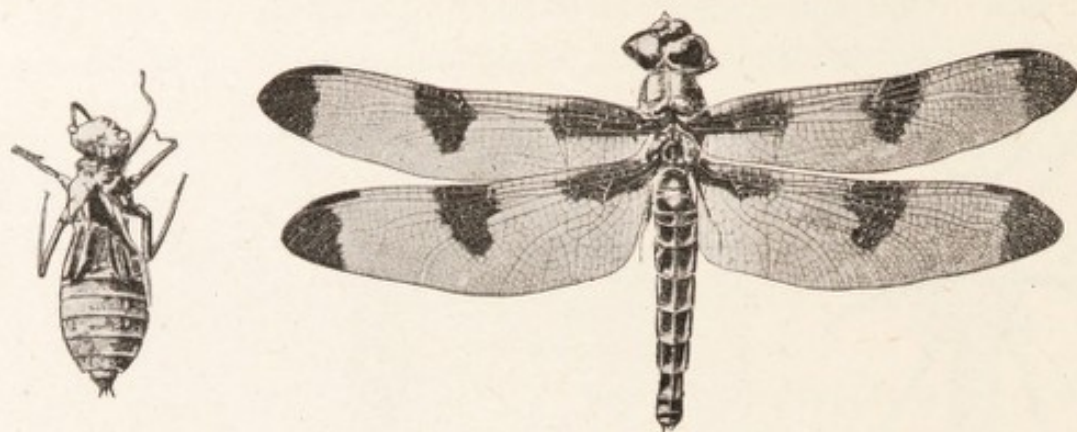


FIG. 21.—*Libellula pulchella*. A, last nymphal skin; B, imago. Slightly reduced.

two pairs, membranous, coarsely and complexly reticulate; equal or else hind wings larger and with an ample plicate anal area. Abdomen



FIG. 22.—*Euthrips tritici*. Length, 1.2 mm.

with ten segments and usually a pair of long multiarticulate cerci. Integument soft. Nymphs thysanuriform, aquatic; adults unique in having tracheal gills. The stone-flies. Example, *Pteronarcys* (Fig. 19). A single family, Perlidæ, comprising two hundred species.

7. **Ephemera**.—Metamorphosis direct. Antennæ bristle-like. Mouth parts mandibulate, but atrophied in the adult. Prothorax small. Wings membranous, minutely reticulate; hind pair much the smaller, rarely absent. Abdomen slender, with ten segments and three or two very long multiarticulate caudal filaments (a pair of cerci, with often a median pseudocercus). Integument delicate. Nymphs thysanuriform, aquatic, with lateral gills. May-flies, or sand-flies. Example, *Hexagenia* (Fig. 20). Three hundred species.

8. **Odonata**.—Metamorphosis direct. Head mobile; eyes large. Antennæ inconspicuous, bristle-shaped. Mouth parts mandibulate. Prothorax small, free; meso- and metathorax intimately united. Tarsi three-segmented. Wings four, elongate, subequal, similar, mem-

branous, minutely reticulate, with characteristic costal joint (nodus), arculus and triangle. Abdomen slender, with ten segments. Cerci one-segmented. Nymphs aquatic; adults predatory. Dragon-flies

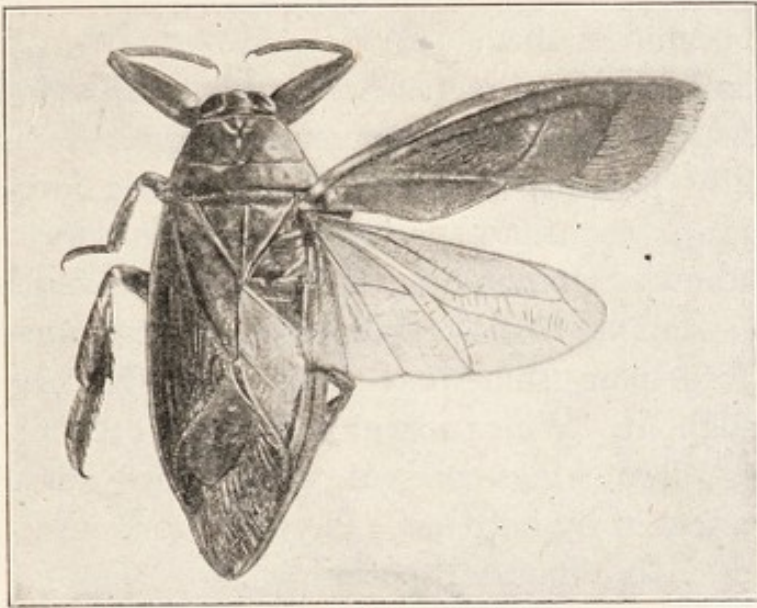


FIG. 23.—*Benacus griseus*. Slightly reduced.



FIG. 24.—Head louse, *Pediculus capitis*, female. Length, 2 mm.

and damsel-flies. Example, *Libellula* (Fig. 21). About two thousand species have been described.

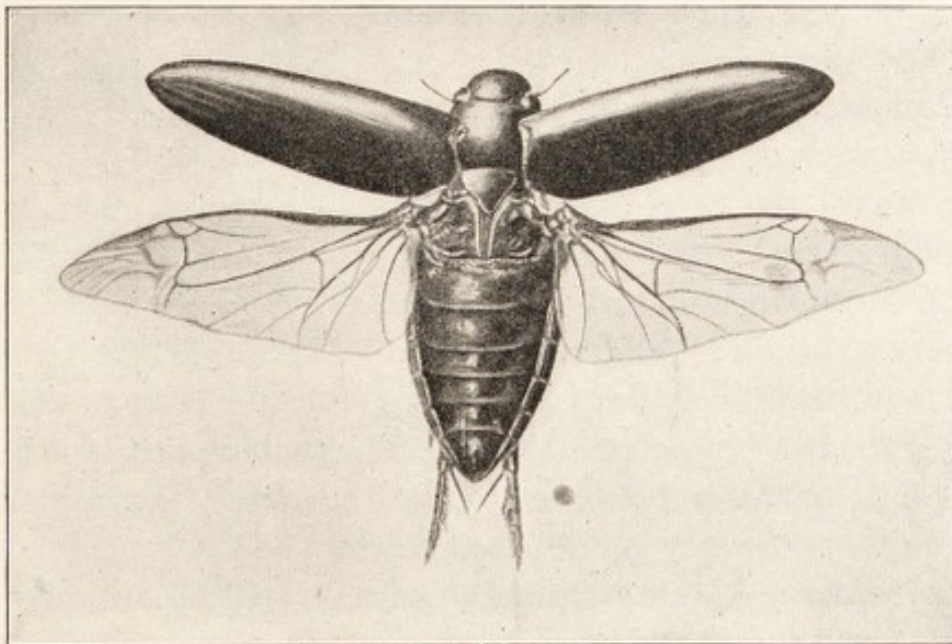


FIG. 25.—*Hydrophilus triangularis*. Natural size.

9. Thysanoptera.—Metamorphosis direct, but including a subpupal stage. Eyes well developed. Mouth parts suctorial, in part asymmetrical. Prothorax long, free. Tarsus one- or two-segmented, ter-

minating in a bladder-like organ. Wings present, rudimentary or absent, the two pairs narrow, equal, similar, with few or no veins and fringed with long hairs. Abdomen with ten segments. Minute, slender insects, known as "thrips." Example, *Euthrips* (Fig. 22). About two hundred species have been described.

10. Hemiptera.—Metamorphosis direct. Antennæ usually few-segmented. Mouth parts suctorial. Prothorax usually large. Wings usually present, except in the parasitic forms. Eighteen thousand species. Two suborders.



FIG. 26.—*Chrysopa plorabunda*. Slightly reduced.

Suborder Homoptera.—Head deflexed. Wings four, sloping roof-like, similar and membranous or fore pair somewhat coriaceous (leathery) throughout. Wings absent in female Coccidæ; in males, fore wings present, hind wings absent, represented by halteres. Phytophagous insects. Example, *Cicada* (Fig. 209). Six thousand species.

Suborder Heteroptera.—Head free, not deflexed. Antennæ often long, few-segmented. Prothorax free. Wings four (sometimes reduced or absent) folded flat; fore wings thickened basally, membranous apically (*hemelytra*), overlapping obliquely; hind wings membranous, with large anal area. Terrestrial or aquatic. The true "bugs." Example, *Benacus* (Fig. 23). About twelve thousand species.

11. Parasita.¹—Metamorphosis direct. Wingless parasites. Eyes simple or absent. Antennæ short, three- to five-segmented. Prognathous. Head with a short tubular beak, crowned with hooks, containing a delicate protrusible sucking tube. Thoracic segments intimately united. Tarsus with a single claw. Integument thin. The sucking lice, blood-sucking parasites of mammals, represented by the "cooties." Example, *Pediculus* (Fig. 24). Some fifty species are known.

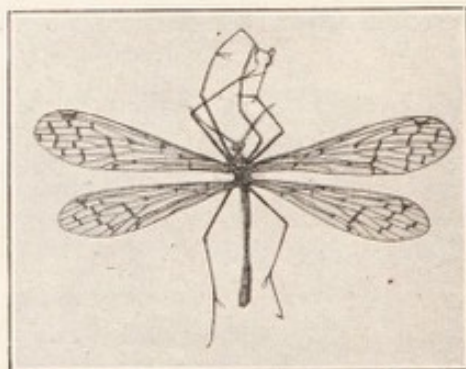


FIG. 27.—*Bittacus strigosus*. Natural size.

12. Coleoptera.—Metamorphosis indirect. Ocelli usually absent. Antennæ of various forms, with segments varying in number (two to twenty-seven) but commonly ten or eleven. Mouth parts mandibulate. Prothorax large, free. Two pairs of wings; fore pair horny or shell-like as

¹ Various names have been used for this group, but the name which has priority and is sanctioned by longest usage is *Parasita* (Latreille, 1796).

a rule (*elytra*), meeting in a straight line; hind pair membranous, often folded. Larvæ sometimes thysanuriform, often eruciform, mandibulate. Hard-bodied insects, the beetles. Example, *Hydrophilus* (Fig. 25). About one hundred and fifty thousand species.

13. Strepsiptera.—Hypermetamorphic; first larva hexapodous, with long anal stylets; later larvæ apodous, degenerate. Female legless, larviform, larviparous, with no pupal stage; male pupa hymenopteroid, within a puparium. Male with large eyes; antennæ seven- to four-segmented, flabellately produced; labrum and labium absent; mandibles ensiform; maxillæ palpiform, two- or three-segmented. Prothorax and mesothorax greatly reduced; metathorax preponderant. One pair of

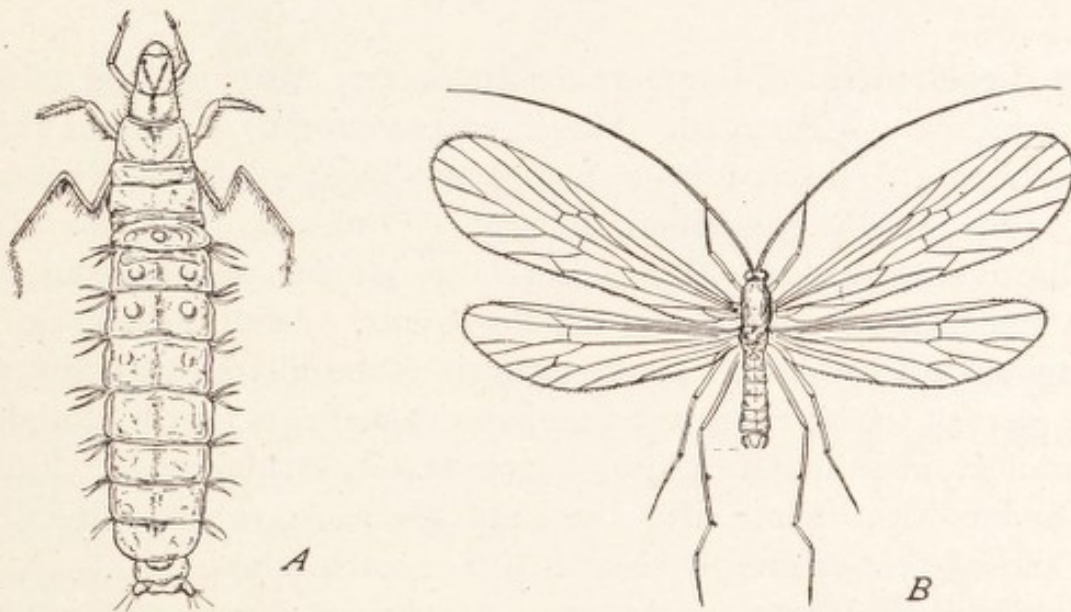


FIG. 28.—*Molanna cinerea*. A, larva; B, imago. $\times 4$ diameters.—After FELT.

wings, the metathoracic, membranous, with only radial veins (eight to five), folding longitudinally. Anterior wings reduced to balancers. Abdomen ten-segmented. Integument thin and soft. Parasitic. About two hundred species are known. Found in all regions of the world.

14. Neuroptera.—Metamorphosis indirect. Antennæ conspicuous. Mouth parts mandibulate. Prothorax large. Wings almost always four, membranous, subequal or else hind pair smaller, complexly reticulate, not plicate, without large anal area. Larvæ thysanuriform or in some cases eruciform, and aquatic or terrestrial, predaceous. Example, lace-winged fly, *Chrysopa* (Fig. 26). About six hundred species have been named.

15. Mecoptera.—Metamorphosis indirect. Antennæ long, filiform. Mouth parts mandibulate, at the end of a deflexed rostrum, or beak. Prothorax small. Tarsi five-segmented. Wings four, elongate, mem-

branous, naked, coarsely reticulate, or else rudimentary or absent. Larvæ eruciform, caterpillar-like, with three pairs of thoracic legs and often eight pairs of abdominal prolegs, carnivorous. Example, *Bittacus* (Fig. 27). A single family, Panorpidæ, comprising but few known species.

16. Trichoptera.—Metamorphosis indirect. Eyes prominent. Antennæ filiform. Mouth parts of imago rudimentary or imperfectly suctorial; mandibles rudimentary or absent. Prothorax small. Tarsi five-segmented. Wings four, membranous, hairy, veins moderate in number, cross veins few; hind pair almost always the larger, with plicate anal area. Larvæ suberuciform, with three pairs of thoracic legs, aquatic, usually case-forming. Caddis worms and caddis flies. Example, *Molanna* (Fig. 28). Between five and six hundred species are known.

17. Lepidoptera.—Metamorphosis indirect. Antennæ long, of various forms, many-segmented. Mouth parts suctorial, mandibles absent or rudimentary (except in a few generalized species). Eyes well developed. Ocelli sometimes present. Prothorax reduced. Tarsi usually five-segmented. Wings four, large, similar, membranous, with veins moderate in number, and few cross veins. Adults usually clothed throughout with scales. Larvæ eruciform (caterpillars), typically with three pairs of thoracic legs and five pairs (sometimes fewer) of abdominal prolegs, mandibulate, phytophagous (rarely carnivorous). Butterflies and moths. Some fifty thousand species have been described. Two suborders, not sharply separated from each other.

Suborder Heterocera.—Antennæ of various forms, but not terminating in a distinct knob or club. Frenulum usually present. Chiefly nocturnal in habit. Example, *Callosamia* (Fig. 239).

Suborder Rhopalocera.—Antennæ simple, terminating in a distinct club and without conspicuous lateral processes. Frenulum absent. Diurnal normally. Examples, *Papilio* (Fig. 29), *Anosia* (Fig. 247, A).

18. Hymenoptera.—Metamorphosis indirect. Mouth parts at the same time mandibulate and suctorial. Prothorax usually small. Tarsi usually five-segmented. Wings two pairs, similar, membranous, transparent or translucent, without scales, with a few irregular veins and cells; venation sometimes reduced; hind wings smaller than fore wings; fore and hind wings held together by a series of hooks (*hamuli*). Abdomen usually with six or seven evident segments. Females with an ovipositor, modified for sawing, boring or stinging. Larvæ eruciform, mandibulate; caterpillar-like, with head and legs, or maggot-like and apodous. Twenty-five or thirty thousand species. Two suborders.

Suborder Terebrantia (Phytophaga, Sessiliventres).—Abdomen broadly attached to the thorax (sessile). Trochanters of posterior legs two-segmented. Ovipositor modified for boring, sawing or cutting. Larvæ with complex mouth parts, frequently caterpillar-like, with three

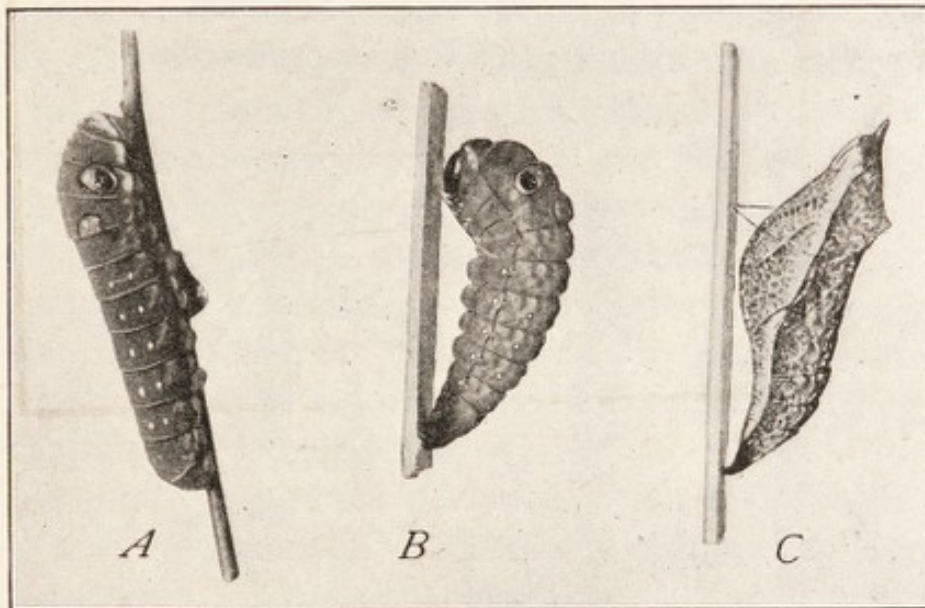


FIG. 29.—*Papilio troilus*. A, larva; B, larva suspended for pupation; C, chrysalis. Natural size.

pairs of thoracic legs and seven or eight pairs of abdominal prolegs. Phytophagous or parasitic. Saw-flies, gall-flies, ichneumon-flies, etc. Example, the pigeon horn-tail, *Tremex* (Fig. 30).

Suborder Aculeata (Heterophaga, Petiolata.)—Abdomen petiolate or subpetiolate (with a deep constriction between the thoracic and abdominal regions). First abdominal segment (*propodeum*) transferred to the thoracic region. Trochanters of posterior legs one-segmented. Ovipositor often modified to form a sting. Larvæ apodous. Ants, bees, wasps, etc. Example, the honey bee, *Apis* (Fig. 284).

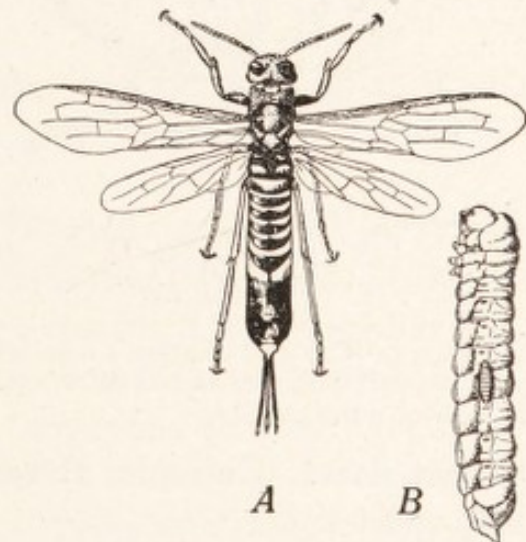


FIG. 30.—*Tremex columba*. A, imago; B, larva (with parasitic larva of *Thalesa* attached). Natural size.—After RILEY.

19. Diptera.—Metamorphosis indirect. Mouth parts typically suctorial, but modified for piercing, lapping, rasping, etc. Prothorax and metathorax small, mesothorax predominant. Tarsi usually five-segmented. One pair of wings (mesothoracic), membranous, transparent, with few veins; wings rudimentary or absent, however, in most of the

parasitic species; hind wings represented by a pair of knobbed threads, or balancers. Larvæ usually eruciform, with the head frequently reduced to a mere vestige with or without a pair of mandibles, and usually without true legs, though pseudopods may be present. Pupa naked, or enclosed in a puparium. The flies. Example, crane-fly, *Tipula* (Fig. 31). About forty thousand described species.

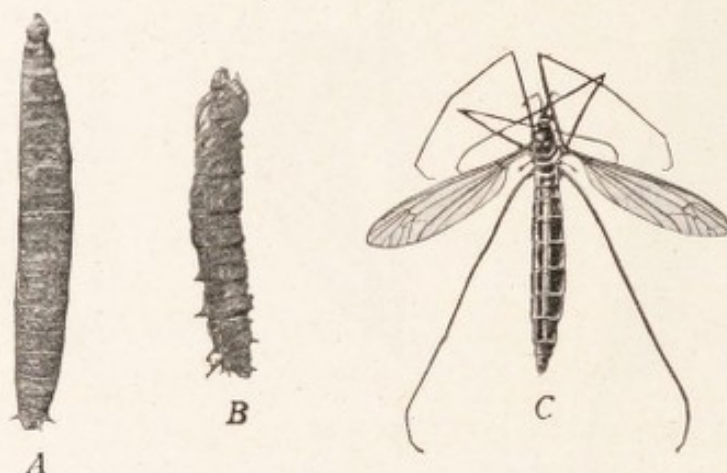


FIG. 31.—*Tipula*. A, larva; B, cast pupal skin; C, imago. Slightly reduced.

20. Siphonaptera.—Metamorphosis indirect. Head small, not sharply separated from the thorax. Eyes minute and simple, or absent. Antennæ short and stout, situated in depressions. Mouth parts suctorial. Body laterally compressed. Thoracic segments subequal, free; coxæ large; tarsi five-segmented. Wings absent or at most quite rudimentary. Larva with a head, mandibulate, apodous, vermiform. Adults saltatorial, parasitic on warm-blooded animals. The well known fleas. Example, *Ctenocephalus* (Fig. 32). One hundred and fifty species.

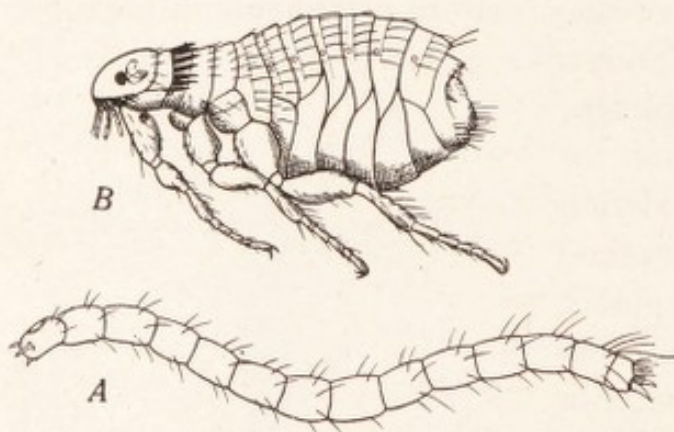


FIG. 32.—Cat and dog flea, *Ctenocephalus canis*. A, larva (after KÜNCKEL D'HERCULAIS); B, adult. Length of adult, 2 mm.

known fleas. Example, *Ctenocephalus* (Fig. 32). One hundred and fifty species.

Interrelations of the Orders.—The modern classification aims to express relationships, and these are most clearly to be ascertained by a comparative study of the facts of anatomy and development.

The most generalized, or primitive, insects are the Thysanura. Subtracting their special, or adaptive, peculiarities, their remaining characters may properly be regarded as inheritances from some vanished

ancestral type of arthropod. This primordial type, then, probably had three simple and equal thoracic segments differing but slightly from the ten abdominal segments; three pairs of legs and no wings; three pairs of exposed biting mouth parts; a pair of long, many-jointed antennæ and a pair of cerci of the same description; a thin naked integument; a simple straight alimentary canal distinctly divided into three primary regions; a ganglion and a pair of spiracles for each of the three thoracic and the first eight abdominal segments, if not all the latter; no metamorphosis; functional abdominal legs and active terrestrial habits.

The existing form that best meets these requirements is *Scolopendrella*, which is not an insect, however, but belongs in the class Symphyla. The most primitive of known insects are *Anajapyx* and *Campodea*, through which other insects trace their origin to the stock from which Symphyla and Diplopoda arose.

There is not the slightest evidence to support the assumption by Handlirsch that Thysanura and Collembola are degenerate descendants of winged ancestors. They are primitively wingless insects (Apterygota); in other words, they originated before insects acquired wings.

Among Thysanura, the genera *Machilis* and *Lepisma* show decided orthopteran affinities; thus their eyes are compound and their mouth parts strongly orthopteran; indeed, the likeness of *Lepisma* to a young cockroach is striking. According to Crampton, *Lepisma* leads to Plecoptera and Ephemera; while *Machilis* has suggestions of affinities with Crustacea.

"The generalized form of Thysanura, and the manner in which it reappears in the larvæ of other insects, is the natural key of the classification" (Hyatt and Arms).

Collembola, though specialized in several important ways, all have the same peculiar kind of entognathous mouth parts as *Campodea* and *Japyx*, for which reason and many others it is believed that Collembola are an offshoot from the thysanuran stem. Collembola are not nearly so primitive as Thysanura, however, for they have fewer abdominal segments than the latter, exhibit much greater concentration of the nervous system, and are uniquely specialized in several respects, notably as regards the ventral tube and the furcula, or springing organ.

Collembola are no longer regarded as a suborder of Thysanura by those who are familiar with the morphology of the two groups. All the specialists in Thysanura and Collembola agree in regarding them as two distinct orders.

Orthoptera probably arose directly from the original thysanuriform stem. Of Orthoptera, Blattidæ are the most primitive, with Mantidæ closely allied to them. In a linear arrangement, Gryllidæ may follow, though not closely related to Mantidæ. Between Gryllidæ and Tettigoniidæ (formerly Locustidæ) comes Walker's new family Grylloblattidæ, which a few authors prefer to regard as a new order. Tettigoniidæ and Locustidæ (formerly Acridiidæ) belong together. Phasmidæ have some affinities with Locustidæ, but show the greatest departure from the primitive orthopteran type.

Dermaptera, represented almost entirely by the family Forficulidæ, which some authorities still retain in the order Orthoptera, must have come from the same ancestors as Orthoptera, needless to say. In some respects they are more primitive than Orthoptera; in others, more specialized. Though the order shows some thysanuran characters, the resemblance between a young earwig and the thysanuran *Japyx* (both having forceps, for example) is on the whole superficial; the mouth parts of the two agreeing only in the broadest way. On the other hand, the resemblances in structure between Dermaptera and Coleoptera are deep-seated. The dermapteran genus *Hemimerus* has strong affinities with the orthopteran family Blattidæ.

The suborders of Platypera are by some raised to the rank of orders. They are so closely related, however, that it seems preferable to the writer to express their resemblances by keeping them together, rather than to emphasize their differences by separating them.

Platypera, as a whole, are most nearly related to Orthoptera on the one hand and to Plecoptera on the other; Isoptera and Embioptera in particular being strongly orthopteran. Mallophaga, aside from their parasitic characters, agree closely with Corrodentia, especially as regards the structure of the head and mouth parts. The bird lice are essentially degenerate descendants of psocid-like ancestors (Snodgrass).

Zoraptera, represented by six species of the genus *Zorotypus*, is held to be a distinct order by some authors. A few years ago, *Zorotypus* would have been placed without hesitation among the termites. The species of the genus are essentially termites, with a wing venation suggesting that of psocids.

Plecoptera, which Packard placed in his order Platypera, show many primitive characters, including thysanuriform nymphs.

The more generalized winged insects fall naturally into two groups, which are not sharply separated, however: orthopteroid and plecopteroid. The latter group consists of the aquatic orders Plecop-

tera, Ephemerida and Odonata. Of these, Plecoptera is probably the most generalized order; though Ephemerida has retained some very primitive structures, notably the paired genital openings and ducts.

It is often stated that Plecoptera are the most primitive of winged insects. According to this view, then, Orthoptera have arisen from the plecopteran stem. They show, however, no evidence of an aquatic ancestry; and everything indicates that terrestrial insects preceded aquatic. Doubtless plecopteroid and orthopteroid insects both arose from a type that was winged, with many wing veins, mandibulate, and terrestrial—a form like a thysanuran but with wings.

On the basis of metamorphosis, Plecoptera, Ephemerida and Odonata form a natural group, Hemimetabola, in which the changes in form during development are greater than in other Heterometabola, the aquatic nymphs of these three orders being termed *naiads* by Comstock.

Odonata are naturally placed next to Ephemerida but are strongly aberrant forms with a unique kind of specialization.

Thysanoptera form a distinct order which is usually placed next to Hemiptera, chiefly on account of the suctorial mouth parts, though even in this respect there is no close agreement between the two orders. They are aberrant and hard to place. Börner and Crampton find resemblances between Thysanoptera and Corrodentia.

Hemiptera form a homogeneous and monophyletic order, characterized by the unique shape and arrangement of the mouth parts, which are always of the same type (Muir). Hemiptera are somewhat like Orthoptera and possibly originated with Thysanoptera from some mandibulate and winged form. The conversion of mandibulate into suctorial organs may be seen within the order Collembola, though it is improbable that Hemiptera arose from forms like Collembola. Hemiptera are exceptional among insects with a direct metamorphosis in their highly developed type of suctorial mouth parts. Homoptera are on the whole more primitive than Heteroptera.

Parasita, long a suborder of Hemiptera, should rank as an order, apparently; though opinions differ in regard to this.

In the early days of the classification, the sucking lice and the biting lice were always grouped together, on account of their resemblances. Then it was found that these similarities, correlated with parasitic existence, were only superficial; and the two groups were separated. Some recent authors have, however, followed one another in the opinion that the two kinds of lice are closely related to each other—an opinion

that is surprising in view of the many strong differences of structure between the two groups, particularly as regards the mouth parts. Though investigators have not agreed as to the morphology of the mouth parts of the sucking lice, a study of cross sections of the mouth parts leads to the conclusion that they conform fundamentally to the hemipteran type.

Metamorphosis offers the broadest criteria for the separation of insects into primary groups. All the orders considered thus far are characterized either by no metamorphosis or by a relatively slight, or so-called direct, or incomplete, transformation. The following orders, on the contrary, are distinguished by an indirect, or complete, metamorphosis, which appears in Coleoptera and attains its maximum development in Hymenoptera and Diptera.

With Coleoptera the eruciform type of larva appears, as a derivative of the earlier thysanuriform type. The larvæ of *Meloë*, *Epicauta* (Fig. 220) and other genera pass from a thysanuriform stage to an eruciform condition during their development.

It was formerly thought that the resemblances between Coleoptera and Dermaptera were superficial, but at present there is reason to believe that these two orders are related. They agree rather closely in structure, especially as regards the structure of the head (Crampton) and the thoracic sclerites (Snodgrass). Coleoptera have affinities with Neuroptera also, that appear in some of the larvæ as well as in the adult forms. Coleoptera are, however, more primitive than Neuroptera, and are placed here at the beginning of the holometabolous series.

Strepsiptera should be separated from Coleoptera as a distinct order, accepting the opinion of Dr. W. D. Pierce, who has studied the group thoroughly. Strepsiptera are aberrant, peculiarly specialized forms. The fact that the male strepsipteran pupa has the form of a hymenopterous pupa may or may not be significant.

In Neuroptera, as in Coleoptera, the transition from the thysanuriform to the eruciform type of larva may take place during the development of the individual, as in the larva of *Mantispa*.

Neuroptera have kinship with Coleoptera; the structure of the head, for one thing, being essentially the same in the two groups. They resemble Plecoptera also; thus a form like *Sialis* may have come from ancestors like perlids.

All the orders that follow are derived from the neuropteran stem, in the opinion of many authorities.

Mecoptera form an isolated order, though their caterpillar-like

larvæ, with eleven or twelve pairs of legs, suggest affinities with Lepidoptera and, more remotely, with the tenthredinid Hymenoptera. Mecoptera are most nearly related to Neuroptera (through the genus *Nemoptera*) and have also certain affinities with Diptera (Crampton).

Trichoptera, while much like Mecoptera in structure and metamorphosis, are undoubtedly closely related to Lepidoptera; in view of the extensive and deep-seated resemblances between caddis flies and the most generalized moths (Micropterygidæ) it must be concluded that Trichoptera and Lepidoptera originated from the same stock, which was doubtless neuropteroid.

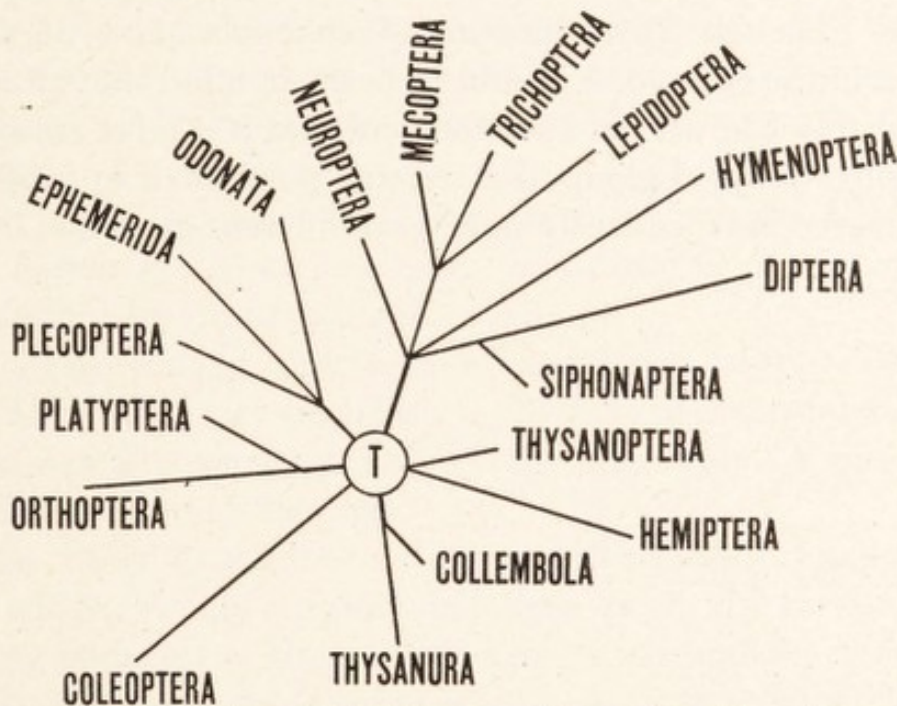


FIG. 33.—Genealogical diagram of the orders of insects.

Hymenoptera also trace their ancestry back to neuropteroid forms. The most generalized hymenopterous larvæ, those of saw-flies, are caterpillar-like; but the most specialized larvæ, as those of ants, bees, wasps, and parasitic Hymenoptera, are more like maggots, in correlation with their sedentary mode of life.

Hymenoptera are often called the “highest” insects, chiefly on account of their highly developed instincts and social life. From this point of view, however, the termites also would rank high, though structurally they belong among the more generalized insects. As a matter of fact, the system of classification is based necessarily on structure, and not on psychology; and structurally Hymenoptera are, taking everything into consideration, less specialized than Diptera.

In Diptera the eruciform type of larva attains its extreme degree of

specialization, as in the family Muscidæ. Such larvæ as those of mosquitoes are comparatively primitive.

The relationships of Diptera to other orders are not evident, but the order is in some respects like Mecoptera. Diptera possibly came from forms like Mecoptera, or both orders may have arisen from neuropteroid ancestors.

The fleas, Siphonaptera, are usually placed next to Diptera, being regarded as degenerate flies.

The preceding diagram (Fig. 33) is a graphic summary of the genealogy of some of the orders of insects. The central group (T) is the hypothetical thysanuroid source of all insects, including Thysanura themselves. Though Thysanura and Collembola show no traces of wings, even in the embryo, it should be borne in mind that all the other insects probably had winged ancestors and that it is more reasonable to assume a single winged group as a starting point than to suppose that wings originated independently in several different groups of insects.

CHAPTER II

ANATOMY AND PHYSIOLOGY

I. SKELETON

Number and Size of Insects.—The number of insect species already known is about 400,000 and it is safe to estimate the total number of existing species as at least one million.

Among the largest living species are the Venezuelan beetle, *Dynastes hercules*, which is 155 mm. long, and the Venezuelan grasshopper, *Tropidacris latreillei*, which has a length of 166 mm. and an alar expanse of 240 mm. Among Lepidoptera, *Attacus atlas* of Indo-China spreads 240 mm.; *Attacus cæsar* of the Philippines, 255 mm.; and the Brazilian noctuid *Erebus agrippina*, 280 mm. Some of the exotic wood-boring larvæ attain a length of 150 mm.

The giants among insects have been found in the Carboniferous, from which Brongniart described a phasmid (*Titanophasma*) as being one-fourth of a meter long, and a huge dragon fly (*Meganeura*) with a spread of more than two feet.

At the other extreme are beetles of the family Trichopterygidæ, some of which are only 0.25 mm. in length, as are also certain hymenopterous egg-parasites of the families Chalcididæ and Proctotrypidæ.

Thus, as regards size, insects occupy an intermediate place among animals; though some insects are smaller than the largest protozoans and others are larger than the smallest vertebrates.

Segmentation.—One of the fundamental characteristics of arthropods is their linear segmentation. The subject of the origin of this segmentation is far from simple, as it involves some of the most difficult questions of heredity and variation. As arthropod segmentation is usually regarded as an inheritance from annelid-like ancestors, the subject resolves itself into the question of the origin of the segmented from the unsegmented "worms." Cope, Packard and others give the mechanical explanation which is here summarized. In a thin-skinned, unsegmented worm, the flexures of the body initiated by the muscular system would throw the integument into folds, much as in the leech, and with the thickening of the integument, segmentation would appear from the fact that the deposit of chitin would be least at the places of

greatest flexure, *i. e.*, the valleys of the folds, and greatest at the places of least flexure, *i. e.*, the crests of the folds. This explanation, which has been elaborated in some detail by the Neo-Lamarckians, applies also to the segmentation of the limbs, as well as the body.

Head.—In an insect several of the most anterior pairs of primary appendages have been brought together to co-operate as mouth parts and sense organs, and the segments to which they belong have become compacted into a single mass—the head—in which the original segmentation is difficult to trace. The thickened cuticula of the head forms a skull, which serves as a fulcrum for the mouth parts, furnishes a base of attachment for muscles and protects the brain and other organs.

While the jaws of most insects can only open and shut, transversely, their range of action is enlarged by movements of the entire head, which are permitted by the articulation between the head and thorax.

As a rule, one segment overlaps the one next behind; but the head, though not a single segment of course, never overlaps the prothorax in the typical manner, but is usually received into that segment. This condition, which may possibly have been brought about simply by the backward pull of the muscles that move the head, has certain mechanical advantages over the alternative condition, in securing, most economically, freedom of movement of the head and protection for the articulation itself.

The size and strength of the skull are usually proportionate to the size and power of the mouth parts. In some insects almost the entire surface of the head is occupied by the eyes, as in Odonata (Fig. 21, *B*) and Diptera (Fig. 40). In muscid and many other dipterous larvæ, or “maggots,” the head is reduced to the merest rudiment.

Though commonly more or less globose or ovate, the head presents innumerable forms; it often bears unarticulated outgrowths of various kinds, some of which are plainly adaptive, while others are apparently purposeless and often fantastic.

Sclerites and Regions of the Skull.—The dorsal part of the skull (Fig. 34) consists almost entirely of the *epicranium*, which bears the compound eyes; it is usually a single piece, or *sclerite*, though in some of the simpler insects it is divided by a Y-shaped suture, the *epicranial suture*. The middle of the face, where the median ocellus often occurs, is termed the *front*; ordinarily this is simply a region, though a frontal sclerite exists in some insects between the branches of the epicranial suture. Just above the front, and forming the summit of the head, is the region known as the *vertex*; it often bears ocelli. The *clypeus* is

easily recognized as being the sclerite to which the upper lip, or *labrum*, is hinged, though the clypeus is not invariably delimited as a distinct sclerite. In certain insects a transverse suture divides the clypeus into an *anteclypeus* and a *postclypeus*. The cheeks of an insect are known as the *gena*, and *post-gena* sometimes occur. On the under side of the head is the *gula*, which bears the under lip, or *labium*. That part of the skull nearest the prothorax is termed the *occiput*; usually it is not delimited from the epicranium, though in some insects it is continuous with the post-gena to form a distinct sclerite. The occiput surrounds the opening known as the *occipital foramen*, through which the œsopha-

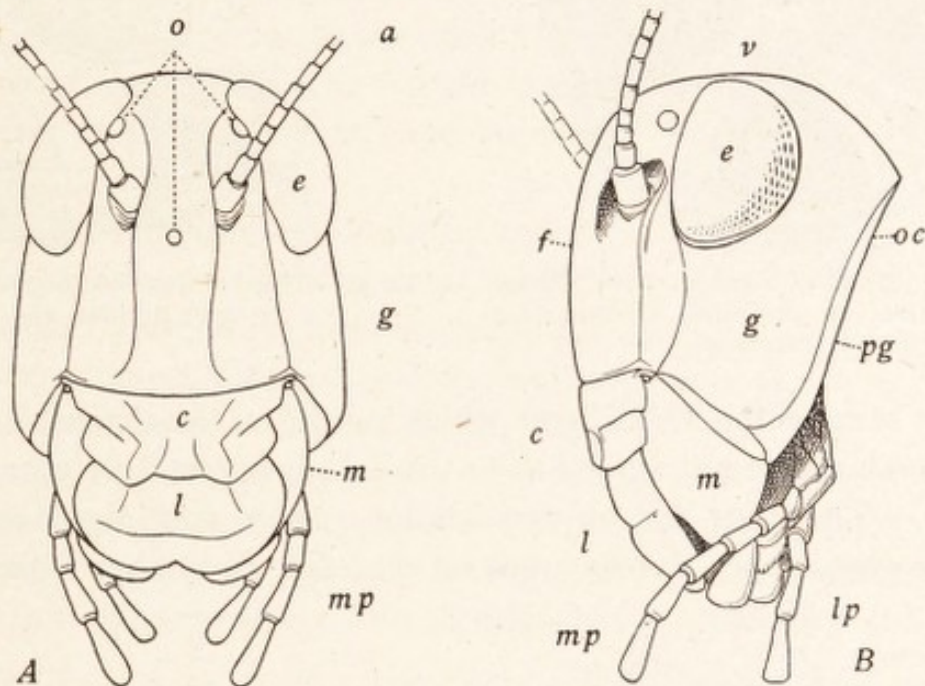


FIG. 34.—Skull of a grasshopper, *Melanoplus differentialis*. *a*, antenna; *c*, clypeus; *e*, compound eye; *f*, front; *g*, gena; *l*, labrum; *lp*, labial palpus; *m*, mandible; *mp*, maxillary palpus; *o*, ocelli; *oc*, occiput; *pg*, post-gena; *v*, vertex.

gus and other organs pass into the thorax. The membrane of the neck in Orthoptera and some other insects contains small *cervical sclerites*, dorsal, lateral or ventral in position; these, in the opinion of Comstock, pertain to the last segment of the head. Besides those described, a few other cephalic sclerites may occur, small and inconspicuous, but nevertheless of morphological importance; for example, *ocular* or *antennal* sclerites, bearing the eyes or the antennæ, respectively; and the *trochantin* of the mandible, situated between the mandible and gena.

Tentorium.—In the head is a chitinous supporting structure known as the *tentorium*. This consists of a central plate from which diverge either two or three pairs of arms (*anterior*, *posterior* and *dorsal*) extending

to the skull (Fig. 35). The central plate, or *body*, lies between the brain and the subœsophageal ganglion and under the œsophagus, which passes between the anterior pair of arms. The tentorium braces the skull, affords muscular attachments and holds the cephalic ganglia and the œsophagus in place. It is not a true internal skeleton, but arises

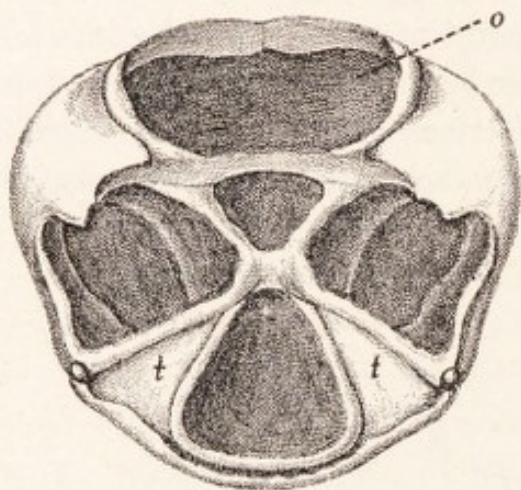


FIG. 35.—Skull of a grasshopper, *Dissosteira carolina*. *o*, occipital foramen; *t*, *t*, anterior arms of tentorium.

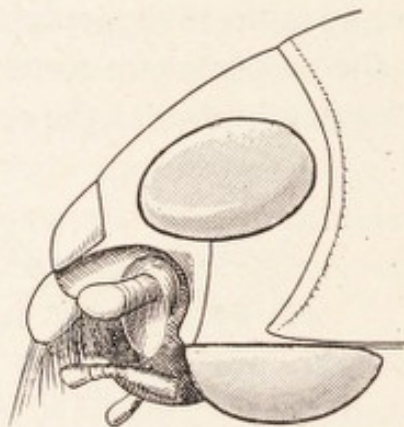


FIG. 36.—Head of a gyrinid beetle, *Dineutus*, to show divided eye.

from the same ectodermal layer which produces the external cuticula; though authors are not agreed as to the details of the development.

Eyes.—The eyes are of two kinds—*simple* and *compound*. The latter, or eyes proper, conspicuous on each side of the head, are of com-

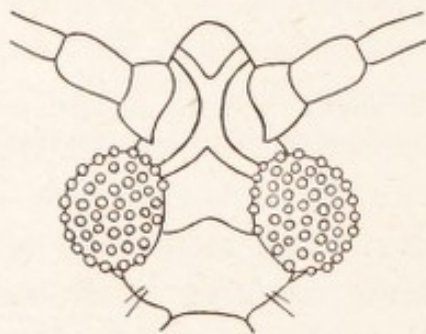


FIG. 37.—Agglomerate eyes of a male coccid, *Leachia fuscipennis*.—After SIGNORET.

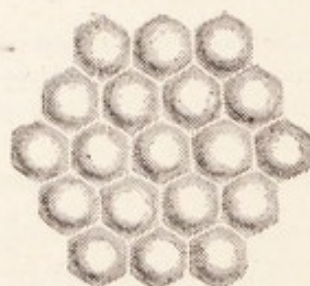


FIG. 38.—Facets of a compound eye of *Melanoplus*. Highly magnified.

mon occurrence except in the larvæ of most holometabolous insects, in some generalized forms (as Collembola) and in parasitic insects. The compound eyes (Fig. 41) are convex and often hemispherical, though their outline varies greatly; thus it may be oval (Orthoptera) or triangular (*Notonecta*), while in the aquatic beetles of the family Gyrinidæ (Fig. 36) each eye has a dorsal and a ventral lobe, enabling the insect to see upward and downward at the same time; so also in *Oberea* and

other terrestrial beetles of the same family. Superficially, a compound eye is divided into minute areas, or *facets*, which though circular in the agglomerate type of eye (Fig. 37) are commonly more or less hexagonal (Fig. 38), as the result of mutual pressure. These facets are not necessarily equal in size, for in dragon flies the dorsal facets are frequently larger than the ventral. In diameter the facets range from .016 mm. (*Lycæna*) to .094 mm. (*Cerambyx*). Their number is often enormous; thus the house fly (*Musca domestica*) has 4,000 to each eye, a butterfly (*Papilio*) 17,000, a beetle (*Mordella*) 25,000 and a sphingid moth 27,000; on the other hand, ants have from 400 down, the worker ant of *Eciton* having at most a single facet on each side of the head.

Ocelli.—The simple eyes, or *ocelli*, appear as small polished lenses, either lateral or dorsal in position. Lateral ocelli (Fig. 39) occur in the larvæ of most holometabolous insects and in parasitic forms. Dorsal ocelli, supplementary to the compound eyes, occur on or near the vertex, and are more commonly three in number, arranged in a triangle, as in Odonata, Diptera (Fig. 40) and Hymenoptera (Fig. 41) as well as many Orthoptera and Hemiptera. Few beetles have ocelli and almost no



FIG. 39.—Head of a caterpillar *Samia cecropia*, to show lateral ocelli.

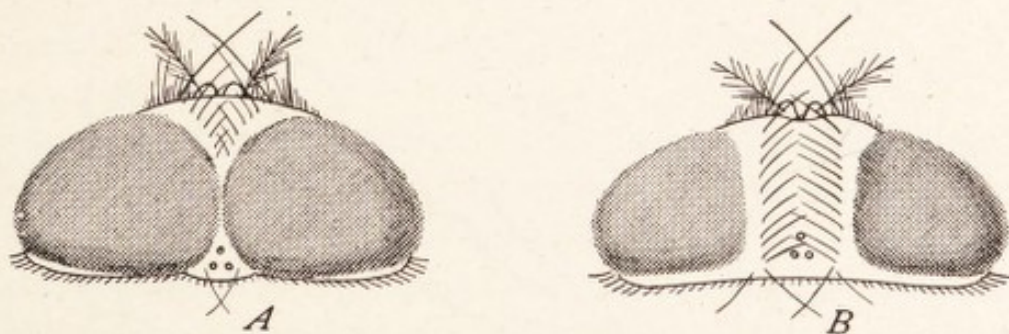


FIG. 40.—Ocelli and compound eyes of a fly, *Phormia regina*. A, male; B, female.

butterflies (*Lerema accius* with its one ocellus being the only exception known), though not a few moths have two ocelli.

As explained beyond, the compound eyes are adapted to perceive form and movements and the ocelli to form images of objects at close range or simply to distinguish between light and darkness.

Sexual Differences in Eyes.—In most Diptera (Fig. 40) and in Hymenoptera (Fig. 41) and Ephemeridæ as well, the eyes of the male are

larger and closer together (*holoptic*) than those of the female (*dichoptic*). This difference is attributed to the fact that the male is more active

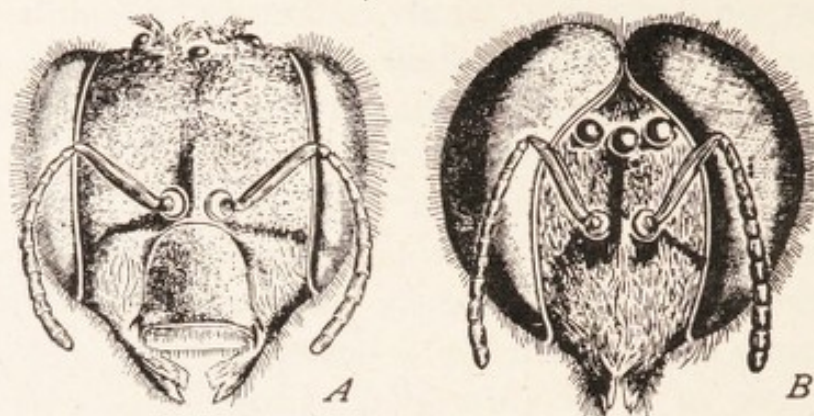


FIG. 41.—Ocelli and compound eyes of the honey bee, *Apis mellifera*. A, queen; B, drone.—After CHESHIRE.

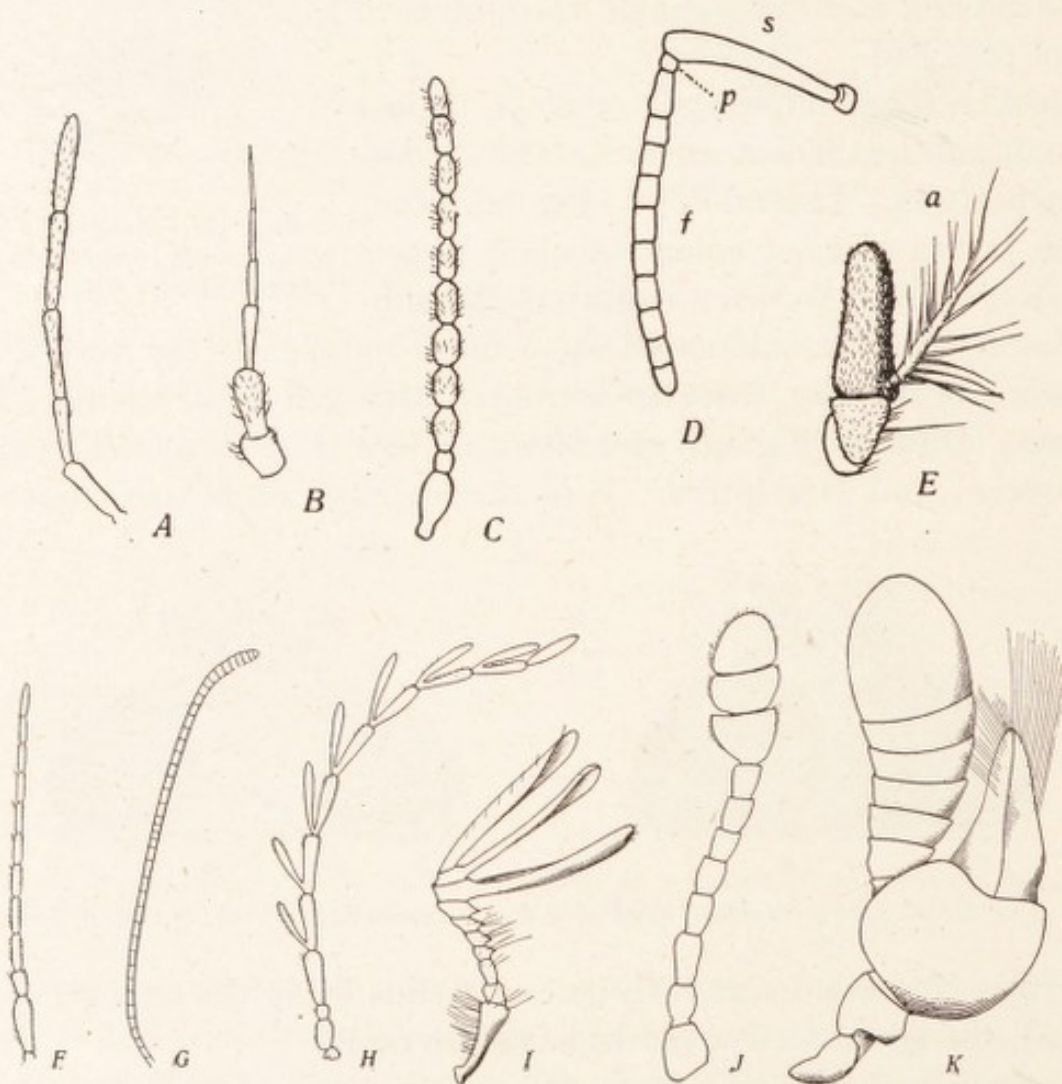


FIG. 42.—Various forms of antennæ. A, filiform, *Euschistus*; B, setaceous, *Plathemis*; C, moniliform, *Catogenus*; D, geniculate, *Bombus*; f, flagellum; p, pedicel; s, scape; E, irregular, *Phormia*; a, arista; F, setaceous, *Galerita*; G, clavate, *Anosia*; H, pectinate, male *Ptilodactyla*; I, lamellate, *Lachnosterna*; J, capitata, *Megalodacne*; K, irregular, *Dineutus*.

than the female, especially in the matter of seeking out the opposite sex.

Among ants of the same species the different forms may differ greatly in the number of lateral facets. Thus in *Formica pratensis*, according to Forel, the worker has about 600 facets in each eye, the queen 800-900 and the male 1,200.

Blind Insects.—Many larvæ, surrounded by an abundance of food and living often in darkness, need no eyes and have none; this is true of the dipterous "maggots" and many other sedentary larvæ, particularly such as are internal parasites (Tachinidæ, Ichneumonidæ), or such as feed within the tissues of plants (many Buprestidæ, Cerambycidæ and Curculionidæ). Subterranean or cavernicolous insects are either eyeless or else their eyes are more or less degenerate, according to the amount of light to which they have access. The statement is made that blind insects never have functional wings.

Antennæ.—The antennæ, never more than a single pair (though embryonic "second antennæ" occur in Thysanura and Collembola), are situated near the compound eyes and frequently between them. With rare exceptions the antennæ have always several and usually many segments. In form these organs are exceedingly varied, though many of them may be referred to the types represented in Figs. 42-44.

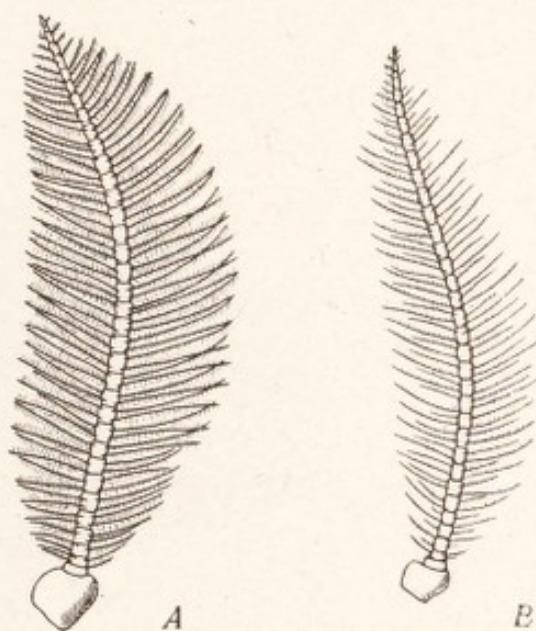


FIG. 43.—Antennæ of a moth, *Samia cecropia*. A, male; B, female.

Though homologous in all insects, the antennæ are by no means equivalent in function. They are commonly tactile (grasshoppers, etc.) or olfactory (beetles, moths) and occasionally auditory (mosquito), as described beyond, but may be adapted for other than sensory functions. Thus the antennæ of the aquatic beetle *Hydrophilus* are used in connection with respiration and those of the male *Meloë* to hold the female.

Sexual Differences in Antennæ.—In moths of the family Saturniidæ (*S. cecropia*, *C. promethea*, etc.) the pectinate antennæ of the male are larger and more feathery than those of the female, and differ also in having more segments (Fig. 43). Here the antennæ are chiefly olfactory, and the reason for their greater development in the male appears from the fact that the male seeks out the female by means of the sense of smell and depends upon his antennæ to perceive the odor emanating from the opposite sex.

The plumose antennæ of the male mosquito (Fig. 44) are highly developed organs of hearing, and are used to locate the female; they have delicate fibrillæ of various lengths, some of which are thrown into sympathetic vibration by the note of the female (p. 94).

Meloë has just been mentioned. In *Sminthurus malmgrenii* (Collembola) the antennæ of the male are provided with hooks and otherwise adapted to grasp those of the female at copulation.

Though systematists have recorded many instances of antennal *antigeny*, the interpretation of these sexual differences has received very little attention; a beginning in the subject has been made by Schenk, whose results will be referred to in connection with the sense organs.

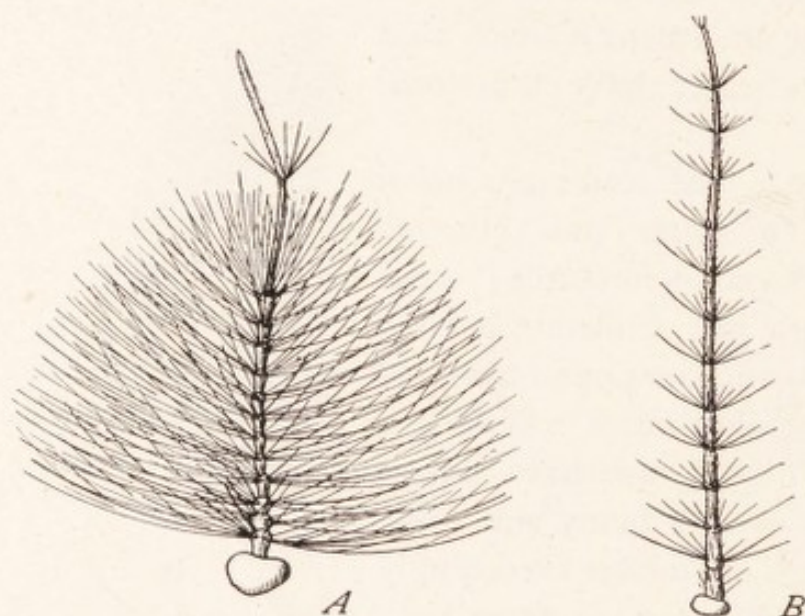


FIG. 44.—Antennæ of mosquito, *Culex pipiens*. A, male; B, female. The antenna has a short basal segment, not shown in the figure.

Mouth Parts.—On account of their great range of differentiation, the mouth parts are of fundamental importance to the systematist, particularly for the separation of insects into orders. Most of the orders fall into two groups according as the mouth parts are either biting (*mandibulate*) or sucking (*suctorial*). Collembola and Hymenoptera, however, combine both functions; Diptera, though suctorial, exhibit various modifications for piercing, lapping or rasping; Thysanoptera are partly mandibulate but chiefly suctorial; and adult Ephemera and Trichoptera have but rudimentary mouth parts.

The mandibulate orders are Thysanura, Collembola (primarily), Orthoptera, Dermaptera, Isoptera, Embioptera, Corrodentia, Mallophaga, Plecoptera, Ephemera (rudimentarily in adult), Odonata, Coleoptera, Strepsiptera, Neuroptera and Mecoptera.

The usual statement is that there are three pairs of mouth parts, namely, *mandibles*, *maxillæ* and *labium*. As a matter of fact, there are four pairs, counting the *superlinguæ*, which are evident in Thysanura and Collembola, become vestigial in Heterometabola, and disappear in the most specialized Holometabola. The mandibulate, or primary type (Fig. 45), from which the suctorial, or secondary type, has been derived, will be considered first.

Mandibulate Type.—The *labrum*, or upper lip, in biting insects is a simple plate, hinged to the clypeus and moving up and down; though capable of protrusion and retraction to some extent. It covers the man-

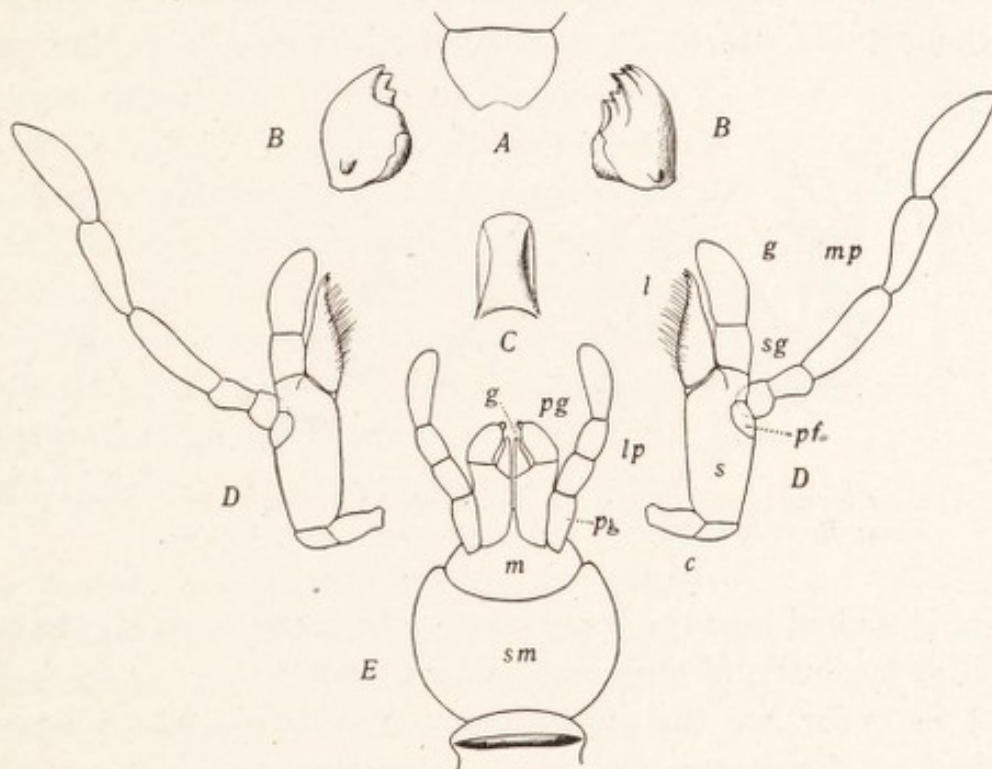


FIG. 45.—Mouth parts of a cockroach, *Parcoblatta pennsylvanica*. A, labrum; B, mandible; C, hypopharynx; D, maxilla; E, labium; c, cardo; g (of maxilla), galea; g (of labium), glossa; l, lacinia; lp, labial palpus; m, mentum; mp, maxillary palpus; p, paraglossa; pf, palpifer; pg, palpiger; s, stipes; sm, submentum. B, D, and E are in ventral aspect.

dibles in front and pulls food back to these organs. On the roof of the pharynx, under the labrum and clypeus, is the *epipharynx*; this consists of teeth, tubercles or bristles, which serve in some insects merely to hold food, though as a rule the epipharynx in mandibulate insects bears end-organs of taste (Packard). The labrum does not represent a pair of primary appendages.

The *mandibles*, or jaws proper, move in a transverse plane, being closed by a pair of strong adductor muscles and opened by a pair of weaker abductors. The mandible is almost always a single solid piece. In herbivorous insects (Fig. 46, A) it is compact, bluntly toothed, and

often bears a molar, or crushing, surface behind the incisive teeth. In carnivorous species (*B*) the mandible is usually long, slender and sharply toothed, without a molar surface. Often, as in soldier ants, the mandibles are used as piercing weapons; in bees (*C*) they are used for various industrial purposes; in some beetles they are large, grotesque in form and apparently purposeless. The mandibles of *Onthophagus* (*D*) and many other dung beetles consist chiefly of a flexible lamella, admirably adapted for its special purpose. In *Euphoria* (Fig. 265), which feeds on pollen and the juices of fruits, the mandibles, and the other mouth parts as well, are densely clothed with hairs. In the larva of *Chrysopa*, the inner face of the mandible (Fig. 46, *E*) has a longitudinal groove against which the maxilla fits to form a canal, through which the blood of

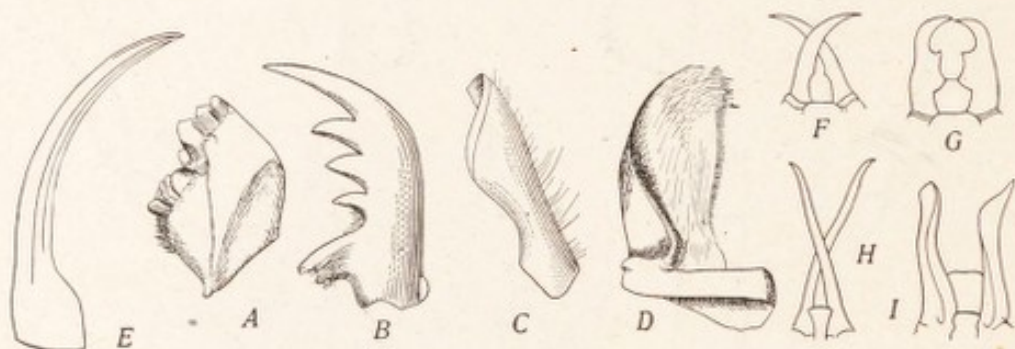


FIG. 46.—Various forms of mandibles. *A*, *Melanoplus*; *B*, *Cicindela*; *C*, *Apis*; *D*, *Onthophagus*; *E*, *Chrysopa*; *F-I*, soldier termites (after HAGEN).

plant lice is sucked into the œsophagus. In termites (*F-I*) the mandibles assume curious and often inexplicable forms.

Next in order are the *superlinguæ* (*maxillulæ*), which have been overlooked or disregarded by most entomologists. The superlinguæ are well developed in Thysanura and Collembola, particularly the former order. In *Machilis*, for example, the superlingua has essentially the same structure as a maxilla, as appears in Fig. 47; in *Japyx* the palpus is three-segmented (Hansen). The superlinguæ, arising in the embryo as a separate pair of appendages (Fig. 198, *sl*), always become united by their bases with the *lingua* (Fig. 198, *ln*), forming a pair of wing-like appendages on the dorsal side of the lingua (Figs. 50, 51).

Among insects, superlinguæ are best developed in Thysanura and Collembola, and are known to occur also in Orthoptera, Dermaptera, Isoptera, Corrodentia, nymphs of Ephemerida and larvæ of some Coleoptera.

Hansen ('93) termed these appendages "maxillulæ," regarding them as homologous with the first maxillæ of Crustacea; and in this

interpretation he was followed by others, including the writer, who (Folsom, '00) termed them "superlinguæ." The writer at present agrees with Crampton, however, that these appendages are homologous with the paragnaths of Crustacea. If they are not equivalent to the first maxillæ of Crustacea, the term "maxillulæ" should not be applied to them; they may be termed "superlinguæ" or "paragnaths," as one prefers.

Following the superlinguæ are the *maxillæ*, or under jaws, which are less powerful than the mandibles and more complex, consisting as they do of several sclerites (Figs. 45, 48). Essentially, the maxilla consists of three lobes, namely, *palpus*, *galea* and *lacinia*, which are borne by a *stipes*, and hinged to the skull by means of a *cardo*. The palpus, always lateral in position, is usually four- or five-segmented and is tactile, olfactory or gustatory in function. The lacinia is commonly provided with teeth or spines. The maxillæ supplement the mandibles by holding the food when the latter open, and help to comminute the food. Additional maxillary sclerites, of minor importance, often occur.

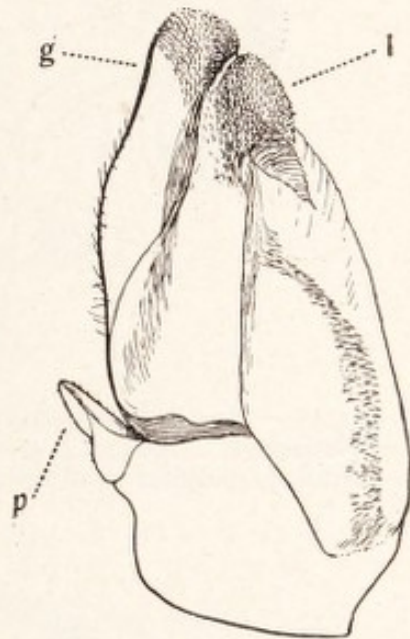


FIG. 47.—Left superlingua of *Machilis variabilis*. g, galea; l, lacinia; p, palpus.

The *labium*, or under lip, may properly be likened to a united pair of maxillæ, for both are formed on the same three-lobed plan. This correspondence is evident in the cockroach, among other generalized insects. Thus, in this insect (Fig. 45):

LABIUM	=	MAXILLÆ
<i>palpus</i>	=	<i>palpus</i>
<i>paraglossa</i>	=	<i>galea</i>
<i>glossa</i>	=	<i>lacinia</i>
<i>palpiger</i>	=	<i>palpifer</i>
<i>mentum</i>	=	<i>stipites</i>
<i>submentum</i> with <i>gula</i>	=	<i>cardines</i>

In most mandibulate orders the glossæ unite to form a single median organ, as in *Harpalus* (Fig. 49, g). The labium forms the floor of the pharynx and assists in carrying food to the mandibles and maxillæ.

The tongue, or *hypopharynx*, is a median fleshy organ (Fig. 45) which is usually united more or less with the base of the labium. In

insects in general, the salivary glands open at the base of the hypopharynx. In the most generalized insects, Thysanura and Collembola, the hypopharynx is a compound organ, consisting of a median ventral lobe, or *lingua*, and two dorsolateral lobes, termed *superlinguæ* by the

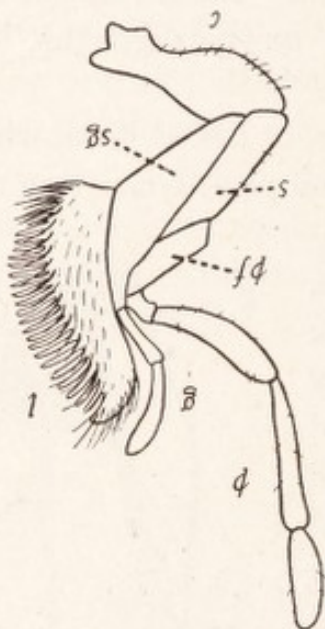


FIG. 48.—Maxilla of *Harpalus caliginosus*, ventral aspect. *c*, cardo; *g*, galea; *l*, lacinia; *p*, palpus; *pf*, palpifer; *s*, stipes; *sg*, subgalea.

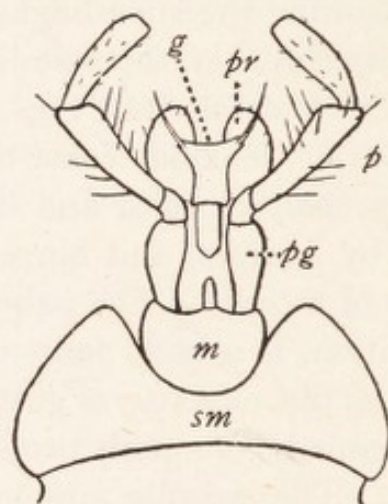


FIG. 49.—Labium of *Harpalus caliginosus*, ventral aspect. *g*, united glossæ, termed the glossa; *m*, mentum; *p*, palpus; *pg*, palpi-ger; *pr*, paraglossa; *sm*, submentum. The median portion of the labium beyond the mentum (excepting the palpi) is termed the ligula.

author. Superlinguæ occur in other mandibulate orders just mentioned, but have not yet been recognized in the most specialized orders of insects.

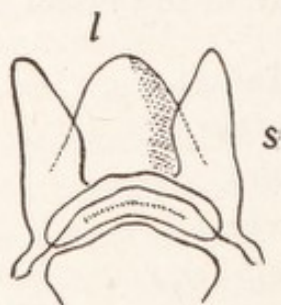


FIG. 50.—Hypopharynx of *Hemimerus talpoides*. *l*, lingua; *s*, superlingua.—After HANSEN.

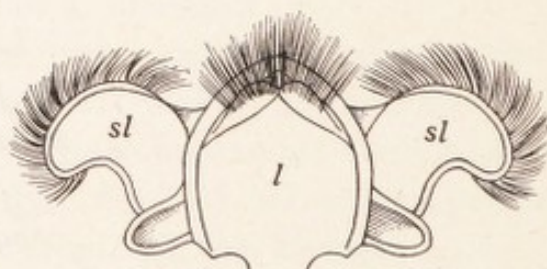


FIG. 51.—Hypopharynx of an ephemerid, *Heptagenia*. *l*, lingua; *sl*, *sl*, superlinguæ.—After VAYSSIÈRE.

Suctorial Types.—The mandibulate type of mouth parts is the primitive type, from which the suctorial types have been derived. Though the latter have evolved in several directions, they may all be homologized with the former.

The suctorial, or haustellate, orders are Collembola (in part), Thysanoptera (in part), Hemiptera, Parasita, Trichoptera (imperfectly), Lepidoptera, Diptera, Siphonaptera and Hymenoptera (which have functional mandibles, however).

Hemiptera.—The beak, or *rostrum*, in Hemiptera consists (Fig. 52) of a conspicuous, one- to four-segmented labium, which ensheathes hair-like mandibles and maxillæ and is covered above at its base by a short

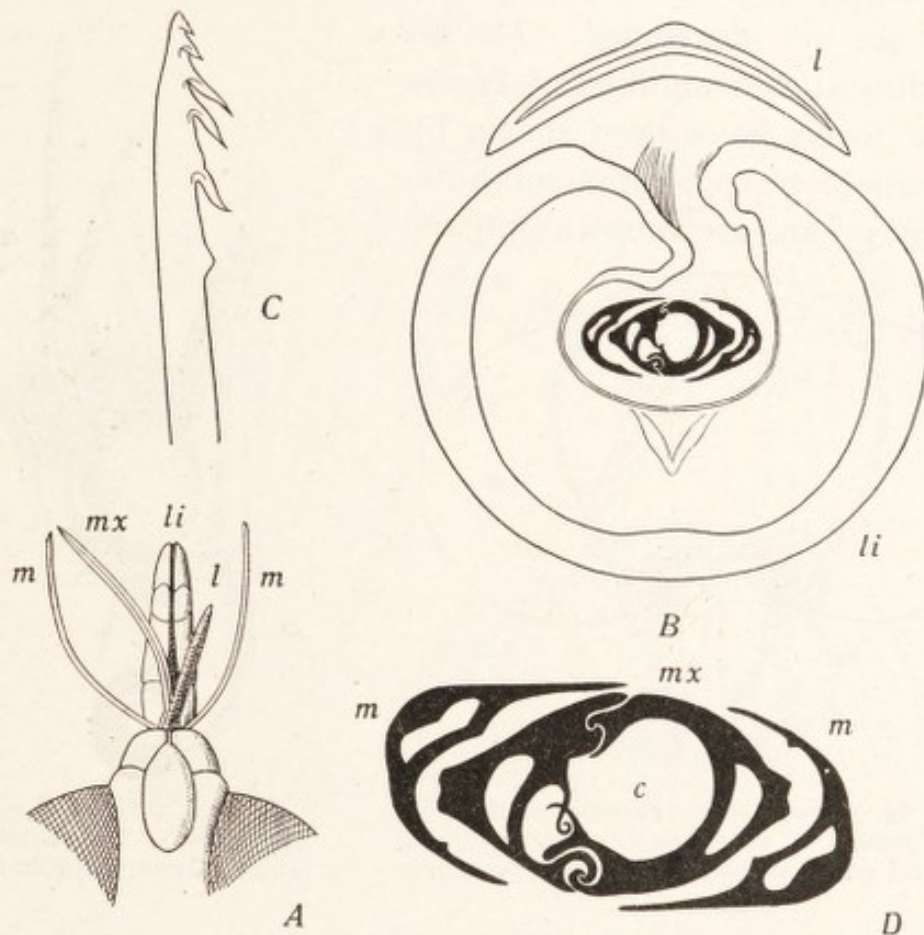


FIG. 52.—Mouth parts of a hemipteron, *Benacus griseus*. A, dorsal aspect; B, transverse section; C, extremity of mandible; D, transverse section of mandibles and maxillæ c, suction canal; l, labrum; li, labium; m, mandible; mx, maxillæ.

labrum. The mandibles and maxillæ are sharply-pointed, piercing organs and the former frequently bear retrorse barbs just behind the tip; the two maxillæ lock together to form a sucking tube with two canals: an upper, suction canal and a lower, salivary canal. Though primarily a sheath, the labium bears at its extremity sensory hairs, which are doubtless used to test the food. This general description applies to all Hemiptera except the parasitic forms, which present special modifications. A pharyngeal pumping apparatus is present, which is similar in its general plan to that of Lepidoptera and Diptera,

as presently described, though it differs as regards the smaller details of construction.

Lepidoptera.—In Lepidoptera, excepting *Eriocephala*, the labrum is reduced (Fig. 53) and the mandibles are either rudimentary or absent (Rhopalscera). The two maxillæ are represented by their galeæ, which form a conspicuous proboscis; the grooved inner faces of the galeæ (or lacinia, according to Kellogg) form the sucking tube, which opens into the œsophagus. The labium is reduced, though the labial palpi (Fig. 54) are well developed. The so-called rudimentary mandibles of *Anosia* and other forms have been shown by Kellogg to be lateral projections of the labrum (Fig. 53) and are known as *pilifers*.

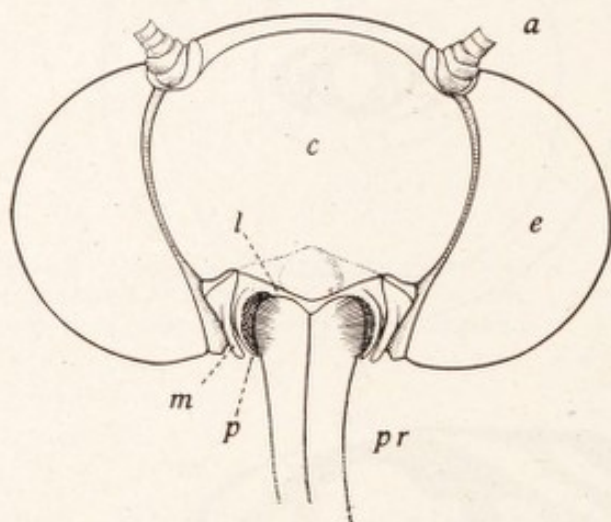


FIG. 53.—Head of a sphingid moth, *Protoparce sexta*. *a*, antenna; *c*, clypeus; *e*, eye; *l*, labrum; *m*, mandible; *p*, pilifer; *pr*, proboscis.



FIG. 54.—Head of a butterfly, *Vanessa*. *a*, antennæ; *l*, labial palpus; *p*, proboscis.

The exceptional structure of the mouth parts in the generalized genus *Eriocephala* (*Micropteryx*) sheds much light on the morphology of these organs in other Lepidoptera, as Walter and Kellogg have shown. In this genus there are functional mandibles; the maxilla presents palpus, galea, lacinia, stipes and cardo, though there is no proboscis; the labium has well developed submentum, mentum and palpi; a hypopharynx is present.

The sucking apparatus, as described by Burgess, is essentially like that of Diptera. Five muscles, originating at the skull and inserted on the wall of a pharyngeal bulb, serve to dilate the bulb that it may suck in fluids, while numerous circular muscles serve by contracting successively to squeeze the contents of the bulb back into the stomach; a hypopharyngeal valve prevents their return forward.

Diptera.—In the female mosquito the mouth parts (Fig. 55) are long and slender. As Dimmock found, the labrum and epipharynx combine¹ to form a sucking tube; the mandibles and maxillæ are delicate, linear, piercing organs, the latter being barbed distally; maxillary palpi are present; the hypopharynx is linear also and serves to conduct saliva; the labium forms a sheath, enclosing the other mouth parts when they are not in use; a pair of sensory lobes, termed *labella*, occur at the extremity of the labium.

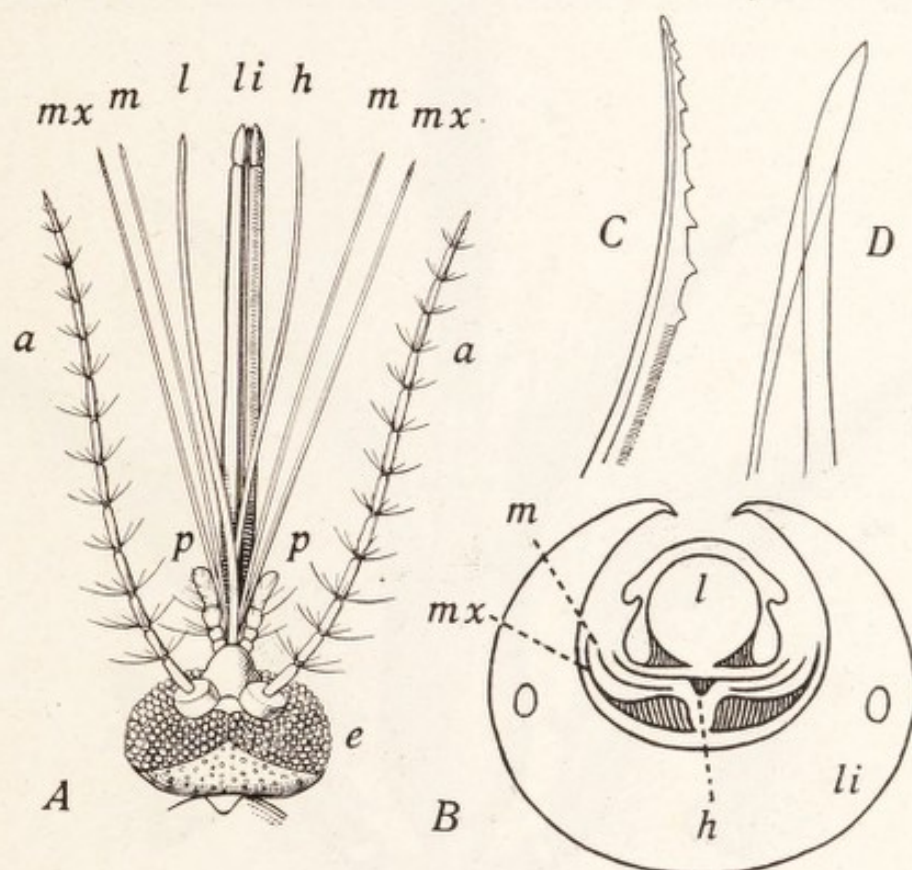


FIG. 55.—Mouth parts of female mosquito, *Culex pipiens*. A, dorsal aspect; B, transverse section; C, extremity of maxilla; D, extremity of labrum-epipharynx; a, antenna; e, compound eye; h, hypopharynx; l, labrum-epipharynx; li, labium; m, mandible; mx, maxilla; p, maxillary palpus.—B, after DIMMOCK.

The œsophagus is dilated to form a bulb, or sucking organ, from which muscles pass outward to the skull; when these contract, the bulb dilates and can suck in fluids, as blood or water, which are forced back into the stomach by the elasticity of the bulb itself, according to Dimmock; the regurgitation of the food is prevented by a valve.

The male mosquito rarely if ever sucks blood, and its mouth parts differ from those of the female in having the mandibles aborted and the maxillæ slightly developed, but with long palpi, while the hypopharynx coalesces with the labium and there is no œsophageal bulb.

¹ Kulagin, however, described them as remaining separate.

Hymenoptera.—In the honey bee, which will serve as a type, the labrum is simple; the mandibles are well developed instruments for cutting and other purposes (Fig. 56) and the remaining mouth parts form a highly complex suctorial apparatus, as follows. The “tongue” (*glossa*) is a long flexible organ, terminating in a “spoon” (*labellum*, Figs. 56, 129) and clothed with hairs of various kinds, for gathering

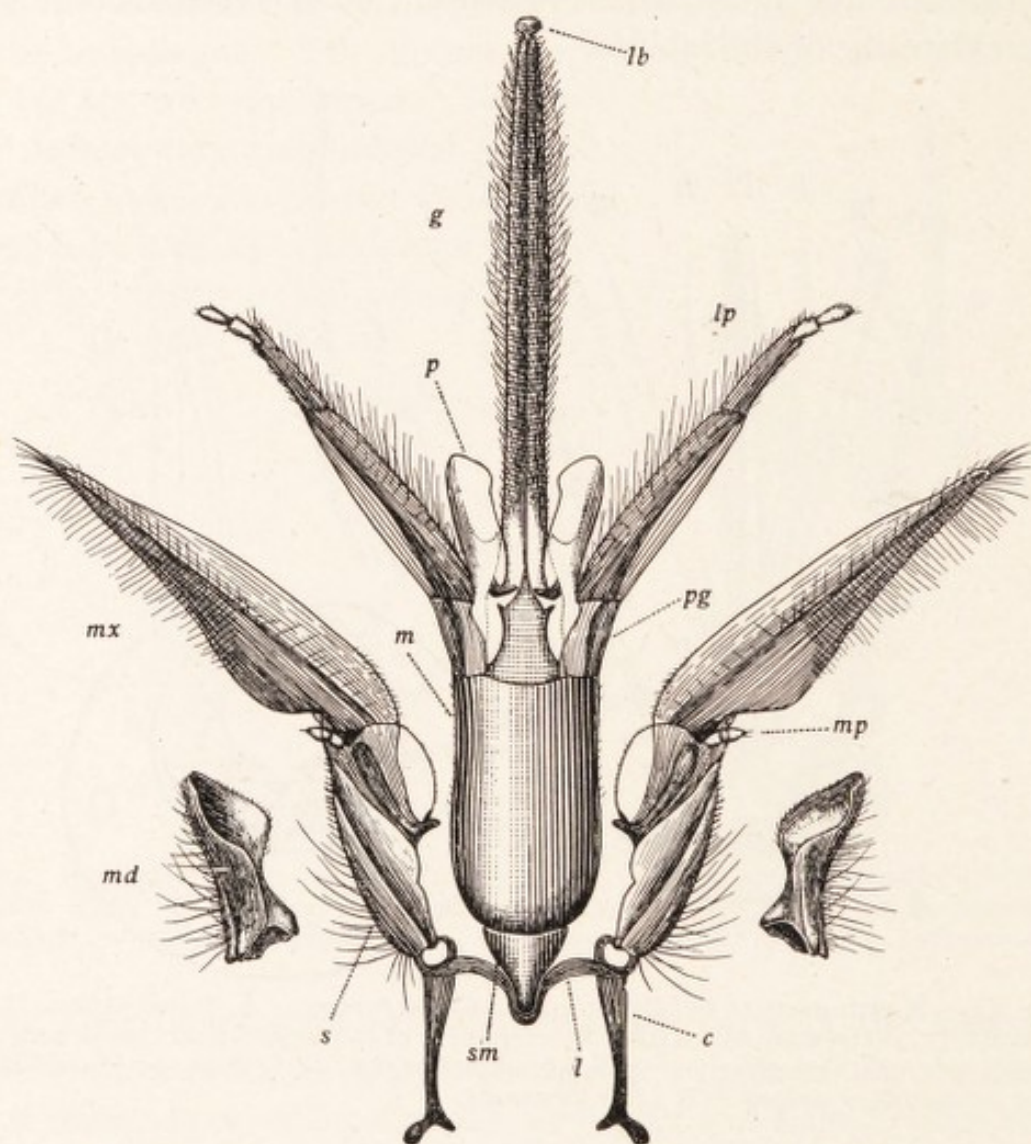


FIG. 56.—Mouth parts of the honey bee, *Apis mellifera*, ventral aspect. *c*, cardo; *g*, glossa (united glossæ); *l*, lorum; *lb*, labellum; *lp*, labial palpus; *m*, mentum; *md*, mandible; *mp*, maxillary palpus; *mx*, maxilla; *p*, paraglossa; *pg*, palpiger; *s*, stipes (plus subgalea and palpifer); *sm*, submentum. The blade of the maxilla is the galea, and the rounded lobe opposite the palpus is the lacinia.

nectar or for sensory or mechanical purposes. The maxillæ and labial palpi form a tube embracing the tongue, while the epipharynx fits into the space between the bases of the maxillæ to complete this tube. Through this canal nectar is driven, by the expansion and contraction of the tube itself, according to Cheshire, except that when only a small quantity of nectar is taken, this passes from the spoon into a fine “cen-

tral duct," or also into the "side ducts," which are specially fitted to convey quantities of fluid too small for the main tube. For a detailed account of the highly complex and exquisitely adapted mouth parts of the honey bee, the reader is referred to Cheshire's admirable work, Packard's *Text-Book*, or Snodgrass' *The Anatomy of the Honey Bee*.

Segmentation of the Head.—The determination of the number of segments entering into the composition of the insect head has been a difficult problem. As no segment bears more than one pair of primary appendages, there are at least as many segments in the head as there are

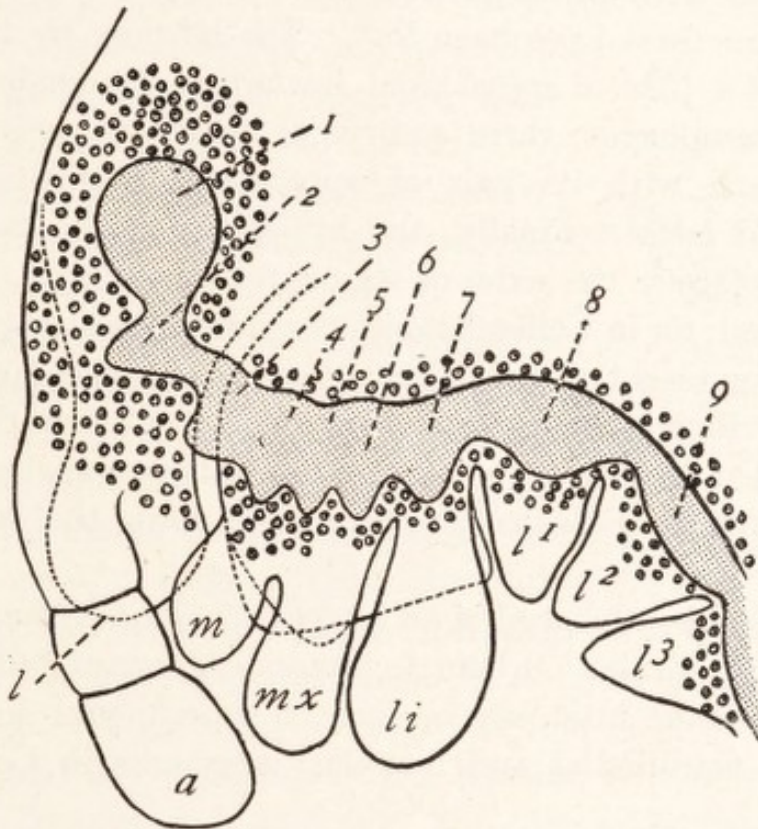


FIG. 57.—Paramedian section of an embryo of the collembolan *Anurida maritima*; to show the primitive cephalic ganglia. 1, ocular neuromere; 2, antennal; 3, intercalary; 4, mandibular; 5, superlingual; 6, maxillary; 7, labial; 8, prothoracic; 9, mesothoracic; a, antenna; l, labrum; li, labium; l¹, l², l³, thoracic legs; m, mandible; mx, maxilla.—After FOLSOM.

pairs of primary appendages. On this basis, then, the antennæ, mandibles, maxillæ and labium may be taken to indicate so many segments; but in order to decide whether the eyes, labrum and hypopharynx represent segments, other than purely anatomical evidence is necessary. The key to the subject is furnished by embryology. At an early stage of development the future segments are marked off by transverse grooves on the ventral surface of the embryo, and the pairs of segmental appendages are all alike (Fig. 197), or equivalent, though later they differentiate into antennæ, mouth parts, legs, etc. Moreover, the nervous

system exhibits a segmentation which corresponds to that of the entire insect; in other words, each pair of primitive ganglia, constituting a *neuromere*, indicates a segment. Now in front of the œsophagus three primitive segments appear, each with its neuromere (Fig. 57): first in position, an *ocular* segment, destined to bear the compound eyes; second, an *antennal* segment; third, an *intercalary* (*premandibular*) segment, which in the generalized orders Thysanura and Collembola bears a transient pair of appendages that are probably homologous with the second antennæ of Crustacea. In the adult, the ganglia of these three segments have united to form the brain, and the original simplicity and distinctness have been lost. The labrum, by the way, does not represent a pair of appendages, but arises as a single median lobe. Behind the œsophagus, three embryonic segments are clearly distinguishable, each with its pair of appendages, namely, *mandibular*, *maxillary* and *labial*. Finally, the hypopharynx, or rather a part of it, claims a place in the series of segmental appendages, as the author has maintained; for in Collembola its two dorsal constituents, or *superlinguæ*, develop essentially as do the other paired appendages and, moreover, a superlingual neuromere (Fig. 57) exists (even though Philipstschenko failed to find it). The four primitive ganglia immediately behind the mouth eventually combine to form the subœsophageal ganglion.

To summarize—the head of an insect is composed of at least six segments, namely, ocular, antennal, intercalary, mandibular, maxillary and labial; and at most seven, since a superlingual segment occurs between the mandibular and maxillary segments in Collembola and Thysanura.

Thorax.—The thorax, or middle region, comprises the three segments next behind the head, which are termed, respectively, *pro-*, *meso-* and *metathorax*. In aculeate Hymenoptera, however, the thoracic mass includes also the first abdominal segment, then known as the *propodeum*, or *median segment*. Each of the three thoracic segments bears a pair of legs in almost all adult insects, but only the meso- and metathorax may bear wings.

The differentiation of the thorax as a distinct region is an incidental result of the development of the organs of locomotion, particularly the wings. Thus in legless (*apodous*) larvæ the thoracic and abdominal segments are alike; when legs are present, but no wings, the thoracic segments are somewhat enlarged; and when wings occur, the size of a wing-bearing segment depends on the volume of the wing muscles,

which in turn is proportionate to the size of the wings. When wings are absent (as in Thysanura and Collembola) or the two pairs equal in area (as in Termitidæ, Odonata, Trichoptera and most Lepidoptera) the meso- and metathorax are equal. If the fore wings exceed the hind ones (Ephemeridæ, Hymenoptera) the mesothorax is proportionately larger than the metathorax; as also in Diptera, where no hind wings occur. If the fore wings are small (Coleoptera) or almost absent (Stylopidae) the mesothorax is correspondingly smaller than the metathorax. The prothorax, which never bears wings, may be enlarged dorsally to form a protective shield, as in Orthoptera, Hemiptera and Coleoptera; or, on the contrary, may be greatly reduced, as in Ephemerida, Odonata, Lepidoptera and Hymenoptera. In the primitive Apterygota the prothorax may become reduced (many Collembola) or slightly enlarged (*Lepisma*).

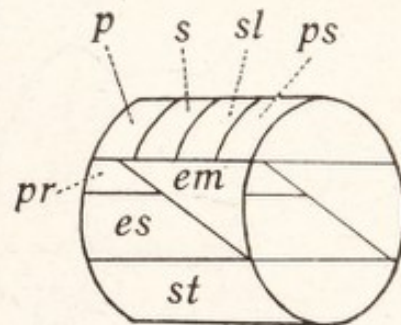


FIG. 58.—Diagram of the principal sclerites of a thoracic segment. *em*, epimeron; *es*, episternum; *p*, præscutum; *pr*, parapteron; *ps*, postscutellum; *s*, scutum; *sl*, scutellum; *st*, sternum.—After COMSTOCK.

The dorsal wall of a thoracic segment is termed the *notum*, or *tergum*; the ventral wall, the *sternum*; and each lateral wall, a *pleuron*; the restriction of these terms to particular segments of the thorax being indicated by the prefixes *pro*-, *meso*- or *meta*-. These parts are usually divided by sutures into distinct pieces, or sclerites, as represented diagrammatically in Fig. 58. Thus the tergum of a wing-bearing segment is regarded as being composed of four sclerites (*tergites*, Fig. 59), namely and in order, *præscutum*, *scutum*, *scutellum* and *postscutellum*. The scutum and scutellum are commonly evident, but the two other sclerites are usually small and may be absent. According to Snodgrass, the tergum consists primitively of a single sclerite, the notum; the four sclerites having arisen as specializations; being not always homologous in different orders of insects. Each pleuron consists chiefly of two sclerites (*pleurites*, Figs. 58 and 60), separated from each other by a more or less oblique suture. The anterior of these two, which joins the sternum, is termed the *episternum*; the other, the *epimeron*. The former is divided into two sclerites in Odonata and both are so divided in Neuroptera.

The sternum, though usually a single plate, is in some instances divided into halves, as in the cockroach, or even into five sclerites (Forficulidæ).

To these should be added the *patagia* of Lepidoptera—a pair of

erectile appendages of the prothorax; and the *tegulae* (*paraptera*) of Lepidoptera, Diptera and Hymenoptera—a pair of small sclerites at the bases of the front wings.

The thorax has also several small sclerites which are not described here, though they are of interest to the morphologist.

Each of the three thoracic segments bears a pair of spiracles in the embryo, but in most imagines there are only two pairs of thoracic spiracles, the suppressed pair being the prothoracic.

The sclerites of the thorax owe their origin probably to local strains on the integument, brought about by the muscles of the thorax. Thus

the primitively wingless Thysanura and Collembola have no hard thoracic sclerites, though certain creases about the bases of the legs may be regarded as incipient sutures, produced mechanically by the movements of the legs. In soft nymphs and larvæ, the sclerites do not form until the wings develop; and in forms that have nearly or quite lost their wings, as Pediculidæ, Mallophaga, Siphonaptera and some parasitic Diptera, the sclerites of the thorax tend to disappear. Furthermore, the absence of sclerites in the prothorax is probably due to the lack of prothoracic wings, notwithstanding the so-called obsolete sutures of the pronotum in grasshoppers.

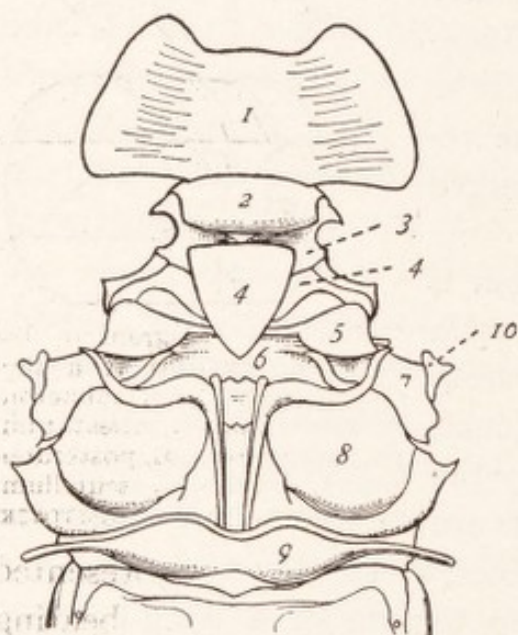


FIG. 59.—Dorsal aspect of the thorax of a beetle, *Hydrous piceus*. 1, pronotum; 2, mesopræscutum; 3, mesoscutum; 4, mesoscutellum; 5, mesopostscutellum; 6, metapræscutum; 7, metascutum; 8, metascutellum; 9, metapostscutellum.—After NEWPORT.

Endoskeleton.—An insect has no internal skeleton, strictly speaking, though the term *endoskeleton* is used in reference to certain ingrowths of the external cuticula which serve as mechanical supports or as protections for some of the internal organs. The tentorium of the head has already been referred to. In the thorax three kinds of chitinous ingrowths may be distinguished according to their positions: (1) *phragmas*, or dorsal projections; (2) *apodemes*, lateral; (3) *furcæ*, or *apophyses*, ventral. The phragmas (Fig. 61) are commonly three large plates, pertaining to the meso- and metathorax, and serving for the origin of indirect muscles of flight in Lepidoptera, Diptera, Hymenoptera and other strong-winged orders. The apodemes are comparatively

small ingrowths, occurring sometimes in all three thoracic segments, though usually absent in the prothorax. The furcæ occur in each thoracic segment as a pair of conspicuous processes, which either remain separate or else unite more or less; leaving, however, a passage for the ventral nerve cord.

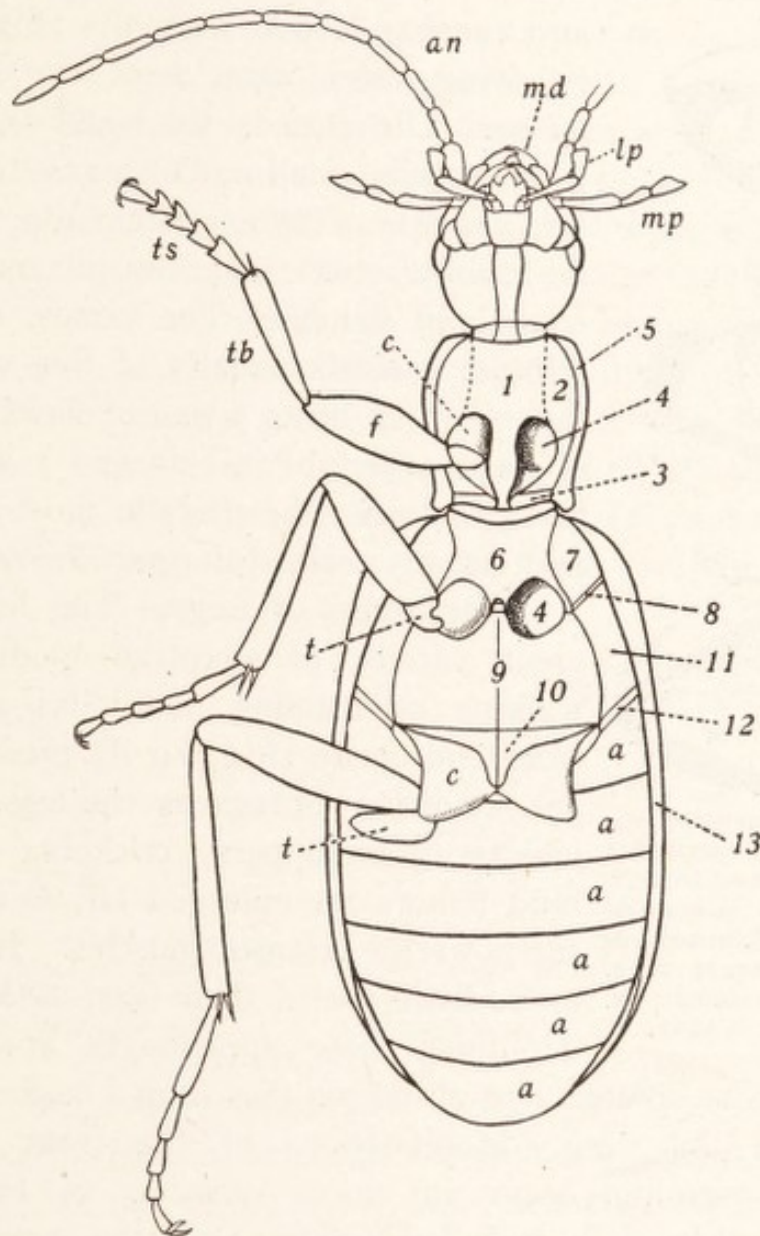


FIG. 60.—Ventral aspect of a carabid beetle, *Galerita janus*. 1, prosternum; 2, proepisternum; 3, proepimeron; 4, coxal cavity; 5, inflexed side of pronotum; 6, mesosternum; 7, mesoepisternum; 8, mesoepimeron; 9, metasternum; 10, antecoxal piece; 11, metaepisternum; 12, metaepimeron; 13, inflexed side of elytron; a, sternum of an abdominal segment; an, antenna; c, coxa; f, femur; lp, labial palpus; md, mandible; mp, maxillary palpus; t, trochanter; tb, tibia; ts, tarsus.

These endoskeletal processes serve chiefly for the origin of muscles concerned with the wings or legs, and are absent in such wingless forms as Thysanura, Pediculidæ and Mallophaga.

Some ambiguity attends the use of these terms. Thus some writers

use the term apodemes for furcæ and others apply the term apodeme to any of the three kinds of ingrowths.

Legs.—In almost all adult insects and in most larvæ each of the three thoracic segments bears a pair of legs. The leg is articulated to the sternum, episternum and epimeron, partly by means of small *articular sclerites* (one of which, the *trochantin*, is shown in Fig. 63)

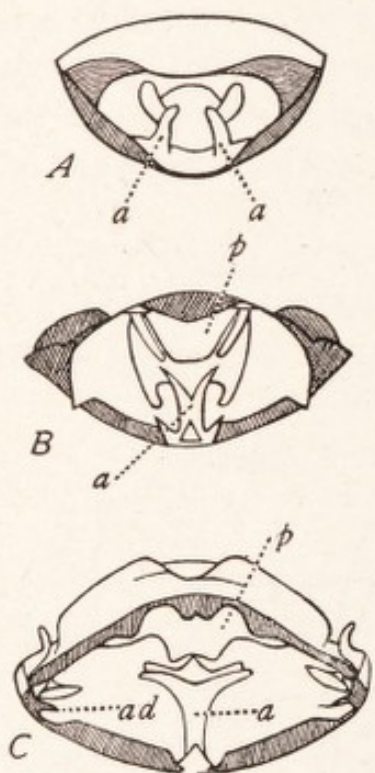


FIG. 61.—Transverse sections of the thoracic segments of a beetle, *Goliathus*, to show the endoskeletal processes. A, prothorax; B, mesothorax; C, metathorax; a, a, furcæ; ad, apodeme; p, phragma.—After KOLBE.

and consists of five segments (Fig. 62), in the following order: *coxa*, *trochanter*, *femur*, *tibia*, *tarsus*. The coxa is the basal segment. The trochanter is small and in parasitic Hymenoptera consists of two subsegments. The femur is usually stout and conspicuous, the tibia commonly slender. The tarsus, rarely single-jointed, consists usually of five segments, the last of which bears a pair of claws in the adults of most orders of insects and a single claw in larvæ; between the claws in most imagines is a pad, usually termed the *pulvillus*, or *empodium*.

Adaptations of Legs.—The legs exhibit a great variety of adaptive modifications. A walking or running insect, as a carabid or cicindelid beetle (Fig. 64, A) presents an average condition as regards the legs. In leaping insects (grasshoppers, crickets, *Haltica*) the hind femora are enlarged (B) to accommodate the powerful extensor muscles. In insects that make little use of their legs, as May flies and

Tipulidæ, these appendages are but weakly developed. The spinous legs of dragon flies form a basket for catching the prey on the wing. Modifications of the front legs for the purpose of grasping occur in many insects, as the terrestrial families Mantidæ (C) and Reduviidæ and the aquatic families Belostomidæ and Naucoridæ (D). Swimming species present special adaptations of the legs (Fig. 231), as described in the chapter on aquatic insects. In digging insects, the fore legs are expanded to form shovel-like organs, notably in the mole-cricket (Fig. 64, E), in which the fore tibia has some resemblance to the human hand, while the tarsus and tibia are remarkably adapted for cutting roots, after the manner of shears. The Scarabæidæ have fossorial legs, the anterior tarsi of which are in some genera reduced (F) or absent; they are rudi-

mentary in the female (G) of *Phanæus carnifex* and absent in the male (H), and absent in both sexes of *Deltochilum*. Though females of *Phanæus* lose their front tarsi by digging, the degenerate condition of these organs cannot be attributed to the inheritance of a mutilation, but may have been brought about by disuse; though no one has explained why the two sexes should differ in this respect. Many insects use the legs to clean the antennæ, head, mouth parts, wings or legs; the honey bee (with other bees, also ants, Carabidæ, etc.) has a special antenna cleaner on the front legs (Fig. 267, D), which is described, with other interesting modifications of the legs, on page 229.

Indeed, the legs serve many such minor purposes in addition to locomotion. They are commonly used to hold the female during coition, and in several genera of Dytiscidæ (*Dytiscus*, *Cybister*) the male (Fig. 64, I) has tarsal disks and cupules chiefly on the front tarsi, for this purpose.

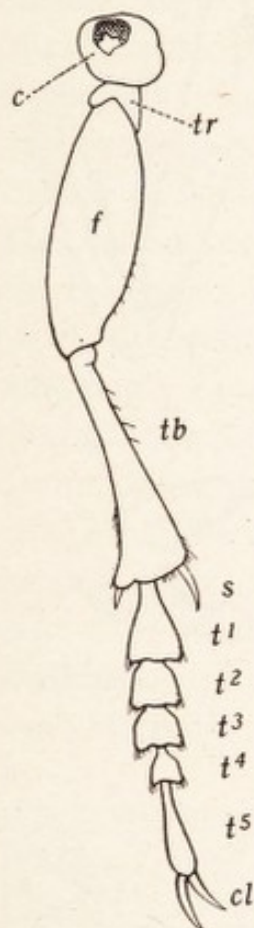


FIG. 62.—Leg of a beetle, *Calosoma calidum*. c, coxa; cl, claws; f, femur; s, spur; t^1 - t^5 , tarsal segments; tb, tibia; tr, trochanter.

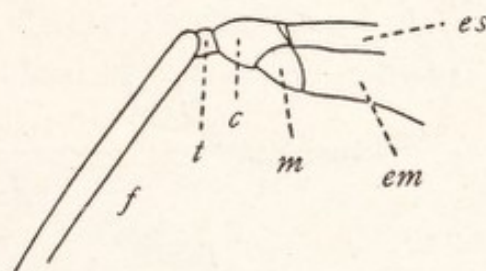


FIG. 63.—Left hind leg of *Bittacus*. c, coxa genuina; em, epimeron; es, episternum; f, femur; m, trochantin; t, trochanter.

Among other secondary sexual peculiarities of the legs may be mentioned the tibial brushes of the male *Catocala concumbens*, regarded as scent organs, and the queer appendages of male Dolichopodidæ that dangle in the air as these flies perform their dances.

The pulvillus is commonly an adhesive organ. In flies it has glandular hairs that enable the insects to walk on smooth surfaces and to walk upside down; so also in many beetles and notably in the honey bee (Fig. 65); in this insect the pulvillus is released rapidly from the surface to which it has been applied, by rolling up from the edges inward.

Sense organs occur on the legs. Thus tactile hairs are almost always present on these appendages, while auditory organs occur on the front tibiæ of Tettigoniidæ, Gryllidæ and some ants. Finally, the

legs may be used to produce sound, as in *Stenobothrus* and such other Locustidæ as stridulate by rubbing the femora against the tegmina.

Legs of Larvæ.—Thoracic legs, terminating in a single claw, are present in most larvæ. Caterpillars have, in addition, fleshy abdominal

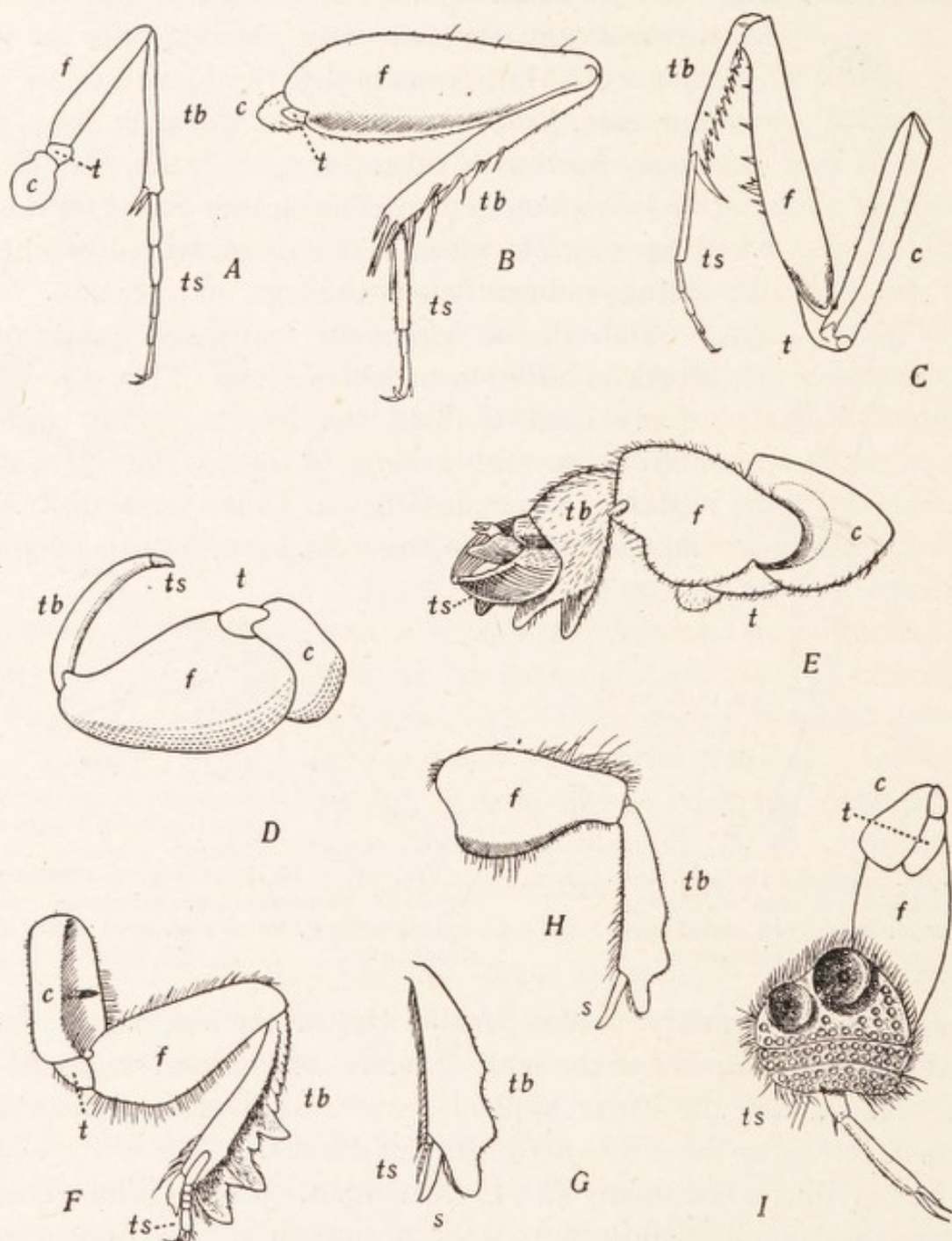


FIG. 64.—Adaptive modifications of the legs. A, *Cicindela sexguttata*; B, *Nemobius vittatus*, hind leg; C, *Stagmomantis carolina*, left fore leg; D, *Pelocoris femoratus*, right fore leg; E, *Gryllotalpa borealis*, left fore leg; F, *Canthion lævis*, right fore leg; G, *Phanæus carnifex*, fore tibia and tarsus of female; H, *P. carnifex*, fore tibia of male; I, *Dytiscus fasciventris*, right fore leg of male; c, coxa; f, femur; s, spur; t, trochanter; tb, tibia; ts, tarsus.

legs (Fig. 64) ending in a circlet of hooks. Most caterpillars have five pairs of these legs (on abdominal segments 3, 4, 5, 6, and 10), but the

rest vary in this respect. Thus *Lagoa* has seven pairs (segments 2-7 and 10) and Geometridæ two (segments 6 and 10), while a few caterpillars (*Tischeria*, *Limacodes*) have none. Larvæ of saw flies (Tenthredinidæ) have seven or eight pairs of abdominal legs and larvæ of most Panorpidæ, eight pairs. Not a few coleopterous larvæ (some Cerambycidæ, *Hypera*) also have abdominal tubercles that represent legs, but are incompletely developed as compared with those of Lepidoptera.

The legless, or *apodous*, condition occurs frequently among larvæ and always in correlation with a sedentary mode of life; as in the larvæ of many Cerambycidæ, almost all Rhynchophora, a few Lepidoptera, all Diptera, and all Hymenoptera except Tenthredinidæ, Siricidæ, and other Terebrantia.

Among adult insects, female scale insects are exceptional in being legless.

Walking.—An adult insect, when walking, normally uses its legs in two sets of three each; thus the front and hind legs of one side and the

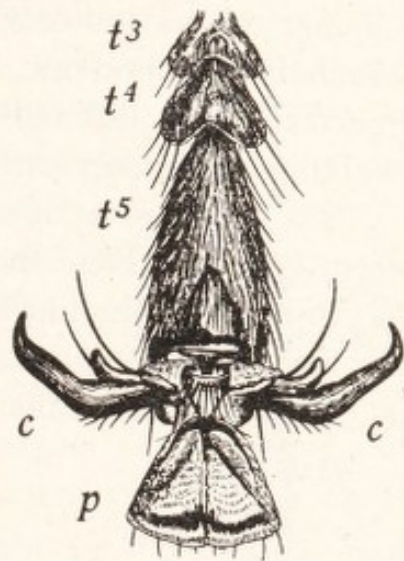


FIG. 65.—Foot of honey bee, *Apis mellifera*. *c, c*, claws; *p*, pulvillus; *t3-t5*, tarsal segments.—After CHESHIRE.

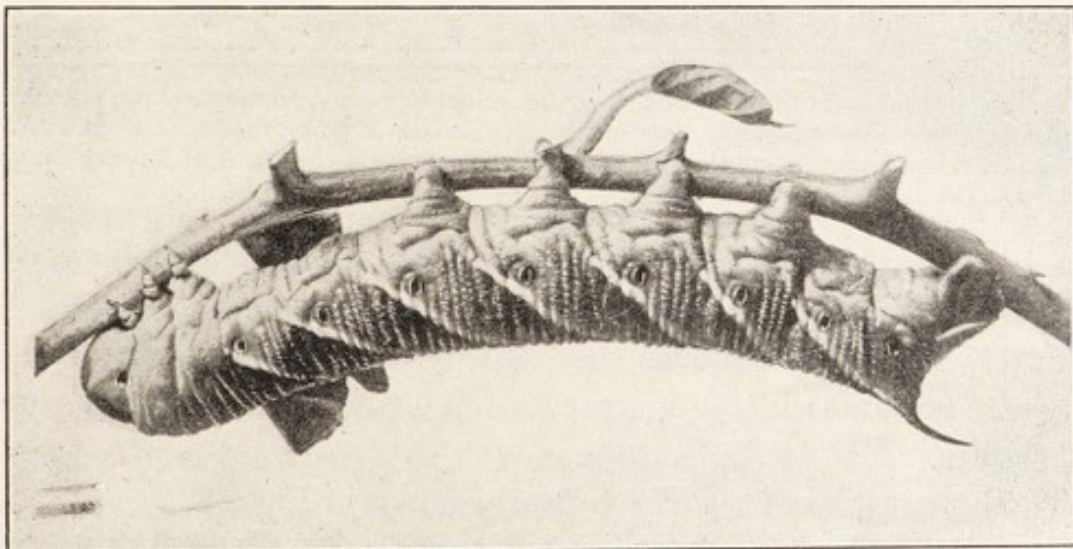


FIG. 66.—Caterpillar of *Protoparce sexta*. Natural size.

middle leg of the other move forward almost simultaneously—though not quite, for the front leg moves a little before the middle one, which, in turn, precedes the hind leg. During these movements the body is supported by the other three legs, as on a tripod. The front leg, having been extended and its claws fixed, pulls the body forward by

Wings.—The success of insects as a class is to be attributed largely to their possession of wings. These and the mouth parts, surpassing all the other organs as regards range of differentiation, have furnished the best criteria for the purposes of classification. The wings of insects present such countless differences that an expert can usually refer a detached wing to its proper genus and often to its species, though no fewer than four hundred thousand species of insects are already known.

Typically, there are two pairs of wings, attached respectively to the mesothorax and the metathorax, the prothorax never bearing wings, as was said. When only one pair is present it is almost invariably the anterior pair, as in *Diptera* and male *Coccidæ*, though in male *Strepsiptera* it is the posterior pair, the fore wings being rudimentary.

In bird lice, fleas and most other parasitic insects, the wings have degenerated through disuse. In *Thysanura* and *Collembola* there are no traces of wings even in the embryo; whence it is inferred that wings originated later than these orders of insects.

Müller and Packard have regarded the wings as tergal outgrowths; Tower, however, has shown that the wings of *Coleoptera*, *Orthoptera* and *Lepidoptera* are pleural in origin, arising just below the line where later the suture between the pleuron and tergum will originate, though the wings may subsequently shift to a more dorsal position.

Modifications of Wings.—Being commonly more or less triangular, a wing presents three margins: front (*costal*), outer (*apical*) and inner (*anal*); and three angles: *humeral* (at the base of the *costa*), *apical* (at the apex of the wing) and *anal* (between outer and inner margins). Various modifications occur in the front wings, which are in many orders more useful for protection than for flight. Thus, in *Orthoptera*, they are leathery, and are known as *tegmina*; in *Coleoptera* they are usually horny, and are termed *elytra*; in *Heteroptera*, the base of the front wing is thickened and the apex remains membranous, forming a *hemelytron*. *Diptera* have, in place of the hind wings, a pair of clubbed threads, known as *balancers*, or *halteres*, and male

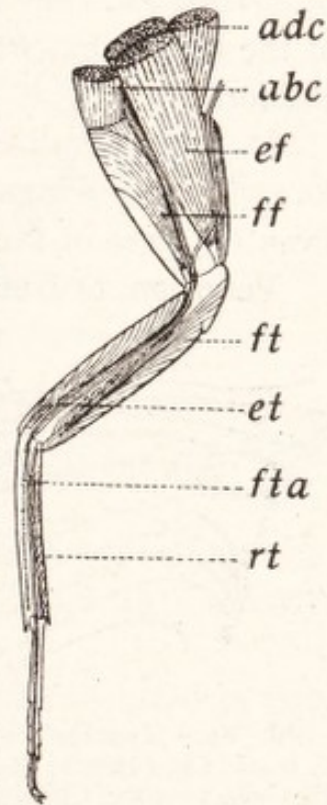


FIG. 68.—Muscles of left mid leg of a cockroach, posterior aspect. *abc*, abductor of coxa; *adc*, adductor of coxa; *ef*, extensor of tibia; *et*, extensor of femur; *ft*, flexor of tibia; *fta*, flexor of tarsus; *rt*, retractor of tarsus.—After MIALl and DENNY.

Coccidæ have on each side a bristle that hooks into a pocket on the wing and serves to support the latter. In many muscid flies a doubly lobed membranous *squama* occurs at the base of the wing.

In Hymenoptera the front and hind wings of the same side are held together by a row of hooks (*hamuli*); these are situated on the costal margin of the hind wing and clutch a rod-like fold of the fore wing. In very many moths, the two wings are enabled to act as one by means of a *frenulum*, consisting of a spine or a bunch of bristles near the base of the hind wing, which, in some forms, engages a membranous loop on the fore wing.

In the generalized moths of the family Hepialidæ, the overlapping fore and hind wings are held together by a *jugum*, projecting backward from the base of the fore wing.

Venation, or Neuration.—A wing is divided by its *veins*, or *nervures*, into spaces, or *cells*.

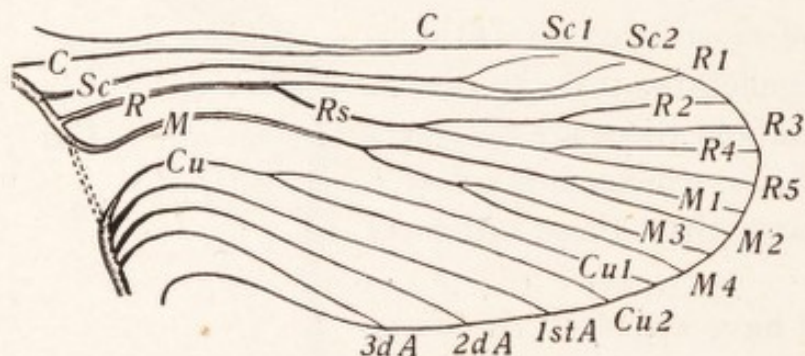


FIG. 69.—Hypothetical type of venation. A, anal vein; C, costa; Cu, cubitus; M, media; R, radius; Sc, subcosta.—Figs. 69–73 after COMSTOCK and NEEDHAM.

The distribution of the veins is of great systematic importance, but formerly, the homologies of the veins in the different orders of insects were not fixed, so that no little confusion resulted. For example, the term *dis-*

cal cell, used in descriptions of Lepidoptera, Diptera, Trichoptera and Psocidæ, was in no two of these groups applied to the same cell. The admirable work of Comstock and Needham, however, seems to settle this disputed subject. By a study of the tracheæ which precede and, in a broad way, determine the positions of the veins, these authors have arrived at a primitive type of tracheation (Fig. 69) to which the more complex types of tracheation and venation may be referred.

In general, the following principal longitudinal veins may be distinguished, in the following order: *costa*, *subcosta*, *radius*, *media*, *cubitus*, and *anal* (Figs. 69–73).

The costa (C) strengthens the front margin of the wing and is essentially unbranched.

The subcosta (Sc) is close behind the costa and is unbranched in the imagines of many orders in which there are few wing veins, though it is typically a forked vein.

The radius (*R*), though subject to much modification, is typically five-branched, as in Fig. 69. The second principal branch of the radius is termed the radial sector (*Rs*).

The media (*M*) is often three-branched and is typically four-branched, according to Comstock and Needham.

The cubitus (*Cu*) has two branches.

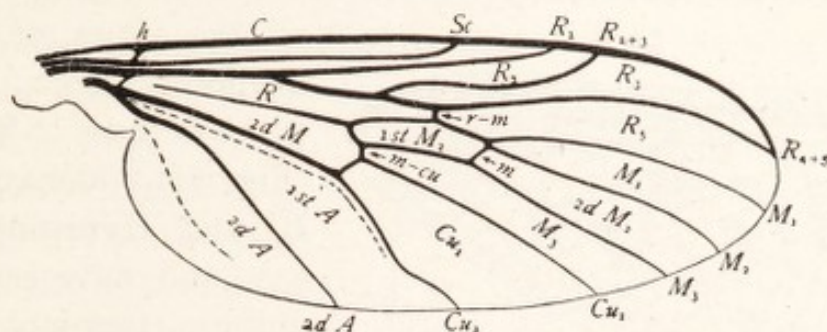


FIG. 70.—Wing of a fly, *Rhyphus*. Lettering as before.

The anal veins (*A*) are typically three, of which the first is usually simple, while the second and third are many-branched in wings that have an expanded anal area.

The Plecoptera, as a whole, show the least departure from the primitive type of venation; which is well preserved, also, in the more generalized genera of the Trichoptera.

Starting from the primitive type, specialization has occurred in two ways: by *reduction* and by *addition*. Reduction occurs either by the *atrophy* of veins or by the *coalescence* of two or more adjacent veins. Atrophy explains the lack of all but one anal vein in *Rhyphus* (Fig. 70) and other Diptera, and the absence of the base of the media in *Anosia* (Fig. 71) and many other Lepidoptera; in the pupa of *Anosia*, the media may be found complete. Coalescence "takes places in two ways: first, the point at which two veins separate occurs nearer and nearer the margin of the wing, until finally, when the margin is reached, a single vein remains where there were two before; second, the tips of two veins may approach each other on the margin of the wing until they unite, and then the coalescence proceeds towards the base of the wing." (Comstock and

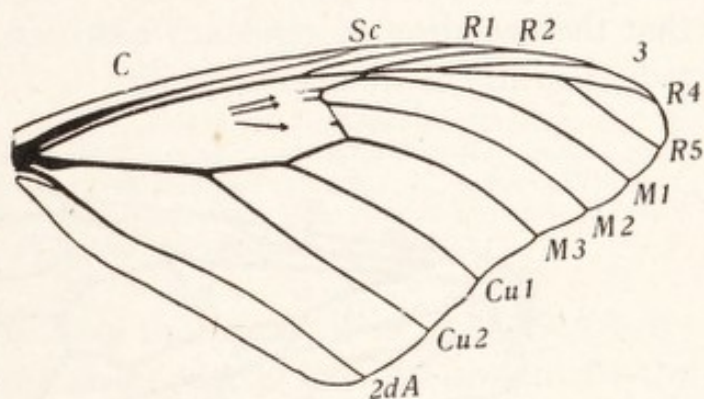


FIG. 71.—Wing of a butterfly, *Anosia*. Lettering as before.

Needham.) The former, or *outward*, kind of coalescence is common in most orders of insects; the latter, or *inward*, kind is especially prevalent in Diptera.

Specialization by addition occurs by a multiplication of the branches of the principal veins, or by the development of secondary longitudinal veins between these branches.

Comstock and Needham have succeeded in homologizing practically

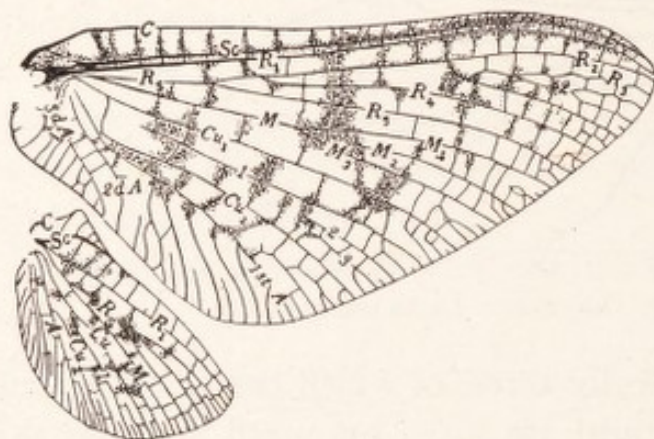


FIG. 72.—Wings of a May fly. Lettering as before.

all the types of neurulation, including such perplexing types as those of Ephemeroptera (Fig. 72), Odonata (Fig. 21, B) and Hymenoptera (Fig. 73), and have established a uniform terminology of the wing veins. The system built up during some twenty-five years by Comstock and his followers is embodied in his great volume, *The Wings of Insects*.

A student of the subject of venation should consult the many articles by Tillyard, a keen investigator, whose point of view is in some respects different from that of Comstock and Needham. He holds, for example, that the primitive type of wing had many veins instead of few, and that the evolutionary tendency has been, generally speaking, toward a reduction in the number of veins.

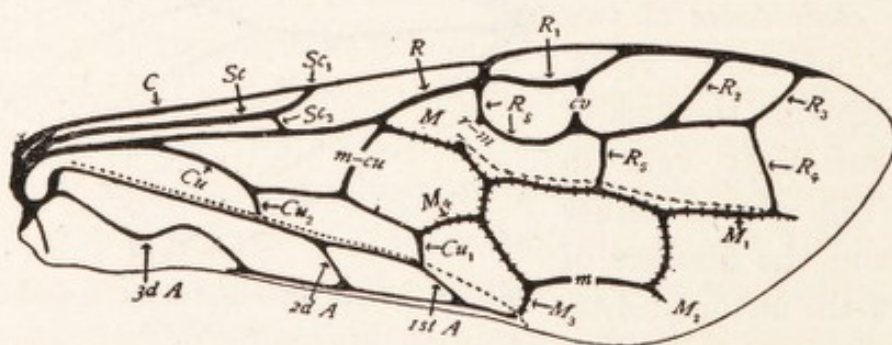


FIG. 73.—A typical hymenopterous wing. Lettering as before.

Folding of Wing.—In some beetles (as *Chrysobothris*) the wings are no larger than the elytra and are not folded; in others the wings exceed the elytra in size, and when not in use are folded under the elytra in ways that are simple but efficient, as described by Kolbe and by Tower. To be understood, the process of folding should be observed in the living insect. As described by Tower for the Colorado potato beetle,

the folded wing (Fig. 74, *B*) exhibits a costal joint (*a*), a fold parallel to the transverse vein (*b*), and a complex joint at *d*. The wing rotates upon the articular head (*ah*) and when folded back beneath the wing-covers the inner end of the cotyla (*c*) is brought into contact with a chitinous sclerite of the thorax, which stops the further movement of the cotyla medianward, and as the wing swings farther back the middle system of veins (*m*) is pushed outward and anteriorly. This motion, combined with the backward movement of the wing as a whole, produces the folding of the distal end of the wing. There are no traces of muscles or elastic ligaments in the wing which could aid in the folding.

Mechanics of Flight.—The mechanism of insect flight is much less complex than one might anticipate. Indeed, owing to the structure of the wing itself, simple up and down movements are sufficient for the simplest kind of flight. During oscillation, the plane of the wing changes, as may be demonstrated by holding a detached wing by its base and blowing at right angles to its surface; the membrane of the wing then yields to the pressure of the air while

the rigid anterior margin does not, to any great extent. Similarly, as the wing moves downward the membrane is inclined upward by the resistance of the air, and as the wing moves upward the membrane bends downward. Therefore, by becoming deflected, the wing encounters a certain amount of resistance from behind, which is sufficient to propel the insect. The faster the wings vibrate, the greater the deflection, the greater the resistance from behind, and the faster the flight of the insect.

The path traced in the air by a rapidly vibrating wing may be determined by fastening a bit of gold leaf to the tip of the wing and allowing the insect—a wasp, for example—to vibrate its wings in the sunlight,

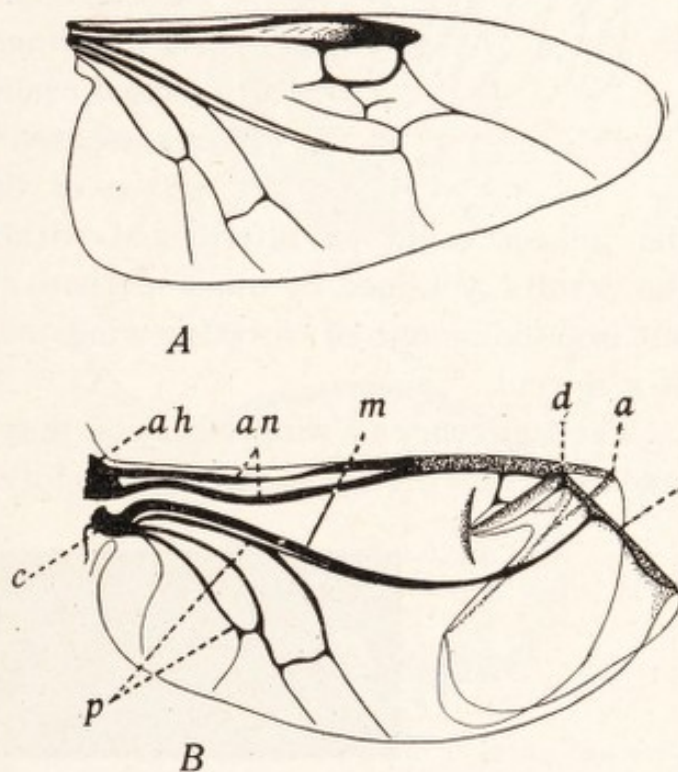


FIG. 74.—Wing of *Leptinotarsa decemlineata*. *A*, spread; *B*, folded; *a*, costal joint; *ah*, articular head; *an*, anterior system of veins; *b*, transverse vein; *c*, cotyla; *d*, joint; *m*, middle system of veins; *p*, posterior system of veins.—After TOWER.

against a dark background. Under these conditions, the trajectory of the wing appears as a luminous elongate figure 8. During flight, the trajectory consists of a continuous series of these figures, as in Fig. 75.

Marey, an authority on animal locomotion, used chronophotography, among other methods, in studying the process of flight, and obtained at first twenty, and later one hundred and ten, successive photographs per second of a bee in flight. As the wings were vibrating 190 times per second, however, the images evidently represented isolated and not consecutive phases of wing movement. Nevertheless,

the images could be interpreted without difficulty, in the light of the results obtained by other methods. At length he obtained sharp but isolated images of vibrating wings with an exposure of only $\frac{1}{25,000}$ of a second.

The frequency of wing vibration may be ascertained from the note made by the wing—if it vibrates rapidly enough to make one; and, in

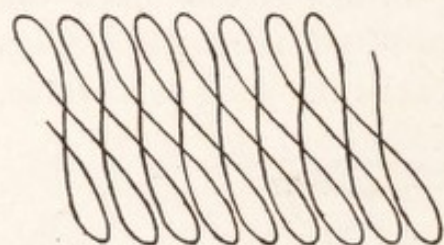


FIG. 75.—Trajectory of the wing of an insect.

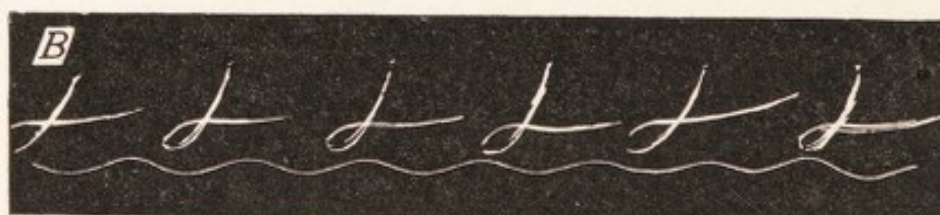


FIG. 76.—Records of wing vibration. *A*, mosquito, *Anopheles*. Above is the wing record and below is the record of a tuning-fork which vibrated 264.6 times per second. *B*, wasp, *Polistes*. The tuning-fork in this instance had a vibration frequency of 97.6.

any case, may be determined graphically by means of a kymograph, which, in one of its forms, consists of a cylinder covered with smoked paper and revolved by clockwork at a uniform rate. The insect is held in such a position that each stroke of the wing makes a record on the smoked paper, as in Fig. 76, *A*. Comparing this record with one made on the same paper by a tuning-fork of known vibration period, the frequency of wing vibration can be determined with great accuracy.

As the wing moves in the arc of a circle, the radius of which is the length of the wing, the extreme tip of the wing records only a short mark; if, however, the wing is pressed against the smoked cylinder, a large part of the figure-8 trajectory may be obtained, as in Fig. 76, *B*. The wings of the two sides move synchronously, as Marey found.

The smaller the wings are, the more rapidly they vibrate. Thus a butterfly (*P. rapæ*) makes 9 strokes per second, a dragon fly 28, a sphingid moth 72, a bee 190 and a house fly 330.

Wing Muscles.—The base of a wing projects into the thoracic cavity and serves for the insertion of the direct muscles of flight. Regarding the wing as a lever (Fig. 77, *A*) with the fulcrum at *p*, it is easy to understand how the contraction of muscle *e* raises the wing and that of muscle *d* lowers it. These muscles are shown diagrammatically in Fig. 77, *B*. Besides these, there are certain muscles of flight which act indirectly upon the wings, by altering the form of the thoracic wall. Thus the muscle *ie* (Fig. 77, *B*) elevates the wing by pulling the tergum toward the sternum; and the longitudinal muscle *id* depresses the wing indirectly by arching the tergum of the thorax.

Though up and down movements are all that are necessary for the simplest kind of insect flight, the process becomes complex in proportion to the efficiency of the flight. Thus in dragon flies there are nine muscles to each wing: five depressors, three elevators and one adductor. The earlier accounts of the mechanics of flight by Marey and others have been modified and improved upon by Stellwaag and by Ritter, whose modern methods of investigation have added considerably to our knowledge of the subject. These later authors have shown, particularly, the parts played by the thoracic sclerites during flight.

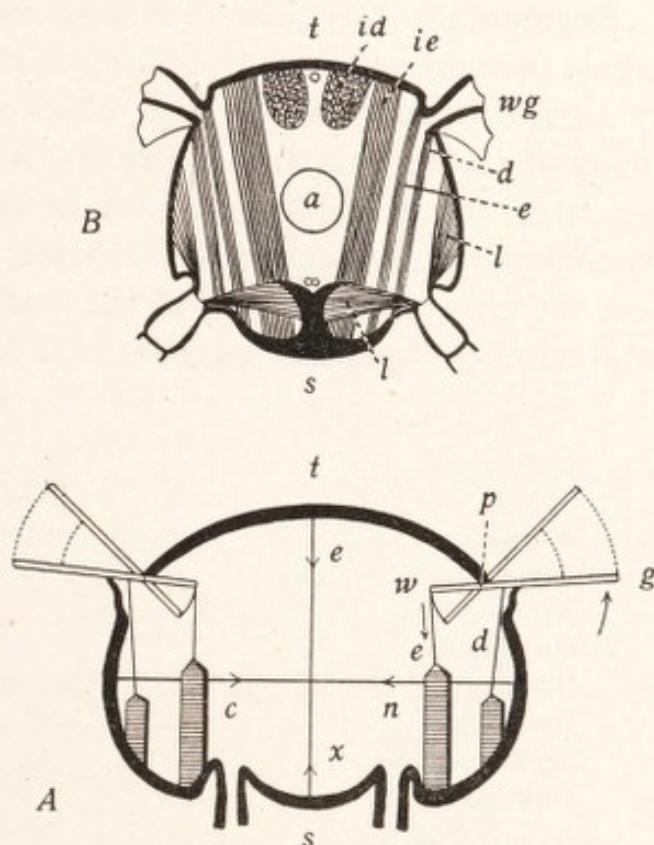


FIG. 77.—*A*, diagram to illustrate the action of the wing muscles of an insect. *B*, diagram of wing muscles. *a*, alimentary canal; *cn*, muscle for contracting the thorax, to depress the wings; *d*, depressor of wing; *e*, elevator of wing; *ex*, muscle for expanding the thorax, to elevate the wings; *id*, indirect depressor; *ie*, indirect elevator; *l*, leg muscle; *p*, pivot, or fulcrum; *s*, sternum; *t*, tergum; *wg*, wing.—After GRABER.

The development of aviation was due largely to thorough studies of the flight of birds and insects.

Abdomen.—The chief functions of the abdomen are respiration and reproduction, to which should be added digestion. The abdomen as a whole has undergone less differentiation than the thorax and presents a simpler and more primitive segmentation.

Segments.—A typical abdominal segment bears a dorsal plate, or *tergum* (*notum*) and a ventral plate, or *sternum*, the two being connected by a pair of *pleural membranes*, which facilitate the respiratory movements of the tergum and sternum. Abdominal tergites and sternites are often termed *urotergites* and *urosternites*, respectively. Most of the abdominal segments have *spiracles*, one on each side, situated in or near the pleural membranes of the first seven or eight segments. The total number of pairs of spiracles is as follows:

	THORACIC	ABDOMINAL	TOTAL
<i>Campodea</i>	2	1	3
<i>Japyx</i> ¹	4	7	11
<i>Machilis</i>	2	7	9
<i>Lepisma</i>	2	8	10
<i>Nicoletia</i>	2	8	10
Orthoptera.....	2	8	10
Odonata.....	2	8	10
Heteroptera.....	2	6(7)	8(9)
Lepidoptera.....	2	7	9
Diptera.....	2	7	9

¹ *Japyx* actually has four thoracic and seven abdominal spiracles, as described and illustrated by Grassi (1888), Willem (1900) and Verhoeff (1904); a study of their figures indicates, however, that the spiracles may have migrated forward, and that the fourth thoracic pair (there being two pairs in the metathorax) belongs morphologically to the first abdominal segment.

Number of Abdominal Segments.—Though only ten abdominal segments are evident in many adult insects and many larvæ as well, the typical number is eleven, and the maximum twelve. In embryos of Thysanura, Orthoptera, Ephemerida, Odonata, Coleoptera and Hymenoptera, eleven abdominal neuromeres (primitive ganglia) have been found by Heymons and others; each neuromere representing a segment; and the twelfth segment is present as a *telson*, a terminal segment containing the anus, but without a neuromere and never bearing a pair of appendages. This telson is present also in the adults of some generalized insects, as Orthoptera. In the more specialized orders, ten may usually be distinguished, with more or less difficulty, though the number is apparently, and in some cases actually, less owing to modifications of

the base of the abdomen in relation to the thorax, but especially to modifications of the extremity of the abdomen, for sexual purposes.

Modifications.—In aculeate Hymenoptera the first segment of the abdomen has been transferred to the thorax, where it is known as the *propodeum*, or *median segment*; in other words, what appears to be the first abdominal segment is actually the second; this, as in bees and wasps, often forms a petiole, which enables the sting to be applied in almost any direction. In Cynipidæ the tergum of segment two or three occupies most of the abdominal mass, the remaining segments being reduced and inconspicuous. The terminal segments of the abdomen often telescope into one another, as in many Coleoptera and Hymenoptera (Chrysididæ), or undergo other modifications of form and position which obscure the segmentation. As to the number of evident (not actual) abdominal segments, Coleoptera show five or six ventrally and seven or eight dorsally; Lepidoptera, seven in the female and eight in the male; Diptera, nine (male Tipulidæ) or only four or five; and Hymenoptera, nine (Tenthredinidæ) or as few as three (Chrysididæ). In the larvæ of these insects, nine or ten abdominal segments are usually distinguishable, though the tenth is frequently modified, being in caterpillars united with the ninth.

Appendages.—Rudimentary abdominal limbs occur in Thysanura (*Machilis*, Fig. 78). Functional abdominal legs do not occur in adult insects, but in larvæ the abdominal *rolegs* (Fig. 66) are homologous with the thoracic legs and the other paired segmental appendages, as the embryology shows. The embryo of *Æcanthus*, according to Ayers, has ten pairs of abdominal appendages (Fig. 199), equivalent to the thoracic legs. Most of these embryonic abdominal appendages are only transitory, but the last three pairs frequently persist to form the genitalia, as in Orthoptera (to which order *Æcanthus* belongs). In

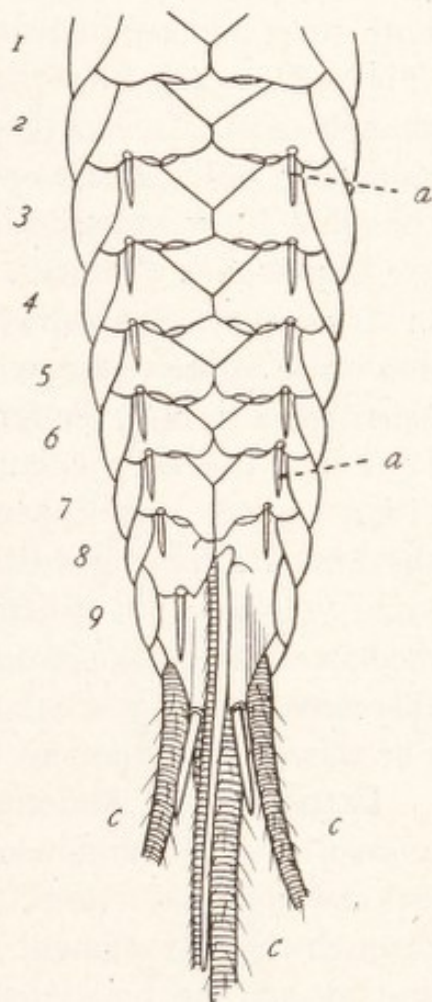


FIG. 78.—Ventral aspect of the abdomen of a female *Machilis maritima*, to show rudimentary limbs (*a*) of segments two to nine. (The left appendage of the eighth segment is omitted.) *c, c, c*, lateral cerci and median pseudocercus.—After OUDEMANS.

Collembola, the embryo has paired abdominal limbs, and those of the first abdominal segment eventually unite to form the peculiar *ventral tube* (Fig. 13) of these insects, while those of the fourth segment form the characteristic leaping organ, or *furcula*, and those of the third, the *tenaculum*.

Cerci.—In many of the more generalized insects the abdomen bears at its extremity a pair of appendages termed *cerci*. These occur in both sexes and are frequently long and multiarticulate, as in Thysanura (Figs. 78, 10, 11), Plecoptera (Fig. 19) and Ephemera (Figs. 20, B; 86) though shorter in cockroaches and reduced to a single sclerite in Locustidae (Fig. 89). The paired cerci, or *cercopoda* of Packard, are usually though not always associated with the eleventh abdominal segment and are homologous with legs, as Ayers has found in *Æcanthus* and Wheeler in *Xiphidium*. As to their function, the cerci of Thysanura are tactile, and those of the cockroach olfactory, while the cerci of male Locustidae often serve to hold the female during copulation.

The so-called "median cercus" or "filum terminale" of Thysanura (Figs. 11, 78) and Ephemera (Fig. 86) resembles the true cerci of these insects in being multiarticulate and usually long, and in having the same function; but differs from these morphologically in arising as a median dorsal prolongation of the eleventh abdominal segment; being therefore not equivalent to one of the paired segmental appendages. For this median filament the term *pseudocercus* is appropriate.

Extremity of Abdomen.—Various modifications of the terminal segments of the abdomen occur for the purposes of defecation and especially reproduction. The anus, dorsal in position, opens always through the last segment and is often shielded above by a *suranal plate* and on each side by a *lateral plate*. The genital orifice is always ventral in position and occurs commonly on the ninth abdominal segment, though there is some variation in this respect. The external, or accessory, organs of reproduction are termed the *genitalia*.

Female Genitalia.—In Neuroptera, Coleoptera, Lepidoptera and Diptera the vagina simply opens to the exterior or else with the anus into a common chamber, or *cloaca*. Often, as in *Cerambyx* (Fig. 79) and *Dasyneura* (Fig. 80) the attenuated distal segments of the abdomen serve the purpose of an ovipositor; thus in Itonididae, the terminal segments, telescoped into one another when not in use, form when extruded a lash-like organ exceeding frequently the remainder of the body in length.

A true *ovipositor* occurs in Thysanura, Orthoptera, Odonata, Hemip-

tera, Hymenoptera and some other orders of insects. The ovipositor consists essentially of three pairs of valves, or *gonapophyses*—a dorsal, a ventral and an inner pair. The two inner valves form a channel through which the eggs are conveyed. In Tettigoniidæ (Fig. 81) the three

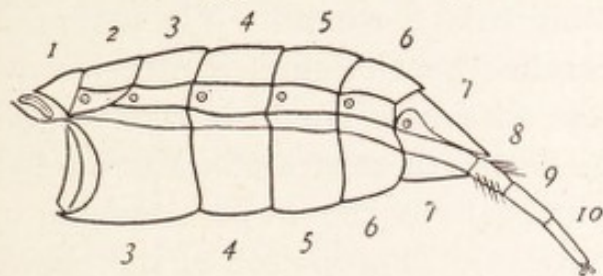


FIG. 79.—Abdomen of female beetle, *Cerambyx*, in which the last three segments are used as an ovipositor.—After KOLBE.

valves of each side are held together by tongues and grooves, which, however, permit sliding

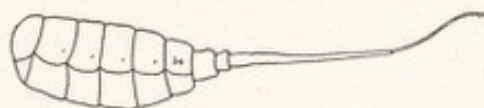


FIG. 80.—Abdomen of a female midge, *Dasyneura leguminicola*, to show the pseudo-ovipositor.

movements to take place. Most authorities have found that the gonapophyses belong to the segmental series of paired appendages—are homodynamous with limbs—and pertain commonly to abdominal

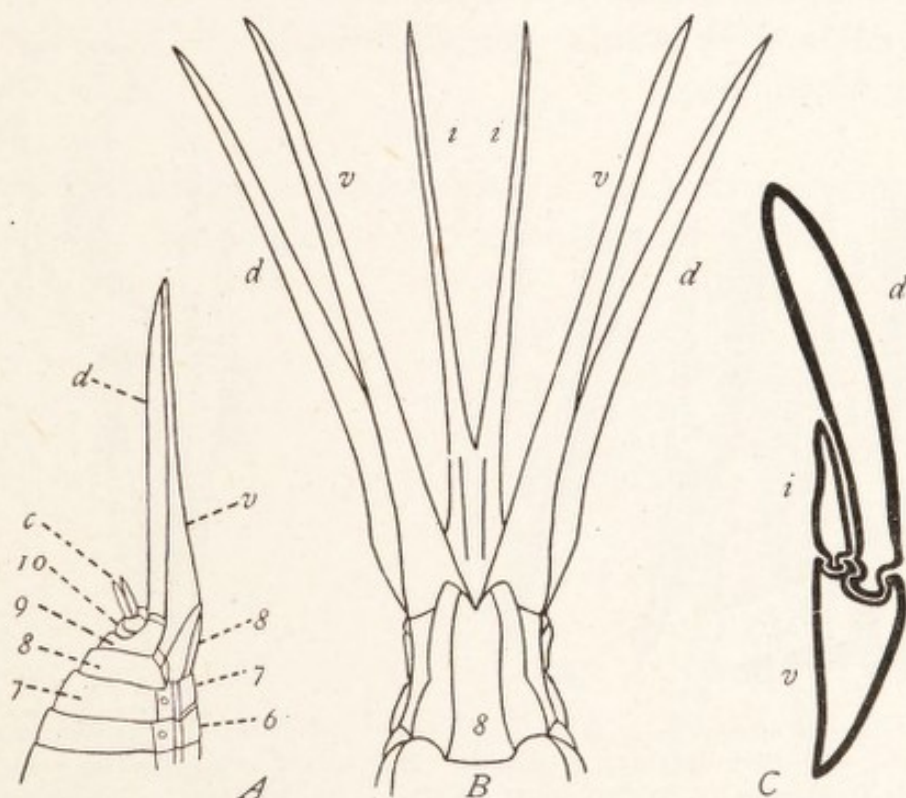


FIG. 81.—Ovipositor of *Phasgonura*.—A, lateral aspect; B, ventral aspect; C, transverse section; c, cerci; d, dorsal valve; i, inner valve; v, ventral valve. The numbers refer to abdominal segments.—After KOLBE and DEWITZ.

segments eight, nine and ten; though there are different views in regard to this.

The ovipositor attains its greatest complexity in Hymenoptera, in which it becomes modified for sawing, boring or stinging. In *Sirex* (Fig.

82) the inner valves are united; in *Apis* the dorsal valves are represented by a pair of *palpi*, the inner valves unite to form the *sheath* (Fig. 83, *B*), and the ventral two form the *darts*, each of which has ten barbed teeth



FIG. 82.—Cross-section of the ovipositor of *Sirex*. *c*, channel; *d*, *d*, dorsal valves; *i*, united inner valves; *v*, *v*, ventral valves.—After TASCHENBERG

behind its apex, which tend to prevent the withdrawal of the sting from a wound. The action of the sting, as described by Cheshire, is rather complex. Briefly, the sheath serves to open a wound and to guide the darts; these strike in alternately, interrupted at intervals by the deeper plunging of the sheath (Fig. 83, *A*). The poison of the honey bee is secreted by two glands, one acid and the other alkaline. The former (Fig. 84) consists of a glandular region which secretes formic acid, of a reservoir, and a duct that empties its contents into the channel of the sheath. The alkaline gland also opens into the reservoir. It is said that both fluids are necessary for a deadly effect; and that in insects which simply paralyze their prey, as the solitary wasps, the alkaline glands are functionless.

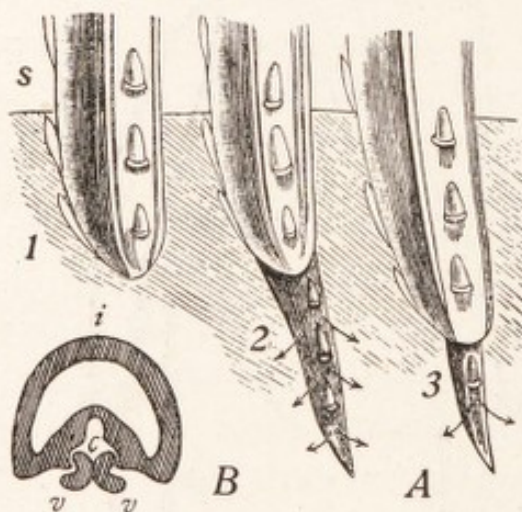


FIG. 83.—Sting of honey bee. *A*, 1, 2, 3, positions in three successive thrusts; *s*, sheath. *B*, cross-section; *c*, channel; *i*, united inner valves, forming the sheath; *v*, *v*, ventral valves, or darts.—*A*, after CHESHIRE; *B*, after FENGER.

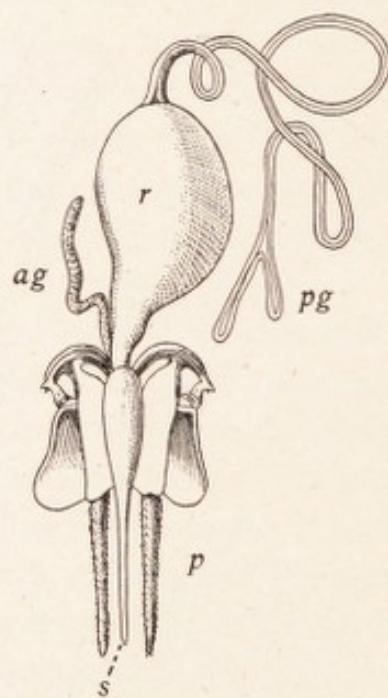


FIG. 84.—Sting and poison apparatus of honey bee. *ag*, accessory gland; *p*, palpus; *pg*, poison gland (formic acid); *r*, reservoir; *s*, sting.—After KRAEPELIN.

Male Genitalia.—The *penis* may be hollow or else solid, and in the latter case the contents of the ejaculatory duct are spread upon its surface. Morphologically, the male gonapophyses correspond to those of the female. The penis (Fig. 85) represents the two inner valves of the ovipositor and is frequently enclosed by one or two pairs of valves.

In Ephemera the two inner valves are partly or entirely separate from each other, forming two intromittent organs (Fig. 86).

In male Odonata, the ejaculatory duct opens on the ninth abdominal segment, but the copulatory organ is placed on the under side of the second segment, to which the spermatozoa are transferred by the bending of the abdomen. At copulation, the abdominal claspers of the male grasp the neck of the female, and the latter bends her abdomen forward until the tip reaches the peculiar copulatory apparatus of the male.

The *claspers* of the male consist of a single pair, variously formed. They are present in Ephemera, Neuroptera, Trichoptera, Lepidoptera (Fig. 87), Diptera and some Hymenoptera, though not in Coleoptera, and often afford good specific characters, as in Odonata. In butterflies of the genus *Thanaos*, the claspers are peculiar in being strongly asymmetrical. In Odonata (Fig. 88, *A*) and Orthoptera (Fig. 89, *A*) the superior appendages of the male often serve as claspers.

In many insects the tergum of the last abdominal segment forms a small *suranal plate* (Fig. 89, *B*, *sp*); this sometimes supplements the claspers of the male in their function, as in Lepidoptera (Fig. 87, *A*, *s*).

2. INTEGUMENT

Insects excel all other animals in respect to adaptive modifications of the integument. No longer a simple limiting membrane, the integu-

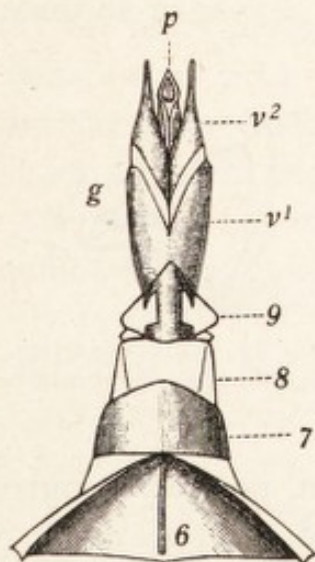


FIG. 85.—Extremity of abdomen of a male beetle, *Hydrophilus*, ventral aspect. *g*, genitalia; *p*, penis; *v*¹, *v*², pairs of valves enclosing the penis; 6-9, sterna of abdominal segments.—After KOLBE.

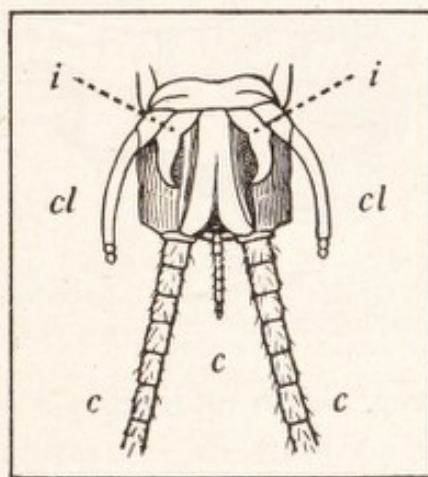


FIG. 86.—Extremity of abdomen of a male May fly, *Hexagenia variabilis*, ventral aspect. *c*, *c*, *c*, cerci and pseudocercus (median); *cl*, *cl*, claspers; *i*, *i*, intromittent organs.

ment has become hardened into an external skeleton, evaginated to form manifold adaptive structures, such as hairs and scales, and

invaginated, along with the underlying cellular layer, to make glands of various kinds.

Chitin.—The skin, or *cuticula*,¹ of an insect differs from that of a worm, for example, in being thoroughly permeated with a peculiar substance known as *chitin*—the basis of the arthropod skeleton. This is a

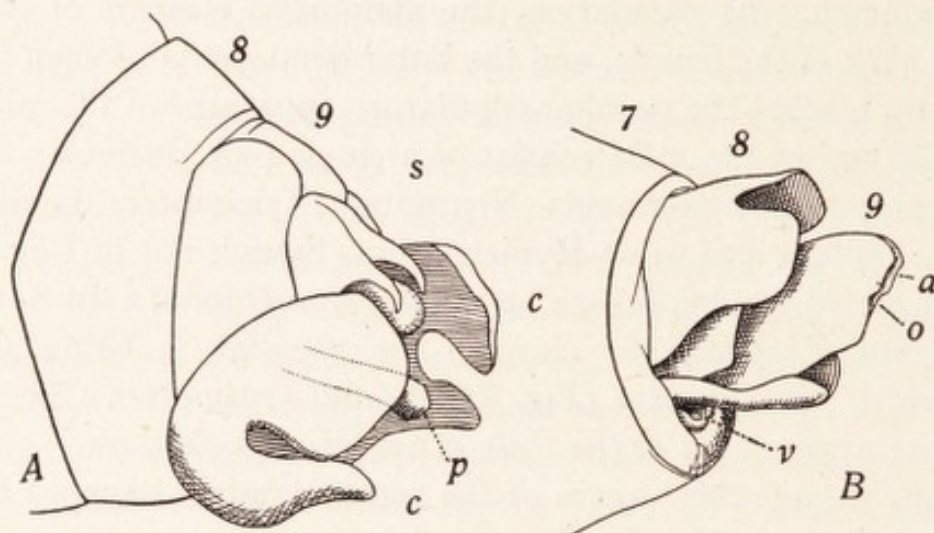


FIG. 87.—Genitalia of a moth, *Samia cecropia*. A, male; B, female; a, anus; c, c, claspers; o, opening of common oviduct; p, penis; s, uncus (the doubly hooked organ); v, vestibule, into which the vagina opens. The numbers refer to abdominal segments.

substance of remarkable stability, for it is unaffected by almost all ordinary acids and alkalis, though it is soluble in sodic or potassic hypochlorite (respectively, Eau de Labarraque and Eau de Javelle) and yields to boiling sulphuric acid. If kept for a year or so under water,



FIG. 88.—Terminal abdominal appendages of a dragon fly, *Plathemis trimaculata*. A, male; B, female. i, inferior appendage; s, s, superior appendages. The numbers refer to abdominal segments.

however, chitin undergoes a slow dissolution, possibly a putrefaction, which accounts in a measure for the rapid disappearance of insect skeletons in the soil (Miall and Denny). By boiling the skin of an insect in potassic hydroxide it is possible to dissolve away the cuticular framework, leaving fairly pure chitin, without destroying the organized

¹ The *cuticula* of an insect should be distinguished from the *cuticle* of a vertebrate, the former being a hardened fluid, while the latter consists of cells themselves, in a dead and flattened condition.

form of the integument, though less than half the weight of the integument is due to chitin. The formula of chitin is given as $C_9H_{15}NO_6$ or $C_{18}H_{30}NO_{12}$ by Krukenberg, and many adopt the formula $C_{15}H_{26}N_2O_{10}$; though no two chemists agree as to the exact proportions of these elements, owing probably to variations in the substance itself in differ-

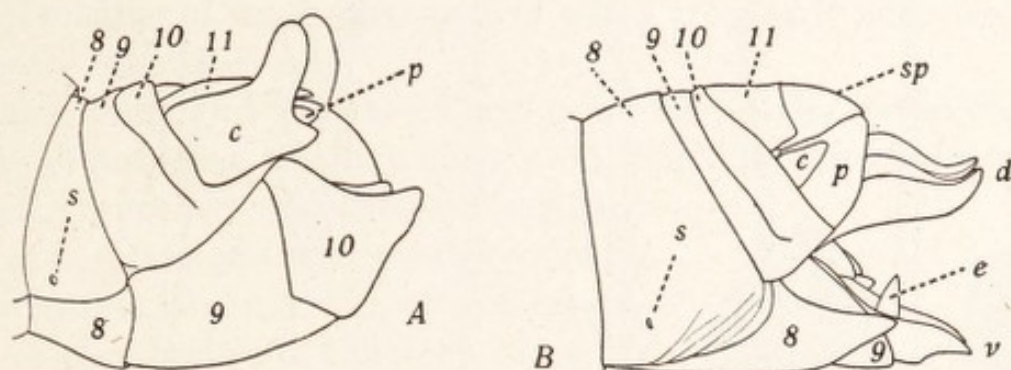


FIG. 89.—Extremity of the abdomen of a grasshopper, *Melanoplus differentialis*. A, male; B, female. The terga and sterna are numbered. c, cercus; d, dorsal valves of ovipositor; e, egg guide; p, podical plate; s, spiracle; sp, suranal plate; v, ventral valves of ovipositor.

ent insects or even in the same species of insect. Iron, manganese and certain pigments also enter into the composition of the integument.

Chitin is not peculiar to arthropods, for it has been detected in the setæ and pharyngeal teeth of annelid worms, the shell of *Lingula* and the pen of the cuttle fish (Krukenberg).

The chitinous integument (Fig. 90) of most insects consists of two layers: (1) an outer layer, homogeneous, dense, without lamellæ or pore canals, and being the seat of the cuticular colors; (2) an inner layer, "thickly pierced with pore canals, and always in layers of different refractive indices and different stainability." (Tower.) These two layers, respectively *primary* and *secondary* cuticula, are radically different in chemical and physical properties. Each layer arises as a fluid secretion from the hypodermis cells, the primary cuticula being the first to form and harden.

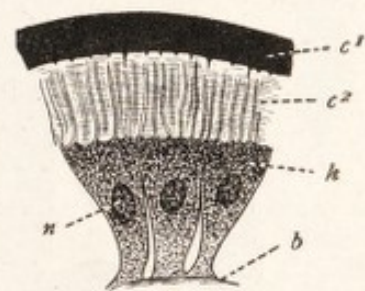


FIG. 90.—Section through integument of a beetle, *Chrysobothris*. b, basement membrane; c¹, primary cuticula; c², secondary cuticula; h, hypodermis cell; n, nucleus.—After TOWER.

The fluid that separates the old from the new cuticula at ecdysis is poured over the hypodermis by certain large special cells, which, according to Tower, "are not true glands, but the setigerous cells which, in early life, are chiefly concerned with the formation of the hairs upon the body; but upon the loss of these, the cell takes on the function of secreting the exuvial fluid, which is most copious at

pupation. These cells degenerate in the pupa, and take no part in the formation of the imaginal ornamentation."

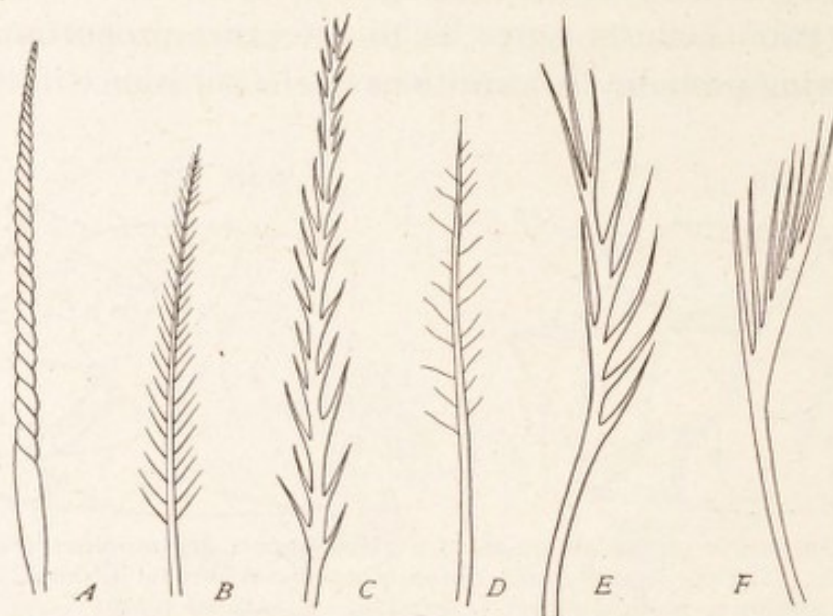


FIG. 91.—Modifications of the hairs of bees. A, B, *Megachile*; C, E, F, *Colletes*; D, *Chelostoma*.—After SAUNDERS.

Histology.—The chitinous cuticula owes its existence to the activity of the underlying layer of *hypodermis* cells (Fig. 90), a single layer,

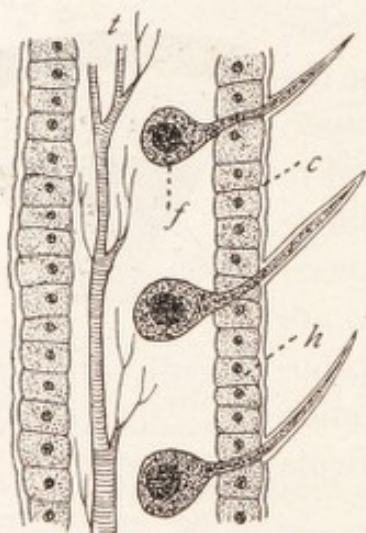


FIG. 92.—Section of antenna of a moth, *Saturnia*, to show developing hairs. c, cuticula; f, formative cell, or trichogen, of hair; h, hypodermis; t, trachea.—After SEMPER.

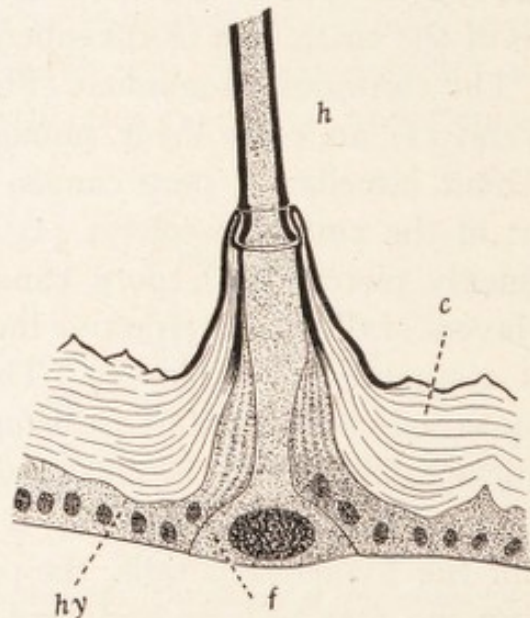


FIG. 93.—Radial section through the base of a hair of a caterpillar, *Pieris rapæ*. c, cuticula; f, formative cell, or trichogen; h, hair; hy, hypodermis.

ectodermal in origin. These cells, distinct in embryonic and often in early larval life, subsequently become confluent by the disappearance of the intervening cell walls, though each cell is still indicated by its

nucleus. The cells are limited outwardly by the cuticula and inwardly by a delicate, hyaline *basement membrane*; they contain pigment granules, fat-drops, etc.

Externally the cuticula may be smooth, wrinkled, striate, granulate, tuberculate, or sculptured in numberless other ways; it may be shaped into all manner of structures, some of which are clearly adaptive, while others are unintelligible.

Hairs, Setæ and Spines.—These occur universally, serving a great variety of purposes; they are not always simple in form, but are often toothed, branched or otherwise modified (Fig. 91). Hairs and bristles are frequently tactile in function, over the general integument or else locally; or olfactory, as on the antennæ of moths; or occasionally auditory, as on the antennæ of the male mosquito; these and other sensory modifications are described beyond. The hairy clothing of some hibernating caterpillars (as *Isia isabella*) probably protects them from sudden changes of temperature. Hairs and spines frequently protect an insect from its enemies, especially when these structures are glandular and emit a malodorous, nauseous or irritant fluid. Glandular hairs on the pulvilli of many flies, beetles, etc., enable these insects to walk on slippery surfaces. The twisted or branched hairs of bees serve to gather and hold pollen grains; in short, these simple structures exhibit a surprising variety of adaptive modifications, many of which will be described in connection with other subjects.

A hair arises from a modified hypodermis cell, *formative cell* or *trichogen* (Fig. 92), the contents of which extend through a pore canal into the interior of the hair (Fig. 93); sometimes, to be sure, as in glandular or sensory hairs, the hair cell is multinucleate, representing, therefore, as many cells as there are nuclei. The wall of a hair is continuous with the general cuticula and at moulting each hair is stripped off with the rest of the cuticula, leaving in its place a new hair, which has been forming inside the old one.

Scales.—Besides occurring throughout the order Lepidoptera and in numerous Trichoptera, scales are found in many Thysanura and

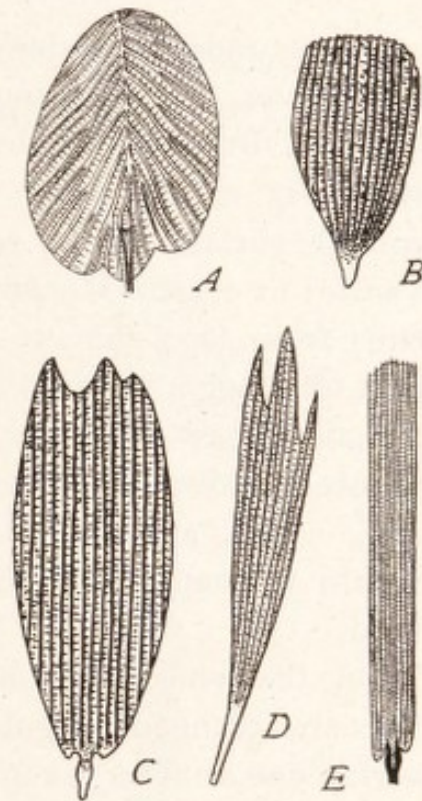


FIG. 94.—Various forms of scales. A, E, thysanuran, *Machilis*; B, beetle, *Anthrenus*; C, butterfly, *Pieris*; D, moth, *Limacodes*.

Collembola, several families of Coleoptera (including Dermestidæ, Cerambycidæ and Curculionidæ), a few Diptera and a few Psocidæ.

Though diverse in form (Fig. 94), scales are essentially flattened sacs having at one end a short pedicel for attachment to the integument. The scales usually bear markings, which are more or less characteristic



FIG. 95.—Cross-section of scale of *Anosia*.—After MAYER.

of the species; these markings, always minute, are in some species so exquisitely fine as to test the highest powers of the microscope; the scales of certain Collembola (*Lepidocyrtus*, etc.) have long been used, under the name of "Podura" scales, to test the resolving power of objectives, for which purpose they are excelled only by some of the diatoms. Butterfly scales are marked with parallel longitudinal ridges (Fig. 94, C), which are confined almost entirely to the upper, or exposed, surface of the scale (Fig. 95) and number from 33 or less (*Anosia*) to 1,400 (*Morpho*) to each scale, the striae being in the latter genus from .002 mm. to .0007 mm. apart (Kellogg); between these longitudinal ridges may be discerned delicate transverse markings. Internally, scales are hollow and often contain pigments derived from the blood.

On the wing of a butterfly the scales are arranged in regular rows and overlap one another, as in Fig. 96; in the more primitive moths and in Trichoptera, however, their distribution is rather irregular.

A scale is the equivalent of a hair, for (1) a complete series of transitions from hairs to scales may be found on a single individual (Fig. 97); and (2) hairs and scales agree in their manner of development, as shown by Semper, Schäffer, Spuler, Mayer and others. Both hairs and scales arise as processes from enlarged hypodermis cells, or *formative cells* (Fig. 98). The scale at first contains protoplasm, which gradually withdraws, leaving short chitinous strands to hold the two membranes of the scale together.

Uses of Scales.—Among Thysanura and Collembola, scales occur only on such species as live in comparatively dry situations, from which

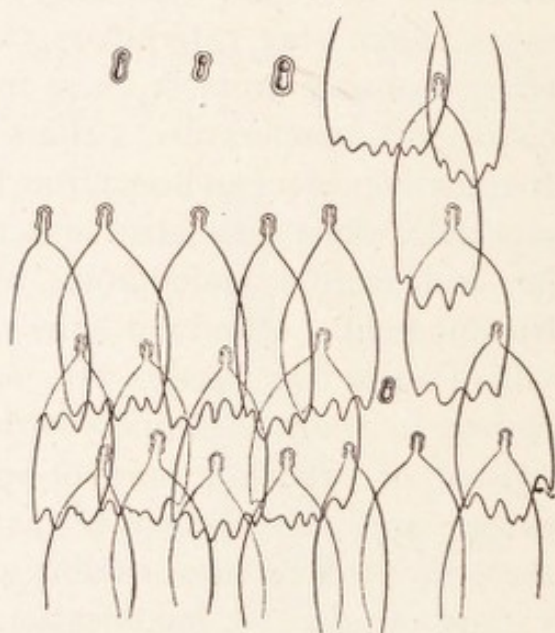


FIG. 96.—Arrangement of scales on the wing of a butterfly, *Papilio*.

it may be inferred that the scales serve to retard the evaporation of moisture through the delicate integument of these insects. This inference is

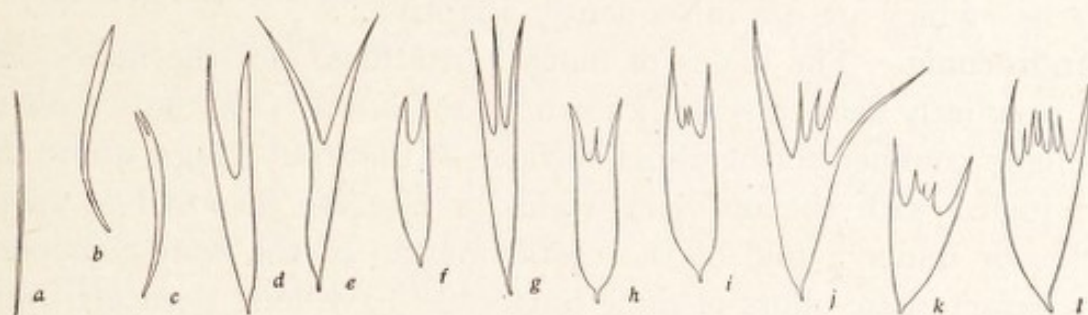


FIG. 97.—Hairs and scales of a moth, *Samia cecropia*.

supported by the fact that none of the scaleless Collembola can live long in a dry atmosphere; they soon shrivel and die even under conditions

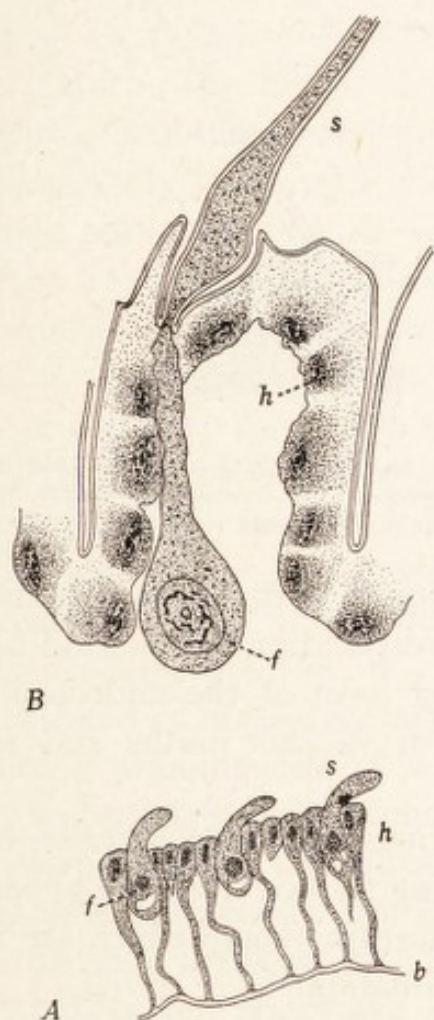


FIG. 98.—Development of butterfly scales. A, *Vanessa*; B, *Anosia*. b, basement membrane; f, formative cell; h, hypodermis; s, scale.—After MAYER.



FIG. 99.—Androconia of butterflies. A, *Pieris rapæ*; B, *Everes comyntas*.

of dryness which the scaled species are able to withstand. In Lepidoptera the scales are possibly of some value as a mechanical protection;

they have no influence upon flight, as Mayer has proved, and appear to be useful chiefly as a basis for the development of color and color patterns—which are not infrequently adaptive.

Androconia.—The males of many butterflies, and the males only, have peculiarly shaped scales known as *androconia* (Fig. 99); these are commonly confined to the upper surfaces of the front wings, where they are mingled with the ordinary scales or else are disposed in special patches or under a fold of the costal margin of the wing (*Thanaos*). The characteristic odors of male butterflies have long been attributed to these androconia, and M. B. Thomas has found that the scales arise

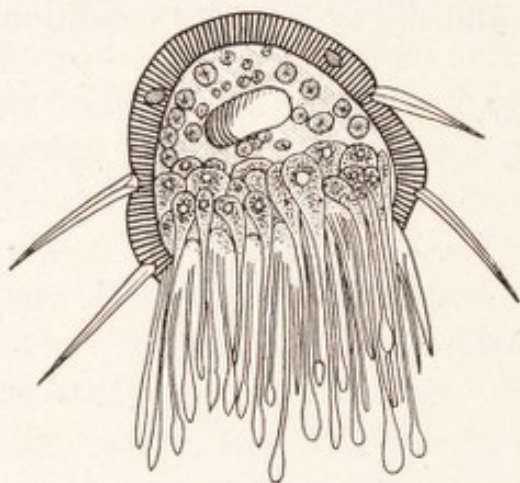


FIG. 100.—Section across tarsus of a beetle, *Hylobius*, to show bulbous glandular hairs.—After SIMMERMACHER.

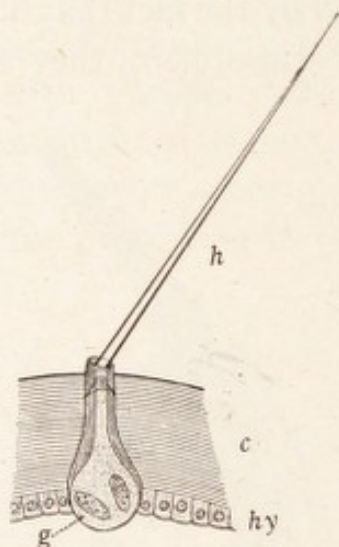


FIG. 101.—Stinging hair of a caterpillar, *Gastropacha*. *c*, cuticula; *g*, gland cell; *h*, hair; *hy*, hypodermis.—After CLAUS.

from glandular cells, which doubtless secrete a fluid that emanates from the scale as an odorous vapor, the evaporation of the fluid being facilitated by the spreading or branching form of the androconium. Similar scales occur also on the wings of various moths and some Trichoptera (*Mystacides*).

Glands.—A great many glands of various form and function have been found in insects. Most of these, being formed from the hypodermis, may logically be considered here, excepting some which are intimately concerned with digestion or reproduction.

Glandular Hairs and Spines.—The presence of adhesive hairs on the empodium of the foot of a fly enables the insect to walk on a smooth surface and to walk upside down; these *tenent hairs* emit a transparent sticky fluid through minute pore canals in their apices. The tenent hairs of *Hylobius* (Fig. 100) are each supplied with a flask-shaped unicellular gland, the glutinous secretion of which issues from the bulbous

extremity of the hair. Bulbous tenent hairs occur also on the tarsi of Collembola, Aphididæ and other insects.

Nettling hairs or spines clothe the caterpillars of certain Saturniidæ (*Automeris*), Liparidæ, etc. These spines (Fig. 101), which are sharp, brittle and filled with poison, break to pieces when the insect is handled and cause a cutaneous irritation much like that made by nettles. In *Lagoa crispata* (Fig. 102) the irritating fluid is secreted, as is usual, by several large hypodermal cells at the base of each spine. These irritating hairs protect their possessors from almost all birds except cuckoos.

Repellent Glands.—The various offensive fluids emitted by insects are also a highly effective means of defense against birds and other insectivorous vertebrates as well as against predaceous insects. The blood itself serves as a repellent fluid in the oil-beetles (Meloidæ) and Coccinellidæ, issuing as a yellow fluid from a pore at the end of the femur. The blood of Meloidæ (one species of which is still used medicinally under the name of "Spanish Fly") contains cantharidine, an extremely caustic substance, which is an almost perfect protection against birds, reptiles and predaceous insects. Coccinellidæ and Lampyridæ are similarly exempt from attack. Larvæ of *Cimbex* when disturbed squirt jets of a watery fluid from glands opening above the spiracles. Many Carabidæ eject a pungent and often corrosive fluid from a pair of anal glands (Fig. 148); this fluid in *Brachinus*, and occasionally in *Galerita janus* and a few other carabids, volatilizes explosively upon contact with the air. When one of these "bombardier-beetles" is molested it discharges a puff of vapor, accompanied by a distinct report, reminding one of a miniature cannon, and this performance may be repeated several times in rapid succession; the vapor is acid and corrosive, staining the human skin a rust-red color. Individuals of a large South American *Brachinus* when seized "immediately began to play off their artillery, burning and staining the flesh to such a degree that only a few specimens could be captured with the naked hand, leaving a mark which remained for a considerable time." (Westwood.)

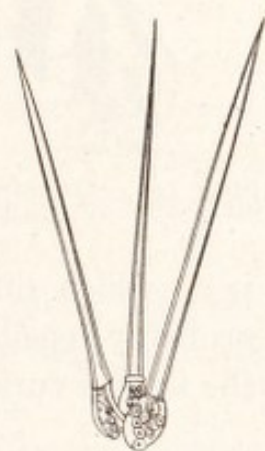


FIG. 102.—Stinging spines of a caterpillar, *Lagoa crispata*.—After PACKARD.

As malodorous insects, Hemiptera are notorious, though not a few hemipterous odors are (apart from their associations) rather agreeable to the human olfactory sense. Commonly the odor is due to a fluid from a mesothoracic gland or glands, opening between the hind coxæ.

Eversible hypodermal glands of many kinds are common in larvæ of Coleoptera and Lepidoptera. The larvæ of *Lina lapponica*, among other Chrysomelidæ, evert numerous paired vesicles which emit a peculiar odor. The caterpillars of our *Papilio* butterflies, upon being irritated, evert from the prothorax a yellow Y-shaped *osmeterium* (Fig.



FIG. 103.—Osmeterium of *Papilio polyxenes*.

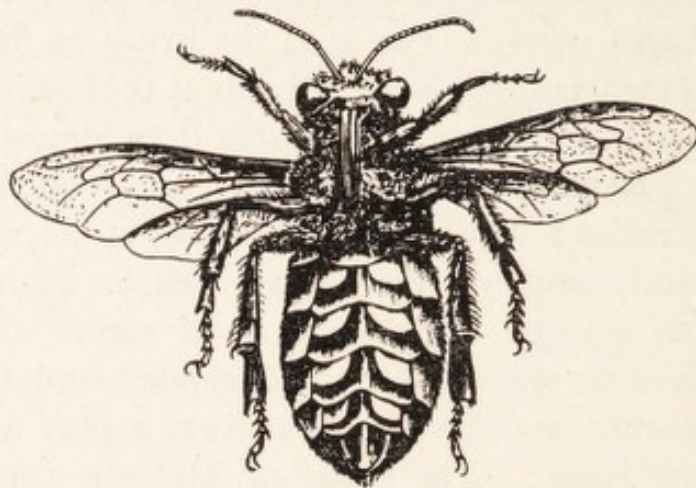


FIG. 104.—Ventral aspect of worker honey bee, showing the four pairs of wax scales.—After CHESHIRE.

103) which diffuses a characteristic but indescribable odor that is probably repellent. The larva of *Cerura* everts from the under side of the neck a curious spraying apparatus which discharges formic acid.

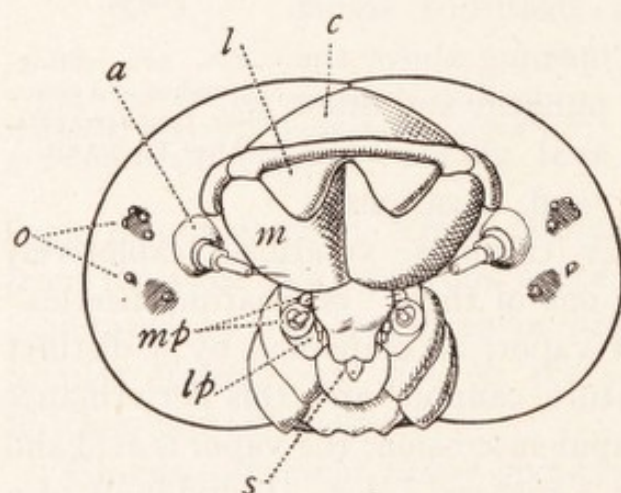


FIG. 105.—Head of caterpillar of *Samia cecropia*. *a*, antenna; *c*, clypeus; *l*, labrum; *lp*, labial palpus; *m*, mandible; *mp*, maxillary palpi; *o*, ocelli; *s*, spinneret.

Alluring Glands.—Odors are largely used among insects to attract the opposite sex. The androconia of male butterflies have already been spoken of. Males of *Catocala concumbens* disseminate an alluring odor from scent tufts on the middle legs. Female saturniid moths (as *cecropia* and *promethea*) entice the males by means of a characteristic odor emanating from the extremity of the abdomen. In lycænid caterpillars, an eversible

sac on the dorsum of the seventh abdominal segment secretes a sweet fluid, for the sake of which these larvæ are sought out by ants.

Wax Glands.—Wax is secreted by insects of several orders, but especially Hymenoptera and Hemiptera. In the worker honey bee the wax exudes from unicellular hypodermal glands and appears on the

under side of the abdomen as four pairs of wax scales (Fig. 104), on the last four of the six evident segments of the abdomen (Dreyling). Plant lice of the genus *Schizoneura* owe their woolly appearance to dense white filaments of wax, which arise from glandular hypodermal cells. In scale insects, waxen threads, emerging from cuticular pores, become matted together to form a continuous shield over and often under the insect itself, the cast skins often being incorporated into this waxen scale. The wax glands in Coccidæ are simply enlarged hypodermis cells.

Some coccids produce wax in quantities sufficient for commercial use. Thus species of *Ceroplastes* (and certain fulgorids as well) in India and China yield a white wax that is used for making candles and for other purposes.

The lac-insect, *Tachardia lacca*, of India, a scale insect living on more than ninety species of trees and shrubs (*Acacia*, *Ficus*, *Zizyphus*, etc.), furnishes the lac from which shellac, lacquer and other varnishes are made. The raw lac is the scale, or shell, of the female insect (the male producing scarcely any lac) and consists of a yellow to reddish brown resinous exudation containing considerable wax, along with the cast skins of the insect. From this material the commercial products are extracted.

Silk Glands.—Larvæ of very diverse orders spin silk, for the purpose of making cocoons, webs, cases, and supports of one kind or another. Silk glands, though most characteristic of Lepidoptera and Trichoptera, occur also in the cocoon-spinning larvæ of not a few Hymenoptera (saw flies, ichneumons, wasps, bees, etc.), in Diptera (Itonididæ), Siphonaptera, Neuroptera (Chrysopidæ, Myrmeleonidæ), and in various larvæ whose pupæ are suspended from a silken support, as in the coleopterous families Coccinellidæ and Chrysomelidæ (in part) and the dipterous family Syrphidæ, as well as most diurnal Lepidoptera.

The silk glands of caterpillars are homologous with the true salivary glands of other insects, opening as usual through the hypopharynx, which is modified to form a spinning organ, or *spinneret* (Fig. 105). The silk glands of Lepidoptera are a pair of long tubes, one on each side of the body, but often much longer than the body and consequently convoluted. Thus in the silk worm (*Bombyx mori*) they are from four to five times as long as the body and in *Telea polyphemus*, seven times as long. In the silk worm the convoluted glandular portion of each tube (Fig. 106) opens into a dilatation, or silk reservoir, which in turn empties into a slender duct, and the two ducts join into a short common

duct, which passes through the tubular spinneret. Two divisions of the spinning tube are distinguished: (1) a posterior muscular portion, or *thread-press* and (2) an anterior *directing tube*. The thread-press combines the two streams of silk fluid into one, determines the form of the silken thread and arrests the emission of the thread at times, besides having other functions. The silk fluid hardens rapidly upon exposure to the air; about fifty per cent. of the fluid is actual silk substance and the remainder consists of protoplasm and gum, with traces of wax, pigment, fat and resin.

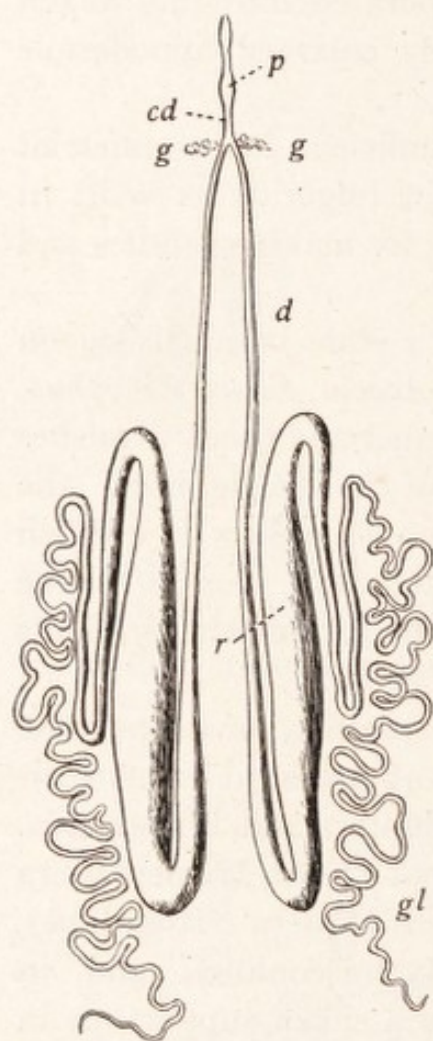


FIG. 106.—Silk glands of the silk worm, *Bombyx mori*. *cd*, common duct; *d*, one of the paired ducts; *g*, *g*, Filippi's glands; *gl*, gland proper; *p*, thread press; *r*, reservoir.



FIG. 107.—Sections of silk gland of the silk worm. *A*, radial; *B*, transverse. *b*, basement membrane; *i*, intima; *s*, glandular cell with branched nucleus.—After HELM.

A transverse or radial section of a silk gland shows a layer of glandular epithelial cells, with the usual intima and basement membrane (Fig. 107); the cells are remarkably large and their nuclei are often branched; the intima is distinctly striated, from the presence of pore-canals. The glands arise as evaginations of the pharynx (ectodermal) and the chitinous intima of each gland is cast at each moult, along with the general integument.

The silk glands of caddis worms (Trichoptera) are essentially like those of caterpillars (Lepidoptera) but the glands of Neuroptera (*Chrysopa*, *Myrmeleon*, etc.) Coccinellidæ, Chrysomelidæ and Syrphidæ, which open into the rectum, are morphologically quite different from those of Lepidoptera.

3. MUSCULAR SYSTEM

The number of muscles possessed by an insect is surprisingly large. A caterpillar, for example, has about two thousand.

The muscles of the trunk are segmentally arranged—most evidently

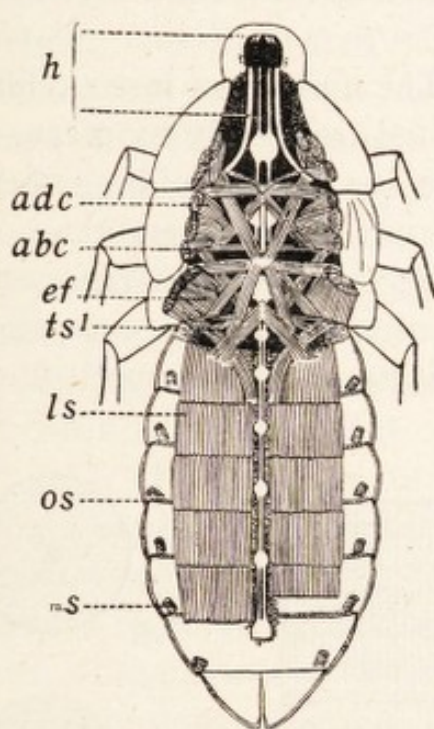


FIG. 108.

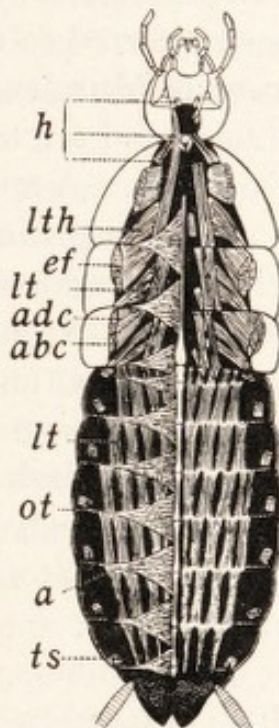


FIG. 109.



FIG. 110.

Muscles of cockroach; of ventral, dorsal and lateral walls, respectively. *a*, alary muscle; *abc*, abductor of coxa; *adc*, adductor of coxa; *ef*, extensor of femur; *h*, head muscles; *ls*, longitudinal sternal; *lt*, longitudinal tergal; *lth*, lateral thoracic; *os*, oblique sternal; *ot*, oblique tergal; *ts*, tergo-sternal; *ts¹*, first tergo-sternal. After MIALl and DENNY.

so in the body of a larva or the abdomen of an imago, where the musculature is essentially the same in several successive segments. In the thoracic segments of an imago, however, the musculature is, at first sight, unlike that of the abdomen, and in the head it is decidedly different; though future studies will doubtless show that the thoracic and cephalic kinds of musculature are only modifications of the simpler abdominal type—modifications brought about in relation to the needs of the legs, wings, mouth parts, antennæ and other movable structures.

The muscular system has been generally neglected by students of insect anatomy; the only comprehensive studies upon the subject being

those of Straus-Dürckheim (1828) on the beetle *Melolontha*; Lyonet (1762), Newport (1834) and Lubbock (1859) on caterpillars; Lubbock and Janet on Hymenoptera; Bauer (1910) on *Dytiscus*; and Berlese (1909-13) on various insects.



FIG. 111.—
Striated muscle
fiber of an insect.

The more important muscles in the body of a cockroach are represented in Figs. 108-110, from Miall and Denny. The *longitudinal sternals* with the *longitudinal tergals* act to telescope the abdominal segments; the *oblique sternals* bend the abdomen laterally; the *tergosternals*, or vertical expiratory muscles, draw the tergum and sternum together. The muscles of the legs and the wings have already been referred to.

Structure of Muscles.—The muscles of insects differ greatly in form and are inserted frequently by means of chitinous tendons. A muscle is a bundle of long fibers, each of which has an outer elastic membrane, or *sarcolemma*, within which are several nuclei; thus the fiber represents several cells, which have become confluent. With rare exceptions ("alary" muscles and possibly a few thoracic muscles) the muscle fibers of an insect present a striated appearance, owing to alternate light and dark bands (Fig. 111), the former being singly refracting, or *isotropic*, and the latter doubly refracting, or *anisotropic*.

The minute structure of these fibers, being extremely difficult of interpretation, has given rise to much difference of opinion. The most plausible view is that of van Gehuchten, Janet and others, who hold that both kinds of dark bands (Fig. 112) consist of highly elastic threads of *spongioplasm* (anisotropic) embedded in a matrix of clear, semi-fluid, nutritive *hyaloplasm* (isotropic). The spongio-plasmic threads of the long bands extend longitudinally and those of the short bands ("Krause's membrane") radially, in respect to the form of the fiber. Moreover, the attenuated extremities of the longitudinal fibrillæ connect with the radial fibrillæ, the points of connection being marked by slight thickenings, or nodes, which go to make up Krause's membrane.

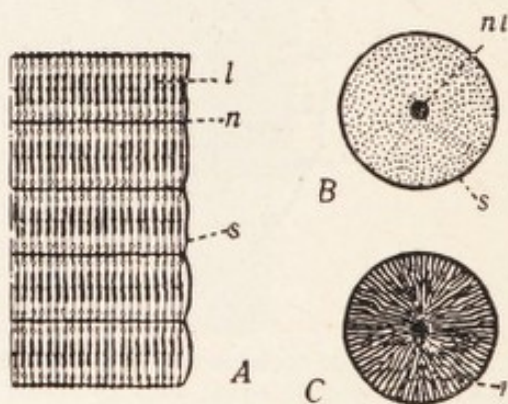


FIG. 112.—Minute structure of a striated muscle fiber. A, longitudinal section; B, transverse section in the region of *l*; C, transverse section in the region of *n*. *l*, longitudinal fibrillæ; *n*, Krause's membrane; *nl*, nucleus; *r*, radial fibrillæ; *s*, sarcolemma.—After JANET.

Under nervous stimulus a muscle shortens and thickens because its component fibers do, and this in turn is attributed to the shortening and thickening of the longitudinal fibrillæ. When the stimulus ceases, the radial fibrillæ, by their elasticity, possibly pull the longitudinal ones back into place. The last word has not been said, however, upon this perplexing subject.

Muscular Power.—The muscular exploits of insects appear to be marvellous beside those of larger animals, though they are often exaggerated in popular writings. The weakest insects, according to Plateau, can pull five times their own weight and the average insect, over twenty times its weight, while *Donacia* (Chrysomelidæ) can pull 42.7 times its weight. As contrasted with these feats, a man can pull in the same fashion but 0.86 of his weight and a horse from 0.5 to 0.83. How are these differences explained?

It is incorrect to say that the muscles of insects are stronger than those of vertebrates, for, as a matter of fact, the contractile force of a vertebrate muscle is greater than that of an insect muscle, other things being equal. The apparently greater strength of an insect in proportion to its weight is accounted for in several ways. The specific gravity of chitin is less than that of bone, though it varies greatly in both substances. Furthermore, the external skeleton permits muscular attachments of the most advantageous kind as compared with the internal skeleton, so that the muscles of insects surpass those of vertebrates as regards leverage. These reasons are only of minor importance, however. Small animals in general appear to be stronger than larger animals (allowing for the differences in weight) for the same reason that a smaller insect has more conspicuous strength than a larger one, when the two are similar in everything except weight. For example: where a bumblebee can pull 16.1 times its own weight, a honey bee can pull 20.2; and where the same bumblebee can carry while flying a load 0.63 of its own weight, the honey bee can carry 0.78. Always, as Plateau has shown, the lighter of two insects is the stronger in respect to external manifestations of muscular force—in the ratio of this muscular strength to its own weight.

To understand this, let us assume that a beetle continues to grow (as never happens, of course). As its weight is increasing so is its strength—but not in the same proportion. For while the weight—say that of a muscle—increases as the cube of a single dimension, the strength of the muscle (depending solely upon the area of its cross-section) is increasing only as the square of one dimension—its diameter. Therefore the

increase in strength lags behind that of weight more and more; consequently more and more strength is required simply to move the insect itself, and less and less surplus strength remains for carrying additional weight. Thus the larger insect is apparently the weaker, though it is actually the stronger, in that its total muscular force is greater.

The writer uses this explanation to account also for the inability of certain large beetles and other insects to use their wings, though these organs are well developed. Increasing weight (due to a larger supply of reserve food accumulated by the larva) has made such demands upon the muscular power that insufficient strength remains for the purpose of flight.

Statements such as this are often seen—a flea can jump a meter, or six hundred times its own length. Almost needless to say, the length of the body is no criterion of the muscular power of an animal.

4. NERVOUS SYSTEM

The central nervous system extends along the median line of the floor of the body as a series of ganglia connected by nerve cords. Typically, there is a ganglion (double in origin) for each primary segment, and the connecting cords, or *commissures*, are paired; these conditions are most nearly realized in embryos and in the most generalized insects—*Thysanura* (Fig. 113). In all adult insects, however, the originally separate ganglia consolidate more or less (Fig. 114) and the commissures frequently unite to form single cords. Thus in *Tabanus* (Fig. 114, C) the three thoracic ganglia have united into a single compound ganglion and the abdominal ganglia are concentrated in the anterior part of the abdomen; in the grasshopper, the nerve cord, double in the thorax, is single in the abdomen. Various other modifications of the same nature occur.

Cephalic Ganglia.—In the head the primitive ganglia always unite to form two compound ganglia, namely, the *brain* and the *subœsophageal ganglion* (disregarding a few anomalous cases in which the latter is said to be absent).

The brain, or *supraœsophageal ganglion* (Fig. 115), is formed by the union of three primitive ganglia, or *neuromeres* (Fig. 57), namely, (1) the *protocerebrum*, which gives off the pair of optic nerves; (2) the *deutocerebrum*, which innervates the antennæ; and (3) the *tritocerebrum*, which in Apterygota bears a pair of rudimentary appendages that are regarded as traces of a second pair of antennæ.

The subœsophageal ganglion (Fig. 115) is always connected with the brain by a pair of nerve cords (*œsophageal commissures*) between which the œsophagus passes. This compound ganglion represents at most four neuromeres: (1) *mandibular*, innervating the mandibles; (2) *superlingual*, found by the author in Collembola, but not yet reported in the less generalized insects; (3) *maxillary*, innervating the maxillæ; (4) *labial*, which sends a pair of nerves to the labium.

The minute structure of the brain, though highly complex, has received considerable study, but will not be described here for the reason that the anatomical facts are of no general interest so long as their physiological interpretation remains obscure.

Sympathetic System.—Lying along the median dorsal line of the œsophagus is a *recurrent*, or *stomatogastric*, nerve (Fig. 116), which arises anteriorly in a *frontal ganglion* and terminates posteriorly in a *stomachic ganglion* situated at the anterior end of the mid intestine. Connected with the recurrent nerve are two pairs of lateral ganglia, the anterior of which innervate the dorsal vessel and the posterior, the tracheæ of the head. The ventral nerve cord may include also a median nerve thread (Fig. 113) which gives off paired transverse nerves to the muscles of the spiracles.

Structure of Ganglia and Nerves.—A ganglion consists of (1) a dense cortex, composed of ganglion cells (Fig. 117), each of which has a large rounded nucleus and gives off usually a single nerve fiber; and (2) a clear medullary portion (*Punksubstanz*) derived from the processes of the cortical ganglion cells and serving as the place of origin of nerve fibrillæ. There are, however, ganglion cells from which processes may pass directly into nerve fibrillæ.

A nerve fiber, in an insect, consists of an *axis-cylinder*, composed of fibrillæ, and an enveloping membrane, or sheath. The axis-cylinder is the transmitting portion and the ganglia are the

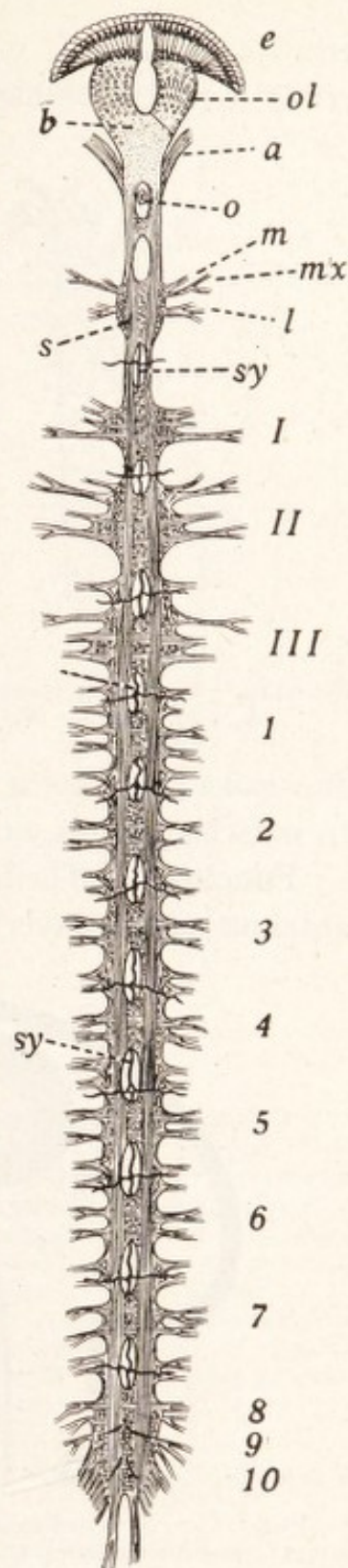


FIG. 113.—Central nervous system of a thysanuran, *Machilis*. The thoracic and abdominal ganglia are numbered in succession. *a*, antennal nerve; *b*, brain; *e*, compound eye; *l*, labial nerve; *m*, mandibular nerve; *mx*, maxillary nerve; *o*, œsophagus; *ol*, optic lobe; *s*, subœsophageal ganglion; *sy*, sympathetic nerve.—After OUDEMANS.

trophic centers, i. e., they regulate nutrition. A nerve is always either *sensory*, transmitting impulses inward from a sense organ; or

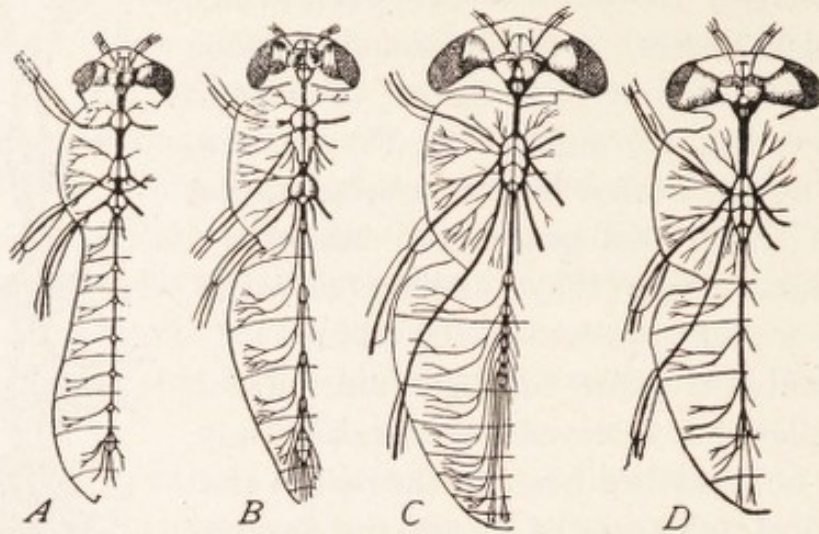


FIG. 114.—Successive stages in the concentration of the central nervous system of Diptera. A, *Chironomus*; B, *Empis*; C, *Tabanus*; D, *Sarcophaga*.—After BRANDT.

else *motor*, conveying stimuli from the central nervous system outward to muscles, glands, or other organs.

Functions.—The brain innervates the chief sensory organs (eyes and antennæ) and converts the sensory stimuli that it receives into motor

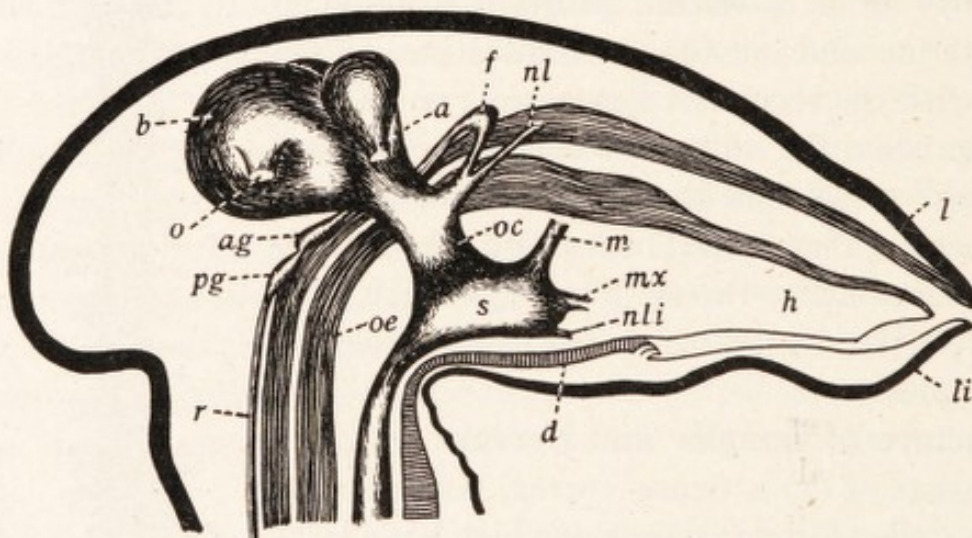


FIG. 115.—Nervous system of the head of a cockroach. a, antennal nerve; ag, anterior lateral ganglion of sympathetic system; b, brain; d, salivary duct; f, frontal ganglion; h, hypopharynx; l, labrum; li, labium; m, mandibular nerve; mx, maxillary nerve; nl, nerve to labrum; nli, nerve to labium; o, optic nerve; oc, oesophageal commissure; oe, oesophagus; pg, posterior lateral ganglion of sympathetic system; r, recurrent nerve of sympathetic system; s, suboesophageal ganglion.—After HOFER.

stimuli, which effect co-ordinated muscular or other movements in response to particular sensations from the environment. The brain is the seat of the will, using the term "will" in a loose sense; it directs locomotor movements of the legs and wings. An insect deprived of its

brain cannot go to its food, though it is able to eat if food be placed in contact with the end-organs of taste, as those of the palpi; furthermore, it walks or flies in an erratic manner, indicating a lack of co-ordination of muscular action.

The subœsophageal ganglion controls the mouth parts, co-ordinating their movements as well as some of the bodily movements.

The thoracic ganglia govern the appendages of their respective segments. These ganglia and those of the abdomen are to a great extent independent of brain control, each of these ganglia being an individual motor center for its particular segment. Thus decapitated insects are still able to breathe, walk or fly, and often retain for several days some power of movement.

In regard to the sympathetic system, it has been shown experimentally that the frontal ganglion controls the swallowing movements and exerts through the stomatogastric nerve a regulative action upon digestion. The dorsal sympathetic system controls the dorsal vessel and the salivary glands, while the ventral sympathetic system is concerned with the spiracular muscles.

5. SENSE ORGANS

For the reception of sensory impressions from the external world, the armor-like integument of insects is modified in a great variety of ways. Though sense

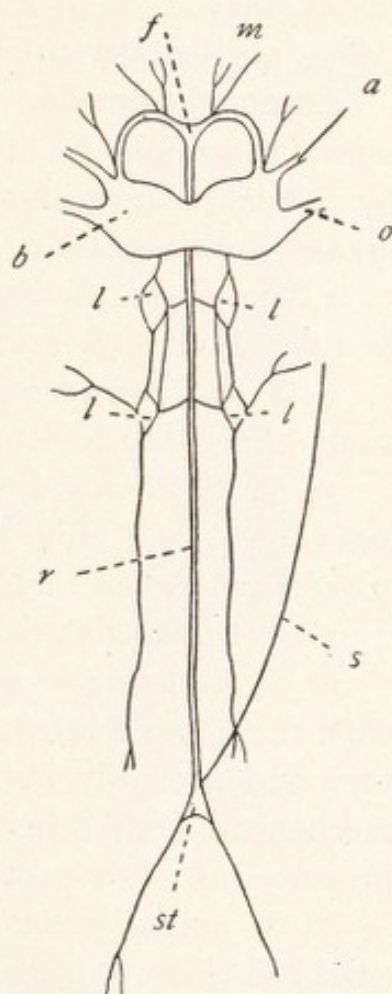


FIG. 116.—Sympathetic nervous system of an insect, diagrammatically represented. *a*, antennal nerve; *b*, brain; *f*, frontal ganglion; *l, l*, paired lateral ganglia; *m*, nerves to upper mouth parts; *o*, optic nerve; *r*, recurrent nerve; *s*, nerve to salivary glands; *st*, stomatogastric ganglion. —After KOLBE.

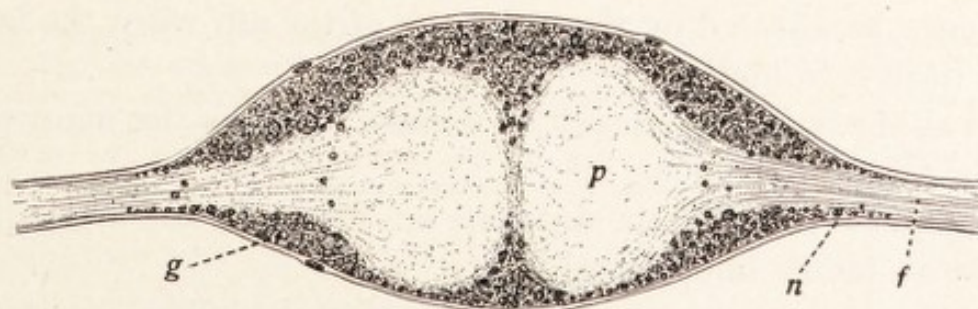


FIG. 117.—Transverse section of an abdominal ganglion of a caterpillar. *f*, nerve fibers; *g*, ganglion cells; *n*, nerve sheath; *p*, Punktsubstanz.

organs of one kind or another may occur on almost any part of an insect, they are most numerous and varied upon the head and its appendages, particularly the antennæ.

Antennal Sensilla.—Some idea of the diversity of form in antennal sense organs may be obtained from Figs. 118–127, taken from a paper by Schenk, whose useful classification of antennal *sensilla*, or sense organs, is here outlined:

1. *Sensillum cæloconicum*—a conical or peg-like projection immersed in a pit (Figs. 118, 119). In all probability olfactory.

2. *S. basiconicum*—a cone projecting above the general surface (Fig. 120). Probably olfactory.

3. *S. styloconicum*—a terminal tooth or peg seated upon a more or less conical base (Fig. 121). Olfactory.

4. *S. chæticum*—a bristle-like sense organ (Fig. 122). Tactile.

5. *S. trichodeum*—a hair-like sense organ (Figs. 123, 124). Tactile.

6. *S. placodeum*—a membranous plate, its outer surface continuous with the general integument (Fig. 125). Function doubtful; not auditory and probably not olfactory, though the function is doubtless a mechanical one; Schenk suggests that this organ is affected by air pressure, as when a bee or wasp is moving about in a confined space.

7. *S. ampullaceum*—a more or less flask-shaped cavity with an axial rod (Figs. 126, 127). Probably auditory.

These types of sensilla will be referred to in physiological order.

Touch.—The tactile sense is highly developed in insects, and end-organs of touch, unlike those of other senses, are commonly distributed over the entire integument, though the antennæ, palpi and cerci are especially sensitive to tactile impressions.

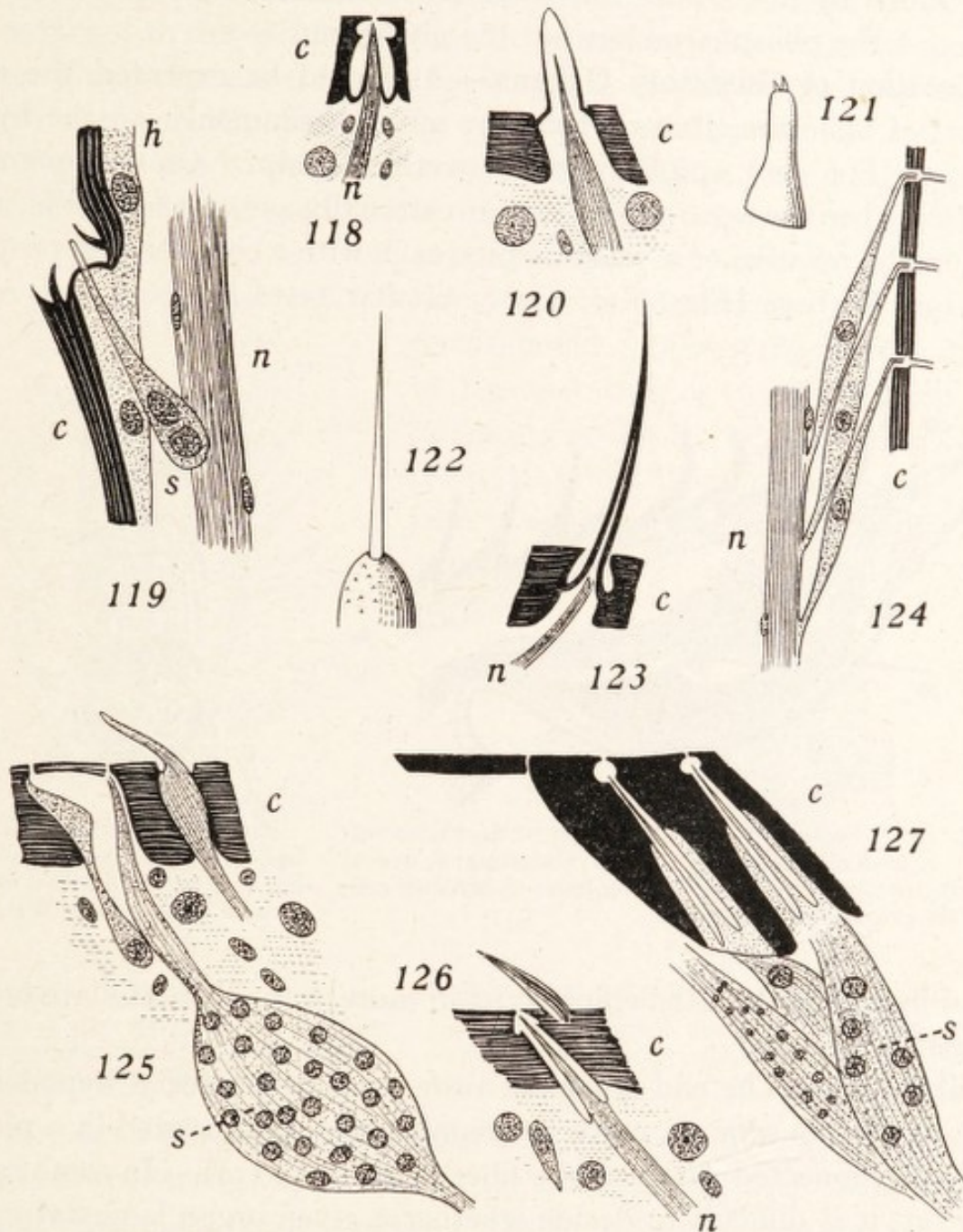
The end-organs of touch are bristles (*sensilla chætica*) or hairs (*sensilla trichodea*), each arising from a special hypodermis cell and having connection with a nerve. *Sensilla chætica* doubtless receive impressions from foreign bodies, while *sensilla trichodea*, being best developed in the swiftest flying insects and least so in the sedentary forms, may be affected by the resistance of the air, when the insect or the air itself is in motion.

Not all the hairs of an insect are sensory, however, for many of them have no nerve connections.

In blind cave insects the antennæ are very long and are exquisitely sensitive to tactile impressions.

Taste.—The gustatory sense is unquestionably present in insects, as is shown both by common observation and by precise experimentation.

Will fed wasps with sugar and then replaced it with powdered alum, which the wasps unsuspectingly tried but soon rejected, cleaning the tongue with the fore feet in a comical manner and manifesting other



FIGS. 118-127.—Types of antennal sensilla, in longitudinal section (excepting Figs. 121 and 122). Fig. 118, sensillum coeloconicum; 119, coeloconicum; 120, basiconicum; 121, styloconicum; 122, chaeticum; 123, trichodeum; 124, trichodeum; 125, placodeum; 126, ampullaceum; 127, ampullaceum; *c*, cuticula; *h*, hypodermis; *n*, nerve; *s*, sensory cell. Figs. 118, 120, 123, 125, 126, honey bee, *Apis mellifera*; 119, 121, 124, *Fidonia piniaria*; 122, moth, *Ino pruni*; 127 wasp, *Vespa crabro*.—After SCHENK.

signs of what we may call disgust. Forel offered ants honey mixed with morphine or strychnine; the ants began to feed but at once rejected the mixture. In its range, however, the gustatory sense of insects differs often from that of man. Thus Will found that Hymenoptera refused

honey with which a very little glycerine had been mixed (though Muscidae did not object to the glycerine) and Forel found that ants ate unsuspectingly a mixture of honey and phosphorus until some of them were killed by it. Under the same circumstances, man would be able to detect the phosphorus but not the glycerine.

Location of Gustatory Organs.—As would be expected, the end-organs of taste are situated near the mouth, commonly on the hypopharynx (Fig. 128), epipharynx and maxillary palpi. On the tongue of the honey bee the taste organs appear externally as short setae (Fig. 129) and on the maxillae of a wasp as pits, each with a cone, or peg, projecting from its base (Figs. 130, 131). Similar taste pits and pegs were

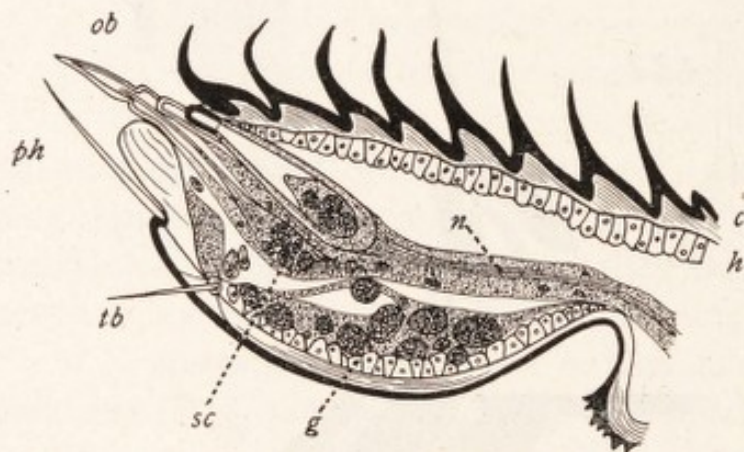


FIG. 128.—Section through tongue of wasp, *Vespa vulgaris*. c, cuticula; g, gland cell; h, hypodermis; n, nerve; ob, gustatory bristle; ph, protecting hair; sc, sensory cell; tb, tactile bristle.—After WILL.



FIG. 129.—Tongue of honey bee, *Apis mellifera*. p, protecting bristles; s, terminal spoon; t, taste setae.—After WILL.

found by Packard on the epipharynx in most of the mandibulate orders of insects.

Histology.—The end-organs of taste arise from special hypodermis cells, as minute setae or, more commonly, pegs, each seated in a pit, or cup, and connected with a nerve fiber (Figs. 131, 132). In some cases, however, it is difficult to decide whether a given organ is gustatory or olfactory, owing to the similarity between these two kinds of structures. In aquatic insects, indeed, the senses of taste and smell are not differentiated, these forms having with other of the lower animals simply a "chemical" sense.

Smell.—In most insects the sense of smell is highly efficient and in many species it is inconceivably acute. Hosts of insects depend chiefly on their olfactory powers to find food, for example many beetles, the flesh flies and the flower-visiting moths; or else to discover the opposite

sex, as is notably the case in saturniid moths. In dragon flies, however, this sense is relied upon far less than that of sight.

Organs of Smell.—By means of simple but conclusive experiments, Hauser and others have shown that the antennæ are frequently olfactory—though not to the exclusion of tactile or auditory functions, of course. Hauser found that ants, wasps, various flies, moths, beetles and larvæ, which react violently toward the vapor of turpentine, acetic acid and other pungent fluids, no longer respond to the same stimuli after their antennæ have been amputated or else covered with paraffine to exclude

the air. His experiments were conducted under conditions such that the results could not be ascribed to the shock of the operation or to effects upon the gustatory or respiratory systems; except for having lost the sense of smell, the insects experimented upon behaved in a normal manner. It should be said,

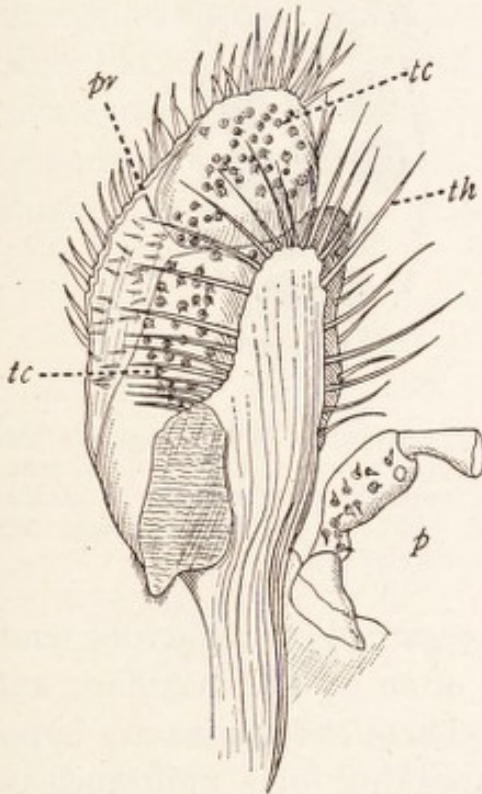


FIG. 130.—Under side of left maxilla of wasp, *Vespa vulgaris*. *p*, palpus; *pr*, protecting hairs; *tc*, taste cup; *th*, tactile hair.—After WILL.

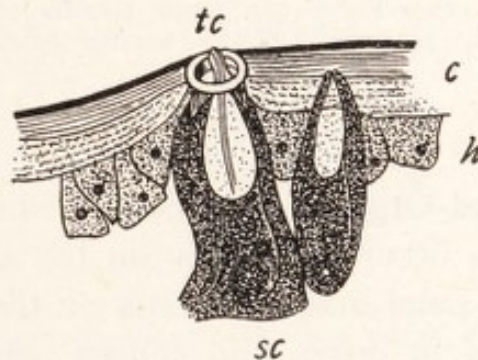


FIG. 131.—Longitudinal section of gustatory end-organ (*tc*, of Fig. 130). *c*, cuticula; *h*, hypodermis; *sc*, sensory cell; *tc*, taste cup.—After WILL.

however, that *Carabus*, *Melolontha* and *Silpha* still reacted to some extent toward strong vapors even after the extirpation of the antennæ; while in Hemiptera the loss of the antennæ did not lessen the response to the odors used. These facts indicate that the sense of smell is not always confined to the antennæ; indeed the maxillary palpi are frequently olfactory, as in *Silpha* and *Hydaticus*; also the cerci, as in the cockroach and other Orthoptera. Experiments indicate that an insect perceives some odors by means of the antennæ and others by the palpi or other organs. Hauser found that the flies *Sarcophaga* and *Calliphora*, after the amputation of their antennæ, became quite indifferent toward decayed meat, to which they had previously swarmed with

great persistence, though their actions in all other respects remained normal. Males of many moths and a few beetles are unable to find the females (see beyond) when the former are deprived of the use of their antennæ.



FIG. 132.—Taste cup from maxilla of *Bombus*. *sc*, sensory cell; *n*, nerve.—After WILL.

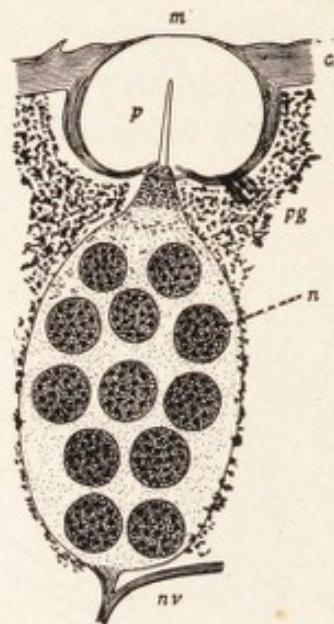


FIG. 133.—Section of antennal olfactory organ of grasshopper, *Caloptenus*. *c*, cuticula; *m*, membrane; *n*, nucleus of sensory cell; *nv*, nerve; *p*, pit with olfactory peg, *pg*, pigment.—After HAUSER.

End-Organs.—Structures which are regarded as olfactory end-organs occur commonly on the antennæ, often on the maxillary and labial palpi and sometimes on the cerci. These end-organs are hypodermal in origin and consist, generally speaking, of a multinucleate cell (Fig. 133) penetrated by a nerve and prolonged into a chitinous bristle or peg, which is more or less enclosed in a pit, as in *Tabanus* (Fig. 134). In many instances, however, the end-organs take the form of teeth or cones projecting from the general surface of the antenna, as in *Vespa* (Fig. 135). These cones are usually less numerous than the pits; in *Vespa crabro*, for example, the teeth number 700 and the pits from 13,000 to 14,000 on each antenna. The pits are even more numerous in some other insects; thus there are as many as 17,000 on each antenna of a blow fly (Hicks). The male of *Melolontha vulgaris*, which seeks out the female by the sense of smell, has according to Hauser 39,000 pits on each antenna, and the female only 35,000. Pits presumably olfactory in function have been found by Packard on the maxillary and labial palpi of *Perla* and on the cerci of the cockroach, *Periplaneta americana*. Vom Rath has described four kinds of sense

hairs from the two larger of the four caudal appendages of a cricket, *Gryllus*; some of these (Fig. 136) may be olfactory, though possibly tactile. The same author found on the terminal palpal segment in various Lepidoptera a large flask-shaped invagination (Fig. 137) into which project numerous chitinous rods, each a process of a sensory cell, which is supplied by a branch of the principal palpal nerve; these peculiar organs are inferred to be olfactory.

The chief reason for regarding these various end-organs as olfactory is that they appear from their structure to be better adapted to receive that kind of an impression than any other, so far as we can judge from our own experience. Though it is easy to demonstrate that the antennæ, for example, are olfactory, it frequently hap-



FIG. 134.—Section through antennal olfactory pit of fly, *Tabanus*. *c*, cuticula; *p*, pit with peg; *pb*, protecting bristles; *s*, sensory cell.—After HAUSER.

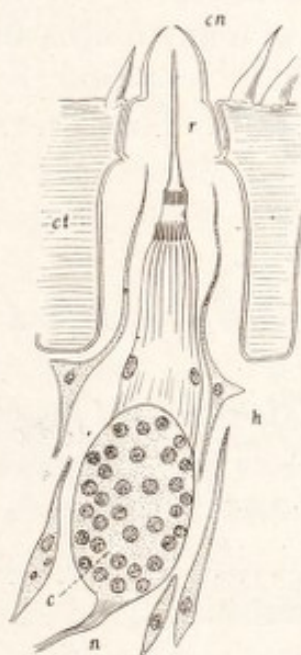


FIG. 135.—Longitudinal section of antennal olfactory organ of wasp, *Vespa*. *c*, olfactory cell; *cn*, olfactory cone; *ct*, cuticula; *h*, hypodermis cells; *n*, nerve; *r*, rod.—After HAUSER.

pens that the antennæ bear several distinct forms of sensory end-organs, so minute and intermingled that their physiological differences can scarcely be ascertained by experiment but must be inferred from their peculiarities of structure. Schenk, however, has arrived at precise results by comparing the antennal sensilla in the two sexes, selecting species in which the antennæ exhibit a pronounced sexual dimorphism, in correlation with sexual differences of behavior. Taking *Notolophus antiqua*, in which the male seeks out the female by means of antennal organs of smell, he finds that the male has on each antenna about 600 sensilla cœloconica and the female only 75; similarly in the geometrid *Fidonia*, in which the ratio is 350 to 100. The sensilla styloconica also, of these two genera, are regarded as olfactory organs. These two kinds of end-

organs are not only structurally adapted for the reception of olfactory stimuli, but their numerical differences accord with the observed differences in the olfactory powers of the two sexes, there being no other antennal end-organs to enter into the consideration.

Dr. N. E. McIndoo has denied that the antennæ are olfactory organs. He finds, in all the large orders of insects, and on almost all parts of the body and legs, on the bases of the wings, and in other situations, the structures that he terms *olfactory pores*, to which he has devoted an immense amount of study.

Assembling.—It is a fact, well known to entomologists, that the females of many moths and some beetles are able by emitting an odor to

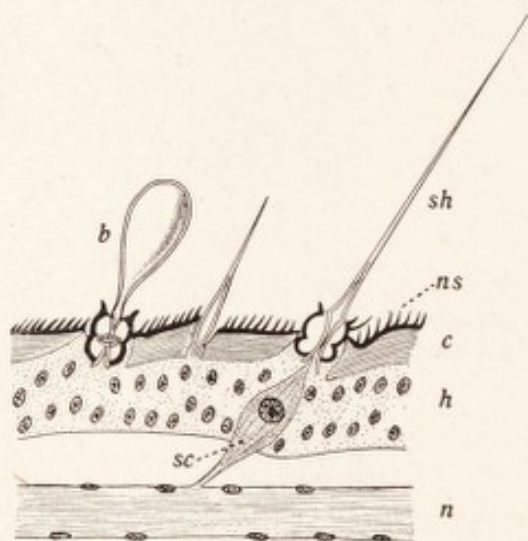


FIG. 136.—Longitudinal section of a portion of a caudal appendage of a cricket, *Gryllus domesticus*. *b*, bladderlike hair; *c*, cuticula; *h*, hypodermis; *n*, nerve; *ns*, non-sensory setæ; *sc*, sense cell; *sh*, sensory hair.—After VOM RATH.

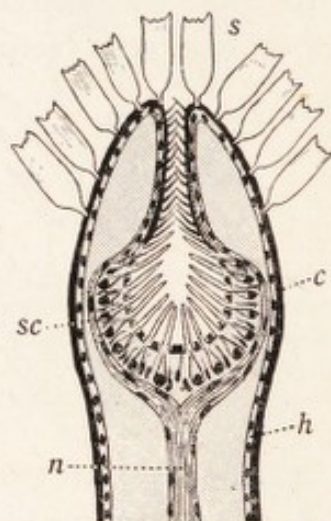


FIG. 137.—Longitudinal section of apex of palpus of *Pieris*. *c*, cuticula; *h*, hypodermis; *n*, nerve; *s*, scales; *sc*, sense cells.—After VOM RATH.

attract the opposite sex, often in considerable numbers. Under favorable conditions, a freshly emerged female of the *promethea* moth, exposed out of doors in the latter part of the afternoon, will attract scores of the males. A breeze is essential and the males come up against the wind; if they pass the female, they turn back and try again until she is located, vibrating the antennæ rapidly as they near her. The female, meanwhile, exhales an appreciable odor, chiefly from the region of the ovipositor, and males will congregate on the ground at a spot where a female has been. If one of these males is deprived of the use of his antennæ, however, he flutters about in an aimless way and is no longer able to find the female.

Among beetles, males of *Polyphylla* gather and scratch at places

where females are about to emerge from the ground. *Prionus* also assembles, as Mrs. Dimmock observed in Massachusetts. In this instance many males, with palpitating antennæ, ran and flew to the female; moreover, a number of *females* were attracted to the scene.

Sounds of Insects.—Before considering the sense of hearing, some account of the sounds of insects is desirable. Most of these are made by the vibrations of a membrane or by the friction of one part against another.

The wings of many Diptera and Hymenoptera vibrate with sufficient speed and regularity to give a definite note. The wing tone of a honey bee is A' and that of a common house fly is F' . From the pitch the number of vibrations may be determined; thus A' means 440^1 vibrations per second and F' , 352. The numbers thus ascertained may be verified by Marey's graphic method (Fig. 76); he found that the fly referred to actually made 330 strokes per second against the smoked surface of a revolving cylinder.

Flies, bees, dragon flies and some beetles make buzzing or humming sounds by means of the spiracles, there being behind each spiracle a membrane or chitinous projection which vibrates during respiration. This "voice" should be distinguished from the wing tone when both are present, as in bees and flies. A fly will buzz when held by the wings, and some gnats continue to buzz after losing wings, legs and head. The wing tone is the more constant of the two; in the honey bee it is A' , falling to E' if the insect is tired, while the spiracular tone of the same insect is at least an octave higher (A'') and often rises to B'' or C'' , according to the state of the nervous system; in fact, it is possible and even probable that various spiracular tones express different emotions, as is indicated by the effects produced by the voice of the old queen bee upon the young queens and the males.

The well-known "shrilling" of the male cicada is produced by the rapid vibration of a pair of membranes, or drums, situated on the basal abdominal segment, and vibrated each by means of a special muscle.

Frictional sounds are made by beetles in a great variety of ways: by the rubbing of the pronotum against the mesonotum (many *Cerambycidae*); or of abdominal ridges against elytral rasps (*Elaphrus*, *Cychrus*); or two dorsal abdominal rasps against specialized portions of the wing folds (*Passalus cornutus*), not to mention other methods. In most cases one part forms a rasp and the other a scraper, for the production of sound.

¹ Upon the basis of C' as 264 vibrations per second. The C' of the physicist has 256 as its frequency of vibration.

In many of these instances the sound serves to bring the two sexes together and is not necessarily confined to one sex; thus in *Passalus cornutus* both sexes stridulate, and the larva as well.

A few moths (Sphingidæ) and a few butterflies make sounds; the South American butterfly *Ageronia feronia* emits a sharp crackling noise as it flies. A rasp and a scraper have been found in several ants, though ants very seldom make any sounds that can be distinguished by the human ear; *Mutilla*, however, makes a distinct squeaking sound by means of a stridulating organ similar to those of ants.

Stridulating organs attain their best development in Orthoptera, in which group the ability to stridulate is often restricted to the male, though not so often as is commonly supposed. Among Locustidæ, *Stenobothrus* rubs the hind femora against the tegmina to make a sound, the femur bearing a series of teeth, which scrape across the elevated veins of the wing-cover; while the male of *Dissosteira* makes a crackling sound during flight or while poising, by means of friction between the front and hind wings, where the two overlap.

Tettigoniidæ and Gryllidæ stridulate by rubbing the bases of the tegmina against each other. Thus in the male *Microcentrum laurifolium* the left tegmen, which overlaps the right, bears a file-like organ of about fifty-five teeth (Fig. 138), while the opposite tegmen bears a scraper, at right angles to the file. The tegmina are first spread a little; then, as they close gradually, the scraper clicks across the teeth, making from twenty to thirty sharp "tic"-like sounds in rapid succession. This call guides the female to the male and when they are a few inches apart she makes now and then a short, soft chirp, to which he responds with a similar chirp, which is quite unlike the first call and, moreover, is made by the opening of the tegmina. These and other details of the courtship may readily be observed in twilight and even under artificial light, as the latter, if not too strong, does not disturb the pair. Something similar may be observed in the daytime in *Orchelimum*, *Xiphidium* and the tree crickets, *Æcanthus*. The stridulating areas are usually membranous and the rasping organs are modified veins. Frequently the wing-covers bulge out to form a resonant chamber that reinforces the sound, as in the katydid.

The naturalist can recognize many a species of grasshopper by its song; Scudder has expressed some of these songs in musical notation. The usual song of the common meadow-grasshopper, *Orchelimum vulgare*, may be represented by a prolonged *zr . . .* sound, followed by a staccato *jip-jip-jip-jip . . .*

In Orthoptera, the frequency of stridulation increases with the temperature; and the correlation between the two is so close that it is easy

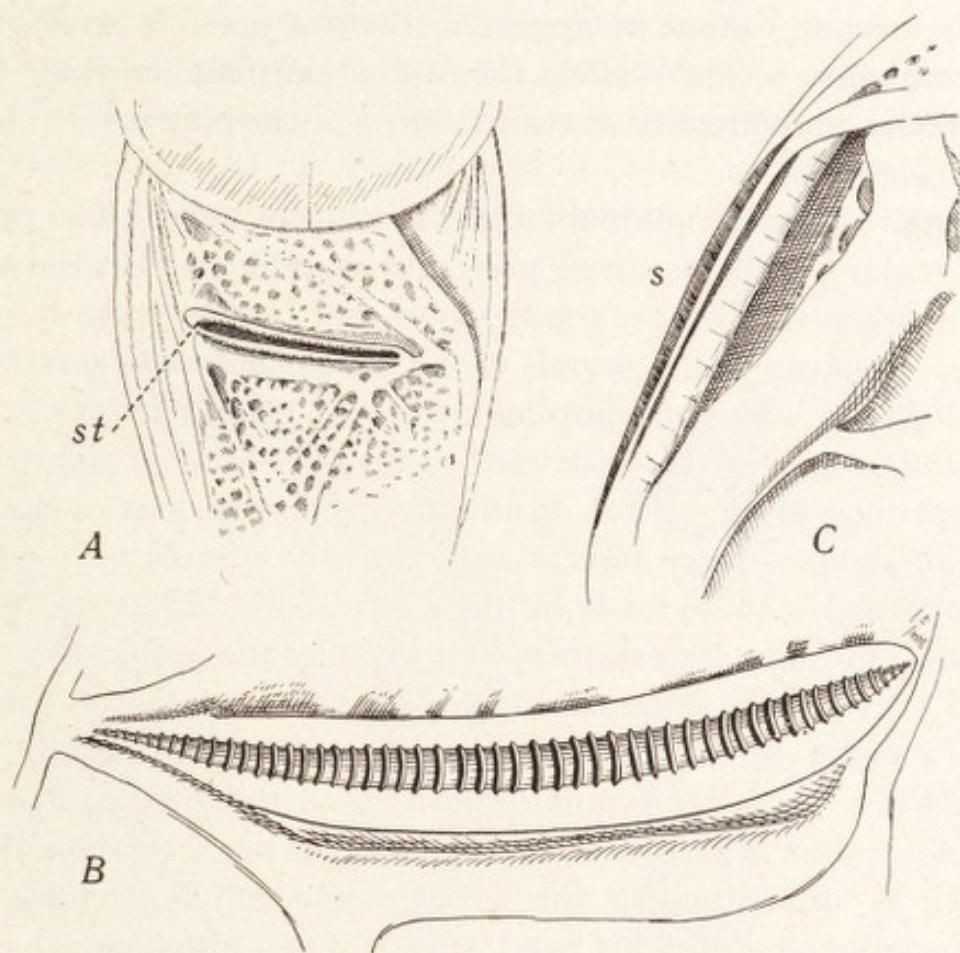


FIG. 138.—Stridulating organs of *Microcentrum laurifolium*. A, dorsal aspect of file (st) when the tegmina are closed; B, ventral aspect of left tegmen to show file; C, dorsal aspect of right tegmen to show scraper (s).

to compute the temperature from the number of calls per minute, by means of formulæ. The formula for a common cricket [probably a tree-cricket, *Ecanthus niveus*], as given by Professor Dolbear, is

$$T = 50 + \frac{N - 40}{4}, \text{ which simplified is } T = 40 + \frac{N}{4}.$$

Here T stands for temperature and N , the rate per minute.

A similar formula for the katydid (*Cyrtophyllus perspicillatus*), based upon observations made by R. Hayward, would be

$$T = 60 + \frac{N - 19}{3}.$$

Here, in computing N , either the "katy-did" or the "she-did" is taken as a single call.

Professor A. F. Shull, who has made precise observations on the stridulation of *Æcanthus*, finds that there are numerous variations of rate that cannot be accounted for by differences of temperature; that Dolbear's formula cannot be applied without a possible error of 6.65° F.; that humidity seems to affect the rate of chirping and that crickets show a certain individuality in their manner of chirping under the same external conditions.

Hearing.—There is no doubt that insects can hear. The presence of sound-making organs is strong presumptive evidence that the sense of hearing is present. Female grasshoppers and beetles make locomotor and other responses to the sounds of the males, and male grasshoppers will answer the counterfeit chirping made with a quill and a file.

Auditory organs are not restricted to any one region of an insect, but occur, according to the species, on antennæ, abdomen, legs, or elsewhere.

The antennæ of some insects are evidently stimulated by certain notes, particularly those made by their own kind. Thus the antennæ of the male mosquito are auditory, as proved by the well-known experiments of Mayer. He fastened a male *Culex* to a microscope slide and sounded various tuning forks. Certain tones caused certain of the antennal hairs to vibrate sympathetically, and the greatest amount of vibration occurred in response to 512 vibrations per second, or the note C'' , which is approximately the note upon which the female hums. The male probably turns his head until the two antennæ are equally affected by the note of the female, when, by going straight ahead, he is able to locate her with great precision.

In the lack of experimental evidence, other organs are inferred to be auditory on account of their structure. Locustidæ bear on each side of the first abdominal segment a *tympanal* sense organ—the subject of Graber's well-known figure (Fig. 139). This organ is admirably adapted to receive and transmit sound-waves. The tympanum, or membrane, is tense, and can vibrate freely, as the air pressure against the two surfaces of the membrane is equalized by means of an adjacent spiracle, which admits air to the inner surface. Resting against the inner face of the tympanum are two processes (Fig. 139, *p*, *p*), which serve probably to transfer the vibrations, and there is also a delicate vesicle connected by means of an intervening ganglion with the auditory nerve, which in this case comes from the metathoracic ganglion. The nerve terminations consist of delicate bristle-like processes which are probably affected by the oscillations of the fluid contained in the vesicle just referred to.

Other tympanal organs, doubtless auditory, are found on the fore tibiae of Tettigoniidæ, ants, termites and Perlidæ, on the femora of Pediculiidæ and the tarsi of some Coleoptera.

Several types of *chordotonal* organs have been described, of which those of the transparent *Corethra* larva may serve as an example. These organs, situated on each side of abdominal segments 4-10, inclusive, consist each (Fig. 140) of a tense cord, probably capable of vibration, which is attached at its posterior end to the integument and at its

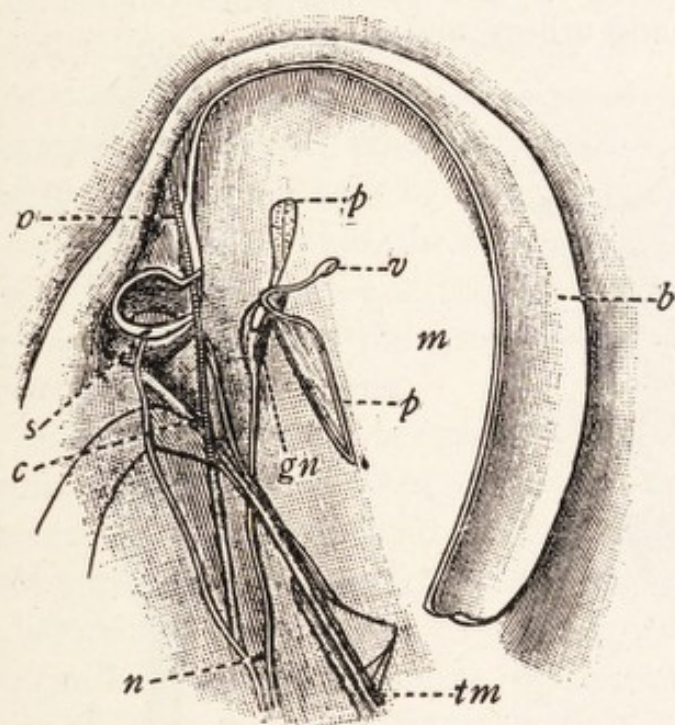


FIG. 139.—Inner aspect of right tympanal sense organ of a grasshopper, *Caloptenus italicus*. *b*, chitinous border; *c*, closing muscle of spiracle; *gn*, ganglion; *m*, tympanum; *n*, nerve; *o*, opening muscle of spiracle; *p*, *p*, processes resting against tympanum; *s*, spiracle; *tm*, tensor muscle of tympanum; *v*, vesicle. After GRABER.

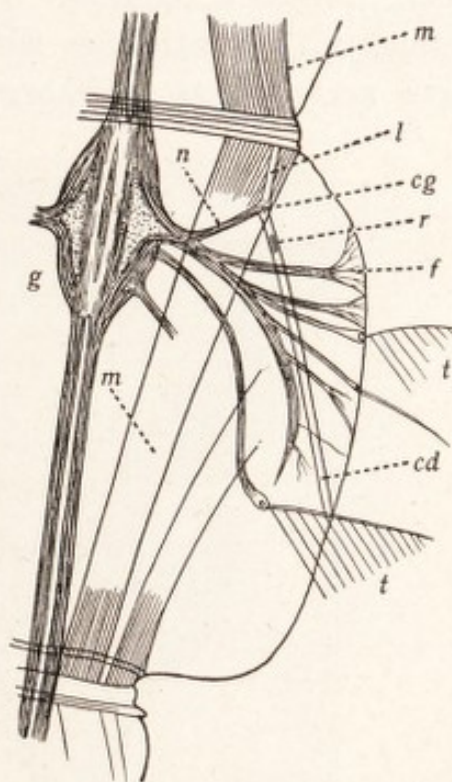


FIG. 140.—Chordotonal sense organ of aquatic dipterous larva, *Corethra plumicornis*. *cd*, cord; *cg*, chordotonal ganglion; *f*, fibers of an integumental nerve; *g*, ganglion of ventral chain; *l*, ligament; *m*, longitudinal muscles; *n*, chordotonal nerve; *r*, rods (nerve terminations); *t*, tactile setae.—After GRABER.

anterior end to a ligament. Between the cord and the supporting ligament is a small ganglion, which receives a nerve from the principal ganglion of the segment.

Vision.—The external characters of the two kinds of eyes—ocelli and compound eyes—have already been described. While the lateral ocelli are comparatively simple in structure, consisting of a small number of cells, the dorsal ocelli almost rival the compound eyes in complexity.

Dorsal Ocelli.—These consist (Fig. 141) of (1) *lens*, (2) *vitreous body*, (3) *retina*, (4) *nerve fibers*, (5) *pigmented hypodermis cells*, and (6)

accessory cells, between the retinal cells and the nerve fibers. The lens, usually biconvex in form, is a local thickening of the general cuticula; it is supplemented in its function by the vitreous body, consisting of a layer of transparent hypodermis cells; these in many insects are elongate, constituting a vitreous layer of rather more importance than the one represented in Fig. 141. The retina consists of cells more or less spindle-shaped and associated in pairs or in groups of two or three, each group being termed a *retinula*. The basal end of each retinal cell is continuous with a nerve fiber (Fig. 142), according to Redikorzew and others, and in

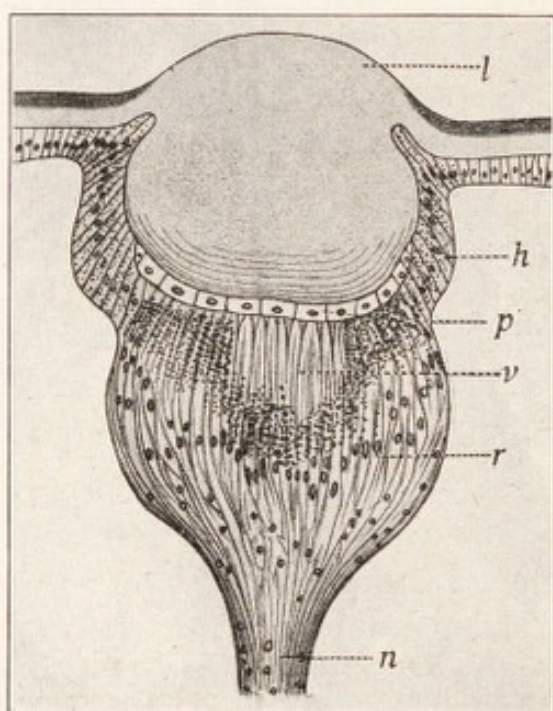


FIG. 141.—Median ocellus of honey bee, *Apis mellifera*, in sagittal section. *h*, hypodermis; *l*, lens; *n*, nerve; *p*, iris pigment; *r*, retinal cells; *v*, vitreous body.—After REDIKORZEW.

some instances (*Calopteryx*) a nerve fiber enters the cell. Each retinula contains a longitudinal rod, or *rhabdom*, in the secretion of which all the cells of the retinula are concerned. Between the retinal cells and nerve fibers are indifferent, or accessory cells. Pigment granules, usually black, are contained in these cells, also in the retinal cells and around the lens, in the last instance forming the *iris*.

Vision by Ocelli.—Though the ocellus is constructed on somewhat the same plan as the human eye, its capacity for forming images must

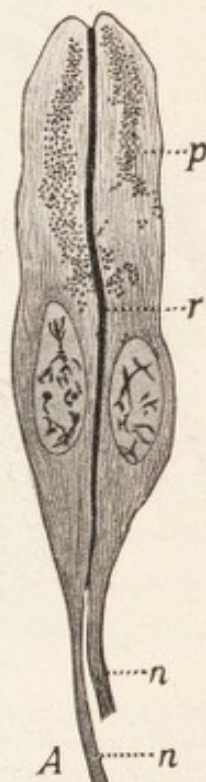
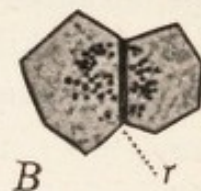


FIG. 142.—An ocellar retinula of the honey bee, composed of two retinal cells. *A*, longitudinal section; *B*, transverse section; *n*, nerves; *p*, pigment; *r*, rhabdom.—After REDIKORZEW.

be extremely limited; for since the form of the lens is fixed and also the distance between the lens and the retina, there is no power of accommodation, and most external objects are out of focus; to make an image, then, the object must be at one definite distance from the lens, and as the lens is usually strongly convex, this distance must be small; in other words, insects, like spiders, are very near-sighted, so far as the ocelli are concerned; furthermore, the small number of retinal rods implies an image of only the coarsest kind.

If the compound eyes of a grasshopper are covered with an opaque varnish and the insect is placed in a box with only a single opening, it readily finds its way out by means of its ocelli; if the three ocelli also are covered, however, it no longer does so, except by accident, though it can make its escape when only one of the ocelli is left uncovered. The ocelli, then, can distinguish light from darkness—and they are probably more serviceable to the insect in this way than in forming images.

Compound Eyes.—As regards delicacy and intricacy of structure, the compound eye of an insect is scarcely if at all inferior to the eye of a vertebrate. In radial section (Fig. 143), a compound eye appears as an aggregation of similar elongate elements, or *ommatidia*, each of which ends externally in a facet. The following structures compose, or are concerned with, each ommatidium: (1) *cornea*, (2) *crystalline lens*, or *cone*, (3) *rhabdom* and *retinula*, (4) *pigment* (*iris* and *retinal*), (5) *fenestrate membrane*, (6) *fibers* of the *optic nerve*, (7) *tracheæ*.

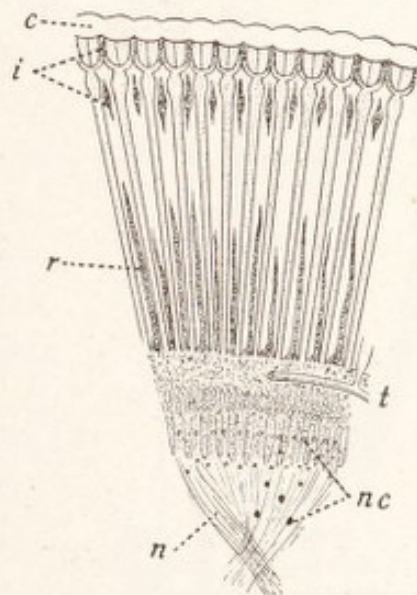


FIG. 143.—Portion of compound eye of fly, *Calliphora vomitoria*, radial section. *c*, cornea; *i*, iris pigment; *n*, nerve fibers; *nc*, nerve cells; *r*, retinal pigment; *t*, trachea.—After HICKSON.

The cornea (Fig. 144) is a biconvex transparent portion of the external chitinous cuticula. Immediately beneath it are the *cone cells*, which may contain a clear fluid or else, as in most insects, solid transparent cones. The rhabdom is a transparent chitinous rod or a group of rods (*rhabdomeres*) situated in the long axis of the ommatidium and surrounded by greatly elongated cells, which constitute the retinula. Two zones of pigment are present: an outer zone, of iris pigment, in which the pigment in the form of fine black granules is contained chiefly in short cells that surround the retinula distally; and an inner zone, of retinal pigment, in which the pigment cells are long and slender,

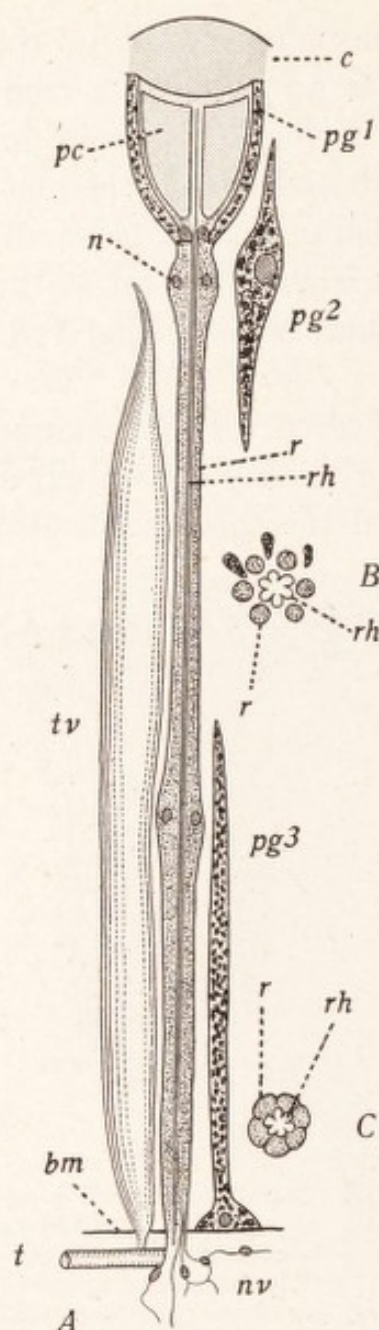


FIG. 144.—Structure of an ommatidium of *Calliphora vomitoria*. A, radial section (chiefly); B, transverse section through middle region; C, transverse section through basal region; *bm*, basement membrane; *c*, cornea; *n*, nucleus; *nv*, nerve fibrillæ; *pc*, pseudocone; *pg*¹, *pg*², cells containing iris pigment; *pg*³, cell containing retinal pigment; *r*, one of the six retinal cells which compose the retinula; *rh*, rhabdom, composed of six rhabdomeres; *t*, trachea; *tv*, tracheal vesicle.—After HICKSON.

and enclose the retinula proximally. All these parts are hypodermal in origin, as is also the fenestrate basement membrane, through which pass tracheæ and nerve fibers. The nerve fibrillæ, which are ultimate branches of the optic nerve, pass into the retinal cells—the end-organs of vision. Under the basement membrane is a fibrous optic tract of complex structure.

Compound eyes are of three types: (1) *eucone*, in which the cone-cells form solid crystalline cones; (2) *pseudocone*, in which the cone-cells contain a transparent fluid; and (3) *acone*, in which there are no cones, though the cone-cells are present.

Physiology.—After much experimentation and discussion upon the physiology of the compound eye—the subject of the monumental works of Grenacher and Exner—Müller's "mosaic" theory is still generally accepted, though it was proposed early in the last century. It is thought that an image is formed by thousands of separate points of light, each of which corresponds to a distinct field of vision in the external world. Each ommatidium is adapted to transmit light along its axis only (Fig. 145), as oblique rays are lost by absorption in the black pigment which surrounds the crystalline cone and the axial rhabdom. Along the rhabdom, then, light can reach and affect the terminations of the optic nerve. Each ommatidium does not itself form a picture; it simply preserves the intensity and color of the light from one particular portion of the field of vision; and when this is done by hundreds or thousands of contiguous ommatidia, an image results. All that the painter does, who copies an object, is to put together patches of light in the same relations of quality and position that he finds in the object itself—and this is essen-

tially what the compound eye does, so far as can be inferred from its structure.

Exner, removing the cones with the corneal cuticula (in *Lampyrus*), looked through them from behind with the aid of a microscope and found that the images made by the separate ommatidia were either very close together or else overlapped one another, and that in the latter case the details corresponded; in other words, as many as twenty or thirty ommatidia may co-operate to form an image of the same portion of the field of vision; this "superposition" image being correspondingly bright—an advantage, probably, in the case of nocturnal insects.

Large convex eyes indicate a wide field of vision, while small numerous facets mean distinctness of vision, as Lubbock pointed out. The closer the object the better the sight, for the greater will be the number of lenses employed to produce the impression, as Mollock says. If Müller's theory is true, an image may be formed of an object at any reasonable distance, no power of accommodation being necessary; while if, on the other hand, each cornea with its crystalline cones had to form an image after the manner of an ordinary hand-lens, only objects at a definite distance could be imaged.

The limit of the perception of form by insects is placed at about two meters for *Lampyrus*, 1.50 meters for Lepidoptera, 68 centimeters for Diptera and 58 centimeters for Hymenoptera.

It is generally agreed, however, that the compound eyes are specially adapted to perceive movements of objects. The sensitiveness of insects to even slight movements is a matter of common observation; often, however, these insects can be picked up with the fingers, if the operation is performed slowly until the insect is within the grasp. A moving object affects different facets in succession, without necessitating any turning of the eyes or the head, as in vertebrates. Furthermore, on the same principle, the compound eyes are serviceable for the perception of form when the insect itself is moving rapidly.

The arrangement of the pigment depends adaptively upon the quality of the light, as Stefanowska and Exner have shown; thus, when the light is too strong, the iris and retinal pigment cells elongate around

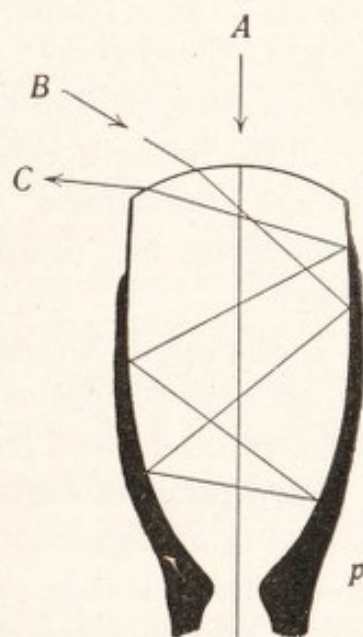


FIG. 145.—Diagram of outer transparent portion of an ommatidium to illustrate the transmission of an axial ray (A) and the repeated reflection and absorption of an oblique ray (B), which at length emerges at C. *p*, iris pigment.

the ommatidium and their pigment granules absorb from the cone cells and rhabdom the excess of light. If the light is weak, they shorten, and absorb but a minimum amount of light. In diurnal insects the pigment is adapted to absorb an excess of light; in nocturnal insects, on the contrary, it is adapted to permit a maximum amount of light to reach the retinal cells.

Origin of Compound Eye.—The compound eye is often said to represent a group of ocelli, chiefly for the reason that externally there appears to be a transition from simple eyes, through agglomerate eyes, to the faceted type. This plausible view, however, is probably incorrect, for these reasons among others. In the ocellus, a single lens serves for all the retinulæ, while in the compound eye there are as many lenses as there are retinulæ. Moreover, ocelli do not pass directly into compound eyes, but disappear, and the latter arise independently of the former.

Probably, as Grenacher holds, both the ocellus and the compound eye are derived from a common and simpler type of eye—are “sisters,” so to speak, derived from the same parentage.

Perception of Light through the Integument.—In various insects, as also in earthworms, blind chilopods and some other animals, light affects the nervous system through the general integument. Thus eyeless dipterous larvæ avoid the light, or, more precisely, they retreat from the rays of shorter wave-length (as the blue), but come to rest in the rays of longer wave-length (red), as if they were in darkness (see page 307). The blind cave-beetles of the genus *Anophthalmus* react to the light of a candle (Packard). Graber found that a cockroach deprived of its eyesight could still perceive light, but Lubbock found that an ant whose eyes had been covered with an opaque varnish became indifferent to light.

Color Sense.—Insects undoubtedly distinguish certain colors, though their color sense differs in range from our own. Thus ants avoid violet light as they do sunlight, but probably cannot distinguish red or orange light from darkness; on the other hand, they are extremely sensitive to the ultra-violet rays. Honey bees frequently select blue flowers: white butterflies (*Pieris*) prefer white flowers, and yellow butterflies (*Colias*) appear to alight on yellow flowers in preference to white ones (Packard). In fact, the color sense is largely relied upon by insects to find particular flowers and by butterflies to a large extent to find their mates. To be sure, insects will visit flowers after the brightly colored petals have been removed or concealed, as Plateau found, but

this does not prove that the colors are of no assistance to the insect, though it does show that they are not the sole attraction—the odor also being an important guide. The honey bee is able to distinguish color patterns, according to the experiments of C. H. Turner.

Problematical Sense Organs.—As all our ideas in regard to the sensations of insects are necessarily inferences from our own sensory experiences, they are inevitably inadequate. While it is certain that insects have at least the senses of touch, taste, smell, hearing and sight, it is also certain that these senses of theirs differ remarkably in range from our own, as we have shown. We can form no accurate conception of these ordinary senses in insects, to say nothing of others that insects have, some of which are probably peculiar to insects. Thus they have many curious integumentary organs which from their structure and nerve connections are inferred to be sensory end-organs, though their functions are either doubtful or unknown. Such an organ is the sensillum placodeum (p. 84), the use of which is very doubtful, though the organ is possibly affected by air pressure. Insects are extremely sensitive to variations of wind, temperature, moisture and atmospheric pressure, and very likely have special end-organs for the perception of these variations; indeed, the sensilla trichodea are probably affected by the wind, as we have said.

The halteres of Diptera, representing the hind wings, contain sensory organs of some sort. They have been variously regarded as olfactory (Lee), auditory (Graber), and as organs of equilibration. When one or both halteres are removed, the fly can no longer maintain its equilibrium in the air, and Weinland holds that the direction of flight is affected by the movements of these “balancers.”

6. DIGESTIVE SYSTEM

The alimentary tract in its simplest form is to be seen in Thysanura, Collembola and most larvæ, in which (Fig. 146) it is a simple tube ex-

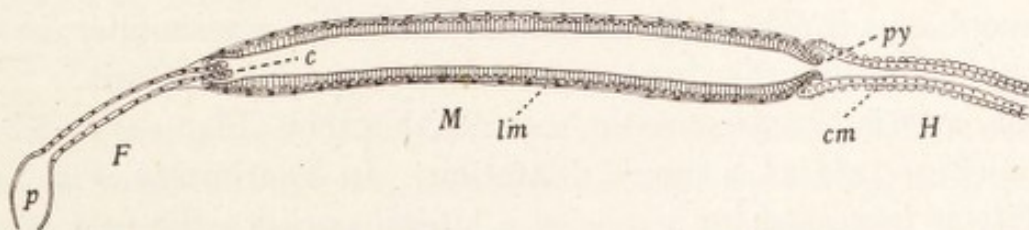


FIG. 146.—Alimentary tract of a collembolan, *Orchesella*. *F*, fore gut; *H*, hind gut; *M*, mid gut; *c*, cardiac valve; *cm*, circular muscle; *lm*, longitudinal muscle; *p*, pharynx; *py*, pyloric valve.

tending along the axis of the body and consisting of three regions, namely, *fore*, *mid* and *hind gut*. These regional distinctions are fundamental, as the embryology shows, for the middle region is entodermal in origin and the two others are ectodermal, as appears beyond.

There are many departures from this primitive condition, and the most specialized insects exhibit the following modifications (Figs. 147, 148) of the three primary regions:

Fore intestine (stomodæum): mouth, pharynx, œsophagus, crop, proventriculus (gizzard), cardiac valve.

Mid intestine (mesenteron): ventriculus (stomach).

Hind intestine (proctodæum): pyloric valve, ileum, colon, rectum, anus.

Stomodæum.—The *mouth*, the anterior opening of the food canal, is to be distinguished from the *pharynx*, a dilatation for the reception of

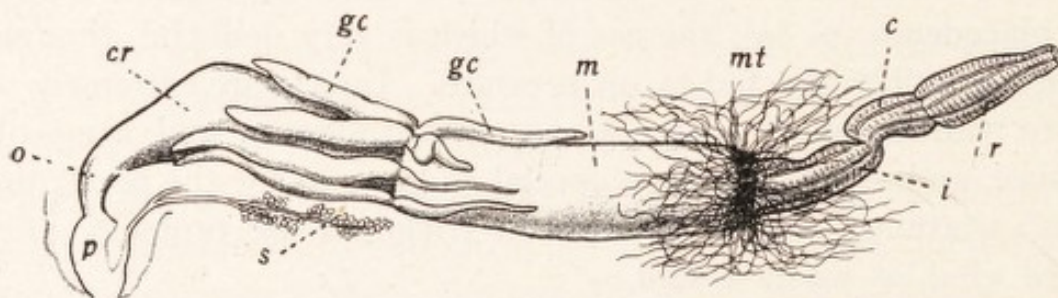


FIG. 147.—Alimentary tract of a grasshopper, *Melanoplus differentialis*. *c*, colon; *cr*, crop; *gc*, *gc*, gastric cæca; *i*, ileum; *m*, mid intestine, or stomach; *mt*, Malpighian, or kidney, tubes; *o*, œsophagus; *p*, pharynx; *r*, rectum; *s*, salivary gland of left side.

food. In the pharynx of mandibulate insects the food is acted upon by the saliva; in suctorial forms the pharynx acts as a pumping organ, in the manner already described.

The *œsophagus* is commonly a simple tube of small and uniform caliber, varying greatly in length according to the kind of insect. Passing between the commissures that connect the brain with the subœsophageal ganglion (Fig. 115), the œsophagus leads gradually or else abruptly into the *crop* or *gizzard*, or when these are absent, directly into the stomach. In addition to its function of conducting food, the œsophagus is sometimes glandular, as in the grasshopper, in which it is said to secrete the "molasses" which these insects emit.

The *crop* is conspicuous in most Orthoptera (Fig. 147) and Coleoptera (Fig. 148) as a simple dilatation. In Neuroptera (Fig. 149) its capacity is increased by means of a lateral pocket—the *food reservoir*; this in Lepidoptera, Hymenoptera and Diptera is a sac (Fig. 150, *c*) communicating with the œsophagus by means of a short neck or a

long tube, and serving as a temporary receptacle for food. In herbivorous insects the crop contains glucose formed from starch by the action of saliva or by the secretion of the crop itself; in carnivorous insects this secretion converts albuminoids into assimilable peptone-like substances.

Next comes the enlargement known as the *proventriculus*, or *gizzard*, which is present in many insects, especially Orthoptera and Coleoptera (Fig. 148), and is usually found in such mandibulate insects as feed upon hard substances. The proventriculus is

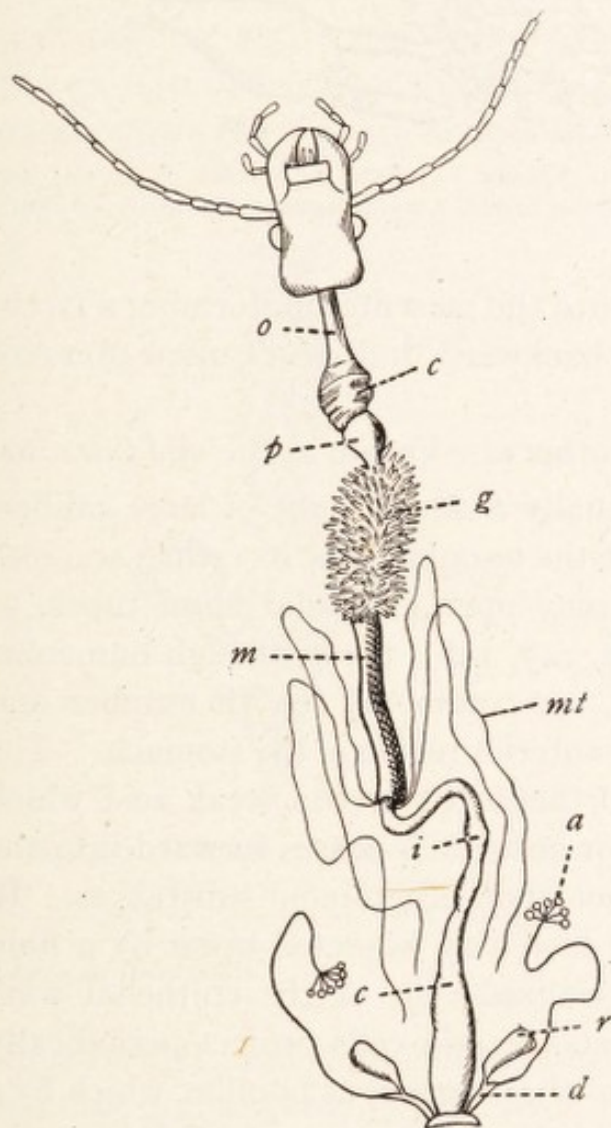


FIG. 148.—Digestive system of a beetle, *Carabus*. *a*, anal gland; *c* (of fore gut), crop; *c* (of hind gut), colon, merging into rectum; *d*, evacuating duct of anal gland; *g*, gastric caeca; *i*, ileum; *m*, mid intestine; *mt*, Malpighian tubes; *o*, oesophagus; *p*, proventriculus; *r*, reservoir.—After KOLBE.

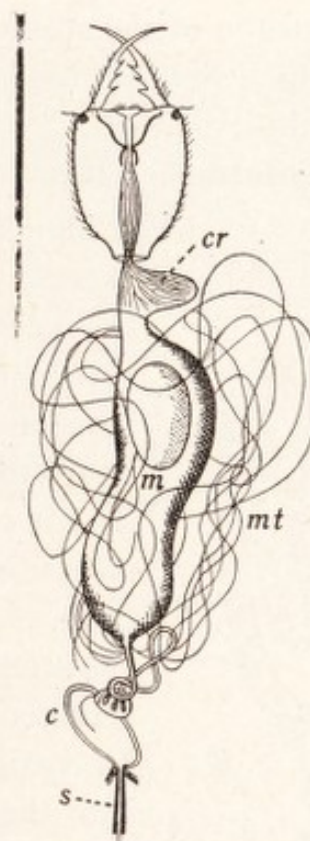


FIG. 149.—Digestive system of *Myrmecoleon* larva. *c*, cæcum; *cr*, crop; *m*, mid intestine; *mt*, Malpighian tubes; *s*, spinneret.—After MEINERT.

lined with chitinous teeth or ridges for straining the food, and has powerful circular muscles to squeeze the food back into the stomach, as well as longitudinal muscles for relaxing, or opening, the gizzard. The proventriculus not only serves as a strainer, but also helps to comminute the food, like the gizzard of a bird.

In most insects a *cardiac valve* guards the entrance to the stomach, preventing the return of food to the gullet. This valve (Figs. 146, 151)

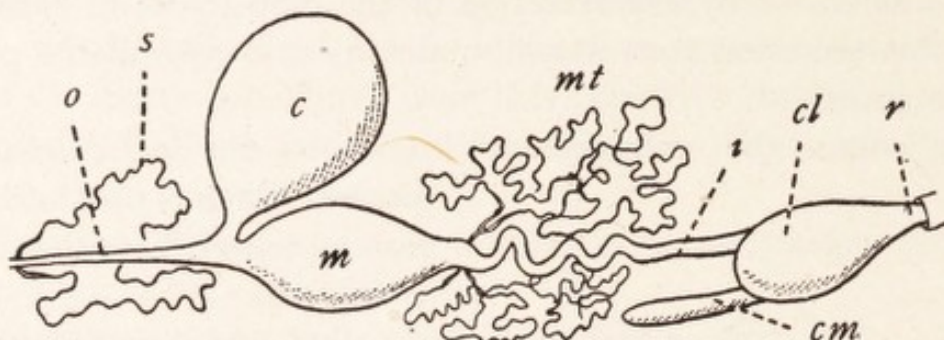


FIG. 150.—Alimentary tract of a moth, *Sphinx*. *c*, food reservoir; *cl*, colon; *cm*, cæcum; *i*, ileum; *m*, mid intestine; *mt*, Malpighian tubes; *o*, oesophagus; *r*, rectum; *s*, salivary gland.—After WAGNER.

is an intrusion of the stomodæum into the mesenteron, forming a circular lip which permits food to pass backward, but closes upon pressure from behind.

Mesenteron.—The *ventriculus*, otherwise known as the *mid intestine*,

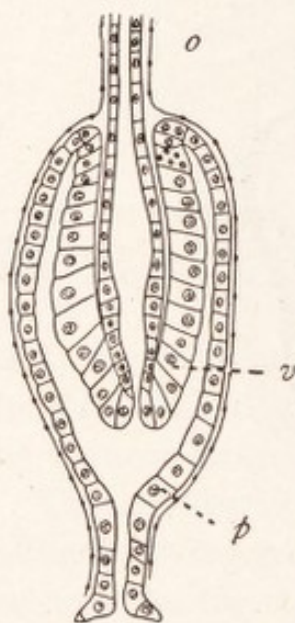


FIG. 151.—Cardiac valve of young muscid larva. *o*, oesophagus; *p*, proventriculus; *v*, valve. In an older larva the valve projects into the mid intestine.—After KOWALEVSKY.

or *stomach*, is usually a simple tube of large caliber, as compared with the oesophagus or intestine, and into the ventriculus may open glandular blind tubes, or *gastric cæca* (Figs. 147, 148); these, though numerous in some insects, are commonly few in number and restricted to the anterior region of the stomach. The gastric cæca of Orthoptera secrete a weak acid which emulsifies fats, or one which passes forward into the crop, there to act upon albuminoid substances. In the stomach the food may be acted upon by a fluid secreted by specialized cells of the epithelial wall. In various insects, certain cells project periodically into the lumen of the stomach as papillæ, which by a process of constriction become separated from the parent cells and mix bodily with the food. This phenomenon takes place in the larva of *Ptychoptera* (van Gehuchten), also in nymphs of Odonata (Needham), and is probably of widespread occurrence among insects. The chief function of the stomach is absorption, which is effected by the general epithelium.

Physiologically, the so-called stomach of an insect is quite unlike the stomach of a vertebrate, being more like an intestine.

Proctodæum.—At the anterior end of the *hind intestine* there is usually a *pyloric valve*, which prevents the contents of the intestine

from returning into the stomach. This valve may operate by means of a sphincter, or constricting, muscle, or may, as in *Collembola* (Fig. 146), consist of a backward-projecting circular ridge, or lip, which closes upon pressure from behind.

In its primitive condition the hind intestine is a simple tube (Fig. 146). Usually, however, it presents two or even three specialized regions, namely and in order, *ileum*, *colon* and *rectum* (Fig. 147). The hind intestine varies greatly in length and is frequently so long as to be thrown into convolutions (Fig. 152). The ileum is short and stout in grasshoppers (Fig. 147); long, slender and convoluted in many carniv-



FIG. 152.—Digestive system of *Belos-toma*. *c*, cæcum; *i*, ileum; *m*, mid intestine; *mt*, Malpighian tubes; *r*, salivary reservoir; *s*, salivary gland.—After Locy, from the *American Naturalist*.

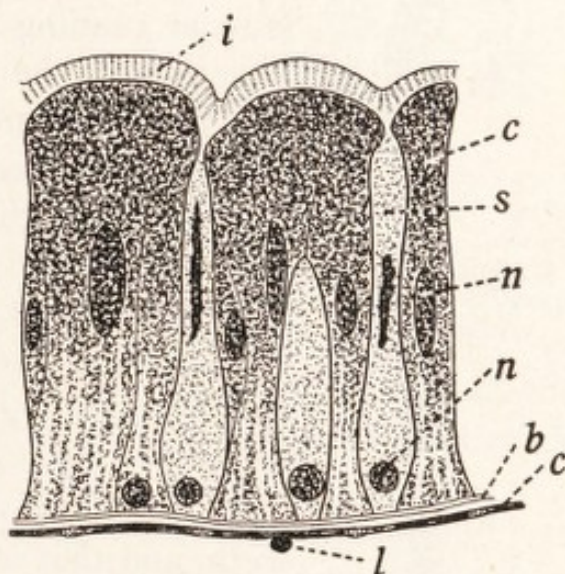


FIG. 153.—Wall of mid intestine of silk-worm, transverse section. *b*, basement membrane; *c*, circular muscle; *i*, intima; *l*, longitudinal muscle; *n*, *n*, nuclei of epithelial cells; *s*, secretory cell.

orous beetles; and quite short in caterpillars and most other larvæ; its function is absorption. The colon, often absent, is evident in Orthoptera and Lepidoptera and may bear (*Benacus*, *Dytiscus*, Silphidæ, Lepidoptera) a conspicuous cæcal appendage (Figs. 150, 152) of doubtful function, though possibly a reservoir for excretions. The colon contains indigestible matter and the waste products of digestion, including the excretions of the Malpighian tubes. The rectum (Fig. 147) is thick-walled, strongly muscular and often folded internally. Its office is to expel excrementitious matter, consisting largely of the indigestible substances chitin, cellulose and chlorophyll. The rectum terminates in the *anus*, which opens through the last segment of the abdomen, always above the genital aperture.

Histology.—The epithelial wall of the alimentary tract is a single layer of cells (Fig. 153), which secretes the *intima*, or lining layer, and the *basement membrane*—a delicate, structureless enveloping layer. The intima, which is continuous with the external cuticula, is chitinous in the fore and hind gut (which are ectodermal in origin), but not in the mid gut (entodermal), and usually exhibits extremely fine transverse striæ, which are due probably to minute pore canals. Surrounding the basement membrane is a series of *circular muscles* and outside these

is a layer of *longitudinal muscles* in the mid gut. In the fore gut the longitudinal muscles are frequently under the circular muscles; and in the hind gut there may be two layers of circular muscles with longitudinal muscles running between them; but there are many variations in the relative positions of the two kinds of muscles in different kinds of insects. The circular muscles serve to constrict the pharynx in sucking insects and, in general, to squeeze backward the contents of the alimentary canal by successively reducing its caliber. The longitudinal muscles, restricted almost entirely to the mid intestine, act in opposition to the constricting muscles to enlarge the lumen of the food canal and in addition to effect peristaltic movements of the stomach.

The intima of the crop is sometimes shaped into teeth, and that of the proventriculus is heavily chitinized and variously modified to form spines, teeth or ridges.

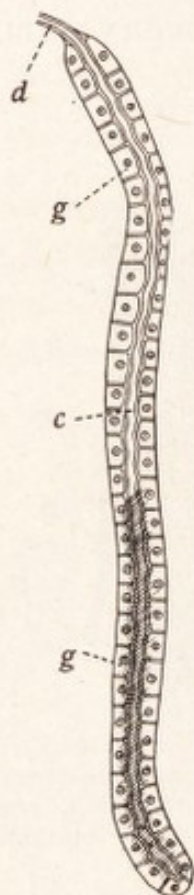


FIG. 154.—A simple salivary gland of *Cæcilius*. *c*, canal; *d*, duct; *g*, *g*, glandular cells.—After KOLBE.

Peritrophic Membrane.—This membrane forms an elastic tube inside the mid intestine and hind intestine; is derived usually from the epithelial cells of the mesenteron; and is, in some instances at least, renewed periodically. The peritrophic membrane, found in ants, wasps, caterpillars, and larvæ and adults of many beetles, etc., is characteristic of insects that consume solid food containing much hard, indigestible matter, and doubtless serves to protect the epithelium of the mid intestine from mechanical injury.

Salivary Glands.—In their simplest condition, the salivary glands are a pair of blind tubes (Fig. 154), one on each side of the œsophagus and opening separately at the base of the hypopharynx. Commonly, however, the glands open through two salivary ducts into a common, or evacuating, duct; a pair of salivary reservoirs (Fig. 155) may be

present and the glands are frequently branched or lobed, and though usually confined to the head, may extend into the thorax or even into the abdomen.

Many insects have more than one pair of glands opening into the pharynx or œsophagus; thus the honey bee has six pairs and Hymenop-

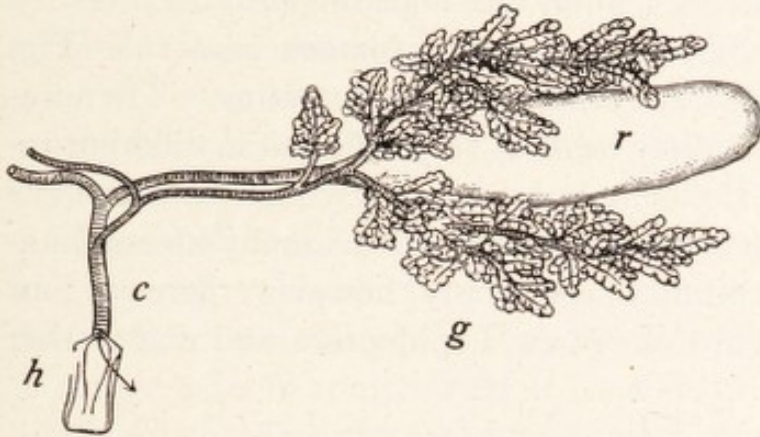


FIG. 155.—Right salivary gland of cockroach, ventral aspect. *c*, common duct; *g*, gland; *h*, hypopharynx; *r*, reservoir.—After MIALl and DENNY.

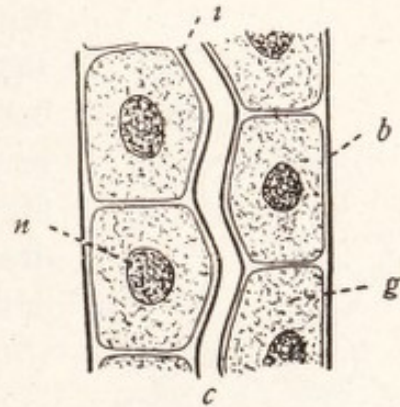


FIG. 156.—Histology of salivary gland of *Cæcilius*, radial section. *b*, basement membrane; *c*, canal; *g*, glandular cell; *i*, intima; *n*, nucleus.—After KOLBE.

tera as a whole have as many as ten different pairs. Though all these are loosely spoken of as salivary glands, it is better to restrict that term to the pair of glands that open at the hypopharynx.

All these cephalic glands are evaginations of the stomodæum (ectodermal in origin) and consist of an epithelial layer with the customary intima and basement membrane (Fig. 156). The nuclei are large, as is usually the case in glandular cells, and the cytoplasm consists of a dense framework (appearing in sections as a network) enclosing vacuoles of a clear substance—the secretion; the chitinous intima is penetrated by fine pore canals through which the secretion passes. In many insects, notably the cockroach, the common duct is held distended by spiral threads which give the duct much the appearance of a trachea.



FIG. 157.—One of the three-lobed salivary glands of a mosquito. The middle lobe secretes the poison.—After MACLOSKIE, from the *American Naturalist*.

In herbivorous insects the saliva changes starch into glucose, as in vertebrates; in carnivorous forms it acts on proteids and is often used to poison the prey, as in the larva of *Dytiscus*. In the mosquito each gland is three-lobed (Fig. 157); the middle lobe is different in appearance from the two others and secretes a poisonous fluid which is carried out

along the hypopharynx. Though this poison is said to facilitate the process of blood-sucking by preventing the coagulation of the blood, its primary use was perhaps to prevent the coagulation of proteids in the juices of plants.

Malpighian Tubes.—The kidney, or Malpighian, tubes, present in nearly all insects, are long, slender, blind tubes opening into the intestine immediately behind the stomach as a rule (Figs 147, 148), but always into the intestine. The number of kidney tubes is very different in different insects; Collembola have none, while Odonata have fifty or more and Locustidæ as many as one hundred and fifty; commonly, however, there are four or six, in Coleoptera, Lepidoptera and many other



FIG. 158.—Portion of Malpighian tube of caterpillar, *Samia cecropia*, surface view.



FIG. 159.—Cross-section of Malpighian tube of silkworm *Bombyx mori*. *b*, basement membrane; *c*, crystals; *i*, intima; *l*, lumen; *n*, nucleus; *p*, peritoneal layer. Greatly magnified.

orders. Not more than six and frequently only four occur in the embryo (Wheeler), though these few embryonic tubes may subsequently branch into many.

The Malpighian tubes (Fig. 158) are evaginations of the proctodæum and are consequently ectodermal. A cross-section of a tube shows a ring of from one to six or more large polygonal cells (Fig. 159), which often project into the lumen of the tube; the nuclei are usually large and may be branched, as in Lepidoptera. A chitinous intima, traversed by pore canals, lines the tube, and a delicate basement membrane is present, surrounded by a peritoneal layer of connective tissue. Furthermore, the urinary tubes are richly supplied with tracheæ. In function, the Malpighian tubes are analogous to the vertebrate kidneys and contain a great variety of substances, chief among which are uric acid and its derivatives (such as urate of sodium and of ammonium), calcium oxalate and calcium carbonate.

Parts of the fat-body may also be concerned in excretion; thus the fat-body in *Collembola* and *Orthoptera* serves for the permanent storage of urates.

7. CIRCULATORY SYSTEM

Insects, unlike vertebrates, have no system of closed blood-vessels, but the blood wanders freely through the body cavity to enter eventually the dorsal vessel, which resembles a heart merely in being a propulsatory organ.

Dorsal Vessel.—The dorsal vessel (Figs. 160, 164) is a delicate tube extending along the median dorsal line immediately under the integument. A simple tube in some larvæ, it consists in most adults chiefly of a series of chambers, each of which has on each side a valvular opening, or *ostium* (Fig. 161), which permits the ingress of blood but opposes its egress; within the chambers occur other valvular folds that allow the blood to move forward only. With few exceptions (*Ephemeridæ*) the dorsal vessel is blind behind and the blood can enter it only through the lateral ostia.

Aorta.—The posterior, or pulsating portion (*heart*) of the dorsal vessel is confined for the most part to the abdomen; the anterior portion, or *aorta*, extends as a simple attenuated tube through the thorax and into the head, where it passes under the brain and usually divides into two branches (Fig. 164), each of which may again branch. In the head the blood leaves the aorta abruptly and enters the general body cavity.

Alary Muscles.—Extending outward from the “heart,” or propulsatory portion, and making with the dorsal wall of the body a *pericardial chamber*, is a loose diaphragm, formed largely by paired fan-like muscles—the *alary muscles* (Figs. 160, 162). These are thought to assist the heart in its propulsatory action.

Structure of the Heart.—The wall of the heart is remarkably thin, and consists essentially of a muscular layer containing closely-set circular or spiral fibers and separated longitudinal fibers, with scattered nucleated cells among the fibers. This muscular tube is between two layers:

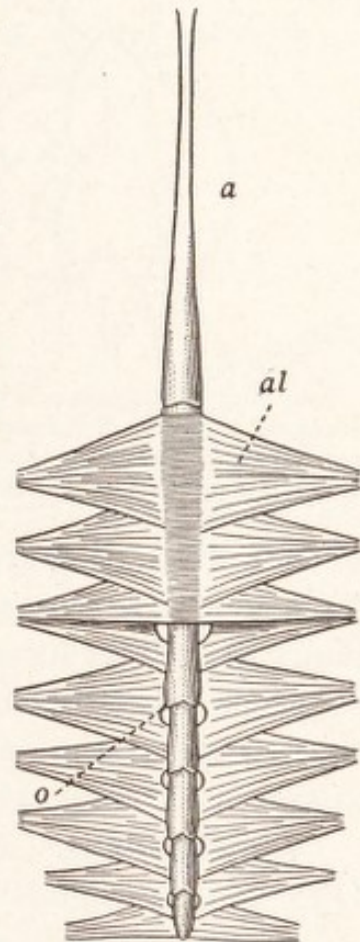


FIG. 160.—Dorsal vessel of beetle, *Lucanus*. *a*, aorta; *al*, alary muscle; *o*, ostium.—After STRAUS-DÜRKHEIM.

an inner membrane, or *sarcolemma*, and an outer layer of elastic connective tissue, the *adventitia*.

Pericardial Cells. Nephrocytes.—The *pericardial cells* occur generally in larvæ and imagines in the vicinity of the heart, usually on each side of the heart, and arranged frequently in longitudinal “garland-like”

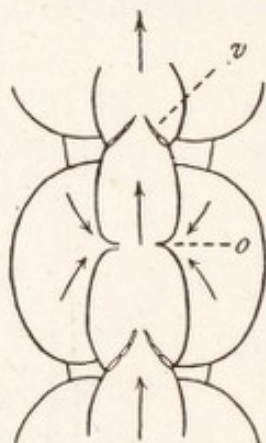


FIG. 161.—Diagram of a portion of the heart of a dragon fly nymph, *Epithea*. *o*, ostium; *v*, valve; the arrows indicate the course of the blood.—After KOLBE.

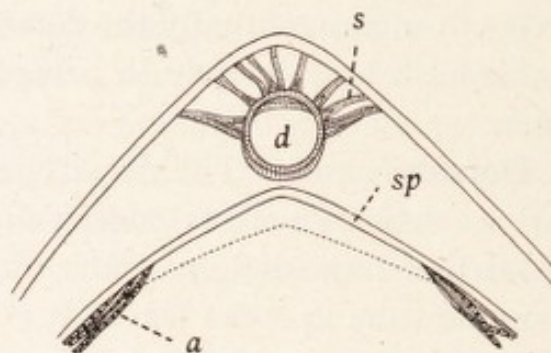


FIG. 162.—Diagrammatic cross-section of pericardial region of a grasshopper, *Edipoda*. *a*, alary muscle; *d*, dorsal vessel; *s*, suspensory muscles; *sp*, septum.—After GRABER.

series. They vary greatly in position, number, form, size and contents, and evidently bear some relation to the circulatory system; though many functions have been assigned to them. In allusion to their supposed excretory function, these cells have been named *nephrocytes*, the term applying particularly to such cells as select and absorb acid ammonia carmine, when that stain is injected into the living insect.

Ventral Sinus.—In many if not most insects a pulsatory septum (Fig. 180, *v*) extends across the floor of the body cavity to form a sinus,



FIG. 163.—Blood corpuscles of a grasshopper, *Stenobothrus*. *a-f*, corpuscles covered with fat-globules; *g*, corpuscle after treatment with glycerine, showing nucleus.—After GRABER.

in which the blood flows backward, bathing the ventral nerve cord as it goes. This ventral sinus supplements the heart in a minor way, as do also the local pulsatory sacs which have been discovered in the legs of aquatic Hemiptera and the head of Orthoptera.

Blood.—The blood, or *hæmolymph*, of an insect consists chiefly of a watery fluid, or *plasma*, which contains *corpuscles* or *leucocytes*. Though

usually colorless, the plasma is sometimes yellow (Coccinellidæ, Meloidæ), often greenish in herbivorous insects from the presence of chlorophyll, and sometimes of other colors; often the blood owes its hue to yellow or red drops of fat on the surface of the blood corpuscles (Fig. 163).

Hæmocytes.—The corpuscles or *hæmocytes* (*leucocytes*) are minute nucleated cells, 6 to 30 μ in diameter, variable in form even in the same species, but commonly (Fig. 163) round, oval or ovate in outline, though often disk-shaped, elongate or amœboid in form.

Function of the Blood.—The blood of insects contains many substances, including egg albumin, globulin, fibrin, iron, potassium and sodium (Mayer), and especially such a large amount of fatty material that its principal function is probably one of nutrition; the blood of an insect contains no red corpuscles and has little or nothing to do with the aeration of tissues, that function being relegated to the tracheal system.

Circulation.—The course of the circulation is evident in transparent aquatic nymphs or larvæ. In odonate or ephemeropterid nymphs, currents of blood may be seen (Fig. 164) flowing through the spaces between muscles, tracheæ, nerves, etc., and bathing all the tissues; separate outgoing and incoming streams may be distinguished in the antennæ and legs; the returning blood flows along the sides of the body and through the ventral sinus and the pericardial chamber, eventually to enter the lateral ostia of the dorsal vessel. A circulation of blood occurs in the wings of freshly emerged Odonata, Ephemeroptera, Coleoptera, Lepidoptera, etc., the currents trending along the tracheæ; this circulation ceases, however, with the drying of the wings.

The chambers of the dorsal vessel expand and contract successively from behind forward. At the expansion (*diastole*) of a chamber its ostia open and admit blood; at contraction (*systole*) the ostia close, as well as the valve of the chamber next behind, while the chamber next in front expands, affording the only exit for the blood. The valves close partly through blood-pressure and partly by muscular action.

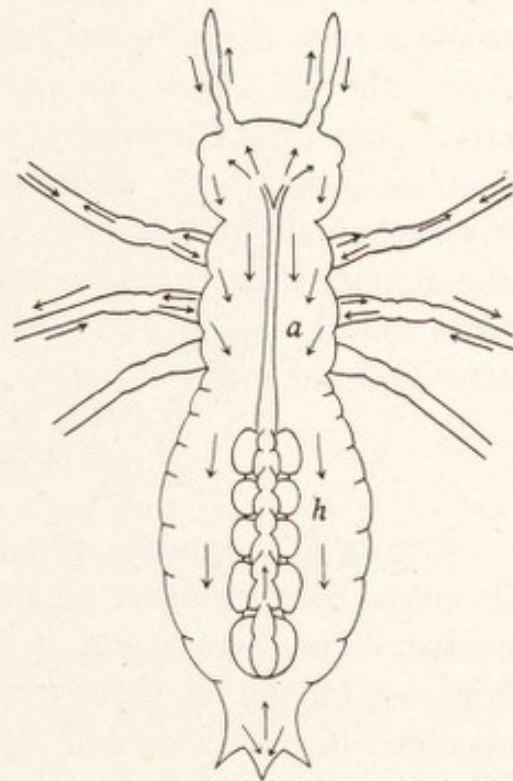


FIG. 164.—Diagram to indicate the course of the blood in the nymph of a dragon fly, *Epiheca*. *a*, aorta; *h*, heart; the arrows show directions taken by currents of blood.—After KOLBE.

The rate of pulsation depends to a great extent upon the activity of the insect and upon the temperature and the amount of oxygen or carbonic acid gas in the surrounding atmosphere. Oxygen accelerates the action of the heart and carbonic acid gas retards it. A decrease of 8° or 10° C. in the case of the silkworm lowers the number of beats from 30 or 40 to 6 or 8 per minute. The more active an insect, the faster its heart beats.

The rate of pulsation is very different in the different stages of the same insect. Thus in *Sphinx ligustri*, according to Newport, the mean number of pulsations in a moderately active larva before the first molt is about 82 or 83 per minute; before the second molt, 89, sinking to 63 before the third molt, to 45 before the fourth, and to 39 in the final larval stage; but the force of the circulation increases as the pulsations decrease in number. During the quiescent period immediately preceding each molt, the number of beats is about 30. In the pupal stage the number sinks to 22, and then lowers until, during winter, the pulsations almost cease. The moth in repose shows 41 to 50 per minute, and after flight as many as 139.

8. FAT-BODY

The *fat-body* appears (Fig. 165) as many-lobed masses of tissue filling in spaces between other organs and occupying a large part of the body cavity. The distribution of the fat-body is to a certain extent definite, however, for the fat-tissue conforms to the general segmentation and is arranged in each segment with an approach to symmetry. Much of this tissue forms a distinct peripheral layer in each segment, and masses of fat-body occur constantly on each side of the alimentary tract and also at the sides of the dorsal vessel, in the latter case forming the *pericardial fat-body*.

Fat-Cells.—The fat-cells (Fig. 166) are large and at first more or less spherical, with a single nucleus (though there are said to be two in *Apis* and several in *Musca*), but the cellular structure of the fat-tissue is often difficult to make out because the cells are usually filled with globules of fat (Fig. 167), while old cells break down, leaving only a disorderly network. The fat-cells sometimes contain an albuminoid substance, and usually the fat-body includes considerable quantities of uric acid or its derivatives, frequently in the form of conspicuous concretions.

Functions.—The physiology of the fat-system is still obscure. Probably the fat-body combines several functions. In caterpillars and other larvæ it furnishes a reserve supply of nutriment, at the expense of

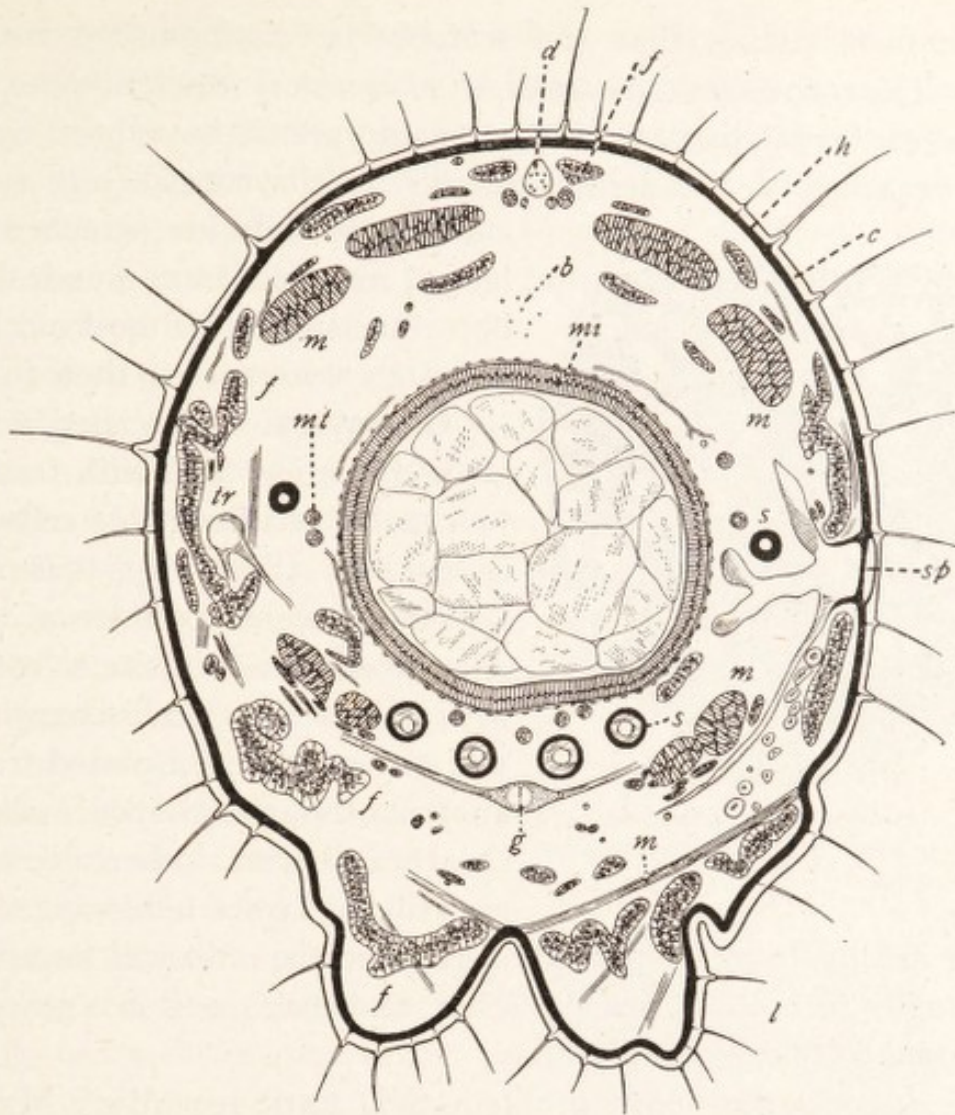


FIG. 165.—Transverse section of the abdomen of a caterpillar, *Pieris rapæ*. *b*, blood corpuscles; *c*, cuticula; *d*, dorsal vessel; *f*, fat-body; *g*, ganglion; *h*, hypodermis; *l*, leg; *m*, muscle; *mi*, mid intestine, containing fragments of cabbage leaves; *mt*, Malpighian tube; *s*, silk gland; *sp*, spiracle; *tr*, trachea.

which the metamorphosis takes place; the amount of fat increases as the larva grows, and diminishes in the pupal stage, though some of it lasts over to furnish nourishment for the imago and its germ cells. The gradual accumulation of uric acid and urates in the fat-body indicates an excretory function, particularly in *Collembola*, which have no Malpighian tubes. The intimate association between the ultimate tracheal branches and the fat-body has led some authorities to ascribe a respiratory function to the latter. A close relation of some sort exists also between the fat-system and the blood-system; fat-cells are found free in the blood, and the blood corpuscles originate in the thorax and



FIG. 166.—Fat-cells of a caterpillar, *Pieris*. *A*, cells filled with drops of fat; *B*, cell freed of fat-drops, showing nucleus.—After KOLBE.

abdomen from tissues that can scarcely be distinguished from fat-tissues. The corpuscles (*leucocytes*, or *phagocytes*) which in some insects absorb effete larval tissues during metamorphosis have been by some authors regarded as wandering fat-cells. Cells constituting the peri-

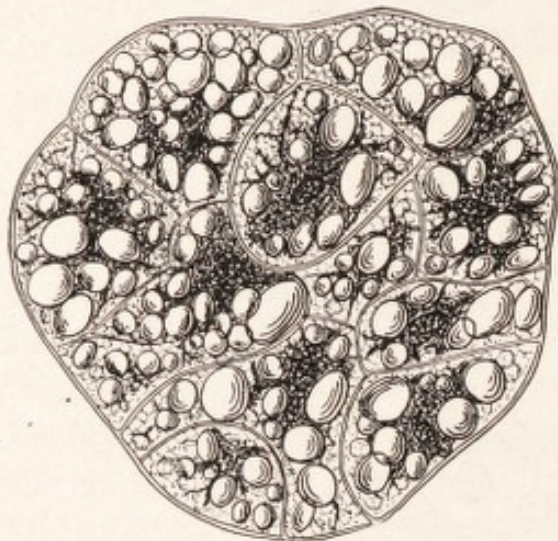


FIG. 167.—Section through fat-body of a silkworm, showing nucleated cells, loaded with drops of fat.

cardial fat-body are attached to the lateral muscles (*alary* muscles) of the dorsal vessel, but almost nothing is definitely known as to their function.

Ænocytes.—Associated with the fat-body proper and with tracheæ as well are the peculiar yellow cells known as *ænocytes* (Fig. 168), that occur in abdominal segments of larvæ. These cells are enormous in size as compared with all other insect-cells excepting ova, and are essentially isolated from one another, though grouped among tracheal branches into loose clusters, one on each side of a spiracle-bearing segment.

After arising from the primitive ectoderm the *ænocytes* never divide, but gradually increase in size (Wheeler), and their size is in a general way proportional to that of the fat-body.

Their function has been problematical until recently. Many observers have regarded them as ductless glands, having seen "microscopical exudations around the periphery of the cytoplasm, especially at times when the nucleus is greatly ramified, and therefore manifesting its great activity" (Glaser).

R. W. Glaser has thrown light upon the nature of the *ænocytic* fluid. By using three-year-old caterpillars of the leopard moth, *Zeuzera pyrina*, which have a great amount of fatty tissue and correspondingly large *ænocytes*, he was able to extract enough of the fluid for chemical experiments. He found by carefully conducted tests that the fluid had the power of oxidizing fats, by means of enzymes known as oxidases (though no fat-splitting enzyme, or lipase, was present), and concluded that the secretion of the *ænocytes* is used to oxidize the reserve food stored up by the larva in the form of fat.

Photogeny.—This phenomenon appears sporadically and by various means in protozoans, worms, insects, fishes and other animals. Lumi-

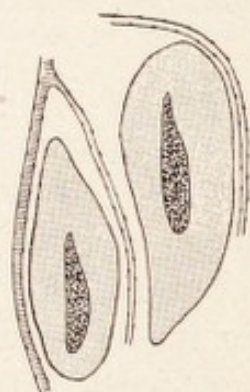


FIG. 168.—Ænocytes and accompanying tracheæ, from abdomen of a silkworm.

nosity in insects, though sometimes merely an incidental and pathological effect of bacteria, is usually produced by special organs in which light is generated, probably by the oxidation of a fatty substance.

There are not many luminous insects. Those best known are the Mexican and West Indian beetles of the genus *Pyrophorus* (Elateridæ), in which the pronotum bears a pair of luminous spots, and the common fireflies (Lampyridæ). In Lampyridæ the light is emitted from the ventral side of the posterior abdominal segments, and the structure of the photogenic organ is essentially the same throughout the family. In *Photinus* this organ (Fig. 169) consists of two layers; a ventral *photogenic layer* and a dorsal *reflecting layer*. The latter, white and opaque, consists of polygonal cells containing large quantities of crystals of urates; the former layer is composed of tracheal structures and intervening parenchyma cells. The tracheæ branch profusely in the photogenic layer, where the larger air-tubes are each surrounded by a more or less cylindrical mass of cells; tracheal branches penetrate between the cells of each *cylinder*, at the edge of which they pass into tracheoles which penetrate the photogenic tissue and anastomose with those of adjacent cylinders; in the meshes of the tracheolar network is a granular substance of fatty nature ("differentiated fat-body"), the oxidation of which is the source of the luminosity, it is inferred. The photogenic tissues of *Photinus*, after being dried and kept in sealed tubes, have retained their photogenic power for more than eighteen months, glowing after this interval upon the "application of water in the presence of air or oxygen" (McDermott). Three factors are involved in the production of the light: a substance to be oxidized, oxygen and water.

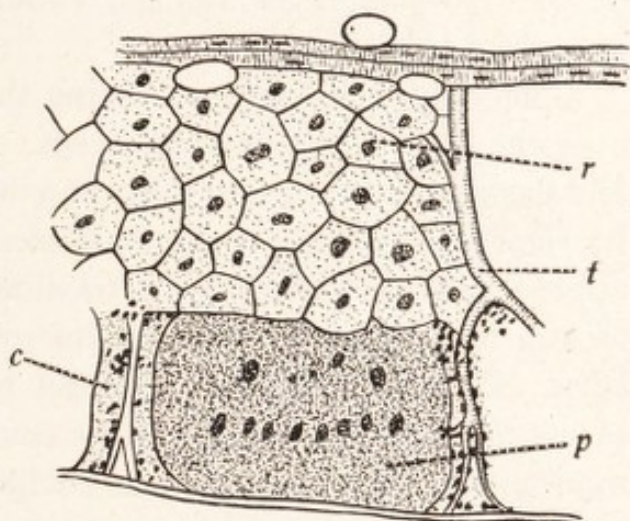


FIG. 169.—Transverse section of portion of photogenic organ of a firefly, *Photinus*. *c*, cylinder; *p*, photogenic layer; *r*, reflecting layer; *t*, trachea.—After TOWNSEND.

Professor W. E. Burge has found that the catalase content of a luminous insect where oxidation is presumably more intense is greater than that of a non-luminous insect where oxidation is less intense.

The rays emitted by the common fireflies are remarkable in being almost entirely light rays. According to Young and Langley, the radiations of an ordinary gas-flame contain less than three per cent. of visible

rays, the remainder being heat or chemical rays, of no value for illuminating purposes; while the light-giving efficiency of the electric arc is only ten per cent. and that of sunlight only thirty-five per cent. The luminous efficiency of the firefly is, however, not much under one hundred per cent.; in *Photuris pennsylvanica* it is about ninety-two per cent., according to Coblentz—an efficiency as yet unapproached by artificial means. The actinic power of the light is so slight that it affects a photographic plate only after a long exposure. Coblentz, who has applied most refined methods of measurement to the radiation of fireflies, found that exposures of one to five hours were necessary with the spectrograph. He was unable to detect any infra-red radiation; the thermal radiation, if present, being immeasurably small as yet. The intensity of the glow averages $\frac{1}{50,000}$ candle power in our common fireflies, according to Coblentz.

This luminosity serves to bring the sexes together. "The male flies over the tops of the grasses, weeds, etc., dropping down between them and flashing; any females that come within the range of his flash, answer by their slower flash; if the male sees this answering flash from one, he approaches her, flashes again, to which she answers, and he then finally locates her definitely by means of subsequent flashes," as McDermott says. He found that he could get responses from the females by imitating the flash of the male with a small electric bulb or even with a common safety match, and that he could deceive the males also by flashing the tiny electric light after the manner of the female.

Synchronism.—Several observers in the Philippines and East Indies have seen the phenomenon of thousands of fireflies flashing exactly in unison; all the fireflies in the same tree, for example, flashing simultaneously (105–109 flashes per minute, in one instance), with regular intervals of darkness. This rare phenomenon, to which Professor E. S. Morse called attention, has attracted considerable interest in the columns of *Science*. There seems to be no doubt as to the accuracy of the observations, but an explanation as to how the synchronism is effected and regulated is still lacking. The phenomenon can hardly be due to chance when thousands of individuals are involved. The fireflies referred to, in Siam and the Philippines, belong to the genus *Calaphotia* (O. A. Reinking).

9. RESPIRATORY SYSTEM

In insects, as contrasted with vertebrates, the air itself is conveyed to the remotest tissues by means of an elaborate system of branching air-

tubes, or *tracheæ*, which receive air through paired segmentally-arranged *spiracles*. Each spiracle is commonly the mouth of a short tube which opens into a *main* tracheal trunk (Fig. 170) extending along the side of the body. From the two main trunks branches are sent which divide and subdivide and terminate in extremely delicate tubes, which penetrate even between muscle fibers; between the ommatidia of the compound eyes and possibly enter cells. In most cases each main longitudinal trunk gives off in each segment (Fig. 171) three large branches: (1) an upper, or *dorsal*, branch which goes to the dorsal muscles; (2) a middle, or *visceral*, branch, which supplies the alimentary tract and the reproductive organs; (3) a lower, or *ventral*, branch, which pertains to the ventral ganglia and muscles.

In many swiftly flying insects (dragon flies, beetles, moths, flies and bees) there occur tracheal pockets, or *air-sacs*, which were formerly and erroneously supposed to diminish the weight of the insect, but are now regarded as simply air-reservoirs. Sacs filled with air lessen the specific gravity of an insect in a fluid medium; but do not increase the buoyancy of an insect in the air, unless the contained air is warmer than the surrounding air; and in the case of birds, it has been found that the air contained in the bones, though warmer than the surrounding medium, has no appreciable effect on flight.

Types of Tracheation.—Two types of tracheal system are distinguished for convenience: (1) the primary, open, or *holopneustic* type described above, in which the spiracles are functional; (2) the secondary, closed, or *apneustic* type, in which the spiracles are either functionless or absent. This type is illustrated in Collembola and such aquatic nymphs and larvæ as breathe either directly through the skin or else by means of gills. The two types are connected by all sorts of intermediate stages.

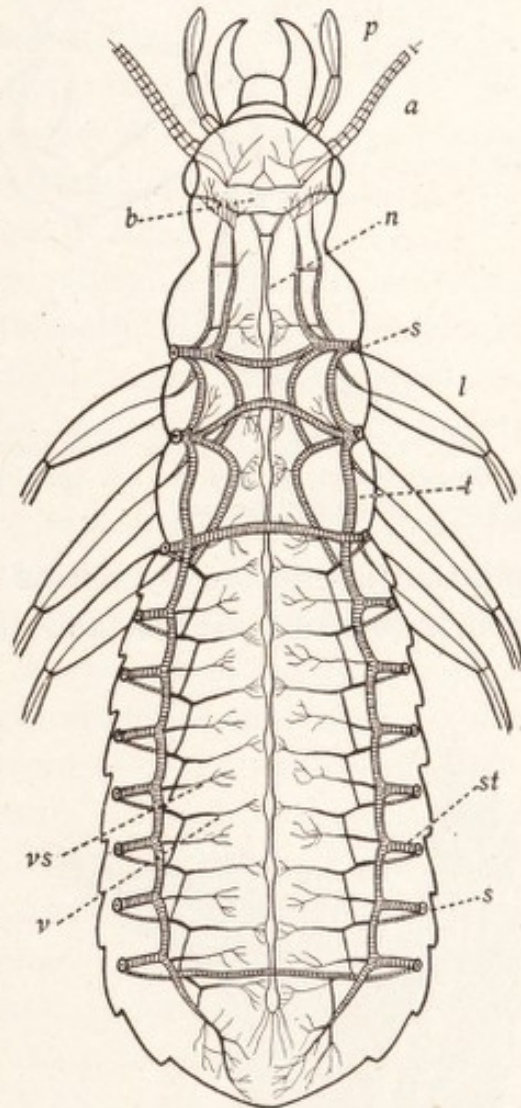


FIG. 170.—Tracheal system of an insect. *a*, antenna; *b*, brain; *l*, leg; *n*, nerve cord; *p*, palpus; *s*, spiracle; *st*, spiracular, or stigmatal, branch; *t*, main tracheal trunk; *v*, ventral branch; *vs*, visceral branch.—After KOLBE.

Tracheal Gills.—In many aquatic nymphs and larvæ the spiracles are suppressed (though they become functional in the imago) and res-

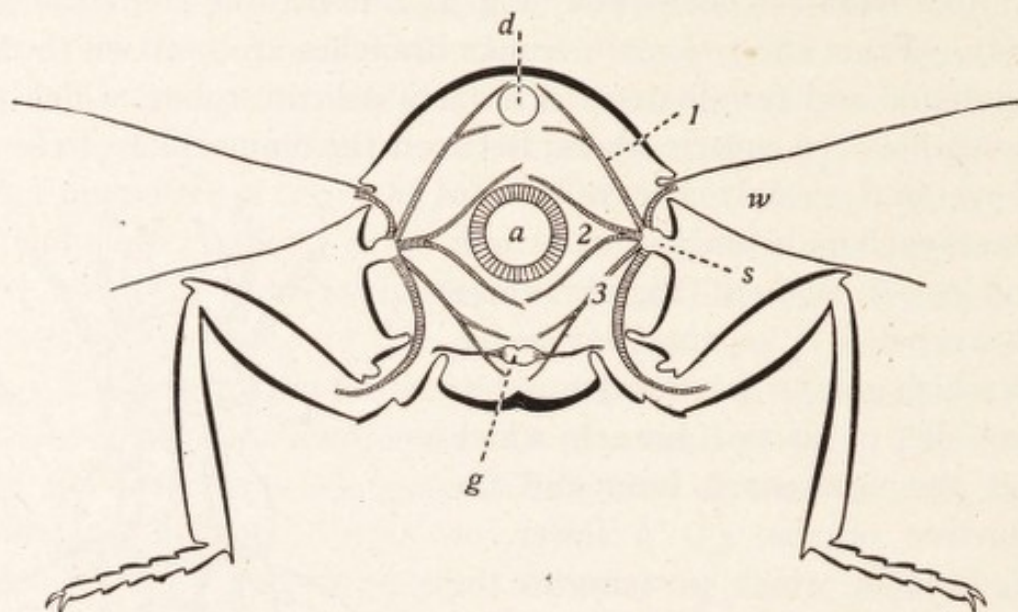


FIG. 171.—Diagrammatic cross-section of the thorax of an insect. *a*, alimentary canal; *d*, dorsal vessel; *g*, ganglion; *s*, spiracle; *w*, wing; *1*, dorsal tracheal branch; *2*, visceral branch; *3*, ventral branch.

piration is effected by means of gills; these are cuticular outgrowths which contain tracheæ and tracheoles and are commonly lateral or

caudal in position. *Lateral tracheal gills* are highly developed in ephemerid nymphs (Fig. 172), in which a pair occurs on some or all of the first seven segments of the abdomen; a few genera have cephalic or thoracic gills. Larvæ of Trichoptera have paired abdominal gills varying greatly in form and position, and Perlidæ often have paired thoracic gills. *Caudal tracheal gills* are conspicuous in nymphs of damselflies (Fig. 173) as three foliaceous appendages. A few coleopterous larvæ of aquatic habit, as *Gyrinus* and *Cnemidotus*, possess tracheal gills, as do also caterpillars of the genus *Paraponyx* (Fig. 174), which feed on the leaves of several kinds of water plants.



FIG. 172.—Lateral gill from abdomen of a May fly nymph, *Hexagenia variabilis*. Enlarged.

Though manifold in form, tracheal gills are usually more or less foliaceous or filamentous, presenting always an extensive respiratory surface; their integument is thin and the tracheæ spread closely beneath

it. These adaptations are often supplemented by waving movements of the gills, as in May fly nymphs, and by frequent movements of the insect from one place to another.

Especially noteworthy are the *rectal tracheal gills* of odonate nymphs. In these insects the lining of the rectum forms numerous papillæ or lamellæ, which contain a profusion of delicate tracheal branches; these are bathed by water drawn into the rectum and then expelled, at rather irregular intervals. A similar rectal respiration occurs also in ephemerid nymphs and mosquito larvæ.

A few forms, chiefly Perlidæ, are exceptional in retaining tracheal gills in the adult stage; in some imagines they are merely vestiges of the nymphal gills, but in others, such as *Pteronarcys* (Fig. 19), which habitually dips into the water and rests in moist situations, the gills probably supplement the spiracles.

Further details on the respiration of aquatic insects are given in Chapter IV.

Blood-gills.—In a few aquatic larvæ, *Simulium* and *Chironomus* for example, there are thin tubular evaginations of the integument known as *blood-gills*, into which the blood flows. In trichopterous larvæ (caddis-worms) the blood-gills are eversible. Some authors regard the ventral eversible sacs of *Scolopendrella* and *Thysanura*, as well as the vesicles of the ventral tube of *Collembola*, as blood-gills.

Spiracles.—The paired external openings of the tracheæ, termed *spiracles* or *stigmata*, occur on the sides of the thorax and abdomen; there being not more than one pair to a segment, though not all segments bear them. As a rule, there are two thoracic and eight abdominal pairs; these belonging to the mesothorax, metathorax, and first eight abdominal segments, respectively. Adult insects do not have more than ten pairs, with the exception of *Japyx* (see page 60, footnote).

The spiracles, variable in position, are situated usually between two segments of the body; but often at the anterior borders of the segments to which they belong; though they may occur farther back on the segments.

In most embryo insects there are eleven pairs of spiracles—three

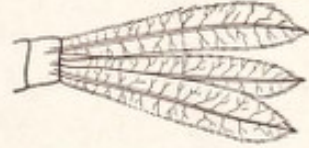


FIG. 173.—Caudal gills of a damselfly nymph, enlarged.

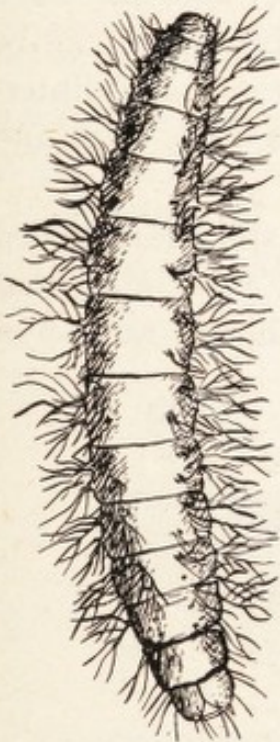


FIG. 174.—Caterpillar of *Paraponyx obscuralis*, to show tracheal gills. Length, 15 mm.—After HART.

thoracic and eight abdominal; but in adults the prothoracic pair is almost always suppressed. (See page 60.)

Though tracheæ are absent in most Collembola, *Sminthurides aquaticus* has tracheæ in the head, which open through a pair of spiracles on the posterior part of the head, there being a spiracle on each side of the neck. Two other species of Collembola, *Sminthurus fuscus* and *Actaletes neptuni*, are likewise known to have such a tracheal system, limited to the head.

The spiracles are usually provided with bristles, hairs or other processes to exclude dust; or the hairs of the body may serve the same purpose, as in Lepidoptera and Diptera; in many beetles the spiracles are protected by the elytra; but in other beetles and in many Hemiptera and Diptera the spiracles are unprotected externally. Larvæ that live in water or mud may have spiracles at the end of a long tube, which can be thrust up into the pure air; this is true of the dipterous larvæ of *Eristalis*, *Bittacomorpha* (Fig. 175) and *Culex* (Fig. 232).

FIG. 175.—Larva of *Bittacomorpha clavipes*, showing respiratory tube.—Natural size.—After HART.

Closure of Spiracles.—As a rule, a spiracle is opened and closed periodically by means of a valve, operated by a special *occludor* muscle. In dipterous larvæ the closure is effected by the contraction of

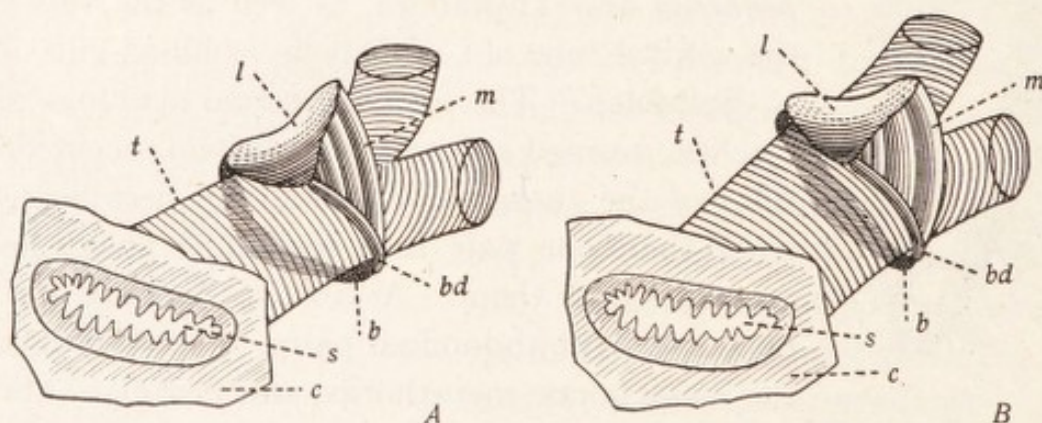


FIG. 176.—Apparatus for closing the spiracular trachea in a beetle, *Lucanus*. A, trachea opened; B, closed; b, bow; bd, band; c, external cuticula; l, lever; m, muscle; s, spiracle; t, trachea.—After JUDEICH and NITSCHÉ.

a circular muscle, but Coleoptera and Lepidoptera, among other insects, have a somewhat complex apparatus for closing the trachea immediately behind the spiracle. Thus, in the stag-beetle, a crescentic *bow* (Fig. 176, b) extends half around the trachea, and the rest of the circumference is spanned by a *lever* (l) and a *band* (bd); these three chitinous parts,

articulated together, form a ring around the trachea. Furthermore, a muscle (*m*) connects the lever and the band. As the muscle shortens, the lever turning upon the end of the band as a fulcrum, pulls the bow

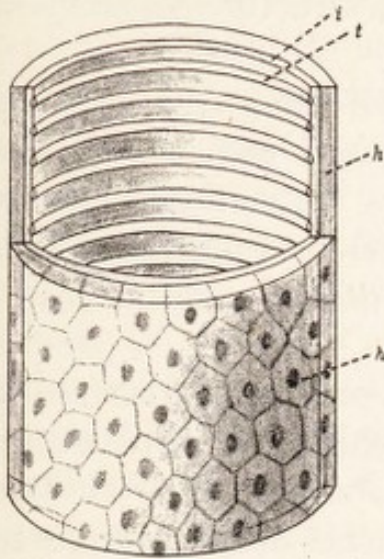


FIG. 177.—Structure of a trachea. *h*, tracheal hypodermis; *i*, intima; *t* taenidium.



FIG. 178.—Tracheolar end-network from silk gland of *Porthetria dispar*. *p*, peritracheal membrane; *t*, tracheal capillary.—After WISTINGHAUSEN.

toward the lever and band until the enclosed trachea is pinched together. When the muscle relaxes, the trachea opens by its own elasticity.

Structure of Tracheæ.—The tracheæ originate in the embryo as simple in-pocketings of the outer germ layer, or ectoderm, and from

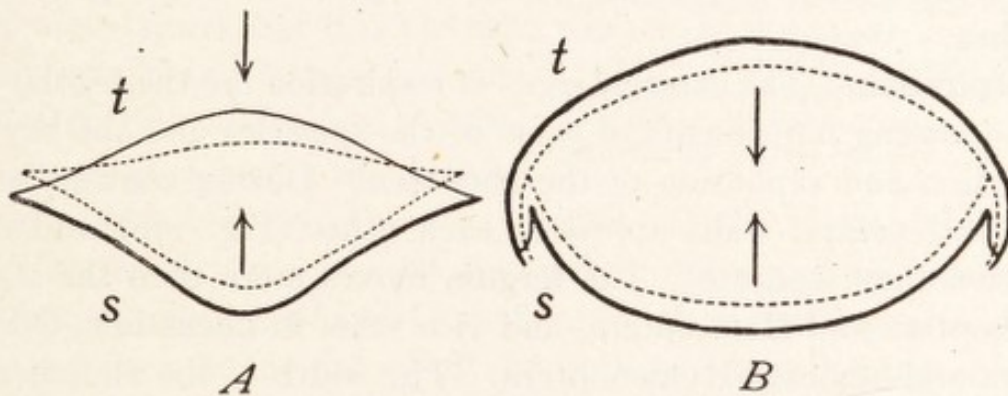


FIG. 179.—Transverse sections of abdominal segments to illustrate respiratory movements. *A*, cockroach (*Blatta*); *B*, bee (*Bombus*); *s*, sternum; *t*, tergum. The dotted lines indicate positions of terga and sterna after expiration; the continuous lines, after inspiration.—After PLATEAU.

these the countless tracheal branches are derived by the same process of invagination. The lining membrane of a trachea is, then, continuous with the external cuticula, and the cellular wall of a trachea is continuous with the rest of the hypodermis. This wall consists of a layer of polygonal cells (Fig. 177) fitting closely together as a *pavement epithelium*. The chitinous lining, or *intima*, is thickened at regular intervals to form thread-like ridges, which course around the inner circumference

in essentially a spiral manner, though the continuity of the so-called spiral thread is frequently interrupted. These elastic threads, or *tænidia*, serve to keep the trachea open without affecting its flexibility.

On the outer surface of the epithelium is a thin structureless *basement membrane*.

Tracheoles.—The ultimate divisions of the air-tubes (Fig. 178) are extremely delicate tubes, or *tracheoles*, which rarely end blindly, but anastomose with one another, forming a capillary network of confluent tubes, measuring less than 0.001 mm. in diameter, and filled, not with air, but with a fluid. Respiration takes place doubtless by means of the tracheoles rather than the tracheæ.

In a caterpillar, these capillary tubes spread out over the surface of the cells of the silk-glands, according to Wistinghausen; and penetrate into the gland-cells themselves, according to Holmgren; other authors differ also as to the relation of the ultimate branches of the air-tubes to the cells which they serve.

The tracheoles consist of (1) a well developed *peritracheal membrane*, which spreads out web-like between the bases of the tubes; and (2) a chitinous *intima* without *tænidia*; the tracheoles being connected with the tracheæ proper by means of (3) *transition cells*.

Unlike tracheæ, the tracheolar tubes do not arise directly by invagination, but develop each within a single cell of the epithelium of a trachea.

Respiration.—The external signs of respiration are the regular opening and closing movements of some of the spiracles and the rhythmic contraction and expansion of the abdomen. During contraction, the dorsal and ventral walls approach each other (Fig. 179) and during expansion they separate. The tergum moves more than the sternum in Coleoptera and Heteroptera, and vice versa in Locustidæ, Odonata, Diptera and aculeate Hymenoptera. The width of the abdomen usually changes but little during respiration, for the tergal and sternal movements are taken up by the *pleural membranes* which, as in the grasshopper, infold at contraction and straighten out at expansion. Other respiratory movements occur, but they are of minor importance.

The rate of respiration increases or diminishes with the activity of the insect and with temperature and other conditions. In six specimens of *Melanoplus differentialis*, held between the fingers, the thoracic spiracles opened and closed respectively 34, 43, 45, 54, 60 and 61 times per minute. Four individuals of *M. femur-rubrum* under the same circumstances gave 70, 78, 90 and 92.

At expansion inspiration takes place, and at contraction expiration occurs. In the grasshopper, the thoracic spiracles open almost simultaneously with the expansion of the abdomen. Contraction is effected by special vertical expiratory muscles (Fig. 180), but expansion is due to the elasticity of the abdominal wall, as a rule; this is the reverse of what occurs in mammals, where expiration is passive and inspiration active. Inspiratory muscles are found, however, in Locustidæ, Trichoptera and Hymenoptera.

Though the respiratory movements of an insect may be studied with a hand-lens, a more precise method is that of Plateau—the chief authority on insect physiology—who made use of the stereopticon to project an enlarged profile of the insect upon a screen, on which could be marked the different contours of the abdomen at its phases of inspiration and expiration.

The way in which the air reaches the finest tracheal branches is not clearly ascertained, but it is thought that air is forced into these tubes by pressure from the abdominal muscles, while its escape through the spiracles

is being prevented by the compression of the stigmal tracheæ.

The respiratory movements are entirely reflex and are independent of the brain or subœsophageal ganglion, for they continue after decapitation and even in the detached abdomen of a grasshopper or dragon fly. Each ventral ganglion of the body is an independent respiratory center for its particular segment.

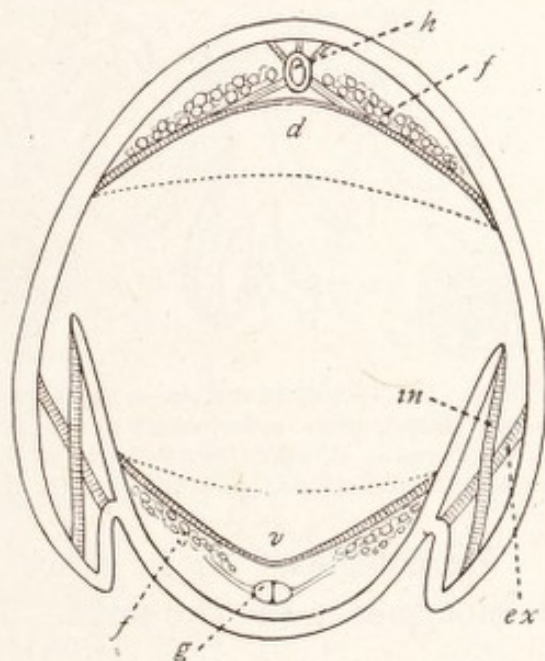


FIG. 180.—Diagrammatic cross-section of abdomen of a grasshopper, *Tropidacris*. *d*, dorsal septum, or diaphragm; *ex*, expiratory muscle; *f*, fat-body; *g*, ganglion; *h*, heart; *in*, inspiratory muscle; *v*, ventral septum, below which is the ventral sinus. The dorsal and ventral septa rise and fall periodically.—After GRABER.

10. REPRODUCTIVE SYSTEM

The sexes are always separate in insects, hermaphroditism occurring only as an abnormal condition. The sexual organs, situated in the abdomen, consist essentially of a pair of ovaries or testes and a pair of ducts (oviducts or seminal ducts, respectively). Primitively, the ducts open separately, as they still do in Ephemeroidea, but in almost all other insects

the two ducts enter a common evacuating duct (*vagina* or *ejaculatory duct*). The vagina commonly opens just behind the eighth abdominal sternite, and the ejaculatory duct behind the ninth.

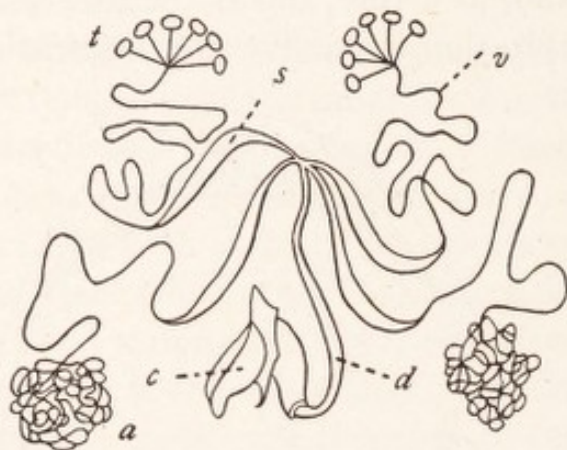


FIG. 181.—Reproductive system of male beetle, *Melolontha*. *a*, accessory gland; *c*, copulatory organ; *d*, ejaculatory duct; *s*, seminal vesicle; *t*, testis; *v*, vas deferens.—After KOLBE.

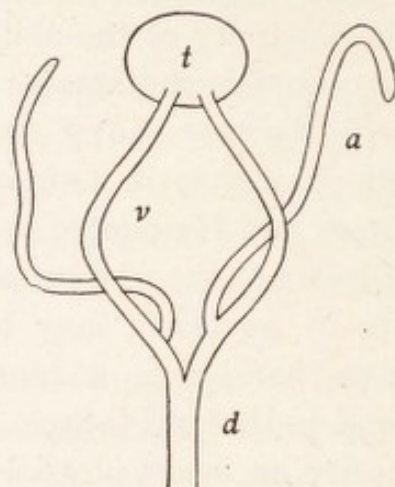


FIG. 182.—Reproductive system of male Lepidoptera. *a*, accessory gland; *d*, ejaculatory duct; *t*, united testes; *v*, vas deferens.—After KOLBE.

Homologies.—As in other animals, the reproductive organs are homologous in the two sexes. Thus:

MALE	FEMALE
<i>Testes</i>	= <i>Ovaries</i>
<i>Seminal ducts</i>	= <i>Oviducts</i>
<i>Ejaculatory duct</i>	= <i>Vagina</i>
<i>Seminal vesicle</i>	= <i>Seminal receptacle</i>
<i>Accessory glands</i>	= <i>Accessory glands</i>
<i>Penis and accessories</i>	= <i>Ovipositor</i>

Male Organs.—Each *testis*, though sometimes a single blind tube, is usually a group of tubes or sacs (Fig. 181), *testicular follicles*, which open into a seminal duct (*vas deferens*). In most Lepidoptera the testes are secondarily united into a single mass (Fig. 182) as also in Locustidæ. The two seminal ducts enter the common *ejaculatory duct*, which terminates in the intromittent organ, or *penis*. Often each vas deferens is dilated near its mouth into a *seminal vesicle*, or reservoir; or there may be only a single seminal vesicle, arising from the common duct. One or more pairs of glands opening into the vasa deferentia or the *ductus ejaculatorius* secrete a fluid which mixes with the spermatozoa and oftentimes unites them into packets, known as *spermatophores*.

All these parts are subservient to the formation, preservation and emission of the *spermatozoa*. These minute, thread-like bodies (Fig.

183) arise in the testicular follicles from a *germinal epithelium*, and consist, as in vertebrates, of a *head*, *middle-piece* and a vibratile *tail*—without entering into the finer structure.

Female Organs.—Each *ovary* (Fig. 184) consists of one or more tubes opening into an *oviduct*. The two oviducts enter a common duct, the *vagina*, which opens to the exterior, often through an *ovipositor*. Frequently the vagina is expanded as a pouch, or *bursa copulatrix*, though in *Lepidoptera* the bursa and the vagina are distinct from each other and open separately (Fig. 185). In most insects a dorsal evagination of the vagina forms a *seminal receptacle*, or *spermatheca*, from which spermatozoa emerge to fertilize the eggs. The *accessory glands*, either paired or single, provide a secretion for attaching the eggs to foreign objects, cementing the eggs together, forming an egg-capsule, etc.

In each ovarian tube, or *ovariole*, are found ova in successive stages of growth, the largest and oldest ovum being nearest the oviduct. In the primitive type of egg-tube, as in *Thysanura* and *Orthoptera* (Fig. 186, *A*) every chamber contains an ovum; in more specialized types, every other chamber contains a nutritive cell instead of a germ cell, the nutritive cells serving as food for the adjacent ova (*B*); or the nutritive cells, instead of alternating with the ova, may be collected in a special chamber, beyond the ovarian chambers (*C*). An egg-tube is usually prolonged distally as a terminal filament or *suspensor*, the free end of which is attached near the dorsal vessel.

Ovaries and testes arise from indifferent cell or primitive germ cells, which are at first exactly alike in the two sexes. In the female, certain of these cells form ova and others form a *follicle* around each ovum (Fig. 187). In the male, the primary germ cells form cells termed *spermatogonia*; each of these forms a *spermatocyte*, and this gives rise to four *spermatozoa*.

Hermaphroditism.—The phenomenon of *hermaphroditism*, defined as “the union, real or apparent, of the two sexes in the same individual,” occurs among insects only as an extremely rare abnormality (except in

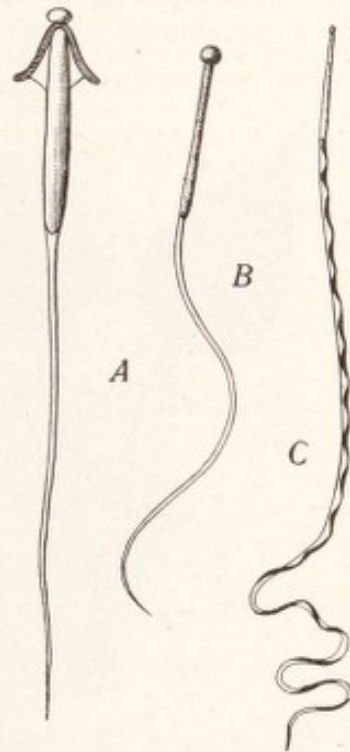


FIG. 183. — Spermatozoa. *A*, grasshopper; *B*, cockroach, *Blatta*; *C*, beetle, *Coprins*.—After BÜTSCHLI and BALLOWITZ.

Termitoxinia, mentioned beyond). Speyer estimated that in Lepidoptera only one individual in thirty thousand is hermaphroditic. Bertkau (1889) listed 335 hermaphroditic arthropods, of which 8 were crustaceans, 2 spiders, 2 Orthoptera, 8 Diptera, 9 Coleoptera, 51 Hymenoptera and 255 Lepidoptera. The large proportion of Lepidoptera is due in great measure to the fact that they are collected oftener than other insects (excepting possibly Coleoptera) and that sexual dimorphism

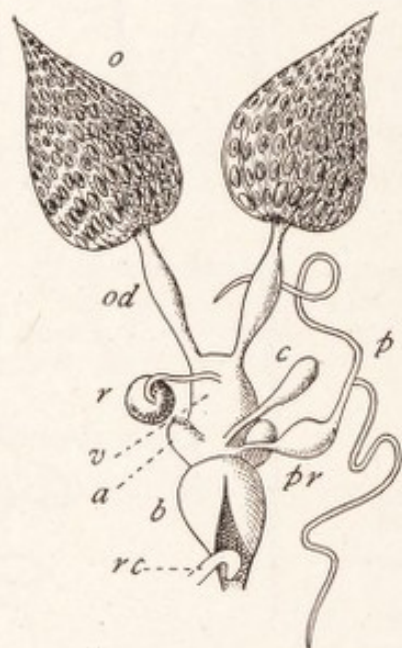


FIG. 184.—Reproductive system of queen honey bee. *a*, accessory sac of vagina; *b*, bulb of stinging apparatus; *c*, colleterial, or cement, gland; *o*, ovary; *od*, oviduct; *p*, poison glands; *pr*, poison reservoir; *r*, receptaculum seminis; *rc*, rectum; *v*, vagina.—After LEUCKART.

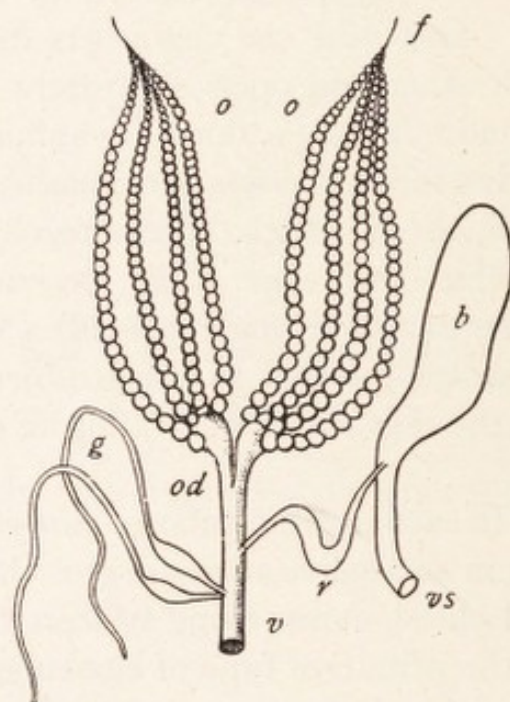


FIG. 185.—Reproductive system of female Lepidoptera. *b*, bursa copulatrix; *f*, terminal filament; *g*, cement glands; *o*, ovaries; *od*, oviduct; *r*, receptaculum seminis; *v*, vagina; *vs*, vestibule, or entrance to bursa.—After KOLBE.

is so prevalent in the order that hermaphrodites are easily recognized.

The most common kind of hermaphroditism is that in which one side is male and the other female, as in Fig. 188. Bertkau found this right-and-left hermaphroditism in 153 individuals. In other instances the antero-posterior kind may occur, as when the fore wings are of one sex and the hind wings of the other; rarely, the characters of the two sexes are intermingled.

Hermaphroditic insects are such rarities that very few of them have been sacrificed to the dissecting needle in order to determine whether the phenomenon involves the primary organs as well as the secondary sexual characters. Where dissections have been made it has been found usually that hermaphroditism does extend to the reproductive

organs themselves. Thus a butterfly with male wings on the right side and female wings on the left would have a testis on the right side of the abdomen and an ovary on the left side.

True hermaphroditism, existing "only when the essential organs of reproduction are united in one individual," and are functional, is said to occur normally in a peculiar wingless termitophilous fly, *Termitoxinia*. Other instances of hermaphroditism among insects are, strictly

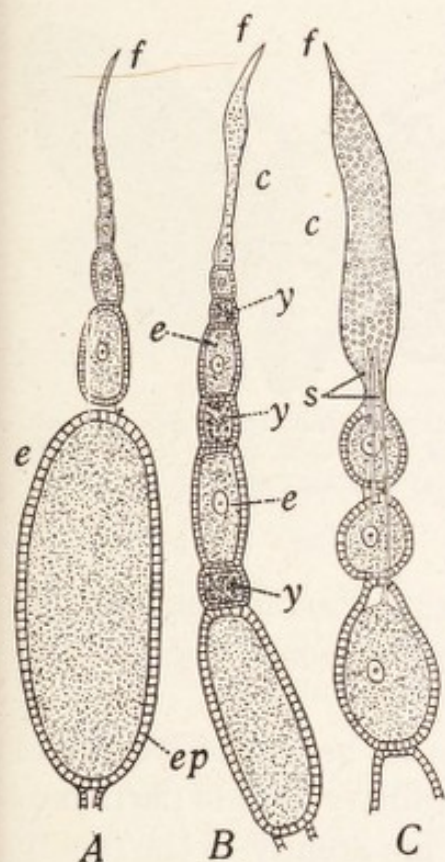


FIG. 186.—Types of ovarian tubes. *A*, without nutritive cells; *B*, with alternating nutritive and egg-cells; *C*, with terminal nutritive chamber, *c*, terminal chamber; *e*, egg-cell; *ep*, follicle epithelium; *f*, terminal filament; *s*, strands connecting ova with nutritive chamber; *y*, yolk, or nutritive cells.—From Lang's *Lehrbuch*.

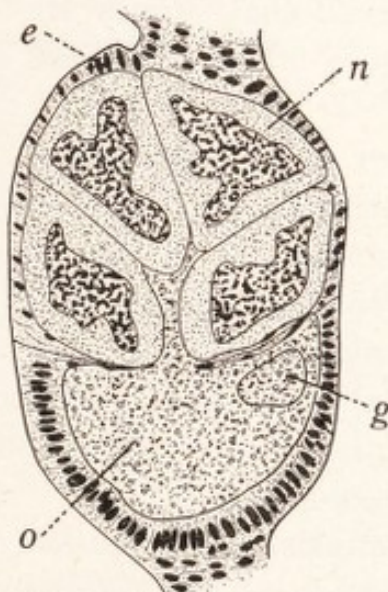


FIG. 187.—Ovum of a butterfly, *Vanessa*, in its follicle. *e*, follicle epithelium; *g*, germinal vesicle; *n*, branching nucleus of nutritive cell; *o*, ovum.—After WOODWORTH.

speaking, examples of *gynandromorphism*, in which secondary sexual characters of both sexes occur in the same individual. A *gynandromorph* often has ovaries and testes at the same time, but both are not functional.

Parthenogenesis.—Reproduction without fertilization is a normal phenomenon in not a few insects. This *parthenogenesis* may easily be observed in plant lice. In these insects there are many successive broods consisting of females only, which bring forth living young; at definite intervals, however, and usually in autumn, males appear also, and fertilized eggs are laid which last over winter. This cyclic reproduction, by the way, is known as *heterogeny*. Among Hymenoptera, parthenogenesis is prevalent, usually alternating with sexual reproduction, as in many Cynipidæ. In some Cynipidæ, however, males are

unknown; such is the case also in some Tenthredinidæ. The statement has long been made that the unfertilized eggs of worker ants, bees and wasps produce invariably males; it has been found, however, that the parthenogenetic worker eggs of the ant *Lasius niger* may produce normal workers (Reichenbach, Mrs. A. B. Comstock).

In the honey bee, unfertilized eggs produce always males; and it is at present rather generally believed that drones are not produced from fertilized eggs.

Professor A. F. Shull determined experimentally that unfertilized eggs of the thysanopter, *Anthothrips verbasci* produce only males; and concluded also that fertilized eggs produce only females. Parthenogenesis has been recorded as occurring also in a few moths, some Coccidæ and many Thysanoptera.

Pædogenesis.—In *Miastor* and a few other genera of Itonididæ young are produced by the *larva*. This extraordinary form of parthenogenesis is termed *pædogenesis*, and is limited apparently to the family



FIG. 189.—Young pædogenetic larvæ of *Miastor* in the body of the mother larva. Greatly enlarged.—After PAGENSTECHER.

Itonididæ. The pædogenetic larvæ of *Miastor* (Fig. 189) develop before the oviducts have appeared and escape by the rupture of the mother. After several successive generations of this kind the result-

ing larvæ pupate and form normal male and female flies:

An excellent account of *Miastor* has been given by Dr. Felt, who has discovered this remarkable genus in New York State.

The *pupa* of a species of *Chironomus* occasionally deposits unfertilized eggs, which develop, however, in the same manner as the fertilized eggs of the species.



FIG. 188.—Gynandromorphic gipsy moth, *Porthetria dispar*; right side, male; left, female. Natural size.—After TASCHENBERG from Hertwig's *Lehrbuch*.

CHAPTER III

DEVELOPMENT

I. EMBRYOLOGY

Ovum.—The ovum of an insect, as of any other animal, is a single cell (Fig. 190), with a large nucleus (*germinal vesicle*), a large *nucleolus*, nutritive matter, or *yolk* (*deutoplasm*), contained in cytoplasm, and a cell wall (*vitelline membrane*) secreted by the ovum. The egg-shell, or *chorion*, is secreted around the ovum by surrounding ovarian cells.

Maturation.—As a preparation for fertilization the germinal vesicle divides twice, forming two *polar bodies*, and as the first of these bodies may itself divide, there result four cells; three of these, however—the polar bodies—are minute and rudimentary.

These phenomena of *ovogenesis* are paralleled in the development of the spermatozoa, or *spermatogenesis*; for the *primary spermatocyte* gives rise to two *secondary spermatocytes*, and these to four *spermatids*, each of which forms a *spermatozoön*.

By means of this *maturation* process the number of *chromosomes* in the *egg-nucleus* is reduced to half the number normal for *somatic cells* (body cells as distinguished from *germ cells*). A similar reduction occurs also during the development of the spermatozoön, and when *sperm-nucleus* and *egg-nucleus* unite, the resulting nucleus contains the normal number of chromosomes. The meaning of these *reduction* phenomena—highly important from the standpoint of heredity—is a much debated subject.

Fertilization.—As the eggs pass through the vagina, they are capable of being fertilized by spermatozoa, previously stored in the seminal receptacle. Through the *micropyle* of the chorion one or more spermatozoa enter and a

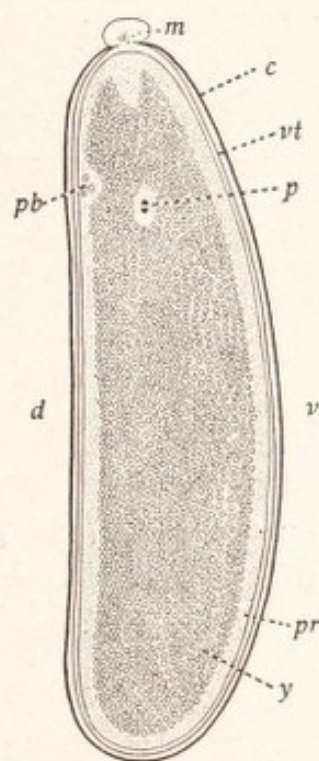


FIG. 190. — Sagittal section of egg of fly, *Musca*, in process of fertilization. *c*, chorion; *d*, dorsal; *m*, micropyle, with gelatinous exudation; *p*, male and female pronuclei, before union; *pb*, polar bodies; *pr*, peripheral protoplasm; *v*, ventral; *vt*, vitelline membrane; *y*, yolk.—After HENKING and BLOCHMANN.

sperm nucleus unites with the egg-nucleus to form what is known as the *segmentation nucleus*. Through this union of nuclear substances the qualities of the two parents are combined in the offspring.

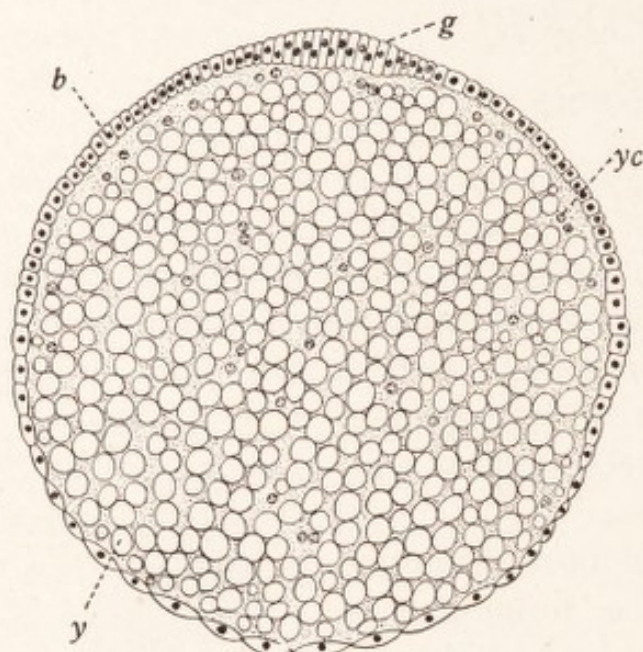


FIG. 191.—Equatorial section of egg of a beetle, *Clytra leviuscula*. *b*, blastoderm; *g*, germ band; *y*, yolk granule; *yc*, yolk cell.—After LÉCAILLON.

Needless to say, the minute details of the process of fertilization are of the highest biological importance.

Blastoderm.—In an arthropod ovum the yolk occupies a central position (*centrolecithal* type), being enclosed in a thin layer of protoplasm. From the segmentation nucleus just mentioned are derived many nuclei, some of which migrate outward with their attendant protoplasm to form with the original peripheral protoplasm a continuous cellular layer, the *blastoderm* (Fig. 191).

Germ Band.—The blastoderm, at first of uniform thickness, becomes thicker in one region, by cell multiplication, forming the *germ band* (*primitive streak*, etc.); this appears in surface view as an oval or elongate area, denser than the remaining blastoderm, with which it is, of course, continuous.

Gastrulation.—The germ band next infolds along the median line,



FIG. 192.—Transverse section of germ band of *Clytra* at gastrulation. *g*, germ band; *i*, inner layer.—After LÉCAILLON.

appearing in cross-section as in Fig. 192; the two lips of the *median groove* close together over the invaginated portion and form an outer layer, or *ectoderm* (Fig. 193), while the invaginated portion spreads

out as an inner layer, which is destined to form two layers, known respectively as *entoderm* and *mesoderm*. This formation of two primary germ layers by invagination or otherwise is termed *gastrulation*; it is an important stage in the development of all eggs, and among insects several variations of the process occur.

Amnion and Serosa.—Meanwhile, the blastoderm has been folding over the germ band from either side, as shown in Fig. 192, and at length the two folds meet and unite to form two membranes (Fig. 194), namely, an inner one, or *amnion*, and an outer one, or *serosa*.

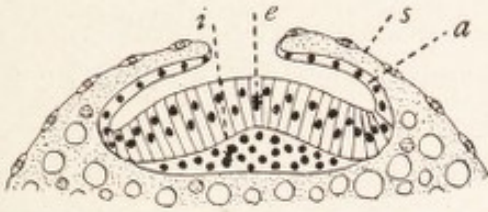


FIG. 193.—Transverse section of germ layers and amnion folds of *Clytra*. *a*, amnion; *e*, ectoderm; *i*, inner layer (meso-entoderm); *s*, serosa.—Original, based on Lécaillon's figures.

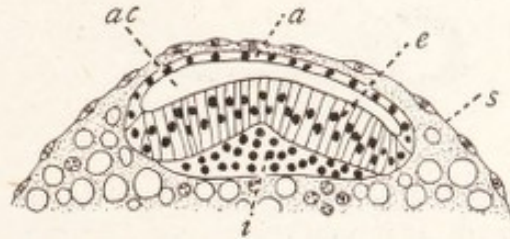


FIG. 194.—Transverse section of germ layers and embryonal membranes of *Clytra*. *a*, amnion; *ac*, amnion cavity; *e*, ectoderm; *i*, inner layer (meso-entoderm); *s*, serosa.—After LÉCAILLON.

Segmentation and Appendages.—On the germ band, which represents the ventral part of the future insect, the body segments are marked off by transverse grooves (Figs. 195, 197); this segmentation beginning

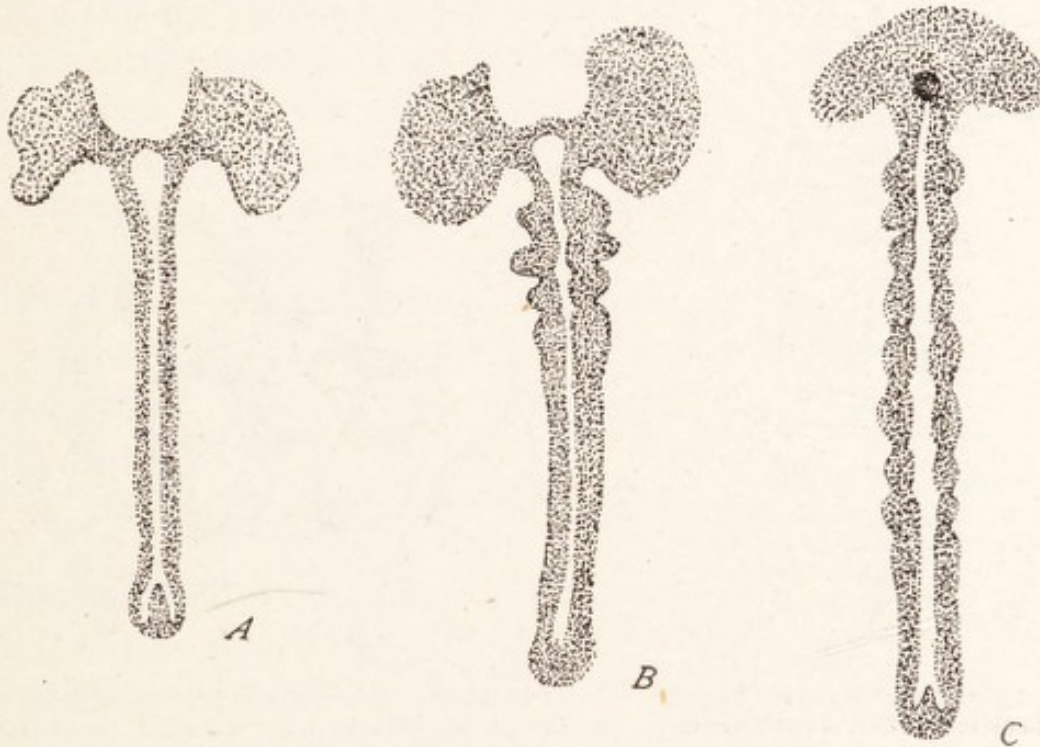


FIG. 195.—Germ band of a beetle, *Lina*, in three successive stages. *A*, unsegmented; *B*, with oral segments demarkated; *C*, with three oral, three thoracic and two abdominal segments.—After GRABER.

usually at the anterior end of the germ band and progressing backward. Furthermore, an anterior infolding occurs (Fig. 196), forming the *stomodæum*, from which the mouth, pharynx, œsophagus and other parts of the fore gut are to arise; a similar but posterior invagination, or *proctodæum* (Fig. 196), is the beginning, or *fundament*, of the hind gut.

At the anterior end of the germ band is a pair of large *procephalic lobes* (Figs. 195, 197), which eventually bear the lateral eyes, and im-



FIG. 196.—Diagrammatic sagittal section of hymenopterous egg to show stomodæal (s) and proctodæal (p) invaginations of the germ band (g).—After GRABER.

mediately behind these are the fundamentals of the antennæ. The fundamentals of the primary paired appendages are out-pocketings of the ectodermal germ band, and at first antennæ, mouth parts and legs are all alike, except in their relative positions. Behind the antennæ (in Thysanura and Collembola at least) appears a pair of rudimentary

appendages (Fig. 197, *i*) which are thought to represent the second antennæ of Crustacea; instead of developing, they disappear in the embryo or else persist in the adult as mere rudiments. In front of these



FIG. 197.—Ventral aspect of germ band of a collembolan, *Anurida maritima*. *a*, antenna; *a*¹–*a*⁵, abdominal appendages; *i*, intercalary appendage; *l*, labrum; *li*, left labial appendage; *m*, mandible; *mx*, maxilla; *p*, procephalic lobe; *pr*, proctodæum; ¹–³, thoracic legs.

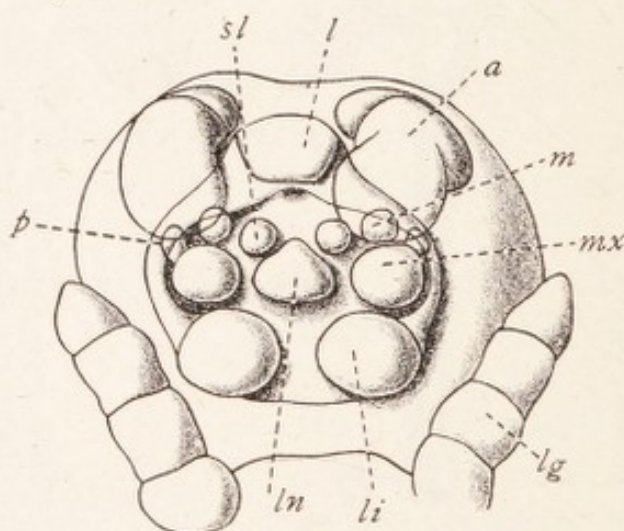


FIG. 198.—Anterior aspect of embryonic mouth parts of a collembolan, *Anurida maritima*. *a*, antenna; *l*, labrum; *lg*, prothoracic leg; *li*, left fundament of labium; *ln*, lingua; *m*, mandible; *mx*, maxilla; *p*, maxillary palpus; *sl*, superlingua.—After FOLSOM.

transitory *intercalary appendages* is the mouth-opening, above which the labrum and clypeus are already indicated by a single, median evagination. Behind the mouth the mandibles, maxillæ and labium are

represented by three pairs of fundamentals, and in Thysanura and Collembola a fourth pair is present to form the superlinguæ (Fig. 198, *sl*), already referred to. Next in order are the three pairs of thoracic legs (Fig. 197) and then, in many cases, paired abdominal appendages (Figs. 197, 199), indicating an ancestral myriopod-like condition; some of these abdominal limbs disappear in the embryo but others develop into abdominal prolegs (Lepidoptera and Tenthredinidæ), external genital organs (Orthoptera, Hymenoptera, etc.) or other structures. The study of these embryonic fundamentals sheds much light upon the morphology of the appendages and the subject of segmentation.

Two Types of Germ Bands.—The germ band described above belongs to the simple *overgrown* type, exemplified in *Clytra*, in which the germ band retains its original position and the amnion and serosa arise by a process of overgrowth (Figs. 193, 194), as distinguished from the *invaginated* type, illustrated in Odonata, in which the germ band invaginates into the egg, as in Fig. 200, until the ventral surface of the embryo becomes turned around and faces the dorsal side of the egg. In this event, a subsequent process of revolution occurs, by means of which the ventral surface of the embryo resumes its original position (Fig. 201).

Dorsal Closure.—As was said, the germ band forms the ventral part of the insect. To complete the general form of the body the margins of the germ band extend outward and upward (Fig. 202) until they finally close over to form the dorsal wall of the insect. Besides this simple method, however, there are several other ways in which the dorsal closure may be effected.

Nervous System.—Soon after gastrulation, the ventral nervous system arises as a pair of parallel cords from cells (Fig. 203, *n*) which have been derived by direct proliferation from those of the germ band,

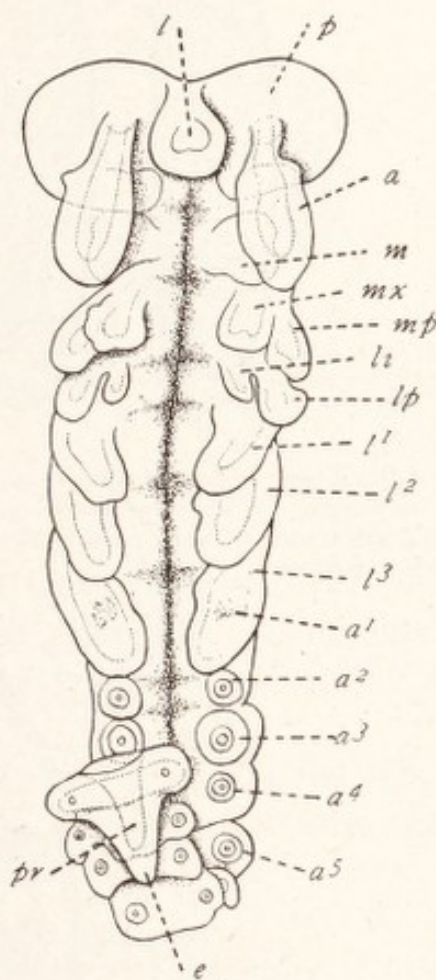


FIG. 199.—Embryo of *Ecanthus*, ventral aspect. *a*, antenna; *a*¹–*a*⁵, abdominal appendages; *e*, end of abdomen; *l*, labrum; *l*₁, left fundament of labium; *lp*, labial palpus; *l*¹–*l*³, thoracic legs; *m*, mandible; *mp*, maxillary palpus; *mx*, maxilla; *p*, procephalic lobe; *pr*, proctodæum. —After AYERS.

and are therefore ectodermal in origin. This primitive double nerve cord becomes constricted at intervals into segments, or *neuromeres*, which correspond to the segments of the germ band. Each neuromere

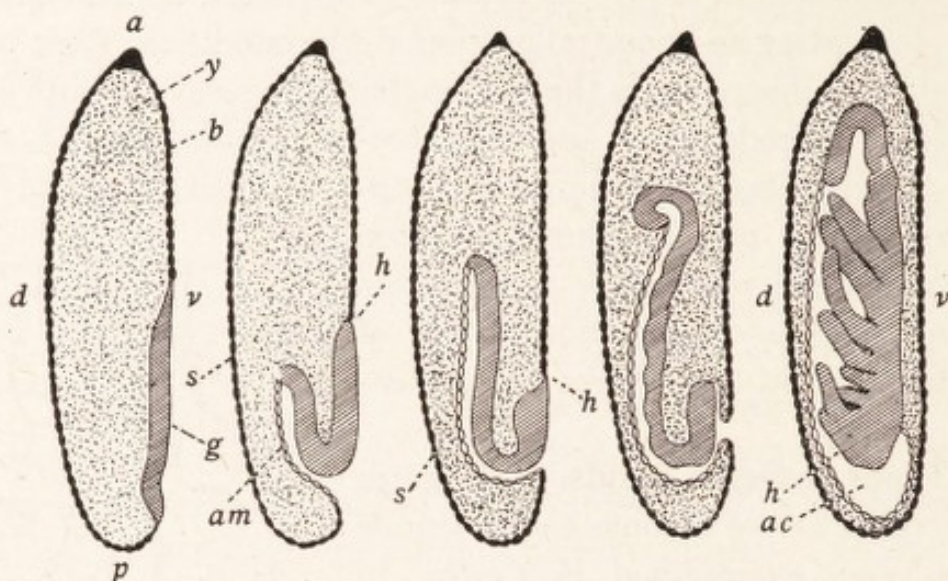


FIG. 200.—Diagrammatic sagittal sections to illustrate invagination of germ band in *Calopteryx*. *a*, anterior pole; *ac*, amnion cavity; *am*, amnion; *b*, blastoderm; *d*, dorsal; *g*, germ band; *h*, head end of germ band; *p*, posterior pole; *s*, serosa; *v*, ventral; *y*, yolk.—After BRANDT.

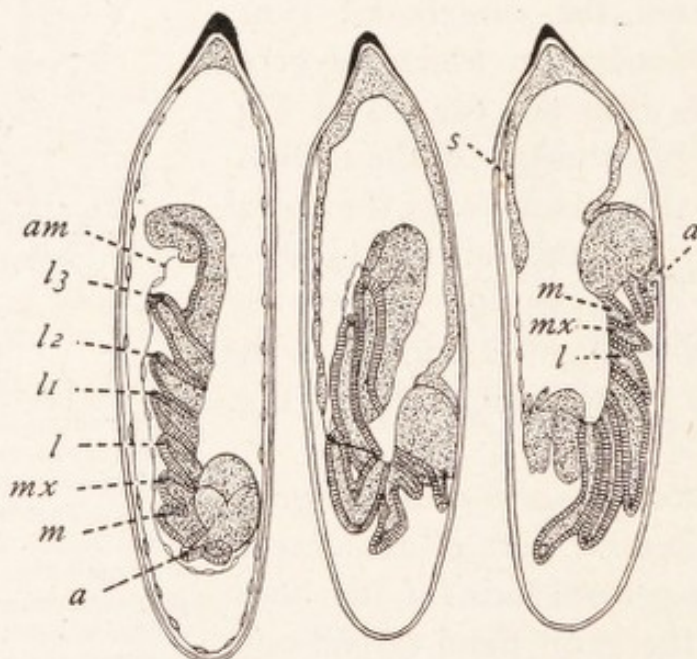


FIG. 201.—Diagrammatic sagittal sections to illustrate revolution of *Calopteryx* embryo. *a*, antenna; *am*, amnion; *l*, labium; *l*¹–*l*³, thoracic legs; *m*, mandible; *mx*, maxilla; *s*, serosa.—After BRANDT.

consists of a pair of primitive ganglia, and these are connected together by paired nerve cords, which later may or may not unite into single cords; moreover, some of the ganglia finally unite to form compound ganglia, such as the brain and the subœsophageal ganglion. In front of

the œsophagus (Fig. 57) are three neuromeres: (1) *protocerebrum*, which is to bear the compound eyes; (2) *deutocerebrum*, or antennal neuromere; (3) *tritocerebrum*, which belongs to the segment which bears the rudimentary intercalary appendages spoken of above. Behind the œsophagus are, at most, four neuromeres, namely and in order, *mandibular*, *superlingual* (found only in Collembola as yet), *maxillary* and *labial*.

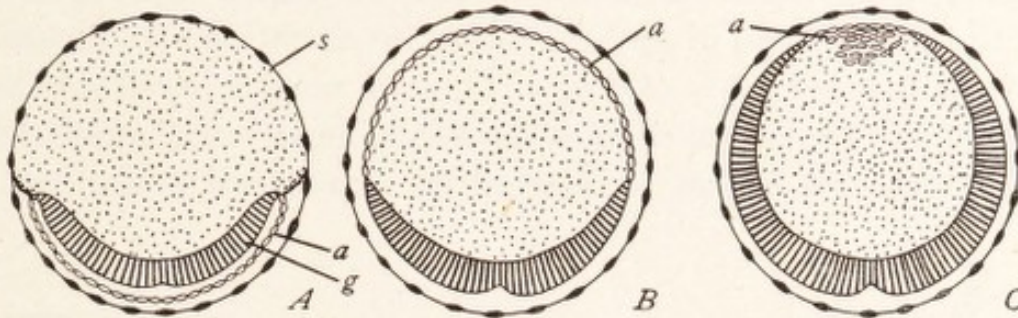


FIG. 202.—Diagrammatic transverse sections to illustrate formation of dorsal wall in the beetle, *Leptinotarsa*. *a*, amnion (breaking up in C); *g*, germ band; *s*, serosa.—After WHEELER, from the *Journal of Morphology*.

Then follow the three thoracic ganglia and ten or eleven abdominal ganglia. The first three neuromeres always unite to form the brain, and the next four (always three; but four in Collembola and perhaps other insects), to form the subœsophageal ganglion. Compound ganglia are frequently formed also in the thorax and abdomen by the union of primitive ganglia.

Tracheæ.—The tracheæ begin as paired invaginations of the ectoderm (Fig. 204, *t*); these simple pockets elongate and unite to form the main lateral trunks, from which arise the countless branches of the tracheal system.

Mesoderm.—From the inner layer which was derived from the germ band by gastrulation (Figs. 192–194) are formed the important germ

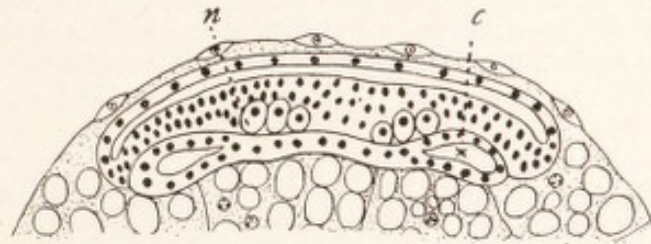


FIG. 203.—Transverse section of germ layers of *Clytra*. *c*, coelom sac; *n*, neuroblasts (primitive nervous cells).—After LÉCAILLON.

layers known as *mesoderm* and *entoderm*. Most of the layer becomes mesoderm, and this splits on either side into chambers, or *cœlom sacs* (Fig. 203, *c*), a pair to each segment. In Orthoptera these cœlom sacs are large and extend into the embryonic appendages, but in Coleoptera, Lepidoptera and Hymenoptera they are small. These sacs may share in the formation of the definite body-cavity, though the last arises independently, from spaces that form between the yolk and the

mesodermal tissues. From the coelom sacs develop the muscles, fat-body, dorsal vessel, blood corpuscles, ovaries and testes; the external sexual organs, however, as well as the vagina and ejaculatory duct, are ectodermal in origin.

Entoderm.—At its anterior and posterior ends, the inner layer just referred to gives rise to a mass of cells which are destined to form the *mesenteron*, from which the mid intestine develops. One mass is adjacent to the blind end of the stomodæal invagination and the other to that of the proctodæal in-folding. The two masses become U-shaped (Fig. 205), and the lateral arms of the two elongate and join so that the entodermal masses become connected by two lateral strands of cells;

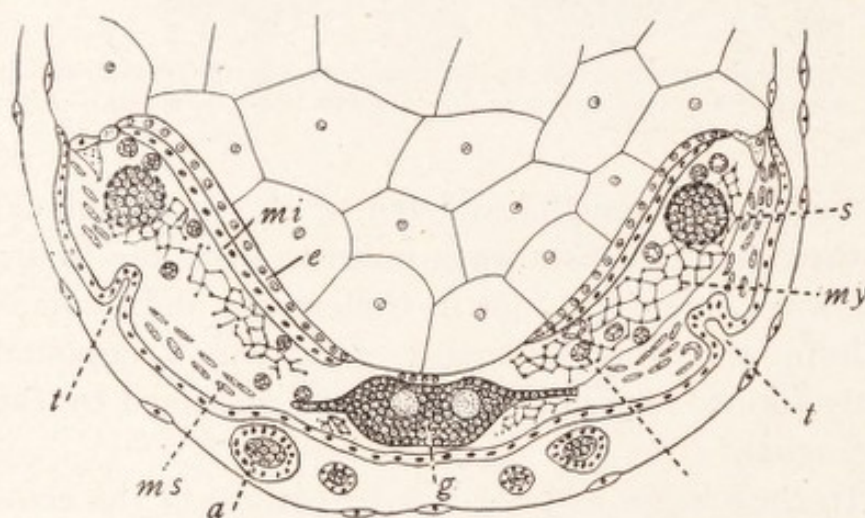


FIG. 204.—Transverse section of abdomen of *Clytra* embryo at an advanced stage of development. *a*, appendage; *e*, epithelium of mid intestine; *g*, ganglion; *m*, Malpighian tube; *mi*, muscular layer of mid intestine; *ms*, muscle elements; *my*, mesenchyme (source of fat-body); *s*, sexual organ; *t*, tracheal invagination.—After LECAILLON.

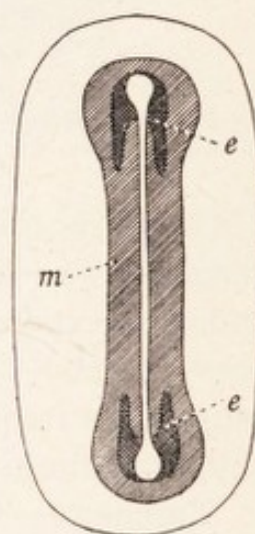


FIG. 205.—Diagram of formation of entoderm in *Lepidoptera*. *e, e*, entodermal masses; *m*, mesoderm.—After WHEELER.

by overgrowth and undergrowth from these lateral strands a tube is formed which is destined to become the stomach, and by the disappearance of the partitions that separate the mesenteron from the stomodæum at one end and from the proctodæum at the other end, the continuity of the alimentary canal is established. The fore and the hind gut, then, are ectodermal in origin, and the mid gut entodermal.

Polyembryony.—In certain Hymenoptera a single egg may give rise to many individuals. Thus in some Chalcididæ and Proctotrypidæ, according to Marchal, the fertilized ovum segments into many (12–100) embryos, which develop into as many adults, all the individuals from the same ovum being of the same sex.

2. EXTERNAL METAMORPHOSIS

Metamorphosis.—One of the most striking phenomena of insect life is expressed by the term *metamorphosis*, which means conspicuous change of form after birth. The egg of a butterfly produces a *larva*; this eats and grows and at length becomes a *pupa*; which, in turn, develops into an *imago*. These stages are so different (Fig. 28) that without experience one could not know that they pertained to the same individual.

Holometabola.—The more specialized insects, namely, Coleoptera (Fig. 206), Strepsiptera, Neuroptera, Mecoptera, Trichoptera, Lepi-

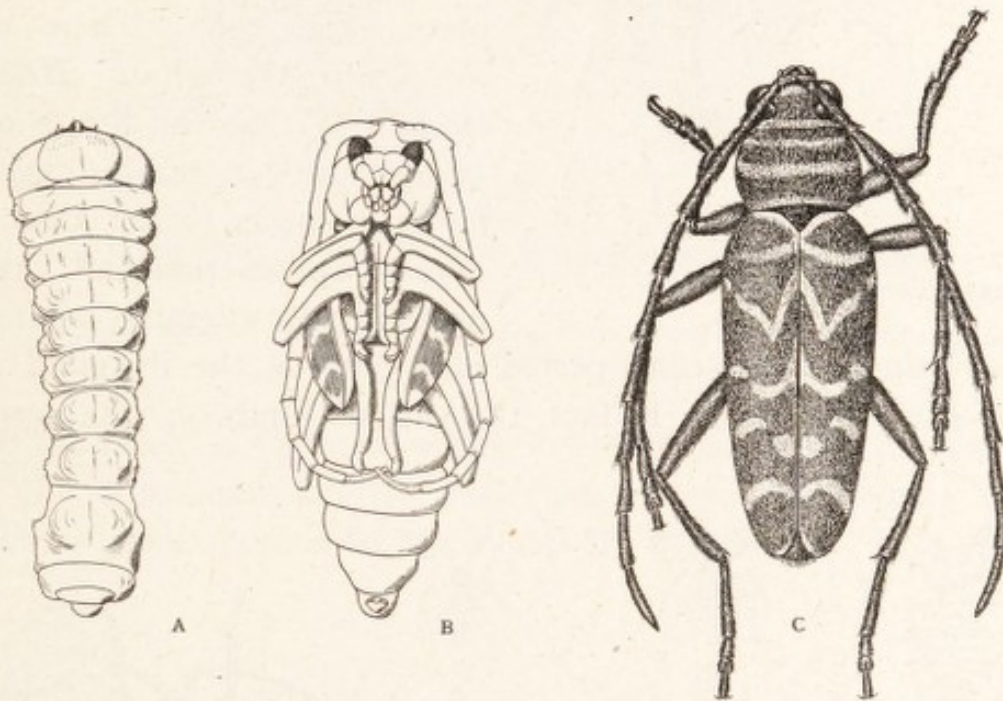


FIG. 206.—*Cyllene caryæ*. A, larva; B, pupa; C, imago. $\times 3$.

doptera, Diptera (Figs. 207, 31), Siphonaptera (Fig. 32) and Hymenoptera (Fig. 287), undergo this *indirect*, or *complete*,¹ metamorphosis, involving profound changes of form and distinguished by the internal development of the wings and by a pupal stage that is usually inactive, though active in mosquitoes and some midges, and in certain Neuroptera just before the transformation. These insects are grouped together as *Holometabola*.

Larvæ receive such popular names as “caterpillar” (Lepidoptera), “grub” (Coleoptera), and “maggot” (Diptera), while the pupa of a moth or butterfly (especially the latter) is called a “chrysalis.”

¹ These terms, though somewhat misleading in implication, are currently used.

Heterometabola.—In a grasshopper, as contrasted with a butterfly, the imago, or adult, is essentially like the young at birth, except in having wings and mature reproductive organs, and the insect is active throughout life, the wings developing externally; hence the metamorphosis is termed *direct*, or *incomplete*. This type of transformation,

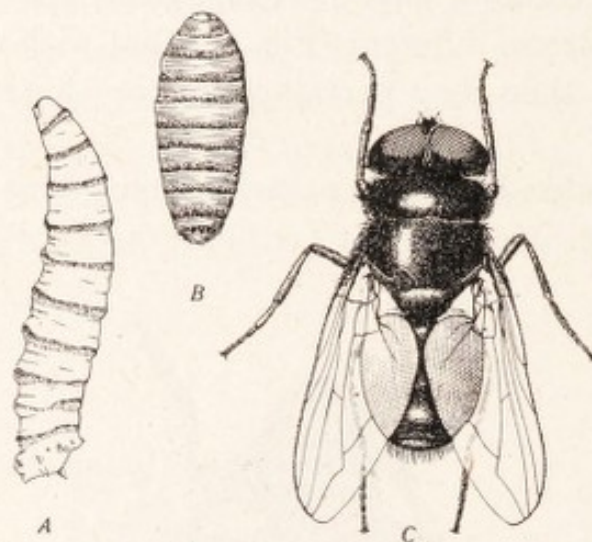


FIG. 207.—*Phormia regina*. A, larva; B, puparium; C, imago. $\times 5$.

without a true pupal period, is characteristic of the more generalized of the metamorphic insects, namely, Orthoptera, Dermaptera, Platyptera, Plecoptera (Fig. 19), Ephemerida (Fig. 20), Odonata (Fig. 21), Thysanoptera and Hemiptera (Fig. 208). These orders constitute the group *Heterometabola*. Within the limits of the group, however, various degrees of metamorphosis occur; thus Plecoptera, Ephemerida and Odonata undergo considerable change of

form; a resting, or quiescent, period may precede the imaginal stage, as in *Cicada* (Fig. 209). In fact, the various kinds of metamorphosis

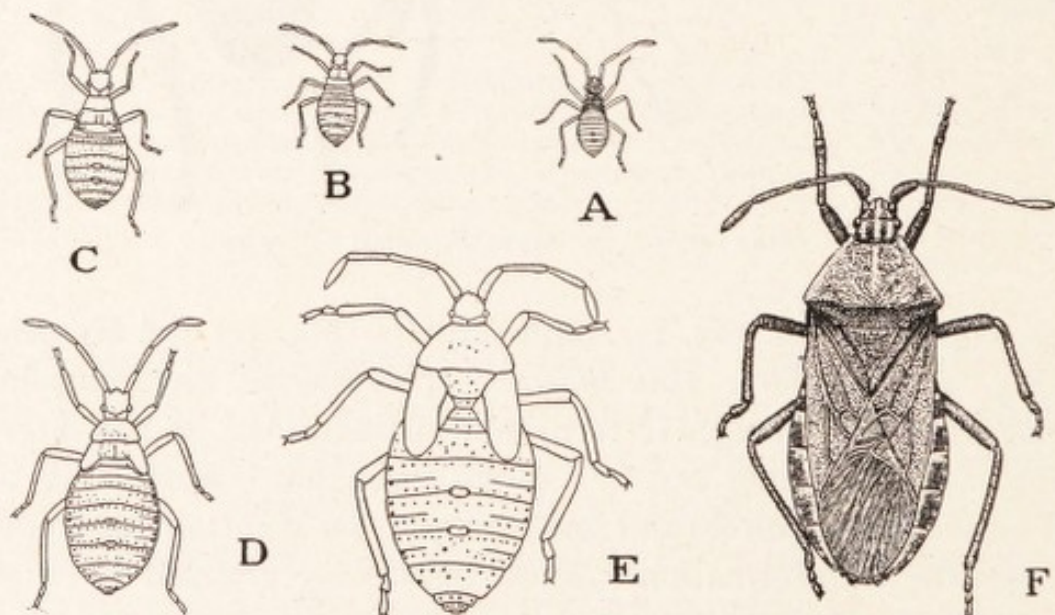


FIG. 208.—Six successive instars of the squash bug, *Anasa tristis*. $\times 2$.

grade into one another in such a way as to make their classification to some extent arbitrary and inadequate.

As there is no distinction between larva and pupa in most hetero-

metabolous insects, it is customary to use the term *nymph* during the interval between egg and imago.

As a rare abnormality, a holometabolous larva may possess two pairs of true external wing-pads. This condition has been reported in

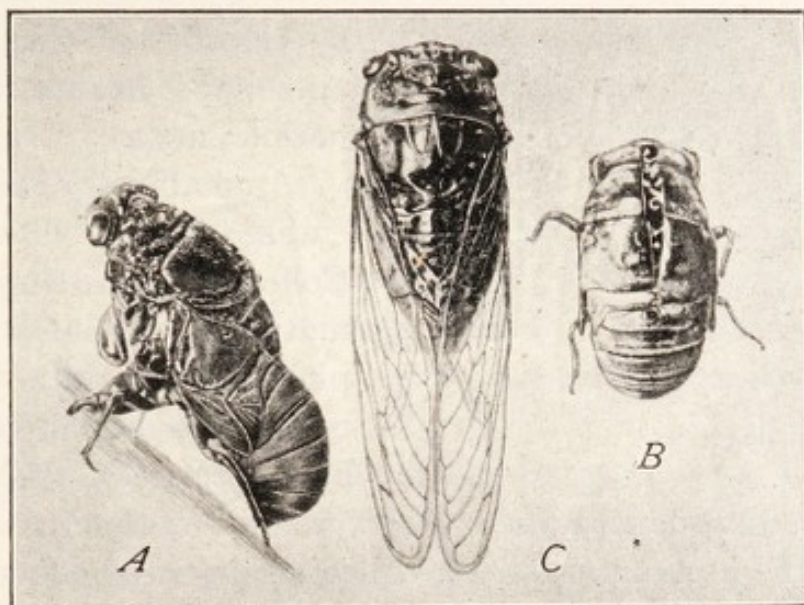


FIG. 209.—*Cicada tibicen*. A, imago emerging from nymphal skin; B, the cast skin; C, imago. Natural size.

several specimens of the meal worm, *Tenebrio molitor* (by Heymons), six larvæ of the museum beetle, *Anthrenus verbasci* (A. Busck) and one pyrochroid larva, *Dendroides canadensis* (P. B. Powell). In these larvæ

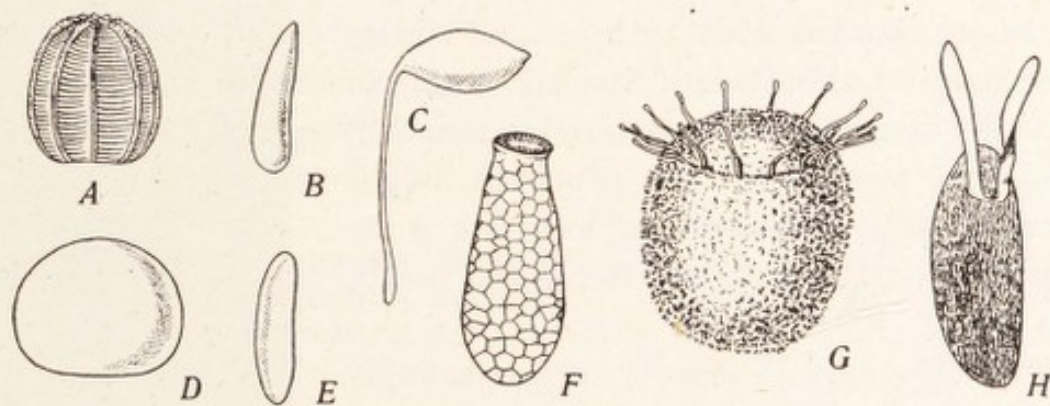


FIG. 210.—Eggs of various insects. A, butterfly, *Polygonia interrogationis*; B, house fly, *Musca domestica*; C, chalcid, *Bruchophagus funebris*; D, butterfly, *Papilio troilus*; E, midge, *Dasyneura trifolii*; F, hemipteron, *Triphleps insidiosus*; G, hemipteron, *Podisus maculiventris*; H, fly, *Drosophila ampelophila*. Greatly magnified.

—all coleopterous—it is comparatively an easy step from the internal wing-rudiment to an external wing-pad, as Dr. W. A. Riley has pointed out. He regards the phenomenon not as an instance of atavism—a harking-back to a period when the larva bore wings—but as an example

of a kind of premature development (known as *prothetaly*) in which characters normally present in the pupal state are present abnormally in the larva. The latter interpretation is supported by the fact that in Mr. Powell's specimen, in addition to the larval ocelli, the compound eyes of the adult are partially developed, and there are more antennal segments than in the normal larva.

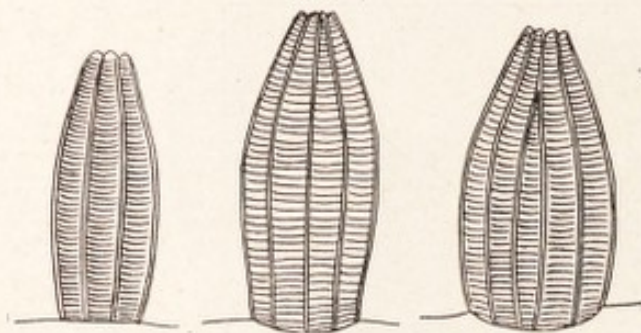


FIG. 211.—Three eggs of the cabbage butterfly, *Pieris rapae*. Greatly magnified, but all drawn to same scale.

Ametabola.—The most generalized insects, Thysanura and Collembola, develop to sexual maturity without a metamorphosis; the form at hatching is retained essentially throughout life, there are no traces of wings

even in the embryo, and there is no change of habit. These two orders form the group *Ametabola*. All other insects have a metamorphosis in the broad sense of the term, and are therefore spoken of as *Metabola*. In this we follow Packard, rather than Brauer, who uses a somewhat different set of terms to express the same ideas.

Stadium and Instar.—During the growth of every insect, the skin is shed periodically, and with each molt, or *ecdysis*, the appearance of the insect changes more or less. The intervals between the molts are termed *stages*, or *stadia*. To designate the insect at any particular stage, the term *instar* was proposed and is much used; thus the insect at hatching is the *first instar*, after the first molt the *second instar*, and so on.

Eggs.—The eggs of insects are exceedingly diverse in form. Commonly they are more or less spherical, oval, or elongate, but there are innumerable special forms, some of which are quite fantastic. Something of the variety of form is shown in Fig. 210. As regards size, most insect eggs can be distinguished by the naked eye; many of them tax the vision, however, for example, the elliptical eggs of *Dasyneura leguminicola*, which are but .300 mm. in length and .075



FIG. 212.—*Chrysopa*, laying eggs. Slightly enlarged.

mm. in width; the oval eggs of the *cecropia* moth, on the other hand, are as long as 3 mm.

The egg-shell, or *chorion*, secreted around the ovum by cells of the ovarian follicle, may be smooth but is usually sculptured, frequently with ridges which, as in lepidopterous eggs, may serve to strengthen the shell. The ornamentation of the egg-shell is often exquisitely beautiful, though the particular patterns displayed are probably of no use, being incidentally produced as impressions from the cells which secrete the chorion. Variations of form, size and pattern are frequent in eggs of the same species, as appears in Fig. 211.

Always the chorion is penetrated by one or more openings, constituting the *micropyle*, for the entrance of spermatozoa.

As a rule, the eggs when laid are accompanied by a fluid of some sort, which is secreted usually by a cement gland or glands, opening into the vagina. This fluid commonly serves to fasten the eggs to appropriate objects, such as food plants, the skin of other insects, the hairs of mammals, etc.; it may form a pedicel, or stalk, for the egg, as in *Chrysopa* (Fig. 212); may surround the eggs as a gelatinous envelope, as in caddis flies, dragon flies, etc.; or may form a capsule enclosing the eggs, as in the cockroach.

The number of eggs laid by one female differs greatly in different species and varies considerably in different individuals of the same species. Some of the fossorial wasps and bees lay only a dozen or so and some grasshoppers two or three dozen, while a queen honey bee may lay a million. Two females of the beetle *Prionus laticollis* had, respectively, 332 and 597 eggs in the abdomen (Mann). A. A. Girault gives the following numbers of eggs per female, from an examination of twenty egg-masses of each species:

	MAXIMUM	MINIMUM	AVERAGE
<i>Thyridopteryx ephemeraformis</i> (bagworm).....	1649	465	941
<i>Malacosoma americana</i> (tent caterpillar).....	466	313	375.5
<i>Chionaspis furfura</i> (scurfy scale).....	84	33	66.5

Hatching.—Many larvæ, caterpillars for example, simply eat their way out of the egg-shell. Some maggots rupture the shell by contortions of the body. Some larvæ have special organs for opening the shell; thus the grub of the Colorado potato beetle has three pairs of hatching spines on its body (Wheeler) and the larval flea has on its head a temporary knife-like egg-opener (Packard). The process of hatching varies greatly according to the species, but has received very little attention.

Larva.—Although larvæ, generally speaking, differ from one another much less than their imagines do, they are easily referable to their orders and usually present specific differences. Larvæ that display individual adaptive characters of a positive kind (Lepidoptera, for example) are easy to place, but larvæ with negative adaptive characters (many Diptera and Hymenoptera) are often hard to identify.

Thysanuriform Larvæ.—Two types of larvæ have been recognized by Brauer, Packard and other authorities: *thysanuriform* and *eruciform*; respectively generalized and specialized in their organization. The former term is applied to many larvæ and nymphs (Fig. 213, C) on

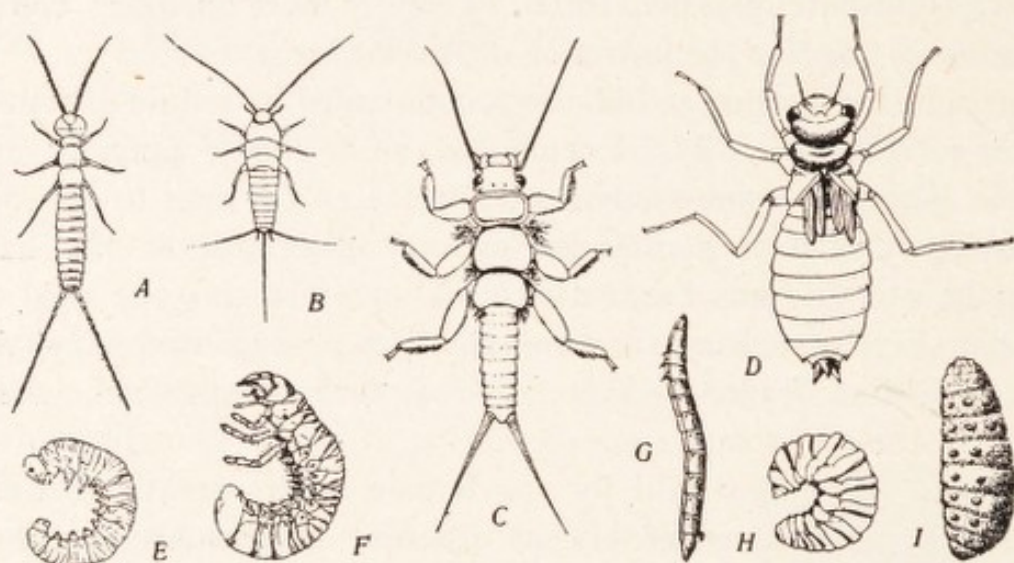


FIG. 213.—Types of larvæ. A, B, Thysanura; C, thysanuriform nymph; E-I, eruciform larvæ. A, *Campodea*; B, *Lepisma*; C, perlid nymph (Plecoptera); D, *Libellula* (Odonata); E, *Tenthredopsis* (Hymenoptera); F, *Lachnosterna* (Coleoptera); G, *Melanotus* (Coleoptera); H, *Bombus* (Hymenoptera); I, *Hypoderma* (Diptera).

account of their resemblance to Thysanura, of which *Campodea* and *Lepisma* are types. The resemblance lies chiefly in the flattened form, long body, hard plates, long legs and antennæ, caudal cerci, well-developed mandibulate mouth parts, and active habits, with the accompanying sensory specializations. These characteristics are permanent in Thysanura, but only temporary in metamorphic insects, and their occurrence in the latter forms may properly be taken to indicate that these insects have been derived from ancestors which were much like Thysanura.

Thysanuriform characters are most pronounced in nymphs of Blattidæ, Forficulidæ, Perlidæ and Ephemeridæ, but occur also in the larvæ of some Neuroptera (*Mantispa*) and Coleoptera (Carabidæ and Meloidæ). These primitive characters are gradually overpowered, in the course of larval evolution, by secondary, or adaptive features.

Eruciform Larvæ.—The prevalent type of larva among holometabolous insects is the *eruciform* (Fig. 213, *E-I*), illustrated by a caterpillar or a maggot. Here the body is cylindrical and often fleshy; the integument weak; the legs, antennæ, cerci, and mouth parts reduced, often to disappearance; the habits sedentary and the sense organs correspondingly reduced. These characteristics are interpreted as being results of partial or entire disuse, the amount of reduction being proportional to the degree of inactivity. Extreme reduction is seen in the maggots of parasitic and such other Diptera as, securing their food with almost no exertion, are simple in form, thin-skinned, legless, with only a mere vestige of a head and with sensory powers of but the simplest kind.

Transitional Forms.—The eruciform is clearly derived from the

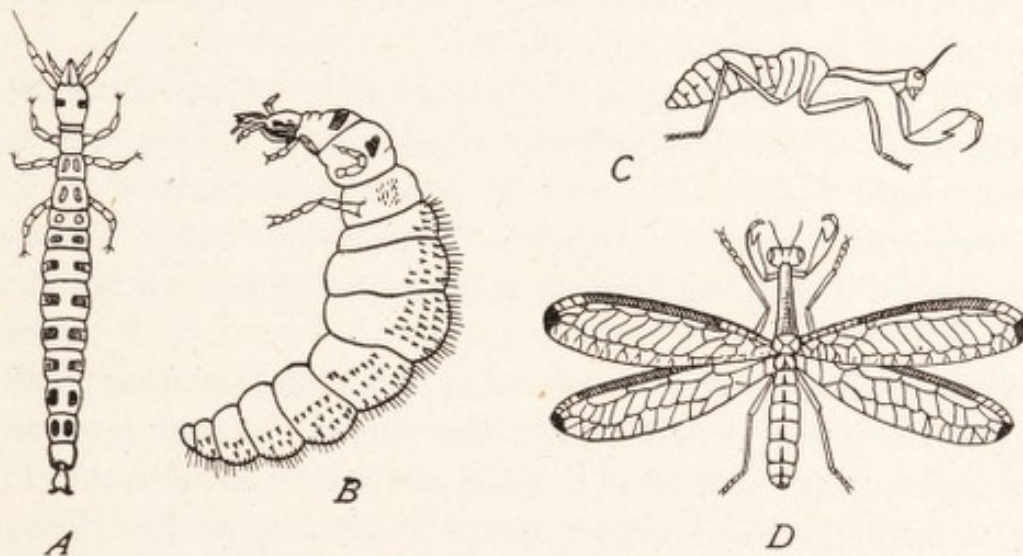


FIG. 214.—*Mantispa*. A, larva at hatching—*thysanuriform*; B, same larva just before first molt—now becoming *eruciform*. C, imago, the wings omitted; D, winged imago, slightly enlarged.—A and B after BRAUER; C and D after EMERTON, from Packard's Text-Book of Entomology, by permission of the Macmillan Co.

thysanuriform type, as Brauer and Packard have shown, the continuity between the two types being established by means of a complete series of intermediate stages. The beginning of the eruciform type is found in Neuroptera, where the campodeoid sialid larva assumes a quiescent pupal condition. The key to the origin of the complete metamorphosis, involving the eruciform condition, Packard finds in the neuropterous genus *Mantispa* (Fig. 214), the first larva of which is truly campodeiform and active. Beginning a sedentary life, however, in the egg-sac of a spider, it loses the use of its legs and the antennæ become partly aborted, before the first molt. In Packard's words, "Owing to this change of habits and surroundings from those of its active ancestors, it

changes its form, and the fully grown larva becomes cylindrical, with small slender legs, and, owing to the partial disuse of its jaws, acquires a small, round head." Meloidæ (Fig. 220) afford other excellent examples of the transition from the thysanuriform to the eruciform condition during the life of the individual.

Thysanuriform characters become gradually suppressed in favor of the eruciform, until, in most of the highly developed orders (Mecoptera, Trichoptera, Lepidoptera, Diptera, Siphonaptera and Hymenoptera), they cease to appear, except for a few embryonic traces—an illustration of the principle of "acceleration in development."

Growth.—The larval period is pre-eminently one of growth. In Heterometabola, growth is continuous during the nymphal stage, but in Holometabola this important function becomes relegated to the larval stage, and pupal development takes place at the expense of a reserve supply of food accumulated by the larva.

The rapidity of larval growth is remarkable. Trouvelot found that the caterpillar of *Telea polyphemus* attains in 56 days 4,140 times its original weight ($\frac{1}{20}$ grain), and has eaten an amount of food 86,000 times its primitive weight. Other larvæ exceed even these figures; thus the maggot of a common flesh fly attains 200 times its original weight in 24 hours.

Ecdysis.—The exoskeleton, unfitted for accommodating itself to the growth of the insect, is periodically shed, and along with it go not only such integumentary structures as hairs and scales, but also the chitinous lining, or intima, of the stomodæum, proctodæum, tracheæ, integumentary glands, etc. The process of molting, or *ecdysis*, in caterpillars is briefly as follows. The old skin becomes detached from the body by an intervening fluid of hypodermal origin; the skin dries, shrinks, is pushed backward by the contractions of the larva, and at length splits near the head, frequently under the neck; through this split appear the new head and thorax, and the old skin is worked back toward the tail until the larva is freed of its *exuviae*. The details of the process are, however, by no means simple. Ecdysis is probably something besides a provision for growth, for Collembola continue to molt long after growth has ceased, and the winged May fly sheds its skin once after emergence. The meaning of this is not known, though ecdysis has an excretory importance in the case of Collembola, which are exceptional among insects in having no Malpighian tubes.

Number of Molts.—The frequency of molting differs greatly in different orders of insects. Locustidæ (formerly "Acridiidae") have

five molts; many Heteroptera, as the chinch bug and squash bug, have five (with six instars); the periodical cicada, six (Marlatt); the larva of the Colorado potato beetle, three; Lepidoptera usually four or five, but often more, as in *Isia isabella*, which molts as many as ten times (Dyar); the house fly, *Musca domestica*, two molts (three larval instars). Packard suggests that cold and lack of food during hibernation in arctians (as *I. isabella*) and partial starvation in the case of some beetles, cause a great number of molts by preventing growth, the hypodermis cells meanwhile retaining their activity.

The appearance of the insect often changes greatly with each molt, particularly in caterpillars, in which the changes of coloration and armature may have some phylogenetic significance, as Weismann has attempted to show in the case of sphingid larvæ.

Adaptations of Larvæ.—Larvæ exhibit innumerable conformities of structure to environment. The greatest variety of adaptive structures occurs in the most active larvæ, such as predaceous forms, terrestrial or aquatic. These have well-developed sense organs, excellent powers of locomotion, special protective and aggressive devices, etc. In insects as a whole, the environment of the larva or nymph and that of the adult may be very different, as in the butterfly or the dragon fly, and the larvæ are modified in a thousand ways for their own immediate advantage, without any direct reference to the needs of the imago.

The chief purpose, so to speak, of the larva is to feed and grow, and the largest modifications of the larva depend upon nutrition. Take as one extreme, the legless, headless, fleshy and sluggish maggot, embedded in an abundance of food, and as the other extreme the active and "wide-awake" larva of a carabid beetle, dependent for food upon its own powers of sensation, locomotion, prehension, etc., and obliged meanwhile to protect or defend itself. Between these extremes come such forms as caterpillars, active to a moderate degree. The great majority of larval characters, indeed, are correlated with food habits, directly or indirectly; directly in the case of the mouth parts, sensory and locomotor organs, and special structures for obtaining special food; indirectly, as in respiratory adaptations and protective structures, these latter being numerous and varied.

Larvæ that live in concealment, as those that burrow in the ground or in plants, have few if any special protective structures; active larvæ, as those of Carabidæ, have an armor-like integument, but owe their protection from enemies chiefly to their powers of locomotion and their aversion to light (*negative phototropism*); various aquatic nymphs (*Zaita*,

Odonata) are often coated with mud and therefore difficult to distinguish so long as they do not move; caddis worms are concealed in their cases, and caterpillars are often sheltered in a leafy nest. There is no reason to suppose that insects conceal themselves consciously, however, and one is not warranted in speaking of an *instinct* for *concealment* in the case of insects—since everything goes to show that the propensity to hide, though advantageous indeed, is simply a reflex, inevitable, negative reaction to light (*negative phototropism*) or a positive reaction to contact (*positive thigmotropism*).

Exposed, sedentary larvæ, as those of many Lepidoptera and Coleoptera, often exhibit highly developed protective adaptations. Caterpillars may be colored to match their surroundings and may resemble twigs, bird-dung, etc.; or larvæ may possess a disagreeable taste or repellent fluids or spines, these odious qualities being frequently associated with warning colors.

Larvæ need protection also against adverse climatal conditions, especially low temperature and excessive moisture. The thick hairy clothing of some hibernating caterpillars, as *Isia isabella*, doubtless serves to mollify sudden changes of temperature. Naked cutworms hibernate in well-sheltered situations, and the grubs of the common "May beetles," or "June bugs," burrow down into the ground below the reach of frost. Ordinary high temperatures have little effect upon larvæ, except to accelerate their growth. Excessive moisture is fatal to immature insects in general—conspicuously fatal to the chinch bug, Rocky Mountain locust, aphids and sawfly larvæ. The effect of moisture may be an indirect one, however; thus moisture may favor the development of bacteria and fungi, or a heavy rain may be disastrous not only by drowning larvæ, but also by washing them off their food plants.

As a result of secondary adaptive modifications, larvæ may differ far more than their imagines. Thus *Platygaster* in its extraordinary first larval form (Fig. 221) is entirely unlike the larvæ of other parasitic Hymenoptera, reminding one, indeed, of the crustacean *Cyclops* rather than the larva of an insect. As Lubbock has said, the characters of a larva depend (1) upon the group of insects to which the larva belongs and (2) upon the special environment of the larva.

Pupa.—The term *pupa* is strictly applicable to holometabolous insects only. Most Lepidoptera and many Diptera have an *obtect* pupa (Fig. 215), or one in which the appendages and body are compactly united; as distinguished from the *free* pupa of Neuroptera, Trichoptera,

Coleoptera and others, in which the appendages are free (Fig. 206); but this distinction cannot always be drawn sharply. Diptera present also the *coarctate* type of pupa (Fig. 207), in which the pupa remains enclosed in the old larval skin, or *puparium*.

Pupal characters, though doubtless of great adaptive and phylogenetic significance, have received but little attention. Lepidopterous pupæ present many puzzling characters, for example, an eye-like structure (Fig. 216) suggesting an ancestral active condition, such as still occurs among heterometabolous insects.



FIG. 215.—Obtect pupa of milkweed butterfly, *Anosia plexippus*, natural size.



FIG. 216.—Head of chrysalis of *Papilio polyxenes*, to show eye-like structure. Enlarged.

Pupation of a Caterpillar.—The process of pupation in a caterpillar has been carefully observed by Riley. The caterpillar of the milkweed butterfly (Pl. I, *A*) spins a mass of silk in which it entangles its suranal plate and anal prolegs and then hangs downward, bending up the anterior part of the body (*B*), which gradually becomes swollen. The skin of the caterpillar splits dorsally from the head backward, and is worked back toward the tail (*C* and *D*) by the contortions of the larva.

The way in which the pupa becomes attached to its silken support is rather complex. Briefly, while the larval skin still retains its hold on the support, the posterior end of the pupa is withdrawn from the old integument while the latter is being temporarily gripped between two of the abdominal segments of the pupa, and by the vigorous whirling and twisting of the body the hooks of the terminal *cremaster* of the pupa are entangled in the silken support. At first the pupa is elongate (*E*) and soft, but in an hour or so it has contracted, hardened, and assumed its characteristic form and coloration (*F*).

Pupal Respiration.—Except under special conditions, pupæ breathe by means of ordinary abdominal spiracles. Aquatic pupæ have special

respiratory organs, such as the tracheal filaments of *Simulium* (Fig. 233), and the respiratory tubes of *Culex* (Fig. 232).

Pupal Protection.—Inactive and helpless, most pupæ are concealed in one way or another from the observation of enemies and are protected from moisture, sudden changes of temperature, mechanical shock and other adverse influences. The larvæ of many moths burrow into



FIG. 217.—Cocoon of *Chrysopa*, after emergence of imago. Slightly enlarged.

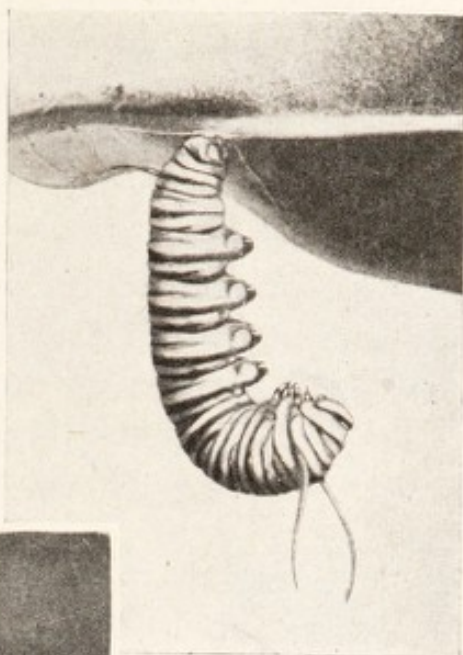
the ground and make an earthen cell in which to pupate; a large number of coleopterous larvæ (*Lachnosterna*, *Osmoderma*, *Passalus*, *Lucanus*, etc.) make a chamber in earth or wood, the walls of the cells being strengthened with a cementing fluid or more or less silk, forming a rude cocoon. Silken cocoons are spun by some Neuroptera (Chrysopidæ, Fig. 217), by Trichoptera (whose cases are essentially cocoons), Lepidoptera, a few Coleoptera (as Curculionidæ, *Donacia*), some Diptera (as Itonididæ), Siphonaptera, and many Hymenoptera (for example, Tenthredinidæ, Ichneumonidæ, wasps, bees and some ants).

The cocoon-making instinct is most highly developed in Lepidoptera and the most elaborate cocoons are those of Saturniidæ. The cocoon of *Samia cecropia* is a tough, water-proof structure and is double (Fig. 218), there being two air spaces around the pupa; thus the pupa is protected against moisture and sudden changes of temperature and from most birds as well, though the downy woodpecker not infrequently punctures the cocoon. *S. cecropia* binds its cocoon firmly to a twig; *Tropæa luna* and *Telea polyphemus* spin among leaves, and their cocoons (with some exceptions) fall to the ground; *Callosamia promethea*, whose cocoon is covered with a curved leaf, fastens the leaf to the twig with a wrapping of silk, so that the leaf with its burden hangs to the twig throughout the winter. The leaves surrounding cocoons may render them inconspicuous or may serve merely as a foundation for the cocoon. While silk and often a waterproof gum or cement form the basis of a cocoon, much foreign material, such as bits of soil or wood, is often mixed in; the cocoons of many common Arctiidæ, as *Diacrisia virginica* and *Isia isabella*, consist principally of hairs, stripped from the body of the larva.

Butterflies have discarded the cocoon, traces of which occur in Hesperiidæ, which draw together a few leaves with a scanty supply of silk to make a flimsy substitute for a cocoon. Papilionid and pierid



A



B



C



D

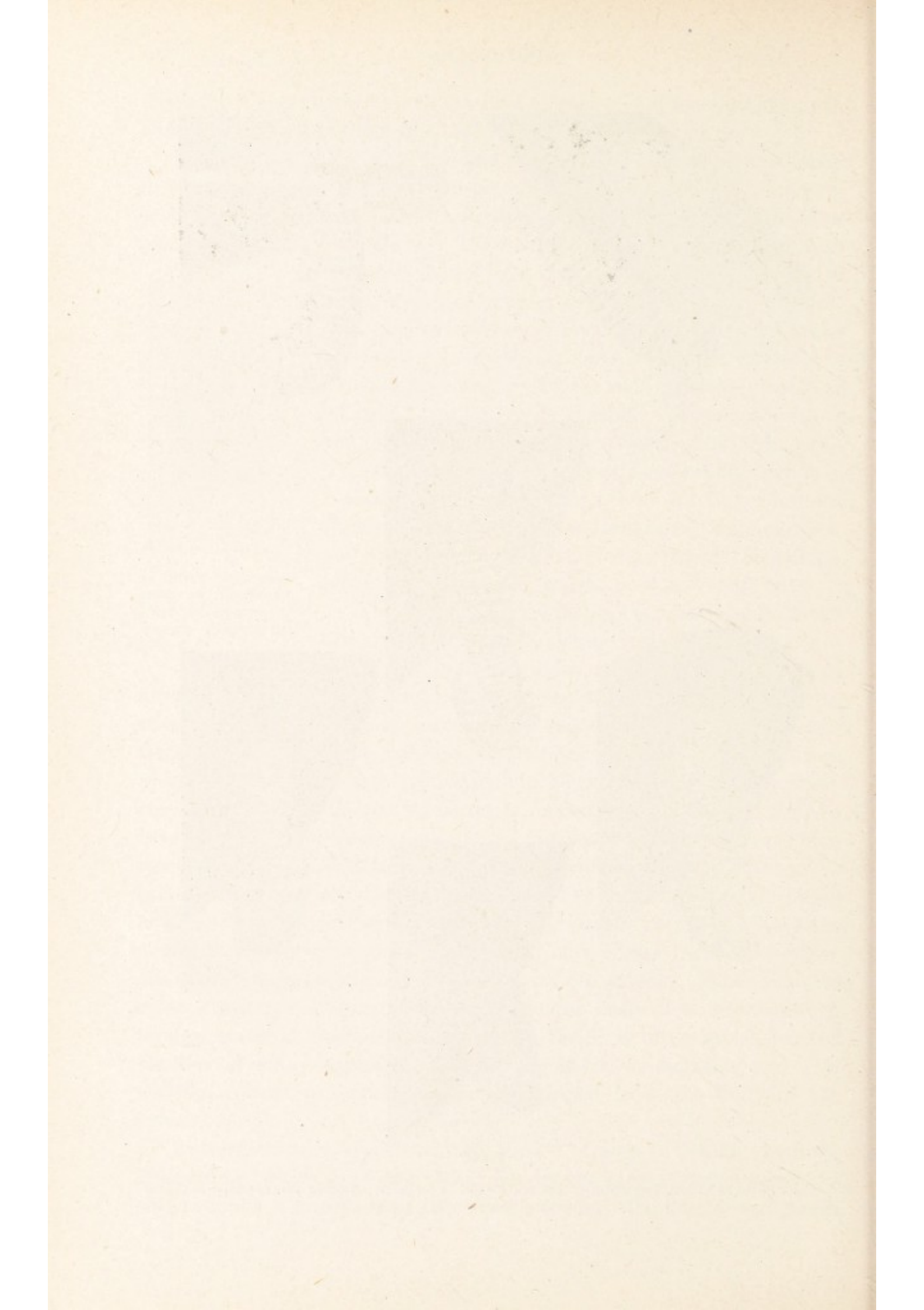


E



F

Successive stages in the pupation of the milkweed caterpillar, *Anosia plexippus*. Natural size.



pupæ are supported by a silken girdle (Fig. 29), and nymphalid chrysalides hang freely suspended by the tail (Fig. 215).

Cocoon-Spinning.—The caterpillar of *Telea polyphemus* “feels with its head in all directions, to discover any leaves to which to attach the fibres that are to give form to the cocoon. If it finds the place suitable, it begins to wind a layer of silk around a twig, then a fibre is attached to a leaf near by, and by many times doubling this fibre and making it shorter every time, the leaf is made to approach the twig at the distance necessary to build the cocoon; two or three leaves are disposed like this one and then the fibres are spread between them in all directions, and soon the ovoid form of the cocoon distinctly appears. This seems to

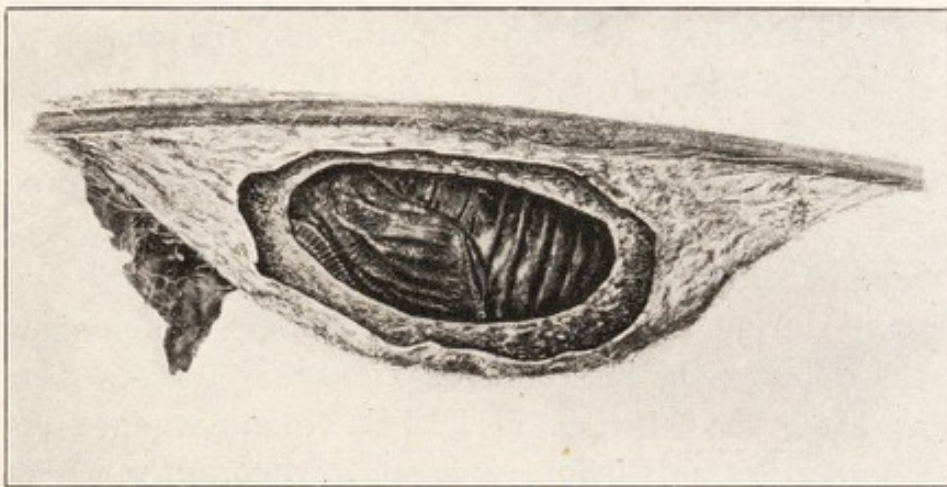


FIG. 218.—Cocoon of *Samia cecropia*, cut open to show the two silken layers and the enclosed pupa. Natural size.

be the most difficult feat for the worm to accomplish, as after this the work is simply mechanical, the cocoon being made of regular layers of silk united by a gummy substance. The silk is distributed in zigzag lines about one-eighth of an inch long. When the cocoon is made, the worm will have moved his head to and fro, in order to distribute the silk, about two hundred and fifty-four thousand times. After about half a day's work, the cocoon is so far completed that the worm can hardly be distinguished through the fine texture of the wall; then a gummy resinous substance, sometimes of a light brown color, is spread over all the inside of the cocoon. The larva continues to work for four or five days, hardly taking a few minutes of rest, and finally another coating is spun in the interior, when the cocoon is all finished and completely air tight. The fibre diminishes in thickness as the completion of the cocoon advances, so that the last internal coating is not half so thick and so strong as the outside ones.” (Trouvelot.)

Emergence of Pupa.—Subterranean pupæ wriggle their way to the surface of the ground, often by the aid of spines (Fig. 219), that catch successively into the surrounding soil. These locomotor spines may occur on almost any part of the pupa, but occur commonly on the

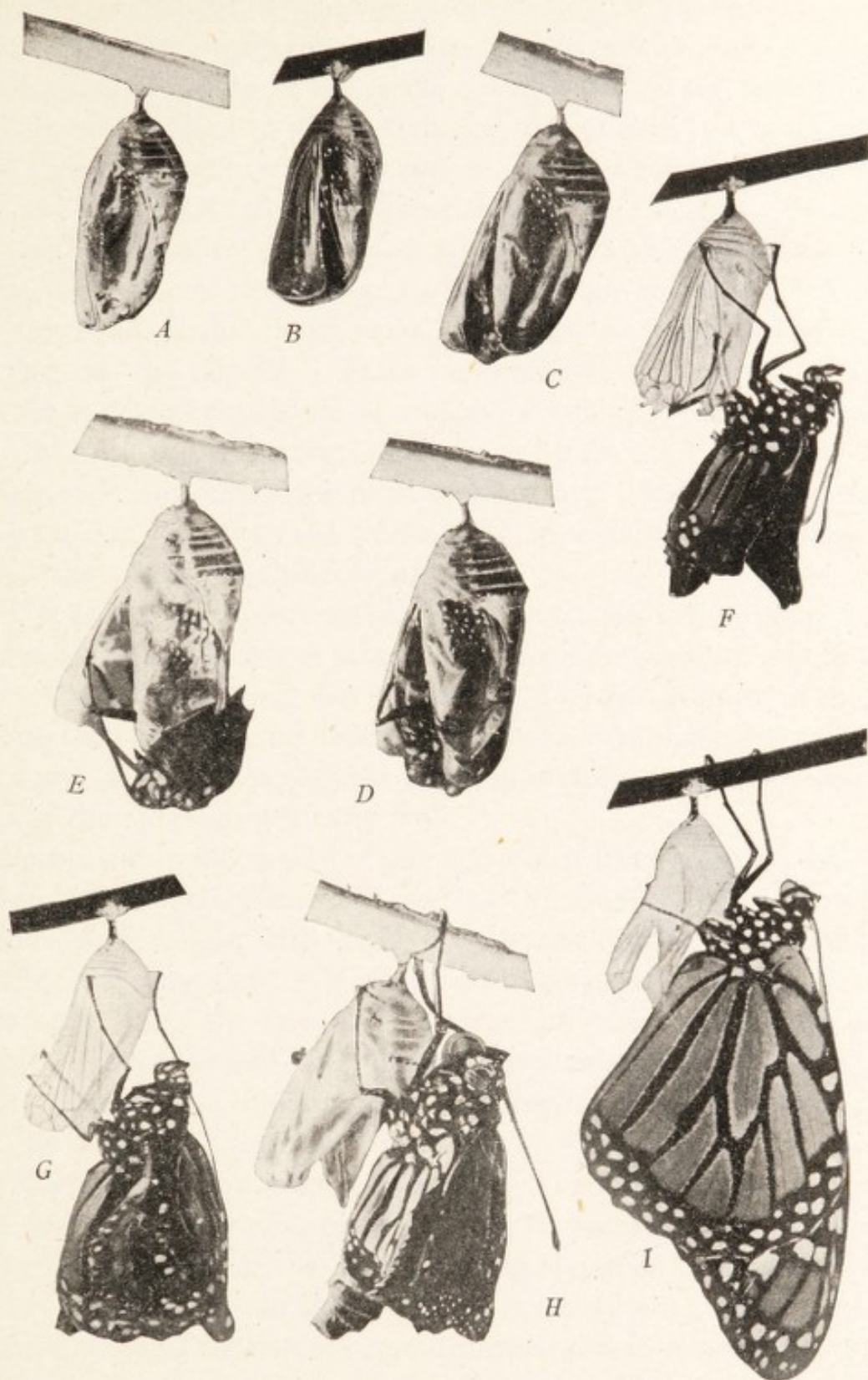


FIG. 219.—Subterranean pupa of *Anisota*. Enlarged.

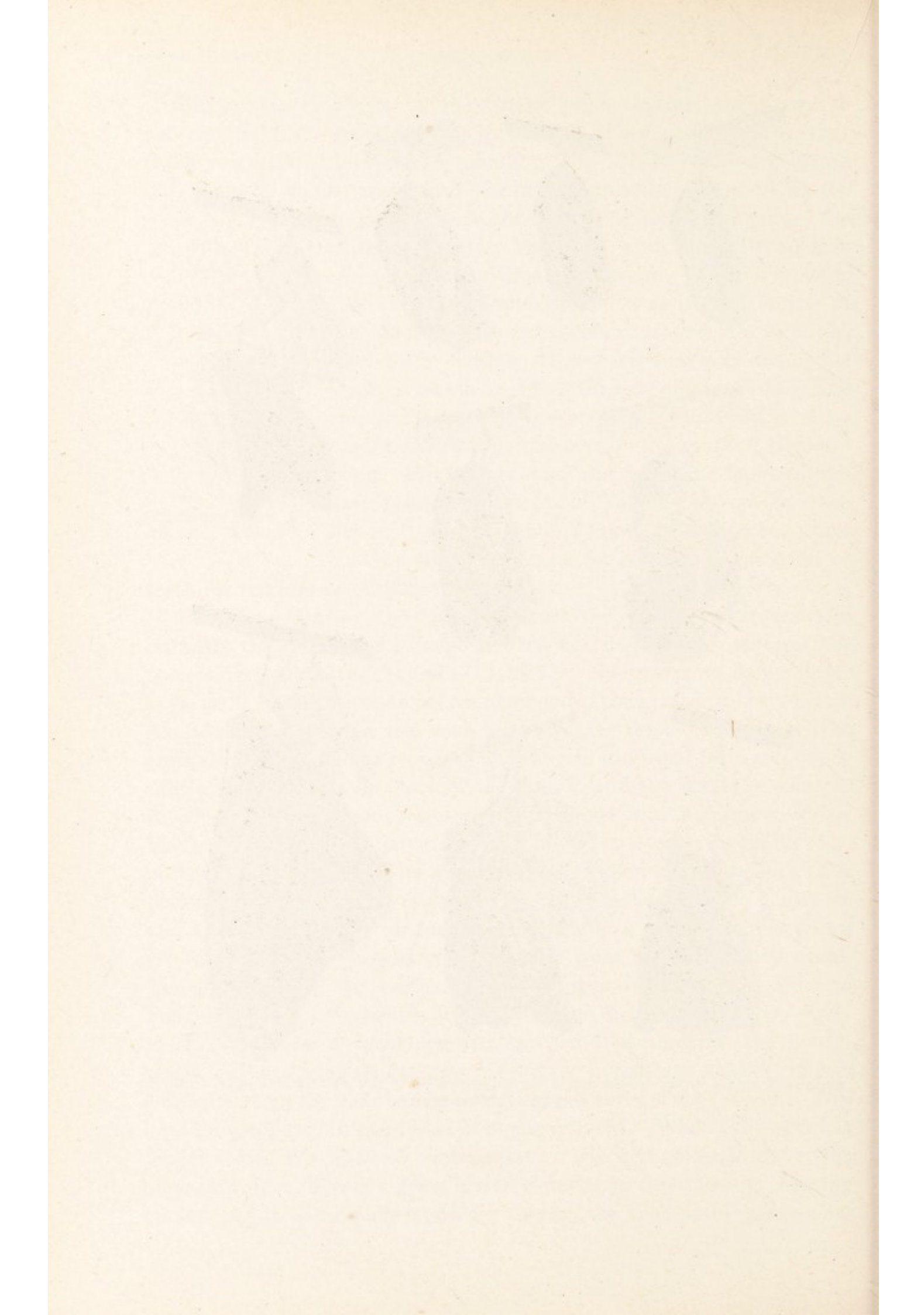
abdominal segments, as in lepidopterous pupæ; the extremity of the abdomen, also, bears frequently one or more spinous projections, as in Tipulidæ, Carabidæ and Lepidoptera, to assist the escape of the pupa. These structures are found also in pupæ, as those of Sesiidæ, that force their way out of the stems of plants in which the larvæ have lived. The emergence from the cocoon is accomplished in some cases by the pupa, in others by the imago. Hemero-biidæ, Trichoptera and the primitive lepidopteron *Eriocephala* use the pupal mandibles to cut an opening in the cocoon; while many lepidopterous pupæ have on the head a beak for piercing the cocoon, or teeth for rending or cutting the silk.

Eclosion.—During the last few hours before the emergence of a butterfly the colors of the imago develop and may be seen through the transparent skin of the chrysalis (Pl. II A). No movement occurs, however, until several seconds before emergence; then, after a few convulsive movements of the legs and thorax of the imprisoned insect, the pupa skin breaks in the region of the tongue and legs (B), a secondary split often occurs at the back of the thorax, and the butterfly emerges (C-E) with moist body, elongated abdomen and miniature wings. Hanging to the empty pupa case (F), or to some other available support, the insect dries and its wings gradually expand (G, H) through the pressure of the blood. At regular intervals the abdomen contracts and the wings fan the air, and sooner or later a drop or two of a dull greenish fluid (the *meconium*) is emitted from the alimentary canal. The expansion of the wings takes place rapidly, and in less than an hour, as a rule, they have attained their full size (I).

T. polyphemus is "provided with two glands opening into the mouth, which secrete during the last few days of the pupa state, a fluid which is a dissolvent for the gum so firmly uniting the fibres of the cocoon. This liquid is composed in great part of bombycic acid. When the insect has accomplished the work of transformation which is going on under the pupa skin, it manifests a great activity, and soon the chrysalis covering bursts open longitudinally upon the thorax; the head and legs are soon



Successive stages in the emergence of the milkweed butterfly, *Anosia plexippus*, from the chrysalis. Natural size.



disengaged, and the acid fluid flows from its mouth, wetting the inside of the cocoon. The process of exclusion from the cocoon lasts for as much as half an hour. The insect seems to be instinctively aware [?] that some time is required to dissolve the gum, as it does not make any attempt to open the fibres, and seems to wait with patience this event. When the liquid has fully penetrated the cocoon, the pupa contracts its body, and pressing the hinder end, which is furnished with little hooks, against the inside of the cocoon, forcibly extends its body; at the same time the head pushes hard upon the fibres and a little swelling is observed on the outside. These contractions and extensions of the body are repeated many times, and more fluid is added to soften the gum, until under these efforts the cocoon swells, and finally the fibres separate, and out comes the head of the moth. In an instant the legs are thrust out, and then the whole body appears; not a fibre has been broken, they have only been separated.

"To observe these phenomena, I had cut open with a razor a small portion of a cocoon in which was a living chrysalis nearly ready to transform. The opening made was covered with a piece of mica, of the same shape as the aperture, and fixed to the cocoon with mastic so as to make it solid and air-tight; through the transparent mica I could see the movements of the chrysalis perfectly well.

"When the insect is out of the cocoon, it immediately seeks for a suitable place to attach its claws, so that the wings may hang down, and by their own weight aid the action of the fluids in developing and unfolding the very short and small pad-like wings. Every part of the insect on leaving the cocoon, is perfect and with the form and size of maturity, except the pad-like wings and swollen and elongated abdomen, which still gives the insect a worm-like appearance; the abdomen contains the fluids which flow to the wings.

"When the still immature moth has found a suitable place, it remains quiet for a few minutes, and then the wings are seen to grow very rapidly by the afflux of the fluid from the abdomen. In about twenty minutes the wings attain their full size, but they are still like a piece of wet cloth, without consistency and firmness, and as yet entirely unfit for flight, but after one or two hours they become sufficiently stiff, assuming the beautiful form characteristic of the species" (Trouvelot). The expansion of the wing is due to blood-pressure brought about chiefly by the abdominal muscles. In the freshly-emerged insect, the two membranes of the wing are corrugated, and expansion consists in the flattening out of these folds. The wing is a sac, which would tend to enlarge

into a balloon-shaped bag, were it not for hypodermal fibres which hold the wing-membranes closely together (Mayer). *Tropæa luna* and *Philosamia cynthia* cut and force an opening through the cocoon by means of a pair of saw-like organs, one at the base of each front wing.

The cocoons of *Samia cecropia* and *Callosamia promethea* do not have a gummy coating over the entire interior. In each case the end through which the moth emerges is composed of silken fibres loosely pulled together and not covered with a gummy substance. It is as if each layer of the cocoon was spun into a fringe at this end, the fringes of all layers being bunched together forming a little cone. In the cocoon of *Samia cecropia*, it is possible to push a pencil through this fringe with apparently no effort. The fibres part readily, it being necessary to break only a few in the extreme outside layer. The same can be said of the cocoon of *C. promethea* (H. B. Weiss).

The temperature inside a cocoon is practically the same as that of the surrounding air, there being a constant tendency for the inside temperature to approach that of its surroundings. Sudden changes of temperature do not occur within a cocoon. When the outside temperature is suddenly lowered, as from 10° C to 0° C., the temperature in a cocoon falls gradually, and even during a gradual rise the cocoon-temperature lags behind that of its surroundings, on account of the poor conducting qualities of air and silk (H. B. Weiss).

Hypermetamorphosis.—In a few remarkable instances, metamorphosis involves more than three stages, owing to the existence of supernumerary larval forms. This phenomenon of *hypermetamorphosis* occurs notably in the coleopterous genera *Meloë*, *Epicauta*, *Sitaris* and *Rhipiphorus*, in Strepsiptera and in several parasitic Hymenoptera.

In the oil-beetle, *Meloë*, as described by Riley, the newly-hatched larva (*triungulin*) is active and campodea-form. It climbs upon a flower and thence upon the body of a bee (*Anthophora*), which carries it to the nest, where it eats the egg of the bee. After a molt, the larva though still six-legged, has become cylindrical, fleshy and less active, resembling a lamellicorn larva; it now appropriates the honey of the bee. With plenty of rich food at hand the larva becomes sluggish, and after another molt appears as a pseudo-pupa, with functionless mouth parts and atrophied legs. From this pseudo-pupa emerges a third larval form, of the pure eruciform type, fat and apodous like the bee-larvæ themselves. After these four distinct stages the larva becomes a pupa and then a beetle.

Epicauta, another meloid, has a similar history. The *triungulin*

(Fig. 220, *A*) of *E. vittata* burrows into an egg-pod of *Melanoplus differentialis* and eats the eggs of that grasshopper. After a molt the *second larva* (*carabidoid* form) appears; this (*B*) is soft, with reduced legs and mouth parts and less active than the triungulin. A second molt and the *scarabæidoid* form of the second larva is assumed; the legs and mouth parts are now rudimentary and the body more compact than before. A third and a fourth molt occur with little change in the form of the second larva, which is now in its *ultimate* stage (*C*). After the fifth molt, however, the *coarctate larva*, or *pseudo-pupa*, appears; this (*D*) hibernates and in spring sheds its skin and becomes the *third larva*,

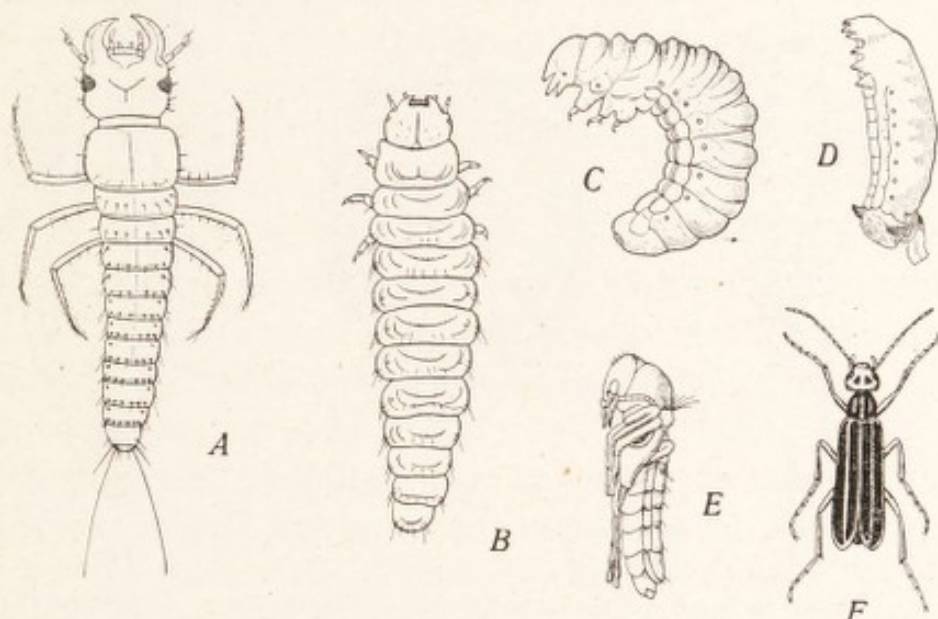


FIG. 220.—Stages in the hypermetamorphosis of *Epicauta*. *A*, triungulin; *B*, carabidoid stage of second larva; *C*, ultimate stage of second larva; *D*, coarctate larva; *E*, pupa; *F*, imago. *E* is species *cinerea*; the others are *vittata*. All enlarged except *F*.—After RILEY, from Trans. St. Louis Acad. Science.

which soon transforms to a true pupa (*E*), from which the beetle (*F*) shortly emerges. Thus the pupal stage is preceded by at least three distinct larval stages.

Strepsiptera, the subject of two important volumes by Dr. W. D. Pierce, are all hypermetamorphic. These parasites affect almost exclusively Hymenoptera and Homoptera, causing the "stylopized" condition known to collectors of bees, wasps or bugs, in which the presence of the parasite is indicated by a flat disk-like plate (in the female parasite) or a tuberculate rounded projection (male) protruding from between segments of the abdomen. The male is winged but the female is maggot-like and sedentary, a mere sac of eggs, often two thousand or more in number, which hatch inside the body of the mother into active little hexapodous thysanuriform larvæ known as *triungulinids*. These

are probably carried by the host to flowers or other places where they are able to attach themselves to the bodies of their future hosts. After penetrating into the body of the host the larva grows rapidly; with the first molt the eyes and legs are lost, the second instar being scarabæidoid in form; after the second molt the male and female larvæ differ in development.

The most extraordinary metamorphoses have been found among parasitic Hymenoptera, as in *Platygaster*, a proctotrypid which infests the larva of *Cecidomyia*. The egg of *Platygaster*, according to Ganin,

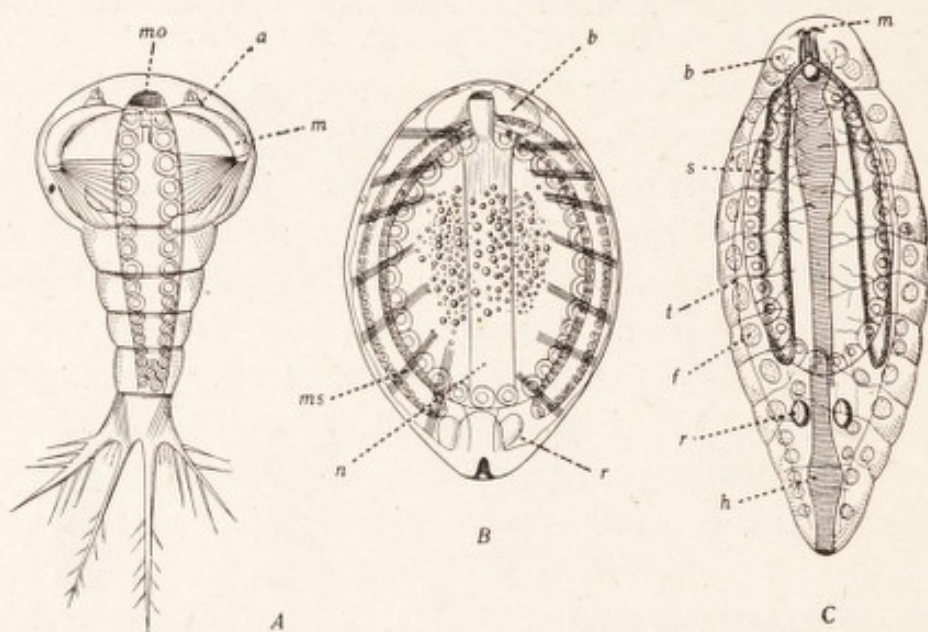


FIG. 221.—Stages in the hypermetamorphosis of *Platygaster*. A, first larva; B, second larva; C, third larva; a, antenna; b, brain; f, fat-tissue; h, hind intestine; m, mandible; mo, mouth; ms, muscle; n, nerve cord; r, reproductive organ of one side; s, salivary gland; t, trachea.—After GANIN.

hatches into a larva of bizarre form (Fig. 221, A), suggesting the crustacean *Cyclops*, rather than an insect. This first larva has a blind food canal and no nervous, circulatory or respiratory systems. After a molt the outline is oval (B), and there are no appendages as yet, though the nervous system is partially developed. Another molt, and the third larva appears (C), elliptical in contour, externally segmented, with tracheæ and a pair of mandibles. From now on, the development is essentially like that of other parasitic Hymenoptera.

Equally anomalous are the changes undergone by *Polynema*, a proctotrypid parasite in the eggs of dragon flies, and by the proctotrypid *Teleas*, which affects the eggs of the tree cricket (*Ecanthus*). In all these cases the larvæ go through changes which in most other insects are confined to the egg stage. In other words, the larva hatches before its embryonic development is completed, so to speak.

Significance of Metamorphosis.—"The essential features of metamorphosis," says Sharp, "appear to be the separation in time of growth and development and the limitation of the reproductive processes to a short period at the end of the individual life."

The simplest insects, Thysanura, have no metamorphosis, and show no traces of ever having had one. Hence it is inferred that the first insects had none; in other words, the phenomenon of metamorphosis originated later than insects themselves. Successive stages in the evolution of metamorphosis are illustrated in the various orders of insects.

The distinctive mark of the simplest metamorphosis, as in Orthoptera and Hemiptera, is the acquisition of wings; growth and sexual development proceeding essentially as in the non-metamorphic insects (Thysanura and Collembola). Here the development of wings does not interfere with the activity of the insect; its food habits remain unaltered; throughout life the environment of the individual is practically the same. Even when considerable difference exists between the nymphal and imaginal environments, as in Ephemerida and Odonata, the activity of the individual may still be continuous, even if somewhat lessened as the period of transformation approaches.

With Neuroptera, the pupal stage appears. In these and all other holometabolous insects the larva accumulates a surplus of nutriment sufficient for the further development, which becomes condensed into a single pupal stage, during which external activity ceases temporarily.

With the increasing contrast between the organization of the larva and that of the imago, the pupal stage gradually becomes a necessity. Metamorphosis now means more than the mere acquisition of wings, for the larva and the imago have become adapted to widely different environments, chiefly as regards food. The caterpillar has biting mouth parts for eating leaves, while the adult has sucking organs for obtaining liquid nourishment; the maggot, surrounded by food that may be obtained almost without exertion, has but minimum sensory and locomotor powers and for mouth parts only a pair of simple jaws; as contrasted with the fly, which has wings, highly developed mouth parts and sense organs, and many other adaptations for an environment which is strikingly unlike that of the larva; so also in the case of the higher Hymenoptera, where maternal or family care is responsible for the helpless condition of the larva.

Thus it is evident that the change from larval to imaginal adaptations is no longer congruous with continuous external activity; a quies-

cent period of reconstruction becomes inevitable (though this statement does not, of course, explain anything).

As was said, the eruciform type of larva has been derived from the thysanuriform type, the strongest evidence of this being the fact that among hypermetamorphic insects, the change from the one to the other takes place during the lifetime of the individual. Furthermore, the eruciform condition is plainly an adaptive one, brought about by an abundant and easily obtainable supply of food. The lack of a thysanuriform stage in the development of the most specialized eruciform larvæ, as those of flies and bees, is regarded by Hyatt and Arms as an illustration of the general principle known as "acceleration of development," according to which newer and useful adaptive characters tend to appear earlier and earlier in the development, gradually crowding upon and forcing out older and useless characters. In connection with this subject, the appearance of temporary abdominal legs in embryo bees is significant, as indicating an ancestral active condition. In accounting for the evolution of metamorphosis, the theory of natural selection finds one of its most important applications.

3. INTERNAL METAMORPHOSES

In Heterometabola, the internal post-embryonic changes are as direct as the external changes of form; in Holometabola, on the contrary, not all the larval organs pass directly into imaginal organs, for certain larval tissues are demolished and their substance reconstructed into imaginal tissues. When indirect, the internal metamorphosis is nevertheless continuous and gradual, without the abruptness that characterizes the external transformation. In the larval stage imaginal organs arise and grow; in the pupal stage the purely larval organs gradually disappear while the imaginal organs are continuing their development.

Phagocytes.—The destruction of larval tissues, or *histolysis*, is due often to the amœboid blood corpuscles, known as *leucocytes* or *phagocytes*, which attack some tissues and absorb their material, but later are themselves food for the developing imaginal tissues. The construction of tissues is termed *histogenesis*.

In Coleoptera the degeneration of the larval muscles is entirely chemical, there being no evidence of phagocytosis, according to Dr. R. S. Breed. Berlese, indeed, goes so far as to deny in general the destructive action of leucocytes on larval tissues.

Imaginal Buds.—The wings and legs of a fly originate in the larva in the form of cellular masses, termed *imaginal buds*, or histoblasts, as Weismann discovered. Thus in the larva of *Corethra*, there are in each thoracic segment a pair of dorsal buds and a pair of ventral buds (Fig. 222), each bud being clearly an evagination of the hypodermis at the bottom of a previous invagination. The six ventral buds form the legs eventually; of the dorsal buds, the middle and posterior pairs form, respectively, the wings and the halteres, and the anterior pair

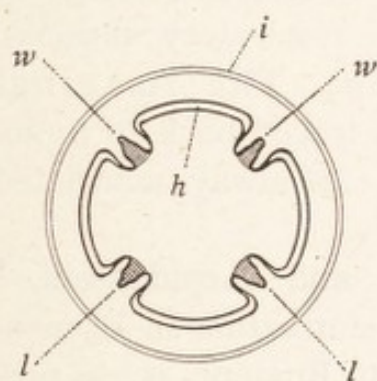
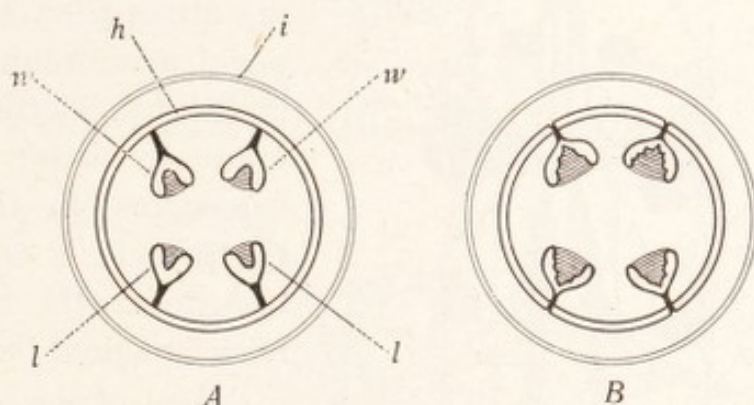


FIG. 222.—Diagrammatic transverse section of *Corethra* larva, to show imaginal buds of wings (*w*) and legs (*l*); *h*, hypodermis; *i*, integument.—Modified from Lang's *Lehrbuch*.

FIG. 223.—Diagrammatic transverse sections of muscid larvæ, to show imaginal buds. *h*, larval hypodermis; *i*, larval integument; *ih*, imaginal hypodermis; *l*, imaginal bud of leg; *w*, imaginal bud of wing.—Modified from Lang's *Lehrbuch*.

form the pupal respiratory processes. Each imaginal bud is situated in a *peripodal cavity*, the wall of which (*peripodal membrane*) is continuous with the general hypodermis; as the legs and wings develop, they emerge from their peripodal sacs and become free.

In *Corethra* but little histolysis occurs, most of the larval structures passing directly into the corresponding structures of the adult. *Corethra* is, indeed, in many respects intermediate between heterometabolous and holometabolous insects as regards its internal changes.

Muscidæ.—In Muscidæ, as compared with *Corethra*, the imaginal buds are more deeply situated, the peripodal membrane forming a

stalk (Fig. 223), and the processes of histolysis and histogenesis become extremely complicated. The hypodermis, muscles, alimentary canal and fat-body are gradually broken down and remodeled, and part of the respiratory system is reorganized, though the dorsal vessel and the

central nervous system, uninterrupted in their functions, undergo comparatively little alteration.

The imaginal hypodermis of the thorax arises from thickenings of the peripodal membrane which spread over the larval hypodermis, while the latter is gradually being broken down by the leucocytes; in the head and abdomen the process is essentially the same as in the thorax, the new hypodermis arising from imaginal buds.

Most of the larval muscles, excepting the three pairs of respiratory muscles, undergo dissolution. The imaginal muscles have been traced back to mesodermal cells such as are always associated with imaginal buds.

Hymenoptera and Lepidoptera.—

The internal transformation in Hymenoptera, according to Bugnion, is less profound than in Muscidae and more extensive than in Coleoptera and Lepidoptera. The internal metamorphosis in Lepidoptera resembles in many respects that of *Corethra*. In both these orders the dorsal pair of prothoracic buds is absent. In

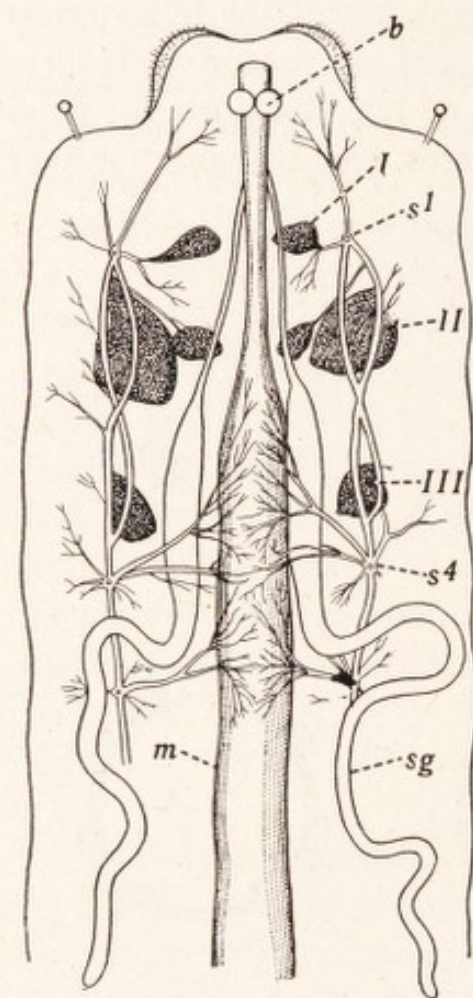


FIG. 224.—Imaginal buds of full grown larva of *Pieris*, dorsal aspect. *b*, brain; *m*, mid intestine; *s¹*, prothoracic spiracle; *s⁴*, first abdominal spiracle; *sg*, silk gland; *I*, prothoracic bud; *II*, bud of fore wing; *III*, bud of hind wing.—After GONIN.

a full-grown caterpillar the fundamentals of the imaginal legs and wings (Fig. 224) may be seen, the wings in a frontal section of the larva appearing as in Fig. 225. Many of the details of the internal metamorphosis in Lepidoptera have been described by Newport and Gonin. Figure 226, after Newport, shows some of the more evident internal differences in the larva, pupa and imago of a lepidopterous insect.

Significance of Pupal Stage.—To repeat—among holometabolous insects the function of nutrition becomes relegated to the larval stage

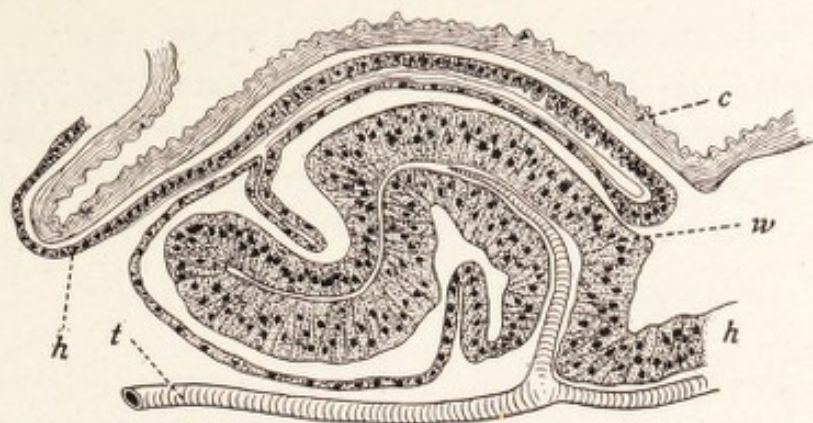


FIG. 225.—Section through left hind wing in larva of *Pieris rapae*, the section being a frontal one of the caterpillar; the base of the wing is anterior in position, and the apex posterior. *c*, cuticula; *h*, hypodermis; *t*, trachea; *w*, developing wing.—After MAYER.

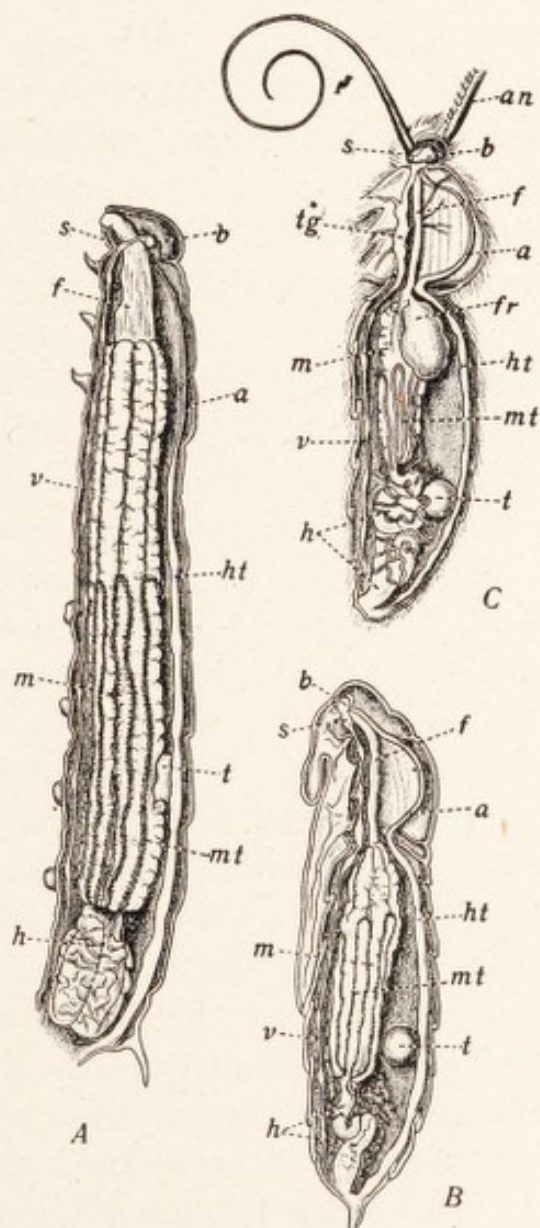


FIG. 226.—Internal transformations of *Sphinx ligustri*. *A*, larva; *B*, pupa; *C*, moth; *a*, aorta; *an*, antenna; *b*, brain; *f*, fore intestine; *fr*, food reservoir; *h*, hind intestine; *ht*, heart; *m*, mid intestine; *mt*, Malpighian tubes; *p*, proboscis; *s*, subcesophageal ganglion; *t*, testis; *tg*, thoracic ganglia; *v*, ventral nerve cord.—After NEWPORT.

and that of reproduction to the imaginal stage. Larva and imago become adapted to widely different environments. So dissimilar are the two environments that a gradual change from the one to the other is no longer possible; the revolutionary changes in structure necessitate a temporary cessation of external activity.

CHAPTER IV

ADAPTATIONS OF AQUATIC INSECTS

Ease, versatility and perfection of adaptation are beautifully exemplified in aquatic insects.

Systematic Position.—Aquatic insects do not form a separate group in the system of classification, but are distributed among several orders, of which Plecoptera, Ephemerida, Odonata and Trichoptera are pre-eminently aquatic. One third of the families of Heteroptera and less than one fourth those of Diptera are more or less aquatic. One tenth of the families of Coleoptera frequent the water at one stage or another, two families of Neuroptera, and only half a dozen genera of Lepidoptera. A few Collembola live upon the surface of water; and several Hymenoptera, though not strictly aquatic, are known to parasitize the eggs and larvæ of aquatic insects.

The change from the terrestrial to the aquatic habit has been a gradual change of adaptation, not an abrupt one. Thus at present there are some tipulid larvæ that inhabit comparatively dry soil; others live in earth that is moist; many require a saturated soil near a body of water and many, at length, are strictly aquatic. Among beetles, also, similar transitional stages are to be found.

Food.—Insects have become adapted to utilize with remarkable success the immense and varied supply of food that the water affords. Hosts of them attack such parts of plants as project above the surface of the water, and the caterpillar of *Paraponyx* (Fig. 174) feeds on submerged leaves, especially of *Vallisneria*, being in this respect almost unique among Lepidoptera. Hydrophilid beetles and many other aquatic insects devour submerged vegetation. The larvæ of the chrysomelid genus *Donacia* find both nourishment and air in the roots of aquatic plants. Various Collembola subsist on floating algæ, and larvæ of mosquitoes and black-flies on microscopic organisms near the surface, while larvæ of midges, *Chironomus*, find food in the sediment that accumulates at the bottom of a body of water.

Predaceous species abound in the water. The backswimmer, *Notonecta* (Fig. 227) approaches its prey from beneath, clasps it with the front pair of legs and pierces it. The water scorpions, *Nepa* and

Ranatra, likewise have prehensile front legs along with powerful piercing organs. The electric light bugs, *Belostoma* and *Benacus* (Fig. 23) even kill small fishes by their poisonous punctures. Some other kinds, as the water-skaters (Gerridæ, Fig. 228), depend on dead or disabled insects. The species of *Hydrophilus* (Fig. 229) are to some extent carnivorous as



FIG. 227.—Backswimmer, *Notonecta insulata*, natural size.



FIG. 228.—Water-skater, *Gerris remigis*, natural size.

larvæ but phytophagous as imagines, while Dytiscidæ (diving beetles) are carnivorous throughout life. Aquatic insects eat not only other insects, but also worms, crustaceans, mollusks or any other available animal matter.

Even aquatic insects are not exempt from the attacks of parasitic species. A few Hymenoptera actually enter the water to find their victims, for example, the ichneumon *Agriotypus*, which lays its eggs on the larvæ of caddis flies.

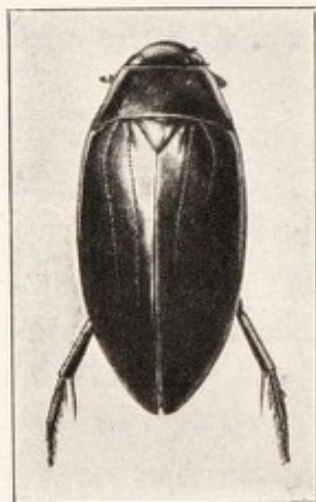


FIG. 229.—*Hydrophilus triangularis*, natural size.

Locomotion.—Excellent adaptations for aquatic locomotion are found in the common *Hydrophilus triangularis* (Fig. 229). Its general form reminds one of a boat, and its long legs resemble oars. The smoothly elliptical contour and the polished surface serve to lessen resistance. Owing to the form of the body (Fig. 230, A) and the presence of a dorsal air-chamber under the elytra, the back of the insect tends to remain uppermost, while in the backswimmer, *Notonecta* (Fig. 230, B), on the other hand, the conditions are reversed, and the insect swims with its back downward. The legs of *Hydrophilus*, excepting the

first pair, are broad and thin (Fig. 231, A) and the tarsi are fringed with long hairs. When swimming, the "stroke" is made by the flat surface, aided by the spreading hairs; but on the "recover," the leg is turned so

as to cut the water, while the hairs fall back against the tarsus from the resistance of the water, as the leg is being drawn forward. The hind

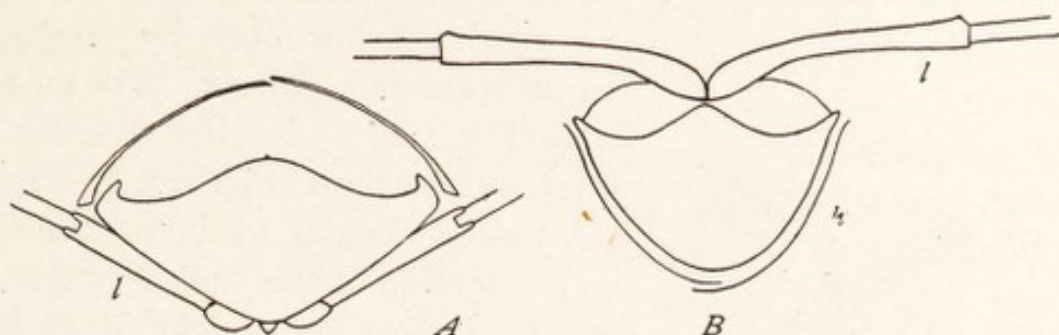


FIG. 230.—Transverse sections of (A) *Hydrophilus* and (B) *Notonecta*. *e*, elytron; *h*, hemelytron; *l*, metathoracic leg.

legs, being nearest the center of gravity, are of most use in swimming, though the second pair also are used for this purpose; indeed, a terrestrial insect, finding itself in the water, instinctively relies upon the third pair of legs for locomotion. *Hydrophilus* uses its oar-like legs alternately, in much the same sequence as land insects, but *Cybister* and other Dytiscidæ, which are even better adapted than *Hydrophilus* for aquatic locomotion, move the hind legs simultaneously, and therefore can swim in a straight line, without the wobbling and less economical movements that characterize *Hydrophilus*.

Larvæ of mosquitoes propel themselves by means of lashing, or undulatory, movements of the

abdomen. A peculiar mode of locomotion is found in dragon fly nymphs, which project themselves by forcibly ejecting a stream of water from the anus.

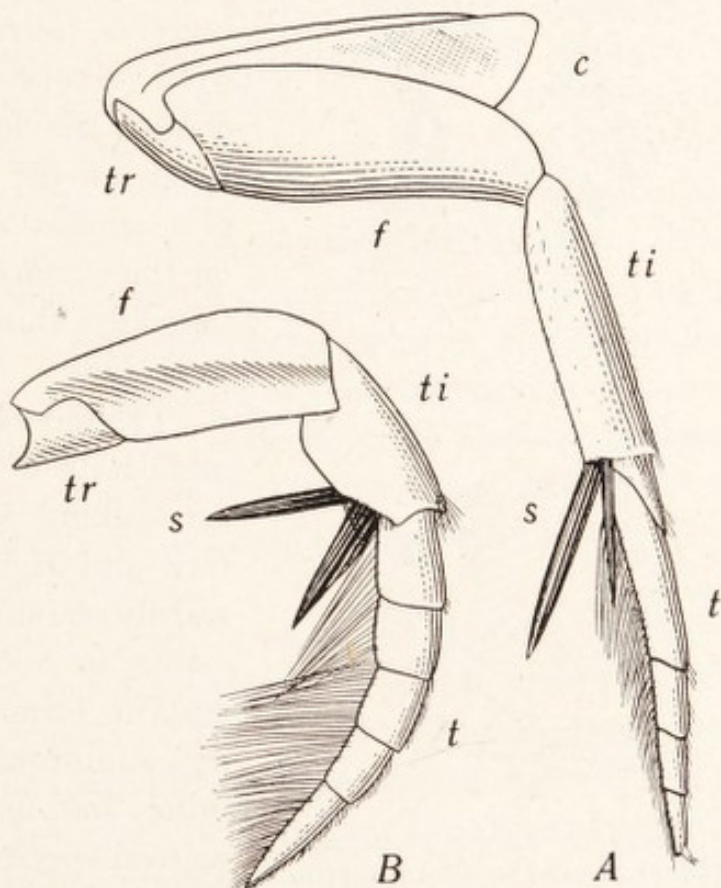
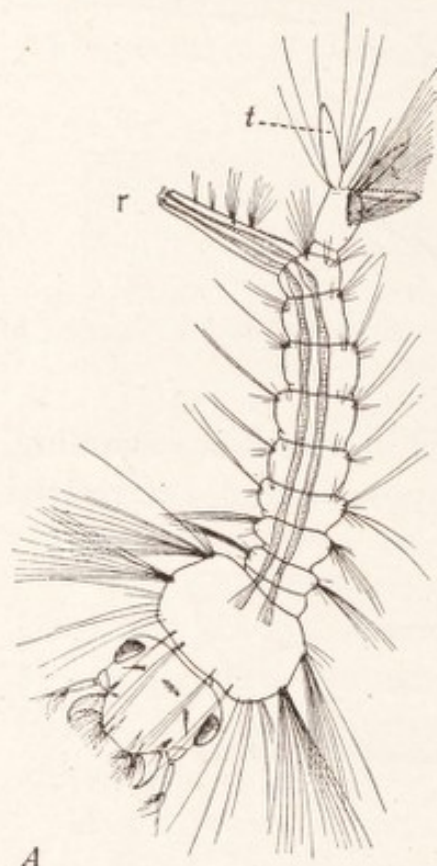
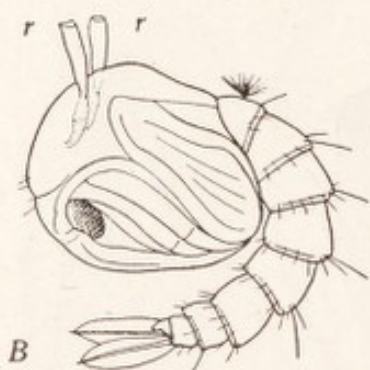


FIG. 231.—Left hind legs of aquatic beetles. A, *Hydrophilus triangularis*; B, *Cybister fimbriolatus*; *c*, coxa; *f*, femur; *s*, spur; *t*, tarsus; *ti*, tibia; *tr*, trochanter.

On account of the large amount of air that they carry about, most aquatic imagines are lighter than the water in which they live, and therefore can rise without effort, but can descend only by exertion, and can remain below only by clinging to chance stationary objects. The mosquito larva (Fig. 232, *A*) is often heavier than water, but the pupa (Fig. 232, *B*) is lighter, and remains clinging to the surface film.



A



B

FIG. 232.—Larva (*A*) and pupa (*B*) of mosquito, *Culex pipiens*. *r*, respiratory tube; *t*, tracheal gills.

The tension of this surface film is sufficient to support the weight of an insect up to a certain limit, provided the insect has some means of keeping its body dry. This is accomplished usually by hairs, set together so thickly that water cannot penetrate between them. As the legs and body of *Gerris* are rendered water-proof by a velvety clothing of hairs, the insect, though heavier than water, is able to skate about on the surface. *Gyrinus*, by means of a similar adaptation, can circle about on the surface film, and minute collembolans leap about on the surface as readily as on land.

The modifications of the legs for swimming have often impaired their usefulness for walking, so that many aquatic Coleoptera and Hemiptera can move but awkwardly on land. When walking, it is interesting to note, *Cybister* and some other aquatic forms no longer move their hind legs simultaneously as they do in swimming, but use them alternately, like terrestrial species.

The adaptations for swimming do not necessarily affect the power of flight.

Dytiscus, *Hydrophilus*, *Gyrinus*, *Notonecta*, *Benacus* and many other Coleoptera and Hemiptera leave the water at night and fly around, often being found about electric lights.

Respiration.—Aquatic insects have not only retained the primitive, or open (*holopneustic*) type of respiration, characterized by the presence

of spiracles, but have also developed an adaptive, or closed (*apneustic*) type, for utilizing air that is mixed with water.

Through minor modifications of structure and habit, many holopneustic insects have become fitted for an aquatic life. In these instances the insects have some means of carrying down a supply of air from the surface of the water. Thus the backswimmer, *Notonecta*, bears on its body a silvery film of air entangled in closely set hairs, which exclude the water. The whirligig beetle, *Gyrinus*, descends with a bubble of air at the end of the abdomen. *Dytiscus* and *Hydrophilus* have each a capacious air-space between the elytra and the abdomen, into which space the spiracles open. The water scorpions, *Nepa* and *Ranatra*, have each a long respiratory organ composed of two valves, which lock together to form a tube that communicates with the single pair of spiracles situated near the end of the abdomen. The mosquito larva, hanging from the surface film, breathes through a cylindrical tube (Fig. 232, *A*, *r*) projecting from the penultimate abdominal segment; the pupa, however, bears a pair of respiratory tubes on the back of the thorax (Fig. 232, *B*, *r*, *r*), which is now upward, probably in order to facilitate the escape of the fly. The rat-tailed maggot (*Eristalis*), three quarters of an inch long, has an extensile caudal tube seven times that length, containing two tracheæ terminating in spiracles, through which air is brought down from above the mud in which the larva lives. Similarly, in the dipterous larva, *Bittacomorpha clavipes* (Fig. 175), the posterior segments of the abdomen are attenuated to form a long respiratory tube. The larva of *Donacia* appears to have no special adaptations for aquatic respiration except a pair of spines near the end of the body, for piercing air chambers in the roots of the aquatic plants in which it dwells.

The simplest kind of apneustic respiration occurs in aquatic nymphs such as those of Ephemerida and Agrionidæ, whose skin at first is thin enough to allow a direct aëration of the blood. This *cutaneous* respiration is possible during the early life of many aquatic species.

Branchial respiration is, however, the prevalent type among aquatic nymphs and is perhaps the most important of their adaptive characteristics. Thin-walled and extensive outgrowths of the integument, containing tracheal branches or, rarely, only blood (*Blood gills*) enable these forms to obtain air from the water. May fly nymphs (Figs. 20, *A*; 170), with their ample waving gills, offer familiar examples of branchial respiration. *Tracheal gills* are very diverse in form and situation, occurring in a few species of May fly nymphs on the thorax or head,

though commonly restricted to the sides of the abdomen, where they occur in pairs or in paired clusters (Fig. 20, A). *Caudal gills* are found in agrionid nymphs (Fig. 173). The aquatic caterpillars of *Paraponyx* (Fig. 174) are unique among Lepidoptera in having gills, which are filamentous in this instance.

Caddis worms, enclosed in their cases, maintain a current of water by means of undulatory movements of the body, and the larvæ and pupæ of most black-flies (Simuliidæ, Fig. 233) secure a continuous supply of fresh air simply by fastening themselves to rocks in swiftly flowing streams.

Rectal respiration is highly developed in dragon fly nymphs. In these, the rectum is lined with thousands of tracheal branches, which are bathed by water drawn in from behind, and then expelled.

All these kinds of respiration—cutaneous, branchial and rectal—occur in young ephemerid nymphs; while mosquito larvæ have in addition spiracular respiration.

With the arrival of imaginal life, tracheal gills disappear, except in Perlidæ, and even in these insects the gills are of little, if any, use.



FIG. 233.—*Simulium*.
A, larva; B, pupa, showing
respiratory filaments.

Marine Insects.—Except along the shore, the sea is almost devoid of insect life, the exceptions being a few chironomid larvæ which have been dredged in deep water, and fifteen species of *Halobates* (belonging to the same family as our familiar pond-skaters), which are found on warm smooth seas, where they subsist on floating animal remains.

Between tide-marks may be found various beetles and collembolans, which feed upon organic débris; as the tide rises, the former retreat, but the latter commonly burrow in the sand or under stones and become submerged, for example the common *Anurida maritima*.

Insect Drift.—Seaweed or other refuse cast upon the shore harbors a great variety of insects, especially dipterous larvæ, staphylinid scavengers and predaceous Carabidæ. On the shores of inland ponds and lakes a similar assemblage of insects may be found feeding for the most part on the remains of plants or animals, or else on one another. During a strong wind, the leeward shore of a lake is an excellent collecting ground, as many insects are driven against it. On the shores of the Great Lakes insects are occasionally cast up in immense numbers, form-

ing a broad windrow, fifty or perhaps a hundred miles long. Needham has described such an occurrence on the west shore of Lake Michigan, following a gale from the northeast. In this instance, a liter of the drift contained nearly four thousand insects, of which 66 per cent. were crickets (*Nemobius*), 20 per cent. Locustidæ, and the remainder mostly beetles (Carabidæ, Scarabæidæ, Chrysomelidæ, Coccinellidæ, etc.), dragon flies, moths, butterflies (*Anosia*, *Pieris*, etc.) and various Hemiptera, Hymenoptera and Diptera. A large proportion of the insects were aquatic forms, such as *Hydrophilus*, *Cybister*, *Zaita*, and a species of caddis fly; these had doubtless been carried out by freshets, while the butterflies and dragon flies had been borne out by a strong wind from the northwest, after which all were driven back to the coast by a northeast wind. While some of these insects survived, notably Coccinellidæ, Trichoptera, Asilidæ, Locustidæ and Gryllidæ, nearly all the rest were dead or dying, including the dragon flies, flies, bumblebees and wasps. Foraging Carabidæ were observed in large numbers, also scavengers of the families Staphylinidæ, Silphidæ and Dermestidæ.

On the seashore and on the shores of the Great Lakes, the salient features of insect life are essentially the same. Similar species occur in the two places with similar biological relations, on account of the general similarity of environment.

Origin of the Aquatic Habit.—The theory that terrestrial insects have arisen from aquatic species is no longer tenable, for the evidence shows that the terrestrial type is the more primitive. Aquatic insects still retain the terrestrial type of organization, which remains unobscured by the temporary and comparatively slight adaptations for an aquatic life. Thus, the development of tracheal gills has involved no important modification of the fundamental plan of tracheal respiration. It is significant, moreover, that the most generalized, or most primitive, insects—Thysanura—are without exception terrestrial. Aquatic insects do not constitute a phylogenetic unit, but represent various orders, which are for the most part undoubtedly terrestrial, notwithstanding the fact that a few of these orders (Plecoptera, Ephemerida, Odonata, Trichoptera) are now wholly aquatic in habit. Adaptations for an aquatic existence have arisen independently and often, in the most diverse orders of insects.

CHAPTER V

COLOR AND COLORATION

The naturalist distinguishes between the terms *color* and *coloration*. A *color* is a single hue, while *coloration* refers to the arrangement of colors.

Sources of Color.—The colors of insects are classed as (1) *pigmental* (*chemical*), those due to internal pigments; (2) *structural* (*physical*), those due to structures that cause interference or reflection of light; and (3) *combination colors* (*chemico-physical*), which are produced in both ways at once.

Structural Colors.—The iridescence of a fly's wing and that of a soap bubble are produced in essentially the same way. The wing, however, consists of two thin, transparent, slightly separated lamellæ, which diffract white light into prismatic rays, the color differences depending upon differences in the distance between the two membranes.

The brilliant iridescent hues of many butterfly scales are due to the diffraction of light by fine, closely parallel striæ (Fig. 95) just as in the case of the "diffraction gratings" used by the physicist, which consist of a glass or metallic plate with parallel equidistant diamond rulings of microscopic fineness. The particular color produced depends in both cases upon the distance between the striæ. Though almost all lepidopterous scales are striated, it is only now and then that the striæ are sufficiently close together to give diffraction colors. In a Brazilian species of *Apatura* the iridescent scales have 1,050 striæ to the millimeter, and in a species of *Morpho*, according to Kellogg, the iridescent pigmented scales have 1,400 striæ per millimeter, the striæ being only .0007 mm. apart; while in some of the finest Rowland gratings they number about 1,200 per millimeter.

In the well known diamond beetle the green dots of the elytra are depressions from which spring brilliant and exquisitely colored scales, the colors varying throughout the range of the spectrum; green, however, predominating. These colors are due to diffraction from regular striations, with a "grating" space of a thousandth to a two-thousandth of a millimeter. On immersing the specimen in oil or other liquid little or no change is observed, except in those specimens in which a small communicating aperture exists in the neck of the scale. The oil can be

seen gradually to fill the interior, and simultaneously all trace of color vanishes (except sometimes a faint greenish surface color). It appears, then, that the color in this case is due to fine striations on the interior surface of the scale. (Michelson.)

The interference colors of butterfly scales may be due, not only to surface markings, but also to the lamination of the scale and to the overlapping of two or more scales. In beetles the brilliant blues and greens, and iridescence in general, are sometimes produced by minute lines or pits that diffract the light. According to Tower, "The pits alone, however, are powerless to produce any color; it is only when they are combined with a highly reflecting and refractive surface lamella and a pigmented layer below that the iridescent color appears. The action of light is in this case the same as in the plain metallic coloring, excepting that each pit acts as a revolving prism to disperse different wave-lengths of light in different directions, and the combined result is iridescence. The existence of minute pits over the body surface is of common occurrence, but it is only when they are combined as above that iridescent colors occur."

The production of color by "metallic" reflection deserves more attention than it has received from naturalists. The metallic colors of birds and insects have been studied precisely by Professor Michelson, who has proved that they are due to the same causes in both animals and metals. The metals, on account of their extraordinary opacity, throw back practically all the light that strikes them, thus giving the characteristic brilliant reflections; the distance to which light can penetrate in most metals being only a small fraction of a light wave, so that a wave-motion such as constitutes light, strictly speaking, can not be propagated at all. As this opacity may be different for different colors, some would be transmitted more freely than others, so that the resulting transmitted light would be colored; and the reflected light would be approximately complementary to the transmitted color. (Michelson.) Thus the reflected light from the metal gold is yellow, the transmitted light being blue. In certain pigeons, peacocks, humming birds, as well as a number of butterflies, beetles and other insects, the brilliant metallic colors are due to an extremely thin surface film which has optical qualities like those of metals. This film in the case of the coppery wing cover of a beetle was calculated by Michelson to be less than a ten-thousandth of a millimeter in thickness.

In animals, as in metals, these colors are brilliant because a large percentage of the incident light is reflected. The color of the reflected

light is complementary to that of the transmitted. Furthermore, the color of the reflected light changes when the surface is inclined, the color always approaching the violet end of the spectrum as the incidence increases. "If the color of the normal reflection is violet the light vanishes (changing to ultra-violet), and if the normal radiation be infra-red it passes through red, orange, and yellow as the incidence increases." (Michelson.)

Professor Michelson states that the metallic and spectrum colors of the tiger beetles, *Cicindelidæ*, are chiefly if not entirely true surface or metallic colors, produced by a film of ultra-microscopic thickness, probably less than a ten-thousandth of a millimeter. This film must be lacking in the dead black variety of *Cicindela scutellaris*, which is without trace of color, like a piece of black paper. Michelson is inclined to attribute differences in the colors to differences in the chemical constitution of the film, and color changes during ontogeny to changes in chemical constitution, but states that this would be very difficult to demonstrate on account of the minuteness of the film. (Shelford.)

Silvery white effects are usually caused by the total reflection of light from scales or other sacs that are filled with air; the same silvery appearance is given also by air-filled tracheæ and by the air bubbles that many aquatic insects carry about under water.

Violet, blue-green, coppery, silver and gold colors are, with few exceptions, structural colors. (Mayer.)

Pigmental Colors.—These are either *cuticular* or *hypodermal*. The predominant brown and black colors of insects are made by pigment diffused in the outer layer of the cuticula (Fig. 90). Cockroaches are almost white just after a molt, but soon become brown, and many beetles change gradually from brown to black. In these cases it is apparently significant that the cuticular pigments lie close to the surface of the skin, i. e., where they are most exposed to atmospheric influences. Gortner found that the black cuticular pigment in the Colorado potato beetle (*Leptinotarsa*) and the brown or black pigments of the tiger beetles (*Cicindela*) belong to the group of melanins and are produced by oxidation, induced by an oxidase; that when all oxygen is absent no pigmentation takes place.

The cuticular pigments are derived, of course, from the underlying hypodermis cells, and these cells themselves, moreover, usually contain (1) colored granules or fatty drops which give red, yellow, orange and sometimes white or gold colors as seen through the skin; (2) diffused

chlorophyll (green) or xanthophyll (yellow), taken from the food plant. Unlike the structural colors, which are persistent, these hypodermal colors often change after death, though less rapidly when the pigments are tightly enclosed, as in scales or hairs. Though white and green are structural colors as a rule, they are due to pigments in Pieridæ, Lycænidæ and some Geometridæ.

Frequently a color pattern consists partly of cuticular and partly of hypodermal colors, the hypodermal or sub-hypodermal color forming "a groundwork upon which the pattern is cut out by the cuticular color." (Tower.) Thus in the Colorado potato beetle, *Leptinotarsa decemlineata*, the pattern "is composed of a dark cuticular pigment upon a yellow hypodermal background."

The pigment present in the cuticula of tiger beetles is essentially all in the primary cuticula, and is always either brown or black. In certain areas the primary cuticula is pigmented and in certain areas clear and transparent. This gives the color pattern. The secondary cuticula beneath the unpigmented areas is full of pore canals and large air-filled interlamellar spaces, and these give the effect of a white or straw color depending upon the color of the secondary cuticula itself. (Shelford.)

Combination Colors.—The splendid changeable hues of *Apatura*, *Euplœa* and other tropical butterflies depend upon the fact that their scales are both pigmented and striated. Under the microscope, certain *Apatura* scales are brown by transmitted light and violet by reflected light, and to the unaided eye the color of the wing is either brown or violet, according as the light is received respectively from the pigment or from the striated surfaces of the scales.

Nature of Pigments.—Some pigments are taken bodily from the food; others are manufactured indirectly from the food, and some of these are excretory products.

The green color of many caterpillars and grasshoppers is due to chlorophyll, which tinges the blood and shows through the transparent integument. Mayer has found that scales of Lepidoptera contain only blood while the pigment is forming; that the first color to appear upon the pupal wings is a dull ochre or drab—the same color that the blood assumes when it is removed from the pupa and exposed to the air; also that pigments like those of the wings may be manufactured artificially from pupal blood. Pieridæ are peculiar in the nature of their pigments, as Hopkins has shown. The white pigment of this family is uric acid and the reds and yellows of *Pieris*, *Colias* and *Papilio* are due to deriva-

tives of uric acid; the yellow pigment, termed lepidotic acid, precedes the red in time of appearance, the latter being probably a derivative of the former. The green pigments of some Papilionidæ, Noctuidæ, Geometridæ and Sphingidæ are also said by some investigators to be products of uric acid, which in insects as in other animals is primarily an excretory, or waste, product.

Effects of Food on Color.—Besides chlorophyll, to which various caterpillars, aphids and other forms owe their green color, the yellow constituent of chlorophyll, namely xanthophyll, frequently imparts its color to plant-eating insects, while some phytophagous species are dull yellow or brown from the presence of tannin, taken from the food plant. Most pigments, however, are elaborated from the food by chemical processes that are not well understood.

Many who have reared Lepidoptera extensively know that the color of the imago is influenced by the character of the larval food, other conditions being equal, and are able at will to effect certain color changes simply by feeding the larvæ from birth upon particular kinds of plants. In this country we have few observations upon the subject, but in Europe the effects of food upon coloration have been ascertained in the case of many species of Lepidoptera. According to Gregson, *Hybernia defoliaria* is richly colored when fed upon birch, but is dull colored and almost unmarked when fed on elm. Pictet, by feeding larvæ of *Vanessa urticæ* on the flowers instead of the leaves of the nettle obtained the variety known as *urticoides*. Food affects the color of the larva also, as Poulton found in the case of caterpillars of *Tryphæna pronuba*, all from the same batch of eggs. When fed with only the white midribs of cabbage leaves, the larvæ remained almost white for a time, but afterward showed a moderate amount of black pigment; when fed with the yellow etiolated heart-leaves or the dark green external leaves, however, the larvæ all became bright green or brown—the same pigment being derived indifferently from etiolin (probably the same substance as xanthophyll) or chlorophyll.

Though the pigments may differ in color or amount according to the kind of food, the color patterns vary without regard to food. Thus *Callosamia promethea*, *Leptinotarsa decemlineata* (Colorado potato beetle), Coccinellidæ (lady-bird beetles) and a host of other insects exhibit extensive individual variations in coloration under precisely the same food conditions. Caterpillars of the same kind and age are often very differently marked when feeding upon the same plant; for example, *Chloridea obsoleta* (corn worm) and the sphingid *Deilephila*

lineata. Furthermore, striking changes of coloration accompany each molt in most caterpillars, but particularly those of butterflies, and these changes may prove to have an important phylogenetic significance. Individual differences of coloration apart from those due to the direct action of food, light, temperature and other environmental conditions are to be explained by heredity.

Effects of Light and Darkness.—Sunlight is an important factor in the development of most animal pigments, as they will not develop in its absence. The collembolan *Anurida maritima* is white at hatching, but soon becomes indigo blue, unless shielded from sunlight, in which event it remains white until exposed to the sunlight, when it assumes the blue color. Subterranean or wood-boring larvæ are commonly white or yellow, but never highly colored. The most notable instances, however, are furnished by cave insects. These, like other cavernicolous animals, are characteristically white or pale from the absence of pigment, if they live in regions of continual darkness, but have more or less pigmentation in proportion respectively to the greater or less amount of sunlight to which they have access.

Curiously enough, light often hastens the destruction of pigment in insects that are no longer alive, for which reason it is necessary to keep cabinet specimens in the dark as much as possible. Life is evidently essential for the sustention or renewal of the pigments.

A chrysalis not infrequently matches its surroundings in color. This phenomenon has been investigated by Poulton, who has proved that the color of the chrysalis is determined largely by the prevalent color of the surroundings during the last few days of larval life. Larvæ of the cabbage butterfly, *Pieris rapæ*, raised upon the same food plant (all other conditions being made as nearly equal as possible) produced dark pupæ if kept in darkness for a few days just before pupation; yellow light arrested the formation of the dark pigment and gave green pupæ; while light colors in general gave light-colored pupæ. This color resemblance is commonly assumed to be of protective value, and perhaps it is. Nevertheless, it is a direct effect of light, and does not need to be explained by natural selection, even though it cannot be denied that natural selection may have helped in its production.

Poulton extended his studies to the adaptive coloration of caterpillars and has published the results of an extensive series of experiments which prove that the colors of certain caterpillars also are directly produced by the same colors in the surrounding light. *Gastropacha quercifolia*, which always rests by day on the older wood of its food plant, was given black

twigs, reddish brown sticks, lichens, etc., to rest upon, and though all the larvæ were from the same cluster of eggs, and had been fed in the same way, each larva gradually assumed the color or colors of its resting place, resulting in exquisite examples of protective resemblance, the most remarkable of which were those in which the larvæ assumed the variegated coloration of lichens. Only the younger larvæ, however, proved to be susceptible to the colors of the environment; unlike those of *Amphidasis betularia*, in which the older larvæ also were sensitive to the surrounding light. Here again, natural selection is unnecessary, even if not superfluous, as an explanation of this kind of protective coloration.

Professor W. M. Wheeler has suggested that "such phenomena as the permanent protective coloration of insects may be regarded as the stereotyped, highly specialized end-stage of a more ancient ability actively to change color in response to color changes in the environment, an ability still possessed by some primitive insects like the grasshoppers and mantids, though much more pronounced in cephalopod mollusks, fishes, amphibia and lizards."

Effects of Temperature.—The amount of a pigment in the wing of a butterfly depends in great measure upon the surrounding temperature during the pupal stage, when the pigments are forming. Black or brown spots have been enlarged artificially by subjecting chrysalides to cold; hence it is probable that the characteristically large black spots on the under side of the wings of the spring brood of our *Cyaniris pseudargiolus* are simply a direct effect of cold upon the wintering chrysalides. Similarly the spring brood (variety *marcia*) of *Phyciodes tharos* owes its distinctive coloration to cold, as Edwards has proved experimentally. Lepidoptera have been the subject of very many temperature experiments, some of which will be mentioned presently in the consideration of seasonal coloration.

Speaking generally, warmth (except in *melanism*) tends to induce a brightening and cold a darkening of coloration, the darkening being due to an increased amount of black or brown pigment. Temperature, whether high or low, seldom if ever produces new pigments, but simply alters the amount and distribution of pigments that are present already.

Effects of Moisture.—Very little is known as to the effects of moisture upon coloration. The dark colors of insular or coastal insects as contrasted with inland forms, and the predominance of dull or suffused species in mountainous regions of high humidity, have led observers occasionally to ascribe *melanism* and *suffusion* to humidity. In these

cases, however, the possible influence of low temperature and other factors must be taken into consideration. The experiments of Merrifield and of Standfuss showed no effect of moisture upon lepidopterous pupæ.

Pictet has found, however, that humidity acting on the caterpillars of *Vanessa urticæ* and *V. polychloros* has a conspicuous effect on the coloration of the butterflies. Thus when the caterpillars were fed for ten days with moist leaves, the resulting butterflies had abnormal black markings on the wings, and the same results followed when the larvæ were kept in an atmosphere saturated with moisture.

Climatal Coloration.—The brilliant and varied colors of tropical insects are popularly ascribed to intense heat, light and moisture; and the dull monotonous colors of arctic insects, similarly to the surrounding climatal conditions. Climate undoubtedly exerts a strong influence upon coloration, but the precise nature of this influence is obscure and will remain so until more is known about the effects separately produced by each of the several factors that go to make up what is called climate.

The prevalence of intense and varied colors among tropical insects is doubtless somewhat exaggerated, for the reason that the highly colored species naturally attract the eye to the exclusion of the less conspicuous forms. Indeed, Wallace assures us that, although tropical insects present some of the most gorgeous colors in the whole realm of nature, there are thousands of tropical species that are as dull colored as any of the temperate regions. Carabidæ, in fact, attain their greatest brilliancy in the temperate zone, according to Wallace, though butterflies certainly show a larger proportion of vivid and varied colors in the tropics. Mayer finds, in the widely distributed genus *Papilio*, that 200 South American species display but 36 colors, while 22 North American species show 17. While the number of species in South America is nine times as great as in North America, the number of colors displayed is only a little more than twice as great; hence Mayer concludes that the richer display of colors in the tropics *may* be due to the far greater number of species, which gives a better opportunity for color sports to arise; and not to any direct influence of the climate. Furthermore, the number of broods which occur in a year is much greater in the tropics than in the temperate zones, so that the tropical species must possess a correspondingly greater opportunity to vary.

Albinism and Melanism.—These interesting phenomena, widespread among the higher animals, have often been attributed to temperature, but albinism and melanism are, in some instances at least, strongly inherited without regard to temperature.

Albinism is exceptional whiteness or paleness of coloration, and is due usually to deficiency of pigment, but in some instances (Pieridæ) to the presence of a white pigment.

The common yellow butterfly, *Colias philodice*, and its relatives, are frequently albinic. Scudder observed that albinism among butterflies in America appears to be confined to a few Pieridæ, and to be restricted to the female sex; is more common in subarctic and subalpine regions than in lower latitudes and altitudes, and only in the former places includes all the females. At low altitudes, however, instead of appearing early in the year as might be expected, the albinic forms appear during the warmer months.

The experiments made by Gerould on *C. philodice* show that the number of albinic female offspring from white females crossed with yellow males is in accordance with Mendelian law. Albinism is not entirely confined to the female as Scudder thought, for white males occur, though they are extremely rare. "They may be expected in regions where the white female is especially abundant" (Gerould).

In Europe there are many albinic species of butterflies, and they are by no means confined to family Pieridæ.

Melanism is unusual blackness or darkness of coloration. As to how it is produced little is known, though warmth is probably the most potent influence, and some attribute it to moisture, as was mentioned. Pictet obtained partial melanism in *Vanessa urticæ* and *V. polychloros* by subjecting the larvæ to moisture.

In warm latitudes, some females of our *Papilio glaucus* are blackish brown with black markings, instead of being, as usual, yellow with black markings. In the South, some males of the spring brood of *Cyaniris pseudargiolus* are partly or wholly brown instead of blue. A melanic male of *Colias philodice* occurs as an extremely rare mutation. A melanic variety of pomace fly, *Drosophila*, with a black body, follows the Mendelian law in its appearance in breeding experiments.

Seasonal Coloration.—When butterflies have more than one brood in a year, the broods usually differ in aspect, sometimes so much that their specific identity is revealed only by rearing one brood from another. The same species may exist under two or more distinct forms during the same season—in other words, may be seasonally *dimorphic*, *trimorphic* or *polymorphic*.

Thus *Polygonia interrogationis* has two forms, *fabricii* and *umbrosa*, which differ not only in coloration, but even in the form of the wings

and the genitalia. In New England *fabricii* hibernates and produces *umbrosa*, as a rule, while *umbrosa* usually yields *fabricii*.

The little blue butterfly, *Cyaniris pseudargiolus* (Fig. 234), is polymorphic to a remarkable degree. In the high latitudes of Canada a

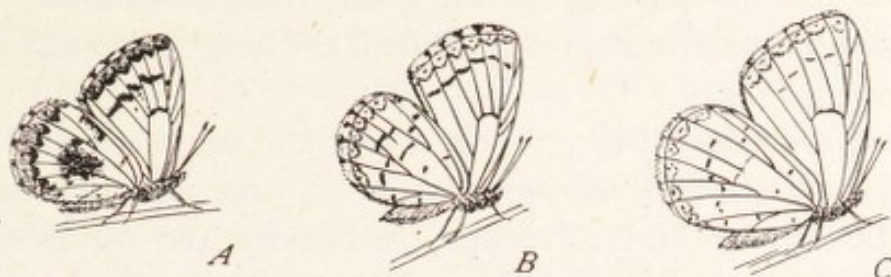


FIG. 234.—*Cyaniris pseudargiolus*; A, form *lucia*; B, *violacea*; C, *pseudargiolus* proper. Natural size.

single brood (*lucia*) occurs. About Boston the same spring brood appears, but under two forms: an earlier variety (*lucia*), which is small, with large black markings beneath; and a later variety (*violacea*), which is typically larger, with smaller black spots, though it varies into the form *lucia*. Finally, in summer, a third form (*pseudargiolus* proper) appears, as the product of *lucia* or else the joint product of *lucia* and *violacea*, and this is still larger, but the black spots are now faint. In the warm South the spring form is *violacea*, but while some of the males are blue, others are melanic, as just mentioned—a dimorphic condition which does not occur in the North. *Violacea* then produces *pseudargiolus*, in which, however, all the males are blue.

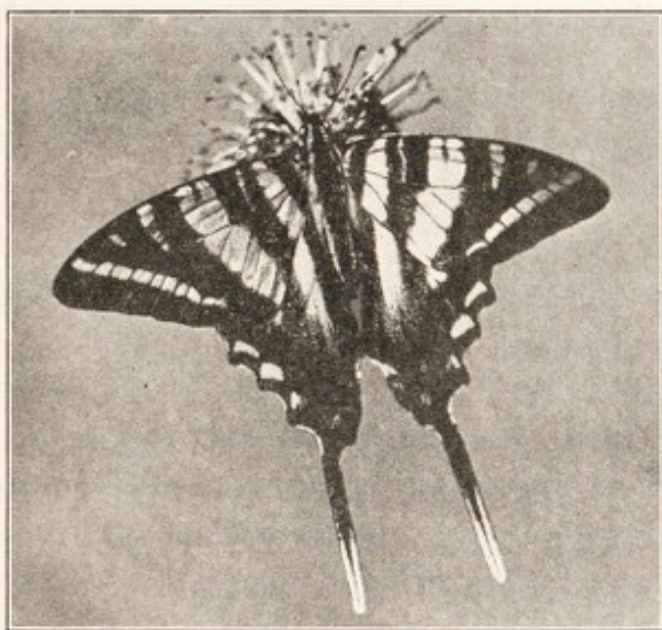


FIG. 235.—*Iphiclides ajax*, form *telamonides*, on flower of button bush. Reduced.

Iphiclides ajax (Fig. 235) is another polymorphic butterfly whose life history is complex. The three principal varieties of this species, known respectively as *marcellus*, *telamonides* and *ajax*, differ not only in coloration, but also in size and form; *marcellus* appears first, in spring; *telamonides* appears a little later (though before *marcellus* has disappeared); and *ajax* is the summer form; as the season advances the

varieties become successively larger, with longer tails to the hind wings.

Now Edwards submitted chrysalides of the summer form *ajax* to cold and thereby obtained, in the same summer, butterflies with the form of *ajax* but the markings of the spring form *telamonides*. Some of the chrysalides, however, lasted over until the next spring and then gave *telamonides*.

In *Phyciodes tharos* (Fig. 236) the spring and summer broods, termed respectively *marcia* and *morpheus*, were at first regarded as distinct species. In *marcia* the hind wings are heavily and diffusely marked beneath with strongly contrasting colors, while in *morpheus* they are plain and but faintly marked. Edwards placed upon ice eighteen chrysalides that normally would have produced *morpheus*; but instead

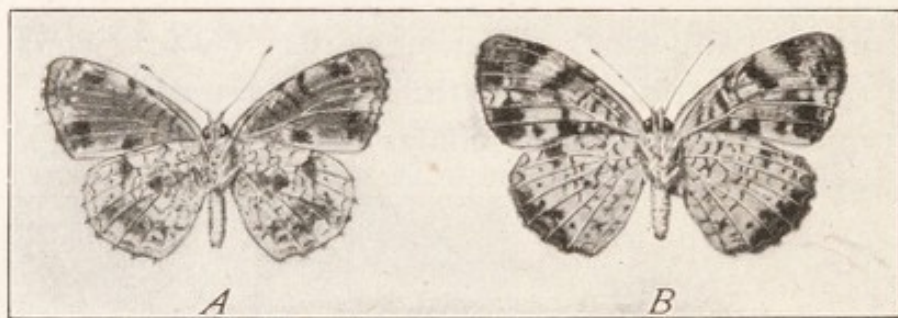


FIG. 236.—*Phyciodes tharos*; A, spring form, *marcia*; B, summer form, *morpheus*; under surfaces. Natural size.

of this, the fifteen imagines that emerged were all of the spring form *marcia* and were smaller than usual. Pupæ derived from eggs of *marcia* gave, after artificial cooling, not *morpheus*, but *marcia* again. The evident conclusion is that the distinctive coloration of the spring variety is brought about by low temperature. In Labrador, only one brood occurs—*marcia*; in New York, the species is *digoneutic* (two-brooded) and in West Virginia *polygoneutic* (several-brooded).

Extensive temperature experiments upon seasonal dimorphism in Lepidoptera have been conducted in Europe by some of the most competent biologists. Weismann found that pupæ of the summer form of *Pieris napi*, if placed on ice, disclosed the darker winter form, usually in the same season, though sometimes not until the next spring. It was found impossible, however, to change the winter variety into the summer one by the application of heat. Similar results have attended the important and much-discussed experiments of Dorfmeister, Weismann and others upon *Vanessa levana-prorsa* and other species, from which it has been inferred by Weismann that the winter form is the primary,

older, and more stable of the two forms, and the summer form a secondary, newer, and less stable variety; since the latter form only, as a rule, responds much to thermal influences. Weismann argued that, in addition to the direct effect of temperature, alternative inheritance also plays an important part in the production of seasonal varieties. He tried to show, moreover, that each seasonal variety is colored in adaptation to its particular environment and that this adaptation may have been brought about by natural selection—though he did not succeed in this respect.

In several instances, local varieties have been artificially produced as results of temperature control. Thus Standfuss produced in Germany, by the application of cold, individuals of *Vanessa urticæ* which were indistinguishable from the northern variety *polaris*; and from pupæ of *Vanessa cardui*, by warmth, a very pale form like that found in the tropics; and, by cold, a dark variety similar to one found in Lapland.

Shelford, by subjecting a pupa of a tiger beetle, *C. tranquebarica* (*vulgaris*) to cold moist conditions (mean temperature, 12° C.; moist) obtained, in Chicago, a color variety like one that occurs naturally in the eastern mountains.

In a second instance, both pattern and color were modified by hot dry conditions (mean temperature, 37° C.; dry), and a variety obtained such as occurs in the western states.

In a third experiment, both pattern and color were modified by hot wet conditions (37° C.; moist), and a variety produced like one in the moist southern states.

These investigators and others, notably Merrifield and Fischer, have accumulated a considerable mass of experimental evidence, the interpretation of which is in many respects difficult, involving as it does, not merely the direct effect of temperature upon the organism, but also deep questions of heredity, including reversion, individual variation, and the inheritance of acquired characters.

The seasonal increase in size that is noticeable, as in *C. pseudargiolus* and *I. ajax*, is doubtless an expression of increasing metabolism due to increasing temperature. Warmth, as is well known, stimulates growth, and cold has a dwarfing effect. While this is true as a rule, there are some apparent exceptions, however. Thus Standfuss found that some caterpillars were so much stimulated by unusual warmth that they pupated before they were sufficiently fed, and gave, therefore, undersized imagines. A moderate degree of warmth, however, undoubtedly hastens growth.

Sexual Coloration.—The sexes are often distinguished by colorational as well as structural differences. Colorational *antigeny* (this word signifying secondary sexual differences of whatever sort) is most prevalent among butterflies, in which it is the extreme phase of that

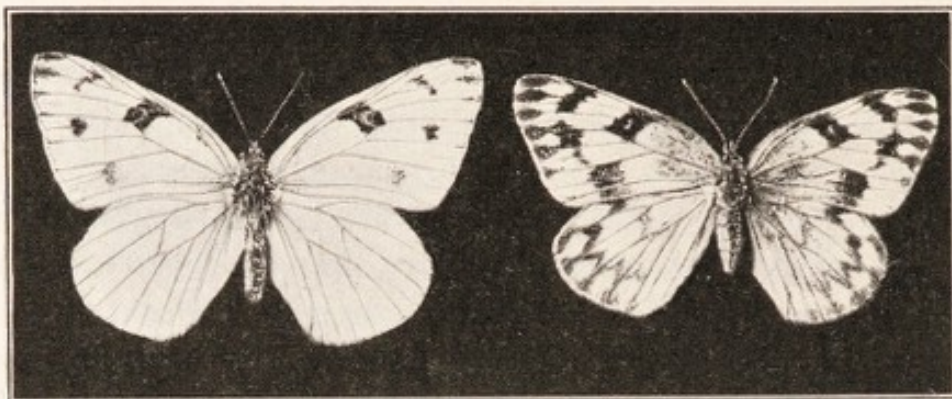


FIG. 237.—*Pieris protodice*; male (on the left) and female (on the right). Natural size.

differentiation of ornamentation for which Lepidoptera are unrivaled.

The male of *Pieris protodice* (Fig. 237) has a few brown spots on the front wings; the female is checkered with brown on both wings. In *Colias philodice* (Fig. 238) and *C. eurytheme* the marginal black band of



FIG. 238.—*Colias philodice*; right fore wing of male (above) and of female (below). Natural size.

the front wings is sharp and uninterrupted in the male, but diffuse and interrupted by yellow spots in the female. In the genus *Papilio* the sexes are often distinguished by colorational differences and in Hesperiidæ the males often have an oblique black dash across the middle of each front wing. *Callosamia promethea* (Fig. 239), the gipsy moth and many other Lepidoptera exhibit colorational antigeny. In not a few Sesiidæ the sexes differ greatly in coloration. Thus in the male of the peach tree borer (*Aegeria exitiosa*) all the wings are colorless and transparent; while in the female the front wings are violet and opaque and the fourth abdominal segment is orange above. The

same sex may present two types of coloration, as in males of *Cyaniris pseudargiolus* and females of *Papilio glaucus*, already mentioned. *Papilio merope*, of South Africa, is remarkable in having three females, which are entirely different in coloration from one another and from the male.

There is no longer any doubt, it may be added, as to the specific identity of these forms.

Next to Lepidoptera, Odonata most frequently show colorational antigeny. The male of *Calopteryx maculata* is velvety black; the female smoky, with a white *pterostigmatal* spot. Among Coleoptera, the male of *Hoplia trifasciata* is grayish and the female reddish brown; a few more examples might be given, though sexual differences in coloration are comparatively rare among beetles. Of Hymenoptera, some of the Tenthredinidæ exhibit colorational antigeny.

Among tropical butterflies there are not a few instances in which the special coloration of the female is adaptive—harmonizing with the surroundings or else imitating the coloration of another species which is known to be immune from the attacks of birds—as described beyond. In this way, as Wallace suggests, the egg-laden females may escape destruction, as they sluggishly seek the proper plants upon which to lay their eggs. Here would be a fair field for the operation of natural selection.

In most insects, however, sexual differences in coloration are apparently of no protective value and are usually so trivial and variable as probably to be of no use for recognition purposes. The usual statement that these differences facilitate sexual recognition is a pure assumption, in the case of insects, and one that is inadequate in spite of its plausibility, for (1) it is extremely improbable from our present

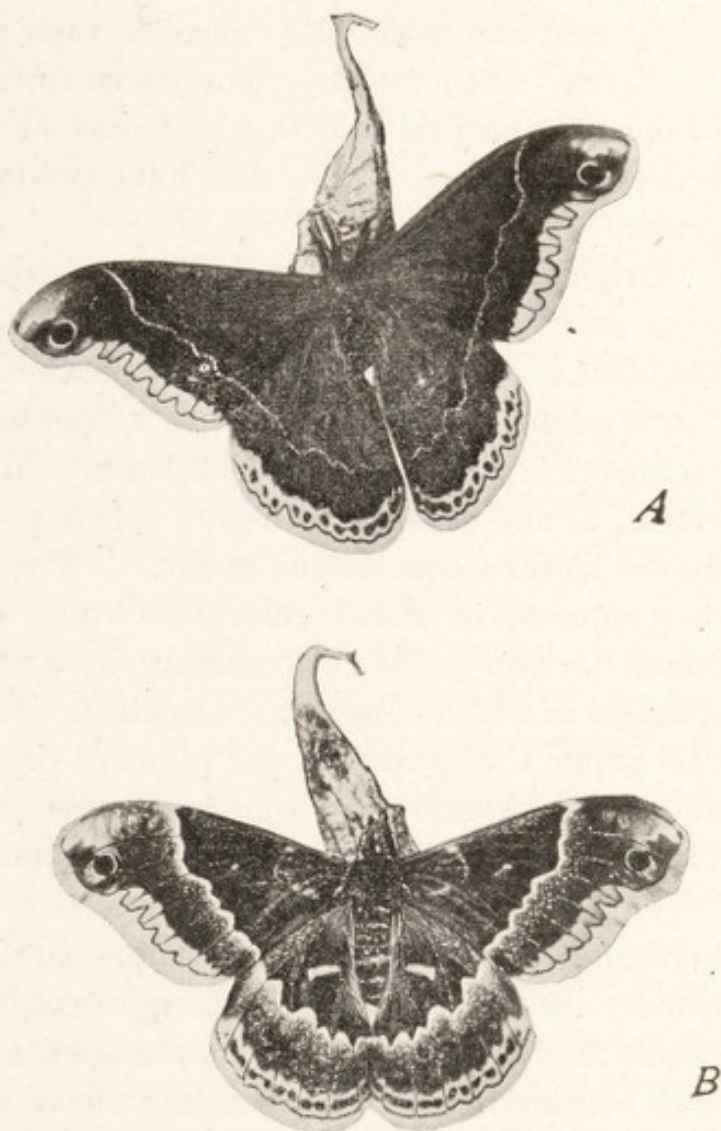


FIG. 239.—*Callosamia promethea*. A, male, clinging to cocoon; B, female. Reduced.

knowledge of insect vision that insects are able to perceive colors except in the broadest way, namely, as masses; (2) the great majority of insect species show no sexual differences in coloration; (3) when colorational antigeny is present it is probably unnecessary, to say the least, for sexual recognition. Thus, notwithstanding the marked dissimilarity of coloration in the two sexes of *C. promethea*, the males, guided by an odor, seek out their mates even when the wings of the female have been amputated and male wings glued in their place, as Mayer found.

Hence, when useless, colorational antigeny cannot have been developed by natural selection and may be due simply to the extended action of the same forces that have produced variety of coloration in general.

Origin of Color Patterns.—Tower, who has written an important work on the colors and color patterns of Coleoptera, finds that each of the black spots on the pronotum of the Colorado potato beetle (Fig. 240) “is developed in connection with a muscle, and marks the point of attachment of its fibres to the cuticula.” Thus the color pattern, in its origin, is not necessarily useful. This point is so important that we quote Tower’s conclusions in full. “The most important and widely disseminated of insect colors are those of the cuticula . . . these colors develop as the cuticula hardens, and appear first, as a rule, upon sclerites to which muscles are attached. In one of the earlier sections of this paper I showed that the pigment develops from before backward and, approximately, by segments, excepting that it may appear upon the head and most posterior segments simultaneously.

“In ontogeny color appears first, as a rule, over the muscles which become active first, or upon certain sclerites of the body. These are usually the head muscles, although exceptions are not infrequent. It should be remembered that as the color appears the cuticula hardens, and, considering that muscles must have fixed ends for their action, it seems that there is a definite relation between the development of color, the hardening of the cuticula, and the beginning of muscular activity; the last being dependent upon the second, and, incidentally, accompanied by the first. As muscular activity spreads over the animal the cuticula hardens and color appears, so that color is nearly, if not wholly, segmentally developed.

“The relation which exists between cuticular color and the stiffening of the cuticula is thus a physiological one, the cuticula not being able to harden without becoming yellow or brown. What bearing has this upon the origin of color patterns? In the lower forms of tracheates,

such as the Myriapods, colors appear as segmental repetitions of spots or pigmented areas which mark either important sclerites or muscle attachments. On the abdomens of insects, where segmentation is best observed, color appears as well-defined, segmentally arranged spots, but on the thorax segmentation is obscured and lost upon the head. Of what importance, then is pigmentation? And how did it arise? If the ontogenetic stages offer any basis for phylogenetic generalization, we may conclude that cuticula color originated in connection with the hardening of the integument of the ancestral tracheates as necessary to the muscular activity of terrestrial life. The primitive colors were yellows, browns and blacks, corresponding well with the surroundings in which the first terrestrial insects are supposed to have lived. The color pattern was a segmental one, showing repetition of the same spots upon successive segments, as upon the abdomen of Coleoptera.

"So firmly have these characters become ingrained in the tracheate series, and so important is this relation of the hardening of the cuticula to the musculature and to the formation of body sclerites, that even the most specialized forms show this primitive system of coloration; and, although there may be spots and markings which have no connection with it, still the chief color areas are thus closely associated."

Development of Color Patterns.—Although the causes of coloration are, for the most part, obscure, it is possible, nevertheless, to point out certain paths along which coloration appears to have developed. These paths have been determined by the comparison of color patterns in kindred groups of insects and the study of colorational variations in adults of the same species. Butterflies, moths and beetles have naturally been preferred as subjects by most students.

The most primitive colors among moths are uniform dull yellows, browns and drabs—the same colors that the pupal blood assumes when it is dried in the air. These simple colors prevail on the hind wings of most moths and on the less exposed parts of the wings of highly colored butterflies. The hind wings of moths are, as a rule, more primitively colored than the front ones because, as Scudder says, "all differentiation in coloring has been greatly retarded by their almost universal concealment by day beneath the overlapping front wings." Exceptions to this statement are found in Geometridæ and such other moths as rest with all the wings spread. "In such hind wings we find that the simplest departure from uniformity consists in a deepening of the tint next the outer margin of the wing; next we have an intensification of the deeper tint along a line parallel to the margin; it is but a step from this

condition to a distinct line or band of dark color parallel to the margin. Or the marginal shade may, in a similar way, break up into two or more transverse and parallel submarginal lines, a very common style of ornamentation, especially in moths. Or, again, starting with the submarginal shade, this may send shoots or tongues of dark color a short distance toward the base, giving a serrate inner border to the marginal shade; when now this breaks up into one, two, or more lines or narrow stripes, these stripes become zigzag, or the inner ones may be zigzag, while the outer ones are plain—a very common phenomenon.

“A basis such as this is sufficient to account for all the modifications of simple transverse markings which adorn the wings of Lepidoptera.”

Briefly, one or more bands may break up into spots or bars, the breaks occurring either between the veins or, more commonly, at the veins; and in the latter event, short bars or more or less quadrate or rounded spots arise in the interspaces. From simple round spots there may develop, as Darwin and others have shown, many-colored eye-like spots, or ocelli.

Mayer gives the following laws of color pattern: “(a) Any spot found upon the wing of a butterfly or moth tends to be bilaterally symmetrical, both as regards form and color; and the axis of symmetry is a line passing through the center of the interspace in which the spot is found, parallel to the longitudinal nervures. (b) Spots tend to appear not in one interspace only, but in homologous places in a row of adjacent interspaces. (c) Bands of color are often made by the fusion of a row of adjacent spots, and, conversely, chains of spots are often formed by the breaking up of bands. (d) When in process of disappearance, bands of color usually shrink away at one end. (e) The ends of a series of spots are more variable than the middle. (f) The position of spots situated near the outer edges of the wing is largely controlled by the wing folds or creases.”

These results have been arrived at chiefly by the study of the variations presented by color patterns.

Variation in Coloration.—It is safe to say that no two insects are colored exactly alike. Some species, however, are far more variable than others. *Catocala ilia*, for example, occurs under more than fifty varieties, each of which might be given a distinctive name, were it not for the fact that these varieties run into one another. One may examine hundreds of potato beetles (*L. decemlineata*) without finding any two that have precisely the same pattern on the pronotum. The range of

this variation in this species is partially indicated in Fig. 240, and that of *Cicindela* in Fig. 241.

Individuals of *Cicindela* vary in pattern in a few definite directions, and the patterns that characterize the various species appear to be fixations of individual variations. According to Dr. G. H. Horn: (1) The *type* of marking is the same in all our species. (2) Assuming a well-marked species, *tranquebarica* (*vulgaris*, Fig. 241, I) as a central type, the markings of other species vary from that type, (a) by a progressive spreading of the white, (b) by a gradual thinning or absorption of the white, (c) by a fragmentation of the markings, (d) by linear supplementary extension. (3) Many species are practically invariable (i.e., the individual variations are small in amount as compared with those in other species). These fall into two series: (a) those of the normal type, as *tranquebarica*, *hirticollis* and *tenuisignata*; (b) those in which some modification of the type has become permanent, probably through isolation, as *marginipennis*, *togata* and *lemniscata*. (4) Those species which vary do so in one direction only. New types of pattern, of specific value, appear to have arisen by the isolation and perpetuation of individual variations.

Professor Shelford, in his important monograph on the colors of these beetles, draws the following conclusions, among others:

Longitudinal stripes in which pigment usually occurs lie in the area of the chief tracheal trunks of the elytron; there are seven cross bands in which pigment does not develop; the second and third and fifth and sixth of these are often joined to make one of each pair.

Pigment usually occurs about the bases of hairs, which usually lie in the lines of the tracheæ.

In ontogeny the elytra show a spotted condition corresponding to the system of cross bands and longitudinal stripes. The longitudinal stripes are usually more pronounced.

The characteristic markings of the group are composed of spots or elements joined in the longitudinal light stripe areas and areas of cross bands, with the loss of various spots or elements which occur in ontogeny; joinings are sometimes oblique, and when so markings are sometimes parallel with the curved end of the elytron.

Certain particular types of markings made up of a few elements joined in a particular way characterize the majority of species of the group.

These markings as derived from the cross and longitudinal bands are angular; reduction of angles, straightening and turning into oblique

positions parallel with the end of the elytron characterize modifications of markings. The response to stimuli (high temperature) is in the same direction.

Response to other stimuli appears to be in the direction of concentric extension of the markings.

The color patterns and structure to which they are related constitute a mechanism, the directions of movement of which are limited, i.e., easier in some directions than others; the color pattern plans break when the related structures do; hereditary changes and fluctuations due to stimulation during ontogeny are in the same direction; laws governing the mechanism are the same throughout.

Variations in general fall into two classes: *continuous* (*individual variations*) and *discontinuous* (*mutations*). The former are always present, are slight in extent and intergrade with one another; they are distributed symmetrically about a mean condition. The latter are occasional, of considerable extent and sharply separated from the normal condition.

R. H. Johnson published an important statistical study on evolution in the color pattern of the lady-beetles. He found both continuous and discontinuous variations present; that the color pattern is capable of modification by the environment; that some modifications are hereditary characters and others not.

Replacements.—Examples of the replacement of one color by another are familiar to all collectors. The red of *Vanessa atalanta* and Coccinellidæ may be replaced by yellow. These two colors in many butterflies and beetles are due to pigments that are closely related to each other chemically. Thus in the chrysomelid *Lina lapponica* the beetle at emergence is pale but soon becomes yellow with black markings, and after several hours, under the influence of sunlight, the yellow changes to red; the change may be prevented, however, by keeping the beetle in the dark. After death, the red fades back through orange to yellow, especially as the result of exposure to sunlight. Yellow in place of red, then, may be attributed to an arrested development of pigment in the living insect and to a process of reduction in the dead insect, metabolism having ceased.

Yellow and green are similarly related. The stripes of *Pæcilocapsus lineatus* are yellow before they become green, and after death fade back to yellow. As the green pigment in most, if not all, phytophagous insects is chlorophyll, these color changes are probably similar to those that occur in leaves. Leaves grown in darkness are yellow, from the

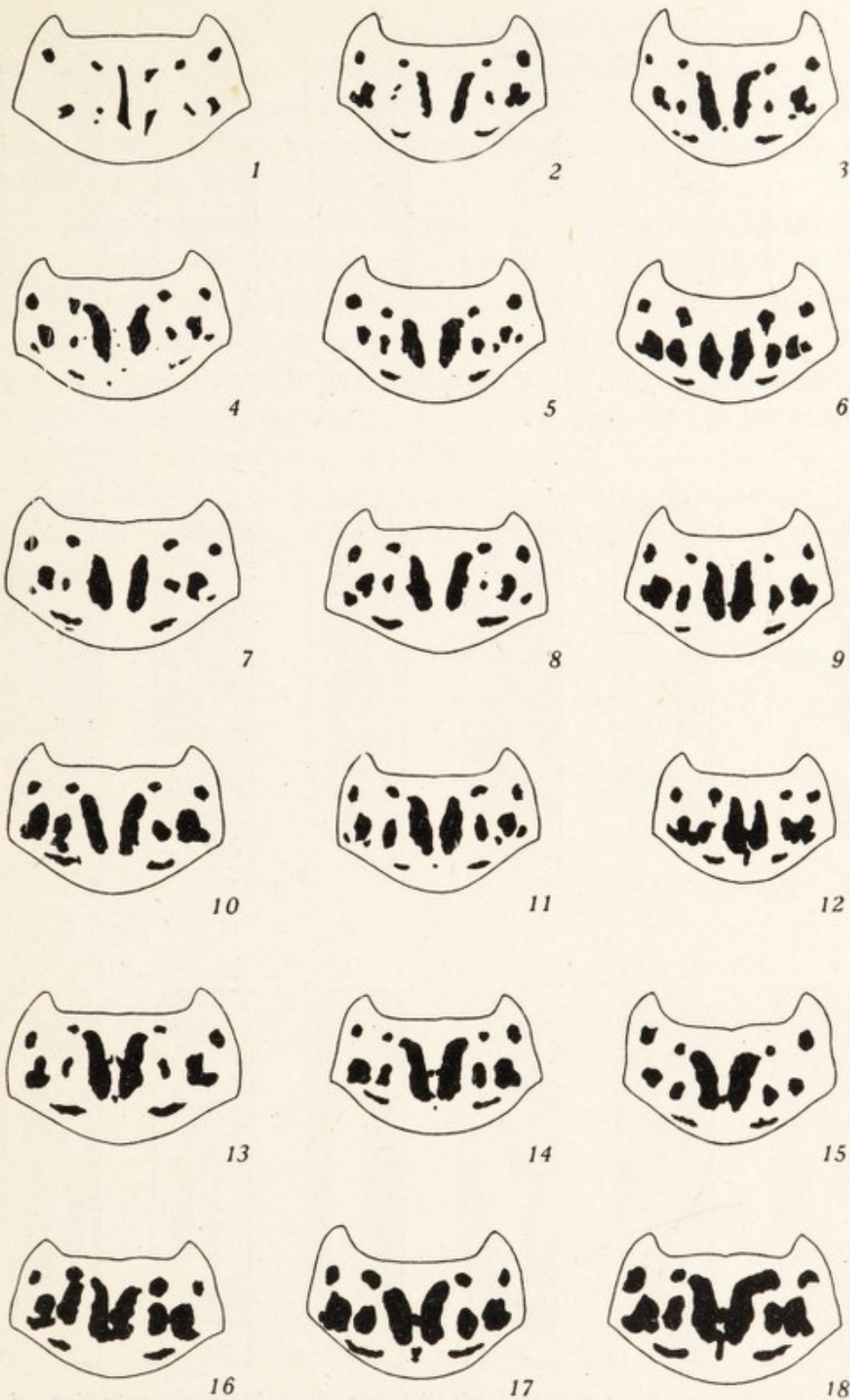


FIG. 240.—Colorational variations of the pronotum of the Colorado potato beetle, *Leptinotarsa decemlineata*.

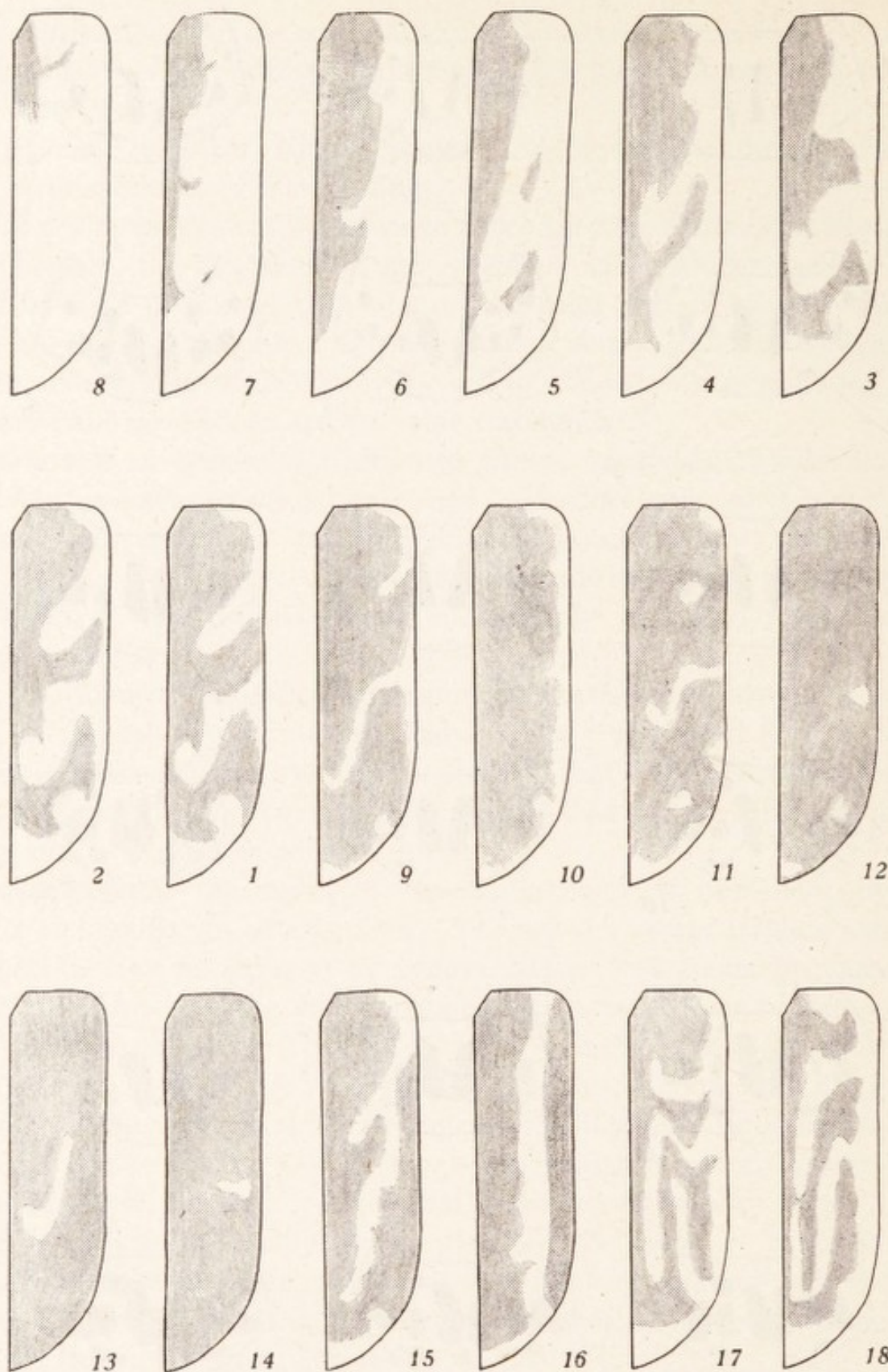


FIG. 241.—Elytral color patterns of *Cicindela*. 1-8 illustrate reduction of dark area; 9-14, extension of dark area; 15, 16, formation of longitudinal vitta; 17, 18, linear extension of markings. 1, *C. tranquebarica*; 2, *formosa*; 3, *formosa*; 4, *pamphila*; 5, *limbata*; 6, *togata*; 7, *gratiosa*; 8, *hamata*; 9, *tenuisignata*; 10, *marginipennis*; 11, *carthagera*; 12, *sexguttata*; 13, *carthagera*; 14, *splendida*; 15, *pusilla*; 16, *lemniscata*; 17, *gabbi*; 18, *dorsalis*.—After HORN, from Entomological News.

presence of etiolin, and do not turn green until they are exposed to sunlight (or electric light), without which chlorophyll does not develop; and as metabolism ceases, chlorophyll disintegrates, as in autumn, leaving its yellow constituent, xanthophyll, which is very likely the same substance as etiolin.

Cicindela sexguttata and *Calosoma scrutator* are often blue in place of green. These colors in these beetles are structural, and their variations are to be attributed to slight differences in the structure of the surface.

Green grasshoppers occasionally become pink toward the close of summer. No explanation has been offered for this phenomenon, though it may be remarked that when grasshoppers are killed in hot water the normal green pigment turns to pink.

These changes of color are apparently of no use to the insect, being merely incidental effects of light, temperature or other inorganic influences.

CHAPTER VI

ADAPTIVE COLORATION

Protective Resemblance.—Every naturalist knows of many animals that tend to escape detection by resembling their surroundings. This phenomenon of *protective resemblance* is richly exemplified by insects, among which one of the most remarkable cases is furnished by the *Kallima* butterflies, especially *K. inachis* of India and *K. paralekta* of the Malay Archipelago. The former species (Fig 242) is conspicuous when on the wing; its bright colors, however, are confined to the upper surfaces of the wings, and when these are folded together, as in repose, the insect

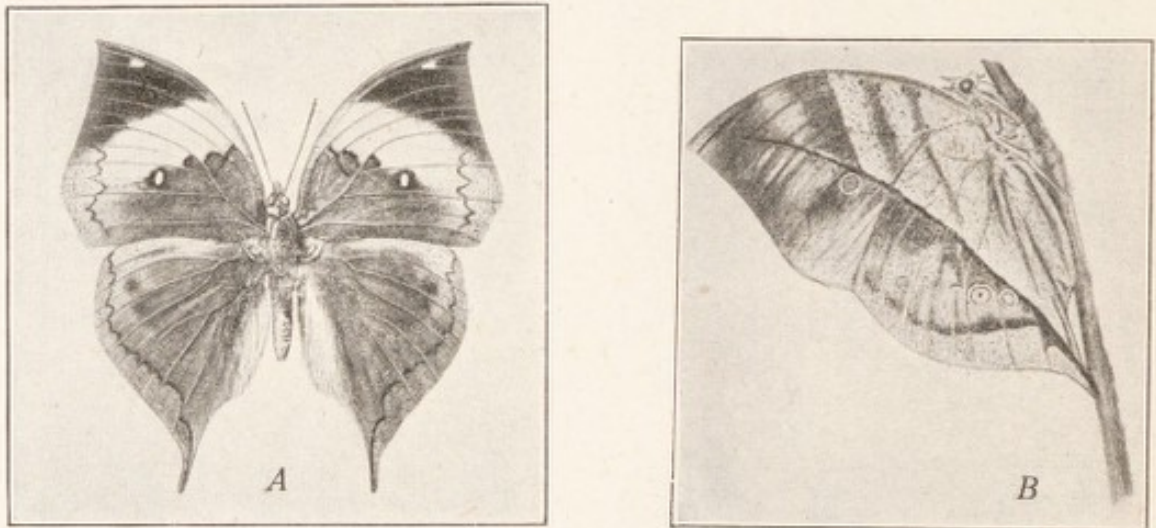


FIG. 242.—*Kallima inachis*; A, upper surface; B, with wings closed, showing resemblance to a leaf. $\times \frac{1}{2}$.

resembles to perfection one of the dead leaves among which it is accustomed to hide. The form, size and color of the leaf are accurately reproduced, the petiole being simulated by the tails of the wings. Two parallel shades, one light and one dark, represent, respectively, the illuminated and the shaded side of a mid-rib, and the side-veins as well are imitated; there are even small scattered black spots resembling those made on the leaf by a species of fungus. Furthermore, the butterfly habitually rests, not among green leaves, where it would be conspicuous, but among leaves with which it harmonizes in coloration. Notwithstanding some discussion as to whether it usually rests in pre

cisely the same position as a leaf, this insect certainly deceives experienced entomologists and presumably eludes birds and other enemies by means of its deceptive coloration.

Some of the tropical Phasmidæ counterfeit sticks, green leaves, or dead leaves with minute accuracy. Our common phasmids, *Diaphero-*

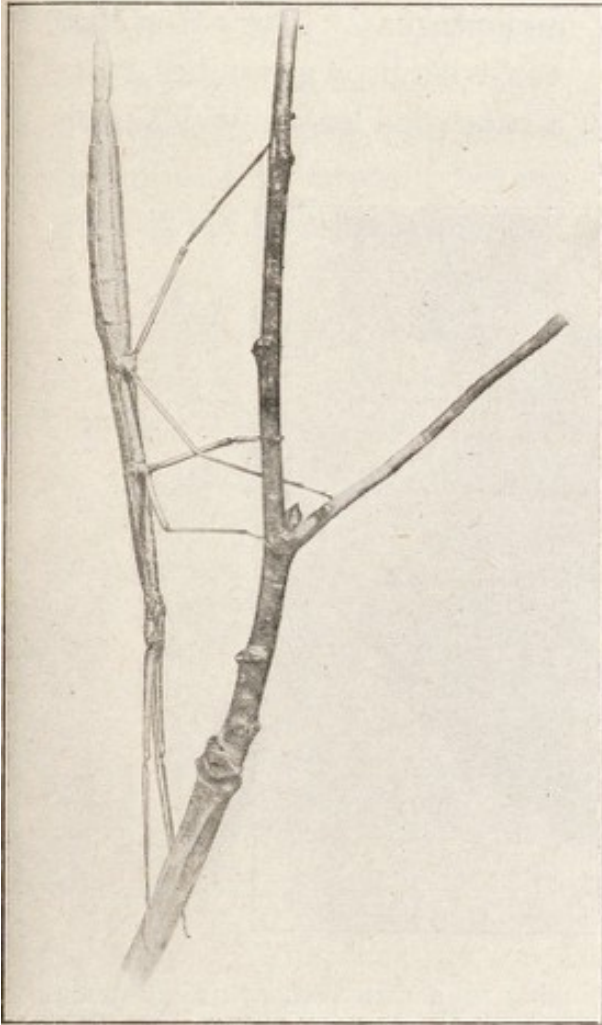


FIG. 243.—*Manomera blatchleyi*, on a twig.
Natural size.

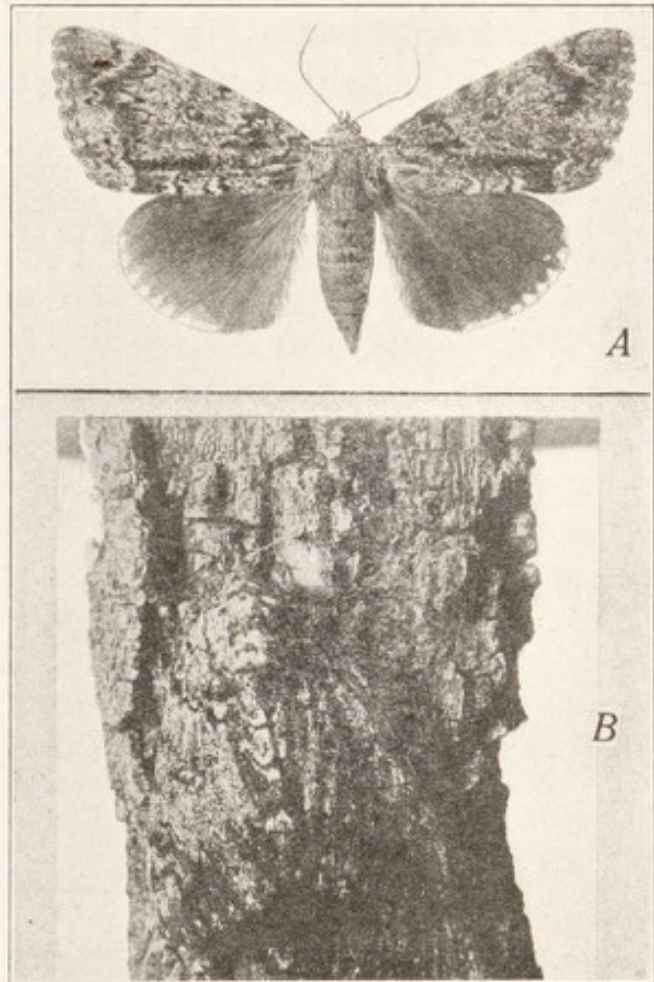


FIG. 244.—*Catocala lacrymosa*; A, upper surface; B, with wings closed, and resting on bark.
Reduced.

mera femorata and *Manomera blatchleyi* (Fig. 243), are well known as "stick insects;" indeed, it is not necessary to go beyond the temperate zone to find plenty of examples of protective resemblance. Geometrid caterpillars imitate twigs, holding the body stiffly from a branch and frequently reproducing the form and coloration of a twig with striking exactitude; and the moths of the same family are often colored like the bark against which they spread their wings. Even more perfectly do the *Catocala* moths resemble the bark upon which they rest (Fig. 244), with their conspicuous and usually showy hind wings concealed under the pro-

tectively colored front wings. The caterpillars of *Basilarchia archippus* and *Papilio thoas*, as well as other larvæ and not a few moths, resemble closely the excrements of birds. Numerous grass-eating caterpillars are striped with green, as is also a sphingid species (*Ellema harrisii*) that lives among pine needles. The large green sphinx caterpillars (Fig. 66) perhaps owe their inconspicuousness partly to their oblique lateral stripes, which cut a mass of green into smaller areas. The caterpillar of *Schizura ipomææ* (Fig. 245), which is green with brown patches, rests for hours along the eaten or torn edge of a basswood leaf, in which posi-



FIG. 245.—Caterpillar of *Schizura ipomææ* clinging to a torn leaf. Natural size.

tion it bears an extremely deceptive resemblance to the partially dead border of a leaf. The weevils that drop to the ground and remain immovable are often indistinguishable to the collector on account of their likeness to bits of soil or little pebbles. Everyone has noticed the extent to which some of the grasshoppers resemble the soil in color. The Carolina locust, *Dissosteira carolina*, which varies greatly in color, ranging from ashy gray to yellowish or to reddish brown, is commonly found on soil of its own color. Along the Atlantic coast, the seaside locust, *Trimerotropis maritima*, is practically invisible against the gray sand of the seashore, to which it restricts itself. The same species of grasshopper occurs inland also, as in Illinois and Michigan, along the shores of lakes, and is then pale brown, like the sands that it

frequents. Another grasshopper of the same genus, *Trimerotropis saxatilis* (Fig. 246) occurs only on rock-surfaces, either bare or lichen-crusted. This grasshopper, mottled with several colors but especially yellow, black and greenish, is conspicuous when flying but indistinguishable when resting on a patch of lichens (Fig. 246 B). Where the grasshopper occurs among lichen-covered rocks, as in southern Illinois, it does not alight by haphazard as a rule, but habitually flies from one patch of lichens to another.

Instances such as this give support to the opinion that "protective resemblances" are not always merely accidental occurrences; since the protective colors are rendered effective by special habits of the insect.

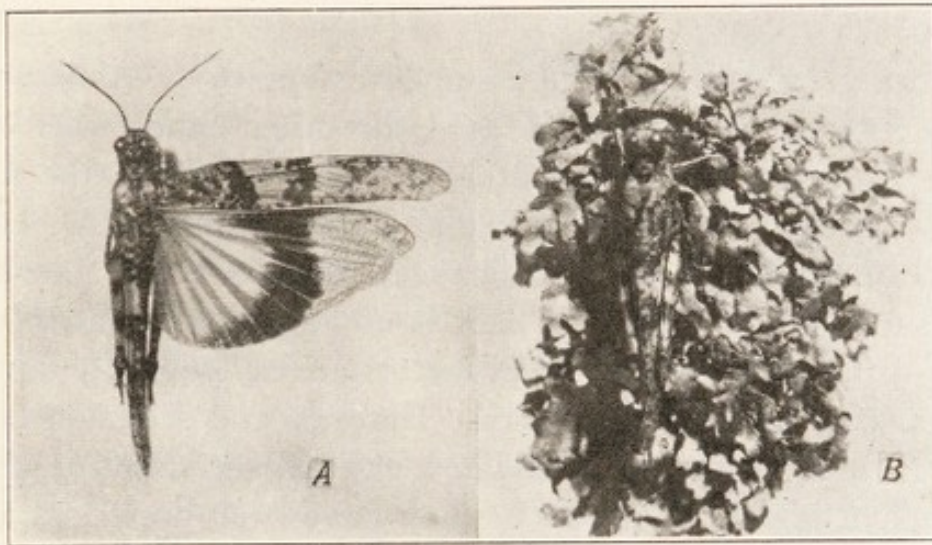


FIG. 246.—*Trimerotropis saxatilis*. A, with wings of right side spread. B, with wings closed, and resting on lichens. Natural size.

This particular grasshopper, it may be added, is sluggish, and inclined to remain where it alights—an advantageous habit under the circumstances. The case is not so simple as that of a caterpillar that is green simply because it feeds on chlorophylls.

Adventitious Resemblance.—If, instead of hastily ascribing all cases apparently of protective resemblance to the action of natural selection, one inquires into the structural basis of the resemblance in each instance, it is found that some cases can be explained, without the aid of natural selection, as being direct effects of food, light or other primary factors. Such cases, then, are in a sense accidental. For example, many inconspicuous green insects are green merely because chlorophyll from the food-plant tinges the blood and shows through the skin. If it be argued that natural selection has brought about a thin and transparent skin, it may be replied that the skin of a green cater-

pillar is by no means exceptional in thinness or transparency. Moreover, many leaf-mining caterpillars are green, simply because their food is green; for, living as they do within the tissues of leaves and surrounded by chlorophyll, their own green color is of no advantage, but is merely incidental.

Again, in the "protectively" colored chrysalides experimented upon by Poulton, the color was directly influenced by the prevailing color of the light that surrounded the larva during the last few days before pupation. Of course, it is conceivable that natural selection may have preserved such individuals as were most responsive to the stimulus of the surrounding light; nevertheless the fact remains that these resemblances do not demand such an explanation, which is, in other words, superfluous.

Indeed, a great many of the assumed examples of "protective resemblance" are very far-fetched. On the other hand, when the resemblance is as specific and minutely detailed as it is in the *Kallima* butterflies—where, moreover, special instincts are involved—the phenomenon can scarcely be due to chance; the direct and uncombined action of such factors as food or light is no longer sufficient to explain the facts—although these and other factors are undoubtedly important in a primary, or fundamental, way. Here natural selection becomes useful, as enabling us to understand how original variations of structure and instinct in favorable directions may have been preserved and accumulated until an extraordinary degree of adaptation has been attained.

Value of Protective Resemblance.—The popular opinion as to the efficiency of protective resemblances is undoubtedly an exaggerated one, owing mainly to the false assumption that the senses of the lower animals are co-extensive in range with our own. As a matter of fact, birds detect insects with a facility far superior to that of man, and destroy them by the wholesale, in spite of protective coloration. Thus, as Judd has ascertained, no fewer than three hundred species of birds feed upon protectively colored grasshoppers, which they destroy in immense numbers, and more than twenty species prey upon the twig-like geometrid larvæ; while the weevils that look like particles of soil, and the green-striped caterpillars that assimilate with the surrounding foliage are constantly to be found in the stomachs of birds.

After all, however, protective resemblance may be regarded as advantageous upon the whole, even if it is ineffectual in thousands of instances. An adaptation may be successful even if it does fall short of perfection; and it should be borne in mind that the evolution of protect-

ive resemblances among insects has probably been accompanied on the part of birds by an increasing ability to discriminate these insects from their surroundings.

Warning Coloration.—In strong contrast to the protectively colored species, there are many insects which are so vividly colored as to be extremely conspicuous amid their natural surroundings. Such are many Hemiptera (*Lygæus*, *Murgantia*), Coleoptera (*Necrophorus*, Lampyridæ, Coccinellidæ, Chrysomelidæ), Hymenoptera (Mutillidæ, Vespidæ), and numerous caterpillars and butterflies. Conspicuous colors, being frequently—though not always—associated with qualities that render their possessors unpalatable or offensive to birds or other enemies, are advantageous if, by insuring ready recognition, they exempt their owners from attack.

Efficiency of Warning Colors.—Owing to much disagreement as to the actual value of “warning” colors, several investigators have made many observations and experiments upon the subject. Tests made by offering various conspicuous insects to birds, lizards, frogs, monkeys and other insectivorous animals have given diverse results, according to circumstances. Thus, one gaudy caterpillar is refused by a certain bird at once, or else after being tasted, but another and equally showy caterpillar is eaten without hesitation. Or, an insect at first rejected may at length be accepted under stress of hunger; or a warningly colored form disregarded by some animals is accepted by others. Moreover, some of the experiments with captive insectivorous animals are open to objection on the score of artificiality.

Nevertheless, from the data now accumulated, there emerge some conclusions of definite value. Frank Finn, whose conclusions are quoted beyond, has found in India that the conspicuous colors of some butterflies, (*Danainæ*, *Acræa*, *violæ*, *Delias eucharis*, *Papilio aristolochiæ*) are probably effective as “warning” colors. Marshall found in South Africa that mantids, which would devour most kinds of butterflies, including warningly colored species, refused *Acræa*, which appeared to be not only distasteful but even unwholesome; *Acræa* is eaten, however, by the predaceous Asilidæ, which feed indiscriminately upon insects—for example, beetles, dragon flies and even stinging Hymenoptera. The masterly studies of Marshall and Poulton strongly support the general theory of warning coloration.

In this country, much important evidence upon the subject has been obtained by Dr. Judd from an extensive examination of the stomach-contents of birds, supplemented by experiments and field observations.

Judd says that the harlequin cabbage bug (*Murgantia histrionica*) and other large showy bugs are usually avoided by birds; that the showy, ill-flavored lady-beetles (Coccinellidæ) and Chrysomelidæ such as the elm leaf beetle, *Diabrotica*, and *Leptinotarsa* (*Doryphora*), possess comparative immunity from birds; and that *Macrodactylus*, *Chauliognathus* and *Cyllene* are highly exempt from attack. Such cases, he adds, are comparatively few among insects, however, and in general, warning colors are effective against some enemies but ineffective against others.

Generally speaking, hairs, stings and other protective devices are accompanied by conspicuous colors—though there are many exceptions to this rule. These warning colors nevertheless fail to accomplish their supposed purpose in the following instances, given by Judd. Taking insects that are thought to be protected by an offensive odor or a disagreeable taste: Heteroptera in general are eaten by all insectivorous birds, the squash bug by hawks and the pentatomids by many birds; among Carabidæ with their irritating fluids, *Harpalus caliginosus* and *pennsylvanicus* are food for the crow, catbird, robin and six others; *Carabus* and *Calosoma* are relished by crows and blackbirds; Silphidæ are taken by the crow, loggerhead shrike and kingbird; and *Leptinotarsa decemlineata* is eaten by at least six kinds of birds: wood thrush, rose-breasted grosbeak, quail, crow, cuckoo and catbird. Of hairy and spiny caterpillars, Arctiidæ are eaten by the robin, bluebird, catbird, cuckoo and others; the larvæ of the gipsy moth are food for the blue-jay, robin, chickadee, Baltimore oriole and many others [thirty-one birds, in Massachusetts]; and the spiny caterpillars of *Vanessa antiopa* are taken by cuckoos and orioles. Of stinging Hymenoptera, bumblebees are eaten by the bluebird, blue-jay and two flycatchers; the honey bee, by the wood pewee, phoebe, olive-sided flycatcher and kingbird; *Andrena* by many birds, and *Vespa* and *Polistes* by the red-bellied woodpecker, kingbird, and yellow-bellied flycatcher.

These facts by no means invalidate the general theory, but they do show that "disagreeable" qualities and their associated color signals are of little or no avail against some enemies. The weight of evidence favors the theory of warning coloration in a qualified form. While conspicuous colors do not always exempt their owners from destruction, they frequently do so, by advertising disagreeable attributes of one sort or another.

The evolution of warning coloration is explained by natural selection; in fact, we have no other theory to account for it. The colors

themselves must have been present, however, before natural selection could begin to operate; their origin is a question quite distinct from that of their subsequent preservation.

Protective Mimicry.—This interesting and highly involved phenomenon is a special form of protective resemblance in which one species

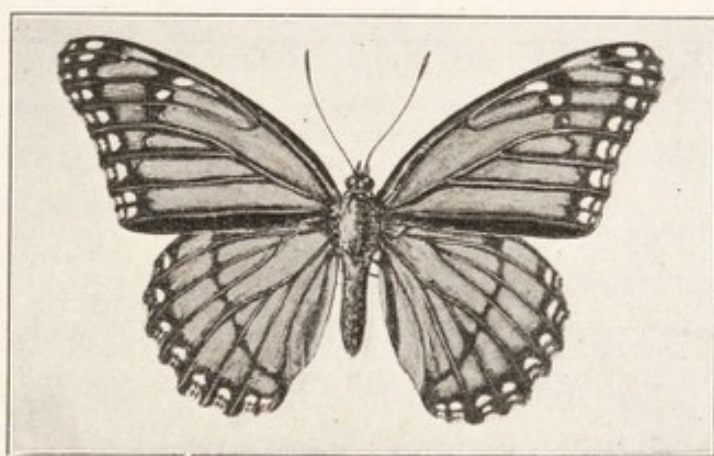
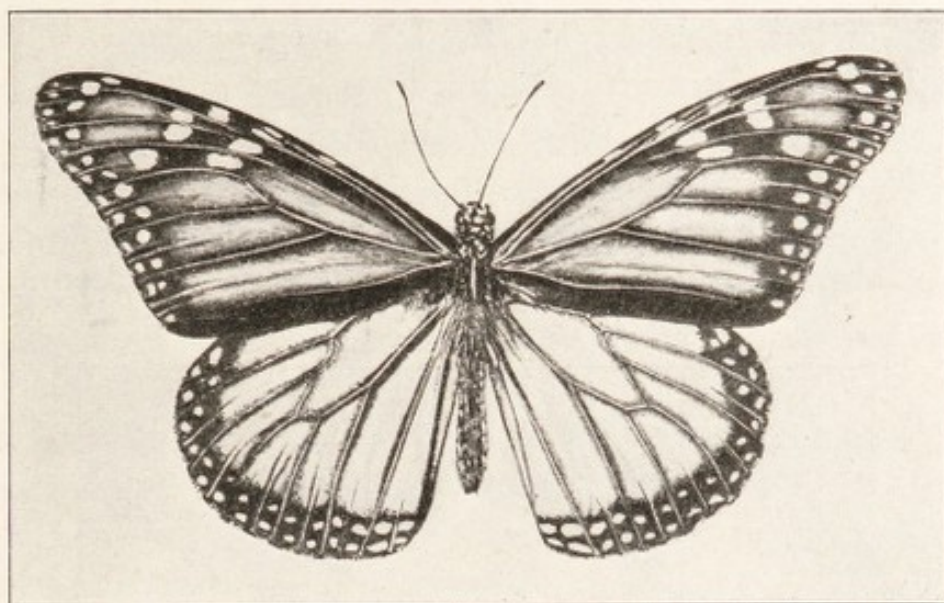


FIG. 247.—A, *Anosia plexippus*, the "model;" B, *Basilarchia archippus*, the "mimic." Natural size.

imitates the appearance of another and better protected species, thereby sharing its immunity from destruction. Though it attains its highest development in the tropics, *mimicry* is well illustrated in temperate regions. A familiar example is furnished by *Basilarchia archippus* (Fig. 247, B), which departs widely from the prevailing dark coloration of its genus to imitate the milkweed butterfly, *Anosia plexippus*. The latter species, or "model," appears to be unmolested by birds, and the former species, or "mimic," is thought to secure the same exemption

from attack by being mistaken for its unpalatable model. The common drone-fly, *Eristalis tenax* (Fig. 248, *B*) mimics a honey bee in form, size, coloration and the manner in which it buzzes about flowers, in company with its model; it does not deceive the kingbird and the flicker, however. Some Asilidæ (robber flies) are remarkably like bumblebees in superficial appearance and certain *Syrphus* flies (flower flies) mimic wasps with more or less success. The beetle *Casnonia* bears a remarkable resemblance to the ants with which it lives.

The classic cases are those of the Amazonian Heliconiidae and Pieridae, in which mimicry was first detected by Bates. The Heliconiidae are abundant, vividly colored and eminently free from the attacks of birds and other enemies of butterflies, on account of their

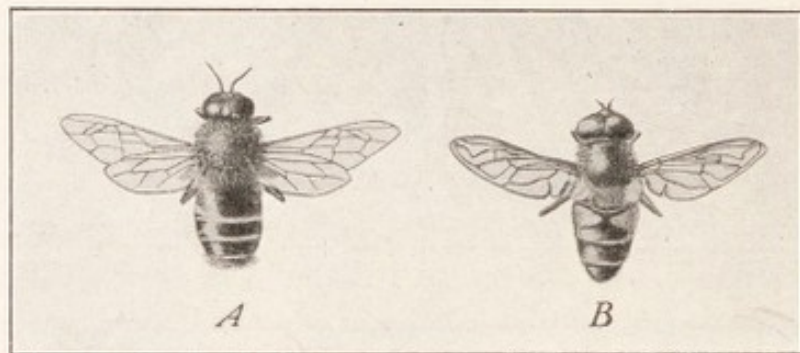


FIG. 248.—Protective mimicry. A, drone bee, *Apis mellifera*; B, drone fly, *Eristalis tenax*. Natural size.

disagreeable odor and taste. Some of the Pieridae—a family fundamentally different from Heliconiidae—imitate the protected Heliconiidae so successfully, in coloration, form and flight, that while other Pieridae are preyed upon by many foes, the mimicking species tend to escape attack.

The family Heliconiidae, referred to by Bates, comprised what are now known as the subfamilies Heliconiinae, Ithomiinae and Danainae; similarly, Pieridae and Papilionidae are now often termed respectively Pierinae and Papilioninae. Ithomiinae are mimicked also by Papilioninae and by moths of the families Castniidae and Pericopidae.

The discoveries of Bates in tropical South America were paralleled and supported by those of Wallace in India and the Malay Archipelago (where Danainae are the chief “models”), and of Trimen in South Africa (where Acræinae and Danainae serve as models). Trimen discovered a most remarkable case, in which three species of *Danaïs* are mimicked, each by a distinct variety of the female of *Papilio cenea* (*merope*).

So much for that kind of mimicry—but how is the following kind to be explained? The Ithomiinæ of the Amazon valley have the same form and coloration as the Heliconiinæ, but the Ithomiinæ themselves are already highly protected. The answer is that this resemblance is of advantage to both groups, as it minimizes their destruction by birds—these having to learn but one set of warning signals instead of two. This is the essence of Müller's famous explanation, which will presently be stated with more precision. There are two kinds of mimicry, then: (1) the kind described by Bates, in which an edible species obtains security by counterfeiting the appearance of an inedible species; (2) that observed by Bates and interpreted by Müller, in which both species are inedible. These two kinds are known respectively as Batesian and Müllerian mimicry, though some writers prefer to limit the term mimicry to the Batesian type.

Wallace's Rules.—The chief conditions under which mimicry occurs have been stated by Wallace as follows:

"1. That the imitative species occur in the same area and occupy the very same station as the imitated.

"2. That the imitators are always the more defenceless.

"3. That the imitators are always less numerous in individuals.

"4. That the imitators differ from the bulk of their allies.

"5. That the imitation, however minute, is external and visible only, never extending to internal characters or to such as do not affect the external appearance."

These rules relate chiefly to the Batesian form of mimicry and need to be altered to apply to the Müllerian kind.

The first criterion given by Wallace is evidently an essential one and it is sustained by the facts. It is also true that mimic and model occur usually at the same time of year; Marshall found many new instances of this in South Africa. In some cases of mimicry, strange to say, the precise model is unknown. Thus some Nymphalidæ diverge from their relatives to mimic the Euploëinæ, though no particular model has been found. In such instances, as Scudder suggests, the prototype may exist without having been found; may have become extinct; or the species may have arrived at a general resemblance to another group without having as yet acquired a likeness to any particular species of the group, the general likeness meanwhile being profitable.

The second condition named by Wallace is correct for Batesian but not for Müllerian mimicry.

The fulfilment of the third condition is requisite for the success

of Batesian mimicry. Bates noted that none of the pierid mimics were so abundant as their heliconiid models. If they were, their protection would be less; and should the mimic exceed its model in numbers, the former would be more subject to attack than the latter. Sometimes, indeed, as Müller found, the mimic actually is more common than the model; in which event, the consequent extra destruction of the mimic would—at least theoretically—reduce its numbers back to the point of protection.

In Müllerian mimicry, however, the inevitable variation in abundance of two or more converging and protected species is far less disastrous; though when two species, equally distasteful, are involved, the rarer of the two has the advantage, as Fritz Müller has shown. His lucid explanation is essentially as follows:

Suppose that the birds of a region have to destroy 1,200 butterflies of a distasteful species before it becomes recognized as such, and that there exist in this region 2,000 individuals of species *A* and 10,000 of species *B*; then, if they are *different* in appearance, each will lose 1,200 individuals, but if they are deceptively alike, this loss will be divided among them in proportion to their numbers, and *A* will lose 200 and *B* 1,000. *A* accordingly saves 1,000, or 50 per cent. of the total number of individuals of the species, and *B* saves only 200, or 2 per cent. Thus, while the relative numbers of the two species are as 1 to 5, the relative advantage from their resemblance is as 25 to 1.

If two or more distasteful species are equally numerous, their resemblance to one another brings nearly equal advantages. In cases of this kind—and many are known—it is sometimes impossible to distinguish between model and mimic, as all the participants seem to have converged toward a common protective appearance, through an interchange of features—the “reciprocal mimicry” of Dr. Dixey.

Marshall argues, however, against this diaposematism, maintaining that in the case of two participants in Müllerian mimicry the evolution of the mimetic pattern has been in one direction only—toward the more abundant species—any variations in the opposite direction being disadvantageous.

From this explanation, the superior value of Müllerian as compared with Batesian mimicry is evident.

The fourth condition—that the imitators differ from the bulk of their allies—holds true to such a degree that even the two sexes of the same species may differ extremely in coloration, owing to the fact that the female has assumed the likeness of some other and protected species.

The female of *Papilio cenea*, indeed, occurs (as was just mentioned) under three varieties, which mimic respectively three entirely dissimilar species of *Danaïs*, and none of the females are anything like their male in coloration.

The generally accepted explanation for these remarkable but numerous cases in which the female alone is mimetic, is that the female, burdened with eggs and consequently sluggish in flight and much exposed to attack, is benefited by imitating a species which is immune; while the male has had no such incentive—so to speak—to become mimetic. Of course, there has been no *conscious* evolution of mimicry.

Wallace's fifth stipulation is important, but should read this way: "The imitation, however minute, is but external and visible *usually*, and never extends to internal characters *which* do not affect the external appearance." For, as Poulton points out, the alertness of a beetle which mimics a wasp, implies appropriate changes in the nervous and muscular systems. In its intent, however, Wallace's rule holds good, and by disregarding it some writers strain the theory of mimicry beyond reasonable limits. Some have said, for example, that the resemblance between caddis flies and moths is mimicry; when the fact is that this resemblance is not merely superficial but is deep-seated; the entire organization of Trichoptera shows that they are closely *related* to Lepidoptera. This likeness expresses, then, not mimicry, but affinity and parallel development. The same objection applies to the assumed cases of mimicry within the limits of a single family, as between two genera of Heliconiidae or between the chrysomelid genera *Lema* and *Diabrotica*. The more nearly two species are related to each other, the more probable it becomes that their similarity is due—not to mimicry—but to their common ancestry.



FIG. 249.—A tettigoniid, *Myrmecophana fallax*, which resembles an ant. Twice natural length. From BRUNNER VON WATTENWYL.

On the other hand, the resemblance frequently occurs between species of such different orders that it cannot be attributed to affinity. Illustrations of this are the mimicry of the honey bee by the drone fly, and the many other instances in which stinging Hymenoptera are counterfeited by harmless flies or beetles. A tettigoniid of the Sudan resembles an ant (Fig. 249), and the resemblance, by the way, is obtained in a most remarkable manner. Upon the stout body of this orthopteron the abdomen of an ant is delineated in black, the rest of the body being light in color and inconspicuous by contrast with the

black. Indeed the various means by which a superficial resemblance is brought about between remotely related insects are often extraordinary.

Irrespective of affinity, insects of diverse orders may converge in wholesale numbers toward a central protected form. The most complete examples of this have been brought to light by Marshall and Poulton, in their splendid work on the bionomics of South African insects, in which is given, for instance, a colored plate showing how closely six distasteful and dominant beetles of the genus *Lycus* are imitated by almost forty species of other genera—a remarkable example of convergence involving no less than eighteen families and five orders, namely, Coleoptera, Hymenoptera, Hemiptera, Lepidoptera and Diptera. Excepting a few unprotected, or Batesian, mimics (a fly and two or three beetles), this association is one between species that are already protected, by stings, bad tastes or other peculiarities. In other words, here is Müllerian mimicry on an immense scale; and if Müllerian mimicry is profitable when only two species are concerned, what an enormous benefit it must be to each of forty participants!

Strength of the Theory.—Evidently the theory of mimicry rests upon the assumption that the mimics, by virtue of their mimicry, are specially protected from insectivorous foes. Formerly, however, there was altogether too little evidence bearing upon the assumption itself, though this was supported by such scattered observations as were available. The oft-repeated assertion that this lack of evidence was due simply to inattention to the subject, has been proved to be true by the decisive results gained in the tropics by several competent investigators who have been able to give the subject the requisite amount of attention.

From his observations and experiments in India, Frank Finn concludes:

“1. That there is a general appetite for butterflies among insectivorous birds, even though they are rarely seen when wild to attack them.

“2. That many, probably most, species dislike, if not intensely, at any rate in comparison with other butterflies, the warningly-colored *Danainæ*, *Acraea violæ*, *Delias eucharis*, and *Papilio aristolochiæ*; of these the last being the most distasteful, and the *Danainæ* the least so.

“3. That the mimics of these are at any rate relatively palatable, and that the mimicry is commonly effectual under natural conditions.

“4. That each bird has separately to acquire its experience, and well remembers what it has learned.

"That therefore on the whole, the theory of Wallace and Bates is supported by the facts detailed in this and my former papers, so far as they deal with birds (and with the one mammal used). Professor Poulton's suggestion that animals may be forced by hunger to eat unpalatable forms is also more than confirmed, as the unpalatable forms were commonly eaten without the stimulus of actual hunger—generally, also, I may add, without signs of dislike."

Though insects have many vertebrate and arthropod enemies, it is probable that the evolution of mimetic resemblance, implying warning coloration, has been brought about chiefly by insectivorous birds.

Neglecting papers of minor importance, we may pass at once to the most important contribution upon this subject—the voluminous work of Marshall and Poulton upon mimicry and warning colors in South African insects. These investigators have found that birds are to be counted as the principal enemies of butterflies; that the *Danainæ* and *Acræinæ*, which are noted as models, are particularly immune from destruction, while unprotected forms suffer; and that mimicking, though palatable, species share the freedom of their models. The same is true of beetles, of which *Coccinellidæ*, *Malacodermidæ* (notably *Lycus*) *Cantharidæ* and many *Chrysomelidæ* serve as models for many other *Coleoptera*, being "conspicuous and constantly refused by insect-eaters." In short, the splendid work of Marshall and Poulton tends to place the theory of Batesian and Müllerian mimicry upon a substantial foundation of observational and experimental evidence.

In regard to the important question—do birds avoid unpalatable insects instinctively or only as the result of experience—the evidence is all one way. Several investigators, including Lloyd Morgan, have found that newly-hatched birds have no instinctive aversions as regards food, but test everything, and (except for some little parental guidance) are obliged to learn for themselves what is good to eat and what is not. This experimental evidence that the discrimination of food by birds is due solely to experience, was evidently highly necessary to place the theory of mimicry—especially the Müllerian theory—upon a sound basis.

Though butterflies as a group are much subject to the attacks of birds in the tropics, it has been asserted that butterflies in temperate regions are as a whole almost exempt from the attacks of birds, and that consequently the mimicry of the monarch (Fig. 247) by the viceroy is of no advantage. In answer to this assertion Marshall has published a long list of references showing that butterflies are attacked by birds

more commonly than has been generally supposed. At the same time there is no proof that the viceroy profits at present by its mimetic pattern, though it may have done so in the past. In any event, the departure of *archippus* from its congeners toward one of the Danainæ—a famous group of “models” in the tropics—is unintelligible except as an instance of mimicry.

Granting that mimicry is upon the whole advantageous, it becomes important to learn just how far the advantage extends; and we find that mimicry is not of universal effectiveness. Even the highly protected Heliconiinae and Danainæ are food for some predaceous insects. In this country, as Judd has observed, the drone-fly (*Eristalis tenax*), which mimics the honey bee, is eaten by the kingbird and the phoebe; the kingbird, indeed, eats the honey bee itself, but is said to pick out the drones; chickens also discriminate between drones and workers, eating the former and avoiding the latter. Bumblebees and wasps, imitated by many other insects, are themselves eaten by the kingbird, catbird and several other birds, though it is not known whether the stingless males of these are singled out or not. Such facts as these do not discredit the general theory of mimicry but point out its limits.

Evolution of Mimicry.—Natural selection gives an adequate explanation of the evolution of a mimetic pattern. Before accepting this explanation, however, we must inquire: (1) What were the first stages in the development of a mimetic pattern? (2) What evidence is there that every step in this development was vitally useful, as the theory demands that it should be? These pertinent questions have been answered by Darwin, Wallace, Müller, Dixey and several other authorities.

The incipient mimic must have possessed, to begin with, colors or patterns that were *capable* of mimetic development; evidently the raw material must have been present. Now Müller and Dixey in particular have called attention to the fact that many pierids have at least touches of the reds, yellows and other colors that are so conspicuous in the heliconiids. More than this, however, Dixey has demonstrated—as appears clearly from his colored figures—a complete and gradual transition from a typical non-mimetic pierid, *Pieris locusta*, to the mimetic pierid *Mylothris pyrrha*, the female of which imitates *Heliconius numata*. He traces the transition chiefly through the males of several pierid species—for the males, though for the most part white (the typical pierid color), “show on the under surface, though in varying degrees, an approach towards the Heliconiine pattern that is so completely imitated by their

mates. These partially developed features on the under surface of the males enable us to trace the history of the growth of the mimetic pattern." Starting from *Pieris locusta*, it is an easy step to *Mylothris lypera*, thence to *M. lorena*, and from this to the mimetic *M. pyrrha*. "Granted a beginning, however small, such as the basal red touches in the normal Pierines, an elaborate and practically perfect mimetic pattern may be evolved therefrom by simple and easy stages."

Furthermore (in answer to the second question), it does not tax the imagination to admit that any one of these color patterns has—at least occasionally—been sufficiently suggestive of the heliconiid type to preserve the life of its possessor; especially when both bird and insect were on the wing and perhaps some distance apart, when even a momentary flash of red or yellow from a pierid might be enough to save it from attack.

It is highly desirable, of course, that this plausible explanation should be tested as far as possible by observations in the field and by experiments as well.

Mimicry and Mendelism.—The weight of evidence is at present vastly in favor of the theory of mimicry as against any other explanation of the facts, even though the theory is sometimes stretched to impossible limits by some of its enthusiastic adherents. The only opposing opinion that has sufficient plausibility to demand much consideration as yet is that of Punnett.

In India and Ceylon the butterfly *Papilio polytes* has in addition to the normal female a second form of female which mimics *P. aristolochiae* and a third which imitates *P. hector*; *polytes* being palatable to birds and its two models unpalatable.

This case, described by Wallace more than fifty years ago, is one of the classic examples of mimicry. Punnett holds, however, that these resemblances are of no practical value and that natural selection has played no part in the formation of these polymorphic forms and suggests that Mendelism offers a better explanation of the phenomenon—a suggestion that should be tested experimentally.

Adaptive Colors in General.—Several classes of adaptive colors have been discriminated and defined by Poulton, whose classification, necessarily somewhat arbitrary but nevertheless very useful, is given below, in its abridged form.

I. APATETIC COLORS.—Colors resembling some part of the environment or the appearance of another species.

A. CRYPTIC COLORS.—Protective and Aggressive Resemblances.

1. *Procryptic colors*.—Protective Resemblances.—Concealment as a protection against enemies. Example: *Kallima* butterfly.
2. *Anticryptic colors*.—Aggressive Resemblances.—Concealment in order to facilitate attack. Example: Mantids with leaf-like appendages.

B. PSEUDOSEMATIC COLORS.—False warning and signalling colors.

1. *Pseudaposematic colors*.—Protective Mimicry. Example: Bee-like fly.
2. *Pseudepisematic colors*.—Aggressive Mimicry and Alluring Coloration. Examples: *Volucella*, resembling bees (Fig. 250); Flower-like mantid.

II. SEMATIC COLORS.—Warning and Signalling Colors.

1. *Aposematic colors*.—Warning Colors.—Examples: Gaudy colors of stinging insects.
2. *Episematic colors*.—Recognition Markings.

III. EPIGAMIC COLORS.—Colors Displayed in Courtship.

Such of these classes as have not already been discussed need brief reference.

Aggressive Resemblances.—The resemblance of a carnivorous animal to its surroundings may not only be protective but may also



FIG. 250.—Aggressive mimicry. On the left, a bee, *Bombus mastrucatus*; on the right, a fly, *Volucella bombylans*. Natural size.

enable it to approach its prey undetected, as in the case of the polar bear or the tiger. Among insects, however, the occurrence of aggressive resemblance is rather doubtful, even in the case of the leaf-like mantids.

Aggressive Mimicry.—Under this head are placed those cases in which one species mimics another to which it is hostile. The best known instance is furnished by European flies of the genus *Volucella*, whose larvæ feed upon those of bumblebees and wasps. The flies bear a close resemblance to the bees, owing to which it is supposed that the former are able to enter the nests of the latter and lay their eggs.

Alluring Coloration.—The best example of this phenomenon is afforded by an Indian mantid, *Gongylus gongyloides*, which resembles so perfectly the brightly colored flowers among which it hides that insects actually fly straight into its clutches.

Recognition Markings.—Though these are apparently important among mammals and birds, as enabling individuals of the same species quickly to recognize and follow one another, no special markings for this purpose are known to occur among insects, not excepting the gregarious migrant species, such as *Anosia plexippus* and the Rocky Mountain locust.

Epigamic Colors.—Among birds, frequently, the bright colors of the male are displayed during courtship, and their evolution has been attributed by Darwin and many of his followers to sexual selection—a highly debatable subject. Among insects, however, no such phenomenon has been found; whenever the two sexes differ in coloration the difference does not appear to facilitate the recognition of even one sex by the other.

Evolution of Adaptive Coloration.—Natural selection is the only theory of any consequence that explains the highly involved phenomena of adaptive coloration. Against such vague and unsupported theories as the action of food, climate, laws of growth or sexual selection, natural selection alone accounts for the multitudinous and intricate correlations of color, pattern, form, attitude, movement, place, time, etc., that are necessary to the development of a perfect case of protective resemblance or mimicry. Natural selection cannot, of course, originate colors or any other characters, its action being restricted to the preservation and accumulation of such advantageous variations as may arise, from whatever causes. As Poulton says, the vast body of facts, utterly meaningless under any other theory, become at once intelligible as they fall harmoniously into place under the principle of natural selection, to which, indeed, they yield the finest kind of support.

CHAPTER VII

INSECTS IN RELATION TO PLANTS

Insects, in common with other animals, depend for food primarily upon the plant world. No other animals, however, sustain such intimate and complex relations to plants as insects do. The more luxuriant and varied the flora, the more abundant and diversified is its accompanying insect fauna.

Not only have insects become profoundly modified for using all kinds and all parts of plants for food and shelter, but plants themselves have been modified to no small extent in relation to insects, as appears in their protective devices against unwelcome insects, in the curious formations known as "galls," the various insectivorous plants, and especially the omnipresent and often intricate floral adaptations for cross-pollination through the agency of insect visitors. Though insects have laid plants under contribution, the latter have not only vigorously sustained the attack but have even pressed the enemy into their own service, as it were.

Numerical Relations.—The number of insect species supported by one kind of plant is seldom small and often surprisingly large. The poison ivy (*Rhus toxicodendron*) is almost exempt from attack, though even this plant is eaten by a leaf-mining caterpillar, two pyralid larvæ and the larva of a scolytid beetle (Schwarz, Dyar). Horse-chestnut and buckeye have perhaps a dozen species at most; elm has eighty; birches have over one hundred, and so have maples; pines are known to harbor 170 species and may yield as many more; while our oaks sustain certainly 500 species of insects and probably twice as many. Turning to cultivated plants, the clover is affected, directly or indirectly, by about 200 species, including predaceous insects, parasites, and flower-visitors. Clover grows so vigorously that it is able to withstand a great deal of injury from insects. Corn is attacked by about 200 species, of which 50 do notable injury and some 20 are pests. Apple insects number some 400 species.

Not uncommonly, an insect is restricted to a single species of plant. Thus the caterpillar of *Heodes hypophlæas* feeds only on sorrel (*Rumex acetosella*), so far as is known. The chrysomelid *Chrysochus auratus* appears to be limited to Indian hemp (*Apocynum androsæmifolium*) and

to milkweed (*Asclepias*). In many instances an insect feeds indifferently upon several species of plants provided these have certain attributes in common. Thus *Argynnis cybele*, *aphrodite* and *atlantis* eat the leaves of various species of violets, and the Colorado potato beetle eats different species of *Solanum*. *Papilio thoas* feeds upon orange, prickly ash and other Rutaceæ. *Anosia plexippus* eats the various species of *Asclepias* and also *Apocynum androsæmifolium*; while *Chrysochus* also is limited to these two genera of plants, as was said. These plants agree in having a milky juice; in fact the two genera are rather nearly related botanically. The common cabbage butterfly (*Pieris rapæ*) though confined for the most part to Cruciferæ, such as cabbage, mustard, turnip, radish, horse-radish, etc., often develops upon *Tropæolum*, which belongs to Geraniaceæ; all its food plants, however, have a pungent odor, which is probably the stimulus to oviposition.

Most phytophagous insects range over many food plants. The *cecropia* caterpillar has more than sixty of these, representing thirty-one genera and eighteen orders of plants; and the tarnished plant bug (*Lygus pratensis*) feeds indifferently on all sorts of herbage, as does also the caterpillar of *Diacrisia virginica*. Many of the insects of apple, pear, quince, plum, peach, and other plants of the family Rosaceæ occur also on wild plants of the same family; and the worst of our corn and wheat insects have come from wild grasses. As regards number of food plants, the gipsy moth "holds the record," for its caterpillar will eat almost any plant. In Massachusetts, according to Forbush and Fernald, it fed in the field upon 78 species of plants, in captivity upon 458 species (30 under stress of hunger, the rest freely), and refused only 19 species, most of which (such as larkspur and red pepper) had poisonous or pungent juices, or were otherwise unsuitable as food. The migratory locust is notoriously omnivorous, and perhaps eats even more kinds of plants than the gipsy moth.

Galls.—Most of the conspicuous plant outgrowths known as "galls" are made by insects, though many of the smaller plant galls are made

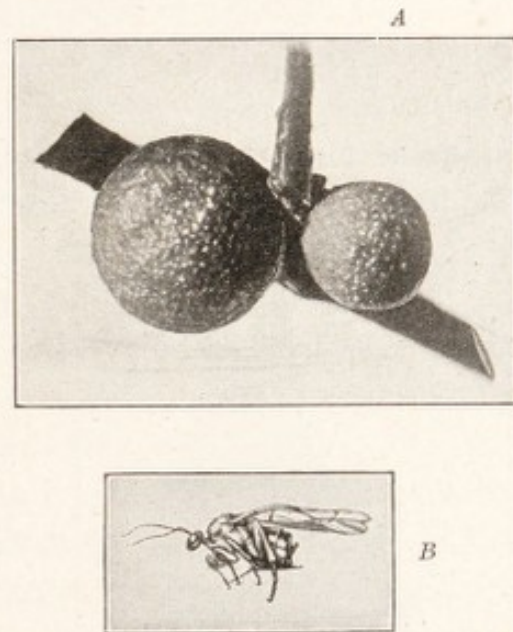


FIG. 251.—*Holcaspis globulus*. A, galls on oak, natural size; B, the gall-maker, twice natural length.

by mites (Acarina) and a few plant excrescences are due to nematode worms and to fungi.

Among insects, Cynipidæ (Hymenoptera) are pre-eminent as gall-

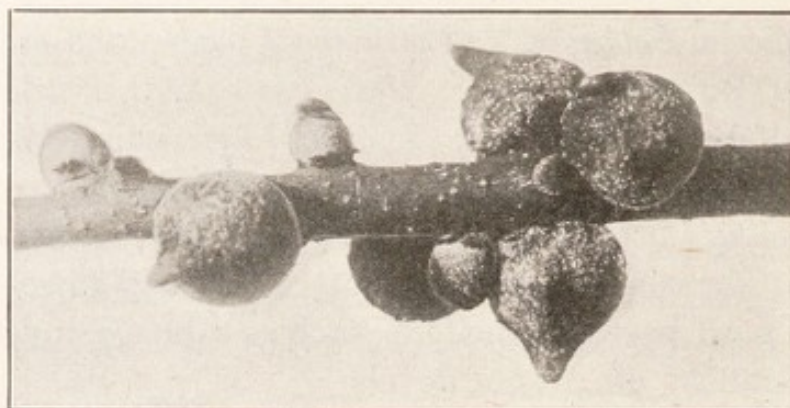


FIG. 252.—Galls of *Holcaspis duricoria*, on oak. Natural size.

makers and next to these, Itonididæ (Diptera), Aphididæ and Psyllidæ (Hemiptera); a few gall-insects occur among Tenthredinidæ (Hymenoptera) and Trypetidæ (Diptera), and one or two among Coleoptera and Lepidoptera.



FIG. 253.—Cockscomb gall of *Colopha ulmicola*, on elm. Slightly reduced.

Cynipidæ affect the oaks (Figs. 251, 252) far more often than any other plants, though not a few species select the wild rose. Itonidid galls occur on a great variety of plants, and those of aphids on elm (Fig. 253), poplar, and many other plants; while psyllid galls are most frequent on hackberry. The galls may occur anywhere on a plant, from the roots to the flowers or seeds, though each gall-maker always works on the same part of its plant,—root, stem, bud, leaf, leaf-vein, flower, seed, etc.

Galls present innumerable forms, but the form and situation of a gall are usually characteristic, so that it is often possible to classify galls as species even before the gall-maker is known.

Gall-Making.—The female simply lays the egg on the epidermis, or else punctures the plant and deposits an egg in or near the cambium, or any other tissue capable of growth; the egg hatches and the surrounding plant tissue is stimulated to grow rapidly and abnormally into a gall,

which serves as food for the larva; this transforms within the gall and escapes as a winged insect. The physiology of gall-formation is far from being understood. It has been found that the mechanical irritation from the ovipositor is not the initial stimulus to the development of a gall; neither is the fluid which is injected by the female during oviposition, this fluid being probably a lubricant; if the egg is removed, the gall does not appear. Ordinarily the gall does not begin to grow until the egg has hatched, and then the gall grows along with the larva; exceptions to this are found in some Tenthredinidæ in which the egg itself increases in volume, when the gall may grow with the egg. It appears that the larva exudes some fluid which acts upon the protoplasm of certain plant cells (the cambium and other cells capable of further growth and multiplication) in such a way as to stimulate their increase in size and number. The following observations on this subject by A. Cosens are important. The cells of the plant that immediately surround the larva are known as nutritive cells. In Cynipidæ the larva gradually withdraws the contents of these cells, by means of the mouth and not by absorption, and the cells gradually collapse. The proportion of sugar to starch decreases from the inside of the nutritive zone (nearest the larva) to the outside. This is owing to an enzyme that changes starch into sugar, the source of this enzyme being probably a pair of salivary glands that open externally on each side just below the mouth of the larva. The larva by accelerating the rate of change from starch to sugar renders available to the plant more food than usual and therefore stimulates the activity of the protoplasm toward greater cell-growth and more rapid cell-reproduction. Thus the gall as well as the larva draws food from the nutritive zone.

Why the gall should have a distinctive, or specific, form, it is not yet known. There is no evidence that the form is of any adaptive importance, and the subject probably admits of a purely mechanical explanation. One factor in determining the form of the gall is the direction in which the stimulus is applied; a spherical cynipid gall arising when the influence is about equally distributed in all directions (Cosens).

Gall Insects.—The study of gall insects is in many respects difficult. It is not at all certain that an insect which emerges from a gall is the species that made it; for many species, even of Cynipidæ, make no galls themselves but lay their eggs in galls made by other species. Such guest-insects are termed *inquilines*. Furthermore, both gall-makers and inquilines are attacked by parasitic Hymenoptera, making the interrelations of these insects hard to determine. Many species of insects

feed upon the substance of galls; thus Sharp speaks of as many as thirty different kinds of insects, belonging to almost all the orders, as having been reared from a single species of gall.

Parthenogenesis and Alternation of Generations.—*Parthenogenesis* has long been known to occur among Cynipidæ. It has repeatedly been found that of thousands of insects emerging from galls of the same kind, all were females. In one such instance the females were induced by Adler to lay eggs on potted oaks, when it was found that the resulting galls were quite unlike the original ones, and produced both sexes of an insect which had up to that time been regarded as another species. Besides parthenogenesis and this *alternation of generations*, many other complications occur, making the study of gall-insects an intricate and highly interesting subject.

Plant-Enemies of Insects.—Most of the flowering plants are comparatively helpless against the attacks of insects, though there are many devices which prevent "unwelcome" insects from entering flowers, for instance the sticky calyx of the catchfly (*Silene virginica*), which entangles ants and small flies. A few plants, however, actually feed upon insects themselves. Thus the species of *Drosera*, as described in Darwin's classic volume on insectivorous plants, have specialized leaves for the purpose of catching insects. The stout hairs of these leaves end each in a globular knob, which secretes a sticky fluid. When a fly alights on one of these leaves the hairs bend over and hold the insect; then a fluid analogous to the gastric juice of the human stomach exudes, digests the albuminoid substances of the insect and these are absorbed into the tissues of the leaf; after which the tentacles unfold and are ready for the next insect visitor. The Venus's flytrap is another well known example; the trap, formed from the terminal portion of a leaf, consists of two valves, each of which bears three trigger-like bristles, and when these are touched by an insect the valves snap together and frequently imprison the insect, which is eventually digested, as before. In the common pitcher-plants, the pitcher, fashioned from a leaf, is lined with downward pointing bristles, which allow an insect to enter but prevent its escape. The bottom of the pitcher contains water, in which may be found the remains of a great variety of insects which have drowned. There are even nectar glands and conspicuous colors, presumably to attract insects into these traps, where their decomposition products are more or less useful to the plant. In *Pinguicula* the margin of a leaf rolls over and envelops insects that have been caught by the glandular hairs of the upper surface of the leaf, a copious secretion

digests the softer portions of the insects, and the dissolved nitrogenous matter is absorbed into the plant. *Utricularia* has little bladders which entrap small aquatic insects. These plants are only partially dependent on insect-food, however, for they all possess chlorophyll.

Bacteria cause epidemic diseases among insects, as in the flacherie of the silkworm; and fungi of a few groups are specially adapted to develop in the bodies of living insects.

Those who rear insects know how frequently caterpillars and other larvæ are destroyed by fungi that give the insects a powdered appearance. These fungi, referred to the genus *Isaria*, are in some cases known to be asexual stages of forms of *Cordyceps*, which forms appear from the bodies of various larvæ, pupæ and imagines as long, conspicuous, fructifying sprouts (Fig. 254).

The chief fungous parasites of insects belong to the large family Entomophthoraceæ, represented by the common *Empusa muscæ* (Fig. 255) which affects various flies. In autumn, especially in warm moist weather, the common house fly may often be seen in a dead or dying condition, sticking to a window-pane, its abdomen distended and presenting alternate black and white bands, while around the fly at a little distance is a white powdery ring, or halo. The white intersegmental bands are made by threads of the fungus just named, and the white halo by countless asexual spores known as *conidia*, which have been forcibly discharged from the swollen threads that bore them (Fig. 255) by pressure, resulting probably from the absorption of moisture. These spores, ejected in all directions, may infect another fly upon contact and produce a growth of fungus threads, or *hyphæ*, in its body. The fungus may be propagated also by means of resting spores, as found by Thaxter, our authority on the fungi of insects.

Empusa aphidis is very common on plant lice and is an important check upon their multiplication. Aphids killed by this fungus are found clinging to their food plant, with the body swollen and discolored. *Empusa grylli* attacks crickets, grasshoppers, caterpillars and other



FIG. 254.—Fructifying sprouts of a fungus, *Cordyceps ravenelii*, arising from the body of a white grub, *Lachnosterna*. Slightly reduced.—After RILEY.

forms. Curiously enough, grasshoppers affected by this fungus almost always crawl to the top of some plant and die in this conspicuous position.

Sporotrichum, a genus of hyphomycetous fungi, affects a great variety of insects, spreading within the body of the host and at length emerging to form on the body of the insect a dense white felt-like covering, this consisting chiefly of myriads of spores, by means of which healthy insects may become infected. Under favorable conditions, especially in moist seasons, contagious fungous diseases constitute one of the most important checks upon the increase of insects and are therefore of vast economic importance. Thus the termination (in 1889)

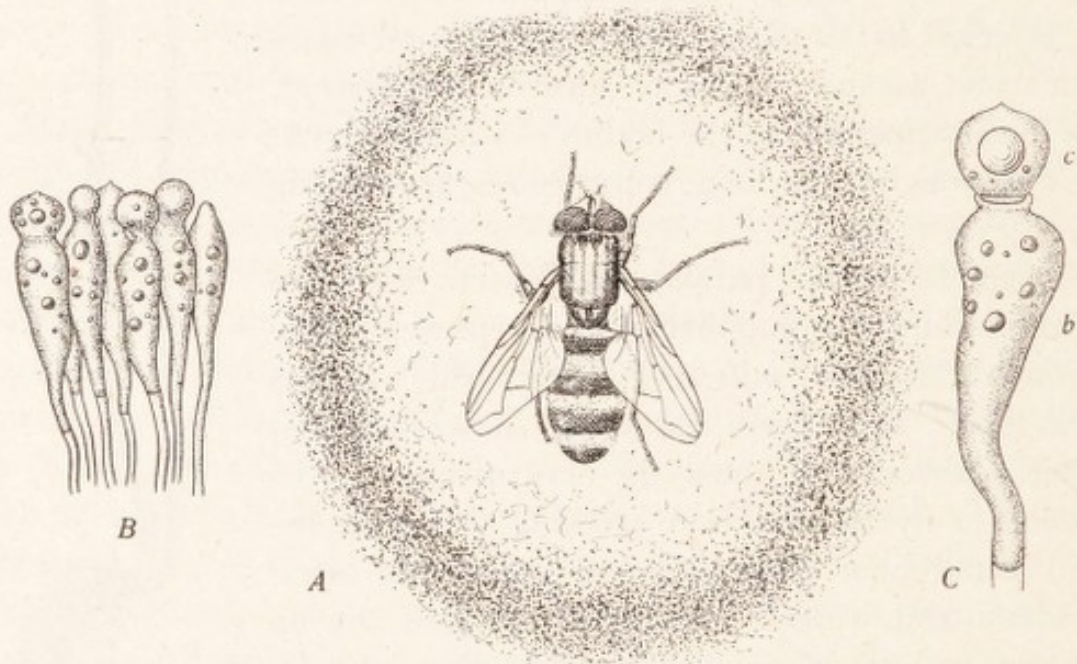


FIG. 255.—*Empusa muscae*, the common fly-fungus. A, house fly (*Musca domestica*), surrounded by fungus spores (conidia); B, group of conidiophores showing conidia in several stages of development; C, basidium (b) bearing conidium (c) before discharge. B and C after THAXTER.

of a disastrous outbreak of the chinch bug in Illinois and neighboring states "was apparently due chiefly, if not altogether, to parasitism by fungi." Artificial cultures of the common *Sporotrichum globuliferum* have been used extensively as a means of spreading infection among chinch bugs and grasshoppers, with, however, but moderate success.

Transmission of Diseases of Plants.—Not a few bacterial and fungous diseases of plants are known to be transmitted by insects. M. B. Waite proved experimentally that the bacillus causing fire blight of pear, apple and other pomaceous trees is carried by honey bees and other insects from flower to flower, multiplies in the nectar, and enters the host plant. Bees, wasps and flies obtain the bacilli from the exudation from old cankers and carry the organisms either to blossoms or to young

growing shoots. Other investigators have found that apple aphids, leafhoppers, the tarnished plant bug (*Lygus pratensis*) and the shot-hole borer (*Scolytus rugulosus*) are also responsible for the inoculation of fruit trees with the bacilli of blight.

Dr. E. F. Smith demonstrated that cucurbit wilt is spread, probably exclusively, by insects, particularly the striped and the twelve-spotted cucumber beetles (*Diabrotica vittata* and *D. duodecimpunctata*, respectively), which introduce the bacilli of the disease into the plants as they feed. Some of the beetles carry the bacillus over winter, in the alimentary tract, and infect young plants with the wilt in spring.

The spores of the fungous disease known as brown rot of peach and plum are probably carried by bees, wasps and certain other insects, and introduced into wounds in the fruits made by themselves or other insects. The plum curculio almost certainly leaves these spores in punctures that it makes.

Cankers of *Leptosphaeria* on apple bark occur around the oviposition wounds made by tree-crickets (*Æcanthus*), and it has been shown experimentally that these insects convey the spores of the disease both externally and internally and inoculate them into the host plant. Typical cankers on apple branches have been obtained artificially by inoculation with feces of tree-crickets fed on spores of the disease.

The mosaic diseases of cucumber, potato and tobacco are transmitted by plant lice. The spores of bitter rot of apples are conveyed from decaying apples to sound fruits by pomace flies (*Drosophila*).

Insects in Relation to Flowers.—Among the most marvelous phenomena known to the biologist are the innumerable and complex adaptations by means of which flowers secure cross pollination through the agency of insect visitors. Cross fertilization is actually a necessity for the continued vigor and fertility of flowering plants, and while some of them are adapted for cross pollination by wind or water, the majority of flowering plants exhibit profound modifications of floral structure for compelling insects (and a few other animals, as birds or snails) to carry pollen from one flower to another. In general, the conspicuous colors of flowers are for the purpose of attracting insects, as are also the odors of flowers. Night-blooming flowers are often white or yellow and as a rule strongly scented. Colors and odors, however, are simply indications to insects that edible nectar or pollen is at hand. Such is the usual statement, and it is indeed probable that insects actually do associate color and nectar, even though they will fly to bits of colored paper almost as readily as they will to flowers of the same colors. It is not

to be supposed, however, that insects realize that they confer any benefit upon the plant in the flowers of which they find food. At any rate, most flowers are so constructed that certain insects cannot get the nectar or pollen without carrying some pollen away, and cannot enter the next flower of the same kind without leaving some of this pollen upon the stigma of that flower. Take the iris, for example, which is admirably adapted for pollination by a few bees and flies.

Iris.—In the common blue-flag (*Iris versicolor*, Fig. 256) each of the



FIG. 256.—Bumblebee (*Bombus*) entering flower of blue-flag (*Iris versicolor*). Slightly reduced.

three drooping sepals forms the floor of an arched passageway leading to the nectar. Over the entrance and pointing outward is a movable lip (Fig. 257, *l*), the outer surface of which is stigmatic. An entering bee hits and bends down the free edge of this lip, which scrapes pollen from the back of the insect and then springs back into place. Within the passage, the hairy back of the bee rubs against an overhanging anther (*an*) and becomes powdered with grains of pollen as the insect pushes down towards the nectar. As the bee backs out of the passage

it encounters the guardian lip again, but as this side of the lip cannot receive pollen, immediate close pollination is prevented. Of course, it is possible for bees to enter another part of the same flower or another flower of the same plant, but as a matter of fact, they habitually fly away to another plant; moreover, as Darwin found, foreign pollen is prepotent over pollen from the same flower. It may be added that bees and other pollenizing insects ordinarily visit in succession several flowers of the same kind.

Orchids.—The orchids, with their fantastic forms, are really elaborate traps to insure cross pollination. In some orchids (*Habenaria* and others) the nectar, lying at the bottom of a long tube, is accessible only to the long-tongued Sphingidæ. While probing for the nectar, a sphinx moth brings each eye against a sticky disk to which a pollen mass is attached, and flies away carrying the mass on its eye. Then these *pollinia* bend down on their stalks in such a way that when the moth thrusts its head into the next flower they are in the proper position to encounter and adhere to the stigma. The orchid *Angræcum sesquipedale*, of Madagascar, has a nectary tube more than eleven inches long, from which Darwin inferred the existence of a sphinx moth with a tongue equally long.

Milkweed.—The various milkweeds are fascinating subjects to the student of the interrelations of flowers and insects. The flowers, like those of orchids, are remarkably formed with reference to cross pollination by insects. As a honey bee or other insect crawls over the flowers (Fig. 258, *A*) to get the nectar, its legs slip in between the peculiar nectariferous *hoods* situated in front of each *anther*. As a leg is drawn upward one of its claws, hairs, or spines frequently catches in a V-shaped fissure (*f*, Fig. 258, *B*) and is guided along a slit to a notched *disk*, or *corpuscle* (Fig. 258, *C*, *d*). This disk clings to the leg of the insect, which carries off by means of the disk a pair of pollen masses, or *pollinia* (Fig. 258, *C*). When first removed from their enclosing pockets, or anthers,

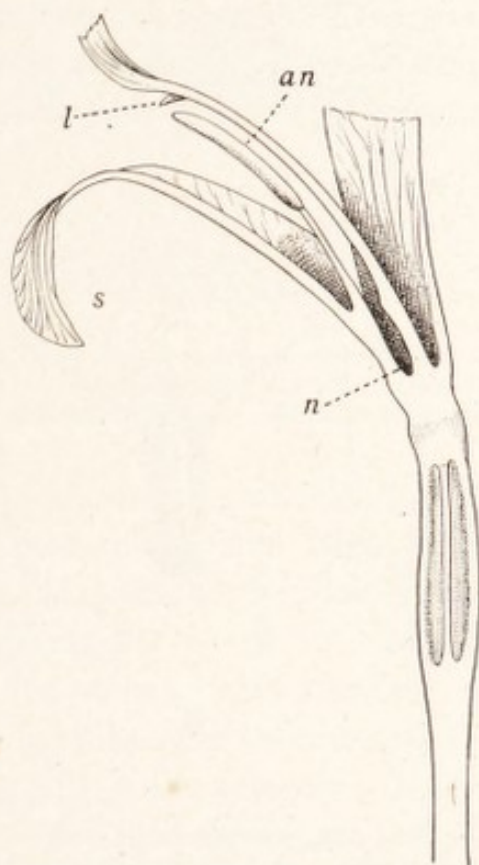


FIG. 257.—Section to illustrate cross pollination of *Iris*. *an*, anther; *l*, stigmatic lip; *n*, nectary; *s*, sepal.

these thin spatulate pollinia lie each pair in the same plane, but in a few seconds the two pollinia twist on their stalks and come face to face in such a way that one of them can be easily introduced into the *stigmatic chamber* of a new flower visited by the insect. Then the struggles of the insect ordinarily break the stem, or *retinaculum*, of the pollinium and free the insect. Often, however, the insect loses a leg or else is permanently entrapped, particularly in the case of such large-flowered milkweeds as *Asclepias cornuti*, which often captures bees, flies and moths of considerable size. Pollination is accomplished by a great

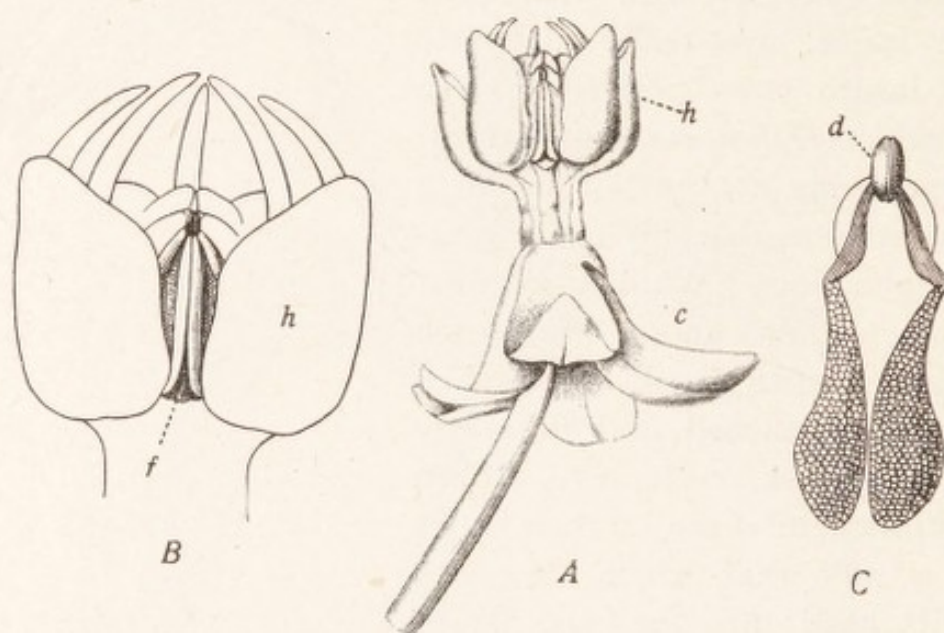


FIG. 258.—Structure of milkweed flower (*Asclepias incarnata*) with reference to cross pollination. A, a single flower; c, corolla; h, hood; B, external aspect of fissure (f) leading up to disk and also into stigmatic chamber; h, hood; C, pollinia; d, disk. Enlarged.

variety of insects, chiefly Hymenoptera, Diptera, Lepidoptera and Coleoptera. These insects when collected about milkweed flowers usually display the pollinia dangling from their legs, as in Fig. 259.

The details of pollination may be gathered by a close observer from observations in the field and may be demonstrated to perfection by using a detached leg of an insect and dragging it upward between two of the hoods of a flower; first to remove the pair of pollinia and then again to introduce one of them into an empty stigmatic chamber.

Yucca.—An extraordinary example of the interdependence of plants and insects was made known by Riley, whose detailed account is here summarized. The yuccas of the southern United States and Mexico are among the few plants that depend for pollination each upon a single species of insect. The pollen of *Yucca filamentosa* cannot be introduced into the stigmatic tube of the flower without the help of a little white

tineid moth, *Pronuba yuccasella*, the female of which pollenizes the flower and lays eggs among the ovules, that her larvæ may feed upon the young seeds. While the male has no unusual structural peculiarities, the female is adapted for her special work by modifications which are unique among Lepidoptera, namely, a pair of prehensile and spinous maxillary "tentacles" (Fig. 260, *A*) and a long protrusible ovipositor (*B*) which combines in itself the functions of a lance and a saw.

The female begins to work soon after dark, and will continue her operations even in the light of a lantern. Clinging to a stamen (Fig. 261) she scrapes off pollen with her palpi and shapes it into a pellet by using the front legs. After gathering pollen from several flowers she flies to another flower, as a rule, thrusts her long flexible ovipositor into the ovary (Fig. 262) and lays a slender egg

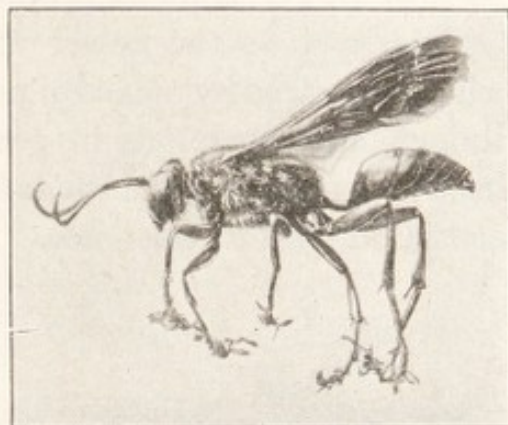


FIG. 259.—A wasp, *Sphex ichneumonea*, with pollinia of milkweed attached to its legs. Slightly enlarged.

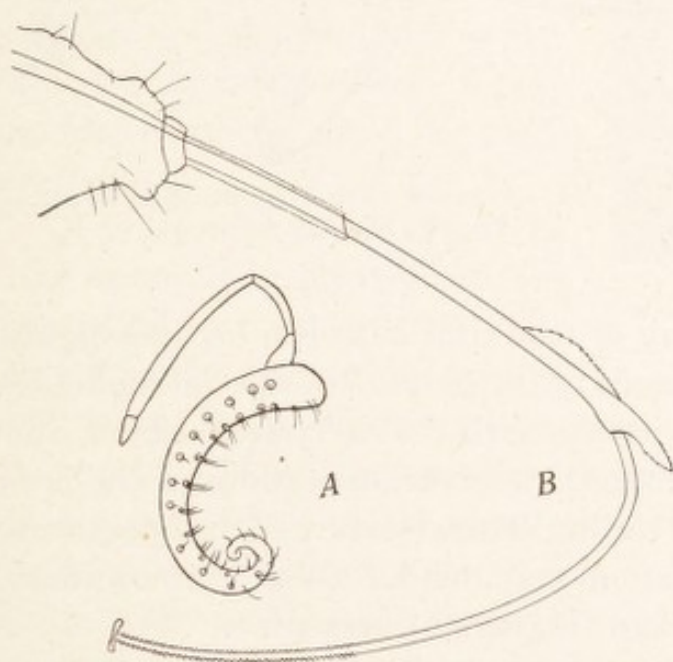


FIG. 260.—*Pronuba yuccasella*. *A*, maxillary tentacle and palpus; *B*, ovipositor.—After RILEY. Figures 260–262 are republished from the Third Report of the Missouri Botanical Garden, by permission.

alongside seven or eight of the ovules. After laying one or more eggs she ascends the pistil and actually thrusts pollen into the stigmatic tube and pushes it in firmly. The ovules develop into seeds, some of which are consumed by the larvæ, though plenty are left to perpetuate the plant itself. Three species of *Pronuba* are known, each restricted to particular species of *Yucca*. Riley says that *Yucca* never produces seed where *Pronuba* does not occur or where she is excluded artificially, and that artificial pollination is rarely so suc-

cessful as the normal method.

Why does the insect do this? The little nectar secreted at the base

of the pistil appears to be of no consequence, at present, and the stigmatic fluid is not nectarian; indeed, the tongue of *Pronuba*, used in clinging to the stamen, seems to have lost partially or entirely its sucking power, and the alimentary canal is regarded as functionless. Ordinarily it is the flower which has become adapted to the insect, which is enticed by means of pollen or nectar, but here is a flower which—though entomophilous in general structure—has apparently adapted itself in no way to the single insect upon which it is dependent for the continuance of its existence. More than this, the insect not only labors

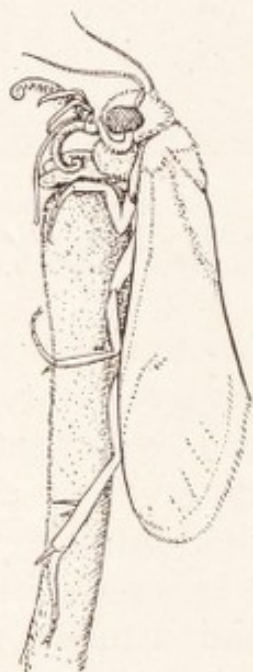


FIG. 261.—*Pronuba yuccasella*, female, gathering pollen from anthers of *Yucca*. Enlarged.

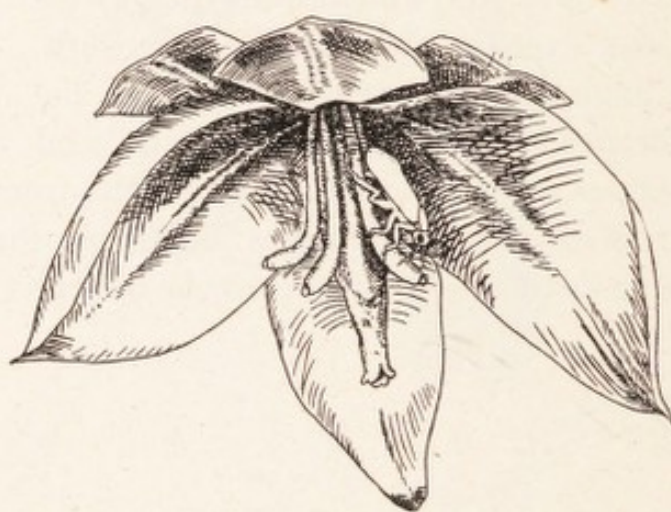


FIG. 262.—*Pronuba* moth ovipositing in flower of *Yucca*. Slightly reduced.

without compensation in the way of food, but has even become highly modified with reference to the needs of the plant,—its special modifications being unparalleled among insects with the exception of bees, and being more puzzling than the more extensive adaptations of the bees when we take into consideration the impersonal nature of the operations of *Pronuba*. Further investigation may render these extraordinary interrelations more intelligible than they are at present.

The bogus Yucca moth (*Prodoxus quinquepunctella*) closely resembles and associates with *Pronuba* but oviposits in the flower stalks of *Yucca* and has none of the special adaptive structures found in *Pronuba*.

As regards floral adaptations, these examples are sufficient for present purposes; many others have been described by the botanist; in fact, the adaptations for cross pollination by insects are as varied as the flowers themselves.

Insect Pollenizers.—The great majority of entomophilous flowers are pollenized by bees of various kinds; the apple, pear, blackberry, raspberry and many other rosaceous plants depend chiefly upon the honey bee, while clover cannot set seed without the aid of bumblebees or honey bees, assisted by wild bees such as *Tetralonia* and *Melissodes*. Lilies and orchids frequently employ butterflies and moths, as well as bees, and the milkweed is adapted in a remarkable manner for pollination by butterflies, moths and some wasps, as was described. Honeysuckle, lilac, azalea, tobacco, *Petunia*, *Datura* and many other strongly scented and conspicuous nocturnal flowers attract for their own uses the long-tongued sphinx moths (Fig. 263); the evening primrose, like milkweed, is a favorite of noctuid moths. Umbelliferous plants are pollenized chiefly by various flies, but also by bees and wasps. Pond lilies, golden rod and some other flowers are pollenized largely by beetles, though the flowers exhibit no special modifications in relation to these particular insects. It is noteworthy that pollination is performed only by the more highly organized insects, the bees heading the list.

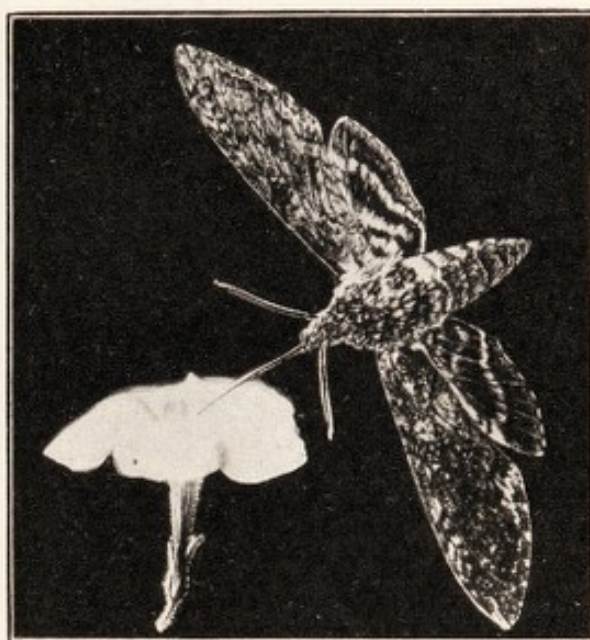


FIG. 263.—*Protoparce sexta* visiting flower of *Petunia*. Reduced.

Of all the insects that haunt the same flower, it frequently happens that only a few are of any use to the flower itself; many come for pollen only; many secure the nectar illegitimately; thus bumblebees puncture the nectaries of columbine, snapdragon and trumpet creeper from the outside, and wasps of the genus *Odynerus* cut through the corolla of *Pentstemon lævigatus*, making a hole opposite each nectary; then there are the many insects that devour the floral organs, and the insects which are predaceous or parasitic upon the others. In the *Iris*, according to Needham, two small bees (*Clisodon terminalis* and *Osmia distincta*) are the most important pollenizers, and next to them a few syrphid flies, while bumblebees also are of some importance. The beetle *Trichius piger* and several small flies obtain pollen without assisting the plant, and *Pamphila*, *Eudamus*, *Chrysophanus* and some other butterflies succeed after many trials in stealing the nectar from the outside (Fig.

264). A weevil (*Mononychus vulpeculus*) punctures the nectary, and the flowing nectar then attracts a great variety of insects. Grasshoppers and caterpillars eat the flowers, an ortalid fly destroys the buds, and several parasitic or predaceous insects haunt the plant; in all, more than sixty species of insects are concerned in one way or another with the *Iris*.



FIG. 264.—A butterfly, *Polites peckius*, stealing nectar from a flower of *Iris versicolor*. Slightly reduced.

Modifications of Insects with Reference to Flowers.—While the manifold and exquisite adaptations of the flower for cross pollination have engaged universal attention, very little has been recorded concerning the adaptations of insects in relation to flowers. In fact, the adaptation is largely one-sided; flowers have become adjusted to the structure of insects as a matter of vital necessity—to put it that way—while insects have had no such urgent need—so to speak—in relation to floral structure. They have been influenced by floral structure to some extent however, and in some cases to a very great extent, as appears from their structural and physiological adaptations for gathering and using pollen and nectar.

Among mandibulate insects, beetles and caterpillars that eat the floral envelopes show no special modifications for this purpose; pollen-feeding beetles, however, usually have the mouth parts densely clothed with hairs, as in *Euphoria* (Fig. 265). In suctorial insects, the mouth parts are frequently formed with reference to floral structure; this is the case in many butterflies and particularly in Sphingidæ, in which the length of the tongue bears a direct relation to the depth of the nectary in the flowers that they visit. According to Müller, the mouth parts of Syrphidæ, Stratyomyiidae and Muscidæ are specially adapted for feed-

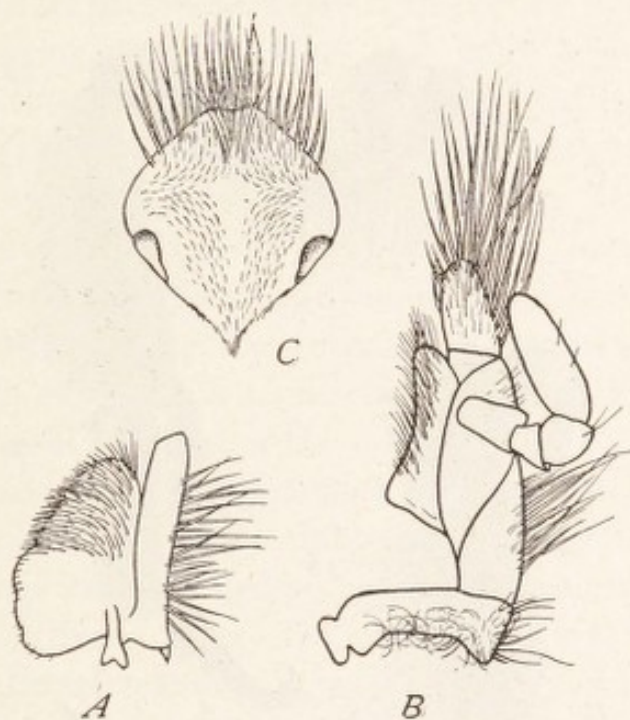


FIG. 265.—A, right mandible; B, right maxilla; C, hypopharynx, of a pollen-eating beetle, *Euphoria inda*. Enlarged. (The mandibles are remarkable in being two-lobed.)



FIG. 266.—Pollen-gathering hair from a worker honey bee, with a pollen grain attached. Greatly magnified.

ing on pollen. In Apidæ, the tongue as compared with that of other Hymenoptera, is exceptionally long, enabling the insect to reach deep into a flower, and is exquisitely specialized (Fig. 129) for lapping up and sucking in nectar.

Pollen-gathering flies and bees collect pollen in the hairs of the body or the legs; these hairs, especially dense and often twisted or branched (Figs. 266, 91) to hold the pollen, do not occur on other than pollen-gathering species of insects. Caudell found that out of 200 species of Hymenoptera only 23 species had branched hairs and that these species belonged without exception to the pollen-gathering group Anthophila, no representative of which was found without such hairs. Similar

branched hairs occur also on the flower-frequenting Bombyliidæ and Syrphidæ.

The most extensive modifications in relation to flowers are found in *Pronuba*, as already described, and above all in Apidæ, especially the honey bee.

Honey Bee.—The thorax and abdomen and the bases of the legs are clothed with flexible branching hairs (Fig. 266), which entangle



FIG. 267.—Adaptive modifications of the legs of the worker honey bee. A, outer aspect of left hind leg; B, portion of left middle leg; C, inner aspect of tibio-tarsal region of left hind leg; D, tibio-tarsal region of left fore leg; a, antenna comb; au, auricle; b, brush; c, coxa; co, corbiculum; f, femur; p, pecten; pc, pollen combs; s, spur; sp, spines; ss, spines; t, trochanter; ti, tibia; v, velum; w, so-called wax pincers; 1-5, tarsal segments; I, metatarsus, or planta.

pollen grains. These are combed out of the gathering hairs by means of special *pollen combs* (Fig. 267, C, pc) on the inner surface of the planta of the hind tarsus, the middle legs also assisting in this operation. From these combs, the pollen is transferred to the *pollen baskets*, or *corbicula* (Fig. 267, A, co), of the outer surface of each hind tibia, the pollen from one side being transferred to the corbiculum of the opposite side. This is accomplished in the following manner: the left *pecten* combs out the pollen from the right planta and a mass of pollen forms just above the left pecten at the lower end of the corbiculum; this mass gradually grows larger and is pushed up along the corbiculum by the

upward movement of the *auricle*: Further details are given by Casteel, whose admirably precise and thorough studies on the manipulation of pollen and wax by the honey bee have corrected certain prevalent errors and added much to our knowledge of the subject. Arriving at the nest, the hind legs are thrust into a cell and the mass of pollen on each corbiculum is pried out by means of a *spur* situated at the apex of the middle tibia (Fig. 267, *B, s*), this lever being slipped in at the upper end of the corbiculum and then pushed along the tibia under the mass of pollen; the spur is used also in cleaning the wings, which explains its presence on queen and drone, as well as worker, but the pollen-gathering structures of the hind legs are confined to the worker. The so-called *wax-pincers* of the hind legs (Fig. 267, *A, C, w*) at the tibio-tarsal articulation, have nothing to do with the transfer of wax scales from the abdomen to the mouth, according to Casteel; a wax scale being removed from its pocket by becoming impaled on stiff spines at the distal end of the inner face of the planta.

For cleaning the antennæ, a front leg is passed over an antenna, which slips into a semicircular *scraper* (Fig. 267, *D, a*) fashioned from the basal segment of the tarsus; when the leg is bent at the tibio-tarsal articulation, an appendage, or *velum* (*v*) of the tibia falls into place to complete a circular comb, through which the antenna is drawn. This comb is itself cleaned by means of a brush of hairs (*b*) on the front margin of the tibia. A series of erect spines (*sp*) along the anterior edge of the first tarsal segment is used as an eye brush, to remove pollen grains or other foreign bodies from the hairs of the compound eyes. The labium and maxillæ (Fig. 56) are exquisitely constructed with reference to gathering and sucking nectar; the maxillæ are used also to smooth the cell walls of the comb; the mandibles (Fig. 56, *md*), notched in queen and drone but with a sharp entire edge in the worker, are used for cutting, scraping and moulding wax, as well as for other purposes. The entire digestive system of the honey bee is adapted in relation to nectar and pollen as food; the proventriculus forms a reservoir for honey and is even provided at its mouth with a rather complex apparatus for straining the honey from the accompanying pollen grains, as described by Cheshire. The wax glands (Fig. 104) are remarkable specializations in correlation with the food habits, as are also the various cephalic glands, the chief functions of which are given as: (1) digestion, as the conversion of cane sugar into grape sugar, and possibly starch into sugar; (2) the chemical alteration of wax; (3) the production of special food substances, which are highly important in larval development.

Numerous special sensory adaptations also occur. In fact, the whole organization of the honey bee has become profoundly modified in relation to nectar and pollen. Many other insects have the same food but none of them sustain such intimate relations to the flowers as do the bees.

Ant-plants.—There are several kinds of tropical plants which are admirably suited to the ants that inhabit them. Indeed, it is often asserted that these plants have become modified with special reference to their use by ants, though this is a gratuitous and improbable assumption.

Belt found several species of *Acacia* in Nicaragua and the Amazon valley which have large hollow stipular thorns, inhabited by ants of the genus *Pseudomyrma*. The ants enter by boring a hole near the apex of

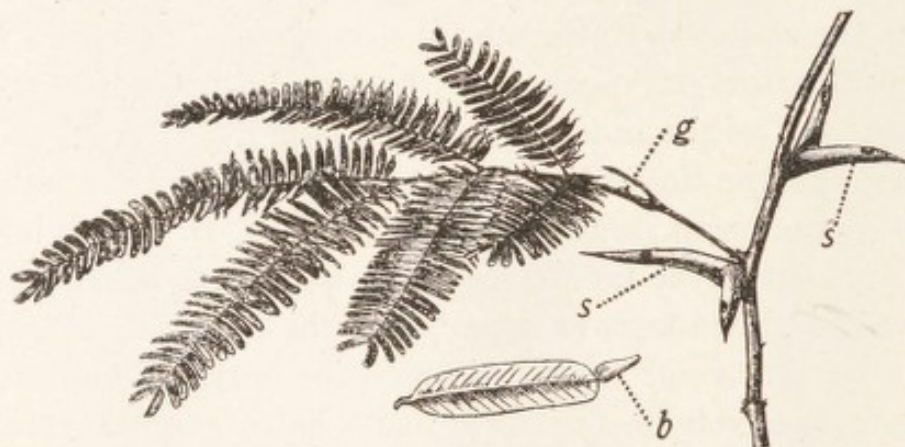


FIG. 268.—*Acacia sphærocephala*, an ant-plant. *b*, one of the "Belt's bodies"; *g*, gland; *s*, *s*, hollow stipular thorns, perforated by ants. Reduced.—From Strasburger's *Lehrbuch der Botanik*.

a thorn (Fig. 268, *s*). The plant affords the ants food as well as shelter, for glands (*g*) at the bases of the petioles secrete a sugary fluid, while many of the leaflets are tipped with small egg-shaped or pear-shaped appendages (*b*) known as "Belt's bodies," which are rich in albumin, fall off easily at a touch, and are eaten by the ants. These ants drive away the leaf-cutting species, incidentally protecting the tree in which they live.

The ant-trees (*Cecropia adenopus*) of Brazil and Central America have often been referred to by travelers. When one of these trees is handled roughly, hosts of ants rush out from small openings in the stems and pugnaciously attack the disturber. Just above the insertion of each leaf is a small pit (Fig. 269, *a*, *b*) where the wall is so thin as to form a mere diaphragm, through which an ant (probably a fertilized female) bores and reaches a hollow internode. To establish communication between the internodal chambers, the ants bore through the intervening

septa (Fig. 270). They seldom leave the *Cecropia* plant, unless disturbed, and even keep herds of aphids in their abode. The base of each petiole bears (Fig. 271) tender little egg-like bodies ("Müller's bodies") which the ants detach, store away and eat; the presence of these bodies is a sure sign that the tree is uninhabited by these ants, which, by the way, belong to the genus *Azteca*.

It is too much to assert that the ants protect the *Cecropia* plant *in return* for the food and shelter which they obtain. All ants are hostile

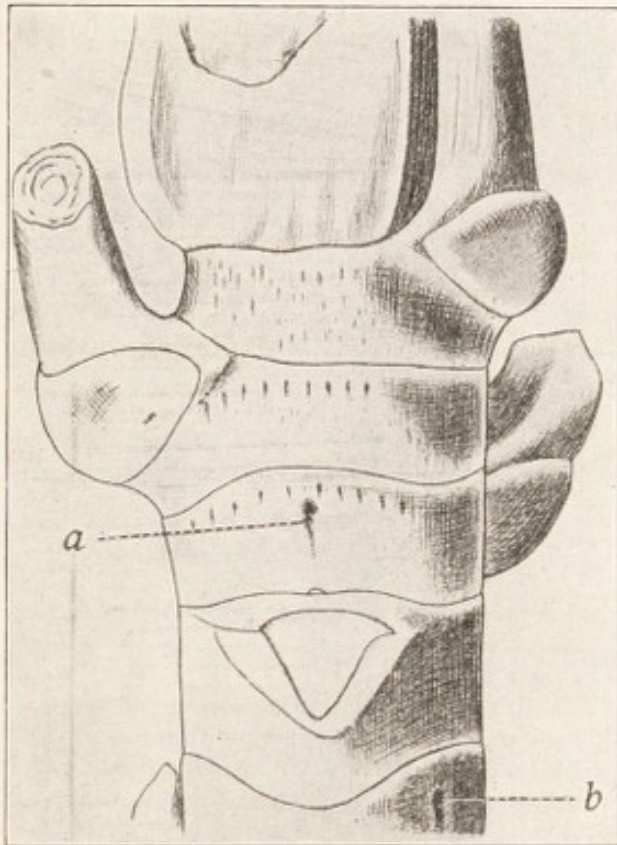


FIG. 269.—Portion of young stem of *Cecropia adenopus* showing internodal pits, *a* and *b*. Natural size. Figures 269-271 are from Schimper's *Pflanzengeographie*.

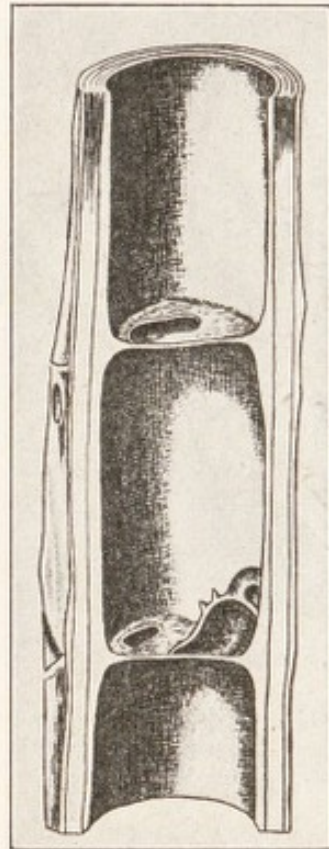


FIG. 270.—*Cecropia adenopus*. Portion of a stem, split so as to show internodal chambers and the intervening septa perforated by ants.

to all other species of ants, with few exceptions, and even to other colonies of their own species; so that their assaults upon leaf-cutting ants are by no means special and adaptive in their nature, and any protection that a plant derives therefrom is merely incidental. Furthermore, hollow stems, glandular petioles and pitted stems are of common occurrence when they bear no relation to the needs of ants. These interrelations of ants and plants are too often misinterpreted in popular and uncritical accounts of the subject.

The interesting habits of the leaf-cutting ants in relation to the

plants that they attack are described¹ in a subsequent chapter, where will be found also an account of the harvesting ants.

The epiphytic plants *Myrmecodia* and *Hydnophytum*, of Java, form



FIG. 271.—*Cecropia adenopus*. Base of petiole showing "Müller's bodies." Slightly reduced.

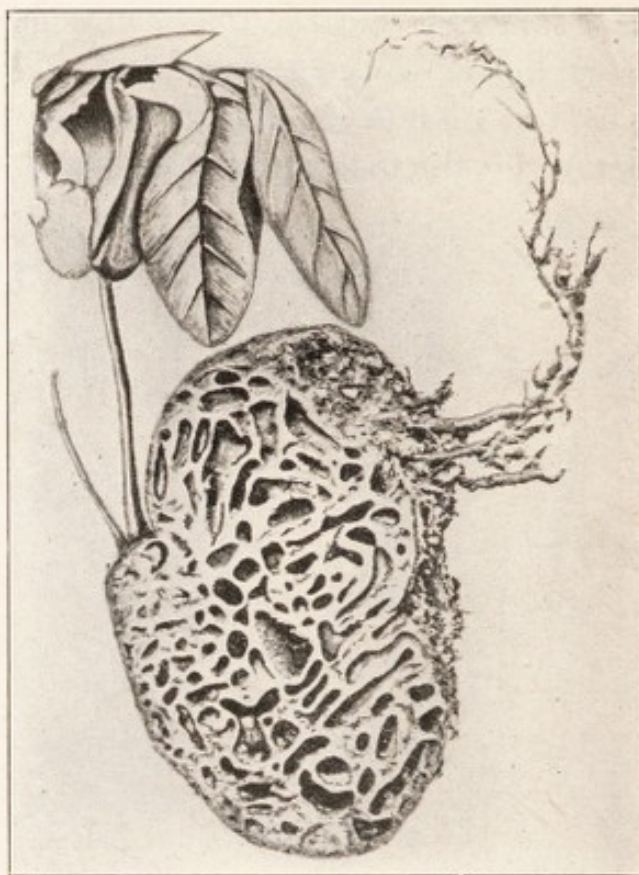


FIG. 272.—*Hydnophytum montanum*. Section of pseudo-bulb, to show chambers inhabited by ants. One-fourth natural size.—After FOREL.

spongy bulb-like masses, the chambers of which are usually tenanted by ants, which rush forth when disturbed. These lumps (Fig. 272) are primarily water-reservoirs, but the ants utilize them by boring into them and from one chamber into another. In plants of the genus *Humboldtia* the ants can enter the hollow internodes through openings that already exist.

CHAPTER VIII

INSECTS IN RELATION TO OTHER ANIMALS

On the one hand, insects may derive their food from other animals, either living or dead; on the other hand, insects themselves are food for other animals, especially fishes and birds, against which they protect themselves by various means, more or less effective. These topics form the principal subject of the present chapter.

Predaceous Insects.—Innumerable aquatic insects feed largely or entirely upon microscopic Protozoa, Rotifera, Entomostraca, etc.; this is especially the case with culicid (mosquito) and chironomid (midge) larvæ. Many aquatic Hemiptera and Coleoptera prey upon planarians, nematodes, annelids, molluscs and crustaceans; *Belostoma* (the electric light bug) sometimes pierces the bodies of tadpoles and small fishes; *Dytiscus* also kills young fishes occasionally and is distinctly carnivorous both as larva and imago. Among terrestrial insects, the ground beetles, Carabidæ, are notably predaceous, preying not only upon other insects but also upon molluscs, myriopods, mites and spiders. Ants do not hesitate to attack all kinds of animals; in the tropics the wandering ants (*Eciton*) attack lizards, rats and other vertebrates, and it is said that even huge serpents, when in a torpid condition, are sometimes killed by armies of these pugnacious insects.

Mosquitoes affect not only mammals but also, though rarely, fishes and turtles. The gadflies (Tabanidæ) torment horses and cattle by their punctures; and the black-flies, or buffalo gnats (*Simulium*), persecute horses, mules, cattle, fowls, and frequently become unendurable even to man. The notorious tsetse fly (*Glossina morsitans*) of South Africa spreads a deadly disease among horses, cattle and dogs, by inoculating them with a protozoan blood-parasite, to the effects of which, fortunately, man is not susceptible.

Parasitic Insects.—Insects belonging to several diverse orders have become peculiarly modified to exist as parasites either upon or within the bodies of birds or mammals.

Almost all birds are infested by Mallophaga, or bird lice, of which Kellogg has catalogued 264 species from 257 species of North American birds. Sometimes a species of Mallophaga is restricted to a single

species of bird, though in the majority of cases this is not so. Several mallophagan species often infest a single bird; thus nine species occur on the hen, and no less than twelve species, representing five genera, on the American coot. These parasites spread by contact from male to female, from old to young, and from one bird to another when the birds are gregarious. When a single species of bird louse occurs on two or more hosts, these are almost always closely allied, and Kellogg has suggested the interesting possibility that such a species has persisted unchanged from a host which was the common ancestor of the two or more present hosts. Mallophaga are not altogether limited to birds, however, for they may be found on cattle, horses, cats, dogs, and some other mammals; Kellogg records eighteen species from fifteen species of mammals. These biting lice feed, not upon blood, but upon epidermal cells and portions of feathers or hairs. They have flat tough bodies (Fig. 18), with no traces of wings, and a large head with only simple eyes; the eggs are glued to feathers or hairs.

Mammals only are infested by the sucking lice, or Pediculidæ. These (Fig. 24) have a large oval or rounded abdomen, no wings, a small head, minute simple eyes or none, and claws that are adapted to clutch hairs; the eggs are glued to hairs. Sucking lice affect horses, cattle, sheep, dogs, monkeys, seals, elephants, etc., and man is parasitized by three species, namely, the head louse (*Pediculus humanus capitis*), the body louse (*Pediculus humanus corporis*), and the crab louse (*Phthirus pubis*).

An anomalous beetle, *Platypsyllus castoris*, occurs throughout North America and also in Europe as a parasite of the beaver.

The fleas, allied to Diptera but constituting a distinct order (Siphonaptera), are familiar parasites of chickens, cats, dogs and human beings. These insects (Fig. 32) are well adapted by their laterally compressed bodies for slipping about among hairs, and their saltatory powers and general elusiveness are well known. Their wings are reduced to mere rudiments, their eyes when present are minute and simple and their mouth parts are suctorial.

Among Diptera, there are a few external parasites, the best known of which is the sheep tick (*Melophagus ovinus*), though several highly interesting but little-studied forms are parasitic upon birds and bats.

The larvæ of the bot-flies (Estridæ) are common internal parasites of mammals. The sheep bot-fly (*Estrus ovis*) deposits her eggs or larvæ on the nostrils of sheep; the maggots develop in the frontal sinuses of the host, causing vertigo or even death, and when full grown escape

through the nostrils and pupate in the soil. The horse bot-fly (*Gastrophilus equi*) glues its eggs to the hairs of horses, especially on the fore legs and shoulders, whence the larvæ are licked off and swallowed; once in the stomach, the bots fasten themselves to its lining, by means of special hooks, and withstand almost all efforts to dislodge them; though when the bots have attained their growth they release their hold and pass with the excrement to the soil. Bots of the genus *Hypoderma* form tumors on cattle and other mammals, domesticated or wild. The ox-warble (*H. lineata*, Fig. 213, I) reaches the œsophagus of its host in the same manner as the horse bot, according to Curtice, but then makes its way into the subcutaneous tissue and causes the well-known tumors on the back of the animal; when full grown the bots squirm out of these tumors and drop to the ground, leaving permanent holes in the hide.

Parasitism in General.—Parasitic insects evidently do not constitute a phylogenetic unit, but the parasitic habit has arisen independently in many different orders. These insects do, however, agree superficially, in certain respects, as the result of what may be termed convergence of adaptation. Thus a dipterous larva, living as an internal parasite, in the presence of an abundant supply of food, has no legs, no eyes or antennæ, and the head is reduced to a mere rudiment, sufficient simply to support a pair of feeble jaws; the skin, moreover, is no longer armor-like but is thin and delicate, the body is compact and fleshy, and the digestive system is of a simplified type. The same modifications are found in hymenopterous larvæ, under similar food-conditions, except that the head undergoes less reduction. The various external parasites lack wings, almost invariably, and the eyes, instead of being compound, are either simple or else absent. In some special cases, as in a few dipterous parasites of birds and bats, the wings are present, either permanently or only temporarily, enabling the insects to reach their hosts.

This so-called parasitic degeneration, widespread among animals in general and consisting chiefly in the reduction or loss of locomotor and sensory functions in correlation with an immediate and plentiful supply of food, results in a simplicity of organization which is to be regarded—not as a primitive condition—but as an expression of what is, in one sense, a high degree of specialization to peculiar conditions of life. This exquisite degree of adaptation to a special environment, however, sacrifices the general adaptability of the animal,—makes it impossible for a parasite to adapt itself to new conditions; and while parasitism may be an immediate advantage to a species, there are few parasites

that have attained any degree of dominance among animals. Ichneumonidæ, to be sure, are remarkably dominant among insects, but their parasitic adaptations are limited for the most part to the larval stage, and the adults may be said to be as free for new adaptations as are any other Hymenoptera.

Scavenger and Carrion Insects.—Not a few families of Diptera and Coleoptera derive their food from dead animal matter. The aquatic families Dytiscidæ and Gyrinidæ are largely scavengers. Among terrestrial forms, Silphidæ feed on dead animals of all kinds; the burying beetles (*Necrophorus*), working in pairs, undermine and bury the bodies of birds, frogs and other small animals, and lay their eggs in the carcasses; Histeridæ and Staphylinidæ are carrion beetles, and Dermestidæ attack dried animal matter of almost every description, their depredations upon furs, feathers, museum specimens, etc., being familiar to all. Ants are famous as scavengers, destroying decaying organic matter in immense quantities, particularly in the tropics. Many Scarabæidæ feed upon excrementitious matter, for example the "tumble-bugs," which are frequently seen in pairs, laboriously rolling along or burying a large ball of dung, which is to serve as food for the larva.

Insects as Food for Vertebrates.—Lizards, frogs, and toads are insectivorous, especially toads. The American toad feeds chiefly upon insects, which form 77 per cent. of its food for the season, the remainder consisting of myriopods, spiders, crustacea, molluscs and worms, according to the observations of A. H. Kirkland, who states that Lepidoptera form 28 per cent. of the total insect food, Coleoptera 27, Hymenoptera 19 and Orthoptera 3 per cent. The toad does not capture dead or motionless insects but uses its extensile sticky tongue to lick in moving insects or other prey, which it captures with surprising speed and precision. In the cities one often sees many toads under an arc-light engaged in catching insects that fall anywhere near them. Though its diet is varied and somewhat indiscriminate, the toad consumes such a large proportion of noxious insects, such as May beetles and cutworms, that it is unquestionably of service to man.

Moles are entirely insectivorous and destroy large numbers of white grubs and caterpillars; field mice and prairie squirrels eat many insects, especially grasshoppers, and the skunk revels in these insects, though it eats beetles frequently, as does also the raccoon, which is to some extent insectivorous. Monkeys are omnivorous but devour many kinds of insects.

With these hasty references, we may pass at once to the subject of the insect food of fishes and birds.

Insects in Relation to Fishes.—Insects constitute the most important portion of the food of adult fresh water fishes, furnishing forty per cent. of their food, according to Dr. Forbes, from whose valuable writings the following extracts are taken.

“The principal insectivorous fishes are the smaller species, whose size and food structures, when adult, unfit them for the capture of Entomostraca, and yet do not bring them within reach of fishes or Mollusca. Some of these fishes have peculiar habits which render them especially dependent upon insect life, the little minnow *Phenacobius*, for example, which, according to my studies, makes nearly all its food from insects (ninety-eight per cent.) found under stones in running water. Next are the pirate perch, *Aphredoderus* (ninety-one per cent.), then the darters (eighty-seven per cent.), the croppies (seventy-three per cent.), half-grown sheepshead (seventy-one per cent.), the shovel fish (fifty-nine per cent.), the chub minnow (fifty-six per cent.), the black warrior sunfish (*Chænobryttus*) and the brook silversides (each fifty-four per cent.), and the rock bass and the cyprinoid genus *Notropis* (each fifty-two per cent.).

“Those which take few insects or none are mostly the mud-feeders and the ichthyophagous species, *Amia* (the dog-fish) being the only exception noted to this general statement. Thus we find insects wholly or nearly absent from the adult dietary of the burbot, the pike, the gar, the black bass, the wall-eyed pike, and the great river catfish, and from that of the hickory shad and the mud-eating minnows (the shiner, the fathead, etc.). It is to be noted, however, that the larger fishes all go through an insectivorous stage, whether their food when adult be almost wholly other fishes, as with the gar and the pike, or molluscs, as with the sheepshead. The mud-feeders, however, seem not to pass through this stage, but to adopt the limophagous habit as soon as they cease to depend upon Entomostraca.

“Terrestrial insects, dropping into the water accidentally or swept in by rains, are evidently diligently sought and largely depended upon by several species, such as the pirate perch, the brook minnow, the top minnows or killifishes (cyprinodonts) the toothed herring and several cyprinoids (*Semotilus*, *Pimephales* and *Notropis*).

“Among aquatic insects, minute slender dipterous larvæ, belonging mostly to *Chironomus*, *Corethra* and allied genera are of remarkable importance, making, in fact, nearly one tenth of the food of all the fishes

studied. They are most abundant in *Phenacobius* and *Etheostoma*, which genera have become especially adapted to the search for these insect forms in shallow rocky streams. Next I found them most generally in the pirate perch, the brook silversides, and the stickleback, in which they averaged forty-five per cent. They amounted to about one third the food of fishes as large and important as the red horse and the river carp, and made nearly one fourth that of fifty-one buffalo fishes. They appear further in considerable quantity in the food of a number of the minnow family (*Notropis*, *Pimephales*, etc.), which habitually frequent the swift waters of stony streams, but were curiously deficient in the small collection of miller's thumbs (*Cottidæ*) which hunt for food in similar situations. The sunfishes eat but few of this important group, the average of the family being only six per cent.

"Larvæ of aquatic beetles, notwithstanding the abundance of some of the forms, occurred in only insignificant ratios, but were taken by fifty-six specimens, belonging to nineteen of the species,—more frequently by the sunfishes than by any other group. The kinds most commonly captured were larvæ of Gyrinidæ and Hydrophilidæ; whereas the adult surface beetles themselves (*Gyrinus*, *Dineutes*, etc.)—whose zigzag-darting swarms no one can have failed to notice—were not once encountered in my studies.

"The almost equally well-known slender water-skipper [*Gerris*] seem also completely protected by their habits and activity from capture by fishes, only a single specimen occurring in the food of all my specimens. Indeed, the true water bugs (Hemiptera) were generally rare, with the exception of the small soft-bodied genus *Corixa* which was taken by one hundred and ten specimens, belonging to twenty-seven species,—most abundantly by the sunfishes and top minnows.

"From the order Neuroptera [in the broad sense] fishes draw a larger part of their food than from any other single group. In fact, nearly a fifth of the entire amount of food consumed by all the adult fishes examined by me consisted of aquatic larvæ of this order, the greater part of them larvæ of day flies (Epheméridæ), principally of the genus *Hexagenia*. These neuropterous larvæ were eaten especially by the miller's thumb, the sheepshead, the white and striped bass, the common perch, thirteen species of the darters, both the black bass, seven of the sunfishes, the rock bass and the croppies, the pirate perch, the brook silversides, the sticklebacks, the mud minnow, the top minnows, the gizzard shad, the toothed herring, twelve species each of the true minnow family and of the suckers and buffalo, five catfishes, the dog-

fish, and the shovel fish,—seventy species out of the eighty-seven which I have studied.

“Among the above, I found them the most important food of the white bass, the toothed herring, the shovel fish (fifty-one per cent.), and the croppies; while they made a fourth or more of the alimentary contents of the sheepshead (forty-six per cent.), the darters, the pirate perch, the common sunfishes (*Lepomis* and *Chænobryttus*), the rock bass, the little pickerel, and the common sucker (thirty-six per cent.).

“Ephemerid larvæ were eaten by two hundred and thirteen specimens of forty-eight species—not counting young. The larva of *Hexagenia*, one of the commonest of the ‘river flies,’ was by far the most important insect of this group, this alone amounting to about half of all the Neuroptera eaten. It made nearly one half of the food of the shovel fish, more than one tenth that of the sunfishes, and the principal food resource of half-grown sheepshead; but was rarely taken by the sucker family, and made only five per cent. of the food of the catfish group.

“The various larvæ of the dragon flies, on the other hand, were much less frequently encountered. They seemed to be most abundant in the food of the grass pickerel (twenty-five per cent.) and next to that, in the croppie, the pirate perch, and the common perch (ten to thirteen per cent.).

“Case-worms (Phryganeidæ) were somewhat rarely found, rising to fifteen per cent. in the rock bass and twelve per cent. in the minnows of the *Hybopsis* group, but otherwise averaging from one to six per cent. in less than half of the species.”

Insects in Relation to Birds.—From an economic point of view the relations between birds and insects are extremely important, and from a purely scientific standpoint they are no less important, involving as they do biological interactions of remarkable complexity.

The prevalent popular opinion that birds in general are of inestimable value as destroyers of noxious insects is a correct one, as Dr. Forbes proved, from his precise and extensive studies upon the food of Illinois birds, involving a laborious and difficult examination of the stomach contents of many hundred specimens. All that follows is taken from Forbes, when no other author's name is mentioned, and though the percentages given by him apply to particular years and would undoubtedly vary more or less from year to year, they are here for convenience regarded as representative of any year and are spoken of in

the present tense. About two thirds of the food of birds consists of insects.

Robin.—The food of the robin in Illinois, from February to May inclusive, consists almost entirely of insects; at first, larvæ of *Bibio albipennis* for the most part, and then caterpillars and various beetles. When the small fruits appear, these are largely eaten instead of insects; thus in June, cherries and raspberries form fifty-five per cent. and insects (ants, caterpillars, wireworms and Carabidæ) forty-two per cent. of the food; and in July, raspberries, blackberries and currants form seventy-nine per cent. and insects (mostly caterpillars, beetles and crickets) but twenty per cent. of the food. In August, insects rise to forty-three per cent. and fruits drop to fifty-six per cent., and these are mostly cherries, of which two thirds are wild kinds. In September, ants form fifteen per cent. of the food, caterpillars five per cent. and fruits (mostly grapes, mountain-ash berries and moonseed berries) seventy per cent. In October, the food consists chiefly of wild grapes (fifty-three per cent.), ants (thirty-five per cent.), and caterpillars (six per cent.).

For the year, judging from the stomach contents of one hundred and fourteen birds, garden fruits form only twenty-nine per cent. of the food of the robin, while insects constitute two thirds of the food. The results are confirmed by those of Professor Beal in Michigan, who found that more than forty-two per cent. of the food of the robin consists of insects with some other animal matter, the remainder being made up of various small fruits, but notably the wild kinds.

Upon the whole, the robin deserves to be protected as an energetic destroyer of cutworms, white grubs and other injurious insects, and the comparatively few cultivated berries that the bird appropriates are ordinarily but a meagre compensation for the valuable services rendered to man by this familiar bird.

Catbird.—Not so much can be said for the catbird, however, for, though its food habits are similar to those of the robin, it arrives later and departs earlier, with the result that it is less dependent than the robin upon insects and that berries form a larger percentage of its total food.

In May, eighty-three per cent. of the food of the catbird consists of insects, mostly beetles (*Carabidæ*, *Rhynchophora*, etc.), crane-flies, ants and caterpillars (*Noctuidæ*); while dry sumach berries are eaten to the extent of seven per cent. For the first half of June, the record is much the same, with an increase, however, in the number of May

beetles eaten; in the second half of the month the food consists chiefly of small fruits, especially raspberries, cherries and currants; so that for the month as a whole, only forty-nine per cent. of the food is made up of insects. This falls to eighteen per cent. in July, when three quarters of the food consists of small fruits, mostly blackberries, however. In August, with the diminution of the smaller cultivated fruits, the percentage of insects rises to forty-six per cent., nearly one half of which is made up of ants and the rest of caterpillars, grasshoppers, Hemiptera, Coleoptera, etc. In September, with the appearance of wild cherries, elderberries, Virginia creeper berries and grapes, these are eaten to the extent of seventy-six per cent., the insect element of the food falling to twenty-one per cent., of which almost half consists of ants, and the remainder of beetles and a few caterpillars.

For the entire year, as appears from the study of seventy specimens by Forbes, insects form forty-three per cent. of the food of the catbird and fruits fifty-two per cent. As the injurious insects killed are offset by the beneficial ones destroyed, "the injury done in the fruit-garden by these birds remains without compensation unless we shall find it in the food of the young," says Professor Forbes. And this has been found, to the credit of the catbird; for Weed learned that the food of three nestlings consisted of insects, sixty-two per cent. of which were cutworms and four per cent. grasshoppers; while Judd found that fourteen nestlings had eaten but four per cent. of fruit, the diet being chiefly ants, beetles, caterpillars, spiders and grasshoppers. In fact, Weed believes that, on the whole, the benefit received from the catbird is much greater than the harm done, and that its destruction should never be permitted except when necessary in order to save precious crops.

Bluebird.—The excellent reputation which the bluebird bears everywhere as an enemy of noxious insects is well deserved. From a study of one hundred and eight Illinois specimens, Forbes finds that seventy-eight per cent. of the food for the year consists of insects, eight per cent. of Arachnida, one per cent. of Julidæ and only thirteen per cent. of vegetable matter, edible fruits forming merely one per cent. of the entire food. The insects eaten are mostly caterpillars (chiefly cutworms), Orthoptera (grasshoppers and crickets) and Coleoptera (Carabidæ and Scarabæidæ). Though some of the insects are more or less beneficial to man, such as Carabidæ and Ichneumonidæ (respectively predaceous and parasitic), the beneficial elements form only twenty-two per cent. of the food for the year, as against forty-nine per cent. of injurious elements, the remaining twenty-nine per cent. consisting of neutral elements. The food

of the nestlings, according to Judd, is essentially like that of the adults, being "beetles, caterpillars, grasshoppers, spiders and a few snails."

Other Insectivorous Birds.—Weed and Dearborn, from whose excellent work the following notes are taken, find that the common chickadee devours immense numbers of capker worms, and that more than half its food during winter consists of insects, largely in the form of eggs, including those of the common tent caterpillar (*C. americana*), the fall webworm (*H. cunea*) and particularly plant lice, whose eggs, small as they are, form more than one fifth of the entire food; more than four hundred and fifty of them are sometimes eaten by a single bird in one day, and the total number destroyed annually is inconceivably large. The house wren is almost exclusively insectivorous, feeding upon caterpillars and other larvæ, ants, grasshoppers, gnats, beetles, bugs, spiders, and myriopods. The swallows, also, are highly insectivorous; "most of their food is captured on the wing, and consists of small moths, two-winged flies, especially crane flies, beetles in great variety, flying bugs, and occasionally small dragon flies. The young are fed with insects." Ninety per cent. of the food of the kingbird "consists of insects, including such noxious species as May beetles, click-beetles, wheat and fruit weevils, grasshoppers, and leafhoppers." The honey bees eaten by this bird are insignificant in number. Woodpeckers destroy immense numbers of wood-boring larvæ, bark-insects, ants, caterpillars, etc. The cuckoos "are unique in having a taste for insects that other birds reject. Most birds are ready to devour a smooth caterpillar that comes their way, but they leave the hairy varieties severely alone. The cuckoos, however, make a specialty of devouring such unpalatable creatures; even stink bugs and the poisonous spiny larvæ of the Io moth are freely taken." Caterpillars form fifty per cent. of the food for the year; Orthoptera (grasshoppers, katydids, and tree crickets), thirty per cent.; Coleoptera and Hemiptera, six per cent. each; and flies and ants are taken in small quantities. "The nestling birds are fed chiefly with smooth caterpillars and grasshoppers, their stomachs probably being unable to endure the hairy caterpillars. All in all, the cuckoos are of the highest economic value. They do no harm and accomplish great good. If the orchardist could colonize his orchards with them, he would escape much loss." The quail feeds largely upon insects during the summer, frequently eating the Colorado potato beetle and the army worm; the prairie hen has similar food habits but lives almost exclusively on grasshoppers, when these are abundant.

The Insect Food of Birds.—"There are few groups of injurious insects that enter so largely into the composition of the food of birds as do the locusts, or short-horned grasshoppers, of the family Acridiidae [now Locustidae]. The enormous destructive power of these insects is well known, but our indebtedness to birds in checking their oscillations is less generally recognized." Professor Aughey, who has made extensive studies upon the relation of birds to the Rocky Mountain locust, found that upon one occasion 6 robins had eaten 265 of these insects, 5 catbirds 152, 3 blue-birds 67, 7 barn swallows 139, 7 night hawks 348, 16 yellow-billed cuckoos 416, 8 flickers 252, 8 screech owls 219, and 1 humming bird 4; while crows and blue-jays had eaten large numbers of the locusts; and grouse, quail and prairie hen, enormous numbers. Even shore birds, such as geese, ducks, gulls and pelicans came to share in the feast. Aughey estimated that the locusts eaten in one day by the passerine birds of the eastern half of Nebraska were sufficient to destroy in a single day 174,397 tons of crops, valued at \$1,743.97.

Weed and Dearborn state that, of Hemiptera, Jassidae are very often found in the stomachs of birds, and that aphids and their eggs form a large part of the food of many of the smaller birds, such as the warblers, nuthatches, kinglets and chickadees. A large proportion of the caterpillars of the Lepidoptera are eagerly devoured by birds, forming an important element of the food of many species. The hairy caterpillars are eaten by cuckoos and blue-jays and the large saturniid caterpillars, such as *cecropia* and *polyphemus*, by some of the hawks. Almost all kinds of Coleoptera are food for birds, but especially the grubs of Scarabæidae, which are eagerly devoured by robins, blackbirds, crows and other birds. Of the Diptera, Itonididae and other gnats are eaten by swallows, swifts and night hawks; while crane flies, Tipulidae, are often found in the stomachs of birds. Among Hymenoptera, ants are eaten extensively by woodpeckers, catbirds and many other species, as are also Ichneumonidae and other parasitic forms—these last by the flycatchers in particular.

The Regulative Action of Birds upon Insect Oscillations.—The worst injuries by insects are done by species that fluctuate excessively in number as the result of variations in those manifold forces that act as checks upon the multiplication of the species.

In order to determine whether birds do anything to reduce existing oscillations of injurious insects, Professor Forbes made studies upon the food of birds which were shot in an Illinois apple orchard which was being ravaged by canker-worms. In this orchard, birds were present in

extraordinary number and variety, there being at least thirty-five species, most of which were studied by Forbes, from whose exhaustive tables the following food-percentages are taken:

	BIRDS EXAMINED	INSECTS, PER CENT.	CANKER-WORMS, PER CENT.
Robin.....	9	93	21
Catbird.....	14	98	15
Brown Thrush.....	4	94	12
Bluebird.....	5	98	12
Black-capped Chickadee.....	2	100	61
House Wren.....	5	91	46
Tennessee Warbler.....	1	100	80
Summer Yellow Bird.....	5	94	67
Black-throated Green Warbler.....	1	100	70
Maryland Yellow-throat.....	2	100	37
Baltimore Oriole.....	3	100	40

To quote Forbes: "Three facts stand out very clearly as results of these investigations: 1. Birds of the most varied character and habits, migrant and resident, of all sizes, from the tiny wren to the blue-jay, birds of the forest, garden and meadow, those of arboreal and those of terrestrial habits, were certainly either attracted or detained here by the bountiful supply of insect food, and were feeding freely upon the species most abundant. That thirty-five per cent. of the food of all the birds congregated in this orchard should have consisted of a single species of insect, is a fact so extraordinary that its meaning can not be mistaken. Whatever power the birds of this vicinity possessed as checks upon destructive irruptions of insect life was being largely exerted here to restore the broken balance of organic nature. And while looking for their influence over one insect outbreak we stumbled upon at least two others, less marked, perhaps incipient, but evident enough to express themselves clearly in the changed food ratios of the birds.

"2. The comparisons made show plainly that the reflex effect of this concentration on two or three unusually numerous insects was so widely distributed over the ordinary elements of their food that no especial chance was given for the rise of new fluctuations among the species commonly eaten. That is to say, the abnormal pressure put upon the cankerworm and vine-chafer was compensated by a general diminution of the ratios of all the other elements, and not by a neglect of one or two alone. If the latter had been the case, the criticism might easily have been made that the birds, in helping to reduce one oscillation, were setting others on foot.

"3. The fact that, with the exception of the indigo bird, the species

whose records in the orchard were compared with those made elsewhere had eaten in the former situation as many caterpillars other than canker-worms as usual, simply adding their canker-worm ratios to those of other caterpillars, goes to show that these insects are favorites with a majority of birds."

The Relations of Birds to Predaceous and Parasitic Insects.—The false assumption is often made that a bird is necessarily inimical to man's interest whenever it destroys a parasitic or a predaceous insect. Weed and Dearborn attack this assumption as follows:

"Suppose an ichneumon parasite is found in the stomach of a robin or other bird: it may belong to any one of the following categories:

"1. The primary parasite of an injurious insect.

"2. The secondary parasite of an injurious insect.

"3. The primary parasite of an insect feeding on a noxious plant.

"4. The secondary parasite of an insect feeding on a noxious plant.

"5. The primary parasite of an insect feeding on a wild plant of no economic value.

"6. The secondary parasite of an insect feeding on a wild plant of no economic value.

"7. The primary parasite of a predaceous insect.

"8. The primary parasite of a spider or a spider's egg.

"This list might easily be extended still farther, and the assumption that the parasite belongs to the first of these categories is unwarranted by the facts and does violence to the probabilities of the case.

"A correct idea of the economic rôle of the feathered tribes may be obtained only by a broader view of nature's methods,—a view in which we must ever keep before the mind's eye the fact that all the parts of the organic world, from monad to man, are linked together in a thousand ways, the net result being that unstable equilibrium commonly called 'the balance of nature.'"

The general subject of food relations and interactions of insects is taken up in the chapter on ecology (page 373).

Efficiency of Protective Adaptations of Insects.—Interesting from a scientific point of view are the various adaptations by means of which insects are protected more or less from their bird enemies. Colorational adaptations having been discussed in another chapter, there remain for consideration—(1) hairs, (2) stings, (3) odors, flavors and irritants. Most of what follows is from an admirable paper by Dr. Judd, whose data are based upon his examination of the stomach contents of fifteen thousand birds.

Hairs.—"Excepting two species of cuckoos, no species of bird in the eastern United States, so far as I am aware, makes a business of feeding upon hairy caterpillars." Judd observed that the fall webworm, *Hyphantria cunea*, infesting a pear tree was not at all molested, in spite of the fact that the tree was tenanted by three broods of birds at the time, namely, kingbirds, orchard orioles and English sparrows. The hairy arctiid caterpillars, however, are eaten by a few birds: the robin, bluebird, catbird, sparrowhawk, cuckoos and shrikes; and the spiny larvæ of *Vanessa antiopa* by cuckoos and the Baltimore oriole; while the hairy caterpillars of the gipsy moth are known to be eaten in Massachusetts by no fewer than thirty-one species of birds, notably cuckoos, Baltimore oriole, catbird, chickadee, blue-jay, chipping sparrow, robin, vireos and the crow, these birds being of no little assistance in the suppression of this pest. These are exceptional cases, however, and in general the hairiness of caterpillars appears to be a highly effective protection against most birds.

Stings.—Some birds (chewink, young ducks) are fatally affected by eating honey bees. The blue-jays, however, will eat *Bombus* (bumblebees) and *Xylocopa*, and flycatchers and swallows feed habitually upon stinging Hymenoptera, particularly Scoliidae, while a great many birds eat Myrmicidae, or stinging ants. The formic acid of ants does not protect them from wholesale destruction by birds; Judd found three thousand ants in the stomach of a flicker. "Stingless ants pretend to sting but many birds they do not deceive." The stinging caterpillar of *Automeris io* is occasionally eaten by the yellow-billed cuckoo. Aside from these exceptions, the stings of insects are an extremely efficient means of defence.

Odors, Flavors and Irritants.—The malodorous Heteroptera in general are food for most birds; *Lygus*, Reduviidae (assassin bugs) and Pentatomidae (stink bugs) are eaten by song sparrows, and *Euschistus* by blackbirds and crows. The odors of Heteroptera are by no means universally protective.

Among Coleoptera, the showy, ill-scented or ill-flavored Coccinellidae (lady beetles) are eaten by very few birds—the flycatchers and swallows—and are refused by caged blue-jays and song sparrows even when these birds are hungry. Of Chrysomelidae, the Colorado potato beetle is refused by the catbird, blue-jay and song sparrow, and *Diabrotica* is not often eaten, except by catbirds and thrushes. "The smaller Carabidae (ground beetles) whether stinking or not, are eaten by practically all land birds." Crows, blackbirds and jays eagerly swallow

the showy *Calosoma scrutator*, and the first two birds are especially fond of *Harpalus caliginosus* and *H. pennsylvanicus*, and feed *Galerita* to their young. "A score of smaller Carabidæ (ground beetles) and Chrysomelidæ (leaf beetles) metallic and conspicuously colored, are habitually eaten by birds that have an abundance of other insect food to pick from."

The stench of Lampyridæ (firefly family) appear to be more effective than those of Carabidæ. *Telephorus* is occasionally eaten, but *Photinus* rarely if at all. *Chauliognathus* is not eaten by many birds (though flycatchers and swallows select this insect) and the genus is regarded unfavorably by caged catbirds and blue-jays.

In regard to other insects, Judd finds that *Epicauta* (blister beetle) with its irritant fluid, is immune from all but the kingbird; *Cyllene* seldom occurs in the stomachs of birds; May flies and caddis flies, however, are terribly persecuted, but swiftly flying Diptera and Odonata are highly immune.

From such facts as these, Judd properly infers, "not cases of protection and non-protection, but cases of greater and lesser efficiency of protective devices."

CHAPTER IX

TRANSMISSION OF DISEASES BY INSECTS

It is commonly known that some kinds of insects are of vital importance to man as agents in the transmission of certain diseases. In recent years immense progress has been made in our knowledge of insect-borne diseases.

MALARIA

So far as is known, malaria is transmissible only through the agency of mosquitoes.

The malaria "germ," discovered in 1880 by the French army surgeon Laveran, may be found as a pale, amœboid organism (*Laverania*, Fig. 273) in the red blood corpuscles of persons afflicted with the disease. This organism (*schizont*, 2) grows at the expense of the hæmoglobin of the corpuscle (3-5) and its growth is accompanied by an increasing deposit of black granules (*melanin*), which are doubtless excretory in their nature. At length, the amœbula divides into many spores (*merozoites*, 6) which by the disintegration of the corpuscle are set free in the plasma of the blood. Here many if not most of the spores, and the pigment granules as well, are attacked and absorbed by leucocytes, or white blood corpuscles, while some of the spores may invade healthy red corpuscles and develop as before. The period of sporulation, as Golgi found, is coincident with that of the "chill" experienced by the patient; and quinine is most effective when administered just before the sporulation period. The destruction of red blood corpuscles explains the pallid, or *anæmic*, condition which is characteristic of malarial patients. In three or four days the number of red corpuscles may be reduced from 5,000,000 per cubic millimeter—the normal number—to 3,000,000; and in three or four weeks of intermittent fever, even to 1,000,000.

Authorities recognize at least three species of malaria parasites affecting man: (1) the *tertian* (*Plasmodium vivax*), with an asexual cycle of forty-eight hours, causing the fever to recur every two days; (2) the *quartan* (*P. malariae*), with a cycle of seventy-two hours, causing fever every third day; and (3) the *subtertian* or malignant form (*Laverania falciparum*) of which there are three varieties (perhaps species), with cycles of twenty-four or forty-eight hours, according to the variety.

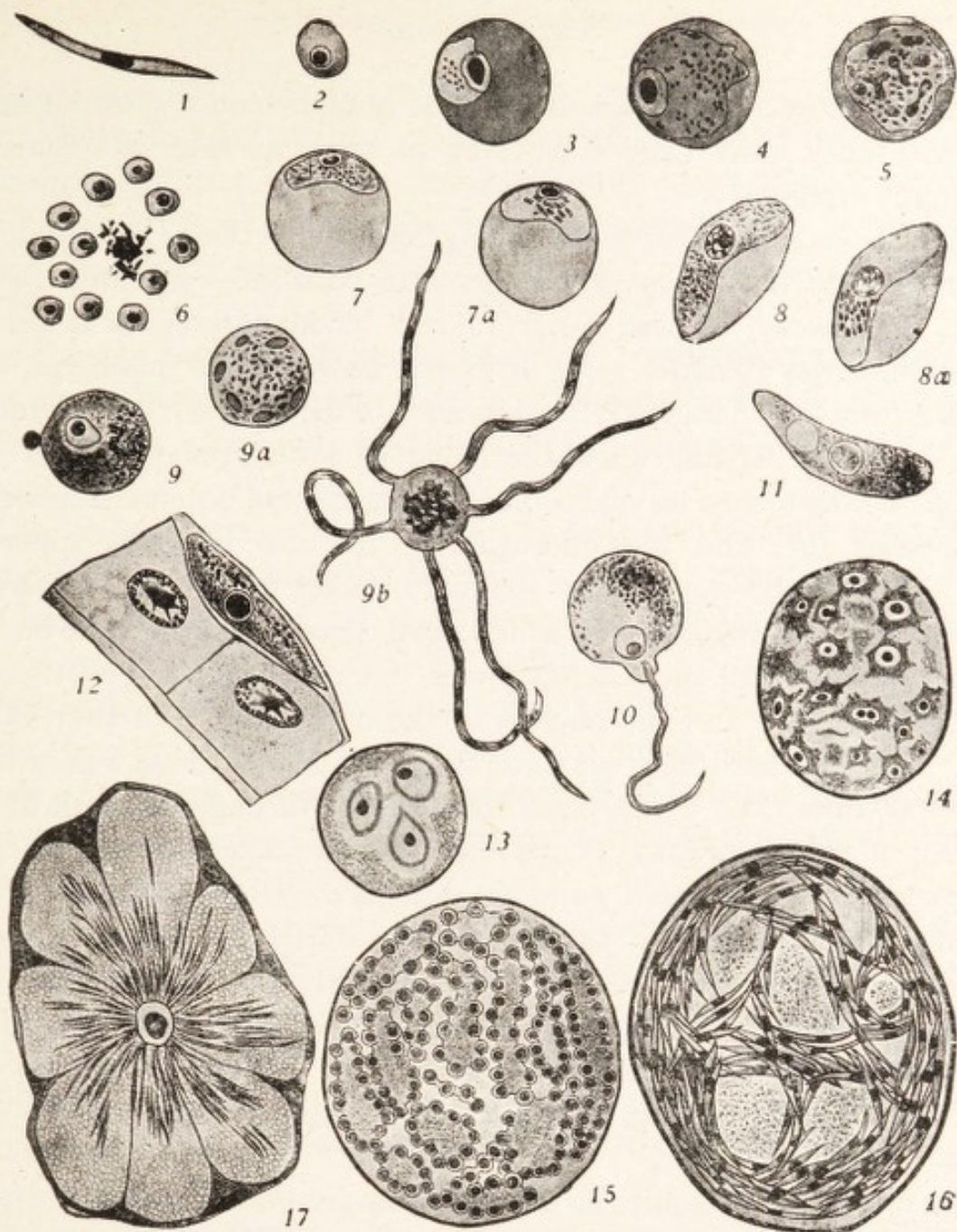


FIG. 273.—Life history of malaria parasite, *Laverania falciparum*. 1, sporozoite, introduced by mosquito into human blood; the sporozoite becomes a schizont. 2, young schizont, which enters a red blood corpuscle. 3, young schizont in a red blood corpuscle. 4, full-grown schizont, containing numerous granules of melanin. 5, nuclear division preparatory to sporulation. 6, spores, or merozoites, derived from a single mother-cell. 7, young macrogametocyte (female), derived from a merozoite and situated in a red blood corpuscle. 7a, young microgametocyte (male) derived from a merozoite. 8, full-grown macrogametocyte. 8a, full-grown microgametocyte. In stages 8 and 8a the parasite is taken into the stomach of a mosquito; or else remains in the human blood. 9, mature macrogamete, capable of fertilization; the round black extruded object may probably be termed a "polar body." 9a, mature microgametocyte, preparatory to forming microgametes. 9b, resting cell, bearing six flagellate microgametes (male). 10, fertilization of a macrogamete by a motile microgamete. The macrogamete next becomes an ookinete. 11, ookinete, or wandering cell, which penetrates into the wall of the stomach of the mosquito. 12, ookinete in the outer region of the wall of the stomach, *i.e.*, next to the body cavity. 13, young oocyst, derived from the ookinete. 14, oocyst, containing sporoblasts, which are to develop into sporozoites. 15, older oocyst. 16, mature oocyst, containing sporozoites, which are liberated into the body cavity of the mosquito and carried along in the blood of the insect. 17, transverse section of salivary gland of an *Anopheles* mosquito, showing sporozoites of the malaria parasite in the gland cells surrounding the central canal.

1-6 illustrate *schizogony* (asexual production of spores); 7-16, *sporogony* (sexual production of spores).

After GRASSI and LEUCKART, by permission of Dr. Carl Chun.

Two or more sets of parasites in the human blood, sporulating at different times, may cause the fever to recur at intervals that are apparently irregular.

After several successive asexual generations, there are produced merozoites which develop—no longer into schizonts—but into sexual forms, or *gametes*. These occur in red blood corpuscles either as *macrogametocytes* (female, 7, 8) or as *microgametocytes* (male, 7a, 8a), in which forms the parasite is introduced into the stomach of a mosquito which has been feeding upon the blood of a malarial patient. The macrogametocyte now leaves its blood corpuscle and becomes a spherical *macrogamete* (9); and the microgametocyte also becomes spherical (9a); but the latter puts forth a definite number (*six*, in *L. falciparum*, 9b) of flagella, or *microgametes*, which separate off as motile male bodies, capable of fertilizing the macrogametes. A microgamete penetrates a macrogamete (10) and the nucleus of the one unites with that of the other. The fertilized macrogamete, or *zygote*, now becomes a migrating cell, or *oökinete* (11), which penetrates almost through the wall of the stomach of the mosquito (12) and then becomes a resting cell, or cyst. This *oöcyst* (13) grows rapidly and its contents develop, by direct nuclear division, into *sporoblasts* (14, 15), which differentiate into spindle-shaped *sporozoites* (16, 17). The sporozoites are liberated into the body cavity of the mosquito, carried in the blood to the salivary glands (as well as elsewhere) and thence along the hypopharynx into the body of a human being, bird or other animal attacked by the insect.

The rôle of the mosquito as the intermediary host of malarial organisms was discovered by Manson and Ross and confirmed by Koch, Sternberg and others. It has been found repeatedly that certain mosquitoes (*Anopheles*) after feeding on the blood of a malarial patient can transmit the disease by means of their "bites" to healthy persons. Thus, *Anopheles* mosquitoes were fed on the blood of malarial subjects in Rome and then sent to London, where a son of Dr. Manson allowed himself to be bitten by the insects. Though previously free from the malarial organism, he contracted a well-marked infection as the result of the inoculation.

Furthermore, it is highly probable that malaria cannot be transmitted to man except through the agency of the mosquito. This appears from the oft-cited experiment of Doctors Sambon and Low on the Roman Campagna, a place notorious for malaria. There the experimenters lived during the malarial season of 1900, freely exposed to the

emanations from the marsh and taking no precautions except to screen their house carefully against mosquitoes and to retire indoors before the insects appeared in the evening. Simply by excluding *Anopheles* mosquitoes, with which the Campagna swarmed, these investigators remained perfectly immune from the malaria which was ravaging the vicinity.

In a later experiment on the island of Formosa, one company of Japanese soldiers was protected from mosquitoes and suffered no malaria, while a second and unprotected company contracted the disease.

The evident preventive measures to be taken against malaria are (1) the avoidance of mosquito bites, by means of screens, and washes of eucalyptus oil, camphor, oil of pennyroyal, oil of tar, etc., applied to exposed parts of the body; (2) the isolation of malarial patients from mosquitoes, in order to prevent infection; (3) the destruction of mosquitoes in their breeding places, especially by the use of kerosene and by drainage. During unavoidable exposure in malarious regions, quinine should be taken in doses of six to ten grains during the day at intervals of four or five days (Sternberg).

In Macedonia in 1916 there were some 800,000 cases of malaria, with 2,000 deaths in the French and Allied army. Where the disease was most severe *Anopheles* mosquitoes were present in enormous numbers. A striking peculiarity of this epidemic was the marked failure of quinine as a preventive or remedy. This failure was explained as being due to the development of quinine-resistant strains of the malaria parasites.

Culex and Anopheles.—More than five hundred species of mosquitoes have been described. Of these only the genus *Anopheles* transmits malaria to man; though in India, Ross found that *Culex* transmits a form of malaria to sparrows. These two common genera are easily distinguishable. In *Culex* the wings are clear; in *Anopheles* they are spotted with brown. In *Culex* when resting, the axis of the body forms a curved line, the insect presenting a hump-backed appearance; in *Anopheles* the axis forms a straight line. *Culex* has short maxillary palpi, while in *Anopheles* they are almost as long as the proboscis. The note of the female *Anopheles* is several tones lower than that of *Culex*, and only the female is bloodthirsty, by the way. As regards eggs, larvæ and pupæ, the two genera differ greatly. The eggs of *Culex* are laid in a mass and those of *Anopheles* singly; the larvæ of *Culex* hang from the surface film of a pool at an angle of about forty-five degrees,

while those of *Anopheles* are almost parallel with the surface of the water in which they live.

The bite of an *Anopheles* is not necessarily injurious, of course, unless the insect has had recent access to a malarious person. *Anopheles* may be present where there is no malaria. On the other hand, it has been found impossible to prove that malaria exists where there are no *Anopheles* mosquitoes. Finally, fevers are sometimes diagnosed as malarial which are not so.

Possibly the malarial parasite can complete its cycle of development in other animals than man. It is also possible that originally the malarial organism was derived by mosquitoes from the stems or other parts of aquatic plants, and that its effects on man are incidental phenomena.

YELLOW FEVER

From 1793 to 1900 there occurred in the United States not less than half a million cases of yellow fever and one hundred thousand deaths from the disease. New Orleans suffered the worst with more than forty-one thousand deaths, followed by Philadelphia with ten thousand and Memphis with almost eight thousand; while Charleston, New York City and Norfolk, Virginia, lost together more than ten thousand lives.

The enormous financial loss from all the epidemics of yellow fever is beyond exact computation; the epidemic of 1878 cost New Orleans more than ten million dollars.

Yellow fever is now within human control; with no thanks to those who at first violently opposed the theory, and later denied the fact, of its transmission by mosquitoes.

Until 1901 yellow fever was fought energetically, but fought in the dark. An immense amount of energy was misdirected and millions of dollars wasted in the fight. On the supposition that bacteria were the cause of the disease, methods of quarantine, burning and fumigation were employed that destroyed an enormous amount of property including valuable cargoes, and paralyzed the business and social activities of great cities.

Official accounts of yellow fever published before 1900 often describe the disease as being due to some insidious poison borne by the air and introduced into the human body, probably through the respiratory system. It was observed that the disease was often conveyed down the wind, that it was not carried far from the nearest focus of infection, that infection was less liable to occur in daylight than by night, and

that cases arose on shore when the only source of infection was a ship that had not yet touched the land. These facts and many others which formerly involved the disease in mystery, are now quite intelligible in the light of the mosquito-theory of transmission.

Finlay's Work.—The pioneer work leading toward the control of yellow fever was done by Dr. Charles J. Finlay, of Havana, Cuba, who not only advocated the mosquito-theory strongly for many years, but also inoculated by means of mosquitoes ninety human subjects, some of whom came down with what he believed to be a mild form of yellow fever. His valuable work prepared the way for the brilliant investigations of Major Reed and his associates.

United States Yellow Fever Commission.—Major Walter Reed was president of the board of medical officers sent to Cuba in June, 1900, to study the acute infectious diseases of the island; his associates were James Carroll, Jesse W. Lazear and A. Agramonte.

At that time Sanarelli's theory as to the bacillary causation of yellow fever was in favor, though Reed and Carroll has already shown that the bacillus of Sanarelli bore no special relation to the disease. After further investigations on this subject in Cuba, with negative results, the commission "concluded to test the theory of Finlay," in Dr. Reed's words. For this purpose General Leonard Wood, the military governor of Cuba, gave permission for experiments on human beings and granted a liberal sum of money for the reward of volunteer subjects.

The commission succeeded in demonstrating how yellow fever is transmitted; after that the methods of prevention to be employed were evident.

The experiments, planned and directed by Major Reed, are models of their kind. All possible sources of error were excluded; hence there was no uncertainty in the interpretation of the results, the accuracy of which has been confirmed by subsequent commissions and by many independent investigators.

In the value of his services Major Walter Reed ranks among the greatest benefactors of mankind. Before his death, which occurred in 1902, he received great honors for his brilliant achievements.

Experiments in Cuba.—For experimental purposes Major Reed established a camp about four miles from Havana. To prevent the introduction of the fever from the outside the inmates of the camp were rigidly quarantined; non-immunes were confined to the camp or, if released, not allowed to return. In order that the study of yellow fever might not be complicated by the presence of any other disease, a com-

plete record was kept of the health of every subject; furthermore, ample time was allowed for any possible development of the disease within the camp before the experiments were begun. In short, the precautions taken were so thorough that yellow fever never appeared in the camp except at the will of the experimenters.

Harmlessness of Fomites.—In a specially constructed building, which was screened against mosquitoes and purposely ill-ventilated, volunteers slept for twenty nights with bedding and clothing that had been contaminated by yellow fever patients, and tried in every other way to contract the disease, if possible, from the fomites, or belongings, of fever subjects; yet the health of these volunteers remained unimpaired; though they were not immunes, for some of them were subsequently infected artificially by means of mosquitoes.

Transmission by Transfusion.—It was found that the disease could be conveyed to non-immunes by the subcutaneous injection of blood taken from the veins of patients during the first three days of the disease.

Experiments with Mosquitoes.—These experiments were made at a time of the year when there was the least chance of acquiring the disease naturally. The mosquitoes used were bred from the eggs and kept active by being maintained at a summer temperature. From time to time some of them were taken away to a yellow fever hospital, fed on the blood of patients and applied to non-immunes in the camp at varying intervals from the time of feeding. The occupants of the camp were, of course, protected carefully from accidental mosquito bites. When a subject came down with yellow fever as the result of an experimental inoculation he was at once removed from the camp to a yellow fever hospital.

In a mosquito-proof building a single room was divided into two compartments simply by means of a partition of wire netting. On one side of the screen infected mosquitoes were liberated; and a brave non-immune, who had been in quarantine for thirty-two days, entered the compartment, allowed himself to be bitten several times, and contracted the disease. In the opposite compartment, free from mosquitoes, non-immunes slept with perfect safety; and the other room became harmless as soon as the mosquitoes were removed.

In another experiment the subject acquired the disease by thrusting his arm into a jar of infected mosquitoes. Eighteen non-immunes were inoculated, ten of them successfully. It was demonstrated that yellow fever is transmitted by the bite of a mosquito, and in no other way except by the artificial injection of diseased blood. The mosquito can

obtain infected blood from a patient during only the first three days of his disease; in other words, the patient is no longer a menace to other persons after three days from the time when he comes down with yellow fever, which is from three to six days after the bite.

After biting a patient the mosquito cannot convey the infection until at least twelve days have elapsed; thereafter it can transmit the disease for certainly six weeks and possibly eight weeks.

Dr. James Carroll allowed himself to be bitten by an infected mosquito and consequently suffered a severe attack of yellow fever. He recovered from this, but was left with an affection of the heart from which he died in 1907.

Dr. Lazear failed to acquire the disease artificially, early in the course of the experiments; but a little later, while visiting yellow fever patients in a hospital, was bitten by a mosquito which he deliberately allowed to remain on his hand. Five days later he came down with yellow fever, which caused his death. His life was a sacrifice for the benefit of the human race.

Yellow Fever Mosquito.—The mosquito that transmits this fever is *Aedes argenteus* (*Aedes calopus*, *Stegomyia fasciata*) and no other species is as yet known to be concerned in the disease. *A. argenteus* is limited to warm regions; at a temperature less than 68° F. the eggs do not hatch, and below 62° F. the female does not bite (Reed). The dependence of the insect upon warmth for its development explains the cessation of the disease in New Orleans in December, with a mean temperature of 55.3° F. and in cities farther north when frost comes. In Cuba and Brazil the fever has occurred every month in the year.

Cause of Yellow Fever.—The specific cause of yellow fever eluded detection for many years and was regarded by many investigators as being ultra-microscopic. The U. S. Commission produced the disease by the injection of blood serum that had been passed through a bacteria-proof filter. Blood from a subject in whom the disease had been produced by transfusion was capable of infecting a third person.

The weight of evidence indicated that the unknown cause of yellow fever was an organism rather than a toxin, and in 1919 the organism was discovered by Noguchi to be a spirochæte, which he named *Leptospira icteroides*. During his investigations in Guayaquil Noguchi succeeded in isolating this spirochæte from the blood of patients and from mosquitoes as well. He obtained pure cultures of the parasite by inoculating guinea pigs with blood from patients, and was able to produce the disease by inoculation in guinea pigs, dogs and marmosets.

Following his discovery, Dr. Noguchi, of the Rockefeller Institute for Medical Research, prepared from the organisms a vaccine, which has been administered to many thousand persons with results that are reported to be distinctly encouraging.

Control of Yellow Fever.—The preventive measures based upon the facts learned by the U. S. Army Commission were wonderfully successful. In February, 1901, Major W. C. Gorgas began a campaign to eradicate the disease in Havana. His efforts were directed against mosquitoes. Every case of fever had to be reported promptly to the authorities. Then the patient was isolated and all the rooms in the building and in neighboring houses fumigated and the doors and windows screened. Standing water in which mosquitoes might develop was drained or treated with petroleum, and water tanks and barrels were screened.

In September, 1901, the last case of yellow fever arose in Havana, where the disease had prevailed for 150 years, with an annual mortality of 500 to 1600 or more. Cases are now and then brought into Havana from Mexico or Central America but are treated under screens in the regular hospitals with impunity.

Yellow Fever in New Orleans.—In 1905 the last epidemic of yellow fever occurred in New Orleans. It might have been checked at its inception had not the authorities adopted a policy of secrecy in regard to the presence of the disease. The city was freed from the fever before frost came, by the same methods that had proved successful in Cuba; but not without organized work of the most strenuous kind on the part of the citizens, under the direction of the U. S. Public Health and Marine-Hospital Service. At present the yellow fever mosquito is said to be a rarity in Louisiana owing to the vigorous measures enforced in its suppression throughout the state.

Fever in the Canal Zone.—The Panama Canal zone was formerly one of the most unhealthful places on earth, chiefly on account of the prevalence of malaria and yellow fever. When the United States acquired the zone in 1904 it was realized that the first step toward building the great canal was to protect the health of all those immediately concerned in the undertaking, and the sanitation of the isthmus was placed in charge of one eminently qualified for the work, Colonel W. C. Gorgas.

He adapted the methods he had used in Cuba to the conditions existing on the isthmus, with the result that every year the death rate decreased until in 1908 it became, among eight thousand white Americans living there, 9.72 per thousand, "a rate no higher than for a

similar population in the healthiest localities in the United States, and much lower than that for most parts of the country." The Sanitary Department has succeeded in driving yellow fever from the isthmus and in checking malaria and other diseases to such a degree that the canal zone is no longer an unhealthful place.

After serving as Surgeon General of the United States Army from 1914 to 1918, W. C. Gorgas entered the service of the International Health Board, and was organizing an international campaign against yellow fever at the time of his death in London, July 4, 1920.

General Gorgas attained international preëminence for his ability in organizing and conducting operations of magnitude against insect-borne diseases. On account of his services in the protection of human life his assistance was sought by foreign nations, and he received high honors.

TYPHOID FEVER

The specific cause of typhoid fever is *Bacillus typhosus*. In the human body this bacillus occurs chiefly in the intestines; but also in the urinary bladder and usually in the blood of infected persons.

The excreta of typhoid subjects contain the virulent bacilli; and some persons, even after recovery, continue to be "chronic carriers" of the disease for many years.

Transmission.—The typhoid bacillus is introduced into the human system by eating or drinking. Most epidemics are due to infected water and many to milk; occasionally the disease is acquired from raw vegetables or from oysters contaminated with sewage. Often the bacillus is conveyed to food by human hands and possibly it is sometimes carried by dust, cockroaches or ants; but there is no doubt that the disease is transmitted by certain flies, particularly the true house fly, *Musca domestica*, which is by far the commonest fly found generally in houses, and becomes a serious menace to health during epidemics of typhoid fever.

The house fly is well adapted by its structure and habits to carry bacteria. The adults often feed on substances contaminated with typhoid or other bacteria and these infected substances cling readily to the hairs of the insect, especially those of the feet, and to the proboscis. The larvæ develop chiefly in horse manure, but also in other kinds of excreta, some of which may contain virulent typhoid bacilli.

Transmission by Flies.—During the Spanish-American war typhoid fever occurred in every American regiment and raged in many of the concentration camps, in consequence of which a special commission was appointed to investigate the origin and spread of the disease in the army. A report by one of the members of the commission, Doctor Vaughan, presents the following conclusions:

“a. Flies swarmed over infected fecal matter in the pits and then visited and fed upon the food prepared for the soldiers at the mess tents. In some instances where lime had recently been sprinkled over the contents of the pits, flies with their feet whitened with lime were seen walking over the food.

“b. Officers whose mess tents were protected by means of screens suffered proportionally less from typhoid than did those whose tents were not so protected.

“c. Typhoid fever gradually disappeared in the fall of 1898, with the approach of cold weather, and the consequent disabling of the fly.

“It is possible for the fly to carry the typhoid bacillus in two ways. In the first place, fecal matter containing the typhoid germ may adhere to the fly and be mechanically transported. In the second place, it is possible that the typhoid bacillus may be carried in the digestive organs of the fly and may be deposited with its excrement.”

Similar conclusions in regard to the agency of flies in the spread of enteric fever among troops have been reached also by investigators in Bermuda, South Africa and India.

Firth and Horrocks fed house flies on material contaminated with *Bacillus typhosus* and then obtained cultures of the bacillus from objects to which the flies had access. In another experiment they obtained cultures from the heads, bodies, wings and legs of such flies. Other investigators have obtained *Bacillus typhosus* from flies captured in rooms occupied by typhoid cases.

Faichnie caught flies in a place where there was an outbreak of typhoid fever, held them on a sterilized needle and passed them through a flame until legs and wings were scorched; after which he obtained the typhoid bacillus from the mashed bodies of the flies, the bacilli having been present in the alimentary tract, without doubt.

Faichnie also obtained cultures of *Bacillus typhosus* from the intestines of flies which had developed from larvæ fed on feces containing the bacillus.

Jordan states that the bacilli survive the passage of the alimentary canal of the fly.

Ficker recovered typhoid bacilli from flies twenty-three days after they had been infected.

In fact, a great amount of evidence has accumulated proving that flies transmit not only the bacilli of typhoid fever, but many other bacteria, and often in enormous numbers. For example, Esten and Mason in their study of the sources of bacteria in milk, collected and examined flies from stables, pig-pens, houses and other places, and found an average of 1,222,570 bacteria per fly; the majority of these being objectionable kinds of bacteria.

Musca Domestica.—A single female of the common house fly lays in all some six hundred eggs. In midsummer, in Washington, D. C., the eggs hatch in about eight hours; the larval period is from four to five days and the pupal period five days, making the cycle about ten days in length. In cooler parts of the season the cycle requires more time and in warm climates it may be as short as eight days. The number of generations in Washington is probably not more than nine (Howard).

Control.—One of the best baits for flies in houses is formalin, which is poisonous to flies but harmless to man. This is prepared by diluting formaldehyde with five or six times as much water and exposing it in shallow dishes, the addition of a little sugar or milk making the solution more attractive to flies, which drink it and quickly die. Pyrethrum is effective against flies, but only when it is pure and has been kept from exposure to the air. Pyrethrum, the chief basis of all the common insect powders, is applied by being puffed through a bellows or by being burned. The powder may be moistened and shaped into cones which when lighted at the top burn slowly and give off fumes that are suffocating to insects.

Dr. Howard estimates that more than ten million dollars are spent every year in screening houses in the United States. Another enormous sum is spent for fly papers and fly traps. The efficient way to deal with the fly problem, however, is to prevent the insects from breeding. Excrementitious substances should be enclosed in such a way as to prevent the access of flies, or should be treated in a way to kill the larvæ therein; one of the simplest methods of treating stable manure being to spread it out to dry, since the maggots cannot develop without moisture.

For detailed information on everything of importance relating to the house fly, and particularly on the mitigation of the fly-nuisance by concerted action in communities, Dr. Howard's admirable book on the house fly should be consulted.

PLAGUE

In the ancient history of Europe epidemics of plague occupy a large place. For many years this pestilence has thrived in China and India, and following an outbreak in 1894 in Hong Kong, the plague reached the western hemisphere for the first time, appearing in Brazil, Argentina and other South American countries, in Mexico and San Francisco.

The cause of plague is *Bacillus pestis*, an organism abundant in the secretions and excretions of plague-stricken animals.

Three varieties of the disease are distinguished as follows:

(1) the *bubonic*, in which the bacilli cause enlargements of lymphatic glands;

(2) the *septicæmic*, characterized by the presence of large numbers of bacilli in the blood and highly virulent;

(3) the *pneumonic*, in which the respiratory organs are affected, the sputum showing the bacilli in enormous numbers; this form, relatively rare, is the most fatal.

Transmission.—Plague is primarily a disease of rats, an epidemic of plague in these animals having often been observed to precede as well as accompany an epidemic among human beings. The disease affects also mice, cats, dogs, calves, sheep, pigs, ducks, geese and many other animals.

Though rats and other of the lower animals may contract the septicæmic type of the disease from feeding on parts of animals killed by plague or on cultures of *Bacillus pestis*, the disease is commonly transmitted among rats neither by contact nor through the atmosphere, but by means of fleas. Healthy rats in association with diseased rats do not become infected as long as fleas are excluded; but a transfer of fleas from the latter to the former starts the disease. By various experiments the Indian Plague Commission demonstrated the important part played by rat-fleas in the transmission of plague. Zirolia found that the bacilli even multiply in the mid-intestine of the flea, retaining their virulence for a week or more. Bacot found that the European rat-flea (*Ceratophyllus fasciatus*) remained infective, when isolated from a host, for forty-seven days.

The weight of evidence, both observational and experimental, shows that plague is transmitted from rats to man by several species of fleas and also by bedbugs. Verjbitski, whose experiments on this subject were particularly precise and thorough, found that plague can be conveyed by the bites of these insects and that the opening made

by the bite affords entrance to plague bacilli when the bodies of the insects are crushed or when the infected feces are introduced by the rubbing or scratching of the wound.

The species of rat-flea most common in the orient is the cosmopolitan "plague flea," *Xenopsylla cheopis*.

In the United States the most common rat flea is *Ceratophyllus fasciatus*. The common cat and dog flea, *Ctenocephalus canis*, affects rats as does the human flea, *Pulex irritans*; and all these species are known to bite man.

Plague in San Francisco.—Plague, long dreaded in American sea-ports, finally entered San Francisco in 1900, killed 114 persons in the next four years, became dormant and broke forth again, with violence, in 1907. The city, just beginning to recover from the great fire of the year before, was in a frightful sanitary condition and most of the population, engaged in the work of reconstruction, paid little attention to the deaths from plague and at first gave little aid toward the suppression of the disease. As may be imagined, the campaign against the disease undertaken by the U. S. Public Health and Marine-Hospital Service was carried on in the face of great odds. It was, however, conducted most efficiently and successfully under the command of Dr. Rupert Blue (later Surgeon-General), who wisely attacked the disease by attacking the rat population.

The labor involved in starving out the rats, trapping or poisoning them, and making buildings rat-proof by the use of concrete or sheet iron, was immense; but the undertaking was nevertheless carried to a successful conclusion. More than one million rats were killed and the disease was checked.

In California plague affects ground squirrels, which doubtless contract the disease from the rats that use the runways of the squirrels in the fields.

TRYPANOSOMIASES

Some of the diseases known as trypanosomiasis are among the deadliest that affect man and other vertebrates, and pathogenic trypanosomes—the organisms causing these diseases—have received an immense amount of study during recent years.

Trypanosomes.—The organisms under consideration are flagellate protozoans. A typical trypanosome, for example, *T. lewisi* (Fig. 274) of the rat, is essentially an elongated cell, tapering at each end, serpen-

tine in form and with no definite cell-wall. A round or oval *nucleus* is present, also a peculiar chromatin body situated often near the posterior end of the cell and termed the *blepharoplast*. Along one side of the cell is a delicate protoplasmic contractile membrane, the *undulating membrane*, along the edge of which is a *marginal cord*, which arises by growth from the blepharoplast and is continued beyond the anterior end of the cell as a vibratile *flagellum*.

Asexual reproduction is by means of a longitudinal division of the cell body, preceded by division of the flagellum, blepharoplast and nucleus, the nucleus dividing amitotically. In regard to the existence of sexual stages, or gametes, the results of investigators seem to be inconclusive as yet.

In a film of fresh blood under the microscope, any active trypanosomes in the field of view attract attention as centers of commotion among the red blood corpuscles, which are pushed aside by the lashing, twisting and other movements of the trypanosomes.

The nutrition is by means of osmosis. Trypanosomes have not been seen to attack erythrocytes, but according to MacNeal and Novy hæmoglobin is useful if not indispensable to them.

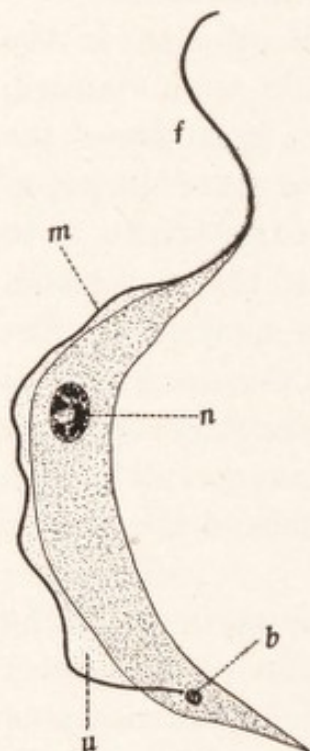


FIG. 274.—*Trypanosoma lewisi*. *b*, blepharoplast; *f*, flagellum; *m*, marginal cord; *n*, nucleus; *u*, undulating membrane. Greatly magnified.

All five classes of vertebrates serve as hosts for trypanosomes, of which more than seventy species have received names. Most of these species are carried from one vertebrate host to another by means as yet unknown, but about 20 per cent. are known or suspected to be transmitted by an intermediate invertebrate host. Thus trypanosomes of frogs are conveyed by leeches; pigeons are infected by mosquitoes, rats by sucking lice and fleas, and many mammals through the agency of blood-sucking flies of the genus *Glossina*, and probably also by *Stomoxys* and certain Tabanidæ.

Tsetse Flies.—The name tsetse fly, originally limited to *Glossina morsitans* (Muscidæ) is now used for any of the fifteen known species of the genus. These flies are a little larger than the common house fly (*Musca domestica*). Their wings, in the resting position, overlap exactly (Fig. 275) instead of being separated at the tips. The proboscis pro-

jects forward, and is stout, owing to the ensheathing palpi; the base of the labium forms a prominent bulb. These are the more conspicuous characters that serve to distinguish tsetse flies from other blood-sucking flies with which they might be confused.

The mode of reproduction as described by Brauer is similar to that of the group of parasitic flies known as Pupipara. The fly produces a full-grown larva, which at once creeps to some resting place and forms a black puparium.

Tsetse flies frequent hot, humid regions, near bodies of water, and are restricted to shaded situations, never occurring on the open plains. Both sexes are bloodthirsty but bite only during the daytime as a rule; though they may bite at night when the moonlight is bright. Travelers take advantage of the habits of the fly to journey by night; spending the day in an open unfested place.

Nagana.—The colonization of South Africa was greatly retarded by *nagana*, a disease invariably fatal to the horse, donkey and dog, and usually fatal to cattle, but not affecting man. Livingstone and other explorers in regions where nagana is prevalent record their having been bitten by tsetse flies thousands of times with no result other than a slight irritation.

Bruce was the first to prove the identity of nagana and tsetse-fly disease and to demonstrate the rôle of the fly in the transmission of the disease. His investigations, begun in Zululand in 1894, are of fundamental importance and have given an immense stimulus to the study of trypanosomes.

After finding that no bacteria were concerned in nagana, Bruce discovered trypanosomes in the blood of cattle affected with the disease. He inoculated their blood into healthy horses and dogs and in a few days the blood of these animals was teeming with trypanosomes. Then he took healthy animals from the mountain on which he had located his headquarters down into the "fly country;" there they contracted the tsetse-fly disease and showed in their blood trypanosomes indistinguishable from those of nagana.

Horses taken into the fly country but not allowed to eat or drink there, took the disease; furthermore, supplies of grass and water brought



FIG. 275.—Tsetse fly, *Glossina morsitans*. $\times 2\frac{1}{2}$.

from the fly country and fed to healthy horses failed to convey the disease.

Then the influence of the fly was tested. Tsetse flies caught in the lowland, carried to the mountain and placed at once on healthy animals gave rise to the disease; but the flies never retained the power of infecting a healthy animal for more than forty-eight hours after feeding upon a sick animal. Thus wild flies, kept without food for three days and then fed on a healthy dog, never gave rise to the disease. The fly alone transmitted the disease; and this by means of trypanosomes adhering to the proboscis either inside or out. Bruce found these organisms in the digestive tract also, but with no change in their form.



FIG. 276.—*Trypanosoma brucei*. Greatly magnified.

He discovered further that buffaloes, antelopes and many other wild animals carried the parasite in their blood, and was able by injecting this blood to transmit the disease to healthy domesticated animals. The parasites were never numerous in the blood of their wild hosts, however, and the latter seemed to be unaffected by their presence. The "big game" of Africa serves, generally speaking, as a reservoir for supplies of trypanosomes.

The species of parasite that Bruce studied is named *Trypanosoma brucei* (Fig. 276). The flies concerned are *Glossina morsitans*, *G. pallidipes* and *G. fusca*, particularly the first two, the distribution of which coincides with that of nagana.

No certain remedies for the disease are yet known. Human serum injected into infected animals causes the trypanosomes to disappear, at least, temporarily; but this fact is of more scientific interest than practical importance. The precaution of traveling by night is often adopted. Creolin and some other substances rubbed on animals serve to repel the flies, and the smoke of encampments drives them away. The protection of horses by means of screens is of course effective.

Human Trypanosomiasis.—Sleeping sickness is most prevalent in the Congo basin, whence it has spread rapidly in equatorial Africa, where it kills about fifty thousand natives every year. The reported cases of recovery are so extremely rare that the mortality is placed at one hundred per cent.

In the first stage of the disease, marked by the appearance of

trypanosomes in the blood, negroes show no symptoms as a rule, though whites are subject to fever. The symptoms may appear as early as four weeks after infection or as late as seven years.

In the second stage trypanosomes appear in the cerebro-spinal fluid and in large numbers in the lymphatic glands, those of the neck, axillæ and groins becoming enlarged. There is tremor of the tongue and hands, drowsiness, emaciation and mental degeneration. The drowsiness passes into periods of lethargy which become gradually stronger until the patient becomes comatose and dies. Some victims do not sleep excessively, but are lethargic, and "profoundly indifferent to all going on around them."

There is some disagreement among authors as to the precise effects of trypanosomes on human tissues and organs, but the evidence indicates at least that trypanosomes produce a toxin which sets up irritations of the lymphatic glands in general and those of the brain in particular. Many of the symptoms of trypanosomiasis are traceable primarily to inflammation of the lymphatics of the nervous system.

The specific cause of sleeping sickness is *T. gambiense*, discovered in 1901 by Forde and named by Dutton. Two eminent English investigators of sleeping sickness, Dutton and Tullock, sacrificed their lives to the disease they were studying.

As the result of the labors of many investigators, human trypanosomiasis is now well understood. Bruce and Nabarro demonstrated by means of inoculation experiments with monkeys that *T. gambiense* is transmitted chiefly, if not solely, by a tsetse fly, *Glossina palpalis*. They and Greig showed that the distribution of the disease in Uganda coincided with that of the fly. In some regions where the fly is present the disease is unknown; which means simply that cases of the disease have not yet been introduced.

Notwithstanding the great activity in the study of this disease no good remedy for it has been found. Wise travelers in tropical Africa take every precaution against being bitten by tsetse flies. Much effort is being exerted to check the spread of the disease among the natives in some of the infected regions; chiefly by removing patients from the fly region, by screening dwellings or by building them away from the damp and marshy areas where the flies breed.

FILARIASIS

The first disease found to be transmitted by an insect was filariasis, the subject of important investigations by Manson, Bancroft and others.

This disease of tropical and subtropical regions is caused by a thread-worm, or nematode, known as *Filaria bancrofti*, which occurs in the blood of man and of several of the lower animals as a slender larva (*microfilaria*) about one-quarter of a millimeter in length. At night these larvæ swarm in the peripheral circulation, from which they are taken into the alimentary canal of a blood-sucking mosquito (chiefly *Culex quinquefasciatus*). In the mid-intestine of the mosquito the larva escapes from its sheath and penetrates into muscular tissue, where it grows and develops for two or three weeks, after which it goes to some other part of the mosquito's body, often to the base of the proboscis, whence the larvæ are carried into the blood of some vertebrate host, there to develop to sexual maturity.

The larvæ are often common in human blood without seeming to injure the host in any way, but the adults (three or four inches long and often found in groups) and ova that have escaped from the parent female sometimes obstruct the lymphatic canals and cause enormous swellings of feet, legs, arms or other parts of the human body; this condition being known as elephantiasis.

TYPHUS

War and typhus have always gone hand in hand. Crowded and uncleanly conditions in camps and prisons are most favorable to the propagation of the disease.

Recent History.—The last scourge of typhus in Serbia began in October, 1914 among Austrian prisoners, who spread the disease over the country. No adequate means of checking the disease existed, and in January, 1915 the epidemic was raging. In April there were 9,000 deaths per day; the total mortality for the first five months of 1915 being more than 100,000. This epidemic was checked largely by the energetic efforts of Dr. R. P. Strong and his fellow-workers.

Syria suffered from typhus in 1916, with more than 1,000 deaths daily. In Roumania, 1916–1919, the mortality was 26,000. Mexico City had 11,000 cases of typhus in December, 1915. In the United States the disease occurs now and then in a small way, but especially among immigrants.

Cause.—The specific cause of typhus can not as yet be named with certainty. It may be a certain spirochæte discovered in 1917 by Futaki, who found it in the liver and urine of typhus victims, as well as in a monkey after inoculation with infected human blood. Others have ascribed the disease to bacilli.

Transmission.—Whatever the organism may be, the fact is now established that typhus is transmitted by human lice. Nicolle, Comte and Conseil, working in northern Africa (1909), conveyed the disease by the injection of human blood to a chimpanzee; then from the chimpanzee to a macaque monkey; and, by means of human body lice, from this animal to other monkeys. Drs. Ricketts and Wilder performed similar experiments in Mexico City (1910) with similar results. They found that monkeys kept free from lice remained healthy, but contracted the disease after inoculation by means of body lice which had fed on the blood of typhus patients. They showed also the strong probability that infection is transmitted through the eggs to the next generation of lice, which through this indirect infection can cause typhus in monkeys and presumably in man also. It has been found that both the body louse (*Pediculus corporis*) and the head louse (*P. capitis*) transmit typhus, but bedbugs and fleas are not implicated.

The brilliant work of Dr. H. T. Ricketts was cut short by his death, in 1910, from typhus contracted during his experiments.

Control.—A typhus patient is harmless as a source of contagion in the absence of human lice, the agents of transmission. Lice, as is well known, crawl readily from man to man in crowded quarters, and inhabit the clothing as well as the body, particularly the underclothing, the seams of which may contain the eggs in immense numbers. Eradication of lousiness means freedom from typhus. During the World War, Great Britain, France and Germany were successful in protecting their armies from the ravages of typhus by the use of methods, often elaborate, directed against the lice, or "cooties." These methods, which are generally known, consisted of (1) the thorough cleansing of the surface of the human body; (2) the disinfection of clothing and other belongings, and of the living quarters, by various physical or chemical processes.

RELAPSING FEVER

Relapsing or recurrent fever is less fatal than typhus, but like the latter is conveyed by lice (though not exclusively) and accompanies war. The disease has often raged in Europe; the last epidemic, early in the recent war, being exceptionally severe in Serbia.

The cause of relapsing fever is the genus *Spirochæta*, of which different species produce various types of the disease in different parts of the world.

Nicolle and his colleagues demonstrated in 1913 that the European and North African form of the disease is transmitted by the body louse, and the head louse as well, though not by their bites. When the lice are crushed and the infected contents of their bodies rubbed into wounds made by the lice, or into abrasions of the skin, or are transferred as by the fingers to a mucous membrane, such as the conjunctiva of the eye, the disease is produced.

It was proved that, in some instances at least, infection could be transmitted through the eggs to the lice of the next generation. The European form of the disease may be conveyed by the bedbug also, according to some investigators. In central Africa a common tick is the agent of transmission, and in Mexico and Central America ticks and bedbugs are suspected.

TRENCH FEVER

One of the most disabling diseases in the Great War was trench fever. The experiments made by British and American investigators in 1918 proved that this disease also is transmitted by the body louse, *Pediculus corporis*. The physical cause of the fever is conveyed in the feces of the lice and inoculation occurs through scratching by the victim, and possibly also by means of punctures made by the lice. The specific cause of trench fever is, however, not actually known as yet.

OTHER DISEASES

Cholera is undoubtedly transmitted by flies. As long ago as 1899 Dr. Nuttall wrote: "The body of evidence as to the rôle of flies in the diffusion of cholera is, I believe, absolutely convincing."

Dysentery is probably carried by flies, as Dr. Orton and others have inferred from their experiments.

Spillman and Haushalter, as well as several others, examined flies that had fed on tubercular sputum and found in the intestinal contents and in the dejections of these flies the bacilli of tuberculosis.

Dr. F. T. Lord summarizes his important investigations on this subject as follows:

"1. Flies may ingest tubercular sputum and excrete tubercle bacilli, the virulence of which may last for at least fifteen days.

"2. The danger of human infection from the tubercular fly-specks is by the ingestion of the specks on food. Spontaneous liberation of

tubercle bacilli from fly-specks is unlikely. If mechanically disturbed, infection of the surrounding air may occur."

If it is true that tuberculosis can be transmitted by means of food, as experiments with some of the lower animals seem to indicate, the house fly is evidently a factor that must be reckoned with in the fight against this disease.

There is conclusive evidence that Egyptian ophthalmia is transmitted by flies and it is highly probable that certain other infections of the eye are conveyed by the same means.

The bacillus of the deadly disease anthrax can be transmitted by tabanid flies and stable flies, *Stomoxys*.

Dr. H. Graham and others have proved that dengue is conveyed by two species of mosquitoes, the common house mosquito of the tropics (*Culex quinquefasciatus*) and the yellow fever mosquito (*Aedes argenteus*).

Phlebotomus fever of Mediterranean regions and India is known to be carried by a sand fly, *Phlebotomus*; and the peculiar Oroya fever of Peru is possibly transmitted by a fly of the same genus.

There is partial proof that the destructive kala-azar in India is disseminated by the common Indian bedbug.

Tropical sore is probably spread by flies of some kind.

In Ceylon, the skin disease known as yaws is conveyed by the common house fly, *Musca domestica*; and in the West Indies, probably by common flies of the genera *Oscinis* and *Sarcophaga*.

In 1912 Professor M. J. Rosenau and Dr. C. T. Brues announced that they had succeeded in transmitting infantile paralysis (polio-myelitis) to monkeys by means of the stable fly, *Stomoxys calcitrans*, and their results were confirmed by Dr. J. F. Anderson. Whether this is the usual means of transmission among human beings it remains to be determined. There is also some experimental evidence that the disease may be carried by the bedbug.

Rocky Mountain spotted fever was proved by Ricketts in 1906 to be conveyed by two or more common species of wood ticks of the genus *Dermacentor*.

Smith and Kilborne demonstrated that the destructive Texas fever of cattle, due to a protozoan parasite, is transmitted by a common tick, *Margaropus annulatus*. The adoption of methods of pasturing that enable cattle to avoid the ticks has been highly successful.

CHAPTER X

INTERRELATIONS OF INSECTS

Insects in general are adapted to utilize all kinds of organic matter as food, and they show all gradations of habit from herbivorous to carnivorous. The many forms that derive their food from the bodies of other insects may conveniently be classed as predaceous or parasitic.

Predaceous Insects.—Among Orthoptera, Mantidæ are notably predatory, their front legs (Fig. 64, C) being well fitted for grasping and killing other insects. The predaceous odonate nymphs have a peculiar hinged extensible labium with which to gather in the prey. The adults

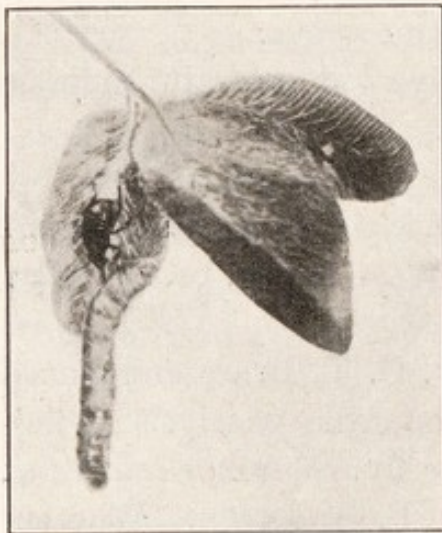


FIG. 277.—Nymph of *Podisus maculiventris* sucking the blood from a clover caterpillar, *Colias philodice*. Natural size.

catch with surpassing speed and precision a great variety of flying insects, mostly small forms, but occasionally butterflies of considerable size. The eyes of a dragon fly are remarkably large; the legs form a spiny basket, probably to catch the prey, which is instantly stripped and devoured, these operations being facilitated by the excessive mobility of the head. The hemipterous families Corixidæ, Notonectidæ (Fig. 227), Nepidæ, Belostomidæ (Fig. 23), Naucoridæ (Fig. 64, D) Reduviidæ and Phymatidæ are predaceous, with raptorial front legs and sharp beaks. Some of the Pentatomidæ (Fig. 277) are of considerable economic value on account

of their predaceous habits. Most of the Neuroptera feed upon other insects. The *Myrmeleon* larva (ant-lion) digs a funnel-shaped pitfall, at the bottom of which it buries itself to await the fall of some unlucky ant. The *Chrysopa* larva (aphis-lion) impales an aphid on the points of its mandibles and sucks the blood through a groove along each mandible (Fig. 46, E), the maxilla fitting against this groove to form a closed channel. Several families of Coleoptera are almost entirely predaceous. Among aquatic beetles, Dytiscidæ are carnivorous both as larvæ and imagines, Gyrinidæ subsist chiefly

upon disabled insects, but occasionally eat plant substances, and Hydrophilidæ as larvæ catch and devour other insects, though some of the beetles of this family (*H. triangularis*, for example, Fig. 229) feed largely if not entirely upon vegetation. Of terrestrial Coleoptera, the tiger beetles (Cicindelidæ) are strictly predaceous upon other insects. The *Cicindela* larva lives in a burrow in the soil and lies in wait for passing insects; a pair of hooks on the fifth segment of the abdomen serves to prevent the larva from being jerked out of its burrow by the struggles of its captive. The large family Carabidæ is chiefly predaceous; these "running beetles," both as larvæ and adults easily overtake and capture other terrestrial insects. The Carabidæ, are by no means exclusively carnivorous, however, for many of them feed to some extent upon fungus spores, pollen, ovules, root-tips and other vegetable matter, as Forbes has found; *Harpalus caliginosus* eats the pollen of the ragweed in autumn; *Galerita janus* eats caterpillars and occasionally the seeds of grasses; but *Calosoma* appears to be strictly carnivorous, feeding chiefly upon caterpillars and being in this respect of considerable economic importance. As a whole, Carabidæ prefer animal food, as appears from the fact that when canker worms, for instance, are unusually abundant these form a correspondingly large percentage of carabid food, the increase being compensated by a diminution in the amount of vegetable food taken. (Forbes.) Coccinellid larvæ (excepting *Epilachna*, which eats leaves) feed almost entirely upon plant lice and constitute one of the most effective checks upon their multiplication; the beetles eat aphides, but also fungus spores and pollen in large quantities. Though Lepidoptera are pre-eminently phytophagous, the larva of *Fenisea tarquinius* is unique in feeding solely upon plant lice, particularly the woolly *Schizoneura tessellata* of the alder. Among Diptera, Asilidæ, Midaidæ, Therevidæ and Empididæ are the chief predaceous families. Asilidæ (robber-flies) ferociously attack not only other flies, but also beetles, bumblebees, butterflies, and dragon flies; as larvæ they feed largely upon the larvæ of beetles. Many of the larvæ of Syrphidæ prey upon plant lice, and the larvæ of *Volucella* feed in Europe on the larvæ of bumblebees and wasps. Of Hymenoptera, the ants are to a great extent predaceous, attacking all sorts of insects, but particularly soft-bodied kinds; while Vespidæ feed largely upon other insects, though like the ants they are fond of the nectar of flowers and the juices of fruits.

Parasitic Insects.—Though very many insects occur as external parasites on the bodies of birds and mammals, very few occur as such on

the bodies of other insects; one of the few is *Braula cæca*, a wingless dipteran found on the body of the honey-bee.

A vast number of insects, however, undergo their larval development as internal parasites of other insects, and most of these parasites belong to the two most specialized orders, Diptera and Hymenoptera.

The larvæ of Bombyliidæ feed upon the eggs of Orthoptera and upon larvæ of Lepidoptera and Hymenoptera. Tachinidæ are the most important dipterous parasites of other insects and lay their eggs most frequently upon caterpillars; the larvæ bore into their victim, develop

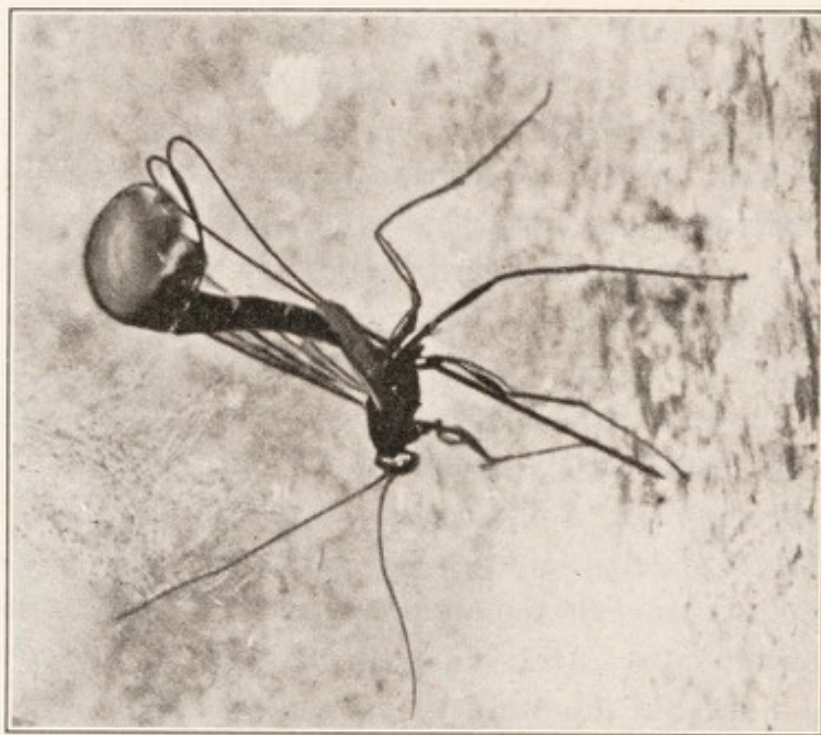


FIG. 278.—*Megarhyssa atrata*, drilling in tree trunk. Natural size.—From CHARLES MACNAMARA.

within its body, and at length emerge as winged insects. These parasites often render an important service to man in checking the increase of noxious Lepidoptera.

The great majority of insect parasites—many thousand species—belong to the order Hymenoptera, constituting one of the primary divisions of the order. They are immensely important from an economic standpoint, particularly the Ichneumonidæ, of which more than ten thousand species are already known. Our most conspicuous ichneumonids are the two species of *Megarhyssa*, *M. atrata* (Fig. 278), and *M. lunator* with their long ovipositors (three inches long in *lunator*, and four to four and three-quarters inches in *atrata*). *Megarhyssa* bores into the trunks of trees in order to reach the burrows of

another large hymenopteron, *Tremex columba* (Fig. 30), upon whose larvæ the larva of *Megarhyssa* feeds.

The enormous family Braconidæ, closely related to Ichneumonidæ, is illustrated by the common *Apanteles congregatus*, which lays its eggs in the caterpillars of various Sphingidæ. The parasitic larvæ feed upon the blood and possibly also the fat-body of their host, and at length emerge and spin their cocoons upon the exterior of the caterpillar (Fig. 279), sometimes to the number of several hundred. Species of *Aphidius* transform within the bodies of plant lice, one to each host, and the imago cuts its way out through a circular opening with a correspondingly

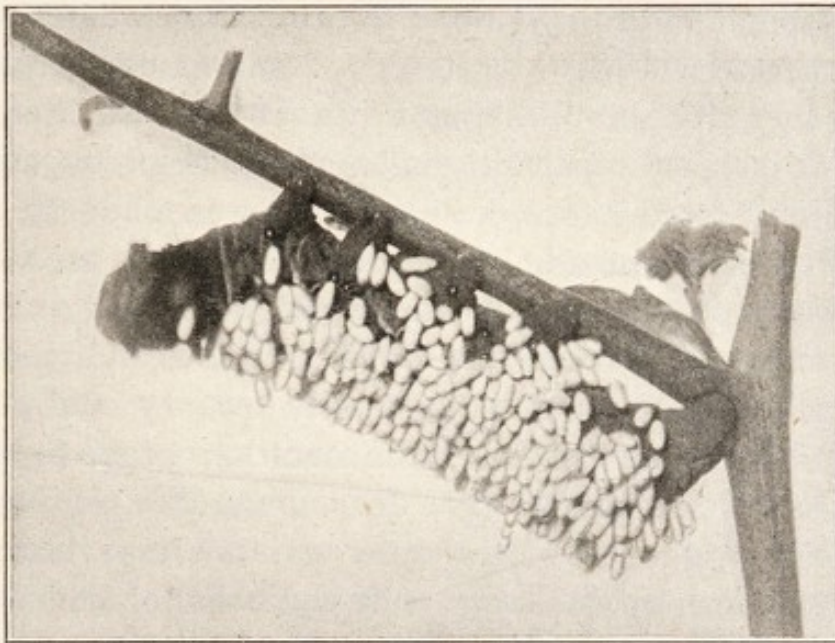


FIG. 279.—A tomato worm, *Protoparce sexta*, bearing cocoons of the parasitic *Apanteles congregatus*. Natural size.

circular lid. Chalcididæ, of which some four thousand species are known, are usually minute and parasitic; though some are phytophagous, for example, species of *Harmolita* (*Isosoma*) which live in wild or cultivated grasses, and the clover seed-midge *Bruchophagus funebris*. Chalcids affect a great variety of insects of one stage or another, such as caterpillars, pupæ, cockroach eggs, plant lice and scale insects; while some of them develop in cynipid galls, either upon the larvæ of the gall-makers or upon the larvæ of inquilines. Giard in France reared more than three thousand chalcids (*Copidosoma truncatellum*) from a single caterpillar of *Plusia*. Proctotrypidæ are remarkable as parasites. Most of them are minute; indeed, this family and the coleopterous family Trichopterygidæ contain the smallest winged insects known—species but one-third or one-fourth of a millimeter long. A large proportion

of the Proctotrypidæ are parasitic in the eggs of other insects or of spiders, several sometimes developing in the same egg; others affect odonate nymphs and coleopterous or dipterous larvæ, while several species have been reared from itonidid and cynipid galls, and many proctotrypids are parasites of other parasitic insects—in other words, are *hyperparasites*.

Hyperparasitism.—Not only are *primary* parasites frequently attacked by other, or *secondary*, parasites, but *tertiary* parasitism is known to occur in a few instances, and there is some reason to believe that even the *quaternary* type exists among insects, as in the following case.

The caterpillar of *Hemerocampa leucostigma* defoliates shade trees in the northeastern United States. An enormous increase of this species in the city of Washington in 1895 was attended by a corresponding increase of parasitic and predaceous species, and this unusual opportunity for the study of parasitism was made the most of by Dr. Howard, from whose admirable paper these facts are taken.

The primary parasites of *H. leucostigma* numbered 23 species—17 Hymenoptera and 6 Diptera; of the hyperparasites (all hymenopterous) 13 were secondary, 2 and probably 5 were tertiary, and one of these (*Asecodes albitarsis*) may under certain conditions prove to be a quaternary parasite. To illustrate—The ichneumon *Pimpla inquisitor*, an important primary parasite of lepidopterous larvæ, lays its eggs in caterpillars of *H. leucostigma*; its larvæ suck the blood of their host and at length spin their cocoons within the loose cocoon of the *Hemerocampa*. These cocoons have yielded a well-known secondary parasite, the chalcid *Dibrachys boucheanus*. Now another chalcid, *Asecodes albitarsis*, has been seen to issue from a pupa of this *Dibrachys*, thus establishing tertiary parasitism. Furthermore, it is quite possible that *Dibrachys* itself is a tertiary parasite, in which event the *Asecodes* might become a parasite of the quaternary order.

Economic Importance of Parasitism.—If a primary parasite is beneficial, its own parasites are indirectly injurious, generally speaking; while those of the third and the fourth order are respectively beneficial and injurious. The last two kinds are so rare, however, as to be of no practical importance from an economic standpoint. The first two kinds are of immense economic importance, particularly the primary parasites. "Outbreaks of injurious insects," says Howard, "are frequently stopped as though by magic by the work of insect enemies of the species. Hubbard found, in 1880, that a minute parasite, *Trichogramma pretiosa*, alone

and unaided, almost annihilated the fifth brood of the cotton worm in Florida, fully ninety per cent. of the eggs of this prolific crop enemy being infested by the parasite. In 1895, in the city of Washington, more than ninety-seven per cent. of the caterpillars of one of our most important shade-tree pests [*Hemerocampa*, as just mentioned] were destroyed by parasitic insects, to the complete relief of the city the following year. The Hessian fly, that destructive enemy to wheat crops in the United States, is practically unconsidered by the wheat growers of certain states, for the reason that whenever its numbers begin to be injuriously great its parasites increase to such a degree as to prevent appreciable damage.

"The control of a plant-feeding insect by its insect enemies is an extremely complicated matter, since, as we have already hinted, the parasites of the parasites play an important part. The undue multiplication of a vegetable feeder is followed by the undue multiplication of parasites, and their increase is followed by the increase of hyperparasites. Following the very instance of the multiplication of the shade tree caterpillar just mentioned, the writer [Howard] was able to determine this parasitic chain during the next season down to quaternary parasitism. Beyond this point, true internal parasitism probably did not exist, but even these quaternary parasites were subject to bacterial or fungus disease and to the attacks of predatory insects.

"The prime cause of the abundance or scarcity of a leaf-feeding species is, therefore, obscure, since it is hindered by an abundance of primary parasites, favored by an abundance of secondary parasites (since these will destroy the primary parasites), hindered again by an abundance of tertiary parasites, and favored again by an abundance of quaternary parasites."

Entomologists have made many attempts to import and propagate insect enemies of various introduced insect pests, and some of their efforts have been crowned with success, as was notably the case when *Novius cardinalis*, a lady-bird beetle, was taken from Australia to California to destroy the fluted scale.

Form of Parasitic Larvæ.—The peculiar environment of parasitic larvæ is responsible for profound changes in their organization. These larvæ, in general, are apodous, the body is compact and the head is more or less reduced, sometimes to the merest rudiment. These characters, occurring also in such dipterous larvæ as live in a mass of decaying organic matter, and again in those hymenopterous larvæ whose food is provided by the mother or by nurses, are to be attributed to the presence

of a plentiful supply of food, obtainable with little or no exertion, and indicate, not primitive simplicity of organization, but a high degree of specialization, as we have said before. The embryonic development of parasitic larvæ is frequently highly anomalous, as appears in the chapter on development.

Maternal Provision.—Excepting several families of Hymenoptera and the Termitidæ, few insects make any special provision for the welfare of the young beyond laying the eggs in some appropriate situation. Many insects, as walking-sticks (Phasmidæ) and some butterflies (*Argynnis*) simply drop their eggs to the ground, leaving the young to shift for themselves. Most insects, however, instinctively lay their eggs in situations where the larva is sure to find its proper food near at hand. Thus various flies and beetles deposit their eggs on decaying animal matter, butterflies and moths are more or less restricted to particular species of plants, and parasitic Hymenoptera to certain species of insects. The beetles of the genus *Necrophorus* go so far as to bury the body of a bird, mouse or other animal in which the eggs are to be laid; and in this instance the male assists the female in undermining and afterward covering the body. A similar co-operation of the two sexes occurs in the scarabæid beetles known as "tumblebugs," a pair of which may often be seen rolling along laboriously a ball of dung which is to serve as larval food. The female mole-cricket (*Gryllotalpa*) is said to care for her eggs and even to feed the young at first.

Hymenoptera display all degrees of complexity in regard to maternal provision. Tenthredinidæ simply lay their eggs on the proper food plants or else insert them into the tissues of the plants. Sphecina make a nest, provision it with food and leave the young to care for themselves. Queen wasps and bumblebees go a step further in feeding the first larvæ and carrying them to maturity. Finally, in the honey bee the care of the young is at once relegated by the queen to other individuals of the colony, as is also the case among ants.

Some of the most elaborate examples of purely maternal provision are found among the digger wasps and the solitary wasps; these instances are highly interesting, involving as they do an intricate co-ordination of many reflex actions—as appears in the discussion of insect behavior.

Among the Sphecina, or digger wasps, the female makes a nest by burrowing into the ground, by mining into such pithy plants as elder or sumach, or else by plastering bits of mud together. The nest is provisioned with insects or spiders which have been stung in such a way as

usually to be paralyzed, without being actually killed. The various species of Sphecina frequently select particular species of insects or spiders as food for the young. *Pepsis formosa* (Pompilidæ) uses tarantulas for this purpose; *Sphecius speciosus* (Bembecidæ) stores her nest with a cicada; Nyssonidæ pick out certain species of Membracidæ; mud-daubers (Sphecidæ) use spiders; and other families of Sphecina capture bees, beetles, plant lice or other insects, as the case may be. The solitary wasps (Eumenidæ) are similar to the digger wasps in habits.

Of the solitary bees, *Megachile* is well known for its habit of cutting pieces out of rose leaves; it uses oblong pieces to form a thimble-shaped tube which, after being stored with pollen and nectar, is plugged with a circular piece of leaf. The larval cells are made either in tunnels excavated in wood by the mother or else in cracks or other chance cavities.

One of the carpenter bees, *Ceratina dupla*, which builds in the hollow stem of a plant a series of larval cells separated by partitions, is said by Comstock to watch over her nest until the young mature.

The transition from the solitary to the social habit is indicated in the life-histories of wasps and bumblebees, where a solitary queen founds the colony but soon relegates to other individuals all duties except that of egg-laying. The social insects will now be considered.

TERMITES

Though popularly known as "white ants," the termites are quite different from true ants, being indeed not very far removed from the most primitive insects. In view of the extreme contrast in structure and development between termites and ants, it is remarkable that the two groups should have much the same kind of complex social organization.

Classes of Termites.—In general, four principal kinds of adults are produced in a community of termites, namely—*workers*, *soldiers*, *fertile males* and *fertile females*.

The workers (Fig. 280, *A*) which are ordinarily the most numerous, are of either sex, but their reproductive organs are undeveloped. A worker ant or bee, is, however, always a female. The termite workers, as the name implies, do most of the work; they make the nest, provide food, feed and care for the young and the royal pair, and attend to many other domestic duties.

The soldiers, like the workers, are of either sex, with undeveloped sexual organs. With monstrous mandibles and head (Fig. 280, *B*),

their chief duty apparently is to defend the colony, though they frequently fail to do so.

The winged males and females (Fig. 280, C) which are sexually ma-

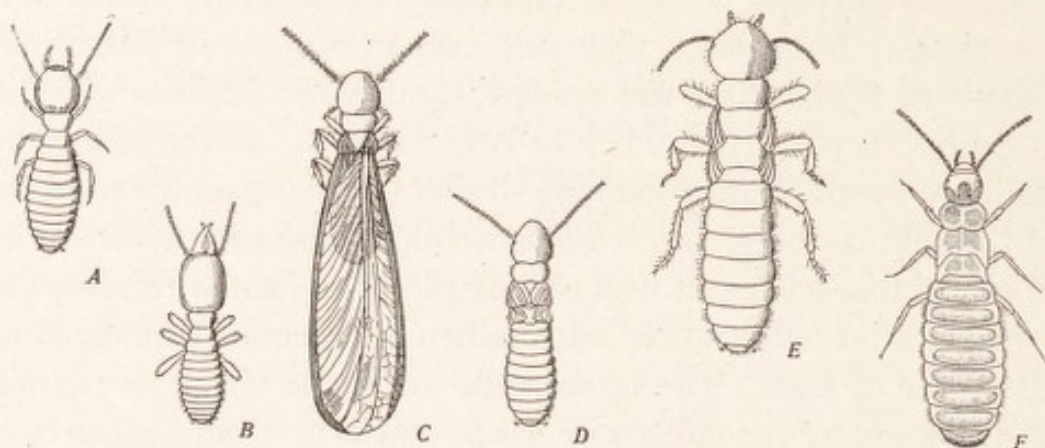


FIG. 280.—Various forms of *Reticulitermes lucifugus*. A, adult worker; B, soldier; C, perfect winged insect; D, perfect insect after shedding the wings; E, young complementary queen; F, older complementary queen. Enlarged.—After GRASSI and SANDIAS.

ture, swarm from the nest and mate. After the nuptial flight the pair burrow into some crevice and shed the wings, which break off each along



FIG. 281.—Queen of *Termes obesus*. Natural size.—After HAGEN.

a peculiar transverse suture, leaving four triangular stumps (Fig. 280, D). The king and queen found a new colony and may live for several years, sheltered in a special chamber; the queen, meanwhile, becoming enormously distended (Fig. 281) with eggs and almost incapable of locomotion. The prolificacy of the queen is astonishing; she can lay thousands of eggs, sometimes at the rate of sixty per minute. She is the nucleus of the colony, and should she become incapacitated, is replaced by one or more *substitute* queens, which have been developed to meet the emergency; similarly, a substitute king is matured upon occasion. These substitutes (Fig. 280, E) differ from the primary pair in having nymphal wing pads in place of the remains of functional wings.

In regard to *Termopsis angusticollis*, in California, Dr. Heath says that if only one of the royal pair be destroyed usually only one substitution form is developed, but when both perish, from ten to forty substitutes appear, according to the size of the colony.

In all, three types of reproductive forms are recognized: *first form*,

true kings and queens, with functional wings or their remnants; *second form*, substitute males or females, with short wing pads; *third form*, ergatoid, or worker-like, males or females, without wings, this type being rather rare.

In certain tropical species there are two types of soldiers, and two of workers; so that adults of either sex may occur under seven different forms in the same colony.

Origin of Castes.—Grassi maintains that all the forms are alike at birth except as regards sex, and that the differences between worker and soldier, which are independent of sex, depend probably upon nutrition. Grassi attributes all the diversities of caste, except the sexual ones, to the character and amount of the food.

C. B. Thompson states that at hatching there are two kinds of nymphs (1) the "reproductive," which develop into the fertile castes, and (2) the "worker-soldier" nymphs, which become the sterile castes; these two types being distinguishable by internal differences in the brain, compound eyes, and sex organs.

Food.—The food of termites is of six kinds: (1) wood; (2) matter emitted from the œsophagus or rectum, termed respectively stomodæal and proctodæal food; (3) cast skins and other exuvial stuff; (4) the bodies of their companions; (5) saliva; (6) water. Of these the proctodæal food is the favorite. Nymphs receive at first only saliva; later they get stomodæal and proctodæal food until, finally, they are able to eat wood—the staple food of a termite.

American Species.—Our common termite is *Reticulitermes flavipes*, which occurs throughout the United States, excavating its galleries in decaying logs, stumps or other dead wood. The nuptial flight of this species takes place in spring, when the two sexes swarm in numbers that are sometimes enormous. One swarm, as recorded by Hagen, appeared as a dense cloud, and was being followed and attacked by no less than fifteen species of birds, among which were robins, bluebirds and sparrows; some of the robins were so gorged to the mouth with termites that their beaks stood open. Though plenty of winged females are said to occur in the swarming season, the true queen of *R. flavipes* is extremely rare, the queen usually found being evidently, from her undeveloped wings, a substitute queen.

The European species *Reticulitermes lucifugus* has been found recently in Massachusetts. Most species of termites occur in warm climates, however. North of Mexico thirty-six species are known,

most of which have come from the south, and more species are liable to be introduced at any time (Banks).

Architecture.—While many termites simply burrow in dead wood, other species construct more elaborate nests. A Jamaican species builds huge nests in the forks of trees, with covered passageways leading to the ground.

In parts of Africa and Australia, where they are free from disturbance,



FIG. 282.—Termite mound, Kimberley type, Australia.—After SAVILLE-KENT.



FIG. 283.—Mound of the "compass" termite of North Australia.—After SAVILLE-KENT.

termites erect huge mounds, frequently six to ten and sometimes eighteen or twenty feet high, with galleries extending as far below the surface of the ground as they do above it. These immense structures (Fig. 282) consist chiefly of earth, cemented by means of some secretion into a stony clay, with which also much excrementitious matter is mixed; they are pyramidal, columnar, pinnacled or of various other forms, according to the species, and are perforated by thousands of passages and chambers, while there are underground galleries extending away from the mound to a distance of often several hundred feet.

An extraordinary type of mound is constructed by the "compass" or "meridian," termites of North Australia, for their wedge-shaped mounds (Fig. 283), commonly eight or ten feet high, though sometimes as high as twenty feet, are directed north and south with surprising accuracy. By means of this orientation the exposure to the heat of the sun is reduced to the minimum, as occurs also in the case of many Australian plants, the leaves of which present their edges instead of their faces to the sun.

More than one species of termite may inhabit a single nest; in one South African nest Haviland found five species of termites and three of ants. The widely distributed genus *Eutermes* is essentially a group of *inquiline*, or guest, species. Termite mounds afford shelter to scorpions, snakes, lizards, rats, and even birds, some of which nest in them. The Australian bushmen hollow out the mounds to make temporary ovens, and even eat the clay of which they are composed, while hill-tribes of India are accustomed to eat the termites themselves, the flavor of which is said to be delicious.

Ravages.—In tropical regions the amount of destruction done by termites is enormous, and these formidable pests are a constant source of consternation and dread. They emit a secretion that corrodes metals and even glass, while anything made of wood is simply at their mercy. Always avoiding the light, they hollow out floors, rafters or furniture, leaving only a thin outer shell, and as a result of their insidious work a chair or a table may unexpectedly crumble at a touch. Jamestown, the capital of St. Helena, was largely destroyed by termites (1870) and had to be rebuilt on that account.

In the United States and Europe few species of termites occur, and they do little injury as compared with the tropical species; though our common *Reticulitermes flavipes* occasionally damages woodwork, books, plants, etc., in an extensive way, particularly in the Southern states.

Termitophilism.—Associating with termites are found various other arthropods, mostly insects. The relations of these termitophilous forms to the termites are, so far as is known, similar to those described beyond between myrmecophilous species and ants.

HONEY BEE

For more than three thousand years the honey bee has been almost unique among insects as an object of human care and study. It was highly prized by the old Greeks and Romans (as appears from the writ-

ings of Aristotle, 330 B. C., and Cato, about 200 B. C.) and actually worshiped as a symbol of royalty by the ancient Egyptians, through whose papyri and scarabs the honey bee may be traced back to the time of Rameses I., or 1400 B. C.

The honey bee, unlike domesticated animals, is so little dependent upon man that it readily returns to a wild life. Under many distinct races, which are due largely to human intervention, *Apis mellifera* is widely distributed over the earth.

Castes.—The species comprises three kinds of individuals: *queen*, *drone* and *worker* (Fig. 284). The workers are females with an atrophied reproductive system. They constitute the vast majority in any colony and are the only kind that is commonly seen out of doors. Upon the industrious workers falls the burden of the labor; they build the comb,

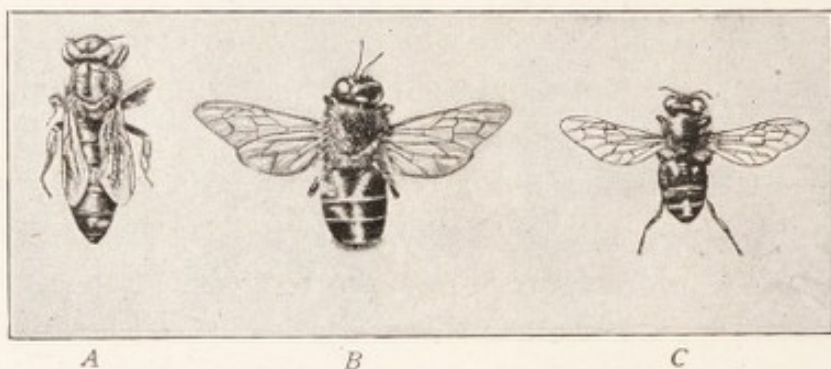


FIG. 284.—The honey bee, *Apis mellifera*. A, queen; B, drone; C, worker. Natural size.

nurse the young, gather food, clean and repair the nest, guard it from intruders, control larval development, expel the drones—briefly, the workers alone are responsible for the general management of the community. Though hibernating workers live eight or nine months, the other workers live but from five to twelve weeks.

The term queen is, of course, a misnomer, for the government of the hive is anything but monarchical. The chief duties of the queen, or mother, are simply to lay eggs and to lead away a swarm. She is able to deposit as many as 4,000 eggs in twenty-four hours. After a single mating, the spermatozoa retain their vitality in the spermatheca of the queen for three or four years—the lifetime of a queen. The males, or drones, apart from their occasional sexual usefulness, are of little or no service, and their very name has become an expression for laziness.

The Comb.—Wax, of which the comb is built, is made from honey or sugar, many pounds (twenty, according to Huber) of honey being required to make one pound of wax. The workers, gorged with nectar, cling to one another in a dense heated mass until the white films of wax

appear underneath the abdomen (Fig. 104); these are transferred to the mouth, as described on page 229, and are masticated with a fluid, secreted by cephalic glands, which alters the chemical composition of the wax and makes it plastic.

The workers now contribute their wax to form a vertical, hanging septum, on the opposite sides of which they proceed to bite out pits—the bottoms of the future cells—using the excavated wax in making the cell walls. The bottom of each cell consists of three rhombic plates (Fig. 285, *A*), and the cells of one side interdigitate with those of the other side (Fig. 285, *B*) in such a way that each rhomb serves for two cells at once. Wax is such a precious substance that it is used (instinctively, however) always with the greatest economy; the cell walls, are scraped to a thinness of $\frac{1}{280}$ or $\frac{1}{400}$ of an inch, and nowhere is more wax used than is sufficient for strength; one pound of wax makes from 35,000 to 50,000 worker cells. The cells, at first circular in cross section, become hexagonal from the mutual interference of workers on opposite sides of the same wall; the form is, however, by no means a regular hexagon in the mathematical sense, for it is difficult to find a cell with errors of less than 3 or 4 degrees in its angles. (Cheshire.) Worker cells are one fifth of an inch in diameter, while the larger cells, destined for drones or to hold honey, are one quarter of an inch across.

To strengthen the edges of cells or to fill crevices, the workers use *propolis*, the sticky exudation from the buds or leaf axils of poplar, fir, horse-chestnut or other trees; though they will utilize instead such artificial substances as grease, pitch or varnish. As winter approaches, the bees apply the propolis liberally, making their abode tight and comfortable.

Larval Development.—When the brood cells are ready, the queen, attended by workers, lays an egg in each cell and has no further concern as to its fate. After three days the egg discloses a footless grub (Figs. 286, 287) which depends at first upon the milky food that bathes it and has been supplied from the mouths of the worker nurses. Later the larva is weaned by its nurses to pollen, honey and water. As the stomach and the intestine of the larva do not communicate with each

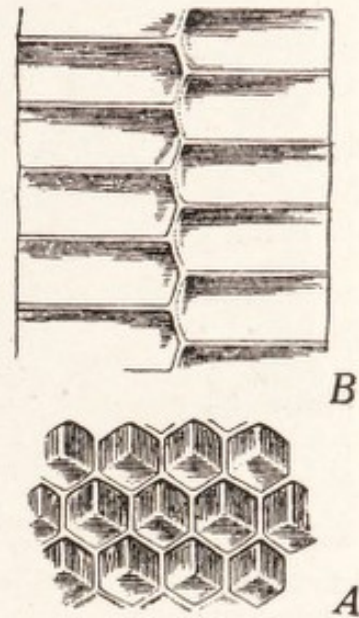


FIG. 285.—*A*, bases of comb cells; *B*, section of comb. Somewhat enlarged.—After CHESHIRE.

other, the excretions of the larva cannot contaminate the surrounding nutriment, and are retained until the final molt. Five days after

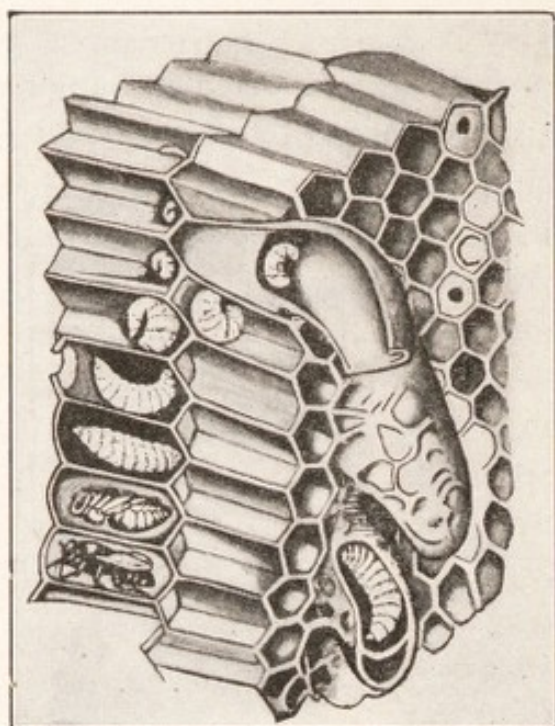


FIG. 286.—Comb of honey bee, showing the insect in various stages. At the right are large queen cells.—After BENTON.

hatching, the larva spins its cocoon, the workers having meanwhile covered the larval cells with a porous cap of wax and pollen (Fig. 287) and on the twenty-first day after the egg was laid the winged worker bee cuts its way out, assisted in this operation by the ever-attentive nurses. Now, after acquiring the use of its faculties, the newly emerged bee itself assumes the duties of a nurse, but as soon as its cephalic nursing glands are exhausted it becomes a forager. This account applies to the worker; the three kinds of individuals differ in respect to the number of days required for development, as appears in the following table, from Phillips:

	EGG.	LARVA.	PUPA.	TOTAL.
Queen.....	3	5½	7½	16
Worker.....	3	6	12	21
Drone.....	3	6½	14½	24

The cells in which queens develop (Fig. 286) are quite different from worker or drone cells, being much larger, more or less irregular in form, and vertical instead of horizontal; they are attached usually to the lower edge of a comb or else to one of the side edges.

Other Facts.—The entire organization of the honey bee has been profoundly modified with reference to floral structure; the life of the bee is wrapped up in that of the flower. The more important structural adaptations of bees in

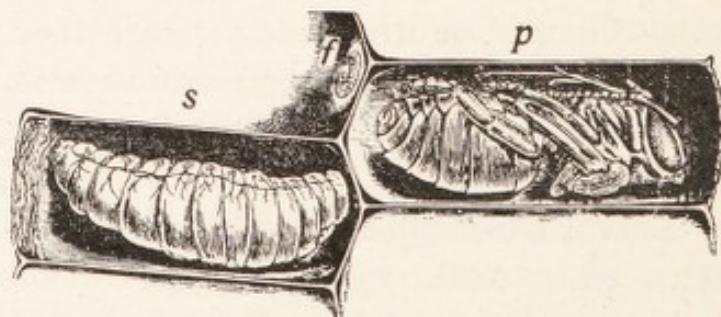


FIG. 287.—Honey bee. *f*, feeding larva; *p*, pupa; *s*, spinning larva.—After CHESHIRE.

relation to flowers have been described, as well as many of their sensory peculiarities; there remain to be added, however, some other items of interest, chosen from the many.

A colony of bees in good condition at the opening of the season contains a laying queen and some 30,000 to 40,000 worker bees, or six to eight quarts by measurement. Besides this there should be four, five, or even more combs fairly stocked with developing brood, with a good supply of honey about it. Drones may also be present, even to the number of several hundred.

Ordinarily the queen mates but once, flying from the hive to meet the drone high in the air, when five to nine days old usually. Seminal fluid sufficient to impregnate the greater number of eggs she will deposit during the next two or three years (sometimes even four or five years) is stored at the time of mating in a sac—the *spermatheca*, opening into the egg-passage.

The liquid secreted in the nectaries of flowers is usually quite thin, containing, when just gathered, a large percentage of water. Bees suck or lap it up from such flowers as they can reach with their flexible, sucking tongue, 0.25 to 0.28 inch long. This nectar is taken into the *honey sac*, located in the abdomen, for transportation to the hive. Besides being thin, the nectar has at first a raw, rank taste, usually the flavor and odor peculiar to the plant from which gathered, and these are frequently far from agreeable. To make from this raw product the healthful and delicious table luxury which honey constitutes—"fit food for the gods"—is another of the functions peculiar to the worker bee. The first step is the stationing of workers in lines near the hive entrances. These, by incessant buzzing of their wings, drive currents of air into and out of the hive and over the comb surfaces. If the hand be held before the entrance at such a time a strong current of warm air may be felt coming out. The loud buzzing heard at night during the summer time is due to the wings of workers engaged chiefly in ripening nectar. Instead of being at rest, as many suppose, the busy workers are caring for the last-gathered lot of nectar and making room for further accessions. This may go on far into the night, or even all night, to a greater or less extent, the loudness and activity being proportionate to the amount and thinness of the liquid. Frequently the ripening honey is removed from one set of cells and placed in others. This may be to gain the use of certain combs for the queen, or possibly it is merely incidental to the manipulation the bees wish to give it. When, finally, the process has been completed, it is found that the water content has usually been re-

duced to 10 or 12 per cent., and that the disagreeable odors and flavors, probably due to volatile oils, have also been driven off in a great measure, if not wholly, by the heat of the hive, largely generated by the bees. During the manipulation an antiseptic (formic acid), secreted by glands in the head of the bee, and possibly other glandular secretions as well have been added. The finished product is stored in waxen cells above and around the brood nest and the main cluster of bees, as far from the entrance as it can be and still be near to the brood and bees. The work of sealing with waxen caps then goes forward rapidly, the covering being more or less porous. Each kind of honey has its distinctive flavor and aroma, derived, as already indicated, mainly from the particular blossoms by which it was secreted, but modified and softened by the manipulation given it in the hives. The last three paragraphs are taken from Benton's useful manual.

The phenomenon of "swarming" results from the tremendous reproductive capacity of the queen, though it is immediately an instance of *positive phototropism*, as Kellogg has shown. Accompanied by most of the workers, the old queen abandons the hive to establish a new colony. The workers that remain behind have provided against this contingency, however, and the departed queen is soon replaced by a new one.

Determination of Caste.—The difference between queen and worker depends solely upon nutrition, both forms being derived from precisely the same kind of egg. To produce a queen, a large cell of special form is constructed, and its occupant, instead of being weaned, is fed almost entirely upon the highly nutritious secretion which worker grubs receive only at first and in limited quantity. This nitrogenous food, the product of cephalic glands, develops the reproductive system in proportion to the amount received. Drone larvæ get much of it, though not so much as queens, while an occasional excess of this "royal jelly" is believed to account for the abnormal appearance of fertile workers.

Parthenogenesis, or reproduction without fertilization, is known to occur in the bee, as well as in various other insects. The always unfertilized eggs of workers produce invariably drones, as do also unfertilized eggs of the queen.

Dzierzon's Theory.—The much discussed theory of Dzierzon, proposed more than seventy-five years ago, is essentially as follows: (1) the queen is able "at will" to lay either male or female eggs; (2) all the eggs in the ovaries would develop into males if unfertilized, but fertilized eggs produce females.

It is a matter of common observation that the queen is able to lay

female eggs in worker or queen cells, and male eggs in drone cells; but the means by which she exercises control over the fertilization of the eggs is not understood.

It is known that unfertilized eggs produce always drones, and at present it is generally believed by geneticists that drones never come from fertilized eggs. The principal reasons for this opinion are these: (1) if a pure-bred queen of one race is crossed with a drone of another race, the female progeny (workers or queens) have hybrid characters, but the male offspring have only characters of the maternal race; (2) eggs from worker or queen cells contain spermatozoa; those from drone cells do not.

BUMBLEBEES

Familiar as the bumblebees are, their habits have been little studied in this country, though in England "humblebees" have formed the subject of an interesting volume by Sladen. The queen hibernates and in spring starts a colony, utilizing frequently for this purpose the deserted nest of a field mouse or sometimes the burrow of a mole or gopher. The queen lays her eggs in a small mass of pollen mixed with nectar (Putnam). The larvæ eat out cavities in the mass of food and when full grown spin silken cocoons, from which the imago cuts its way out; the empty cocoon being subsequently used as a receptacle for honey. At first only workers are produced and they at once relieve the queen of the duties of collecting nectar and pollen, caring for the young, etc. The workers are of different sizes, the smaller ones being nurses or builders and the larger ones foragers—the kind commonly seen out of doors. In the latter part of summer both males and females are produced, but when severe frost arrives, the old queen, the workers and the males succumb, leaving only the young queens to survive the winter.

SOCIAL WASPS

The Social Wasps constitute the family Vespidae, of which we have three genera, namely, *Vespa*, *Polistes* and *Polybia*, the last genus being represented by a single Californian species.

Vespa.—Some species of *Vespa*, as *V. maculata*, make a nest which consists of several tiers of cells protected by an envelope (Fig. 288), attaching the nest frequently to a tree; other species, as *germanica* and *vulgaris*, make a nest underground. The paper of which the nests are

composed is manufactured from weather-worn shreds of wood, which are torn off by the mandibles and then masticated with a secreted fluid which cements the paper and makes it waterproof.

A solitary queen founds the colony in spring; she starts the nest, lays eggs, feeds the young and brings forth the first workers; these then relieve her—continue the building operations, collect food, nurse the young; in short, assume the burden of the labor. In the latter part of summer, fertile males and females appear and pairing occurs. Though the statement has often been made that only the young queens survive

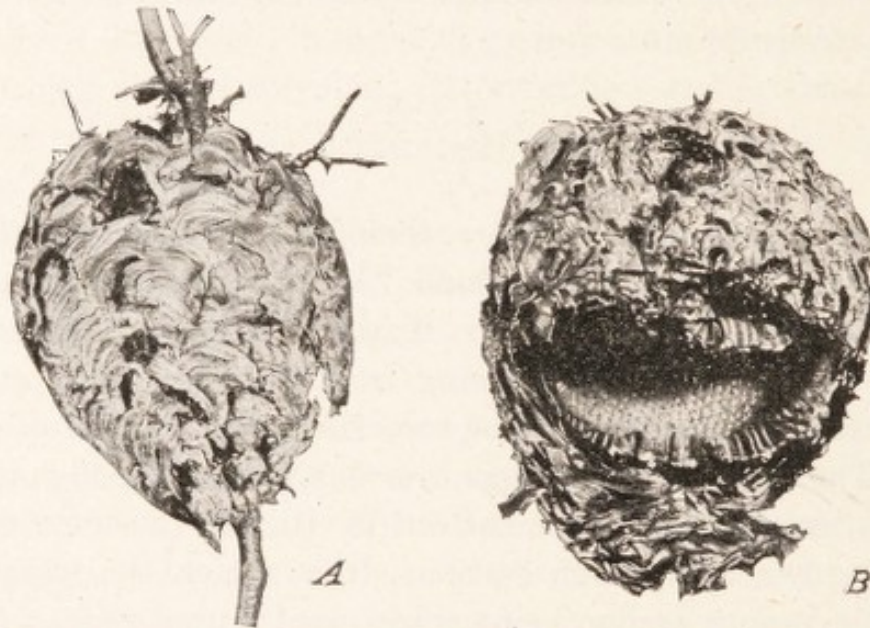


FIG. 288.—Nest of wasp, *Vespa maculata*. A, outer aspect; B, with envelope cut away to show combs. Greatly reduced.

the winter, there is some reason to believe that not only the queens but also males and workers may hibernate successfully in the nest.

The larvæ are fed at first, by regurgitation, upon the sugary nectar of flowers and the juices of fruits, and later upon more substantial food, such as the softer parts of caterpillars, flies, bees, etc., reduced to a pulp by mastication; occasionally wasps steal honey from bees.

The workers, as is usual among social Hymenoptera, are modified females, incapable of reproduction as a rule, though the distinction between worker and queen is not nearly so sharp among wasps as it is among bees. Worker eggs are said to be parthenogenetic and to produce only males. The males, unlike those of the honey bee, are active laborers in the colony. In the tropics there are wasps that form permanent colonies, store honey and swarm, after the manner of honey bees.

Polistes.—The preceding description of *Vespa* applies equally well to our several species of *Polistes*, except that the nest of *Polistes* is a

single comb hanging by a pedicel and without a protecting envelope. Miss Enteman, who has carefully studied the habits of *Polistes*, finds that the larva spins a lining as well as a cap for its cell, by means of a fluid from the mouth, and that the adults emerge after a pupal period of three weeks, males and females appearing (in the vicinity of Chicago) in the latter part of August and early in September.

ANTS

The habits of ants have engaged the serious attention of some of the most sagacious students of the phenomena of life. Any species of ant presents innumerable problems to the thoughtful investigator and about five thousand species, subspecies and varieties of ants have been described.

A large part of our knowledge of the habits of these remarkable insects has been obtained by the use of artificial formicaries, which are easily constructed and have yielded important results in the hands of Lubbock, Forel, Janet, Wasmann, Fielde, Wheeler and other well-known students of ants. We have an important comprehensive volume on these insects by Wheeler.

Castes.—In a colony of ants three kinds of individuals are produced as a rule: *males*, *females* and *workers*, the last being sexually imperfect females.

The males and females swarm into the air for a nuptial flight, after which the males die, but the females shed their wings and enter upon a new and prolific existence, which may last for many years; a queen of *Lasius niger* was kept alive by Lubbock for nine years, and one of *Formica fusca*, fifteen years, and then its death was due to an accident.

The workers live from one to seven years, according to the same authority. They constitute the vast majority in any colony and are the familiar forms that so often command attention by their industry and pertinacity. In some species certain of the workers are known as *soldiers*; these may be recognized by their larger head and mandibles.

Polymorphism.—Ants and termites surpass all other insects in respect to the number of forms under which a single species may occur. In some species of ants several types of workers exist; these are distinguished by structural peculiarities of one kind or another, which possibly indicate special functions, for the most part as yet unascertained. Furthermore, the sexual individuals are not necessarily winged; some or all of them may be wingless, especially the females.

These wingless males and females are termed *ergatoid*, on account of their resemblance to workers.

As to how these various forms are produced, very little is known. Probably, as among bees, workers and queens are produced from the same kind of eggs, which have been fertilized, and the differences between worker and queen and between workers themselves may be due to the quality and quantity of the food that is supplied to the larvæ by their nurses. As in bees, the parthenogenetic eggs laid by abnormal workers may produce males, as Forel, Lubbock and Miss Fielde have found; or they may produce normal workers, as Reichenbach and Mrs. A. B. Comstock have found to be the case in *Lasius niger*. Wheeler points out the possibility of the inheritance of worker characters through the male offspring of workers.

Larvæ.—The numerous eggs laid by one or more queens are taken in charge by the young workers, through whose assiduous care the helpless larvæ are carried to maturity. The nurses feed the larvæ from their own mouths, clean the larvæ, and carry them from one place to another in order to secure the optimum conditions of temperature, moisture, etc. When a nest is broken open, the workers seize the larvæ and pupæ and hurry into some dark place. The pupa is either naked or else enclosed in a cocoon, spun by the larva.

Nests.—The species of the tropical genus *Eciton* do not make nests but occupy temporarily any suitable retreat which they may happen to find in the course of their wanderings. Ants in general know how to utilize all sorts of existing cavities as nests; they make use of crevices in rocks and under stones or bark, the holes made by bark-beetles, hollow stems or roots, plant-galls, fruits, etc. The extraordinary "ant-plants" have already received special consideration.

Very many ants excavate their nests in the ground; after a rain these ants are especially industrious in the improvement of the nest, pressing the wet earth into the walls of the galleries and adding probably a secreted fluid which acts as a cement; stones and sticks are often worked into the walls of a nest and the mounds of ants are frequently fashioned about blades of grass or growing herbage of whatever kind. The subterranean galleries are often complex labyrinths; frequently there are long underground passages extending out in all directions, sometimes to aphid-infested roots of plants or, as in the case of the leaf-cutting ants of the tropics, to trees which are destined to be attacked; special chambers are set apart for the storage of food and others for eggs, larvæ or pupæ.

Often a nest is excavated under a stone. As Forel observes, the stone warms speedily under the rays of the sun, and in damp or cool weather the ants are always in the highest story of the nest as soon as the sun's warmth begins to penetrate the soil, while they go below as soon as the sun disappears or when its heat becomes too strong. They select stones that are neither too large nor too small to regulate the temperature well, while other ants attain the same object by making the nest under sheltering herbage or by making a mound with a hard cemented roof.

The well-known ant-hills may consist simply of excavated particles of soil or else, as in the huge mounds of *Formica exsectoides*, may contain labyrinthine passages in addition to those underground. The mounds of this species are elaborate structures which may last a man's lifetime at least. *F. exsectoides* is accustomed to form new colonies in connection with the parent nest; McCook found in the Alleghanies no less than 1,600 nests, forming a single enormous community with hundreds of millions of inhabitants, hostile to all other colonies of ants, even those of the same species. This ant covers its mound with twigs, dead leaves, grass and all sorts of foreign material, and is said to close the exits of the nest with bits of wood at night and in rainy weather, removing them in the morning or when the weather becomes favorable.

As Forel says [translation]: "The chief feature of ant architecture, in contradistinction to that of the bees and the wasps, is its irregularity and want of uniformity—that is to say, adaptability, or the capacity of making all the surroundings and incidents subserve the purpose of attaining the greatest possible economy of space and time and the greatest possible comfort. For instance, the same species will live in the Alps under stones which absorb the rays of the sun; in a forest it will live in warm, decayed trunks of trees; in a rich meadow it will live in high, conical mounds of earth." Some species construct peculiar pasteboard nests, as *Lasius fuliginosus* of Europe and tropical species of *Crematogaster*; and others spin silk to fasten leaves together, as *Polyrhachis* of India and *Ecophylla* of tropical Asia and tropical Africa, the silk being probably a salivary secretion, according to Forel.

Habits in General.—The habits of ants are an inexhaustible and ever-fascinating subject of study to the naturalist, and well repay the most critical observation. While each species has its characteristic habits, ants in general have many customs in common.

Thus ants of one colony exhibit, as a rule, a pronounced hostility toward ants of any other colony, even one of the same species, but

recognize and spare members of their own colony, even after many months of separation and though the colony may number half a million individuals. This recognition is effected by means of an odor, distinctive of the colony and apparently inheritable. When an ant is washed and then restored to its fellows, it is treated at first as an intruder and may even be killed. The same is true when the ant has been smeared with juices from the bodies of alien ants. According to Miss Fielde, workers of colony *A*, smeared with the juices from crushed ants of colony *B* and then placed in colony *B* are received amicably, but at once set about to destroy their hosts, like "wolves in sheep's clothing." These statements apply only to workers, however, for alien larvæ and pupæ are frequently captured and reared by ants, and Miss Fielde states that kings of one colony of *Stenamma* when introduced into another colony are even cordially received.

Some of the most careful students of the habits of ants agree that these insects can communicate with one another. An ant discovers a supply of food, returns toward the nest, meets a fellow worker, the two stroke antennæ and then both start back to the food; before long other members of the colony swarm to the prize. It has been thought that the odor of the food or some other odor, left by the first ant, serves as a trail for the other ants to follow. Bethe, indeed, infers from his experiments that this phenomenon is purely mechanical and involves no psychical qualities on the part of the ants. His own experiments, however, show that one ant can inform another by means of an odor as to the whereabouts of food—which is certainly one form of communication.

Ants avoid sunlight as a rule but prefer rays of lower refrangibility to those of higher. Upon exposing ants to the colors of the spectrum, as transmitted through glasses of different colors, Lubbock found that they congregated in greatest numbers under the red glass and that the numbers diminished regularly from the red to the violet end of the spectrum, there being very few individuals under the violet glass.

Miss Fielde, experimenting with queens, workers and young of *Stenamma fulvum piceum* in an artificial nest, covered half the nest with orange glass and half with violet. "The ants removed hastily from under the violet as often as an interchange of the panes was made, once or twice a day, for about twenty days. Thereafter they became indifferent to the violet rays." "The plasticity of the ants is remarkably shown in their gradually learning to stay where they were never disturbed by me, under rays from which their instincts at first withdrew them."

Ants are sensitive not only to the different colors of the spectrum

but also to the ultra-violet rays, which produce no appreciable effect on the human retina (though they induce chemical changes). If obliged to choose between the two, ants prefer violet to ultra-violet rays, as Lubbock found. If, however, the ultra-violet rays are intercepted, by means of a screen of sulphate of quinine or bisulphide of carbon, the ants then collect under the screen in preference to under the violet rays.

From lack of experience we can form no adequate idea as to the range of sensation in ants or other insects. Ants can taste substances that we cannot, and *vice versa*. They show no response to sounds of human contrivance, yet many of them possess stridulating organs and organs that are doubtless auditory; whence it may be inferred that ants can communicate with one another by means of sounds. In rare instances the stridulation of an ant can impress the human ear, as in a species of *Atta* mentioned by Sharp.

Experiments show that ants, as well as bees and wasps, find their way back to the nest, not by a mysterious "sense of direction," but by remembering the details of the surroundings, and in the case of ants, by means of an odor left along the trail.

In studying the habits of ants, the greatest care must be exercised in order to discriminate between actions that may be regarded as purely instinctive and those that may indicate some degree of intelligence. If any insects show signs of intelligence, the social Hymenoptera do; but in the study of this recondite subject, false conclusions can be avoided only by observation and experimentation of the most critical kind.

Hunting Ants.—Some ants, as *Formica fusca*, live by the chase, hunting their prey singly. The African "driver ants" (*Anomma arcens*), although blind, hunt in immense droves, consuming all the animal refuse in their way, devouring all the insects they meet, and not hesitating to attack all kinds of vertebrates; these ants ransack houses from time to time and clear them of all vermin, though they themselves are a great nuisance to the householder. The Brazilian species of *Eciton* (Fig. 290, B, C) have similar habits and are likewise blind, or else have but a single lens on each side of the head. These insects hunt in armies of hundreds of thousands, to the terror of every animate thing they come across. They have no permanent abode, but now and then appropriate some convenient hole for the purpose of raising a new brood of marauders.

Slave-making Ants.—It is a fact that some ants make slaves of other species. *Formica sanguinea*, for example, will attack a colony of *Formica fusca*, kill its active members in spite of their determined resistance, kidnap the larvæ and pupæ and carry them home, where the

captives receive every care, and at length, as imagines, serve their masters as faithfully as they would serve their own species. In the Alleghanies, according to McCook, colonies of *F. fusca* occur where there are no "red ants" (*F. sanguinea*), but are hard to find where the enslaving species occurs.

Although *F. sanguinea* can exist very well without slaves, *Polyergus rufescens*, of Europe, is notoriously dependent upon their services, it being doubtful whether it is capable of feeding itself. This species is powerful as a warrior, but its mandibles are of little use, except to pierce the head of an adversary. *Strongylonotus* is still more helpless, while *Anergates* (also of Europe) is said to depend absolutely upon its slaves.

Polyergus lucidus occurs in the Alleghanies, where the colonies of this species, according to McCook, contain large numbers of the workers of *Formica schaufussi*. The masters are good fighters but do no other work, and have not been seen to feed themselves, though they may often be seen feeding from the mouths of their slaves.

Honey Ants.—Among ants in general, the workers that stay in the



FIG. 289.—Honey ants, *Myrmecocystus melliger*, clinging to the roof of their chamber. About natural size.—After McCook.

nest receive food from the mouths of the foragers—a custom which has led to the extraordinary conditions found in the "honey ants," in which certain of the workers sacrifice their own activity in order to act as living reservoirs of food (*repletes*) for the benefit of the other members of the colony. This remarkable habit has arisen independently, in different genera of ants, in North America, Australia and South Africa, as Lubbock observes.

The honey ant whose habits are best known, through the studies of McCook and others, is *Myrmecocystus melliger*, of Mexico, New Mexico and southern Colorado. In this species some of the workers hang sluggishly from the roof of their little dome-like chamber, several inches underground, and act as permanent receptacles for the so-called honey, which is a transparent sugary exudation from certain oak-galls; it is gathered at night by the foraging workers and regurgitated to the mouths of the "honey-bearers," whose crops at length become distended with honey to such an extent that the insects (Fig. 289) look like so many little translucent grapes or good-sized currants. This stored food is in all probability drawn upon by the other ants when necessary.

Leaf-cutting Ants.—The most dangerous foes to vegetation in tropical America are the several species of *Atta* (Fig. 290, A). Living

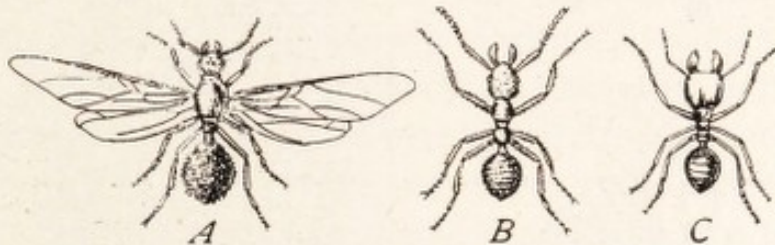


FIG. 290.—A, leaf-cutting ant, *Atta cephalotes*. B, wandering ant, *Eciton drepanophorum*; C, *Eciton omnivorum*. Natural size.—After SHIPLEY.

in enormous colonies and capable of stripping a tree of its leaves in a few hours, these formidable ants are the despair of the planter; where they are abundant it becomes impossible to grow the orange, coffee, mango and many other plants. These ants dig an extensive underground nest, piling the excavated earth into a mound, sometimes thirty or forty feet in diameter, and making paths in various directions from the nest for access to the plants of the vicinity; Belt often found these ants at work half a mile from their nest; they attack flowers, fruits and seeds, but chiefly leaves. Each ant, by laboring four or five minutes, bites out a more or less circular fragment of a leaf (Fig. 291) and carries it home, or else drops it for another worker to carry; and two strings of ants may be seen, one carrying their leafy burdens toward the nest, the other returning for more plunder.

The use made of these leaves has been the subject of much discussion. Belt found the true explanation, but it remained for Möller to investigate the subject so thoroughly as to leave no room for doubt. The ants grow a fungus upon these leaves and use it as food. The bits of leaves are kneaded into a pulpy, spongy mass, upon which the

fungus at length appears. The food for the sake of which the ants carry on their complex operations consists of the knobbed ends of fungus threads (Fig. 292), and these bodies, rich in fluid, form the most important, if not the sole food of the leaf-cutting ants. By assiduously weeding out all foreign organisms the ants obtain a pure culture of the

fungus, and by pruning the fungus they keep it in the vegetative condition and prevent its fructification; under exceptional circumstances, nevertheless, the fungus develops aerial organs of fructification of the

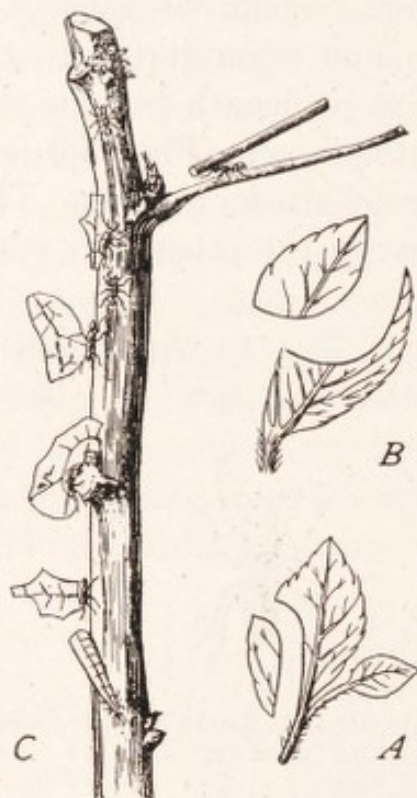


FIG. 291.—A, B, cuts made in *Cuphea* leaves in four or five minutes by *Atta discigera*; natural size. C, *Atta discigera* transporting severed fragments of leaves; reduced.—After MÖLLER.

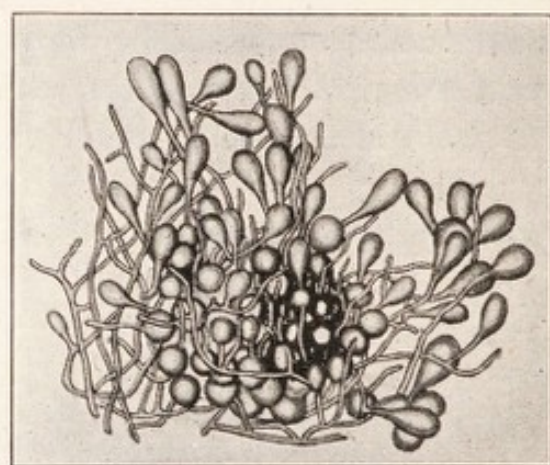


FIG. 292.—Fungus clumps (*Rozites gongylophora*) cultivated by ants of the genus *Atta*. Greatly magnified.—After MÖLLER.

agaricine type, but this species (*Rozites gongylophora*) has never been found outside of ants' nests. The peculiar clubbed threads were produced by Möller in artificial cultures and are not spores, but products of cultivation. Other ants are known to cultivate other kinds of fungi for similar purposes.

McCook has found a leaf-cutting ant (*Atta fervens*) in Texas, and mentions that it cuts circular pieces out of leaves of chiefly the live-oak, these being dropped to the ground and taken to the nest by another set of workers. He records an underground tunnel of *Atta fervens* which extended 448 feet from the nest and then opened into a path 185 feet in length; the tunnel was 18 inches below the surface on an average, though occasionally as deep as 6 feet, and the entire route led with remarkable precision to a tree which was being defoliated.

The same observer has given also a brief account of a leaf-cutting ant that lives in New Jersey. This species (*Trachymyrmex septentrionalis*) cuts the needle-like leaves of seedling pines into little pieces, which are carried to the nest. Two columns of workers may be seen, one composed of individuals returning to the nest, each with a piece of pine needle, the other of outgoing workers. The nest is a simple structure, extending some seven inches underground and ending in a chamber in which are several small pulpy balls, consisting probably of masticated leaves. Further studies upon our own leaf-cutting ants, modeled after the admirable studies of Möller, are much to be desired.

Harvesting Ants.—Lubbock observes that some ants collect the seeds of violets and grasses and preserve them carefully for some purpose as yet unknown. From such a beginning as this may have arisen the extraordinary habits of the agricultural, or harvesting, ants, of which some twenty species are known from various parts of the world.

The Texas species *Pogonomyrmex barbatus*, studied by Lincecum and by McCook, clears away the herbage around its nest (even plants several feet high and as thick as a man's thumb) and levels the ground, forming a disk often 10 or 12 and sometimes 15 to 20 feet in diameter, from which radiating paths are made, from 60 to 300 feet in length. The ants go back and forth along these roads, carrying to the nest seeds which they have collected from the ground or else have cut from plants; these seeds are stored in "granaries" several feet underground and are eventually used as food. The ants prefer the seeds of a grass, *Aristida oligantha*, but the oft-repeated statement that they *sow* the seeds of this "ant-rice," guard it and weed it, is denied by Wheeler.

Notwithstanding the elaborate studies of McCook upon this subject, there still remain not a few essential questions to be answered.

Myrmecophilism.—To add to the complexity of ant-life, the nests of ants, when at all extensive, are frequented by a great variety of other arthropods, which on account of their association with ants are termed *myrmecophiles*. Most of these are insects, of which Wasmann has catalogued 1,200 species, but not a few are spiders, mites, crustaceans, etc. Though the diverse relations between myrmecophiles and ants are but partially understood, these aliens may for convenience be considered under five groups: *captives*, *guests*, *visitors*, *intruders* and *parasites*.

Captives.—Besides enslaving other species, as already mentioned, ants make use of aphids and some coccids for the sake of their palatable products. The attendance of ants upon colonies of plant lice is a common occurrence and one that repays careful observation. With the

aid of a hand-lens, one may see the ants hastening about among the plant lice and patting them nervously with the antennæ until at length some aphid responds by emitting from the end of the abdomen a glistening drop of watery fluid, which the ant snatches. This fluid, contrary to prevalent accounts, is not furnished by the so-called honey-tubes of the aphid, but comes from the alimentary canal; the "honey-tubes" are glandular indeed, but are probably repellent in function. In some instances ants give much care to their aphids, for example covering them with sheds of mud, which are reached through covered passageways. More than this, however, some ants actually collect aphid eggs and preserve them over winter as carefully as they do their own eggs. In one such instance Lubbock found that the aphids upon hatching, after six months, were brought out by the ants and placed upon young shoots of the English daisy, their proper food plant. In our own country, as Forbes has discovered, the eggs of the corn root louse (*Aphis maidiradicis*) are collected in autumn by ants (especially of the genus *Lasius*) and stored in the underground nests. In winter the eggs are taken to the deepest parts of the nest, and on bright spring days they are brought up and even scattered about temporarily in the sunshine; while if a nest is opened, the ants carry off the aphid eggs as they would their own. In spring the ants tunnel to the roots of pigeon grass and smartweed, seize the aphids and carry them to these roots, and later to the roots of Indian corn. Throughout the year the ants exercise supervision over these aphids; occasionally, as Forbes says, an ant seizes a winged louse in the field and carries it down out of sight, and in one such instance it appeared that the wings had been gnawed away near the body, as if to prevent the escape of the louse. Similar relations exist also between ants and some species of scale insects.

Guests.—Though Aphididæ and Coccidæ are able almost always to live without the help of ants, there are some insects which have never been found outside the nests of ants. Most of these insect guests are beetles, notably Staphylinidæ and Pselaphidæ. The rove-beetles make themselves useful by devouring refuse organic matter, and these scavengers are unmolested by the ants with which they live. A few myrmecophilous beetles furnish their hosts with a much-coveted secretion and receive every attention from the ants, which clean these valuable beetles and even feed them mouth to mouth, as the ants feed one another. *Lomechusa* (Fig. 293) is one of these favored guests, as it has abdominal tufts of hairs from which the ants secure a secreted fluid. *Atemeles* (Fig. 294) is another; it solicits and obtains food from the mouth of a

foraging ant as if it were an ant itself. In the Alleghanies, *Atemeles cava* occurs in the nests of *Formica rufa*, and is much prized by this ant on account of the fluid which the beetle secretes from glandular hairs on the sides of the abdomen.

The beetle *Claviger* has at the base of each elytron a tuft of hairs,

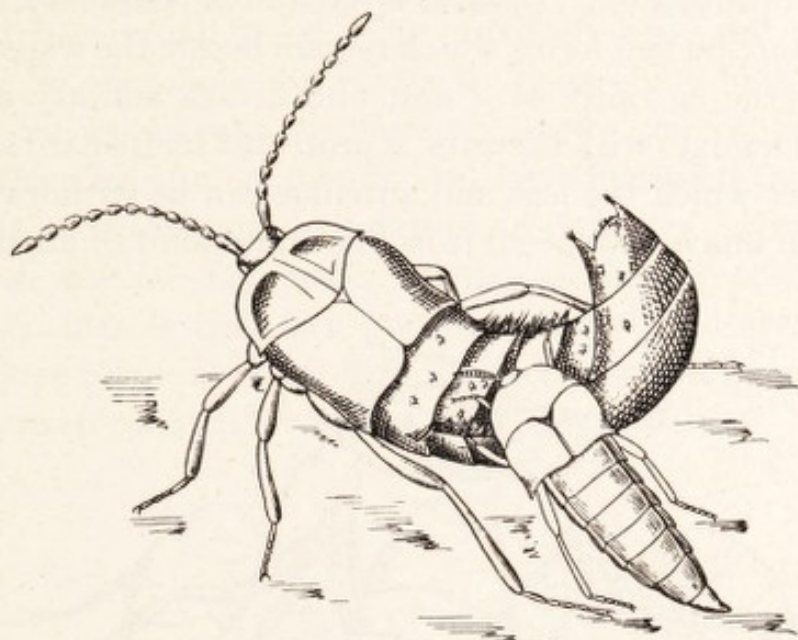


FIG. 293.—*Lomechusa strumosa* being freed of mites by *Dinarda dentata*.—After WASMANN.



FIG. 294.—*Atemeles emarginatus* being fed by an ant, *Myrmica scabrinodis*.—After WASMANN.

which the ants lick persistently. This beetle is blind and appears to be incapable of feeding itself; for when deprived of ant-assistance it dies, even though surrounded by food. These cases of *symbiosis*, or mutual benefit, are well authenticated.

Visitors.—Many myrmecophilous insects are not restricted to ants' nests, but are free to enter or to leave. This is true of such Staphylinidæ as visit formicaries simply for shelter or to feed upon detritus, and these visitors are treated with indifference by the ants.

Intruders.—Not so, however, with species that are inimical to the interests of the ants, such as many species of Staphylinidæ and Histeridæ, which steal food from the ants, kill them or devour their larvæ or pupæ at every opportunity. The ants are hostile to these marauders, though the latter often escape through their agility or else rely upon their armor for protection. *Quedius brevis* and *Myrmedonia*, as Schwarz observes, are soft-bodied forms which remain beside the walls of the galleries or near the entrance of a nest and attack solitary ants; while *Helærius*, which mixes with the ants, is protected by its hard and smooth covering, under which the legs and antennæ can be withdrawn. Such an enemy is an unavoidable evil from the standpoint of an ant.

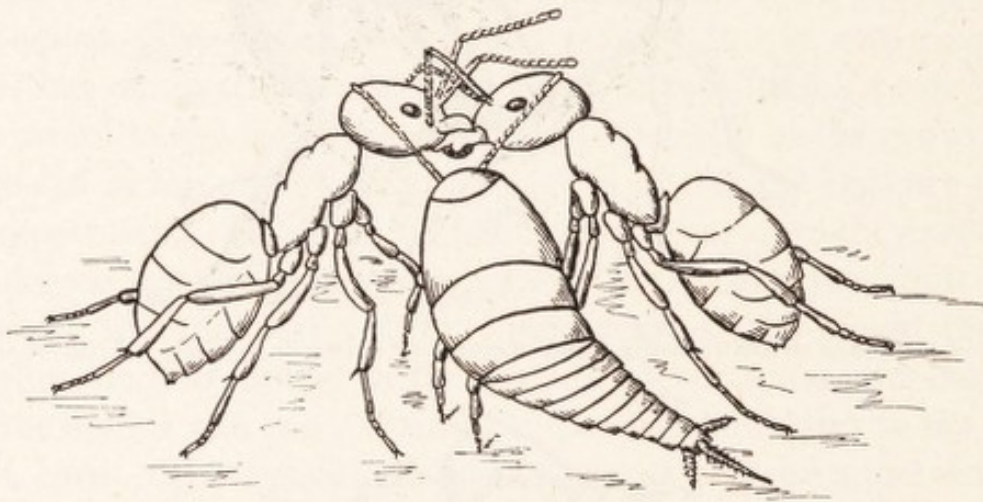


FIG. 295.—*Atelura formicaria* stealing food from a pair of ants.—After JANET.

Janet has described the amusing way in which an audacious species of *Atelura* steals food from the very mouths of ants. As is well known, ants are accustomed to feed one another from mouth to mouth. When the foragers, filled with honey or other food, return to the nest, they are solicited for food by those that have remained at home; as a forager and a beggar stand head to head, the former disgorges small drops of food, which are seized by the latter. While a pair of ants are engaged in this performance (Fig. 295), and a drop of honey is being passed, the *Atelura* rushes in, grabs the drop and hurries away. As might be expected, these interlopers are constantly being chased by their victims from one corner of the nest to another.

Parasites.—Nematode worms occupy the pharyngeal glands of ants; larvæ of *Stylops* inhabit their bodies; more than thirty kinds of mites attach themselves to the heads or feet of ants; while Chalcididæ and Proctotrypidæ parasitize ants' eggs.

Origin of the Social Habit.—Wheeler regards “trophallaxis,” meaning exchange of nourishment, as the source of the social habit in wasps, ants, and termites; though admitting that the phenomenon has not been observed in the social bees. He says: “If we confine our attention largely to the ants, I believe it can be shown that trophallaxis, originally developed as a mutual trophic relation between the mother insect and her larval brood, has expanded with the growth of the colony like an ever-widening vortex till it involves, first, all the adults as well as the brood and therefore the entire colony; second, a great number of species of alien insects that have managed to get a foothold in the nest as scavengers, prædators or parasites (symphily); third, alien social insects—*i.e.*, other species of ants (social parasitism); fourth, alien insects that live outside the nest and are “milked” by the ants (trophobiosis); and, fifth, certain plants which are visited or sometimes partly inhabited by the ants (phytophily).”

CHAPTER XI

INSECT BEHAVIOR

The subject of insect behavior will be considered under three heads: (1) Tropisms, (2) Instinct, (3) Intelligence.

I. TROPISMS

Environmental influences, such as light, temperature or moisture, may control the direction of locomotion of an organism by determining the orientation of its body. The reaction of the organism under these circumstances is known as a *tropic*, or *tactic*, reaction. A moth, for example, flies toward a flame—is *positively phototropic*; a cockroach, on the contrary, avoids the light—is *negatively phototropic*. A plant turns toward the sun—in other words, is positively *heliotropic*.

An insect flies toward the light as inevitably and as mechanically as a plant turns toward the sun; indeed, the two phenomena are fundamentally the same. Some students prefer, however, to use the term *taxis* for bodily movements of motile organisms, and the term *tropism* for turning movements of fixed organisms.

The study of tropic reactions has already illuminated the entire subject of the behavior of organisms and placed it on a rational basis, and the complex tropisms of insects offer a fresh and large field to the investigator.

Chemotropism.—Positive and negative *chemotropism*, as Wheeler observes, “are among the most potent factors in the lives of insects.” Insects are affected positively or negatively by such substances as can affect their end-organs of smell or taste. Positive chemotropism enables many insects to find their food or their mates; and negative chemotropism enables them to avoid injurious substances. This negative reaction on the part of other organisms is made use of also by such insects as emit repellent odors.

A maggot orients its body with reference to a source of food and then moves toward the food just as mechanically as a moth flies to a flame. The maggot, as Loeb maintains, is influenced chemically by the radiating diffusion from a piece of meat, and follows a line of diffusion to the

center of diffusion in much the same way that a moth follows a ray of light to its source. In both cases a stimulus affects muscular tissue; the animal orients its body until the muscular tension is symmetrically distributed, and then locomotion brings the animal to the source of the stimulus, whether it be food or light.

The remarkable "instinctive" action of the fly in laying her eggs on meat is due, according to Loeb, simply to the fact that both the fly and the maggot have the same kind of positive chemotropism. Similarly also in the case of such butterflies or other insects as lay their eggs on a special kind of plant. It is certain that "neither experience nor volition plays any part in these processes."

W. M. Barrows determined experimentally that the well-known pomace fly, *Drosophila ampelophila*, is positively chemotropic to amyl alcohol, ethyl alcohol, acetic acid, lactic acid and other chemical substances, all of which occur in fermenting fruits. The fly finds its food, not by sight, but by smell, and when this sense is lost it reaches its food only by accident. The olfactory sense organs that are concerned with finding food are located in the third or terminal segment of the antenna. When one antenna is lost and the other antenna is stimulated by food odor, circus movements are carried out in such a way as to prove that the fly orients normally by an unequal stimulation of the antennæ. *Drosophila*, when stimulated by a weak food odor, first shows random movements, *i.e.*, it attempts to find the food by the method of trial and error, but as the fly passes into an area of greater stimulation, these movements give way to a direct orientation.

Hydrotropism.—Wheeler observed that beetles of the genera *Haliplus* and *Hydroporus* were positively *hydrotropic*; that when released on the shore from a bunch of water plants, they scrambled toward the lake, twenty feet away. Collectors take advantage of the negative hydrotropism of *Bembidion*, *Elaphrus*, *Omophron* and other shore-dwelling beetles by splashing the water upon the dry bank, when the beetles leave their places of concealment and are easily caught.

It is well known that after a rain ants carry their young out into the sunshine, though when the upper parts of the nest become too dry, the ants transfer their eggs, larvæ and pupæ to lower and moister galleries. In these instances, however, we have to deal with *thermotropism* as well as hydrotropism.

Thigmotropism.—Negative *thigmotropism* (*stereotropism*) as displayed in the withdrawal from contact, is a common phenomenon among animals, from Protozoa to Vertebrata, and is often conducive

to the safety of an organism; though the negative response occurs none the less, whether it is to prove useful or not, and occurs as automatically as the collapse of a sensitive plant at a touch.

Positive thigmotropism is less common, though nevertheless widespread among animals. Protozoa and Infusoria cling to solid bodies and become aggregated about them. Cockroaches squeeze themselves into crevices until their bodies come into close contact with surrounding surfaces. A moth, *Pyrophila* (*Amphipyra*) *pyramidoides*, is accustomed to squeeze into crevices under loose bark or elsewhere, though this habit, though doubtless protective, is not performed *for the purpose of* self-concealment. That this is not a case of negative phototropism, it was proved by Loeb, who wrote: "I placed some of these animals in a box, one-half of which was covered with a non-transparent body, the other half with glass. I covered the bottom of the box with small glass plates which rested on small blocks, and were raised just enough from the bottom to allow an *Amphipyra* to get under them. Then the *Amphipyra* collected under the little glass plates, where their bodies were in contact with solid bodies on every side, not in the dark corner where they would have been concealed from their enemies. They even did this when in so doing they were exposed to direct sunlight. This reaction also occurred when the whole box was dark. It was then impossible for anything but the stereotropic [thigmotropic] stimuli to produce the reaction."

Among the water-striders, Gerridæ, thigmotropism is strongly in evidence at the inception of and during the hibernation period. The gerrids hibernate in large groups or clusters under dead leaves, in holes in banks of streams, under logs, etc., with their bodies in close contact with the substratum. The acts of crawling into and remaining in such places are evidently due to the contact stimuli that impinge on them at such times (C. F. C. Riley).

Rheotropism.—Fishes swimming or heading directly against a current of water illustrate positive *rheotropism*. When facing the current, the resistance of the water is symmetrically distributed on the body of the animal and is met by symmetrical muscular action, in the most economical manner. Many aquatic insects offer such examples of rheotropism, either positive or negative.

E. P. Lyon gives, however, a different explanation. He found that fishes orient themselves just as well when they are put into a closed glass bottle, which is dragged through the water, although in this case they are not under the influence of any friction from the current. When the bottle is not moved the fishes swim in any direction inside the

bottle. It is obviously the motion of the retina images of the objects on the bank of the brook which causes the "rheotropic" orientation of fishes. When driven backward by the current or when dragged backward in a bottle through the water, the objects on the bank of the river seem to move in the opposite direction. The animal being compelled to keep the same object fixed, an apparent forward motion of the fixed object changes the muscles of the fins in such a sense as to cause the animal to follow the fixed object automatically. When such rheotropic fishes were kept in an aquarium and a white sheet of paper with black stripes was moved constantly in front of the aquarium the fishes oriented themselves against the direction in which the paper and its stripes moved. The phenomenon was more marked in young than in older specimens. All the phenomena of rheotropism ceased in the dark or when the fishes were blind. (J. Loeb.)

Anemotropism.—Various flies orient the body with reference to the direction of the wind. Wheeler observed swarms of the male of *Bibio albipennis* poising in the air, with all the flies headed directly toward the gentle wind that was blowing. If the wind shifted, the insects at once changed their position so as again to face to windward; a strong wind, however, blew them to the ground. The males of an anthomyiid (*Ophyra leucostoma*), according to the same naturalist, hover in swarms in the shade for hours at a time; if the breeze subsides they lose their definite orientation, but if it is renewed they face the wind with military precision. In Syrphidæ, he finds, either males or females are positively *anemotropic*. Midges of the genus *Chironomus*, which on summer days dance in swarms for hours over the same spot, orient themselves to every passing breeze. So also in the case of Empididæ, which Wheeler has observed swarming in one spot every day for no less than two weeks, possibly on account of "some odor emanating from the soil and attracting and arresting the flies as they emerged from their pupæ."

The Rocky Mountain locusts "move with the wind and when the air-current is feeble are headed away from its source;" when the wind is strong, however, they turn their heads toward it.

Anemotropism and rheotropism are closely allied phenomena. As Wheeler says, "The poising fly orients itself to the wind in the same way as the swimming fish heads upstream," adjusting itself to a gaseous instead of a liquid current. "In both cases the organism naturally assumes the position in which the pressure exerted on its surface is symmetrically distributed and can be overcome by a perfectly symmetrical action of the musculature of the right and left halves of the body."

Geotropism.—Gravity frequently determines the orientation and direction of locomotion of an animal. A freshly emerged moth hangs with the abdomen downward and remains in this position until the wings have expanded. Certain dolichopodid flies found on the bark of trees “rest or walk with the long axis of the body perpendicular to the earth and parallel with the long axis of the trunk of the tree and the head pointing upwards. When disturbed they fly off, but very soon alight nearer the earth and again walk upward.” (Wheeler.) Coccinellidæ (lady beetles) and cockroaches are also negatively *geotropic*.

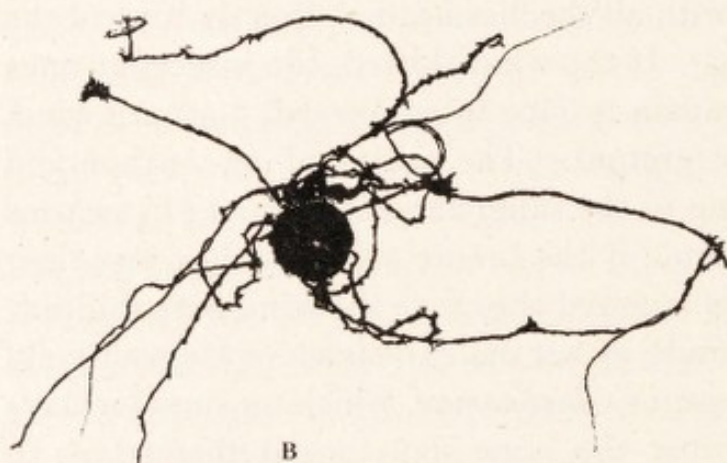


FIG. 296.—A, tracks made on paper by a larva of *Lucilia caesar* moving out of a spot of ink under the influence of light; A and B show respectively the first and second directions of the light. B, tracks made in the dark.—After POUCHET.

The latter insects, as Loeb has observed, tend to leave a horizontal surface but come to rest on a surface that is vertical or as nearly so as possible.

Wheeler says, “Geotropic as well as anemotropic orientation is not altered for the sake of response to light. Even if the insect be strongly heliotropic, as is the case in most Diptera, it orients itself to the wind or to gravity no matter whence the light may fall.”

Experiments by W. H. Cole show that the pomace fly, *Drosophila ampelophila*, when creeping, reacts negatively to grav-

ity, to a centrifugal force which is equal to or slightly greater than gravity, and to air currents without regard to other stimuli. Gravity is, then, a kinetic as well as a directive stimulus. The stimuli causing these reactions are probably received by the sensory nerves of the leg muscles. (Cole.)

Phototropism.—It is a matter of common observation that house flies, butterflies, bees and many other diurnal insects fly toward the light; and that cockroaches and bedbugs avoid the light. These are familiar examples of *phototropism* (*heliotropism*) or the “control of the direction of locomotion by light.” The phototropic response is

either positive or negative according as the organism moves, respectively, toward or away from the source of light. Maggots of *Lucilia caesar* and of many other flies are negatively phototropic as a rule (Fig. 296, *A*), but in the absence of light (other directive stimuli being excluded, of course) wander about indifferently (Fig. 296, *B*).

Do the different rays of the spectrum differ in phototropic power? This question has occurred to many investigators, who have found that, in general, the rays of shorter wave length, as violet or blue, are more effective than those of longer wave length, as yellow or red; the latter in fact acting like darkness. Ants avoid violet rays as they would avoid direct sunlight, but carry on their operations under yellowish red light as they would in darkness. Miss Fielde has made use of this fact in studying the habits of ants, by using as a cover for her artificial formicaries an orange-red sheet of glass such as the photographer uses for his dark room. Though ants avoid violet rays, they prefer them to ultra-violet rays, as Lubbock found.

These responses to light are inevitable on the part of the organism, whether they are beneficial or harmful, and it is now becoming recognized that the reactions of both plants and animals to light are fundamentally the same.

Phototaxis and Photopathy.—A phototropic organism, if bilaterally symmetrical, orients itself with the head directly toward or else directly away from the source of light and moves toward or away from the light, as the case may be. In either event the long axis of the organism becomes parallel with the rays of light. Now a ray of light is ever diminishing in intensity from its source, and it would seem that differences of intensity along the paths of light rays determine the orientation and consequent direction of locomotion of the organism. Some investigators, however, distinguish between the effects of *intensity* of light and those of its *direction*. Thus by ingeniously contrived experiments, it has been found, apparently, that *Protista* (Strasburger), *Daphnia* (Davenport and Cannon) and the caterpillars of *Porthesia* (Loeb) move toward a *source* of light even while, in so doing, they are passing into regions of *less* intensity of illumination. For this migration as determined by the *direction* of the light rays, the term *phototaxis* is by some authors (as Davenport) reserved. Usually, however, the direction of locomotion *does* depend on differences of intensity, without regard to the direction whence the light comes. This "migration towards a region of greater or less intensity of light" has been termed *photopathy*, and organisms are said to be *photophil* or *photophob*, accord-

ing as they move, respectively, toward or away from a more intensely illuminated area.

Verworn and others maintain, however, that differences of intensity are sufficient to account for all phototropic phenomena.

Optimum Intensity.—It has been found that there is a certain *optimum* degree of light, differing according to the organism, toward which the organism will move, from either a region of greater illumination or one of less. The organism appears to be *attuned* to a "certain range of intensity." This attunement is used by Davenport to explain apparent anomalies between the response to light of a butterfly and that of a moth. Butterflies are positively phototropic to sunlight and most moths are negatively so. Why, then, do moths fly toward a lamp or an electric light? The answer is given that the moth is positively phototropic up to a certain intensity of light, at which it becomes negatively phototropic. "Butterflies are attuned to a high intensity of light, moths to a low intensity; so that bright sunlight, which calls forth the one, causes the other to retreat. On the other hand, a light like that of a candle, so weak as not to stimulate a butterfly, produces a marked response in the moth." (Davenport.)

The circling of moths and other insects about a light is a matter of common observation, an explanation for which has been given by Loeb. Loeb says, "If a moth be struck by the light on one side, those muscles which turn the head toward the light become more active than those of the opposite side, and correspondingly the head of the animal is turned toward the source of light. As soon as the head of the animal has this orientation and the median-plane (or plane of symmetry) comes into the direction of the rays of light, the symmetrical points of the surface of the body are struck by the rays of light at the same angle. The intensity of light is the same on both sides, and there is no reason why the animal should turn to the right or left, away from the direction of the rays of light. Thus it is led to the source of the light. Animals that move rapidly (like the moth) get into the flame before the heat of the flame has time to check them in their flight. Animals that move slowly are affected by the increasing heat as they approach the flame; the high temperature checks their progressive movement and they walk or fly slowly about the flame." As Loeb insists, the moth "does not fly into the flame out of 'curiosity,' neither is it 'attracted' by the light; it is only *oriented* by it and in such a manner that its median-plane is brought into the direction of the rays and its head directed toward the

source of light. In consequence of this orientation its progressive movements must lead it to the source of light."

Factors Influencing Phototropism.—The response of an organism to light is influenced by previous exposure to light, by temperature, moisture, nutrition and other factors, all of which have to be taken into account in experiments on phototropism.

Loeb found that larvæ of the brown-tail moth, *Euproctis chrysorrhæa*, driven by the warm sunshine out of the nest in which they have hibernated, crawl upward to the tips of branches and feed upon the buds and new leaves. This self-preservative "instinct" is purely a response to light. The caterpillars are positively phototropic, and as the horizontal components of the surrounding light neutralize each other, only the light from above is effective as a stimulus to orientation. After feeding, however, the larvæ are no longer positively phototropic and crawl downward; in other words, they are positively phototropic only so long as they are unfed. Here the kind of phototropism is dependent upon nutrition.

Phototropism may be overruled by chemotropism and influenced by conditions of metabolism, as Parker found for the butterfly *Vanessa antiopa*. In his words: *Vanessa antiopa*, in bright sunlight, comes to rest with the head away from the source of light, that is, it is negatively phototropic, when the surface on which it settles is not perpendicular or very nearly perpendicular to the direction of the sun's rays. When, however, this surface is perpendicular to the sun's rays the insect settles without reference to the direction of the rays. When feeding or near food [such as running sap] the butterflies do not respond phototropically.

This negative phototropism is seen only in intense sunlight and after the butterfly has been on the wing, *i.e.*, after a certain state of metabolism has been established.

V. antiopa creeps and flies toward a source of light, that is, it is positively phototropic in its locomotor responses. Positive phototropism also occurs in intense sunlight, and is not dependent upon any particular phase of metabolism.

Both negative and positive phototropism in this species are independent of the "heat rays" of sunlight.

The position assumed in negative phototropism exposes the color patterns of the wings to fullest illumination, and probably has to do with bringing the sexes together during the breeding season.

To these may be added other important conclusions of Parker's:

No light reactions are obtained from the butterfly when shadows are thrown upon any part of the body except the head. When one eye is painted black the butterfly creeps or flies in circles ("circus movements") with the unaffected eye always toward the center. When both eyes are painted black all phototropic responses cease and the insect flies upward. Butterflies with normal eyes liberated in a perfectly dark room come to rest near the ceiling. This upward flight in both cases is due to negative geotropism, not to phototropic activity.

V. antiopa does not discriminate between lights of greater or less intensity provided they are all of at least moderate intensity and of approximately equal size. *V. antiopa* does discriminate between light derived from a large luminous area and that from a small one, even when the light from these two sources is of equal intensity as it falls on the animal. These butterflies usually fly toward the larger areas of light. This species remains in flight near the ground because it reacts positively to large patches of bright sunlight rather than to small ones, even though the latter, as in the case of the sun, may be much more intense.

V. antiopa retreats at night and emerges in the morning, not so much because of light differences, as because of temperature changes. On warm days it will, however, become quiet or active, without retreating, depending upon a sudden decrease or increase of light.

The maggots of the muscid *Phormia regina* are, as the author has observed, negatively phototropic until full grown, when they become positively phototropic for an hour or less, leave the decaying matter in which they have developed and wriggle along the ground toward the sun; or if the sunlight is diffused by clouds, wander about aimlessly, but at length bury themselves in the ground to pupate. Here the positive phototropism just before pupation is adaptive.

The swarming of the honey bee is likewise a case of periodic positive phototropism, as Kellogg has observed.

Winged ants of both sexes are strongly positively phototropic when they swarm from the ground for the nuptial flight. After mating, however, the female becomes negatively phototropic and positively thigmotropic; enters the ground, sheds her wings, and enters upon a subterranean existence, during which she is intensely positively thigmotropic. In connection with this subject, it is a significant fact that the pomace fly, *Drosophila*, loses its phototropism when its wings are removed artificially.

In autumn, gravid females of the mosquito, *Culex pipiens*, become

strongly negatively phototropic and seek dark hibernation quarters, in spite of warm temperatures that may prevail. If hibernating in a warm place the mosquito becomes positively thigmotropic, and loses its phototropism, prolonged exposure to strong lights producing no response, though the insect responds actively to mechanical stimuli. It is also negatively geotropic, as it always assumes a position with the long axis of the body perpendicular to the earth and the head pointing upward. (H. B. Weiss.)

Though adaptive in their results, these phototropic reactions can scarcely be said to be performed *on account of* their usefulness. They are performed anyway, and may result harmfully, as when they lead a moth into a flame or, to take a more natural example, when they expose an insect to its enemies.

Phototropism and thermotropism, either together or singly, as Wheeler suggests, may explain the up and down migration of insects in vegetation. "On cold, cloudy days few insects are taken because they lurk quietly near the surface of the soil and about the roots of the vegetation, but with an increase in warmth and light they move upwards along the stems and leaves of the plants, and, if the day be warm and sunny, escape into the air."

F. Payne bred sixty-nine successive generations of the pomace fly, *Drosophila ampelophila* in the dark without any resultant effect upon either the eyes or the phototropism of the flies.

Drosophila is usually positively phototropic, but R. S. McEwen obtained a mutant which is not phototropic; this character being "linked" with a characteristic "tan" color.

Muscle Tension Theory.—Experiments by Professor S. J. Holmes with water scorpions (*Ranatra*) showed that when the insect is illuminated from the right side the legs on the right side are flexed and those of the left side are extended, with a resultant locomotion toward the light. These and other experiments "leave no doubt that the primary effects of light consist in changes in the tension of muscles." (Loeb.) The muscle tone is dependent upon the intensity of the light. If a positively phototropic insect is illuminated from one side only it turns toward the light until the muscle tension is equal on the two sides of the body; then locomotion is inevitably toward the source of light. The stimulus is received through the eyes.

Artificial Heliotropic Machine.—As illustrating the purely mechanical nature of the response to light, the artificial heliotropic machine, as described by Loeb, may be referred to. Briefly, this

electrically-operated machine, invented by Mr. John Hays Hammond, Jr., is a box containing the mechanism and mounted on three wheels. Two of these are geared to a driving motor and the third, on the rear end, can be turned by means of electro-magnets in a horizontal plane. A pair of five-inch condensing lenses on the front end look like large eyes. If a portable electric light, as a hand flashlight, be turned on in front of the machine this will immediately move toward the light and will follow the light all around the room in complex manœuvres at a speed of about three feet per second. Upon shading or switching off the light the "dog," as it is called, can be stopped at once, but will resume its uncanny movements as soon as the light reaches the "eyes" of the machine in sufficient intensity. The orientation mechanism possesses two selenium cells, one behind each "eye," which when influenced by light effect the control of sensitive relays, analogous to the nervous system of a moth. These relays operate electro-magnetic switches, which control the driving motors and the steering wheel.

The principle of this mechanism has been applied to the "Hammond dirigible torpedo."

Thermotropism.—Ants are strongly *thermotropic*; they carry their eggs, larvæ and pupæ from a cooler to a warmer place or vice versa, and thus secure optimum conditions of temperature. Caterpillars and cockroaches migrate to regions of optimum temperature.

In thermotropism it appears that the *direction* of heat rays has little or no effect as compared with differences of *intensity*.

Tropisms in General.—Other kinds of tropisms are known, for example, *tonotropism*, or the control of the direction of locomotion by density, and *electrotropism* (*galvanotropism*); not to mention any more.

All these phenomena are responses of protoplasm to definite stimuli and are almost as inevitable as the response of a needle to a magnet.

The tropisms of the lower organisms have been experimented upon by many skilled investigators, whose results furnish a broad basis for the study of the subject in the higher animals. Even in the simplest organisms, behavior is the resultant effect of several or many stimuli acting at once, and the precise effect of each stimulus can be ascertained only by the most guarded kind of experimentation; while in the higher animals, with their complex organization, including specialized sense organs, the study of behavior becomes intricate and cannot be carried on intelligently without an extensive knowledge of the behavior of unicellular organisms. The properties of protoplasm are the key to the

behavior of organisms. Furthermore, the study of tropic reactions is complicated by the fact that they are due not only to external stimuli, but also to little-understood internal stimuli, arising from unknown conditions of the alimentary canal, muscles, reproductive organs, etc.

A recognized property of protoplasm is that of adaptation, as manifested in the acclimatization of protoplasm to untoward conditions of temperature, light, contact and other stimuli; and this adaptation to unusual conditions may take place without the aid of natural selection.

A tropic reaction occurs, whether it is to prove useful to the organism or not. Thus a lady-bird beetle walks upward, on a branch, on a fence, on one's finger. It walks upward as far as possible and then flies into the air. If it happens to reach the tip of a twig and finds aphids there, the beetle stops and feeds upon them. This adaptive result is in a sense incidental. Yet, upon the whole, tropic reactions are wonderfully adaptive in their results. Here natural selection is of special value as affording an explanation of the phenomena.

As Loeb and Davenport have insisted, the mechanical reactions to gravity, light, heat and other influences determine the behavior of the organism.

2. INSTINCT

Insects are eminently instinctive; though their automatic behavior is often so remarkably successful as to appear rational, instead of purely instinctive.

A satisfactory definition of "instinct" seems to be impossible, though some of the characteristics of instinctive behavior are quite evident.

Instinct, as distinguished from reason, attains adaptive ends without prevision and without experience. For example, a butterfly selects a particular species of plant upon which to lay her eggs. Caterpillars of the same species construct the same kind of nest, though so isolated from one another as to exclude the possibility of imitation. Every caterpillar that pupates accomplishes the intricate process after the manner of its kind, without the aid of experience.

Instinctive actions belong to the reflex type—they consist of co-ordinated reflex acts. A complex instinctive action is a chain, each link of which is a simple reflex act. In fact, no sharp line can be drawn between reflexive and instinctive actions.

Basis of Instinct.—Reflex acts, the elements from which instinctive actions are compounded, are the inevitable responses of particular organs

to appropriate stimuli, and involve no volition. The presence of an organ normally implies the ability to use it. The newly born butterfly needs no practice preliminary to flight. The process of stinging is entirely reflex; a decapitated wasp retains the power to sting, directing its weapon toward any part of the body that is irritated; and a freshly emerged wasp, without any practice, performs the stinging movements with greatest precision.

As Whitman observes, the roots of instincts are to be sought in the constitutional activities of protoplasm.

Apparent Rationality.—The ostensible rationality of behavior among insects, as was said, often leads one to attribute intelligence to them, even when there is no evidence of its existence. As an illustration, many plant-eating beetles, when disturbed, habitually drop to the ground and may escape detection by remaining immovable. We cannot, however, believe that these insects “feign death” with any consciousness of the benefit thus to be derived. This act, widespread among animals in general, is instinctive, or reflex, as Whitman maintains, being at the same time, one of the simplest, most advantageous and deeply seated of all instinctive performances.

Take the many cases in which an insect lays her eggs upon only one species of plant. The *philenor* butterfly hunts out *Aristolochia*, which she cannot taste, in order to serve larvæ, of whose existence she can have no foreknowledge. Oviposition is here an instinctive act, really a chemotropism, which is not performed until it is evoked by some sort of stimulus—probably an olfactory one—from a particular kind of plant.

Stimuli.—Some determinate sensory stimulus is, indeed, the necessary incentive to any reflex act. The first movements of a larva within the egg-shell are doubtless due to a sensation, probably one of temperature. Simple contact with the egg-shell is probably sufficient to stimulate the jaws to work, and the caterpillar eats its way out; yet it cannot foresee that its biting is to result in its liberation. Nor, later on, when voraciously devouring leaves, can the caterpillar be supposed to know that it is storing up a reserve supply of food for the distant period of pupation and the subsequent imaginal stage. The ends of these reflex actions are proximate and not ultimate, except from the standpoint of higher intelligence.

Just as simple reflexes link together to form an instinctive action, so may instincts themselves combine. The complex behavior of a solitary wasp is a chain of instincts, as the Peckhams have shown. All the operations of making the nest, stinging the prey, carrying it to the nest, etc.,

are performed as a rule in a definite, predicable sequence, and even a slight interference with the normal sequence disconcerts the insect. Just as the performance of one reflex act may serve as the stimulus for the next reflex in order, so the completion of one instinctive action may be in part the stimulus for the next one.

Modification of Instincts.—An action can be regarded as purely instinctive in its initial performance only, because every subsequent performance may have been modified by experience; in other words, habits may have been forming and fixing, so that the results of instinct become blended with those of experience. Thus the first flight of a dragon fly is instinctive and erratic, but later efforts, aided by experience, are well under control.

When once shaped by experience, reflex or instinctive actions tend to become intense habits. Thus, certain caterpillars, having eaten all the available leaves of a special kind, will almost invariably die rather than adopt a new food plant, whereas larvæ of the same species will eat a strange plant if it is offered to them at birth. An act is strengthened in each repetition by the influence of habit, to the increasing exclusion of other possible modes of action. Many a caterpillar, having eaten its way out of the egg-shell, does not stop eating, but consumes the remainder of the shell—a reflex act, started by a stimulus of contact against the jaws and continued until the cessation of the stimulus, unless some stronger stimulus should intervene. It has been said that the larva eats the remains of the shell because they might betray its presence to its enemies. Whether this is true or not, to assume conscious foresight of such a result on the part of an inexperienced caterpillar is worse than unnecessary.

With insects, as with other animals, many instincts are transitory; even when partially fixed by habit, they are replaceable by stronger instincts. Thus the gregarious habit of larvæ is finally overpowered by a propensity to wander, which does not mature, however, until the approach of the transformation period. The reproductive instinct is another of those impulses that do not ripen until a certain age in the individual.

Inflexibility of Instincts.—Broadly speaking, instinctive actions lack individuality—are performed in the same way by every individual of the species. The solitary wasps of the same species are remarkably consistent in architecture, in the selection of a special kind of prey, in the way they sting it, carry it to the nest and dispose of it; all these operations, moreover, are performed in a sequence that is characteristic

of the species. Examples of this so-called inflexibility of instinct are so omnipresent, indeed, that insect behavior as a whole is admitted to be instinctive, or automatic. Insects are capable of an immense number of reflex impulses, ready to act singly or in intricate correlation, upon the requisite stimuli from the environment.

To normal conditions of the environment, the behavior of an insect is accurately adjusted; but in the face of abnormal circumstances demanding the exercise of judgment, most insects are helpless. The specialization to one kind of food, though usually advantageous, is fatal if the supply becomes insufficient and the larva is unable to adopt another food. A species of *Sphex* habitually drags its grasshopper victim by one antenna. Fabre cut off both antennæ and then found that the wasp, after vain efforts to secure its customary hold, abandoned the prey. Under such unaccustomed conditions, insects often show a surprising stupidity, capable as they are amid ordinary circumstances.

Flexibility of Instincts.—Notwithstanding such examples, the common assertion that instincts are absolutely “blind,” or inflexible, is incorrect. Instinctive acts are not mechanically invariable, though their variations are so inconspicuous as frequently to escape casual observation. A precise observer can detect individual variations in the performance of any instinctive act—variations analogous to those of structure.

To take extreme examples, the Peckhams found that an occasional queen of *Polistes fusca* would occupy a comb of the previous year, instead of building a new one; and that an individual of *Pompilus marginatus*, instead of hiding her captured spider in a hole or under a lump of earth as usual, hung it up in the fork of a purslane plant. They observed also that one *Ammophila*, in order to pound down the earth over her nest, actually used a stone, held between the mandibles (Fig. 297).

This performance, which has been witnessed also by Professor Williston and a few other observers, illustrates the flexibility of instinctive action, and has been cited as an instance of adaptability, or intelligence. It can not be supposed, however, that the insect is conscious of the efficiency of a stone as a tool. The performance may be an accident. If one observes an *Ammophila* at work he will notice that she not only pounds down the earth with her head, but also lifts and lays aside small stones with her mandibles. Possibly she now and then chances to begin the pounding movement before she has happened to release a stone from her jaws.

Even the despotic power of habit may be overborne by individual adaptability. Among caterpillars that have exhausted their customary food, there are often a few that will adopt a new food plant and survive, leaving their more conservative fellows to starve.

As Darwin himself held, the doctrine of natural selection is applicable to instincts as well as structures. All reflex acts are to some extent variable. Disadvantageous reflexes or combinations of reflexes eliminate themselves, while advantageous ones persist and accumulate.

Indeed, structures and instincts must frequently have evolved hand in hand. The remarkable protective resemblance of the *Kallima* butter-

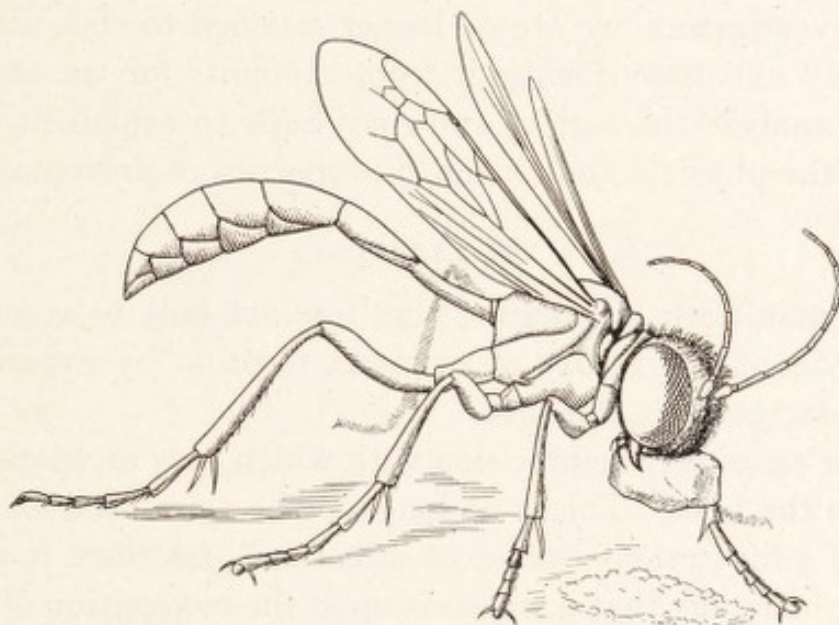


FIG. 297.—*Ammophila urnaria* using a stone to pound down the earth over her nest. Greatly enlarged.—After PECKHAM, from Bull. Wisconsin Geol. and Nat. Hist. Survey.

fly would be useless, did not the insect instinctively rest among dead leaves of the appropriate kind.

Origin of Instinct.—There are two leading theories as to the origin of instinct. Lamarck, Romanes and their followers have regarded instinct as inherited habit; have supposed that instincts have originated by the relegation to the reflex type of actions that at first were rational, and that instincts represent the accumulated results of ancestral experience. This *habit* theory, however, has little to support it, and assumes the inheritance of acquired characters—which has not been proved.

The selection theory of Darwin, Weismann, Morgan and others has much in its favor. It regards reflex acts as primitive, as the raw material from which natural selection, as the chief factor, has effected those combinations that are termed instincts.

Instincts and Tropisms.—We have already emphasized the fact that an instinct is a reflex act or a combination of reflex acts. The same fact may now be stated in these words: an instinct is a *tropism* or a combination of *tropisms*. The more important of these tropisms have been considered. Whenever possible it is better to discard the ambiguous term *instinct* in favor of such more precise terms as *phototropism*, *geotropism*, etc.; though the term *instinct* remains useful as applied to an action that is the resultant of several tropic responses.

The modern student of instincts aims to resolve them into their component reflexes and to determine as precisely as possible the influence of each reflex component. Thanks to the labors of a great number of skilled investigators, we are no longer satisfied to class an action as "instinctive" and then dismiss it from thought; for we are now in a position to analyze the action, and may hope to explain it eventually in terms of the physical and chemical properties of protoplasm.

3. INTELLIGENCE

Though manifestly dominant, pure instinct fails to account for all insect behavior. The ability of an insect to profit by experience indicates some degree of intelligence.

Take, for example, the precision with which bees or wasps find their way back to the nest. This is no longer to be accounted for on the assumption of a mysterious "sense of direction," for there is the best of evidence for believing that it depends upon the recognition of surrounding objects. When leaving the nest for the first time, these insects make "locality studies," which are often elaborate. Referring to a digger-wasp, *Sphex ichneumonea*, the Peckhams write: "At last, the nest dug, she was ready to go out and seek for her store of provision and now came a most thorough and systematic study of the surroundings. The nests that had been made and then deserted had been left without any circling. Evidently she was conscious of the difference and meant, now, to take all necessary precautions against losing her way. She flew in and out among the plants first in narrow circles near the surface of the ground, and now in wider and wider ones as she rose higher in the air, until at last she took a straight line and disappeared in the distance. The diagram [Fig. 298, A] gives a tracing of her first study preparatory to departure. Very often after one thorough study of the topography of her home has been made, a wasp goes away a second time with much less circling or with none at all. The second diagram [Fig. 298, B] gives a fair illustration of one of these more hasty departures. . . .

"If the examination of the objects about the nest makes no impression upon the wasp, or if it is not remembered, she ought not to be inconvenienced nor thrown off her track when weeds and stones are removed and the surface of the ground is smoothed over; but this is just what happens. *Aporus fasciatus* entirely lost her way when we broke off the leaf that covered her nest, but found it without trouble when the missing object was replaced. All the species of *Cerceris* were extremely annoyed if we placed any new object near their nesting-places. Our *Ammophila* refused to make use of her burrow after we had drawn

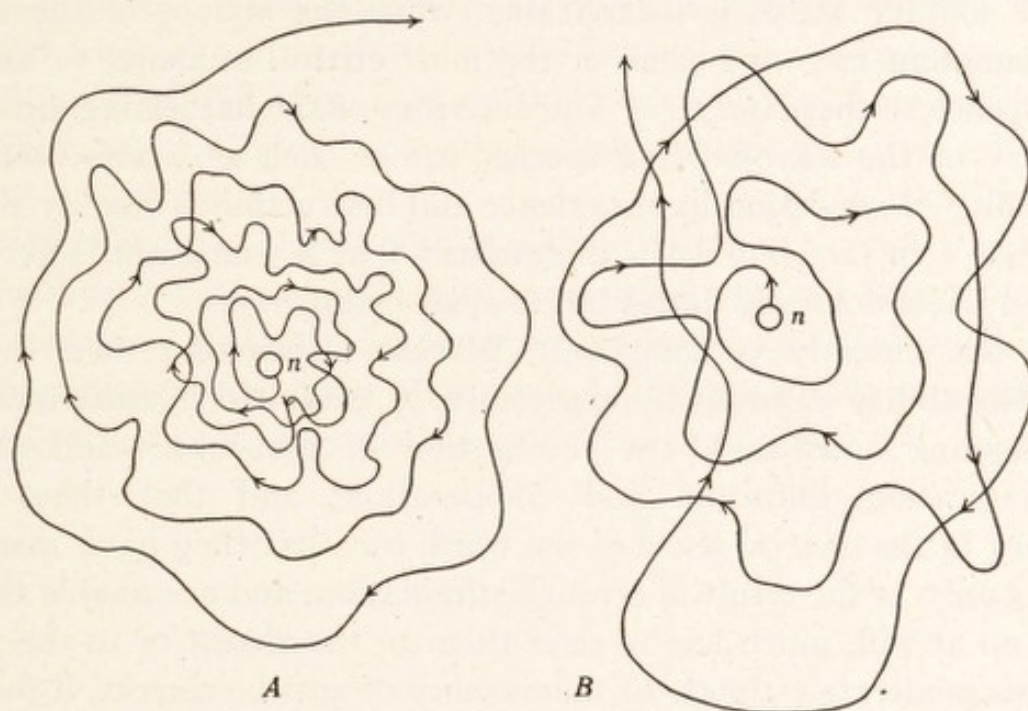


FIG. 298.—Locality studies made by a wasp, *Sphex ichneumonea*. A, a thorough study; B, a hasty study; n, nest.—After PECKHAM, from Bull. Wisconsin Geol. and Nat. Hist. Survey.

some deep lines in the dust before it. The same annoyance is exhibited when there is any change made near the spot upon which the prey of the wasp, whatever it may be, is deposited temporarily."

If we take, as one criterion of intelligence, the power to choose between alternatives, then insects are more intelligent than is generally admitted. The control of locomotion, the selection of prey, and the avoidance of enemies, as results of experience, indicate powers of discrimination. The power of intercommunication, conceded to exist among social Hymenoptera, implies some degree of intelligence.

If instinct is blind, or mechanical, with no adjustment of means to ends, then a pronounced individuality of action must signify something more than instinct. In regard to a female *Pompilus scelestus*, which had dragged a large spider nearly to her nest, the Peckhams observe:

"presently she went to look at her nest and seemed to be struck with a thought that had already occurred to us—that it was decidedly too small to hold the spider. Back she went for another survey of her bulky victim, measured it with her eye, without touching it, drew her conclusions, and at once returned to the nest and began to make it larger. We have several times seen wasps enlarge their holes when a trial had demonstrated that the spider would not go in, but this seemed a remarkably intelligent use of the comparative faculty."

From the standpoint of pure instinct, indeed, much of the behavior of the solitary wasps is inexplicable; while the actions of the social Hymenoptera have led some of the most critical students to ascribe intelligence to these insects. The activities of the harvesting ants, the military or the slave-holding species, are of such a nature that the possibility of education by experience and instruction is strong, to say the least. In fact, Forel has maintained that a young ant is actually trained to its domestic duties by its older companions.

In his scholarly volume, *Ants*, Wheeler shows that these insects have the ability to profit by experience, as exhibited in their foraging and homing operations, the recollection of nest-mates and aliens, communication, imitation and co-operation; and that they have memory in the general sense of the word, but that they have memory images only as the result of sensory stimulation, and are unable to call them up at will, much less to refer them to the absent or to the past. "If this moderate estimate of the memory of ants be correct, it follows that they must be incapable of reasoning—of 'focusing the wherefore,' to use Lloyd Morgan's expression, for a mere association of sense impressions is not deducing conclusions from premises." (Wheeler.)

It is extremely difficult, if not impossible, however, to draw the line between instinct and intelligence; and in doubtful cases there is a general tendency to exaggerate the importance of intelligence rather than that of instinct. For example, the well-known discrimination on the part of ants between members of their own colony and those of other colonies, even of the same species, would seem to imply intelligent recognition. This recognition is due, however, to a characteristic odor, which is derived from the mother of the community. An ant after being washed receives hostile treatment from others in its own colony; while an alien ant after being smeared with the juices of hostile ants is treated by the latter as a friend.

Each instance of apparent intelligence must be examined impartially on its own merits. At present it may be said that, while most of the

behavior of insects is purely instinctive, there is some reason to believe that at least gleams of intelligence appear in the most specialized Hymenoptera.

Lack of Rationality.—However intelligent the social Hymenoptera may be in their way, they show no signs of the power of abstract reasoning. Even ants, according to the experiments of Lubbock, display profound stupidity in the face of novel emergencies from which they might extricate themselves by abstract reasoning of the simplest kind. The thoughts of an ant or bee seem to be limited to simple associations of concrete things. Miss Enteman observed a *Polistes* worker which gnawed a piece out of the side of a dead larva of its own kind and, turning, actually offered it as food to the mouth of the same larva. In another instance a larva was attacked and killed, and then offered a piece of its own body.

Such examples as these emphasize the strength of the reflex factor in the behavior of insects. Indeed, the basis of all behavior is being sought in the reactions of protoplasm to external stimuli. Possibly even memory, consciousness and other attributes of intelligence will eventually be reduced to this basis, improbable as it may now seem.

CHAPTER XII

DISTRIBUTION

I. GEOGRAPHICAL

Importance of Dispersion.—Dispersion enables species to mitigate the intense competition and the rigid selection that result from crowded numbers; hence the tendency to disperse, being self-preservative, has become universal. Some species habitually emigrate in prodigious numbers: the African migratory locust, the Rocky Mountain locust, and the milkweed butterfly, which annually leaves the Northern states for the South in immense swarms, in autumn, and in the following spring straggles back to the North. *Vanessa cardui* occasionally migrates in immense numbers, as do also *Pieris*, some dragon flies and some beetles, notably Coccinellidæ.

Wide Distribution of Insects.—Insects have been found in almost every latitude and altitude explored by man. Butterflies and mosquitoes occur beyond the polar circle, the former in Lat. 83° N., the latter in Lat. 72° N., and a species of *Emesa* closely allied to our common *E. longipes* is recorded by Whymper from an altitude of 16,500 ft. in Ecuador, where, according to the same traveler, Orthoptera occur at 16,000 ft., *Pieris xanthodice* ranges above 15,000 ft., and dragon flies, Hymenoptera and scorpions reach a height of 12,000 ft., while twenty-nine species of Lepidoptera range upward of 7,300 ft. A very few species of insects inhabit salt water, *Halobates* being found far at sea; some kinds live in arid regions and a few even in hot springs, while caves furnish many peculiar species. In short, insects are the most widely distributed of all animals, excepting Protozoa and possibly Mollusca.

While all the large orders of insects are world-wide in distribution, the most richly distributed are Coleoptera, Thysanura and Collembola, the last two feeding usually upon minute particles of organic matter in the soil and being remarkably tolerant of extremes of temperature. The four chief families of butterflies occur the world over, as do several families of beetles. Of species that are essentially cosmopolitan we may mention the collembolan *Folsomia fimetaria*, and the butterflies *Vanessa cardui* and *Anosia plexippus*, while among beetles no less than one hun-

dred species are cosmopolitan or subcosmopolitan, including *Tenebrio molitor*, *Silvanus surinamensis*, *Dermestes lardarius*, *Attagenus piceus* and *Calandra oryzae*. The coccinellid genus *Scymnus* occurs in North America, Europe, Hawaii, Galapagos Islands and New Zealand, and *Anobium* and *Hydrobius* are distributed as widely. The huge noctuid, *Erebus odora*, occurring in Brazil on the lowlands, and in Ecuador at an altitude of 10,000 ft., finds its way up into the United States and even into Canada. The chinch bug and many other Central American forms also spread far northward, as described beyond.

Means of Dispersal.—This exceptional range of insects is due to their exceptional natural advantages for dispersal, chief among which are the power of flight and the ability to be carried by the wind. The migratory locust, *Schistocerca peregrina*, has been found on the wing five hundred miles east of South America. The home of the genus, according to Scudder, is Mexico and Central America, where 23 species are found; 20 occurring in South America, including the Galapagos Islands, 11 in the United States and 6 in the West Indies; and there is every reason to believe that *S. peregrina*—the biblical locust and the only representative of its genus in Africa—crossed over from South America, where it is found indeed at present. Darwin and others have recorded many instances of insects being taken alive far at sea; Trimen mentions moths and longicorn beetles as occurring 230 miles west of the African coast and *Sphinx convolvulus* as flying aboard ship 420 miles out. In these instances the insects have usually been assisted or carried by strong winds, particularly the trade-winds, and oceanic islands have undoubtedly been colonized in this way. On land, Webster has found that the direction in which the Hessian fly spreads is determined largely by the prevailing winds at the time when these delicate insects are on the wing, and that the San José scale insect spreads far more rapidly with the prevailing winds than against them, the wind carrying the larvæ as if they were so many particles of dust. The pernicious buffalo-gnat of the South emerges from the waters of the bayous and may be carried on a strong wind to appear suddenly in enormous numbers twenty miles distant from its breeding place. Mosquitoes are distributed locally by light breezes, but cling to the herbage during strong winds.

Ocean currents may carry eggs, larvæ or adults on vegetable drift to new places thousands of miles away. Thus the Gulf Stream annually transports thousands of tropical insects to the shores of Great Britain, where they do not survive, however.

Fresh-water streams convey incalculable numbers of insects in all stages; and insects as a whole are very tenacious of life, being able to withstand prolonged immersion in water, and even freezing, in many instances, while they can live for a long time without food.

The universal process of soil-denudation must aid the diffusion of insects, slowly but constantly.

Birds and mammals disseminate various insects in one way or another, while the agency of man is, of course, highly important. Intentionally, he has spread such useful species as the honey bee, the silkworm and certain useful parasites; incidentally he has distributed the San José scale, Colorado potato beetle, gipsy moth and many other pests.

Barriers.—The most important of the mechanical barriers which limit the spread of terrestrial species is evidently the sea. Mountain ranges retard distribution more or less successfully, though a species may spread along one side of a range and sooner or later pass through a break or else around one end. Mountain chains act as barriers, however, chiefly because they present unendurable conditions of climate and vegetation. For the same reason deserts are highly effective barriers. Indeed the most important checks upon distribution are those of climate, and of climatal factors temperature is the most powerful. Tropical species cannot, as a rule, survive and reproduce in regions of frost; most of the tropical species which have entered the United States are restricted to its narrow tropical belts (Plate IV). The stages of an insect are frequently so accurately adjusted to particular climatal conditions that an unfamiliar climate deranges the life cycle. Thus many Southern butterflies find their way every year to the Northern states, only to perish without reproducing their kind. Insects are, nevertheless, more adaptable than most other animals in respect to climate, and frequently follow their food plants into new climates, as in the case of the harlequin cabbage bug, which has pushed north from the tropics to Missouri, southern Illinois and Indiana.

Humidity ranks next to temperature in the importance of its influence upon the distribution of organisms, but in the case of animals acts for the most part indirectly, by its effects upon vegetation. Thus the effectiveness of an arid region as a barrier is due chiefly to the lack of vegetation in consequence of the lack of moisture. Excessive moisture, on the other hand, may act as a barrier. The Rocky Mountain locust, which formerly migrated eastward in immense swarms, succumbed in the moist valley of the Mississippi; the chinch bug is never seriously injur-

ous in wet years. Moisture checks the development of these and other insects in ways as yet unascertained; possibly it acts indirectly by favoring the growth of fungus diseases, to which insects are much subject.

The absence of proper food is more effective than climate, as a *direct* check upon the spread of an animal; food itself being, of course, dependent ultimately upon climatal factors and soil. Many insects, being confined to a single food plant, can not exist long where this plant does not occur; but they will follow the plant, as was just said, into new climates; thus *Anosia plexippus* is following the milkweed over the world. The butterfly *Euphydryas phaeton* is remarkably local in its occurrence, being limited to swamps where its chief food plant (*Chelone glabra*) grows; and *Epidemia epixanthe* is similarly restricted to cranberry bogs.

Former Highways of Distribution.—Many facts of distribution which are inexplicable under the present conditions of topography and climate become intelligible in the light of geological history. The marked similarity between the fauna of Europe and that of North America means community of origin; and though the Arctic zone now interposes as a barrier, there was once an opportunity for free dispersion when, in the early Pleistocene or late Pliocene, a land connection existed between Asia and North America and a warm climate prevailed throughout what is now the Arctic region.

The extraordinary isolation of the butterfly *Æneis semidea* on mountain summits in New Hampshire and Colorado (particularly Mt. Washington, N. H., and Pikes Peak, Col.) is explained by glacial geology. The ancestors of this species, it is thought, were driven southward before an advancing ice-sheet and then followed it back as it retreated northward, adapted as they were to a rigorously cold climate. Some of those ancestors presumably followed the melting ice up the mountain sides, until they found themselves stranded on the summits. Other individuals, undiverted from the lowlands, followed the retreating glacier into the far north; and at present there occurs throughout Labrador a species of *Æneis* which differs but slightly from its lonely ally of the mountain tops.

Glaciation undoubtedly had a profound effect upon the fauna and flora of North America. "With the slow southward advance of the ice, animals were crowded southward; with its recession they advanced again northward to reoccupy the desolated region, until now it has long been repopulated, either with the direct descendants of its former inhabitants or with such limitations to the integrity of the fauna as this

interruption of local life may have caused." (Scudder.) Probably many species were exterminated and many others became greatly modified, though little is known as to the relationship of the present fauna to the preglacial fauna. "The glacial cold still lingers over the northern part of this continent and our present animals are only a remnant of the rich fauna that existed in former ages, when the magnolia and the sassafras thrived in Greenland."

Island Faunæ.—The ability of insects to surmount barriers, under favorable circumstances, is strikingly shown in the colonization of oceanic islands. Not a few insects, including *Vanessa cardui*, have found their way to the isolated island of St. Helena. In the Madeira Islands, according to Wollaston, there are 580 species of Coleoptera, of which 314 are known to occur in Europe, while all the rest are closely allied to European forms. Subtracting 120 species as having been introduced probably or possibly through the agency of man, there remain 194 that have been introduced by "natural" means. The rest, 266 species, are endemic, though akin to European species.

The scanty insect fauna of the Galapagos Islands includes twenty species of Orthoptera, which have been studied by Scudder and by Snodgrass. Five of these are cosmopolitan cockroaches, doubtless introduced commercially, and the remaining fifteen are all "distinctly South and Central American in their affinities." Three of these fifteen are strong-winged species which doubtless arrived by flight from the neighboring mainland; indeed, Scudder records a *Schistocerca* (*S. exsul*) as having been taken at sea two hundred miles off the west coast of South America, or nearly half way to the Galapagos Islands. Thirteen of the fifteen are endemic, and five are apterous or subapterous, while a sixth has an apterous female. Apterous insects, noticeably common on wind-swept oceanic islands, may have been carried thither on driftwood, though it is more likely that the apterous condition arose on the islands, where the better-winged and more venturesome individuals may have been constantly swept out to sea and drowned, leaving the more feeble-winged and less venturesome individuals behind, to reproduce their own life-saving peculiarities.

The Coleoptera of the Hawaiian Islands, studied by Dr. Sharp, number 428 species, representing 38 families, and "are mostly small or very minute insects," the few large forms being non-endemic, with little or no doubt; 352 species are at present known only from this archipelago. Dr. Sharp distinguishes three elements in the fauna: "first, species that have been introduced, in all probability comparatively recently, by arti-

ficial means, such as with provisions, stores, building timber, ballast, or growing plants; many of these species are nearly cosmopolitan. Second, species that have arrived in the islands, and have become more or less completely naturalized; they are most of them known to be wood- or bark-beetles, but some that are not so may have come with the earth adhering to the roots of floating trees; a few, such as the Dytiscidæ, or water beetles, may possibly have been introduced by violent winds. Third, after making every allowance for introduction by these artificial and natural methods, there still remains a large portion standing out in striking contrast with the others, which we are justified in considering strictly endemic or autochthonous." Among the introduced genera are *Coccinella*, *Dermestes*, *Aphodius*, *Buprestis*, *Ptinus* and *Cerambyx*. The immigrant longicorns appear to have been derived "from the nearest lands in various directions"—the Philippine Islands, tropical America and the Polynesian Islands—and the same conclusion will probably be found to hold for the other immigrants, when their general distribution shall have been sufficiently studied. The endemic species number 214, or exactly half the total number of species, and are distributed among 9 families, as follows:

FAMILIES.	SPECIES.	GENERA.	ENDEMIC GENERA.
Carabidæ.....	51	7	7
Staphylinidæ.....	19	3	1
Nitidulidæ.....	38	2	1
Elateridæ.....	7	1	1
Ptinidæ (Anobiini).....	19	3	3
Cioidæ.....	19	1	0
Aglycyderidæ.....	30	1	1
Curculionidæ (Cossonini).....	21	3	3
Cerambycidæ.....	10	1	1

Sharp writes: "I think it may be looked on as certain that these islands are the home of a large number of peculiar species not at present existing elsewhere, and if so it follows that either they must have existed formerly elsewhere and migrated to the islands, and since have become extinct in their original homes, or that they must have been produced within the islands. This last seems the simpler and more probable supposition, and it appears highly probable that there has been a large amount of endemic evolution within the limits of these isolated islands."

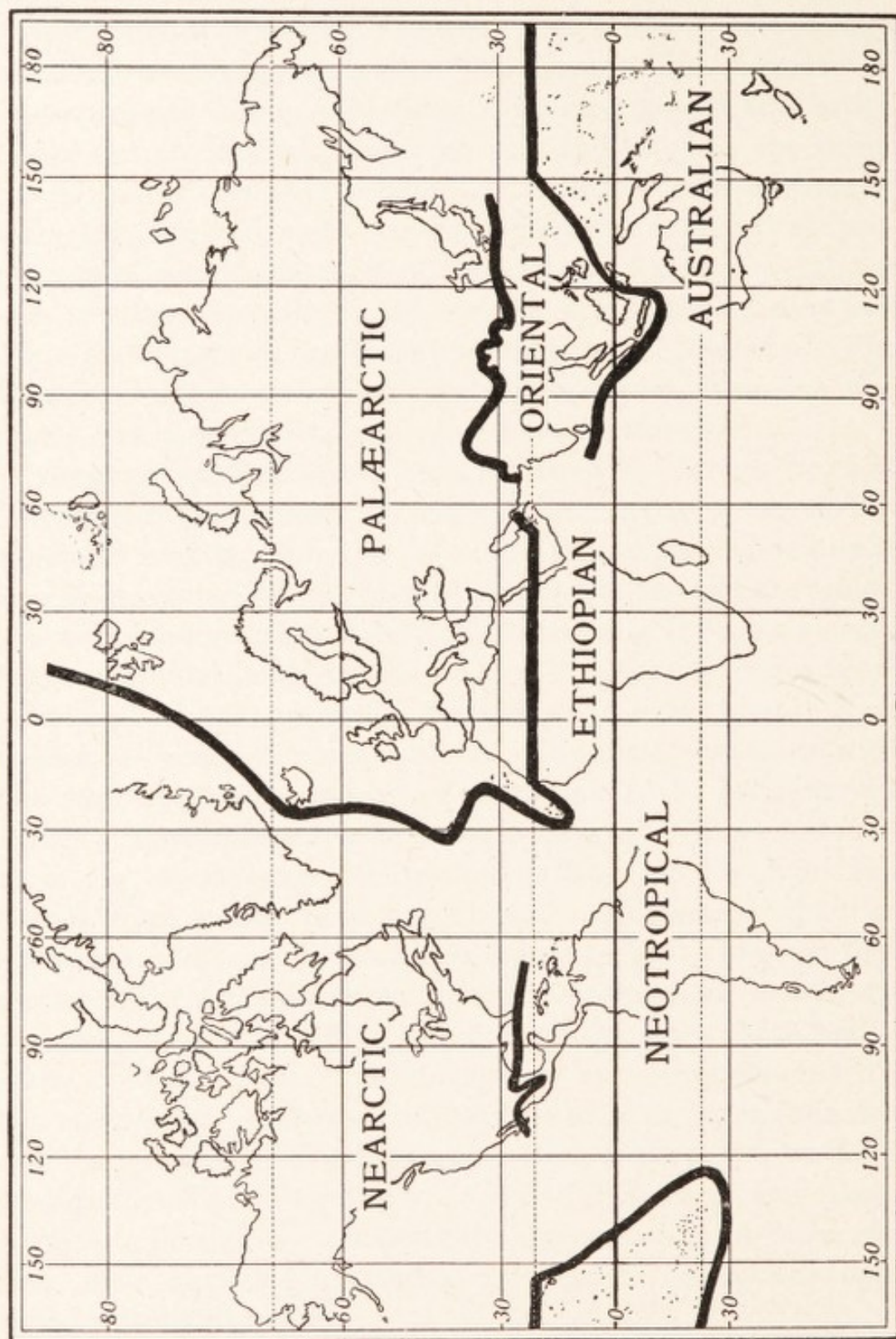
The parasitic Hymenoptera of Hawaii, according to Ashmead, number 14 families, 69 genera and 128 species; only eleven genera are endemic and most of the other genera are represented in nearly all the

known faunæ of the earth. Ashmead concurs in the view that the Hawaiian fauna was originally derived from the Australasian fauna—the view held by all the specialists who have studied Hawaiian insects.

Geographical Varieties.—Darwin found that wide-ranging species are as a rule highly variable. The cosmopolitan butterfly *Vanessa cardui* presents striking variations in different parts of the earth, largely on account of climatal differences, as is indicated by the temperature experiments of several investigators. Standfuss exposed German pupæ of this insect to cold, and obtained thereby a dark variety such as occurs in Lapland; and by the influence of warmth, obtained a very pale form such as occurs normally in the tropics only. Our *Cyaniris pseudargiolus*, which ranges from Alaska into Mexico and from the Pacific to the Atlantic, exhibits many geographical varieties, some of which are clearly due to temperature, as experiments have shown.

Geographical isolation is often followed by changes in the specific characters of an organism, as witness the endemic species and varieties of oceanic islands. Even in the same archipelago, the different islands may be characterized by different varieties of one and the same species, or even by different but closely allied species of the same genus. Thus Darwin and Alexander Agassiz found that in the Galapagos Islands each island had its own species of *Tropidurus* (a lizard) and had only one species, with almost no exceptions. The same phenomenon occurs in the two Galapagan species of *Schistocerca*—*S. melanocera* and *S. literosa*. In *melanocera*, as Scudder discovered, "Three or four distinct types are becoming gradually differentiated on the eight [now ten] islands from which they are known." Snodgrass, who has made important additions to Scudder's account, says, in regard to the two species, "The specimens from the different islands show striking though, in most cases, slight differences distinguishing the individuals of each island as a race, from those inhabiting any other island. There are two exceptions. Abingdon and Bindloe have the same form, and Albermarle supports at least two races." Each of these two species presents no less than five racial types, to which distinctive names have been applied. Though the relationships and evolution of these races have been ably discussed by Snodgrass, definite conclusions upon these subjects are still needed.

Faunal Realms.—The general distribution of life is such that naturalists divide the earth into several *realms*, each of which has its characteristic fauna and flora. As to the precise boundaries of these faunal realms, zoölogists do not all agree, owing chiefly to the fact that



Faunal Realms.—After SCLATER and WALLACE.

faunæ overlap one another to such an extent as to render their exact separation more or less arbitrary. Five realms, at least, are generally recognized: *Holarctic*, *Neotropical*, *Ethiopian*, *Oriental* and *Australian* (Plate III).

The *Holarctic* realm comprises the whole of Europe, Northern Africa as far south as the Sahara, Asia down to the Himalayas, and North America down to Mexico. Though the faunæ of all these areas are fundamentally alike (as Merriam and other authorities maintain), it is often convenient to divide the Holarctic into two parts: the *Palearctic*, including Europe and most of temperate Asia, being limited roughly by the Tropic of Cancer; and the *Nearctic*, occupying almost the entire continent of North America, including Greenland. The northern portion of the Holarctic realm forms a circumpolar belt with a remarkably homogeneous fauna and flora; therefore some authors distinguish an *Arctic* realm, limited by the isotherm of 32° , which marks very closely the tree-limit.

The boreal insects of Eurasia and North America are strikingly alike. Dr. Hamilton has catalogued almost six hundred species of beetles as being holarctic in distribution; five hundred of these are common to Europe, Asia and North America, and the remainder are known to occur in North America and also in Europe or Asia; one hundred are cosmopolitan or sub-cosmopolitan, to be sure, but fifty of these are probably holarctic in origin, for example—*Dermestes lardarius* (larder beetle) and *Tenebrio molitor* (meal-worm). Of butterflies, out of some two hundred and fifty species that are found in the United States east of the Rocky Mountains, scarcely more than a dozen occur also in the old world. North of the United States, however, as Scudder finds, no fewer than thirteen genera are represented in the old world by the same or by allied species.

The *Neotropical* realm embraces South America, Central America, the West Indies and the coasts of Mexico; Mexico being for the most part a transition tract between the Neotropical and the Nearctic. The richest butterfly fauna in the world is found in tropical South America. To this region are restricted, almost without exception, the Euplœinæ and Lemoniinæ and over ninety-nine per cent. of the Libytheinæ; here the Heliconiidæ and Papilionidæ attain their highest development, as do also the Cerambycidæ, or longicorn beetles.

The *Ethiopian* realm consists of Africa south of the Sahara, Southern Arabia and Madagascar; though some prefer to regard Madagascar as a distinct realm, the *Lemurian*. According to Wallace, the Ethiopian

realm has seventy-five peculiar genera of Carabidæ and is marvelously rich in Cetoniidæ and Lycænidæ.

The *Oriental* realm includes India, Ceylon, Tropical China, and the Western Malay Islands. In the richness of its insect fauna, this realm vies with the Neotropical. Danaidæ and Papilionidæ are abundant, while the genus *Morpho* is represented by some forty species; of Coleoptera, Buprestidæ are important and Lucanidæ especially so.

The *Australian* realm embodies Australia, New Zealand, the Eastern Malay Islands and Polynesia. Buprestidæ are here represented by forty-seven genera, of which twenty are peculiar; against this showing, the Oriental has forty-one genera and the Neotropical thirty-nine (Wallace). Strong affinities are said to exist between the Australian and Neotropical insect faunæ.

Life Zones of North America.—Merriam, the chief authority upon the subject, says: "The continent of North America may be divided,



FIG. 299.—Distribution of *Erynnis manitoba*, a butterfly restricted to subarctic and subalpine regions.—After SCUDDER.

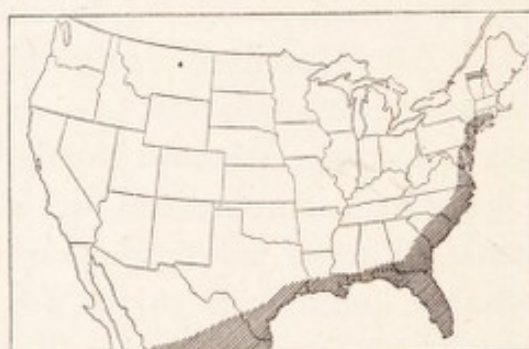


FIG. 300.—Distribution in the United States of *Eudamus proteus*, primarily a tropical butterfly.—After SCUDDER.

according to the distribution of its animals and plants, into three primary transcontinental regions—*Boreal*, *Austral* and *Tropical*." (Plate IV).

The *Boreal* region covers the northern part of the continent to about the northern boundary of the United States and continues southward along the higher portions of the mountain ranges. This region is divided into three transcontinental zones: (1) the *Arctic-Alpine*, lying above the limits of tree growth, in latitude or altitude; (2) the *Hudsonian*, comprising the northern part of the great transcontinental coniferous forest and the upper timbered slopes of the highest mountains of the United States and Mexico; (3) the *Canadian*, covering the remainder of the Boreal region. The butterfly *Erynnis manitoba* (Fig. 299) is strictly boreal in distribution.



Life Zones of the United States.—After MERRIAM.

The *Austral* region "covers the whole of the United States and Mexico, except the Boreal mountains and the Tropical lowlands." It comprises three transcontinental belts: (1) the *Transition* zone, in which the Boreal and the Austral overlap; (2) the *Upper Austral*; (3) the *Lower Austral*. The butterfly *Eudamus proteus* (Fig. 300) is restricted, generally speaking, to the Tropical region and the warmer and more humid portions of the Austral.

The *Tropical* region covers the southern extremity of Florida and of Lower California, most of Central America and a narrow strip along the two coasts of Mexico, the western strip extending up into California and Arizona.

These divisions are based primarily upon the distribution of mammals, birds and plants, and the three primary divisions serve almost equally well for insects also. In regard to the *zones*, however, not so much can be said—for insects are to a high degree independent of minor differences of climate. Many instances of this are given beyond.

The insect fauna of the United States is upon the whole a heterogeneous assemblage of species derived from several sources, and the foreign element of this fauna we shall consider at some length.

Paths of Diffusion in North America.—It may be laid down as a general rule that every species tends to spread in all directions and does so spread until its further progress is prevented, in one way or another. The paths along which a species spreads are determined, then, by the absence of barriers. The diffusion of insects in our own country has received much attention from entomologists, especially in the case of **such insects as are important from an economic standpoint.** The accessions to our insect fauna have arrived chiefly from Asia, Central and South America, and Europe.

Webster, our foremost student of this subject, to whom the author is indebted for most of his facts, names four paths along which insects have made their way into the United States: (1) *Northwest*—Northern Asia into Alaska and thence south and east; (2) *Southwest*—Central America through Mexico; (3) *Southeast*—West Indies into Florida; (4) *Eastern*—from Europe, commercially.

Northwest.—The northern parts of Europe, Asia and North America have in common very many identical or closely allied species, whose distribution is accounted for if, as geologists assure us, Asia and North America were once connected, at a time when a subtropical climate prevailed within the Arctic Circle; in fact, the distribution is scarcely explicable upon any other theory. Curiously enough, the trend of

diffusion seems to have been from Asia into North America and rarely the reverse, so far as can be inferred.

The lady-beetle, *Coccinella quinque-notata*, occurring in Siberia and Alaska, has spread to Hudson Bay, Greenland, Kansas, Utah, California and Mexico; while *C. sanguinea*, well known in Europe and Asia, ranges from Alaska to Patagonia; and *Ceratomegilla fuscilabris* from Vancouver and Canada to Chile. About six hundred species of beetles are holarctic in distribution, as was mentioned. Some of them inhabit different climatal regions in different parts of their range; thus *Lina lapponica* in the Old World "occurs only in the high north and on high mountain ranges, whereas in North America it extends to the extreme southern portion of the country," being widely diffused over the lowlands (Schwarz). Similarly, *Silpha lapponica* is strictly arctic in Europe, but is distributed over most of North America; *Silpha opaca*, on the contrary, is common all over Europe, but is strictly arctic in North America. *Silpha atrata*, common throughout Europe and western Siberia, was introduced into North America, but failed to establish itself.

Southwest.—Very many species have come to us from Central America and even from South America. South America appears to be the home of the genus *Halisidota*, according to Webster, who has traced several of our North American species as offshoots of South American forms. Many of our species may be traced back to Yucatan. *H. cinctipes* ranges from South America to Texas and Florida; *H. tessellaris* has spread northward from Central America and now occurs over the middle and eastern United States, while a form closely like *tessellaris* ranges from Argentina to Costa Rica; *H. caryæ* follows *tessellaris*, and appears to have branched in Central America, giving off *H. agassizii*, which extends northward into California. Similarly in the case of the Colorado potato beetle (*Leptinotarsa decemlineata*) and its relatives. According to Tower, the parent form, *L. undecimlineata*, seems to have arisen in the northern part of South America, to have migrated northward and, in the diversified Mexican region, to have split into several racial varieties. The parent form grades into *L. multilineata* of the Mexican table lands, which in turn, in the northern part of the Mexican plateau, passes imperceptibly into *L. decemlineata*, which last species has spread northward along the eastern slope of the western highlands, west of the arid region. In the lower part of the Mexican region the parent form may be traced into *L. juncta*, which has spread along the low humid Gulf Coast, up the Mississippi valley to southern Illinois, and along the Gulf Coast and up the Atlantic coast to Maryland, Delaware and New

Jersey. In general, the mountains of Central America and Mexico and the plateau of Mexico have been barriers to the northward spread of many species, which have reached the United States by passing to the east or to the west of these barriers, in the former case skirting the Gulf of Mexico and spreading northward along the Mississippi valley or along the Atlantic coast, in the latter event traveling along the Pacific coast to California and other Western states. Not a few species, however, have made their way from the Mexican plateau into New Mexico and Arizona; this is true of many Sphingidæ. The butterfly *Anosia berenice* ranges from South America into New Mexico, Arizona and Colorado; while many of the Libytheidæ have entered Arizona and neighboring states from Mexico. The chrysomelid genus *Diabrotica* is almost exclusively confined to the western hemisphere and its home is clearly in South America, where no fewer than 367 species are found. About 100 species occur in Venezuela and Colombia, "of which 11 extend into Guatemala, 8 into Mexico, and 1 into the United States." We have 18 species of *Diabrotica*, almost all of which can be traced back to Mexico, and several of them—as the common *D. longicornis*—to Central America. "The common *Dynastes tityus* occurs from Brazil through Central America and Mexico, and in the United States from Texas to Illinois and east to southern New York and New England." *Erebus odora* ranges from Ecuador and Brazil to Colorado, Illinois, Ohio, New England and into Canada, though it is not known to breed in North America, being in fact a rare visitor in our northern states.

Southeast.—Many South American species have made their way into southern and western Florida by way of the West Indies, while some subtropical species have reached Florida probably by following around the Gulf coast. The semitropical insect fauna of southern and southwestern Florida, including about 300 specimens of Coleoptera, according to Schwarz, is entirely of West Indian and Central American origin, the species having been introduced with their food plants, chiefly by the Gulf Stream, but also by flight, as in the case of Sphingidæ. Ninety-five species of Hemiptera collected in extreme southern Florida by Schwarz and studied by Uhler are distinctly Central American and West Indian in their affinities. Indeed Uhler is inclined to believe that the principal portion of the Hemiptera of the United States has been derived from the region of Central America and Mexico.

Eastern.—On the Atlantic coast are many European species of insects which have arrived through the agency of man. Most of them have not as yet passed the Appalachian mountain system, but some

have worked their way inland. Thus the common cabbage butterfly (*Pieris rapæ*), first noticed in Quebec about 1860, was found in the northern parts of Maine, New Hampshire and Vermont five or six years later, was established in those states by 1867, entered New York in 1868 and then Ohio. *Aphodius fossor* followed much the same course from New York into northeastern Ohio, as did also the asparagus beetle (*Crioceris asparagi*), the clover leaf weevil (*Hypera punctata*), the clover root borer (*Hylastinus obscurus*) and other species. In short, as Webster has pointed out, New York offers a natural gateway through which species introduced from Europe spread westward, passing either to the north or to the south of Lake Erie.

Inland Distribution.—*Pieris rapæ*, the spread of which in North America has been thoroughly traced by Scudder, reached northern New York in 1868 (as above), but appears to have been independently introduced into New Jersey in 1868, whence it reached eastern New York again in 1870; it was seen in northeastern Ohio in 1873, Chicago 1875, Iowa 1878, Minnesota 1880, Colorado 1886, and has extended as far south as northern Florida, but is apparently unable to make its way down into the peninsula.

The asparagus beetle, *Crioceris asparagi*, another native of Europe, became conspicuous in Long Island in 1856, spread southward to Virginia and westward to Ohio, where it was taken in 1886; it is frequent now in Illinois and Wisconsin and is known in Colorado and California. This insect, as Howard observes, flies readily, and may be introduced commercially in the egg or larval stage on bunches of asparagus.

The clover leaf weevil, *Hypera punctata*, common over Europe and most of Asia, was found in Canada some seventy years ago, has spread into Mississippi, Texas, Utah and Idaho, and is present on the Pacific coast also.

The lesser clover leaf weevil, *Phytonomus nigrirostris*, introduced from Europe into the United States, has spread steadily westward and has now reached Illinois, where it has been common since 1919.

Cryptorhynchus lapathi, a beetle destructive to willows and poplars, and common in Europe, Siberia and Japan, was found in New Jersey in 1882 and in New York in 1896, though known for many years previously in Massachusetts. It became noticeable in Ohio in 1901, and is steadily extending its ravages, being known now in Minnesota.

From Colorado the well-known potato beetle (*Leptinotarsa decemlineata*) has worked eastward since 1840, reaching the Atlantic coast,

and has even made its way several times into Great Britain, only to be stamped out with commendable energy. The box-elder bug (*Leptocoris trivittatus*) is similarly working eastward, having now reached Ohio. Formerly the Rocky Mountain locust periodically migrated eastward, but always met a check in the moist valley of the Mississippi.

The chinch bug (*Blissus leucopterus*), the distribution of which has been traced by Webster, has spread from Central America and Mexico northward along the Gulf coast into the United States, following three paths: (1) along the Atlantic coast to Cape Breton; (2) along the Mississippi valley and northward into Manitoba; (3) along the western coast of Central America and Mexico into California and other Western states. Everywhere this insect has found wild grasses upon which to feed, but has readily forsaken these for cultivated grasses upon occasion.

Every year some of the southern butterflies reach the Northern states, where they die without finding a food plant, or else maintain a precarious existence. Thus *Iphiclides ajax* occasionally reaches Massachusetts as a visitor and a visitor only; *Lærtias philenor*, however, finds a limited amount of food in the cultivated *Aristolochia*. *P. thoas*, one of the pests of the orange tree in the South, is highly prized as a rarity by New England collectors and is able to perpetuate itself in the Middle States on the prickly ash (*Xanthoxylum*). The strong-winged grasshopper, *Schistocerca americana*, belonging to a genus the center of whose dispersion is tropical America, ranges freely over the interior of North America, sometimes in great swarms, and its nymphs are able to survive in moderate numbers in the southern parts of Illinois, Ohio and other states of as high latitude, while the adults occasionally reach Ontario, Canada.

Many species are now so widely distributed that their former paths of diffusion can no longer be ascertained. The army worm (*Cirphis unipuncta*), feeding on grasses, and occurring all over the United States south of Lat. $45^{\circ} 23' N.$, is found also in Central America, throughout South America, and in Europe, Africa, Japan, China, India, etc.; in short, it occurs in all except the coldest parts of the earth, and where it originated no one knows.

Determination of Centers of Dispersal.—In accounting for the present distribution of life, naturalists employ several kinds of evidence. Adams recognizes ten criteria, aside from palæontological evidence, for determining centers of dispersal:

1. Location of greatest differentiation of a type.

2. Location of dominance or great abundance of individuals.
3. Location of synthetic or closely related forms (Allen).
4. Location of maximum size of individuals (Ridgway-Allen).
5. Location of greatest productiveness and its relative stability, in crops (Hyde).
6. Continuity and convergence of lines of dispersal.
7. Location of least dependence upon a restricted habitat.
8. Continuity and directness of individual variations or modifications radiating from the center of origin along the highways of dispersal.
9. Direction indicated by biogeographical affinities.
10. Direction indicated by the annual migration routes, in birds (Palmén).

2. GEOLOGICAL

Means of Fossilization.—Abundant as insects are at present, they are comparatively rare as fossils, the fossil species forming but one per cent. of the total number of described species of insects. The absence of insect remains in sedimentary rocks of marine origin is explained by the fact that almost no insects inhabit salt water; and terrestrial forms in general are ill-adapted for fossilization. The hosts of insects that die each year leave remarkably few traces in the soil, owing perhaps, in great measure, to the dissolution of chitin in the presence of moisture.

Most of the fossil insects that are known have been found in vegetable accumulations such as coal, peat and lignite, or else in ancient fresh-water basins, where the insects were probably drowned and rapidly imbedded. At present, enormous numbers of insects are sometimes cast upon the shores of our great lakes—a phenomenon which helps to explain the profusion of fossil forms in some of the ancient lake basins.

Insects in rich variety have been preserved in amber, the fossilized resin of coniferous trees. This substance, as it exuded, must have entangled and enveloped insect visitors just as it does at present. Many of these amber insects are exquisitely preserved, as if sealed in glass. Copal, a transparent, amber-like resin from various tropical trees, particularly Leguminosæ, has also yielded many interesting insects.

Ill-adapted as insects are by organization and habit for the commoner methods of fossilization, the number of fossil species already described is no fewer than three thousand.

Localities for Fossil Insects.—The Devonian of New Brunswick has furnished a few forms, found near St. John, in a small ledge that

outcrops between tide-marks; these forms, though few, are of extraordinary interest, as will be seen.

For Carboniferous species, Commentry in France is a noted locality, through the admirable researches of Brongniart, who described from there 97 species of 48 genera, representing 12 families or higher groups, 10 of which are regarded as extinct; without including many hundred specimens of cockroaches which he found but did not study. In this country many species have been found in the coal fields of Illinois, Nova Scotia, Rhode Island, Pennsylvania and Ohio.

Many fine fossils of the Jurassic period have been found in the lithographic limestones of Bavaria; 143 species from the Lias—four fifths of them beetles—were studied by Heer.

The Tertiary period has furnished the majority of fossil specimens. To the Oligocene belong the amber insects, of which 900 species are known from Baltic amber alone, and to the same epoch are ascribed the deposits of Florissant and White River in Colorado and of Green River, Wyoming. These localities—the richest in the world—have been made famous by the monumental works of Scudder. At Florissant there is an extinct lake, in the bed of which, entombed in shales derived from volcanic sand and ash, the remains of insects are found in astonishing profusion. For Miocene forms, of which 1,550 European species are known, the Eningen beds of Bavaria are celebrated as having furnished 844 species, described by the illustrious Heer.

Pleistocene species are supplied by the peats of France and Europe, the lignites of Bavaria, and the interglacial clays of Switzerland and Ontario, Canada.

Silurian and Devonian.—The oldest fossil insect known consists of a single hemipterous wing, *Protocimex*, from the Lower Silurian of Sweden. Next in age comes a wing, *Palæoblattina* (Fig. 301), of doubtful position,¹ from the Middle Silurian of France. Following these are six specimens of as many remarkable species from the Devonian shales of New Brunswick. The specimens, to be sure, are nothing but broken wings, yet these few fragments, interpreted by Dr. Scudder, are rich in meaning. All are neuropteroid, but they cannot be classified satisfactorily with recent forms on account of being highly synthetic in structure. Thus *Platephemera antiqua* (Fig.



FIG. 301.—*Palæoblattina douvillei*, natural size.—After BRONGNIART.

¹There is some evidence, it should be said, that this species is not an insect. Handlirsch denies also that *Protocimex* is an insect.

302), though essentially a May fly of gigantic proportions (spreading probably 135 mm.), has an odonate type of reticulation; while *Xenoneura* (Fig. 303) combines characters which are now distributed among Ephemeridæ, Sialidæ, Raphidiidæ, Coniopterygidæ, and other families, besides being in many respects unique. These Devonian forms attained huge dimensions as compared with their recent representatives; *Gerephmera*, for example, had an estimated expanse of 175 millimeters.

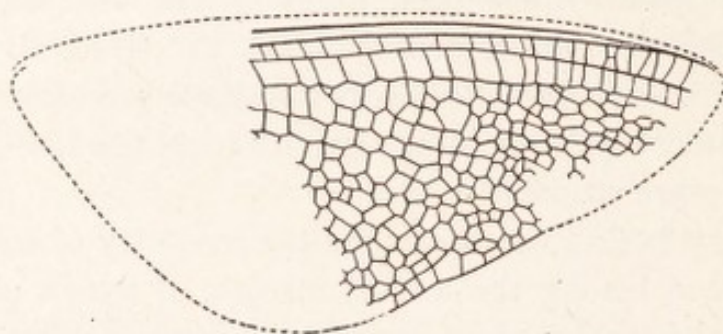


FIG. 302.—*Platephemera antiqua*, natural size.—After SCUDDER.

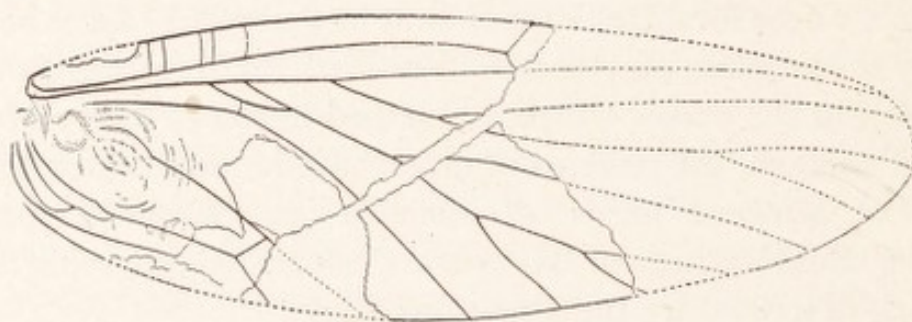


FIG. 303.—*Xenoneura antiquorum*, five times natural size.—After SCUDDER.

Carboniferous.—The Carboniferous age, with its luxuriant vegetation, is marked by the appearance of insects in great number and variety, still restricted, however, to the more generalized orders. The dominance of cockroaches in the Carboniferous is especially noteworthy, no fewer than 200 Palæozoic species being known from Europe and North America. These ancient roaches (Fig. 304) differed from their modern descendants in the similarity of the two pairs of wings, which were alike in form, size, transparency and general neuration, with six principal nervures in each wing; while in recent cockroaches the front wings have become tegmina, with certain of the veins always blended together, though the hind wings have retained their primitive characteristics with a few modifications, such as the expansion of the anal area. Carboniferous cockroaches furthermore exhibit ovipositors, straight, slender, and half as long again as the abdomen—organs which do not exist in recent species.

Lithomantis (Fig. 305), a remarkable form from Scotland, possessed in addition to its four large neuropteroid wings, a pair of prothoracic



FIG. 304.—*Etolblattina mazona*, a Carboniferous cockroach from Illinois. Twice natural size.—After SCUDDER in Miall and Denny.

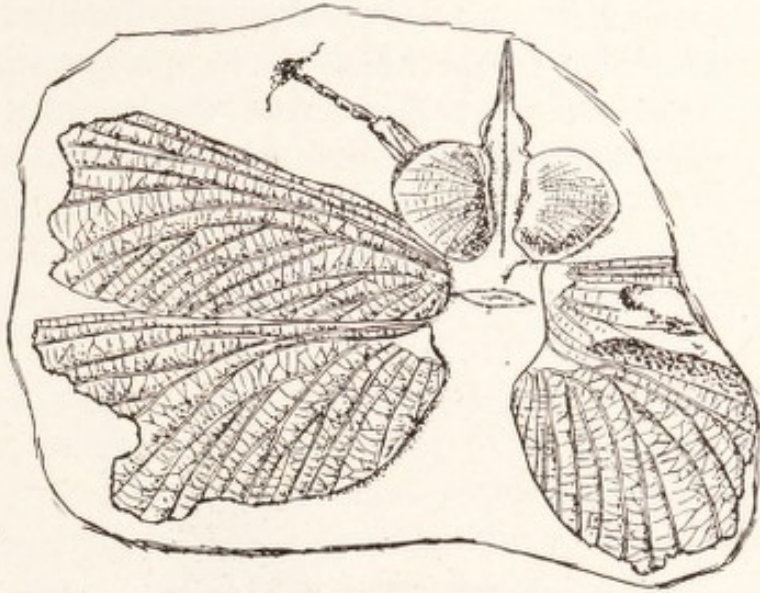


FIG. 305.—*Lithomantis carbonarius*, showing prothoracic appendages. Two thirds natural size.—After WOODWARD.

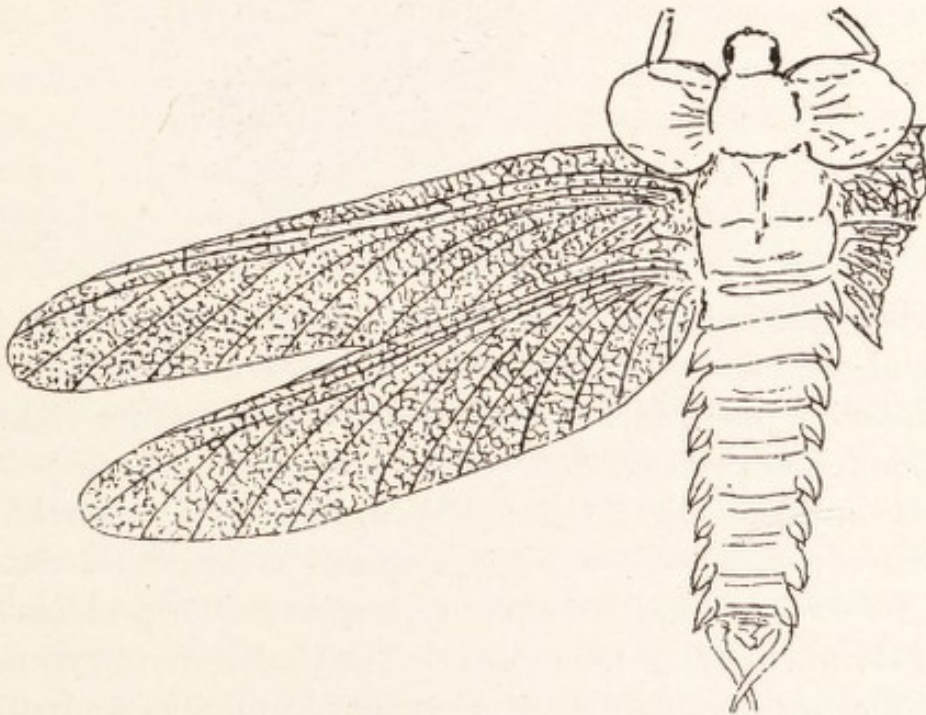


FIG. 306.—*Stenodictya lobata*, showing wing-like appendages of prothorax and abdomen. Natural size.—After HANDLIRSCH.

wing-like appendages which, provided they may be regarded as homologous with wings, represent a third pair, either atrophied or undeveloped

—a condition which is never found today, unless the patagia of Lepidoptera represent wings, which is unlikely.

Stenodictya lobata (Fig. 306) described by Brongniart from the Upper Carboniferous of Commentry, France, also bears prothoracic "wings" and, in addition, eight pairs of abdominal wing-like or gill-like appendages. No fewer than five families of Palæozoic insects are represented by specimens having prothoracic wings.

From the rich deposits of Commentry, Brongniart has described several forms of striking interest. *Dictyoneura* is a Carboniferous genus

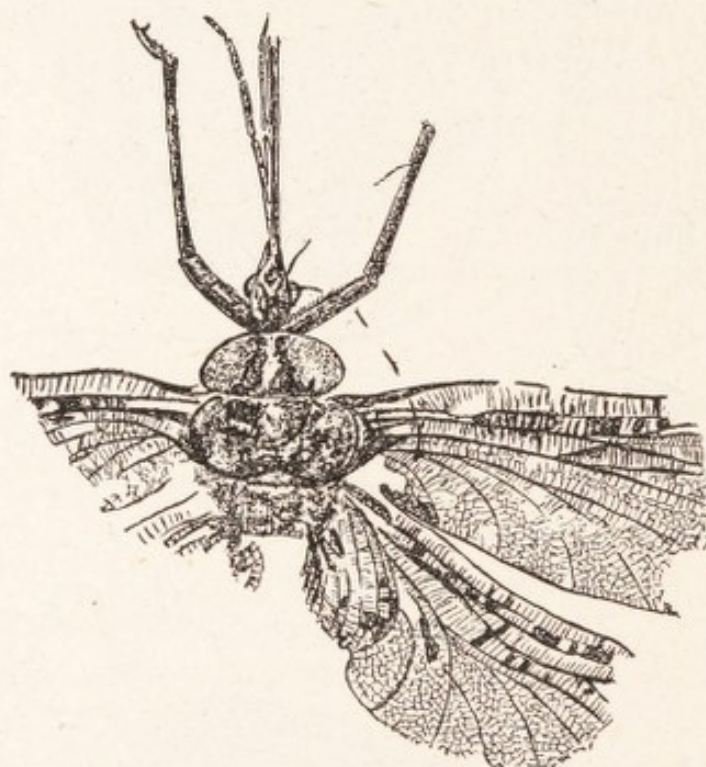


FIG. 307.—*Eugereon böckingi*. Three quarters natural size.—After DOHRN.

with neuropteroid wings and an orthopteroid body, having, in common with several contemporary genera, strong isopteran affinities. *Corydaloides scudderi*, a phasmid, has an alar expanse of twenty-eight inches. The Carboniferous prototypes of our Odonata were gigantic beside their modern descendants, one of them (*Meganeura*) having a spread of more than two feet; they were more generalized in structure than recent Odonata, presenting a much simpler type of neurulation and less differentiation of the segments of the thorax. The Carboniferous precursors of our May flies attained a high development in number and variety; in fact, the Ephemeridæ, like the Blattidæ, achieved their maximum development ages ago, when they attained an importance strongly contrasting with their present meager representation.

The Permian has supplied a remarkable genus *Eugereon* (Fig. 307)

with hemipterous mouth parts associated with filiform antennæ and orthopteroid wings. The earliest unquestionable traces of insects with an indirect metamorphosis are found in the Permian of Bohemia, in the shape of caddis-worm cases.

Triassic.—Triassic cockroaches present interesting stages in the evolution of their family. Through these Mesozoic species the continuity between Palæozoic and recent cockroaches is clearly established—which can be said of no other insects; and in fact of no other animals, the only comparable cases being those of the horse and the molluscan genus *Planorbis*. In the Triassic period occur the first fossils that can be referred indisputably to Coleoptera and Hymenoptera, the latter order being represented first, as it happens, by some of its most specialized members, namely ants.

Jurassic.—At length, in the Jurassic, all the large orders except Lepidoptera occur; Diptera appear for the first time, and Odonata are represented by many well-preserved specimens, while the Liassic Coleoptera studied by Heer number over one hundred species. The Cretaceous has yielded but few insects, as might be expected.

Tertiary.—In the rich Tertiary deposits all orders of insects occur. Baltic amber has yielded Collembola, some remarkable Psocidæ, many Diptera, and ants in abundance. Of 844 species taken from the noted Miocene beds of Æningen, nearly one half were Coleoptera, followed by neuropteroid forms (seventeen per cent.) and Hymenoptera (fourteen per cent.); ants were twice as numerous in species as they are at present in Europe. Almost half the known species of fossil insects have been described from the Miocene of Europe. To the Miocene belongs the indusial limestone of Auvergne, France, where extensive beds—in some places two or three meters deep—consist for the most part of the calcified larval cases of caddis flies.

At Florissant, as contrasted with Æningen by Scudder, Hymenoptera constitute 40 per cent. of the specimens, owing chiefly to the predominance of ants; Diptera follow with 30 per cent. and then Coleoptera with 13 per cent. Modern families are represented in great profusion. The material from Florissant and neighboring localities includes a *Lepisma*, fifteen species of Psocidæ, more than thirty species of Aphididæ, and more than one hundred species of Elateridæ, while the Rhynchophora number 193 species as against 150 species from the Tertiary of Europe. Tipulidæ are abundant and exquisitely preserved, while Bibionidæ, as compared with their present numbers, are surprisingly common. Numerous masses of eggs occur, undoubtedly sialid and closely like those of

Corydalis. Sialid characters, indeed, appear in the oldest fossils known, and are strongly manifest throughout the fossil series, though among recent insects Sialidæ occupy only a subordinate place. Strange to say, few aquatic insects have been found in this ancient lake basin.

Fossil butterflies are among the greatest rarities, only seventeen



FIG. 308.—*Prodryas persephone*, a fossil butterfly from Colorado. Natural size.—After SCUDDER.

being known; yet Florissant has contributed eight of these, a few of which are marvelously well preserved (Fig. 308), as appears from Scudder's figures. Two of the Florissant specimens belong to *Libytheinæ*, a group now scantily represented, though widely distributed over the earth. The group is structurally an archaic one, and its recent members (forming only one eight-hundredth of the described species of butterflies) are doubtless

relicts.

Taken as a whole, the insect facies of Tertiary times was apparently much the same as at present. The Florissant fauna and flora indicate, however, a former climate in Colorado as warm as the present climate of Georgia.

Quaternary.—The interglacial clays of Toronto, Ontario, have yielded fragments of the skeletons of beetles to the extent of several hundred specimens, about one third of which (chiefly elytra) were sufficiently complete or characteristic to be identified by Dr. Scudder, who found in all 76 species of beetles, representing 8 families, chiefly Carabidæ and Staphylinidæ. All these interglacial beetles are referable to recent genera, but none of them to recent species, though the differences between the interglacial species and their recent allies are very slight. As a whole, these species "indicate a climate closely resembling that of Ontario to-day, or perhaps a slightly colder one. . . . One cannot fail, also, to notice that a large number of the allies of the interglacial forms are recorded from the Pacific coast." (Scudder.) The writer, who has studied these specimens, has been impressed most by their likeness to modern species. It is indeed remarkable that so little specific differentiation has occurred in these beetles since the interglacial epoch—certainly ten thousand and possibly two to three hundred thousand years ago.

General Conclusions.—Unfortunately, the earliest fossils with which we are acquainted shed much less light upon the subject of insect phylogeny than one might expect. The few Devonian forms, though synthetic indeed as compared with their modern allies, are at the same time highly organized, or far from primitive, and their ancestors have been obliterated.

The general plan of wing structure, as Scudder finds, has remained unaltered from the earliest times, though the Devonian specimens exhibit many peculiarities of venation, in which respect some of them are more specialized than their nearest living allies, while none of them have much special relation to Carboniferous forms.

Carboniferous insects are more nearly related to recent forms than are the Devonian species, but present a number of significant generalized features. Generally speaking, the thoracic segments were similar and unconsolidated, and the two pairs of diaphanous wings were alike in every respect—in groups that have since developed tegmina and dissimilar thoracic segments. The Carboniferous precursors of our cockroaches, phasmids and May flies have been mentioned. Palæozoic insects were grouped by Scudder into a single order, Palæodictyoptera, on account of their synthetic organization, though other authors have tried to distribute them among the modern orders. This disagreement will continue until, with increasing knowledge, our classification becomes less arbitrary and more natural.

Mesozoic insects are interesting chiefly as evolutionary links, notably so in the case of cockroaches—the only insects whose ancestry is continuously traceable. In this era the large families became differentiated out.

Most of the Tertiary species are referable to recent genera, peculiar families being highly exceptional, while all the Quaternary species belong to recent genera.

Hemiptera appear in the Silurian; Neuroptera (in the old sense) in the Devonian; Thysanura and Orthoptera, Carboniferous; Coleoptera and Hymenoptera, Triassic; Diptera, Jurassic; and Lepidoptera not until the Tertiary.

Since Scudder's day, considerable additions to the knowledge of our fossil insects have been made by Professor T. D. A. Cockerell and by Professor H. F. Wickham.

A comprehensive and richly illustrated account of fossil insects is given by Handlirsch in his great work, *Die fossilen Insekten*.

CHAPTER XIII

INSECT ECOLOGY

Ecology is the physiology of organisms in relation to environment. It is the physiology of entire organisms rather than of organs. It deals with the reactions of organisms to the conditions of their existence, including the modification of these reactions in relation to changes of environment.

Though its subject matter is primarily animals and plants, ecology is based upon all the sciences, and cannot be pursued most precisely without the aid of some mathematics.

Insect life in its omnipresence and diversity affords countless illustrations of ecological principles, under which innumerable isolated observations fall into organization.

The qualitative study of the subject is simply a matter of accurate and thorough observation and correct inference, with the aid of the simplest kind of experimentation. Even in quantitative investigation, the ecological principles may be brought out with the use of such inexpensive means as thermometers, ice-boxes, weather maps, etc. For the most refined work, however, elaborate appliances for controlling ecological factors are often necessary.

It should be remembered that the study of insects alone gives only a partial understanding of ecology, with an imperfect perspective of the subject.

The ecology of individuals is known as *Autecology*; that of communities, as *Synecology*.

I. CONDITIONS OF TERRESTRIAL EXISTENCE

I. SOIL

The *edaphic* conditions of existence (those relating to the soil) are the same for animals and plants, but are utilized in different ways by these organisms. Plants can utilize inorganic constituents of the soil as food, but animals can not. All the food of animals, with such exceptions as water and salt, is derived in the last analysis from plants.

Structure.—The retention of water by the soil depends largely upon the size of the soil particles; soil of small particles holding more water

than one of large particles. Water evaporates more rapidly from coarse soils than from fine ones, but in loose soils the more rapid evaporation from the surface forms an aerated "mulch" which retards further evaporation. The different capacities of different soils for absorbing or retaining moisture affects insects indirectly by its effects on vegetation, or may affect them directly. The compactness of loose soils varies with the amount of water present, which is of importance to burrowing insects. A good example of this is seen in the sandy beach of a lake, when the sand wet by waves becomes firm; the water evaporates rapidly, however, until the sand is dry again, in proportion to its nearness to the surface. In such sand, with frequent alternations from wet to dry, insects do not live; though some forms, as tiger beetles and beetles of the genus *Bembidion*, burrow in the sand a little farther back from the shore, where the fluctuations in the water content are not so great.

In a loose soil white grubs or wireworms go easily and rapidly from one plant to another. Tiger beetles and ants need soil of a consistence which will maintain the burrows after they are made. Caterpillars, grubs, etc., about to pupate, can not burrow in soil that is too hard, and frequently avoid also soil that is too loose. The bollworm if unable to dig into hard baked soil will enter cracks in the soil. Some grasshoppers, on the other hand, prefer hard-packed soil in which to lay their eggs. In making their pupal cells in the ground, larvæ press the surrounding soil into a compact wall, often adding a cementing fluid which is frequently waterproof. The bollworm, or corn ear worm, lines its burrow with silk.

A soil of loose texture facilitates the emergence of adult insects. If the soil is too hard they may not be able to emerge until it has been softened by rain. Plowing and rolling the soil of a stubble field in summer is known to prevent the exit of Hessian flies.

The depth to which insects burrow in the ground depends upon the physical nature of the soil, and temperature and moisture as well.

Chemical Conditions.—In addition to oxygen, carbon dioxide and nitrogen, the soil contains other gases and various chemical compounds, some of which are essential to plant life and therefore indirectly to the welfare of animals. The character of the vegetation as determined by the acidity or alkalinity of the soil affects the character of the insect fauna. The acid water of bogs is directly unfavorable to insect life, but is favorable to the growth of peculiar plants which are selected as food by certain insects. In New Jersey, Mr. H. Bird, by acidulating soil with an artificial bog water made with the extract of hemlock used

for tanning leather, succeeded in growing the pitcher plant, *Sarracenia purpurea*, and in raising thereon a species of rare moth, *Papaipema appassionala*, known for thirty years only by a unique type in the British Museum.

Plants of alkaline desert soils have their characteristic insect fauna.

Air.—The oxygen content of subterranean air is important directly for respiration; indirectly for its effects on vegetation. Aeration of the soil is essential to subterranean life. In too compact a soil insects suffer from lack of oxygen and excess of carbon dioxide, and may experience also the effects of excessive evaporation and mechanical difficulties in burrowing.

Water.—For their welfare, soil insects must have neither too much nor too little water. They may be drowned by gravitational water, which acts also by filling the air spaces around soil particles. Submersion was used effectively in France against the destructive *Phylloxera* of the grape. Capillary water is, on the contrary, favorable to the insect life until it evaporates to excess. As with terrestrial insects, the vital effects of water and temperature are produced through evaporation, in relation to which soil forms exhibit various adaptations. As the soil dries, ants dig deeper. The depth of pupal chambers, their compact waterproofed walls, and the air space around the pupa, and the closing of the entrance to the burrow, all tend to protect the pupa from undue loss of bodily moisture.

With the tiger beetles, the amount of moisture determines whether eggs are to be laid, and their number if laid; eggs being absent in dry soil (Shelford).

Temperature.—There are great differences in the temperatures of different soils, from dry sands to moist shaded humus. Temperature and moisture determine largely the character of the flora and of the accompanying fauna. The greater the depth of soil the lower the temperature as a rule. Ants and other insects will dig deeper to avoid heat as well as dryness. Ants often find suitable conditions of temperature and moisture under stones or logs.

In the case of insects that are said to be killed by heat, the mortality is due primarily to evaporation and secondarily to the coagulation of the protoplasm; perhaps also to ultra-violet rays.

Physiographic Conditions.—As environmental factors there must be considered also the nature of the surface of the soil as regards exposure or cover, the slope of the soil, and the altitude at which it is found. All these things affect the fauna. Angle of slope has an effect in

determining the presence or absence of oviposition burrows of tiger beetles, and the presence, absence, or number of eggs laid (Shelford).

Nutriments.—The food of soil insects may be roots or stems of plants, dead animal or vegetable matter, other insects or other animals. Some insects are parasitic on burrowing mammals. Many ants derive part of their nourishment from the root-sucking aphids or coccids which they attend. Ants and termites sustain diverse relations as regards food with various other insects and other arthropods that live in their nests. Some species that burrow near the surface, as tiger beetles and ant-lions, capture their prey from the surface of the ground.

Soil that contains no organic matter, as pure quartz sand, is food for no insect. Some larvæ, as white grubs and wireworms, that subsist primarily on roots of plants, can if necessary thrive for many months on a diet of soil alone, but only because of the organic matter that it contains.

Interactions.—The subject of interactions in the soil environment can only be touched upon here. The character of the soil itself is changed by the plants and animals that inhabit it. Thus burrowing animals, as worms, crawfishes, insects, moles, mice, many larger mammals, etc., alter the distribution and the physical and chemical composition of the soil. Bacteria and fungi play important parts. The soil is not fully effective in protecting its insect inhabitants from predaceous and parasitic enemies among other insects, and soil insects are themselves food for many birds, mammals, and other of the larger animals.

2. ATMOSPHERE

LIGHT

The most conspicuous effect of light is its directive effect on locomotion. This phenomenon is discussed in another chapter (p. 306), where it is shown that insects react either positively or negatively to light, are often attuned to definite ranges of light intensity, and react differently to light of different wave lengths. The results of phototropism are often incidentally adaptive. As examples, the positive reaction may take insects to their food, cause the nuptial flight of ants or termites, or the swarming of bees; while the negative response may lead insects into places of concealment, pupation, or hibernation. Structures and functions are correlated with the presence or the absence of light; for example, those of the eyes. Insects that live in darkness, as boring species, subterranean forms, and cave insects, exhibit special

modifications in relation to the absence of light that are mentioned in other parts of this book.

Growth.—In nature the effects of light on growth are bound up with those of temperature. The temperature of the air varies with light (*insolation*, or exposure to the sun's rays). Cloudy summer days are cooler than sunny days. Cloudy winter days are warmer. (Shelford.) Light affects the rate of growth, or more precisely, some wave lengths are more effective than others. Beclard reared larvæ of the flesh-fly, *Musca carnivora*, from the eggs, under glass bells of different colors. The largest larvæ were found under violet or blue; the smallest under green; the colors producing their effects in the following order: violet, blue, red, yellow, white, green. Under violet the larvæ were three-quarters greater than under green. Green rays retarded growth, as did also white light. (C. B. Davenport.)

Activity.—Sunshine, aside from temperatures, unless they are extreme, has a stimulating effect on reproduction and other activities in flies (Bishopp, Dove, Parman); and this is true probably for most diurnal insects. On cloudy days the boll weevil and most other insects as well are less active than on clear days, without regard to temperature.

Exposure to hot sunshine kills pupæ of the bollworm, plum curculio and other forms. This result is due primarily to heat with evaporation, but possibly the ultra-violet rays also exert some influence.

Sleep.—Whatever the temperature may be, insects go to sleep when night falls, and do so during the daytime if clouds diminish the sunlight beyond a certain point which varies for different species. If it becomes very cloudy, the mourning-cloak, *Vanessa antiopa*, seeks some crevice and goes to sleep, but is quickly aroused, however, by returning sunshine. The sleep of insects doubtless has the same physiological results as that of other animals.

"A few species seem to choose protectively colored situations, and others select sites which are in various ways protective. Some which are solitary by day are gregarious at night, and some insects sleep with all the regularity of a theoretical modern infant, while others of a more unsystematic life snatch a wink when they can." (P. Rau and N. Rau.)

TEMPERATURE

Temperature Limits.—It goes without saying that the life-processes and the activities of every animal or plant are confined within a certain range of temperature, outside of which the organism cannot exist.

This range is different for different species, for the same species in different seasons or places, and is different even for different individuals of the same species under apparently equal conditions, and for different stages in the growth or development of the same individual. The temperature-range is affected by food, moisture, evaporation, and several other factors.

Growth and development proceed most rapidly in a certain *optimum* range of temperature, within which there is, at least theoretically, an optimum degree of temperature. At and above a certain degree of high temperature heat-rigor sets in, and may or may not be fatal to an organism, according to the duration of the exposure to the temperature. This *maximum* temperature has as its upper limit the *ultramaximum*, at which the organism dies at once, probably because of the coagulation of proteids in the protoplasm. At a certain degree of low temperature, cold-rigor takes place; the point at which it occurs being near the freezing point, on account of the fluid content of protoplasm. Below this *minimum* is an *ultraminimum* temperature, at which the organism dies.

The following examples of temperature-limits are from Davenport's *Experimental Morphology*.

INSECT	MAXIMUM	ULTRAMAXIMUM
Springtail, <i>Podura similata</i>	27° C.	36.0° C.
Mosquito, <i>Culex pipiens</i>	40° C.
Larva of fly, <i>Musca vomitoria</i>	42.5° C.
Pupa of fly, <i>Musca vomitoria</i>	43.7° C.
Silkworm, <i>Bombyx mori</i>	42.5° C.
Back-swimmer, <i>Notonecta</i>	45.0° C.

It should be noted that the *Podura* (near *Achorutes*) has a thin integument, and can not live in a dry atmosphere. The pupa of the fly is protected somewhat by its puparium, and the back-swimmer by a fairly thick integument.

INSECT	ULTRAMINIMUM
Honey bee, <i>Apis mellifera</i>	— 1.5° C.
House fly, <i>Musca domestica</i>	— 5.0° C.
Larva of cockchafer, <i>Melolontha</i>	— 15.0° C.
Adult cockchafer, <i>Melolontha</i>	— 18.0° C.

Davenport notes that the large size and thick covering of the beetle, *Melolontha* prevent the rapid loss of heat.

Activity in Relation to Temperature.—The range of activity of the adult cotton boll weevil lies between 56° F. and 95° F. From 95° to 122° is the range of æstivation, within which the beetles are inactive. From 122° to 140° (soil temperature) is an upper range of fatal tem-

peratures, in which the weevil dies in 15 minutes to 1 second, according to the temperature, 140° being the maximum fatal temperature.

In the descending scale of temperature, there is a range between 56° to 24° within which the beetles hibernate. Below 24° is the lower range of fatal temperatures, with 7° as the minimum fatal temperature. As the limits of these ranges vary with moisture and other factors, these ranges, as given by Hunter and Pierce (1912) are necessarily approximations; but they serve to illustrate the fact that such ranges exist, and are accurate for the particular conditions under which they were made.

It may be mentioned that Hunter and Pierce found that the winter cold is, on the average, almost twice as effective as summer heat in killing the beetle; which has several times been greatly reduced in numbers by early freezes in the South.

High temperatures are more favorable to the activities of insects than to those of human beings. The temperature range of activity varies with different species.

The effect of temperature upon the locomotor activity of the boll weevil was tested by Dr. A. W. Morrill, who found that as the temperature was gradually raised the activity of the weevils increased up to 105° F. At 95° the beetles were very active; at 86° they began to lose their activity; and at 37° all movement ceased. Out of doors, weevil activity began and ceased at about 75° ; feeding continuing at lower temperatures than oviposition.

The number of daily feeding punctures of the weevil was found to be greatest at about 80° F., as was also the number of eggs laid. (Hunter and Hinds.)

The curve representing the average number of eggs deposited daily by the alfalfa weevil, *Phytonomus posticus*, follows the curve of the mean daily temperature in all its major fluctuations, the highest record (twenty-six eggs) occurring on the day (May 18) with the highest mean temperature (72° F.) of any day previous to June 6. (T. H. Parks.)

By stimulating the activities of insects, high temperatures diminish the longevity. Thus a worker honey bee that hibernates may live for six or seven months, but an active worker in summer lives only five or six weeks.

Other things being equal, the longevity of insects in general is lengthened by a decrease in temperature and shortened by an increase (when these temperatures are between about 42° and 72° F.); the difference in longevity of a species at different temperatures corresponding roughly to the difference in temperature. (J. P. Baumberger.)

Development in General.—The effects of temperature on the development of insects are known in a qualitative way, and considerable progress has been made in the quantitative study of the subject. At a certain degree of low temperature during development an insect becomes physiologically inactive, or dormant, without being killed, and may resume activity when the temperature rises. This point is termed the *threshold of development* (*critical point*, *developmental zero*). Temperatures above this point that are conducive to development are termed *effective temperatures*, and in ascertaining the number of temperature units requisite to development, all temperatures below the threshold of development are disregarded. The effects of high temperatures in accelerating development, and of low temperatures in retarding development, are known to all who have raised butterflies or moths from pupæ.

The theory used to be that the entire development of an insect, from the time the egg is laid until the adult emerges, requires a fixed number of effective degrees of temperature; the same being true also for any stage of the insect, as egg, larva or pupa; that the entire development, or any phase of the development, will not be completed until a definite number of temperature units have been experienced, whether the time required be long or short. The number expressing the total temperature, or *temperature constant*, is obtained by multiplying the mean daily temperature by the number of days required for the development. Needless to say, the effects of temperature are obscured by those of humidity, light, and several other influences in nature, and become evident only under the exact conditions of experimentation.

For the development of the boll weevil, Hunter and Hinds (1905) give the following summary:

Stage	Total observations	Average period for stage, Days	Average ¹ effective temperature, ° F.	Total effective temperature, ° F.
Egg.....	616	4.0	34.0	136.0
Larva.....	313	9.8	32.2	315.6
Pupa.....	530	5.5	33.2	182.6
Total development, sum of stages	1,459	19.3	32.9	634.2
Observations on entire period of development.....	887	19.6	32.2	632.0

¹ For the average mean temperatures, add 43 degrees to the average effective temperatures.

Exact experimental studies of the effects of temperature, moisture, and other conditions have undoubtedly an important economic bearing. For example: it was found, from experiments made by Professor. T. J. Headlee in Manhattan, Kansas, that the cycle of the codling moth required an average of 39 days with an average of 1,006 degrees of effective temperature (temperatures above the threshold of development, given at that time as about 50° F.). With as exact a knowledge of the other factors, particularly moisture, one ought to be able, with the aid of weather reports, to foretell when a given brood of the codling moth will appear; which would evidently be of advantage to fruit-growers.

The subject is, however, not so simple as it was thought to be. Sanderson (1908, 1910), who has given a useful discussion of this subject, showed "that upon purely theoretical grounds there could be no uniform accumulation of temperature or 'thermal constant' for the various stages of insect growth, but that the relation of temperature to growth phenomena was probably different for each species and might be expressed by a curve, the abscissas of which represent degrees of temperature and the ordinates represent the time factor. The importance of considering the so-called law of the velocity of chemical reaction as influenced by temperature was pointed out and it was shown that the velocity of reaction varies at different temperatures. It was shown that both the so-called thermal constant and coefficient of velocity increase as the temperature is lowered from the optimum of the species, and that the curve for each species and phase of growth or activity of that species must be plotted before the influence of temperature can be exactly stated." Sanderson defined the "thermal constant" for insects as "that accumulation of mean daily temperature above the 'critical point' of the species, which will cause it to emerge from hibernation or to transform from any given stage." (1) There is no uniform minimum above which the temperature may be accumulated as effective, but this varies with each species and phase of growth; (2) there is no "thermal constant" as far as a mere accumulation of temperatures is concerned; and (3) the velocity of reaction varies according to the range of temperatures (Sanderson). To illustrate the first of these three statements, Sanderson cites the green-bug, *Toxoptera graminum*, which, as Hunter and Glenn showed, begins to develop at 1.65° C., while its parasite, *Lysiphlebus tritici*, shows no activity below about 4° or 5° C. For the bollworm the point of cold rigor is about 10° C. In regard to the second statement, Sanderson adds: "It is evident that any accumulation of

temperature to secure a thermal or physiological constant cannot be based on a mere addition where variable temperatures are involved, for it is evident that every degree has a different value in relation to the time factor. Thus as the mean temperature rises with the advance of the season both the time for the pupal stage and the total accumulated temperature for the pupal stage of the codling moth decrease with the advancing season. Though a fairly constant 'total effective temperature' for any given phase of an insect's life or activity may be secured for the summer months when there is a fairly constant mean temperature, such an accumulation will have no meaning in regard to the same phenomena in spring and fall when the temperatures are more variable. If we wish to be exact, we must secure the temperature curve for the species, based on the observation of a considerable number of individuals kept at different constant temperatures, or possibly better at temperatures having a diurnal variation with constant maximum and minimum, and with fairly constant moisture conditions."

Krogh on Temperature-velocity.—The results obtained by Krogh, which differ in some respects from those of other investigators, are regarded as highly important. He finds that the temperature-velocity curve expressing the rate at which segmentation takes place in frog's eggs is, between 7° and 20.7° , a straight line. "An increase in temperature between these limits produces a proportional increase in the velocity with which the processes in the egg leading up to segmentation take place. Below 7° the curve deviates from the straight line and the reaction takes place more rapidly than one would expect from the results obtained at higher temperatures. At the lowest temperature, where the development certainly is no longer normal the curve turns downward once more."

"The relation between the temperatures and the velocity of embryonic development is algebraic over a range of temperatures which corresponds approximately to that at which normal development can take place, and the curve representing the relation is consequently a straight line." The velocity of embryonic development is a linear function of the temperature.

In regard to the relation between temperature and the later stages of development of the frog, Krogh says: "Between the temperatures 12° and 25° the increment in velocity of the embryonic development of the frog is therefore proportional to the temperature increment, but below 12° the development is more rapid than one would expect from the formula."

Concerning the time of incubation of the eggs of a water beetle, *Acilius sulcatus*, Krogh found that "when the reciprocal values of the hatching times at the three temperatures are plotted against the temperatures, they are found to lie in a straight line." (See also Krogh's results on Pupal Development, p. 359.)

From all that has been said, then, it appears that there is a threshold of development, which varies for different species and under different conditions of existence, and that there is such a thing as an accumulation of effective temperatures, or thermal constant. This constant is limited, however, to a certain range of temperature, below which growth or development is faster than the constant requires, and above which it is slower. This fact has an economic consequence; for basing predictions upon the thermal constant alone, the spring brood of the codling moth or other insect would appear earlier than would be expected, and the autumn brood later.

Reproduction.—Among plant lice *parthenogenesis* (reproduction without fertilization) is apparently continuous and uninterrupted under favorable environmental conditions; *amphigony* (reproduction by fertilization) occurring only under the influence of low temperatures and, as certain authors claim, inadequate food supply. Aphids in tropical and other warm climates appear to have the tendency to reproduce exclusively by parthenogenesis. The same condition apparently obtains among greenhouse aphids in temperate climates. Aphids in colder climates undergo *heterogony* (reproduction both by parthenogenesis and amphigony) as an adaptation to adverse environmental conditions. In certain species, the appearance of the amphigonous generation seems to be a rhythmic process, which continues to occur at definite cyclical intervals for some time after the influence of low temperature has been eliminated. (L. B. Uichanco.)

Incubation.—The length of the egg period varies greatly according to surrounding conditions, chiefly those of temperature. First brood eggs of the codling moth in Michigan hatched at outdoor temperatures in 4 to 10 days, average 8 days, at an average mean temperature of about 67.6° F.; eggs not hatching readily, however, during extremely dry weather. (A. G. Hammar.)

In regard to the eggs of this species, C. B. Simpson says: "(1) Under a low temperature the length of the egg stage is longer than at high temperatures. (2) Under normal field conditions a small difference in temperature causes but little change in the length of the stage. (3)

The eggs are not in the same stage of maturity at the time of oviposition, as at 24° F. we have from 9 to 18 days as the length of the stage."

As regards the threshold of development, Sanderson found that eggs of the meal worm, *Tenebrio molitor*, failed to hatch at 9° or 10° C. but hatched at 12° C.

The time from the deposition of the eggs to hatching of the chinch bug is variable, being longer if temperature is low, or shorter if high. Thus first brood eggs (June) with an average mean temperature of 73° F. hatch in 17.3 days; and second brood eggs (August) at 76.58° F. in 11.45 days; the average for both broods being 14.4 days (Headlee and McColloch).

Larval Development.—The discussion already given of growth and development in relation to temperature applies of course to the larval stage as well as to all other stages of development.

Larvæ of the cotton boll weevil in squares developed in 7 days at an average mean temperature of 75° F.; the total of effective temperatures being 280 degrees F. (Hunter and Hinds.)

The bollworm, or corn ear worm, developed in 21 days at an average mean temperature of 77° F.; the total of effective temperatures being 617 degrees F. (Quaintance and Brues.)

In these experiments it was assumed, as was formerly customary, that only temperatures above 43° F. were effective for growth; this is known to be a mistake. A small percentage of bollworms survive a temperature of 34° F.; but larvæ subjected to temperatures somewhat below freezing for one to two days are killed outright.

A constant temperature of 90° F. prevents the development of the plant louse, *Aphis avenæ*; the optimum temperature for the production of the wingless agamic forms being about 65° F. (H. E. Ewing.)

Warmth and dryness are favorable to the development of species of "thrips" (Thysanoptera) and of the "red spider," a well known mite that injures plants, especially in greenhouses.

Molting.—In the walking-stick, *Diapheromera femorata*, a low temperature lengthens, while a high temperature shortens, on an average, the interval between molts. A low temperature has a tendency to decrease the number of molts, while a high temperature increases the number. (H. H. P. and H. C. Severin.)

Pupal Development.—Krogh found that the extremely simple relation (already described) between temperature and the velocity of embryonic development held good also for the changes taking place during the pupal life of the meal worm, *Tenebrio molitor*. He says:

(1) "The relation between the temperature and the velocity of pupal development in *Tenebrio* cannot be expressed in terms of Van't Hoff's formula, but between 18.5° and 28° the relation is algebraic and the curve representing it is a straight line. (2) Beyond these limits the curve is not straight, but bends upwards at the lower temperature and downwards at the higher. Normal development is still possible at temperatures between 15° (13.5°) and 33° . (3) In the metabolic activity of the chrysalides of *Tenebrio* three stages are recognizable, corresponding roughly to periods of disintegration of larval tissues, comparative rest and formation of imago tissues. The metabolism in the tissue disintegration period is practically of the same intensity as in the tissue formation period. (4) The total amount of CO_2 produced during the pupal life is the same at all the temperatures examined (21° – 33°). There is no optimum temperature with regard to metabolism. The relation between the temperature and the average CO_2 production per hour follows the same curve as that found for the velocity of development."

Sanderson found that pupæ of the meal worm, *Tenebrio molitor*, failed to transform at 9° or 10° C. but transformed at 12° C.; and that pupæ of the codling moth underwent little development below 55° F. As a rule, the length of the pupal period is rapidly shortened by increase of temperature. In Michigan, in spring, pupæ of the codling moth developed in an average of 18.4 days at an average mean temperature of 66° F. (A. G. Hammar.) The boll weevil in summer had a pupal period of 5.1 days at an average mean temperature of 74.3° F. (Hunter and Pierce.)

Life Cycle.—The total life cycle of the boll weevil, as obtained by adding egg, larval, and pupal periods, was found to be 17.65 days, at an average mean temperature of 77.8° F.; or an average of effective temperatures of 34.8 degrees; the total of effective temperatures being 614.2 degrees. As found by continuous observations on the same individuals, the life cycle was 17.7 days, with average mean temperature 76.9° F.; average of effective temperatures 33.9 degrees, and total of effective temperatures 600 degrees. (Hunter and Hinds.) Here, again, 43° F. was assumed to be the "zero of development."

Acclimatization.—A few insects have become adapted to survive and thrive under extremely high temperatures. Larvæ of a fly, *Stratiomys*, have been found in a hot spring in Colorado with a temperature of 69° C. A water beetle in India was found in a warm spring at 44.4° C. Few organisms, however, resist temperatures over 45° C. (Dr. C. B. Davenport.) Probably in successive generations of the ancestors of these forms

there were some individuals that could endure a little more heat than the others, and gradually a resistant strain of a species was built up.

Hibernation.—Temperature manifestly bears an important relation to hibernation, the phenomenon of passing the winter in seclusion, usually in a quiescent or inactive condition. The stimulus leading to hibernation is usually decreased temperature in autumn. Thus the cotton boll weevil begins to hibernate with the decrease in mean average temperature to about 55° . (Hinds and Yothers.) Low temperature is not always, however, the immediate incentive to hibernation. The codling moth larva begins to hibernate before the temperature falls and before food fails. The woolly bear caterpillars (*Isia isabella*) show great regularity in the date at which they stop feeding, under conditions of high temperature, different degrees of relative humidity, and an abundance of fresh food. (Baumberger.) Mosquitoes begin to hibernate before cold weather sets in. Among other influences there may be a "tendency" to hibernate in many species.

The period of hibernation is prolonged by low temperatures. The emergence of *Cecropia* moths from their cocoons may be delayed for more than one year by placing the cocoons in cold storage with the temperature a little above the freezing point.

Warm periods during winter may arouse insects to more or less activity. It is commonly thought by collectors that a uniformly cold winter is more favorable to a subsequent abundance of insect life than a winter interrupted by mild spells.

Some insects do not awaken easily from the condition of hibernation, while others respond readily to an increase of temperature. Examples of the latter kind are the pomace flies (*Drosophila*), the house fly (*Musca domestica*) and other flies, and cockroaches.

The temperature requisite to emergence varies with the species. The boll weevil, in hibernation by the time of the first hard frost, continues to hibernate until the mean average temperature has been for some time above 65° F. (Hunter and Hinds.) In the case of the brown-tail moth 34° F. is the threshold above which the temperature accumulates in determining the time of emergence of the caterpillars from their winter nests. (Sanderson.)

According to J. P. Baumberger, insects hibernate as (1) adults, when their food habits are such that oviposition can take place on the proper food at the earliest warm weather; (2) as larvæ, when protected from the cold and thus able to continue feeding to the latest date possible; (3) as pupæ or eggs, because they are nonfeeding resistant stages.

Many examples of adaptation in relation to winter conditions will suggest themselves. Insects when about to hibernate seek shelter or construct shelter, or both. They may simply crawl into existing crevices or holes, as in the ground or in plants, under stones, logs, loose bark, dead leaves, among stems or roots of plants, or may burrow into the ground or into living or dead plants; or may make cocoons or silken nests or earthen cells, in which protection is afforded by surrounding air-spaces. A curious situation for hibernation is that of back-swimmers (*Notonecta*), which have been found clustered in small cavities in thick ice. Hibernating insects protect themselves more or less successfully from such adverse influences as sudden changes of temperature, excess of moisture or of dryness, invasion by fungi and bacteria, and from attacks by other insects or by birds or mammals.

There are, however, many examples of unsuccessful hibernation. Exceptionally low temperatures occasionally exterminate the boll weevil in certain areas, the mortality being increased by excessive rainfall. Concerning the caterpillars of the brown-tail moth in their winter nests, Sanderson says that where nests of average size containing 300-400 larvæ were subjected to -24° F. or lower, from 72 to 100 per cent. of the larvæ were killed, but that in large nests from the same locality only 57 per cent. were killed; the larvæ in the outer parts of the nests dying first.

Following a period of subnormal temperatures in the state of Washington, 1919, examinations were made of larvæ of the codling moth under bark or burlap bands. It was found that wherever the minimum temperature had been lower than -25° F. all larvæ were killed. On higher ground, where the minimum temperatures ranged from -20° to -25° , 80 to 90 per cent. of the larvæ were killed. On still higher ground, with minimum temperatures of -15° to -20° , the mortality was approximately 70 per cent. One interesting fact noted was that frequently, on tearing away the burlap band, one or two living larvæ would be found in the midst of a number of dead ones. It seems impossible, in these cases, that the living larvæ had any more protection than the others. They must simply have had more vitality. (E. J. Newcomer.)

Distribution.—Minimum temperatures exert an important influence in limiting the northern distribution of insects, according to Sanderson, from whose article on the subject the following extracts have been taken. In New Hampshire (January, 1907) most of the hibernating caterpillars of the brown-tail moth (excepting those in large nests) were killed off by

a temperature of -24° F. and below. The northern limit of the San José scale insect corresponds approximately with the average annual minimum isotherm of -15° F. This species dies out in central Wisconsin and cannot survive in Minnesota. The wide-ranging cotton bollworm, or corn ear worm, does not winter in Minnesota and no records of injury occur in Montana, Wyoming or the Dakotas. The harlequin cabbage bug maintains a foothold in the latitude of Long Island, southern Ohio and southern Illinois, but has been unable to extend its permanent range farther north on account of being killed off by cold during hibernation.

A blanket of snow may offset the effects of minimum temperatures, as with the striped cucumber beetle, which hibernates in the soil, the codling moth, which passes the winter as a caterpillar in a cocoon under bark, the scale insects, and many other species.

Occasional periods of extremely low temperature, occurring at long intervals, are temporary checks upon the distribution, but the exact northern limits of distribution depend rather upon the average minimum temperature.

PRESSURE

From the few observations that have been made upon the subject it appears that insects are sensitive to variations in atmospheric pressure, as birds and mammals, including man, are said to be. Atmospheric pressure as correlated with humidity affects animals indirectly through its effects on evaporation. Thus high pressure with low humidity means increased evaporation, and vice versa.

The following extracts are from an interesting article by D. C. Parman on the effect of storm phenomena on insect activity.

With a rapidly falling barometer several species of flies (Muscidæ) first become nervously active and then go into a state of partial coma, in which state they are more subject to the action of other destructive agencies, diseases probably included. The decrease in the number of flies is quite appreciable after a severe tropical storm.

The adults of the fly *Chrysomya macellaria* apparently will not chill and die under the effect of a rising barometer as under a lowering barometric pressure.

Insects attracted to lights are more active during high barometric periods and especially while the barometer is rising.

Bred adult Diptera tend to emerge on periods of rising barometer.

The heavy emergences apparently always have been during periods of high barometric pressure. Trappings and observations indicate that muscoid Diptera are most abundant during long periods with slight variations in barometric pressure, provided, of course, temperature, humidity and rainfall are favorable.

Migration of the butterfly, *Hypatus bachmani* was observed during the summer and fall of 1916 to take place after storms, which indicates that the flights were during high barometric pressure.

MOISTURE

Moisture ranks with temperature as a highly essential condition of existence. Moisture affects terrestrial animals most vitally through evaporation, which will be considered beyond. Here we may state the effects of moisture without special reference to evaporation, but it should be borne in mind that, in most of the phenomena discussed, evaporation is an important factor.

Metabolism.—"Water plays a part in growth second in importance to no other agent, so that in its absence growth cannot occur. As the quantity is increased, growth is increased until an optimum is reached. The amount imbibed does not, however, depend directly upon the amount available, but rather upon the needs and habits of the species." (Dr. C. B. Davenport.)

1. There is an optimum moisture for insect development. 2. This optimum is not the same for different species. 3. The moisture which may hasten the development of one species may retard the development of another. (Bachmetjew.) Headlee adds that the rate of metabolism in certain actively feeding insects with an abundant supply of succulent food is not affected by large differences in atmospheric moisture. He found that the green-bug, *Toxoptera graminum*, required six days to pass from birth to maturity under a constant temperature of 80° F. and relative humidities of 37, 50, 70, 80 and 100 per cent. Professor Headlee found also that, with the angoumois grain moth and the bean weevil (1) increase in atmospheric humidity means increase in speed of metabolism as measured by length of life cycle; (2) the optimum per cent. of atmospheric humidity is the highest which will not encourage a heavy growth of fungi; (3) 100 per cent. atmospheric humidity destroys by encouraging the growth of fungi, and low atmospheric moisture destroys directly—probably by the extraction of water; (4) while the egg stage of the bean weevil, at least, is most sensitive to the effect

of low atmospheric humidity, other stages are unfavorably affected; (5) low atmospheric moisture might be developed into an efficient insecticide for certain species of stored grain insects.

Eclosion.—Moisture frequently determines the time of eclosion, or the emergence of an insect from the pupa. Hessian flies do not emerge from the puparia in dry weather, but issue in abundance after rainfall in the proper season. When bred indoors, the flies do not emerge from dry soil, even though the temperature be favorable, but emerge shortly when the soil is moistened.

Activity.—Wet weather lessens the activities of insects exposed to it. There are some exceptions, however. Larvæ of the midges, Itonididæ, are all very sensitive to the presence of moisture, to which they react positively. Larvæ of the clover seed midge emerge from the clover heads usually in damp weather and often in large numbers when the plants are wet with rain. Even when full grown and contracted in readiness to form the puparium, they revive and move about if moistened with water.

Oviposition.—It has been found that with the house fly, when temperatures are high or moderately high, increased humidity hastens egg-laying. This may be partially due to the effect of humidity on the food and breeding substances—keeping them moist and attractive. (Bishopp, Dove, Parman.)

Mortality.—Changes in relative humidity produce striking changes in the mortality of *Drosophila*, the mortality increasing with a decrease of humidity, the optimum humidity being 100 per cent. The effects of low humidity on mortality are most marked with very young pupæ, whose covering permits a rapid evaporation of body moisture. After a few hours, when integumental changes making evaporation more difficult have set in, the effects of low humidity are correspondingly decreased. (A. Elwyn.)

Hibernation.—As a preparation for hibernation, the water content of an organism is frequently reduced; as also in seeds or spores. Thus the Colorado potato beetle loses about 30 per cent. of its gross weight through the loss of water, which enables it to withstand a lower freezing point and higher temperatures than if the protoplasm were not thus condensed. (Tower.) As Sanderson notes, the time of emergence from hibernation is controlled by moisture conditions as well as temperature, or independent of temperature. Tower kept potato beetles for eighteen months at a high temperature, but with a dry atmosphere, and they emerged as soon as normal moisture conditions were produced.

Æstivation.—In the case of the potato beetle, hibernation and *æstivation*, or the condition of dormancy in summer, are practically the same as regards the life history of the insect, according to Tower. In the tropics, where there is no hibernation, *æstivation* occurs over the dry season. Though *æstivation* is associated mainly with heat, relative humidity is also a factor, and “undoubtedly has the most important influence upon the time of emergence of forms in *æstivation* during the summer or in arid regions. (Sanderson.) During intense heat (95° to 122° F.) the boll weevil *æstivates* temporarily on the ground under protecting objects.

Drought.—Drought accompanies heat and affects animals and plants through evaporation. It affects them directly, by desiccation; or indirectly, by drying out the food plants or other food substances; as with larvæ of the boll weevil or the house fly. The range of dryness within which insects can exist varies greatly with different species. The chinch bug, unlike the Hessian fly, thrives in hot dry summers; and species that inhabit arid regions are exceptionally resistant to conditions of drought.

Precipitation.—Rainfall is direct or indirect in its influence on the life and activities of insects. Eggs of the cotton bollworm are destroyed in immense numbers by the mechanical force of the rain during violent storms. The combined effects of rain, wind, and sandy particles washed against the plants removes many eggs. (Quaintance and Brues.) Young larvæ of the bollworm feeding on corn early in the spring are often washed down by rain and submerged for considerable periods. Of twenty newly hatched larvæ submerged for seventeen hours, all but four survived the immersion. Larger larvæ cannot stand such long periods, but when dropped into water become stupefied after a few minutes. Pupæ could not withstand twenty-four hours' submergence in rain water at normal summer temperatures, but at a temperature of from 50° to 60° F. they were unharmed by from four to six days' submergence. (Quaintance and Brues.) In the case of the cotton boll weevil, a pupa survived an immersion of six hours; and 60 per cent. of adults, one of fifteen hours. Ten adults were floated for one hundred and twelve hours, after which only one was dead, but only two were normal; after floating for only twenty-five hours, however, six of the ten were normal. The floating of adults and infested squares explains the appearance of weevils in great numbers along high-water line immediately after a flood. (Hunter and Hinds.)

Rains favor weevil increase in several ways. Frequent rains in-

crease the growth of the plant and lead to the production of a larger number of squares which may become infested. Driving rains knock off infested squares, and by softening and moistening the food hasten the development of the larvæ within. Squares which are already upon the ground are protected during rainy weather from sunshine and drying. Rain hinders the enemies of the weevil far more than it does the development of the weevils themselves. On the other hand, it seems probable that as many of the hibernating weevils perish from frequent wetting as from exposure to the cold. (Hunter and Hinds.)

Frequent heavy rains in spring reduce greatly the numbers of immature chinch bugs.

Moisture increases the mortality of insects indirectly by favoring the growth of parasitic fungi or bacteria. Thus, in moist weather chinch bugs may be almost exterminated by the fungus *Sporotrichum*, as described with other examples in a preceding chapter. (See page 218.)

This chinch bug fungus will not grow in a relative humidity of 90 per cent. or less, but will remain dormant in the spore stage for an indefinite period (more than eighteen months, in dryness.) The fungus can hardly have too much moisture in a state of nature; dashing and washing rains serving merely to distribute it. (Headlee and McColloch.)

COMPOSITION

The fact that animals require oxygen for respiration, and give off carbon dioxide, while plants utilize carbon dioxide and set free oxygen, need only be alluded to.

The chief constituents of air are oxygen, nitrogen, carbon dioxide, water-vapor in varying amounts, with small quantities of gaseous ammonia and hydrogen dioxide, and extremely small amounts of argon. The organic matters present, as bacteria, spores of fungi, pollen grains, etc., are highly important biologically.

In atmospheric air there are very nearly three parts of nitrogen to one part of oxygen, whether by volume or by weight; with slight variations in these proportions.

The carbon dioxide is present in relatively small quantity, about three parts in ten thousand, the proportion varying according to the locality and season; being greater in cities than in the country; in summer than in winter; in warm climates than in cold; in lower altitudes than in higher; and "greatest near the ground where decomposition is taking place."

MOVEMENT

The movement of air is physiologically important in affecting the rate of evaporation from the bodies of animals. With other conditions constant, the rate of evaporation is proportional to the strength of the air-current.

The directive effect of currents of air (*anemotropism*) has been discussed (page 305). Some insects turn away from currents of air because of increased evaporation. (Shelford.)

Winds are highly effective agents in the distribution of insects. To what has been said on this subject (page 323) these remarks may be added.

In the case of the cotton boll weevil, "prevailing winds frequently cause the majority of the insects to follow one course." (Hunter and Pierce.)

The natural spread of the gipsy moth is accomplished chiefly by means of winds, acting on the hairy first-stage larvæ. (A. F. Burgess.)

Hessian flies are often carried two miles, in an uninjured condition, by strong winds. One female must have been carried five miles. (J. W. McColloch.) These flies may be borne by winds with a velocity of twenty-five miles or more per hour; mosquitoes, on the other hand, cling to herbage near the ground during strong winds, but are conveyed many miles by gentle breezes.

The green-bug, *Toxoptera graminum*, and many other plant lice are widely distributed, as winged viviparous females, by the wind. "If the temperature be below the point of activity for the species, it is very clear that the velocity of the wind would have no effect whatever upon the diffusion of the insect. The conditions necessary, then, for the wind to exert its greatest influence will be a decreasing food supply for the insect under a temperature considerably above that actually necessary for its activity, with numbers not seriously reduced by parasites; under these conditions, many species of aphids are known to be carried about in immense numbers by the winds." (Webster and Phillips.)

ELECTRICITY

Electric currents have a directive effect on animals (*electrotropism*, *galvanotropism*) but the conditions under which this effect is obtained are artificial, and may or may not be paralleled in nature.

Atmospheric electricity, the effects of which vary with variations

in other conditions of the atmosphere (Shelford), doubtless exerts some influence on the activities of insects and other animals, but in regard to this subject little is known.

In the literature there are observations of the effects of electrical storms on insects, but these effects are results of several influences operating in combination (as temperature, moisture, pressure, light, and wind and rain acting mechanically); and possible effects of electricity alone are not distinguishable.

EVAPORATION

Evaporation depends upon air-temperature, pressure, relative humidity, air-movement and, indirectly, light. The amount of evaporation expresses the total effect of these factors. The evaporating power of the air is "by far the best index of physical conditions surrounding animals wholly or partly exposed to the atmosphere." (Shelford.) The rate of evaporation is directly correlated with temperature and illumination, but most closely correlated with relative humidity. (Yapp.)

In the experimental study of evaporation Livingston's atmometer is usually employed. This consists essentially of a cup of porous clay which is filled with water, that is replaced as it evaporates, from a reservoir of water. The amount of evaporation is easily measured by the amount of water necessary to restore the water in the reservoir to its original level.

Few precise studies have been made upon the effects of evaporation on insects, though many have been made with man and other warm-blooded animals.

Metabolism in Relation to Evaporation.—"Metabolism results in heat, and the temperatures of the bodies of animals both warm and cold blooded, is nearly always higher than the surrounding medium, at least during activity. The surrounding conditions may be stated as usually acting on metabolism, etc., as follows: (a) A moist cold atmosphere (very low evaporation) causes body temperature to fall more rapidly than a dry cold one at the same temperature, because of the more rapid conduction of heat. Such a fall in temperature *decreases* metabolism of *cold blooded* animals, and *increases* metabolism of *warm blooded* animals within their capacity for heat regulation. In a dry cold atmosphere the heat loss is less pronounced because of the less rapid conduction of heat. (b) In a dry warm atmosphere (high evaporation) rapid evaporation keeps down the peripheral temperature, and prevents death from over-heating and destructive metabolism in cold blooded animals,

and makes possible body temperature regulation and thus prevents heat stroke and death in warm blooded animals. In a moist warm atmosphere, death and heat stroke occur because of lack of evaporation and lack of peripheral cooling in the case of warm blooded animals even when the surrounding temperature is at or below the normal body temperature. (c) Wind movement (which increases evaporation) increases radiation of body heat and of heat due to insolation. It increases evaporation and further cools the body, thus within certain limits increasing the metabolism of warm blooded animals and decreasing it in cold blooded animals. (d) Decrease of pressure increases evaporation and radiation both of which lower the temperature of animal bodies and influence metabolism.

"Conditions which withdraw water from organisms (evaporation as influenced by various factors) influence irritability, activity and length of life history. Thus Hennings found that low humidity increased insect metabolism and Sanderson found that in dry air the optimum temperature of the growth of insects was lower than in moist air. Factors probably operate with reference to an optimum." (Shelford.)

Professor Headlee raised bean weevils, *Bruchus obtectus*, from the eggs at a constant temperature of 80° F., but with various degrees of atmospheric moisture, from less than 1 per cent. to approximately 100 per cent. The optimum relative humidity was found to lie between 80 and 89 per cent. At 89.7 and 100 fungi developed and greatly reduced the numbers of the insects. Comparatively few individuals reached maturity in an atmospheric moisture of 25 per cent. and none in one of less than 1 per cent.

Burger, as reported by Shelford, studied the water relations of the meal worm, *Tenebrio molitor* when kept in dry air and fed on bran which had been dried at 105° C. He believed that the animals were in essentially absolute dryness. Here they lived for weeks, but lost weight. He found, however, that the per cent. of water in the animals remained practically the same until after death and came to the conclusion that the insect larvæ could not use their food to produce water and so the living substance itself was used. No doubt the food taken produced water but this was not sufficient in quantity. The most important fact brought out was that the per cent. of water remained about the same in spite of the extreme dryness and rapid loss of moisture.

Reactions.—Professor Shelford, who studied experimentally the behavior of various animals under different rates of evaporation, found

that in dry air (evaporation 0.06 cc. per hour) running beetles of the genus *Pterostichus* were very sensitive, exhibiting a preference for moist air. Digger wasps, *Microbembex*, were slightly positive to dry air, their chief reaction being digging, which took place in medium and moist air but not in the dry. A tiger beetle, *Cicindela*, gave a negative reaction to air evaporating 3.6 cc. per hour, and a positive reaction to air evaporating 1.56 cc. per hour.

Shelford studied also the influence of rapidly flowing and of warm air in increasing evaporation. All the animals that he studied could be killed by loss of water, when other conditions remained favorable to their existence. The smaller animals died from loss of water much more quickly than the larger, the surface being greater in proportion to the volume in the smaller animals. The animals died after a smaller amount of evaporation when the rate was slow than when it was more rapid. The most remarkable fact brought out was that the animals died more quickly from evaporation due to rapid movement of air than due to dryness.

With a total evaporation of 31.0 cc. in a dry atmosphere *Pterostichus* died in twenty-two hours.

The *Pterostichus* referred to came from under leaves on the ground in a dense forest—a moist habitat; and *Microbembex* is a resident of dry open sand areas.

Hatching.—With fertile eggs of plant lice (*Aphis avenæ* and *A. pomi*) air of high moisture content is more favorable to hatching than air having a lower moisture content. The moisture content of the air influences the evaporation from the eggs, determines the percentage of hatching, and probably influences the rate of splitting of the outer layer of the egg shell. (A. Peterson.)

Nymphs of walking-sticks, Phasmidæ, frequently fail to extract themselves from the egg shell, owing to dryness at the time of hatching. Most of them succeed in escaping, however, if supplied with moisture. In this instance evaporation has the mechanical effect of causing the appendages or the abdomen to adhere to the amniotic membrane. (H. P. and H. C. Severin.)

Life Cycle.—The length of the life cycle is often influenced greatly by evaporation as determined by temperature and relative humidity. With the Hessian fly, high temperature and low humidity lengthen the cycle. In a dry atmosphere the eggs shrivel; in periods of drought most of the puparia dry out and die. High temperature with high humidity, however, does not retard the development, and is not fatal.

Low temperatures lengthen the cycle and may be fatal to prepupal stages. Low humidity also increases the length of the cycle, and if extreme is fatal in all stages of development. (Headlee.)

Eclosion.—Every one who has had experience in raising moths from pupæ knows that the pupæ must have a certain amount of moisture or they will dry out and die. Out of doors the rainfall supplies the requisite moisture, but even there pupæ may succumb to too much or too little moisture.

Moths and butterflies upon emerging from the pupa can not expand their wings if the air is too dry, on account of the rapid evaporation of moisture from the wings. Indoors the moisture must be supplied if necessary. It has often been observed that moths emerge from cocoons in greater numbers on damp days. In dry weather many insects emerge at night, when the relative humidity is higher than in the daytime. This incidentally protects the helpless insect from its diurnal enemies.

Adaptations.—Many thin-skinned larvæ, as those of the house fly and the plum curculio, that live in a moist environment of decaying substance, die quickly if subjected to a dry atmosphere, when the temperature alone is not sufficiently high to kill them. On the other hand, larvæ with a thick integument, like the meal worm, resist evaporation more successfully.

An immense number of dipterous larvæ, those of the Hessian fly and the house fly, for example, when full grown retain the larval skin instead of shedding it; this skin drying and hardening to form a *puparium*, which retards evaporation from the developing pupa within. An unusually hot dry summer will, however, kill most of the puparia of the Hessian fly, excepting such as may be protected by their depth in the soil.

Some of our large silkworms smear the inner surface of the cocoon with a waterproof gum or varnish which undoubtedly prevents the undue escape of water from the enclosed pupa.

Larvæ that burrow into the ground (for example many caterpillars and maggots, white grubs, larvæ of the plum curculio, Colorado potato beetle, and numerous others) and make earthen cells in which to pupate, secure thereby protection from evaporation as well as from other influences. Larvæ of the late fall brood of the bollworm (corn ear worm) dig much deeper than those pupating earlier in the season. (Quaintance and Brues.)

The beetles of the subfamily Eleodinæ (Tenebrionidæ) that are characteristic of arid and semi-arid regions, have a thick integument and

are quite at home in the desert. The integument is possibly no thicker than in other tenebrionids, but having a thick skin to begin with, these forms have found a suitable environment and have thrived in arid places.

3. FOOD RELATIONS

As regards its kind and quantity, food is, needless to say, a most important condition of existence. Examples of food habits have been given (page 212); here should be mentioned some of the more essential facts concerning food as an ecological factor.

Classification of Food Habits.—According to the nature of their food, most insects may be classified as follows: *pantophagous* (omnivorous); *phytophagous* (plant-eating, referring usually to the flowering plants); *monophagous* (with a single food plant); *oligophagous* (with several definitely fixed food plants); *polyphagous* (feeding indiscriminately on many plants); *sarcophagous* (carnivorous); *harpactophagous* (predatory); *entomophagous* (parasitic on insects); *saprophagous* (feeding on decaying substances); *necrophagous* (feeding on dead animals); *coprophagous* (eating excrementitious material); *mycetophagous* (feeding on fungi); *microphagous* (on micro-organisms, as bacteria, yeasts, etc.).

Not all these categories will be considered here, but a few of them need special mention.

Microphaga.—The pomace flies (*Drosophila*) famous as subjects of investigation by geneticists, feed naturally in fermenting fruits, where they find nourishment, not in the products of fermentation, but chiefly in the yeasts that cause the fermentation. On sterilized glucose-agar the larvæ cannot grow unless yeast is added; and a medium of yeast nucleo-protein, sugars and inorganic salts is a complete food for this insect. (Loeb and Northrop, Baumberger.)

Sarcophaga.—Dipterous larvæ that normally feed on decaying animal tissue were raised from eggs to adults on a diet of banana and yeast-agar, by Baumberger, who says that we must consider the probability that all decaying or fermenting substrata are merely the media on which fungous or bacterial food of insects is growing.

Coprophaga.—Larvæ of the house fly were raised on bran mash containing a heavy growth of molds. Sections through these larvæ showed a complete absence of all material except bacteria, fungous spores, and yeast cells in the digestive tract. It appears probable that the larvæ feed on micro-organisms, and are associated with them in the same manner as that of *Drosophila* and yeasts. (Baumberger.)

Mycetophaga.—Many, though not all, of the fungus flies (*Mycetophilidæ*) feed on fungi. Larvæ of a species of *Sciara* that feeds in woody tissue were found to contain in the digestive tract fungous mycelia along with considerable woody material. Larvæ of the same species were reared on a medium of bran-agar, which they soon infected with molds, upon which they were subsequently observed to feed. The wood is merely the substratum in which the food material develops. (Baumberger.)

The ambrosia beetles, of which there are many species, make their tunnels in damp wood of weak or dead trees. Their food is not wood, however, but a fungous growth which develops rapidly on the walls of the galleries—so rapidly often as to choke the galleries and kill their inmates. The fungus begins its growth on a bed of chips which the female prepares, and on which she lays eggs. The fresh tender growth of the fungus is food for both larvæ and beetles, but only the latter can eat the older growth. “Different species of fungi are associated with different species of beetles, and these associations are constant for the same species in spite of changes of host plants.” (Baumberger.)

In connection with this subject the elaborate fungus-gardens of leaf-cutting ants and of termites should be recalled (page 295).

Selection of Food.—Insects find food for themselves or for their future larvæ by means of the senses of (1) *smell*, the most widespread method; (2) *taste*, as with butterflies, pomace flies, flesh flies and other forms that feed as adults; (3) *vision*, as with dragon flies, which after capturing their prey test it, however, and reject portions unsuitable as food; also bees, which can discriminate between flowers of different colors.

Brues adds, in his paper on this subject, that the selection of food plants by *Lepidoptera* depends also on (1) “Some attribute of the plant, perhaps an odor but far less pronounced to our own senses than those mentioned above. Species restricted to plants like *Leguminosæ* or *Violaceæ* may be considered in this category. Undoubtedly there is some attribute of such plants which insects can recognize in a general way and not as a specific characteristic of some single plant species or genus. (2) A similarity in the immediate environment or general form of the food plant. The effect of something of this sort is seen particularly in oligophagous and also polyphagous caterpillars feeding mainly on trees or shrubs, such as the gipsy moth, *Cecropia* moth, etc., and those of certain species like some of the *Arctiid* moths that feed upon a great variety of low plants. (3) Apparently chance associations that have

become fixed, whereby diverse plants are utilized by oligophagous species."

The selection of food by means of its odor is simply a case of positive chemotropism (see page 302), a blind reaction to a chemical substance. Pomace flies, which feed on and lay their eggs in fermenting fruits, are positively chemotropic to weak percentages of certain alcohols and acetic acid, which are products of fermentation. House flies are stimulated to oviposition by ammonium carbonate, with its odor like that of manure. The cabbage butterfly is induced to lay eggs by mustard oils, which occur naturally in its usual food plants, Cruciferae.

Growth.—Other things equal, the length of the larval stage depends upon the kind, condition, and amount of food. With the house fly, it is primarily temperature and moisture that determine the rate of development; but with an average temperature of about 21° C., the maggots develop in horse manure in fourteen to twenty days, and on a diet of bananas, in twenty-seven days. At the same temperature, the rate of development is directly proportional to the condition of the food as regards moisture. Dry conditions may retard development five or six weeks, tend to produce flies of subnormal size, or may be fatal. (C. G. Hewitt.)

If the mother insect lays her eggs in a considerable supply of food substance, as happens usually in the case of the house fly, pomace fly, carrion beetles, dung beetles, and many other insects, the development of the larva is assured, so far as the amount of food is concerned. The quantity of food present becomes important, however, for insects that are restricted to one kind of food plant, or to a food of low nutritive value. The nutritive content of wood is small, and wood-boring caterpillars and grubs frequently require long periods for their growth, even several years (Cerambycidae); though less time is needed if the larvæ, like those of the peach tree borers and the flat-headed apple borer, feed largely on the inner bark, which is more nutritive than the wood.

Size.—Under-nourished larvæ produce small adults, as might be expected. The size of boll weevils depends upon the abundance of the food supply and also upon the nature of the food. The smallest weevils develop from squares which are very small, and which fall very soon after the egg is deposited; the largest, from bolls which grow to maturity. In bolls the food supply is most abundant, and the period of larval development is several times as long as it is in squares. (Hunter and Pierce.)

Reproduction.—It goes without saying that constant feeding is necessary in the case of long-lived prolific females, such as queen bees, ants, or termites.

With plant lice, it has long been known that the drying up of the food plant causes the appearance of large numbers of winged, or migrant females. In experiments with the pea louse, *Macrosiphum pisi*, it was found that the subjection of parthenogenetic (reproducing without fertilization) females to periods of partial starvation induced the production of winged offspring from the wingless mothers. These winged young would otherwise have been wingless, as check experiments showed. (L. H. Gregory.)

In regard to the relation of food to the production of the males and oviparous (egg-laying) females of plant lice, not much seems to be definitely known.

Fecundity.—The kind and amount of food influence fecundity. If female boll weevils are fed on leaves alone, eggs do not develop; while a diet of squares leads to the development of eggs in about four days. More eggs are laid when squares are abundant than when they are few. (Hunter and Pierce.)

Guyénot found that pomace flies (*Drosophila*) reared from aseptic larvæ on sterile potato (without yeast) did not produce offspring. The flies themselves, if fed on potato alone, were much less prolific than when fed on potato and yeast.

Oviposition.—With many adult insects feeding is not necessary for oviposition; in fact the mouth parts are often rudimentary, as in some of the moths. Such insects owe their activity to the presence of a supply of food stored up by the larva. Other insects, however, must feed in order to lay eggs; the queen honey bee, for example.

Adults of *Pteromalus puparum*, a parasite of the cabbage butterfly, *Pieris rapæ*, if kept without food for three days, attempt to oviposit but are physically unable to do so. If then fed, however, with honey-water or with blood from punctured chrysalides (their natural food), they succeed in drilling into the chrysalides of their hosts. When supplied with fresh pupæ one of these females may feed and lay eggs for three weeks; and if given honey-water also, for two months. (S. B. Doten.)

Sex-determination.—One of the most plausible of the theories of sex-determination has been that high nutrition produces females and low nutrition, males. In raising moths or butterflies from caterpillars males and females occur in about equal numbers, as a rule. If, however,

the caterpillars are almost starved, some will die, and there will result many more male adults than female. Dr. C. V. Riley explained this long ago, by pointing out the fact that female caterpillars require a longer time for growth than males (having sometimes one more molt than the males); so that conditions of starvation would kill chiefly female caterpillars, that had not completed their growth, and affect male caterpillars less. T. H. Morgan, in a discussion of the subject, adopts this view, and points out the fact that the sex of the caterpillar is determined before the egg is laid; furthermore, that an excess of food does not cause an excess of females.

Longevity.—The duration of life is evidently related to food. Insects cannot live long, if active, without food; and activity is correlated with the amount of food utilized.

Females live longer than males, with some exceptions, particularly if they have not laid their eggs, and frequently possess an ample supply of reserve food accumulated by the larva, as in the case of many moths, particularly such as do not themselves feed as adults (silkworm moth).

With cotton boll weevils after emergence from hibernation, unfed beetles of both sexes were found to live ten days, and fed beetles, twenty-five days. (Hinds and Yothers.)

A queen honey bee, constantly fed with highly nutritious food, may live more than four years; a queen ant, fifteen years (one instance). On the other hand, the Hessian fly, which does not feed and has little reserve nutriment, lives only from one day (males) to four days (females).

A remarkable instance of longevity under starvation conditions is given by J. E. Wodsdalek. Finding that larvæ of the common museum beetle, *Trogoderma tarsale*, would live a long time without food, molting meanwhile but not eating the cast skins, he tested their longevity by keeping them individually in glass vials without food. The larvæ gradually decreased in size to almost their length at hatching, but were surprisingly tenacious of life. Newly hatched larvæ that had never eaten lived four months without food; quarter-grown larvæ, fourteen months; half-grown larvæ, three years; three-quarters-grown larvæ, four years; and full grown individuals, from four years to five years, one month and twenty-nine days (one larva). If stunted specimens were given food they began to grow again, and could again be reduced in size by a second period of starvation. By alternate periods of feasting and fasting, larvæ were three times brought to their maximum size and three times reduced to the minimum size.

Hibernation.—Food is of minor importance as an incentive to hibernation. Codling moth caterpillars, woolly bears (*Isia isabella*) and many other insects enter hibernation before there is any failure of the food supply.

Insects which feed on evergreen trees are not as rhythmical in their hibernation as those which feed on deciduous trees. (Pictet, Baumberger.)

Some larvæ are full-fed upon entering hibernation (codling moth); while others are not (brown-tail moth). Emergence from hibernation depends immediately upon temperature, but it is possible that hunger also is a stimulus to the renewal of activity.

As metabolism is at its minimum in hibernating insects, their food requirement is similarly small.

Coloration.—Food, as regards kind and condition, often affects coloration, particularly pigmental coloration (see page 176).

In the cotton boll weevil the color becomes darker with age; consequently, hibernated individuals are the darkest found; but food also influences the color. The smaller the size of the weevil, the darker brown is its color; the largest weevils are light yellowish brown. The principal reason for the variation, in the opinion of Dr. W. E. Hinds, lies in the degree of development of the minute, hair-like scales, which are much more prominently developed in the large than in the small specimens, although the color of old specimens is often changed by the abrasion of the scales. These scales are yellow in color, while the ground color of the integument bearing them is a dark brown or reddish brown. The development of the scales appears to take place mostly after the adult weevils have become quite dark in color, but before the chitin becomes fully hardened. They seem, therefore, to be, to a certain extent, an aftergrowth which depends upon the surplus food supply remaining after the development of the essential parts of the weevil structure. (Hunter and Pierce.)

Food Relations in General.—A phytophagous species which is limited to one species of food plant frequently dies out in a locality from having consumed or fatally weakened all its food plants (the butterfly *L. philenor*, on *Aristolochia*, in the North).

Evidently, a species which has many kinds of food plants has an advantage (gipsy moth, grasshoppers, army worm, etc.).

The quantity of food present becomes important for an insect that is restricted to a single species of plant. It may be a plant that is

always abundant, like the pawpaw, to which the Ajax butterfly is confined; or it may not be.

In a state of nature, if food plants of one species are scattered among other plants, their insect enemies do not become injurious; but in a state of nature, if many plants of one species grow together, insects may injure them (in forests, for example). Where man grows one kind of plant over a large area, insect enemies flourish (Hessian fly, chinch bug, cotton boll weevil, codling moth, etc.).

The same relations exist between parasites or predators and their hosts. A parasitic species of insect that is limited to one species of host will die if it destroys all the individuals of the host species. The successful parasites (as Ichneumonidæ, Chalcididæ, and Braconidæ) are those that have available immense numbers of a single species of host, or a large number of species as hosts.

Most predaceous insects, however, feed indifferently on almost any species of insects that they can overcome, and often do not limit themselves to insects for food; therefore their numbers are not affected by the absence of this or that species of possible victim.

These food relations form a most important factor in the interactions of organisms, the subject next to be considered.

4. BIOTIC CONDITIONS

The animals and plants of a region form a vast complex, in which every organism affects every other, directly or indirectly, and is in turn affected by all the others. Furthermore, all the organisms are influenced by their environment, and in turn affect the character of the environment itself more or less. All the organisms are bound up with one another in an intricate network of interactions which the mind can only partially comprehend.

Interactions.—As a familiar illustration of these interactions, take the case of any common plant louse and the extensive society, or consocieties, which it dominates.

To begin with, the numbers of aphids depend greatly upon inorganic influences, as heat or cold, dryness or moisture; evaporation being important. Aphids are often blown off their plants, or washed off by rains, and killed mechanically. When they are abundant, many are squeezed to death between branches that are blown against each other. Bacteria and fungi destroy the lice. The fungus, *Empusa aphidis*, is the most important enemy, for in damp weather it can almost extermi-

nate plant lice locally. Weather conditions may render the plants unfit for food, or may prevent the eggs from hatching. In short, aphids are affected for good or ill by all the influences that act upon their food plants.

Enemies are abundant. Many kinds of spiders and a few kinds of mites kill the lice. The English sparrow eats the pea louse voraciously, and the chickadee in winter consumes enormous numbers of aphid eggs. Most of the enemies are, however, other insects. Here are lists of the insects known to affect, directly or indirectly, the common pea louse, or clover louse, *Macrosiphum pisi*.

PREDATORS¹

<i>Coccinellidæ</i> (lady beetles)	<i>Chrysopidæ</i> (lace-wings)
<i>Ceratomegilla fuscilabris</i>	<i>Chrysopa oculata</i>
<i>Hippodamia tredecimpunctata</i>	<i>Chrysopa rufilabris</i>
<i>Hippodamia parenthesis</i>	<i>Chrysopa plorabunda</i>
<i>Hippodamia glacialis</i>	<i>Gryllidæ</i> (tree-cricket)
<i>Hippodamia convergens</i>	<i>Æcanthus confluens</i>
<i>Coccinella novemnotata</i>	<i>Pentatomidæ</i> (stink bugs)
<i>Cycloneda sanguinea</i>	<i>Podisus maculiventris</i>
<i>Adalia bipunctata</i>	<i>Euschistus variolarius</i>
<i>Chilocorus bivulnerus</i>	<i>Anthocoridæ</i> (flower bugs)
<i>Syrphidæ</i> (flower flies)	<i>Triphleps insidiosus</i>
<i>Ocyptamus fuscipennis</i>	<i>Cantharidæ</i> (cantharids)
<i>Platychirus quadratus</i>	<i>Podabrus rugulosus</i>
<i>Syrphus americanus</i>	<i>Podabrus tomentosus</i>
<i>Syrphus ribesii</i>	<i>Itionididæ</i> (gall gnats)
<i>Allograpta obliqua</i>	<i>Aphidoletes meridionalis</i>
<i>Mesogramma marginata</i>	
<i>Mesogramma polita</i>	
<i>Sphærophoria cylindrica</i>	

PARASITES

<i>Ichneumonidæ</i> (ichneumons)	<i>Aphidius washingtonensis</i>
<i>Praon simulans</i>	<i>Aphidius rosæ</i>
<i>Trioxys cerasaphis</i>	<i>Miscogasteridæ</i> (miscogasterids)
<i>Aphidius fletcheri</i>	<i>Megorismus fletcheri</i>

The species of the preceding list feed directly on the pea louse. Those of the following list affect the louse indirectly, by feeding on the preceding species or on one another.

¹Additional details in regard to all these insects will be found in Bull. Ill. Agr. Exp. Sta., No. 134, and Bull. U. S. Dept. Agr., No. 276.

AFFECTING *M. PISI* INDIRECTLY*Braconidæ* (braconids)

Perilitus americanus, parasitic on the beetles, *Ceratomegilla fuscilabris* and *Coccinella novemnotata*.

Bassus lætоторius, a parasite bred from larvæ and pupæ of *Allograpta obliqua* and five other species of *Syrphidæ*.

Figitidæ (figitids)

Solenaspis hyalinus, a parasite from larvæ of *Mesogramma polita*.

Pteromalidæ (pteromalids)

Pachyneuron syrphi, a parasite of *Bassus lætоторius*.

Encyrtidæ (encyrtids)

Encyrtus mesograptae, a parasite from larvæ of *Mesogramma polita*.

Chalcididæ (chalcids)

Isocratus vulgaris, a parasite of *Bassus lætоторius*.

Proctotrypidæ (proctotrypids)

Telenomus podisi, a parasite of the eggs of *Podisus* and *Euschistus*.

A few examples will illustrate the intricacy of the interrelations of these insects that are dominated by *Macrosiphum pisi*.

M. pisi is preyed upon by lady beetles, the pupæ of which are sucked by the stink bugs, the eggs of which are parasitized by a proctotrypid.

M. pisi is food for larvæ of flower flies, the larvæ and pupæ of which are parasitized by a braconid, which is itself parasitized by a pteromalid and a chalcid.

M. pisi is destroyed by larvæ of flower flies, the larvæ of which are attacked by stink bugs, while the adults are eaten by robber flies, toads, and various birds, as the kingbird, flicker and phoebe.

Thus forty species of insects are known to be vitally concerned with the pea louse. There should be added the mite, *Rhyncholophus parvus*, which feeds on the louse.

The writer has found more than two hundred species of insects in a field of red clover. All these have some influence on the pea louse (clover louse) and on each other; though the influence is often remote in its effects and practically insignificant. The scavenger insects on the ground, and collembolans etc., in the soil, feeding on organic matter, affect the texture and composition of the soil and consequently the plant. Without considering earthworms, moles, mice, birds and many other animal factors that might be thought of, we shall mention insects only. The bees that pollenize the flowers, and the various insects that destroy the roots, stems, leaves or flowers, all affect indirectly the louse. As illustrating interactions, though it is of no practical consequence, we may say that the yield of clover seed depends slightly upon the structure of the milkweed flower; for flower flies whose larvæ destroy plant

lice are sometimes fatally entangled in the flowers of milkweed. We might even go farther, and implicate all the factors that control milkweed; and so on indefinitely. Such speculation is not altogether profitless, if one bears in mind the fact that only the more immediate influences are of any practical importance, and that the effect of one factor may be increased, diminished, or neutralized by that of another.

Every one of the insects or other animals that affect the clover louse directly or indirectly, is itself the center of a little world of interactions. Though we cannot follow all these interactions, their total effect at any given time is expressed by the existing number of individuals of each of the species involved; which measures also the success of each species from its own point of view, so to speak.

Equilibrium.—It is not surprising, then, that species fluctuate in number of individuals. The presence or absence, or increase or decrease, of one influence may affect many other factors, and disturb preexisting relations. This is seen in the case of the rapid multiplication of the gipsy moth and the San José scale insect, when introduced into this country without their natural enemies.

Evidently there is actually no such thing as a "balance of nature," a true equilibrium; on the contrary there is continual fluctuation within wider or narrower limits. The so-called equilibrium is simply a condition of relatively small fluctuation. Under conditions of nature, animals and plants approximate a condition of stability, or fluctuation within comparatively narrow limits, to the benefit of all concerned. Under artificial conditions, however, as when man grows one kind of plant over a large area, the insects of the plant multiply rapidly. Man is able to remedy such disturbances of the "order of nature" in proportion to his knowledge of the factors concerned, especially of their relative importance. He has unwisely introduced the English sparrow to subdue caterpillars; but has wisely imported and propagated the native enemies of the fluted scale, the gipsy moth, and other pests.

II. CONDITIONS OF AQUATIC EXISTENCE

The fundamental physiological requirements are the same for aquatic as for terrestrial animals, but these conditions are often met in different ways in the two groups. Though insects may broadly be divided into these two groups, there are many kinds whose environment is intermediate between water and land, and many forms are aquatic in their immature stages and terrestrial as adults.

1. CHEMICAL CONDITIONS

Animals cannot exist in water that does not contain certain gases and chemical compounds in solution.

Gases.—Oxygen is a necessity, and most aquatic animals select water with a high oxygen content. In air dissolved in water the proportion of oxygen to nitrogen is much larger than it is in atmospheric air; because oxygen is more soluble in water than nitrogen. The oxygen content of the water is more variable than that of the atmosphere. The importance of the oxygen factor is indicated by the many elaborate adaptations for respiration displayed by aquatic insects.

Carbon dioxide given off by animals during respiration, acts in small quantities as a stimulation to respiration, and in large amounts as a narcotic capable of fatal effects. Aquatic animals react negatively to even a small increase of carbon dioxide. This is due to the increase in hydrogen-ion concentration which it causes. Since a large amount of dissolved carbon dioxide is commonly accompanied by a low oxygen content as well as other important factors, the hydrogen-ion concentration of waters of low alkalinity is probably the best single index of the suitability of the water for animals. (Shelford.)

“Nitrogen has little effect upon animals except when present in excess.” (Shelford.)

“Oxygen and nitrogen go into solution from the atmosphere and oxygen is also produced by green plants. The other gases are produced chiefly by organisms as excretory and decomposition products.” (Shelford.)

Chemical Compounds.—Carbonates, sulphates, and chlorides of magnesium, calcium, and sodium, and salts of potassium, iron, and silicon are practically always present in solution in water, and their presence in definite proportions is essential to the life of the animals. (Shelford.) Sodium chloride, or common salt, is unfavorable to insect life. Almost no insects live in the ocean (see p. 170). In fact, if an insect larva be taken from a brook and put in a brackish pool it will actually lose water through its skin; it will partly dry up. (F. E. Lutz.) Flies of the genus *Ephydra* are, however exceptional in this respect. Two species of these “salt-flies” are abundant in Great Salt Lake, the salinity of which is greater than that of the ocean. The flies and puparia sometimes occur in inconceivable numbers, the latter forming large brown patches on the water or windrows on the shore. The larvæ, which feed on an alga, are active even when the water evaporates

down until covered with a crust of salt. (J. M. Aldrich.) Not a few insects live in brackish water, however; some of them occurring also in fresh water; as the nymphs of certain dragon flies, which inhabit also salt, sulphurous, or slightly alkaline ponds in the West. (R. C. Osburn.) A few Hemiptera of fresh-water occur also in brackish water or in water strongly impregnated with various mineral salts. (H. G. Barber.) Several species of mosquitoes confine themselves for breeding purposes to salt marshes, where *Aedes sollicitans* is always the most abundant and is found in practically all the temporary pools uninhabited by fish. (J. A. Grossbeck.)

Larvæ of the malaria mosquitoes (*Anopheles*) also develop in brackish water. The salt marsh mosquito (*Aedes sollicitans*) was found to develop in water so strongly polluted with acid waste from a "guano factory" that all other animal life appeared to be extinct. (S. F. Hildebrand.)

Water containing certain acids, as the humic acids of peat bogs, is deleterious to insect life.

2. PHYSICAL CONDITIONS

Circulation.—"The distribution of dissolved salts and gases is dependent upon the circulation of the water, as their diffusion is too slow to keep them evenly distributed. The circulation of water in streams is probably such as to keep all dissolved gases and salts about equally distributed. The water of streams has been found to be supersaturated with oxygen. Oxygen is taken up by the water near the surface. Nitrogen and carbon dioxide are produced especially near the bottom, and if the water did not circulate they would be too abundant in some places and deficient in others for animals to live." (Shelford.)

The flowing or splashing of water increases the oxygen content. Larvæ such as the hellgrammite, those of black-flies (*Simulium*) and of some caddis flies (as *Hydropsyche*) require well-aerated water, and are found always in moving water, often in strong currents. They occur in flowing water not *primarily* on account of its greater oxygen content, however, but because, as Shelford has shown, such animals orient themselves toward a strong current of water (positive rheotaxis) and move against the current. Furthermore, they are positively thigmotactic and show a strong preference for hard surfaces, as those of large stones; with an avoidance of sand; the members of a rapids community differing from those of a pool community in this respect.

Hydropsyche reacts positively to the direction of light, though indifferent to its intensity; but some other members of the rapids community, as hellgrammites and burrowing caddis worms, avoid light.

"Current is an important factor of aquatic environments which finds its terrestrial counterpart in winds. That it is a very important factor is shown by the numerous devices aquatic insects have to keep their position, and it varies from nothing in puddles to the rush of Niagara." (F. E. Lutz.) Larvæ of the black-flies are fastened to stones or other objects; some caddis worms anchor their cases securely; beetles of the family Elmidae cling with their claws tightly to submerged objects. With caddis flies of the family Hydropsychidae, which live in swift streams, the instantaneous emergence of the adult as soon as the pupa reaches the surface prevents the fly from being swept away. (C. E. Sleight.)

Temperature.—Temperature is of great indirect importance in the control of the distribution of life in water. (Shelford.) It is "more constant in aquatic environments than in terrestrial, although it is somewhat variable from place to place and month to month. In the summer, a spring hole is cooler than a rainwater puddle and the opposite is apt to be true in the winter. In general, a running stream is apt to be cooler in summer than a stagnant one. In the spring a deep pond is generally cooler than a shallow one, and the opposite is true in the autumn. But aquatic insects are never subject to the sharp daily fluctuations of temperature that most of their terrestrial relatives must bear, and even the annual range of temperature variations is slight." (F. E. Lutz.) Such differences as there are have, however, an influence on aquatic life. Temperature affects activities of various kinds, as locomotion and oviposition; may determine the length of the egg-period; or may act in other ways.

Light.—Light controls distribution and activities. Its intensity decreases rapidly, particularly that of the orange and red rays, with the depth of the water. Aquatic insects, like terrestrial, react either positively or negatively to the directive action of light (*phototropism*, p. 306). Some of them frequent shaded or dark places, while others, as the whirligig-beetles (*Gyrinidae*) and the water-striders (*Gerridae*) are at home on the surface of the water in the strongest sunlight.

Pressure.—Pressure in water increases with depth, at the rate of about one atmosphere for each thirty-three feet (Shelford). Its effects on aquatic insects are for the most part indirect; the pressure affecting other conditions of existence.

Depth.—Depth is mostly important indirectly, on account of its influence on other conditions, such as circulation, temperature, light, and pressure; but is in itself a determining condition in some instances. Thus such larvæ of horse-flies (*Tabanidæ*) as have a posterior respiratory tube bearing the spiracles must have shallow water, where the spiracles can be raised to the surface; though sometimes these larvæ are found in moist earth where there is no standing water. (R. C. Osburn.)

Bottom.—"The character of materials and topography of the bottom are very important to animals living on the bottom, but it has its effect also on free swimming animals as a determining factor in the amount of sediment. The kind of bottom is important because many animals are dependent upon solid objects for attachment and are absent from bottoms made up of fine materials. Others must burrow into mud or creep on sand and gravel." (Shelford.)

Most *Dytiscidæ* prefer clean live water, being averse to very muddy bottoms. (J. D. Sherman.) On the other hand, nymphs of various dragon flies bury themselves in the mud. Some of the caddis worms prefer a clear sandy bottom; others, a bottom with slime, or one with sticks, dead leaves or other debris.

Vegetation.—It goes without saying that vegetation, in its amount and kind, is extremely important as a condition of aquatic existence. The green plants give off oxygen. Plants are used for shelter, escape from enemies, as places in which to wait for the prey (dragon fly nymphs, *Zaitha*), as surfaces for locomotion (non-swimming larvæ of diving beetles, whirligig beetles and others), especially as a means of reaching the surface for air or for the transformation (dragon fly nymphs, etc.). Eggs may be laid on the plants (electric light bugs, back-swimmers, May flies, caddis flies, etc.) or inserted into plant tissues (diving beetles, water scorpions).

3. FOOD CONDITIONS

The small beetles of the family *Haliplidæ* are said to feed on algæ. The water-scavenger beetles (*Hydrophilidæ*) feed mostly on decaying vegetable matter, but are sometimes carnivorous, and some of the adults will eat green vegetation. The diving beetles (*Dytiscidæ*) are carnivorous; the whirligig beetles (*Gyrinidæ*) feed on small insects found on the surface of the water. The water-striders (*Gerridæ*) capture disabled or living insects for food; the water boatmen (*Corix-*

idæ) are predaceous. Nymphs of dragon flies are predaceous, catching other insects by means of their peculiar extensile lower lip, and even young fishes, tadpoles and smaller nymphs of their own kind. (R. C. Osburn.) Most caddis worms are plant-eating, but some are insectivorous, as *Hydropsyche*, which catches its victims in the nets that it spreads in swift currents. May fly nymphs are carnivorous, or feed on plants or mud. Additional examples of food habits are given on p. 165.

4. BIOTIC CONDITIONS

Aquatic animals and plants, like terrestrial, form a vast complex of organisms that interact upon one another in innumerable ways and are acted upon by the environment; but the interactions are different to the extent that the aquatic environment differs from the terrestrial. As a whole, the physical and chemical conditions of existence are more uniform in water than on land. Furthermore, the number of species concerned is fewer; thus aquatic insects form only 3 per cent. of all insects. As regards food supply, the truism that its diminution lessens the numbers of the animals dependent upon it, applies of course, as with terrestrial forms. Aquatic insects are, however, much less specialized than terrestrial as regards food habits. Thus the plant-eating species are seldom limited to one species of plant, therefore can always find food, even though there are fewer species of aquatic plants than of terrestrial. The great majority of aquatic insects are, however, carnivorous, and many are omnivorous, and rarely suffer from lack of food. Though the predaceous habit is highly developed among aquatic insects, the parasitic habit has developed almost entirely among terrestrial forms; and aquatic insects, while actually in the water, are practically free from the attacks of parasitic insects.

On the whole, the interrelations of aquatic forms, though inconceivably complex, are less extensive than those of terrestrial species.

The so-called equilibrium or "balance of nature" is maintained, which is, as on land, a condition of continual fluctuation within relatively narrow limits; with a smaller range of fluctuation in the aquatic environment.

III. ENVIRONMENTAL FACTORS IN GENERAL

The important factors of the environment have been considered individually. In nature they do not operate singly, however, and by

simple observation, unaided by experimentation, one cannot disentangle the effects of one factor from those of others acting with it. The environment is a complex of many interdependent factors.

The factors control one another, but those that are more immediate in their operation are controlled by the larger influences of physiography and vegetation.

Physiography.—"In streams, current and oxygen content are determined very largely by physiographic conditions. Current is a function of volume of water and slope of stream bed. Oxygen content is largely determined by the rate of flow, and therefore is influenced by physiography. In lakes, oxygen content is determined by the depth, the temperature, and winds—physiographic factors are again important. On land, moisture and light are in a measure controlled by physiographic features. Slope and direction of facing profoundly affect vegetation, moisture, and light." (Shelford.)

Surface Materials and Vegetation.—"Materials for abode are largely the surface soil or rock or the vegetation. Surface soil or rock influences the moisture. Both moisture and surface materials influence the kind and amount of vegetation. All are interdependent.

"Physiographic features change with time. Erosion changes the gradient of streams, the width of valleys, the steepness of valley walls and cliffs, the ground-water level, etc. The weathering of rock is a process familiar to all. It is the aggregate of processes by which the coarse and hard or massive materials are reduced to clay and soil. This requires time.

"The fact that vegetation grows upon the so-called sterile, coarse, rough-surface materials, usually scattered or ephemeral at first, but increasing in denseness with each generation, is also familiar. Plants add organic matter to the soil. This organic matter holds the water so that moisture increases and plants may increase. With such changes it is obvious that an area of sterile soil will support more animals as time goes on, than at the outset, when the conditions were such that only a few hardy species could live. Here again, then, time is the important factor in determining the change of the area, so as to be suitable for more species (because more species are adapted to live in the resulting than in the initial conditions). The length of time which has elapsed since a given set of surface and physiographic conditions became exposed to the atmosphere is very important in governing the number, kind, and distribution of animals in a given area." (Shelford.)

IV. CLASSIFICATION OF ENVIRONMENTS

The distinction must be made between *climatic* environmental complexes and *local* complexes. "The climate, and such features as types of vegetation covering large areas, e.g., steppe, deciduous forest, etc., are commonly regarded as climatic. Opposed to these, and lying within them, are the local conditions, such as streams, lakes, soils, exposure, etc., which are only indirectly dependent upon climate." (Shelford.)

The classification of animal environments is based upon vegetation, physiography, or both. Where vegetation exists, animal communities are referred to the plant communities which form their environments. (Plate V.)

The simple and natural classification of plant communities recommended by Livingston and Shreve is illustrated as follows:

"The extensive areas such as the sagebrush plains of the Great Basin, the grasslands of Nebraska and Kansas, or the pine forests of the Atlantic Coastal Plain are designated as *formations*. The smaller and less markedly differentiated areas within a formation are designated as *associations*, as, for example, the forests of shortleaf pine in New Jersey, those of loblolly pine in Maryland and Virginia, and those of longleaf pine in the Gulf States, all lying within the Coastal Plain formation. The smallest units of vegetation are [sometimes] termed *societies*, and these are of small area and represent portions of the association in which a definite aggregation of species is to be found." (Livingston and Shreve.)

An outline of the content of animal ecology prepared by a committee of the Ecological Society of America, in 1920, contains the following useful synopsis.

DISTRIBUTION OF COMMUNITIES

1. Land communities.

(a) Forests with broad thin leaves.

1. Continuously moist and evergreen.

(a) Uniformly warm, affording habitats in six or more strata. (Tropical rain forests.)

(b) With cool season. (Temperate rain forests.)

2. Intermittently dry or cold, and deciduous.

(a) Warm with distinct dry season. (Tropical deciduous forest.)

(b) With cold winter, little winter shelter. (Temperate deciduous forest.)

(b) Communities of evergreen forests of narrow, thick leaves.

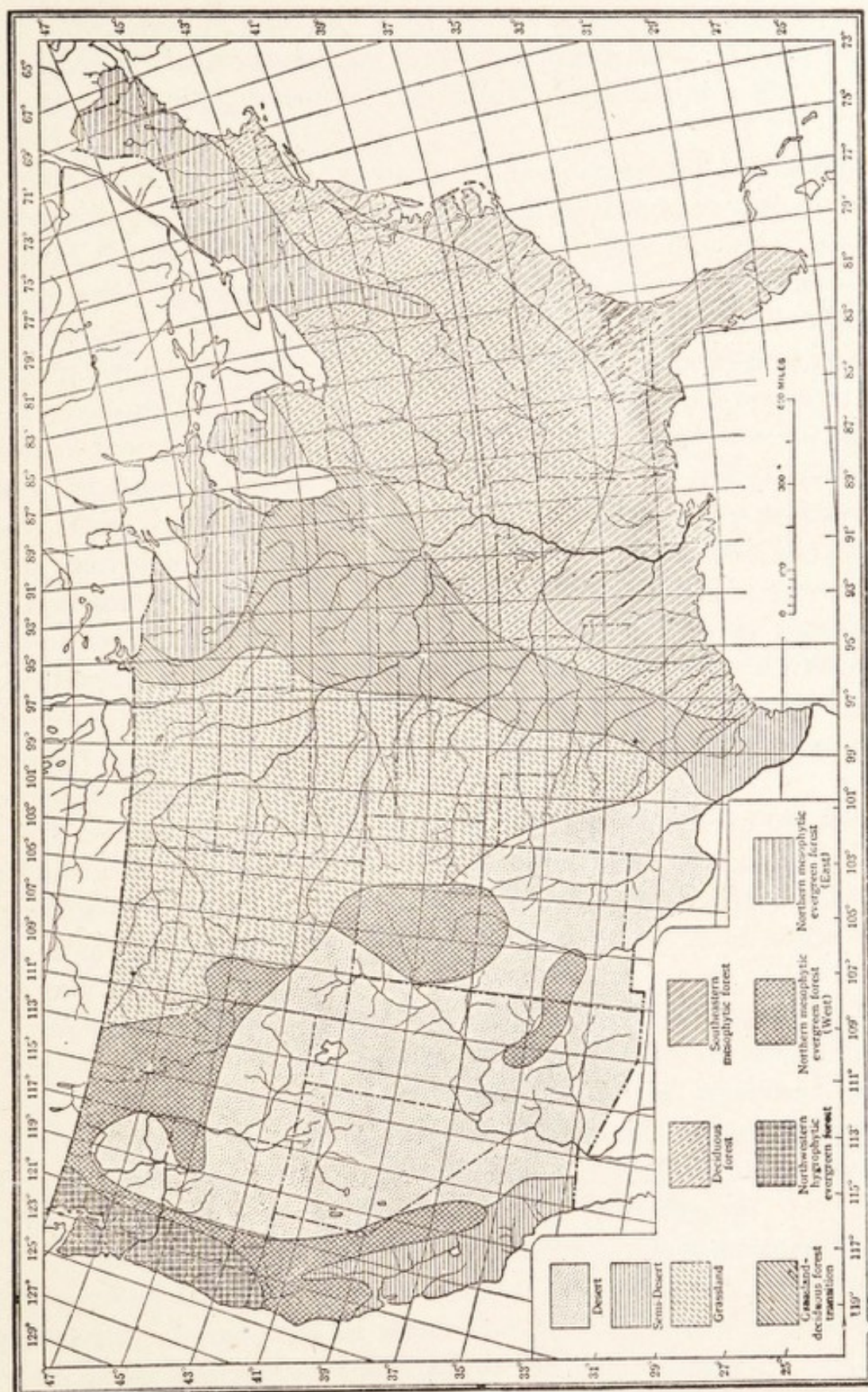
1. Moist conifer forest with little undergrowth.

2. Rainy conifer forest with shrub undergrowth.

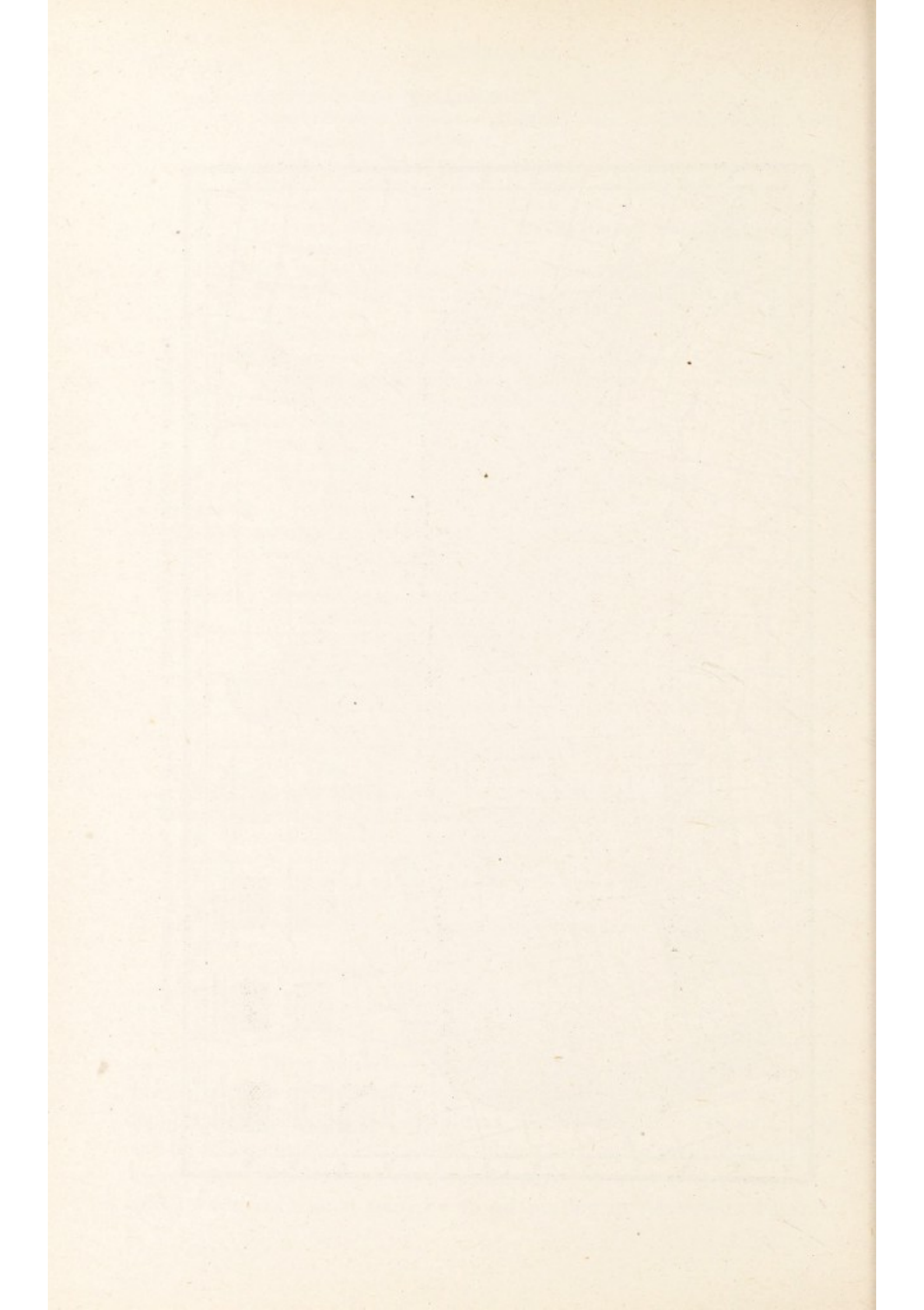
3. Open, arid, conifer forest.

- (c) Communities of savanna and grassland.
 - 1. Tropical savanna (dry season) affording habitats in groves, thickets, forest margins and grasslands.
 - 2. Tropical steppe; large herds of mammals.
 - 3. Temperate savanna; habitats in groves, thickets, forest margins and grasslands.
 - 4. Temperate steppe with cold or dry winters and usually large herds of mammals.
 - 5. Arid, broken, bush-covered steppe with small herds of mammals.
- (d) Communities of winter rain (forests with broad thick leaves) e.g., California semi-desert.
- (e) Communities of desert and semi-desert.
 - 1. Grass, cactus, tree semi-desert with grazing mammals (e.g., South Texas semi-desert); succulent semi-desert; shrub-covered semi-desert.
 - 2. Extreme desert without large diurnal mammals.
- (f) Arctic and Alpine lands.
 - 1. Tundra.
 - 2. Alpine meadows.
 - 3. Ice fields.
- 2. Communities of waters and shores.
 - (a) Communities of the sea (Marine).
 - 1. Communities of the open sea (Pelagic).
 - (a) Mid-oceanic communities.
 - (b) Oceanic island communities.
 - (c) Sargassum communities.
 - (d) Coastal oceanic communities.
 - 2. Communities of the sea bottom (Benthic).
 - 3. Littoral communities.
 - (a) Communities of eroding shores; subdivisions based on exposure, bottom material and latitude.
 - (b) Communities of depositing shores; subdivisions as above plus vegetation.
 - (c) Special communities: coral; tidepools; kelp.
 - 3. Communities of the sea shores. Animals feeding in the sea and breeding on the land, or vice versa. Classification based on climate.
 - 4. Communities of the fresh waters.
 - (a) Communities of still waters. Subdivisions based on size, depth and vegetation; littoral, pelagic, benthic.
 - (b) Communities of turbulent waters. Subdivisions based on character of water movement.
 - (c) Swamps, marshes, etc.

Ecology finds its distinctive field of study in *communities* and *succession*. These important subjects can not, however, be adequately presented from an entomological viewpoint alone. Furthermore, little has been published on the subject as regards insects. The most that can be done here is to illustrate the subject by naming some of the better known insects as being characteristic of a few typical environments, and to add occasional remarks on adaptation in relation to habitat.



Generalized Vegetation map of the United States. (AFTER LIVINGSTON AND SHREVE.)



V. COMMUNITIES

In a given habitat the fauna and flora together constitute a *biota*. The term *fauna* is generally used in connection with classification or geographical distribution, as is also the term *flora*. In reference to ecological relations, however, the animals or plants of a given habitat constitute a *community*.

As animals and plants, according to their structural resemblances or differences, fall into species, genera, families, orders, etc., so do animal or plant communities, according to their ecological likenesses or unlikenesses, fall into *mores*, *consocieties*, *strata*, *associations*, and *formations*; each of these orders being inclusive of the preceding kind; there the resemblance ends. The animals of a community agree in their reactions to the factors that they encounter. If they meet environmental influences in the same way, they are said to be *ecologically similar*; if they meet the same influences in different ways, they are *ecologically equivalent*. Thus a caterpillar that meets low temperature by making a cocoon, and one that gets the same result by digging into the ground, are ecologically equivalent. Animals select their habitats, probably by trial and error; and their behavior becomes adjusted to the surrounding conditions. (Shelford.) "The habitat is the *mold* into which the organism fits. Since habitats are different, animal communities occupying different habitats are physiologically different. Communities are systems of correlated working parts." (Shelford.)

"*Mores* are groups of organisms in full agreement as to physiological life histories as shown by the details of habitat preference, time of reproduction, reactions to physical factors of the environments, etc. The organisms constituting a *mores* usually belong to a single species but may include more than one species.

"*Consocieties* are groups of *mores* usually dominated by one or two of the *mores* concerned and in agreement as to the main features of habitat preference, reaction to physical factors, time of reproduction, etc. Example: the prairie aphid consocieties. The aphids dominate a group of organisms which for the most part prey upon them, as, for instance, certain species of lacewing, lady beetles, syrphus-flies, etc.

"*Strata* are groups of consocieties (and animals not so grouped) occupying the recognizable vertical divisions of a uniform area. Strata are in agreement as to material for abode and general physical conditions but in less detail than the consocieties which constitute them.

"For example, a forest-animal community is clearly divisible into

the *subterranean-ground* stratum, the *field* stratum (zone of the tops of the herbaceous vegetation), the *shrub* stratum (zone of the tops of the dominant shrubs), the *lower tree* stratum (zone of the shaded branches of the trees), and the *upper tree* stratum. A given animal is classified primarily with the stratum in which it breeds, as being most important to it, and secondarily with the stratum in which it feeds, etc., as in many cases most important to other animals. The migration of animals from one stratum to another makes the division lines difficult to draw in some cases. Still, the recognition of strata is essential but a rigid classification undesirable. Consocieties boring into the wood of living trees probably should be considered as consocieties relatively independent of stratification phenomena.

"*Associations* are groups of strata uniform over a considerable area. The majority of mores, consocieties, and strata are different in different associations. A minority of strata may be similar. The term is applied in particular to stages of formation development of this ranking. The unity of associations is dependent upon the migration of the same individual and the same mores from one stratum to another at different times of day or at different periods of their life histories. Migration is far more frequent from stratum to stratum than from one association to another.

"*Formations* are groups of physiologically similar associations. Formations differ from one another in all strata, no two being closely similar. The number of species common to two formations is usually small (e.g., 5 per cent.). Migrations of individuals from one formation to another are relatively rare." (Shelford.)

VI. EXAMPLES OF INSECT COMMUNITIES

The article by A. G. Vestal, from which the following extracts are taken, though limited to a single group of insects, the grasshoppers, is a good example of how entomological field observations may be organized on an ecological basis. The observations were made at Douglas Lake, Michigan.

COMMUNITY-RELATIONS OF GRASSHOPPERS

Northeastern Conifer Formation.—*Thuja Association.*—Cedar and peat bog. *Melanoplus islandicus* the only species.

Aspen Association.—In treeless parts, *M. angustipennis* is the common species. *M. luridus* is found sparingly in scattered aspen

growths. *Scirtetica marmorata* occurs usually on or near the lichen-covered surfaces.

Eastern Deciduous Forest Formation.—*Herbaceous Associations.*—Hot dry clearings. Grasshoppers are numerous both in individuals and in species. In order of abundance: *Melanoplus atlanis*, *Camnula pellucida*, *Dissosteira carolina* (Carolina locust), etc.

Thicket and Bramble Associations.—*M. bivittatus* occasional on shrubs. *M. atlanis* and others occur on the ground.

Local Associations.—*Dry Beach.*—Pure sand, dry and shifting, with full exposure to sun and wind. Here are several species of grasshoppers, which occur also in other habitats. *Trimerotropis maritima* (the seaside grasshopper, p. 196) is, however, limited to this habitat, and has the same brownish color as the sand.

Marsh Associations.—Several species of grasshoppers are found in the tall, rather close, sedge or grass growths. *Stenobothris curtippennis* is the characteristic grasshopper of littoral situations.

Ruderal Associations.—*Dry Grassland.*—Waste places, dry pastures, abandoned fields, roadsides, etc. In order of importance: *M. atlanis*, *Camnula pellucida*, *M. bivittatus*, *Dissosteira carolina*, *Arphia pseudonietana*. All these species, with the possible exception of the last, are more abundant in ruderal than in native vegetation.

Sparsely Vegetated or Bare Soil.—The *Oedipodinae* normally rest on bare soil and oviposit in it. Bare soil as a habitat is, however, not sufficient; nearby vegetation is necessary. Grasshoppers are rare on extensive areas of bare soil, except at the borders. They are conspicuous on bare places, but are more abundant in the interspaces between plants, in open growths. The Carolina locust, *Dissosteira carolina*, is the most familiar species of bare soil, though other species have the same habitat.

Meadow Associations.—Variable in character. In a bluegrass-white clover meadow, *M. atlanis* and *Stenobothris curtippennis* are of about equal abundance. The red-legged locust, *M. femur-rubrum* is more abundant than these in such places, in some localities. The differential locust, *M. differentialis*, is typical in meadow habitats.

1. Grasshoppers are more abundant, in species and in individuals, in herbaceous or grassland habitats than in forest, and more abundant in dry than in moist or wet situations.

2. Certain species are much more restricted than others in range of habitats, and in accompanying range of toleration of physical and vegetational factors of the environment.

3. Although a species may be found over several associations, it is more abundant in one, or two, of these, than in others. Certain activities take place in more restricted habitats; chief of these restricted activities is the laying of eggs.

4. No two plant associations have identical grasshopper assemblages.

5. No two grasshopper species have identical habitat-preferences.

It should be said that these scanty excerpts give no idea of the scope of Vestal's article; most important in which are the ecological generalizations.

Mr. A. P. Morse, authority on Orthoptera, has paid particular attention to the subjects of distribution and adaptation. His data were given according to life zones and habitats, but are rearranged here as follows.

Shores of Seas and Lakes.—Bare sands, hot and dry. Ground Stratum. The seaside locust, *Trimerotropis maritima*, found along the Atlantic coast from Maine to North Carolina, and inland about the Great Lakes, is a characteristic *arenicolous* (sand-dwelling) species, which varies in color from gray to brown, in harmony with its local habitat (see p. 196).

Salt Marshes and Vegetation Bordering Brackish Waters.—Moist Soil. Ground and Herbaceous Strata. *Orphulella olivacea*, occurring along the Atlantic coast from Connecticut to Florida and Texas; the only *halophilous* (inhabiting salty soil) locust of the Eastern States.

Semi-Arid Areas.—Hot and Dry. Herbaceous and Shrub Strata. *Hesperotettix pratensis*, ranging from Mexico and Texas to Washington, and California to Indiana; occurring also in the Southeastern States amid conditions much resembling those of its habitats in the arid West; for example along the Gulf shore of Florida, among the *xerophytic* (inhabiting hot, dry places) strand vegetation.

Temperate Savanna and Grassland Formation.—Herbaceous Stratum. *Orphulella picturata* and *Melanoplus bispinosus* are common on the prairies west of the Mississippi. In damp grassy fields the red-legged locust, *Melanoplus femur-rubrum*, is common; in dry grassy fields, *M. attanis*. On ruderal dry grasslands are species of *Arphia*, *Syrbula*, etc. On bare soil, hot and dry, are the Carolina locust, *Dissosteira carolina*, and *Trimerotropis citrina*. On the moist banks of streams, *M. femoratus*. On moist soil of sandy loam, or the banks or beds of freshwater streams, somewhat exposed, are the grouse locusts, Tetriginæ, some of which feed sometimes on humus. On bunch-grass in fields or openings in the forest is *Hesperotettix brevipennis*, limited to this plant.

Temperate Deciduous Forest Formation.—In the undergrowth is *Mela-*

noplus strumosus. On bare or lichen-cruste rock occurs *Trimerotropis saxatilis* (see page 197), which occupied that station before the forest came.

Adaptations.—"Brachypterism (the short-winged condition) in locusts is a more complete adaptation to a leaping mode of progression brought about by life in situations where flight is difficult or impracticable, and consequently disadvantageous. That this is the true explanation is indicated by the habits and haunts of the majority of the flightless species (sylvan surroundings or tangled undergrowth wherever found); by their distribution locally, horizontally, and vertically; and by the equally characteristic habits, haunts, and distribution of *macrop-terous* (long-winged) species as inhabitants of the open field, desert, or savanna.

"The advantages of progression by flight—dispersal widely and easily effected, often aided by the wind, ease of escape from many enemies, etc., and the superiority of this mode in open lands—are evident to all. On the other hand, long wings and locomotion by flight are disadvantageous amid dense underbrush, where a leaping mode of progression has decided advantages. Organs unused or disadvantageous tend to dwindle and disappear; hence the loss of wings.

"It is found that Orthoptera frequenting habitats involving passage over open spaces of considerable extent, such as fields, between trees in forests, and bushes or thickets in deserts, are usually long-winged, flying species; and others dwelling in an environment of more or less dense, intricate, interlacing vegetal growth, be it sub-alpine or sub-tropical, in forest or swamp—or in burrows, crevices, etc.,—in short, in stations where wings are not needed or are at a disadvantage, are very generally *apterous* (wingless) or *brachypterous* (short-winged).

"Brachypterism, therefore, appears to be largely not so much a case of natural selection through the agency of the wind as an adaptation in structure to habits. The fact that the heavier-bodied female is more frequently or completely brachypterous than the male and that the tegmina in the latter sex when used as musical organs are retained in a less degenerate condition (even when entirely useless in flight), confirms this explanation of brachypterism." (A. P. Morse.)

COMMUNITIES OF STREAMS

From Shelford's notable volume, *Animal Communities in Temperate North America*, we may take, from the wealth of data given, examples of common insects representing the various communities of streams.

Intermittent Stream Communities. *Temporary rapids consocieties.*—The larva of the black-fly, *Simulium*, found in the smallest trickle of water. Nymphs of May flies, as the stream grows a little larger. No permanent aquatic residents, however, in these temporary streams. The temporary residents may fail to transform if the water dries out too soon. *Temporary pool consocieties.*—Somewhat more permanent. Insects that belong primarily to stagnant ponds make their appearance. *Permanent pool communities.*—A practically permanent fauna. Water striders, back-swimmers, water boatmen, etc. are common. Dragon fly nymphs, diving beetles, crane fly larvæ, and many other insects.

Spring Brook Associations.—In streams fed by springs. On the stones, larvæ of the black-fly, *Simulium*, and the caddis fly, *Hydropsyche*. Under the stones, nymphs of May flies and larvæ of flies and midges (*Chironomus*, *Dixa*).

Swift-stream Communities. *Hydropsyche or Rapids Formation.*—Three ecologically equivalent modes of life, each meeting the current in a different way. These are (1) clinging to stones in the current, (2) avoiding the current by creeping under stones, (3) self-maintenance by strong swimming powers. Upper surface of stones (stratum 1): black-fly larvæ, hanging from stones to which they are attached by means of a sucker at the posterior end of the body. Caddis worms, *Hydropsyche*, in cases made of pebbles; with a net for catching floating food. Among the stones (stratum 2): miscellaneous insects, also of the following stratum. Under the stones (stratum 3): May fly nymphs, larvæ of midges, *Chironomus*, and of horse flies, *Tabanus*. Stone fly nymphs, Perlidæ, with flattened bodies. Larvæ of the parnid beetle *Psephenus*. Caddis worms, *Helicopsyche*. Nymphs of the damselfly, *Calopteryx*, if vegetation is present. *Sandy and gravelly bottom formation (pools).*—Bloodworms, *Chironomus*. The burrowing dragon fly nymph, *Gomphus exilis*, a burrowing May fly nymph, caddis worms.

Sandy Bottomed Streams.—With shifting bottom, the animals present being those which belong to moderately swift water. Brook beetles, Parnidæ, attached to the few scattered plants. On logs and roots, many Parnidæ; predaceous diving beetles, Dytiscidæ, hiding in the crevices; a few caddis worms, *Hydropsyche*; the little dytiscid, *Hydroporus mellitus*, which buries itself in the sand.

Sluggish Stream Communities. *Sand and Silt Bottom Formations.*—Bloodworms, Chironomidæ; green midge larvæ, Chironomidæ; occasional caddis worms, *Hydropsyche*; a burrowing May fly nymph, *Hexagenia*. *Formation of the Vegetation.*—A densely rooted vegetation,

as in ponds. Large numbers of diverse insects, many of which come to the surface for air, both in the adult and the young stages. Water scorpions, *Ranatra*; creeping water bugs, *Pelocoris femoratus*; small water bug, *Zaitha fluminea*; water boatmen, *Corixa*; predaceous diving beetles, Dytiscidæ; water scavenger beetles, Hydrophilidæ. The gilled aquatic insects are the May fly nymphs, *Cænis* and *Callibaetis*; damsel fly nymphs, *Ischnura verticalis*; dragon fly nymphs, *Æschnidæ* and Libellulidæ; these utilizing the vegetation as resting-places or clinging-places, or as a means of creeping to the surface to transform.

Tension Lines.—Margins of bodies of water, swamps and marshes, and temporary ponds are on the border line between land and water. The classification of the communities of such *tension lines* of overlapping environments is often difficult. (Shelford.)

Along the margins of young ponds and lakes is an area which is characterized by being made up of wet sand or mud which is submerged at high water and moist at other times. Here we find springtails (especially *Podura aquatica*), shore bugs (Saldidæ), many tiger beetles (Cicindelidæ) and numerous small flies. The ground beetle (*Bembidion carinula*) and numerous scavengers (Staphylinidæ, Histeridæ, etc.) are common because the beach is often strewn with dead animals which have floated ashore. (Shelford.)

In Shelford's *Animal Communities* there are extended accounts of communities of streams, lakes, ponds, prairies, and forests.

COMMUNITY RELATIONS IN NEW MEXICO

The notes that follow on the insect ecology of New Mexico are taken from an interesting report by Professor J. R. Watson. They are here arranged under four of Livingston's vegetational areas.

Northern Mesophytic Evergreen Forest Formation. *Douglas Spruce Association.*—Poor in insect life. Some thirty species listed. The carpenter ant, *Camponotus pennsylvanicus*, is common here and in the yellow pine association, but was not seen outside of the mountains. The butterfly, *Grapta zephyrus*, is also limited to these two associations. The familiar mourning cloak butterfly, *Vanessa antiopa*, is present. *Yellow Pine Association.*—About fifty species of insects listed. *Machilis* sp. The hemipteron *Oncometopia lateralis* is confined to this association. *Circotettix undulatus* is very rare outside of this association; it makes the loudest noise of any grasshopper in the region. Another locust, *Arphia acta*, noteworthy for its loud crackling noise, is common, and descends into the cedar association.

Western Xerophytic Evergreen Forest Formation.—A dwarf and open form of semi-forest that characterizes the edges of the preceding formation. *Pinon Association.*—The locust, *Trimerotropis cyanea*, is especially at home here. The hemipteron, *Peribalus limbolarius*, is very abundant on blossoms of *Yucca*. The skipper butterfly *Epargyreus tityrus* seems to belong here. *Cedar Association.*—The tarantula killer, *Pepsis formosa*, is particularly abundant here. On milkweed, which is more abundant here than elsewhere, is the cerambycid beetle, *Tetraopes femoratus*, and the hemipteron, *Lygæus turcicus*.

Desert-grassland Transition Formation.—Intermediate between the Grasslands to the east and the Desert regions to the west. *Opuntia arborescens Society.*—Several insect species are quite characteristic of this society. The nitidulid beetle, *Carpophilus pallipennis*, eats the pollen and petals of the *Opuntia* and every blossom commonly shows from a dozen to a hundred or more individuals. The peculiar cerambycid beetle, *Presmis pocularis*, and the next insect are chiefly responsible for weakening and killing the cactus plants. The beetle apparently never leaves the plant, and its wings are degenerate. The female is usually seen carrying her much smaller mate. The larvæ bore in the tissues of the plant. The cicada, *Cacama valvata*, is very abundant on the tree cactus, but, unlike the last, also occurs on the prickly pears. The loud calls of the males are heard on every hand when the sun is shining. But let a cloud obscure the sky for a moment and all is hushed. The larvæ feed on the roots of the cactus. *Shortgrass Association.*—The mesa grasshopper, *Trimerotropis vinculata* is extremely numerous, ascending even into the yellow pine association. It is very variable in color and the variations have a very definite relation to that of the ground around them, being very light on sandy soil, mottled on pebbly hills and darker among the pines where there is more vegetation. The species migrates in large numbers when the rains cease and the grasses on which it feeds dry out. Many species of insects inhabit the mesa. Here lives the harvesting ant, *Pogonomyrmex occidentalis* (see page 297). It is well known that these ants bring their stores of grain out to air occasionally. Professor Watson relates that "One somewhat windy day in September, a hill was visited in which part of the ants were busily engaged in bringing out the grain to air and others were as busily engaged in carrying it back again. One ant would drop a grain and at once start back without a load into the hill for another, whereupon the grain would be at once seized by another ant and carried back into the granary. It is possible that this treatment is what the grain needed but it

looked to the interested observer like a serious disagreement in the colony as to where that grain should be, a case illustrating the limitations of instinct in developing 'team work.'"

Large centipedes, *Scolopendra*, are quite common, often entering houses and being much feared; though their bite is by no means as serious as represented. The whip-scorpion, *Thelyphonus*, "is rarely met with on the mesa. Though probably poisonous, its bite is also grossly exaggerated in popular belief." (Watson.) Tarantulas, *Lycosa*, "are somewhat more common than the last but much less so than the centipedes. Their bite is more serious than any of the above, but still not dangerous to most people." (Watson.)

Rio Grande Semi-desert Formation.—Hot and dry. *Gutierrezia Association.*—The big clumsy sand-cricket, *Stenopelmatus fasciatus*, is common under stones, etc. Several species of the tenebrionid subfamily Eleodinae are characteristic. One of these beetles, *Eleodes longicollis*, when held, can squirt an ill-smelling fluid to a distance of eight inches. The large black tenebrionid beetles, *Eusattus convexus*, "form a very large and characteristic feature of the fauna of this region. They are true children of the desert. Their elytra are grown together and to their backs, an adaptation to the fierce sand storms of the mesa. These wind storms drifting sand and gravel with them are a source of grave danger to the fauna of the region, even to man himself. The author has several times been caught out on the mesa when one struck the region with its usual suddenness and has stopped to observe the behavior of the animals. The prairie horned larks sought the shelter of the friendly arroyo banks. (The author has picked up these birds on the mesa during one of these storms. They were so exhausted by the buffeting that they had received that they made no effort to escape.) The digger wasps climbed into the *Gutierrezia* bushes and hung on for dear life with all of their feet wrapped about the stem, an attitude that they also assume during a shower; the snout beetles on the other hand backed down off the *Gutierrezia* and sought shelter in the ground; the woolly bears and other caterpillars curled up under the shelter of tufts of grass; most of the lizards sought their holes as did the harvester ants; but these Tenebrionidæ went about their business as usual entirely oblivious, apparently, of the storm. Their heavy bodies kept them from being blown away and their heavy coat of chitin (it is hardly possible to force a heavy insect pin through some species) defied the drifting wind. In their disposition not to be too particular as to what they eat they again show that they are true children of the desert. Anything

from the tender green seedling leaves of a *Hoffmanseggia* to a dead member of their own species is good. They collect in large numbers about the carcass of a dead mammal. They will come out from their winter quarters under the rosettes of *Yucca* and other sheltered places any time in winter if it is as warm as 60° F. They have been taken by the author on January 15. On the other hand they seem somewhat to shun the hottest hours of the day in summer, being then much more noticeable toward sunset." (J. R. Watson.)

In the shallow depressions or "draw" in the mesa above the place where a definite arroyo develops, there is found a society of which certain quick-growing annual grasses are most conspicuous. "Here and here only have I ever found this big, nearly wingless, 'lubberly locust' (*Brachystola magna*), a good illustration of an insect restricted to a very limited habitat." (Watson.) The grasshopper, *Heliastus aridus*, is particularly abundant in these arroyos, where its mottled colors agree perfectly with the gravelly surface.

Chrysothamnus Association.—Occupying such rapidly eroding and hence unstable situations as the dissected edge of the mesa and the higher gravelly parts of the valley of the Rio Grande, this is the most xerophytic (inhabiting hot dry places) of the associations. The characteristic tenebrionid beetle, *Cysteodemus wislizeni*, is very common in colonies, which are spread over much ground. The ambush bug, *Phymata erosa fasciata* is very abundant; it is almost perfectly concealed in yellow blossoms, as those of golden rod, where it occurs more commonly than in white blossoms. The clear-winged moth, *Calesesia coccinea*, is exceedingly abundant on *Hymenopappus* during the third week in May; its conspicuous colors blending perfectly with those of the blossoms of this plant. The insect disappears by the first of June. The magnificent noctuid moth, *Erebus odora*, is occasionally taken.

The sand dunes are entirely barren of vegetation and of insect life except for a species of digger-wasp, *Bembex*, which here finds conditions favorable for its colonies. "All the specimens of the scorpion (*Buthus*) that I have seen have come from this association. Its sting is, to most people, not nearly as serious as it is represented to be. Persons that have experienced it say that for a short time only is the pain more severe than that resulting from the sting of a hornet and that it does not last as long." (Watson.) In the *Croton Society* the short-winged, tricolored, or "barber-pole" grasshopper, *Dactylotum pictum*, occurs wherever its food plant, *Croton texensis*, occurs in sufficient abundance. The walking-stick, *Diapheromera femorata*, is present also. It is, of

course, perfectly harmless, but is charged by the natives with causing the death of many a poor horse.

In the "Valley" insects are abundant in number of species and of individuals; but the term *valley* does not signify much, ecologically, since it may mean anything from mud flats to desert. On the mesa, dragon flies range five or six miles from any possible breeding place, but the feebler damsel flies never fly far from home. The harlequin cabbage bug is sometimes abundant on *Cleome* and on cabbage sprouts, but does not seem to be a very serious pest, possibly because it prefers the *Cleome*. The squash bug, *Anasa tristis*, is very abundant on cultivated squashes, and commonly hibernates under yucca stems miles from any cultivated fields. The well-known Carolina locust, *Disosteira carolina*, which in the East frequents the driest of situations, in New Mexico clings very closely to the moist valleys, like other eastern forms (as tiger beetles) that occur also in New Mexico. In both east and west, however, the species frequents places of about the same degree of humidity. In the *Alkaline Meadow Society*, the lesser migratory locust, *Melanoplus atlanis*, occurs in the more moist situations, and damages alfalfa in the valleys. The red-legged locust is common, inhabiting somewhat drier situations than the last species. Mosquitoes, *Culex pipiens*, breed in countless millions in the ponds that form in the valley whenever the Rio Grande is high, usually in May and June. All the mosquitoes seen on the mesa come from the valley; sometimes they are five miles from any possible breeding place. They are carried by a gentle breeze, but a brisk breeze causes them to seek shelter low down among the herbage and not to venture forth.

The following species, of wide distribution and not characteristic of any particular formation, are of interest as occurring in New Mexico, because they are some of the most familiar insects of more eastern states under quite different climatal conditions. *Coleoptera*.—The metallic leaf-beetle, *Chrysochus auratus*, occurs on *Apocynum* as usual, but at an altitude sometimes of ten to eleven thousand feet. *Euphoria inda* occurs from the valley up to the yellow pine association and doubtless higher. The lady-beetle, *Hippodamia convergens*, is abundant everywhere from the tops of the highest mountains to the lowest parts of New Mexico. *Lepidoptera*.—*Colias eurytheme*, is common in the mountains and in the valley wherever there is damp soil, but is absent from the mesa. The checkered white, *Pieris protodice*, is found from the valley to the spruce association. The painted lady, *Pyrameis cardui*, is abundant wherever the thistle grows; and more abundant up in the

blue spruce association than anywhere else. *Hymenoptera*.—The social wasp, *Polistes variatus*, nests from the valley of the Rio Grande up into the spruce forest at eight thousand feet. The pigeon Tremex, *T. columba*, is equally abundant in the cottonwoods of the valley and in the Douglas spruce of the mountains. *Hemiptera*.—*Gerris remigis*, the well known water strider of eastern states, is found on all suitable ponds and streams in both valley and mountains. The plant-feeding bug, *Lygus pratensis*, is as ubiquitous here as it is elsewhere in the United States.

VII. SUCCESSION

“Succession is no doubt one of the most important and widespread of the phenomena discovered by the ecologists up to the present time. Simply stated, it means that on a given fixed area organisms succeed one another, because of changes in conditions. These changes make impossible the continued existence of the forms present at any given time; with the death or migration of such forms, others adapted to the changed conditions occupy the area, whenever such adapted forms are available. The changes referred to result from physical or biological causes, or combinations of the two. It is probable that the causes of the changes are frequently complex combinations of various factors.

“We have among the physical causes changes in climate and changes in topography. All degradation of land is a cause of succession. Such geological processes are well understood and treated in textbooks on geology and physiography.

“The biological causes of succession lie chiefly in the fact that organisms frequently so affect their environment that neither they themselves nor their offspring can continue to live at the point where they are now living. Every organism adds certain poisonous substances to its surroundings, and takes away certain substances needed by itself. It frequently thus so changes conditions that its offspring cannot live and grow to maturity in the same locality as the parents. However, by these same processes it prepares the way for other organisms which can live and grow in the conditions thus produced.” (Shelford.)

“The general growth or evolution of environmental conditions and the communities which belong to them are included under *succession*. The word *succession* is used in three distinct senses. We speak of (a) *geological succession*, (b) *seasonal succession*, and (c) *ecological succession*.” (Shelford.)

Geological.—“Geological succession is primarily a succession of species throughout a period or periods of geological time. It is due

mainly to the dying-out of one set of species and the evolution of others which take their places, or in some cases to migration." (Shelford.)

Many species of insects owe their present distribution primarily to the phenomena of the glacial epoch. An excellent example of this is the White Mountain butterfly (page 325). In Arkansas mountains, the "elevation is not sufficient to provide true boreal conditions, but does modify the temperature so that certain species, abundant at the north, and forced southward during the glacial epoch, have been enabled to exist in this latitude till the present time. Such are the grasshoppers *Tettix hancocki*, *Chloealtis conspersa*, and *Melanoplus fasciatus*." (Morse.)

"The chief biological importance of the Southeastern United States, comprising Virginia, North and South Carolina, Georgia, Florida, Alabama, eastern Tennessee, and West Virginia, is connected with two facts: First, this region served during the Glacial Epoch as a refuge for boreal forms of life which had been pushed southward by the climatal conditions of the Ice Age, and at the close of that period it became the center of dispersal whence these forms were able to restock the opening country at the north. Second, during this later period its lowland plains served, and probably continue to serve, as a highway of dispersal for austral forms entering the country from the south and southwest, many of which have penetrated far into the heavily glaciated region of the Northern States." (Morse.)

Seasonal.—"Seasonal succession is the succession of species or stages in the life histories of species over a given locality, due to hereditary and environic differences in the life histories (time of appearance) of species living there." (Shelford.) "Successful species are those that fit into the seasonal rhythm with respect to physical conditions, food, and numerous other relations." (Shelford.)

Many examples of seasonal succession among insects will occur to the student of insect life. The seasonal succession of insects is frequently correlated with that of plants. The cycle of an insect may be adjusted to that of a plant upon which it depends.

Thus "the Membracidæ or tree hoppers are celebrated for the wonderful variety and complexity of their adaptations to their food plants. . . . The tree hoppers of the genus *Telamona*, for example, feed very largely on the sap of the trees and mainly on the tender growing twigs. They find optimum conditions for such feeding only during the comparatively short period in which the tree is making its

growth. They also must find a location and deposit their eggs while the wood is still soft and tender; otherwise they will be unable to penetrate to a sufficient depth to protect the eggs from predaceous and parasitic insects. The result is that we find that they, with a possible exception, pass the winter in the egg stage and have a single annual generation. . . . A striking adaptation to a special period in a plant's growth is shown in the life cycle of *Micrutalis calva*, the little shining black seed-like tree hopper. The nymphs are found between the branches of the blossom head of the Ironweed, *Vernonia*. This purple flower appears only in the fall, so that the single generation of nymphs comes on over 70 days later than its relative that lives in the tree.

"In the case of *Ceresa bubalis* (the Buffalo tree hopper) and its vegetation-feeding allies the need of haste is not so great as their food plants, Composites, Legumes and others, grow all summer, so we find the nymphal period both longer and later and the adults extending into the fall." (E. D. Ball.)

The time of appearance of the locust borer, *Cyllene robiniae*, in the fall coincides with that of the flowers of golden rod, on which the beetles feed; the coloration of the beetles being protective, as Prof. H. Garman has observed in Kentucky.

Ecological.—"Ecological succession of animals is succession of *mores* over a given locality as conditions change. If species have relatively fixed mores we have succession of species. When mores are flexible we may have the same species remaining throughout, with changes in mores." (Shelford.)

A few examples, from Shelford's *Vegetation and the Control of Land Animal Communities*, will serve to illustrate this kind of succession.

The stages of forest development are marked by the dominance of certain species of trees which succeed one another in a rather definite order. On the sand areas at the head of Lake Michigan, the sequence is as follows (Cowles). 1. *Cottonwood Stage*. Near the lake shore, with the sand more or less shifting and rarely with more than a trace of humus. 2. *Pine Stage*. With stable sand, considerably blackened by humus, except in blowouts. 3. *Black Oak Stage*. With the sand much darkened by humus and locally covered with a dry moss or with dead leaves; grasses and a shrubby undergrowth occur. 4. *Red Oak Stage*. Ground with a carpet of leaves and humus; with a well marked shrubby and herbaceous growth. Red oak, black oak, and white oak; often hickory also. 5. *Beech Stage*. The mineral soil is covered with a thick layer of leaves and humus. Fewer species of trees than in the

preceding stage, but a greater number of species of small shrubs, with a smaller number of individual shrubs. The trees close the overhead spaces and make a dense shade, while the lower forest is open. Beech and sugar maple are characteristic. These five stages are linked together by transitional stages.

Of the many species tabulated by Shelford, the tiger beetles and grasshoppers may be selected to illustrate succession in relation to forest development. The tiger beetles, *Cicindela*, breed in the subterranean stratum and feed in the ground stratum.

TIGER BEETLES OF FOREST SUCCESSION (SHELFORD)

In these tables *C* signifies common; *F*, few; *P*, present

	Stage 1 Cottonwood	1-2	2 Pine	2-3	3 Black Oak	4 Red Oak- Hickory	5 Beech
<i>C. lepida</i>	<i>C</i>	<i>F</i>					
<i>C. formosa generosa</i>	<i>F</i>	<i>C</i>	<i>F</i>				
<i>C. scutellaris lecontei</i>	<i>F</i>	<i>C</i>	<i>C</i>	<i>F</i>		
<i>C. sexguttata</i>	<i>C</i>	<i>F</i>

With the tiger beetles the character of the soil, as regards suitability for oviposition, is the chief factor that determines the presence or absence of this or that species. *C. sexguttata*, which comes in with the white oak- red oak- hickory forest, lays its eggs under loose leaves or in little irregularities in the ground, which contain a little humus and are slightly shaded; it is rare, however, in very shady situations, such as those of the beech and maple forest.

Of the orthoptera named in the following table, numbers 1 to 6 breed in the subterranean stratum and feed in the ground stratum; 6 feeds also in the vegetation strata; 7 breeds in the ground stratum, feeds in the herbaceous; 8 and 9 breed and feed in the herbaceous; 10 and 11 breed and feed in the tree stratum; 12 breeds and feeds in the subterranean-ground stratum; and 13 in the ground stratum.

The table indicates that the successive changes in vegetation are accompanied by corresponding changes in the character of the orthopteran fauna. Other insects or other animals also illustrate the same phenomenon of ecological succession. During the successive vegetational stages the numbers of a species increase until optimum conditions of habitat are attained, and thereafter decrease.

ORTHOPTERA OF FOREST SUCCESSION (SHELFORD)

	Stage I Cottonwood	1-2	2 Pine	2-3	3 Black Oak	4 Red Oak- Hickory	5 Beech
1. Seaside locust, <i>Trimerotropis maritima</i>	C	F					
2. Long-horned grasshopper, <i>Pseudis fenestralis</i>	C	C	C	C			
3. Sand locust, <i>Agenotettix arenosus</i>	P	P				
4. Mottled sand locust, <i>Spharagemon wyomingarum</i>	C	C	C			
5. Migratory locust, <i>Melanoplus atlantis</i>	C	C	C			
6. Locust, <i>Melanoplus angustipennis</i>	C	C	C			
7. Sprinkled locust, <i>Chloealtis conspersa</i>	C		
8. Texas grasshopper, <i>Scudderella texensis</i>	F		
9. Tree cricket, <i>Oecanthus fasciatus</i>	C		
10. Tree cricket, <i>Oecanthus angustipennis</i>	C	
11. Katydid, <i>Cyrtophyllus perspicillatus</i>	F	
12. Camel cricket, <i>Ceuthophilus</i>	C	F
13. Locust, <i>Melanoplus islandicus</i>	C

Some species of insects do not appear until the Black Oak stage, and others not until the Red Oak-Hickory or the Beech-Maple stage.

The causes of animal succession and the control of animal communities are discussed by Shelford, who draws these conclusions, among others:

"The development of forest on sand or other mineral soil is accompanied by an almost complete change of animal species and probably by a complete change of animal mores.

"Forest development is accompanied by marked changes in soil and physical factors; animal distribution is more closely correlated with differences in physical factors than with species of plants.

"Succession of all the animals of the forest communities under consideration is comparable in principle to that in ponds. Succession is due to an increment of changes in conditions produced by the plants and animals living at a given point. Animals through their effect upon the soil play an important though minor part in the process.

"The various animal species are arranged in these communities in an orderly fashion and the dominating animal mores are correlated with the dominating conditions.

"Taxonomic (structural) species usually have distinct mores,

though the same species often has different mores under different conditions, and different species may have the same mores. *Species* and *mores* are therefore not synonymous.

"Ecology considers together mores that are alike or similar in their larger characters."

CHAPTER XIV

INSECTS IN RELATION TO MAN

A great many insects, eminently successful from their own standpoint, so to speak, nevertheless interfere seriously with the interests of man. On the other hand, many insects are directly or indirectly so useful to man that their services form no small compensation for the damage done by other species.

Injurious Insects.—Insects destroy cultivated plants, infest domestic animals, injure food, manufactured articles, etc., and molest or harm man himself.

The cultivation of a plant in great quantity offers an unusual opportunity for the increase of its insect inhabitants. The number of species affecting one kind of plant—to say nothing of the number of individuals—is often great. Thus about 200 species attack Indian corn, 50 of them doing notable injury; 200 affect clover, directly or indirectly; and 400 the apple; while the oaks harbor probably 1,000 species.

The average annual loss through the cotton worm, 1860 to 1874, was \$15,000,000, according to Packard; the loss from the Rocky Mountain locust, in 1874, in Iowa, Missouri, Kansas and Nebraska, \$40,000,000 (Thomas); and the total loss from this pest, 1874 to 1877, \$200,000,000. The loss through the chinch bug, in 1864, was \$73,000,000 in Illinois alone, as estimated by Riley. The ravages of the Hessian fly, fluted scale, San José scale, gipsy moth and cotton boll weevil need only be mentioned.

At times, an insect has been the source of a national calamity, as was the case for forty years in France, when *Phylloxera* threatened to exterminate the vine. In Africa the migratory locust is an unmitigated evil.

Probably at least ten per cent. of every crop is lost through the attacks of insects, though the loss is often so constant as to escape observation. Regarded as a direct tax of ten cents upon the dollar, however, this loss becomes impressive. Webster says: "It costs the American farmer more to feed his insect foes than it does to educate his children." The average annual damage done by insects to crops in the United States was conservatively estimated by Walsh and Riley to be \$300,000,-

000—or about \$50 for each farm. “A recent estimate by experts put the yearly loss from forest insect depredations at not less than \$100,000,000. The common schools of the country cost in 1902 the sum of \$235,000,000, and all higher institutions of learning cost less than \$50,000,000, making the total cost of education in the United States considerably less than the farmers lost from insect ravages. Thus it would be within the statistical truth to make a still more startling statement than Webster’s, and say that it costs American farmers more to feed their insect foes than it does to maintain the whole system of education for everybody’s children.

“Furthermore, the yearly losses from insect ravages aggregate nearly twice as much as it costs to maintain our army and navy; more than twice the loss by fire; twice the capital invested in manufacturing agricultural implements; and nearly three times the estimated value of the products of all the fruit orchards, vineyards, and small fruit farms in the country.” (Slingerland.)

Though most of the parasites of domestic animals are merely annoying, some inflict serious or even fatal injury, as has been said. The gad flies persecute horses and cattle; the maggots of a bot fly grow in the frontal sinuses of sheep, causing vertigo and often death; another bot fly develops in the stomach of the horse, enfeebling the animal. The worst of the bot flies, however, is *Hypoderma lineata*, the ox-warble, which not only impairs the beef but damages the hide by its perforations; the loss from this insect for one period of six months (Chicago, 1889) was conservatively estimated as \$3,336,565, of which \$667,513 represented the injury to hides.

All sorts of foodstuffs are attacked by insects, particularly cereals; clothing, especially of wool, fur or feathers; also furniture and hundreds of other useful articles.

As carriers of disease germs, insects are of vital importance to man, as we have shown.

Beneficial Insects.—The vast benefits derived from insects are too often overlooked, for the reason that they are often so unobvious as compared with the injuries done by other species. Insects are useful as checks upon noxious insects and plants, as pollenizers of flowers, as scavengers, as sources of human clothing, food, etc., and as food for birds and fishes.

Almost every insect is subject to the attacks of other insects, predaceous or parasitic—to say nothing of its many other enemies—and but for this a single species of insect might soon overrun the earth.

There are only too many illustrations of the tremendous spread of an insect in the absence of its accustomed natural enemies. One of these examples is that of the gipsy moth, artificially introduced into Massachusetts from Europe; another is the fluted scale, transported from Australia to California. Some conception of the vast restricting influence of one species upon another may be gained from the fact that the fluted scale was practically exterminated in California as the result of the importation from Australia of one of its natural enemies, a lady-bird beetle known as *Novius cardinalis*. The plant lice, though of unparalleled fecundity, are ordinarily held in check by a host of enemies (p. 379).

An astonishingly large number of parasites may develop in the body of a single individual; thus over 3,000 specimens of a hymenopterous parasite (*Copidosoma truncatellum*) were reared by Giard from a single *Plusia* caterpillar.

Parasites themselves are frequently parasitized, this phenomenon of hyperparasitism being of considerable economic importance. A beneficial primary parasite may be overpowered by a secondary parasite, evidently to the indirect disadvantage of man, while the influence of a tertiary parasite would be beneficial again. Now parasites of the third order occur and probably of the fourth order, as appears from Howard's studies, which we have already summarized. Moreover, parasites of all degrees are attacked by predaceous insects, birds, bacteria, fungi, etc. The control of one insect by another becomes, then, a subject of extreme intricacy.

Insects render an important, though commonly unnoticed, service to man in checking the growth of weeds. Indeed, insects exercise a vast influence upon vegetation in general. A conspicuous alteration in the vegetation has followed the invasions of the Rocky Mountain locust, as Riley has said; many plants before unnoticed have grown in profusion and many common kinds have attained an unusual luxuriance.

As agents in the cross pollination of flowers, insects are eminently important. Darwin and his followers have proved beyond question that as a rule cross pollination is indispensable to the continued vitality of flowering plants; that repeated close pollination impairs their vigor to the point of extermination. Without the visits of bees and other insects our fruit trees would yield little or nothing, and the fruit grower owes these helpers a debt which is too often overlooked.

As scavengers, insects are of inestimable benefit, consuming as they do in incalculable quantity all kinds of dead and decaying animal and

vegetable matter. This function of insects is most noticeable in the tropics, where the ants, in particular, eradicate tons of decomposing matter that man lazily neglects.

Of insects that are directly useful to man, the silkworms and the several species of honey bees are the most important. Silk is most valuable as a textile material, but has minor uses. Some of the best fishing lines are made of silk; and the best "leaders"—long, tapering, strong, and practically invisible in the water—are the silk glands themselves, after being stretched and dried. These leaders are imported from the Mediterranean region, but may easily be made from the glands of our large native silkworms, such as the *Cecropia*.

Though honey as a food is not as indispensable to us as it was to the ancients, immense quantities of it are produced annually, and the demand for it is usually greater than the supply. Beeswax has more uses than one might suppose. One of its chief uses is for the manufacture of comb "foundation" for bee hives. Beeswax, though rivaled by paraffin and ceresin, is better than these for some purposes. It is used in polishes for furniture, floors, carriages, automobiles, shoes and other leather articles, and steel tools; as a coating for shoemaker's thread and for steel nails; as an ingredient of some varnishes; for the insulation of electric wires, etc.; for church candles; salves and cosmetics; in sealing wax and grafting wax; by sculptors for making models; by dentists for taking impressions; and was anciently used on writing tablets.

Lac, commonly used as shellac and for lacquer and other resistant varnishes, is yielded by several species of scale insects, but chiefly *Tachardia lacca*, which is abundant in many parts of India on a variety of plants (*Zizyphus*, *Acacia*, *Butea*, etc.). The lac is a resinous secretion, produced abundantly by the female, and forming with the exuviae a protective covering over her body.

A coccid that produces considerable quantities of lac occurs in Arizona on *Larrea mexicana*.

Several coccids of the genus *Ceroplastes*, in India and China, produce white wax, which is highly valued for some purposes but has been replaced by paraffin for other uses.

The brilliant crimson pigment of the lac-insect of India is extracted and known to artists as "lake."

The cochineal insect, *Dactylopius coccus*, is indigenous to Mexico, but has been transported with its food plant, the prickly pear, to Spain, India, and elsewhere. From the dried bodies of the females, carmine is extracted. The cochineal industry, which dates back to the time of the

Aztecs, attained an immense development until some fifty years ago, when it began to decline with the discovery of aniline dyes. Even at present, however, there is a constant demand for cochineal, which is used for coloring confectionery, fabrics, inks, and druggists' preparations.

The cottony cochineal insect, *Dactylopius confusus*, ranges throughout the cactus region of the United States, and contains the same crimson fluid as its ally.

The Greeks and Romans obtained a red dye from species of *Kermes* living on an oak. Galls of Cynipidæ were once important as a source of ink.

As articles of human food, some insects are highly nutritious, but are appreciated chiefly by savages. Not exclusively, however, for the "manna" of biblical times was almost certainly the honey-dew from a coccid. It is still used by Arabs as food under the name of "man." The flavor of the large black carpenter ants, *Camponotus*, which can be scooped up with the hands in large numbers, appeals to some who would resent being called savages. White grubs, available in any desirable quantity, are said to make an excellent salad, high in protein content. Used in connection with corn they furnish almost a balanced ration for hogs.

The red Indians formerly used many kinds of insects as food. Especially delicious was a bushel of grasshoppers roasted in a hole in the ground. After all, the grasshopper is more attractive in appearance and more refined in its choice of food than the much-esteemed lobster. The Pah Utes of Utah eke out an existence on dried caterpillars, and annually flock from far and near to harvest the salt-fly of the salt lakes. The puparia of these flies (*Ephydra hians*) are washed up on the shore in such enormous numbers that they can be collected by hundreds of bushels. After the dirt is removed and the puparium shelled off, the pupa, which is rather large, supplies a food which is said to be not unpleasant to the taste (Aldrich).

According to Dr. Aldrich, the Indians in the vicinity of Mono Lake, California, collect for food the caterpillars of the saturniid moth, *Coloradia pandora*, from a species of pine tree. The great event of gathering the crop comes, unfortunately, only every other year; as the insect has a two-year cycle and only one brood. The Indians dig a trench around a tree, making the outer wall of the trench vertical; then beat the caterpillars off the branches and collect them in the trench. The dried caterpillars are a great delicacy to the Indians. Aldrich says they taste like linseed oil.

Water-boatmen (*Corixa*) and their eggs are used as food in Mexico, and are said to have a fine flavor. In Australia the Bugong moth occurs in millions in certain localities, and the moth itself was formerly an important article of food with the aborigines (Sharp). The bushmen of Australia find that the clay of termite mounds makes a solid meal; and hill tribes of India eat the termites, which have a flavor like that of almonds. In Africa the migratory locust has been eaten since history began.

The wise fisherman knows that certain kinds of insects are excellent bait for fishes, especially at certain seasons. The better known of these insects are grub worms, grasshoppers and hellgrammites.

A few insects have medicinal properties. Coccids of the genus *Kermes* that live on an oak in the Mediterranean region yield a medicinal syrup. Another coccid, *Llaveia axinus*, of Mexico, produces a peculiar substance known as axin. This is used as an external medicinal application, and is of considerable value as a varnish. (Sharp.) Our native blister beetles and oil beetles possess a blistering or vesicant property, which is due to the presence of cantharidin in their blood. The crushed bodies of a Mediterranean species are still used medically under the name of Spanish fly. In China medicinal properties are ascribed to many different kinds of insects.

The use of insects as ornaments must not be forgotten. Beetles with metallic colors or with iridescence, like the diamond beetle of Brazil, are made up into jewelry. A coccid, *Margarodes formicarium*, of the West Indies, found in the soil, where it lives on roots of plants and is often plowed up, resembles a pearl, and is strung into necklaces, etc. (Comstock.) The cucujo beetles (*Pyrophorus*) of tropical America are the most brilliantly luminous of insects. They are used for ornamental display and are said to be serviceable as candles. Their diffused light is pleasing in its quality, and it is reported that "the smallest print may be read by moving one of these insects along the lines."

The showy butterflies, moths, and beetles, mounted for purposes of display, are familiar to all.

In Japan a "fire-box" to hold a charcoal fire is made from a section of a log, placed on end. For this purpose a log is frequently selected on account of its natural ornamentation made by the engraver beetles; or a screen may be made of wood that is carved with tunnels made by termites.

The unimportant use of insects as playthings need only be alluded to. In the south, children amuse themselves by attaching the green June

bugs to threads and letting them fly about. In China crickets are matched against each other in fighting contests.

Many other examples of insects beneficial, more or less, to man could be given if space permitted.

Doubtless many of us have now and then kept crickets or katydids in cages because we liked to hear them sing; or have put fire flies in bottles to watch them glow.

The Japanese, with a national appreciation of nature which is foreign to this country, are accustomed to do these things. Crickets and katydids are sold on the streets, at prices equivalent to two to fifteen cents each, much as flowers are sold here.

As they have a cherry blossom season, they have also a fire fly season, when it is the common custom to make visits to the country to procure fire flies. Special trains are even run for these excursions.

Annually the people of Gifu collect many thousands of fire flies, which are sent to Tokyo and on a certain night are liberated for the enjoyment of the emperor.

As objects of scientific investigation insects are important, as no entomologist will deny. They are even economically important in this respect, for some of the principles of heredity, applicable to the breeding of domesticated animals, have been worked out with the aid of insects, particularly the pomace flies, *Drosophila*.

Introduction and Spread of Injurious Insects.—Many of our worst insect pests were brought accidentally from Europe, notably the Hessian fly, wheat midge, codling moth (probably), gipsy moth, brown-tail moth, European corn borer, elm leaf beetle, leopard moth, woolly apple aphid, cabbage butterfly, cabbage aphis, clover leaf beetle, clover root borer, asparagus beetle, imported currant worm and many cutworms; though few American species have obtained a foothold in Europe, one of the few being the dreaded *Phylloxera*, which appeared in France in 1863.

The gipsy moth (*Porthetria dispar*), a native of Europe, where it is at times a serious pest, was liberated in eastern Massachusetts in 1868, and has spread over the eastern half of the state and into New Hampshire, Maine and Connecticut, in spite of all efforts to control it. Small infestations occur also in New York and Pennsylvania, and in July, 1920, a colony was found in New Jersey, where at present (1922) 410 square miles are infested. The cost of controlling this omnivorous pest is enormous (see beyond). "The amount expended by the Bureau in the campaign against the Gipsy Moth, including the appropriation for

the current fiscal year, is \$4,650,000." (Dr. L. O. Howard, March 28, 1922.)

The brown-tail moth (*Euproctis chrysorrhæa*) is a native of the Old World "where it is found from Algiers on the South to Sweden on the North and from England on the West to the Himalaya Mountains on the East. Over most of this area it is recognized as a pest of orchards and forests." (Dr. W. E. Britton.) This moth was accidentally introduced into eastern Massachusetts on nursery stock, and first attracted the attention of entomologists in 1897, since when it has spread over most of Massachusetts and New Hampshire, into Vermont, Maine, Nova Scotia and New Brunswick, over all of Rhode Island, half of Connecticut, and into New York. The brown-tail moth has accompanied the gipsy moth in its work of destruction.

The brown-tail moth spreads locally by means of flight, mostly; but may be carried great distances commercially, on shipments of young trees bearing young caterpillars in their winter nests. The first nests found in Connecticut came on fruit tree seedlings imported in 1909 from a French nursery. (Britton.) The pest has several times reached nurseries in Illinois on young trees from Belgium and France, but has each time been eradicated by the state inspection service before it could spread from the nurseries. In 1921 the federal inspectors intercepted nests of the brown-tail moth on forty-two shipments from France, and egg masses of the gipsy moth on one shipment.

These two pests have been fought most vigorously but are not yet under complete control. It is worth while to give here an account of the expenditures made up to date (April 5, 1922) in the fight against the gipsy moth and the brown-tail moth. Mr. A. F. Burgess, who is in charge of the work, has kindly furnished these figures.

EXPENDITURES BY INFESTED STATES
(Federal Funds Not Included)

States	Expenditures	From beginning of work to—	Expenditures by towns, in- dividuals, etc.	Totals
Connecticut.....	183,715.55	Dec. 1, 1921	229.50	183,945.05
Maine.....	435,000.00	do	180,000.00	615,000.00
Massachusetts.....	5,137,000.00	do	9,126,927.97	14,263,927.97
New Hampshire.....	186,500.00	Sept. 30, 1921	No record	186,500.00
Rhode Island.....	179,600.00	Dec. 31, 1921	20,000.00	199,600.00
Vermont.....	24,409.72	do	No record	24,409.72
New Jersey.....	161,883.73	do	25,000.00	186,883.73
New York.....	175,000.00	do	No record	175,000.00
Pennsylvania.....	600.00	do	No record	600.00
	\$6,483,709.00		\$9,352,157.47	\$15,835,866.47

Add to this the amount supplied by the Federal Government, and the total is more than twenty million dollars.

The San José scale insect (*Aspidiotus perniciosus*), a native of North China, was introduced into the San José valley, California, about 1870, probably upon the flowering Chinese peach, became seriously destructive there in 1873, was carried across the continent to New Jersey in 1886 or 1887 on plum stock, and thence distributed directly to several other states upon nursery stock. At present the San José scale is a permanent menace to horticulture throughout the United States, and is being checked or subdued only by the vigorous and continuous work of official entomologists, acting under special legislation. This pernicious insect occurs also in Japan, Hawaii, Australia and Chile.

The Mexican cotton boll weevil (*Anthonomus grandis*), which is found throughout Mexico and in Guatemala, Costa Rica and western Cuba, crossed the Rio Grande river and appeared in Brownsville, Texas, about 1892. It either flew across the river or was carried across in seed cotton. Since then it has extended its range every year until in 1921 it had practically "reached the limit of cotton cultivation."

The beetle hibernates and lays its eggs in the squares or bolls of cotton; these are injured both by the larva feeding within and by the beetles, whose feeding-punctures destroy the bolls and cause them to drop. The annual loss from the weevil is far in excess of \$200,000,000. The pest has now been thoroughly studied by the Bureau of Entomology, and the adoption of the control methods recommended by the Bureau enables cotton to be grown at a fair profit; though the days of "bumper crops" have gone.

The European corn borer (*Pyrausta nubilalis*), long known in Europe as a pest of corn, hemp, hops and millet, was discovered near Boston, Massachusetts, in 1916, having been introduced probably in hemp sent to a cordage factory, or in broom corn. In 1919 the borer was found to be infesting four hundred square miles in the vicinity of Schenectady, New York, having arrived possibly in bales of broom corn from Austria. In 1920 the insect had established itself in an area of nineteen hundred square miles in eastern Massachusetts, southern New Hampshire, and New York, and appeared in Ontario, Canada. The borer feeds not only on cultivated plants but also on a great variety of weeds. Energetic efforts are being made to prevent this destructive insect from spreading westward into the corn belt.

The green Japanese beetle (*Popillia japonica*), which in its native home is not an important pest, was discovered in New Jersey in August,

1916, and in Pennsylvania in 1920. It came from Japan probably as grubs in soil about the roots of iris or azalea plants, but brought none of its native enemies with it, and spread rapidly in its new environment. In 1921 it occupied two hundred and thirteen square miles in New Jersey and fifty-seven in Pennsylvania.

The injury is done mostly by the beetles, which skeletonize the leaves of trees and shrubs, both wild and cultivated, destroy ripening fruits, and have a longer list of food plants than the brown-tail moth.

Extensive operations against the beetle are being conducted by the Bureau of Entomology in co-operation with the Departments of Agriculture of New Jersey and Pennsylvania.

The elm leaf beetle (*Galerucella luteola*), notorious in southern Europe as a defoliator of elm trees, entered Maryland about 1837, spread along the coast as far as southern New Hampshire, and has made its way into New York, Ohio and Kentucky, killing off thousands of fine old elms on its way. The only effective means of controlling this beetle seems to be an arsenical spray.

The leopard moth (*Zeuzera pyrina*), another European species accidentally introduced into New Jersey some time before 1879, spread north into Massachusetts, assisting the elm leaf beetle in its injurious activity. The leopard moth is not confined to elms, however, though it injures chiefly elms and silver maples, but attacks more than eighty kinds of trees and shrubs, and affects fruit trees as well as shade trees. The caterpillar does not feed on the leaves but bores into the branches, which become weakened as a result and are broken off by the wind.

The pink bollworm (*Pectinophora gossypiella*), a cotton pest which is probably a native of southern Asia and occurs also in Africa, Hawaii and Brazil, entered Mexico and was recently introduced into Texas. This serious pest is now being eradicated by the Department of Agriculture, at an annual expense of about half a million dollars.

An insect often passes readily from a wild plant to a nearly related cultivated species. Thus the Colorado potato beetle passed from the wild species *Solanum rostratum* to the introduced species, *Solanum tuberosum*, the potato. Many of our fruit-tree insects feed upon wild, as well as cultivated, species of Rosaceæ; the peach borer, a native of this country, probably fed originally upon wild plum or wild cherry. Many of the common scarabæid larvæ known as "white grubs" are native to prairie sod, and attack the roots of various cultivated grasses, including corn, and those of strawberry, potato and other plants. The chinch bug fed originally upon native grasses, but is equally at home on cul-

tivated species, particularly millet, Hungarian grass, rice, wheat, barley, rye and corn. In fact, the worst corn insects, such as the chinch bug, wireworms, white grubs and cutworms, are species derived from wild grasses.

Even in the absence of cultivated plants their insect pests continue to sustain themselves upon wild plants, as a rule; the larva of the codling moth, for example, is very common in wild apples and wild haws.

The Economic Entomologist.—To mitigate the tremendous damage done by insects, the individual cultivator is almost helpless without expert advice, and the immense agricultural interests of this country have necessitated the development of the economic entomologist, the value of whose services is universally appreciated by the intelligent.

Almost every State now has one or more economic entomologists, responsible to the State or else to a State Experiment Station, while the general Government attends to general entomological needs in the most comprehensive and thorough manner.

"It is the special object of the economic entomologist," says Dr. Forbes, "to investigate the conditions under which these enormous losses of the food and labor of the country occur, and to determine, first, whether any of them are in any degree preventable; second, if so, how they are to be prevented with the least possible cost of labor and money; and, third, to estimate as exactly as possible the expenses of such prevention, or to furnish the data for such an estimate, in order that each may determine for himself what is for his interest in every case arising.

"The subject matter of this science is not insects alone, nor plants alone, nor farming alone. One may be a most excellent entomologist or botanist, or he may have the whole theory and practice of agriculture at his tongue's end, and at his fingers' ends as well, and yet be without knowledge or resources when brought face to face with a new practical problem in economic entomology. The subject is essentially that of the relations of these things to each other; of insect to plant and of plant to insect, and of both these to the purposes and operations of the farm, and it involves some knowledge of all of them.

"As far as the entomological part of the subject is concerned, the chief requisites are a familiar acquaintance with the common injurious insects, and especially a thorough knowledge of their life histories, together with practical familiarity with methods of entomological study and research. The life histories of insects lie at the foundation of the whole subject of economic entomology; and constitute, in fact, the

principal part of the science; for until these are clearly and completely made out for any given injurious species, we cannot possibly tell when, where or how to strike it at its weakest point.

"But besides this, we must also know the conditions favorable and unfavorable to it; the enemies which prey upon it, whether bird or insect or plant parasite; the diseases to which it is subject, and the effects of the various changes of weather and season. We should make, in fact, a thorough study of it in relation to the whole system of things by which it is affected. Without this we shall often be exposed to needless alarm and expense, perhaps, in fighting by artificial remedies, an insect already in process of rapid extinction by natural causes; perhaps giving up in despair just at the time when the natural checks upon its career are about to lend their powerful aid to its suppression. We may even, for lack of this knowledge, destroy our best friends under the supposition that they are the authors of the mischief which they are really exerting themselves to prevent. In addition to this knowledge of the relations of our farm pests to what we may call the natural conditions of their life, we must know how our own artificial farming operations affect them, which of our methods of culture stimulate their increase, and which, if any, may help to keep it down. And we must also learn where strictly artificial measures can be used to advantage to destroy them.

"For the life histories of insects, close, accurate and continuous observation is of course necessary; and each species studied must be followed not only through its periods of destructive abundance, when it attracts general attention, but through its times of scarcity as well, and season after season, and year after year.

"The observations thus made must of course be collected, collated and most cautiously generalized, with constant reference to the conditions under which they were made. No part of the work requires more care than this.

"This work becomes still more difficult and intricate when we pass from the simple life histories of insects to a study of the natural checks upon their increase. Here hundreds and even thousands of dissections of insectivorous birds and predaceous insects are necessary, and a careful microscopic study of their food, followed by summaries and tables of the principal results, a tedious and laborious undertaking, a specialty in itself, requiring its special methods and its special knowledge of the structures of insects and plants, since these must be recognized in fragments, while the ordinary student sees them only entire.

"If we would understand the relations of season and weather to the

abundance of injurious insects, we are led up to the science of meteorology; and if we undertake to master the obscure subject of their diseases, especially those of epidemic or contagious character, we shall find use for the highest skill of the microscopist, and the best instruments of microscopic research.

"All these investigations are preliminary to the practical part of our subject. What shall the farmer do to protect his crops? To answer this question, besides the studies just mentioned, much careful experiment is necessary. All practical methods of fighting the injurious insects must be tried—first on a small scale, and under conditions which the experimenter can control completely, and then on the larger scale of actual practice; and these experiments must be repeated under varying circumstances, until we are sure that all chances of mistake or of accidental coincidence are removed. The whole subject of artificial remedies for insect depredations, whether topical applications or special modes of culture, must be gone over critically in this way. So many of the so-called experiments upon which current statements relating to the value of remedies and preventives are based have been made by persons unused to investigation, ignorant of the habits and the transformations of the insects treated, without skill or training in the estimation of evidence, and failing to understand the importance of verification, that the whole subject is honeycombed with blunders. Popular remedies for insect injuries have, in fact, scarcely more value, as a rule, than popular remedies for disease.

"Observation, record, generalization, experiment, verification—these are the processes necessary for the mastery of the subject, and they are the principal and ordinary processes of all scientific research."

The official economic entomologist uses every means to reach the public for whose benefit he works. Bulletins, circulars and reports, embodying most serviceable information, are distributed freely where they will do the most good, and timely advice is disseminated through newspapers and agricultural journals. An immense amount of correspondence is carried on with individual seekers for help, and personal influence is exerted in visits to infested localities and by addresses before agricultural meetings. Special emergencies often tax every resource of the official entomologist, especially if he is hampered by inadequate legislative provision for his work. Too often the public, disregarding the prophetic voice of the expert, refuses to "close the door until the horse is stolen."

Aside from these emergencies, such as outbreaks of the Rocky Moun-

tain locust, chinch bug, Hessian fly, San José scale and others, the State or Experiment Station entomologist has his hands full in any State of agricultural importance; in fact, can scarcely discharge his duties properly without the aid of a corps of competent assistants.

This chapter would be incomplete without some mention of the progress of economic entomology in this country, especially since America is pre-eminently the home of the science. The history of the science is largely the history of the State and Government entomologists, for the following account of whose work we are indebted chiefly to the writings of Dr. Howard, to which the reader is referred for additional details as well as for a comprehensive review of the status of economic entomology in foreign countries.

Massachusetts.—Dr. Thaddeus W. Harris, though preceded as a writer upon economic entomology by William D. Peck, was our pioneer official entomologist—official simply in the sense that his classic volume was prepared and published at the expense of the state of Massachusetts, first (1841) as a "Report" and later as a "Treatise." The splendid Flint edition (1862), entitled "A Treatise on Some of the Insects Injurious to Vegetation," is still "the *vade mecum* of the working entomologist who resides in the northeastern section of the country."

Dr. Alpheus S. Packard gave the state three short but useful reports from 1871 to 1873.

As entomologist to the Hatch Experiment Station of the Massachusetts Agricultural College, Prof. Charles H. Fernald issued important bulletins upon injurious insects, and published in collaboration with Edward H. Forbush a notable volume upon the gipsy moth.

New York.—Dr. Asa Fitch, appointed in 1854 by the New York State Agricultural Society, under the authorization of the legislature, was the first entomologist to be officially commissioned by any state. His fourteen reports (1855 to 1872) embody the results of a large amount of painstaking investigation.

In 1881 Dr. James A. Lintner became state entomologist of New York. Highly competent for his chosen work, Lintner made every effort to further the cause of economic entomology, and his thirteen reports, accurate, thorough and extremely serviceable, rank among the best. Lintner has had a most able successor in Dr. E. P. Felt, who is continuing the work with exceptional vigor and the most careful regard for the entomological welfare of the state. Felt has published at this writing thirty-eight bulletins (including twenty-one annual reports), besides important papers on forest and shade-tree insects, and has

directed the preparation by Needham and his associates of three notable volumes on aquatic insects.

The Cornell University Agricultural Experiment Station, established in 1879, has issued many valuable publications upon injurious insects, written by the master-hand of Professor Comstock or else under his influence. The studies of Comstock and Slingerland were always made in the most conscientious spirit and their bulletins—original, thorough and practical—are models of what such works should be.

More recently, Prof. C. R. Crosby and Prof. G. W. Herrick, of Cornell, have published important contributions to economic entomology.

The Geneva station has issued many excellent entomological bulletins, the results of investigations by V. H. Lowe, F. A. Sirrine, H. E. Hodgkiss, P. J. Parrott, and W. J. Schoene.

Illinois.—Mr. Benjamin D. Walsh, engaged in 1867 by the Illinois State Horticultural Society, published in 1868, as acting state entomologist, a report in the interests of horticulture—an accurate and altogether excellent piece of original work. Like many other economic entomologists he was a prolific writer for the agricultural press and his contributions, numbering about four hundred, were in the highest degree scientific and practical.

Walsh was succeeded by Dr. William LeBaron, who published (1871 to 1874) four able reports of great practical value. In the words of Dr. Howard, "He records in his first report the first successful experiment in the transportation of parasites of an injurious species from one locality to another, and in his second report recommended the use of Paris green against the canker worm on apple trees, the legitimate outcome from which has been the extensive use of the same substance against the codling moth, which may safely be called one of the great discoveries in economic entomology of late years."

Following LeBaron as state entomologist, Rev. Cyrus Thomas and his assistants, G. H. French and D. W. Coquillett, produced a creditable series of six reports (1875 to 1880) as part of a projected manual of the economic entomology of Illinois.

In 1882 Prof. S. A. Forbes was appointed state entomologist. His reports and bulletins, based upon the labors of an able corps of assistants, are among the best that have been produced. Of the eighteen reports issued by Dr. Forbes, those dealing with the chinch bug, San José scale, corn insects and sugar beet insects are especially noteworthy.

The office of state entomologist was discontinued in 1917, without, however, any interruption of the entomological work, which is now

carried on by Dr. Forbes, as director of the Natural History Survey, with W. P. Flint as chief entomologist.

Missouri.—Appointed in 1868, Prof. Charles V. Riley published (1869 to 1877) nine reports as state entomologist. To quote Dr. Howard, "They are monuments to the state of Missouri, and more especially to the man who wrote them. They are original, practical and scientific. . . . They may be said to have formed the basis for the new economic entomology of the world." Riley's subsequent work will presently be spoken of.

Minnesota.—The reports that Dr. O. Lugger issued in Minnesota, though compiled for the most part, contain much serviceable information, presented in a popularly attractive manner. Following Lugger, F. L. Washburn published several useful reports. The present state entomologist is Prof. A. G. Ruggles.

New Jersey.—New Jersey has long been active and progressive in state entomological work. Dr. J. B. Smith, state entomologist from 1894 until his death in 1912, was a most energetic investigator and prolific writer of useful bulletins and reports. He was succeeded by Dr. T. J. Headlee, well known for his work in Kansas.

Connecticut.—Dr. W. E. Britton has published twenty reports as state entomologist. These are of a high degree of excellence, are well illustrated, and are most useful treatises on the injurious insects of the state.

Maine.—Dr. C. H. Fernald and Prof. F. L. Harvey formerly rendered entomological service to the state of Maine. The work is now in the efficient hands of Dr. Edith M. Patch, an authority on Aphididæ, who has made a reputation for the state by her excellent publications and those of her co-workers.

California.—The progressive spirit of California has been carried into the entomological work of the state. Many excellent investigations, chiefly upon insects affecting citrus plants and the grape, and upon means of control, have been made by Prof. C. W. Woodworth, Prof. W. B. Herms, Prof. H. J. Quayle, and Prof. E. O. Essig.

Ohio.—F. M. Webster became known as one of the leading investigators in economic entomology by his work in Ohio. Since then Prof. H. A. Gossard and J. S. Houser have made important contributions to the literature of economic entomology.

Kansas.—Manhattan, Kansas, is a well-known center of entomological activity, from which have appeared many important publications on economic entomology. Prof. G. A. Dean, Dr. J. H. Merrill, and Dr.

R. C. Smith, with their efficient assistants, are carrying on the work there. At the University of Kansas, Prof. S. J. Hunter is in charge of entomological work.

Iowa.—At Ames, Iowa, Prof. H. E. Summers was formerly state entomologist, followed by R. L. Webster as acting state entomologist, who was succeeded by Dr. E. D. Ball, now Director of Research of the U. S. Department of Agriculture. All these men, with Dr. C. P. Gillette (now of Colorado) and Prof. Herbert Osborn (now of Ohio), have greatly aided entomological progress by their studies.

Other States.—The states just mentioned are those in which economic entomology has long been encouraged and developed. In almost all the other states, however, the value of the science is at present appreciated. In the following states the work of the entomologists who are named has been especially noteworthy. *Alabama*: Dr. W. E. Hinds. *Delaware*: Prof. E. D. Sanderson. Prof. C. O. Houghton. *Florida*: Prof. P. H. Rolfs. Prof. H. A. Gossard. *Idaho*: Prof. J. M. Aldrich. *Indiana*: Prof. W. S. Blatchley. Prof. J. J. Davis. *Kentucky*: Prof. H. Garman. *Louisiana*: Prof. H. A. Morgan. Wilmon Newell. *Maryland*: W. G. Johnson. Prof. T. B. Symons. *Massachusetts*: Prof. C. H. Fernald. Prof. H. T. Fernald. *Michigan*: Prof. A. J. Cook. Prof. R. H. Pettitt. *Mississippi*: Prof. G. W. Herrick. Prof. R. W. Harned. *Missouri*: Prof. J. M. Stedman. *Montana*: Prof. R. A. Cooley. *Nebraska*: Prof. L. Bruner. Prof. M. H. Swenk. *Nevada*: Prof. S. B. Doten. *New Hampshire*: Dr. C. M. Weed. Prof. E. D. Sanderson. Prof. W. C. O'Kane. *New Mexico*: Prof. C. H. T. Townsend. Prof. T. D. A. Cockerell. *North Carolina*: Prof. F. Sherman, Jr. *Oregon*: Dr. A. B. Cordley. *South Carolina*: Prof. A. F. Conradi. *Tennessee*: Dr. H. A. Morgan. *Washington*: Prof. A. L. Melander. *West Virginia*: Dr. A. D. Hopkins. Prof. L. M. Peairs.

State Experiment Stations.—The organization of State Agricultural Experiment Stations in 1888, under the Hatch Act, gave economic entomology an additional impetus. At present at least one experiment station is in operation in every state and territory; there being stations in Alaska, Hawaii, Porto Rico, Virgin Islands, and Guam. These stations, often in connection with state agricultural colleges, maintain altogether more than two hundred workers in entomology, and have issued a great number of bulletins upon injurious insects. These publications are extremely valuable as a means of disseminating entomological information, and most of them are based upon the investigations of their authors.

While these workers have been conspicuously active in the publication of their investigations, there are many other station entomologists and state entomologists who devote themselves entirely to the practical application of entomological knowledge, and whose work in this respect is highly important, even though its influence does not extend beyond the limits of the state.

The U. S. Entomological Commission.—This commission, founded under a special Act of Congress in 1877 to investigate the Rocky Mountain locust, consisted of Dr. C. V. Riley, Dr. A. S. Packard and Rev. Cyrus Thomas, remained in existence until 1881, and published five reports and seven bulletins, all of lasting value. The first two reports form a most elaborate monograph of the Rocky Mountain locust; the third report includes important work upon the army worm and the canker worm; the fourth, written by Riley, is an admirable volume on the cotton worm and boll worm; and the fifth, by Packard, is a useful treatise on forest and shade-tree insects.

The U. S. Department of Agriculture.—The first entomological expert appointed under the general government was Townend Glover, in 1854. He issued a large number of reports (1863–1877), which “are storehouses of interesting and important facts which are too little used by the working entomologists of to-day,” as Howard says. Glover prepared, moreover, a most elaborate series of illustrations of North American insects, at an enormous expense of labor, out of all proportion, however, to the practical value of his undertaking.

Glover was succeeded in 1878 by Riley, whose achievements have aroused international admiration. He resigned in a year, after writing a report, and was succeeded by Prof. Comstock, who held office for two years, during which he wrote two important volumes (published respectively in 1880 and 1881) dealing especially with cotton, orange and scale insects. His work on scale insects laid the foundation for all our subsequent investigation of the subject.

Riley, assuming the office of government entomologist, published up to 1894, “12 annual reports, 31 bulletins, 2 special reports, 6 volumes of the periodical bulletin *Insect Life* and a large number of circulars of information.” During his vigorous and enterprising administration economic entomology took an immense step in advance. The life histories of injurious insects were studied with extreme care and many valuable improvements in insecticides and insecticide machinery were made. One of the notable successes of Dr. Riley and his co-workers, which has attracted an exceptional amount of public attention, was the

practical extermination of the fluted scale (*Icerya purchasi*), which threatened to put an end to the cultivation of citrus trees in California. This disaster was averted by the importation from Australia, in 1888, of a native enemy of the scale, namely the lady-bird beetle *Novius* (*Vedalia*) *cardinalis*, which, in less than eighteen months after its introduction into California, subjugated the noxious scale insect. The United States has since sent *Novius* to South Africa, Egypt and Portugal with similar beneficial results.

The Department of Agriculture succeeded in starting a new and important industry in California—the culture of the Smyrna fig. The superior flavor of this variety is due to the presence of ripe seeds, in other words, to fertilization, and for this it is necessary for pollen of the wild fig, or “caprifig,” to be transferred to the flowers of the Smyrna fig. Normally this pollination, or “caprification,” is dependent upon the services of a minute chalcid, *Blastophaga grossorum*, which develops in the gall-like flowers of the caprifig. The female insect, which in this exceptional instance is winged while the male is not, emerges from the gall covered with pollen, enters the young flowers of the Smyrna fig to oviposit, and incidentally pollenizes them.

After many discouraging attempts, *Blastophaga*, imported from Algeria, was established in California, and the new industry has developed rapidly.

Based upon the foundation laid by Riley, the work of the Bureau of Entomology has steadily progressed, under the leadership of Dr. Leland O. Howard. With a comprehensive and firm grasp of his subject, alert to discover and develop new possibilities, energetic and resourceful in management, Dr. Howard has brought the government work in applied entomology to its present position of commanding importance. Admirably organized, the Bureau now (1922) requires the services of 460 employes, 386 of whom are directly engaged in scientific work.

In the magnitude and importance of its contributions to economic entomology the Bureau is unapproached by any other organization.

The Bureau of Entomology has always secured the services of the best entomologists available, and its staff of experts includes many of the leading entomologists of the world. Those in charge of the work are as follows: Dr. L. O. Howard, entomologist and chief of bureau. C. L. Marlatt, entomologist and assistant chief of bureau. W. D. Hunter, southern field crop insect investigations. W. R. Walton, cereal and forage insect investigations. Prof. A. L. Quaintance, decidu-

ous-fruit insect investigations, tropical and subtropical fruit insect investigations. C. L. Marlatt, investigations of the Mediterranean and other fruit flies. Dr. F. H. Chittenden, truck-crop insect investigations. E. A. Back, stored-product insect investigations. Dr. A. D. Hopkins, forest insect investigations. Dr. L. O. Howard, W. D. Hunter, and J. L. Webb, investigations of insects affecting the health of man and animals. Dr. E. F. Phillips, investigations in bee culture. A. F. Burgess, gipsy moth and brown-tail moth investigations.

The U. S. Department of Agriculture publishes annually a *List of Workers in Subjects Pertaining to Agriculture*, which contains the names of all the entomological workers in the Department of Agriculture, in State Agricultural Colleges and in Experiment Stations.

Canada.—The development of economic entomology in Canada was due largely to the efforts of Dr. James Fletcher, of the Dominion Experimental Farms, Ottawa, whose annual reports and other writings were of exceptional value. His work was furthered in every way by the "eminent director of the experimental farms system, Dr. William Saunders, himself a pioneer in economic entomology in Canada and the author of one of the most valuable treatises upon the subject that has ever been published in America." Dr. Fletcher was Government entomologist from 1884 until his death, in 1908. Dr. C. Gordon Hewitt, who was appointed Dominion entomologist in 1909, made in ten years a brilliant record in public service. His remarkable work was cut short by his death in February, 1920. In October, 1920, Arthur Gibson was made Dominion entomologist. He is well fitted by ability and experience to maintain the standard of excellence set by his eminent predecessors.

Outside of the government work, entomology in Canada centers around the Entomological Society of Ontario, whose excellent publications, sustained by the government, are of great scientific and educational importance. In addition to its annual reports, this society issues the *Canadian Entomologist*, one of the leading serials of its kind, edited for many years by its founder, the Rev. C. J. S. Bethune, whose devoted services have been appreciated by every entomologist.

The Association of Official Economic Entomologists.—Organized in 1889 by a few energetic workers, this association has had a rapid and healthy growth and now numbers among its members all the leading economic entomologists of America and a large number of foreign workers. The annual meetings of the association impart a vigorous stimulus to the individual worker and tend to promote a well-balanced development of the science of economic entomology.

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INDEX

An asterisk * denotes an illustration.

- Abbott, 461
 Abdomen, 60; appendages of, *61, *132, *133; extremity, 62; modifications, 61; segments, 60
Acacia, *230
 Accessory glands, *124, 125
 Acclimatization, 360
Acerentomon, *6
Achorutes, *10
 Acone, 98
 Acridiidae (see *Locustidae*).
 Aculeata, 19
 Adams, 339, 472, 475
 Adaptations, of larvæ, 145; of legs, 48, *50; of mandibles, *36; protective, 245
 Adaptive coloration, 194; classification, 210; evolution, 211
 Adelung, von, 444
 Adler, 439, 462
 Adventitia, 110
 Adventitious resemblance, 197
Aedes, 255, 269
Egeria, sexual coloration, 184
 Æstivation, 366
Ageronia, 92
 Aggressive resemblance, 210
 Agrionidae, caudal gills, *119
 Air, movement, 368; of soil, 350; of water, 383
 Air-sacs, 117
 Alary muscles, *109
 Albinism, 179
 Aldrich, 384, 414, 426
 Alexander, 460
 Alimentary tract (see *Digestive system*).
 Allard, 445
 Alluring coloration, 210
 Alternation of generations, 216
 Amans, 437, 455
 Amber insects, 341, 345
 Ametabola, 140
Ammophila, *317
 Amnion, *131, 135
Amphidasis, 178
 Amphigony, 358
Amphipyra, 304
 Ampullaceum, *85
Anajapyx, *6, 21
 Anal glands, 73, *103
Anasa, *138
 Anderson, 269
 Androconia, *71, 72
 Anemotropism, 305
Anergates, 294
Angræcum, 221
Anisota, *152
 Anisotropic, 78
 Annelids, in relation to arthropods, 5, *8
Anomma, 293
Anopheles, 250, 251
Anophthalmus, 100
Anosia berenice, 337; *plexippus*, antenna of, *32; dispersal, 325; eclosion, 152; so-called mandibles, 40; mimicry, *201, 207; pupa, *147; pupation, 147; scale, *70; wing, *55
 Anteclypeus, 29
 Antecoxal piece, *47
 Antennæ, forms of, *32; functions, 33; sexual differences, *33
 Antennal comb, *228, 229; neuromere, *43; segment, 44; sensilla, 84, *85
Anthonomus grandis, activity, 353; æstivation, 366; coloration, 378; development, 355, 359, 360; fecundity, 376; food, 376; hibernation, 361; longevity, 377; rainfall on, 366; spread in U. S., 418; winds on, 368
 Anthrax, 269
Anthrenus, *69
 Antigeny, 34, *184
 Ant-plants, *230
 Ants, castes of, 289; color sense, 100; facets, 31; general account, 289; habits, 291; harvesting ants, 297, 400; honey ants, *294; hunting ants, 293; larvæ, 290; leaf-cutting, *295; nests, 290; phototropism, 310; slavemaking, 293

- Anurida*, development of mouth parts, *132; germ band, *132; habits, 170; pigment, 177
 Anus, *66, 105
 Aorta, *109
Apanteles, *273
 Apatetic colors, 210
Apatura, scales, 172; colors, 175
Aphididæ, development, 359; galls of, *214; reproduction, 358
Aphidius, 273
Apis mellifera, antennal sensilla, *85; cephalic glands, 107; comb, 282, *283; control of sex, 286; determination of caste, 286; foot, *51; general account, 281; hair, *227; larvæ, *284; legs, *228; mandible, *36; mimicry, *202; modifications in relation to flowers, *228; mouth parts, *42; ocellus, *96; ovipositor, *64; pupa, *284; reproductive system, *126; tongue, *86; wax, *74, 282
 Apneustic, 117, 169
 Apodemes, *48
 Apodous larvæ, 44, 51
 Apophyses, *48
Aporus, 319
 Appendages, development of, *131
 Apple, insects of, 212, 410
 Apter, 7
 Apterygota, 9
 Aquatic insects, adaptations of, 165; conditions of existence, 382; food, 165, 386; locomotion, 166; origin, 171; respiration, 168; systematic position, 165
 Arachnida, *2
 Arctic realm, 331
 Arista, *32
Aristida, 297
Arixeniidæ, 10
 Arms, J. M., 21, 431, 432, 454
 Army worm, 339
 Arthropoda, characters of, *1; classes, 2; interrelationships, 4; naturalness of phylum, 7; phylogeny, *8
Asclepias, 221, *222, *223
Asecodes, 274
 Ashmead, 327
Aspidiotus perniciosus, spread of, 418; winter-killing of, 363
 Assembling, 90
 Associations, 393, 394
 Ast, 446
Atelura, *300
Atemeles, *299
 Atmosphere, 351; composition of, 367; movement, 368; temperature, 352
Atta, 293, *295
Attacus, 27
 Auditory hairs, 94; organs, 94, *95
 Aughey, on insectivorous birds, 243, 463
 Auricle, *228, 229
 Austen, 465
 Australian realm, 332
 Austral region, 332
 Autecology, 348
Automeris, 73
 Ayers, 61, 452
 Bachmetjew, 364
 Back, E. A., 429
 Backswimmers (see *Notonecta*).
 Baldwin, 469
 Ball, E. D., 426
 Ballowitz, 450
 Banks, 430, 434
 Barber, 384, 456
 Barriers, 324
 Barrows, 303, 470
 Basement membrane, *67, 69, *105
 Basiconicum, 84, *85
 Basidium, *218
Basilarchia, mimicry, *201, 207; protective resemblance, 196
 Bates, on mimicry, 202, 459, 470, 471
 Batesian mimicry, 203
 Bateson, 458
 Bauer, 442
 Baumberger, 354, 361, 373, 374, 475, 476
 Beal, 240, 463
 Bean weevil (see *Bruchus*).
 Beddard, 457, 460, 472
 Bees, color sense of, 100; hairs, *68
 Beetles, sounds of, 91
 Behavior of insects, 302
 Bellesme, de, 446
Belostoma, digestive system of, *105; predaceous, 166, 233
 Belt, on leaf-cutting ants, 295, 471
Bembidion, 303, 349
Benacus, *15; cæcum, 105; mouth parts, *39; predaceous, 166
 Beneden, van, 466
 Beneficial insects, 411
 Benton, on honey bee, 286, 466

- Berlese, 160, 431, 433
 Bernard, 432
 Bertkau, 126
 Bethe, 292, 469
 Bethune, 429
 Betten, 456
 Binet, 442
 Biotic conditions, 379, 387
 Birches, insects of, 212
 Bird, H., 349
 Birds, insectivorous, 239; regulating insect oscillations, 243
 Bishopp, 352, 365, 475
Bittacomorpha, *120, 169
Bittacus, *16, *49
 Bitter rot, 219
 Black-flies, 233
 Blackiston, 460
 Blanc, 436, 447
 Blanchard, 464
 Blandford, 464
 Blastoderm, *130
Blastophaga, 428
 Blatchley, 426
Blatta, muscles of, *77; respiration, *121
 Blattidæ, 10
 Blind insects, 33
Blissus leucopterus, distribution of, 339; drought on, 366; incubation, 359; losses through, 410; rainfall on, 367
 Blochmann, 452
 Blood, corpuscles, *110; course of, 110, *111; function, 111; gills, 119
 Bluebird, food of, 241
 Blunck, 453
 Boas, 455
 Bobretzky, 452
 Boll weevil (see *Anthonomus*).
 Bollworm (see *Chloridea*).
 Bolton, 430
Bombus, antenna of, *32; general account, 287; larva, *142; mimicry, *210; respiration, *121; taste cup, *88
Bombyx mori, Malpighian tubes of, *108; mid intestine, *105; œnocytes, *114; silk glands, *76
 Bordas, 441, 447
 Boreal region, 332
 Borgert, 441
 Börner, 433, 434
 Bot flies, 234
 Bourcart, 477
 Bouvier, 433, 470
 Boyce, 465
Brachinus, 73
 Brachypterism, 397
 Braconidæ, 273
 Brain, 80, *82; functions of, 82
 Branchial respiration, 169
 Brandt, 451
 Brauer, on classification, 7; types of larvæ, 142; 432, 453
Braula, 272
 Braun, 464, 465
 Breed, on phagocytosis, 160
 Breithaupt, 436
 Bridges, 461
 Britton, 425
 Brongniart, on Carboniferous insects, 341, 344, 473
 Brown-tail moth (see *Euproctis*).
 Bruce, 263, 264, 465
Bruchophagus, *139
Bruchus, metabolism, 364, 370
 Brues, 269, 359, 366, 372, 374, 434, 465, 467, 476
 Bruner, 426
 Brunner von Wattenwyl, 458
 Bruntz, 448
 Buckingham, 470
 Bugnion, 162, 454
 Bumblebees, general account, 287
 Bureau of Entomology, 428
 Burge, 115
 Burger, 370
 Burgess, A. F., 368, 429
 Burgess, E., 436
 Burmeister, 431, 432
 Bursa copulatrix, 125
 Busck, 139
Buthus, *2
 Butler, 459
 Bütschli, 442, 450, 451, 452
 Butterflies, eclosion of, 152, *153; fossil, *346
 Cabbage butterfly (see *Pieris rapæ*).
 Cæca, gastric, *102, *103, 104
Cæcilius, *106
 Cæcum, *104, *105
 Cæsar, 445
 Cajal, 449
 Calkings, 465
Calliphora, compound eyes of, *97, *98

- Callosamia*, antennæ, 33; assembling, 90; cocoon, 356; sexual coloration, *185
Caloptenus, olfactory organ of, *88; tympanal organ, *95
Calopteryx, development of, *134; sexual coloration, 185
 Calvert, 465
 Cameron, 475
Campodea, 6, *9, 21, 60, *142
 Candèze, 440
 Canker worms, as food of birds, 243
 Cannon, 307
Canthon, *50
 Capitate, *32
Carabidæ, anal glands of, 73, *103; food of, 233; predaceous, 271
Carabidoid larva, *157
Carabus, alimentary tract of, *103
 Carboniferous insects, 341, 342
 Cardiac valve, *101, 102, *104
 Cardo, *37
 Carlet, 439
 Carpenter, F. W., 469
 Carpenter, G. H., 5, 7, 431, 433, 455, 456, 461, 472
Carpocapsa pomonella, development, 356, 360; hibernation, 361; incubation, 358; temperature on, 356; winter-killing of, 362
 Carrière, 444, 452
 Carrion insects, 236
 Carroll, 253, 255, 465
 Carus, 430
 Casteel, 229, 463
 Catbird, foot of, 240
 Caterpillar, 137; pupation of, 147, *149
Catocala, protective resemblance, *195; scent tufts, 49
Catogenus, antenna of, *32
 Caudal gills, 170
 Caudell, 434, 435
Cecidomyiidae (see *Itonididae*).
Cecropia adenopus, 230, *231, *232
Cecropia moth (see *Samia*).
 Centipede, *5
 Centrolecithal, *130
Cerambyx, facets of, 31; ovipositor, *63
Ceratina, 277
Ceratomegilla, 336
Cerceris, 319
 Cerci, *9, 62, *63, *65
 Cercopoda, 62
Ceroplastes, 75
Cerura, 74
 Cervical sclerites, 29
 Chadwick, 463
 Chæticum, 84, *85
 Chalcididae, 27, 273
 Chandler, 465
 Chapman, 453
Chelostoma, *68
 Chemotropism, 302
 Cheshire, 42, 64, 229, 283
 Child, 444
 Chilopoda, 3, *5
 Chinch bug (see *Blissus*).
Chionaspis, 141
Chironomus, nervous system, *82; pupal eggs, 128
 Chitin, 66
 Chittenden, 429, 474, 477
Chloridea obsoleta, development, 359; rainfall on, 366
 Chlorophyll, as a pigment, 175
 Cholera, 268
 Cholodkovsky, 432, 447, 452
 Chordotonal organs, *95
 Chorion, *129, 141
 Christophers, 465
 Christy, 464
 Chromosomes, 129
 Chrysalis, 137
Chrysobothris, integument of, *67
Chrysomelidae, silk glands of, 77
Chrysopa, *16; cocoon of, *148; laying eggs, *140; mandibles, *36; predaceous, 270; silk glands, 77
 Chun, 440
Cicada, metamorphosis of, *139; molts, 145; sound, 91
Cicindela, leg of, *50; mandible, *36; predaceous, 271; variation in coloration, 183, 189, *192
Cicindelidae, ecological succession of, 407; eggs, 350, 351
Cimbex, repellent glands, 73
 Circular muscles, *105, 106
 Circulation, *111
 Circulatory system, 109
Cirphis unipuncta, 339
 Claassen, 476
 Claspers, *65, *66
 Claus, 432
 Clavate, *32

- Claypole, 453
 Clements, 474
 Climatal coloration, 179
Clisodon, 225
 Cloaca, 62
 Clover, insects of, 212, 410; pollination of, 225
 Clypeus, 28, *40
Clytra, embryology of, *130, *131, *135, *136
Cnemidotus, 118
 Coarctate pupa, 147
 Coblentz, 116, 449
Coccinella, distribution of, 336
 Coccinellidæ, predaceous, 271; silk glands, 77
 Cochineal, 413
 Cockerell, 347, 426
 Cockroach, cephalic ganglia of, *82; fossil, *343, 345; mouth parts, *35; muscles, *53, *77; respiration, *121; salivary gland, *107; spermatozoön, *125
 Cocoon, *148, *151
 Codling moth (see *Carpocapsa*).
 Cæloconicum, 84, *85
 Cælom sacs, *135
 Coleoptera, 16, *15, 24
Colias, albinism of, 180; color sense, 100; sexual coloration, *184
 Collembola, alimentary tract of, *101; defined, 9; furcula, 62; primitive condition, 21; ventral tube, 62
Colletes, hairs of, *68
 Colon, *102, 105
Colopha, gall of, *214
Coloradia, 414
 Color, effects of food on, 176; sources of, 172
 Colorado potato beetle (see *Leptinotarsa*).
 Coloration, adaptive, 194, 210; climatal, 179; development of, 187; effects of moisture and temperature on, 178; seasonal, 180; sexual, 184; variation in, 188; warning, 199
 Color patterns, development of, 187; origin, 186
 Colors, combination, 175; pigmental, 174; structural, 172
 Color sense, 100
 Commissures, 80, *82
 Communities, 393; classification of, 389, 393; distribution of, 389; examples of, 394; grasshopper, 394; stream, 397; in New Mexico, 399
 Complete metamorphosis, 137
 Compound eyes, *25; origin, 100; physiology, 98; structure, *97, *98
 Comstock, A. B., 128, 290
 Comstock, J. H., 56, 424, 427, 431, 432, 433, 434, 435, 436, 438, 455, 456
 Comte, 267
 Cone cells, 97, *98
 Conidia, *218
 Conidiophores, *218
 Connold, 462
 Conradi, 426
 Conseil, 267
 Consociates, 393
 Cook, A. J., 426
 Cook, M. T., 462
 Cooke, 462
 Cooley, 426
 Cooties (see *Pediculus*).
 Cope, on segmentation, 27
Copidosoma, 273, 412
Copris, spermatozoön of, *125
 Coprophaga, 373
 Coquillett, 424
 Corbiculum, *228
 Cordley, 426
Cordyceps, *217
Corcthra, chordotonal organs of, *95; imaginal buds, *161
 Corn borer (see *Pyrausta*).
 Corn ear worm (see *Chloridea*).
 Corn insects, 212, 410
 Cornea, *97, *98
 Corrodentia, *12
Corydaloides, 344
 Cosens, 215, 463
 Costa, *54
 Coste, 457
 Cotton boll weevil (see *Anthonomus*).
 Cotton bollworm (see *Chloridea*).
 Cotton worm, 410
 Cowan, 462
 Coxa, 48
 Craig, 465
 Craighead, 476
 Crampton, 21, 23, 25, 434, 435, 437, 438, 440
 Crawley, 467
 Cremaster, 147
Cremastogaster, 291
 Cricket, stridulation of, 93
Crioceris, 338
 Crop, *102, *103

- Crosby, 424, 477
 Crustacea, 2
Cryptorhynchus, 338
 Crystalline cone, 97, *98
Ctenocephalus, *20
 Cubitus, *54
 Cucurbit wilt, 219
 Cuénot, 441, 447, 448
Culex, antennæ of, *34; characteristics, 251; filariasis transmitted by, 265; hibernation, 310; larva, *168; mouth parts, *41; respiration, 169; tropisms, 310
 Cutaneous respiration, 169
 Cuticula, 66, *67, *68
 Cuticular colors, 174
Cyaniris pseudargiolus, coloration of, 178; geographical varieties, 328; melanism, 180; polymorphism, *181; sexual coloration, 184
Cybister, leg of, *167; locomotion, 167, 168
Cychnus, 91
Cyllene, metamorphosis of, *137
 Cynipidæ, abdomen of, 61; galls, *213, *214; parthenogenesis, 127, 216
Cyrtophyllus, stridulation of, 93

 Dahl, 437, 440, 442
 Darkness, as affecting pigmentation, 177
 Darts, *64
 Darwin, 317, 412, 461, 462, 470
Dasyneura, egg of, *139, 140; ovipositor, *63
 Davenport, 308, 352, 353, 360, 364, 469, 474
 Davis, J. J., 426
 Davis, K. C., 456
 Dean, 425
 Dearborn, on insectivorous birds, 242, 243, 245, 464
 Deegener, 441, 442, 443, 445, 447, 448, 450, 451, 455
 Demoll, 437, 445, 446
 Demoor, 437
 Denny, 66, 78, 431, 435, 442
 Dermaptera, 10
 Dermestidæ, 236
 Deutocerebrum, 80, 135
 Deutoplasm, *129
 Development, 129
 Development, threshold of, 355
 Developmental zero, 355
 Devonian insects, 340, 341
 Dewar, 461
 Dewitz, 437, 439, 448, 454

Diabrotica, distribution of, 337
Diacrisia, cocoon of, 148
Diapheromera, 195, 359
 Diastole, 111
Dibrachys, 274
 Dichoptic, *32
 Dickel, 467
Dictyoneura, 344
 Dietrich, 445
 Digestive system, 101; of beetle, *103; *Belostoma*, *105; Collembola, *101; grasshopper, *102; histology, *105; 106; moth, *104; *Myrmeleon*, *103
 Digoneutic, 182
 Dimmock, on assembling, 91; on mouth parts of mosquito, *41; 436, 440, 457, 463
 Dimorphism, 180
Dinarda, *299
Dineutus, antenna of, *32; eyes, *30
 Diplopoda, *3
 Diptera, 19, *20; eyes of, *31; halteres, 101; mouth parts, *41; origin, 25; sounds, 91; spiracles, 60
 Direct metamorphosis, 138
 Directing tube, 76
 Diseases, their transmission by insects, 218, 248
 Dispersal, 322; centers of, 339; means of, 323; in North America, 335
Dissosteira, protective resemblance of, 196; stridulation, 92
 Distant, 471
 Distribution, former highways of, 325; geographical, 322; geological, 340; temperature on, 362
 Diving beetles (see *Dyliscidæ*).
 Dixey, 208, 457, 458, 460
 Doane, 465
 Dogiel, 447
 Dolbear, on stridulation, 93
 Dolichopodidæ, 49
 Dolley, 470
Donacia, 79, 165, 169
 Doncaster, 451
 Donisthorpe, 467
 Dorfmeister, 457
 Dorsal vessel, *109, *110
 Doten, 376, 426, 474
 Dove, 352, 365, 475
 Dozier, 476
 Drift, insect, 170

- Drone, *282
Drosophila, chemotropism of, 303; egg, *139; food, 373, 376; humidity on, 365; melanism, 180; phototropism, 310, 311
Drought, 366
Dubois, 448
Ductus ejaculatorius, *124
Dufour, 449, 455
Durham, 464
Dürken, 438
Dyar, on molts, 145
Dynastes hercules, 27; *tityus*, distribution of, 337
Dysentery, 268
Dytiscidae, 166, 167
Dytiscus, caecum of, 105; leg of, *50; predaceous, 233; respiration, 169
Dzierzon's theory, 286

Ecdysis, 140, 144
Eciton, *295; eyes of, 31; habits, 233, 290, 293
Eckstein, 462
Eclosion, 152
Ecology, 348
Economic entomologist, 420
Ectoderm, 130, *131
Edwards, on *I. ajax*, 182; on *P. tharos*, 182
Effective temperatures, 355
Egg-guide, *67
Egg-nucleus, *129
Eggs, form of, *139; number, 141; size, 140
Eimer, 468
Ejaculatory duct, *124
Elaphrus, stridulation of, 91
Electricity, 368
Eleodinae, 372
Ellema, protective resemblance of, 196
Elm, insects of, 212
Elm leaf beetle (see *Galerucella*).
Eltringham, 446, 461
Elwes, 471
Elwyn, 365, 475
Ely, 476
Elytra, 53
Embia, 12
Embiopoda, 11
Embryology, 129
Emery, 448, 467
Emesa, 322
Empis, nervous system of, *82
Empodium, 48

Empusa, *218
Enderlein, 433
Endoskeleton, 46, *48
Engelmann, 430
Enteman, 289, 321, 459, 467, 469
Entoderm, 130, 135, *136
Entomophagous, 373
Entomophthoraceae, 217, *218
Environment, 387, 389
Ephemerida, *13, 14; abdominal segments of, 60; eyes, 31; origin, 23
Ephydra, 383, 414
Epicaula, hypermetamorphosis of, 156, *157
Epicranium, 28
Epigamic colors, 211
Epimeron, *45, *47
Epipharynx, 35
Episternum, *45, *47
Epithea, dorsal vessel of, *110
Equilibrium, 382
Erebus agrippina, 27; *odora*, 323, 337
Ergatoid, 290
Erioccephala, mouth parts of, 40
Eristalis, mimicry by, *202; respiration, 169
Eruciform larvæ, 24, *143, 160
Erynnis manitoba, distribution of, *332
Escherich, 439, 451
Essig, 425
Ethiopian realm, 331
Etiolin, 193
Etolblattina, 343
Eucone, 98
Eudamus proteus, distribution of, *332
Eugereon, *344
Euphoria, mouth parts of, 36, *227
Euplexoptera (see *Dermaptera*).
Euplæa, colors of, 175
Euproctis chrysorrhæa, phototropism of, 309; spread, 417; winter-killing of, 362
European corn borer (see *Pyrusta*).
Euschistus, antenna of, *32
Eutermes, 281
Euthrips, *14
Evaporation, 369; adaptations to, 372; on eclosion, 372; gradients, 371; on hatching, 371; on life cycle, 371; on metabolism, 369; reactions to, 370
Everes, androconium of, *71
Ewing, 4, 359, 435
Excrements, 105
Exner, on compound eyes, 98, 444, 468
Expiration, 123

- Exuviae, 144
 Eyes, compound, *30, *97; kinds of, *30; sexual differences in, *31; simple, *30, *31
 Fabre, J. H., 316, 466, 468
 Fabre, J. L., 446
 Facets, *30
 Fat-body, distribution of, 112, *113; functions, 112; structure, 112, *113, *114
 Fat-cells, 112, *113
 Faunæ of islands, 326
 Faunal realms, 328, *329
 Faussek, 447
 Felt, E. P., 423, 451, 463
 Female genitalia, 62, *63
 Femur, *47, 48, *49
 Fenard, 451
 Fenestrate membrane, 97, *98
Feniseca, 271
 Fernald, C. H., 213, 423, 425, 426
 Fernald, H. T., 426, 432, 477
 Fertilization, 129
Fidonia, antennal sensilla, *85
 Fielde, 290, 292, 307, 466, 467, 469
 Fielding-Ould, 464
 Filariasis, 265
 Filiform, *32
 Filippi's glands, *76
 Finlay, 253, 464
 Finn, on mimicry, 206; on warning coloration, 199; 460, 461
 Fire blight, 218
 Fire-flies, 115, 116
 Fischer, 458
 Fishes, insectivorous, 237
 Fitch, 423
 Flagellum, *32
 Fleas, *20, 234
 Fletcher, 429
 Flight, mechanics of, 57
 Flint, W. P., 425
 Flögel, 442
 Fluted scale, 428
 Follicles, 124, *127
 Folsom, 433, 436, 447
 Food, its effects on color, 176, 378; on fecundity, 376; on growth, 375; habits, 373; on hibernation, 378; on longevity, 377; on oviposition, 376; plants, 373; relations, 378; on reproduction, 376; selection, 374; on sex-determination, 376
 Food reservoir, 102, *104
 Forbes, H. O., 471
 Forbes, S. A., on corn root louse, 298; on economic entomologist, 420; food of *Carabidae*, 271; insectivorous birds, 239; insectivorous fishes, 237; insect oscillations, 243; 424, 462, 463, 464, 466
 Forbush, 213, 423
 Fore intestine, *101, *102
 Forel, on ants, 291; on taste, 85; 440, 443, 444, 445, 467, 469
 Forficulidæ, 10
 Formations, 393, 394
 Formative cells, 69, *71
Formica, *exsectoides*, mounds of, 291; *fusca*, 289, 293, 294; *pratensis*, eyes of, 33; *sanguinea*, 294
 Fossil insects, localities for, 340
 Fossilization, 340
 Free pupa, 146
 French, G. H., 424
 Frenulum, 54
 Frenzel, 446, 447
 Friese, 459
 Front, *28, *29
 Frontal ganglion, 81, *82
 Fuller, 467
 Fundament, 131
 Fungi of insects, *217, *218
 Furcæ, 46, *48
 Furcula, 62
 Futaki, 266
 Gadeau de Kerville, 448
 Gad flies, 233
 Galapagos Islands, Orthoptera of, 326
 Galea, *35, 37, *38
Galerita, anal glands of, 73; antenna, *32; sternites, *47
Galerucella luteola, 419
 Galls, *213, *214
 Ganglia, cephalic, *43, 80, *82; functions of, 82
 Ganglion, structure of, 81, *83; subœsophageal, *81, *82; suprœsophageal, 80, *82
 Ganglion cells, 81, *83
 Ganin, on *Platygaster*, *158, 454
 Garman, 426, 456
 Gastric cæca, *102, *103, *104
Gastropacha, larval coloration, 177; stinging hair, *72

- Gastrophilus*, 235
 Gastrulation, *130
 Gee, 470
 Gehuchten, van, on digestion, 104; 442, 447
 Genæ, *29
 Geniculate, *32
 Genitalia, 62; of female, 62; grasshopper, *67; male, 64; moth, *66
 Geographical, distribution, 322; varieties, 328
 Geological distribution, 340
 Geometridæ, legs of larvæ, 51
 Geotropism, 306
Gerephmera, 342
 Germ band, *130; types of, 133
 Germ cells, 129
 Germinal vesicle, 129
 Gerould, 180, 459, 461
Gerris, *166; locomotion of, 168; thigmotropism, 304
 Gerstäcker, 449
 Gibson, A., 429
 Gibson, W. H., 462
 Gill, T., 471
 Gillette, 426
 Gills, *118, *119, 169
 Gilson, 447, 450, 456
 Gipsy moth (see *Porthetria*).
 Girault, on numbers of eggs, 141
 Gizzard, 102, *103
 Glaciation, its effects on distribution, 325
 Glands. 72: accessory, *124, *126; alluring, 74; repellent, 73; salivary, *106, *107; silk, 75, *76, wax, 74
 Glandular hairs, *72, *73
 Glaser, 114, 449
 Gleason, 474
 Glenn, 356
 Glossa, *35, 37, *42
Glossina, 262, *263
 Glover, 427
 Golgi, on malaria, 248
Goliathus, endoskeleton of, *48
 Gonapophyses, *63, *64
Gongylus, 210
 Gonin, 454
 Goossens, 439, 440
 Gorgas, 256, 465
 Gortner, 174, 459
 Goss, 473
 Gossard, 425, 426
 Gould, 457
 Graber, on chordotonal organ, *95; halteres, 101; hearing, 94; 431, 437, 439, 443, 447, 452, 468
 Graham, 269
 Grasshopper, adaptations, 397; alimentary tract, *102; communities, 394; genitalia, *67; hearing, *94
 Grassi, on *Termes*, 279; 432, 464, 466
 Green bug (see *Toxoptera*).
 Gregory, 376
 Gregson, 176
 Grenacher, on compound eye, 98, 100, 443
 Grobben, 432
 Gross, 451
 Grossbeck, 384, 456
 Growth, 144
 Grub, 137
 Grünberg, 451, 465
 Gryllidæ, 10
 Grylloblattidæ, 10
Gryllotalpa, leg of, *50; maternal care, 76
Gryllus, sense hairs, *90; stridulation, 92
 Gula, 29, 37
 Günther, 445
 Guyénot, 376
 Gynandromorphism, 127, *128
 Gyrinidæ, eyes of, *30
Gyrinus, locomotion of, 168; respiration, 169; tracheal gills, *118
 Haase, 432, 439, 449, 460
 Hæmolymp, 110
 Hagen, 279, 430, 455, 457
 Hairs, development of, *68, 69; functions, 69; histology, *69; modifications, *68; pollen-gathering, *60, *227; protective, 245; tenent, *72
Halisidota, distribution of, 336
Halobates, 170
 Halteres, 53, 101
 Hamilton, on holarctic beetles, 331, 471
 Hammar, 358, 360
 Hammond, A. R., 454
 Hammond, J. H., Jr., 312
 Hamuli, 54
 Handlirsch, 8, 347, 433, 434, 435, 474
 Hansen, 432, 433, 436
Harmolita, 273
 Harned, 426
 Harpactophagous, 373
Harpalus, labium of, *38; maxilla, *38
 Harris, 423, 476

- Hart, 456, 474
 Hartman, 469
 Harvey, 425
 Hatching, 141
 Hatschek, 452
 Hauser, on smell, 87, 443
 Haushalter, 268
 Haviland, on termites, 281
 Hawaii, beetles of, 326; Hymenoptera, 327
 Hayward, on stridulation, 93
 Head, 28; segmentation of, *43
 Headlee, 356, 359, 364, 367, 370, 372, 425, 475, 476
 Hearing, 94
 Heart, *109, *110, *111
 Heath, on *Termopsis*, 278, 467
 Heer, on fossil insects, 341, 473
 Heider, 452, 454
 Heilprin, 472
 Heim, 462
 Heinemann, 448
 Heliconiidae, mimicry, 202
Heliophila (see *Cirphis*).
 Heliotropism, 306; machine to illustrate, 311
 Helm, 446
 Hemelytra, 53
Hemerocampa, parasites of, 274
 Hemimeridae, 10
Hemimerus, *11; hypopharynx of, *38
 Hemiptera, 16; mouth parts, *39; odors, 73; origin, 23
 Henking, 450, 452
 Henneguy, 431
 Hennings, 370
 Henshaw, 430
Heptagenia, hypopharynx of, *38
 Hermaphroditism, 125
 Herms, 425, 465, 470, 474
 Herrick, 424, 426, 477
 Hesse, 445
 Hessian fly (see *Mayetiola*).
Hetarius, 300
 Heterocera, 18
 Heterogeny, 127
 Heterogony, 358
 Heterometabola, 138
 Heterophaga, 19
 Heteroptera, *16; spiracles of, 60
 Hewitt, 375, 429, 436, 477
Hexagenia, *13, 14; male genitalia, *65; tracheal gills, *118
 Hexapoda, defined, 4
 Heymons, 139, 433, 439, 451, 453
 Hibernation, 361
 Hicks, on olfactory pits, 88
 Hickson, 444
 Higgins, 456
 Hildebrand, 384
 Hilton, 441
 Hind intestine, *102, *104
 Hinds, 354, 355, 359, 360, 361, 366, 367, 377, 378, 426
 Histogenesis, 160
 Histolysis, 160
 Hochreuther, 445
 Hodgkiss, 424
 Hoffbauer, 438
 Holarctic realm, 331
Holcaspis, galls of, *213, *214
 Holmes, 69, 470
 Holmgren, 436, 443, 450, 451, 467
 Holometabola, 137
 Holopneustic, 117, 168
 Holoptic, *32
 Homoptera, 16
 Honey, 285, 413
 Honey ants, *294
 Honey bee (see *Apis mellifera*).
 Hopkins, A. D., 426, 429
 Hopkins, F. G., on pigments, 175, 458
Hoplia, sexual coloration of, 185
 Horn, on *Cicindela*, 189
 Houghton, 426
 House fly (see *Musca*).
 Houser, 425
 Howard, 274, 338, 423, 428, 429, 431, 464, 465, 466, 472, 477
 Howes, 470
 Hubbard, on parasitism, 274
 Huber, on wax, 282
 Hudson, 471
Humboldtia, 232
 Hunter, S. J., 356, 426, 431
 Hunter, W. D., 354, 355, 359, 360, 361, 366, 367, 368, 375, 376, 378, 428, 429
 Huxley, 450
 Hyaloplasm, 78
 Hyatt and Arms, 21, 160, 431, 432, 454
Hybernia, 176
Hydnophyllum, *232
Hydrophilus, *15, *166; antennae, 33; leg, *167; locomotion, 166; male genitalia, *65; respiration, 169

- Hydrotropism, 303
Hydrous, tergites of, *46
Hylastinus, 338
Hylobius, glandular hairs of, *72
 Hymenoptera, defined, 18; cephalic glands, 107; eyes of sexes, *32; internal metamorphosis, 162; mouth parts, *42; ocelli, 31; origin, 25; sounds, 91; wing, *56
Hypatus, 364
Hypera, 338
 Hypermetamorphosis, 156
 Hyperparasitism, 274
Hyphæ, 217
Hyphantria, 246
Hypoderma, larva of, *142; *lineata*, habits of, 235; losses through, 411
 Hypodermal colors, 174
 Hypodermis, *67, *68
 Hypognathous, 11
 Hypopharynx, *35, 37, *38, *41

Icerya, 428
 Ichneumonidæ, *272
 Ileum, *105
 Imaginal buds, *161, *162
 Imago, 137
 Imms, 477
 Incomplete metamorphosis, 138
 Incubation, 358
 Indirect metamorphosis, 137
 Ingenitzky, 451
 Injurious insects, 410; introduction of, 416
Ino, antennal sensilla of, *85
 Inquilines, 215, 281
 Insecta, defined, 4
 Insectivorous birds, 239; fishes, 237; plants, 216; vertebrates, 236
 Inspiration, 123
 Instar, 140
 Instinct, 313; apparent rationality of, 314; basis of, 313; flexibility, 316; inflexibility, 315; modifications, 315; origin, 317; stimuli, 314; and tropisms, 318
 Integument, 65
 Intelligence, 318
 Interactions of organisms, 379
 Intercalary, appendages, *132; neuromere, *43; segment, 44
 Interglacial beetles, 346
 Interrelations, of insects, 270; of orders, 20
 Intima, *76, 106, *121

Iphiclides ajax, polymorphism of, 181
 Iridescence, 172
 Iris pigment, *96, *97
Iris versicolor, *220, *221
 Irritants, 246
Isaria, 217
Isia, cocoon of, 148; hairs, 69, 146; hibernation, 361; molts, 145
 Island faunæ, 326
 Isolation, 328
 Isoptera, 11
Isosoma (see *Harmolita*).
 Isotropic, 78
 Ithomiinæ, mimicry, 202, 203
 Itonididæ, galls of, 214; pædogensis, 128

 Jackson, C. F., 431
 Jackson, T. W., 465
 Jacobi, 461, 472
 James, W., 468
 Janet, on *Atelura*, *300; on muscles, *78; 436, 439, 440, 442, 466, 467
 Japan, 415
 Japanese beetle (see *Popillia*).
Japyx, 9, 22; spiracles of, 60
 Jennings, 469
 Johannsen, 456, 465
 Johnson, R. H., 459
 Johnson, W. G., 426, 477
 Jordan, 436
 Jörschke, 445
 Judd, on food of bluebird, 242; mimicry, 208; protective adaptations, 245; protective resemblance, 198; warning coloration, 199; 460, 463, 464
 Jugum, 54
 Jurassic insects, 341, 345

 Kala-azar, 269
Kallima, protective resemblance of, *194
 Kanthack, 464
 Kapzov, 441
 Kathariner, 469
 Katydid, stridulation of, 93
 Kellogg, on Mallophaga, 233; mouth parts, 40; phototropism, 310; pilifers, *40; scales, 70, 172; swarming, 286; 431, 435, 436, 458
 Kenyon, 432, 443
 Kidney tubes, *108
 Kielich, 442
 Kilborne, 269

- Kingsley, on Arthropoda, 7
 Kirby, 431, 432
 Kirkland, 463
 Klemensiewicz, 440
 Kluge, 451
 Knüppel, 447
 Koch, 250
 Kochi, 436
 Koestler, 442
 Kolbe, 431
 K  lliker, 442
 Korotneff, 452
 Korschelt, 450, 452, 453, 454
 Kowalevsky, 447, 448, 451, 454
 Kraepelin, 436
 Krancher, 449
 Krause's membrane, *78
 Krogh, on temperature-velocity, 357; pupal development, 359
 Krukenberg, 67
 Kulagin, 41, 436, 453, 454

 Labellum, *41, *42
 Labial, neuromere, *43, 81, 135; segment, 44
 Labium, 29, *35, 37, *38, *39, *41
 Labrum, *29, *35, *39
 Lac, 75, 413
Lachnosterna, antenna of, *32; cocoon, 148; larva, *142
 Lacinia, *35, 37, *38
Lagoa, legs of, 51; stinging hairs, *73
 Lamarck, on instinct, 317
 Lameere, 455
 Lamellate, *32
 Landois, 449
 Lang, 435
 Langley, on luminosity, 115
 Lankester, 433
 Larv  , 137; adaptations of, 145; legs, 50; nutrition, 145; parasitic, 275; types of, *142
Lasius, age of, 289; nest, 291; parthenogenesis, 128
 Lathrop, 470
 Laveran, on malaria, 248, 465
Laverania, 248, *249
Leachia, eyes of, *30
 Leaping, 52
 LeBaron, 424
 LeConte, 470
 Lee, on halteres, 101; 444
 Legs, adaptations of, 48, *50; larval, 50; Legs, mechanics, *52; muscles, *53; segments, *49
 Lendenfeld, von, 437, 441
 Leng, 456
 Lens, *96
 Leonard, 477
 Leopard moth (see *Zeuzera*).
Lepidocyrtus, scales of, 70
 Lepidoptera, defined, 18; internal metamorphosis, *162; molts, 145; mouth parts, *40; origin, 25; reproductive organs, *124, *126; silk glands, *76; spiracles, 60
 Lepidotic acid, 176
Lepisma, *9, 21, *142; spiracles of, 60
Leptinotarsa decemlineata, aestivation, 366; color pattern, 175, 186, *191; distribution, 336, 338; dorsal wall, *135; endoderm, *136; folding of wing, *57; hibernation, 365; spread, 338; variation in coloration, *191
Leptocoris, 339
Leptosphaeria, 219
Leptospira, 255
Lerema, ocellus of, 31
 Leuckart, 451
 Leucocytes, *110, 114, 160
 Leydig, 442, 446, 450
Libellula, *14, *142
 Lice, biting, *12, 223; sucking, *15, 234
 Life zones, 332, *333
 Light, 351; on activity, 352; growth, 352; pigments, 177
 Ligula, *38
Limacodes, scale of, *69
Lina, color changes of, 190; distribution, 336; germ band, *131; glands, 74
 Linden, von, 458, 459
 Lingua, *38
 Link, 445
 Linn  us, on orders of insects, 7
 Lintner, 423, 476
Lithomantis, *343
 Livingston, 369, 389, 391, 476
 Lloyd, 456
 Locality studies, 319
 Lochhead, 477
 Locustid  , 10; molts of, 144
 Locy, 446
 Lodeman, 477
 Lodge, 470
 Loeb, 302, 304, 305, 306, 308, 309, 311, 373, 468, 469, 470, 476

- Lomechusa*, *299
 Longitudinal muscles, *105, 106
 Lord, 268
 Lorum, *42
 Losses through insects, 410
 Lovell, 445
 Low, on malaria, 250
 Lowe, 424
 Lowne, 435, 443, 444, 450
 Lubbock, on ants, 289, 290, 292, 294, 297, 298, 307; larval characters, 146; muscles, 78; vision, 99; 432, 441, 443, 444, 454, 462
Lucanus, cocoon of, 148; dorsal vessel, *109; spiracles, *120
Lucilia, *306
 Lugger, 425
 Lühe, 465
 Luks, 442
 Luminosity, 114
 Lund, 448
 Lutz, 383, 385, 432, 456
Lycæna, facets of, 31
 Lycænid larvæ, alluring gland of, 74
Lycus, mimicked, 206, 207
 Lyon, 304
 Lyonet, on muscles, 78; 435, 441

 MacGillivray, 456
Machilis, 9, 21; abdominal appendages, *61; nervous system, *81; scales, *69; spiracles, 60
 Macloskie, 449, 455
Macrosiphum pisi, interactions of, 380
 Madeira Islands, beetles of, 326
 Maggot, 137
 Malacopoda (see *Onychophora*).
Malacosoma, eggs, 141
 Malaria, 248, *249
 Male genitalia, 64, *65, *66
 Mallock, A., 444
 Mallock, H. R. A., 438
 Mallophaga, *12, 233
 Malpighian tubes, *108
 Mammen, 450
 Mandibles, *35; adaptations of, *36; *Culex*, *41; Lepidoptera, *40
 Mandibular, neuromere, *43, 81, 135; segment, 44
 Mandibulate mouth parts, *35; orders, 34
 Mandus, 461
 Mann, 141

Manomera, *195
 Manson, on filariasis, 265; malaria, 250; 465
 Mantidæ, 10, 270
Mantispa, 24; metamorphosis of, *143
 Maples, insects of, 212
 Marchal, 136, 453
 Marey, on wing vibration, 58; 437, 438
Margaropus, 269
 Marine insects, 170
 Mark, E. L., 444
 Marlatt, 428, 429
 Marshall, on adaptive coloration, 206, 207, 460, 461
 Martin, 438
 Mast, 470
 Maternal provision, 276
 Maturation, 129
 Maxillæ, 37, *38
 Maxillary, neuromere, *43, 81, 135; segment, 44
 Maxillulæ, 36
 Mayer, A. G., on color pattern, 188; *Papilio*, 179; scales, 71; 441, 458, 460
 Mayer, A. M., on *Culex*, 94, 443
 Mayer, P., 432, 443
Mayetiola destructor, distribution, 368; evaporation on, 371; longevity, 377; losses through, 410; moisture on, 365
 May fly, male genitalia of, *65; wings, *56
 McAtee, 461
 McColloch, 359, 367, 368
 McCook, on ants, 291, 294, 295, 296, 297, 466
 McDermott, 449
 McEwen, 311
 McIndoo, 90, 445, 446, 470
 Mealworm (see *Tenebrio*).
 Meconium, 152
 Mecoptera, defined, 17; origin, 24
 Media, *54, 55
 Median segment, 44, 61
 Meek, 436
Megachile, hairs of, *68
Megalodacne, antenna of, *32
Meganeura, 344
Megarhyssa, *272
Megilla (see *Ceratomegilla*).
 Melander, 426, 467
 Melanism, 180
Melanoplus, alimentary tract of, *102; facets, *30; genitalia, *67; mandible, *36; respiration, 122; skull, *29

- Melanotus*, larva of, *142
 Meldola, 460
Melissodes, 225
 Melnikow, 451
Meloë, antenna of, 33; hypermetamorphosis, 156
Melolontha, male reproductive system, *124; olfactory pits, 88
 Mendelism, 209
Menopon, *12
 Mentum, *35, 37
 Merriam, on life zones, 332, 471, 472
 Merrifield, 457, 458
 Merrill, 425
 Mesenchyme, *136
 Mesenteron, *102, *103, *104, 136
 Mesnil, 465
 Mesoderm, 130, *136
 Meso-entoderm, *131
 Mesothorax, 44
 Metabola, 140
 Metallic colors, 173
 Metamorphosis, defined, 137; external, 137; internal, 160; significance, 159; systematic value, 24
 Metatarsus, *228
 Metathorax, 44
 Metschnikoff, 446, 451, 454
 Miall, on chitin, 66; muscles, 78, 431, 435, 442, 450, 454, 456
Miastor, pædogenesis of, *128
 Michels, 442
 Michelson, 173, 174
Microcentrum, stridulation of, 92, *93
 Microphaga, 373
Micropteryx, mouth parts of, 40
 Micropyle, 129, 141
 Mid intestine, *102, *103, *104
 Milkweed, pollination of, 221, *222
 Mimicry, 201; evolution of, 208
 Minot, 440
 Miocene insects, 341, 345
 Mitchell, 465
 Moisture, 364; its effects on activity, 365; aestivation, 366; coloration, 178; eclosion, 365; hibernation, 365; metabolism, 364; mortality, 365; oviposition, 365
Molanna, *17
 Moles, insectivorous, 236
 Möller, on leaf-cutting ants, 295, 462
 Mollock, on vision, 99
 Molting, 144, 359
 Molts, number of, 144
 Moniliform, *32
Mononychus, 226
 Monophagous, 373
Mordella, facets of, 31
 Mores, 393
 Morgan, C. Lloyd, 207, 468, 469
 Morgan, H. A., 426
 Morgan, T. H., 377, 469, 474
Morpho, scales of, 70, 172
 Morrill, 354
 Morse, A. P., 396, 397, 472, 474
 Mosaic diseases, 319
 Mosquito, antennæ of, *34; hearing, 94; hibernation, 311; locomotion of larvæ, 167; in relation to malaria, 248, 250; mouth parts, *41; respiration, 169; tropisms, 311
 Moulton, 461
 Mouth parts, dipterous, *41; hemipterous, *39; hymenopterous, *42; lepidopterous, *40; mandibulate, *35; orthopterous, *35; suctorial, 38
 Muir, 23
 Müller, F., on mimicry, 204; wings, 53; 460
 Müller, H., 462
 Müller, J., mosaic theory of, 98, 443
 Müllerian mimicry, 203, 204
 Murray, 471
Musca, egg of, *139; facets, 31; fungus of, *218; molts, 145; oviposition, 365; ovum, *129; in relation to typhoid fever, 257, 258, 259
 Muscidæ, cardiac valve of, *104; imaginal buds, *161
 Muscles, circular and longitudinal, 106; of cockroach, *53, *77; of leg, *53; number, 77; structure, *78; of wing, *59
 Muscle-tension theory, 311
 Muscular, power, 79; system, 77
Mutilla, stridulation of, 92
 Muttikowski, 456
 Mycetophaga, 374
 Myrientomata, 6, *7
 Myriopoda, 5
Myrmecocystus, 295
Myrmecodia, 232
Myrmecophana, mimicry, by, *205
 Myrmecophilism, 297
Myrmedonia, 300

- Myrmeleon*, digestive system of, *103; pre-daceous, 270; silk glands, 77
Myrmica, *299
Mystacides, androconia of, 72

 Nagana, 263
 Nagel, 444
 Nearctic realm, 331
 Necrophagous, 373
Necrophorus, 236, 276
 Needham, 54, 104, 424, 438, 447, 456, 462
 Nelson, 453
Nemobius, leg of, *50
 Neotropical realm, 331
Nepa, respiration of, 169
 Nephrocyte, 110
 Nerves, of head, 81, *82; structure, *81
 Nervous system, 80; development of, 133, *135
 Nervures, 54
 Neurulation, *54, *55, *56
 Neuroblasts, *135
 Neuromeres, 44, 134; of head, *43, 80
 Neuroptera, defined, 17; metamorphosis of, 24, *143
 Newbigin, 458, 460
 Newcomer, 362
 Newell, A. G., 440
 Newell, W., 426
 New Mexico, insect communities in, 399
 Newport, on metamorphosis, 162; muscles, 78; 435, 441, 442
 Newton, 442
 Nicolle, 267
 Noguchi, 255, 256
 Northrop, 373, 476
Notolophus, olfactory organs of, 89
Notonecta, *166; locomotion of, *166; respiration, 169
 Notum, 45
Novius, 275, 412, 428
 Nucleolus, 129
 Number of insects, 27
 Nuttall, 464
 Nymph, 139

 Oaks, insects of, 212, 410
Oberea, eyes of, 30
 Obtect pupa, *147
 Occipital foramen, 29, *30
 Occiput, 29
 Ocelli, *31; structure of, 95; vision by, 96
 Ockler, 437
 Ocular, neuromere, *43; segment, 44
 Odonata, abdominal segments of, 60; copulation of, 65; defined, 14; ocelli, 31; origin, 23; spiracles, 60
 Odors, 73; efficiency of, 246
Odynerus, 225
Oecanthus, abdominal appendages of, 61, *133; embryo, *133; stridulation, 93
Oecophylla, 291
Oedipoda, dorsal vessel of, *110
Oeneis, distribution of, 325
 Enocytes, *114
 Esophageal commissures, *82
 Esophagus, *102, *103, *104
 Estridae, 234
 O'Kane, 426, 477
 Olfactory organs, 87, *88, *89
 Oligocene insects, 341
 Oligophagous, 373
Oligotoma, *11
 Ommatidium, *97, *98
Onthophagus, mandible of, *36
 Onychophora, 2, *3
 Ophthalmia, 269
Orchelimum, stridulation of, 92
 Orders of insects, 7, *25
 Oriental realm, 332
 Origin of arthropods, *8; of insects, 6
 Oroya fever, 269
 Orthoptera, abdominal segments of, 60; defined, 9; ecological succession, 408; origin, 22; stridulation, 92, *93
 Osborn, 426, 477
 Osburn, 384, 386, 387, 456
 Osmeterium, *74
Osmia, 225
Osmoderma, cocoon of, 148
 Osten-Sacken, 440
 Ostium, *109, *110
 Oudemans, 450
 Oustalet, 455
 Ovaries, 123, *126
 Ovariole, 125
 Oviducts, 125, *126
 Ovipositor, 62, *63, *67
 Ovogenesis, 129
 Ovum, of *Musca*, *129; *Vanessa*, *127
 Ox-warble, *142, 235

- Paasch, 443
 Packard, on *Anophthalmus*, 100; Arthropoda, 7; classification, 7; *Mantispa*, 143; olfactory pits, 88; relationships of orders, 22; segmentation, 27; types of larvæ, 142; wings, 53; 423, 427, 431, 432, 433, 439, 442, 444, 449, 454, 455, 461, 476
 Pædogenesis, 128
 Palæarctic realm, 331
Palæoblattina, *341
 Palæodictyoptera, 347
 Palmén, 449, 450
 Palmer, 464
 Palpifer, *35, 37, *38
 Palpiger, *35, 37, *38
 Palpus, *35, 37, *38, *40
 Pankrath, 444
 Panorpidæ, 18; legs of, 51
 Pantophagous, 373
Papilio, colors of, 179; egg, *139; facets, 31; head of pupa, *147; melanism, 180; mimicry, 202, 205; osmeterium, *74; protective resemblance, 196; *cenea*, mimicry by, 202, 205
 Paraglossa, *35, 37, *38
 Paragnaths, 37
 Paralysis, infantile, 269
Paraponyx, *119, 170
 Paraptera, 46
 Parasita, defined, 16
 Parasitic insects, 233, 271, 275; in relation to birds, 245
 Parasitism, 235, 271; economic importance of, 274
Parcoblatta, mouth parts of, *35
 Parker, on phototropism, 309, 469
 Parks, 354, 475
 Parman, 352, 363, 365, 475, 476
 Parrott, 424
 Parthenogenesis, 127, 216, 286, 290, 358
Passalus, cocoon of, 148; stridulation, 91
 Patagia, 45
 Patch, E. M., 425
 Patten, B. M., 470
 Patten, W., 444, 452
 Pawlovi, 443
 Pawlowa, 448
 Payne, 311
 Peacock, 437
 Peairs, 426, 431, 475, 477
 Pea louse (see *Macrosiphum*).
 Peck, W. D., 423
 Peckham, on behavior, 316, 318, 319, 466, 467, 469
 Pecten, *228
 Pectinate, *32
Pectinophora gossypiella, 419
 Pedicel, *32
 Pediculidæ, 234
Pediculus, *15, 234, 267, 268
Pelocoris, leg of, *50
 Penis, 64, *65, 124
Pepsis, 277
 Pérez, 455
 Pericardial, cells, 110; chamber, *109, *123
Peripatus, characters of, 2, *3, 5; systematic position, 5
Periplaneta, olfactory pits of, 88
 Peripodal, cavity, 161; membrane, 161; sac, 161
 Peritrophic membrane, 106
Perla, olfactory pits of, 88
 Perlidæ, *13, 14; nymph, *142; tracheal gills, *118
 Permian insects, 344
 Peterson, 371, 437, 476
 Petiolata, 19
 Pettigrew, 437
 Pettit, 426
Petunia, *225
 Peytoureau, 439, 451
 Pflugstaedt, 438
 Phagocytes, 114, 160
Phanæus, legs of, 49, *50
 Pharynx, 102
 Phasmidæ, 10, *195
 Philiptschenko, 44
 Phillips, E. F., 429
 Phillips, W. J., 368
 Phlebotomus fever, 269
Phormia, antenna of, *32; eyes, *31; metamorphosis, *138; phototropism, 310
 Phosphorescence, 114
Photinus, luminosity of, *115
 Photogeny, 114
 Photopathy, 307
 Photophil, 307
 Photophob, 307
 Phototaxis, 307
 Phototropism, 306
Photuris, 116
 Phragmas, 46, *48
Phthirus, 234

- Phyciodes*, coloration of, 178, *182
Phylloxera, 350, 410, 416
 Phylogeny, 5, *8, *25
Phytonomus, spread of, 338
 Phytophaga, *19
 Phytophagous, 373
 Pictet, on coloration, 176, 179
 Piepers, 460
 Pierce, 24, 157, 354, 360, 368, 375, 376, 378, 434, 463, 466
Pieris, color sense of, 100; dispersion, 322; fat-cells, *113; imaginal buds, *162; olfactory organs, *90; scale, *69; *napi*: temperature experiments on, 182; *protodice*: sexual coloration of, *184; *rapæ*: androconium of, *71; developing wing, *163; distribution, 338; eggs, *140; food plants, 213; hair, *68; larval tissues, *113; pupal coloration, 177; wing vibration, 59; *xanthodice*, distribution of, 322
 Pigmental colors, 174
 Pigments, of eyes, *96, *97, *98, *99; nature of, 175; of Pieridæ, 175
 Pilifers, *40
Pimpla, 274
 Pine, insects of, 212
 Ping, 476
Pinguicula, 216
 Pink bollworm (see *Pectinophora*).
 Placodeum, *85
 Plague, 260
 Planta, *228
 Plant lice (see *Aphididæ*).
 Plants, diseases of, 218; insectivorous, 216; insects in relation to, 212
 Plasma, 110
Plasmodium, 248
 Plateau, on color sense, 100; muscular power, 79; respiration, 123; 441, 444, 446, 449, 468
Platephemera, *342
Plathemis, abdominal appendages of, *66; antenna, *32
Platygaster, hypermetamorphosis of, 146, *158
Platypteryx, 234
 Platyptera, defined, 10; origin of, 22, *25
 Plecoptera, defined, 14, *13; nymph, *142; origin, 22, *25
 Pleistocene insects, 341
 Pleurites, *45, *47
 Pleuron, 45
 Plotnikow, 441
 Pocock, 432
 Podical plate, *67
Podisus, egg of, *139; predaceous, *270
Pæcilocapsus, color changes of, 190
Pogonomyrmex, 297
 Polar bodies, *129
 Poletajew, 449, 455
 Poliomyelitis, 269
Polistes, behavior of, 316, 321; habits, 288; wing vibration, *58
Polites, on Iris, *226
 Pollenizers, insect, 225
 Pollination, 219, 225; of *Iris*, *220; milkweed, 221, *222; orchids, 221; *Yucca*, 222, *224
 Pollinia, *222
Polybia, 287
 Polyembryony, 136
Polyergus, 294
 Polygoneutic, 182
Polygonia, dimorphism of, 180; egg, *139
 Polymorphism, 289
Polynema, 158
 Polyphagous, 373
Polyphemus (see *Telea*).
Polyphylla, assembling of, 90
Polyrhachis, 291
 Pomace flies (see *Drosophila*).
Pompilus, behavior of, 316, 319
Popillia japonica, 418
Porthetria dispar, damage by, 416; distribution by winds, 368; gynandromorphism, *128; tracheoles, *121
 Postclypeus, 29
 Postgenæ, 29
 Postscutellum, *45, *46
 Potato beetle (see *Leptinotarsa*).
 Pouchet, 468
 Poulton, on adaptive coloration, 206, 207, 209; on colors of larvæ and pupæ, 177; 454, 457, 458, 459, 460, 461
 Powell, 139, 455
 Pratt, 454, 455
 Precipitation, 366
 Predaceous insects, 233, *270; in relation to birds, 245
 Prell, 434
 Premandibular, appendages, *132; segment, *43, 44
 Pressure, 363

- Pricer, 467
 Primitive insects, 20
 streak, 130
 Primordial insect, 21
Prionus, assembling of, 91; eggs, 141
 Proboscis, *40
 Procephalic lobes, *132, *133
 Prochnow, 438, 445
 Proctodæum, *102, 104, 131
 Proctotrypidæ, 27, 274
Prodoxus, 224
Prodryas, *346
 Prognathous, 11
Promethea (see *Callosamia*).
 Pronotum, *46
Pronuba, *223, *224
 Propodeum, 44
 Propolis, 283
Protapteron, 6
 Protective, adaptations, 245; mimicry, *201, 206; resemblance, *194, 198
 Prothorax, 44
 Protocerebrum, 80, 135
Protoparce, head of moth, *40; larva, *51; moth, *225; parasitized larva, *273
Protura, 6, *7
 Proventriculus, *102, *103, *104
 Pseudocercus, *61, 62, *65
 Pseudocone, *98
Pseudomyrma, 230
 Psocidæ, *12
Pteromalus, oviposition of, 376
Pteronarcys, *13; tracheal gills of, 119
 Pterygota, 9
Ptilodactyla, antenna of, *32
 Pulvillus, 48, *51
 Punksubstanz, 81
 Punnett, 209, 461
 Pupæ, 137, 146; emergence of, 152; protection, 148; respiration, 147
 Pupal stage, significance of, 159, 162
 Puparium, 147, 372
 Pupation of a caterpillar, 147, *149
 Putnam, on habits of *Bombus*, 287
 Pyloric valve, 104
Pyrausta nubilalis, spread of, 418
Pyrophila, thigmotropism of, 304
Pyrophorus, luminosity of, 115
Pyrrharctia (see *Isia*).
 Quaintance, 359, 366, 372, 428
 Quaternary insects, 346
 Quayle, 425
Quedius, 300
 Queen, honey bee, *282; termite, *278
 Radius, *54
 Rádl, 469
 Rainfall, 366
Ranatra, 166; phototropism of, 311; respiration, 169
 Rand, 463
 Raschke, 449
 Rath, vom, on sense hairs, *90; 444, 445
 Rathke, 449
 Rationality, apparent, 314; lack of, 321
 Rau, 352, 470
 Realms, faunal, 328, *329
 Réaumur, de, 435
 Receptaculum seminis, 125, *126
 Recognition markings, 211
 Rectal respiration, 119, 170
 Rectum, 105
 Recurrent nerve, 81, *83
 Redikorzew, on ocelli, *96, 445
 Redtenbacher, 437
 Reed, on yellow fever, 253, 465
 Rees, van, 454
 Reichenbach, on ants, 128
 Relapsing fever, 267
 Relationships, of arthropods, 4, *7; of orders, 20, *25
 Repellent glands, 73
 Replacements, 190
 Reproduction, of plant lice, 358
 Reproductive system, 123
 Respiration, 122, 147, 155
 Respiratory system, 116, *117
Reticulitermes, 279, 281
 Retina, *96
 Retinula, *96, *98
 Reuter, 445
 Rhabdom, *96, 97, *98
 Rheotropism, 304
Rhipiphorus, 156
 Rhopalocera, 18
Rhyphus, *55
 Ricketts, 267, 269
 Riley, C. F. C., 304, 470, 474, 476
 Riley, C. V., on hypermetamorphosis, 156; losses through insects, 410; pollination of *Yucca*, 222; pupation, 147; 377, 410, 412, 425, 427, 454, 462
 Riley, W. A., 139, 465

- Rimsky-Korsakow, 6, 434
 Ritter, 438
 Robertson, 462
 Robin, food of, 240
 Rocky Mountain locust, dispersion of, 322;
 as food of birds, 243
 Rocky Mountain spotted fever, 269
 Rolfs, 426
 Rollet, 442
 Romanes, on instinct, 317, 468
 Rosenau, 269
 Ross, on malaria, 250, 464
 Rössig, 462
 Rostrum, 39
Rozites, *296
 Ruggles, 425
 Ruland, 444

 Sadones, 450, 455, 456
 Saliva, of *Dytiscus*, 107; mosquito, 107
 Salivary glands, *106, *107
 Sambon, on malaria, 250
Samia cecropia, antennæ of, *33; cocoon,
 *151; egg, 141; food plants, 213; geni-
 talia, *66; head of larva, *74; Malpigh-
 ian tubes, *108; ocelli, *31; odor, 74,
 scales, *71
 Sanderson, 356, 359, 360, 362, 365, 366, 370,
 426, 431, 474, 477
 Sandias, 466
 San José scale insect (see *Aspidiotus pern-
 ciosus*).
 Saprophagous, 373
 Sarcolemma, *78
Sarcophaga, nervous system of, *82
 Sarcophagous, 373
Saturnia, hairs of, *68
 Saunders, 429, 476
 Saville-Kent, 472
 Scales, arrangement of, *70; development,
 70, *71; form, *69, *71; occurrence of,
 69; uses, 70
 Scape, *32
 Scarabæidoid larva, 157
 Scavenger insects, 236
 Schäffer, on scales, 70; 435, 441, 448
 Schenk, on sensilla, 84, *85, 89, 445
 Schepotieff, 6, 434
 Scheuring, 445
 Schewiakoff, 442
 Schiemenz, 446
 Schimper, 462
 Schindler, 446
Schistocerca, distribution of, 323, 339; of
 Galapagos Islands, 326; isolation, 328
Schizoneura, wax of, 75
Schizura, protective resemblance of, *106
 Schmidt, O., 454
 Schmidt, P., 433, 448
 Schmidt-Schwedt, 449
 Schneider, A., 450
 Schneider, R., 440
 Schoene, 424
 Schön, 445
 Schröder, 436
 Schwarz, on distribution, 336, 337; myrme-
 cophilism, 300, 471
 Schwedt, 455
 Sclerite, 28
Scolopendra, *5, 401
Scolopendrella, *6, 21
 Scorpion, *2, 401
 Scudder, on albinism, 180; coloration, 187;
 fossil insects, 341, 345, 346, 347; glaci-
 ation, 326; mimicry, 203; Orthoptera
 of Galapagos Islands, 326, 328; spread
 of *P. rapæ*, 338; stridulation, 92; 443,
 457, 471, 473, 474
 Scutellum, *45
 Scutum, *45
 Seasonal coloration, 180
 Sedgwick, 433
 Segmentation, of arthropods, 27; germ
 band, *131, 132; head, *43.
 Segments of abdomen, 60
 Seitz, 457, 462, 466, 468, 471
 Sematic colors, 210
 Seminal ducts, 124; receptacle, 125, *126;
 vesicle, *124
 Semon, 472
 Semper, C., on scales, 70
 Semper, K., 471
 Sempers, 477
 Sense organs, 83
 Sensilla, 84, *85
 Serosa, *131, *134
 Sessiliventre, *19
 Setaceous, *32
 Setæ, modifications of, 69
 Seventeen-year locust, 145
 Severin, 359, 371, 470
 Sex-determination, 376
 Sexual coloration, 184
 Shannon, 472

- Sharp, on *Atta*, 293; Hawaiian beetles, 326; metamorphosis, 159; 415, 431, 433, 449, 455
 Sheath, *64
 Shelford, R., 460
 Shelford, V. E., on chemical conditions, 383; communities, 393, 397; environments, 388, 389; evaporation, 368, 369, 370, 371; physical conditions, 384; succession, 404, 406, 407, 408; tension lines, 399; tiger beetles, 174, 175, 183, 189, 350; 459, 472, 474, 475, 576
 Sherman, F., Jr., 426
 Sherman, J. D., Jr., 386, 456
 Shreve, 389, 391, 476
 Shull, 94, 445
 Silk, 76
 Silk glands, 75, *76
 Silkworm (see *Bombyx mori*).
Silpha, distribution of, 336
 Silurian insects, 341
 Silvestri, on *Anajapyx*, *6; 433, 434
 Simmermacher, 440
 Simpson, 358
Simulium, 233; respiration, 170
 Sinclair, 433
 Siphonaptera, *20; origin of, *25, 26
Sirex, ovipositor of, *64
 Sitrine, 424
Silaris, 156
 Size of insects, 27
 Skin, 66
 Skull, 28, *29
 Skunk, insectivorous, 236
 Sladen, 287, 467
 Sleep of insects, 352
 Sleight, 385, 456
 Slingerland, 411, 424, 477
 Smell, 87; end-organs of, *88, *89
Sminthurus, *10
 Smith, E. F., 219
 Smith, J. B., 425, 477
 Smith, R. C., 426
 Smith, T., 269
 Snodgrass, 24, 326, 328, 436, 438
 Snow flea, *10
 Snyder, 468
 Societies, 389
 Soil, 348; nutriment in, 351; structure of, 348; temperature, 350
 Soldier, ants, 289; termites, *277
 Somatic cells, 129
 Sørensen, 433
 Sounds, 91
 Spence, 431, 432
 Spermatheca, 125, *126
 Spermatogenesis, 129
 Spermatophores, 124
 Spermatozoa, 124, *125
 Sperm-nucleus, 129
 Speyer, on hermaphroditism, 126
 Sphecina, 277
Sphecius, 277
Sphex, *223; behavior of, 316, 318, *319
 Spingidæ, as pollenizers, 221, *225
Sphinx, alimentary tract of, *104; dispersal, 323; pulsations of heart, 112; transformation, *163
 Spichardt, 450
 Spillman, 268
 Spines, 69
 Spinneret, *74, 75
 Spiracles, closure of, *120; number, 60, 119
Spirobolus, *3
Spirocheta, 267
 Spongioplasm, 78
Sporotrichum, 218, 367
 Spuler, on scales, 70; 438, 441, 458
 Spur, *49
 Squama, 54
 Squash bug, metamorphosis of, *138
 Stadium, 140
Stagmomantis, leg of, *50
 Standfuss, temperature experiments of, 183, 458
 Stedman, 426
 Stefanowska, on pigment, 99; 444
Stegomyia, 255
 Stellwaag, 438
Stenamma, 292
Stenobothrus, blood corpuscles of, *110; stridulation of, 92
Stenodictya, *343, 344
 Stephens, 465
 Stereotropism, 303
 Sternberg, 250, 251, 464
 Sternum, *47
 Stigmata (see *Spiracles*).
 Sting of honey bee, *64
 Stinging hairs, *73
 Stings, efficiency of, 246
 Stipes, *35, 37, *38
 Stokes, 449
 Stomach, *104

- Stomachic ganglion, 81, *83
 Stomatogastric nerve, 81, *83
 Stomodæum, *102, 131
 Strata, 393
Stratiomys, 360
 Straton, 462
 Straus-Dürckheim, on muscles, 78; 435, 441
 Strength, muscular, 79
 Strepsiptera, 17, 137, 157
 Stridulation, 92, *93
 Strindberg, 453
 Strong, R. P., 266
Strongylonotus, 294
 Structural colors, 172
 Styloconicum, 84, *85
Stylops, hypermetamorphosis of, 157
 Subcosta, *54
 Subgalea, *38
 Submentum, *35, *38
 Subœsophageal ganglion, *81, *82
 Succession, 404; causes of, 404; ecological, 406; of forest communities, 406; geological, 404; of Orthoptera, 408; seasonal, 405; of tiger beetles, 407
 Suctorial mouth parts, 38
 Suffusion, 178
 Summers, 426
 Superlinguæ, 36, *38, *132, 133
 Superlingual, neuromere, *43, 81, 135; segment, 44
 Supræœsophageal ganglion, 80, *82
 Suranal plate, 62, *67
 Surface film, 168
 Suspensor, 125
 Suspensory muscles, *110
 Swarming, 286
 Swenk, 426
 Symbiosis, 299
 Symons, 426
 Sympathetic system, *81, *83
 Symphyla, 3, *6
 Synchronism, of fireflies, 116
 Synecology, 348
 Syrphidæ, silk glands of, 77
 Systole, 111

 Tabanidæ, 233
Tabanus, nervous system, *82; olfactory organ, *89
Tachardia, 75
 Tactile hairs, 69, 84, *85
Tanidia, *122

 Tarantula, 401
 Tarsus, *48
 Taschenberg, 430
 Taste, 84; end-organs of, *86, *87, *88
 Taxis, 302
 Tegmina, 53
 Tegulæ, 46
Telea polyphemus, cocoon of, 148; eclosion, 152; larval growth, 144; silk glands, 75; spinning, 151
Teleas, 158
 Telson, 60
 Temperature, 352; acclimatization to, 360; on activity, 353; on coloration, 182; on distribution, 362; on hibernation, 361; on incubation, 358; limits, 352; on reproduction, 358; of soil, 350
 Temperature-constant, 355
Tenebrio molitor, development, 359, 360; incubation, 359; metabolism, 370
 Tenent hairs, *72
 Tension lines, 399
 Tenthredinidæ, larval legs of, 51
Tenthredopsis, larva of, *142
 Tentorium, 29, *30
 Terebrantia, *19
 Tergites, *45, *46
 Tergum, 45
 Termites, American species of, 279; architecture, *280; classes of, *277; "compass," *280; food of, 279; mandibles, *36; origin of castes, 279; queen, *278; ravages, 281
 Termitidæ, 11
 Termitophilism, 281
Termitoxinia, 126, 127
Termopsis, 278
 Tertiary insects, 341, 345
 Testes, *124
Tetralonia, 225
 Tettigoniidæ, 10; ovipositor, *63; spermatozoön, *125
 Texas fever, 269
Thalessa (see *Megarhyssa*).
Thanaos, androconia of, 72; claspers, 65
 Thayer, 461
 Thaxter, on *Empusa*, 217, *218; 462
 Thelen, 449
 Theobald, 477
 Thermotropism, 312
 Thigmotropism, 303
 Thimm, 465

- Thomas, 424, 427
 Thompson, C. B., 443, 468
 Thompson, S. M., 463
 Thorax, differentiation of, 44; parts of, *45;
 sclerites of, *45, *46, *47
 Thread-press, *76
Thyridopteryx, eggs of, 141
 Thysanoptera, *14, 15; origin of, 23, *25
 Thysanura, 8, *9; abdominal segments, 60;
 primitive, 20
 Thysanuriform, 24, *142, *143, 160
 Tibia, 48, *49
 Tiger beetles (see *Cicindelidæ*).
 Tillyard, 438, 476
Tipula, *20
Titanophasma, 27
 Toad, insectivorous, 236
 Tongue, 37
 Torre-Bueno, 475
 Touch, 84
 Tower, D. G., 437
 Tower, W. L., on color patterns, 186;
 cuticular colors, 175; distribution of
 Leptinotarsa, 336; folding of wing, 56,
 *57; hibernation, 365; integument,
 *67; origin of wings, 53; structural
 colors, 173; 441, 459, 472
 Townsend, A. B., 448
 Townsend, C. H. T., 426
Toxoptera graminum, development of, 356,
 364; distribution of, 368
 Toyama, 451
 Tracheæ, development of, 135, *136; dis-
 tribution, *117, *118; structure, *121
 Tracheal gills, *118, 169
 Tracheation, types of, 117
 Tracheoles, *121, 122
 Trelease, 462
Tremex, *19
 Trench fever, 268
 Triassic insects, 345
Trichius, 225
 Trichodeum, 84, *85
 Trichogen, *68, 69, *71
Trichogramma, 274
 Trichoptera, 18, *17; origin of, *25; silk
 glands, 77
 Trichopterygidæ, size of, 27; 273
 Trimen, on dispersal, 323; on *P. cenea*, 202,
 205; 459, 460
Trimerotropis, protective resemblance of,
 196, *197
 Trimorphism, 180
Triphleps, egg of, *139
 Tritocerebrum, 80, 135
 Triungulin, 156, *157
 Trochanter, 48, *49, 50
 Trochantin, 48
Trogoderma, 377
Tropæa luna, cocoon of, 148
 Trophallaxis, 301
 Tropical region, 335
Tropidacris, 27; respiratory muscles of, *123
 Tropisms, 302
 Trouessart, 471
 Trouvelot, on cocoon-spinning, 151; eclo-
 sion, 152; larval growth, 144; 453
 Trypanosomes, 261, *262, *264
 Trypanosomiasis, 261, 263, 264
Tryphæna, 176
 Tsetse fly, 262, *263
 Tuberculosis, 269
 Turner, 101, 445
 Tutt, 472
 Typhoid fever, 257
 Typhus, 266
 Uhler, on distribution, 337
 Uichanco, 358
 Underhill, 464
 Urech, 457, 458
 Uric acid, 108; as a pigment, 175
 Urosternite, 60
 Urotergite, 60
 Useful insects, 411
Utricularia, 217
 Uzel, 453
 Vagina, 125, *126
 Valette St. George, la, 450
Vanessa, development of scales of, *71; head
 of butterfly, *40; *antiopa*: 246; photo-
 tropism, 309; *atalanta*: color change,
 190; *cardui*: dispersion, 322, 326; geo-
 graphical variation, 328; *polychloros*:
 coloration, 179; melanism, 180; *urtica*:
 coloration, 176; melanism, 180; tem-
 perature experiments, 183
 Variation in coloration, 188, *191, *192
 Variations, 190
 Vas deferens, *124
 Vayssièrè, 447, 449, 455
Vedalia (see *Novius*).
 Vegetation map of U. S., *391

- Veins, *54
 Velum, *228
 Venation, *54
 Ventral sinus, 110, *123
 Ventral tube, 62
 Ventriculus, *104
 Verhoeff, 438, 439, 440, 466
 Vernon, 459
 Vertex, 28
 Verworn, on phototropism, 308; 469
Vespa, nests of, *288; olfactory organ, *89;
 sensillum, *85; taste cups, *87; tongue,
 *86
Vespidæ, 287
 Vestal, 394, 475
 Viallanes, 435, 442, 448, 454
 Vinal, 450
 Vision, 95
 Vitelline membrane, *129
 Vitreous body, 95, *96
Volucella, mimicry by, *210; predaceous, 271
 Voss, F., 438
 Voss, H. v., 459

 Wagner, F. v., 459
 Wagner, J., 433
 Wagner, N., 450
 Wahl, 455
 Walker, E. M., 434, 435
 Walker, J. J., 456
 Walking, 51
 Walking-stick, *195
 Wallace, on mimicry, 203; 459, 460, 471
 Walsh, on losses through insects, 410; 424
 Walter, on mouth parts, 40; 436
 Walton, 428
 Warming, 474
 Warning coloration, 199
 Washburn, 425, 464
 Wasmann, on myrmecophilism, 297; 466,
 469, 470
 Wasps, 287
 Wasteneys, 470
 Wataſe, 444
 Water, 382; circulation of, 384; contents
 of, 383; depth, 386; pressure, 385; of
 soil, 350; temperature of, 385; vegeta-
 tion of, 386
 Watson, 474
 Wax, 413
 Wax, glands, 74; pincers, *228, 229
 Webb, 429

 Webster, F. M., on dispersal, 323, 335, 338,
 368; losses through insects, 410; 425,
 460, 462, 466, 471, 472
 Webster, R. L., 426
 Wedde, 436
 Weed, C. M., on birds in relation to insects,
 242, 243, 245; 426, 464
 Weinland, 444
 Weismann, on imaginal buds, 161; instinct,
 317; temperature experiments, 182;
 451, 453, 457, 458, 459, 460, 469
 Weiss, 156, 311, 475
 Welch, 456
 Welles, 447
 Wesché, 437
 Westwood, on *Brachinus*, 73; 431, 432
 Wheeler, on ants, 289, 297, 320; Malpighian
 tubes, 108; protective coloration, 178;
 trophallaxis, 301; tropisms, 302, 303,
 305, 306, 311; 439, 447, 448, 452, 453,
 467, 468, 469
 White, F. B., 455
 Whitman, 469
 Whymper, on distribution, 322; 472
 Wickham, 347
 Wielowiejski, von, 448, 450
 Wilcox, 451, 463
 Wilde, 446
 Wilder, 267
 Will, F., on taste, 85; 444
 Will, L., 450, 452
 Williams, C. B., 434
 Williams, T., 449, 455
 Wilson, 453
 Wilt, cucurbit, 219
 Wind, distribution by, 323, 368
 Wings, 53; folding of, 56, *57; modifications
 of, 53; muscles of, *59; venation, *54;
 vibration, 57, *58, 91
 Wistinghausen, von, 449
 Witlaczil, 440, 447, 452, 454
 Wodsedalek, 377
 Wollaston, on beetles of Madeira Islands,
 326
 Woodward, 453
 Woodworth, 425, 438
 Worker, ant, 289; bee, *282, 286; termite,
 277, *278; wasp, 288

 Xanthophyll, as a pigment, 176, 193
Xenoncura, *342
Xiphidium, stridulation of, 92

- Yapp, 369
Yaws, 269
Yellow fever, 252
Yolk, *129, *130
Yothers, 361, 377
Young, R. T., 461
Yuasa, 437
Yucca, pollination of, 222, *224
- Zailha*, 171
Zander, 440
Zeuzera pyrina, 419
Zittel, von, 433
Zones, life, *333
Zoraptera, 12, 22
Zorotypus, 12, 22
Zugmayer, 461









