ENTOMOLOGY

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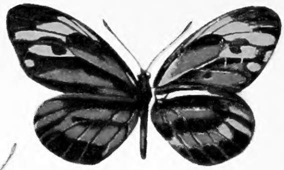
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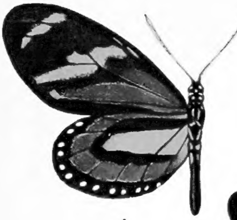
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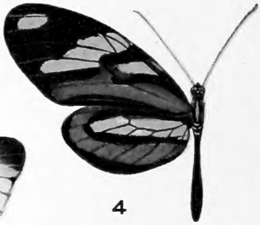
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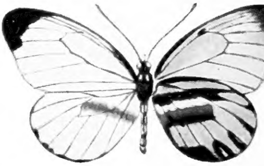
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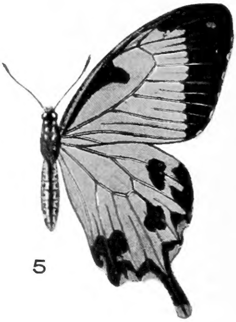
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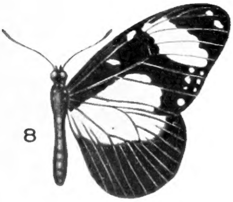
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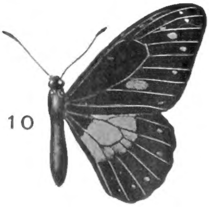
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DESCRIPTION OF FRONTISPIECE.

PROTECTIVE MIMICRY AMONG BUTTERFLIES.

FIG. 1.—*Heliconius eucrate,* one of the Heliconiinæ, which are naturally immune from the attacks of birds. From Brazil.

FIG. 2.—*Perhybris pyrrha,* female (Pierinæ), which is edible by birds but probably secures immunity by means of its resemblance to such species as No. 1 or No. 4. Brazil.

FIG. 3.—*Perhybris pyrrha,* male, to show the colorational basis from which the mimetic pattern of the female has been developed; under surface on right. Brazil.

FIG. 4.—*Mechanitis lysimnia* (Ithomiinæ), naturally immune, but nevertheless sharing a common color pattern with Heliconiinæ (No. 1). Brazil.

FIG. 5.—*Papilio merope,* male, having three forms of females (Nos. 7, 9 and 11), which mimic, respectively, three species of Danainæ (Nos. 6, 8 and 10). South Africa.

FIG. 6.—*Danais chrysippus,* immune, mimicked by No. 7. South Africa.

FIG. 7.—*Papilio merope,* female, which mimics No. 6. South Africa.

FIG. 8.—*Amauris niavius,* "model" of No. 9. South Africa.

FIG. 9.—*Papilio merope,* female, "mimic" of No. 8. South Africa.

FIG. 10.—*Amauris echeria,* "model" of No. 11. South Africa.

FIG. 11.—*Papilio merope,* female, "mimic" of No. 10. South Africa.

The figures are about one half the natural size. Compiled, largely from Trimen and Weismann.

ENTOMOLOGY

WITH SPECIAL REFERENCE TO

ITS BIOLOGICAL AND ECONOMIC ASPECTS

BY

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With Five Plates (One Colored)
and 300 Text-Figures

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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 Lake Forest University; Dr. S. H. Scudder of Cambridge, Mass.; 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. Henry C. McCook of Devon, Penn.; Dr. William Trelease, Director of the Missouri Botanical Garden; Dr. Henry Skinner, as editor of "Entomological News"; the editors of "The American Naturalist"; and W. Saville-Kent, of Wallington, England.

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.

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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 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 subœsophageal ganglion passes the œsophagus. These relations appear in Figs. 1 and 163.

FIG. 1.

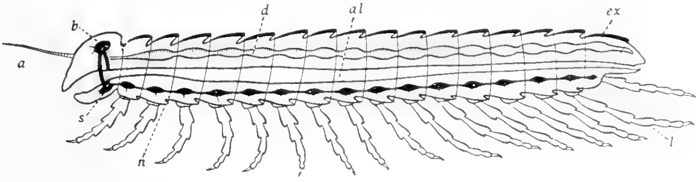
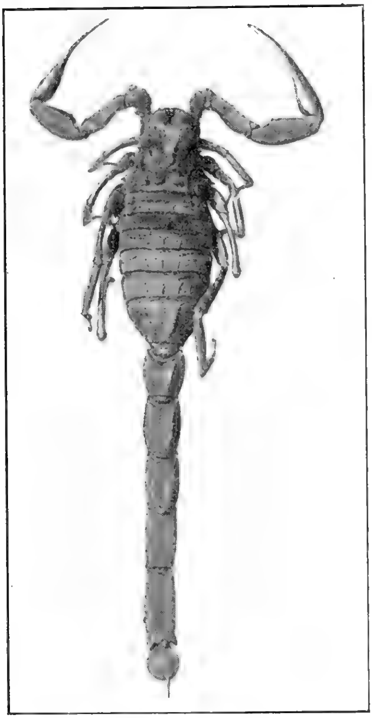


Diagram to express the fundamental structure of an arthropod. *a*, antenna; *al*, alimentary canal; *b*, brain; *d*, dorsal vessel; *ex*, exoskeleton; *l*, limb; *n*, nerve chain; *s*, subœsophageal ganglion.—After SCHMEIL.

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.

FIG. 2.



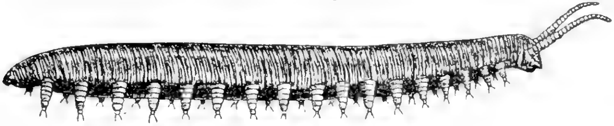
A scorpion, *Buthus*. Natural size.

Classes of Arthropoda.—Excepting the king-crab, trilobites and a few other aberrant forms of uncertain position, the members of the series, or phylum, Arthropoda fall into six distinct classes, namely, Crustacea, Arachnida, Malacopoda, Diplopoda, Chilopoda and Insecta. These classes 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. 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).

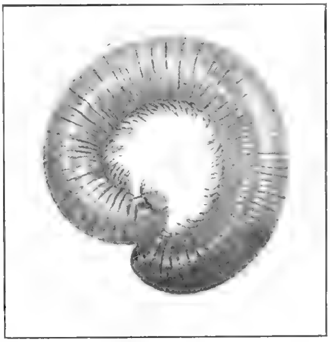
FIG. 3.



Peripatus capensis. Natural size.—After MOSELEY.

Malacopoda.—Terrestrial. Vermiform (worm-like), unsegmented externally. One pair of antennæ, a pair of jaws and a pair of oral slime papillæ. Legs numerous, paired, imperfectly segmented. Respiration by means of tubular tracheæ, the stigmata of which are scattered over the surface of the body. Numerous nephridia (excretory) are present and these are arranged segmentally in pairs. Two separate longitudinal nerve cords, connected by transverse commissures. Integument delicate. A single genus, *Peripatus* (Fig. 3), comprising many species.

FIG. 4.

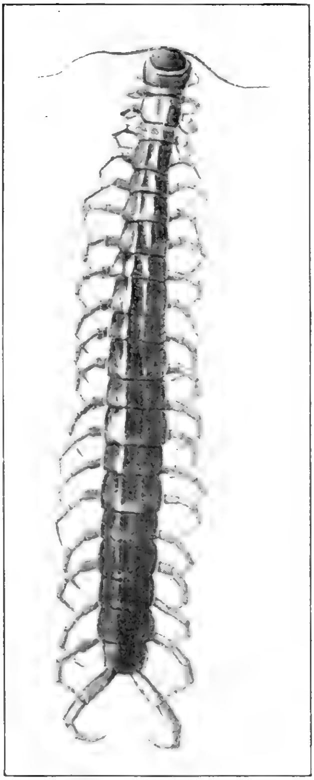


A diplopod, *Spirobolus marginatus.* Natural size.

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, 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).

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-jointed limbs, which are not inserted near the median line. Eyes simple and numerous (agglomerate in *Scutigera*), antennæ long. A pair of mandibles and two pairs of maxillæ. A single genital opening, on the preanal segment. Example, *Scolopendra* (Fig. 5).

Fig. 5.



A centipede, *Scolopendra heros*. About two thirds the maximum length.

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 three pairs of mouth parts—mandibles, maxillæ and labium—besides which a hypopharynx, or tongue, is present. 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 and male Coccidæ); the prothorax never bears wings. Abdomen typically with ten segments (seldom more) 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 lately insisted.

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

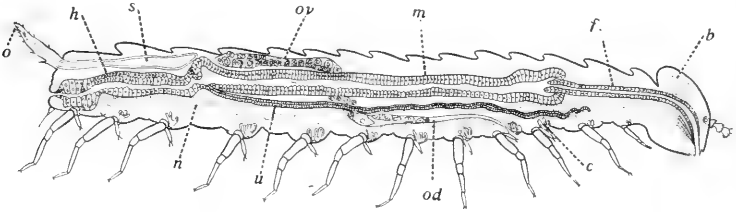
Malacopoda, as represented by *Peripatus*, are often spoken of as bridging the gulf that separates Insecta, Chilopoda and Diplopoda from Annelida. *Peripatus* indeed resembles the chætopod annelids in its segmentally arranged nephridia, dermo-muscular tube, coxal glands and soft integument, and resembles the three other classes in its tracheæ, dorsal vessel, lacunar circulation, mouth parts and salivary glands. These resemblances, however, are by no means close, 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.

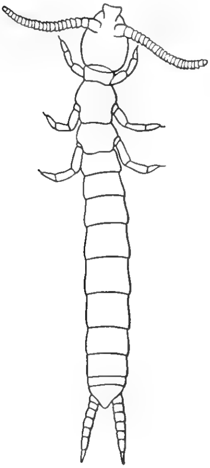
Scolopendrella, now placed either among Diplopoda or else in a class by itself, Symphyla, presents a remarkable combination of diplopodan and insectean characters. *Scolopendrella* (Fig. 6) and the thysanuran *Campodea* have the same kind of head, with its long moniliform antennæ, and agree in the general 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 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), has lately been discovered by Silvestri, who regards it as being in many respects the most primitive insect known, combining as it does characters of Symphyla, Diplopoda and *Campodea.*

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.

FIG. 7.



Anajapyx vesiculosus. Length, 2 mm.—After SILVESTRI.

The following diagram (Fig. 8) expresses very crudely one view as to the annelid origin of the chief classes of Arthropoda.

The naturalness of the phylum Arthropoda has been questioned by Kingsley and Packard. The latter author recently divided Arthropoda into five independent phyla, holding that

Fig. 8.

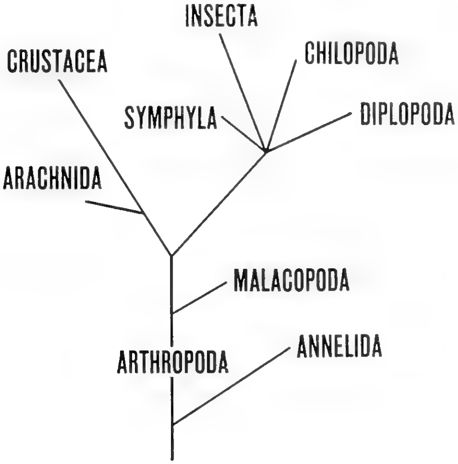


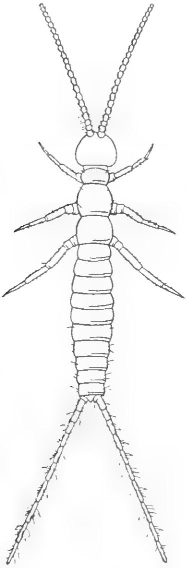
Diagram to indicate the origin of Arthropoda.

"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, has recently brought together no little evidence in favor of a revised form of the old Müllerian theory of crustacean origins. He traces all the classes of Arthropoda back to common arthropodan ancestors with a definite number of segments and distinctly crustacean in character; then traces 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.

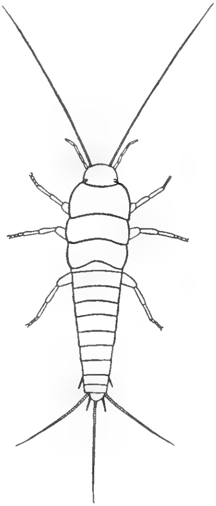
Orders of Insects.—Linnæus arranged insects in seven orders, namely, Coleoptera, Hemiptera, Lepidoptera, Neuroptera, Hymenoptera, Diptera and Aptera. The wingless insects termed Aptera were soon found to belong to diverse orders and the name has now become so ambiguous as to meet with little approbation.

FIG. 9.



Campodea. Length, 3 mm.

FIG. 10.



Lepisma. Length, 10 mm.

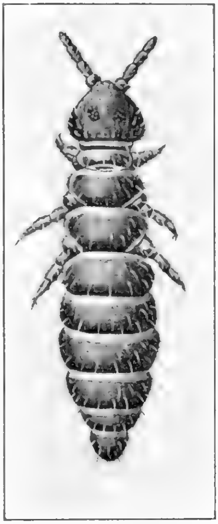
From the Linnæan group Hemiptera, the Orthoptera were set apart; the old order Neuroptera, a heterogeneous and unnatural group, has been split into several distinct orders, and many other changes in the classification have been necessary.

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, until our present system has been attained.

Owing to the incomplete condition of entomological knowledge, however, the best system as yet proposed is but tentative and more or less open to objection. The most competent and widely approved classifications are those of Brauer and Packard, and the system here adopted is essentially that of Brauer, with certain important modifications made by Packard.

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.

FIG. 11.



The snow flea, *Achorutes nivicola*. Length, 2 mm.

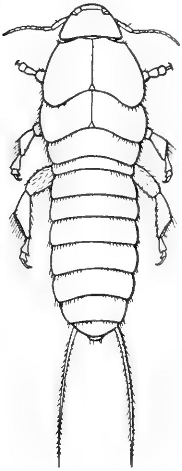
1. **Thysanura.**—No metamorphosis. Mouth parts mandibulate, either free (ectognathous) or enclosed in the head (entognathous). Wings invariably absent. Thoracic segments simple and similar. Abdominal segments ten, with two to eight pairs of rudimentary limbs and two or three anal cerci. Eyes aggregate, compound or absent. Antennæ multiarticulate. Integument thin. Examples, *Campodea* (Fig. 9), *Japyx*, *Machilis*, *Lepisma* (Fig. 10). Some one hundred and seventy-five species are known.

FIG. 12.

Sminthurus hortensis. Length, 1.2 mm.

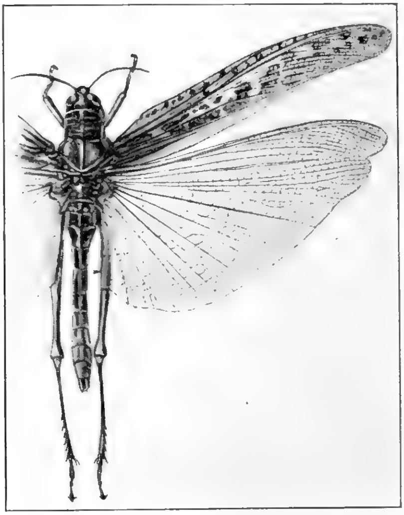
2. **Collembola.**—No metamorphosis. Mouth parts entognathous and typically mandibulate, with occasional secondary suctorial modifications. Wings invariably absent. Thoracic segments simple and similar or prothorax reduced. Body cylindrical or globular; abdomen with six segments. Ventral tube and furcula usually present, rarely rudimentary. Eyes ocelliform or absent. Antennæ of four segments in most genera; five or six in a few genera. Integument delicate. Examples, *Achorutes* (Fig. 11), *Sminthurus* (Fig. 12). About seven hundred species have been described.

FIG. 13.



Hemimerus talpoides. Length, 11.5 mm.—After HANSEN.

FIG. 14.



Schistocerca americana. **Slightly reduced.**

Under the term *Apterygota* (Apterygogenea, Brauer; Synaptera, Packard) the Thysanura and Collembola, as primitively wingless insects, are conveniently distinguished from all other insects, or *Pterygota* (Pterygogenea, Brauer).

3. **Orthoptera.**—Metamorphosis direct. Mouth parts mandibulate. Wings two pairs as a rule, though not infrequently reduced or absent; front wings coriaceous (tegmina); hind

pair membranous, ample, closely reticulate, plicate along the numerous radiating principal veins. Abdomen with ten or eleven segments. Eight families: Forficulidæ, Hemimeridæ (Fig. 13), Blattidæ, Mantidæ, Phasmidæ (Fig. 240), Acridiidæ (Fig. 14), Locustidæ, Gryllidæ. Over ten thousand species are known.

Some authors prefer to separate Forficulidæ from Orthoptera as a distinct order, for which Brauer and Packard preserve the old term *Dermaptera* of Leach, while Comstock uses Westwood's term *Euplexoptera*.

Hemimeridæ consist at present of two African species whose affinities appear to lie with Forficulidæ, but deserve further study.

4. **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. Integument usually thin. Nymphs thysanuriform. Two suborders.

Suborder Corrodentia.—Including three families, as follows:

Termitidæ. — Eyes facetted. Antennæ 9–31 jointed. Mouth parts prognathous or hypognathous.[1] Prothorax large. Wings elongate, alike, membranous, delicate, with indefinite reticulation and with a characteristic basal suture. Abdomen elongate, with ten segments and a pair of short, two-jointed anal cerci. Integument delicate. Social in habit. Example, *Termes* (Fig. 273). Over one hundred species are known.

Comstock places Termitidæ in an order by themselves, *Isoptera*.

Embiidæ. — Eyes facetted. Antennæ 15–32 jointed. Mouth parts prognathous. Thorax elongate, prothorax reduced. Wings (sometimes absent) elongate, membranous, delicate, with few and feebly developed longitudinal and cross veins. Abdomen elongate, with ten or possibly eleven seg-

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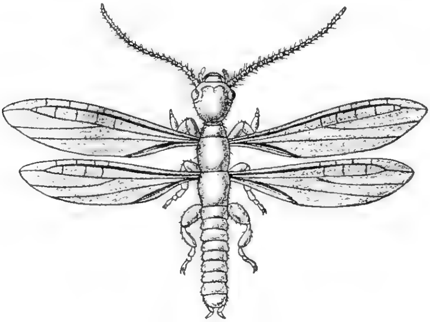
[1] *Prognathous,* directed forward; *hypognathous,* directed downward.

ments, and a pair of stout biarticulate cerci. Integument delicate. Not social in habit. Examples, *Embia, Oligotoma* (Fig. 15). Some twenty species, all from warm climates. These insects are most nearly related to Termitidæ and Psocidæ.

Fig. 15.



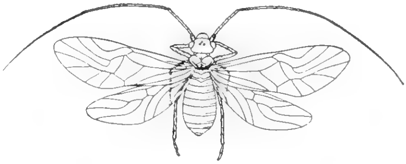
Oligotoma michaeli. Length, 10.5 mm.—After McLachlan.

Psocidæ. — Eyes facetted. Antennæ 13–50 jointed. Mouth parts hypognathous. Prothorax reduced. Wings present, rudimentary or absent; front pair the larger; veins few and irregular. Abdomen with nine or ten segments and no cerci. Integument delicate. Example, *Psocus* (Fig. 16). About two hundred species.

Comstock raises Psocidæ to the rank of an order, for which he employs, in a new sense, Brauer's term *Corrodentia.*

Suborder Mallophaga.—Wingless flattened insects, of parasitic habit. Head large. Eyes consisting of a few isolated ocelli or else absent. Antennæ 3–5 jointed. Mouth parts prognathous. Prothorax distinct; mesothorax often and metathorax usually transferred to the abdominal region. Abdominal segments eight to ten in number; no cerci. Parasitic upon birds and a few mammals. Example, *Menopon* (Fig. 17). More than fifteen hundred species have been described.

Fig. 16.



Psocus venosus. Length, 5 mm.

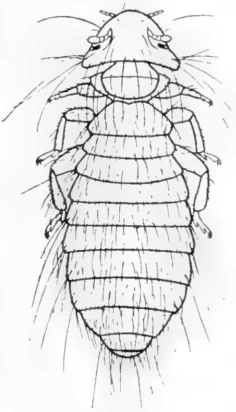
Packard's order *Platyptera* originally included Perlidæ. Brauer's order *Corrodentia* consisted of Termitidæ, Psocidæ and Mallophaga; Perlidæ being set apart as an order (*Plecop-*

tera) and Embiidæ being transferred doubtfully to Orthoptera.

Enderlein's recent and thorough studies confirm the view that Termitidæ, Embiidæ, Psocidæ and Mallophaga constitute a single order.

5. **Plecoptera.** — Metamorphosis direct. Antennæ long, multiarticulate. Mouth parts mandibulate. Prothorax large. Wings two pairs, membranous, coarsely and complexly reticulate; equal or else hind wings larger and with an ample plicate anal area. Abdomen with ten segments and usually a pair of long multiarticulate cerci. Nymphs thysanuriform, aquatic; adults unique in having tracheal gills. Example, *Pteronarcys* (Fig. 18). A single family, Perlidæ, comprising two hundred species.

Fig. 17.



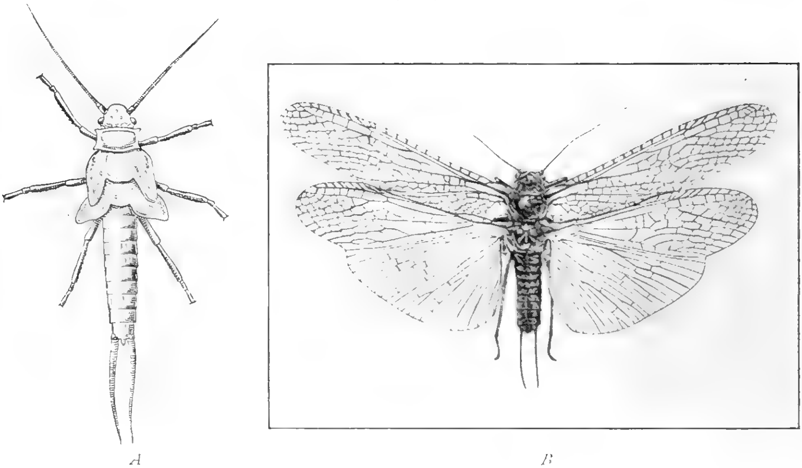
A chicken louse, *Menopon*. Length, 2 mm.

6. **Ephemerida.** — 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 cerci. Integument delicate. Nymphs thysanuriform, aquatic. Example, *Hexagenia* (Fig. 19). Three hundred species.

7. **Odonata.**—Metamorphosis direct. Antennæ inconspicuous, bristle-shaped. Mouth parts mandibulate. Prothorax small. Wings four, elongate, subequal, similar, membranous, minutely reticulate, with a costal joint, or nodus. Abdomen slender, with ten segments. Nymphs thysanuriform, aquatic. Example, *Libellula* (Fig. 20). About two thousand species have been described.

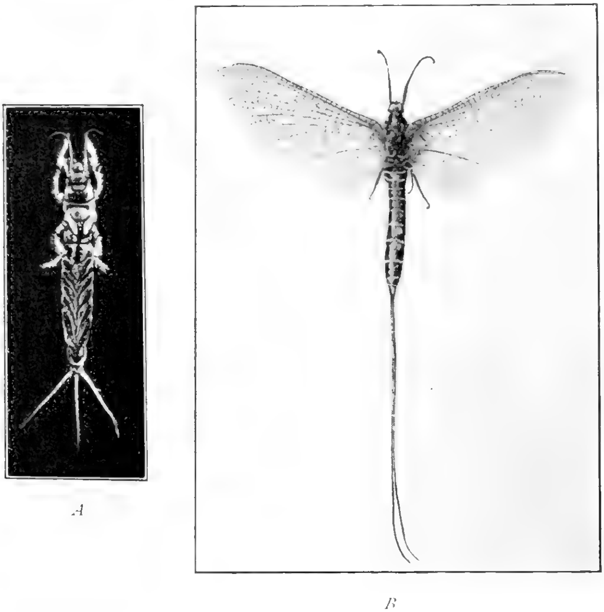
8. **Thysanoptera (Physopoda).** — Metamorphosis direct.

FIG. 18.



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

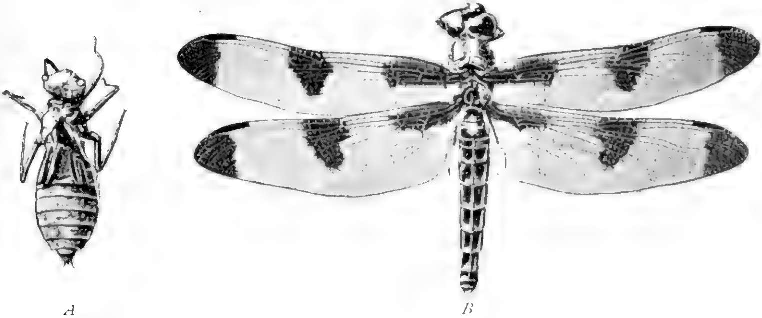
FIG. 19.



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

but including a subpupa stage. Mouth parts suctorial. Prothorax long. Tarsus terminating in a bladder-like organ.

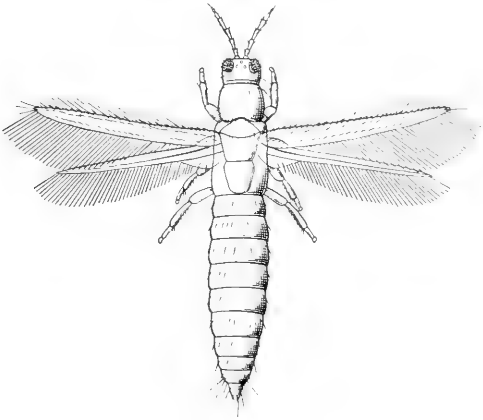
FIG. 20.



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

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 insects. Example, *Euthrips* (Fig. 21). About one hundred and fifty species have been described.

FIG. 21.

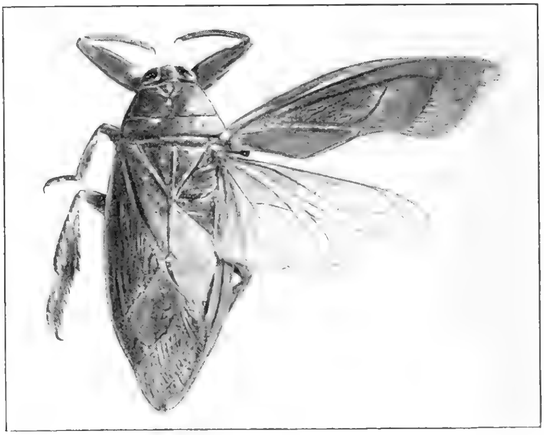


Euthrips tritici. Length, 1.2 mm.

9. **Hemiptera.** — Metamorphosis direct (excepting male Coccidæ). Antennæ usually few-jointed. Mouth parts suctorial. Prothorax usually large. Wings usually present, except in the parasitic forms. Eighteen thousand species. Three suborders:

Suborder Heteroptera.—Wings four, folded flat; front wings thickened basally, membranous apically (hemelytra), overlapping obliquely; hind wings membranous. Head not deflexed. Example, *Benacus* (Fig. 22). About twelve thousand species.

FIG. 22.



Benacus griseus. Slightly reduced.

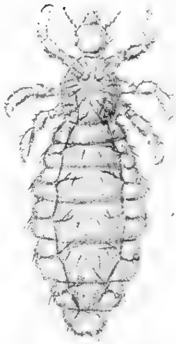
Suborder Homoptera.—Wings four, sloping roof-like, similar and membranous or front pair somewhat coriaceous throughout. Head deflexed. Example, *Cicada* (Fig. 206). Six thousand species.

Suborder Parasita. — Wingless. Eyes simple or none. Thoracic segments intimately united; tarsus with a single claw. Integument thin. Parasites upon mammals. Example, *Pediculus* (Fig. 23). Some fifty species are known.

10. **Neuroptera.**—Metamorphosis indirect. Antennæ con-

spicuous. Mouth parts mandibulate. Prothorax large. Wings almost always four, membranous, subequal or else hind pair smaller, complexly reticulate, not plicate. Larvæ thysanuriform or in some cases eruciform, and aquatic or terrestrial. Example, *Chrysopa* (Fig. 24). About six hundred species have been named.

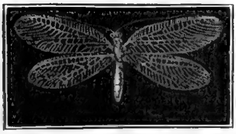
FIG. 23.



Head louse, *Pediculus capitis,* female. Length, 2 mm.

11. **Mecoptera.**—Metamorphosis indirect. Mouth parts mandibulate, at the end of a deflexed rostrum, or beak. Prothorax small. Wings four, elongate, membranous, naked, coarsely reticulate, or else rudimentary or absent. Larvæ eruciform, caterpillar-like, with numerous prolegs, carnivorous. Example, *Bittacus* (Fig. 25). A single family, Panorpidæ, comprising but few known species.

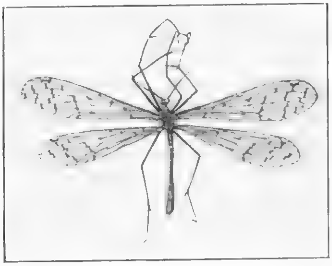
FIG. 24.



Chrysopa plorabunda. Slightly reduced.

12. **Trichoptera.**—Metamorphosis indirect. Antennæ filiform. Mouth parts of imago rudimentary or imperfectly suctorial; mandibles rudimentary or absent. Prothorax small. Wings four, membranous, hairy, veins moderate in number, cross veins few; hind pair almost always the larger, with plicate anal area. Larvæ suberuciform, aquatic, usually case-forming. Example, *Molanna* (Fig. 26). Between five and six hundred species are known.

FIG. 25.



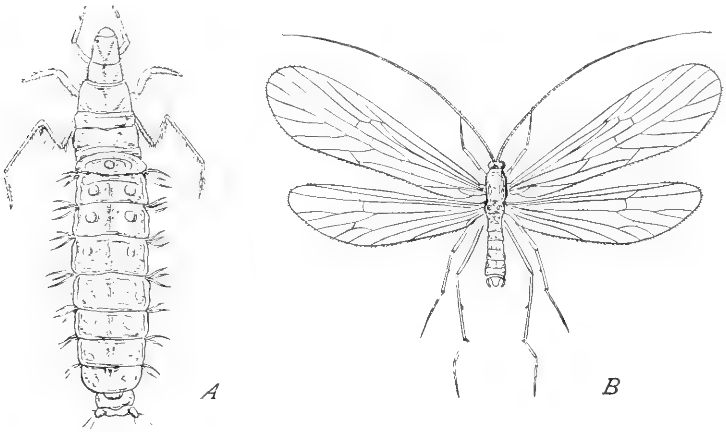
Bittacus strigosus. Natural size.

13. **Lepidoptera.**—Metamorphosis indirect. Mouth parts suctorial, mandibles absent or rudimentary (except in a few

generalized species). Prothorax small. Wings four, similar, membranous, clothed with scales, veins moderate in number, cross veins few. Larvæ eruciform (caterpillars), phytophagous (almost never carnivorous), mandibulate. 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. 236).

FIG. 26.



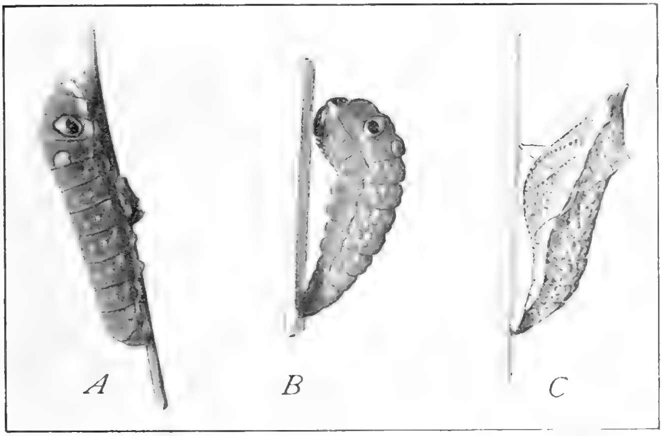
Molanna cinerea. *A*, larva; *B*, imago. × 4 diameters.—After FELT.

Suborder Rhopalocera.—Antennæ simple, terminating in a distinct club and without conspicuous lateral processes. Frenulum absent. Diurnal normally. Examples, *Papilio* (Fig. 27), *Anosia* (Fig. 243, *A*).

14. **Coleoptera.**—Metamorphosis indirect. Mouth parts mandibulate. Prothorax large, as a rule. Wings four; front pair horny (elytra), meeting in a straight line; hind pair membranous, often folded. Larvæ thysanuriform or eruciform. Example, *Hydrophilus* (Fig. 28). About fifteen thousand species.

15. **Diptera.**—Metamorphosis indirect. Mouth parts typically suctorial, but modified for piercing, lapping, rasping, etc. Prothorax small. 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 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. Example, *Tipula* (Fig. 29). About forty thousand described species.

FIG. 27.



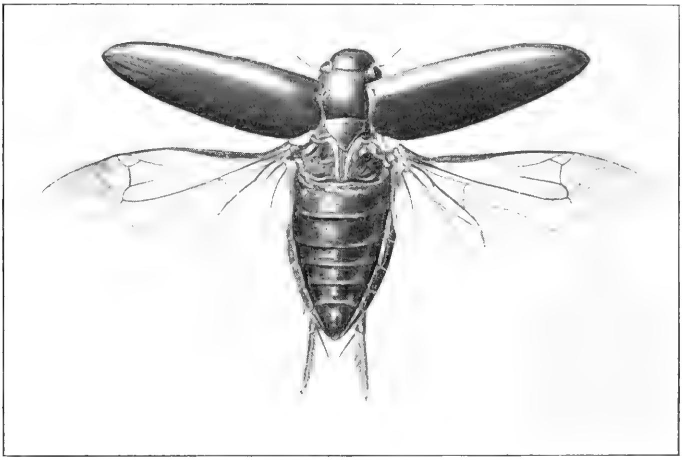
Papilio troilus. *A*, larva; *B*, larva suspended for pupation; *C*, chrysalis. Natural size.

16. **Siphonaptera (Aphaniptera).**—Metamorphosis indirect. Head small. Eyes simple or absent. Mouth parts suctorial. Body laterally compressed. Thoracic segments subequal. Wings absent or at most quite rudimentary. Larvæ with a head, mandibulate, apodous. Parasitic insects. Example, *Ctenocephalus* (Fig. 30). One hundred and fifty species.

17. **Hymenoptera.**—Metamorphosis indirect. Mouth parts at the same time mandibulate and suctorial. Prothorax usually small. Wings four, similar, membranous, transparent,

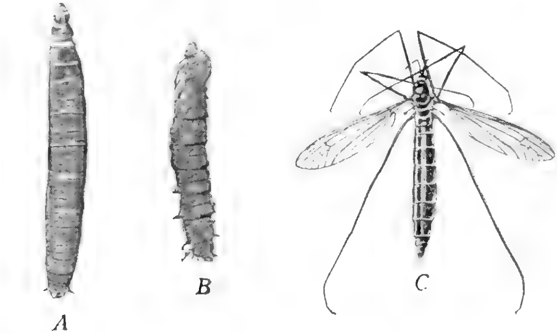
with a few irregular veins and cells; hind pair the smaller. Females with an ovipositor, modified for sawing, boring or stinging. Larvæ eruciform, mandibulate, caterpillar-like, with head and legs, or else maggot-like and apodous. Twenty-five or thirty thousand species. Two suborders.

FIG. 28.



Hydrophilus triangularis. Natural size.

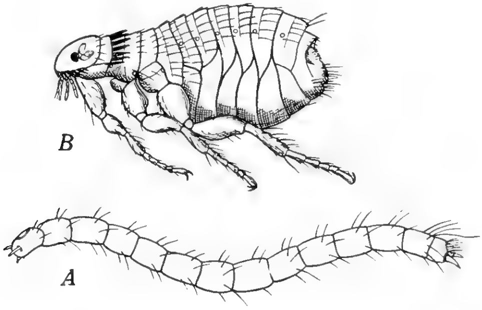
FIG. 29.



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

Suborder Terebrantia (Phytophaga, Sessiliventres).—Abdomen broadly attached to the thorax. Ovipositor modified for boring, sawing or cutting. Larvæ with complex mouth parts and frequently abdominal legs. Phytophagous. Example, *Tremex* (Fig. 31).

FIG. 30.

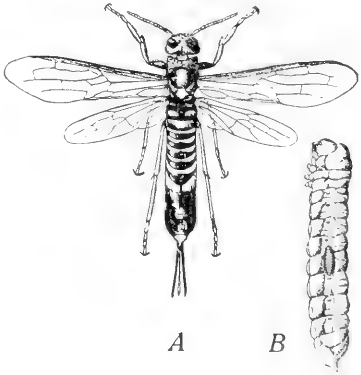


Cat and dog flea, *Ctenocephalus canis*. *A*, larva (after KÜNCKEL D'HERCULAIS); *B*, adult. Length of adult, 2 mm.

Suborder Aculeata (Heterophaga, Petiolata).—Abdomen petiolate or subpetiolate; first abdominal segment transferred to the thorax. Ovipositor often modified to form a sting. Larvæ apodous. Example, *Apis* (Fig. 277).

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.

FIG. 31.



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

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 among or near the diplopods. 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.

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, however, are not nearly so primitive as Thysanura, for the former 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.

Returning to 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, as is also that of *Japyx* to a young forficulid.

In short, as Hyatt and Arms express it, " 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."

Orthoptera probably arose directly from the original thysanuriform stem.

Platyptera, as a whole, are most nearly related to Orthoptera on the one hand and to Plecoptera on the other. Termitidæ have strong orthopteran affinities and Embiidæ have even been placed in the order Orthoptera, though the latter family is most nearly allied to Termitidæ and Psocidæ. These two are approached rather closely by Mallophaga and exhibit, by the way, some collembolan characters, as Enderlein has lately pointed out.

Plecoptera, which Packard placed in his group Platyptera, are better regarded as a distinct order with some orthopteran and many ephemerid and odonate affinities. The strong resemblance between nymphs of Plecoptera, Ephemerida and Odonata indicates community of origin.

Ephemerida and Odonata are well circumscribed orders, most nearly related to each other, but sharply separated, nevertheless, by differences in the wings, mouth parts and other organs. Ephemerida are almost unique among insects in having a pair of genital openings—a primitive condition.

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.

Hemiptera stand alone and give few hints of their ancestry. They are least unlike 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, but it is highly 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.

Metamorphosis offers, upon the whole, 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 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 Neuroptera and attains its maximum development in Diptera and Hymenoptera.

With Neuroptera the eruciform type of larva appears, as a derivative of the earlier thysanuriform type. The larva of *Mantispa*, as Packard has shown, actually passes, during its individual development, from the primary, thysanuriform stage to the secondary, eruciform condition.

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.

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) there is little doubt that Trichoptera and Lepidoptera originated from the same stock.

The origin of the coherent group Coleoptera is by no means clear, although thysanuriform larvæ occur frequently in this order. Packard suggests that both beetles and earwigs arose from some thysanuroid form or that the primitive coleopterous larva sprang from some metabolous neuropteroid form. In any linear arrangement of the orders the position of Coleoptera is largely arbitrary, and here the order is intruded between Lepidoptera and Diptera simply for want of a more satisfactory place.

Lepidoptera, Trichoptera and Mecoptera are probably branches from one stem. Lepidoptera, Diptera and Hymenoptera are regarded by Packard as having had a common origin from metabolic Neuroptera.

Among Diptera, such larvæ as those of Culicidæ are comparatively primitive, according to Packard, and larvæ of Muscidæ are secondary, or adaptive, forms.

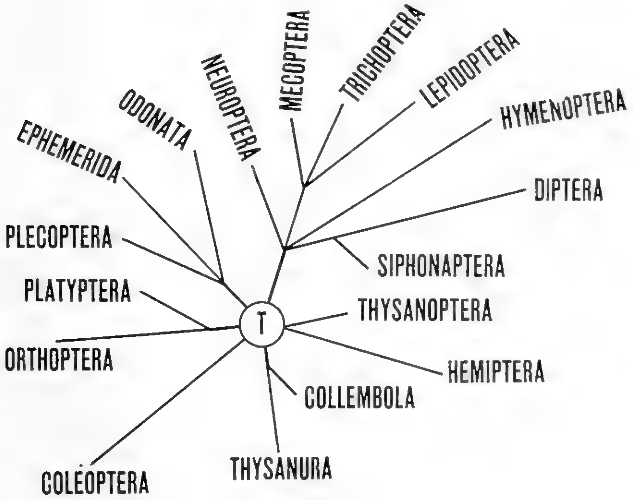
Siphonaptera used to be regarded as Diptera and are probably an offshoot from the dipteran stem.

The most primitive hymenopterous larvæ are those of the sawflies (Tenthredinidæ), judging from their resemblance to mecopterous and lepidopterous larvæ; and the simple, maggot-like form of the larvæ of ants, bees, wasps and parasitic Hymenoptera is due to secondary modifications in correlation with their sedentary mode of life.

In Diptera and Hymenoptera the phenomenon of metamorphosis attains its greatest complexity, as was remarked. Opinions differ as to which of these two orders is the more specialized. Hymenoptera are commonly called the "highest" insects, when their remarkable psychological development is taken into account; but from a purely structural standpoint it is hard to say which order is the more complex—indeed, the two orders are specialized in so many different ways that no precise comparison can be made between them.

The following diagram (Fig. 32) is a graphic summary of what has just been said in regard to the genealogy of the orders of insects. The positions of Hemiptera and Coleoptera are most open to criticism. The central group (*T*) is the

Fig. 32.



Genealogical diagram of the orders of insects.

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 300,000 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 *Acridium 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.

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.

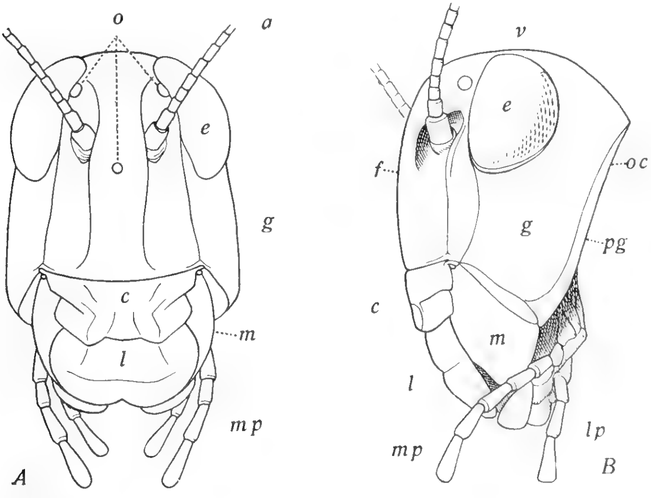
As a rule, one segment overlaps the one next behind; but the head, though not a single segment of course, never overlaps the prothorax in the typical manner, but is usually received into that segment. This condition, which may possibly have been brought about simply by the backward pull of the muscles 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. 20, *B*) and Diptera (Fig. 39). 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. 33) consists almost entirely of the *epicranium*,

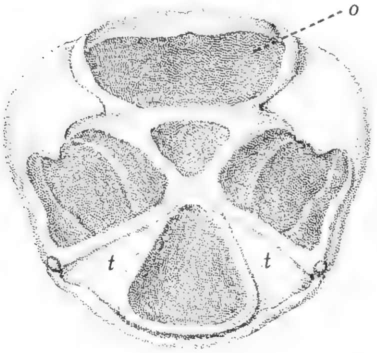
FIG. 33.



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.

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 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. Just above the front, and forming the sum-mit 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. The cheeks of an insect are known as the *genæ,* and *post-genæ* 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-genæ to form a distinct sclerite. The occiput surrounds the opening known as the *occipital foramen,* through which the œsophagus 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 considerable morphological importance.

Fig. 34.

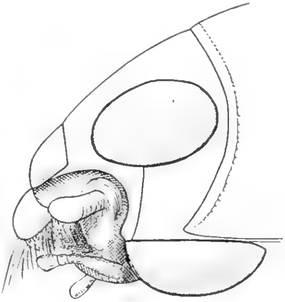


Skull of a grasshopper, *Dissosteira carolina.* *o,* occipital foramen; *t, t,* anterior arms of tentorium.

Tentorium.—In the head is a chitinous supporting structure known as the *tentorium.* This consists of a central plate from which diverge two pairs of arms extending to the skull (Fig. 34). The central plate 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 from the same ectodermal layer which produces the external cuticula; though authors are not agreed as to the details of the development.

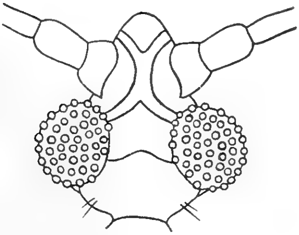
Eyes.—The eyes are of two kinds—*simple* and *compound.* The latter, or eyes proper, conspicuous on each side of the head, are of common occurrence except in the larvæ of most holometabolous insects, in some generalized forms (as Collembola) and in parasitic insects. The compound eyes (Fig. 40) are convex 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. 35) 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. 36) are commonly more or less hexagonal (Fig. 37), 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 diam-

FIG. 35.



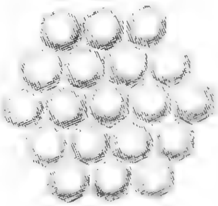
Head of a gyrinid beetle, *Dineutus,* to show divided eye.

FIG. 36.



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

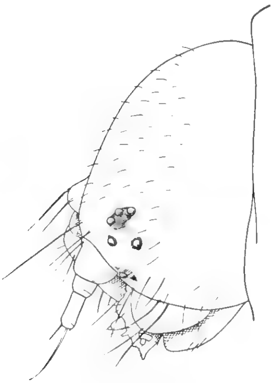
FIG. 37.



Facets of a compound eye of *Melanoplus.* Highly magnified.

eter 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.

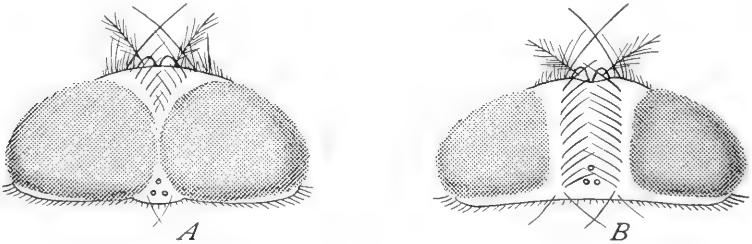
FIG. 38.



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

Ocelli.—The simple eyes, or *ocelli*, appear as small polished lenses, either lateral or dorsal in position. Lateral ocelli (Fig. 38) 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. 39) and Hymenoptera (Fig. 40) as well as many Orthoptera and Hemiptera. Few beetles have ocelli and almost no butterflies (*Lerema accius* with its one ocellus being the only exception known), though not a few moths have two ocelli.

FIG. 39.

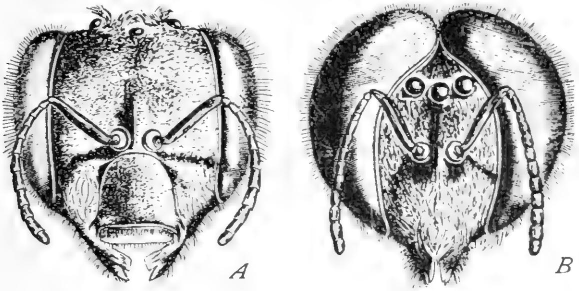


Ocelli and compound eyes of a fly, *Phormia regina*. *A*, male; *B*, female.

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. 39) and in Hymenoptera (Fig. 40) 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 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.

FIG. 40.

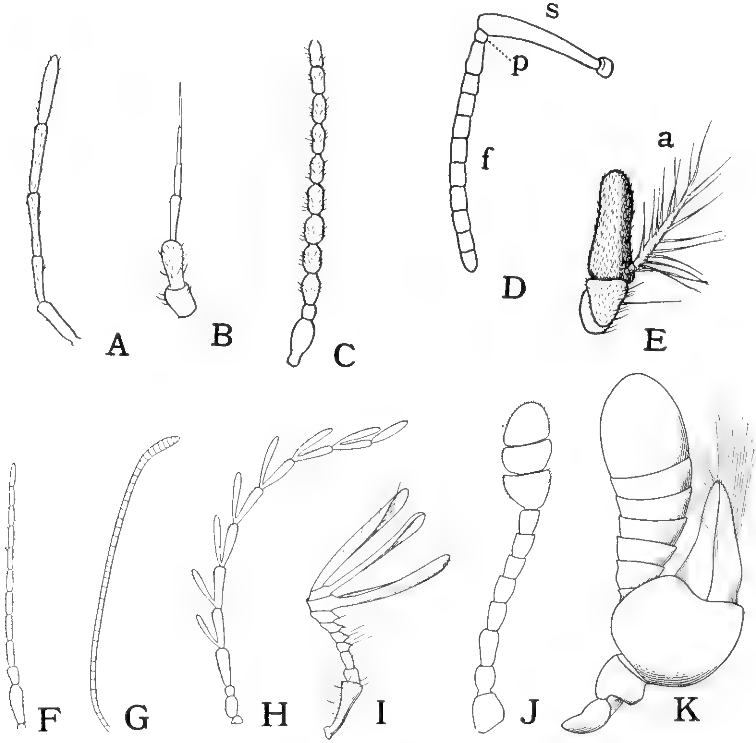


Ocelli and compound eyes of the honey bee, *Apis mellifera*. *A*, queen; *B*, drone.—After CHESHIRE.

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. 41–43.

FIG. 41.

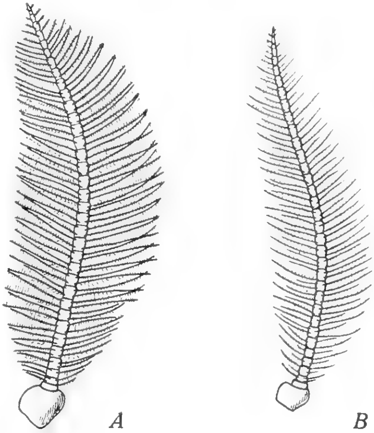


Various forms of antennæ. *A*, filiform, *Euschistus; B*, setaceous, *Plathemis; C*, moniliform, *Catogenus; D*, geniculate, *Bombus; f*, flagellum; *p*, pedicel; *s*, scape; *E*, irregular, *Phormia; a*, arista; *F*, setaceous, *Galerita; G*, clavate, *Anosia; H*, pectinate, male *Ptilodactyla; I*,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

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 *Meloe* 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 feathered than those of the female, and differ also in having more segments (Fig. 42). 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.

FIG. 42.



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

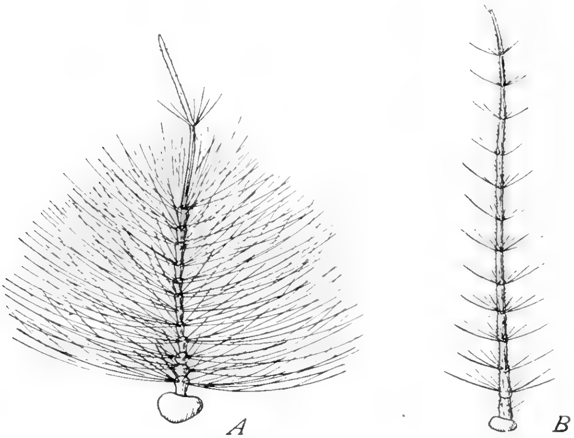
The plumose antennæ of the male mosquito (Fig. 43) are highly developed organs of hearing, and are used to locate the female; they have delicate fibrillæ of various lengths, some of which are thrown into sympathetic vibration by the note of the female (p. 107).

Meloe 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; though a beginning in the subject has been made by Schenk, whose results will be referred to in connection with the sense organs.

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 Ephemerida and Trichoptera have but rudimentary mouth parts.

Fig. 43.



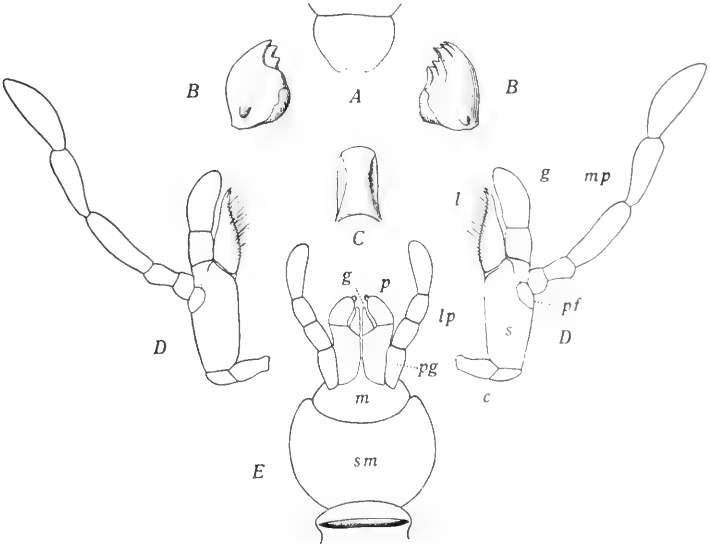
Antennæ of mosquito, *Culex pipiens*. *A*, male; *B*, female.

The mandibulate orders are Thysanura, Collembola (primarily), Orthoptera, Platyptera, Plecoptera, Ephemerida (rudimentarily in adult), Odonata, Neuroptera, Mecoptera and Coleoptera.

The mouth parts of an insect consist typically of *labrum, mandibles, maxillæ, labium* and *hypopharynx* (Fig. 44), though these organs differ greatly in different orders of insects. The mandibulate, or primary type, 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 mandibles 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).

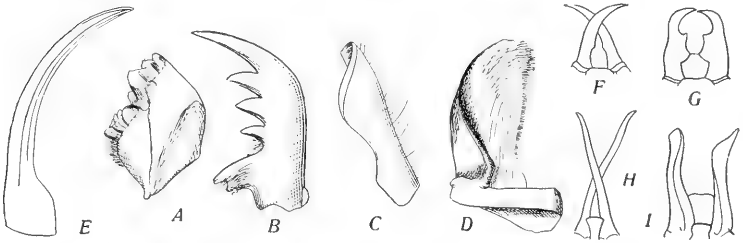
FIG. 44.



Mouth parts of a cockroach, *Ischnoptera 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.

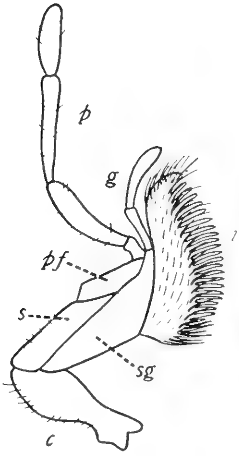
The *mandibles,* or jaws proper, move in a transverse plane, being closed by a pair of strong adductor muscles and opened by a pair of weaker abductors. The mandible is almost always a single solid piece. In herbivorous insects (Fig. 45, *A*) it is compact, bluntly toothed, and often bears a molar, or 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. 261), 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. 45, *E*) has a longitudinal groove against which the maxilla fits to form a canal, through which the blood of plant lice is sucked into the œsophagus. In termites (*F–I*) the mandibles assume curious and often inexplicable forms.

Fig. 45.



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

Fig. 46.



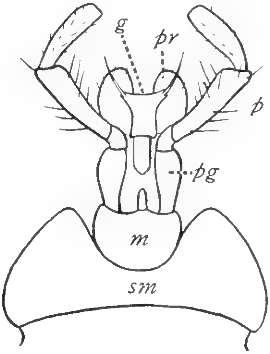
Maxilla of *Harpalus caliginosus*, ventral aspect. *c*, cardo; *g*, galea; *l*, lacinia; *p*, palpus; *pf*, palpifer; *s*, stipes; *sg*, subgalea.

Next in order are the *maxillæ*, or under jaws, which are less powerful than the mandibles and more complex, consisting as they do of several sclerites (Figs. 44, 46). 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-jointed 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.

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. 44):

LABIUM = MAXILLÆ
palpus = *palpus*
paraglossa = *galea*
glossa = *lacinia*
palpiger = *palpifer*
mentum = *stipites*
submentum with *gula* = *cardines*

FIG. 47.



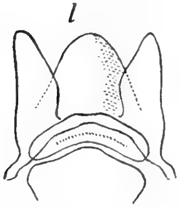
Labium of *Harpalus caliginosus,* ventral aspect. *g,* united glossæ, termed *the glossa*; *m,* mentum; *p,* palpus; *pg,* palpiger; *pr,* paraglossa; *sm,* submentum. The median portion of the labium beyond the mentum is termed the *ligula*

In most mandibulate orders the glossæ unite to form a single median organ, as in *Harpalus* (Fig. 47, *g*). The labium forms the floor of the pharynx and assists in carrying food to the mandibles and maxillæ.

The use of the term "second maxillæ" for the labium of an insect is open to objection, as it implies an equivalence with the second maxillæ of Crustacea—which is by no means established.

The tongue, or *hypopharynx,* is a median fleshy organ (Fig. 44) 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 dorso-lateral lobes, termed *superlinguæ* by the author. Superlinguæ occur in a few other mandibulate orders (Orthoptera, Fig. 48; Ephemerida, Fig. 49), but have not yet been recognized in the more specialized orders of insects.

Fig. 48.

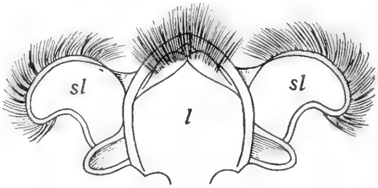


Hypopharynx of *Hemimerus talpoides.* *l,* lingua; *s,* superlingua.—After Hansen.

Suctorial Types.—Owing to their greater complexity, suctorial mouth parts are not nearly so well understood as the mandibulate organs, but enough has been learned to enable us to homologize the two types, even though morphologists still disagree in regard to minor details of interpretation.

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

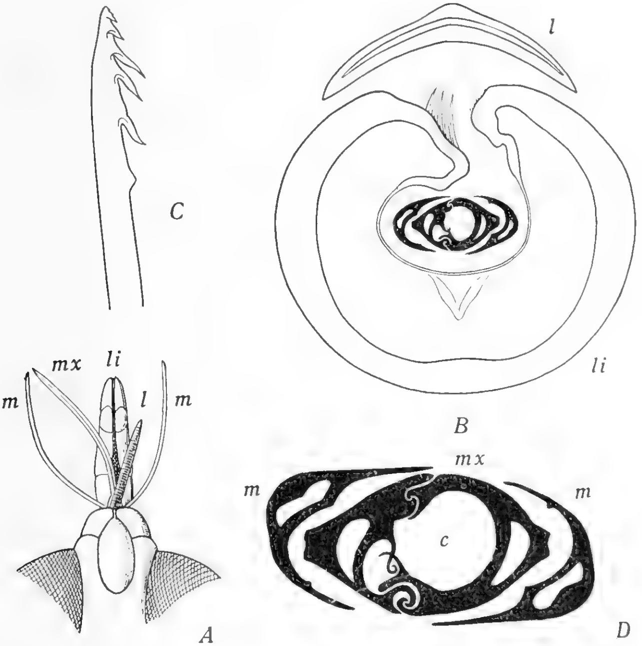
Fig. 49.



Hypopharynx of an ephemerid, *Heptagenia.* *l,* lingua; *sl, sl,* superlinguæ.—After Vayssière.

Hemiptera. — The beak, or *rostrum,* in Hemiptera consists (Fig. 50) of a conspicuous, one- to four-jointed labium, which ensheathes hair-like mandibles and maxillæ and is covered above at its base by a short 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. 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.

FIG. 50.

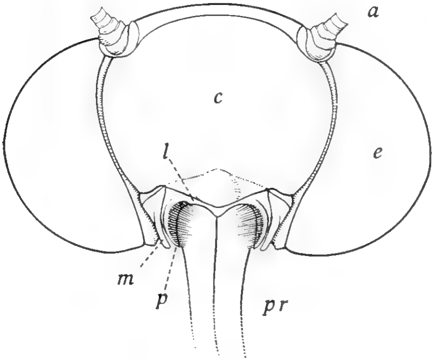


Mouth parts of a hemipteron, *Benacus griseus*. *A*, dorsal aspect; *B*, transverse section; *C*, extremity of mandible; *D*, transverse section of mandibles and maxillæ; *c*, canal; *l*, labrum; *li*, labium; *m*, mandible; *mx*, maxillæ.

Lepidoptera.—In Lepidoptera, excepting *Eriocephala*, the labrum is reduced (Fig. 51) and the mandibles are either rudimentary or absent (Rhopalocera). The two maxillæ are represented by their galeæ, which form a conspicuous proboscis; the grooved inner faces of the galeæ (or laciniæ, according to Kellogg) form the sucking tube, which opens into the œsophagus. The labium is reduced, though the labial palpi (Fig. 52) 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. 51) and he terms them *pilifers*.

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.

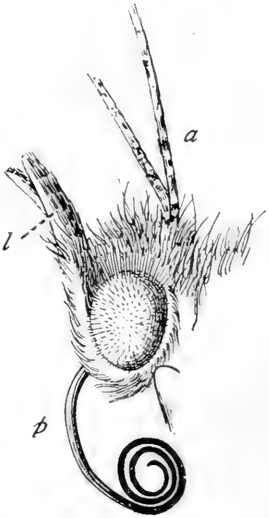
Fig. 51.



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

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.

Fig. 52.



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

Diptera.—In the female mosquito the mouth parts (Fig. 53) are long and slender. As Dimmock has found, the labrum and epipharynx combine[1] to form a sucking tube; the mandibles and maxillæ are delicate, linear, piercing organs, the latter being barbed distally; maxillary palpi are pres-

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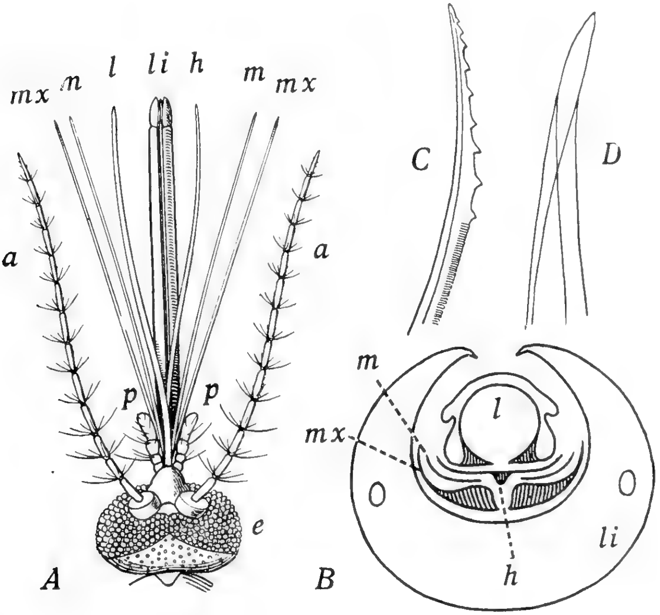
[1] Kulagin, however, describes them as remaining separate.

ent; 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. 53.



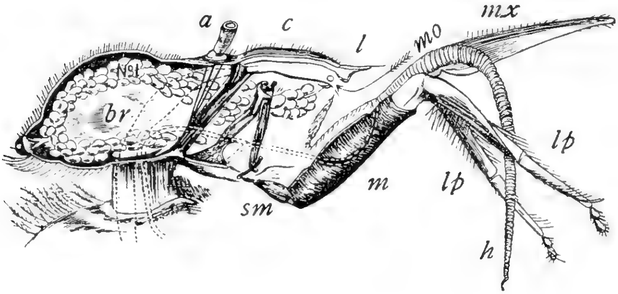
Mouth parts of female mosquito, *Culex pipiens.* *A,* dorsal aspect; *B,* transverse section; *C,* extremity of maxilla; *D,* extremity of labrum-epipharynx; *a,* antenna; *e,* compound eye; *h,* hypopharynx; *l,* labrum-epipharynx; *li,* labium; *m,* mandible; *mx,* maxilla; *p,* maxillary palpus.—*B,* 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 that the mandibles are aborted and the maxillæ slightly developed, but with long palpi, while the hypopharynx coalesces with the labium, and there is no œsophageal bulb.

Hymenoptera.—In the honey bee, which will serve as a type, the labrum (Fig. 54) is simple; the mandibles are well developed instruments for cutting and other purposes and the remaining mouth parts form a highly complex suctorial apparatus, as follows. The tongue is a long flexible organ, terminating in a "spoon" (Fig. 127) and clothed with hairs of various kinds, for gathering 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 "central 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 or to Packard's Text-Book.

Fig. 54.

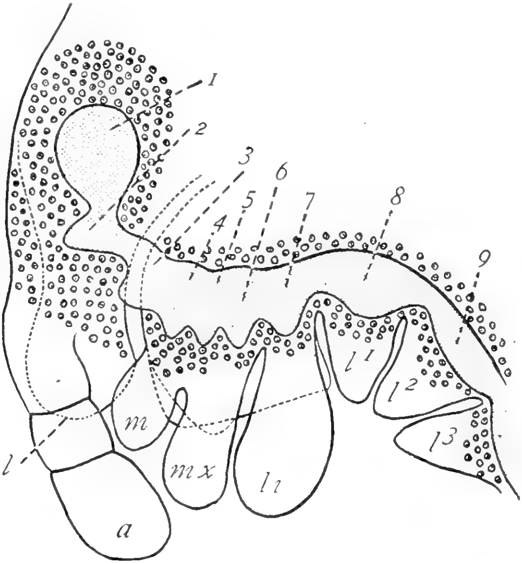


Mouth parts of the honey bee, *Apis mellifera*. *a*, base of antenna; *br*, brain; *c*, clypeus; *h*, hypopharynx; *l*, labrum; *lp*, labial palpus; *m*, mentum; *mo*, mouth; *mx*, maxilla; *sm*, submentum.—After Cheshire.

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 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. 194), 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. 55): 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. 55) exists. 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 probably Thysanura, though it has not yet been discovered in the more specialized insects.

FIG. 55.



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; l^1, l^2, l^3, thoracic legs; *m*, mandible; *mx*, maxilla. —After FOLSOM.

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 (Stylopidæ) 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. 56.

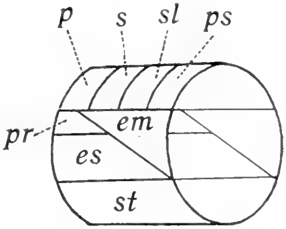
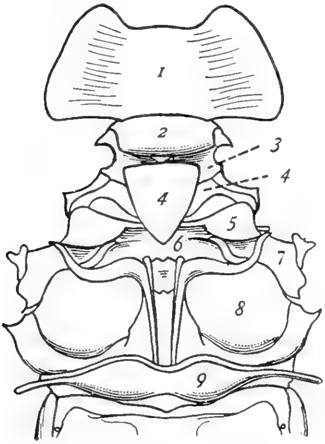


Diagram of the principal sclerites of a thoracic segment. *em*, epimeron; *es*, episternum; *p*, præscutum; *pr*, parapteron; *ps*, postscutellum; *s*, scutum; *sl*, scutellum; *st*, sternum.—After COMSTOCK.

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. 56. Thus the tergum of a wing-bearing segment is regarded as being composed of four sclerites (*tergites*, Fig. 57), 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. Each pleuron consists chiefly of two sclerites (*pleurites*, Fig. 58), 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.

Fig. 57.



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.

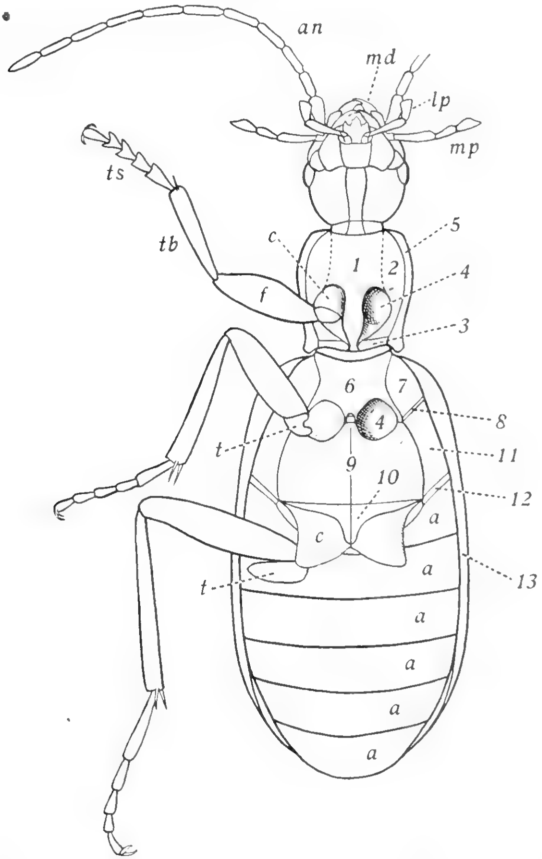
The sternum, though usually a single plate, is in some instances divided into halves, as in the cockroach, or even into five sclerites (Forficulidæ).

To these should be added the *patagia* of Lepidoptera—a pair of erectile appendages of the prothorax; and the *paraptera*, or *tegulæ*, of Lepidoptera and Hymenoptera—a pair of small sclerites at the bases of the front wings.

Each thoracic segment bears a pair of spiracles in the embryo and in some adults as well (*Campodea*, Heteroptera), but in most imagines there are only two pairs of thoracic spiracles, the suppressed pair being usually 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

Fig. 58.

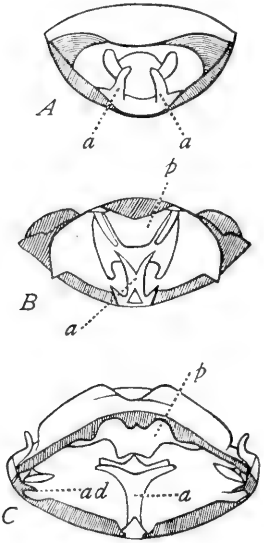


Ventral aspect of a carabid beetle, *Galerita janus*. *1*, prosternum; *2*, proepisternum, *3*, proepimeron; *4*, coxal cavity; *5*, inflexed side of pronotum; *6*, mesosternum; *7*, mesoepisternum; *8*, mesoepimeron; *9*, metasternum; *10*, antecoxal piece; *11*, metaepisternum; *12*, metaepimeron; *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.

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.

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) *apophyses,* ventral. The phragmas (Fig. 59) 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 apophyses 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. 59.



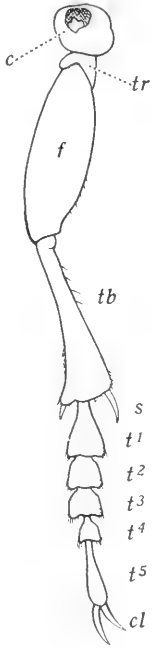
Transverse sections of the thoracic segments of a beetle, *Goliathus*, to show the endoskeletal processes. *A*, prothorax; *B*, mesothorax; *C*, metathorax; *a*, *a*, apophyses; *ad*, apodeme; *p*, phragma.—After KOLBE.

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 apophyses 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 and consists of five segments (Fig. 60), in the following order: *coxa, trochanter, femur, tibia, tarsus.* The coxa, or basal segment, often has a posterior sclerite, the *trochantine.*[1] 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.*

FIG. 60.



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

Adaptations of Legs.—The legs exhibit a great variety of adaptive modifications. A walking or running insect, as a carabid or cicindelid beetle (Fig. 62, *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

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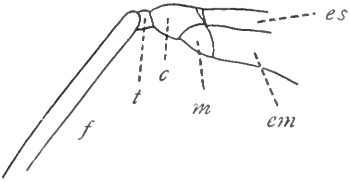
[1] But on account of the ambiguous use of this last term, the name *meron* (Fig. 61), proposed by Walton, is to be preferred.

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. 228), 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. 62, *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 rudimentary 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. 263, *D*), which is described, with other interesting modifications of the legs, on page 271.

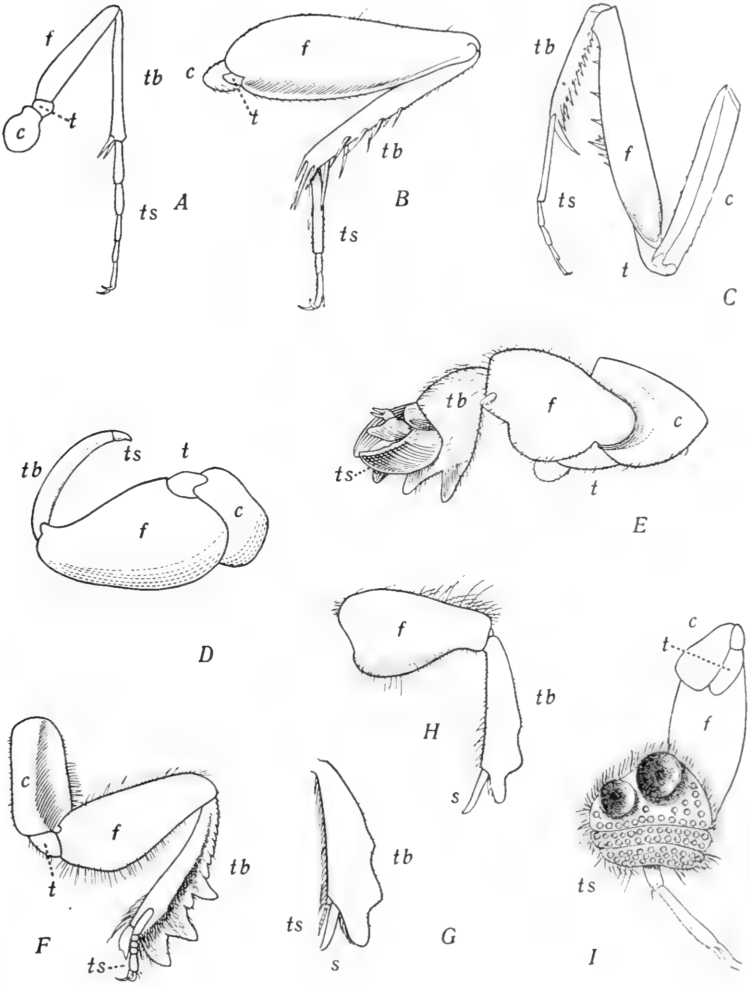
FIG. 61.



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

Indeed, the legs serve many such minor purposes in addition to locomotion. They are generally used to hold the female during coition, and in several genera of Dytiscidæ (*Dytiscus*, *Cybister*) the male (Fig. 62, *I*) has tarsal disks and cupules, chiefly on the front tarsi, for this purpose. Among

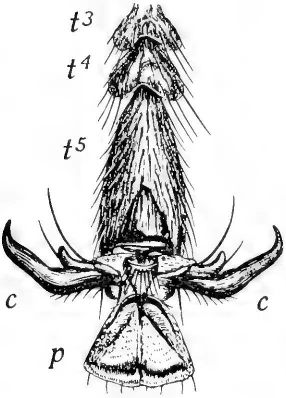
FIG. 62.



Adaptive modifications of the legs. *A, Cicindela sexguttata; B, Nemobius vittatus,* hind leg; *C, Stagmomantis carolina,* left fore leg; *D, Pelocoris femorata,* right fore leg; *E, Gryllotalpa borealis,* left fore leg; *F, Canthon 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.

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.

Fig. 63.

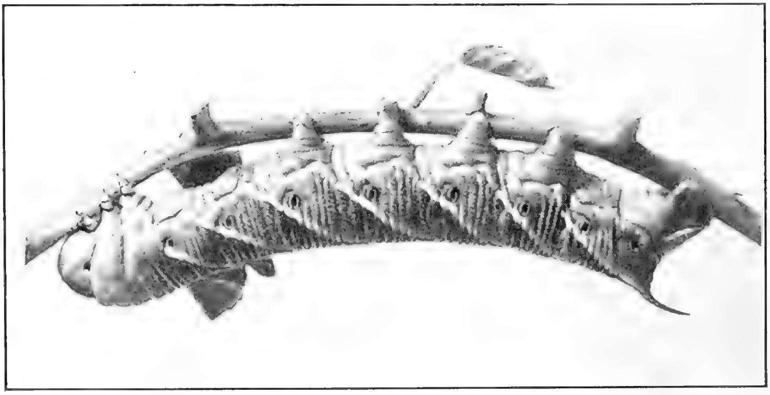


Foot of honey bee, *Apis mellifera.* *c, c,* claws; *p,* pulvillus; t^3–t^5, tarsal segments.—After Cheshire.

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. 63); 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 Locustidæ, Gryllidæ and some ants. Finally, the legs may be used to produce sound,

Fig. 64.

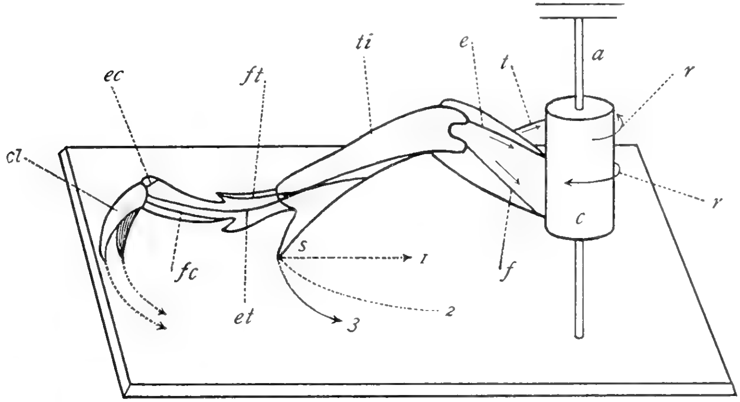


Caterpillar of *Phlegethontius sexta.* Natural size.

as in *Stenobothrus* and such other Acridiidæ 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 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, *Phytonomus*) also have abdominal legs, which are incompletely developed, however, as compared with those of Lepidoptera.

FIG. 65.



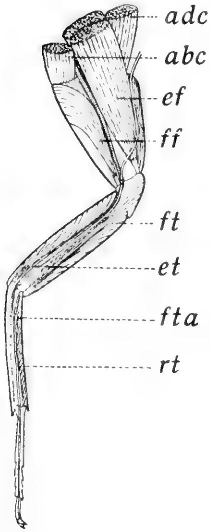
Mechanics of an insect's leg. *a*, axis of coxa; *c*, coxa; *cl*, claw; *e*, extensor of tibia; *ec*, extensor of claw; *et*, extensor of tarsus; *f*, flexor of tibia; *fc*, flexor of claw; *ft*, flexor of tarsus; *r*, *r*, rotators of coxa; *s*, spur; *t*, trochanter muscle (elevator of femur); *ti*, tibia.—After GRABER.

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, nearly 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 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 means of the contraction of the tibial flexors; the hind leg, on the contrary, pushes the body, by the shortening of the tibial extensors, against the resistance afforded by the tibial spurs; the middle leg acts much like the hind one, but helps mainly to steady the body. Different species show different peculiarities of gait. In its analysis, the walking of an insect is rather intricate, as Graber and Marey have shown.

FIG. 66.



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

The mode of action of the principal leg muscles may be gathered from Fig. 65. Here the flexion of the tibia would cause the tibial spur (*s*) to describe the line *s 1*; and the backward movement of the leg due to the upper coxal rotator *r* would cause the spur to follow the arc *s 3*. As the resultant of both these movements, the path actually described by the tibial spur is *s 2*; then, as the leg moves forward, the curve is continued into a loop.

Caterpillars use their legs successively in pairs, and when the pairs of legs are few and widely separated, as in Geometridæ, a curious looping gait results.

The leg muscles of a cockroach are shown in Fig. 66.

Leaping.—The hind legs, inserted nearest the center of gravity, are the ones employed in leaping, and they act together. A grasshopper prepares to jump by bending the femur back against the tibia; to make the jump, the tibia is jerked back against the ground, into which the tibial spurs are driven, and the straightening of the leg by means of the powerful extensors throws the insect into the air. At the distal end of the femur are two lobes, one on each side of the tibia, which prevent wobbling movements of the tibia.

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 less than three 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 Stylopidæ 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 recently 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.

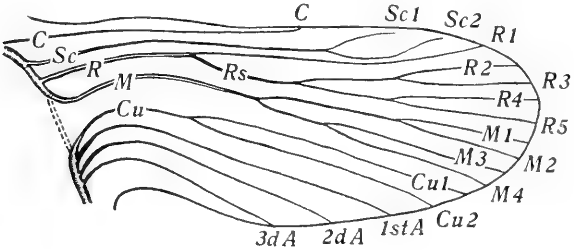
Modifications of Wings.—Being commonly more or less triangular, a wing presents three margins: front (*costal*), outer (*apical*) and inner (*anal*). Various modifications occur in the front wings, which are in many orders more useful for protection than for flight. Thus, in Orthoptera, they are leathery, 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 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, engage a membranous loop on the fore wing.

Venation, or Neuration.—A wing is divided by its *veins,* or *nervures,* into spaces, or *cells.* The distribution of the veins is of great systematic importance but, unfortunately, the homologies of the veins in the different orders of insects have not been fixed, until recently, so that no little confusion has existed upon the subject. For example, the term *discal cell,* used in descriptions of Lepidoptera, Diptera, Trichoptera and Psocidæ, has in no two of these groups been 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. 67) 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. 67–71).

FIG. 67.



Hypothetical type of venation. *A*, anal vein; *C*, costa; *Cu*, cubitus; *M*, media; *R*, radius; *Sc*, subcosta.—Figs. 67–71 after COMSTOCK and NEEDHAM.

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. 67. 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.

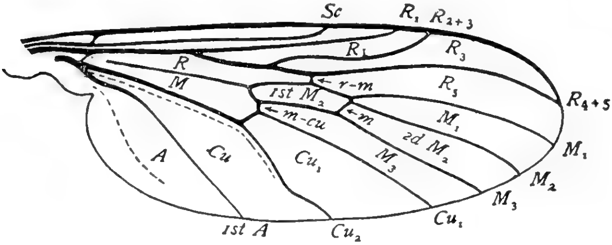
The cubitus (*Cu*) has two branches.

The anal veins (*A*) are typically three, of which the first is generally 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 of the Trichoptera.

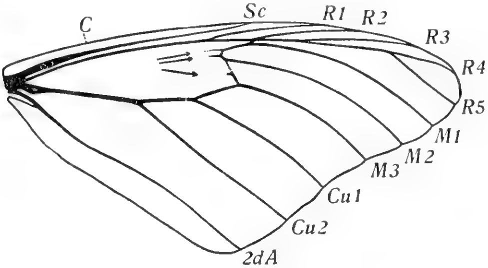
Starting from the primitive type, specialization has occurred in two ways: by *reduction* and by *addition*. Reduction occurs either by the *atrophy* of veins or by the *coalescence* of two or more adjacent veins. Atrophy explains the lack of all but one anal vein in *Rhyphus* (Fig. 68) and other Diptera, and the absence of the base of the media in *Anosia* (Fig. 69) and many other Lepidoptera; in the pupa of *Anosia*, the media may be found complete. Coalescence "takes place 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 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.

Fig. 68.



Wing of a fly, *Rhyphus*. Lettering as before.

Fig. 69.

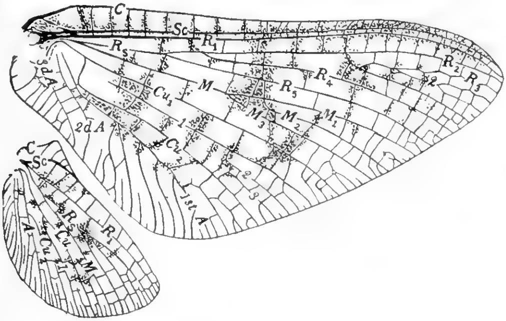


Wing of a butterfly, *Anosia*. Lettering as before.

Specialization by addition occurs by a multiplication of the branches of the principal veins.

Comstock and Needham have succeeded in homologizing practically all the types of neuration, including such perplexing types as those of Ephemerida (Fig. 70), Odonata (Fig. 20, *B*) and Hymenoptera (Fig. 71), and their thorough work affords a sound basis for a rational terminology of the wing veins; there is no longer any excuse for the lamentable confusion that has hitherto attended the study of venation.

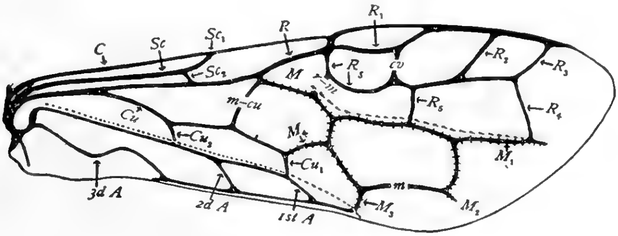
Fig. 70.



Wings of a May fly. 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, however, 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

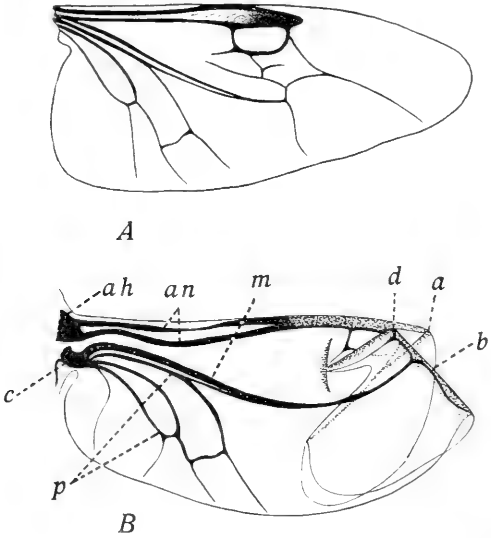
Fig. 71.



A typical hymenopterous wing. Lettering as before.

beetle, the folded wing (Fig. 72, *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.

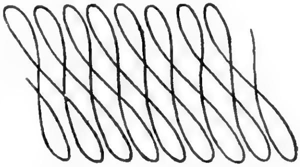
Fig. 72.



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.

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.

FIG. 73.



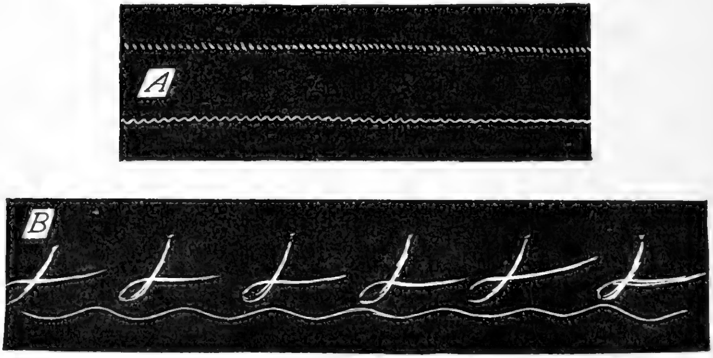
Trajectory of the wing of an insect.

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, 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. 73.

Marey, the chief 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 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 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. 74. 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. 74, *B*. The wings of the two sides move synchronously, as Marey found.

Fig. 74.

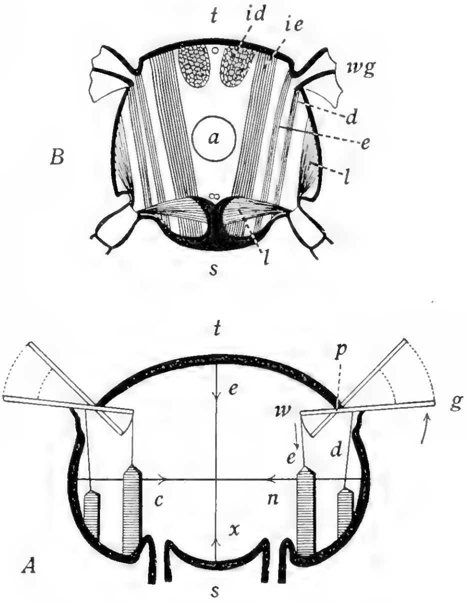


Records of wing vibration. *A*, mosquito, *Anopheles*. Above is the wing record and below is the record of a tuning fork which vibrated 264.6 times per second. *B*, wasp, *Polistes*. The tuning fork in this instance had a vibration frequency of 97.6.

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. 75, *A*), with the fulcrum at *p*, it is easy to understand how the contraction of muscle *c* raises the wing and that of muscle *d* lowers it. These muscles are shown diagrammatically in Fig. 75, *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. 75, *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.

Fig. 75.



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.

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.

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*, 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. 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.
Campodea,	3	0	3
Japyx,	4	7	11
Machilis,	2	7	9
Lepisma,	2	8	10
Blattidæ, Acridiidæ,	2	8	10
Odonata,	2	8	10
Heteroptera,	3	7	10
Lepidoptera,	2	7	9
Diptera,	2	7	9

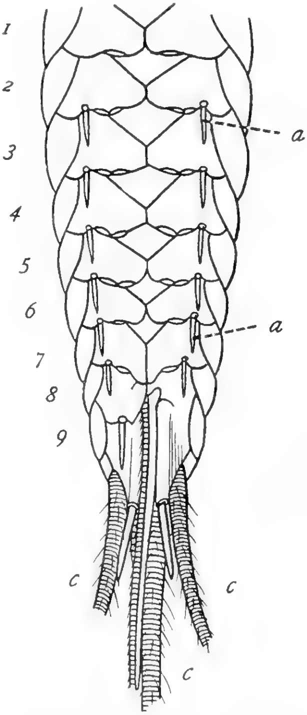
In most embryo insects there are eleven pairs of spiracles (three thoracic and eight abdominal); in adults, however, two pairs are commonly suppressed—the prothoracic and the eighth abdominal.

Number of Abdominal Segments.—Though consisting typically of ten segments—the number evident in such generalized insects as Thysanura and Ephemerida—eleven occur in various adult Orthoptera, with traces of a twelfth, while Heymons has detected twelve abdominal segments in embryos of Orthoptera and Odonata. 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, however, 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. 76). Functional abdominal legs do not occur in adult insects, but in larvæ the abdominal *pro-legs* (often called "false legs," Fig. 64) are homologous with the thoracic legs and the other paired segmental appendages, as the embryology shows. The embryo of *Œcanthus,* according to Ayers, has ten pairs of abdominal appendages (Fig. 196), 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

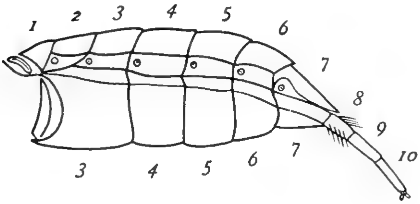
FIG. 76.



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 ninth segment is omitted.) *c, c, c, cerci.*—After OUDEMANS.

Orthoptera (to which order *Œcanthus* belongs). In Collembola, the embryo has paired abdominal limbs, and those of the first abdominal segment eventually unite to form the peculiar *ventral tube* (Fig. 12) of these insects, while those of the fourth segment form the characteristic leaping organ, or *furcula.*

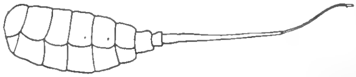
Fig. 77.



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

Cerci.—In many of the more generalized insects, the abdomen bears at its extremity two or three appendages termed *cerci.* These occur in both sexes and are frequently long and multiarticulate, as in Thysanura (Figs. 76, 9, 10) and Ephemerida (Figs. 19, *B;* 84), though shorter in cockroaches and reduced to a single sclerite in Acridiidæ (Fig. 87). The paired cerci, or *cercopoda* of Packard, are usually though not always associated with the tenth abdominal segment and are homologous with legs, as Ayers has found in *Œcanthus* 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 Acridiidæ often serve to hold the female during copulation.

Fig. 78.

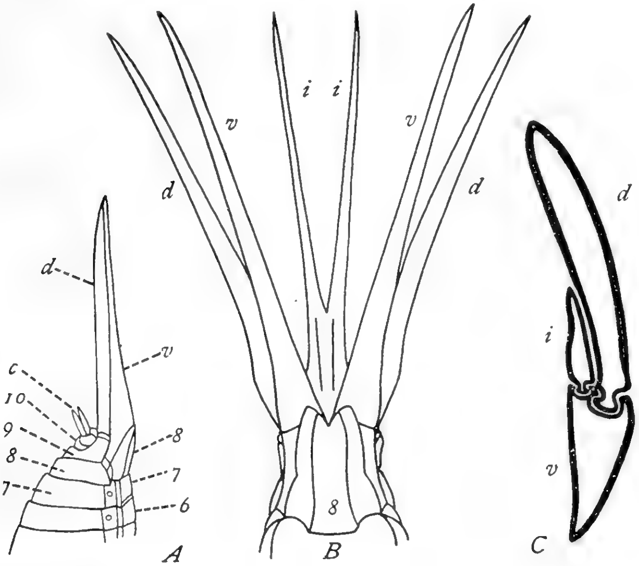


Abdomen of a female midge, *Cecidomyia leguminicola,* to show the pseudo-ovipositor.

Extremity of Abdomen.—Various modifications of the terminal segments of the abdomen occur for the purposes of defæcation 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. 77) and *Cecidomyia* (Fig. 78) the attenuated distal segments of the abdomen serve the purpose of an ovipositor; thus in Cecidomyiidæ, 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.

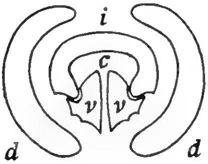
Fig. 79.



Ovipositor of *Locusta*. *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.

A true *ovipositor* occurs in Thysanura, Orthoptera, Odonata, Hemiptera, 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 Locustidæ (Fig. 79) the three

Fig. 80.

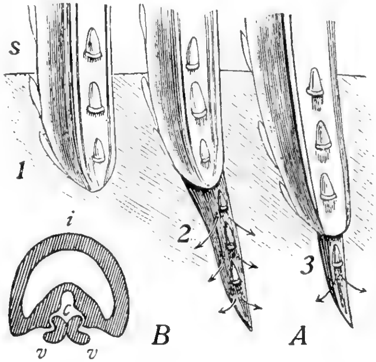


Cross section of the ovipositor of *Sirex*. *c*, channel; *d*, *d*, dorsal valves; *i*, united inner valves; *v*, *v*, ventral valves.—After Taschenberg.

valves of each side are held together by tongues and grooves, which, however, permit sliding 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 segments seven, eight and nine.

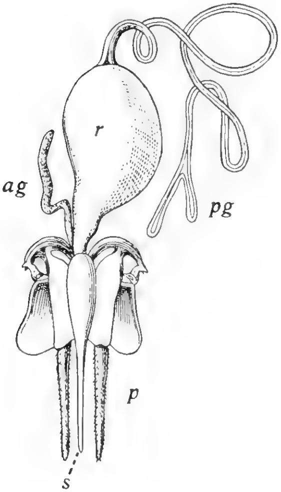
The ovipositor attains its greatest complexity in Hymenoptera, in which it becomes modified for sawing, boring or stinging. In *Sirex* (Fig. 80) the inner valves are united together; in *Apis* the dorsal valves are represented by a pair of *palpi*, the inner valves unite to form the *sheath* (Fig. 81, *B*), and the ventral two form the *darts*, each of which has ten barbed teeth behind its apex, which tend to prevent the withdrawal of the sting from a wound. The action of the sting, as

Fig. 81.



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.

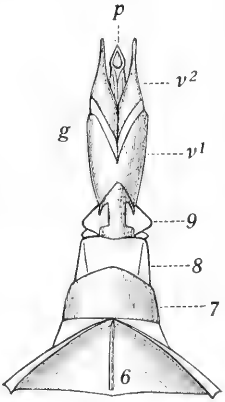
Fig. 82.



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

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. 81, *A*). The poison of the honey bee is secreted by two glands, one acid and the other alkaline. The former (Fig. 82) 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.

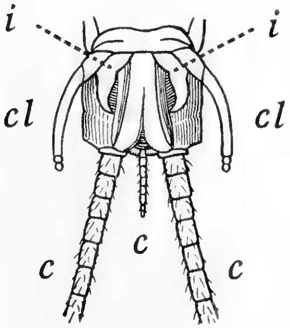
FIG. 83.



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.

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. 83) represents the two inner valves of the ovipositor and is frequently enclosed by one or two pairs of valves. In Ephemerida the two inner valves are partly or entirely separate from each other, forming two intromittent organs (Fig. 84).

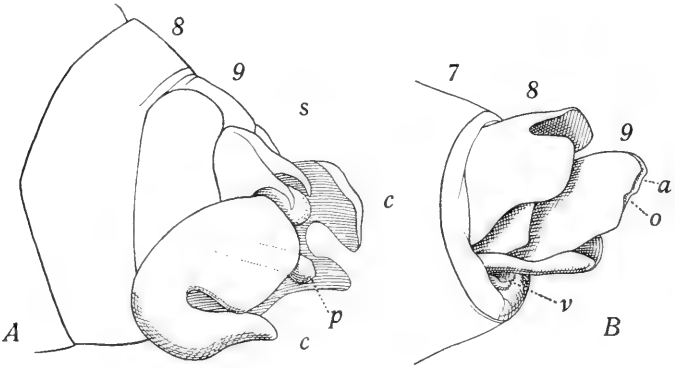
FIG. 84.



Extremity of abdomen of a male May fly, *Hexagenia variabilis*, ventral aspect. *c, c, c*, cerci; *cl, cl*, claspers; *i, i*, intromittent organs.

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.

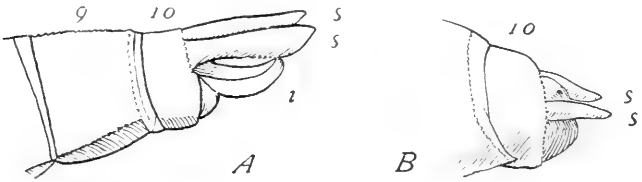
FIG. 85.



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.

The *claspers* of the male consist of a single pair, variously formed. They are present in Ephemerida, Neuroptera, Trichoptera, Lepidoptera (Fig. 85), 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. 86, *A*) and Orthoptera (Fig. 87, *A*) the cerci of the male often serve as claspers.

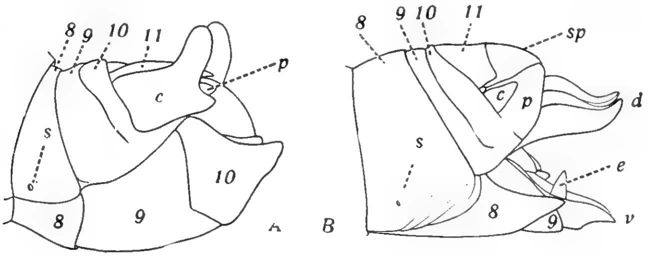
FIG. 86.



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

In many insects the tergum of the last abdominal segment forms a small *suranal plate* (Fig. 87, *B, sp*); this sometimes supplements the claspers of the male in their function, as in Lepidoptera (Fig. 85, *A, s*).

Fig. 87.



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.

2. INTEGUMENT

Insects excel all other animals in respect to adaptive modifications of the integument. No longer a simple limiting membrane, the integument 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 substance of remarkable stability, for it is unaffected by almost all ordinary acids and alkalies, 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, however, chitin undergoes a slow dissolution,

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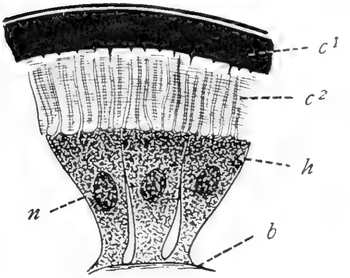
[1] The *cuticula* of an insect should be distinguished from the *cuticle* of a vertebrate, the former being a hardened fluid, while the latter consists of cells themselves, in a dead and flattened condition.

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 hydrate it is possible to dissolve away the cuticular framework, leaving fairly pure chitin, without destroying the organized 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 $C_{18}H_{15}NO_{12}$ by Krukenberg, and Packard adopts 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 different 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).

FIG. 88.

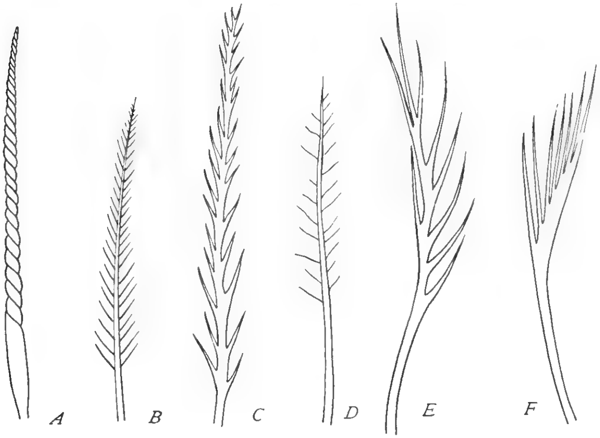


Section through integument of a beetle, *Chrysobothris*. *b*, basement membrane; c^1, primary cuticula; c^2, secondary cuticula; *h*, hypodermis cell; *n*, nucleus.—After TOWER.

The chitinous integument (Fig. 88) 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. The chitinous cuticula is secreted, as a fluid, from the hypodermis cells. Each layer arises as a fluid secretion from the hypodermis cells, the primary cuticula being the first to form and harden.

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. 89.



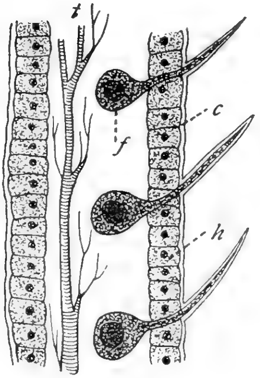
Modifications of the hairs of bees. *A, B, Megachile; C, E, F, Colletes; D, Chelostoma.*—After SAUNDERS.

Histology.—The chitinous cuticula owes its existence to the activity of the underlying layer of *hypodermis* cells (Fig. 88). 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.

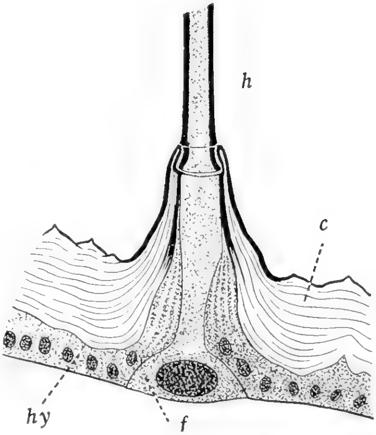
Hairs, Setæ and Spines.—These occur universally, serving a great variety of purposes; they are not always simple in form, but are often toothed, branched or otherwise modified (Fig. 89). Hairs and bristles are frequently tactile in function, over the general integument or else locally; or olfactory, 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.

FIG. 90.



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

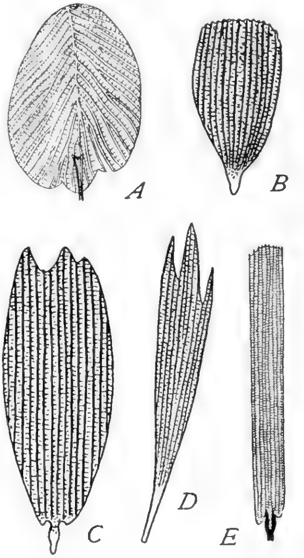
FIG. 91.



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

A hair arises from a modified hypodermis cell (Fig. 90), the contents of which extend through a pore canal into the interior of the hair (Fig. 91); 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.

Fig. 92.

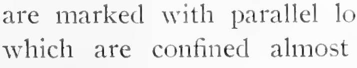


Various forms of scales. *A, E,* thysanuran, *Machilis; B,* beetle, *Anthrenus; C,* butterfly, *Pieris; D,* moth, *Limacodes.*

Scales. — Besides occurring throughout the order Lepidoptera and in numerous Trichoptera, scales are found in many Thysanura and Collembola, several families of Coleoptera (including Dermestidæ and Curculionidæ), a few Diptera and a few Psocidæ.

Though diverse in form (Fig. 92), 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 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. 92, *C*), which are confined almost entirely to the upper, or ex-

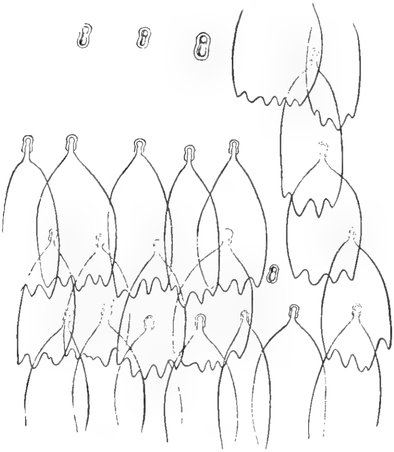
Fig. 93.



Cross section of scale of *Anosia*.— After Mayer.

posed, surface of the scale (Fig. 93) and number from 33 or less (*Anosia*) to 1,400 (*Morpho*) to each scale, the striæ being 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.

Fig. 94.

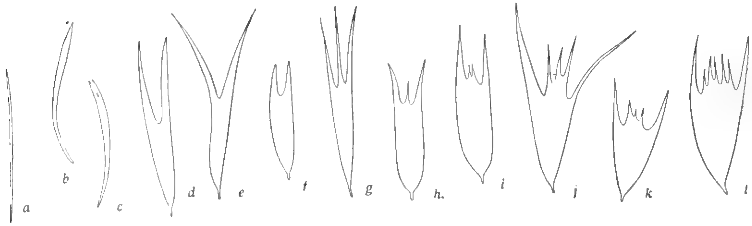


Arrangement of scales on the wing of a butterfly, *Papilio*.

On the wing of a butterfly the scales are arranged in regular rows and overlap one another, as in Fig. 94; 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. 95); 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. 96). The scale at first contains protoplasm, which gradually withdraws, leaving short chitinous strands to hold the two membranes of the scale together.

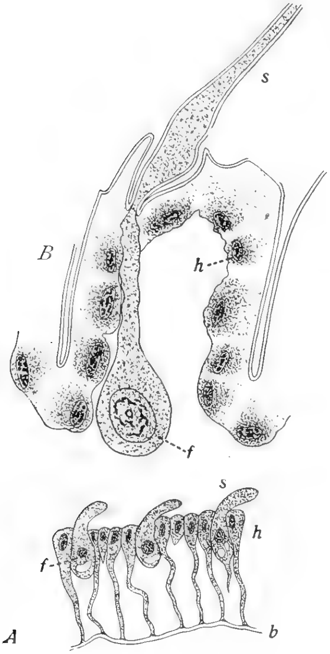
Fig. 95.



Hairs and scales of a moth, *Samia cecropia*.

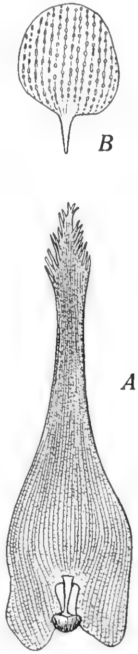
Uses of Scales.—Among Thysanura and Collembola, scales occur only on such species as live in comparatively dry situations, from which it may be inferred that the scales serve to retard the evaporation of moisture through the delicate integument of these insects. This inference is supported by the fact that none of the scaleless Collembola can live long in a dry atmosphere; they soon shrivel and die even under conditions 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

FIG. 96.



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

FIG. 97.

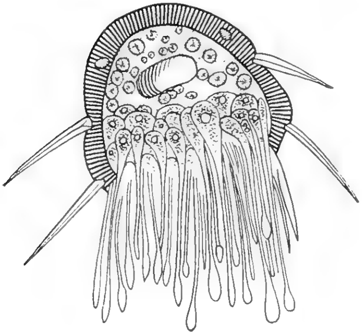


Androconia of butterflies. *A, Pieris rapæ; B, Everes comyntas.*

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. 97); 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 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*).

Fig. 98.



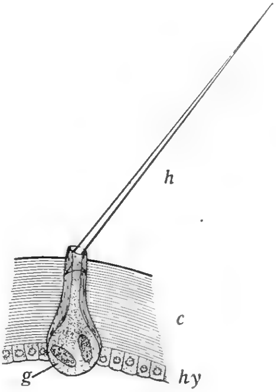
Section across tarsus of a beetle, *Hylobius*, to show bulbous glandular hairs.—After Simmermacher.

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. 98) 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. 99), 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. 100) 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.

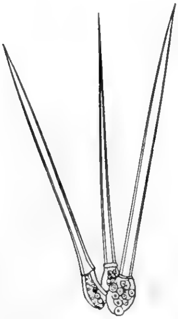
FIG. 99.



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

Repellent Glands.—The various offensive fluids emitted by insects are also a highly effective means of defence 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

FIG. 100.



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

glands (Fig. 146); 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. 101.

Osmeterium of *Papilio polyxenes.*

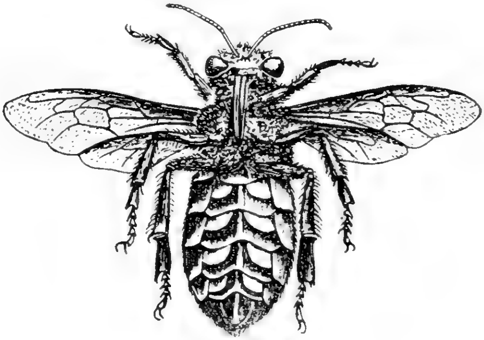
As malodorous insects, Hemiptera are notorious, though not a few hemipterous odors are (apart from their associations) rather agreeable to the human olfactory sense. Commonly the odor is due to a fluid from a mesothoracic gland or glands, opening between the hind coxæ.

Eversible hypodermal glands of many kinds are common in larvæ of Coleoptera and Lepidoptera. The larvæ of *Melasoma 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. 101) which diffuses a characteristic but indescribable odor that is probably repellent. The larva of *Cerura* everts a curious spraying apparatus from the under side of the neck.

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. 102). 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.

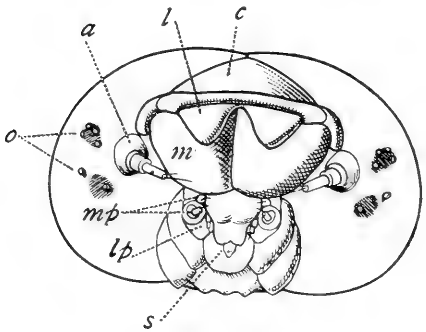
FIG. 102.



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

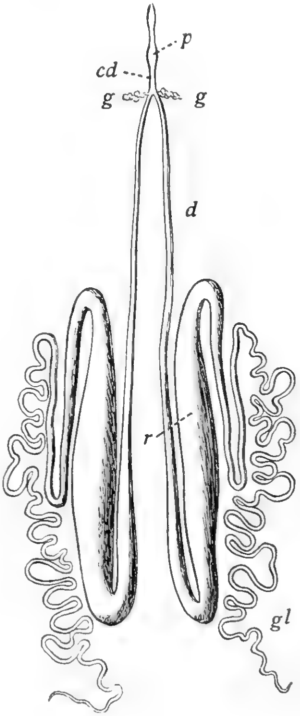
Silk Glands.—Larvæ of very diverse orders spin silk, for the purpose of making cocoons, webs, cases, and supports of one kind or another. Silk glands, though most characteristic of Lepidoptera and Trichoptera, occur also in the cocoon-spinning larvæ of not a few Hymenoptera (saw flies, ichneumons, wasps, bees, etc.), in Diptera (Cecidomyiidæ), 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.

FIG. 103.



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

FIG. 104.

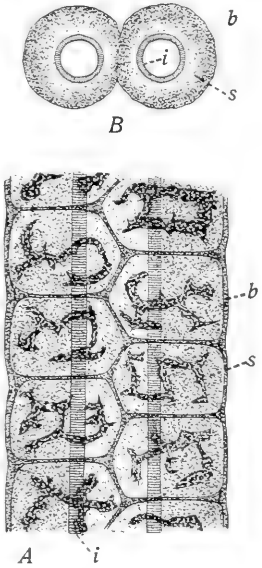


Silk glands of the silk worm, *Bombyx mori*. *cd*, common duct; *d*, one of the paired ducts; *g*, *g*, Filippi's glands; *gl*, gland proper; *p*, thread press; *r*, reservoir.

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. 103). 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. 104) 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.

A transverse or radial section of a silk gland shows a layer of glandular epithelial cells, with the usual intima and basement membrane (Fig. 105); 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.

FIG. 105.



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.

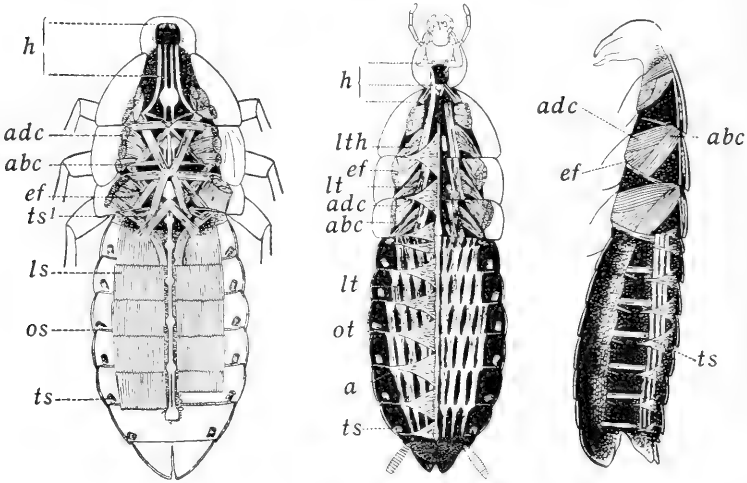
The silk glands of Trichoptera are essentially like those of Lepidoptera, but the glands of *Chrysopa*, *Myrmeleon*, Coccinellidæ, Chrysomelidæ and Syrphidæ, which open into the rectum, are morphologically quite different from those of Lepidoptera.

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 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.

Fig. 106. Fig. 107. Fig. 108.



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; *ts*¹, first tergo-sternal.—After Miall and Denny.

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; and the more recent studies of Lubbock and Janet on Hymenoptera.

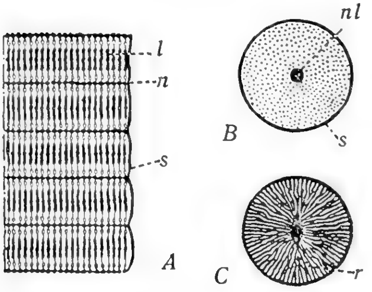
The more important muscles in the body of a cockroach are represented in Figs. 106–108, from Miall and Denny. The *longitudinal sternals* with the *longitudinal tergals* act to telescope the abdominal segments; the *oblique sternals* bend the abdomen laterally; the *tergo-sternals,* or vertical expiratory muscles, draw the tergum and sternum together. The muscles of the legs and the wings have already been referred to.

FIG. 109.

Striated muscle fiber of an insect.

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. 109), the former being singly refracting, or *isotropic,* and the latter doubly refracting, or *anisotropic.*

FIG. 110.



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.

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 110) consist of highly elastic threads of *spongioplasm* (anisotropic) embedded in a matrix of clear, semi-fluid, nutritive *hyaloplasm* (isotropic). The spongioplasmic 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.

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 .86 of his weight and a horse from .5 to .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 bumble bee can pull 16.1 times its own weight, a honey bee can pull 20.2; and where the same bumble bee 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.

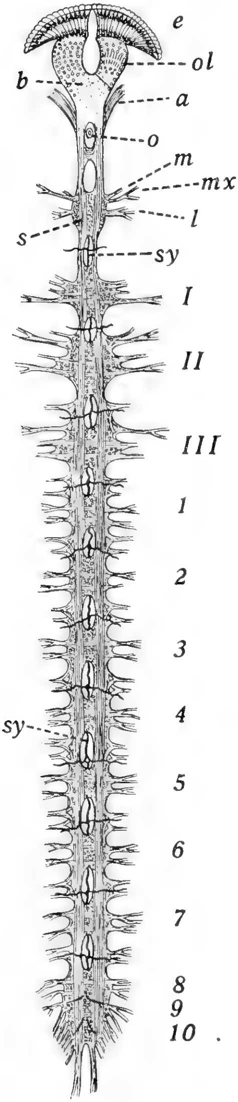
4. Nervous System

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. 111). In all adult insects, however, the originally separate ganglia consolidate more or less (Fig. 112) and the commissures frequently unite to form single cords. Thus in *Tabanus* (Fig. 112, *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. 113), is formed by the union of three primitive ganglia, or *neuromeres* (Fig. 55), namely, (1) the *protocerebrum*, which gives off the pair of optic nerves; (2) the *deutocerebrum*, which

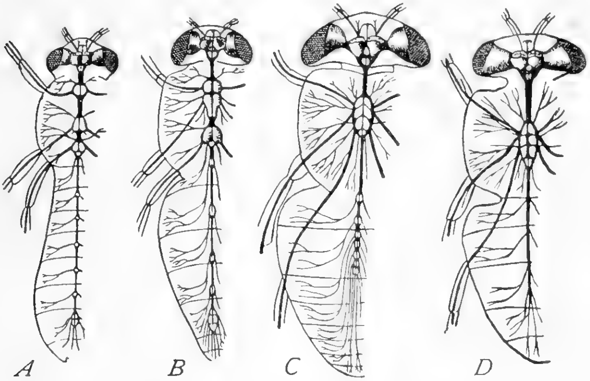
Fig. 111.



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.

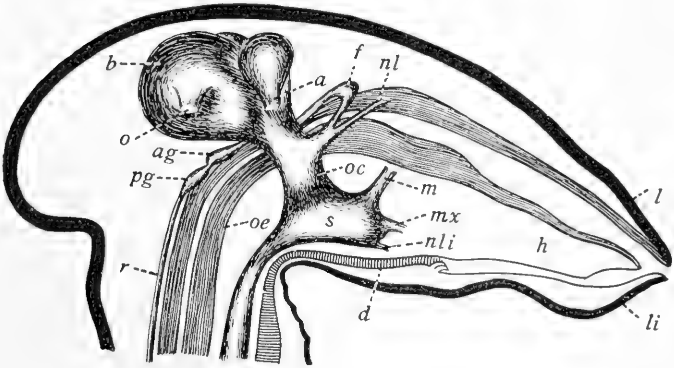
innervates the antennæ; and (3) the *tritocerebrum*, which in Apterygota bears a pair of rudimentary appendages that are regarded as traces of a second pair of antennæ.

FIG. 112.



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

FIG. 113.

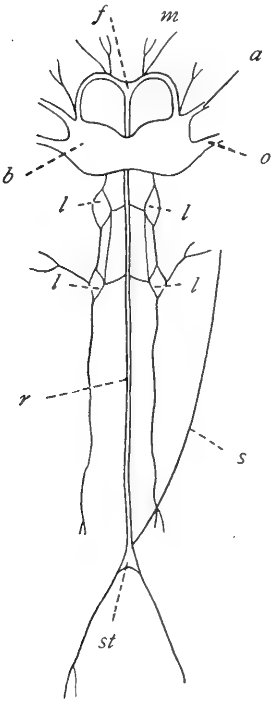


Nervous system of the head of a cockroach. *a*, antennal nerve; *ag*, anterior lateral ganglion of sympathetic system; *b*, brain; *d*, salivary duct; *f*, frontal ganglion; *h*, hypopharynx; *l*, labrum; *li*, labium; *m*, mandibular nerve; *mx*, maxillary nerve; *nl*, nerve to labrum; *nli*, nerve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

The subœsophageal ganglion (Fig. 113) 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.

FIG. 114.



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,* stomachic ganglion.—After KOLBE.

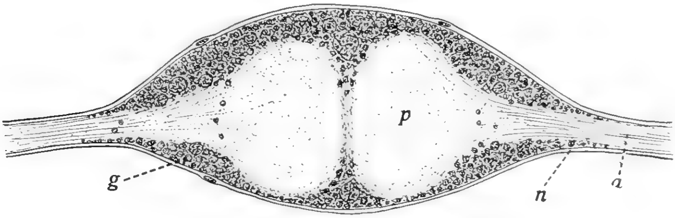
Sympathetic System.—Lying along the median dorsal line of the œsophagus is a *recurrent,* or *stomatogastric,* nerve (Fig. 114), which arises anteriorly in a *frontal ganglion* and terminates posteriorly in a *stomachic ganglion* situated at the anterior end of the mid intestine. Connected with the recurrent 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. 111) 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. 115), each of which has a large rounded nucleus and gives off usually a single nerve fiber; and (2) a clear medullary portion

(*Punktsubstanz*) 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, in an insect, consists of an *axis-cylinder,* composed of fibrillæ, and an enveloping membrane, or *neurilemma.* The axis-cylinder is the transmitting portion and the ganglia are the trophic centers, i. e., they regulate nutrition. A nerve is always either *sensory,* transmitting impulses inward from a sense organ; or else *motor,* conveying stimuli from the central nervous system outward to muscles, glands, or other organs.

FIG. 115.



Transverse section of an abdominal ganglion of a caterpillar. *a,* axis-cylinder; *g,* ganglion cells; *n,* neurilemma; *p,* Punktsubstanz.

Functions.—The brain innervates the chief sensory organs (eyes and antennæ) and converts the sensory stimuli that it receives into motor 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 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. 116–125, taken from a recent paper by Schenk, whose useful classification of antennal *sensilla,* or sense organs, is here outlined:

1. *Sensillum cœloconicum*—a conical or peg-like projection immersed in a pit (Figs. 116–117). In all probability olfactory.

2. *S. basiconicum*—a cone projecting above the general surface (Fig. 118). Probably olfactory.

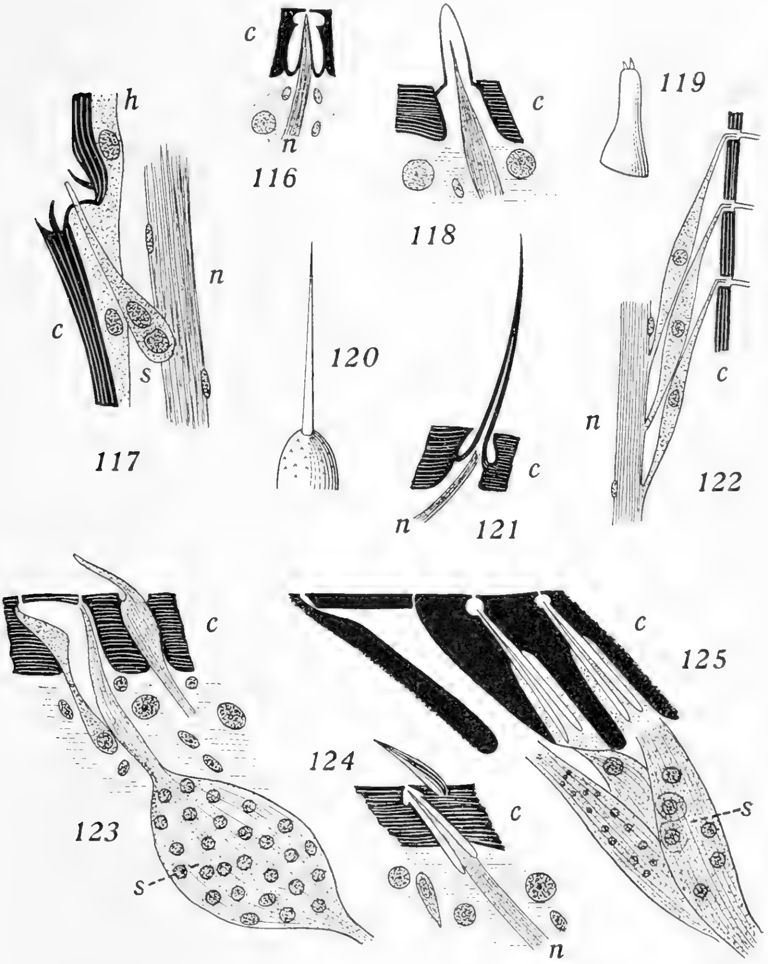
3. *S. styloconicum*—a terminal tooth or peg seated upon a more or less conical base (Fig. 119). Olfactory.

4. *S. chæticum*—a bristle-like sense organ (Fig. 120). Tactile.

5. *S. trichodeum*—a hair-like sense organ (Figs. 121, 122). Tactile.

6. *S. placodeum*—a membranous plate, its outer surface continuous with the general integument (Fig. 123). Func-

FIGS. 116–125.



Types of antennal sensilla, in longitudinal section (excepting Figs. 119 and 120). Fig. 116, sensillum cœloconicum; 117, cœloconicum; 118, basiconicum; 119, styloconicum; 120, chæticum; 121, trichodeum; 122, trichodeum; 123, placodeum; 124, ampullaceum; 125, ampullaceum; *c*, cuticula; *h*, hypodermis; *n*, nerve; *s*, sensory cell. Figs. 116, 118, 121, 123, 124, honey bee, *Apis mellifera;* 117, 119, 122, moth, *Fidonia piniaria;* 120, moth, *Ino pruni;* 125, wasp, *Vespa crabro.*—After SCHENK.

tion doubtful; not auditory and probably not olfactory, though the function is doubtless a mechanical one; Schenk suggests that they are 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. 124, 125). 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.

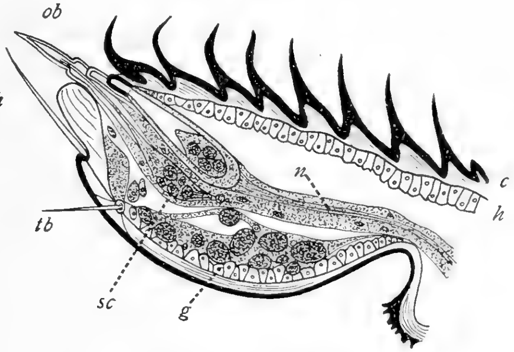
The end-organs of touch are bristles (sensilla chætica) or hairs (sensilla trichodea), each arising from a special hypodermis cell and having connection with a nerve. Sensilla chætica doubtless receive impressions from foreign bodies, while sensilla trichodea, being best developed in the swiftest flying 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.

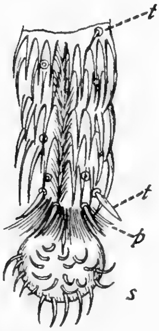
Taste.—The gustatory sense is unquestionably present in insects, as is shown both by common observation and by precise experimentation. Will fed wasps with sugar and then replaced it with powdered alum, which the wasps unsuspectingly tried but soon rejected, cleaning the tongue with the fore feet in a comical manner and manifesting other 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 Muscidæ 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.

Fig. 126.



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. 127.

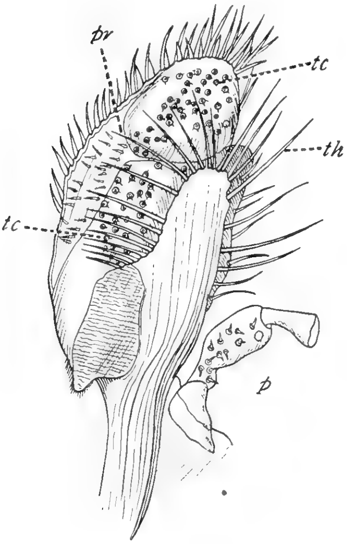


Tongue of honey bee, *Apis mellifera*. *p*, protecting bristles; *s*, terminal spoon; *t*, taste setæ.—After Will.

Location of Gustatory Organs.—As would be expected, the end-organs of taste are situated near the mouth, commonly on the hypopharynx (Fig. 126), epipharynx and maxillary palpi. On the tongue of the honey bee the taste organs appear externally as short setæ (Fig. 127) and on the maxillæ of a wasp as pits, each with a cone, or peg, projecting from its base (Figs. 128, 129). Similar taste pits and pegs have been 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 setæ or, more commonly, pegs each seated in a pit, or cup, and connected with a nerve fiber (Figs. 129, 130). 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.

FIG. 128.

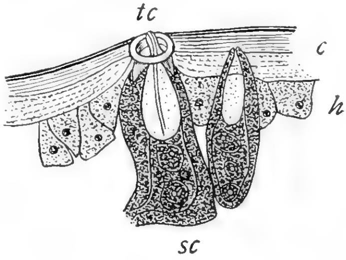


Under side of left maxilla of wasp, *Vespa vulgaris*. *p*, palpus; *pr*, protecting hairs; *tc*, taste cup; *th*, tactile hair.—After WILL.

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 turpen-

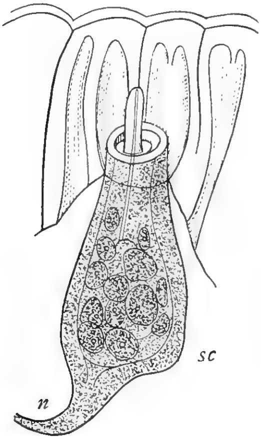
FIG. 129.



Longitudinal section of gustatory end-organ (*tc*, of Fig. 128). *c*, cuticula; *h*, hypodermis; *sc*, sensory cell; *tc*, taste cup.—After WILL.

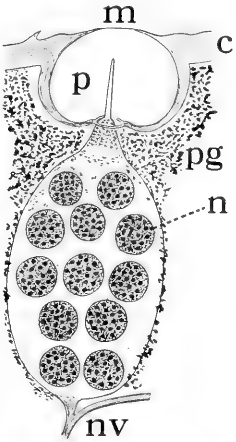
tine, acetic acid and other pungent fluids, no longer respond to the same stimuli after their antennæ have been amputated or else covered with paraffine to exclude the air. His experiments were conducted under conditions such that the results could not be ascribed to the shock of the operation or to 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, 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

FIG. 130.



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

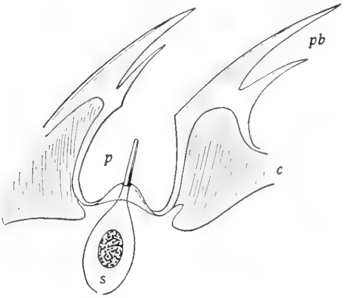
FIG. 131.



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.

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.

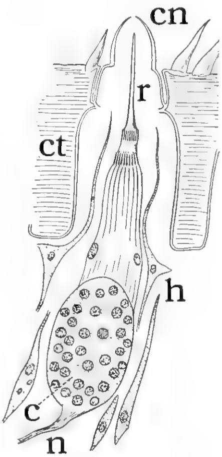
Fig. 132.



Section through antennal olfactory pit of fly, *Tabanus.* *c,* cuticula; *p,* pit with peg; *pb,* protecting bristles; *s,* sensory cell.—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. 131) 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. 132). 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. 133). 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

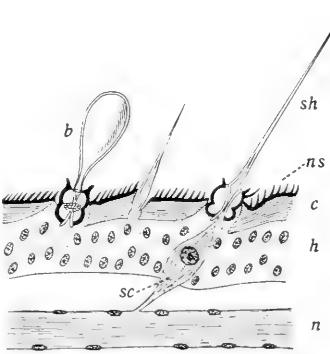
Fig. 133.



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.

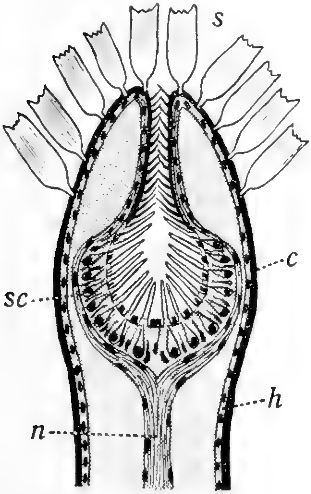
insects; thus there are as many as 17,000 on each antenna of a blow fly (Hicks). The male of *Melolontha vulgaris,* which seeks out the female by the sense of smell, has according to Hauser 39,000 pits on each antenna, and the female only 35,000. Pits presumably olfactory in function have been found 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. 134) may be olfactory, though possibly tactile. The same author found on the terminal palpal segment in various Lepidoptera a large flask-shaped invagination (Fig. 135) 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.

FIG. 134.



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

FIG. 135.



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

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 happens 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* (*Orgyia*) *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.

Assembling.—It is a fact, well known to entomologists, that the females of many moths and some beetles are able by exhaling an odor to 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. 74); 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.

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[1] Upon the basis of *C′* as 264 vibrations per second. The *C′* of the physicist has 256 as its frequency of vibration.

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 Cerambycidæ); 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.

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.

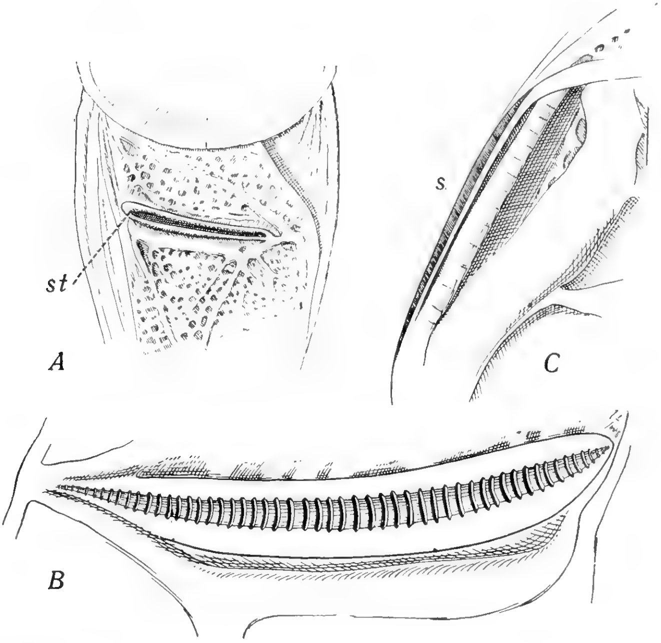
A few moths (Sphingidæ) and a few butterflies make sounds; the South American butterfly *Ageronia feronia* emits a sharp crackling noise as it flies. A rasp and a scraper have been found in several ants, though ants very seldom make any sounds that can be distinguished by the human ear; *Mutilla,* however,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

Locustidæ 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. 136), 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, *Œcanthus*. The stridulating areas are usually membranous and the rasping organs are modified veins.

Fig. 136.



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*).

Frequently the wing-covers bulge out to form a resonant chamber that reinforces the sound.

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

$$T = 50 + \frac{N - 40}{4}.$$

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

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

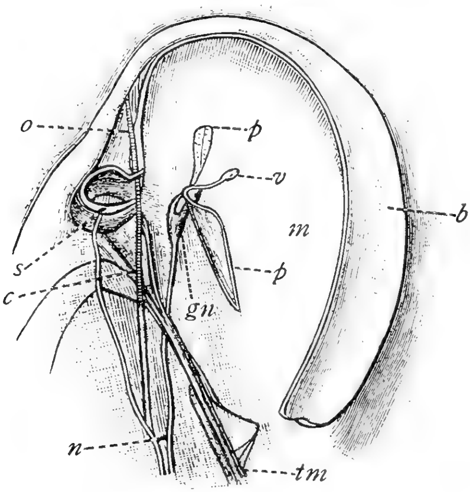
Here, in computing N, either the "katy-did" or the "she-did" is taken as a single call.

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.

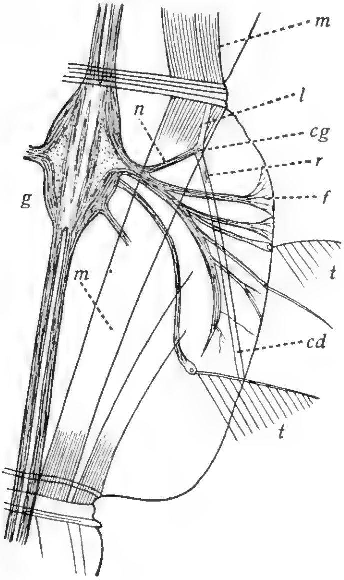
Fig. 137.



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.

In the lack of experimental evidence, other organs are inferred to be auditory on account of their structure. Acridiidæ bear on each side of the first abdominal segment a *tympanal* sense organ—the subject of Graber's well-known figure (Fig. 137). 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. 137, *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.

FIG. 138.



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 setæ.—After GRABER.

Other tympanal organs, doubtless auditory, are found on the fore tibiæ of Locustidæ, ants, termites and Perlidæ, on the femora of Pediculidæ and the tarsi of some Coleoptera.

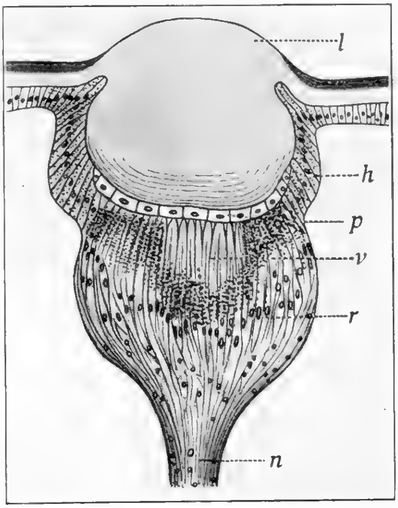
Several types of *chordotonal* organs have been described, of which those of the transparent *Corethra* larva may serve as an example. These organs, situated on each side of abdominal segments 4–10, inclusive, consist each (Fig. 138) of a tense cord, probably capable of vibration, which is attached at its posterior end to the integument and at its 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. 139) 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. 139. 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. 140), according to Redikorzew and others, and in 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.*

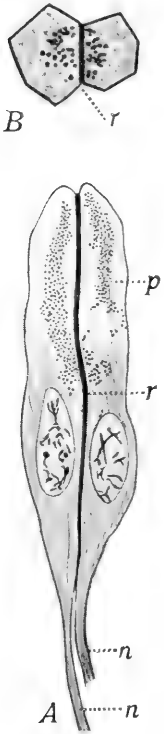
FIG. 139.



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.

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

FIG. 140.



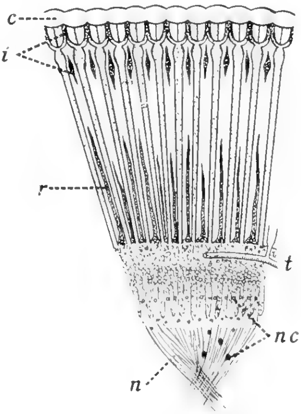
An ocellar retinula of the honey bee, composed of two retinal cells. *A*, longitudinal section; *B*, transverse section; *n*, *n*, nerves; *p*, pigment; *r*, rhabdom. — After REDIKORZEW.

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 all three ocelli are also 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. 141), 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*.

The cornea (Fig. 142) 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, 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.

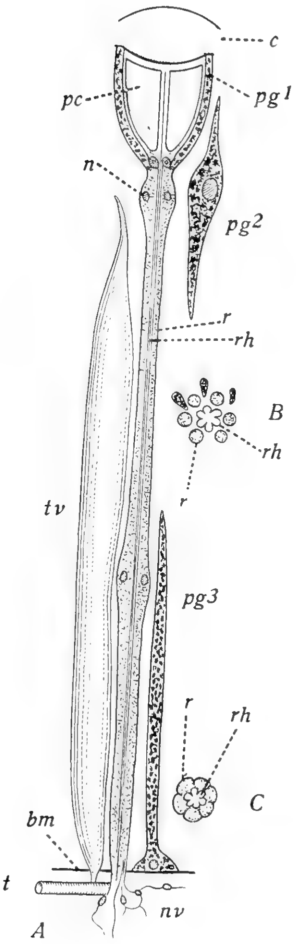
FIG. 141.



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.

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.

FIG. 142.



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.

Each ommatidium is adapted to transmit light along its axis only (Fig. 143), 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 essentially what the compound eye does, so far as can be inferred from its structure.

Exner, removing the cones with the corneal cuticula (in *Lampyris*), 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 coöperate 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 has 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 *Lampyris,* 1.50 meters for Lepidoptera, 68 cm. for Diptera and 58 cm. 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.

FIG. 143.

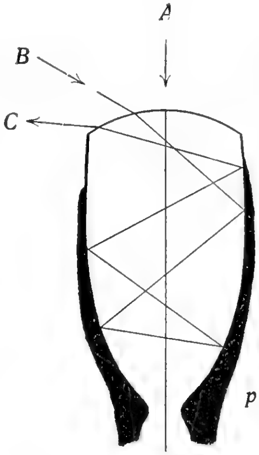


Diagram of outer, transparent portion of an ommatidium to illustrate the transmission of an axial ray (*A*) and the repeated reflection and absorption of an oblique ray (*B*), which at length emerges at *C*. *p*, iris pigment.

The 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 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.

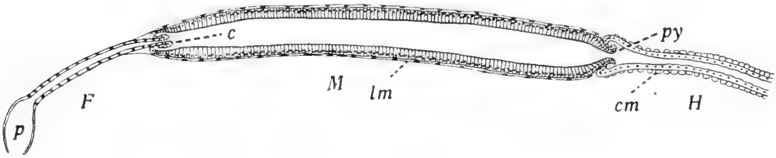
Origin of Compound Eye.—The compound eye is often said to represent a group of ocelli, chiefly for the reason that externally there appears to be a transition from simple eyes, through agglomerate eyes, to the facetted type. This plausible view, however, is probably incorrect, for these reasons among 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 350). 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, which make no sensible impression upon us. 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.

FIG. 144.



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.

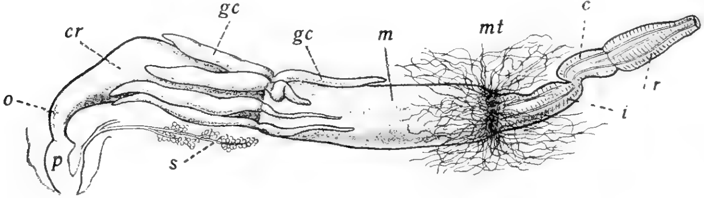
Problematical Sense Organs.—As all our ideas in regard to the sensations of insects are necessarily inferences from our own sensory experiences, they are inevitably inadequate. While it is certain that insects have at least the senses of touch, taste, smell, hearing and sight, it is also certain that 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 probably sensory end-organs, though their functions are either doubtful or unknown. Such an organ is the sensillum placodeum (p. 95), 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. 144) it is a simple tube extending 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.

Fig. 145.



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.

There are many departures from this primitive condition, and the most specialized insects exhibit the following modifications (Figs. 145, 146) of the three primary regions:

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

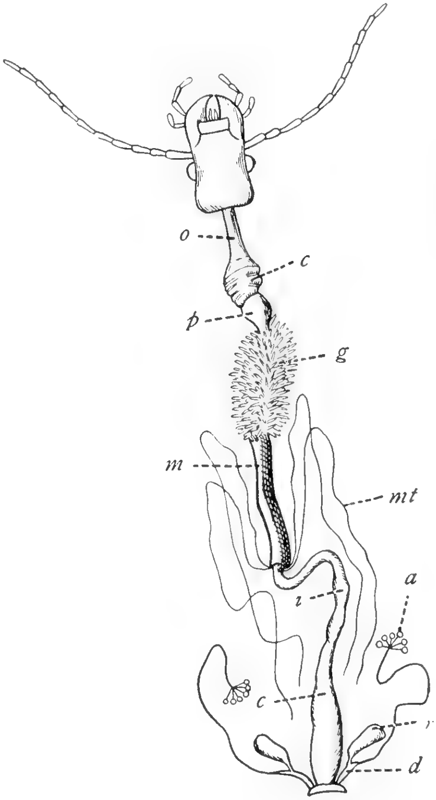
Mid intestine (*mesenteron*): ventriculus (stomach).

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 reception of 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. 113), 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.

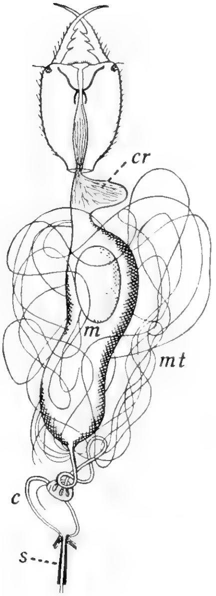
Fig. 146.



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 cæca; *i*, ileum; *m*, mid intestine; *mt*, Malpighian tubes; *o*, œsophagus; *p*, proventriculus; *r*, reservoir.—After Kolbe.

The *crop* is conspicuous in most Orthoptera (Fig. 145) and Coleoptera (Fig. 146) as a simple dilatation. In Neuroptera (Fig. 147) its capacity is increased by means of a lateral pocket—the *food reservoir;* this in Lepidoptera, Hymenoptera and Diptera is a sac (Fig. 148, *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 the secretion of the crop itself; in carnivorous insects this secretion converts albuminoids into assimilable peptone-like substances.

Fig. 147.



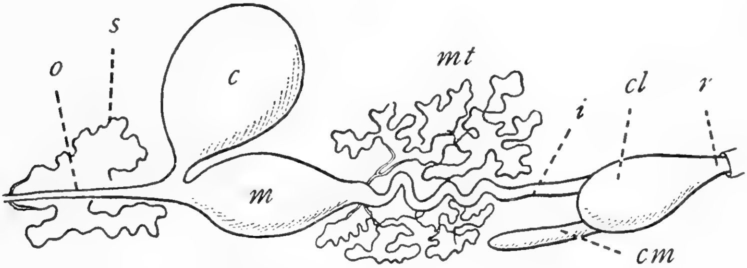
Digestive system of *Myrmeleon* larva. *c*, cæcum; *cr*, crop; *m*, mid intestine; *mt*, Malpighian tubes; *s*, spinneret.—After Meinert.

Next comes the enlargement known as the *proventriculus*, or *gizzard*, which is present in many insects, especially Orthoptera and Coleoptera (Fig. 146), and is usually found in such mandibulate insects as feed upon hard substances. The proventriculus is 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. Some authors maintain that 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. 144, 149) 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.

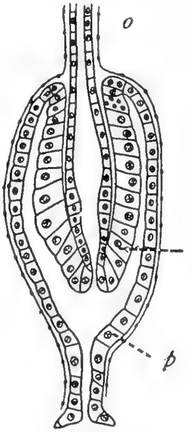
Mesenteron.—The *ventriculus,* otherwise known as the *mid intestine,* or *stomach,* is usually a simple tube of large caliber, as compared with the œsophagus or intestine, and into the ventriculus may open glandular blind tubes, or *gastric cæca* (Figs. 145, 146); these, though numerous in some insects, 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

Fig. 148.



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

Fig. 149.

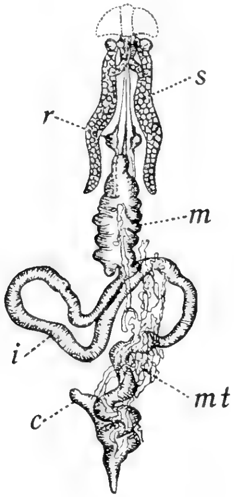


Cardiac valve of young muscid larva. *o,* œsophagus; *p,* proventriculus; *v,* valve. In an older larva the valve projects into the mid intestine.—After Kowalevsky.

stomach, however, 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. 144), consist of a backward-projecting circular ridge, or lip, which closes upon pressure from behind.

FIG. 150.

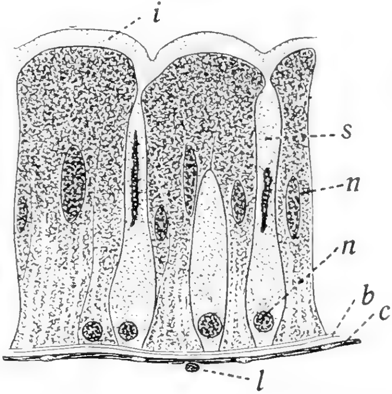


Digestive system of *Belostoma*. *c*, cæcum; *i*, ileum; *m*, mid intestine; *mt*, Malpighian tubes; *r*, salivary reservoir; *s*, salivary gland. —After LOCY, from the *American Naturalist*.

In its primitive condition the hind intestine is a simple tube (Fig. 144). Usually, however, it presents two or even three specialized regions, namely and in order, *ileum, colon* and *rectum* (Fig. 145). The hind intestine varies greatly in length and is frequently so long as to be thrown into convolutions (Fig. 150). The ileum is short and stout in grasshoppers (Fig. 145); long, slender and convoluted in many carnivorous 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. 148, 150) 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. 145) 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. 151), 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*. 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.

FIG. 151.

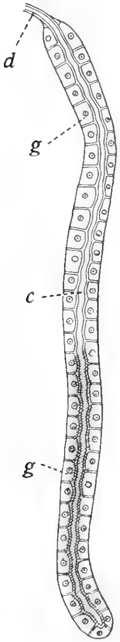


Wall of mid intestine of silk worm, transverse section. *b*, basement membrane; *c*, circular muscle; *i*, intima; *l*, longitudinal muscle; *n*, *n*, nuclei of epithelial cells; *s*, secretory cell.

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.

Salivary Glands.—In their simplest condition, the salivary glands are a pair of blind tubes (Fig. 152), 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. 153) 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.

FIG. 152.

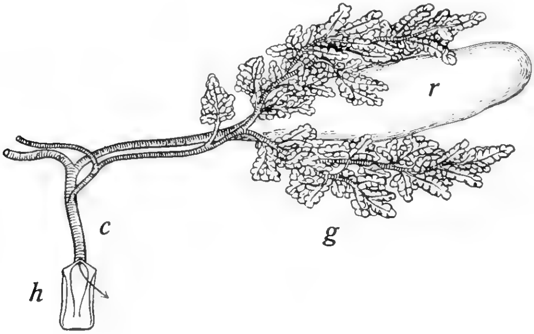


A simple salivary gland of *Cæcilius*. *c*, canal; *d*, duct; *g*, *g*, glandular cells.—After KOLBE.

Many insects have more than one pair of glands opening into the pharynx or œsophagus; thus the honey bee has six pairs and Hymenoptera 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. 154). 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

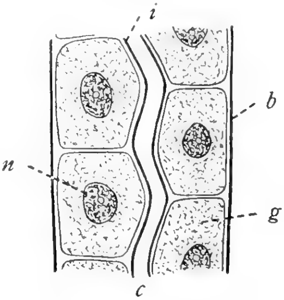
FIG. 153.



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

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. 154.

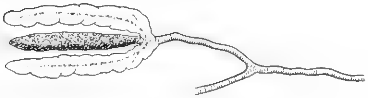


Histology of salivary gland of *Cæcilius*, radial section. *b*, basement membrane; *c*, canal; *g*, glandular cell; *i*, intima; *n*, nucleus.—After KOLBE.

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. 155); 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 act upon 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. 145, 146), 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 Acridiidæ as many as one hundred and fifty; commonly, however, there are four or six, as in Coleoptera, Lepidoptera and many other orders. Not more than six and frequently only four occur in the embryo (Wheeler), though these few embryonic tubes may subsequently branch into many.

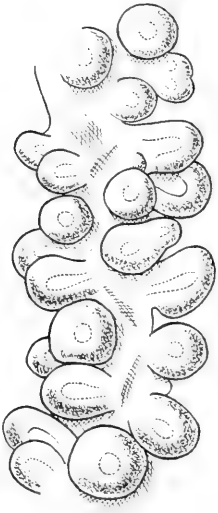
FIG. 155.



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

The Malpighian tubes (Fig. 156) 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. 157), 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.

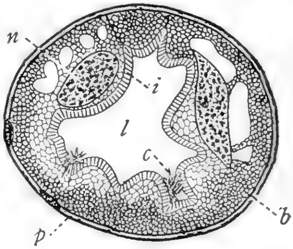
Fig. 156.



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

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.

Fig. 157.



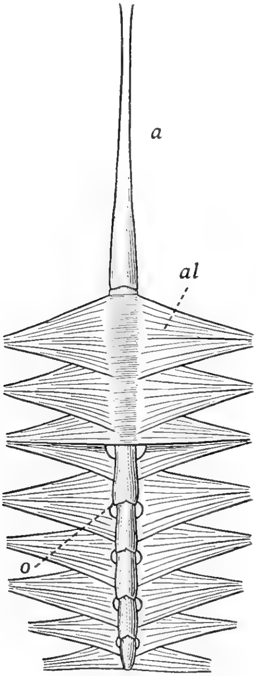
Cross section of Malpighian tube of silkworm, *Bombyx mori*. *b*, basement membrane; *c*, crystals; *i*, intima; *l*, lumen; *n*, nucleus; *p*, peritoneal layer. Greatly magnified.

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. 158, 162) 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

FIG. 158.



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

FIG. 159.

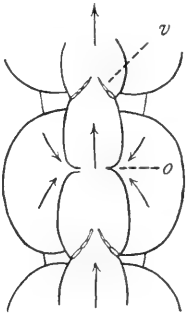
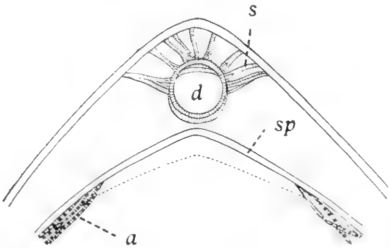


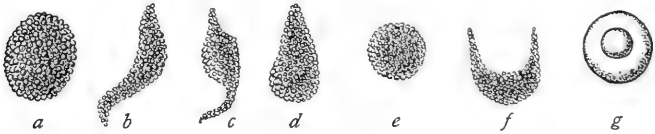
Diagram of a portion of the heart of a dragon fly nymph, *Epitheca*. *o*, ostium; *v*, valve; the arrows indicate the course of the blood. — After KOLBE.

FIG. 160.



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

FIG. 161.



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

which has on each side a valvular opening, or *ostium* (Fig. 159), 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. 162), each of which may again branch. In the head the blood leaves the aorta abruptly and enters the general body cavity.

Fig. 162.

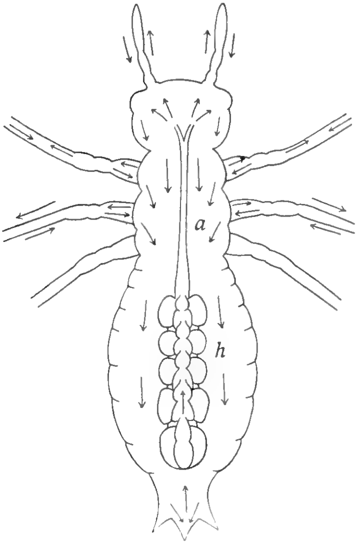


Diagram to indicate the course of the blood in the nymph of a dragon fly, *Epitheca*. *a*, aorta; *h*, heart; the arrows show directions taken by currents of blood.—After Kolbe.

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. 158, 160). These are thought to assist the heart in its propulsatory action.

Structure of the Heart.—The dorsal vessel has a delicate lining-membrane, or intima, and a thin enveloping membrane; between these, in the heart, is a layer of fine muscle fibers, circular or spiral in direction, which effect the contractions of the organ.

Ventral Sinus.—In many if not most insects a pulsatory septum (Fig. 177, *v*) extends across the floor of the body cavity to form a *sinus*, 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. 161).

Leucocytes.—The corpuscles, or leucocytes, are minute nucleated cells, 6 to 30 μ in diameter, variable in form even in the same species but commonly (Fig. 161) round, oval or ovate in profile, 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 ephemerid nymphs, currents of blood may be seen (Fig. 162) 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, Ephemerida, 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.

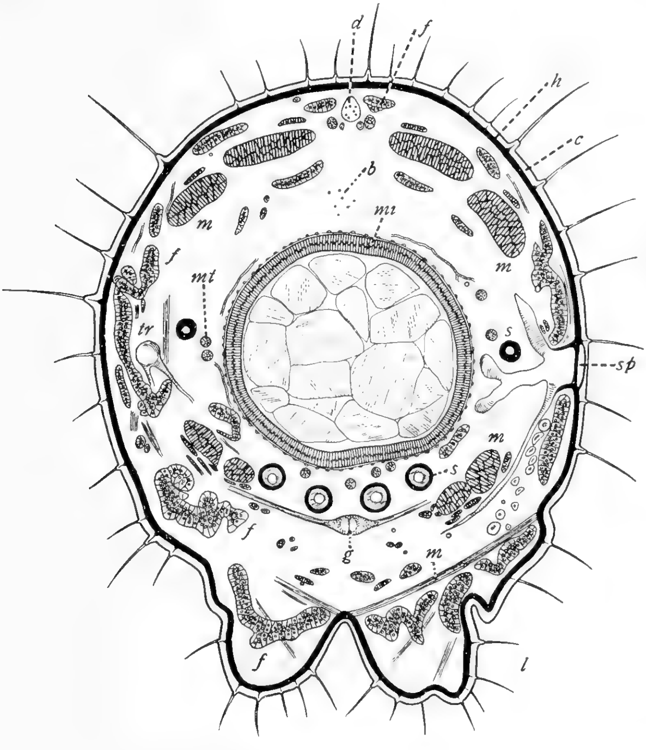
The rate of pulsation depends to a great extent upon the activity of the insect and upon the temperature and the amount of oxygen or carbonic acid gas in the surrounding atmosphere. Oxygen accelerates the action of the heart and carbonic acid gas retards it. A decrease of 8° or 10° C. in the case of 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 moult is about 82 or 83 per minute; before the second moult, 89, sinking to 63 before the third moult, to 45 before the fourth, and to 39 in the final larval stage; the force of the circulation, however, increases as the pulsations decrease in number. During the quiescent period immediately preceding each moult, 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. 163) 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.

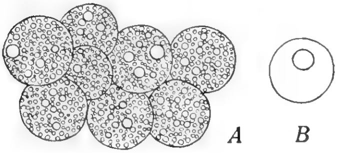
FIG. 163.



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.

Fat-Cells.—The fat-cells (Fig. 164) 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. 165), 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.

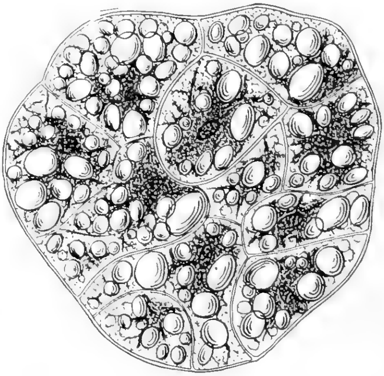
FIG. 164.



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

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 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 abdomen from tissues that can scarcely be distinguished from

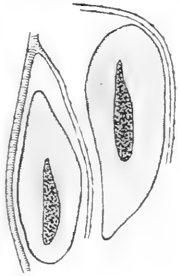
FIG. 165.



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

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 pericardial fat-body are attached to the lateral muscles (*alary* muscles) of the dorsal vessel, but almost nothing is known as to their function. Associated with the fat-body proper are the peculiar cells known as *œnocytes.* These occur in most insects, in segmentally-arranged clusters on each side of the abdomen, and consist of exceptionally large cells, more or less round or oval (Fig. 166), each with a large round, oval or elongate nucleus. These peculiar cells are usually separate from one another, but are held in clusters by tracheal branches. Their function is unknown. Finally, the fat-body is the basis of the luminosity, or so-called phosphorescence, of insects.

FIG. 166.

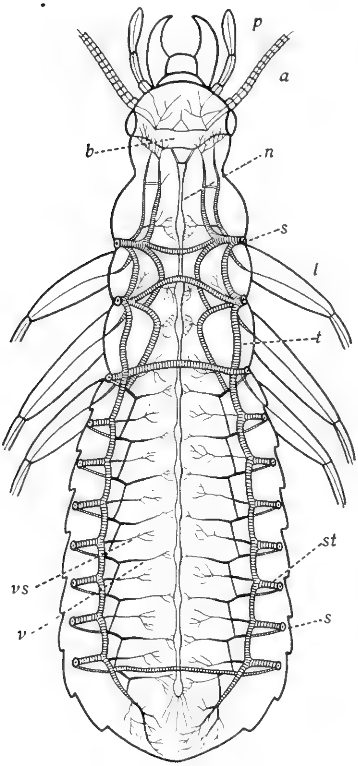


Œnocytes and accompanying tracheæ, from abdomen of a silkworm.

Luminosity.—This phenomenon appears sporadically and by various means in protozoans, worms, insects, fishes and other animals. Luminosity 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 fire-flies (Lampyridæ). In Lampyridæ, the light is emitted from the ventral side of the posterior abdominal segments. In our common *Photinus,* the seat of the light is a modified portion of the fat-body—a *photogenic plate,* situated immediately under the integument and supplied with a profusion of fine tracheal branches. The cells of the photogenic plate, it is said, secrete a substance which undergoes rapid combustion in the rich supply of oxygen furnished by the tracheæ.

Fig. 167.



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.

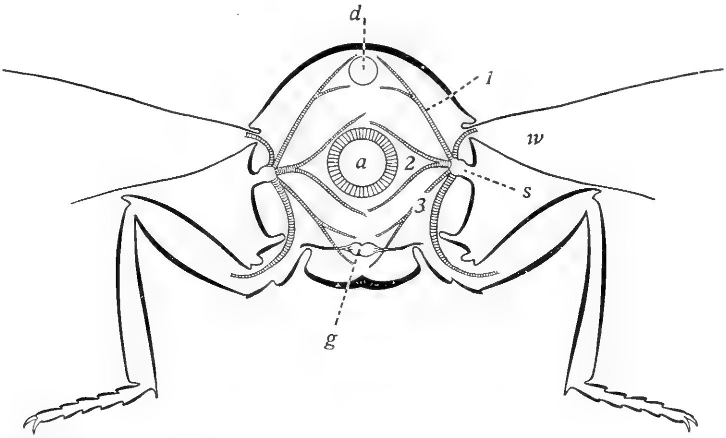
The rays emitted by the common fire-flies are remarkable in being almost entirely light rays, with almost no thermal or actinic rays. According to Young and Langley, the radiations of an ordinary gas-flame contain less than three per cent. of visible rays, the remainder being heat or chemical rays, of 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 light of the fire-fly, however, may be rated at one hundred per cent.; this light, then, is perfect, and as yet unapproached by artificial means.

As to the use of this luminosity, there is a general opinion that the light exists for the purpose of sexual attraction—a belief held by the author in regard to *Photinus,* at least. Another view is that the light is a warning signal to nocturnal birds, bats or other insectivorous animals; this is supported by the fact that lampyrids are refused by birds in general, after experience; young birds readily snap at a fire-fly for the first time, but at once reject it and thereafter pay no attention to these insects.

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. 167) extending along the side of the body. From the two main trunks branches are sent which divide and subdivide until they become 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. 168) 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.

Fig. 168.



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.

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.

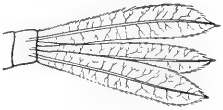
Types of Tracheation.—Two types of tracheal system are distinguished for convenience: (1) The primary, open, or *holopneustic* type described above, in which the spiracles are functional; (2) the secondary, closed, or *apneustic* type, in which the spiracles are either functionless or absent. This type 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, however, are connected by all sorts of intermediate stages.

Fig. 169.

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

Tracheal Gills.—In many aquatic nymphs and larvæ the spiracles are suppressed (though they become functional in the imago) and respiration is effected by means of gills; these are cuticular outgrowths which usually, though not invariably, contain tracheæ, and are commonly lateral or caudal in position. *Lateral tracheal gills* are highly developed in ephemerid nymphs (Fig. 169), in which a pair occurs on some or all of the first seven segments of the abdomen; a few genera, however, 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 Agrionidæ (Fig. 170) as three foliaceous appendages. A few coleopterous

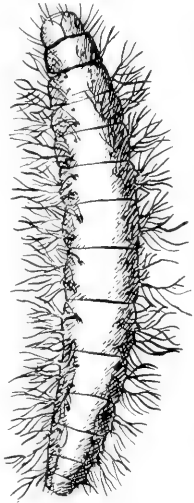
Fig. 170.



Caudal gills of an agrionid nymph, enlarged.

larvæ of aquatic habit, as *Gyrinus* and *Cnemidotus*, possess tracheal gills, as do also caterpillars of the genus *Paraponyx* (Fig. 171), which feed on the leaves of several kinds of water plants.

FIG. 171.



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

Though manifold in form, tracheal gills are generally 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.

FIG. 172.

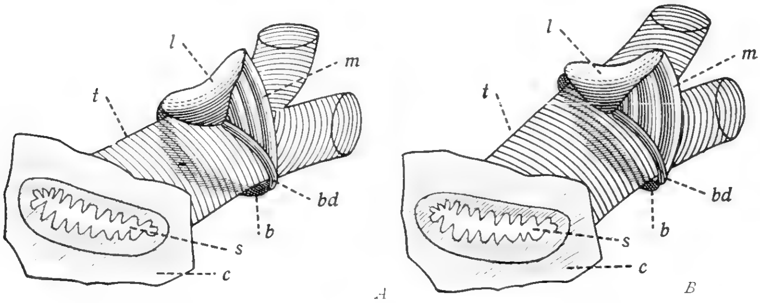
Larva of *Bittacomorpha clavipes*, showing respiratory tube. Natural size. — After HART.

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. 18), 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.

Spiracles.—The paired external openings of the tracheæ occur on the sides of the thorax and abdomen, there being never more than one pair to a segment. Though the thysanuran *Japyx* has 11 pairs, no winged insect has more than 10; although there are in all 12 segments which may bear spiracles—the three thoracic and the first nine abdominal segments. (Additional details are given on page 66.)

The *spiracles*, or *stigmata*, 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; in other beetles, however, 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. 172) and *Culex* (Fig. 229).

FIG. 173.

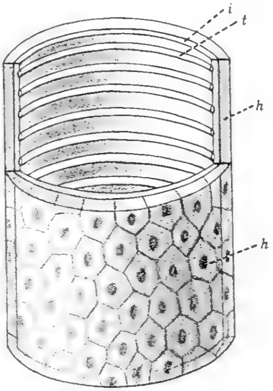


Apparatus for closing the spiracular trachea in a beetle, *Lucanus*. *A*, trachea opened; *B*, closed; *b*, bow; *bd*, band; *c*, external cuticula; *l*, lever; *m*, muscle; *s*, spiracle; *t*, trachea.—After JUDEICH and NITSCHE.

Closure of Spiracles.—As a rule, a spiracle is opened and closed periodically by means of a valve, operated by a special *occlusor* muscle. In dipterous larvæ the closure is effected by the contraction of 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. 173, *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 toward the lever and band until the enclosed trachea is pinched together. When the muscle relaxes, the trachea opens by its own elasticity.

FIG. 174.



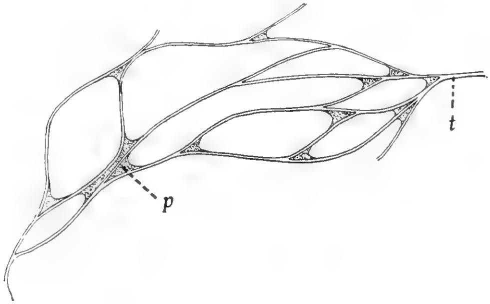
Structure of a trachea. *h*, tracheal hypodermis; *i*, intima; *t*, tænidium.

Structure of Tracheæ. — The tracheæ originate in the embryo as simple in-pocketings of the outer germ layer, or ectoderm, and from 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. 174) 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.

The ultimate tracheal branches (Fig. 175) are extremely delicate tubes, which do not end blindly, but anastomose with one another, forming a capillary network of confluent tubes. Some authors have held that the finest tracheal filaments penetrate epithelial or other cells.

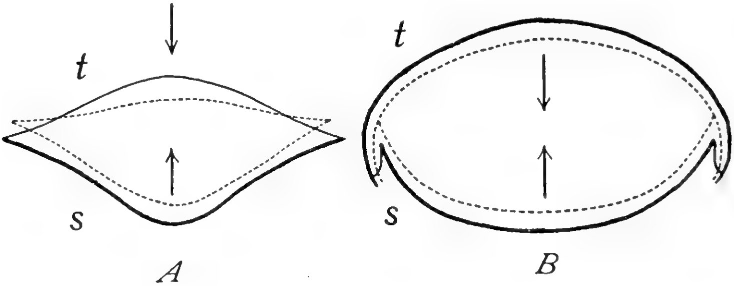
Respiration.—The external signs of respiration are the regular opening and closing movements of some of the spiracles and the rhythmic contraction and expansion of the abdomen. During contraction, the dorsal and ventral walls approach each other (Fig. 176) and during expansion they separate. The tergum moves more than the sternum in Coleoptera and Heteroptera, and vice versa in Acridiidæ, 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.

FIG. 175.



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

FIG. 176.

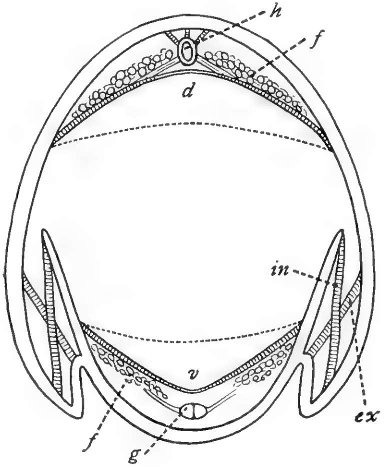


Transverse sections of abdominal segments, to illustrate respiratory movements. *A*, cockroach (*Blatta*); *B*, bee (*Bombus*); *s*, sternum; *t*, tergum. The dotted lines indicate positions of terga and sterna after expiration; the continuous lines, after inspiration.—After PLATEAU.

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. 177), 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 Acridiidæ, Trichoptera and Hymenoptera.

FIG. 177.



Diagrammatic cross section of abdomen of a grasshopper, *Acridium.* *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.

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.

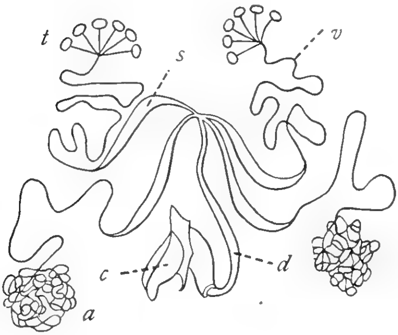
The way in which the air reaches the finest tracheal branches is not clearly ascertained, but it is thought that air is forced into these tubes by pressure from the abdominal muscles, while its escape through the spiracles is being prevented by the compression of the stigmatal tracheæ.

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.

10. Reproductive System

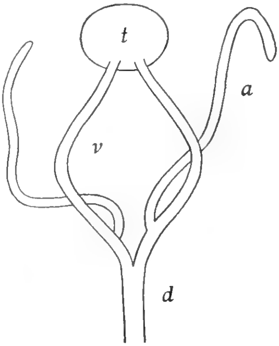
The sexes are always separate in insects, hermaphroditism occurring only as an abnormal condition. The sexual organs, situated in the abdomen, consist essentially of a pair of *ovaries* or *testes* and a pair of ducts (*oviducts* or *seminal ducts,* respectively). Primitively, the ducts open separately, as they still do in Ephemeridæ, but in nearly all other insects the two ducts enter a common evacuating duct (*vagina* or *ejaculatory duct*); this opens ordinarily between the penultimate and antepenultimate segments of the abdomen, i. e., usually the ninth and eighth, at any rate never through the last abdominal segment.

Fig. 178.



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. 179.



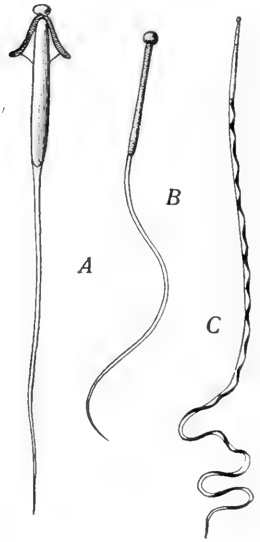
Reproductive system of male Lepidoptera. *a*, accessory gland; *d*, ejaculatory duct; *t*, united testes; *v*, vas deferens.—After Kolbe.

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

MALE. FEMALE.
Testes = *Ovaries*
Seminal ducts = *Oviducts*
Ejaculatory duct = *Vagina*
Seminal vesicle = *Seminal receptacle*
Accessory glands = *Accessory glands*
Penis and accessories = *Ovipositor*

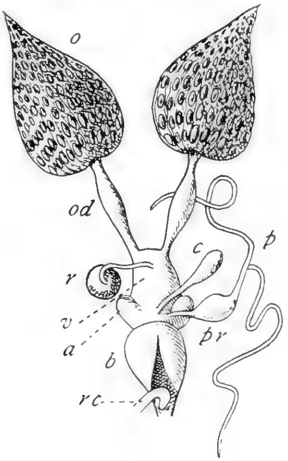
Male Organs.—Each *testis*, though sometimes a single blind tube, is usually a group of tubes or sacs (Fig. 178), *testicular follicles*, which open into a seminal duct (*vas deferens*). In most Lepidoptera the testes are secondarily united into a single mass (Fig. 179) as also in Acridiidæ. The two seminal ducts enter the common *ejaculatory duct*, which ter-

FIG. 180.



Spermatozoa. *A*, locustid grasshopper; *B*, cockroach, *Blatta*; *C*, beetle, *Copris*. —After BÜTSCHLI and BALLOWITZ.

FIG. 181.

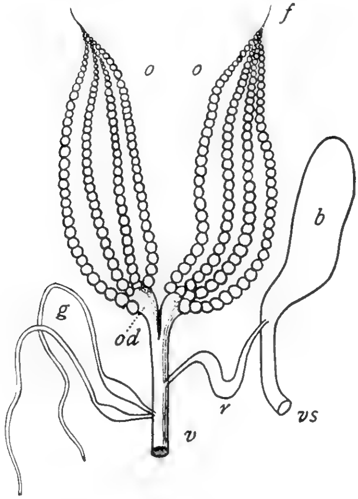


Reproductive system of queen honey bee. *a*, accessory sac of vagina; *b*, bulb of stinging apparatus; *c*, colleterial, or cement, gland; *o*, ovary; *od*, oviduct; *p*, poison glands; *pr*, poison reservoir; *r*, receptaculum seminis; *rc*, rectum; *v*, vagina.—After LEUCKART.

minates 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. 180) 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.

FIG. 182.

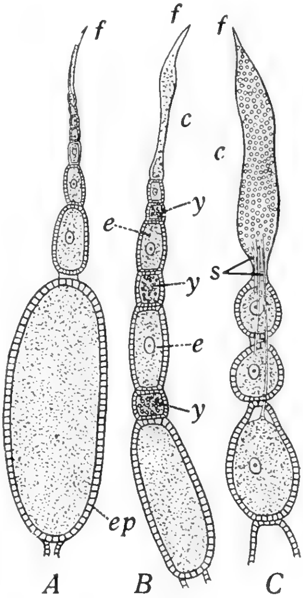


Reproductive system of female Lepidoptera. *b,* bursa copulatrix; *f,* terminal filament; *g,* cement glands; *o, o,* ovaries; *od,* oviduct; *r,* receptaculum seminis; *v,* vagina; *vs,* vestibule, or entrance to bursa.—After KOLBE.

Female Organs. — Each *ovary* (Fig. 181) 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. 182). 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. 183, *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.

Fig. 183.

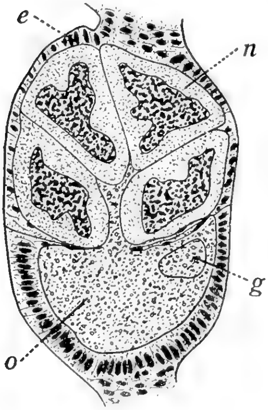


Types of ovarian tubes. *A,* without nutritive cells; *B,* with alternating nutritive and egg-cells; *C,* with terminal nutritive chamber; *c,* terminal chamber; *e,* egg-cell; *ep,* follicle epithelium; *f,* terminal filament; *s,* strands connecting ova with nutritive chamber; *y,* yolk, or nutritive,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

Ovaries and testes arise from indifferent cells, 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. 184). 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,* or the combination of male and female characters in the same individual, occurs only as an extremely rare abnormality among insects. 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 is so prevalent in the order that hermaphrodites are easily recognized.

Fig. 184.

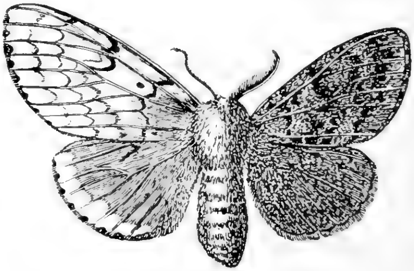


Ovum of a butterfly, *Vanessa*, in its follicle. *e*, follicle epithelium; *g*, germinal vesicle; *n*, branching nucleus of nutritive cell; *o*, ovum.—After Woodworth.

The most common kind of hermaphroditism is that in which one side is male and the other female, as in Fig. 185. 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.

Fig. 185.

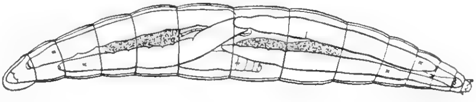


Hermaphrodite gypsy moth, *Porthetria dispar;* right side, male; left, female. Natural size.—After Taschenberg, from Hertwig's *Lehrbuch*.

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 recently, however, that the parthenogenetic worker eggs of the ant *Lasius niger* may produce normal workers (Reichenbach, Mrs. A. B. Comstock). Males may, of course, result from fertilized eggs, as in the honey bee, according to Dickel, who maintains, indeed, that all the eggs laid by the queen bee are fertilized. Parthenogenesis has been recorded as occurring also in a few moths, some Coccidæ and many Thysanoptera.

Pædogenesis.—In *Miastor* and some species of *Cecidomyia,* young are produced by the *larva.* This extraordinary form of parthenogenesis is termed *pædogenesis,* and is limited apparently to the family Cecidomyiidæ. The pædogenetic larvæ of *Miastor* (Fig. 186) develop before the oviducts have appeared and escape by the rupture of the mother. After several successive generations of this kind the resulting larvæ pupate and form normal male and female flies. 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. 186.



Young pædogenetic larvæ of *Miastor* in the body of the mother larva. Greatly enlarged.—After PAGENSTECHER.

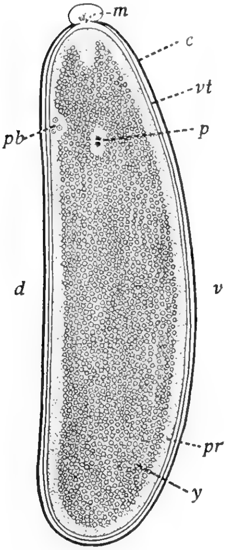
CHAPTER III

DEVELOPMENT

1. Embryology

Ovum.—The ovum of an insect, as of any other animal, is a single cell (Fig. 187), with a large nucleus (*germinal vesicle*), a large *nucleolus*, nutritive matter, or *yolk* (*deutoplasm*), contained in the 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.

Fig. 187.



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.

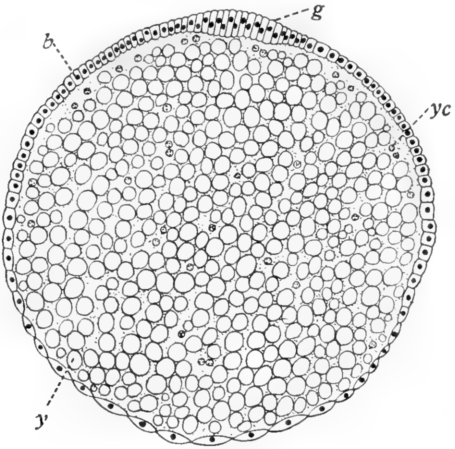
Maturation.—As a preparation for fertilization the germinal vesicle divides twice, forming two *polar bodies*, and as the first of these bodies may itself divide, there result four cells; three of these, however—the polar bodies—are minute and rudimentary.

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 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. Needless to say, the minute details of the process of fertilization are of the highest biological importance.

FIG. 188.

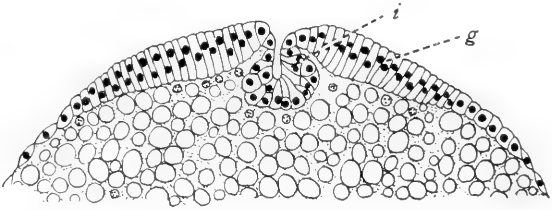


Equatorial section of egg of a beetle, *Clytra læviuscula.* *b*, blastoderm; *g*, germ band; *y*, yolk granule; *yc*, yolk cell.—After LÉCAILLON.

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. 188).

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.

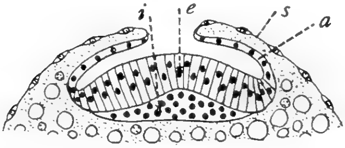
Fig. 189.



Transverse section of germ band of *Clytra* at gastrulation. *g,* germ band; *i,* inner layer.—After Lécaillon.

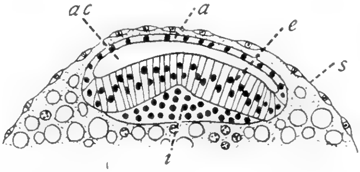
Gastrulation.—The germ band next infolds along the median line, appearing in cross section, as in Fig. 189; the two lips of the *median groove* close together over the invaginated portion and form an outer layer, or *ectoderm* (Fig. 190), while the invaginated portion spreads out as an inner layer, which 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.

Fig. 190.



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.

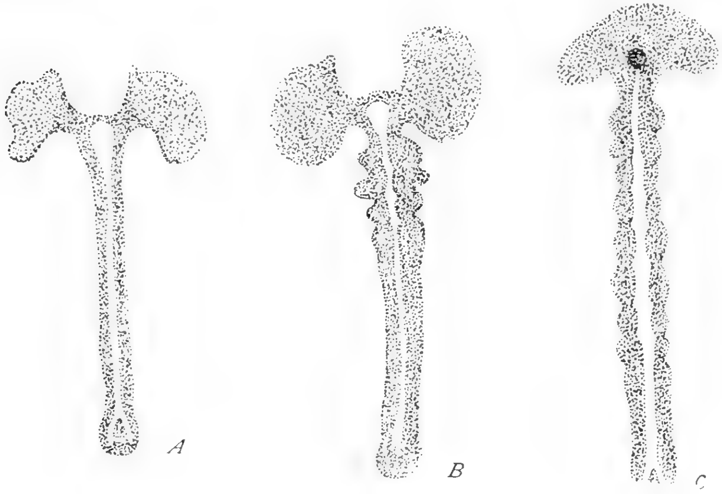
Fig. 191.



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.

Amnion and Serosa.—Meanwhile, the blastoderm has been folding over the germ band from either side, as shown in Fig. 190, and at length the two folds meet and unite to form two membranes (Fig. 191), namely, an inner one, or *amnion,* and an outer one, or *serosa.*

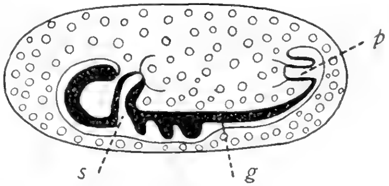
FIG. 192.



Germ band of a beetle, *Melasoma,* in three successive stages. *A,* unsegmented; *B,* with oral segments demarkated; *C,* with three oral, three thoracic and two abdominal segments.—After GRABER.

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. 192, 194); this segmentation beginning usually at the anterior end of the germ band and progressing backward. Furthermore, an anterior infolding occurs (Fig. 193), 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. 193.

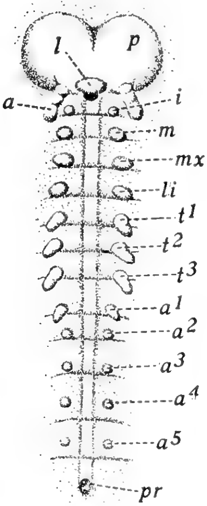


Diagrammatic sagittal section of hymenopterous egg to show stomodæal (*s*) and proctodæal (*p*) invaginations of the germ band (*g*).—After GRABER.

(Fig. 193), 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. 192, 194), which eventually bear the lateral eyes, and immediately behind these are the fundaments of the antennæ. The fundaments 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. 194, *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 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 fundaments, and in Thysanura and Collembola a fourth pair is present to form the superlinguæ (Fig. 195, *sl*), already referred to. Next in order are the three pairs of thoracic legs (Fig. 194) and then, in many cases, paired abdominal appendages (Figs. 194, 196), 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 fundaments sheds much light upon the morphology of the appendages and the subject of segmentation.

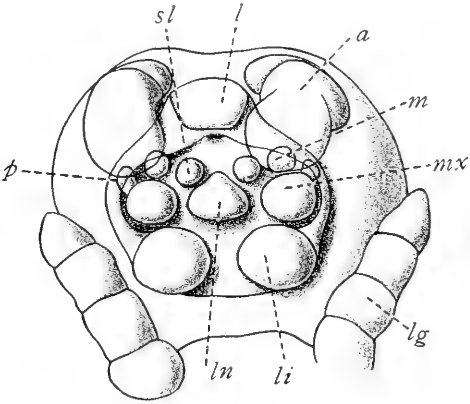
Fig. 194.



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; t^1–t^3, thoracic legs.

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. 190, 191), as distinguished from the *invaginated* type, illustrated in Odonata, in which the germ band invaginates into the egg, as in Fig. 197, 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. 198).

FIG. 195.



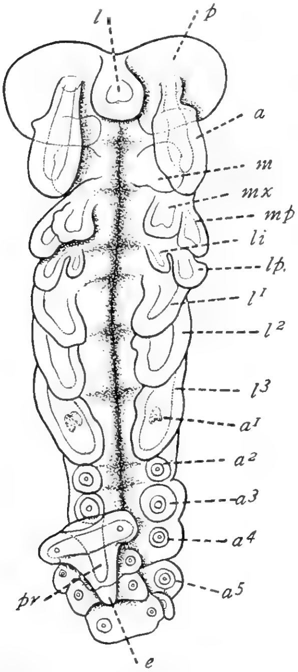
Anterior aspect of embryonal mouth parts of a collembolan, *Anurida maritima.* *a,* antenna; *l,* labrum; *lg,* prothoracic leg; *li,* left fundament of labium; *ln,* lingua; *m,* mandible; *mx,* maxilla; *p,* maxillary palpus; *sl,* superlingua.—After FOLSOM.

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. 199) 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.

200, *n*) which have been derived by direct proliferation from those of the germ band, 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 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. 55) 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.* Then follow the three thoracic ganglia and ten (usually) abdominal ganglia. The first three neuromeres always unite together 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.

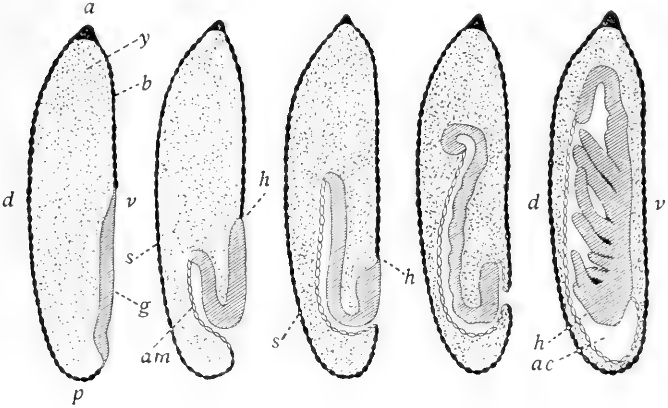
FIG. 196.



Embryo of *Œcanthus,* ventral aspect. *a,* antenna; a^1–a^5, abdominal appendages; *e,* end of abdomen; *l,* labrum; *li,* 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.

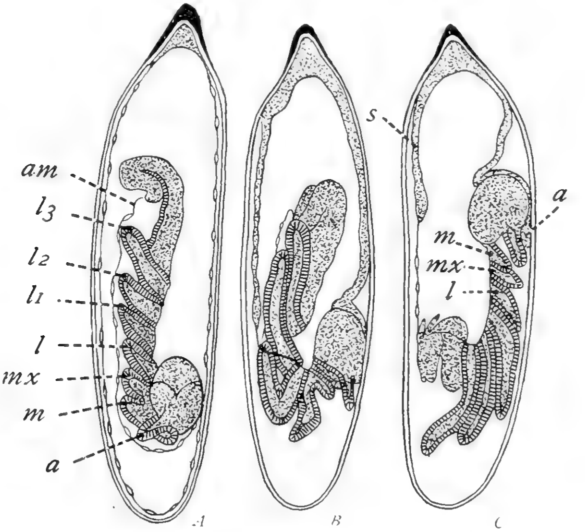
Tracheæ.—The tracheæ begin as paired invaginations of the ectoderm (Fig. 201, *t*); these simple pockets elongate and

FIG. 197.



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. 198.

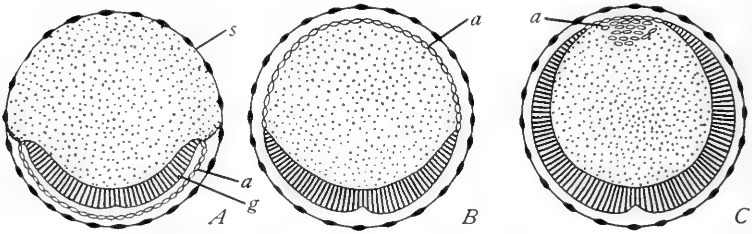


Diagrammatic sagittal sections to illustrate revolution of *Calopteryx* embryo. *a*, antenna; *am*, amnion; *l*, labium; l^1–l^3, thoracic legs; *m*, mandible; *mx*, maxilla; *s*, serosa.—After BRANDT.

unite to form the main lateral trunks, from which arise the countless branches of the tracheal system.

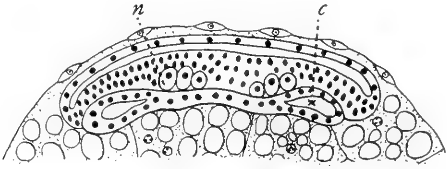
Mesoderm.—From the inner layer which was derived from the germ band by gastrulation (Figs. 189–191) are formed the important germ layers known as *mesoderm* and *entoderm*. Most of the layer becomes mesoderm, and this splits on either side into chambers, or *cœlom sacs* (Fig. 200, *c*), a pair to each 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 cœlom 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.

Fig. 199.



Diagrammatic transverse sections to illustrate formation of dorsal wall in a beetle, *Leptinotarsa*. *a*, amnion (breaking up in *C*); *g*, germ band; *s*, serosa.—After Wheeler, from the *Journal of Morphology*.

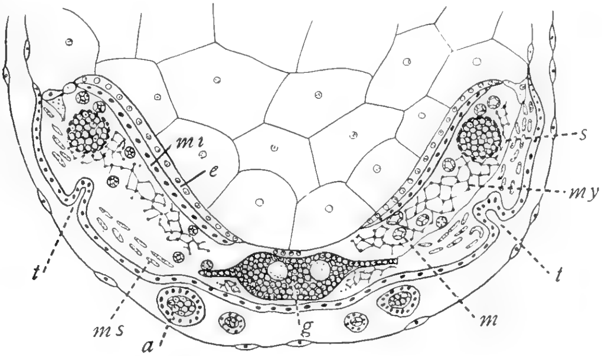
Fig. 200.



Tansverse section of germ layers of *Clytra*. *c*, cœlom sac; *n*, neuroblasts (primitive nervous cells).—After Lécaillon.

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. 202), and the lateral arms of the two elongate and join so that the entodermal masses become connected by two lateral strands of cells; 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.

FIG. 201.



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 LÉCAILLON.

FIG. 202.

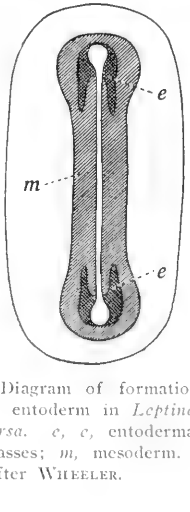
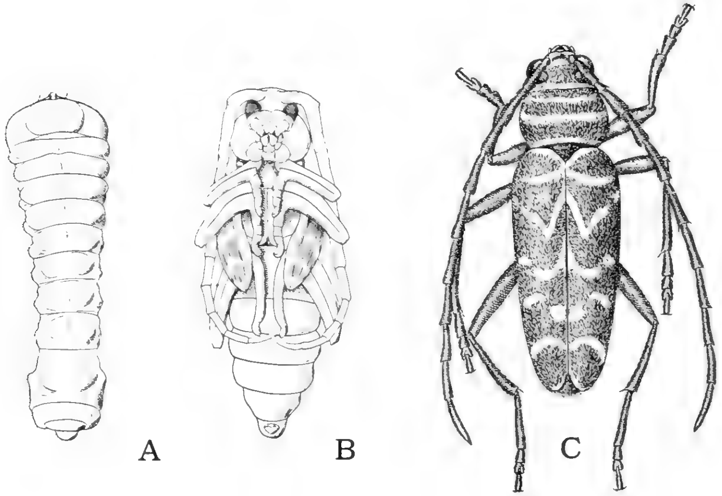


Diagram of formation of entoderm in *Leptinotarsa*. *e*, *e*, entodermal masses; *m*, mesoderm.—After WHEELER.

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. 27) that without experience one could not know that they pertained to the same individual.

Fig. 203.



Cyllene pictus. *A,* larva; *B,* pupa; *C,* imago. × 3.

Holometabola.—The more specialized insects, namely, Neuroptera, Mecoptera, Trichoptera, Lepidoptera, Coleoptera (Fig. 203), Diptera (Figs. 204, 29), Siphonaptera (Fig. 30) and Hymenoptera (Fig. 280), undergo this *indirect,* or *complete,*[1] metamorphosis, involving profound changes of form and distinguished by an inactive pupal stage. These insects are grouped together as *Holometabola.*

Larvæ receive such popular names as "caterpillar" (Lepi-

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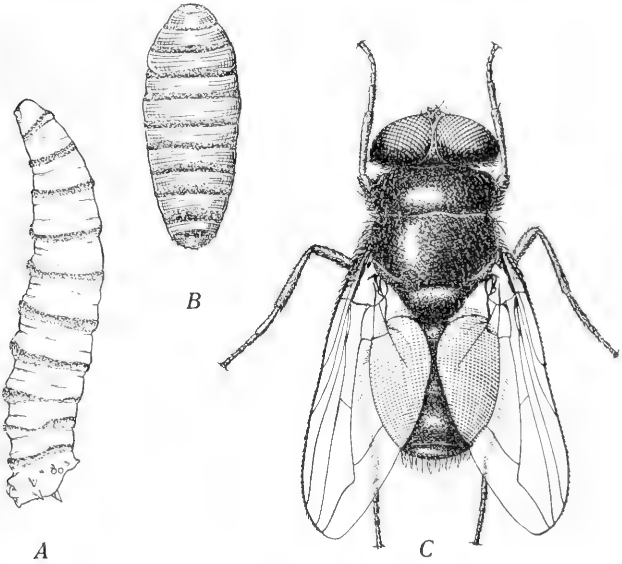
[1] These terms, though somewhat misleading in implication, are currently used.

doptera), "grub" (Coleoptera), and "maggot" (Diptera), while the pupa of a moth or butterfly (especially the latter) is called a "chrysalis."

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; hence the metamorphosis is termed *direct,* or *incomplete.* This type of transformation, without a true pupal period, is characteristic of the more generalized of the metamorphic insects, namely, Orthoptera, Platyptera, Plecoptera, Ephemerida (Fig. 19), Odonata (Fig. 20), Thysanoptera and Hemiptera (Fig. 205). 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.

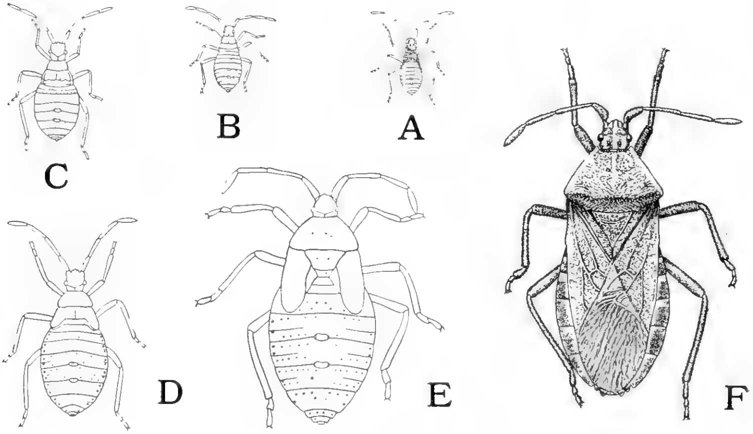
FIG. 204.



Phormia regina. *A,* larva; *B,* puparium; *C,* imago. × 5.

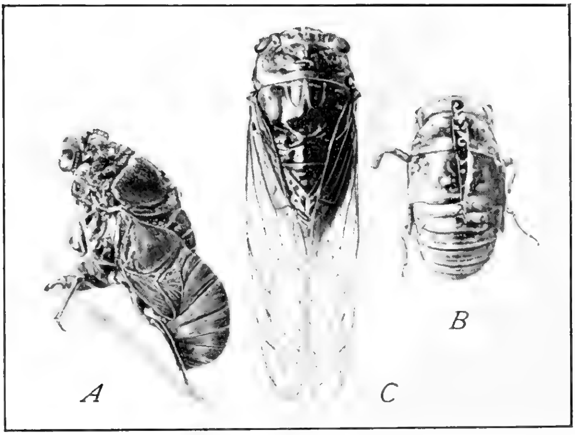
206); while male Coccidæ have what is essentially a complete metamorphosis. In fact, the various kinds of metamorphosis grade into one another in such a way as to make their classification to some extent arbitrary and inadequate.

Fig. 205.



Six successive instars of the squash bug, *Anasa tristis*. × 2.

Fig. 206.



Cicada tibicen. *A,* imago emerging from nymphal skin; *B,* the cast skin; *C,* imago. Natural size.

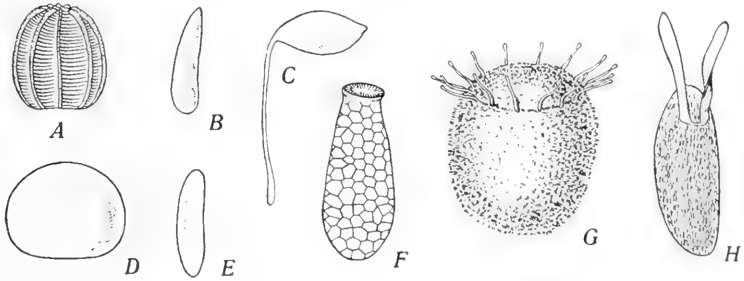
As there is no distinction between larva and pupa in most heterometabolous insects, it is customary to use the term *nymph* during the interval between egg and imago.

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 moult, or *ecdysis,* the appearance of the insect changes more or less. The intervals between the moults are termed *stages,* or *stadia.* To designate the insect at any particular stage, the term *instar* has been proposed and is growing in favor; thus the insect at hatching is the *first instar,* after the first moult the *second instar,* and so on.

Egg.—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

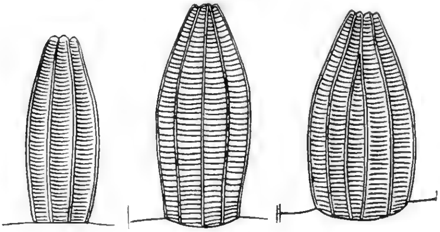
FIG. 207.



Eggs of various insects. *A,* butterfly, *Polygonia interrogationis; B,* house fly, *Musca domestica; C,* chalcid, *Bruchophagus funebris; D,* butterfly, *Papilio troilus; E,* midge, *Cecidomyia trifolii; F,* hemipteron, *Triphleps insidiosus; G,* hemipteron, *Podisus spinosus; H,* fly, *Drosophila ampelophila.* Greatly magnified.

quite fantastic. Something of the variety of form is shown in Fig. 207. 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 *Cecidomyia leguminicola,* which are but .300 mm. in length and .075 mm. in width; the oval eggs of the *cecropia* moth, on the other hand, are as long as 3 mm.

FIG. 208.



Three eggs of the cabbage butterfly, *Pieris rapæ.* Greatly magnified, but all drawn to same scale.

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. 208.

Always the chorion is penetrated by one or more openings, constituting the *micropyle,* for the entrance of spermatozoa.

FIG. 209.

Chrysopa, laying eggs. Slightly enlarged.

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. 209); 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:

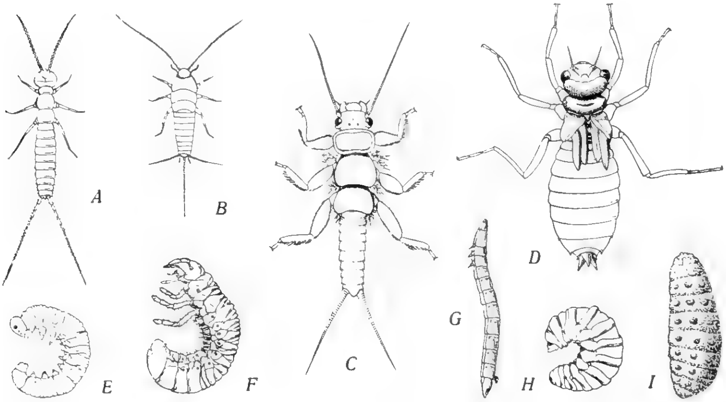
	Maximum.	Minimum.	Average.
Thyridopteryx ephemeræformis	1076	753	941
Clisiocampa americana	466	313	375.5
Chionaspis furfura	84	33	66.5

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 are recognized by Brauer, Packard and other authorities: *thysanuriform* and *cruciform;* respectively generalized and specialized in their organization. The former term is applied to many larvæ and nymphs (Fig. 210, *C, D*) on account of their resemblance to Thysanura, of which *Campodea* and *Lepisma* are types. The resemblance lies chiefly in the flattened form, 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.

Fig. 210.



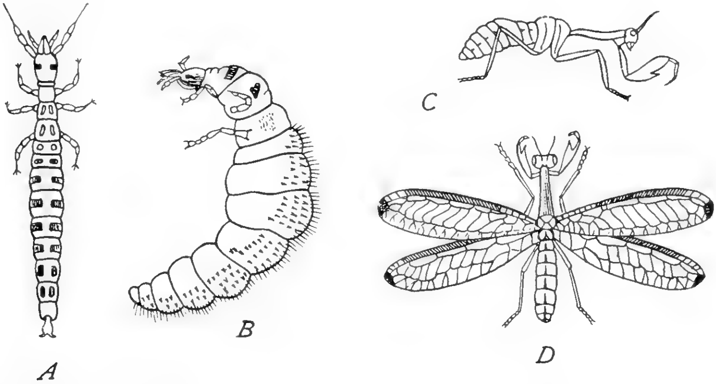
Types of larvæ. *A, B,* Thysanura; *C, D,* thysanuriform nymphs; *E–I,* eruciform larvæ. *A, Campodea; B, Lepisma; C,* perlid nymph (Plecoptera); *D, Libellula* (Odonata); *E, Tenthredopsis* (Hymenoptera); *F, Lachnosterna* (Coleoptera); *G, Melanotus* (Coleoptera); *H, Bombus* (Hymenoptera); *I, Hypoderma* (Diptera).

Thysanuriform characters are most pronounced in nymphs of Blattidæ, Forficulidæ, Perlidæ, Ephemeridæ and Odonata, 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. 210, *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 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,

FIG. 211.



Mantispa. *A*, larva at hatching—*thysanuriform*; *B*, same larva just before first moult—now becoming *cruciform*. *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.

involving the eruciform condition, Packard finds in the neuropterous genus *Mantispa* (Fig. 211), the first larva of which is truly campodea-form 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 moult. 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. 217) 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 (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 moulting, 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 *exuviæ.* The details of the process, however, are by no means simple. Ecdysis is probably something besides a provision for growth, for Collembola continue to moult long after growth has ceased, and the winged May fly sheds its skin once after emergence. The meaning of this is not known, though perhaps ecdysis has an excretory importance in the case of Collembola, which are exceptional among insects in having no Malpighian tubes.

Number of Moults.—The frequency of moulting differs greatly in different orders of insects. Acridiidæ have five moults; Lepidoptera usually four or five, but often more, as in *Isia* (*Pyrrharctia*) *isabella,* which moults as many as ten times (Dyar); *Musca domestica* has three (Packard); the honey bee probably six (Cheshire); and the seventeen-year locust about twenty-five or thirty (Riley). 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 moults by preventing growth, the hypodermis cells meanwhile retaining their activity.

The appearance of the insect often changes greatly with each moult, 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 are very different, as in the dragon fly or the butterfly, 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 (*Zaitha,* 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*).

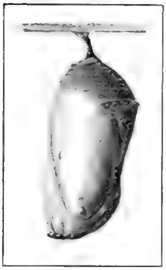
Exposed, sedentary larvæ, as those of many Lepidoptera and Coleoptera, often exhibit highly developed protective adaptations. Caterpillars may be colored to match their surroundings and may resemble twigs, bird-dung, etc.; or larvæ may possess a disagreeable taste or repellent fluids or spines, these 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* (*Pyrrharctia*) *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. 218) 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. 212), 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. 203). This distinction, however, cannot always be drawn sharply. Diptera present also the *coarctate* type of pupa (Fig. 204), in which the pupa remains enclosed in the old larval skin, or *puparium*.

FIG. 212.

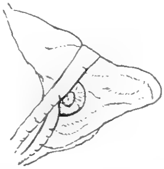


Obtect pupa of milkweed butterfly, *Anosia plexippus*, natural size.

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. 213) suggesting an ancestral active condition, such as still occurs among heterometabolous insects.

Pupation of a Caterpillar.—The process of pupation in a caterpillar has been carefully observed by Riley. The caterpillar of the milkweed butterfly (Pl. 1, *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.

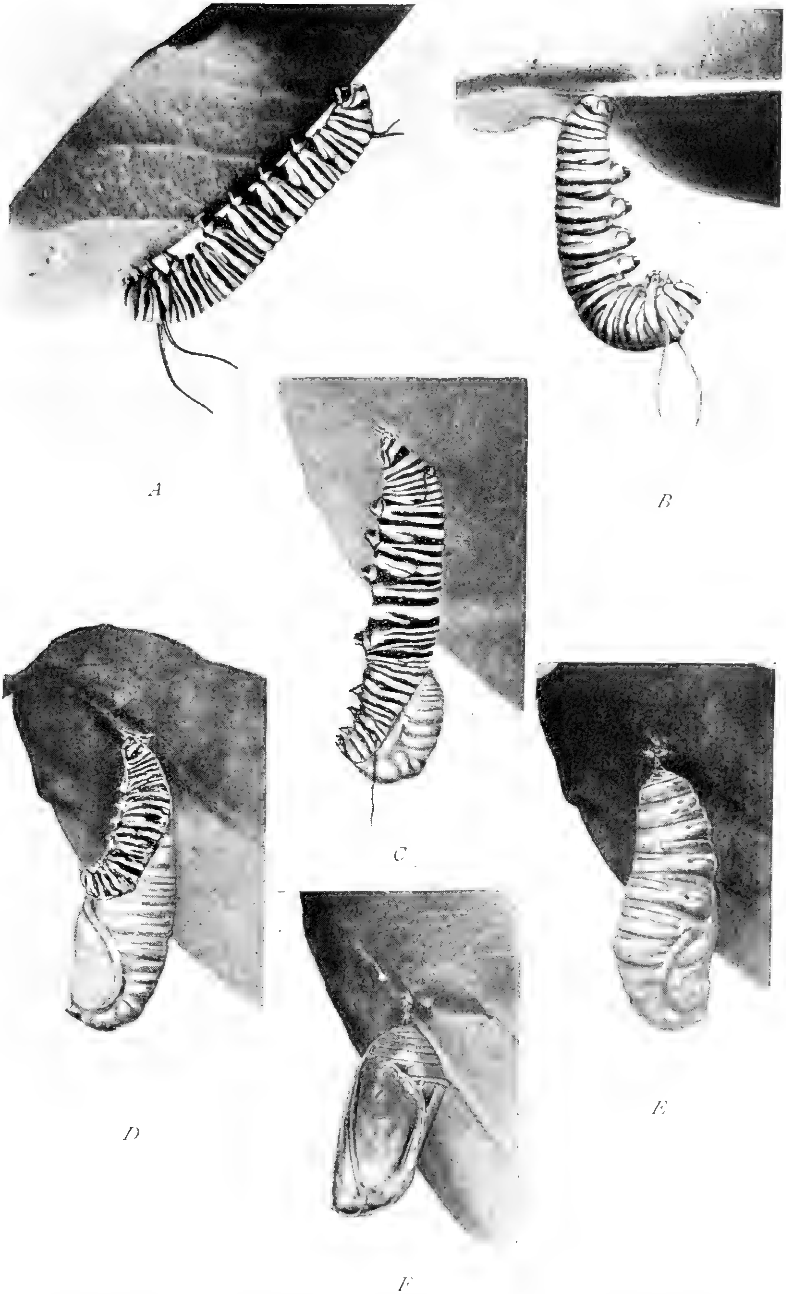
FIG. 213.



Head of chrysalis of *Papilio polyxenes*, to show eye-like structure. Enlarged.

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 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

PLATE I.

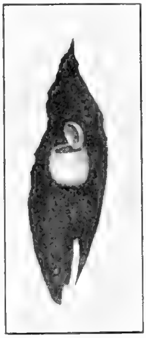


Successive stages in the pupation of the milkweed caterpillar, *Anosia plexippus.*
Natural size.

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. 230), and the respiratory tubes of *Culex* (Fig. 229).

FIG. 214.

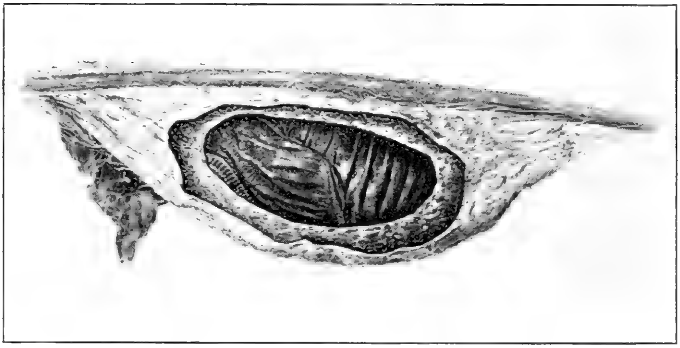


Cocoon of *Chrysopa*, after emergence of imago. Slightly enlarged.

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 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 cell being strengthened with a cementing fluid or more or less silk, forming a rude cocoon. Silken cocoons are spun by some Neuroptera (Chrysopidæ, Fig. 214), by Trichoptera (whose cases are essentially cocoons), Lepidoptera, a few Coleoptera (as Curculionidæ, *Donacia*), some Diptera (as Cecidomyiidæ), 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. 215), 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 water-proof 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.

Fig. 215.

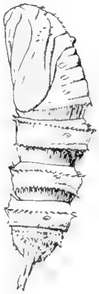


Cocoon of *Samia cecropia*, cut open to show the two silken layers and the enclosed pupa. Natural size.

Butterflies have discarded the cocoon, the last 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 pupæ are supported by a silken girdle (Fig. 27), and nymphalid chrysalides hang freely suspended by the tail (Fig. 212).

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 fibres are spread between them in all directions, and soon the ovoid form of the cocoon distinctly appears. This seems to 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 of 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.)

Fig. 216.



Subterranean pupa of *Anisota*. Enlarged.

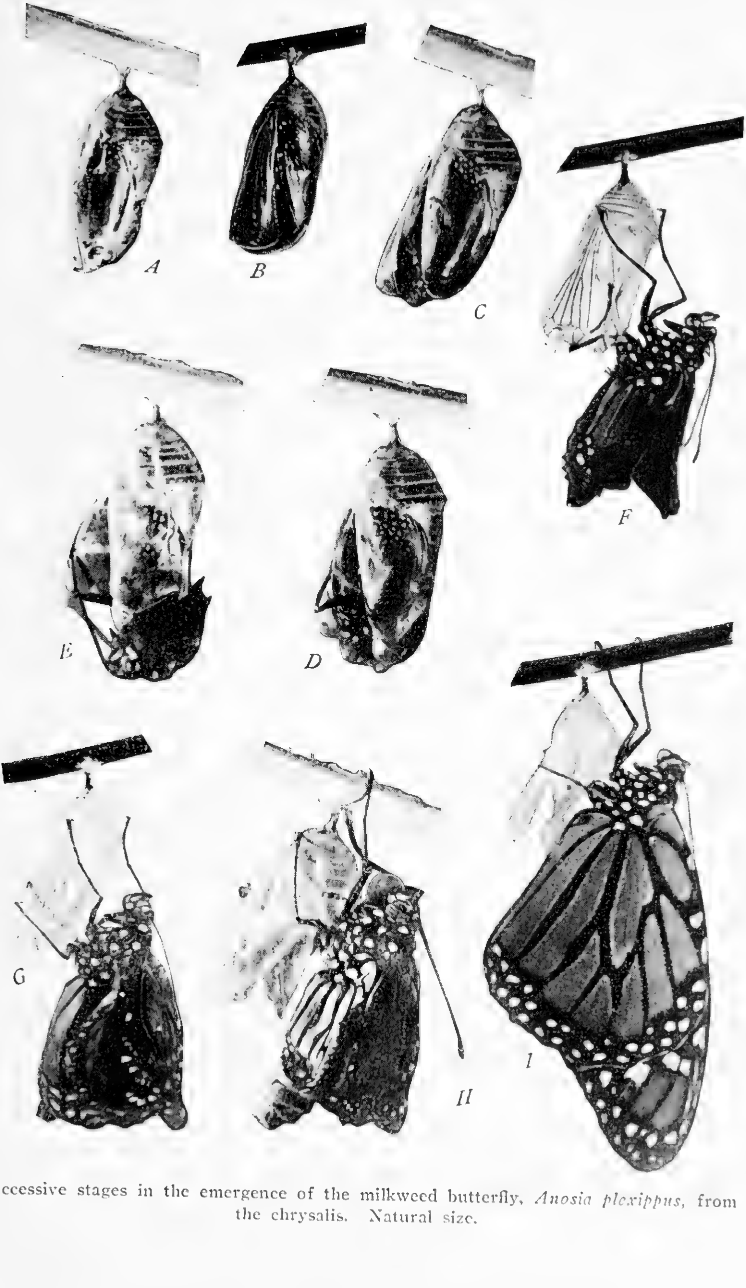
Emergence of Pupa.—Subterranean pupæ wriggle their way to the surface of the ground, often by the aid of spines (Fig. 216) that catch successively into the surrounding soil. These locomotor spines may occur on almost any part of the pupa, but occur commonly on the abdominal segments, as in lepidopterous 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. Hemerobiidæ, 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. 2, *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 disengaged, and the acid fluid flows from its

PLATE II.



Successive stages in the emergence of the milkweed butterfly, *Anosia plexippus*, from the chrysalis. Natural size.

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.

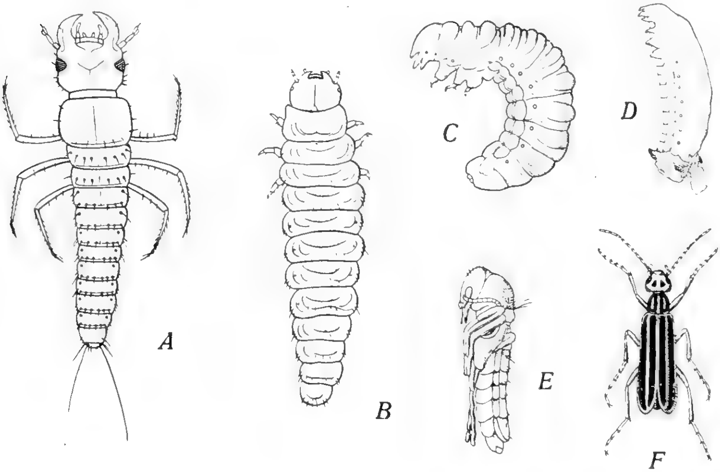
"When the still immature moth has found a suitable place, it remains quiet for a few minutes, and then the wings are seen to grow very rapidly by the afflux of the fluids from the abdomen. In about twenty minutes the wings attain their full size, but they are still like a piece of wet cloth, without 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 fibers which hold the wing-membranes closely together (Mayer). *Samia cecropia* also uses a dissolvent fluid; *Tropæa luna, Philosamia cynthia* and others 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.

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 *Meloe, Epicauta, Sitaris, Rhipiphorus* and *Stylops,* in male Coccidæ and several parasitic Hymenoptera.

In *Meloe,* as described by Riley, the newly-hatched larva (*triungulin* form) 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 moult, 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 moult 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. 217, *A*) of *E. vittata* burrows into an egg-pod of *Melanoplus differentialis* and eats the eggs of that grasshopper. After a moult the *second larva* (*carabidoid* form) appears; this (*B*) is soft, with reduced legs and mouth parts and less active than the triungulin. A second moult and the *scarabœidoid* 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 moult occur with little change in the form of the second larva, which is now in its *ultimate* stage (*C*). After the fifth moult, however, the *coarctate larva*, or *pseudo-pupa*, appears; this (*D*) hibernates and in spring sheds its skin and becomes the *third larva*, 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.

FIG. 217.

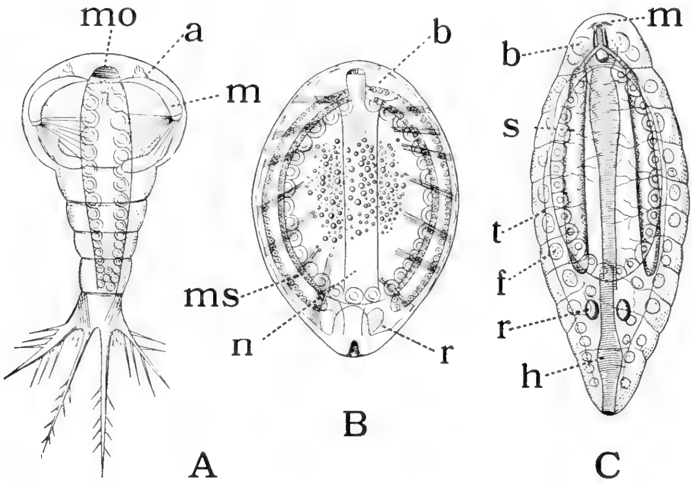


Stages in the hypermetamorphosis of *Epicauta*. *A*, triungulin; *B*, carabidoid stage of second larva; *C*, ultimate stage of second larva; *D*, coarctate larva; *E*, pupa; *F*, imago. *E* is species *cinerea;* the others are *vittata*. All enlarged except *F*.—After RILEY, from Trans. St. Louis Acad. Science.

In the anomalous beetle *Stylops*, the males are winged, but the females are maggot-like and sedentary, living in the bodies of bees and wasps. Packard found as many as three hundred triungulin larvæ issuing from a female *Stylops* in the body of an *Andrena*. The further life history of *Stylops* is but imperfectly known; probably the triungulin climbs upon a bee or a wasp and enters its body, after the manner of the European *Rhipiphorus paradoxus*, whose life-history is much better understood.

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, hatches into a larva of bizarre form (Fig. 218, *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 moult the outline is oval (*B*), and there are no appendages as yet, though the nervous system is partially developed. Another moult, and the third larva appears (*C*), elliptical in contour, externally segmented, with tracheæ and a pair of mandibles.

Fig. 218.



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.

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 (*Œcanthus*). 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.

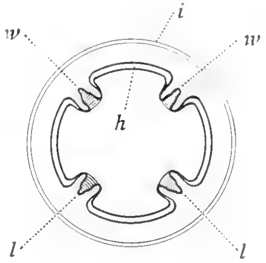
With Neuroptera, the pupal stage appears. In these and all other holometabolous insects the larva accumulates a surplus of nutriment sufficient for the further development, which becomes condensed into a single pupal stage, during which external activity ceases temporarily.

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 quiescent period of reconstruction becomes inevitable.

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.

FIG. 219.

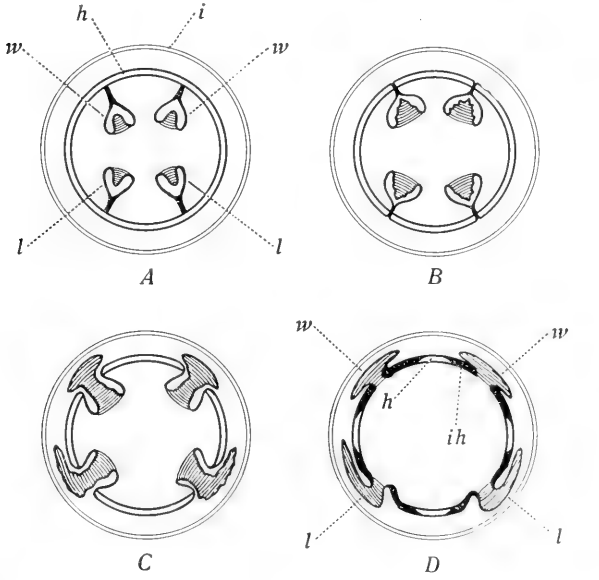


Diagrammatic transverse section of *Corethra* larva, to show imaginal buds of wings (*w*) and legs (*l*); *h*, hypodermis; *i*, integument.—Modified from Lang's *Lehrbuch*.

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

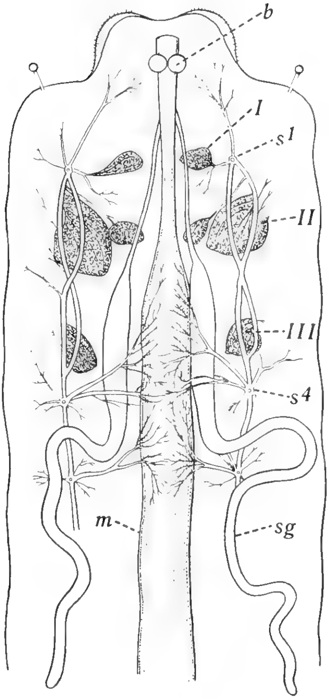
FIG. 220.



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*.

indirect, however, 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.

FIG. 221.



Imaginal buds of full grown larva of *Pieris*, dorsal aspect. *b*, brain; *m*, mid intestine; s^1, prothoracic spiracle; s^4, first abdominal spiracle; *sg*, silk gland; *I*, prothoracic bud; *II*, bud of fore wing; *III*, bud of hind wing.—After GONIN.

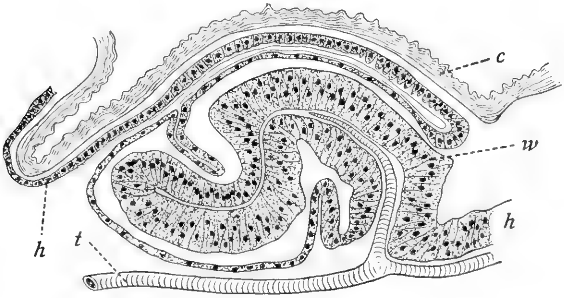
Phagocytes.—The destruction of larval tissues, or *histolysis*, is due often to the amœboid blood corpuscles, known as *leucocytes* or *phagocytes*, which attack some tissues and absorb their material, but later are themselves food for the developing imaginal tissues. The construction of tissues is termed *histogenesis*.

In Coleoptera, however, 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, or *imaginal buds*, 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. 219), 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 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,* indeed, is in many respects intermediate between heterometabolous and holometabolous insects as regards its internal changes.

FIG. 222.



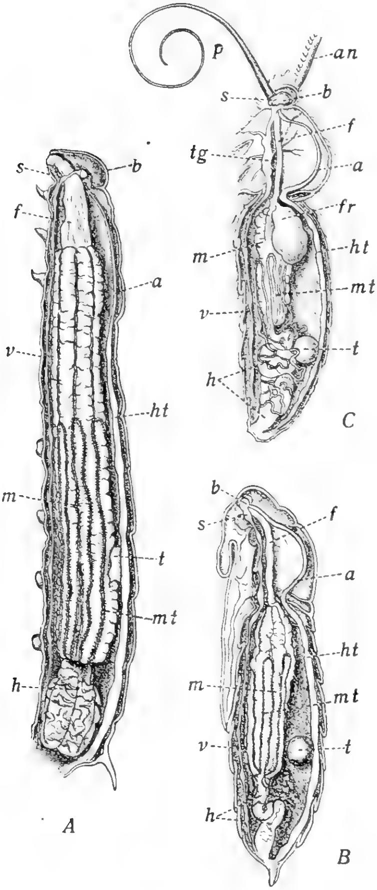
Section through left hind wing in larva of *Pieris rapæ,* the section being a frontal one of the caterpillar; the base of the wing is anterior in position,. and the apex posterior. *c,* cuticula; *h,* hypodermis; *t,* trachea; *w,* developing wing.—After MAYER.

Muscidæ.—In Muscidæ, as compared with *Corethra,* the imaginal buds are more deeply situated, the peripodal membrane forming a stalk (Fig. 220), 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.

FIG. 223.



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*, subœsophageal ganglion; *t*, testis; *tg*, thoracic ganglia; *v*, ventral nerve cord.—After NEWPORT.

Hymenoptera and Lepidoptera.—The internal transformation in Hymenoptera, according to Bugnion, is less profound than in Muscidæ 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 a full-grown caterpillar the fundaments of the imaginal legs and wings (Fig. 221) may be seen, the wings in a frontal section of the larva appearing as in Fig. 222. Many of the details of the internal metamorphosis in Lepidoptera have been described by Newport and Gonin. Figure 223, 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 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 many 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, but 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.

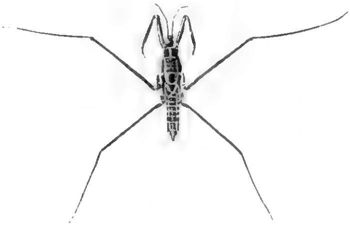
Food.—Insects have become adapted to utilize with remarkable success the immense and varied supply of food that the water affords. Hosts of them attack such parts of plants as project above the surface of the water, and the caterpillar of *Paraponyx* (Fig. 171) feeds on submerged leaves, especially of *Vallisneria*, being in this respect 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 *Chironomus* find food in the sediment that accumulates at the bottom of a body of water.

Predaceous species abound in the water. *Notonecta* (Fig. 224) approaches its prey from beneath, clasps it with the front pair of legs and pierces it. *Nepa* and *Ranatra* likewise have prehensile front legs along with powerful piercing organs. *Belostoma* and *Benacus* (Fig. 22) even kill small fishes by their poisonous punctures. Some other kinds, as the water-skaters (Gerridæ, Fig. 225), depend on dead or disabled insects. The species of *Hydrophilus* (Fig. 226) are to some extent carnivorous as larvæ but phytophagous as imagines, while Dytiscidæ are carnivorous throughout life. Aquatic insects eat not only other insects, but also worms, crustaceans, mollusks or any other available animal matter.

FIG. 224.

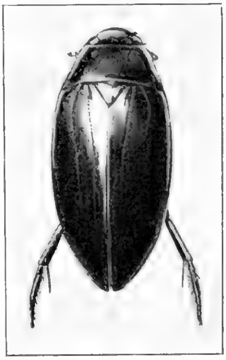
Backswimmer, *Notonecta insulata*, natural size.

FIG. 225.



Water-skater, *Gerris remigis*, natural size.

FIG. 226.

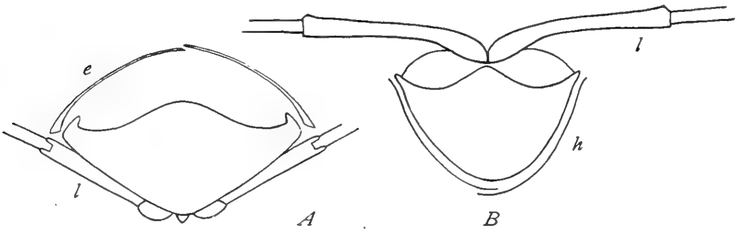


Hydrophilus triangularis, natural size.

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.

Locomotion.—Excellent adaptations for aquatic locomotion are found in the common *Hydrophilus triangularis* (Fig. 226). 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 friction. Owing to the form of the body (Fig. 227, *A*) and the presence of a dorsal air-chamber under the elytra, the back of the insect tends to remain uppermost, while in *Notonecta* (Fig. 227, *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. 228, *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 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*.

FIG. 227.

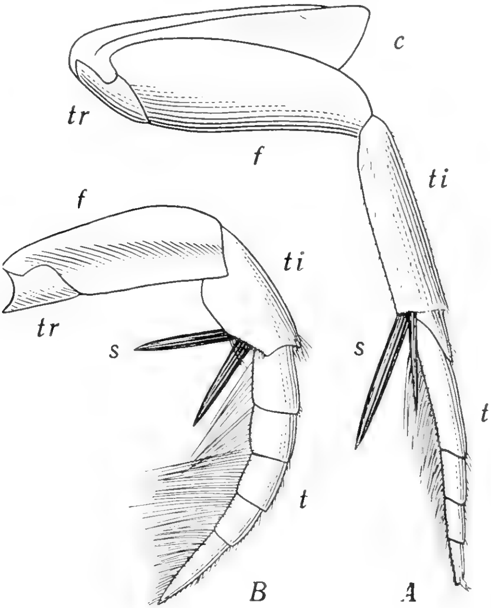


Transverse sections of (*A*) *Hydrophilus* and (*B*) *Notonecta*. *e*, elytron; *h*, hemelytron; *l*, metathoracic leg.

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.

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. 229, *A*) is often heavier than water, but the pupa (Fig. 229, *B*) is lighter, and remains clinging to the surface film.

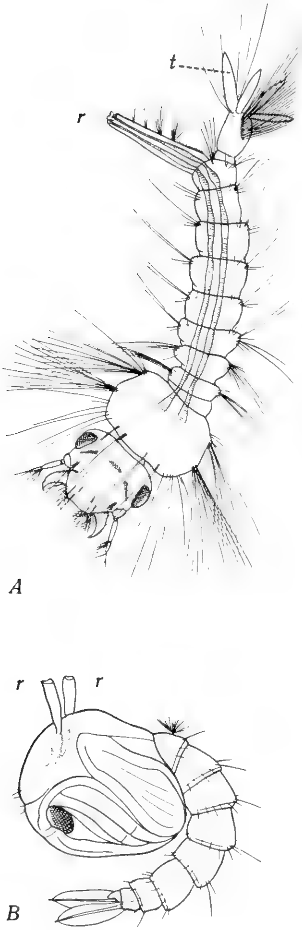
FIG. 228.



Left hind legs of aquatic beetles. *A*, *Hydrophilus triangularis*; *B*, *Cybister fimbriolatus*; *c*, coxa; *f*, femur; *s*, spur; *t*, tarsus; *ti*, tibia; *tr*, trochanter.

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.

FIG. 229.



Larva (*A*) and pupa (*B*) of mosquito, *Culex pipiens*. *r*, respiratory tube; *t*, tracheal gills.

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.

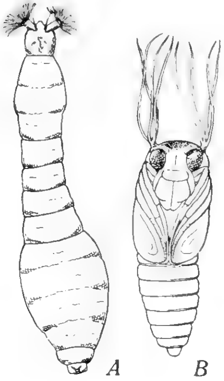
Respiration.—Aquatic insects have not only retained the primitive, or open (*holopneustic*), type of respiration, characterized by the presence of spiracles, but have also developed an adaptive, or closed (*apneustic*), type, for utilizing air that is mixed with water.

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 *Notonecta* bears on its body a silvery film of air entangled in closely set hairs, which exclude the water. *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. *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. 229, *A, r*) projecting from the penultimate abdominal segment; the pupa, however, bears a pair of respiratory tubes on the back of the thorax (Fig. 229, *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. 172), 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, however, is 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, enable these forms to obtain air from the water. May fly nymphs (Figs. 19, *A*; 169), 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. 19, *A*). *Caudal gills* are found in agrionid nymphs (Fig. 170). The aquatic caterpillars of *Paraponyx* (Fig. 171) are unique among Lepidoptera in having gills, which are filamentous in this instance.

Fig. 230.



Simulium; *A*, larva; *B*, pupa, showing respiratory filaments.

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. 230) secure a continuous supply of fresh air simply by fastening themselves to rocks in swiftly flowing streams.

Rectal respiration is highly developed in odonate and ephemerid 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.

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 debris; 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, forming 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. Acridiidæ, 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, Zaitha,* 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, Acridiidæ and Gryllidæ, nearly all the rest were dead or dying, including the dragon flies, flies, bumble bees 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. 92) just as in the case of the "diffraction gratings" used by the physicist, which consist of a glass or metallic plate with parallel 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 1050 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 are as far apart as .0015 mm., though numbering 1,700 per millimeter.

These 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 metallic blues and greens, and iridescence in general, are often produced by minute lines or pits that diffract the light. Purely structural colors, however, are not so common as might be supposed, according to Tower, who says, "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."

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. 88). Cockroaches are almost white just after a moult, 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. Tower finds, however, that cuticular colors "are not due to drying, oxidation, secretion, or like processes," but are due to "some katalytic agent or enzyme [formed by the hypodermis] which, passing out through the pore canals, comes in contact with the primary cuticula and there becomes the active factor in the production of cuticula colors."

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 *Leptinotarsa decemlineata* the pattern "is composed of a dark cuticular pigment upon a yellow hypodermal background."

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. According to Tower, chemico-physical colors "which are of exceedingly wide occurrence, are also the most brilliant and varied of all those found in insects. To this class belong all metallic, iridescent, pearly, and translucent colors, as well as blue, green, and violet in almost every case."

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 derivatives 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, *Heliothis armiger* (corn worm) and the sphingid *Deilephila linaata.* Furthermore, striking changes of coloration accompany each moult 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 sustension 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 *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.

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 recently 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, are little understood, but appear to be due chiefly to temperature.

Albinism is exceptional whiteness or paleness of coloration, and is due usually to lack or 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. Indeed, as Scudder observes, albinism among butterflies in America appears to be confined to a few Pieridæ, and to be restricted to the female sex; it is more common in subarctic and subalpine regions than in lower latitudes and altitudes, and only in the former places does it include all the females. At low altitudes, instead of appearing early in the year as might be expected, the albinic forms appear during the warmer months.

In Europe there are many albinic species of butterflies, and they are by no means confined to the 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.

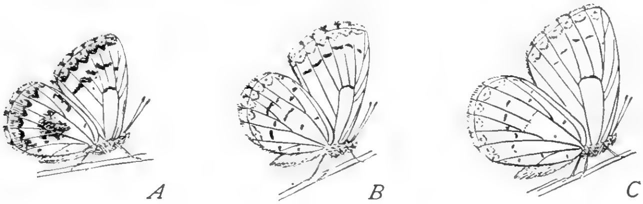
In warm latitudes, some females of our *Papilio glaucus* are blackish brown with black markings, instead of being, as usual, yellow with black markings. In the South, some males of the spring brood of *Cyaniris pseudargiolus* are partly or wholly brown instead of blue.

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. 231), is polymorphic to a remarkable degree. In the high latitudes of Canada, a 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. 231.



Cyaniris pseudargiolus; A, form *lucia; B, violacea; C, pseudargiolus* proper. Natural size.

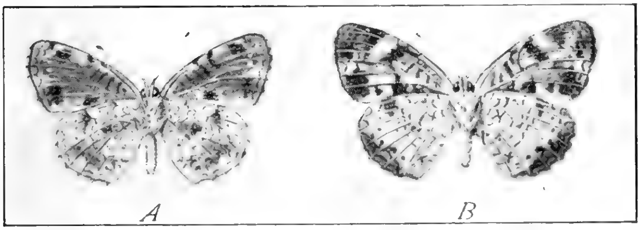
Iphiclides ajax (Fig. 232) is another polymorphic butterfly whose life history is complex. The three principal varieties of this species, known respectively as *marcellus, telamonides* and *ajax,* differ not only in coloration, but also in size and form; *marcellus* appears first, in spring; *telamonides* 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.

FIG. 232.

Iphiclides ajax, form *telamonides*, on flower of button bush. Reduced.

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*.

FIG. 233.



Phyciodes tharos; A, spring form, *marcia; B*, summer form, *morpheus;* under surfaces. Natural size.

In *Phyciodes tharos* (Fig. 233) 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 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 argues that, in addition to the direct effect of temperature, alternative inheritance also plays an important part in the production of seasonal varieties. He tries 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 does 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.

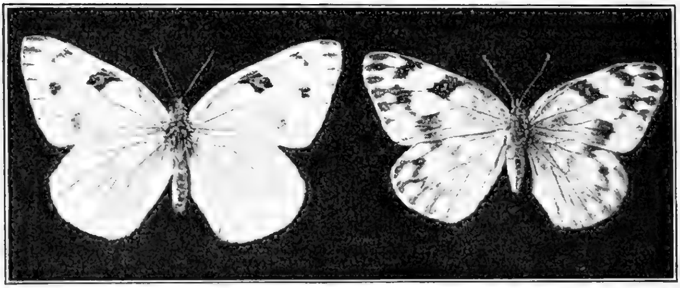
These investigators and others, notably Merrifield and Fischer, have accumulated a considerable mass of experimental evidence, the interpretation of which is in many respects difficult, involving as it does, not merely the direct effect of temperature upon the organism, but also deep questions of heredity, 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 differentiation of ornamentation for which Lepidoptera are unrivaled.

The male of *Pieris protodice* (Fig. 234) has a few brown spots on the front wings; the female is checkered with brown on both wings. In *Colias philodice* (Fig. 235) and *C. eurytheme* the marginal black band of 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

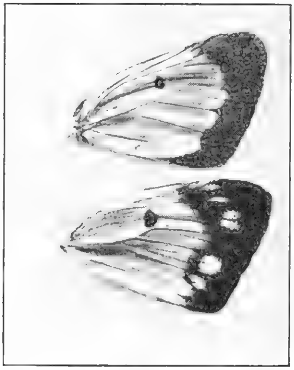
FIG. 234.



Pieris protodice; male (on the left) and female (on the right). Natural size.

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. 236), the gypsy 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 (*Sanninoidea 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 do males of *Cyaniris pseudargiolus* and females of *Papilio glaucus,* already mentioned. *Papilio merope,* of South Africa, is remarkable in having three females (Frontispiece, Figs. 5, 7, 9, 11) 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.

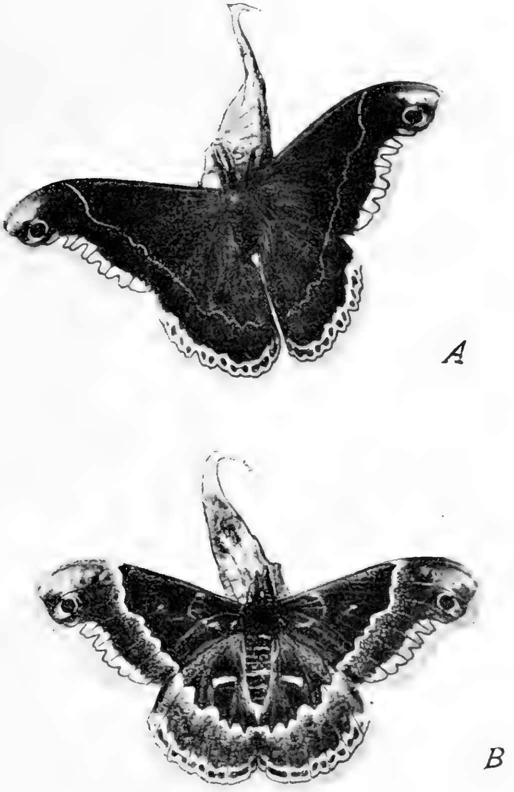
FIG. 235.



Colias philodice; right fore wing of male (above) and of female (below). Natural size.

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.

Fig. 236.



Callosamia promethea; A, male, clinging to cocoon; *B,* female. Reduced.

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 with remarkable precision 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 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. 237) "is developed in connection with a muscle, and marks the point of attachment of its fibers 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. The development of coloration in the individual, however, has as yet received but little attention—excepting the excellent studies of Mayer and of Tower. Butterflies, moths and beetles have naturally been preferred by most students of the subject.

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."

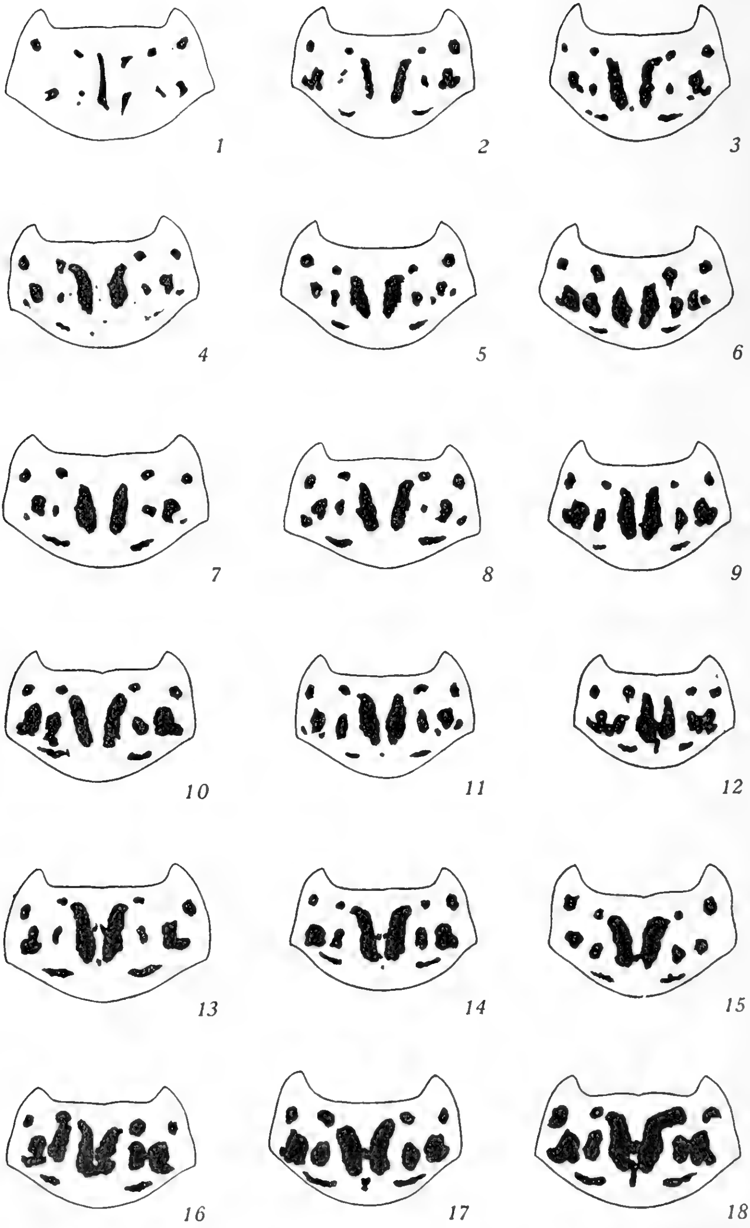
Briefly, one or more bands may break up into spots or bars, the breaks occurring either between the veins or, more commonly, at the veins; and in the latter event, short bars or more or less quadrate or rounded spots arise in the interspaces. From simple round spots there may develop, as Darwin and others 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.

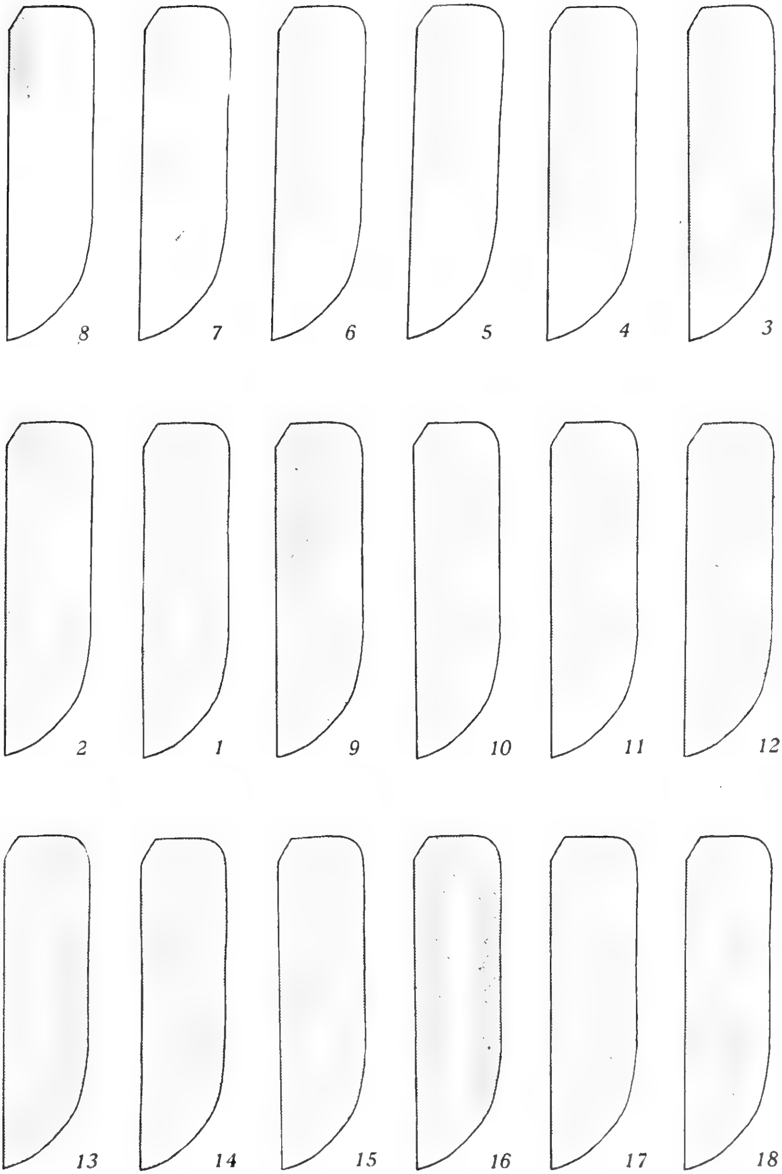
Variation in Coloration.—It is safe to say that no two insects are colored exactly alike. Some species, however, are

FIG. 237.



Colorational variations of the pronotum of the Colorado potato beetle, *Leptinotarsa decemlineata.*

FIG. 238.



Elytral color patterns of species 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. vulgaris; 2, generosa; 3, generosa; 4, pamphila; 5, limbata; 6, togata; 7, gratiosa; 8, canosa; 9, tenuisignata; 10, marginipennis; 11, hentzii; 12, sexguttata; 13, hæmorrhagica; 14, splendida; 15, imperfecta; 16, lemniscata; 17, gabbii; 18, saulcyi.*—After HORN, from Entomological News.

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. 237, and that of *Cicindela* in Fig. 238.

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. In the words of Dr. Horn: " (1) The *type* of marking is the same in all our species. (2) Assuming a well-marked species (*vulgaris,* Fig. 238, *1*) 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 *vulgaris, 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.

Variations in general fall into two classes: *continuous* (*individual variations*) and *discontinuous* (*sports*). 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.

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 *Melasoma 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 *Pœcilocapsus 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 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. Here, however, these colors are structural, and their variations are to be attributed to slight differences in the spacing of the surface elevations or depressions.

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.

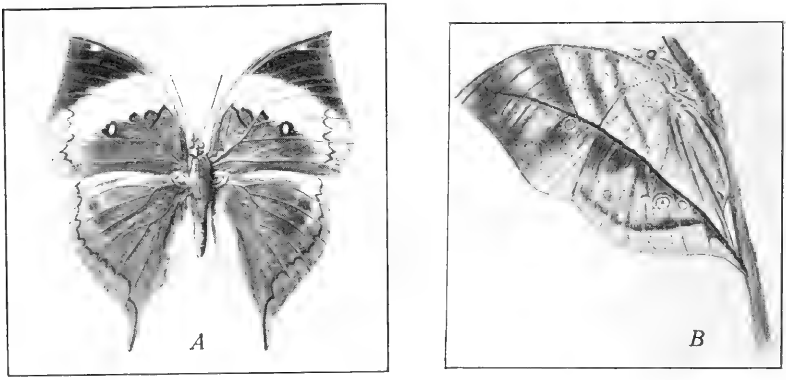
These changes of color are apparently of no use to the insect, being merely incidental effects of light, temperature or other inorganic influences.

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. paraklcta* of the Malay Archipelago. The former species (Fig. 239) 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 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,

FIG. 239.



Kallima inachis; A, upper surface; *B,* with wings closed, showing resemblance to a leaf. × ½.

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 a recent discussion as to whether it usually rests in precisely 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.

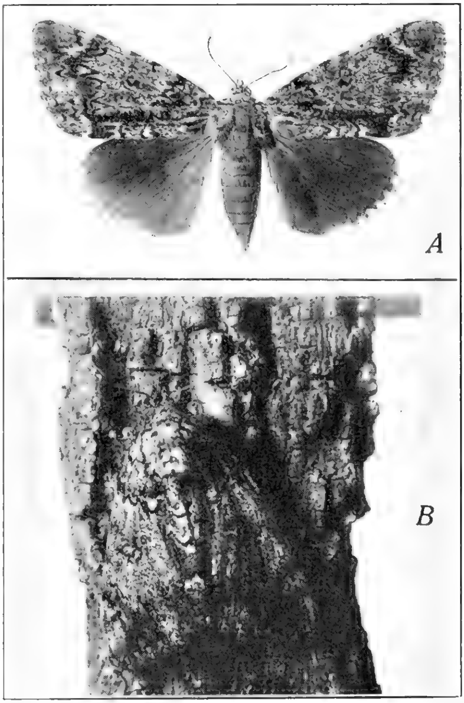
Some of the tropical Phasmidæ counterfeit sticks, green leaves, or dead leaves with minute accuracy. Our common phasmids, *Diapheromera femorata* and *velici* (Fig. 240), are well known as "stick insects"; indeed, it is not necessary to go beyond the temperate zone to find plenty of examples of protective 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

Fig. 240.

Diapheromera velici, on a twig. Natural size.

they rest (Fig. 241), with their conspicuous and usually showy hind wings concealed under the protectively 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 perhaps owe their inconspicuousness partly to their oblique lateral stripes, which cut a mass of green into smaller areas. The caterpillar of *Schizura ipomœæ* (Fig. 242), which is green with brown patches, rests

Fig. 241.



Catocala lacrymosa; A, upper surface; *B,* with wings closed, and resting on bark. Reduced.

for hours along the eaten or torn edge of a basswood leaf, in which position 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

FIG. 242.

Caterpillar of *Schizura ipomææ* clinging to a torn leaf. Natural size.

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; *Trimerotropis maritima* is practically invisible against the gray sand of the seashore or other places to which it restricts itself; and *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.

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 caterpillar 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, their 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 less 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 protective 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 *Murgantia histrionica* and other large showy bugs are usually avoided by birds; that the showy, ill-flavored 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.

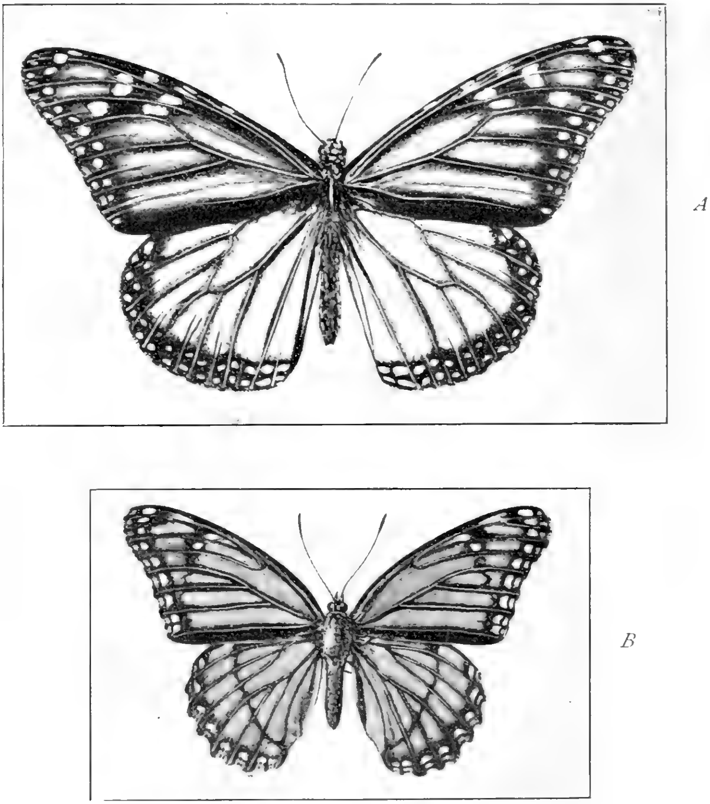
Generally speaking, hairs, stings and other protective devices are accompanied by conspicuous colors—though there are many exceptions to this rule. These warning colors, however, fail to accomplish their supposed purpose in the following instances, given by Judd. Taking insects that are thought to be 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 gypsy 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, bumble bees are eaten by the bluebird, blue-jay and two flycatchers; the honey bee, by the wood pewee, phœbe, 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, however, must have been present 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 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. 243, *B*), which departs widely from the prevailing dark coloration of its genus to imitate the milkweed butterfly, *Anosia*

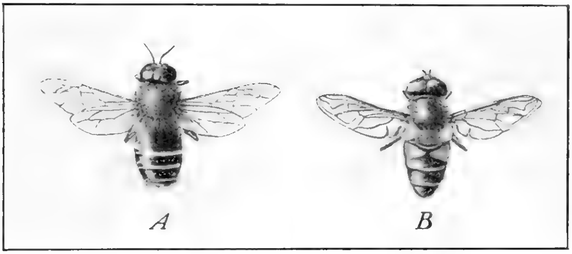
Fig. 243.



A, Anosia plexippus, the "model"; *B, Basilarchia archippus,* the "mimic." Natural size.

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. 244, *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 are remarkably like bumble bees in superficial appearance and certain *Syrphus* flies mimic wasps with more or less success. The beetle *Casnonia* bears a remarkable resemblance to the ants with which it lives.

Fig. 244.



Protective mimicry. *A*, drone bee, *Apis mellifera*; *B*, drone fly, *Eristalis tenax*. Natural size.

The classic cases are those of the Amazonian Heliconiidæ and Pieridæ, in which mimicry was first detected by Bates. The Heliconiidæ (Frontispiece, Fig. 1) are abundant, vividly colored and eminently free from the attacks of birds and other enemies of butterflies, on account of their disagreeable odor and taste. Some of the Pieridæ—a family fundamentally different from Heliconiidæ—imitate (Frontispiece, Fig. 2) the protected Heliconiidæ so successfully, in coloration, form and flight, that while other Pieridæ are preyed upon by many foes, the mimicking species tend to escape attack.

The family Heliconiidæ, referred to by Bates, comprised what are now known as the subfamilies Heliconiinæ, Ithomiinæ and Danainæ; similarly, Pieridæ and Papilionidæ are now often termed respectively Pierinæ and Papilioninæ. Ithomiinæ are mimicked also by Papilioninæ and by moths of the families Castniidæ and Pericopidæ.

The discoveries of Bates in tropical South America were paralleled and supported by those of Wallace in India and the Malay Archipelago (where Danainæ are the chief "models"), and of Trimen in South Africa (where Acræinæ and Danainæ serve as models). Trimen discovered a most remarkable case, in which three species of Danainæ are mimicked, each by a distinct variety of the female of *Papilio merope* (Frontispiece, Figs. 5–11).

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 (Frontispiece, Figs. 1, 4), 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 Euplœinæ, 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.

From this explanation, the superior value of Müllerian as compared with Batesian mimicry is evident.

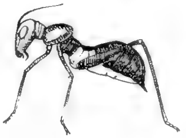
The fourth condition—that the imitators differ from the bulk of their allies—holds true to such a degree that even the two sexes of the same species may differ extremely in coloration, owing to the fact that the female has assumed the likeness of some other and protected species. The female of *Papilio merope,* indeed, occurs (as was just mentioned) under three varieties, which mimic respectively three entirely dissimilar species of Danainæ, and none of the females are anything like their male in coloration (Frontispiece, Figs. 5–11). The specific identity of these four South African varieties of *merope* has been established by Trimen, Marshall and other investigators.

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 Heliconiidæ or between the chrysomelid genera *Lema* and *Diabrotica*. The nearer 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.

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 locustid of the Soudan resembles an ant (Fig. 245), 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

FIG. 245.



A locustid, *Myrmecophana fallax*, which resembles an ant. Twice natural length. From BRUNNER VON WATTENWYL.

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 recently 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 nearly 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. Until the last few years, however, there was altogether too little positive 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 recently 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, *Acræa 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, there are very few recorded instances of this for our temperate region. It may then be asked, what advantage does the "viceroy" (Fig. 243, *B*) gain by resembling the "monarch," in a region where *all* butterflies are exempt from destruction by birds? In reply, it may be said that the premise of the argument is as yet little more than an assumption, because so little attention has been given to the relations between birds and butterflies in our own country. Or, admitting the premise, it may be said that the resemblance was advantageous once, if not now; and that 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 Heliconiinæ 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 phœbe; 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. Bumble bees 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 heliconids. 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 [compare Figs. 2 and 3 of Frontispiece] 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 heliconid 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.

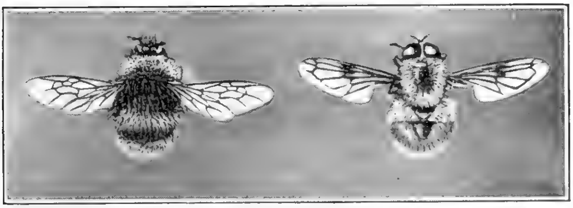
It is highly desirable, of course, that this plausible explanation should be tested as far as possible by observations in the field and by experiments as well.

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. 246); 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.

FIG. 246.



Aggressive mimicry. On the left, a bee, *Bombus mastrucatus;* on the right, a fly, *Volucella bombylans.* Natural size.

Aggressive Resemblances.—The resemblance of a carnivorous animal to its surroundings may not only be protective but may also 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 bumble bees 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

ORIGIN OF ADAPTATIONS AND OF SPECIES

1. ADAPTATIONS

Organic Evolution.—Organic evolution is essentially the evolution of adaptive structures and functions. There remain to be explained, however, non-adaptive structures and functions, and no theory of evolution is adequate which does not account for the useless as well as the useful characters.

Existing structures are due to the nature of the organism and the nature of the environment; in other words, are results of the activity of protoplasm under the influence of environmental forces. Variations arise which are useful or not and either transmissible or not. Useful transmissible variations not only remain but tend to become more nearly perfect; while useless variations tend to disappear.

The various theories of organic evolution differ chiefly in their answers to these questions: (1) What is the nature of variations and how do they arise? Variations are classed as either continuous or discontinuous; adaptive or unadaptive. In asexual organisms, variations are brought about by the direct influence of temperature, light and other primary factors upon protoplasm; in sexual organisms, variations are due to another cause as well, namely, the union of two kinds of protoplasm. In any given case of variation, how much is due immediately to protoplasm and how much to the environment? (2) What kinds of variations are transmissible? Discontinuous variations (sports) are strongly transmissible as a rule, while continuous (individual) variations are often non-transmissible; though it is often difficult to decide whether they are transmissible or not. Each kind of variation has to be examined separately, on its own merits. Difficulties arise from the fact that some variations which appear in successive generations are due not to inheritance but to the direct action of the environment on each successive generation; also to the fact that some structural changes may have been brought about by selection of some sort, rather than by inheritance. Are the results of use or disuse or mutilation inheritable? It has not been proved as yet that these "acquired characters" are transmissible. On the other hand, experiments show that some organisms can become acclimatized to unusual degrees of heat, density, etc., through inheritance, in cases where selection does not enter into the problem. Much of the confusion attending the discussion of "the inheritance of acquired characters" has been due to disagreements as to what is meant by the term "acquired characters." (3) What are the secondary influences that have brought about the evolution of structures? Of these influences, natural selection and isolation are by far the most important; while in some instances extensive structural adaptations have arisen spontaneously, without a long course of evolution.

Natural Selection.—The more intricate adaptations of organism to environment, however, are for the most part inexplicable without the aid of Darwin's and Wallace's theory of natural selection. After almost fifty years of searching criticism and even violent opposition, this theory, though modified in some respects, remains essentially as it was formulated, and is at present the working hypothesis of most naturalists. This doctrine is here outlined in its several factors.

Excessive Multiplication.—Any one species of animal or plant, were its multiplication unchecked, would soon cover the earth. The progeny of a single aphid in ten generations, as calculated by Huxley, would "contain more ponderable substance than five hundred millions of stout men; that is, more than the whole population of China." The hop aphid (*Phorodon humuli*), studied by Riley, has thirteen generations a year, consisting entirely of females up to the last generation. Assuming that each female produces 100 young and that the increase is unchecked, the number of individuals of the twelfth generation, as the descendants of a single female of the first generation, would be ten sextillions. These if placed in a single file, allowing 10 aphids to an inch, would form a line so long that light itself, traveling at the rate of 186,000 miles per second, would require over 2,690 years to go from one end of the line to the other.

As it is, many species become temporarily dominant under favorable conditions; for example, the Rocky Mountain locust, chinch bug and gypsy moth. Even one of the least prolific species would predominate in a surprisingly short time, were it permitted to increase in its normal geometrical ratio. The rate of sexual reproduction is highest in fishes and insects. An insect averages one or two hundred eggs, while some forms, as queen termites, lay them by thousands.

Struggle for Existence.—Although a single species is potentially capable of covering the earth, there actually are at least 1,000,000 species of insects, not to mention 250,000 species of other animals and some 500,000 kinds of plants. This means a tremendous prevention of reproduction among the individuals of any one species—an intense " struggle for existence," as Darwin termed it. Among plants and the lower animals, comparatively few individuals survive and reproduce; the majority die. The agents of destruction are manifold, each species having its own army of enemies, organic and inorganic. Thus insects are subject to unfavorable conditions of temperature and moisture, to bacterial and fungous diseases, vertebrate and invertebrate enemies, accidents, etc. The aphids are at the same time among the most prolific and the most defenceless of animals. These delicate insects succumb to very slight mechanical shocks and are killed by extremes of temperature that most other insects can endure. They are often washed off their food plants by rain. Their rate of reproduction decreases if their food plant receives insufficient moisture. Aphids form the chief food of coccinellid larvæ and beetles, are preyed upon by chrysopid and syrphid larvæ, parasitized by Braconidæ and Chalcididæ, carried off by some of the digger-wasps (Mimesidæ, Pemphredonidæ), and devoured by ants, carabids, other insects, spiders, and some birds, as the chickadee. In damp weather, aphids are killed in countless numbers by a fungous disease. In short, the aphid is threatened in every direction.

Elimination of the Unfit.—In the intense "struggle for existence," as it is commonly, though misleadingly, called, those comparatively few individuals that survive do so manifestly by virtue of certain advantages over their less fortunate fellows. One egg can stand a little more cold than another; one beetle drops to the ground when disturbed and thus escapes an attacking bird, while its companions remain in place and are destroyed; some individuals escape by surpassing their fellows in locomotor ability or by resembling the surface on which they happen to rest.

Such fortunate individuals live to transmit their advantageous peculiarities to their progeny, while the less favored individuals succumb. The progeny inherit the life-saving peculiarities in differing degrees, and the least favored of the progeny are again weeded out. Thus by the continual elimination of individuals that vary in unfavorable directions, the individuals that remain become better and better adapted to the surrounding conditions of life, through the preservation and accumulation of advantageous variations. This preservation and accumulation of advantageous variations through the destruction of disadvantageous ones is the essence of natural selection, or the "survival of the fittest."

Favorable variations may have been so slight and infrequent as to have required geological ages for their accumulation. On the other hand, adaptive variations are sometimes so extensive from the beginning as to lead some writers to doubt that these variations are preserved and improved by natural selection.

Variation.—Natural selection cannot *originate* useful characters, of course, but is limited to the preservation and accumulation of such advantageous variations as already exist. Variation, then, is the basis of natural selection. Though the question of the origin of variations is still unsettled, the fact of their occurrence in a manner sufficient for the purposes of natural selection is beyond dispute. No two individuals of a species are ever exactly alike in structure or behavior, and their differences furnish the material for the operation of natural selection.

Two classes of variations are distinguished on the basis of the amount of variation: (1) *continuous* (*individual*) variations, of small extent, intergrading with one another and with the typical form; and (2) *discontinuous* variations (*sports*), or considerable and isolated departures from the normal condition. Furthermore, variations of either class are adaptive or unadaptive, the latter kind being either harmful or simply neutral.

Origin of Adaptive Variations.—Natural selection, as was said, does not begin to operate until useful variations are already in existence; and the origin of these primary adaptive variations is a question quite distinct from that of their subsequent preservation and accumulation by natural selection.

That all adaptive variations are due to the response of protoplasm to environmental influences (using the term "environment" in its widest sense), it goes without saying. These variations are, however, either *direct* or *indirect*. Direct variations, appearing first in the *soma,* or body, of the organism, are termed *somatogenic;* indirect variations, apparently spontaneous, and due immediately to the germ cells, are termed *blastogenic.* Weismann places somatogenic variations, according to their origin, into three categories: (1) *injuries,* (2) *functional variations,* and (3) variations depending on the so-called "influences of environment," these influences being mainly *climatic.* These three kinds will receive brief consideration.

Injuries.—There appears to be no good evidence that injuries or mutilations can be transmitted. Nearly all the experiments upon the subject have given decidedly negative results. Thus Weismann found that the amputation of the tails of hundreds of mice, down to the nineteenth generation, had no influence on the tails of the descendants.

Mechanical injuries to the body of an organism are merely casual, or accidental, effects of the environment and appear to have no influence upon the germ cells. From the standpoint of adaptation, injuries are only of minor importance.

Functional Variations.—While it is certain that the use or disuse of organs affects their form in the individual, it remains doubtful whether the effects of use and disuse are transmissible. Weismann and his followers contend that they are not. On the other hand, Neo-Lamarckians, as Cope, Hyatt, H. F. Osborn, Packard and Eimer, have maintained that they are. Weismann admits, however, that both use and disuse may lead indirectly to variations, "the former whenever an increase as regards the character concerned is useful, and the latter in all cases in which an organ is no longer of any importance in the preservation of the species"; and that these variations may be acted upon by natural selection. Thus, in a few words, the question stands.

Environmental Variations.—Under this head may be classed such variations as are due directly to climate, nutrition and other primary environmental influences. It is certain that changes of temperature, light, and food, for example, cause corresponding changes of form and function in the individual organism; though the inheritance of these changes directly induced by the environment is the subject of much debate.

Dallinger took flagellate infusorians that at first would die at a temperature of 23° C., and by slowly raising the temperature through several years, brought them safely to a temperature of 70° C. There was some mortality, to be sure, in his experiments, but other experimenters have obtained similar results without the loss of a single individual, and therefore—it is important to note—without the entrance of natural selection. This progressive acclimatization of successive generations of an organism to heat is clearly due in large measure to heredity. So also in the case of the entomostracan *Artemia,* whose specific form Schmankewitsch succeeded in changing, by increasing the salinity of the water in which the animal lived. Here, again, the adaptation was brought about without the aid of selection.

Poulton's already-mentioned experiments on larvæ and pupæ show that these may become protectively colored as the direct effect of the surrounding light on the organism. Here, of course, the possible influence of natural selection can scarcely be excluded, though the fact remains that the color resemblances are initiated directly by the stimulus of light upon protoplasm.

Protoplasm itself is to a certain extent adaptive, in that it may become acclimatized to untoward conditions of heat, light and other stimuli. From this point of view, Henslow's theory of self-adaptation in plants deserves more consideration than it has received, though Henslow did not adopt the theory of natural selection.

Blastogenic Variations.—According to Weismann, only *congenital* variations are inheritable, i. e., only those that result from modifications of the germ plasm. He holds that while all variations are due ultimately to external influences, the processes of reproduction (conjugation in unicellular, and sexual reproduction in multicellular organisms) furnish fresh combinations of individual variations for the operation of natural selection, and that this is the chief purpose of *amphimixis,* or " the mingling of two individuals or of their germs."

Inheritance of Acquired Characters.—Weismann and his followers, in opposition to the Neo-Lamarckians, hold that somatogenic, or acquired, characters are not transmissible; that every permanent (hereditary) variation proceeds from the germ.

The subject of the inheritance of acquired characters has aroused no end of discussion, much of which has been fruit-less, chiefly for two reasons. First, there is no little disagreement as to what is meant by the term "acquired characters." An acquired character arises, not in the germ cells, but in the soma, or body, and for the theoretical transmission of the character the soma must affect the germ cells subsequently; though some maintain that a given external influence may affect both soma and germ plasm at the same time. The definition of acquired characters excludes (1) sports; (2) changes due to the renewed action of the environment upon successive generations of an organism; (3) changes which *may* have been due to selection. Second, having defined the term, it is often difficult if not impossible to say whether a given character is acquired or not. Thus in an acclimatization experiment, if heat, for example, affects first the soma and the latter affects the germ cells subsequently, we have an example of the inheritance of an acquired character. If, however, the heat affects soma and germ plasm simultaneously, the result is or is not the inheritance of an acquired character, according as one defines the term. Indeed, Weismann himself has found the greatest difficulty in trying to explain the inheritance of "climatic" variations in terms of his well-known hypothesis. In fact, the distinction between acquired and non-acquired characters is to no little extent artificial and arbitrary; and too strong an insistence upon the distinction bars the way to the solution of the more important question—What *kinds* of variations are inheritable and what are not?

To summarize: Of somatogenic, or acquired, characters, (1) injuries or mutilations are unadaptive and probably uninheritable. (2) Functional variations are adaptive, but the subject of their transmissibility is involved in doubt. As yet there is no adequate experimental evidence upon the subject, the discussion of which, therefore, is based chiefly on theoretical grounds. There is a strong tendency, however, to believe that results of use or disuse are to some extent transmissible to the benefit of succeeding generations, and even Weismann, the chief opponent of the Neo-Lamarckians, admits that the effects of use and disuse are important in organic evolution. (3) Effects of climatal influences and of nutrition are frequently adaptive and often transmissible, as experiments have proved. There is, however, much difference of opinion as to the precise way in which these effects are transmitted.

Incidental Adaptations.—Many leaf-eating caterpillars and grasshoppers are green from the presence of chlorophyll in their bodies; they owe their color directly to their food. Now it may be admitted that this green color is often protective, without admitting that the color was acquired for that purpose. In the case of green leaf-mining caterpillars, certainly, the color appears to be superfluous for protective purposes. Even variegated protective coloration may be simply a direct effect of the surrounding kinds of light, as Poulton proved.

Again, take the various *tropisms,* described in another chapter. Often they are adaptive and often they are not; but they occur inevitably, whether they result advantageously or not. It is too much to say that a useful structure or function appeared *because* of its usefulness. It first *appeared,* and then proved to be either useful or not useful. If useful, a structure may save the life of its possessor and possibly be transmitted to the next generation; if harmful, it is self-eliminating.

2. SPECIES

Modifications arise, and are either useful or not to their possessors. For the systematist who aims merely to distinguish one species from another, this distinction matters but little. To the biologist, however, the difference is an essential one, and he draws a line between specific peculiarities that are adaptive and those that are not adaptive. The origin of species and the origin of adaptations are by no means the same thing.

Darwin's Origin of Species.—At the time Darwin's great work was written, its immediate purpose was to demonstrate a process of organic evolution; and this object was accomplished in the most forcible way, namely, by shattering the traditional belief in the immutability of species. Nowhere does Darwin imply that nature is striving to produce "species" for their own sake. A process of evolution was the theme of Darwin and its key-note was adaptation.

Indeed, for the purposes of the present generation, Darwin's immortal work would more properly be entitled—The Evolution of Adaptations by Means of Natural Selection. And to us, who now ridicule the old notion of the special creation of species, the doctrine of natural selection appears in a fresh light, with a new mission. For, in the words of Romanes, the theory is "primarily, a theory of adaptations, and only becomes secondarily a theory of species in those comparatively insignificant cases where the adaptations happen to be distinctive of the lowest order of taxonomic division." The opposite view he compares "to that of an astronomer who should define the nebular hypothesis as a theory of the origin of Saturn's rings. It is indeed a theory of the origin of Saturn's rings; but only because it is a theory of the origin of the entire solar system, of which Saturn's rings form a part. Similarly, the theory of natural selection is a theory of the entire system of organic nature in respect of adaptations, whether these happen to be distinctive of particular species only, or are common to any number of species." It should be remembered, of course, in using this comparison, that not all specific characters are adaptive.

As regards the origin of species, however, there are several processes at work besides natural selection. Indeed, Darwin himself knew this, for he expressly stated: "I am convinced that natural selection has been the most important, but not the exclusive, means of modification."

The Conception of "Species."—What is a "species"? The only practical criterion of species is isolation, or separateness, of one kind or another. The majority of our "species" are sharply separated from one another by structural differences; the minority, however, blend into one another, and have so many characters in common that the separation into species becomes an arbitrary matter, depending upon the good judgment of the systematist, who if wise, is neither a "lumper" nor a "splitter." At present, the minutely discriminating powers of an unfortunately large number of entomological systematists are displayed in an extraordinary multiplication of generic and specific names, often to the sacrifice of convenience and stability of nomenclature. This has been carried to such an extent, however, that a reaction has already set in, and there is now some promise of a rational terminology.

Considering characters as of specific importance only, it makes no immediate difference whether they are adaptive or not. If adaptive, whatever their origin, they may have been developed by natural selection; if not, they are incidental, and may be due to such influences as those next to be referred to.

Climate and Food.—Naturalists have recorded many instances in which plants or animals when transferred to a new climate have produced offspring markedly different from the parent form. The term *climate,* however, has no precise meaning for the naturalist, referring as it does collectively to several distinct influences, chief among which are temperature, moisture, light and (indirectly) food conditions. Experimental evidence has already been adduced to show that color changes in insects may be brought about as direct effects of warmth, cold, light or food. Some of these color variations are possibly inheritable, and many of them, artificially produced, would be regarded as distinctive of new species, if found in a state of nature. In fact, the distinction between varieties and species is often entirely arbitrary; varieties are incipient species and it is often impossible to draw any sharp line between the two.

Mutation Theory.—De Vries' *mutation theory*, expounded in 1901 as the result of nearly twenty years of experimentation, is at present an absorbing subject of study and discussion in the biological world, and will continue to be for many years, until the full bearing of the theory is ascertained.

De Vries has produced new species by experimental means and without the aid of selection. Moreover, he has produced them at once, showing that a species does not necessarily require hundreds of years to develop, by means of a long-continued process of selection.

It has long been customary to draw a distinction between *individual variations* and *sports.* Darwin recognized the distinction and was one of the first to notice the extraordinary persistence with which sports are transmitted, as compared with the relative instability of individual variations. Not a few dominant races of plants and animals are known to have arisen from sports, and the belief has been gaining ground with Bateson and others that species also have to some extent arisen from sports, rather than from individual variations; though the rarity of sports as compared with individual variations is the strongest objection to this theory as a theory of the origin of species in general.

De Vries, however, was the first to make extensive experiments on sports, or *mutations,* as he calls them, and to formulate a definite theory of the subject from a considerable body of evidence. He regards the qualities of organisms as being built up of definite but sharply separated units, or elements, which combine in groups. The addition of a new unit means a *mutation,* a sudden departure from the normal specific form; in other words, a new species may arise from the parent form without any evident gradation. The mutable condition exists only at times, and some species are more mutable than others. Acting upon this as a hypothesis, De Vries made a preliminary study of a great number of plants in order to find one in its period of mutation, and at length selected *Œnothera Lamarckiana* (probably a variety of our *E. biennis,* introduced into Holland from America), because of its exceptionally vigorous multiplication, dispersion and variation. By careful cultivation and by means of artificial pollination, he succeeded in obtaining seven or more new species. Most of these remained constant from year to year in spite of intercrossing. Moreover, cross pollination was not necessary to the production of new species by mutation, and when employed did not accelerate the results materially. As a botanist, De Vries confined his investigations to plants, but his general conclusions are perhaps equally applicable to animals, and his experiments are doubtless being repeated by zoölogists.

Through his exhaustive experiments, De Vries has partly attained a long-desired object, in that he has removed the question of the origin of some species "from the purely theoretical to the concrete."

The mutation theory is not primarily a theory of the origin of adaptive characters. It endeavors to account for the origin of certain characters, which may or may not prove useful to their possessors. Indeed, one great merit of De Vries' theory is that it affords an explanation for the existence of variations which are not useful. Now Darwin does not pretend to account for the *origin* of variations, but he shows how given variations, if useful, may be preserved and accumulated. Thus the theory of De Vries supplements that of Darwin and does not antagonize it; even though De Vries himself takes much pains to contrast the two theories, and even asserts that new species arise exclusively as mutations. Both theories, indeed, are theories of the origin of species; but according to De Vries, specific characters spring into existence, irrespective of their usefulness; while according to Darwin, useful characters, and these only, are *premised*, as the starting point of the evolution of certain kinds of species. Thus, as another has said, natural selection begins where the mutation theory leaves off.

Isolation.—The theory of isolation as given by Gulick and by Romanes is highly important as affording an explanation of "the rise and continuance of specific characters which need not necessarily be adaptive characters." By isolation is meant "simply the prevention of intercrossing between a separated section of a species or kind and the rest of that species or kind. . . . So long as there is free intercrossing, heredity cancels variability, and makes in favor of fixity of type. Only when assisted by some form of discriminate isolation, which determines the exclusive breeding of like with like, can heredity make in favour of change of type, or lead to what we understand by organic evolution." (Romanes.)

"As soon as a portion of a species is separated from the rest of that species, so that breeding between the two portions is no longer possible, the general average of characters in the separated portion not being in all respects precisely the same as it is in the other portion, the result of in-breeding among all individuals of the separated portion will eventually be different from that which obtains in the other portion; so that, after a number of generations, the separated portion may become a distinct species from the effect of isolation alone. Even without the aid of isolation, any original difference of average characters may become, as it were, magnified in successive generations, provided that the divergence is not harmful to the individuals presenting it, and that it occurs in a sufficient proportional number of individuals not to be immediately swamped by intercrossing." (Romanes.)

Of the many modes of isolation, the most important are the *geographical* and the *physiological*, both of which have received elaborate treatment by Romanes.

The doctrine of geographical isolation offers a partial explanation of the origin of the peculiar faunæ and floræ of remote islands. These island species, however peculiar, doubtless came originally from the mainlands where their nearest allies now occur; thus the endemic insects of the Galapagos Islands are most nearly related to species of western South America.

The first individuals of *Schistocerca* doubtless reached the Galapagos Islands by means of the wind or on driftwood. These individuals, separated from the main body of their species, would interbreed and might thereby give rise to a new variety or species, if we may assume that the average of characters of the detached portion of the species differed from that of the main body of individuals; in other words, that the isolated forms varied around a mean condition of their own, and no longer around the mean of the species as a whole.

Besides this, the influences of new food and new climatal conditions as means of modification must be taken into account. Furthermore, though a new species might conceivably arise on an island without the aid of natural selection, it is very likely that selection has often played a part in the formation of such a species, as in the apterous or subapterous forms that predominate on oceanic islands. While it is possible that the earliest arrivals were already apterous, and arrived safely because on that account they clung to driftwood instead of flying away, it is probable, on the other hand, that on wind-swept islands the full-winged and more venturesome individuals would be carried out to sea and drowned, leaving the poorly winged and less venturesome ones to remain and transmit their own life-saving peculiarities; which would become intensified by continual selection of the same kind. Romanes, indeed, regards natural selection itself as but one form of isolation.

Physiological isolation, which though important will not be discussed here, "arises in consequence of mutual infertility between the members of any group of organisms and those of all other similarly isolated groups occupying simultaneously the same area." (Romanes.)

CHAPTER VIII

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.

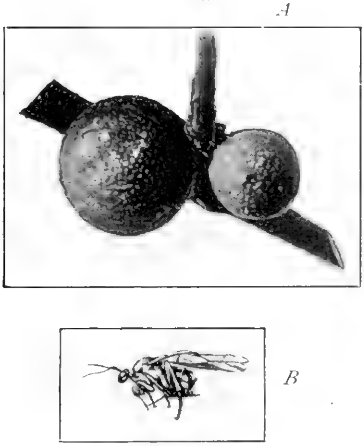
Not only have insects become profoundly modified for using all kinds and all parts of plants for food and shelter, but plants themselves have been modified to no small extent in relation to insects, as appears in their protective devices against unwelcome insects, in the curious formations known as "galls," 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, horseradish, 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, however, 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 gypsy 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 gypsy moth.

Fig. 247.

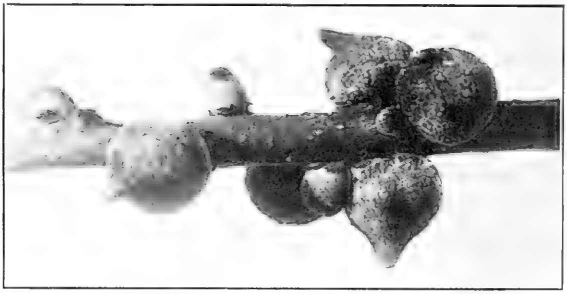


Holcaspis globulus. *A*, galls on oak, natural size; *B*, the gall-maker, twice natural length.

Galls.—Most of the conspicuous plant outgrowths known as "galls" are made by insects, though many of the smaller plant galls are made 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-makers and next to these, Cecidomyiidæ (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. 248.



Galls of *Holcaspis duricoria*, on oak. Natural size.

Cynipidæ affect the oaks (Figs. 247, 248) far more often than any other plants, though not a few species select the wild rose. Cecidomyiid galls occur on a great variety of plants, and those of aphids on elm (Fig. 249), 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.

FIG. 249.

Cockscomb gall of *Colopha ulmicola*, on elm. Slightly reduced.

Gall-Making.—The female cynipid punctures the plant and lays an egg in the wound; 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 Hymenoptera 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. 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 — a problem for the future.

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 nearly 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 depend-

FIG. 250.

Fructifying sprouts of a fungus, *Cordyceps ravenelii,* arising from the body of a white grub, *Lachnosterna.* Slightly reduced.—After RILEY.

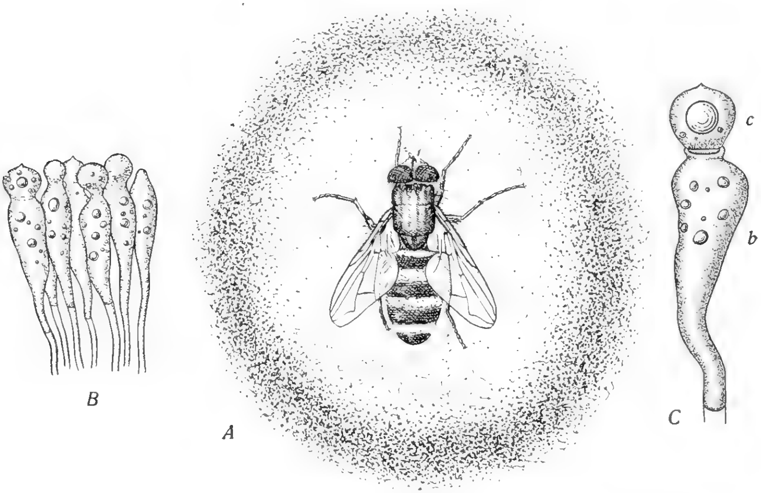
ent on insect-food, however, for they all possess chlorophyll.

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. 250).

The chief fungus parasites of insects belong to the large family Entomophthoraceæ, represented by the common *Empusa muscæ* (Fig. 251) 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

FIG. 251.



Empusa muscæ, 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.

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. 251) 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 upon 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 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 fungus 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) 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 as yet.

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

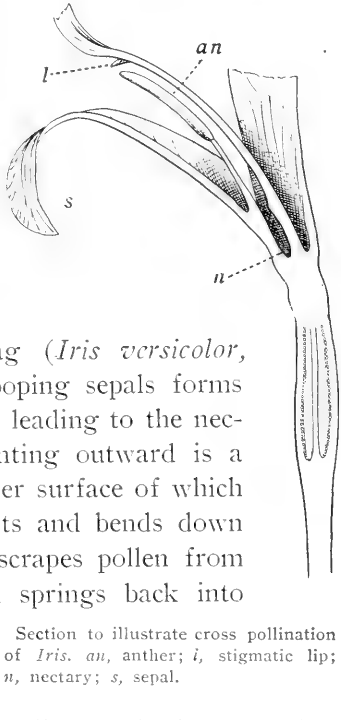
FIG. 252.

Bumble bee (*Bombus*) entering flower of blue-flag (*Iris versicolor*). Slightly reduced.

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. 252), each of the 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. 253, *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 can not 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

FIG. 253.



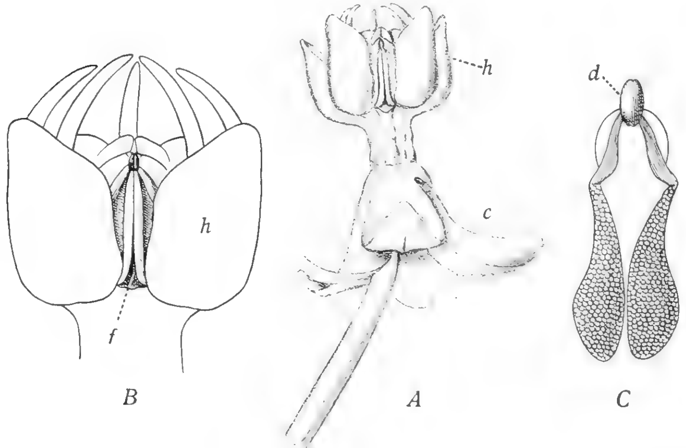
Section to illustrate cross pollination of *Iris*. *an*, anther; *l*, stigmatic lip; *n*, nectary; *s*, sepal.

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,—an inference which proved to be correct.

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

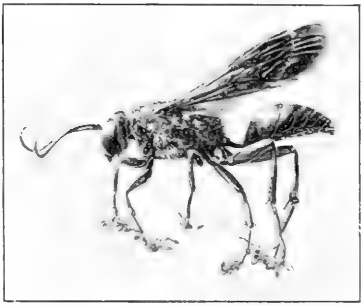
FIG. 254.



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.

reference to cross pollination by insects. As a honey bee or other insect crawls over the flowers (Fig. 254, *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. 254, *B*) and is guided along a slit to a notched *disk*, or *corpuscle* (Fig. 254, *C*, *d*). This disk clings to the leg of the insect, which carries off by means of the disk a pair of pollen masses of *pollinia* (Fig. 254, *C*). When first removed from their enclosing pockets, or anthers, these thin spatulate pollinia lie each pair in the same plane, but in a few minutes 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 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. 255.

FIG. 255.

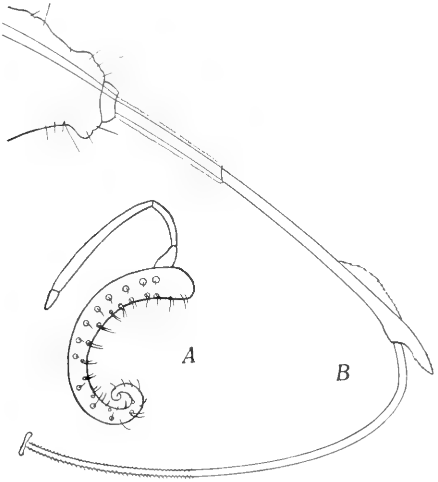


A wasp, *Sphex ichneumonea*, with pollinia of milkweed attached to its legs. Slightly enlarged.

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. 256, *A*) and a long protrusible ovipositor (*B*) which combines in itself the functions of a lance and a saw.

FIG. 256.



Pronuba yuccasella. *A*, maxillary tentacle and palpus; *B*, ovipositor.—After RILEY. Figures 256–258 are republished from the Third Report of the Missouri Botanical Garden, by permission.

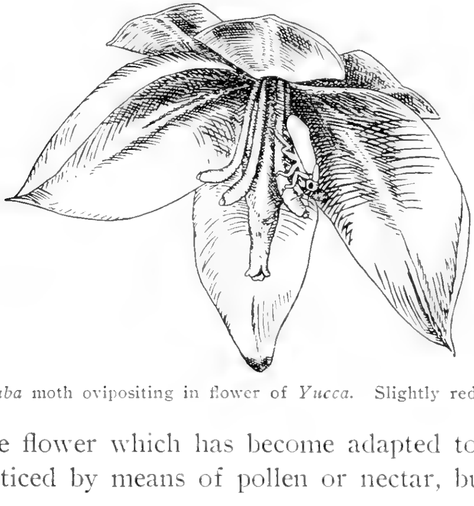
The female begins to work soon after dark, and will continue her operations even in the light of a lantern. Clinging to a stamen (Fig. 257) she scrapes off pollen with her palpi and shapes it into a pellet by using the front legs. After gathering pollen from several flowers she flies to another flower, as a rule, thrusts her long flexible ovipositor into the ovary (Fig. 258) and lays a slender egg 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 successful 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

FIG. 257.

Pronuba yuccasella, female, gathering pollen from anthers of *Yucca*. Enlarged.

FIG. 258.

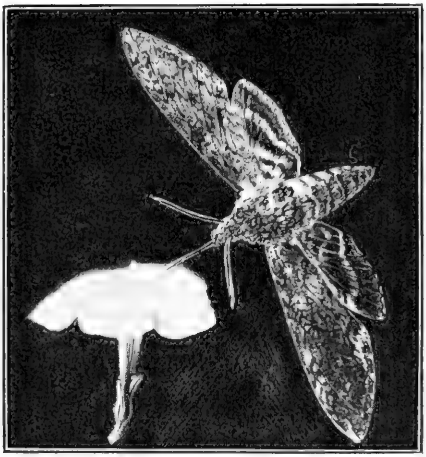


Pronuba moth ovipositing in flower of *Yucca*. Slightly reduced.

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 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, or less mysterious, 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*.

FIG. 259.



Phlegethontius sexta visiting flower of *Petunia*. Reduced.

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 bumble bees or honey bees, assisted possibly by butterflies. 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-tonged sphinx moths (Fig. 259); 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

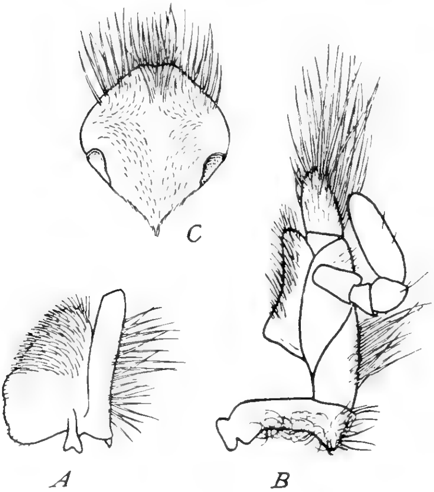
FIG. 260.

A butterfly, *Polites peckius,* stealing nectar from a flower of *Iris versicolor.* Slightly reduced.

is noteworthy that pollination is performed only by the more highly organized insects, the bees heading the list.

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 bumble bees 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 bumble bees 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. 260). 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, over sixty species of insects are concerned in one way or another with the *Iris*.

Fig. 261.



A, right mandible; *B*, right maxilla; *C*, hypopharynx, of a pollen-eating beetle, *Euphoria inda*. Enlarged. (The mandibles are remarkable in being two-lobed.)

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.

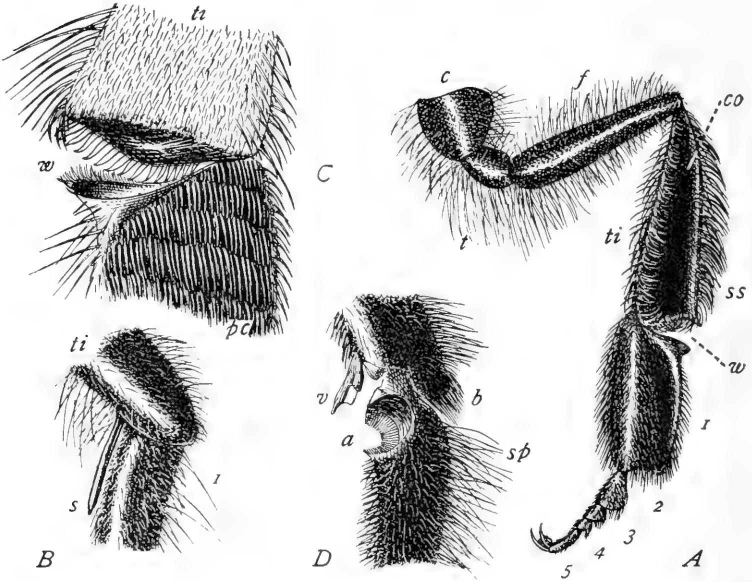
FIG. 262.

Pollen-gathering hair from a worker honey bee, with a pollen grain attached. Greatly magnified.

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. 261). 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, Stratyomyiidæ and Muscidæ are specially adapted for feeding 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. 127) 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. 262, 89) 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.

Fig. 263.



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; *b*, brush; *c*, coxa; *co*, corbiculum; *f*, femur; *pc*, pollen combs; *s*, spur; *sp*, spines; *ss*, spines; *t*, trochanter; *ti*, tibia; *v*, velum; *w*, wax pincers; *1–5*, tarsal segments; *1*, metatarsus, or planta.

The most extensive modifications in relation to flowers are found in *Pronuba*, as already described, and above all in Apidæ, especially the honey bee.

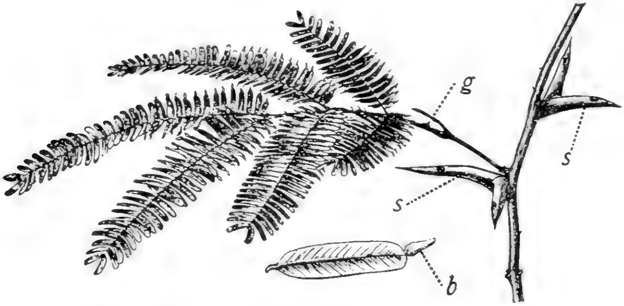
Honey Bee.—The thorax and abdomen and the bases of the legs are clothed with flexible branching hairs (Fig. 262), which entangle pollen grains. These are combed out of the gathering hairs by means of special *pollen combs* (Fig. 263, *C, pc*) on the inner surface of the proximal segment of the hind tarsus, the middle legs also assisting in this operation. From these combs, the pollen is transferred to the *pollen baskets,* or *corbicula* (Fig. 263, *A, co*), of the outer surface of each hind tibia; by crossing the legs, the pollen from one side is transferred to the corbiculum of the opposite side, the spines (*ss*) on the posterior margin of the tibia serving to scrape the pollen from the combs. 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. 263, *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. This is true also of the *wax-pincers* of the hind legs (Fig. 263, *A, C, w*) at the tibio-tarsal articulation; these nippers are used by the worker to remove the wax plates from the abdomen.

For cleaning the antennæ, a front leg is passed over an antenna, which slips into a semicircular *scraper* (Fig. 263, *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 metatarsus is used as an eye brush, to remove pollen grains or other foreign bodies from the hairs of the compound eyes. The labium, hypopharynx and maxillæ (Fig. 54) 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. 45, *C*), 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. 102) 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

FIG. 264.

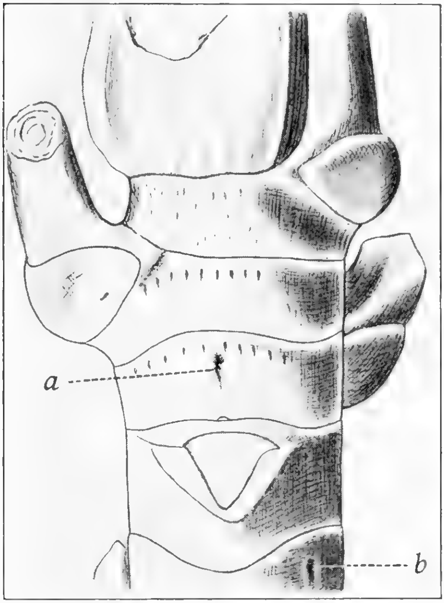


Acacia sphærocephala, an ant-plant. *b*, one of the "Belt's bodies"; *g*, gland; *s*, *s*, hollow stipular thorns, perforated by ants. Reduced.—From Strasburger's *Lehrbuch der Botanik*.

with special reference to their use by ants, though this is a gratuitous and improbable assumption.

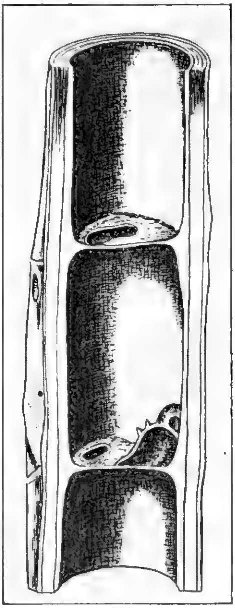
Belt found several species of *Acacia* in Nicaragua and the Amazon valley which have large hollow stipular thorns, inhabited by ants of the genus *Pseudomyrma*. The ants enter by boring a hole near the apex of a thorn (Fig. 264, *s*). The plant affords the ants food as well as shelter, for glands (*g*) 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.

FIG. 265.



Portion of young stem of *Cecropia adenopus*, showing internodal pits, *a* and *b*. Natural size. Figures 265-267 are from Schimper's *Pflanzengeographie*.

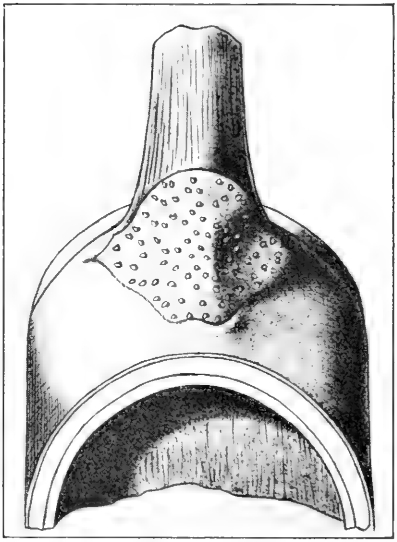
FIG. 266.



Cecropia adenopus. Portion of a stem, split so as to show internodal chambers and the intervening septa perforated by ants.

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. 265, *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. 266). They seldom leave the *Cecropia* plant, unless disturbed, and even keep herds of aphids in their abode. The base of each petiole bears (Fig. 267) 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*.

FIG. 267.



Cecropia adenopus. Base of petiole showing "Müller's bodies." Slightly reduced.

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 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 thereby 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 described in a subsequent chapter, where will be found also an account of the harvesting ants.

FIG. 268.

Hydnophytum montanum. Section of pseudo-bulb, to show chambers inhabited by ants. One fourth natural size.—After FOREL.

The epiphytic plants *Myrmecodia* and *Hydnophytum*, of Java, form spongy bulb-like masses, the chambers of which are usually tenanted by ants, which rush forth when disturbed. These lumps (Fig. 268) 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 IX

INSECTS IN RELATION TO OTHER ANIMALS

1. The General Subject

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 and chironomid larvæ. Many aquatic Hemiptera and Coleoptera prey upon planarians, nematodes, annelids, molluscs and crustaceans; *Belostoma* 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, 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 gad flies (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. 17), 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 (Hemiptera). These (Fig. 23) 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 capitis*), the body louse (*Pediculus vestimenti*), and the crab louse (*Phthirius pubis*), though the first two are possibly the same species.

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. 30) 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 (Œstridæ) are common internal parasites of mammals. The sheep bot fly (*Œstrus 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. 210, *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 usually 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, however, 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 here the 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 fat-head, 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-skippers (*Hygrotrechus*) 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 *Corisa,* 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 (Ephemeridæ), 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 larvæ 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. They made nearly one half of the food of the shovel fish, more than one tenth that of the sunfishes, and the principal food resources of half-grown sheepshead; but were 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 Forbes 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, wire-worms 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 cankerworms, 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 in 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 Acridiidæ. 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 bluebirds 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, Jassidæ 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 Scarabæidæ, which are eagerly devoured by robins, blackbirds, crows and other birds. Of the Diptera, Cecidomyiidæ and other gnats are eaten by swallows, swifts and night hawks; while Tipulidæ are often found in the stomachs of birds. Among Hymenoptera, ants are eaten extensively by woodpeckers, catbirds and many other species, as are also Ichneumonidæ 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 some admirable 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.	Canker-worms.
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 canker-worm and vinechafer 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.' "

This broader view was first elaborated by Professor Forbes, in his masterly paper, " On Some Interactions of Organisms," the substance of which is given below.

" Evidently a species can not long maintain itself in numbers greater than can find sufficient food, year after year. If it is a phytophagous insect, for example, it will soon dwindle if it seriously lessens the numbers of the plants upon which it feeds, either directly, by eating them up, or indirectly, by so weakening them that they labor under a marked disadvantage in the struggle with other plants for foothold, air, light and food. The interest of the insect is therefore identical with the interest of the plant it feeds upon. Whatever injuriously affects the latter, equally injures the former; and whatever favors the latter, equally favors the former. This must, therefore, be regarded as the extreme normal limit of the numbers of a phytophagous species,—a limit such that its depredations shall do no especial harm to the plants upon which it depends for food, but shall remove only the excess of foliage or fruit, or else superfluous individuals which must perish otherwise, if not eaten, or, surviving, must injure their species by over-crowding. If the plant-feeder multiply beyond the above limit, evidently the diminution of its food supply will soon react to diminish its own numbers; a counter reaction will then take place in favor of the plant, and so on through an oscillation of indefinite continuance.

" On the other hand, the reduction of the phytophagous insect below the normal number, will evidently injure the food plant by preventing a reduction of its excess of growth or numbers, and will also set up an oscillation like the preceding, except that the steps will be taken in reverse order.

"I next point out the fact that precisely the same reasoning applies to predaceous and parasitic insects. Their interests, also are identical with the interests of the species they parasitize or prey upon. A diminution of their food reacts to decrease their own numbers. They are thus vitally interested in confining their depredations to the excess of individuals produced, or to redundant or otherwise unessential structures. It is only by a sort of unlucky accident that a destructive species really injures the species preyed upon.

"The discussion has thus far affected only such organisms as are confined to a single species. It remains to see how it applies to such as have several sources of support open to them,—such, for instance, as feed indifferently upon several plants or upon a variety of animals, or both. Let us take, first, the case of a predaceous beetle feeding upon a variety of other insects,—either indifferently, upon whatever species is most numerous or most accessible, or preferably upon certain species, resorting to others only in case of an insufficiency of its favorite food.

"It is at once evident that, taking the group of its food-insects as a unit, the same reasoning applies as if it were restricted to a single species for food; that is, it is interested in the maintenance of these food-species at the highest number consistent with the general conditions of the environment,—interested to confine its own depredations to that surplus of its food which would otherwise perish if not eaten—interested, therefore, in establishing a rate of reproduction for itself which will not unduly lessen its food supply. Its interest in the numbers of each species of the group it eats will evidently be the same as its interest in the group as a whole, since the group as a whole can be kept at the highest number possible only by keeping each species at the highest number possible. . . .

"This argument holds for birds as well as for insects, for animals of all kinds, in fact, whether their food be mixed or simple, animal or vegetable, or both. It also applies to parasitic plants. The ideal adjustment is one in which the reproductive rate of each species should be so exactly adapted to its food supply and to the various drains upon it that the species preyed upon should normally produce an excess sufficient for the species it supports. And this statement evidently applies throughout the entire scale of being. Among all orders of plants and animals, the ideal balance of Nature is one promotive of the highest good of all the species. In this ideal state, towards which Nature seems continually striving, every food-producing species of plant or animal would grow and multiply at a rate sufficient to furnish the required amount of food, and every depredating species would reproduce at a rate no higher than just sufficient to appropriate the food thus furnished. . . .

"Exact adjustment is doubtless never reached anywhere, even for a single year. It is usually closely approached in primitive nature, but the chances are practically infinite against its becoming really complete, and mal-adjustment in some degree is therefore the general rule. All species must oscillate more or less."

Professor Forbes then shows that oscillations are injurious to a species and that the tendency of things is toward a healthy equilibrium. If the rate of reproduction, as in a parasite for instance, is too small in relation to the food supply, the species will eventually yield to its more prolific competitors in the general struggle for existence. If, on the other hand, its rate of multiplication is too high, the species will be at a disadvantage in the search for food, as compared with better adjusted species, and must again suffer. "The fact of survival is therefore usually sufficient evidence of a fairly complete adjustment of the rate of reproduction to the drains upon the species." . . . "We may be sure, therefore, that, as a general rule, in the course of evolution, only those species have been able to survive whose parasites, if any, were not prolific enough sensibly to limit the numbers of their hosts for any length of time.

"We notice incidentally that it is thus made unlikely that an injurious species can be exterminated, can even be permanently lessened in numbers, by a parasite strictly dependent upon it,—a conclusion which remarkably diminishes the economical rôle of parasitism. The same line of argument will, of course, apply, with slight modifications, to any animal, or even to any plant dependent upon any other animal or any other plant for existence.

"It is a general truth, that those animals and plants are least likely to oscillate widely which are preyed upon by the greatest number of species, of the most varied habit. Then the occasional diminution of a single enemy will not greatly affect them, as any consequent excess of their own numbers will be largely cut down by their other enemies, and especially as, in most cases, the backward oscillations of one set of enemies will be neutralized by the forward oscillations of another set. But by the operations of natural selection, most animals are compelled to maintain a varied food habit,—so that if one element fails, others may be available. Thus each species preyed upon is likely to have a number of enemies, which will assist each other in keeping it properly in check.

"Against the uprising of inordinate numbers of insects, commonly harmless but capable of becoming temporarily injurious, the most valuable and reliable protection is undoubtedly afforded by those predaceous birds and insects which eat a *mixed food*, so that in the absence or diminution of any one element of their food, their own numbers are not seriously affected. Resorting, then, to other food supplies, they are found ready, on occasion, for immediate and overwhelming attack against any threatening foe. Especially does the wonderful locomotive power of birds, enabling them to escape scarcity in one region which might otherwise decimate them, by simply passing to another more favorable one, without the loss of a life, fit them, above all other animals and agencies, to arrest disorder at the start,—to head off aspiring and destructive rebellion before it has had time fairly to make head. But we should not therefrom derive the general, but false and mischievous notion, that the indefinite multiplication of either birds or predaceous insects is good. Too many of either is nearly or quite as harmful as too few.

" There is a general consent that primeval nature, as in the uninhabited forest or the untilled plain, presents a settled harmony of interaction among organic groups which is in strong contrast with the many serious mal-adjustments of plants and animals found in countries occupied by man.

" To man, as to nature at large, the question of adjustment is of vast importance, since the eminently destructive species are the widely oscillating ones. Those insects which are well adjusted to their environments, organic and inorganic, are either harmless or inflict but moderate injury (our ordinary crickets and grasshoppers are examples) ; while those that are imperfectly adjusted, whose numbers are, therefore, subject to wide fluctuations, like the Colorado grasshopper, the chinch-bug and the army worm, are the enemies which we have reason to dread. Man should then especially address his efforts, first, to prevent any unnecessary disturbance of the settled order of the life of his region which will convert relatively stationary species into widely oscillating ones; second, to destroy or render stationary all the oscillating species injurious to him; or, failing in this, to restrict their oscillations within the narrowest limits possible.

" For example, remembering that every species oscillates to some extent, and is held to relatively constant numbers by the joint action of several restraining forces, we see that the removal or weakening of any check or barrier is sufficient to widen and intensify this dangerous oscillation; may even convert a perfectly harmless species into a frightful pest. Witness the maple bark louse, which is so rare in natural forests as scarcely ever to be seen, limited there as it is by its feeble locomotive power and the scattered situation of the trees it infests. With the multiplication and concentration of its food in towns, it has increased enormously, and, if it has not done the gravest injury, it is because the trees attacked by it are of comparatively slight economical value, and because it has finally reached new limits which hem it in once more.

" We are therefore sure that the destruction of any species of insectivorous bird or predaceous insect, is a thing to be done, if at all, only after the fullest acquaintance with the facts. The natural presumptions are nearly all in their favor. It is also certain that the species best worth preserving are the mixed feeders and not those of narrowly restricted dietary (parasites, for instance),—that while the destruction of the latter would cause injurious oscillations in the species affected by them, they afford a very uncertain safeguard against the rise of such oscillations. In fact, their undue increase would be finally as dangerous as their diminution.

" Notwithstanding the strong presumption in favor of the natural system, when we remember that the purposes of man and what, for convenience' sake, we may call the purposes of Nature do not fully harmonize, we find it incredible that, acting intelligently, we should not be able to modify existing arrangements to our advantage,—especially since much of the progress of the race is due to such modifications made in the past. . . .

" But far the most important general conclusion we have reached is a conviction of the general beneficence of nature, a profound respect for the natural order, a belief that the part of wisdom is essentially that of practical conservatism in dealing with the system of things by which we are surrounded."

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 *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, sparrow-hawk, cuckoos and shrikes; and the spiny larvæ of *Vanessa antiopa* by cuckoos and the Baltimore oriole; while the hairy caterpillars of the gypsy moth are known to be eaten in Massachusetts by no less 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* and *Xylocopa,* and flycatchers and swallows feed habitually upon stinging Hymenoptera, particularly Scoliidæ, while a great many birds eat Myrmicidæ, 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, however, 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,* Reduviidæ and Pentatomidæ 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

Coccinellidæ are eaten by but very few birds— the flycatchers and swallows—and are refused by caged blue-jays and song sparrows even when these birds are hungry. Of Chrysomelidæ, 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 Carabidæ, whether stinking or not, are eaten by practically all land birds." Crows, blackbirds and jays eagerly swallow *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 and Chrysomelidæ, metallic and conspicuously colored, are habitually eaten by birds that have an abundance of other insect food to pick from."

The stenches of Lampyridæ 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,* 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.

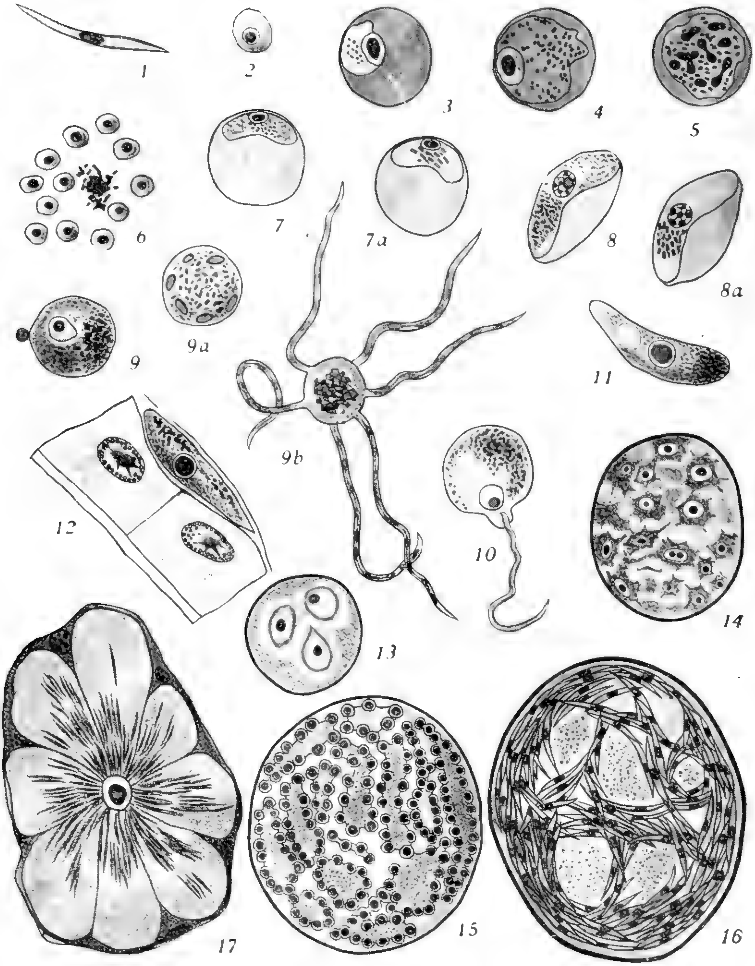
From such facts as these, Judd properly infers, "not cases of protection and non-protection, but cases of greater and lesser efficiency of protective devices."

2. The Transmission of Diseases by Insects.

It is now known that several kinds of insects are of vital importance to man as agents in the transmission of certain diseases. This recently demonstrated rôle of insects now commands universal attention.

Malaria.—So far as is known, malaria is transmissible only through the agency of mosquitoes.

FIG. 269.



Life history of malaria parasite, *Plasmodium præcox*. *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 macrogamete (female), derived from a merozoite and situated in a red blood corpuscle. *7a*, young microgametoblast (male), derived from a merozoite. *8*, full-grown macrogamete. *8a*, full-grown microgametoblast. 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 microgametoblast, preparatory to

The malaria "germ," discovered in 1880 by the French army surgeon Laveran, may be found as a pale, amœboid organism (*Plasmodium,* Fig. 269) 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.

Three types of malaria are recognized: (1) the tertian, in which the paroxysm recurs every two days; (2) the quartan, in which it happens every third day; and (3) the æstivo-autumnal type (Fig. 269). These three kinds are by some

forming microgametes. *9b,* resting cell, bearing six flagellate microgametes (male). *10,* fertilization of a macrogamete by a motile microgamete. The macrogamete next becomes an oökinete. *11,* oökinete, or wandering cell, which penetrates into the wall of the stomach of the mosquito. *12,* oökinete in the outer region of the wall of the stomach, i. e., next to the body cavity. *13,* young oöcyst, derived from the oökinete. *14,* oöcyst, containing sporoblasts, which are to develop into sporozoites. *15,* older oöcyst. *16,* mature oöcyst, 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.

investigators thought to be due to different species of parasites; and when, as often happens, the malarial chill occurs every day, this is attributed to two sets of tertian amœbulæ, sporulating on alternate days.

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 *macrogametes* (female, *7, 8*) or as *microgametoblasts* (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 macrogamete now leaves its blood corpuscle and becomes spherical (*9*), as does also the microgametoblast (*9a*); but the latter puts forth a definite number (*six,* in *P. præcox, 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 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, 1*). 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 of 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).

Culex and Anopheles.—The mosquitoes of North America number one hundred and twenty-five known species. 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.—It has now been demonstrated that the dreaded disease, yellow fever, is transmitted from one human being to another by the bite of a mosquito (*Stegomyia fasciata*) and in no other way excepting, of course, by the artificial injection of diseased blood. The discovery of the mode of transmission of the disease was made in Cuba during 1900 and 1902 by Dr. Reed and his corps of United States army surgeons. These investigators succeeded in transmitting the disease to healthy subjects by inoculation from mosquitoes which had previously fed on the blood of yellow fever patients. To convey the disease, however, a period of ten to thirteen days was necessary between the original biting of a patient and the inoculation of a healthy subject. The disease followed the bite of an infected *Stegomyia* with remarkable precision.

Furthermore, Dr. Reed and his associates found that yellow fever could not be conveyed by means of the clothing, bedding, etc., of fever patients, so long as mosquitoes were excluded. In the absence of the mosquito the yellow fever patient is harmless and in the absence of a patient the mosquito is harmless (Sternberg). The disease terminates in cold weather with the disappearance of the mosquito.

Preventive measures based upon these recently acquired facts have been wonderfully successful. The city of Havana, in which yellow fever had always prevailed, has now been freed of the disease.

The specific cause of yellow fever has as yet eluded detection in the human body. There has been discovered, however, in the stomach and salivary glands of mosquitoes infected with yellow fever, a protozoan parasite (order Coccidiida), the sexual cycle of which, ending in the development of sporozoites, has been traced in the body of the *Stegomyia.* This coccidium may or may not prove to be concerned in the transmission of the disease.

Other Diseases.—Typhoid fever is transmitted frequently by the common house fly, which may carry the bacillus from the excreta of typhoid patients to food supplies in kitchens or elsewhere. The spread of the disease in army camps is due chiefly to the house fly (*Musca domestica*), as was demonstrated in 1898 by a commission of the United States army.

The dreaded disease filariasis (elephantiasis) of Oriental tropical regions is transmitted by mosquitoes of the genus *Culex,* as Dr. Manson discovered many years ago. The disease is due to a parasitic worm (*Filaria*), both sexes of which lodge in the lymphatic vessels, obstruct the flow of the lymph and thereby cause an abnormal enlargement of the parts in which they occur. The embryos of the parasite pass into the blood and thence into the body of the mosquito; there they remain in the thoracic muscles for a time and become larvæ, which at length pass through the proboscis of the mosquito into the skin of man. It is possible, though not proved, that other mosquitoes than *Culex* and indeed other kinds of insects are involved in the transmission of filariasis.

In Egypt, an eye disease is transmitted by the house fly. There is some evidence that the bubonic plague is spread through the agency of fleas. Anthrax of cattle is carried by gad flies (Tabanidæ). A South African disease fatal to horses, cattle and dogs, though not to man, is transmitted from infected to healthy animals by the proboscis of a muscid fly, *Glossina morsitans,* as has been mentioned. The specific cause of this disease is a blood parasite similar to that of malaria. Finally, the destructive Texas fever of cattle is undoubtedly transmitted by the common cattle-tick, as was discovered by Theobald Smith, though the tick is not, properly speaking, an insect.

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. 62, *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 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. 224), Nepidæ, Belostomidæ (Fig. 22), Naucoridæ (Fig. 62, *D*), Reduviidæ and Phymatidæ are predaceous, with raptorial front legs and sharp beaks. Some of the Pentatomidæ (Fig. 270) are of considerable economic value on account of their predaceous habits. Most of the Neuroptera feed upon other insects.

FIG. 270.

Nymph of *Podisus spinosus* sucking the blood from a clover caterpillar, *Colias philodice*. Natural size.

The *Myrmeleon* larva digs a funnel-shaped pitfall, at the bottom of which it buries itself to await the fall of some unlucky ant. The *Chrysopa* larva impales an aphid on the points of its mandibles and sucks the blood through a groove along each mandible (Fig. 45, *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. 226) 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, however, are by no means exclusively carnivorous, 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; *Calosoma,* however, 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 they 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 *Feniseca 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 ferociously attack not only other flies, but also beetles, bumble bees, 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 bumble bees 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.

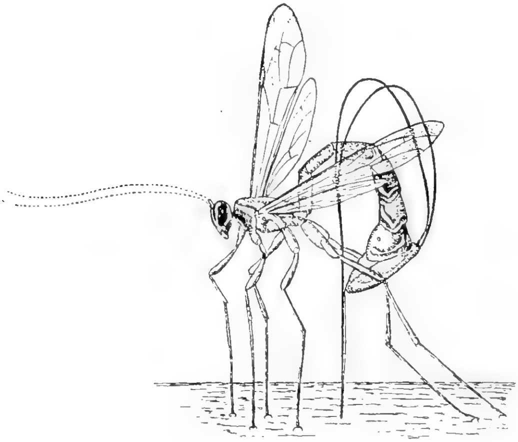
Parasitic Insects.—Though very many insects occur as external parasites on the bodies of birds and mammals, very few occur as such on the bodies of other insects; one of the few is *Braula cæca,* a wingless dipteron found on the body of the honey bee.

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 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 *Thalessa, T. atrata* and *T. lunator* (Fig. 271), with their long ovipositors (three inches long in *lunator*, and four to four and three quarters inches in *atrata*). *Thalessa* bores into the trunks of trees in order to reach the burrows of another large hymenopteron, *Tremex columba* (Fig. 31), upon whose larvæ the larva of *Thalessa* feeds.

FIG. 271.



Oviposition of *Thalessa lunator*. Natural size.—After RILEY.

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. 272), 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 circular lid. Chalcididæ, of which some four thousand species are known, are usually minute and parasitic;

though some are phytophagous, for example, *Isosoma hordei,* which lives in the stems of grasses, especially wheat, rye and barley. 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 cecidomyiid and cynipid galls, and many proctotrypids are parasites of other parasitic insects—in other words, are *hyperparasites.*

FIG. 272.

A tomato worm, *Phlegethontius sexta,* bearing cocoons of the parasitic *Apanteles congregatus.* Natural size.

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* (*Orgyia*) *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. Not longer ago than 1895, in the city of Washington, more than ninety-seven per cent. of the caterpillars of one of our most important shade-tree pests [*Orgyia,* 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 in 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 May beetles (*Lachnosterna*) 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 "tumble-bugs," 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 bumble bees 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.

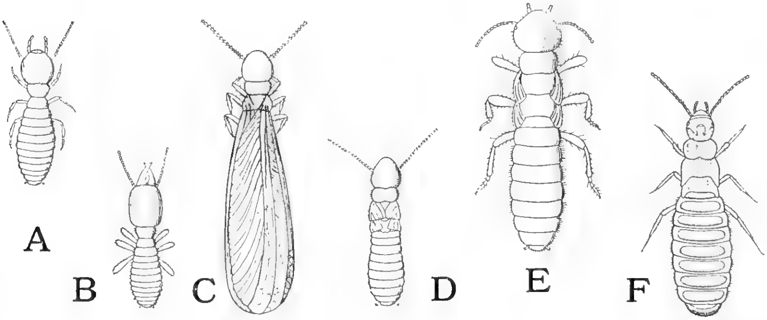
One of the carpenter bees, *Ceratina dupla,* which builds in the hollow stem of a plant a series of larval cells separated by partitions, is said by Comstock to watch over her nest until the young mature.

The transition from the solitary to the social habit is indicated in the life-histories of wasps and bumble bees, 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.

FIG. 273.



Various forms of *Termes 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.

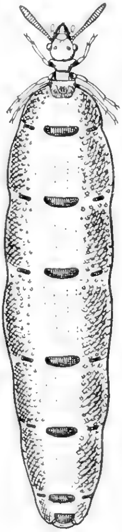
Classes of Termites.—In general, four kinds of adults are produced in a community of termites, namely—*workers, soldiers, winged males* and *winged females.*

The workers (Fig. 273, *A*), which are ordinarily the most numerous, are of either sex, but their reproductive organs are undeveloped. A worker-ant or bee, however, is 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. 273, *B*), their chief duty apparently is to defend the colony, though they frequently fail to do so.

The winged males and females (Fig. 273, *C*) which are sexually mature, 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 a peculiar transverse suture, leaving four triangular stumps (Fig. 273, *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. 274) 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. 273, *E*) differ from the primary pair in having nymphal wing-pads in place of the remains of functional wings.

Fig. 274.



Queen of *Termes obesus.* Natural size.—After Hagen.

These six kinds are by no means all that may occur in a single colony. *Termes lucifugus,* according to Grassi, has no less than fifteen kinds of individuals, counting nymphs in various stages of development toward workers, soldiers, and primary or else complementary, or reserve, kings or queens.

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.

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.

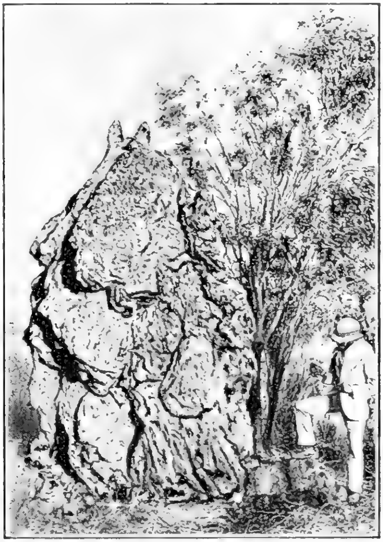
American Species.—Our common termite is *Termes flavipes*, which occurs throughout the United States, excavating its galleries in decaying logs, stumps or other dead wood. The nuptial flight of this species takes place in spring, when the two sexes swarm in numbers that are sometimes enormous. One swarm, 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, a true queen of *T. flavipes* is as yet unknown, the queen described by Hubbard being evidently, from her undeveloped wings, a substitution queen.

In the Western states, six species of termites are known, including *Termes lucifugus*, which has probably been introduced from Europe. In this species the primary queen is known to exist. Regarding the Californian *Termopsis angusticollis*, 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; furthermore—a remarkable fact—these substitution royalties may contain workers or even soldiers capable of laying eggs.

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, 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. 275) 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.

Fig. 275.



Termite mound, Kimberley type, Australia. —After Saville-Kent.

An extraordinary type of mound is constructed by the "compass," or "meridian," termites of North Australia, for their wedge-shaped mounds (Fig. 276), 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 natives of India and Africa are accustomed to eat the termites themselves, the flavor of which is said to be delicious.

FIG. 276.

Mound of the "compass" termite of North Australia.—After SAVILLE-KENT.

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 *Termes 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. Their relations to the termites are, so far as is known, similar to those described beyond between myrmecophilous species and ants. These *termitophilous* forms, however, have received as yet but little attention.

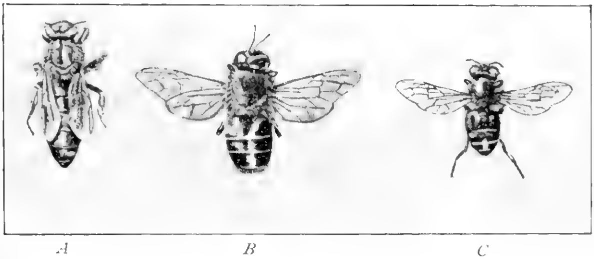
Honey Bee

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 writings 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.

Though its habits have been somewhat modified by domestication, the honey bee, unlike most domesticated animals, is still 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. 277). The workers are fe-

FIG. 277.

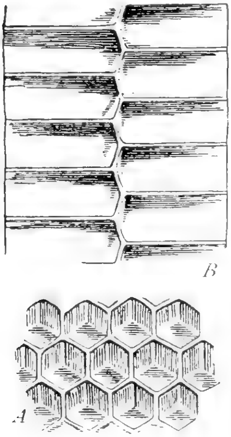


The honey bee, *Apis mellifera*. *A*, queen; *B*, drone; *C*, worker. Natural size.

males 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, 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 monarchial. 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.

Fig. 278.

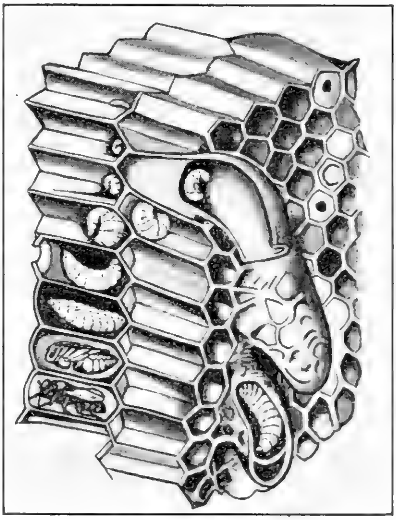


A, bases of comb cells; *B*, section of comb. Somewhat enlarged.—After Cheshire.

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. 102); these are transferred to the mouth by means of the wax-pincers (Fig. 263, *C*) of the hind legs 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. 278, *A*), and the cells of one side interdigitate with those of the other side (Fig. 278, *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 1/280 or even 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, however, is 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.

FIG. 279.

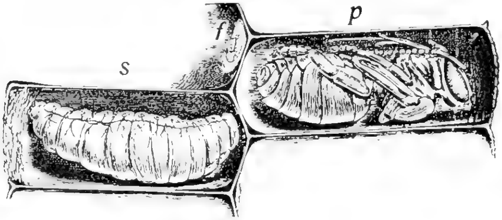


Comb of honey bee, showing the insect in various stages. At the right are large queen cells.—After BENTON.

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, horsechestnut 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. 279, 280) 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 other, the excretions of the larva cannot contaminate the surrounding nutriment, and they are retained until the final moult. Five days after hatching, the larva spins its cocoon, the workers having meanwhile covered the larval cell with a porous cap of wax and pollen (Fig. 280) and on the twenty-first day after the egg was laid the winged 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 Benton:

FIG. 280.



Honey bee. *f*, feeding larva; *p*, pupa; *s*, spinning larva.—After CHESHIRE.

	Egg.	Larva.	Pupa.	Total.
Queen,	3	5½	7	15½
Worker,	3	5	13	21
Drone,	3	6	15	24

The cells in which queens develop (Fig. 279) 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 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 generally. 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. At the time the queen mates, there are in the hive neither eggs nor young larvæ from which to rear another queen; hence, should she be lost, no more fertilized eggs would be deposited, and the old workers gradually dying off without being replaced by young ones, the colony would become extinct in the course of a few months at most, or meet a speedier fate through intruders, such as wax-moth larvæ, robber bees, wasps, etc., which its weakness would prevent its repelling longer; or cold is very likely to finish such a decimated colony, especially as the bees, because queenless, are uneasy and do not cluster compactly.

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, generally 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 reduced 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, if not already, 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. Probably the queen cannot control the sex of her eggs, as she has long been supposed to do, for Dickel has recently found, among other revolutionary facts, that *all* the eggs of the normal mother bee are fertilized.

Bumble Bees

Familiar as the bumble bees are, their habits are but imperfectly known. 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

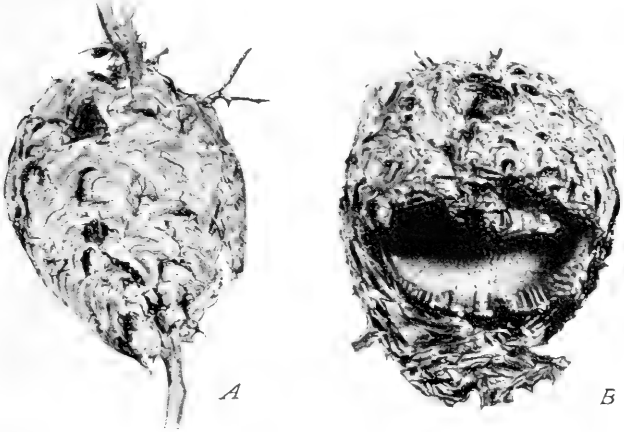
The Social Wasps constitute the family Vespidæ, of which we have three genera, namely, *Vespa, Polistes* and *Polybia,* the last genus being represented by a single Californian species.

Vespa.—Some species of *Vespa,* as *V. maculata,* make a nest which consists of several tiers of cells protected by an envelope (Fig. 281), 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 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.

FIG. 281.



Nest of wasp, *Vespa maculata.* *A*, outer aspect; *B*, with envelope cut away to show combs. Greatly reduced.

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 fashion 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 no less than two thousand species of ants are already known.

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.

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 heads 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, its 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 *Cremastogaster;* and others spin silk to fasten leaves together, as *Polyrhachis* of India and *Œcophylla* 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 so; but in the study of this recondite subject, false conclusions can be avoided only by observation and experiment 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. 283, *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 that 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.

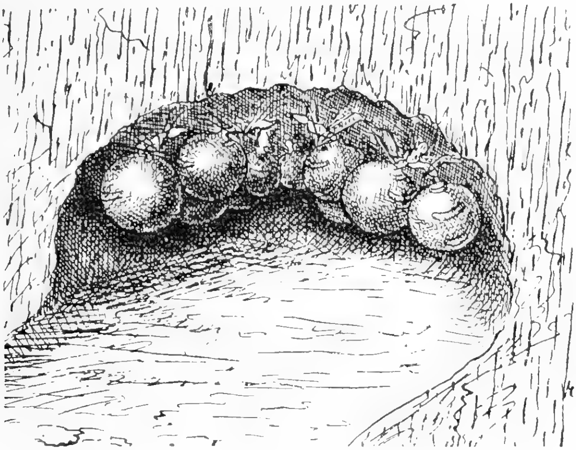
Polyergus lucidus occurs in the Alleghanies, where the colonies of this species, according to McCook, contain large numbers of the workers of *Formica schaufussi.* The masters are good fighters but do no other work, and have not been seen to feed themselves, though they may often be seen feeding from the mouths of their slaves.

Honey Ants.—Among ants in general, the workers that stay in the 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 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. 282) 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.

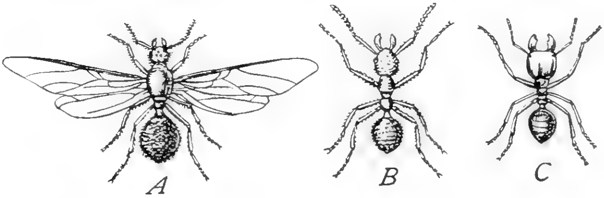
Fig. 282.



Honey ants, *Myrmecocystus melliger,* clinging to the roof of their chamber. About natural size.—After McCook.

Leaf-cutting Ants.—The most dangerous foes to vegetation in tropical America are the several species of *Atta* (*Œcodoma,* Fig. 283, *A*). Living 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. 284) 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.

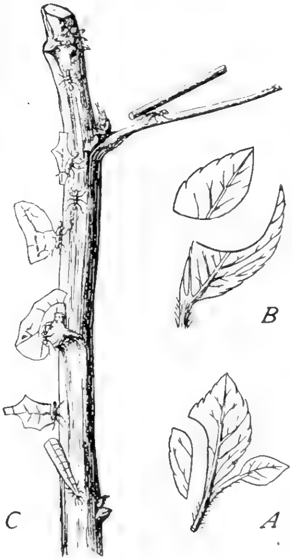
FIG. 283.



A, leaf-cutting ant, *Atta cephalotes*. *B*, wandering ant, *Eciton drepanophorum; C*, *Eciton omnivorum*. Natural size.—After SHIPLEY.

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

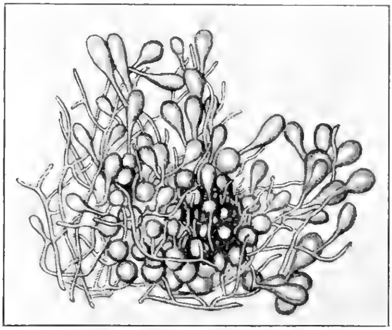
FIG. 284.



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.

the sake of which the ants carry on their complex operations consists of the knobbed ends of fungus threads (Fig. 285), 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, however, the fungus develops aërial organs of fructification of the 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.

Fig. 285.



Fungus clumps (*Rozites gongylophora*) cultivated by ants of the genus *Atta*. Greatly magnified.—After Möller.

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 (*Atta 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 a 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.

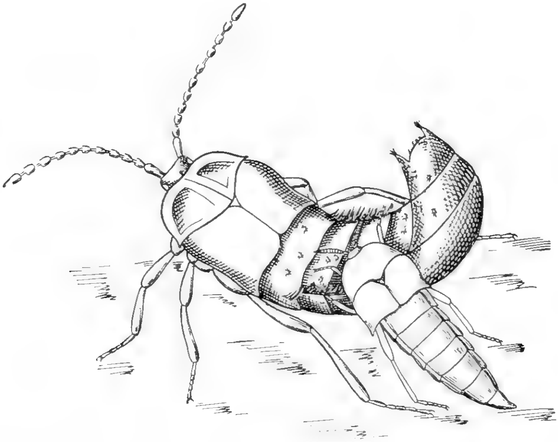
Myrmecophilism.—To add to the complexity of ant-life, the nests of ants, when at all extensive, are frequented by a great variety of other arthropods, which on account of their association with ants are termed *myrmecophiles.* Most of these are insects, of which Wasmann has catalogued 1,200 species, 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 Aphidæ 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. 286) is one of these favored guests, as it has abdominal tufts of hairs from which the ants secure a secreted fluid. *Atemeles* (Fig. 287) is another; it solicits and obtains food from the mouth of a foraging ant as if it were an ant itself. In the Alleghanies,

Fig. 286.

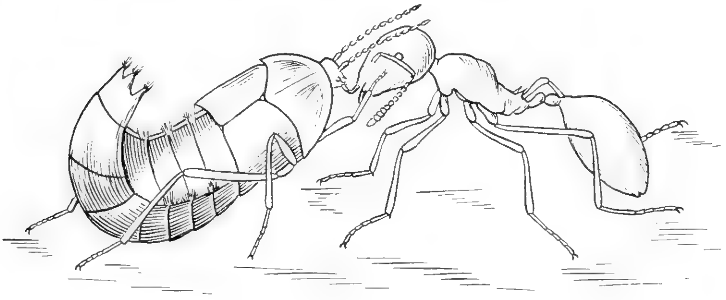


Lomechusa strumosa being freed of mites by *Dinarda dentata.*—After Wasmann.

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, 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.

Fig. 287.



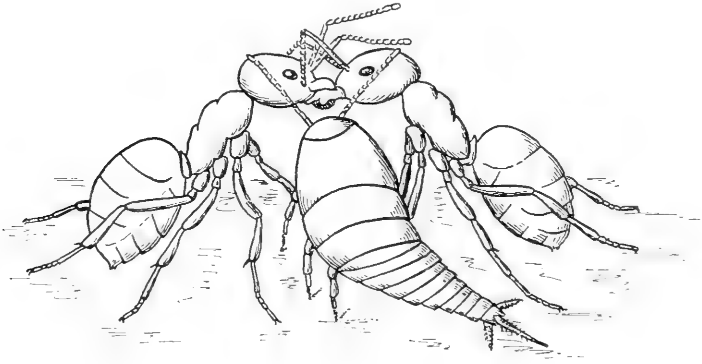
Atemeles emarginatus being fed by an ant, *Myrmica scabrinodis*.—After Wasmann.

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 *Hetærius*, 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.

Janet has described the amusing way in which an audacious species of *Lepismina* 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. 288), and a drop of honey is being passed, the *Lepismina* 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.

Fig. 288.



Lepismina stealing food from a pair of ants.—After Janet.

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.

CHAPTER XI

INSECT BEHAVIOR

The subject of insect behavior will be considered under three heads: (1) Tropisms, (2) Instinct, (3) Intelligence.

1. 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, however, prefer 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, though comparatively new, has already illuminated the whole subject of the behavior of organisms and placed it on a rational basis. The complex tropisms of insects offer a fresh and large field to the investigator, comparatively little having as yet been published upon the subject.

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 or something else.

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."

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 *Bembidium, 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,* 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."

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.

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*. The 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.

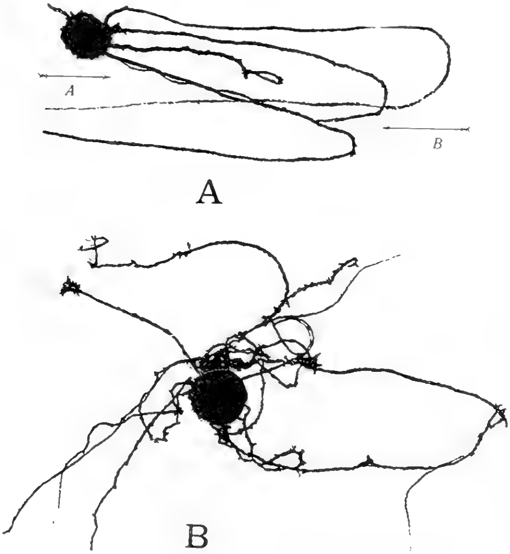
Anemotropism and rheotropism are closely allied phenomena. As Wheeler says, " The poising fly orients itself to the wind in the same way as the swimming fish heads upstream," adjusting itself to a gaseous instead of a liquid current. " In both cases the organism naturally assumes the position in which 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 and cockroaches are also negatively *geotropic.* 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."

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,* or the "control of the direction of locomotion by light." The pho-

Fig. 289.



A, tracks made on paper by a larva of *Lucilia cæsar* 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.

totropic response is either positive or negative according as the organism moves, respectively, toward or away from the source of light. Maggots of *Lucilia cæsar* and of many other flies are negatively phototropic as a rule (Fig. 289, *A*), but in the absence of light (other directive stimuli being excluded, of course) wander about indifferently (Fig. 289, *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; though the latter rays produce no sensible effect on the human organism.

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,* according as they move, respectively, toward or away from a more intensely illuminated area.

Verworn and others maintain 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 moth *Euproctis chrysorrhœa,* 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 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, as it is in the case of sexually mature ants, which make a nuptial flight into the sunlight when they have acquired wings. The swarming of the honey bee is likewise a case of periodic positive phototropism, as Kellogg has observed.

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."

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;* 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—a study which has scarcely begun. 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, though comparatively little is known as yet in regard to these properties. 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, reproductive organs, etc.

A newly 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.

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, not performed until it is evoked by some sort of stimulus—perhaps an olfactory one—from a particular kind of plant.

Stimuli.—Some determinate sensory stimulus, indeed, is 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.

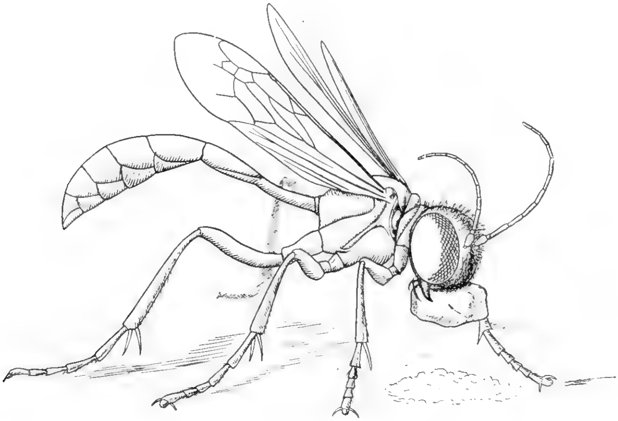
With insects, as with other animals, many instincts are transitory; even when partially fixed by habit, they are replaceable by stronger instincts. Thus the gregarious habit of larvæ is finally overpowered by a propensity to wander, which does not mature, however, until the approach of the transformation 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; in the face of abnormal circumstances, however, 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 *Sphex,* 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.

FIG. 290.



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.

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. 290).

While most of the variations that one encounters are small and, in a sense, accidental, or purposeless, such novel departures as those of the *Polistes* or the *Ammophila* would seem to denote adaptability.

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* butterfly 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 now we are 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

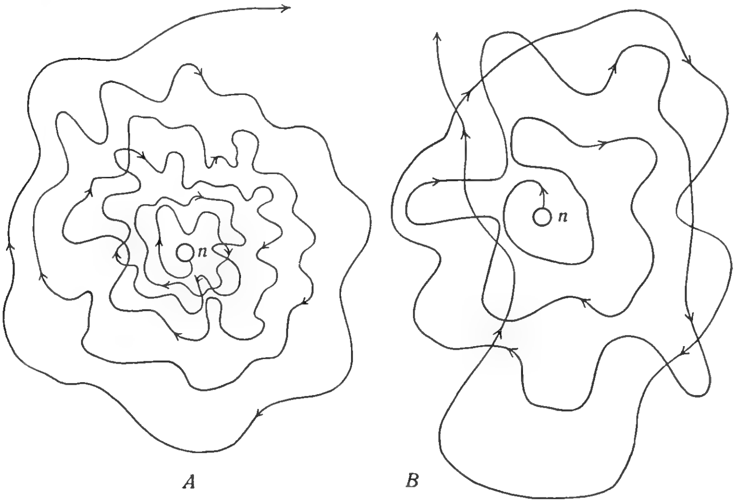
Though manifestly dominant, pure instinct fails to account for all insect behavior. The ability of an insect to profit by experience indicates some degree of intelligence.

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 *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. 291, *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. 291, *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 some deep lines in the dust before it. The same annoyance is exhibited when there is any change

FIG. 291.



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.

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 the 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—as in the case of the *Ammophila*. 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. Miss Enteman, on the contrary, says: " Wasps do not imitate one another. Instinct and individual experience account sufficiently for their powers, and their apparent coöperation is due entirely to the accident of their being born in the same nest." She finds that the worker *Polistes* does not learn to feed the larvæ by imitating the queen.

It is extremely difficult, however, if not impossible, 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, however, is due simply to a characteristic odor, which is derived from the mother of the community. An ant after being washed receives hostile treatment from others of 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 when 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

1. 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 *Isotoma fimetaria,* and the butterflies *Vanessa cardui* and *Anosia plexippus,* while among beetles no less than one hundred species are cosmopolitan or subcosmopolitan, including *Tenebrio molitor, Silvanus surinamensis, Dermestes lardarius, Attagenus piceus* and *Calandra oryzæ.* 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 tradewinds, 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, gypsy 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, as a rule, cannot 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 (Pl. 4). 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, however, are 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, migrating eastward in immense swarms, succumbs in the moist valley of the Mississippi; the chinch bug is never seriously injurious 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, cannot 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, though its food-habits are as yet unknown.

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 *Œneis semidea* on mountain summits in New Hampshire and Colorado (particularly Mt. Washington, N. H., and Pike's 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 these 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 *Œneis* 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 artificial 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."

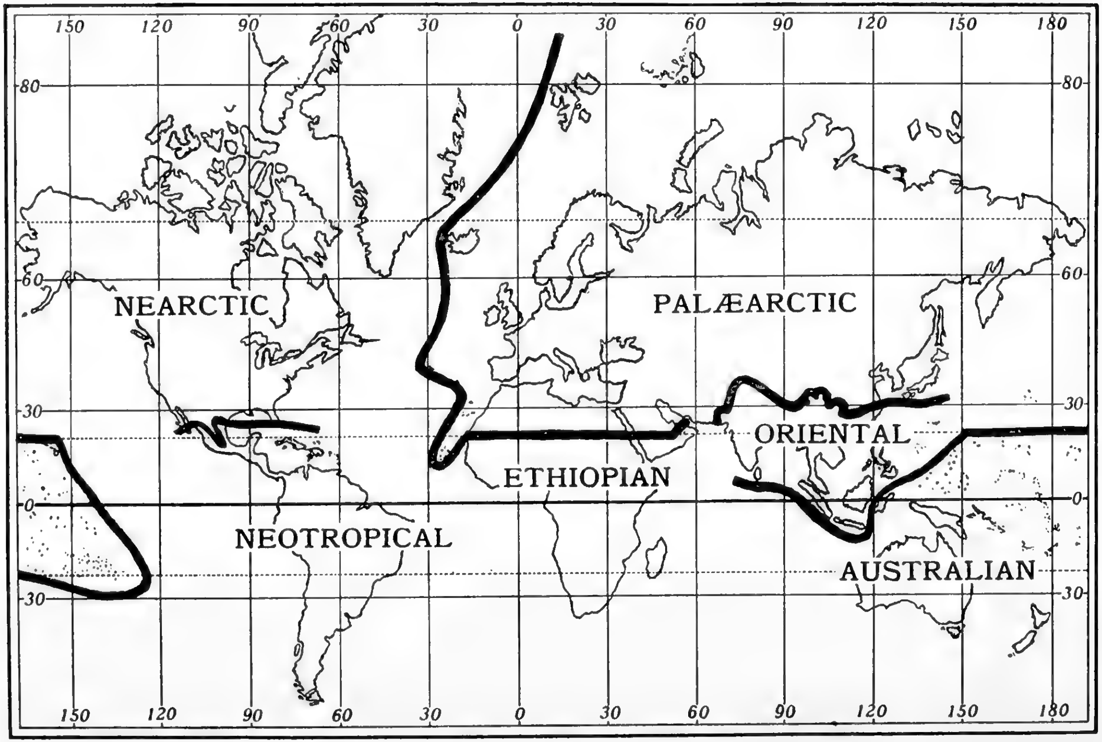
The parasitic Hymenoptera of Hawaii, according to Ashmead, number 14 families, 69 genera and 128 species; only eleven genera are endemic and most of the other genera are represented in nearly all the known faunæ of the earth. Ashmead concurs in the view that the Hawaiian fauna was originally derived 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 recently 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 Albemarle 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. Isolation in general we have considered briefly in Chapter VII.

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 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:

PLATE III.



Faunal Realms.—After Sclater and Wallace.

Holarctic, Neotropical, Ethiopian, Oriental and *Australian* (Pl. 3).

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 *Palæarctic*, 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 remarkable 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 nearly 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 subcosmopolitan, to be sure, but fifty of these are probably holarctic in origin, for example—*Dermestes lardarius* and *Tenebrio molitor*. 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 less 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.

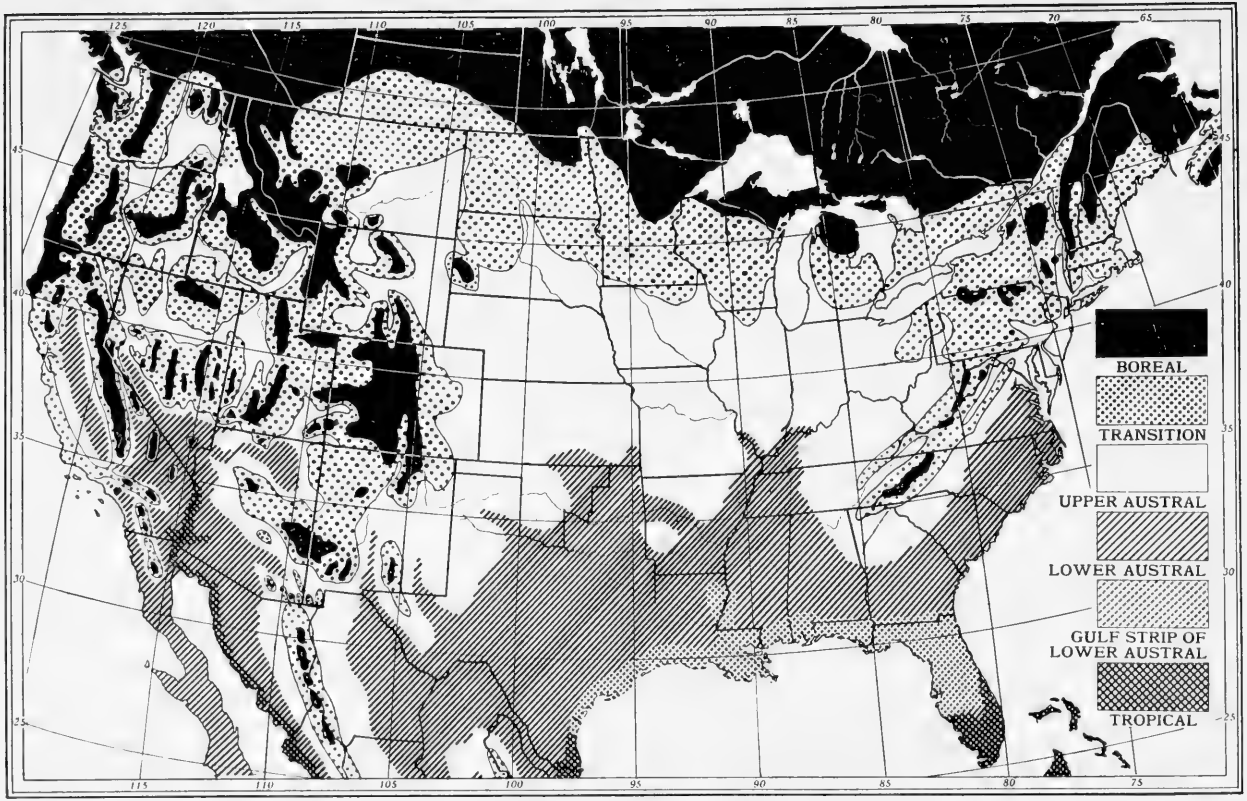
The *Oriental* realm includes India, Ceylon, Tropical China, and the Western Malay Islands. In the richness of its insect fauna, this realm vies with the Neotropical. Danaidæ and Papilionidæ are abundant, while the genus *Morpho* is represented by some forty species; of Coleoptera, Buprestidæ are important 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, according to the distribution of its animals and plants, into three primary transcontinental regions —*Boreal, Austral* and *Tropical*." (Pl. 4.)

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. 292) is strictly boreal in distribution.

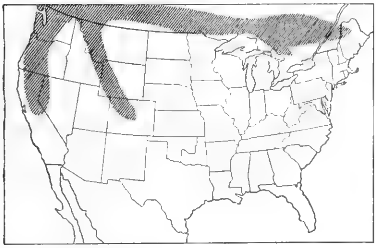
PLATE IV.



Life Zones of the United States.—After MERRIAM.

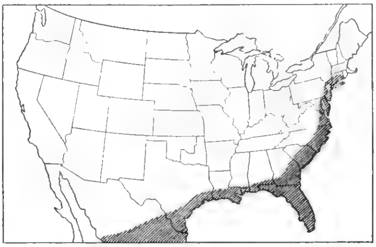
The *Austral* region "covers the whole of the United States and Mexico, except the Boreal mountains and the Tropical lowlands." It comprises three transcontinental belts: (1) the *Transition* zone, in which the Boreal and the Austral overlap; (2) the *Upper Austral;* (3) the *Lower Austral.* The butterfly *Eudamus proteus* (Fig. 293) is restricted, generally speaking, to the Tropical region and the warmer and more humid portions of the Austral.

FIG. 292.



Distribution of *Erynnis manitoba,* a butterfly restricted to subarctic and subalpine regions.—After SCUDDER.

FIG. 293.



Distribution in the United States of *Eudamus proteus,* primarily a tropical butterfly.—After SCUDDER.

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.

Coccinella quinquenotata, 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 *Megilla maculata* 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 *Melasoma* (*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. undecemlineata,* 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 less 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 (*Phytonomus punctatus*), the clover root borer (*Hylastes 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.

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 occurs now in Illinois. This insect, as Howard observes, flies readily, and may be introduced commercially in the egg or larval stage on bunches of asparagus.

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 reported recently from Minnesota.

From Colorado the well-known potato beetle (*Leptinotarsa decemlineata*) has worked eastward since 1840, reaching the Atlantic coast within twenty years, 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 Indiana. The Rocky Mountain locust periodically migrates eastward, but meets a check in the moist valley of the Mississippi, as has been said.

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. The harlequin cabbage bug (*Murgantia histrionica*) has spread from Central America into California and Nevada, and has steadily progressed in the Mississippi basin as far north as Illinois, Indiana and Ohio, though it appears to be unable to maintain itself in the northern parts of these states. This insect required about twenty-five years to pass from Louisiana (1864) to Ohio, spreading through its own efforts and not commercially to any great extent.

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 (*Heliophila unipuncta*), feeding on grasses, and occurring all over the United States south of Lat. 44° 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 found 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 less than three thousand.

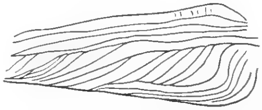
Localities for Fossil Insects.—The Devonian of New Brunswick has furnished a few forms, found near St. John, in a small ledge that outcrops between tide-marks; these forms, though few, are of extraordinary interest, as will be seen.

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 Œningen beds of Bavaria are celebrated as having furnished 844 species, described by the illustrious Heer.

FIG. 294.



Palæoblattina douvillei, natural size.—After BRONGNIART.

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. 294), of doubtful position,[1] from the Middle Silurian of France. Following these are six specimens of as many remarkable species from the Devonian shales

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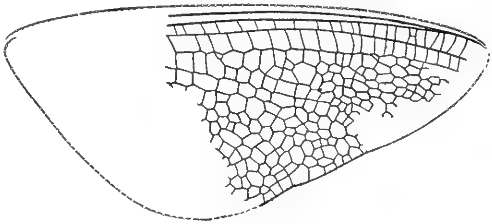
[1] There is some evidence, it should be said, that this species is not an insect. Handlirsch denies also that *Protocimex* is an insect.

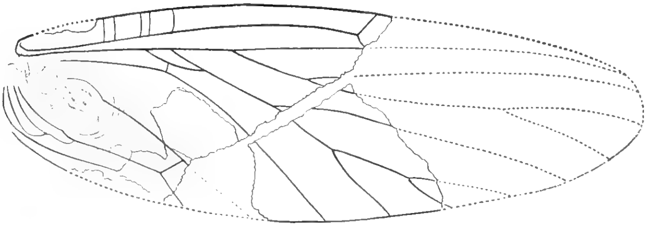
of New Brunswick. The specimens, to be sure, are nothing but broken wings, yet these few fragments, interpreted by Dr. Scudder, are rich in meaning. All are neuropteroid, but they cannot be classified satisfactorily with recent forms on account of being highly synthetic in structure. Thus *Platephemera antiqua* (Fig. 295), though essentially a May fly of gigantic proportions (spreading probably 135 mm.), has an odonate type of reticulation; while *Xenoneura* (Fig. 296) combines characters which are now distributed among Ephemeridæ, Sialidæ, Rhaphidiidæ, Coniopterygidæ, and other families, besides being in many respects unique. These Devonian forms attained huge dimensions as compared with their recent representatives; *Gerephemera,* for example, had an estimated expanse of 175 millimeters.

FIG. 295.



Platephemera antiqua, natural size.—After SCUDDER.

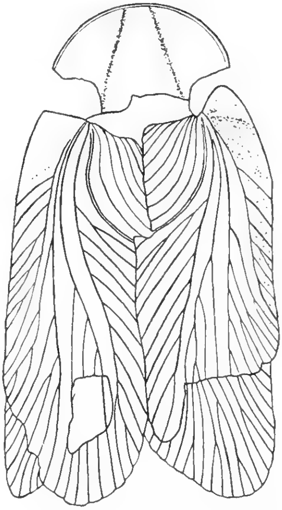
FIG. 296.



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 less than 200 Palæozoic species being known from Europe and North America. These ancient roaches (Fig. 297) 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.

Fig. 297.



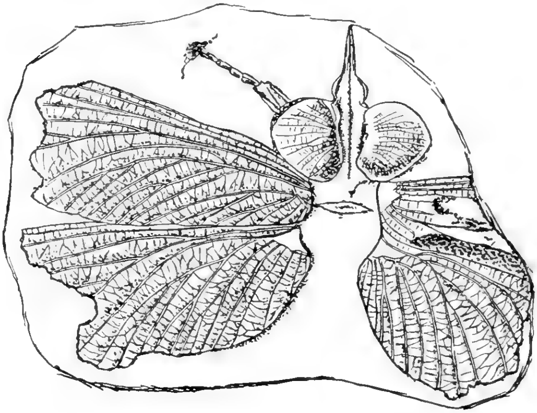
Etoblattina mazona, a Carboniferous cockroach from Illinois. Twice natural size. —After Scudder in Miall and Denny.

Lithomantis (Fig. 298), a remarkable form from Scotland. possessed in addition to its four large neuropteroid wings, a pair of prothoracic 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.

From the rich deposits of Commentry, Brongniart has described several forms of striking interest. *Dictyoneura* is a Carboniferous genus 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 over two feet; they were more generalized in structure than recent Odonata, presenting a much simpler type of neuration 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.

FIG. 298.

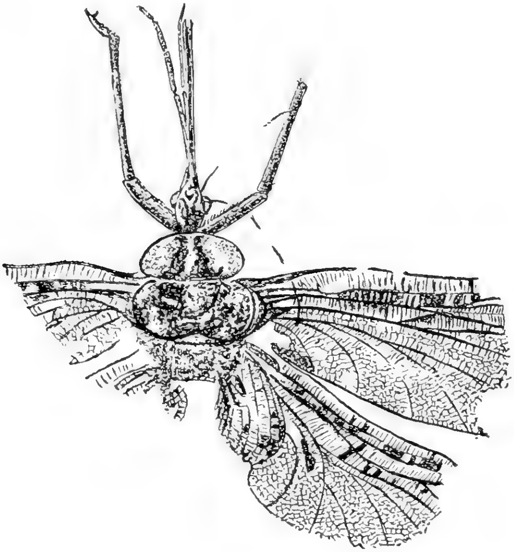


Lithomantis carbonarius, showing prothoracic appendages. Two thirds natural size.—After WOODWARD.

The Permian has supplied a remarkable genus *Eugereon* (Fig. 299) 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.

FIG. 299.



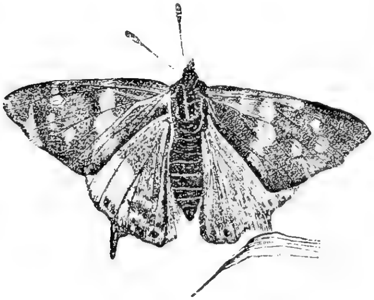
Eugereon böckingi. Three quarters natural size.—After DOHRN.

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 Œningen, 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 Œningen 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, over thirty species of Aphididæ, and over 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.

FIG. 300.



Prodryas persephone, a fossil butterfly from Colorado. Natural size. — After SCUDDER.

Fossil butterflies are among the greatest rarities, only seventeen being known; yet Florissant has contributed eight of these, a few of which are marvelously well preserved (Fig. 300), 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 has 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 or 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 are 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.

CHAPTER XIII

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, gypsy 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 annoyances, 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 food stuffs 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 gypsy 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 has practically been 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, as was described.

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.

The usefulness of the silkworms and the honey bee need only be mentioned, and after these, the cochineal insect and the lac insects. The " Spanish fly "—a meloid beetle—is still used medicinally, and in China medicinal properties are ascribed to many different insects. As human food, insects are of considerable importance among semi-civilized races; the migratory locust is eaten in great quantities in Africa, and termites in Africa and Australia, the latter insects being said to have a delicious flavor; in Mexico the eggs and adults of an aquatic hemipteron, *Corixa,* are highly relished by the natives. As food for fishes, game birds, song birds and poultry, insects are of vast importance, it is needless to say.

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), gypsy moth, 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 gypsy moth, liberated in Massachusetts in 1868, cost the state over one million dollars in appropriations (1890–1899) and is not yet under control. The San José scale, a native of North China according to Marlatt, 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, in these places probably as a recent introduction.

The Mexican cotton boll weevil (*Anthonomus grandis*) crossed the Rio Grande river and appeared in Brownsville, Texas, about 1892, since when it has spread over eastern Texas and even into western Louisiana. Advancing as it does at the rate of fifty miles a year, the insect would require but fifteen or eighteen years to cover the entire cotton belt. The beetle hibernates and lays its eggs in the cotton bolls; these are injured both by the larva feeding within and by the beetles, whose feeding-punctures destroy the bolls and cause them to drop. If unchecked, this pest would destroy fully one half the cotton crop, entailing an annual loss of $250,000,000. As it is, the universal adoption of the cultural methods recommended by the Bureau of Entomology promises to reduce the damage to a point at which cotton can still be grown at a fair profit.

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 cultivated species, particularly millet, Hungarian grass, rice, wheat, barley, rye and corn. In fact, the worst corn insects, such as the chinch bug, wire worms, 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 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.

Nearly 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 a 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 this 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 Mountain 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 has issued important bulletins upon injurious insects, and has published in collaboration with Edward H. Forbush a notable volume upon the gypsy moth. For the suppression of this pest, which threatened to exterminate vegetation over one hundred square miles, the state of Massachusetts made annual appropriations amounting in all to more than one million dollars, and the operations, carried on by a committee of the State Board of Agriculture, rank among the most extensive of their kind.

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 eighteen bulletins (including seven 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 are always made in the most conscientious spirit and their bulletins—original, thorough and practical—are models of what such works should be.

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, sagacious 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.

Since 1882, Prof. Stephen A. Forbes has fulfilled the duties of state entomologist in the most efficient manner. Thoroughly scientific, with a broad view and a clear insight into the agricultural needs of the state, his authoritative and scholarly works upon economic entomology rank with those of the highest value. Of the twelve reports issued thus far by Dr. Forbes, those dealing with the chinch bug, San José scale, corn insects and sugar beet insects are especially noteworthy.

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.

State Experiment Stations.—The organization of State Agricultural Experiment Stations in 1888, under the Hatch Act, gave economic entomology an additional impetus. At present, all the states and territories, except Indian Territory, have an experiment station, and in a few instances two or even three; while there are stations in Alaska, Hawaii and Porto Rico. These stations, often in connection with state agricultural colleges, maintain altogether over forty men who concern themselves more or less with 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 not a few of them are based upon the investigations of their authors. Especially noteworthy as regards originality, volume and general usefulness are the publications of Slingerland in New York, Smith in New Jersey, Webster in Ohio (formerly), Hopkins in West Virginia, Gillette and Osborn in Iowa and Gillette in Colorado. The reports that Lugger issued in Minnesota, though compiled for the most part, contain much serviceable information, presented in a popularly attractive manner.

While these workers have been conspicuously active in the publication of their investigations, there are many other station entomologists who devote themselves altogether 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.

Based upon the foundation laid by Riley, the work of the Division (now 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 maintains a corps of about fifty experts, and the total output of the Division and the Bureau now amounts to nearly one hundred bulletins and more than half as many circulars.

The Department of Agriculture has recently 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, or, 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, has now been established in California, and the new industry is developing rapidly.

Canada.—The development of economic entomology in Canada has been due largely to the efforts of Dr. James Fletcher, of the Dominion Experimental Farms, Ottawa, whose annual reports and other writings indicate ability of an exceptional order. His work has been 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."

Outside of this, the work 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 by its founder, the Rev. C. J. S. Bethune, whose devoted services are 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.

Conclusion.—While working for the material welfare of the agriculturist, the economic entomologist discovers phenomena which are of the highest value to the purely scientific mind. Indeed it is remarkable to notice the extent to which the professedly practical entomologist is animated—not to say dominated—by the same spirit which has led many of the most profound thinkers that the world has ever produced to devote their lives to the study of life itself.

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