PRINCIPLES OF INSECT MORPHOLOGY

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PREFACE

The principal value of facts is that they give us something to think about. A scientific textbook, therefore, should contain a fair amount of reliable information, though it may be a matter of choice with the author whether he leaves it to the reader to formulate his own ideas as to the meaning of the facts, or whether he attempts to guide the reader's thoughts along what seem to him to be the proper channels. The writer of the present text, being convinced that generalizations are more important than mere knowledge of facts, and being also somewhat partial to his own way of thinking about insects, has not been able to refrain entirely from presenting the facts of insect anatomy in a way to suggest relations between them that possibly exist only in his own mind. Each of the several chapters of this book, in other words, is an attempt to give a coherent morphological view of the fundamental nature and the apparent evolution of a particular group of organs or associated structures. It is more than likely, practically certain, that many of the generalizations here offered will soon be modified or superseded by other generalizations, but they will have served their purpose if they induce critical students to make a wider and more thorough study of the problems of insect morphology.

Two notable books have appeared recently in entomology: one, "Lehrbuch der Entomologie," by Dr. Hermann Weber of Danzig, in its first edition; the other, "A General Textbook of Entomology," by Dr. A. D. Imms of Cambridge, England, in its third edition. In preparing the present text the writer has made a special effort to concur with the authors of these books in the matter of anatomical terms, in order that students may as far as possible be spared confusion in turning from one treatise to another. Unfortunately, however, there is still much unavoidable discrepancy in the use and application of anatomical names in entomology. The trouble, in large measure, can be blamed on the insects themselves, since they will not entirely conform with any plan of nomenclature or with any scheme we can devise for naming their parts consistently. To make clear the meaning of terms as used in this text, therefore, a glossary of definitions is appended to each chapter, wherein, also, will be found the German equivalents of many of our English and Latinized technical names.

In making acknowledgments, the writer must first of all declare his indebtedness to the Bureau of Entomology, United States Department of Agriculture, for the experience and information acquired in the course of his many years of official service. Most of the illustrations accompanying the text that are not accredited to particular sources are the property of the Bureau of Entomology and Plant Quarantine, and many of them have been published in the *Miscellaneous Collections* and the *Annual Reports* of the Smithsonian Institution of Washington, D.C. For the use of these figures the writer hereby expresses his thanks both to the Bureau and to the Smithsonion Institution. With regard to illustrations borrowed from other works, the writer is particularly indebted to Professor Hermann Weber, of Danzig, for permission to use figures from his "Biologie der Hemipteren" and "Lehrbuch der Entomologie." The rest of the illustrations, each accredited to its proper source in the scientific journals, have been freely drawn from the common heritage of entomology contributed by the many workers in many lands who have devoted themselves to the study of insects. To my wife, Ruth H. Snodgrass, credit is due for the typing of the manuscript and for much of the work of indexing and proofreading.

R. E. SNODGRASS.

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CONTENTS

CHAPTER VIII

CHAPTER IX

CHAPTER X

CHAPTER XI

CHAPTER XII

CHAPTER XIII

CHAPTER XIV

CHAPTER XV

CHAPTER XVI

CHAPTER XVII

CHAPTER XVIII

CHAPTER XIX

PRINCIPLES OF INSECT MORPHOLOGY

CHAPTER I

INTRODUCTION

Morphology, in the biological sense, is the science of form in living organisms. Anatomy is the determination of structural facts. Morphology seeks to find the reason for structure, and to understand the relation of different structural forms to one another. Morphology, therefore, must be intimate with function, since it must see forms as plastic physical adaptations to the work to be performed. A few physiological functions are basic to all organisms; they are essential to the continuance of matter in a living state. The various structural types of organisms are special ways of accomplishing these functions, that is, for doing the same things in different ways or under different circumstances. Some represent improvements in the machinery along established lines; others represent changes or new ideas developed along new and divergent lines. The morphologist, therefore, though primarily a comparative anatomist, in order properly to develop his subject, must give attention to the working of the physical mechanisms with which he deals in his anatomical studies, he must look for the significance of structural modifications and innovations, and he must understand the basic physiological functions that underlie organic form.

In the study of insect morphology we cannot confine ourselves to the limits of entomology. The fundamental organization of insects was established long before insects became a specialized group within the phylum of the Arthropoda, and the basic structure of the arthropods is much older than the arthropods themselves. As organisms evolve, important structures are often so modified that their true nature becomes obscured; but the same structure is not likely to be modified to the same degree in all related groups, or in all members of the same group. Structural modification has been carried to a high degree in all the arthropods, affecting some organs in one group, others in another group; and particularly is this true of the insects. Hence, in the discussion of the morphology of insect organs given in the following chapters, many references will be made to corresponding parts in other arthropods, while, for an understanding of the more fundamental structures of the arthropods, it will be found necessary to go back to the segmented worms and to those wormlike creatures known as onychophorans. Before taking up the particular subject in hand, therefore, we must know something of the distinctive structural features of the Annelida the Onychophora, and the major groups of the Arthropoda.

THE ANNELIDA

The typical annelid worms are elongate cylindrical animals divided transversely into a series of segments. The mouth is situated ventrally between the first segment and a preoral lobe (prostomium); the anus is terminal in the last segment (periproct). The segments between the prostomium and the periproct are true metameres, or somites, produced by segmentation of the primitive body region anterior to the periproct. Some of the annelids are provided with lateral segmental appendages (parapodia), which are hollow evaginations of the body wall, movable by muscles inserted on or within their bases.

The body cavity of the Annelida is the coelome. It is often divided transversely by intersegmental septa into segmental coelomic cavities. The alimentary canal is a tube extending through the body from the mouth, situated ventrally between the prostomium and the first somite, to the anus, which is terminal on the periproct. A blood vascular system is well developed in some forms by enclosure of tracts of the haemocoele in mesodermal walls. Usually there is a median dorsal vessel and a median ventral vessel connected by lateral trunks, from which are given off branches to the various organs of the body. The excretory system consists of paired segmental tubes (nephridia) opening, on the one hand, into the coelome, and, on the other, to the exterior. Respiration takes place either directly through the body wall or by means of gills, which are evaginations of the integument.

The annelid nervous system includes a median prostomial ganglion, the brain (archicerebrum), lying dorsal to the alimentary canal, and a ventral nerve cord consisting of double segmental ganglia united by paired connectives. The brain and the first ventral ganglia are united by connectives embracing the oesophagus. The brain innervates whatever sense organs, such as palpi, tentacles, and eyes, may be located on the prostomium; it is often differentiated into a forebrain (protocerebrum) and a hindbrain (deutocerebrum). The forebrain may contain well-developed association centers in the form of stalked bodies, or corpora pedunculata.

The germ cells of the mature annelid occur in groups imbedded in the mesodermal lining of the coelome, the simple organs thus formed being the gonads (ovaries and testes). The ripening ova and spermatozoa are discharged from the gonads either into the general coelomic cavity, from which they escape through the nephridia or through pores of the body wall, or into special coelomic receptacles connected by ducts with the exterior. The young annelid larva has a characteristic form and is known as a trochophore.

THE ONYCHOPHORA

The onychophorans, including *Peripatus* and related genera, are wormlike animals resembling the annelids in many respects. Though segmentation is not evident in the cylindrical body or in the somatic musculature, the presence of a series of paired lateroventral ambulatory appendages gives the animal a segmented appearance. The "legs" resemble the annelid parapodia in that each is a hollow evagination of the body wall movable by four sets of muscles reflected into the appendage from the somatic wall. The mouth is situated anteriorly on the ventral surface at the base of a prostomial lobe. The prostomium bears a pair of tentacles and a pair of simple eyes. An extraoral mouth cavity contains the true oral opening and a pair of strongly musculated mouth hooks.

The body cavity of the Onychophora is continuous through the length of the animal. The circulatory system consists of a dorsal vessel only, which has paired openings into the body cavity between each pair of legs. The excretory organs are nephridia similar to those of Annelida, opening externally on the bases of the legs. Delicate internal air tubes (tracheae), arising in groups from pits scattered irregularly over the integument, probably subserve respiration. The nervous system consists of a dorsal brain located in the head, and of two long lateral nerve cords in which ganglia are but little differentiated. The brain innervates the tentacles, the eyes, and the mouth hooks. The reproductive organs in each sex are a pair of long tubular sacs, the ducts of which unite in a median exit tube that opens ventrally near the posterior end of the body. Most species of Onychophora are viviparous, the embryo being developed within the oviducts of the female. The young animal takes on directly the form of the adult.

The Onychophora have often been regarded as primitive arthropods, but there is little in their organization that conforms with arthropod structure. Their relationships are undoubtedly with the Annelida, but the fact that the young at no stage have any resemblance to a trochophore larva would seem to indicate that the Onychophora are not derived from typical annelids. The Onychophora, in fact, have an ancient lineage of their own; fossil forms are known from the Middle Cambrian that closely resemble modern species, except for the smaller number of legs.

THE ARTHROPODA

The arthropods have an annulate body and segmental appendages. Their distinctive features are the jointing of the appendages and a grouping of the body segments, each appendage being composed of a number of limb segments (podites) individually movable by muscles, while the body segments are segregated to form more or less distinct trunk sections (tagmata). The integument is usually hardened by the deposition of sclerotizing substances in definite areas of the cuticula, forming exoskeletal plates (sclerites) to which most of the muscles are attached. The intervening membranous areas allow of movement between the plates. This character has given the arthropods an unlimited field for the development and evolution of exoskeletal mechanisms both in the trunk and in the appendages.

The composition and specialization of the trunk sections, or tagmata, are characteristic of each of the several major groups of arthropods. The most constant and distinctive tagma is the head. In its simplest form the definitive head represents the embryonic protocephalon, consisting of a large preoral region and usually the first postoral somite. Generally, however, it includes a gnathal region (gnathocephalon) formed of at least three succeeding somites. The body region following the head may preserve a uniform segmentation and simple structure, or it may be variously differentiated into a thorax and an abdomen. In some forms the cephalic region and a varying number of succeeding somites are combined in a "cephalothorax," or prosoma, distinct from the abdomen. The primitive terminal segment (telson) is probably not a true somite, but an endpiece of the body bearing the anus, corresponding to the periproct of the Annelida.

The appendages of the trunk include a pair of procephalic antennae (antennules), and a double series of segmented, postoral, ventrolateral limbs, potentially a pair on each segment but the last. The postoral appendages become variously modified in adaptation to functional specializations. A typical arthropod limb consists of a basis (coxopodite) movable anteroposteriorly on the body, and of a six-segmented shaft (telopodite) movable in a vertical plane on the basis. Endite and exite lobes of the limb segments are frequently developed into specialized appendicular processes.

The definitive alimentary canal includes long anterior and posterior sections (stomodaeum and proctodaeum) derived from the ectoderm. Typical segmental nephridia are absent. The blood vascular system is variously developed, but in plan it conforms with that of the Annelida. Respiration takes place either through the general body integument or by means of evaginations (gills) or invaginations (tracheae) of the body wall.

The nervous system of the arthropods has the same general structure as that of the Annelida. The primitive brain consists of a preoral body of nerve tissue lying above the stomodaeum, which is differentiated into protocerebral (ocular) and deutocerebral (antennular) regions, except in forms lacking antennae. The definitive brain in most groups, however, is a syncerebrum, since it includes also the first pair of ganglia of the ventral nerve cord, which secondarily become tritocerebral brain lobes. The protocerebrum contains often highly developed corpora pedunculata and the ocular centers; the deutocerebrum innervates the antennules (first antennae); and the tritocerebrum the first pair of postoral appendages (chelicerae or second antennae).

The visual organs of the arthropods include dorsal (median) and lateral eyes innervated from the protocerebrum. The dorsal eyes are always simple ocelli, located usually on the upper or anterior surface of the head, but in *Xiphosura*, and possibly in the trilobites and eurypterids, there is a pair of rudimentary ventral eyes on the deflected under surface of the head before the mouth. The number of dorsal eyes varies from one to eight, but often none is present; primitively there were perhaps two pairs; a single median dorsal ocellus probably represents the ocelli of one pair united. The lateral eyes are typically compound, being formed of groups of simple optic units composing a single organ, but often they are represented by groups of distinct ocelli.

The reproductive organs are mesodermal sacs enclosing the germ cells. The paired mesodermal exit ducts open either separately to the exterior or into a common median outlet tube of ectodermal origin. The position of the genital aperture is variable.

The Arthropoda include three major groups, namely, the *Trilobita*, the *Chelicerata*, and the *Mandibulata*.

THE TRILOBITA

The trilobites are extinct creatures that flourished throughout the Paleozoic era but were most abundant during the Cambrian and Ordovician periods. They are the most generalized of known arthropods. The body is usually oval and flattened and carries ventrally a double series of jointed limbs. The trunk is divided into a head and two body regions known as the thorax and the pygidium, but the name "trilobite" is derived from the apparent triple division of the trunk lengthwise into an elevated median area (the axis, or rhachis) and two depressed lateral areas (pleurae). The head, which appears to include the prostomium and four somites, is covered by a dorsal carapace; the thorax consists of a variable number of free segments; the pygidium contains several segments, which, except in certain earlier forms, are united in a caudal shield. Each body segment, except the last, bears ventrally a pair of jointed appendages. On the upper surface of the head in most species are a pair of compound lateral eyes, and in some forms a median tubercle which appears to be a simple dorsal eye; on the under surface is a pair of small spots which some writers believe to be ventral eyes.

The distinctively generalized feature of the trilobites, as compared with the other arthropods, is the lack of specialization and structural differentiation in the segmental appendages. The first pair of appendages, which probably are procephalic antennules, are filamentous and multiarticulate. The rest are without doubt postoral limbs. They are practically all alike except that some of the more anterior ones may have a greater number of segments than the others. The trilobite limb preserves the typical form and fundamental structure of all arthropod appendages. The basis supports a large exite (epipodite) bearing a series of thin, closely set plates or filaments, which probably functioned as gills. The telopodite is usually six segmented.

The trilobites appear to be related, on the one hand, to the Xiphosura, and, on the other, to the phyllopod crustaceans, since they have features characteristic of both these groups. They are not literally the ancestors of the other arthropods, however, since along with the trilobites there lived the highly specialized eurypterids and a large and varied crustacean fauna, but the trilobites are probably more closely related to the ancestral arthropods than are any other known forms.

THE CHELICERATA

In both the chelicerate and the mandibulate arthropods the segmental appendages are diversified in form and function, and some of them are suppressed. The most generally distinctive features that separate the Chelicerata from the Mandibulata are the suppression of the antennules, and the modification of the *first* postoral appendages to form a pair of *chelicerae,* which typically are pincerlike feeding organs.

The body segments are grouped into two trunk regions, a prosoma and an abdomen. The first includes the protocephalon and the first six postoral somites, which are always more or less united. The abdomen varies in length and may be distinctly segmented, though in the higher forms it is usually short and its segmentation indistinct or suppressed. The prosoma bears six pairs of limbs, including the chelicerae, all of which, except the chelicerae, are generally leglike in form. The telopodites of some of the appendages often contain seven segments instead of six by the interpolation of a "patella" between the femur (meropodite) and the tibia (carpopodite). Abdominal appendages are usually absent, but in the more generalized forms they are retained in modified shape and may have gill-bearing epipodites as in the Trilobita.

The brain of the Chelicerata is a syncerebrum composed of the primitive cerebrum and the ganglia of the cheliceral segment, but, owing to the loss of the procephalic antennules, the deutocerebral centers are suppressed, and the brain consists of the protocerebrum, which innervates the eyes, and of the tritocerebrum, which innervates the chelicerae. The ocular organs include median dorsal eyes, lateral eyes, and in some cases ventral eyes. The lateral eyes are compound in more primitive forms; in others they are represented by groups of simple eyes.

The Chelicerata include the *Eurypterida,* the *Xiphosura,* the *Pycnogonida,* and the *Arachnida.*

Eurypterida.—The eurypterids are extinct Paleozoic arthropods that lived from the Cambrian to the Carboniferous period but attained their greatest development in the Silurian and Devonian. They were aquatic, mostly fresh-water, or mud-inhabiting creatures. While the majority were relatively small, less than a foot in length, some became the largest of all known arthropods, reaching a length of 6 or 7 feet. The segments of the prosoma are united; the abdomen consists of 12 free segments, the last bearing a telson, which is usually a long tapering spine but is plate-like in some forms. The chelicerae are long or short. The next four pairs of limbs are generally small, and the sixth pair long and flat, evidently swimming organs; but in some species the legs are all long and slender. The first five segments of the abdomen have plate-like appendages overlapping each other and concealing gills. On the upper surface of the cephalic region are a pair of compound lateral eyes and two small simple dorsal eyes; on the under surface, according to Störmer (1934), there appears to be in some forms a pair of ventral eyes.

Xiphosura.—The modern members of this group, commonly known as horseshoe crabs or king crabs, have so many points of resemblance with the ancient eurypterids that the two groups are often classed together as the Merostomata, and certain extinct forms make the connection even closer. The body of the horseshoe crab is distinctly divided between the prosoma and the abdomen; in each part the segments are united and covered by a large dorsal carapace, the second ending in a long spine-like telson. The six thoracic appendages are all chelate in the female. The abdomen contains only six segments, which bear plate-like appendages very similar to those of the anterior part of the abdomen of the eurypterids, each except the first having a large gill-bearing epipodite. On the head are a pair of compound lateral eyes, a pair of simple median dorsal eyes, and a pair of rudimentary median ventral eyes.

Pycnogonida, or Pantapoda.—The pycnogonids are aberrant arthropods commonly known as sea spiders. From the nature of their appendages they appear to belong to the Chelicerata.

Arachnida.—Here are included the scorpions, the solpugids, the phalangids, the spiders, the ticks, and the mites. In most forms the trunk is divided in the typical chelicerate manner into a prosoma and an abdomen, but in the solpugids the prosoma is constricted between the fourth and fifth pairs of limbs. The abdomen may be long and distinctly segmented, in which case the distal part is narrowed and has the form of a jointed "tail," but in the spiders and mites the abdomen is short and rotund, with indistinct or suppressed segmentation. The prosomal appendages include the chelicerae, a pair of pedipalps, and four pairs of legs. Abdominal appendages are either absent or represented by modified rudimentary structures. The cephalic region of the prosoma generally bears a group of simple dorsal eyes, and, in some forms, on each side one to five simple lateral eyes; the lateral eyes are never compound. Paleontologically the oldest known arachnids are contemporaneous with the trilobites and eurypterids.

THE MANDIBULATA

The mandibulate arthropods differ from the Chelicerata in two characteristic features, namely, (1) the retention of the procephalic antennules, and (2) the modification of the bases of the *second* postoral appendages to form a pair of biting, jawlike feeding organs, the *mandibles*. The appendages of the first postoral segment, corresponding to the chelicerae of the Chelicerata, are present in most Crustacea as a pair of large biramous antennae (second antennae), but in the other mandibulate groups they are suppressed or are represented only by embryonic rudiments. The telopodites of the mandibles may be retained in Crustacea in the form of "palpi," but otherwise they are lost. The first two postmandibular appendages are generally modified as accessory feeding organs (the first and second maxillae), though in some forms they are reduced and more or less rudimentary. The following appendages may all have a uniform structure, or they may be variously modified on different regions of the body; but a patellar segment is never present in any of them.

Tagmosis is variable in the Mandibulata. The head may consist of the protocephalon only (including the second antennal somite), but generally it contains a gnathocephalic section composed of the mandibular and the two maxillary somites, to which may be added the appendages, at least, of the next trunk segment. In the malacostracan Crustacea the protocephalon, the gnathal segments, and a varying number of succeeding segments are more or less combined in a "cephalothorax." The Myriapoda and Hexapoda have a distinct head including four postoral somites; the body of the first group shows no tagmosis, but in the hexapods it is differentiated into a thorax and an abdomen.

The brain of the Mandibulata is well differentiated into a protocerebrum and a deutocerebrum, innervating respectively the eyes and the antennules (first antennae); generally it includes also the first postoral ganglia of the ventral nerve cord, innervating the second antennae when these appendages are present; these ganglia become the tritocerebral lobes of the definitive brain, though they retain their primitive ventral commissure. The mandibular and both maxillary pairs of ganglia are united in a composite suboesophageal ganglion contained in the head when the latter includes the gnathal segments. A stomodaeal nervous system is usually present, having its principal connections with the tritocerebral ganglia.

The major groups of the Mandibulata are the *Crustacea,* the *Myriapoda,* and the *Hexapoda.*

Crustacea.—The crustaceans include the phyllopods, the barnacles, the shrimps, crayfish and lobsters, the crabs, and related forms. The Crustacea are distinguished from all the other arthropods by a biramous structure of the limbs, each appendage typically having an outer branch (exopodite), arising from the basal segment (basipodite) of the telopodite, and an inner branch (endopodite), which is the shaft of the telopodite distal to the basipodite. The coxopodite, in many forms, supports a gill-bearing epipodite, which apparently corresponds to the similar basal appendicular organ of the limbs of Trilobita and the abdominal appendages of Xiphosura.

Tagmosis is variable in the Crustacea. The protocephalon, including the tritocerebral somite, may constitute a small primitive head distinct from the rest of the trunk, or it may be united with several somites following to form a composite head; or, again, a variable number of segments in the thoracic region are more or less united with the head in a cephalothorax distinct from an abdomen.

The first antennal appendages (antennules) are usually filamentous and multiarticulate; they are never biramous. The tritocerebral appendages (second antennae) are typically biramous and thus show that they belong to the series of postoral limbs, though the body segment bearing them forms a part of the protocephalon. The mandibles are always well developed; the two pairs of maxillae are small, sometimes rudimentary. The next three pairs of appendages are termed maxillipeds; the following five are differentiated in higher forms primarily as ambulatory organs (periopods). The abdominal appendages (pleopods) are usually different from the thoracic appendages and are often specially modified. Most of the appendages may be modified for purposes of swimming.

The brain in some of the lower Crustacea is a primitive cerebrum differentiated into a protocerebrum and deutocerebrum containing respectively the ocular and first antennal centers. In most forms, however, the definitive brain is a syncerebrum including the second antennal ganglia as tritocerebral lobes. The Crustacea have compound lateral eyes similar in structure to those of insects.

Myriapoda.—The common myriapods are easily distinguished from the other terrestrial arthropods by their slender forms and many legs, but a more generally distinctive character is the division of the trunk into only two parts, a head and a body. The head bears a pair of preoral antennae (antennules) and probably includes not more than four postoral somites. The appendages of the first somite are absent, those of the second are the mandibles, the other two pairs are variable in structure. The body is typically long and uniformly segmented, though some of the segments may be reduced, and in two groups the segments are united in pairs. Most of the primitive segments bear each a pair of legs. The myriapods are terrestrial animals; the majority of them have tracheal invaginations of the body wall for respiration. Eyes, when present in modern forms, consist of groups of simple lateral eyes, which approach the compound type in *Scutigera.* Certain Permian diplopods are said to have had large compound eyes.

The Myriapoda include two principal groups. In the members of one group (progoneate forms) the reproductive organs open near the anterior end of the body; in those of the other group (opisthogoneate forms) the genital opening is at the posterior end of the body. The progoneate myriapods include the Diplopoda, the Pauropoda, and the Symphyla; the opisthogoneate group consists of the Chilopoda (centipedes). In the diplopods and pauropods most of the body somites appear to be united in successive pairs, at least dorsally; the legs of the diplopods occur in pairs on each double segment. The pauropods have branched antennae.

Hexapoda.—The hexapods are well characterized by the feature of their organization from which they get their name, which is the invariable specialization of three pairs of appendages as legs. The legs are always the appendages of the first three postgnathal somites; the latter constitute a definite locomotor center, the thorax, distinct from the abdomen, which seldom bears organs of locomotion. The head has apparently the same composition as in the Myriapoda, since it always includes three pairs of gnathal somites. The abdomen never has more than 12 segments (11 true somites), of which the last is the periproct.

The appendages of the head include a pair of procephalic antennae (antennules), embryonic rudiments of second antennae, a pair of mandibles, and two pairs of maxillae. The second maxillae are united in a median composite organ known as the labium. The thoracic appendages are the three pairs of legs. Abdominal appendages may be present on any of the 11 true somites of the abdomen, but they are always greatly modified or rudimentary and when present assume a variety of forms; generally most of them are absent in the adult stage. The appendages are never biramous in a manner comparable with the appendages of Crustacea, but epipodites may be present on the coxopodites.

The brain of the hexapods has distinct protocerebral, deutocerebral, and tritocerebral centers, the last formed of the ganglia of the second antennal somite. The lateral eyes, when present, are typically compound, but in some adults and in many larval forms they are replaced by groups of simple eyes. Three dorsal ocelli are commonly present, the unpaired ocellus being median, anterior (or ventral) to the others, and probably double in its origin.

The genital ducts open either separately or through a median tube of ectodermal origin. The paired ducts of the female may open between the eleventh and twelfth segments of the abdomen (Protura), or between the seventh and eighth (Ephemerida). The median oviduct opens on the seventh, eighth, or ninth abdominal segment, the median ejaculatory duct on the ninth segment, except in Collembola where the genital opening in each sex is between the fifth and sixth definitive segments of the abdomen.

The Hexapoda include several more or less distinct groups, which are the *Protura*, the *Collembola*, the *Diplura*, the *Thysanura*, and the *Pterygota*, but systematists are not agreed as to the relationships of these groups. Since the Pterygota are the winged insects, the other forms are generally termed collectively the Apterygota. Or, again, the Protura are set apart from the others, which are regarded as the true Insecta. The Diplura are usually classed with the Thysanura, the two groups then being distinguished as Thysanura entotrophica and Thysanura ectotrophica.

Protura.—The proturans are minute creatures resembling insects except that they lack antennae. They are more fundamentally distinguished from the other hexapods by the fact that the body does not contain the definitive number of segments at hatching, there being added during growth two segments between the periproct and the preceding somite. This postembryonic development of segments is unknown in the other hexapods but is usual in the myriapods. The reproductive ducts in both sexes of Protura open behind the penultimate segment of the adult, as in Chilopoda. Notwithstanding these features, however, the Protura appear to be more closely allied to the insects than to the myriapods. The body is differentiated into a principal locomotor center, the thorax, composed of three segments bearing three pairs of legs, and into an abdomen of 12 complete segmental annuli, which has small or rudimentary tubular appendages on its first three segments only. The thoracic legs end each in a simple clawlike segment (dactylopodite)—

another myriapod feature, but one occurring also in some apterygote insects and in many pterygote larvae.

Collembola.—The collembolans are small creatures that constitute a sharply defined group of hexapods with many distinctive features. The abdomen never has more than six segments and is usually provided with three highly specialized appendicular organs. The first of these appendages is a large thick tube, the collophore, that projects from the ventral side of the first abdominal segment. The third is a leaping organ, the furcula, arising from the fifth segment, consisting of a large base and two long terminal prongs. When bent forward in repose, the furcula is held in place by the small forked second appendage, or tenaculum, arising from the third abdominal segment. The genital opening in both sexes occurs between the fifth and sixth segments of the abdomen. The reproductive organs closely resemble those of Protura.

Diplura (*Thysanura entotrophica*).—The members of this group are characterized by having the mandibles and maxillae retracted into a pouch above the labium. In this respect and in certain other respects they are more specialized than the true Thysanura, but the latter are more closely related to the Pterygota. The common genera are *Campodea* and *Japyx*.

Thysanura (*Thysanura ectotrophica*).—The thysanurans have the mandibles and maxillae exposed in the usual manner, and they retain more complete remnants of abdominal appendages than do the Diplura. The coxopodites of the genital appendages in most species are provided with gonapophyses that form an ovipositor in the female, which appears to be the prototype of the egg-laying organ of pterygote insects. Of the two principal families, Machilidae and Lepismatidae, the second shows closer affinities with the Pterygota in the structure and mechanism of the mandibles.

Pterygota.—The Pterygota include all the winged insects and their wingless relatives; the latter presumably have lost their wings secondarily. The wings are lateral extensions of the dorsum of the second and third thoracic segments and were fully developed as organs of flight in the oldest known fossil insects. During the Carboniferous period, or probably earlier, a group of winged insects evolved a mechanism in the wing base for flexing the wings horizontally over the back when not in use. The descendants of this group (Neopterygota) include the majority of modern winged insects, while the more primitive nonwing-flexing insects are represented today by only two orders (Odonata and Ephemerida), both of which have descended from Carboniferous times but are not closely related to each other.

Ontogenetically the wings are developed during postembryonic growth, and a postembryonic metamorphosis, in varying degrees, is common in all the Pterygota. Among the wing-flexing insects, the wings in one group are developed during the larval stages within closed pouches of the body wall, and the larvae of members of this group have become so specialized that their transformation to the adult involves the interpolation of a preimaginal instar, the pupa, between the larva and the fully formed adult. Insects of this group are known as the Endopterygota, because of the internal development of the wings, or as the Holometabola, in reference to their high degree of metamorphosis. Most of the other wing-flexing insects, as well as those that do not flex the wings, develop the wings externally in the usual manner of growth of appendicular organs, and they have in general a simpler metamorphosis that allows the nymph or larva to change directly into the form of the adult. These insects are distinguished, therefore, as the Exopterygota, or Hemimetabola, but it should be observed that they do not constitute a monophyletic assemblage of forms, since they include a large group of wing-flexing insects and also the nonwing-flexing Odonata and Ephemerida.

CHAPTER II

GENERAL ORGANIZATION AND DEVELOPMENT

To understand the structural organization of any animal, it is necessary to know that animal's history, for no living creature has arrived at its present organization by a direct line of development from its beginning. Structure generally is an adaptation to function; but many of the organs of complex animals have served a series of quite different functions during the course of their evolution and, as a consequence, have had their structure many times remodeled by way of adaptation to their changing function or to new functions.

The history of an animal cannot be known from the imperfectly preserved records of its past. Embryonic development may give us a suggestion of phylogenetic evolution, since in a general way the embryo repeats the history of its race; but the embryo, for purposes of its own, usually digresses much from the ancestral story, and it commonly abbreviates its version of the earlier chapters or often omits these parts altogether. Fortunately, however, the less highly evolved the final form of an organism, the more of its early history is it likely to retain in its ontogeny. Hence, we may approximate a reconstruction of the phylogeny of a species by filling out the obscure passages in its embryonic story, or by supplying those deleted, with material judiciously selected from the facts of embryonic development in related forms successively lower in the scale of organization. To the evidence derived from embryology, however, we must always add that to be deduced from a study of comparative anatomy, for in the structure of serially related adult animals we often get an insight into the course of evolution more reliable than that to be obtained from any other source.

In the present chapter, therefore, we shall endeavor to build up a concept of the fundamental organization of an insect on evidence derived from embryology and from a study of the adult structure of other arthropods, of *Peripatus*, and of the annelid worms.

The Germ Cells and the Soma.—The generative cell from which any individual of the metazoic animals is produced begins development by division. After successive repetitions of division there are soon formed two distinct groups of cells in the resulting cell mass; those of one group continue to be *germ cells*, those of the other group become the *somatic cells*. It is the organization of this second and always larger group of cells forming the *soma,* or body of the future animal, that we study in ordinary anatomy.

The purpose of the soma primarily is to give protection to the germ cells during the period in which these cells develop to maturity. It then becomes obligatory upon the soma, in most forms of animals, to bring the germ cells of opposite sexes together in such a manner that a sufficient number of them may unite to insure perpetuation of the species. In the higher forms of animals, the soma has also taken upon itself the responsibility of securing protection to the fertilized eggs and to the early developmental stages of the new somata formed by them. Some animals acquit themselves of this duty merely by depositing their eggs in places where the developing embryos will have a reasonable guaranty against destruction; others retain the fertilized eggs and give the embryos space for development within their own bodies. Finally, assuming still greater responsibility, the soma of the more highly endowed types of animals charges itself with the duty of protecting and nourishing the young during the adolescent period of postembryonic life. In addition to fulfilling its many parental functions, and in order to accomplish these functions, the soma must also maintain itself as a living unity.

The methods that the soma has adopted for carrying on its various functions are the reasons for its structure; and the continual reorganizing of its structure in adaptation to more efficient ways of accomplishing its functions has resulted in its evolution from a simple to a complex organization. The different methods that the somata of different animals have adopted and perfected to meet their obligations are expressed in the many forms of life existing today and in those that have existed during the past. Structure, vegetative functions, sensitivity to environmental conditions and changes, the power of automatic reaction to impinging forces, instincts, consciousness, intelligence, and the faculty of making voluntary adjustments to external conditions—all these things are properties developed and perfected in the soma for the benefit of the germ cells or for the somata that are to accompany the succeeding generations of germ cells. The soma of the more complex animals cannot reproduce itself; when its purposes are accomplished, its physical elements disintegrate, its vitality is reduced, and sooner or later its enemies or adverse circumstances bring about its death.

The germ cells appear to be the reproductive agents of the soma; but "reproduction," so called, is more truly a repeated production of somata and germ cells. Each germ cell multiplies by division, and the resulting cells undergo a development into *spermatozoa* or *ova,* according to their sex, or some of them may become merely nutritive cells for the others. The persisting germ cells remain as separate entities, except in the union of male and female cells to form a composite cell from which the development of both germ cells and soma usually proceeds. The ovum alone, however, may produce a complete soma; in insects parthenogenesis is of frequent occurrence. The germ cells carry the *determinants of heredity, called genes,* whatever they may be, and apparently in most cases receive no direct influence from the accompanying soma.

Typical Early Stages of Development.—The egg, being a cell, has all the constituent parts of an ordinary cell; but, since it is destined to a much greater activity than any of the body cells, it is provisioned with a supply of nutritive material, known as *yolk*, or *deutoplasm*, stored in the meshes of its cytoplasm. The known facts of comparative embryology lead us to believe that the early developmental stages in all animals were once essentially the same, though actually they may now be very different in different animals. Some of the differences are clearly correlated with the quantity of yolk contained in the egg; others are to be attributed to other causes, which may be termed embryonic expediency, for the embryo, as well as the postembryonic instars of the animal, departs from the ancestral line of development wherever an advantage is offered in so doing.

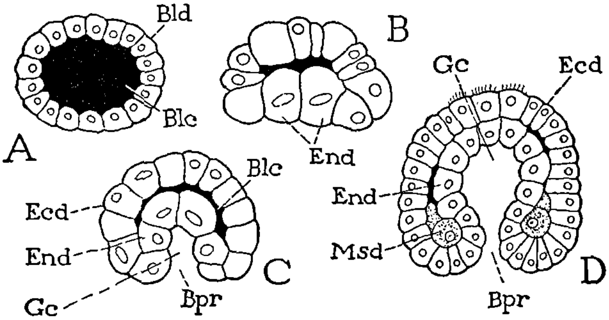

FIG. 1.—Typical early stages in general embryonic development. A, the blastula (diagrammatic). B, C, D, three stages in the differentiation and invagination of the endoderm (*End*), and the formation of the mesoderm (*Msd*) of a chiton. (*From Kowalevsky*, 1883.)

The development of the insect presents one of the greatest puzzles that the embryologist encounters, and it is certain that the insect embryo does not structurally reproduce free-living stages of its ancestry. In order to understand insect structure as presented by the embryo, therefore, we must discover the fundamental things in its development that underlie those that have been built up to suit the convenience of the embryo.

In the typical, generalized form of animal development, which proceeds from eggs containing a minimum quantity of yolk, the first division, or *cleavage*, of the egg cuts the egg into approximately equal halves, and the similar succeeding divisions soon produce a globular mass of cells, or *blastomeres,* called a *morula.* Then a cavity, the *blastocoele,* appears in the center of the mass, and the cells become arranged in a single layer at the surface. This stage is the *blastula* (Fig. 1 A); the superficial layer of cells is the *blastoderm* (*Bld*). The term *blast,* so frequently recurring in embryological names, comes from the Greek word βλαστός, meaning a bud or sprout.

The cells on one side of the blastula become distinguished from the others by an increase in size (Fig. 1 B). The larger cells then sink into the blastocoele cavity, usually as a hollow invagination of the blastula wall, and the primitive creature takes on the form of a double-walled sac (C). This stage in general embryonic development is the *gastrula.* The blastoderm is now differentiated into an outer layer, or *ectoderm* (*Ecd*), and an inner layer, or *endoderm* (*End*), between which is the remnant of the blastocoele (*Blc*). The new cavity is the *gastrocoele* (*Gc*), or *archenteron,* and its external opening is the *blastopore* (*Bpr*).

The endoderm is not necessarily produced in all animals by invagination. Gastrulation is often accomplished by an internal proliferation of cells from the blastoderm forming an inner cell mass that later becomes excavated by a cavity which is the gastrocoele. Invagination and proliferation, therefore, are but two variants of the developmental process of gastrulation.

Some of the lowest metazoic animals, such as the Coelenterata, never progress beyond the two-layered stage; but in all higher forms the two-layered gastrula becomes three layered by the differentiation of a middle layer, or *mesoblast,* from the primary inner layer or from points where the outer and inner layers meet. The mesoblast may be produced from scattered cells proliferated from the outer layer, and in such cases it is called a *mesenchyme;* but generally it takes the form of a definite cell layer, known as the *mesoderm.* The definitive middle layer may include cells produced in both ways.

In the three-layered stage, the embryo thus has become differentiated into an outer ectoderm (Fig. 1 D, *Ecd*), an innermost endoderm (*End*) lining the gastrocoele (*Gc*), and an intermediate mesoderm (*Msd*). The gastrocoele becomes the stomach of the future animal, the epithelial walls of which are formed of the endoderm. The mesoderm, in its typical mode of development, is given off laterally in each side of the body where the endoderm joins the ectoderm just within the lips of the blastopore (Figs. 1 D, 3 A, *Msd*). Animals possessing a mesoderm are typically elongate in form and are bipolar, since one end is habitually forward in progression; they acquire a dorsoventral differentiation of structure and consequently have a bilateral symmetry in their organization. The blastopore, originally posterior, as in the free-swimming larvae of certain Coelenterata, becomes ventral either by a migration in position or by a forward elongation on the under surface of the embryo. These stages of development, which probably took place in the ancestors of the arthropods, are well illustrated in the larvae of annelid worms and in the embryo of *Peripatus* (Fig. 2).

Few animals, however, actually follow the simple form of early development outlined above; many appear to depart widely from it. Yet it is believed that in all cases the actual development is but a modification of the simple type. The arthropods particularly are aberrant in their ontogeny. The student of entomology, therefore, must keep clearly in mind the basic course of development in order to understand the departures from it that will be encountered in the growth of the insect embryo.

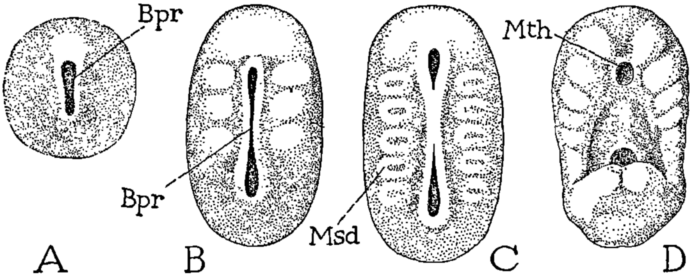

FIG. 2.—Early stages in the embryonic development of *Peripatus capensis*. (*From Balfour*, 1883.)

The Insect Egg.—The egg of an insect is usually contained in a shell, called the *chorion* (Fig. 4 B, *Cho*). The chorion has the appearance and texture of the body-wall cuticula, but it is said to be nonchitinous. It is formed in the ovary as a product of the walls of the egg follicle, and it bears externally the imprint of the follicular cells. At the anterior end of the egg in most cases the chorion is perforated by a minute opening or group of pores known as the *micropyle* (*Mi*), which permits the entrance of the spermatozoa. The delicate cell wall of the ovum becomes the *vitelline membrane* (*Vit*) of the mature egg. When the egg contains much yolk, or deutoplasm (Fig. 4 B), most of its cytoplasmic material is distributed in a layer of clear *cortical cytoplasm* (*cpl*) about the periphery

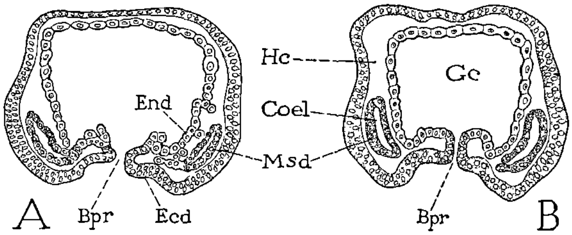

FIG. 3.—Transverse sections of a young embryo of *Peripatus capensis*, showing the lateral mesoderm bands and their coelomic cavities. (*From Balfour*, 1883.)

of the egg, and in a small mass of *nuclear cytoplasm* (*npl*) around the nucleus, the remainder being reduced to a network of strands or sheets, in the meshes of which is held the yolk material (*Y*). The typical shape of an insect egg rich in deutoplasm is elongate oval, which is the usual form of the egg within the ovarian tubule (Fig. 287); but when extruded the egg may take on various shapes, ranging from that of an elliptical globe to that of a flattened disc. The chorion may be a smooth shell having the form of the egg, or it may assume curious and bizarre shapes. Protected eggs are usually of the simple elliptical, oval, or elongate type (Fig. 4 B), with one side commonly a little less convex than the other or sometimes slightly incurved. A few insects enclose their eggs in cases, or *oöthecae*, formed by a secretion discharged from the oviduct or from special *colleterial glands.*

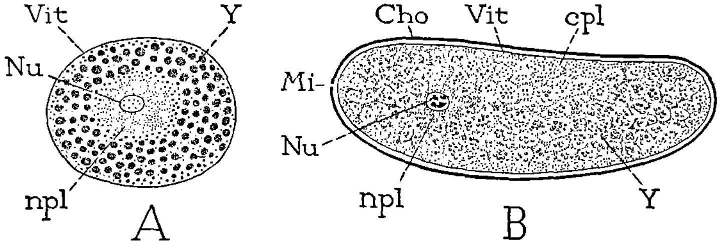

FIG. 4.—Two types of insect eggs, sectional views. A, egg of a collembolan, *Isotoma cinerea*, with small quantity of yolk. (*From Philiptschenko*, 1912.) B, diagram of usual type of insect egg containing much yolk.

Cleavage and the Formation of the Blastoderm.—Most insect eggs contain such a large quantity of yolk that their size is quite out of proportion to the amount of their protoplasmic matter. The ordinary insect egg, therefore, to avoid what would be a cumbrous procedure if its first cleavage division were to cut through its entire mass, limits its activities to the nucleus and the nuclear cytoplasm. This method of cleavage in the egg is called *meroblastic,* in distinction from total cleavage, which is *holoblastic.*

Not all insect eggs, however, are meroblastic; the eggs of Collembola, which have a comparatively small quantity of yolk (Fig. 4 A), divide by entire cleavage, and the holoblastic form of division continues until a typical morula is formed (Fig. 5). The early development of *Anurida* has been described by Claypole (1898), that of *Isotoma* by Philiptschenko (1912).

The blastomeres in the morula of *Anurida,* Claypole says, are practically all of equal size (Fig. 5 G, H). In the following stage, however, there ensues a period of disintegration in the blastomeres (Fig. 6 A, *Blm*), accompanied by a migration of the nuclei in small masses of cytoplasm (*a*) toward the periphery of the egg. The yolk is thus left behind in the central part of the egg as an inert mass in which the original cell boundaries are lost. The migrating nucleated fragments of cytoplasm, which are now virtually small cells, divide as they proceed to the exterior and arrange themselves in two layers (B). The outer, continuous layer is the ectoderm (*Ecd*), the inner, incomplete layer is the mesoderm (*Msd*). Some of the cells, however, remain behind in the yolk (B, *End*). These cells, according to Claypole, later form the stomach epithelium in *Anurida* and are therefore endodermal.

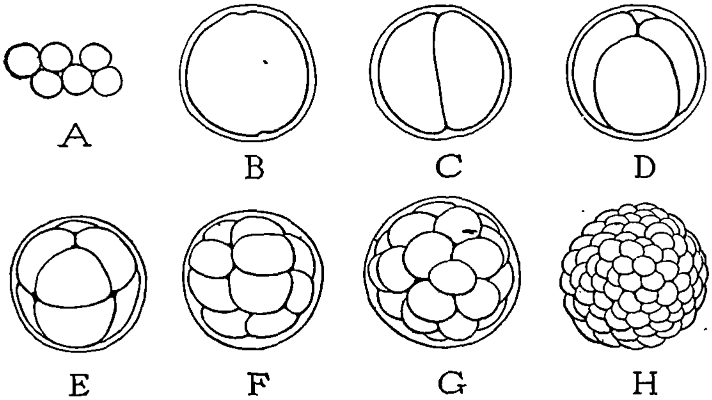

FIG. 5.—Example of holoblastic cleavage in an insect egg, *Anurida maritima*. (*From Claypole*, 1898.) A, group of eggs. B-G, successive stages of cleavage resulting in a typical morula (H).

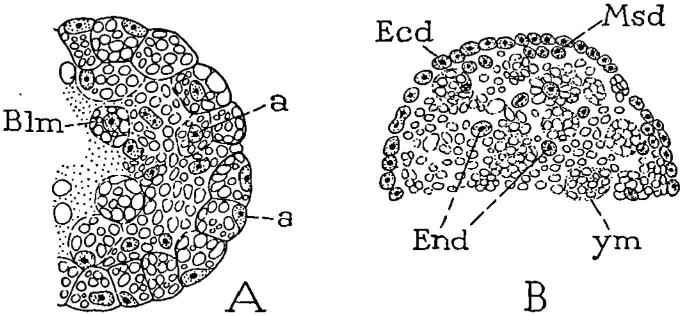

FIG. 6.—Developmental stages of *Anurida maritima* following holoblastic cleavage of the egg. (*From Claypole*, 1898.) A, disintegration of the blastomeres. B, differentiation of the germ layers.

In *Isotoma*, as described by Philiptschenko, the holoblastic cleavage of the egg produces a compact morula in which the cleavage cavity disappears. Then each of the blastomeres divides into a smaller outer cell containing the nucleus, and into a large, nonnucleate inner sphere which retains the yolk. The small nucleated cells migrate outward between the yolk spheres and come to rest at the surface of the egg, where they form at first a single continuous layer, which is the blastoderm. The blastoderm cells later differentiate into an outer layer of ectoderm and an inner layer, which, in *Isotoma*, Philiptschenko claims is the common rudiment of the future mesoderm and endoderm.

In meroblastic eggs the nucleus and its containing mass of cytoplasm, situated in the interior of the egg, behave in the manner of an ordinary cell. By repeated division, together with division of the daughter cells (Fig. 7 A), they produce an increasing number of cleavage cells (*CCls*), which migrate to the periphery of the egg (B) and there become disposed in a single layer just beneath the vitelline membrane (B, C). The cortical cytoplasm then unites with the cleavage bodies to form definitive cells, which constitute the blastoderm (C, D, *Bld*). In this stage, the insect embryo derived from a meroblastic egg is equivalent to the blastula in the generalized form of development (Fig. 1 A), but the cells of the blastoderm are all contained within the original egg wall, or vitelline membrane.

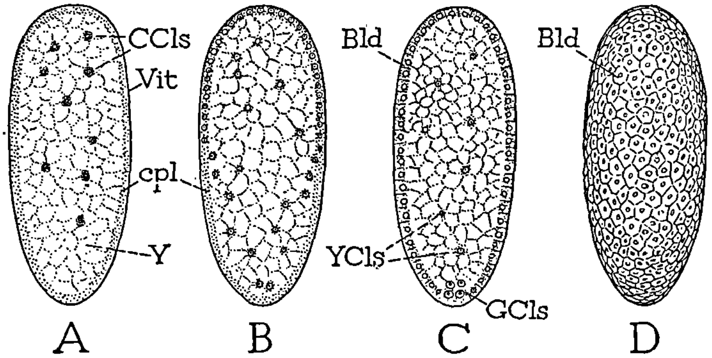

FIG. 7.—Diagrams of meroblastic cleavage and the process of blastoderm formation typical of insect eggs having a large quantity of yolk.

Within the blastoderm is the mass of yolk material held in the meshes of the inner cytoplasm of the egg, and usually a few *yolk cells* (Fig. 7 C, *YCls*). The latter are nucleated cytoplasmic masses derived from the egg nucleus that did not take part in the formation of the blastoderm. In addition to these primary yolk cells, other cells are often found in the yolk after the completion of the blastula, which are said to be proliferated from the blastoderm. These cells, some investigators claim, are endoderm cells that accomplish a partial digestion of the yolk before the embryonic stomach is formed, and for this reason they have been named *vitellophags*. It appears, as we shall presently see, that the walls of the stomach in some insects are formed in part or entirely from migratory endoderm cells proliferated into the yolk at an early stage of development.

The Germ Cells.—The germ cells of many insects become recognizable at the time the blastoderm is being formed. In the collembolan *Isotoma*, Philiptschenko (1912) says, the germ cells first appear as a small, compact group of cells in the yolk near the posterior end of the blastula (Fig. 8 A, *GCls*). In insects with meroblastic cleavage the germ cells are usually observed first at the posterior end of the blastoderm (Fig. 7 C, *GCls*), where they lie in a differentiated protoplasmic area called the *germ tract* (*Keimbahn*) and in some cases protrude somewhat from the surface of the blastoderm (Fig. 8 B, *GCls*). The protoplasm of the germ tract is often marked by the presence of dark-staining granules, and certain writers have suggested that it is some peculiar quality of the germ-band protoplasm (Huettner, 1923), or even of the granules themselves (Hegner, 1914), that differentiates as germ cells whatever cleavage cells happen to wander into the germ tract. Huettner shows that even at this early stage there is a difference in the nuclei between the germ cells and the blastoderm cells.

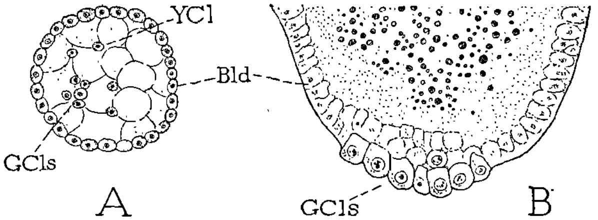

FIG. 8.—Early differentiation of the germ cells (*GCls*) from the somatic cells. A, blastula of *Isotoma cinerea*. (*From Philiptschenko*, 1912.) B, blastula of *Drosophila melanogaster* with germ cells segregated at posterior pole. (*From Huettner*, 1923.)

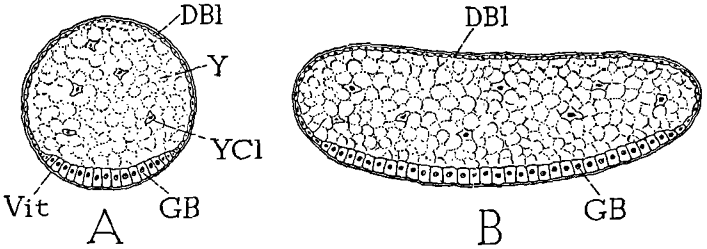

FIG. 9.—Diagrams of the formation of the germ band (*GB*) on the ventral side of the blastoderm. A, cross section. B, longitudinal section.

The germ cells undergo a short period of activity during which they increase slightly in numbers, and then they enter a long period of rest while the somatic cells are developing. The germ cells move into the interior of the body and are finally lodged in the dorsal part of the mesoderm that forms the ovaries or testes (Fig. 22, *GCls*).

The Germ Band.—When the insect blastoderm has completely surrounded the egg, the creature is in the blastula stage (Figs. 1 A, 7 C). Its cleavage cavity, or blastocoele, is filled with the yolk. The first differentiation that leads to the formation of the specific embryo consists of a thickening of the cells in that wall of the blastula which is to be the ventral side of the future insect (Fig. 9). This region of enlarged cells (*GB*) appears on the surface as an opaque oval or elongate area, which is known as the *germ band, germinal disc,* or *primitive streak* (*Keimscheibe, Keimstreif*). The blastoderm is now differentiated into an embryonic area (*GB*) and an extraembryonic field (*DBl*), the latter being the dorsal part of the blastoderm, composed of small, flat, often attenuate cells, termed the *dorsal blastoderm,* or *serosa.*

Formation of the Inner Germ Layers.—This subject is a most difficult one to understand in insect embryology, if by "understanding" we mean an interpretation of the known facts of the formation of the germ layers in insects according to the terms of the general gastrulation theory. The crux of the difficulty lies in the fact that the apparent gastrulation of the insect embryo gives rise directly to a cell layer that forms the tissues which are of mesoblastic origin in other animals, while the epithelium of the mesenteron, which should be the endodermal wall of the gastrulation cavity, appears in most cases to be derived independently from the blastoderm.

In the typical and general mode of development, as we have seen, the embryo becomes two layered by the invagination of one side of the blastoderm (Fig. 1 C); but it was noted also that the invagination method of gastrulation may be modified into a process of internal proliferation of cells from a closed blastopore area of the blastoderm. The typical embryo next becomes three layered by the generation of a mesoderm from invaginations or proliferations of cells from the blastoderm just within the lips of the blastopore where the ectodermal and endodermal layers meet (Figs. 1 D, 3 A, *Msd*). It is evident, therefore, that the normal relations of the endoderm and the mesoderm might be obscured if the endoderm were formed in part or entirely by the proliferation of scattered cells, for it would then appear that gastrulation produces only the mesoderm. A discontinuous formation of the endoderm commonly takes place in the arthropods, and this condition has led to much misunderstanding of the true relations of the germ layers; but if we keep in mind the important fact that it is the function of the endoderm to absorb and digest the yolk, we need not be disconcerted by the various ways it adopts for fulfilling its destiny.

In some of the Crustacea an archenteron is formed by typical gastrulation in which an invaginated endoderm becomes directly the stomach of the mature animal. In such cases the endoderm *absorbs* the yolk mass and passes it into the archenteric cavity, from which it is drawn for use by the growing tissues. In certain other crustaceans the walls of the archenteron disintegrate, and the liberated endoderm cells migrate into the yolk, whence they later emerge and arrange themselves again in an epithelial layer, but this time *surrounding* the yolk to form the walls of the definitive stomach. In other cases, again, though the major part of the endoderm is fragmented, two flat masses of its cells remain intact beneath the yolk, and from these rudiments the mesenteron epithelium is later regenerated. In this case the endoderm cells lost to the yolk remain there as vitellophags. These various modifications of mesenteron formation by the endoderm are generally correlated with the amount of yolk in the egg.

When we turn now to the insects, we find, so far as known, that the primitive method of forming the mesenteron by the typical invagination process of gastrulation does not exist. We must presume, then, that, having become impracticable owing to the amount of yolk in the insect egg, it has been completely eliminated from insect ontogeny. Various stages may be traced, however, in the fragmentation of the major part of the endoderm, and the differentiation of its ventral remnant into several groups of cells that *regenerate* the embryonic stomach, or mesenteron. These groups of cells are the so-called *mesenteron rudiments.*

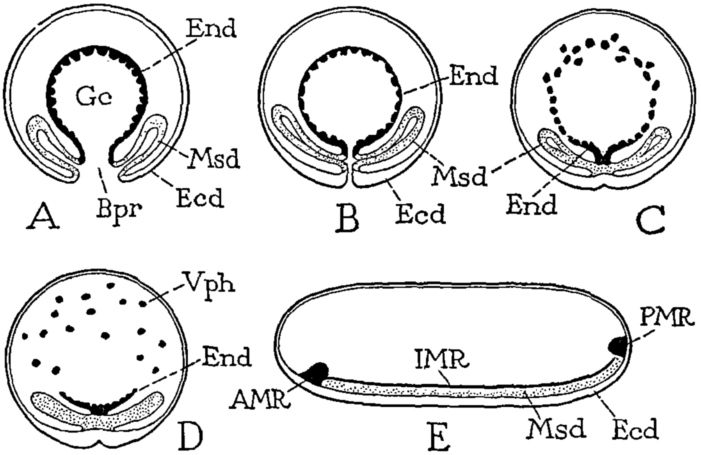

Fig. 10.—Diagrams suggesting the evolution of germ-layer formation in pterygote insects. A, primitive gastrula with open blastopore and lateral bands of mesoderm. B, blastopore closing. C, blastopore closed, the archenteron in state of disintegration. D, most of endoderm cells dispersed in yolk as vitellophags (*Vph*), leaving only a ventral remnant (*End*) intact. E, differentiation of the ventral endoderm remnant into anterior, intermediate, and posterior mesenteron rudiments (*AMR, IMR, PMR*).

In the insect embryo the blastopore is never an open aperture, but the blastopore area, as indicated by the region from which the endoderm and mesoderm are formed, becomes elongated forward on the ventral side of the embryo, appearing sometimes as a groove (Fig. 23 A, *Bpr*) comparable with the long, open, slitlike blastopore of *Peripatus* (Fig. 2 B). We may assume, therefore, that gastrulation and the formation of the mesoderm originally took place along this line (Fig. 10 A). With the closure of the blastopore, then, the mesoderm comes to be the first layer immediately within the blastopore area (B, C, *Msd*). In this case it is clear that the endoderm (*End*) would appear to be generated from the mesoderm, and that by complete disintegration it might take the form of cells scattered through the yolk (C) or, on the other hand, a ventral remnant of it might be preserved beneath the yolk (D). In the light of this concept we can understand many of the processes of mesoderm and endoderm formation described by different writers on insect embryology, the discrepancies between which have seemed irreconcilable.

The Mesoderm.—In the Collembola, according to Claypole (1898) and Philiptschenko (1912), the first-formed inner layer is the mesoderm. It is produced by a general tangential division of the blastoderm cells, the division taking place either at the time the cleavage cells reach the surface of the egg (*Anurida*, Claypole) or afterwards (*Isotoma*, Philiptschenko). This method of mesoderm formation may be conceived as an unlocalized form of proliferation from the blastoderm.

In the Thysanura the mesoderm is formed by a localized proliferation of cells from the midventral line of the blastoderm, the area of proliferation being sometimes marked externally by a pit or a groove. In *Campodea*, according to Uzel (1897), and in *Lepisma*, as described by Heymons (1897), the mesoderm proliferation arises at a central point of the blastoderm, the cells spreading out into a disc as they are given off. Heymons does not believe that the limited extent of the proliferation area here represents a polar gastrulation; he attributes it rather to the small size of the egg and to the oval shape of the germ band.

In the Pterygota the surface of the usually elongate germ band becomes differentiated into a median area, or *middle plate* (Fig. 11 A, *MP*), and into two lateral areas known as the *lateral plates* (*LP*). From the middle plate is formed the mesoderm, usually in one of three ways: in some cases by an infolding or invagination of the middle plate (B, C), in others by an overgrowth of the median plate by the lateral plates (D, E), and in still others by a proliferation of cells from the inner surface of the middle plate (F). In any case the formation of the mesoderm evidently represents a modified gastrulation, from which the endoderm appears to have been eliminated; but, as we shall presently see, the middle plate more probably represents a common mesoderm-endoderm rudiment, since a part of the endoderm is usually generated from the mesoderm or in close association with it.

The Endoderm.—Where the processes of gastrulation take place by proliferation from the area of a closed blastopore, it is clear, as we have already noted (Fig. 10 C), that the endoderm, if produced in connection with the mesoderm, will appear to arise from the latter. In the collembolan *Isotoma*, Philiptschenko (1912) says, the endoderm is generated from that part of the inner germ layer along the midventral line of the embryo that does not take part in the formation of the mesoderm somites (see Fig. 19 A). The endoderm tissue consists at first of three groups of cells—an anterior group, which is the *anterior mesenteron rudiment,* a posterior group, which is the *posterior mesenteron rudiment,* and a median strand of loosely associated cells forming an *intermediate mesenteron rudiment* lying beneath the yolk and connecting the two terminal rudiments. The definitive embryonic stomach, or mesenteron, is produced by the multiplication of cells in each of the rudiments and the growth of the cells around the yolk until they form an epithelial sac enclosing the latter. Here, therefore, it is clear that the primitive inner layer is a mesoderm-endoderm layer, since the endoderm is differentiated from its entire length. A similar condition is said by Strindberg (1913) to exist in termites (*Eutermes*) and in ants, where the endoderm arises by a proliferation of cells from the entire length of the mesoderm (or mesoderm-endoderm rudiment); these cells lie beneath the yolk and eventually surround it to form the walls of the mesenteron.

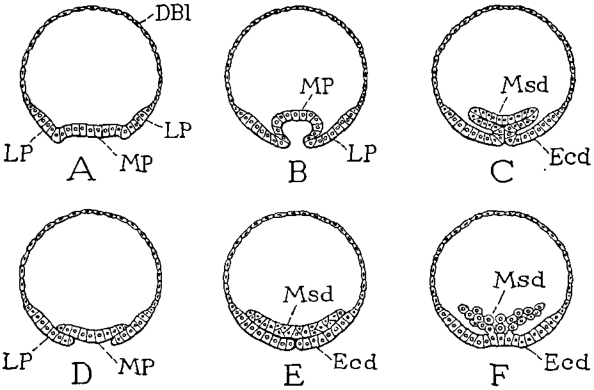

Fig. 11.—Diagrams showing three methods of mesoderm formation in pterygote insects. A, cross section of egg with germ band differentiated into middle plate (*MP*) and lateral plates (*LP*). B, C, the middle plate invaginated to form the mesoderm. D, E, the middle plate overgrown by the lateral plates. F, mesoderm proliferated internally from the middle plate.

There is reason to believe that the enclosure of the yolk by endoderm cells derived from the mesoderm-endoderm rudiment does not strictly represent the process of gastrulation in insects, but that it is a secondary regeneration of the mesenteron taking place subsequent to an earlier fragmentation of the walls of the true gastrulation cavity. This conclusion is to be deduced from the observation of several investigators.

According to Claypole (1898), the endoderm cells of the collembolan *Anurida* originate during cleavage of the egg, but they remain in the yolk, while the blastoderm cells that give rise to the ectoderm and mesoderm are migrating to the surface. Finally, however, the endoderm cells engulf the yolk and then arrange themselves to form the definitive mesenteron, which contains practically no yolk except that in the bodies of its cells.

A similar method of mesenteron formation is described by Heymons (1897) for *Lepisma.* In this insect, Heymons says, the mesenteron epithelium is generated from cells found at an early stage of development within the yolk. These cells later migrate to the periphery of the yolk mass where they become aggregated into scattered islands that grow in extent by multiplication of their cells until eventually they surround the yolk and constitute the wall of the definitive mesenteron.

In the Odonata the mesenteron is said by Tschuproff (1904) to be a composite organ made up of cells derived from three distinct sources, its anterior and posterior parts being formed from cells proliferated from the inner ends of the stomodaeum and proctodaeum (Fig. 13, *Stom, Proc*), while its middle part is formed of cells that migrate outward from the yolk. The cells derived from the yolk Tschuproff regards as the true endoderm; the others she claims are ectoderm cells. This conclusion concerning the nature of the anterior and posterior parts of the mesenteron is not necessary, for it is well known that the anterior and posterior mesenteron rudiments derived from the middle plate of the embryo may be carried inward by the stomodaeal and proctodaeal invaginations; but the observations of Tschuproff, if true, do show that the Odonata present a gradient condition in the endodermal activities between one in which the mesenteron is re-formed from a disintegrated archenteron and one in which it is regenerated from anterior and posterior groups of endodermal cells.

It is interesting to note that Eastham (1927) finds in *Pieris rapae* a median proliferation of cells from the middle plate of the embryo (Fig. 12, *MPCls*); these cells take no part in the mesoderm formation but pass into the yolk and there disintegrate. The proliferation of these cells, Eastham says, begins at the anterior end of the middle-plate region and "continues along the middle line of the embryo from before backward," until there is formed "a median track of proliferation passing almost from end to end of the embryo." While Eastham apparently does not definitely commit himself to the view that these cells are endodermal, he mentions having observed in one series of sections a continuity at an early stage of development between them and the posterior mesenteron rudiment. It seems clear, however, that the line of proliferating cells must represent the true gastrulation of the insect in a rudimentary and disintegrated state. The cells, Eastham says, "in all probability help in the liquefaction of the yolk, rendering the latter capable of being assimilated by the germ band." These "middle-plate cells" that wander into the yolk are evidently endodermal vitellophags.

In the majority of pterygote insects, mesenteron rudiments have been found only at the two ends of the mesoderm (Fig. 13 B, *AMR*, *PMR*); but, as we have observed, it is claimed by Strindberg that in the termites and in ants the anterior and posterior rudiments are connected by an intermediate rudiment (A, *IMR*), thus duplicating the condition described by Philiptschenko in *Isotoma*. It is evident, therefore, that the usual condition, in which the mesenteron is formed from anterior and posterior rudiments alone, has resulted from a suppression of the intermediate rudiment, or from the migration of its cells into the yolk, as in *Pieris*, and that the two persisting end rudiments represent the final remnants of a disintegrated archenteron (Fig. 10 C). In the Lepidoptera, according to Schwangart (1904) and Eastham (1927), the anterior and posterior mesenteron rudiments are formed in continuity with the mesoderm; but in other insects the two rudiments often appear to arise either directly from the blastoderm at the two ends of the mesoderm (Fig. 10 E) or from the walls of the ectodermal stomodaeal and proctodaeal invaginations (Fig. 13).

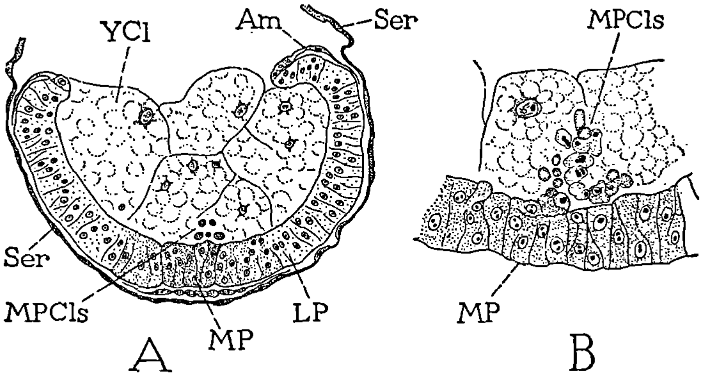

FIG. 12.—Proliferation of cells (*MPCls*) from the middle plate of the germ band of *Pieris rapae*. (*From Eastham*, 1927.)

Résumé of Gastrulation.—The formation of a stomach by the ancestral process of open gastrulation (Fig. 10 A) becomes impracticable in embryos containing a large quantity of yolk. In insect phylogeny the blastopore, after elongating forward on the ventral side of the embryo, has become permanently closed (B, C) and gastrulation takes place by proliferation instead of by open invagination, the cells thus formed migrating separately into the yolk. This process represents a fragmentation of most of the walls of the archenteron (C), an embryonic device by which the endoderm cells may surround the yolk. In some of the Apterygota the definitive stomach (mesenteron) is said to be regenerated by the scattered endoderm cells; in Odonata it is perhaps regenerated in part by these cells. In some of the Apterygota and in most of the Pterygota, however, the proliferated endoderm cells remain as vitellophags in the yolk (D, *Vph*), and the definitive stomach is regenerated from a ventral remnant of the endoderm (C, D, *End*) that remains in contact with the mesoderm below the yolk. This ventral endoderm remnant may consist of a continuous band of cells coextensive with the mesoderm (E, *AMR*, *IMR*, *PMR*), or it may be reduced to anterior and posterior groups of cells, which are the usual anterior and posterior mesenteron rudiments (*AMR*, *PMR*). Throughout the entire course of the life cycle of most insects the endodermal epithelium of the mesenteron is subject to disintegration and regeneration.

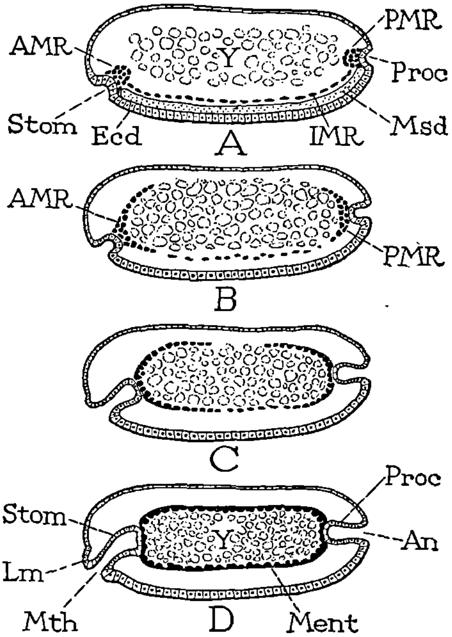

FIG. 13.—Diagrams showing the formation of the definitive alimentary canal in pterygote insects. A, the germ layers in longitudinal section, including the three regenerative endodermal rudiments of the mesenteron (*AMR*, *IMR*, *PMR*). B, C, D, envelopment of the yolk by the growth of the mesenteron rudiments to form the stomach (*Ment*), and the ingrowth of the ectodermal stomodaeum (*Stom*) and proctodaeum (*Proc*).

The Alimentary Canal.—The stomach, or mesenteron, of the insect embryo is clearly not the primitive archenteron, though when completed it is a sac composed of endoderm cells. As we have just seen, it may be formed by the reassembling of the primitive endoderm cells scattered in the yolk, or in part from such cells and in part from ventral endoderm remnants. In most insects, however, it is regenerated entirely from a median ventral remnant of the archenteron, including anterior, intermediate, and posterior rudiments (Fig. 13 A, *AMR*, *IMR*, *PMR*) or more commonly from anterior and posterior rudiments only (B, C, D, *AMR*, *PMR*). The cells of these mesenteron rudiments multiply and extend over the surface of the yolk (C) until those proliferated from opposite ends meet and finally constitute a complete epithelial sac containing the yolk (D). The sac is later enswathed by sheets of muscle tissue and eventually becomes the definitive stomach, or *ventriculus*, of the adult insect.

The complete alimentary canal (Figs. 13 D, 14) comprises, in addition to the stomach, anterior and posterior sections derived as secondary invaginations from the ectoderm. These parts, known respectively as the *stomodaeum* (*Stom*) and *proctodaeum* (*Proc*), later open into the mesenteron and thus give the alimentary canal its final form of a complete tube extending through the body (Fig. 20). The embryonic development of the alimentary canal, however, may entirely ignore the phylogenetic order of events, for it is often found that the stomodaeal and proctodaeal invaginations are formed prior to the generation of the mesenteron. The rudiments of the latter may then be carried inward by the ectodermal ingrowths, in which case the mesenteron appears to be generated from the opposing ends of the ectodermal parts of the alimentary canal.

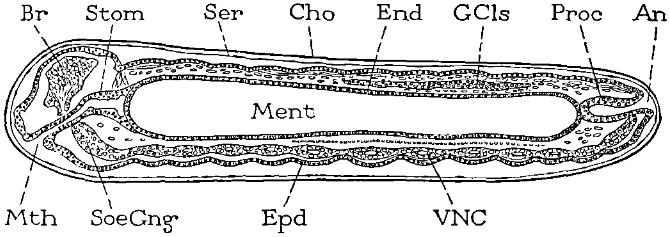

FIG. 14.—Median longitudinal vertical section of a mature male embryo of the honey bee surrounded by the serosa and chorion. (*From Petrunkevitch*, 1901.)

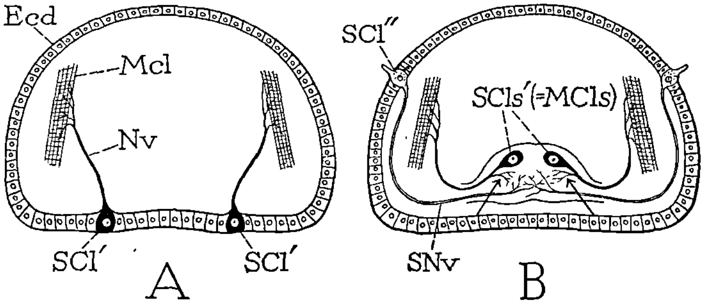

FIG. 15.—Diagrams suggesting the evolution of the synaptic sensory-motor nervous system. A, the primary sensory nerve cells (*SCl′*) located in the ectoderm and connected directly with muscles (*Mcl*). B, the primary nerve cells internal (now motor cells) and stimulated indirectly by nerves from a second set of sensory cells (*SCl″*) in the ectoderm.

Origin of the Nervous System.—All nerve tissue originates in the ectoderm. Nerve cells are ectodermal cells in which the properties of irritability and conductivity are highly developed. If their inner ends are connected with the motor tissues, the primary nerve cells (Fig. 15 A, *SCl′*) become the agents for transmitting external stimuli to the motor elements (*Mcl*), and thus they may directly incite the latter to action. In most animals, however, the nerve cells connected with the effector mechanisms sink beneath the surface of the ectoderm where they become shut off from direct contact with the outer world (B, *SCls'*). The sunken nerve cells must then be themselves stimulated through the agency of other nerve cells (*Scl''*) that retain surface relations. In this way the general nervous system of complex animals comes to consist functionally of a *motor system* lying entirely within the body and of a *sensory system* maintaining, on the one hand, a connection with the exterior and, on the other, establishing connections with the motor system (B).

In the annelids and arthropods the motor nerve cells are contained mostly in two more or less closely associated tracts of nerve tissue forming the *ventral nerve cord* (Fig. 16 C, *VNC*) lying along the midventral line of the body. It is probable that this double median nerve cord has been evolved from two lateroventral bands of ectodermal nerve cells forming two primitive lateral cords (A, B) which have approached each other medially. In the annelids the two cords are united anteriorly with a small nerve mass, or primitive brain, the so-called *archicerebrum* (*Arc*), lying in the anterior end of the body primarily before the mouth.

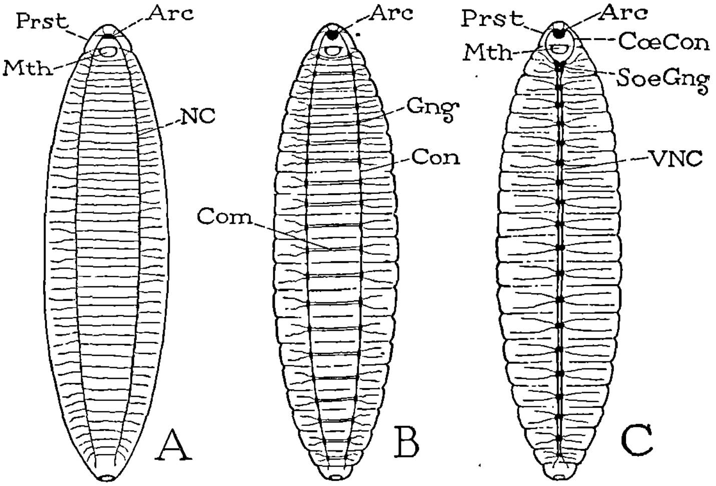

FIG. 16.—Diagrams showing the probable evolution of the annelid-arthropod type of central nervous system from a preoral nerve center (*Arc*) and two lateroventral nerve cords (*NC*).

In the ontogeny of insects most of the nerve tissues originate at an early stage of development from two longitudinal thickenings of the ectoderm near the midline of the germ band, known as the *neural ridges* (Fig. 17 A, *NlR*), between which is a median *neural groove* (*NlG*). From the inner surfaces of the ridges are proliferated longitudinal rows of large cells, the *neuroblasts* (*Nbl*), which are the primary nerve cells of the future nerve cords. A median row of neuroblasts also is formed above the neural groove. The neuroblasts multiply by division and produce three strands of ganglionic cells (B, *GngCls*). Thus the definitive ventral nerve cord of insects appears to take its origin from two primitive *lateral cords* of nerve cells (*LC*) and a *median cord* (*MC*). The nerve cells formed from the neuroblasts send out processes which become the *nerve fibers.* Some of the fibers remain in the nerve cords where they establish communication between the nerve cells; others extend outward to the other body organs and constitute the motor nerves.

The sensory nerves of insects proceed inward from sensory cells of the ectoderm to the ventral nerve cord and here form intimate associations with the motor cells. Little is definitely known, however, concerning the actual development of the sensory nerves in arthropods.

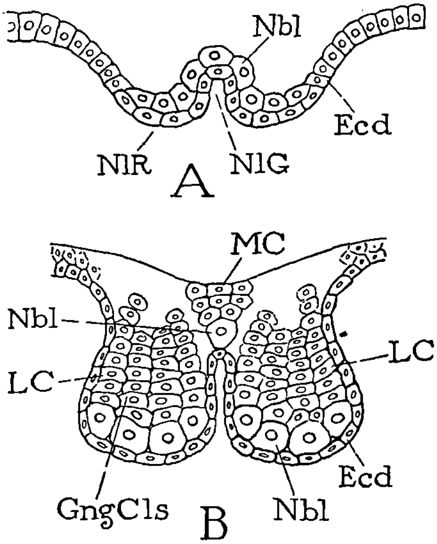

Fig. 17.—Embryonic origin of the ventral nervous system from the ectoderm. (*Diagrams based on figures from Wheeler,* 1891.) *Ecd,* ectoderm; *GngCls,* ganglion cells; *LC,* lateral nerve cords; *MC,* median nerve cord; *Nbl,* neuroblasts; *NlG,* neural groove; *NlR,* neural ridge.

When segmentation takes place in the body, the nerve cords are differentiated into segmental regions, or *ganglia* (Fig. 16 B, *Gng*), containing the nerve cells and into intersegmental *connectives* (*Con*) composed of nerve fibers. The two ganglia of each segment become connected crosswise by fibrous *commissures* (*Com*) and finally are so closely approximated and bound to each other that they constitute a single segmental ganglion (C), though the intersegmental connectives remain double. The successive paired ganglia in the future head region of the insect always coalesce in two groups: those of the anterior part of the head unite with the primitive archicerebrum to form the *brain* (Fig. 14, *Br*), which lies above the stomodaeum (*Stom*); those of the posterior part compose the *suboesophageal ganglion* (*SoeGng*), which lies below the stomodaeum.

The Embryonic Coverings.—The embryos of most insects become separated in one way or another from contact with the egg shell during a part or all of the period of their development. We may distinguish four methods of separation, namely, (1) by invagination of the embryo, (2) by involution of the embryo, (3) by the formation of cellular protective membranes, (4) by the production of cuticular coverings. The last constitutes a distinct process, probably allied to moulting; the others intergrade, and the second and third are possibly derivations from the first.

Invagination of the Embryo.—In the Apterygota the germ band doubles upon itself ventrally at an early stage of development and sinks into the egg or the yolk in the form of an inverted U, in which position it may remain until the embryo is almost fully formed (Fig. 18 A, B). This method of development is characteristic of many other arthropods, and its retention in the apterygote insects apparently has a phylogenetic significance. In the Collembola (Fig. 18 A) the embryo fills the entire egg after the ventral flexure takes place. In *Lepisma,* as described by Heymons (1897), the embryo begins its development on the surface of the egg in the usual manner, but soon it curves ventrally and sinks into the yolk (B). As the submergence increases, a part of the surrounding extraembryonic blastoderm is turned in also, and the mouth of the cavity contracts to a small pore, but it does not entirely close. Later, the *Lepisma* embryo partially emerges and completes its development with its head and thoracic parts again on the surface (C).

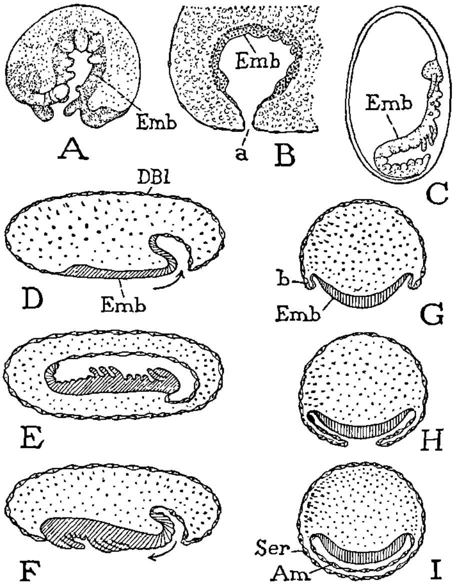

Fig. 18.—Three methods by which the insect embryo may become separated from the egg shell. A–C, *invagination* of the embryo (A, *Isotoma cinerea, from Philiptschenko* 1912; B, C, *Lepisma, from Heymons,* 1897). D–F, *involution* of the embryo and its return to the surface of the egg, diagrammatic. G–I, formation of *cellular covering membranes,* diagrammatic.

Involution of the Embryo.—In several other orders of insects, including the Odonata, some of the Orthoptera, and the Homoptera, the embryo, which begins its development on the surface of the egg (Fig. 18 D), turns into the yolk tail end first, by a process of revolving on its transverse axis, and stretches out within the egg in a reversed and inverted position (E). The revolution of the embryo carries a part of the extraembryonic blastoderm into the yolk, and when the reversal of the embryo is complete the opening into the embryonic cavity is closed. There is thus differentiated from the extraembryonic blastoderm an inner part lining the embryonic cavity, which is the *amnion* (*Am*), and an outer part, or *serosa* (*Ser*), which surrounds the egg. Before the odonate or hemipteran embryo completes its development, it reverts again to the surface by a counter-revolution that restores it to its original position (F).

Cellular Embryonic Membranes.—The more usual type of embryonic covering is that produced by outgrowths of the blastoderm forming a cellular sheath over the embryo. In typical cases of this kind folds from the extraembryonic part of the blastoderm grow out around the ends or along the sides of the germ band (Fig. 18 G, *b*), the edges of which come together (H) and unite beneath the embryo (I). The corresponding layers of the opposite folds then become continuous, and the embryo is shut in beneath two cellular membranes, the outer of which is the serosa (*Ser*), the inner the amnion (*Am*). Usually the amnion and serosa remain in contact over the ventral surface of the embryo; but in some cases, particularly in the Lepidoptera, the embryo and the amnion sink into the yolk, and a part of the yolk then fills the space between the amnion and the serosa, producing a submerged condition of the embryo. In the honey bee, according to Nelson (1915), the embryonic covering consists of a single layer of cells, formed by two outgrowths from the serosa along the edges of the germ band, which eventually meet and unite beneath the embryo.

The cellular embryonic membranes usually disappear before the embryo reaches maturity. In most cases they separate in a longitudinal cleft beneath the embryo, and the resulting folds are carried upward as the dorsal blastoderm contracts above the expanding lateral walls of the growing embryo. The cells of the dorsal blastoderm and the amniotic folds eventually sink into the yolk on the dorsal side of the egg, where they are finally absorbed. In the honey bee, the single embryonic membrane is said to persist until the time of hatching, when it is broken up by the movements of the young larva in the egg.

Embryonic coverings formed of blastodermic folds are characteristic of insects; a similar structure is said to be found in other arthropods only in the scorpions.

Cuticular Embryonic Membranes.—Embryonic coverings of a non-cellular structure are of common occurrence in all groups of the Arthropoda. These membranes, apparently, are of the nature of cuticular exuviae, for it is stated by Campbell (1929) that the embryonic investment of the cockroach is a chitinous tissue. Their separation from the embryo, therefore, may be regarded as an embryonic moult. The embryonic membranes are shed at the time the young arthropod leaves the egg or shortly thereafter.

Cuticular embryonic coverings occur in all insects with incomplete metamorphosis and have been observed in some holometabolous forms. In *Anurida*, as recorded by Claypole (1898), three distinct membranes are given off from the entire surface of the embryo before the appendages are formed and before the embryo curves into the egg. In most insects, however, only one cuticular embryonic membrane is known to exist. In some cases, as in the aphids, the membrane has the form of a simple sac enveloping the embryo, but in other insects the sac may be provided with pouches that individually ensheath the appendages. Evidently, then, the period of embryonic growth at which the moult is given off varies in different insects. A similar embryonic covering occurs in Arachnida, Crustacea, Chilopoda, and Diplopoda, in some cases enveloping the embryo as a cuticular sac, in others having close-fitting extensions over the appendages.

Segmentation of the Body.—The first important step in the evolution of the annelids and arthropods was that by which the body lost its unity of structure and became broken up into a series of parts, or *somites.* The somites are in general called *body segments,* but in the embryo they are more specifically termed *metameres.*

In ontogenetic development, metamerism is usually described as originating in the mesoderm, the segmental regions being first marked by a closer massing of the mesodermal cells, which thus appear as a series of opaque areas in the germ band alternating with more transparent lines. It is pointed out by Eastham (1927, 1930), however, that in the embryo of *Pieris* external segmentation, shown by indentations of the ectoderm, precedes the formation of the mesodermal somites. In the larvae of the annelid worms, which develop two lateral bands of mesoderm tissue, the segmental masses of mesodermal cells soon become hollowed by the formation of clefts between their dorsal and ventral cells, there being thus produced a series of paired mesodermal pouches that eventually extends through the entire length of the body. These pouches are the *coelomic sacs.* As development proceeds, the coelomic sacs enlarge upward in the sides of the body and either remain thus as definitive segmental body cavities or unite in a common body cavity coextensive with the length of the animal.

In the Arthropoda the mesoderm becomes distinctly segmented, but coelomic cavities are not so definitely formed as in the Annelida, and in many cases they are entirely absent. Where they appear they generally take the form of small clefts in the lateral parts of the mesoderm (Fig. 19 A, *Coel, Coel*), but the series on each side soon becomes converted into a coelomic tube by the disappearance of the partitions, and the inner walls of the tubes break down (B), so that the segmental cavities are at best but evanescent.

Segmentation in the arthropods, as in the annelids, is not a process of "budding." The somites are formed always anterior to a small terminal piece, the *telson,* or *periproct* (Fig. 20, *Prpt*), which contains the anus and gives rise to the proctodaeal invagination. Even in arthropods in which segmentation is not complete at hatching, the segments added during postembryonic development are formed in the region immediately anterior to the periproct. Embryonic segmentation usually appears first in the gnathal region and proceeds posteriorly, though there is often much irregularity in the sequence of the newly forming somites. The segmented area of the trunk, however, finally extends from the mouth to the periproct, but, since the mouth lies a short distance behind the anterior pole of the embryo, there is always an unsegmented preoral region of the animal, which is the *prostomium* (Fig 20, *Prst*). The prostomium is represented in the arthropod embryo probably by the cephalic lobes (Fig. 23, *Prc*); in the annelid trochophore larvae it is the large preoral swelling of the trunk. The segments between the prostomium and the periproct are the true somites, of which in the insects there are at least 18 when segmentation is complete. The insect embryo attains its defini-

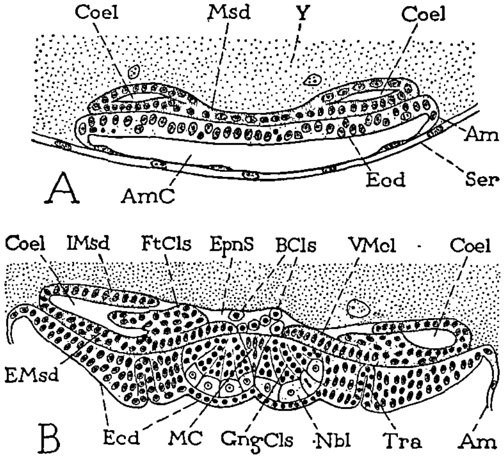

FIG. 19.—Formation of the coelomic sacs and the ventral nerve cord in the embryo of *Forficula*. (*From Heymons*, 1895.) A, cross-section of young embryo showing coelomic clefts (*Coel*) in the mesoderm. B, later stage in which the ventral nerve cord is differentiated from the ectoderm, and the coelomic sacs open into the epineural sinus (*EpnS*) of the haemocoele.

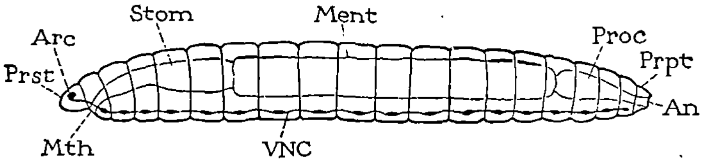

FIG. 20.—Diagram of the fundamental structure of a segmented animal of the annelid-arthropod type. *An*, anus; *Arc*, archicerebrum; *Ment*, mesenteron; *Mth*, mouth; *Prpt*, periproct; *Proc*, proctodaeum; *Prst*, prostomium; *Stom*, stomodaeum; *VNC*, ventral nerve cord.

tive segmentation before leaving the egg, but in the Protura the last two somites are formed just anterior to the periproct during postembryonic life.

Since segmentation affects primarily the mesoderm and the ectoderm, but not the endoderm, the alimentary canal is never segmented; but the metamerism of the body influences most of the organs subsequently formed, such as the nervous system, the circulatory organs, the body appendages, the tracheal invaginations, and the reproductive organs.

The Segmental Appendages.—The acquisition of segmentation was undoubtedly in itself an important event in the evolution of the segmented animals toward a higher development because of the increased facilities of movement that came with it; but the advantages of metamerism were not fully available until the segments became equipped with movable appendages.

The segmental appendages of arthropods are developed in the embryo as hollow, paired outgrowths of the body wall, appearing soon after segmentation, on the lateroventral parts of the germ band (Fig. 23 B). Each appendage contains an extension of the mesoderm and becomes differentiated into a series of parts, the limb segments, or *podites*, which are eventually movable on each other through the development of muscle fibers in the mesoderm of the appendage. Each body segment between the prostomium and the periproct potentially may develop a pair of appendages; but various appendages suppressed in the adult may not appear even in the embryo. The possession of jointed segmental appendages separates the arthropods from the annelids and undoubtedly has given them the possibility of attaining the high degree of development that sets them so far above their wormlike relatives.

Completion of the Body Wall.—The embryo, we have seen, begins its development as a disc or band of thickened cells on the ventral side of the egg (Fig. 9, *GB*). The germinal area may be but a small part of the blastoderm, or it may almost encircle it, but there is always left a dorsal region (*DBl*) consisting of very thin attenuate cells that take no direct part in the formation of the definitive insect. As the marginal parts of the germ band increase in extent, they spread dorsally over the egg, and the extraembryonic field of the blastoderm contracts until it is condensed into a cell mass that sinks into the yolk. The contracting dorsal blastoderm carries with it the ruptured amniotic folds, if the embryo has an amniotic covering, and all these tissues drawn into the yolk are there absorbed to be utilized as nutriment by the growing embryo. With the disappearance of the dorsal blastoderm, the back of the embryo is completed by the dorsal closure of the extended lateral plates, and the body of the embryo thus becomes an oval or elongate sac with continuous walls formed from the ectodermal layer of the primitive germ band.

The Definitive Body Cavity.—In many adult annelids the body cavity consists of a series of segmental compartments which are the enlarged cavities of the coelomic sacs of the embryo. The arthropods have a continuous body cavity formed in part only from the rudimentary coelomic clefts in the embryonic mesoderm (Fig. 19 A, *Coel*). As the arthropod embryo develops, the median strand of the mesoderm breaks apart and some of its cells are said to be converted into free blood cells (Fig. 19 B, *BCls*). The space in which the blood cells lie is known as the *epineural sinus* (*EpnS*); it is a part of the *haemocoele*, or blood cavity of the insect, which is the remnant of the blastocoele after the invasion of the latter by the mesoderm. The coelomic clefts become continuous in each side of the body by a disintegration of the transverse partitions, and their inner walls more or less break down. The epineural sinus thus becomes continuous with the coelomic spaces. The cavity so formed enlarges upward with the growth of the mesoderm around the yolk or the alimentary canal, penetrates into the appendages, and forms eventually the continuous *body cavity* of the segmented body of the arthropod (Fig. 21, *BC*).

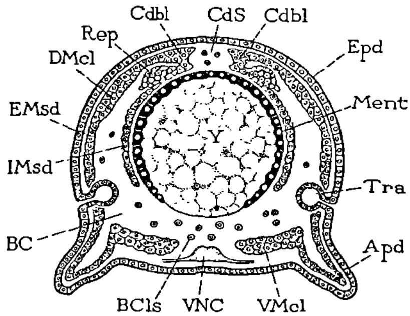

FIG. 21.—Diagrammatic cross section of a nearly mature insect embryo. *Apd*, segmental appendage; *BC*, definitive body cavity; *BCls*, blood cells; *Cdbl*, cardioblasts; *CdS*, cardiac sinus; *DMcl*, rudiment of dorsal muscles; *EMsd*, external mesoderm layer (somatopleure); *Epd*, epidermis; *IMsd*, inner mesoderm layer (splanchnopleure); *Ment*, mesenteron; *Rep*, rudiment of reproductive organ; *Tra*, trachea; *VMcl*, rudiment of ventral muscles; *VNC*, ventral nerve cord; *Y*, yolk.

The mesoderm in each side of the body is split by the coelomic clefts into an outer lamina, or *somatic layer* (Fig. 21, *EMsd*), and into an inner lamina, or *splanchnic layer* (*IMsd*). The first becomes applied to the body wall, the second to the wall of the alimentary canal.

The Mesodermal Organs.—From the mesoderm are formed the muscles, the heart, the blood cells, the fat body, connective tissue, and the parts of the reproductive organs that are not of ectodermal origin. Since the development of the principal mesodermal organs will be given in the chapters on the circulatory system, the fat body, and the reproductive system, we need give but brief attention to the subject here.

The Muscles.—The muscle fibers of arthropods are all of the striated type of structure and are multinucleate, the nuclei in some cases being superficial and in others buried within the body of the fiber. Investigators differ as to whether each fiber represents a single multinucleate cell or is the product of many united cells. The muscles of the body wall and the appendages and probably the dilator or suspensory muscles of the alimentary canal are derived from the somatic layer of the mesoderm; those that surround the digestive tube, including the ectodermal stomodaeum and proctodaeum, are said to be all derived from the splanchnic layer.

The Dorsal Blood Vessel.—The dorsal blood vessel, or principal circulatory organ of the insect, is a muscular tube lying along the dorsal midline of the body. Its lumen is derived from the dorsal part of the haemocoele which formed a *cardiac sinus* (Fig. 21, *CdS*) enclosed between the upper undivided ends of the lateral mesoderm bands. As the latter, or *cardioblasts* (*Cdbl*), approach each other above the alimentary canal, their inner faces become hollowed as two opposing furrows; and when finally the two layers meet, the margins of their grooves unite to form a tube, which is the dorsal blood vessel (Fig. 22, *DV*). The walls of the vessel are converted into transverse muscle fibers, which give the tube a strong contractile power. The blood gains access to the heart cavity through lateral openings, *ostia*, in its walls; it is driven forward and expelled from the anterior end beneath the brain.

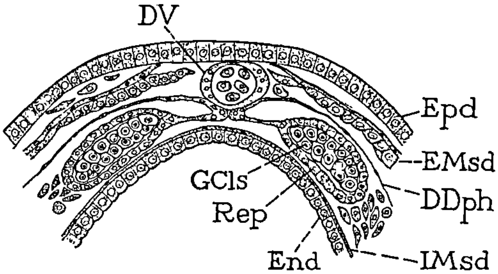

FIG. 22.—Cross section through the dorsal part of the abdomen of a male embryo of the honey bee. (*From Petrunkevitch*, 1903.)

The Fat Body.—The principal fat-containing tissue of insects constitutes a definite structure known as the *fat body*, which consists of a loose aggregate of mesodermal cells lying in the body cavity. The first cells of the fat body are formed in the embryo, but the organ increases greatly in size by cell multiplication and cell growth during postembryonic stages, when the cells take on other functions besides that of fat storage.

The Organs of Reproduction.—The internal parts of the reproductive organs, in which the germ cells are lodged, and in which these cells undergo their subsequent development into the spermatozoa or eggs, according to their sex, appear first as thickenings of the splanchnic walls of the mesoderm in the abdominal region of the body. The cell groups that form these thickenings, or *genital ridges*, are the rudiments of the *testes* or *ovaries* (Fig. 22, *Rep*). From each a strand of cells continues rearward, which becomes the duct of the organ, a *vas deferens* in the male, an *oviduct* in the female. In a few of the lower insects each duct opens by an independent aperture near the posterior end of the body; but in most insects the two vasa deferentia or the paired oviducts unite in a single median tube produced by an invagination of the ectoderm. The ectodermal tube thus formed becomes the *ductus ejaculatorius* in the male (Fig. 292 A, *Dej*), and the *oviductus communis* of the female (Fig. 284 A, *Odc*).

The Tracheal System.—The respiratory organs of insects are entirely ectodermal; they consist both of evaginations and of invaginations of the body wall. The latter, taking the form of branching tubes, or *tracheae,* ramifying minutely throughout the body cavity, constitute the usual respiratory system of all insects whether aquatic or terrestrial. Respiratory evaginations form "blood gills" and occur only in a few aquatic larvae. The rudiments of the tracheae appear first at a comparatively late stage of embryonic growth as segmental pits in the ectoderm along the sides of the body (Fig. 19 B, *Tra*). The pits deepen into tubes, the tubes fork out into branches, the branches subdivide until the tracheae from each primitive pit, the opening of which is now a *spiracle,* form a finely branched system in the corresponding half of the body segment. By the union of some of the branches from successive and opposite spiracles, longitudinal trunks and transverse commissures are established. Since the tracheal system is evidently a comparatively late acquisition in insects, it is not necessary to assume that all the segments once bore spiracles. There is embryonic evidence, however, of the former existence of spiracles on at least each of the segments from the last head segment to the tenth abdominal segment, as will be shown in Chap. XV.

The Definitive Body Form.—The final external form of the insect may be traced through five theoretical evolutionary stages.

First is the wormlike stage (Fig. 24 A) in which the animal consists of a long segmented part coextensive with the length of the alimentary canal and of a short unsegmented preoral part, or prostomium (*Prst*). The mouth (*Mth*) is situated ventrally between the prostomium and the first segment; the anus is terminal in the last segment, or periproct (*Prpt*). The prostomium contains the principal sensory ganglion and may be regarded as the primitive head, or *archicephalon.*

In the second stage (Fig. 24 B) each body segment between the prostomium and the periproct acquires a pair of movable lateroventral appendages, and one or two pairs of antennal organs may be developed on the prostomium.

The third stage (Fig. 24 C) is characterized by the union of the first postoral somite with the primitive head to form a composite head structure, which, being the first stage in the evolution of the definitive head, may be termed the *protocephalon* (*Prc*). The somite involved is that bearing the postantennal appendages, or second antennae (Fig. 23 B, *Pnt*), which in insects are reduced in the embryo and disappear in the adult, while the somite itself loses its identity after union with the procephalic lobes (C), though its ganglia become the tritocerebral lobes of the brain. The protocephalon forms the procephalic part of the definitive insect head, but in some Crustacea it remains as a distinct cephalic structure bearing the eyes, the labrum, and the two pairs of antennae. The protocephalon, or the procephalic part of the definitive arthropod head, is commonly regarded as containing two primitive somites between the prostomium and the tritocerebral segment, corresponding to preantennal and the first antennal appendages, but there is reason to believe that the antennal and preantennal regions of the head are prostomial in origin, and that the postantennal, or tritocerebral, region represents the first primitive somite, which is postoral. This view is expressed in the diagrams (Fig. 24) and will be amplified in subsequent chapters on the head and the nervous system.

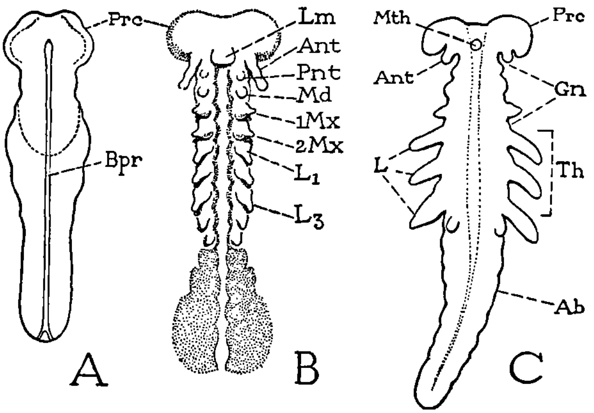

Fig. 23.—Differentiation of the sections (tagmata) of the insect trunk during embryonic development. A, young embryo of *Leptinotarsa*. (*From Wheeler*, 1889.) B, embryo of *Anurida* with appendage rudiments. (*From Wheeler*, 1893.) C, embryo of *Naucoris*, with trunk differentiated into protocephalic, gnathal, thoracic, and abdominal sections. (*From Heymons*, 1899.)

The fourth stage in the development of the body form (Fig. 24 D) differentiates the insects from all other arthropods. It is well shown in the embryo of many insects (Fig. 23 C). In this stage the trunk segments back of the protocephalon (*Prc*) become segregated into three regions. The first may be called the *gnathal region* (*Gn*), since its appendages are destined to become feeding organs; the second is the *thoracic region* (*Th*), set apart as the locomotor center of the insect by the special development of its appendages as locomotory organs; the third is the *abdominal region* (*Ab*), on which the appendages are reduced and mostly obliterated.

In the fifth stage (Fig. 24 E) the body of the insect attains its final form. The gnathal segments are now united with the protocephalon in the *definitive head* (*H*), which thus comprises the prostomium and four succeeding segments and carries the gnathal appendages as well as the protocephalic appendages. In the Pterygota the thorax acquires wing rudiments in the form of paranotal lobes, two pairs of which eventually become wings, and is finally evolved into a highly perfected locomotor mechanism. The abdomen loses most of its appendages, becoming principally a container of the more important viscera and the seat of respiratory and reproductive activities.

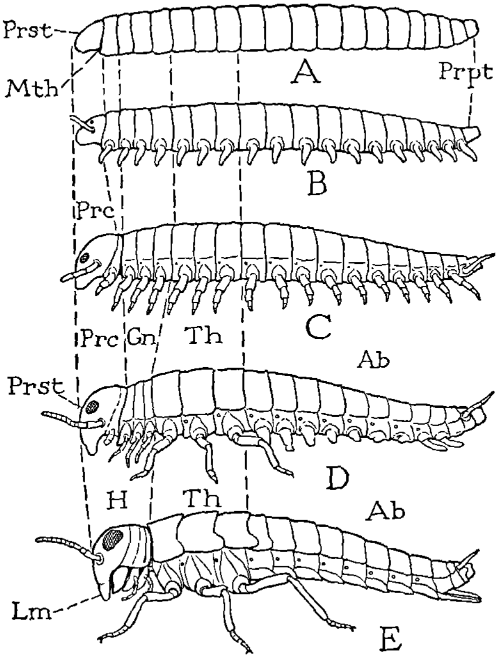

Fig. 24.—Diagrams suggesting the evolution of the definitive insect structure from that of a theoretical wormlike ancestor. *Ab*, abdomen; *Gn*, gnathal segments; *H*, definitive head; *Lm*, labrum; *Mth*, mouth; *Prc*, protocephalon (prostomium and at least one somite), or procephalic part of definitive head; *Prpt*, periproct; *Prst*, primitive head, or archicephalon (prostomium); *Th*, thorax.

From this general review of the processes of development by which a single cell, the egg, after dividing into a group of cells like itself, sets aside a few cells to procreate its species and then forms a highly organized soma from the others, we may proceed to a closer study of the various systems of organs by which the insect soma maintains itself as a living entity and fulfills its destiny as guardian of the germ cells entrusted to it. Before the insect can proceed with its life functions, however, it must get out of the egg shell.

Hatching.—A young animal enclosed in a hard-shelled egg is left to gain its liberty by its own exertions; with most insects maternal responsibility ends with the deposition of the eggs. Many insects at hatching, moreover, find themselves in a situation where it is yet impossible to begin their destined postembryonic life, for the eggs may be buried in the ground, contained in a chamber excavated in the wood of a tree by the mother, hidden in a deep crevice, covered with a protective substance, or enclosed in a horny case. Hence the young creature is often confronted with a hard task to be performed during the first few minutes or half hour of its active existence. Its escape from its first surroundings, however, is not made in a haphazard manner but is orderly directed by "instincts," and often the young insect is provided with special structures to lighten its task.

The first adult function to become active in the hatching insect larva is tracheal respiration. The embryo within the egg makes use of the oxygen that diffuses through the egg shell and is dissolved in the body fluid; the entire tracheal system at this time is filled with a clear liquid. With the first movements of the young larva preparatory to hatching, however, the tracheal liquid is quickly replaced by free air, the liquid being drawn back from the main tracheal branches into the tracheoles, from which it finally disappears, while air simultaneously fills the tubes as the liquid retreats. So mysterious in aspect is this rapid aeration of the tracheal system that various impossible theories have been proposed to account for it on the assumption that the entering air drives out the liquid. It has been shown by Keilin (1924*a*), however, that the activating force must be the retraction of the liquid, and that the air automatically fills the emptied tracheae, since the walls of the latter are constructed to withstand atmospheric pressure. Sikes and Wigglesworth (1931) point out that the mechanism that brings about the absorption of the tracheal liquid at this time is probably the same as that which is functional after hatching, namely, that it is osmotic tension created in the blood by the discharge of metabolites resulting from the first muscular activities of the larva, which causes the tracheal liquid to be drawn into the blood or the tissues through the semipermeable walls of the tracheae, as in ordinary tracheole respiration (see page 459). If the larva has an open tracheal system, air can enter the tracheae through the spiracles, but if the latter are closed it must diffuse into the tracheae from the blood.

The process of hatching, or eclosion from the egg, is accomplished by some insects simply by gnawing a hole through the chorion with the mandibles. With most insects, however, the jaws are not free organs at the time of hatching, or they may not be of the biting type of structure. In such cases the insect must rupture the egg shell by body movements, and it often gives itself for this purpose a closer contact against the chorion by swallowing the amniotic fluid or air that has diffused through the chorion. The anterior end of the egg shell, or sometimes both ends, may be merely pushed off by the muscular exertions of the larva; but often the young insect is equipped with a special instrument, known as the "egg burster," having the form of spines, a series of teeth, or a sharp ridge on the top of the head, with which a slit is made in the chorion over the head. Once the chorion is split, the insect, usually distending itself by copious draughts of air, issues rapidly from the cleft.

All insects with incomplete metamorphosis and some holometabolous species are invested at the time of hatching in a thin cuticular sheath formed during embryonic development. The membrane has not been generally observed in holometabolous insects, but Smith (1922) has described it in three species of Neuroptera, and Sikes and Wigglesworth (1931) note its presence in the mealworm *Tenebrio molitor.* It seems probable, therefore, that the membrane occurs in other holometabolous insects, but that it is perhaps shed before hatching and is thus unobserved. A similar hatching membrane is of common occurrence in many other arthropods than insects.

The hatching membrane may be a smooth, tightly stretched pellicle investing the body, or it may have extensions over the appendages, which are then cramped and folded in their pouches. The egg burster is a part of this embryonic investiture in most cases, though in the fleas it is said to be a strong ridge on the head of the definitive first-instar larva. Some insects shed the embryonic cuticula at the time of hatching and leave the shriveled membrane in the egg; others reject it just after emergence; but young grasshoppers retain it until they have burrowed upward to the surface of the ground from their subterranean egg pods, and young cicadas work their way out of the egg pockets in the twigs of trees still bound in their hatching vestments, which are discarded at the mouth of the cavity.

GLOSSARY OF EMBRYOLOGICAL TERMS

Amnion (*Am*).—The cellular, membranous covering of the embryo formed from folds of the extraembryonic blastoderm; or, specifically, the inner layer of each amniotic fold, or of the completed covering.

Amniotic Cavity (*AmC*).—The cavity between the amnion and the embryo.

Anterior Mesenteron Rudiment (*AMR*).—The anterior group of cells of the ventral endoderm remnant that regenerates the mesenteron.

Archenteron (*Gc*).—The gastrocoele, or cavity of the endoderm.

Archicephalon (*Prst*).—The primitive annelid-arthropod head, or prostomium.

Archicerebrum (*Arc*).—The primitive suprastomodaeal nerve mass of the prostomium. (*Archencephalon.*)

Blastocoele (*Bc*).—The cavity of the blastula. (*Segmentation cavity.*)

Blastoderm (*Bld*).—The surface layer of cells of the blastula before gastrulation.

Blastomeres.—The cleavage cells, or cells produced by the division of the egg or its nucleus that form the blastoderm.

Blastopore (*Bpr*).—The mouth of the gastrulation cavity.

Blastula.—The early stage of the embryo in which the only cell layer is the blastoderm.

Body Cavity (*BC*).—The definitive cavity of the body and appendages, not strictly equivalent in all animals.

Cardiac Sinus (*CdS*).—The channel of the haemocoele dorsal to the yolk or alimentary canal.

Cardioblasts (*Cdbl*).—The dorsal strands of mesodermal cells that form the dorsal blood vessel.

Cephalic Lobes (*Prc*).—The head lobes of the embryo, comprising the region of the prostomium and usually that of the tritocerebral somite.

Chorion (*Cho*).—The nonchitinous shell of an insect egg, formed in the egg follicle.

Cleavage.—The division of the egg or its nucleus and of the resulting cells forming the blastoderm. (*Segmentation of the egg.*)

Cleavage Cells (*CCls*).—The cells formed during cleavage.

Coelome.—A body cavity formed of the coelomic sacs only.

Coelomic Sacs (*Coel*).—The paired segmental cavities of the mesoderm. (*Primitive segments, Ursegmente.*)

Cortical Cytoplasm (*cpl*).—The peripheral layer of cytoplasm in the egg. (*Keimhautblastem.*)

Deutoplasm (*Y*).—The yolk, or nutritive materials of the egg enmeshed in the cytoplasm. (See *yolk.*)

Dorsal Blastoderm (*DBl*).—The extraembryonic part of the blastoderm. (*Serosa.*)

Dorsal Organ (*DO*).—A mass of cells in the dorsal part of the embryo apparently produced by the invaginated serosa.

Ectoderm (*Ecd*).—The outer cell layer of the embryo.

Endoderm (*End*).—The innermost cell layer of the embryo, forming the epithelium of the stomach.

Epineural Sinus (*EpnS*).—The channel of the embryonic haemocoele beneath the yolk or alimentary canal.

Gastrocoele (*Gc*).—The gastrulation cavity. (*Archenteron.*)

Gastrula.—The embryo after gastrulation.

Gastrulation.—The formation of the endoderm, either by invagination of one wall of the blastula or by internal proliferation of cells from the blastoderm.

Germ Band (*GB*).—The area of thickened cells on the ventral side of the blastoderm that becomes the embryo. (*Embryonic rudiment, germ disc, primitive streak, Keimstreif, Keimscheibe, bandelette primitive, plaque ventrale, piastra germinativa.*)

Germ Cells (*GCls*).—Cells destined to become ova or spermatozoa, differentiated from the somatic cells during cleavage.

Germ Tract.—The cytoplasmic area of the blastula containing the germ cells. (*Posterior polar plasm, Keimbahn.*)

Gnathal Segments (*Gn*).—The segments of the insect embryo the appendages of which become the mandibles and first and second maxillae.

Haemocoele.—The blood cavity or cavities of the embryo between the mesoderm and the other germ layers, probably a remnant of the blastocoele.

Hatching Membrane.—A membranous sheath investing the young insect at the time of hatching, probably an embryonic exuvial cuticula, shed during hatching or shortly after. (Not the amnion.)

Holoblastic Division.—The type of cleavage in which the entire egg is divided.

Intermediate Mesenteron Rudiment (*IMR*).—A median strand of cells of the ventral endoderm remnant taking part in the regeneration of the mesenteron in some insects.

Invagination of the Embryo.—The direct infolding of the embryo into the egg.

Involution of the Embryo.—Invagination of the embryo accompanied by a revolution and final reversal of position in the egg.

Lateral Nerve Cords (*LC*).—The lateral strands of nerve tissue produced from the ventral neuroblasts.

Lateral Plates (*LP*).—The lateral areas of the germ band after differentiation of the middle plate.

Median Nerve Cord (*MC*).—The median strand of nerve tissue produced from the ventral neuroblasts.

Meroblastic Division.—The type of egg cleavage in which only the nucleus and the nuclear cytoplasm are divided.

Mesenchyme.—Mesoblastic tissue formed of loosely connected or scattered cells.

Mesenteron (*Ment*).—The stomach of the embryo; in insects regenerated from scattered endodermal cells or from intact endodermal remnants; becomes the epithelium of the adult stomach, or ventriculus.

Mesenteron Rudiments.—The groups of endoderm cells that regenerate the mesenteron, including an anterior, a posterior, and sometimes an intermediate rudiment.

Mesoblast.—The middle cell tissue of the embryo, including mesenchyme and mesoderm.

Mesoderm (*Msd*).—The mesoblastic tissue that takes the form of a definite middle cell layer.

Metamere.—One of the body divisions of the embryo; an embryonic somite or primary body segment.

Micropyle.—The pore or group of pores in the egg chorion giving entrance to the spermatozoa.

Middle Plate (*MP*).—The median strip of cells in the germ band between the lateral plates.

Morula.—The mass of cells formed by holoblastic cleavage of the egg.

Neural Groove (*NlG*).—The median ventral groove of the embryo between the neural ridges.

Neural Ridges (*NlR*).—The two longitudinal ventral ridges of the embryo in which are formed the lateral cords of neuroblasts.

Neuroblasts (*Nbl*).—The primitive nerve cells differentiated from the ectoderm.

Nuclear Cytoplasm (*npl*).—The small mass of egg cytoplasm containing the egg nucleus.

Oötheca.—An egg case formed of secretion products of accessory genital glands or the oviducts.

Ovum.—The mature female germ cell.

Periproct (*Prpt*).—The terminal piece of the body containing the anus, anterior to which segmentation takes place. (*Telson.*)

Posterior Mesenteron Rudiment (*PMR*).—The posterior group of cells of the ventral endoderm remnant that regenerates the mesenteron.

Proctodaeum (*Proc*).—The posterior ectodermal part of the alimentary canal.

Prostomium (*Prst*).—The anterior preoral unsegmented part of the trunk of a segmented animal. (*Acron.*)

Protocephalon (*Prc*).—A general early stage in the evolution of the arthropod head, corresponding to the cephalic lobes of the embryo, comprising the prostomium and usually the first postoral somite, forming the procephalic region of the definitive insect head.

Segment.—A subdivision of the body or of an appendage between areas of flexibility associated with muscle attachments. A primitive body segment is a *somite;* a segment of an appendage is a *podite.* An embryonic body segment is a *metamere.*

Segmental Appendages.—The paired ventrolateral segmental outgrowths of the body wall serving primarily for locomotion.

Serosa (*Ser*).—The dorsal blastoderm or its extension as the outer layer of the amniotic covering of the embryo.

Soma.—The body of an animal as distinguished from the germ cells.

Somatic Cells.—The body cells as distinguished from the germ cells.

Somatic Layer (*EMsd*).—The external layer of the mesoderm applied against the body wall. (*Somatopleure.*)

Somite.—A primary body segment, or metamere.

Spermatozoon.—A mature male germ cell.

Splanchnic Layer (*IMsd*).—The inner layer of the mesoderm applied to the walls of the alimentary canal. (*Splanchnopleure.*)

Stomodaeum (*Stom*).—The anterior ectodermal part of the alimentary canal.

Syncephalon.—A secondary composite head, formed of the prostomium and one or more succeeding somites.

Ventriculus (*Vent*).—The stomach of the adult insect, the epithelial wall of which is the endodermal mesenteron of the embryo.

Vitelline Membrane (*Vit*).—The wall of the egg cell; undivided in meroblastic cleavage, surrounding the blastoderm.

Vitellophags (*Vph*).—Endoderm cells proliferated into the yolk and accomplishing a partial digestion of the latter.

Yolk (*Y*).—Deutoplasm. When the yolk is small in quantity or evenly distributed through the cytoplasm, the egg is said to be *alecithal* or *hololecithal;* when the yolk has a central position, the egg is *centrolecithal;* if the yolk lies at one end of the egg, the latter is *telolecithal.* Insect eggs are centrolecithal.

Yolk Cells (*YCls*).—Cleavage cells remaining in the yolk and taking no part in the blastoderm formation.

Yolk Cleavage.—The division of the yolk into masses containing from one to several cleavage nuclei.

Zygote.—The fertilized egg or egg nucleus.

CHAPTER III

THE BODY WALL AND ITS DERIVATIVES

The body wall of an animal is that part of the ectoderm which remains at the surface in the fully developed stage and serves to maintain anatomical integrity in the rest of the organism. Though primarily an integument, because of its position numerous responsibilities devolve upon the body wall: it must bear the brunt of all external things and forms of energy that touch upon the animal; it must be able to receive impressions of changes in the environment to which it is advantageous or necessary that the creature should respond; and in the arthropods it is the principal agent of the motor mechanism.

In following the development of the arthropod embryo we have seen how one group of cells after another becomes inflected from the ectoderm and specialized to form some internal organ or group of organs. The body wall, therefore, is an undifferentiated remnant of the ectoderm, and as a consequence its cells preserve in a high degree the potentiality of primitive functions, which may be expressed in the adult as absorption, transpiration, secretion, excretion, and sensitivity, while, furthermore, they retain a large capacity for development, as shown in the many specialized organs that have been evolved in the integument. In a study of the insect body wall, therefore, while we give chief attention to its fundamental structure and to the modifications adaptive to protection and locomotion, we must recognize that the various ectodermal glands and the sense organs are directly parts of it, and that, more remotely, the invaginations forming the anterior and posterior sections of the alimentary canal, the respiratory organs, the unpaired reproductive ducts, and the entire nervous system are derivatives from it.

1. THE BODY WALL

The arthropod body wall is reinforced by a *cuticula* covering its outer surface. The cuticular substances are products of the body-wall cells, but the protective layer formed by them becomes the most important part of the integument, and the matrix cells, after having generated the cuticula, take a subordinate place in the tegumentary structure. The cuticula may be entirely soft and flexible, but characteristically it becomes *sclerotized,* or hardened in certain areas, forming body-wall plates, or *sclerites.* The sclerites, which usually have definite shapes and interrelations, constitute the *exoskeleton* of the arthropod and play an important role in the motor mechanisms of the animal. Inflections of the body wall containing rigid ingrowths of the cuticula, or *apodemes,* form collectively the *endoskeleton* of the arthropod organization. The flexible lines of the integument between sclerites are usually called *sutures,* and movable points of contact are termed *articulations.* The hard exoskeleton produces a mechanical and physiological condition in the arthropods quite different from that of soft-skinned animals, and Kennedy (1927) in an interesting paper has pointed out many ways in which the exoskeleton has been a factor both in limiting and in directing the evolution of insects.

Structure of the Body Wall.—The arthropod integument, because of the presence of the cuticula, has a stratified structure (Fig. 25 A), since it consists of both the inner cellular epithelium (*Epd*) and the outer noncellular cuticula (*Ct*). In entomology the cell layer of the body wall is commonly called the "hypodermis," but the term *epidermis* is preferable inasmuch as the integumental epithelium is the homologue of the ectodermal layer of the skin so designated in vertebrate anatomy, though either term is illogical when applied to invertebrates having no accompanying "dermis." Internally the epidermis is limited by a very thin noncellular *basement membrane* (*BMb*).

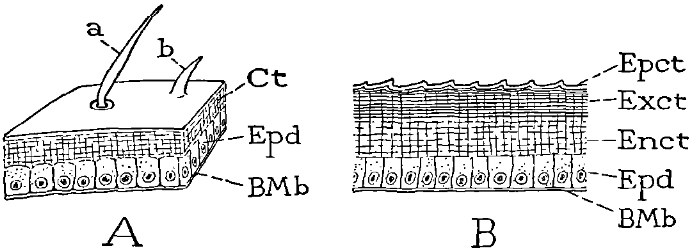

FIG. 25.—Structure of the body wall, diagrammatic. A, piece of body wall bearing a movable external process, or seta (*a*), and an immovable process (*b*). B, vertical section of body wall. *BMb*, basement membrane; *Ct*, cuticula; *Enct*, endocuticula; *Epct*, epicuticula; *Epd*, epidermis; *Exct*, exocuticula.

The Cuticula.—The cuticula itself generally has a stratified appearance in sections, since it usually exhibits two distinct principal layers, namely, an outer *primary cuticula,* or *exocuticula* (Fig. 25 B, *Exct*), and an inner *secondary cuticula,* or *endocuticula* (*Enct*), while on the exterior there is a very thin surface layer, or *epicuticula* (*Epct*), which appears in sections as a clear border line about one micron in thickness. The characteristic constituent of the exocuticula and endocuticula is chitin, but the exocuticula contains also other substances and is generally distinguishable from the endocuticula by its darker pigmentation and its denser structure, since it is the layer of the body wall containing the hardening substances that form the sclerites. The epicuticula is a nonchitinous layer, but its component materials also permeate the exocuticula (Wigglesworth, 1933*b*).

The cuticular substance known as *chitin* is a colorless nitrogenous polysaccharide, perhaps of microcrystalline structure (Gonell, 1926). Chemically, as stated by W. J. Schmidt (1930), "chitin is characterized by its decomposition product, glucosamine, as an animopolysaccharide, one of those interesting compounds intermediate between carbohydrates and proteins." Its chemical formula as given by Brach (1912) is $(C_{32}H_{54}N_4O_{21})_x$. As stated by Campbell (1929), chitin is insoluble in water, alcohol, ether, dilute acids, and dilute or concentrated alkalies. It is dissolved, with or without decomposition, by concentrated mineral acids and, according to Schulze and Kunike, by water-free formic acid. It is hydrolyzed by concentrated mineral acids, with the formation of a glucosamine salt or chitose, a sugar, and fatty acids, chiefly acetic. Treatment of chitin with potassium or sodium hydroxide at high temperatures also hydrolyzes it, producing *chitosan* and acetic acid, but without change in appearance. Chitin is oxidized and dissolved at room temperature by a solution of sodium hypochlorite containing 5 per cent of available chlorine. It is not attacked by mammalian digestive enzymes but is broken down by *Bacillus chitinovorus* (Benecke, 1905), which may be the agent of its decomposition in nature.

Röntgenographic tests and polarized light studies, as described by W. J. Schmidt (1930), have shown that chitin has a fibrous structure, and that the fibers are composed of elongate, submicroscopic, crystalline parts (micellae) which lie parallel with the fiber axes. The chitinous mass, furthermore, is penetrated by fine intermicellar spaces and therefore possesses submicroscopic pores. This porous character, Schmidt points out, accounts for the permeability of chitin to gases and liquids, as in the chitin-covered chemoreceptive sense organs, tracheae, absorptive surfaces of the alimentary canal, and discharging surfaces of glands.

The common laboratory practice of soaking or boiling parts of the insect body wall in caustic solutions to soften and clear the cuticula removes the coloring and hardening substances from the latter and may change the chitin into chitosan; but it does not disintegrate the cuticula or produce any visible change in its chitinous parts because chitosan does not differ in appearance from chitin. The insect cuticula can be stained with acid fuchsin after soaking in potassium hydroxide until translucent and then washing thoroughly, finally in acidulated water.

For determining the presence of chitin, Campbell (1929) gives the following practical test, a modification of the more difficult Van Wisselingh-Brunswick method. Material suspected of being chitinous is placed in potassium hydroxide solution saturated at room temperature and kept at 160°C. for 15 minutes in a tube closed by a Bunsen valve.

Since chitosan gives a violet color reaction with solutions of iodine in weak acids, this test may now be applied to a sample on a slide, after which the material should be dissolved on the slide at room temperature in a drop of 75 per cent (by volume) sulphuric acid. This gives chitosan sulphate, crystals of which, precipitated by slow dilution of the drop in moist air, cling to the slide, where they may be washed, stained with an acid dye, and mounted in balsam.

Chitin is of wide distribution among invertebrate animals, being found, according to Wester (1910), in the Porifera, Hydrozoa, Bryozoa, Brachiopoda, Mollusca, Annelida, and Arthropoda. It is unknown in the Protozoa and Vertebrata; among plants it is restricted to the fungi, in which group it was first discovered. Chitin is perhaps the organic foundation of the cuticula of all arthropods; it occurs also in the intima of the various ectodermal invaginations and has been reported to be present in the lining (peritrophic membrane) of the mesenteron in several species of insects. In the Annelida chitin forms the bristles or setae of the skin but it is not present in the cuticula. In the Onychophora, however, the integument is said to be chitinous.

It is a common mistake to suppose that the sclerites of the insect body wall are "strongly chitinized" areas of the cuticula. The reverse probably is more generally true, since sclerotization results from the deposit of nonchitinous substances in the exocuticula. Campbell (1929) has shown that the exocuticula of *Periplaneta* contains only about 22 per cent of chitin, while the soft endocuticula contains about 60 per cent, and Kunike (1926) found that the wing covers of a May beetle contain by weight 75 per cent of nonchitinous substances, and those of a grasshopper as much as 80 per cent. The chemical nature of the hardening substances that form the sclerites of the insect cuticula is not known, though there is some evidence of their being carbohydrates. In the Crustacea the sclerotic matter of the integument is largely calcium salts.

The nonchitinous epicuticula is composed of substances that, it has been shown by Wigglesworth (1933*b*), are also constituents of the exocuticula. According to Kühnelt (1928, 1928*a*), this surface film (*Grenzlamelle*) of the exocuticula is highly resistant to acids, but when heated in caustics it is saponified and can be shown to contain fatty acids and cholesterin. From its chemical reactions the epicuticula of the insect body wall appears to be closely related to the surface cuticula of plants. As Kühnelt points out, it protects the insect against many harmful external influences, such as excessive humidity, dryness, and disease organisms, and makes it possible for insects to live under a great variety of environmental conditions.

The histological appearance of the cuticula varies somewhat in different insects and in different parts of the integument of the same insect. Most investigators find that the endocuticula has a faint horizontally lamellate structure, in which usually there are visible fine vertical striations. The striations appear to be canals left by protoplasmic filaments that, during the formative stage of the cuticula, extend outward from the epidermal cells. The cuticular material is probably laid down in layers between these filaments, which are later retracted. N. Holmgren (1902) has suggested that the protoplasmic strands of the epidermis represent primitive cilia that once may have covered the bodies of the arthropod ancestors.

In some of the Coleoptera the cuticula has a highly specialized structure. The cuticula of the larva of *Dytiscus* or *Lucanus,* according to Kapzov (1911), is composed of stratified lamellae having a distinctly spongy or alveolate structure. In the endocuticula coarsely and finely alveolated lamellae alternate, the plates becoming thinner toward the periphery,. while in the exocuticula the lamellae are condensed into a more compact fabric in which the alveolation is almost obliterated. In the adult beetles, as shown by the studies of Biedermann (1903) and Kapzov (1911) on *Lucanus cervus,* and of Casper (1913; Korschelt, 1924) on *Dytiscus,* the cuticula has a much more complicated structure. The exocuticula is a simple alveolar tissue showing no stratification or striation. The endocuticula, on the other hand, consists of horizontal bars, or trabeculae, arranged in well-defined strata. The trabeculae lie parallel in each stratum, but those of successive strata are crossed at definite angles. In *Lucanus* the trabeculae are bound together by bundles of fibrous strands that extend between them from the epidermal cells; in *Dytiscus,* according to Casper, the uniting strands are visible only in an early formative stage. The strands would appear to represent the protoplasmic processes of the epidermal cells observed in other insects.

The Epidermis.—The ectodermal cells of the body wall are primarily arranged in a single layer (Fig. 25, *Epd*), and in most places they preserve the form of a simple epithelium. Secondarily they may become separated into two layers or disposed irregularly; in most such cases, however, each cell maintains its attachments both to the cuticula and to the basement membrane, though the connection with one or the other is reduced to a fine strand of protoplasmic tissue. In the growing stages of insects, the epidermal cells are usually cubical or columnar, with the nuclei near their bases; but in adult insects, after the activity of cuticula formation is over, the matrix cells become more or less degenerate and appear in most places as a thin protoplasmic layer beneath the cuticula, in which cell boundaries are indistinct and the cell areas are marked only by the nuclei.

The Basement Membrane.—The thin membrane that forms the inner lining of the body wall (Fig. 25, *BMb*) is so closely adherent to the epidermis that it appears to be a product of the latter similar to the cuticula covering the outer surface. It has often been stated that this basement membrane is a connective tissue layer, itself composed of greatly flattened and attenuated cells, but in sections of the body wall of insects we may look in vain for positive evidence of cellular structure in the basement membrane. Though the membrane may often appear at first sight to be nucleated, a closer inspection will show that the visible nuclei belong to blood cells or to a sheet of connective tissue that is here and there applied against the basement membrane.

Sclerotization.—From the standpoint of morphology the most important feature of the arthropod body wall is its ability to produce definitely limited sclerotic areas in the cuticula. It is probable that sclerotization served first as a means of protection; but the presence of integumental plates in animals having the muscles attached on the body wall gave at once the possibility of a new mechanism of movement and of locomotion; and the development of refined interrelations between muscles and sclerites has been the principal line of evolution in the arthropods. The study of insects has been largely a study of sclerites. And yet we know practically nothing of the chemical or physical processes of cuticular sclerotization in insects. It is obvious, however, that only when we have learned something of the physiological nature of sclerites can we give them their proper status in comparative anatomy; and only on such a basis can we intelligently judge the value of sclerites as taxonomic characters.

Sutures.—The term "suture" comes from the Latin word *suere*, "to sew." In anatomy it properly applies, therefore, to the lines along which adjoining plates have united, as those between the centers of ossification in the vertebrate cranium. In entomology, however, almost any kind of line or narrow space separating sclerotic areas of the cuticula is called a *suture*. We may distinguish at least four distinct varieties of entomological sutures: (1) external grooves of linear inflections of the cuticula that form internal ridges or plates to strengthen the skeletal walls or to furnish increased surfaces for muscle attachments; (2) lines where the sclerotization of the cuticula has become secondarily discontinuous in order to give flexibility; (3) lines where sclerotization has never taken place; and (4) true sutures or lines of union between originally distinct sclerites. Perhaps the majority of insect sutures belong to the first category. In descriptive works they are recorded as lines delimiting subdivisions in a larger sclerotized field. It should be recognized, however, that in most such cases the "sclerite" so defined is merely an incidental result of the cuticular infoldings, and that the true functional characters are the endoskeletal structures formed by the inflections of the body wall, the lines of which appear externally as "sutures."

Apodemes.—Any internal cuticular process of the body wall is an apodeme (from ἀπό, "away," and δέμασ, "body"). The cuticular part of an apodeme is always contained in a matrix of the epidermis (Fig. 26 C, *Epd*) and is usually an inflection of the cuticula (A, B, C), though in some cases it appears to be a solid cuticular ingrowth (D, E). The site of a hollow apodeme is marked externally by a depressed line (suture) or a pit, according to the form of the apodemal invagination, and at ecdysis the cuticular core is withdrawn and regenerated. Apodemes ordinarily take the form of ridges, plates, or arms formed in multicellular invaginations of the epidermis (A, B, C), and they have definite mechanical purposes. Most of them are ridges which evidently serve to strengthen the exoskeleton, either forming a brace between two points of stress or giving rigidity to an area subject to special strain. Armlike apodemes, or apophyses, usually furnish attachment points for muscles, though some muscle-bearing apodemes have the form of ridges or plates. Individual muscles are frequently attached to the body wall by long, slender, threadlike apodemes, often called "tendons," which may have an expansion at the end for the reception of the muscle. In some cases very slender, tendonlike muscle apodemes are extensions of the cuticula formed within a single cell of the epidermis (E, F). These unicellular tendons give attachment each to a single muscle fiber.

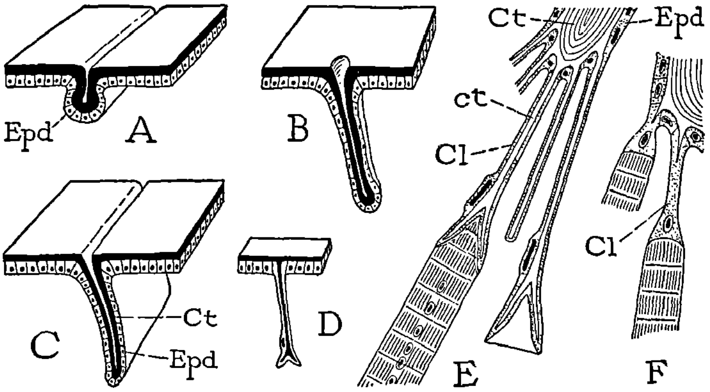

Fig. 26.—Apodemes, or internal processes of the body wall. A, B, C, various forms of multicellular apodemes, diagrammatic. D, a unicellular apodeme. E, unicellular muscle "tendons" at the end of a multicellular apodeme. F, formative stage of the same. (E, F *from Janet*, 1907.)

Articulations.—Wherever there is a line of movement in the body wall, the flexible area, or "joint," is merely the nonsclerotized cuticula between two neighboring regions of sclerotization (Fig. 27 A, *mb*). The movable area is known as an *articular membrane*, or *corium*.

The movements possible at a joint will depend on the extent of the articular membrane; if the latter is ample and completely separates the sclerotic parts, as between the segments of the abdomen (Fig. 27B, *Mb*), the movement is unrestricted. In most cases, however, particularly at the joints of the appendages, movement is limited by the special development of one or two pairs of contiguous points on the adjacent ends of the adjoining segments. Limited joints of this nature may be distinguished as articulated joints, since the points of contact constitute specific *articulations*. According to whether an articulated joint has one pair or two pairs of articulating surfaces, it is said to be *monocondylic* or *dicondylic*. A monocondylic joint may have a partial rotary movement; a dicondylic joint is restricted to a hinge movement.

Articulations are of two types of structure; in one the points making contact are sclerotic prolongations within the articular membrane (Fig. 27 C, *e, f*), in the other the articulating surfaces are areas of contact on the outside of the skeletal parts (D, *a, c*). The two forms of articulations may be distinguished as *intrinsic* and *extrinsic*, respectively. Extrinsic articulations are usually of the ball-and-socket type and are particularly characteristic of the articulations of the mouth appendages with the wall of the cranium (D). The articulations of the legs with the body (the pleuro-coxal articulations) are intrinsic, as are usually also the articulations between the leg segments (C), though monocondylic leg articulations may be extrinsic.

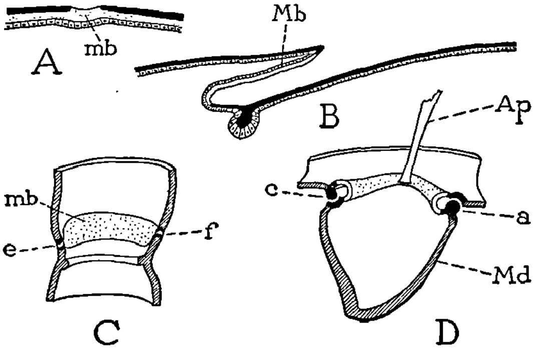

FIG. 27.—Sutures, joints, and articulations, diagrammatic. A, section through a simple membranous "suture." B, a conjunctival membrane (*Mb*) between two body segments. C, a dicondylic leg joint with intrinsic articulations (*e, f*). D, the typical extrinsic dicondylic articulation of the mandible with the cranium.

2. EXTERNAL PROCESSES OF THE BODY WALL

The outer surface of the cuticula is seldom smooth or bare; it presents a great variety of microscopic roughenings in the form of points, pits, ridges, and sculptured designs, and it is covered with larger outgrowths that take the shape of spicules, spines, hairs, and scales. All the external processes of the body wall, however, may be classed in two groups according to whether the epidermal cells take a direct part in their production or do not; that is, they are either *cellular* or *noncellular* outgrowths. Of the cellular processes, some are unicellular, others are multicellular.

Noncellular Processes of the Body Wall.—The noncellular projections of the outer surface of the body wall are purely cuticular structures (Fig. 28 A, B). They have the form of minute points or nodules (scobinations), spicules, small spines, hairs, corrugations, and ridges, the last often enclosing regular polygonal areas. The pattern of these surface characters appears in some cases to have a relation to that of the underlying epidermal cells, but in others it seems to be entirely unrelated to the cell arrangement. These surface structures of the mature body wall are probably formed over cytoplasmic processes of the epidermis when the outer layers of the cuticula are being generated, and later become solid.

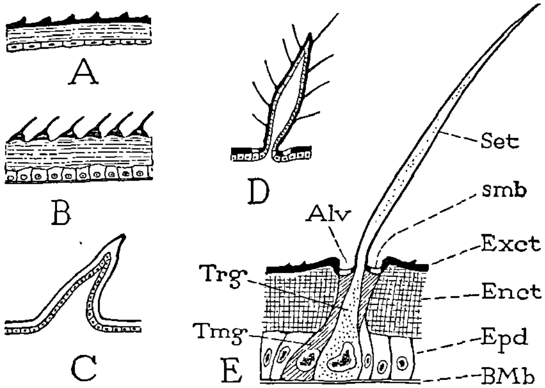

Fig. 28.—External processes of the body wall, diagrammatic. A, B, noncellular cuticular processes. C, D, multicellular processes. E, a typical unicellular process, or seta. *Alv*, setal socket, or alveolus; *Set*, seta; *smb*, setal membrane; *Tmg*, tormogen, or socket-forming cell; *Trg*, trichogen, or seta-forming cell.

Multicellular Processes of the Body Wall.—Cuticular structures of this nature are hollow outgrowths of the entire body wall and are therefore lined by a layer of formative epidermal cells (Fig. 28 C). They are usually large and spine-like in form. Most of them are solidly fixed to the surrounding cuticula (C), but some are set in a membranous ring and are movable (D). The immovable varieties are specifically termed *spines*, the movable ones are distinguished as *spurs*. Examples of fixed multicellular processes are seen in the spines of the hind tibiae of certain Orthoptera, while the spurs at the ends of the tibiae are examples of the movable variety. The lateral claws of the feet of insects are large movable spurs. Both spines and spurs may themselves bear unicellular processes, or setae (D).

Unicellular Processes of the Body Wall.—The typical outgrowths of the body wall in this class are the hairlike processes, termed *setae*, that constitute the principal body covering of most insects. Some unicellular processes, however, are thick and spinous, such being distinguished as *spine-like setae;* others are branched or featherlike and are termed *plumose hairs;* still others are flat squamous structures of various shapes, known as *scales.* Also there are unicellular outgrowths of many other varieties having the form of cones, pegs, hooks, spatulae, knobbed hairs, etc., but all are fundamentally setal structures.

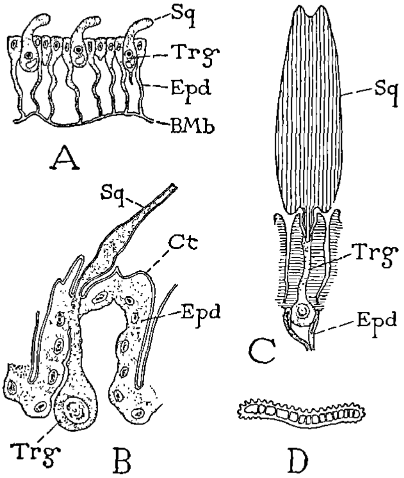

Fig. 29.—Development and structure of lepidopterous wing scales. (*From Mayer*, 1896.) A, early stage of scale cells (*Sq*) in section of a wing of *Vanessa antiope.* B, later stage of scale growth on pupal wing of *Danais plexippus.* C, a mature wing scale of *D. plexippus.* D, cross section of mature scale of *D. archippus.*

Structure of a Seta.—A typical seta is a slender hairlike process of the cuticula formed by a plasmatic outgrowth from a single large epidermal cell (Fig. 28 E). In the mature condition the plasmatic core usually shrinks and more or less withdraws from the cavity of the seta, but at each moult the seta may be re-formed by a new outgrowth from the generative cell. The base of the seta is set in a small membranous ring of the body wall, known as the *setal membrane* (*smb*), which may be depressed in a hair socket, or *setal alveolus* (*Alv*), and the latter may be elevated on a *tubercle.* Beneath the base of the seta a cylindrical internal cavity of the cuticula, called the *trichopore*, contains the distal parts of the cells associated with the seta.

The epidermal cell that forms a seta, or any hairlike structure, is termed the trichogenous cell, or *trichogen* (Fig. 28 E, *Trg*). Closely associated with the trichogen there is usually a second cell that forms the setal membrane, and which for this reason is sometimes called the membrane cell, but since the setal membrane is usually the floor of an alveolus its generative cell has been named by Wigglesworth (1933*b*) the socket-forming cell, or *tormogen* (*Tmg*). The seta-forming process of the trichogen, during the period of the setal growth, is said to penetrate the tormogen like a finger thrust through a ring (Haffer, 1921; Wigglesworth, 1933*b*). In the mature condition, therefore, the distal part of the socket cell surrounds the neck of the hair cell, and the seta rises from the center of the setal membrane. Finally, there is associated with many insect setae, if not the majority of them, a sensory nerve cell, lying in or just beneath the epidermis, that is connected with the seta by a distal nerve process. Setae thus innervated become setal sense organs.

Scales.—The small, flat, scale-like structures that constitute the body covering of adult Lepidoptera and of some other insects are greatly modified unicellular outgrowths of the body wall, which probably have been evolved from ordinary setae. Several stages in the development of a scale from a single cell of the wing epidermis of butterflies are shown in Fig. 29. Each scale arises as a blunt process (A, *Sq*) formed by an outgrowth from a special scale cell (*Trg*) of the wing epidermis. As the process elongates (B), it takes on the shape of a small bag and finally flattens out to form the scale (C). When the scale nears completion, the scale-forming cell degenerates and withdraws from the lumen of the scale. The two horizontal walls of the scale are united by vertical cuticular bars (D), which serve to give rigidity to the scale by binding its upper and lower surfaces together. The pigmentation of the scale is said to be formed by blood corpuscles that enter the fully formed scale after the retraction of the primary scale cell. The iridescent colors so characteristic of most insect scales are the result of the surface sculpturing of the scale itself.

Poison Setae.—The larvae of certain Lepidoptera are provided with setae from which is discharged an irritant venom formed in special poison gland cells associated with the trichogenous cell (Fig. 30 A). The poison issues from the ends of the setae when the tips of the latter (*a*) are broken off. A concise and comprehensive account of the poison apparatus of North American caterpillars is given in a paper by Gilmer (1925), to which the student is referred also for references to the work of other investigators on this subject. Species of caterpillars known to be poisonous occur in the Notodontidae, Liparidae, Megalopygidae, Arctiidae, Noctuidae, Eucleidae, Saturniidae, and Nymphalidae.

According to Gilmer, there are two principal types of stinging structures in caterpillars. In one type (Fig. 30 A) the apparatus consists of an ordinary seta (*Set*) that has become toxic by the development of a poison gland cell (*GlCl*) immediately adjacent to the trichogen (*Trg*), which extends into the lumen of the seta. In the other type (B) the stinging elements are the same as in the first, but the seta has been carried out on the end of a multicellular spine or spur (*Spi*) and becomes thus a terminal armature of the latter. The gland cell may lie within the spine (*GlCl*), or it may become so greatly enlarged that its base projects beneath the inner end of the spine. In the spine type of apparatus the terminal seta in some cases is a long, piercing needle, in others it is reduced to a thick apical point. In many of the Liparidae and in some of the Notodontidae, including the caterpillar of the brown-tail moth *Euproctis* *chrysorrhea,* the seta is replaced by a group of small spicules, which, Gilmer believes, are derived from an original branched seta, the main shaft of which has been shortened and finally obliterated. A spicule of the brown-tail moth caterpillar is composed of a series of dartlike pieces, each of which is inserted by its tapering base into the larger distal end of the piece proximal to it.

The poison cell of the stinging apparatus (Fig. 30 A, *GlCl*) extends into the seta along with the trichogen cell, and Gilmer suggests that it is

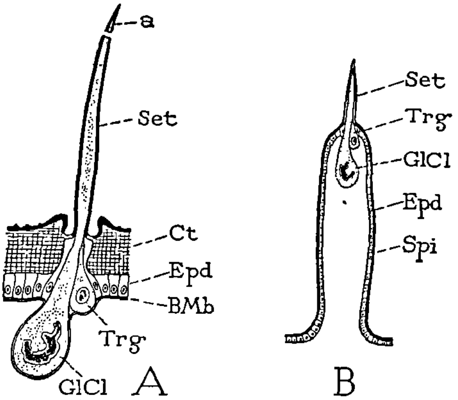

FIG. 30.—Poison setae of certain caterpillars. (*Diagrams based on figures from Gilmer,* 1925.) A, typical structure of a poison seta, with a large gland cell (*GlCl*) discharging through broken tip of seta. B, a poison spine, or multicellular process armed with a stinging seta.

a "sister cell" of the latter, the two being formed probably by the division of a single primary seta-forming cell. The gland cell is always distinguished by its greater size, and particularly by its large, irregular, branched nucleus. The trichogen commonly disintegrates between moults and is often inconspicuous or not discernible in sections. Setal glands have been observed on the larvae of other insects than Lepidoptera. Woods (1929) says that all the setae of the larva of the alder flea beetle have, in addition to the trichogen, a gland cell that opens through a pore on the tip of the seta.

3. SENSE ORGANS

The reaction of a complex animal to the environment, that is, its adjustment to external changes by movement or other forms of response activated from within, is dependent on two accessory conditions. First, the outer surface of the animal must be in part at least "sensitive" to environmental changes; second, the sensitive areas must be in connection with the motor mechanism. The first condition is realized in most Invertebrata by the special development of cells of the body wall that are particularly sensitive to external stimuli (Fig. 31, *SCl*); the second is established by the propagation of nerve tracts that go either directly or indirectly from the receptive parts to the motor tissues, or effectors. In all but the lowest Metazoa the sensory nerves from the receptor organs proceed to a central nerve organ, which in arthropods is the brain or the ganglia of the ventral nerve cord (*VNC*), and here make a connection (synapse) with the roots of the motor nerves (*MNv*) which proceed outward to the muscles (*Mcl*) or other effectors.

Both the sensory cells and the sensory nerves are derived from the ectoderm, as are also the motor cells and the motor nerves; but, whereas the motor nerve tissues lose their connections with the exterior (see page 30), the sensory tracts maintain their continuity with it in the sensory cells of the epidermis. The body wall in the immediate neighborhood of a sensitive cell, or group of such cells, is usually modified to form a more efficient receptor apparatus, designed to admit some particular kind of impinging stimulus, or a certain group of stimuli; and these special receptors constitute the so-called *sense organs* of the animal (Fig. 31, *SO*). The sense organs of insects are widely distributed over the surface of the body and the appendages, and they occur also in the anterior and posterior parts of the alimentary canal. Each is a more or less complex structure elaborated from the several layers of the body wall, the various forms of which and their possible functions will be discussed in Chap. XVII.

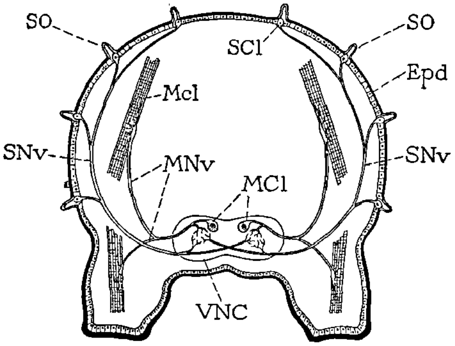

FIG. 31.—Diagram of the relation of the epidermal sense cells to the central nervous system and the motor mechanism. *Epd*, epidermis; *MCl*, motor cell; *Mcl*, muscle; *MNv*, motor nerve; *SCl*, sense cell; *SNv*, sensory nerve; *SO*, sense organ; *VNC*, ganglion of ventral nerve cord.

4. ECTODERMAL GLANDS, CORPORA ALLATA, OENOCYTES

The ectoderm is the seat of much cellular activity, mostly of a secretory nature. All the ectoderm cells produce the cuticular substances, which, being largely nitrogenous compounds, are regarded by some writers as excretory products. In addition to the general chitinogenous function, however, many cells or groups of cells have highly specialized secretory functions, and in these cells are elaborated a great variety of substances which are discharged at the exterior or into invaginations of the body wall. The true gland cells of the body wall always remain in anatomical continuity with the epidermis, though their bases may push far into the body cavity, or the cells themselves may be carried inward by deep invaginations of the integument. On the other hand, certain cells are given off from the epidermis into the body cavity where they become free internal organs. Such cells form the *corpora allata* in the head, and the *oenocytes* in the abdomen, which are possibly of the nature of endocrine glands (see Chap. XIV).

The glands of the ectoderm discharging their secretion externally are too numerous to be described here in detail. They arise from all parts of the body wall, from the stomodaeal and proctodaeal sections of the alimentary canal, and from the ectodermal ducts of the reproductive organs. Classified according to their function they include salivary glands, silk glands, wax glands, lac glands, food glands, trophallactic glands, scent glands, adhesive glands, excretory glands, poison glands, stinging glands, defensive glands, repellent glands, moulting glands, colleterial or egg-covering glands, mucous glands, and others.

Structurally the ectodermal glands are specialized cells of the epidermis or of the walls of ectodermal invaginations. Gland cells are usually distinguished by their large and often irregular or branched nuclei, the nuclei being probably the source of the substances that activate the secretory properties of the cytoplasm. The simplest gland form consists of a single cell, but the majority of insect glands are multicellular.

Unicellular Glands.—A one-celled gland is usually of greater size than the cells surrounding it and, in its simplest form (Fig. 32 A), discharges its products directly through the covering cuticula. A larger glandular area may include a group of secretory cells (B). Some writers have claimed that the cuticular covering of such glands is penetrated by fine pores, but in most insect glands the secretion escapes by diffusion through the very thin cuticula covering the surface of the cells. In many glands, however, a minute cuticular ductule extends from the exterior into the body of each cell (C, H, *a*), thus allowing the secretion to pass out through an extremely thin layer of cuticula. Unicellular glands of this kind often have the distal end of the cell drawn out into a slender neck, or duct (C, *Dct*).

Multicellular Glands.—The many-celled glands may be, as we have just noted, merely a group of cells situated at the surface of the body (Fig. 32 B); but most of them are invaginations of the body wall. A simple multicellular gland is a mere tube of secretory cells lined with a delicate cuticular intima (D). Such glands are sometimes eversible. By a specialization in function between its outer and inner parts a tubular gland may become differentiated into a duct (E, *Dct*) and a true glandular part (*Gl*), while a widening of the duct may constitute a reservoir (F, *Res*) for the storage of the secretion products. Glands are frequently branched, the branches in some cases being long and tubular and in others sacculated at the ends, giving the gland a racemous structure (G). In all forms of multicellular glands the intima is continuous over the inner surfaces of the cells, but in some it gives off minute capillary ductules into the individual cells (H), as in some of the unicellular glands (C).

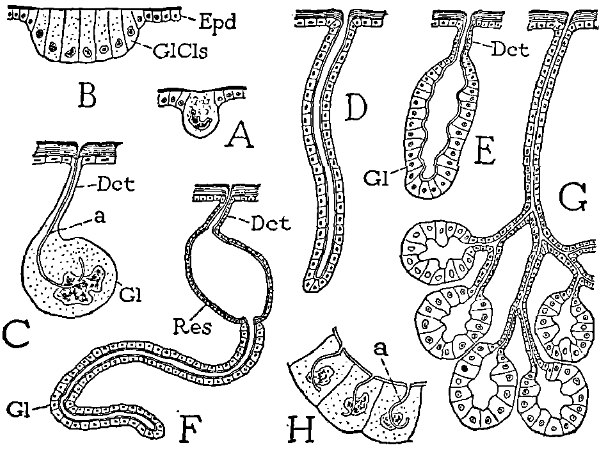

FIG. 32.—Various structural types of ectodermal glands, diagrammatic.

5. MUSCLE ATTACHMENTS ON THE BODY WALL

A most important mechanical feature of arthropod organization is the intimate connection between the body wall and the muscles. Yet, in their origin, the epidermis and the muscle tissue are entirely distinct, the first being derived from the ectoderm, the second from the mesoderm. In the embryo the mesodermal cells of the developing muscle fibers attach themselves to the inner face of the epidermis (Fig. 33 B), and in some larval insects (C, D) this condition appears to be preserved, though the basement membrane disappears at the end of the muscle and becomes continuous with the sarcolemma of the latter. In postembryonic stages of most insects, however, the muscle fibers are attached to the cuticula by fine connective fibrils, *tonofibrillae* (A, *Tfbl*), that traverse the epidermal layer. The dilator muscles of the ectodermal parts of the alimentary canal are said by Boelitz (1933) to be inserted in the same manner by tonofibrillae attached on the cuticular intima.

The tonofibrillae are produced by a transformation of the epidermal cells at the ends of the muscles into cuticular fibrils that are continuous, on the one hand, with the cuticula and, on the other, with the muscle fibrillae. The plasmatic parts of the cells may entirely disappear, but in most cases nucleated remnants of the cells are to be seen between groups of the tonofibrillae (Fig. 33 F) or at the end of the muscle tissue (E, *Nu*). The striated part of the muscle, according to recent investigators (Munscheid, 1933; Boelitz, 1933), ends with a Q-disc (A, *Q*), though other writers have claimed a Z-disc is final. At each moult the muscles are detached from the tonofibrillae, which are discarded with the cuticula. The epidermis at the end of a muscle is renewed either from persisting cell remnants or from the surrounding epithelium, and, as shown by Munscheid, a new set of tonofibrillae is generated.

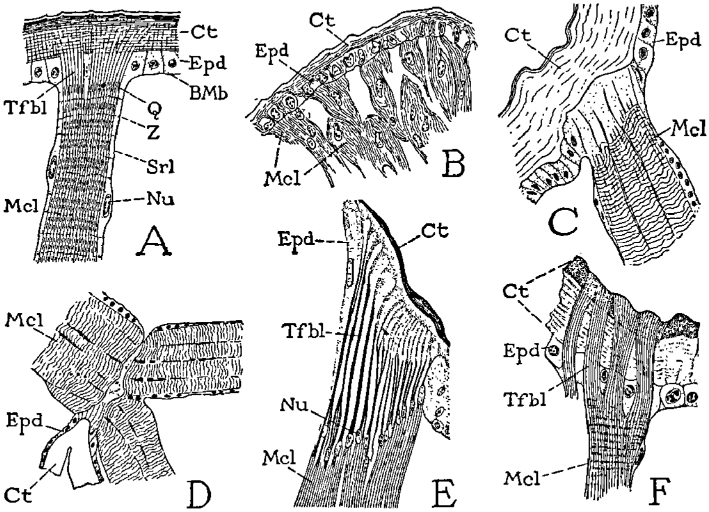

FIG. 33.—Muscle attachments on the body wall. A, diagram showing tonofibrillae (*Tfbl*) traversing the epidermis from muscle to cuticula. B, muscle tissue in embryo of *Periplaneta* attached to epidermis. (*From Henneguy*, 1906.) C, end of larval muscle of *Phlegothontius sexta*. D, muscles of larva of *Balaninus caryae* attached on fold of body wall. E, attachment of labial muscle of a dragonfly larva, tonofibrillae stained dark. (*From Munscheid*, 1933.) F, muscle attachment in adult *Chrysobothrus femorata*. (*From W. L. Tower*, 1906.)

It frequently appears not only that the tonofibrillae traverse the epidermal layer, but that they penetrate a varying distance into the cuticula, even to the outer part of the latter (Fig. 33 F). In this case it must be supposed, as pointed out by Henneguy (1906), that the tonofibrillae, being differentiated at an early stage in the formation of the cuticula, are first connected with the outer layers of the exocuticula, and their proximal extensions are then imbedded in the endocuticula subsequently laid down beneath the former.

6. MOULTING

The nonelastic nature of the arthropod cuticula gives the body wall but little tensibility. When the cuticula is once formed, therefore, the integument can ordinarily increase in extent only in so far as the wrinkles and folds of the cuticula may be straightened out. Before reaching mature size all arthropods cast off the cuticula at intervals and thus release the epidermis from the limitations of its external covering, allowing the epidermal cells to undergo a brief period of development while a new cuticula is being formed.

The shedding of the cuticula is known as *moulting,* or *ecdysis.* Moulting affects the entire body wall and all internal parts that are formed as invaginations of it. The discarded slough constitutes the *exuviae.* (This word in its Latin usage has no singular form; "exuvium," sometimes used, is without grammatical standing.)

The succession of ecdyses divides the life span of the animal into a series of *stages,* while the animal itself appears as a series of *instars.* The number of moults varies with different species or groups of insects and is frequently different with individuals of the same species reared under the same conditions. It is influenced somewhat by temperature, humidity, and the amount of feeding. Yet, notwithstanding all irregularities, the number of moults is surprisingly constant for each species and may be characteristic of families and even orders. Most insects moult from four to six times before they become mature; some normally shed the skin only two or three times or but once, but only abnormal conditions induce a very large series of moultings. The majority of pterygote insects do not moult after reaching the adult form; most of the mayflies, however, undergo a complete ecdysis shortly after becoming winged, and some of the Apterygota moult irregularly throughout life, as do many arthropods other than insects.

The beginning of an instar is not marked by the discarding of the old cuticula, though in "life-history" studies the length of a developmental stage is usually measured from the time the exuviae are cast. Physiologically, however, it should be reckoned from the time the old cuticula is loosened from the epidermis, which more approximately marks the beginning of the short period of development that is to give the increased size and the characteristics of the following instar. The loosened cuticula may not be shed for several days, and in some cases it remains intact as a protective capsule about the insect through a part or all of its subsequent development. When the cuticula begins to separate from the epidermis preparatory to ecdysis, the insect usually ceases to feed and becomes more or less quiescent. Each active stage in the insect's life is thus followed by a sluggish premoulting period.

Ecdysis begins with a splitting of the old cuticula, within which is contained the new instar of the insect. The cleft usually forms over the forward part of the body and over the top of the head, but the details vary much in different insects. The released insect issues from its covering as quickly as possible before the latter becomes dry. At least a part of the cuticular linings of the tracheal tubes and the stomodaeal and proctodaeal parts of the alimentary canal are usually drawn out attached to the slough from the body wall, but it is not clear just how the intima of the minute ramifications of the tracheal system is cast out. The cuticular intima of the stomodaeum of the cockroach, Eidmann (1924) has shown, is broken in the region of the foramen magnum, and only the head part is drawn out with the cuticula of the body wall; the rest, as is also the intima of the proctodaeum, is fragmented and discharged through the alimentary canal.

The cuticula at ecdysis evidently ruptures along predetermined lines of weakness, though the splitting may be expedited by muscular contractions that produce contortionistic movements of the body. When the rupture in the old cuticula is once formed, the insect, in many cases, appears automatically to swell out from the cleft. The enlargement of the body is produced by the taking of air or water into the alimentary canal through the mouth. Generally it is the crop that is distended. The air or liquid must enter the alimentary canal either around the stomodaeal lining being discarded or through a rupture in the latter. Eidmann (1924) points out that the breaking of the old stomodaeal intima in the back part of the head in the cockroach allows air to be swallowed into the lumen of the crop. He fully demonstrates, moreover, that the presence of air in the crop is a necessary condition for successful ecdysis in the cockroach.

The mechanism of moulting is perhaps not yet entirely understood, but the weight of evidence seems to uphold the current view that the separation of the old cuticula from the epidermis is accomplished by a moulting liquid formed by the epidermal cells, or by special *exuvial glands* of the epidermis, that dissolves the inner layers of the endocuticula and thus frees the rest of the cuticula from the cellular matrix. It is true at least that in many insects a copious liquid appears beneath the loosened cuticula just before ecdysis, and that special glands appear in the epidermis and become active at the time of the moult.

Glands of the epidermis supposed to secrete the exuvial liquid have been described in Apterygota, Hemiptera, Neuroptera, Coleoptera, Lepidoptera, and Hymenoptera, in some cases arranged segmentally, in others scattered over the general surface of the body. They are functional during larval stages and may be carried over into the pupa, but they are absent in adults of pterygote insects. In Collembola, which moult during the adult stage, the glands are said to persist throughout life. Some writers, however, particularly von Buddenbrock (1930, 1931) and Hoop (1933), claim that these supposed exuvial glands do not produce the moulting fluid, which, they believe, is secreted by the cells of the general epidermal epithelium. The relative scarcity of the glands in most cases and their absence in certain parts of the body, as in the head, the appendages, and the tracheae, would seem to indicate that they are not adequate to furnish the large amount of subcuticular fluid that appears at ecdysis. Hoop concludes that moulting results from a rhythmically repeated activity of the epidermal cells, causing them to secrete first the exuvial fluid and then the new cuticula.

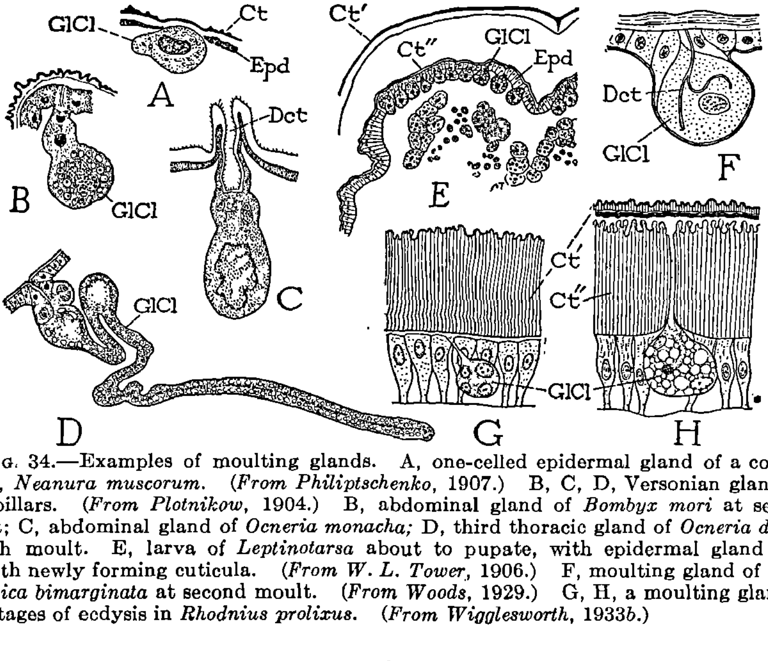

FIG. 34.—Examples of moulting glands. A, one-celled epidermal gland of a collembolan, *Neanura muscorum*. (*From Philiptschenko*, 1907.) B, C, D, Versonian glands of caterpillars. (*From Plotnikow*, 1904.) B, abdominal gland of *Bombyx mori* at second moult; C, abdominal gland of *Ocneria monacha;* D, third thoracic gland of *Ocneria dispar* at fifth moult. E, larva of *Leptinotarsa* about to pupate, with epidermal gland cells beneath newly forming cuticula. (*From W. L. Tower*, 1906.) F, moulting gland of larva of *Altica bimarginata* at second moult. (*From Woods*, 1929.) G, H, a moulting gland at two stages of ecdysis in *Rhodnius prolixus*. (*From Wigglesworth*, 1933*b*.)

Epidermal glands to which the formation of a moulting liquid is ascribed were first described in the silkworm by Verson (1890), and these glands of lepidopterous larvae are known as the Versonian glands. They are three-celled structures of various shapes (Fig. 34 B, C, D) situated along the sides of the body, two on each side of each thoracic segment, and one on each of the first nine abdominal segments. The function of the Versonian glands in connection with moulting has been questioned by von Buddenbrock (1930), who claims that the outlet ducts open at the surface of the old cuticula, and that the secretion, therefore, could not have a dissolving effect on the inner layers of the latter. Furthermore, since he finds that the glands do not reach their maximum secretory activity until ecdysis is completed, he postulates that the large inner cell is an organ of internal secretion that activates the moulting process. The moulting fluid of lepidopterous larvae, von Buddenbrock believes, is formed by the ordinary epidermal cells and not by the glands. Wachter (1930), however, figures the Versonian glands of the silkworm as opening *beneath* the cuticula, and it is perhaps possible that the vacuolization of the active inner cells of these organs observed by von Buddenbrock is a final degenerative process.

The supposed moulting glands of some insects are said to consist each of a single specialized epidermal cell (Fig. 34 A, E). According to Tower (1906), the exuvial glands of the potato beetle (*Leptinotarsa*) are of this kind (E), being formed during embryonic and larval stages by a modification of certain cells of the epidermis; after each ecdysis the gland cells rapidly degenerate and finally disappear. Woods (1929) describes the moulting glands of the alder flea beetle (*Altica*) as comprising each three cells (Fig. 34 F), two of which, however, are small and serve merely as neck or guard cells, while the large third cell (*GlCl*) is the true glandular organ. The gland cell contains a branched canaliculus (*Dct*) through which the exuvial fluid is discharged beneath the old cuticula as the new is being formed. These glands are found to persist from the embryo to the pupal stage, becoming functional at each ecdysis. Wigglesworth (1933*b*) gives a concise description of the development and secretory activity of one-celled epidermal glands in the hemipteron *Rhodnius prolixus*, which, he says, are without doubt responsible for the formation of the moulting fluid. The glands (Fig. 34 G, H, *GlCl*) have distinct ducts that terminate at the surface of the epidermis beneath the cuticula. They are formed anew at each moult from undifferentiated cells in the epidermis and are functional only during moulting; after ecdysis they break down, their nuclei undergoing chromatolysis. New glands do not appear in the adult stage.

Little is known concerning the chemical nature of the moulting fluid. Verson says the moulting fluid of the silkworm contains a solution of oxalic acid salts at the fourth larval moult, and uric acid at the time of the moult to the pupa. It is known, however, that products of the Malpighian tubules discharged from the anus may find their way beneath the loosened cuticula. Wigglesworth (1933*b*) finds that the moulting fluid of *Rhodnius* is a neutral liquid, which appears to be free from chloride and gives no precipitate with silver nitrate and nitric acid but shows protein color reactions.

There is evidence that moulting is induced by a moulting hormone produced within the head, possibly, as suggested by Wigglesworth (1934), secreted by the corpora allata. It has been found that transfusion of blood from an insect about to moult into another not yet in a moulting condition will induce ecdysis in the latter. Wigglesworth has demonstrated that in the case of the hemipteron *Rhodnius prolixus* an insect with its head cut off prior to a certain period before the moulting time, though it may live indefinitely, will not normally moult, but it can be caused to moult by transfusion of blood into its body from an insect after the "critical" period.

Since the somatic muscles must be detached from the cuticula of the body wall at each moult, it is necessary that they become reattached to the newly forming cuticula. The new attachments, Munscheid (1933) has shown, in dragonfly larvae are formed by new tonofibrillae differentiated in the regenerated epidermis at the end of the muscle, not as Tower (1906) supposed by the imbedding of the old tonofibrillae in the new cuticula. If the formation of new muscles takes place at the time of moulting, these muscles may become attached to the cuticula in the usual manner. But in holometabolous insects the imaginal muscles are formed *after* the last larval, or pupal, ecdysis, and Poyarkoff (1914) sees in this condition the reason for a subsequent moult, and hence the establishment of a pupal stage in the life cycle of insects in which the muscles undergo histolysis and regeneration after the end of the larval stage. It is clear that another, preimaginal moult then becomes necessary in order that the new muscles may become affixed to the cuticula. Thus Poyarkoff holds that the pupa is a secondary preimaginal stage interpolated into the life cycle of holometabolous insects and is not to be regarded as representing the last larval or nymphal stage of other insects.

GLOSSARY OF TERMS APPLIED TO THE BODY WALL

Alveolus (*Alv*).—A hair socket.

Apodeme (*Ap*).—Any cuticular ingrowth of the body wall, usually formed in a multicellular matrix, but sometimes in a single cell.

Apophysis.—Any tubercular or elongate process of the body wall, external or internal.

Articulation.—A movable point of contact between two sclerotic parts of the body wall.

Basement Membrane (*BMb*).—The inner noncellular membranous lining of any epithelial layer.

Body Wall. (*BW*).—The integument of the body, formed of the ectoderm, consisting of epidermis, cuticula, and basement membrane.

Chitin.—The chemical substance that forms the groundwork of the cuticula, but not necessarily the principal part of it.

Cuticula (*Ct*).—The outer noncellular layers of the body wall.

Ecdysis.—The shedding of the cuticula. (*Moulting.*)

Ectoderm (*Ecd*).—The outer embryonic layer from which the epidermis of the body wall is derived.

Endocuticula (*Enct*).—The inner softer layer of the cuticula.

Endoskeleton.—Collectively the internal cuticular, or apodemal, ridges and processes of the body wall.

Epicuticula (*Epct*).—The nonchitinous external filmlike covering of the exocuticula. (*Grenzlamelle.*)

Epidermis (*Epd*).—The epithelium of the body wall. (*Hypodermis.*)

Exocuticula (*Exct*).—The outer chitinous layer of the cuticula, containing the sclerotic deposits of the cuticula when the latter are present.

Exoskeleton.—Collectively the external plates of the body wall.

Exuviae.—The cuticular parts discarded at a moult.

Exuvial Glands.—Glands of the epidermis supposed to secrete the exuvial or moulting liquid.

Hypodermis.—See *epidermis.*

Moulting.—The periodic process of loosening and discarding the cuticula, accompanied by the formation of a new cuticula, and often by structural changes in the body wall and other organs.

Moulting Glands.—See *exuvial glands.*

Scale (*Sq*).—A flat unicellular external process of the body wall, probably a modified seta.

Sclerite.—Any of the large or small sclerotized areas of the body wall.

Sclerotization.—The hardening of the body wall by the deposit of sclerotizing substances in the exocuticula.

Sense Organ (*SO*).—Any specialized innervated structure of the body wall receptive to external stimuli; most insect sense organs are innervated setae.

Seta (*Set*).—A hairlike unicellular external process of the body wall or of any derivative of the latter.

Setal Membrane (*smb*).—The membranous floor of the hair socket, or alveolus, supporting the seta.

Spine.—A multicellular external process of the body wall.

Spur.—A movable spine-like process.

Suture.—Any of the external grooves of the body wall forming internal cuticular inflections, or any narrow membranous areas between sclerites.

Tonofibrillae (*Tfbl*).—Cuticular fibrils connecting the muscle fibers with the inner surface of the cuticula.

Tormogen (*Tmg*).—The epidermal cell associated with a seta that forms the setal membrane or socket.

Trichogen (*Trg*).—An epidermal cell that generates a seta.

Trichopore.—The opening in the cuticula beneath a seta, giving passage to the hair-forming process of the trichogen.

CHAPTER IV

BODY REGIONS, SCLERITES, AND SEGMENTATION

An arthropod, in a final anatomical analysis, consists of a cylindrical *trunk* containing the visceral organs and of a series of ventrolateral *limbs.* The part of the trunk traversed by the alimentary canal becomes divided, by the process of metamerism, into a succession of *somites,* or body segments corresponding to the series of limbs. Anterior to the first somite is the preoral *prostomium,* and the segmented body terminates with an endpiece, the *periproct,* or *telson,* which contains the anus (Fig. 24 B). The trunk segments, including the prostomium and the periproct, become segregated in the adult animal into two or three distinct body sections, or *tagmata,* the limits of which vary in the different arthropod groups. Those of the Hexapoda are the *head,* the *thorax,* and the *abdomen.* The limbs are characteristically segmented. Primarily they were all organs of locomotion, but in modern arthropods they are variously modified for many purposes.

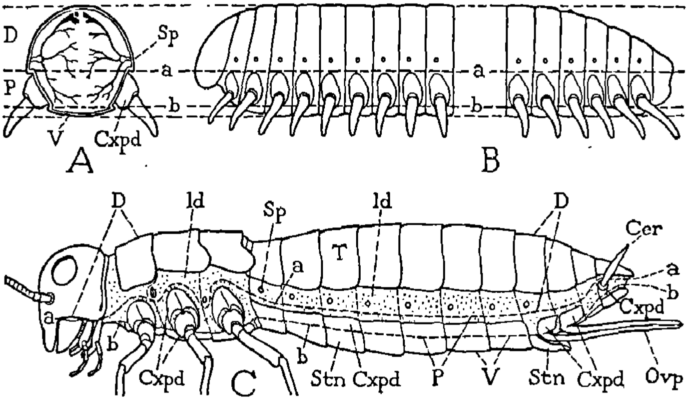

FIG. 35.—Diagrams showing the lengthwise regional divisions of an arthropod as determined by the position of the limb bases. *a-a,* dorso-pleural line; *b-b,* pleuro-ventral line; *Cer,* cercus; *Cxpd,* limb basis, or coxopodite; *D,* dorsum; *ld,* laterodorsum; *Ovp,* ovipositor; *P,* podial, or pleural, region; *Sp,* spiracle; *Stn,* sternum; *T,* tergum; *V,* venter.

The Surface Regions of the Body.—The implantation of the bases of the limbs along the lower lateral parts of the trunk divides the body surface longitudinally into four principal regions, namely, a dorsal region lying above the bases of the limbs, a ventral region lying between the limb bases of opposite sides, and a ventrolateral region on each side containing the limb bases. These regions are respectively the *dorsum* (Fig. 35 A, *D*), the *venter* (*V*), and the *podial,* or *pleural, regions* (*P*).

The lateral line on each side between the limb bases and the dorsum is the *dorso-pleural line* (A, B, *a-a*); that between the limb bases and the venter is the *pleuro-ventral line* (*b-b*). There is reason to believe that the spiracles, or segmental apertures of the tracheal system (*Sp*), are situated in the lower lateral parts of the dorsum just above the limb bases.

Each segment of the trunk presents the same surface regions as does the body as a whole. In studying any individual segment, therefore, we must distinguish a *segmental dorsum*, a *segmental venter*, and *segmental pleural areas*.

Sclerites.—The arthropod integument may remain soft and flexible in all its parts, as in the larvae of many insects, but usually it is hardened, or *sclerotized*, in definite areas owing to the deposit or formation of other substances than chitin in its cuticula. These hardened areas are the *sclerites*.

Sclerites primarily may be intrasegmental and intersegmental and may occupy any of the several regions of an individual segment. A major segmental plate of the dorsum is a *tergum*, or *notum;* a major segmental plate of the venter is a *sternum;* plates of the pleural areas are designated *pleural sclerites*. Subdivisions of a principal segmental plate or the component sclerites of a major area of sclerotization, then, become *tergites*, *sternites*, and *pleurites*, respectively, since the suffix *-ite* has a fractional significance. Unfortunately there is little uniformity in the usage of these terms. Some entomologists use the words "tergum" and "sternum" to designate the dorsal and ventral regions of a segment and distinguish the regional plates as "tergites" and "sternites." This practice, however, leaves us without suitable terms for the minor divisions or component sclerites of major areas of sclerotization. Hence, while the nomenclature given above, and adopted in the present text, may be somewhat arbitrary, it is practicable in application and for the most part can be consistently followed.

Sclerites do not define anatomical areas. The student must recognize this fact as fundamentally important. Much inaccuracy of thought, as well as confusion in descriptive statements, has resulted from identifying areas of sclerotization with the morphological regions they occupy.

The pleural regions of the arthropod body wall are typically membranous, allowing a free movement to the appendages arising from them, as is well illustrated in the centipedes. Pleural sclerites may be developed in the pleural walls about the bases of the limbs; but in most cases it appears that the major pleural sclerotization in each segment is derived from the limb basis, representing either the entire basis of the appendage or the proximal, subcoxal part of the basis.

The spiracles are contained in the lateral parts of the terga if the tergal sclerotizations extend downward on the sides to the lower limits of the dorsum; otherwise they generally lie free in the membranous parts of the dorsum below the edges of the terga, though in some cases they are contained in lateral tergal sclerites, which may be distinguished from the principal dorsal tergites as *paratergites*, or *laterotergites*.

Identification of the Body Regions.—In the study of insects it is of prime importance to be able to determine the limits of the surface regions of the body, and to identify the corresponding parts in the several sections of the trunk. The diagram given at C of Fig. 35 shows a typical form of the body structure in an immature generalized pterygote insect. The spiracles lie between the subcoxal plates of the leg bases on the thorax and in the membranous lower parts of the dorsum on the abdomen. The series of lateroventral appendages begins on the head with the mandibles (or theoretically with the second antennal appendages), followed by the first and second maxillae, which are all articulated to the lower edge of the cranium. On the thorax are the legs, the bases of which (*Cxpd*) form the subcoxal pleural plates, which in the second and third segments are extended upward to the bases of the wings in the adult stage. Appendages are generally absent on the pregenital part of the abdomen in adult pterygote insects, but the eighth and ninth segments, in the female, may bear each a pair of gonopods, which contribute to the formation of the ovipositor (*Ovp*), and the eleventh segment supports the cerci (*Cer*), which are known to be true appendages.

If the dorso-pleural and pleuro-ventral lines are not marked by evident structural features, their positions can be determined by applying the principles already explained. The dorso-pleural line (Fig. 35 C, *a-a*) begins on the head between the bases of the gnathal appendages and the lower edge of the cranium; on the thorax it goes over the subcoxal plates of the leg bases but dips down between them to pass beneath the spiracles, since the latter belong to the dorsum; on the abdomen it follows a straight course through the lateral membrane below the spiracles and finally runs out dorsal to the base of the cercus. The pleuro-ventral line (*b-b*) begins on the head mesad of the bases of the gnathal appendages; on the thorax it separates the leg bases from the primary sternal areas; on the abdomen it traverses the lateral parts of the definitive ventral plates until it comes to the genital segments, where it passes beneath the bases of the gonopods, and then finally ends between the base of the cercus and the paraproct.

The corresponding surface regions of the head, the thorax and the abdomen can now be identified with one another. The dorsum is the entire surface above the dorso-pleural lines, containing the spiracles and the segmental terga of the thorax and abdomen and the principal part of the cranial capsule of the head. The venter is the region below the pleuro-ventral lines, including the under surface of the head between the gnathal appendages, and the true sternal parts of the thorax and abdomen. The pleural region is that containing the bases of the gnathal appendages, the subcoxal plates of the leg bases, the lateral parts of the pregenital ventral plates of the abdomen, the bases of the gonopods, and the base of the cercus. The ventral plates, or definitive sterna, of the pregenital part of the abdomen are thus seen to be really pleurosternal plates, since they cover the areas of the primitive limb bases (*Cxpd*) and those of the primary sterna (*Stn*). In some of the Apterygota the limb bases of the entire abdomen are plates distinct from the primitive sterna and bear appendicular parts of the limbs in the form of styli; in others the styli are borne by lateral parts of the definitive sterna, which are thus seen to be composite pleurosternal (that is, coxosternal) plates.

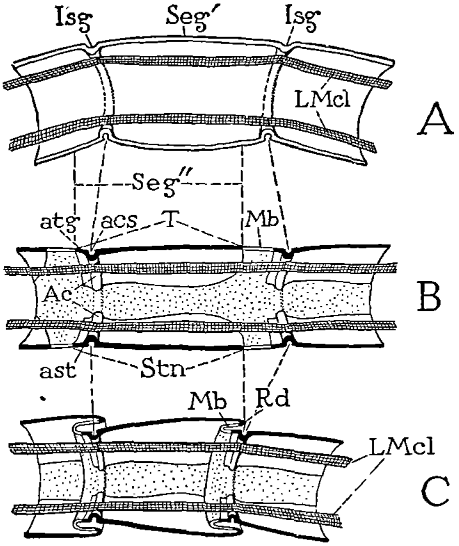

FIG. 36.—Types of body segmentation. A, primary segmentation. B, C, secondary segmentation. *Ac*, antecosta; *acs*, antecostal suture; *ast*, acrosternite; *atg*, acrotergite; *Isg*, intersegmental fold; *LMcl*, longitudinal muscles; *Mb*, conjunctival, secondary intersegmental, membrane; *Rd*, posterior fold of secondary segment; *Seg′*, primary segment (somite); *Seg″*, secondary segment.

Segmentation.—In soft-bodied segmented animals, as in the annelid worms and in the wormlike larvae of certain insects, the segmental regions of the body (Fig. 36 A, *Seg′*) are separated by circular constrictions of the integument (*Isg*). Internally the intersegmental grooves form folds, and on these folds are attached the fibers of the principal longitudinal bands of somatic muscles (*LMcl*). Animals having this type of structure can bend the body freely in any direction, and they can shorten it by a lengthwise contraction of the segments. In the typical adult arthropod structure the segmental areas of the body are hardened by the deposition of sclerotizing substances in the cuticula, forming usually tergal and sternal plates (B, *T*, *Stn*). The areas of sclerotization, however, do not coincide with the areas of the original segments, since they do not cover the posterior parts of the latter and may extend anteriorly a short distance before the intersegmental grooves on which the muscles are attached. The trunk thus becomes differentiated into a series of sclerotic annuli, the *scleromata* (B, *Seg″*), and intervening membranous *conjunctivae* (*Mb*). The former not only are movable upon each other by reason of the flexible conjunctivae but can be partially retracted each into the posterior end of the one preceding by the contraction of the longitudinal muscles attached upon them (C).

On comparing the two kinds of organization described in the preceding paragraph, it becomes evident that we must distinguish two types of segmental structure included under the general term "segmentation." The first type (Fig. 36 A), which occurs in all soft-bodied arthropods and in annelid worms, is the embryonic form of segmentation. It is, therefore, the more primitive one, and we may designate it *primary segmentation.* The other type (B, C) is clearly a secondary differentiation of the body into successive parts by the formation of plates in the integument alternating with nonsclerotized areas. This type of body segmentation we may distinguish as *secondary segmentation.*

Primary Segmentation.—In soft-bodied larval insects, as in the annelid worms, the principal longitudinal muscles are attached typically on the primary intersegmental folds. It is evident, therefore, that there is a close relation between this more primitive form of body segmentation and the segmentation of the muscle-forming parts of the mesoderm into myotomes. We may, then, define as primary segmentation that form of segmentation (Fig. 36 A) in which the functional intersegmental lines of the body wall (*Isg*) coincide with the lines of attachment of the principal longitudinal muscle fibers (*LMcl*). The segments in this type of segmentation (*Seg′*) correspond with the true somites, or embryonic metameres.

Secondary Segmentation.—The development of hardened areas or plates in the body wall, a feature distinguishing most of the arthropods from the annelids, was perhaps in the first place a protective device. But, since in the arthropods the muscles have their attachments on the body wall, an advantage is gained if the muscles are affixed to the integumental plates, because the latter become, in this case, not only protective coverings but elements of the motor mechanism as well. Hence the sclerotized areas of the arthropod body wall, such as the major tergal and sternal plates (Fig. 36 B, *T*, *Stn*), usually include the parts of the primary intersegmental folds (A, *Isg*) on which the longitudinal muscles are attached. In order to retain the power of motion, however, there must be left a flexible nonsclerotized area (B, *Mb*) at the opposite end of the segment. These flexible conjunctival areas of the integument now become the functional intersegmental membranes. For this reason the limits of the definitive segments in arthropods that have body-wall plates (B, *Seg″*) are not coincident with the primary intersegmental folds (A, *Isg*). The areas of flexibility between the sclerotic parts of the segments (B, *Mb*) divide the body in a new way, which is clearly secondary and therefore constitutes a secondary segmentation. In primary segmentation the longitudinal muscles are intrasegmental, inasmuch as they are coextensive with the segmental areas of the body (A); in secondary segmentation the muscles become intersegmental (B). The flexible areas of the body wall in secondary segmentation (B, *Mb*) are usually the posterior parts of the primary segments. This arrangement allows the muscles of each segment to draw the following segment forward (C), and the infolding of the conjunctival membranes gives the characteristic posterior overlapping to the successive segmental plates.

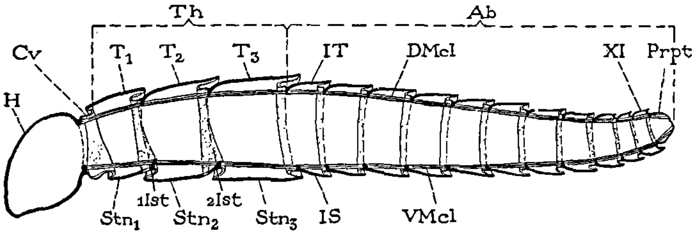

Fig. 37.—The body sections (tagmata) of an insect and their typical segmentation. Note free intersternites (*1Ist*, *2Ist*) in the thorax, and reversed overlapping of the thoracic sterna.

In adult insects, secondary segmentation in its typical form prevails throughout the length of the abdomen, where the limits of the tergal and sternal plates coincide morphologically with each other (Fig. 37, *Ab*).

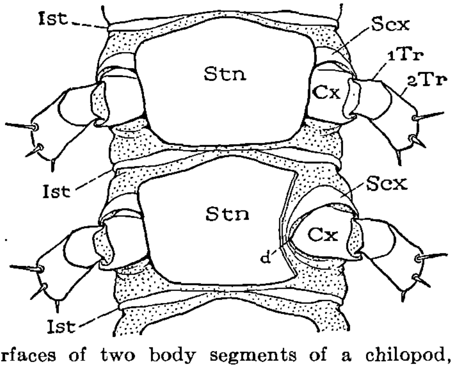

Fig. 38.—Ventral surfaces of two body segments of a chilopod, showing alternating segmental sternal plates (*Stn*) and intersegmental intersternites (*Ist*).

In the thorax (*Th*), however, the terga, though fundamentally secondary segmental plates of the usual form, may undergo modifications that alter this structure, and the thoracic sternal sclerotizations are characteristically of a different type of structure, which is best illustrated in the Chilopoda.

The secondary segmentation of the chilopods has produced typical secondary segmental plates only in the dorsum. In most of the centipedes, excepting *Scutigera*, the ventral sclerotizations throughout the length of the body have taken the form of independent segmental and intersegmental sclerites, the former occupying the primary segmental regions, the latter being confined to the intersegmental folds (Fig. 38, *Stn*, *Ist*). In some families the ventral longitudinal muscles retain their attachments on the intersegmental plates, in others they have migrated to the segmental plates, or to supporting arms or ligaments of the latter. This same type of sclerotization occurs in the venter of the thorax of many insects, in which there is a small intersternite (Fig. 37, *1Ist*, *2Ist*) situated posterior to the principal sternal plate of the prothorax and the mesothorax (Stn_1, Stn_2).

Structure of a Typical Secondary Segment.—A typical segment of an adult arthropod is in general one of the secondary annular sections of the body defined by the lengthwise extent of its dorsal and ventral plates (Fig. 36 C). A considerable part of the true segmental area, however, is formed by the posterior conjunctival membrane (B, C, *Mb*), which is usually infolded and more or less concealed within the posterior ends of the tergal and sternal plates (C). The wall of each segment, as we have seen, contains typically a dorsal sclerotic area, or tergum (B, *T*), and a ventral sclerotic area, or sternum (*Stn*), while the lateral or pleural walls may contain each one or more pleural sclerites.

The Tergum.—In its typical form the back plate of a secondary segment includes the sclerotization of the dorsum of the primary intersegmental area preceding (Fig. 36 B, *T*). The primitive intersegmental fold (A, *Isg*), therefore, becomes a submarginal ridge near the anterior edge of the inner surface of the tergum (B, *Ac*). This ridge is the *antecosta* of the tergum. The corresponding external groove, or transverse line of inflection forming the antecosta, is the *antecostal suture* (*acs*). The narrow precostal lip of the tergum is the *acrotergite* (*atg*). The postcostal tergal sclerotization usually forms a simple plate, which is subject to modifications in various ways, especially in the wing-bearing segments of pterygote insects, but it may be broken up into smaller sclerites, as in many holometabolous larvae. The dorsal longitudinal muscles, primarily attached on the intersegmental folds (A), usually retain their attachments on the antecostae in the secondary segments (B, C), though some or all of their fibers may migrate to the precostal or postcostal areas of the tergum.

Tergal plates are present in the adult stages of nearly all arthropods. Their principal variation in size with relation to the shape of the segment is in a transverse direction. They may be limited to the median part of the back, or their lateral areas may be extended downward a varying distance in the lateral walls of the dorsum, and the lateral margins may project as free folds either horizontally extended or ventrally deflected over the sides of the segment, sometimes concealing the bases of the legs. Frequently laterodorsal sclerites are distinct from a principal median tergite.

In the thoracic segments of winged insects the typical structure of the dorsal plates is generally obscured by a modification in the intersegmental sclerotization, correlated with the development of the wings as efficient organs of flight. The intertergal parts of the conjunctivae between the mesothorax and metathorax and between the metathorax and first abdominal segment are almost obliterated by an anterior extension of the acrotergites of the metathoracic and first abdominal terga (Fig. 39 B). Furthermore a secondary membranous suture may appear in the tergal region just behind the antecosta (*Ac*) of each of these segments. There is thus formed posterior to each wing-bearing tergal plate (T_2, T_3) a *postnotal plate* (PN_2, PN_3) bearing the intersegmental attachments of the dorsal muscles (*DMcl*). Since the dorsal muscles are greatly enlarged in the thorax, the antecostae develop large lobes, the *phragmata* (*Ph*), for their accommodation. The postnotal plates are usually regarded as belonging to the segment preceding in each case, but it is clear that they are intersegmental structures analogous to the intersternites of the venter between the prothorax and mesothorax and between the mesothorax and metathorax (A, *Ist*), which are usually more closely associated with the preceding sterna (Fig. 37, *1Ist*, *2Ist*).

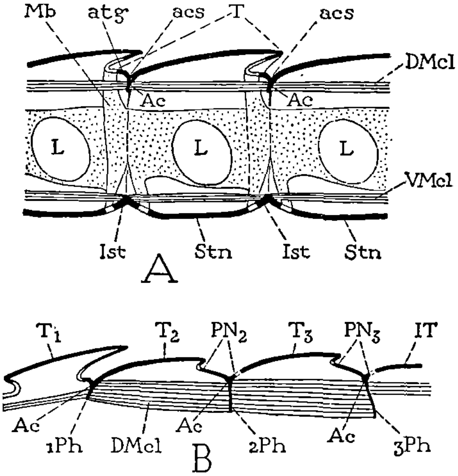

Fig. 39.—Diagrams showing intersegmental relations of the skeletal plates in secondary segmentation. A, generalized condition. B, specialized condition in the dorsum of the thorax of winged insects, in which the enlarged acrotergites (A, *atg*) become the postnotal plates (B, *PN*) of the second and third segments.

The Sternum.—Sternal plates are not so constant a feature of the arthropod skeleton as are the tergal plates. They may be present or absent within the same major group, and, where present, they are often highly variable in both shape and size between closely related forms, and even in different body regions of the same species.

The ventral plate of a segment usually has the same structure as the tergum (Fig. 36 B, *Stn*), as in the abdomen of insects (Fig. 37, *Ab*), where the sternum generally is an inverted replica of the tergum. In this case each sternum bears anteriorly a submarginal antecosta on its inner surface (Fig. 36 B, *Ac*), on which the ventral longitudinal muscles are usually attached, and presents a narrow precostal lip, or *acrosternite* (*ast*), corresponding to the acrotergite of the dorsal plate. In the thorax of many insects, however, the intersegmental sclerotizations of the venter form small independent plates, or intersternites (Figs. 37, 39 A, *Ist*), as they do in the whole length of the body in most of the chilopods (Fig. 38). The intersternites of the thorax of insects, which may occur between the prothorax and mesothorax and between the latter and the metathorax, are known as *spinasterna* because each usually bears an internal spine-like process giving attachment to some of the ventral muscles. The spinasterna are often united with the segmental sterna preceding them, but never with those following. A definitive thoracic sternum, therefore, never has a true antecosta. Most of the ventral muscles of the thorax are attached (probably secondarily) on apodemal processes of the segmental plates; a few fibers, however, usually retain the primitive connections with the median processes, or *spinae*, of the intersegmental spinasterna (Figs. 87, 103 A).

The definitive sterna of insects are usually composite plates, each comprising a median region representing the area of the primitive segmental sternum and lateral parts derived from the limb bases. In the thorax the adjoined lateral elements are the ventral arcs of the subcoxal parts of the leg bases; in the abdomen the sternal plates appear to contain, in most cases, the entire basal parts of the otherwise suppressed limbs. The term "sternum" is usually applied to the principal ventral plate of a segment regardless of the real or theoretical composition of the latter.

The Pleural Sclerites.—The podial areas of arthropod body segments, that is, the so-called pleural areas in which the limbs are implanted, are usually membranous and seldom contain any extensive sclerotization that can be attributed to the wall of the body itself. The proximal, or subcoxal, parts of the limb bases, however, are often expanded in the pleural wall and separated by an articular ring from the coxal parts of the limbs. The coxae thus become the functional bases of the appendages, and the subcoxae serve as supports for the latter in the podial areas of the body wall. Wherever sclerotizations occur in the podial areas, therefore, they appear generally to be derived from the bases of the limbs, though it is probable that certain small sclerites may belong also to the region of the peripodial membranes. All sclerotizations of the podial areas of the body segments, however, are in general termed *pleurites.* In the thorax of pterygote insects the subcoxal sclerotization above, before, and behind the coxa is known as the *pleuron.*

Subcoxal pleurites occur in most of the body segments of the Chilopoda (Fig. 52 A, *Scx*), where they have the form of small sclerites of various shapes more or less closely associated with the bases of the coxae. Similar sclerites are present in the pleural areas of the thorax in apterygote Hexapoda, but here they frequently appear as two crescentic arches over the bases of the coxae (Fig. 89). In adult pterygote insects the thoracic pleural plates are much enlarged, especially in the wing-bearing segments, where they form supports for the wings as well as giving articulation to the coxae of the legs. In the decapod Crustacea the inner walls of the gill chambers are evidently of subcoxal origin, but in most of the Crustacea and in the Arachnida there is little evidence of the presence of pleurites derived from the limb bases.

In the abdominal segments of insects the limb bases are sometimes represented by distinct plates occupying the pleural areas between the terga and sterna, as in certain Thysanura (Fig. 138 A, *Cxpd*) and in many larval forms (Fig. 150 A, *Cxpd*); in the genital segments they are retained as the basal plates of the gonopods (Fig. 35 C). In general, however, the abdominal pleurites appear to be fused with the primitive sterna in continuous plates, which are the definitive sterna.

Intersegmental Relations.—The primary intersegmental grooves, we have seen, are the functional segmental limits only in soft-bodied arthropods or in forms with but a weak or partial sclerotization of the integument (Fig. 36 A). In all arthropods with well-developed body-wall plates, the definitive segmentation is a secondary one; but the limits of the secondary segments differ according to the relations of the sclerotization in the primary intersegmental regions to that of the segmental regions before and behind them.

In the insect abdomen, where both the dorsal and the ventral primary intersegmental areas of sclerotization are continuous with the segmental plates following, a typical secondary segmentation prevails (Fig. 37, *Ab*), and the functional intersegmental rings are the membranous posterior parts of the primary segments (Fig. 40 A, *Mb*). The primitive intersegmental fold (*Isg*) forms an antecosta (*Ac*) on both the tergum and the sternum, and the precostal lip forms an acrotergite (*atg*) of the dorsal plate and an acrosternite (*ast*) of the ventral plate. Wherever there is a difference between the dorsum and the venter in the sclerotization of the intersegmental region, however, the intersegmental relations are less simple. If the dorsal plates retain the form typical of secondary segmentation, while the ventral sclerotization takes the form of independent sternites and intersternites, as often occurs in the thorax, the ventral half of each intersegmental membrane will embrace the intersternite (B, *Ist*) and will include a part of the two adjoining primary segmental regions. Again, if the intersternite is united with the segmental sternum preceding (C), while the intertergal sclerotization remains continuous with the tergum following, the conjunctival membrane (*Mb*) will cross obliquely on the side of the body from the posterior part of the anterior segment to the anterior part of the posterior segment, and the ventral postcostal lip becomes a *poststernite* (*pst*) of the anterior segment. Finally, if both the dorsal and ventral intersegmental sclerotizations are united or closely associated with the segmental plates preceding, the functional intersegmental membrane becomes the anterior part of the posterior segment (D, *Mb′*), and the postcostal lip forms a *posttergite* (*ptg*) dorsally and a poststernite (*pst*) ventrally.

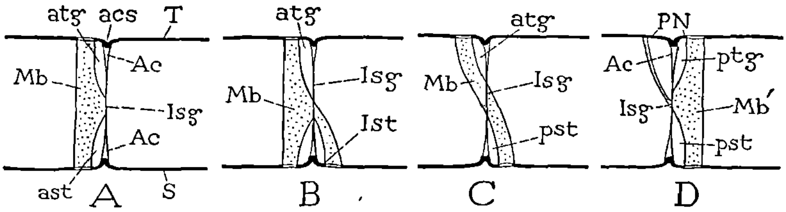

FIG. 40.—Four types of intersegmental relations, according to the position of the secondary intersegmental membrane, or conjunctiva (*Mb*, *Mb′*). *Ac*, antecosta; *acs*, antecosta suture; *ast*, acrosternite; *Isg*, primary intersegmental line; *pst*, poststernite; *ptg*, posttergite

Tagmosis.—In all adult arthropods some of the segments are more or less united into groups forming distinct trunk sections, or *tagmata*. The number of tagmata, and the number of segments in each tagma vary in different arthropods. The most constant tagmosis of the trunk is that which differentiates, in the embryo, the protocephalic head region from the primitive body (Fig. 23 A). The definitive head of most mandibulate arthropods, however, contains a second tagma, which is that of the gnathal segments (C, *Gn*). In the Hexapoda a third embryonic tagma (*Th*) becomes the thorax, or second tagma of the adult, which is usually composed of three segments, though in most Hymenoptera it contains four. A fourth embryonic tagma (*Ab*) becomes the adult hexapod abdomen, which has at most 12 segments, including the periproct. Tagmosis is more variable in the Crustacea; in the Chilopoda and Diplopoda it results only in the formation of a head, including the gnathal segments, and a body; in the Chelicerata again it is variable, but the principal division of the trunk is into a "cephalothorax" and an "abdomen."

GLOSSARY OF GENERAL TERMS APPLIED TO THE BODY SEGMENTS AND THE SKELETAL PLATES

Acrosternite (*ast*).—The narrow marginal flange anterior to the antecosta of a definitive sternal plate that includes the preceding primary intersegmental sclerotization; characteristic of abdominal sterna of insects, but absent on thoracic sterna.

Acrotergite (*atg*).—The anterior precostal part of the tergal plate of a secondary segment; usually a narrow flange, but sometimes greatly enlarged, and frequently reduced or obliterated.

Antecosta (*Ac*).—The anterior submarginal or marginal ridge on the inner surface of a tergal or sternal plate corresponding to the primary intersegmental fold, on which typically the longitudinal muscles are attached.

Antecostal Suture (*acs*).—The external groove of the antecosta.

Conjunctiva (*Mb*).—See *intersegmental membrane*. (*Gelenkhaut.*)

Dorso-pleural Line (*a-a*).—The line of separation between the dorsum and the pleural region of the body, often marked by a fold or groove.

Dorsum (*D*).—The entire back of an animal above the pleural regions; or specifically, when qualified by the designation of a segment, the back region of a segment.

Intersegmental Membrane (*Mb*).—The flexible conjunctiva between two secondary segments; usually the nonsclerotized posterior part of a primary segment, but variable as shown in Fig. 40.

Intersternite (*Ist*).—An intersegmental sclerotization of the venter, such as the thoracic spinasterna.

Laterotergite (*ltg*).—A lateral sclerotization of the dorsum distinct from a principal median tergite. (*Paratergite.*)

Limb Basis (*Cxpd*).—The primitive basal part of a limb, implanted in the pleural area of the body wall, bearing the telopodite. (*Coxopodite.*)

Metamere.—An embryonic somite, or primary body segment.

Myotome.—A division of the body muscles corresponding to a metamere.

Notum.—See *tergum.*

Paratergite.—See *laterotergite.*

Pleural Region (*P*).—The podial region, or ventrolateral parts of the body on which the limbs are implanted, metamerically divided into segmental *pleural areas.*

Pleurite (*pl*).—Any minor sclerite of the pleural area of a segment, or one of the component sclerites of a pleuron.

Pleuron (*Pl*).—The sclerotization of the pleural area of a segment, apparently derived from the proximal part of the limb basis, and usually subdivided into pleurites.

Pleuro-ventral Line (*b-b*).—The line of separation between the pleural region and the venter; lying mesad of the limb bases, but obscured when the latter are fused with the sterna.

Postnotum (*PN*).—An intersegmental plate of the dorsum of the thorax associated with the tergum of the preceding segment, bearing the antecosta and usually a pair of phragmatal lobes. (*Phragmanótum.*)

Poststernite (*pst*).—The postcostal lip of a definitive sternal plate that includes the intersegmental sclerotization following.

Posttergite (*ptg*).—The narrow postcostal lip of a postnotal thoracic plate.

Primary Segmentation.—A segmental division of the body corresponding to the embryonic metamerism.

Sclerite.—Any sclerotized area of the body wall, or of internal parts derived from the body wall.

Scleroma.—The sclerotic annulus of a body segment in distinction to the membranous conjunctiva.

Secondary Segmentation.—Any form of body segmentation that does not strictly conform with the embryonic metamerism; the usual segmentation of arthropods having a well-developed exoskeleton, in which the membranous intersegmental rings are the posterior parts of the primary segments.

Segment.—A body segment is any of the successive annular subdivisions of the arthropod trunk, whether corresponding to the embryonic metameres or produced secondarily.

Somite.—A primitive, or primary, body segment corresponding to an embryonic metamere or myotome.

Sternite.—A subdivision of a sternal plate, or any one of the sclerotic components of a definitive sternum.

Sternum.—Either the primary ventral plate (*Stn*) of a body segment or a composite definitive sternum (*S*).

Subcoxa (*Scx*).—The proximal part of the limb basis when differentiated from the coxa; usually incorporated into the pleural wall of the body segment.

Tagma.—A group of successive segments forming a distinct section of the trunk.

Tergite.—A subdivision of a definitive tergum, or any one of several sclerites in the dorsum of a body segment.

Tergum (*T*).—The dorsal sclerotization of a body segment; called also *notum*, especially in the thorax.

Trunk.—The entire series of body segments of an arthropod, including the cephalic, thoracic, and abdominal sections.

Venter (*V*).—The entire under surface of the animal between the two series of limb bases, or, when qualified by the designation of a segment, the corresponding surface of a single body segment.

CHAPTER V

THE SEGMENTAL APPENDAGES OF ARTHROPODS

The Arthropoda are well named from the fact that they have jointed segmental appendages (from ἄρθρον, a "joint," and πούς, ποδός, a "foot" or "leg"), for no other feature of their organization is so characteristic of them. While segmented limbs are possessed by other groups of animals, they have nowhere attained such a diversity of form in adaptation to so wide a range of uses as have the appendages of the arthropods. Primarily the segmental appendages are organs of locomotion; but in the evolution of the Arthropoda they have developed into a great assortment of tools. The effective use of tools involves a high degree of efficiency in the muscular and nervous systems and the possession of varied and discriminating organs of perception. As a consequence, the arthropods are endowed with the highest mechanical, nervous, and sensory organization attained within the Invertebrata.

General Structure of the Appendages.—The segmental appendages of arthropods are hollow outgrowths of the lateral or lateroventral regions of the body wall (Fig. 41). The early, perhaps wormlike, ancestors of the Arthropoda probably had a pair of appendages on each of the true somites between the prostomium and the periproct and may thus have resembled the onychophorans in general appearance. The appendages of modern arthropods are characteristically segmented, but the embryonic rudiments of the organs are simple lobes. We must assume, therefore, that the jointing of the limb is a secondary development, and that the primitive appendage was an undivided lobe or tubular outgrowth of the body wall, serving as an aid in locomotion.

The Basal Mechanism of a Primitive Appendage.—To be functionally effective, an organ of locomotion must be movable. There can be little question that the primitive arthropod appendages, whether used for progression on solid surfaces or in water, turned forward and rearward in the manner of an annelid parapodium, each on an approximately vertical axis of flexibility at its base (Fig. 41, *a-b*). A comparative study of the basal limb muscles in Annelida, Onychophora, and Arthropoda suggests that the simplest effective musculature of a primitive appendage comprises *dorsal promotor* and *remotor muscles* (*I*, *J*) arising on the dorsum of the body segment, and *ventral promotors* and *remotors* (*K*, *L*) arising on the venter. An actual musculature of this pattern is present in connection with all the locomotor appendages of Onychophora (Fig. 42, F), and with the simpler anterior parapodia of some Annelida (D), and occurs in a somewhat modified form in the entire series of annelid parapodia (E), while the basal limb musculature of arthropod appendages can in most cases be analyzed into the same functional groups of muscles. The relation of the limb muscles to the muscles of the body wall, however, differs in these three groups of animals, so that it is evident there is no real homology involved in the similarity of the limb muscles; each case probably represents an independent structural adaptation to a common function. We may not suppose, therefore, that the arthropod appendages have necessarily had a common origin with the parapodia of Annelida or with the tubular legs of Onychophora.

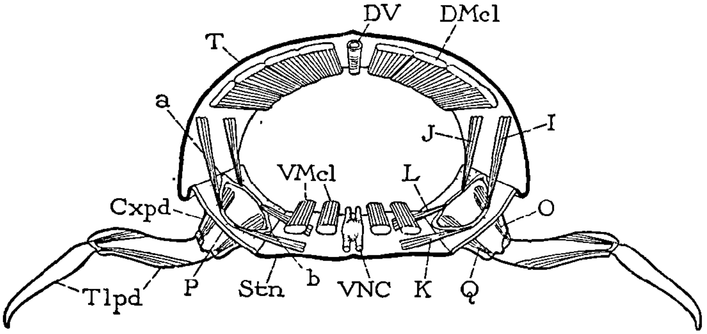

Fig. 41.—Diagrammatic cross section of an arthropod segment showing the relation of the legs and the basal leg muscles to the areas of the body wall. *a-b*, axis of movement of leg base; *Cxpd*, coxopodite; *DMcl*, dorsal longitudinal muscles; *DV*, dorsal blood vessel; *I*, *J*, dorsal promotor and remotor muscles of leg; *K*, *L*, ventral promotor and remotor muscles of leg; *O*, levator muscle of telopodite; *P*, podial, or pleural, area of body wall; *Q*, depressor of telopodite; *Stn*, sternum; *Tlpd*, telopodite; *VMcl*, ventral longitudinal muscles; *VNC*, ventral nerve cord.

Segmentation of the Appendages.—The limbs of the earliest known fossil arthropods are fully segmented; the legs of the Cambrian trilobites and crustaceans have all the segments that occur in modern arthropods. Embryology throws little light on the evolution of the arthropod appendages, and we can deduce a working hypothesis as to the homologies of the limb segments only from a comparative study of the structure of the segments in the several arthropod groups, and from a theoretical consideration of the mechanical demands in an organ of locomotion.

An appendage having the form of a hollow outgrowth of the body wall and containing an extension of the body muscles is capable of segmentation in the same way as the cylindrical body itself, namely, by the attachment of its muscles to successive parts of its wall. An incipient limb segmentation is to be seen in the onychophoran leg (Fig. 42 H), in the distal part of which are several distinct annuli separated by infoldings of the integument, on some of which muscles are attached (*15, 16, 19*), but there is nothing here closely resembling the definite relation between muscles and segments so characteristic of an arthropod limb.

A clearly defined limb segment, definitely correlated with muscle attachments, is termed a *podomere*, or *podite*. In the typical arthropods the limb segmentation is so thoroughly standardized that the number of segments seldom if ever exceeds eight; but with specialization there is often a union of two consecutive primitive segments, accompanied by the loss of the muscles of the more distal segment, or segments may be reduced or obliterated. On the other hand, a segment may become secondarily divided into two or more nonmusculated *subsegments*. A true limb segment, or podite, therefore, must be defined as *any part of an appendage independently movable in some member of the Arthropoda by muscles inserted on its base*. The areas of flection between the podites are the *joints* of the limb; particular sclerotic points of contact in the joints are *articulations*.

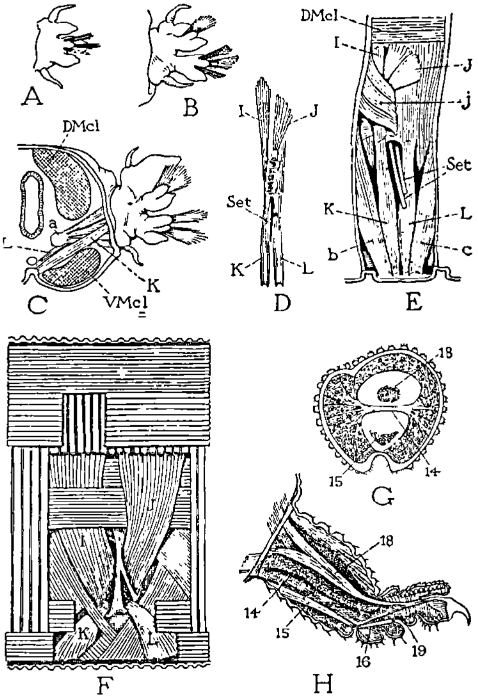

FIG. 42.—Appendages of Annelida and Onychophora. A, B, C, parapodia of *Nereis virens*. D, muscles of an anterior parapodium. E, lateral muscles of a typical segment of *Nereis*, showing muscles (*I*, *J*, *j*, *K*, *L*) attached to base of parapodium. F, musculature of right half of a body "segment" of *Peripatoides*, showing four muscles (*I*, *J*, *K*, *L*) entering base of leg. G, cross section of leg of *Peripatoides*. H, longitudinal section of same.

The names used generally in zoology to designate the arthropod leg segments, beginning at the base of the appendage, are as follows: *coxopodite, basipodite, ischiopodite, meropodite, carpopodite, propodite, dactylopodite.* In entomology the following terms are more commonly used for the same segments: *coxa, first trochanter, second trochanter* (or *prefemur*), *femur, tibia, tarsus, pretarsus.* In some of the Chelicerata an extra segment, the *patella,* is interpolated between the femur (meropodite) and the tibia (carpopodite). Strictly speaking, the term "coxa" refers to a distal subdivision of the coxopodite when the latter is divided into a subcoxa and a coxa.

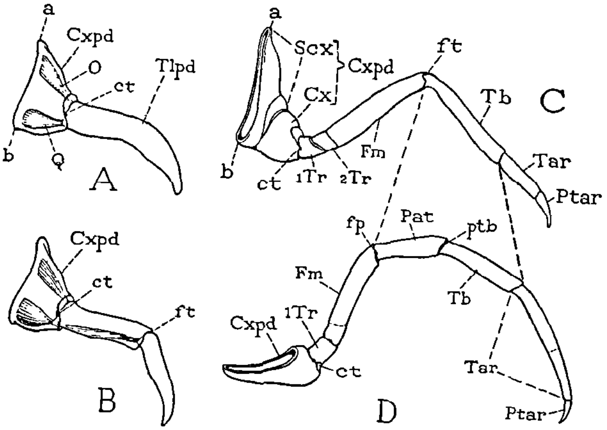

Fig. 43.—Diagrams of the evolution of the segmentation of an arthropod leg. A, theoretically primitive limb divided into coxopodite (*Cxpd*) and telopodite (*Tlpd*). B, the telopodite segmented at the femoro-tibial joint (*ft*). C, a primitive insect leg, with coxopodite divided into subcoxa (*Scx*) and coxa (*Cx*), the telopodite six-segmented. D, a typical arachnid limb with a patella (*Pat*) interpolated between femur and tibia.

In an elongate appendage turning forward and rearward on its base, the first demand for a point of movement in the shaft would establish a joint near the base allowing movement of the distal part in a vertical plane. Thus we may assume that the primitive arthropod limb first became divided into a *basis,* which is the coxopodite (Fig. 43 A, *Cxpd*), and a distal arm, or *telopodite* (*Tlpd*).

Further evolution toward mechanical efficiency in an elongate appendage evidently would result in the production of a "knee" joint in the telopodite, giving the part beyond the knee a principal downward flection in a vertical plane (Fig. 43 B). Hence there have come to be two primary points of bending in the limb, which persist in all typical arthropod appendages as the *coxo-trochanteral joint* (*ct*), and the *femoro-tibial joint* (*ft*). By a further segmentation, the proximal piece of the telopodite may have one or two trochanters (C, 1*Tr*, 2*Tr*) cut off from its base, leaving the rest as the femur (*Fm*), while the part of the limb distal to the knee becomes divided into a tibia (*Tb*), a tarsus (*Tar*), and a pretarsus (*Ptar*). This type of limb segmentation is characteristic of all the mandibulate arthropods. In many of the Chelicerata there is in some of the appendages an additional segment, the patella (D, *Pat*), interpolated between the femur and the tibia. The patella and the tibia together in this type of limb segmentation apparently represent the tibia alone of the Mandibulata (C, *Tb*). In the Arachnida, Pycnogonida, Chilopoda, and Insecta, the tarsus is commonly divided into movable subsegments; but since these parts are not provided with muscles, they are evidently secondary and are not to be regarded as true podites; they are *tarsites*, or *tarsomeres*.

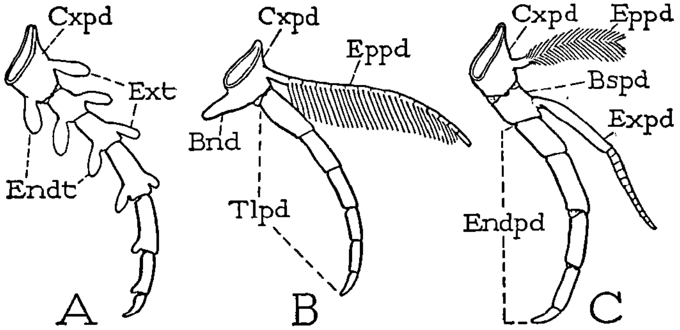

FIG. 44.—Comparative structure of a theoretically generalized arthropod limb (A), a trilobite leg (B), and a crustacean leg (C). *Bnd*, coxal endite; *Bspd*, basipodite; *Cxpd*, coxopodite; *Endpd*, endopodite; *Endt*, endites; *Eppd*, epipodite; *Expd*, exopodite; *Ext*, exites; *Tlpd*, telopodite.

Lobes of the Appendages.—Along the outer and inner margins of an appendage there may be developed movable lobes often individually provided with muscles arising in the shaft of the limb. An outer lobe is known as an *exite* (Fig. 44 A, *Ext*), an inner lobe as an *endite* (*Endt*). Usually there is not more than one lobe in each position on a single segment, though sometimes two occur.

The Limb Basis, or Coxopodite.—The basal segment of a generalized arthropod appendage is implanted in the membranous pleural wall of the body segment and may be articulated to the tergum or the sternum or to both. Upon its proximal margin are inserted the muscles that move the appendage as a whole, which take their origins on the dorsal and ventral walls of the body segment. A limb basis, or coxopodite, having this relatively primitive structure appears to be preserved in the limbs of the Trilobita, Xiphosura, many of the Arachnida, and most of the Crustacea.

In some cases the limb basis loses its mobility and becomes merely a support for the rest of the appendage by assuming the form of a lobe or plate of the body wall. When this occurs, the basal muscles are reduced or suppressed, and the muscles of the first trochanter, arising in the basis, become the motors of the free part of the limb, which is the telopodite.

In most cases, however, when the basis forms an immovable or but slightly movable support for the rest of the limb, it becomes subdivided into a proximal stationary part, or *subcoxa* (Fig. 43 C, *Scx*), and a distal freely movable part, or *coxa* (*Cx*). The subcoxa is usually incorporated into the pleural wall of the body segment, where it forms a group of sclerites or a plate known as the *pleuron*. The coxa now becomes the functional basis of the appendage.

The subcoxae appear in a relatively primitive condition in some of the Chilopoda, where their sclerotized parts may form complete rings about the bases of the coxae, though more commonly each is broken up into several small sclerites lying in the pleural wall of the body segment close to the coxa (Fig. 52 A, *Scx*). In the insects the pleural plates of the thoracic segments appear also to be derived from the subcoxal parts of the leg bases. Those of the Apterygota (Fig. 89) consist of small sclerites as in the Chilopoda, but in adult Pterygota the pleura are extensive plates in the lateral walls of the thoracic segments, which, in the second and third segments, are extended upward to form supports for the wing bases (Fig. 91 B). In the decapod Crustaceans subcoxal extensions from the bases of the pereiopods on each side of the body are united in a large pleural plate forming the inner wall of the branchial chamber. The ventral arcs of the subcoxae are generally reduced to narrow folds between the coxae and the sterna, or they unite with the primary sterna to become laterosternal elements of the definitive sternal plates.

The coxa and subcoxa of an appendage never have in all respects the structural relations of true primary segments to each other. The body muscles of the limb are usually inserted on both the subcoxa and the coxa or are taken over entirely by the coxa. The coxa, however, generally is provided also with muscles arising in the subcoxa. The subcoxo-coxal articulation is variable, though it appears that the primary hinge of the coxa on the subcoxa was approximately in a vertical plane with dorsal and ventral points of articulation.

Exite and endite lobes are of frequent occurrence on the appendage basis. In the Trilobita and some of the phyllopod Crustacea basendites are present on the majority of the appendages (Figs. 45, 50 B, *Bnd*), forming a double row of lobes converging along the midventral line of the body. Basendites of the gnathal appendages function as feeding accessories. The maxillae of crustaceans and insects usually have each a pair of basendites, known as the lacinia and galena. The diplopods have a freely movable mandibular endite, but in the chilopods, crustaceans, and insects the mandibular endite is consolidated with the basis of the appendage to form a solid jawlike organ. Baseendites are of less frequent occurrence in the Chelicerata, but they are often present on the pedipalps and other appendages associated with the mouth.

An exite, or outer lobe, of the coxopodite is commonly termed an *epipodite* and is often a highly developed or specially modified structure (Fig. 44 B, C, *Eppd*). The epipodite is an important feature of all the legs of Trilobita and of some of the limbs of many Crustacea, since in both these groups it may be converted into a branchial organ (Fig. 45). Gill-bearing epipodites are present also on the abdominal appendages of Xiphosura. The epipodite of Crustacea, however, is often a simple lobe or is sometimes represented by a pair of lobes (Fig. 50 A, *Eppds*) and may be absent. Epipodites seldom occur on the appendages of terrestrial arthropods, though the appendicular processes known as styli, present on the coxae of the second and third legs of the apterygote insect *Machilis* (Fig. 148 A, *Sty*), are of the nature of epipodites.

The Telopodite.—The distal shaft of the limb, or telopodite, is highly variable in size and segmentation since it takes on numerous forms in adaptation to different functions, such as walking, running, leaping, climbing, grasping, or swimming, and it may be rudimentary or suppressed; in the gnathal appendages it becomes the "palpus." The identity of the telopodite, however, is seldom to be mistaken. Except in rudimentary appendages and in some crustacean limbs in which the basipodite is united with the coxopodite, the telopodite almost universally articulates with the coxopodite on a horizontal hinge with anterior and posterior articular points. Allowance must be made, of course, for an axial revolution of the limb, which may actually lie in an oblique or even a horizontal plane. The basal muscles of the telopodite are the levator and depressor of the first trochanter (basipodite), which arise in the coxopodite (Fig. 43 A, *O*, *Q*), except that in insects the levator of the legs usually has one or more branches arising in the body segment. Elevation and depression of all the appendages in an entire lateral series thus take place uniformly along the line of the coxo-trochanteral joints, except, as in some Crustacea, where the first trochanters are united with the coxae.

Endite and exite lobes are of frequent occurrence on the segments of the telopodite in the Crustacea; and in this group an exite of the basipodite (first trochanter) is of particular importance, since it is often highly developed as an accessory outer branch of the limb called the *exopodite* (Figs. 44 C, 50 A, *Expd*). The crustacean limb thus acquires its characteristic "biramous" structure, the shaft of the telopodite beyond the basipodite being known as the *endopodite* (*Endpd*). It should be observed that a branched limb of this type occurs only in the Crustacea, and that there is no sound evidence of its being the primitive limb form of arthropods generally.

The maximum number of segments in the telopodite appears to be six in Mandibulata and seven in Chelicerata, with six as the usual number in Trilobita. The number may be variously reduced, however, either by a union of successive segments or by suppression of certain segments. The second trochanter (ischiopodite) is perhaps the most variable segment. In some forms it is not differentiated from the femur (meropodite) in all the appendages; in the legs of most Hexapoda it is united with the first trochanter (basipodite) in a single trochanteral segment (Fig. 53 A, *Tr*). The tarsus is variable in its subsegmentation. In Chelicerata and Chilopoda it is frequently divided into two subsegments, a *basitarsus* and a *telotarsus* (Figs. 48 D, 49, 52), and sometimes it is further broken up into a large number of small articles (Fig. 47 A). Among the Hexapoda the tarsus may be a simple segment, or it may be divided into from two to a maximum of five subsegments. The pretarsus (dactylopodite) is typically a simple clawlike segment; but it may be armed with a pair of lateral claws, as in some Arachnida, Pycnogonida, and most insects, in which case the median claw is usually reduced or obliterated, and the pretarsus becomes secondarily a two-clawed structure.

The joints of the telopodite usually have a characteristic movement. The trochanteral and trochantero-femoral joints commonly have a movement of production and reduction; the femoro-tibial joint has a downward flexure, and the tibio-tarsal and tarso-pretarsal joints move likewise in the axial plane of the limb. The patello-tibial joint, when present, is variable in respect to the direction of its axis, but it generally gives a movement of production and reduction to the tibia. The limb joints are monocondylic or dicondylic according to whether they contain one or two points of contact between the adjacent segments. The articulation in a monocondylic joint is usually dorsal; in a dicondylic joint the articular points are commonly anterior and posterior, though they may be dorsal and ventral.

Legs of Trilobita.—The trilobites present the most generalized condition of the appendages found in the Arthropoda, since limbs occur on all the body segments but the last, and they are all practically alike in form. The first pair of appendages arises behind the base of the labrum (hypostoma); they are possibly procephalic antennae, since they are usually long, simple, and multiarticulate. The rest of the appendages are leglike in structure and are undoubtedly postoral limbs. Each consists of a large basal segment, or coxopodite (Fig. 45, *Cxpd*), and of a slender telopodite (*Tlpd*) containing usually six segments. The coxopodites have large endite processes (*Bnd*) directed mesally, and, except some of the more anterior appendages, each supports a long fringed epipodite (*Eppd*), which is probably, as shown by Störmer (1933), a branchial organ. The trilobite appendages are often described as being biramous, but it should be observed that the outer branch is an epipodite of the coxopodite and therefore does not represent the exopodite of biramous crustacean limbs.

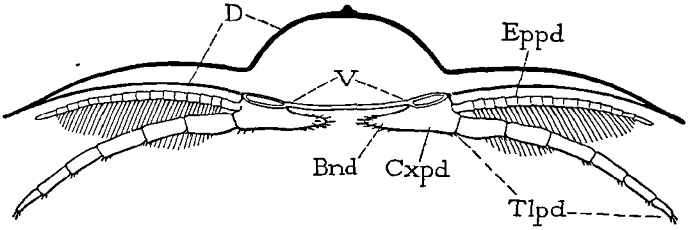

FIG. 45.—Diagrammatic cross section of a trilobite.

Legs of Xiphosura.—The first three of the four pairs of legs of *Xiphosura polyphemus* have only six distinct segments; the last leg (Fig. 46), however, has seven. The large first segment of each appendage is the coxopodite (*Cxpd*), which in the hind leg bears dorsally a spatulate epipodite (*Eppd*). The next segment is evidently a trochanter (*Tr*), and the third the femur (*Fm*). The fourth segment of the last leg appears

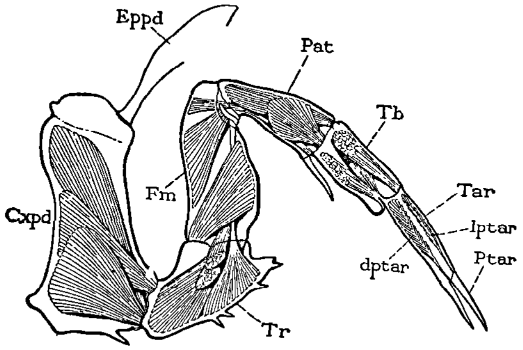

FIG. 46.—Last leg of *Xiphosura polyphemus*, left side, anterior view.

to be a patella (*Pat*), since it is followed by a tibia (*Tb*), a tarsus (*Tar*), and a pretarsus (*Ptar*). In the other legs, which have one less segment, either the patella or the tibia is lacking. The musculature suggests that the missing segment is the tibia. The presence of a patella gives the xiphosuran leg a resemblance to the leg of an arachnid, especially to that of a scorpion (Fig. 48 D); but the origin of the levator and depressor muscle of the pretarsus in the tarsus (Fig. 46) is a primitive character found in Crustacea and Pycnogonida, and not in Arachnida. The abdominal appendages of Xiphosura are reduced and have the form of wide transverse plates. Each consists of a large coxopodite supporting a broad, flat epipodite and of two or three small distal segments.

Legs of Arachnida.—The arachnid limb, in its fullest segmentation, shown in the leg of a solpugid (Fig. 48 B), a tick (Fig. 47 C), or a phalangid (Fig. 47 A), consists of a coxopodite, two trochanters, a femur, a patella, a tibia, a tarsus, and a pretarsus.

The coxopodite is never subdivided into a subcoxa and a coxa. It is inserted in the lateral or ventrolateral wall of the body (Fig. 47 A), where, if movable, it turns forward and rearward and may be articulated to the tergum if there are well-developed plates in the body wall. When movable, the basis is provided typically with dorsal (*I*, *J*) and ventral (*K*, *L*) promotor and remotor muscles, though one set may be lacking. The dorsal muscles have their origin on the tergum; the ventral muscles arise on the sternum or on sternal apophyses, or on a transverse ligament suspended in the body, which probably is derived from the sternum.

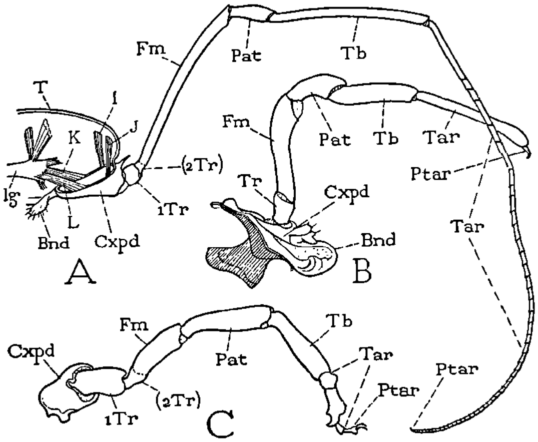

FIG. 47.—Appendages of Arachnida. A, second right leg of a phalangid, *Liobunum*. B, left pedipalp of *Liobunum*. C, fourth leg of a tick, *Amblyomma tuberculatum*.

The segments of the arachnid telopodite are variable in different appendages and in corresponding appendages in the several arachnid groups. Two well-defined trochanters are present in some of the legs of Solpugida (Fig. 48 B, 1*Tr*, 2*Tr*), and an indistinct second trochanter, or prefemur, appears to be only partially separated from the base of the femur in phalangids (Fig. 47 A) and ticks (C). The legs of pseudoscorpions, scorpions (Fig. 48 D), and spiders, however, have only one trochanter, and two trochanters are never present in the pedipalp (Fig. 47 B). The patella is absent in the pseudoscorpions. The tarsus is often divided into two subsegments (Fig. 48 D), either one or both of which may be further subdivided (Figs. 47 A, 48 C). The pretarsus is a single claw in the phalangids and has a simple, dactylopodite-like form in the primitive genus *Holosiro*. In most of the arachnids, however, the pretarsus bears two lateral claws (Fig. 48 E, *Un*) and is itself reduced to a median hook or spur (*Ptar*), though it retains the dicondylic hinge (*r*) with the tarsus and has both levator and depressor muscles (*lptar, dptar*). The pretarsal muscles in all Arachnida arise in segments proximal to the tarsus.

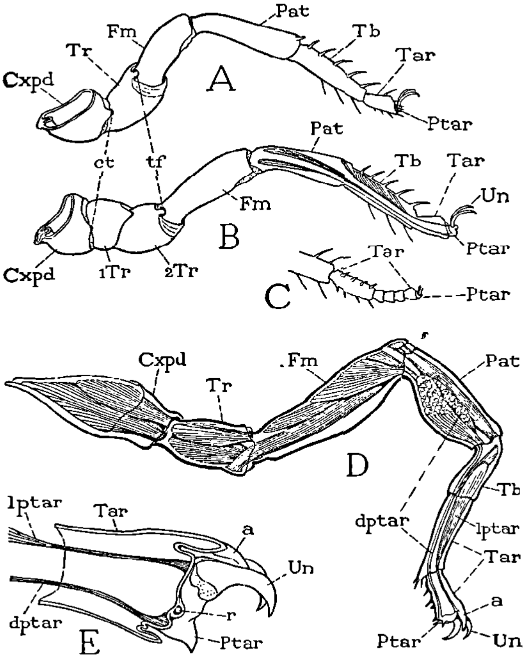

Fig. 48.—Legs of Arachnida. A, B, second and third legs of a solpugid. C, distal part of a solpugid leg with segmented tarsus. D, leg of a scorpion. E, terminal parts of a scorpion leg, showing reduced pretarsus (*Ptar*), with apodemes of levator and depressor muscles and lateral pretarsal claws (*Un*).

Legs of Pycnogonida.—The pycnogonid leg (Fig. 49 A) resembles the leg of an arachnid in having a patella (*Pat*) interpolated between the femur and the tibia. The distinctive feature of the pycnogonid appendage is in its proximal part, where there are three small segments intervening between the femur (*Fm*) and a supporting lobe (*L*) of the body segment. At first glance these segments might appear to be the coxopodite and the usual two trochanters, but their articulations are not typical of these segments. The horizontal dicondylic hinge of the first segment on the body lobe, or that between the second and third segments, suggests the characteristic coxo-trochanteral joint of other arthropods, while a vertical hinge such as that between the first and second segments never occurs elsewhere between the coxa and trochanter. Some writers regard the body lobe as the limb basis or as a subcoxal limb segment united with the body.

The pretarsus of the pycnogonids is a small dactylopodite with levator and depressor muscles arising, as in Xiphosura and Crustacea, in the tarsus (Fig. 49 B), which in Pycnogonida is divided into two subsegments. In some species there is a pair of small accessory claws (*B, Un*) arising dorsally from the base of the pretarsus.

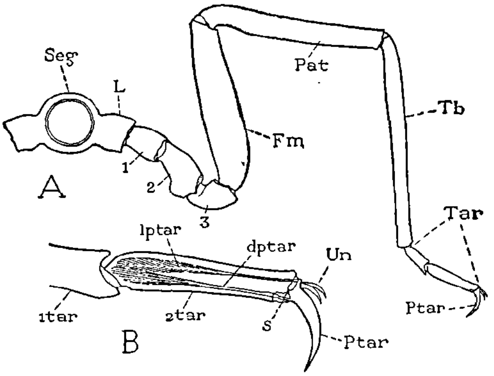

FIG. 49.—Leg structure of Pycnogonida. A, third right leg of *Chaetonymphon spinosum* and attachment to body. B, distal part of leg, showing levator and depressor muscles of pretarsus arising in tarsus, and small pretarsal claws (*Un*).

Legs of Crustacea.—A typical crustacean appendage has the usual seven limb segments of the Mandibulata (Fig. 50 A). The coxopodite is generally undivided, but in the Decapoda the gill-bearing plates forming the inner walls of the branchial chambers appear to be expansions of the subcoxal parts of the bases of the ambulatory legs. Ordinarily the gills are modified epipodites of the coxopodites or filamentous structures borne on the epipodites. The segments of the telopodite may be variously modified, reduced, or eliminated, and in simplified appendages the basipodite is sometimes united with the coxopodite, forming a composite limb base termed the *protopodite*. The dactylopodite is usually a simple clawlike segment, though it may be opposed by a process of the propodite, forming a *chela*. In some of the Isopoda, however, the dactylopodite bears a pair of small claws on its base similar to the lateral claws of insects and some arachnids. The dactylopodite is provided with levator and depressor muscles, which arise in the propodite (tarsus).

A distinctive feature of crustacean appendages in general, though one by no means always present, is the special development of an exite lobe on the basipodite into a long, often jointed arm known as the exopodite (Fig. 50 A, *Expd*). The presence of the exopodite gives the limb its so-called biramous structure, the inner arm, or endopodite, being the shaft of the telopodite distal to the basipodite. In some cases the exopodite exceeds the endopodite in size; or the endopodite may be suppressed, resulting in a monoramous limb of which the distal part is the exopodite. In most of the Crustacea some of the appendages are modified in structure for purposes of swimming. In certain groups the swimming organs are large, flat exite lobes (Fig. 50 B, *Ext*); in others the exopodite and endopodite branches of a group of appendages set apart as natatory organs take on the form of broad overlapping plates.

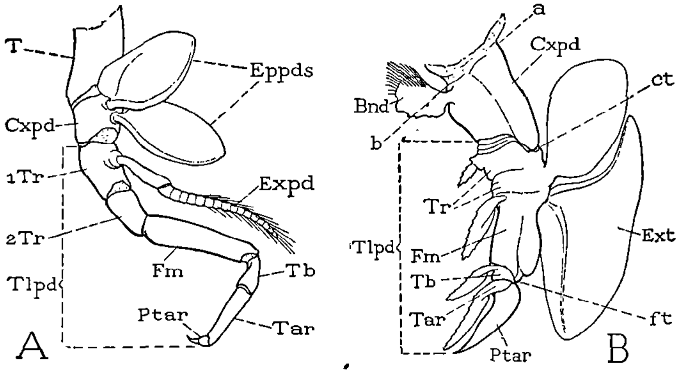

FIG. 50.—Appendages of Crustacea. A, fourth right pereiopod of *Anaspides tasmaniae.* B, third maxilliped of *Apus longicaudata.*

Legs of Diplopoda and Symphyla.—In the diplopods the legs arise from the ventral plates of the body segments, and it is impossible to determine in the adult whether subcoxal parts of the limb bases are incorporated in these plates are not. The first segment of the leg (Fig. 51, A, *Cx*), however, is evidently the homologue of the coxa in the Chilopoda. The second segment, then, is the first trochanter (1*Tr*), the third, though from its size it may have the appearance of a femur, is probably the second trochanter (2*Tr*), and the small fourth segment the femur (*Fm*). Distal to the femur are the usual tibia (*Tb*), tarsus (*Tar*), and pretarsus (*Ptar*). The pretarsus has a single muscle, the depressor (A, B, *13*), arising in the tibia, which is inserted on the base of the pretarsus by a long tendinous apodeme (*x*) traversing the tarsus. The pretarsal musculature of the diplopods thus corresponds to that of the chilopods and hexapods, in which a levator of the pretarsus is absent, and the depressor arises proximal to the tarsus (Figs. 52 B, 53).

The legs of Symphyla (Fig. 51 C), except those of the small first pair, closely resemble the diplopod legs both in segmentation and in the relative size of the second trochanter and the femur. Each leg carries a small styluslike basal process (*Bnd*), which, in *Hanseniella* at least, is an endite of the coxa and is therefore not comparable with the thoracic styli of Machilidae (Fig. 148 A, *Sty*), which are coxal exites. The clawlike pretarsus has a small posterior claw arising from its base (Fig. 51 C, *Ptar*). The pretarsal musculature, according to H. E. Ewing (1928), consists of a depressor muscle only, the fibers of which, as in Diplopoda, arise in the tibia.

In the Pauropoda the legs have only six segments, there being but a single trochanter. The pretarsus lacks a levator muscle, and the fibers of the depressor arise in the tibia and femur. In certain forms the tarsus is divided into two or three subsegments.

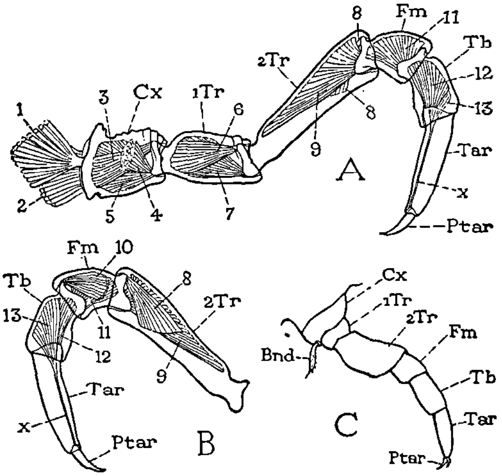

FIG. 51.—Legs of progoneate Myriapoda. A, left leg of a diplopod, *Euryurus*, anterior view. B, distal segments of same, posterior view. C, right leg of a symphylid, *Hanseniella*.

Legs of Chilopoda.—The legs of the chilopods are implanted in broad membranous pleural areas of the body segments, in which there is always a distinct and more or less sclerotized fold surrounding the base of the coxa, that evidently represents a subcoxal part of the limb basis (Fig. 52 A, *Scx*). The dorsal muscles of the appendage are inserted on the subcoxa, and the coxa turns on the subcoxa by a vertical hinge with dorsal and ventral articular points (*c*, *d*). The subcoxal sclerotization is continuous around the base of the coxa in some Geophilidae, but in most of the other chilopods it is broken up into one or more small sclerites (*Cxpl*, *Spl*). Two trochanters are always present, which in Geophilidae are movably articulated to each other. In *Lithobius* and *Scolopendra* they are united, and if the leg is broken off in these forms it comes free at the coxotrochanteral joint; in *Scutigera* the break occurs between the two trochanters. The tarsus (*Tar*) is usually divided into two subsegments; in *Scutigera* each subsegment is again subdivided into a large number of small articles. The pretarsus (*Ptar*) is a small dactylopodite-like claw; it is provided with a depressor muscle only, the fibers of which arise in the tibia and the femur (B, *dptar*) and are inserted by a long tendon (*x*) on the ventral edge of the base of the pretarsus.

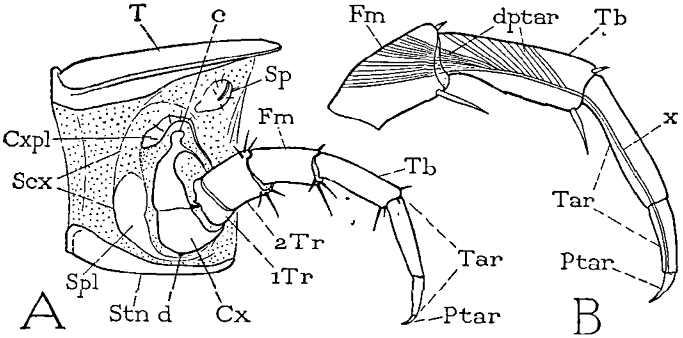

FIG. 52.—Leg structure of Chilopoda. A, leg and left side of body segment of *Lithobius*, showing subcoxa (*Scx*) incorporated into pleural area of body wall. B, distal part of leg, showing single muscle (depressor) of pretarsus, with branches arising in tibia and femur.

Legs of Hexapoda.—In the proturans and insects the free part of the leg comprises at most but six independently movable segments (Fig. 53 A), namely, a coxa, one trochanter, a femur, a tibia, a tarsus, and a pretarsus. In the Odonata there are two trochanters, though they are not movable on each other. The second contains a reductor muscle of the femur. The femur is usually the largest segment of the leg. Beyond the knee joint the segmentation is variable, and there is often a reduction

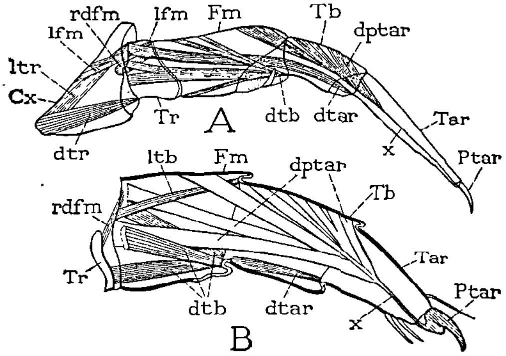

FIG. 53.—Legs of Hexapoda. A, third leg of *Eosentomon germanicum*. (*From Prell*, 1912.) B, third right leg of a caterpillar, *Estigmene acraea*, posterior view, coxa removed.

in the number of segments, resulting either from a fusion of adjacent segments or from the obliteration of a segment. In many such cases a careful study of the leg musculature will help establish the identity of the parts present. The tarsus may be an undivided segment, or it may be broken up into two, three, four, or five subsegments; but it is not characteristically divided into a basitarsus and telotarsus as in the Chilopoda and some Arachnida. No muscles have their origins within the tarsus in insects.

The hexapod pretarsus in its simplest form consists of a small clawlike segment (Fig. 53, *Ptar*) similar to the terminal claw of a chilopod or diplopod limb, and, as in these two groups, it is provided with a depressor muscle only. This muscle arises usually by several branches distributed in the tibia and the femur (*dptar*), which are inserted on a long slender apodeme or "tendon" (*x*) that traverses the tarsus to its attachment on the ventral lip of the base of the pretarsus. The usual pretarsus of adult insects comprises a pair of lateral claws, the *ungues*, articulated dorsally to the end of the tarsus (Fig. 111 A, *Un*), and a median structure (*Ar*) which is probably a remnant of the primary dactylopodite. A condition intermediate between the one-clawed and two-clawed types of structure is found in certain Collembola that have a pair of small lateral claws developed from the base of a larger median claw, and in some of the Thysanura where there are two articulated lateral claws (Fig. 110 C, D), and a small median claw (*dac*), to the base of which is attached the tendon (*x*) of the depressor muscle. In adult pterygote insects the tendon of the depressor muscle ("retractor of the claws") is usually attached to a small ventral sclerite in the base of the pretarsus (Fig. 111 C, E, *Utr*). The lateral claws (*Un*) are clearly secondary structures developed dorsally from the base of the pretarsus.

GLOSSARY OF TERMS APPLIED TO THE APPENDAGES

Arolium (*Ar*).—The median terminal lobe of an insect's foot, probably a remnant of the dactylopodite.

Basipodite (*Bspd*).—The basal segment of the telopodite, or second segment of a generalized appendage; in Crustacea bearing the exopodite. (*First trochanter.*)

Basitarsus (*Btar*).—The proximal subsegment of the tarsus.

Carpopodite (*Crpd*).—The fifth segment of a generalized appendage. (*Tibia.*)

Coxa (*Cx*).—The distal part of the coxopodite serving as the functional basal segment of the leg when separated from the proximal part (subcoxa).

Coxopodite (*Cxpd*).—The primary basal segment of an appendage, representing the primitive limb basis.

Dactylopodite (*Dac*).—The terminal segment of a generalized appendage; typically clawlike in form, with levator and depressor muscles arising in the propodite; represented by a median claw of the pretarsus in some apterygote insects.

Endite.—A mesal lobe of any limb segment.

Endopodite (*Endpd*).—The mesal branch of a biramous appendage; the main shaft of the limb beyond the basipodite.

Epipodite (*Eppd*).—An exite of the coxopodite; often a gill-bearing organ.

Exite.—An outer lobe of any limb segment.

Exopodite (*Expd*).—An exite of the basipodite in Crustacea, often highly developed, giving the limb a biramous structure.

Femur (*Fm*).—The third segment of the telopodite, usually the principal segment of the insect leg. (*Meropodite.*)

First Trochanter (*1Tr*).—The first segment of the telopodite. (*Basipodite.*)

Ischiopodite.—The third segment of a generalized limb, or second segment of the telopodite. (*Second trochanter, prefemur.*)

Limb Basis (*Cxpd*).—The primary basal segment of an appendage (*coxopodite*) supporting the telopodite; sometimes subdivided into a proximal *subcoxa* (*pleuropodite*, or *pleuron*), and a distal *coxa*.

Meropodite.—The fourth segment of a generalized limb. (*Femur.*)

Patella (*Pat*).—A segment between the meropodite (femur) and the carpopodite (tibia) in the legs of Pycnogonida, most Arachnida, and in the last legs of Xiphosura.

Podite, or Podomere.—A limb segment.

Pretarsus (*Ptar*).—The terminal limb segment (*dactylopodite*); in insects comprising usually a pair of lateral claws (*ungues*), and reduced median parts (*arolium, unguitractor plate*, or *median claw*).

Propodite.—The penultimate segment of a generalized limb. (*Tarsus.*)

Protopodite.—The basal stalk of some crustacean limbs composed of the united coxopodite and basipodite.

Second Trochanter (*2Tr*).—The second segment of the telopodite, often not distinct from the base of the femur; in insects usually fused with the first trochanter. (*Prefemur, ischiopodite.*)

Subcoxa (*Scx*).—A secondary proximal subdivision of the coxopodite present in some arthropods, forming a support in the pleural wall of the body segment for the rest of the appendage. (*Pleuron.*)

Tarsomere, or Tarsite.—One of the subsegments of the tarsus.

Tarsus (*Tar.*)—The penultimate segment of the limb, commonly divided into two principal subsegments or into a number of small parts, none of which is individually provided with muscles except the first. (*Propodite.*)

Telopodite (*Tlpd*).—The primary shaft of the limb distal to the coxopodite, the basal segment of which is the first trochanter (*basipodite*).

Telotarsus.—The distal of the two principal subsegments of the tarsus in Arachnida and Chilopoda.

Tibia (*Tb*).—The fourth segment of the telopodite in an appendage lacking a patella. (*Carpopodite.*)

Trochanters (*Tr*).—The first and second segments of the telopodite (*basipodite* and *ischiopodite*); in insects generally united in a single trochanteral segment.

Ungues (*Un*).—Lateral claws of the foot secondarily developed from the base of the dactylopodite; characteristic of insects, but occurring in several arthropod groups.

Unguitractor Plate (*Utr*).—A ventral sclerite in the base of the pretarsus of insects upon which the depressor muscle of the pretarsus, or retractor of the claws, is inserted by a long tendinous apodeme.

CHAPTER VI

THE HEAD

The head of an elongate animal is the compact anterior end of the trunk in which are crowded the principal instruments necessary to the creature for finding its way about in its medium, and usually the implements essential to it for procuring and swallowing its food. The head is always at the anterior end of the body because the original direction of movement determined the pole at which cephalization should take place. Habitual progression in one direction made it necessary that the guiding sense organs should be located at the forward pole and also made this extremity of the animal the most practical location for the intake orifice of the alimentary canal. With the principal sense organs and the mouth located in the head, it follows that the head should contain the major sensory ganglia and should bear the organs for grasping and manipulating the food. Thus it comes about that in the head are associated the two extremes of animal activity, the highest mental powers, and the most primitive function of ingestion.

1. GENERAL MORPHOLOGY OF THE ARTHROPOD HEAD

In the evolutionary history of the arthropods the first well-defined head must have been an anterior section of the trunk corresponding to the region of the procephalic lobes of the embryo (Fig. 23, *Prc*). Considered phylogenetically, therefore, we may term this primitive head the *protocephalon.* The protocephalon, as represented by the procephalic lobes of the embryo, consists of the circumoral region bearing the labrum, the eyes, and the antennae and usually includes the postoral somite of the second antennae, though the latter may be a distinct segmental region of the trunk immediately behind the cephalic lobes. The protocephalon persists in some Crustacea as a small definitive head carrying the labrum, the eyes, and both pairs of antennae, but in most of the mandibulate arthropods the adult head is a more complex structure (syncephalon) including the protocephalon and a variable number of succeeding somites, all more or less intimately united. Since the appendages of the added somites are transformed into organs of feeding, these somites are known as the *gnathal segments.* The embryonic gnathal segments constitute a distinct gnathal section of the trunk (Fig. 23 C, *Gn*) between the protocephalon (*Prc*) and the thorax (*Th*). Inasmuch as the definitive arthropod head of the composite type is thus formed by the union of two primitive sections of the trunk, we may distinguish in its composition a protocephalic region, or *procephalon*, and a gnathal region, or *gnathocephalon*. An understanding of the morphology of the arthropod head depends largely on a study of the head appendages and the cephalic nervous system.

The Procephalon.—The region of the procephalic lobes in the arthropod embryo bears the mouth, the labrum, the eyes, and at most three pairs of appendage rudiments. There is no doubt concerning the existence of two pairs of procephalic appendages, namely, the antennae and postantennae (second antennae or chelicerae), but the claim that there are three is based only on the presence of two small, evanescent preantennal lobes that have been observed to arise at the sides of the mouth in young embryos of a centipede and of a phasmid insect (Fig. 70 A, B, *Prnt*). The antennal and postantennal appendages (Fig. 23 B, *Ant*, *Pnt*) may also be suppressed in the adult, but one or both pairs of them are usually retained and variously developed in different arthropod groups.

The procephalic region of the embryo shows no clear external segmentation, but it is said that its mesoderm in lower insects contains three pairs of coelomic sacs corresponding to the preantennal, antennal, and postantennal appendages. This, together with the triple division of the brain into protocerebral, deutocerebral, and tritocerebral lobes, is usually taken as evidence of a corresponding metamerism in the procephalon. It is necessary to assume, however, that the procephalon contains also a prostomial element (acron), and that the protocerebral lobes of the brain are largely made up of the primitive prostomial ganglion, or archicerebrum, which innervates the eyes. The antennae are the deutocerebral appendages, and the postantennae are the tritocerebral appendages.

The general structure of the arthropod head and the cephalic nervous system is not entirely in accord with the foregoing theory of the procephalic segmentation. The mouth appears to lie immediately before the tritocerebral somite, and the first ventral dilator muscles of the stomodaeum are said by Smreczynski (1932) to be formed from the mesoderm of this somite. The tritocerebral ganglia, though united with the brain, are the first ganglia of the ventral nerve cord, and they innervate the oral and ventral preoral region of the head. The protocerebral and deutocerebral lobes of the brain, on the other hand, are always suprastomodaeal in position and thus appear to be preoral nerve centers, but there is no evidence whatever of cephalic segmentation between the labrum and the mouth. A comparative study of the histology of the arthropod brain made by Holmgren and by Hanström, as will be shown in Chap. XVI, suggests that the protocerebrum and deutocerebrum are secondary subdivisions of a primitive preoral nerve mass evolved directly from the prostomial archicerebrum. According to this view the tritocerebral segment is the first true cephalic somite, and paired mesodermal cavities anterior to it are to be regarded as secondary in origin and not as representative of primitive metamerism in the antennal and preantennal regions of the head. As a corollary, the antennae and preantennae become prostomial appendages comparable with the cephalic tentacles of the annelid worms. The slightly postoral position of the antennal rudiments in the embryos of some insects (Fig. 23 B, C) has no morphological significance, since the nerve centers of the appendages are not derived from the ventral postoral wall of the head.

The accompanying diagram of the head segmentation (Fig. 54 A) expresses the idea that the tritocerebral segment is the first true somite of the arthropod trunk, and that the entire preoral region of the head bearing the labrum, the eyes, and the antennae is prostomial. The tritocerebral ganglia are thus regarded as the first ganglia of the primitive ventral nerve cord (Fig. 244 B); they innervate the oral and labral regions and are connected with both the prostomial nerve mass and the first ganglion of the stomodaeal nervous system (*FrGng*).

The Gnathocephalon.—The gnathocephalon is the region of the insect head that supports the mandibles, the maxillae, and the labium. It contains, therefore, at least three somites (Fig. 54 A, *II*, *III*, *IV*), and these somites are always distinct in the gnathal region of the embryo (Fig. 23 B, C). Some entomologists, however, have contended that lateral lobes of the hypopharynx, known as the superlinguae (Fig. 77 A, *Slin*), represent a pair of appendage rudiments behind the mandibles, and that the gnathocephalon, therefore, must contain four somites. Since the appendicular nature of the superlingue has not been demonstrated, only the three known segments of the gnathocephalon are recognized in the present discussion. The ganglia of the gnathal somites in insects are always combined in a single nerve mass, which is the ventral, or suboesophageal, ganglion of the definitive head.

While in the insects and the myriapods the gnathal segments are always completely united with the protocephalon in the adult head, there are many Crustacea, including the shrimps, crayfish, and crabs, in which the gnathal segments form a part of the body and are included with the segments of the maxillipeds and pereiopods in a gnathothoracic section of the trunk, which may be covered by a carapace. In certain other crustaceans, however, as in the amphipods and isopods, the gnathal segments are united with the protocephalon in a composite head structure resembling that of the insects. Intermediate stages occur in some of the phyllopods, as in *Eubranchipus* (Fig. 55 A), in which the mandibular segment (*II*) is intimately associated with the large protocephalon (*Prc*), while the maxillary segments (*III* + *IV*), though united with each other, form a distinct postcephalic region. The Arachnida cannot be said to have a head, since in most forms the protocephalon is combined with the following five segments to form the prosoma or anterior body section known as the cephalothorax.

The Definitive Insect Head.—After the union of the gnathal segments with the protocephalon there are in general no visible marks in the resulting head capsule showing the lines of fusion between the component segments. A subterminal groove (postoccipital suture) of the definitive cranium, however, surrounding the foramen magnum dorsally and laterally (Fig. 57 A, *pos*), is apparently the persisting suture between the first maxillary and the labial segments (Fig. 54 A, *z*). In the adult head of *Machilis* a transverse suture on the rear part of the head (Fig. 55 B, *y*), ending ventrally on each side between the bases of the mandible and the maxilla, may represent the suture between the mandibular and maxillary segments (Fig. 54 A, *y*), since it is suggestive of this suture in *Eubranchipus* (Fig. 55 A, *y*). Attempts have been made to determine the segmental limits in the cranial wall of insects by the muscle attachments, but the bases of the muscles appear in many instances to have migrated without regard to segment areas after the latter have become continuous. The various sutures that appear in the definitive head capsule, with the exception of the subterminal postoccipital suture, as shown by Smreczynski (1932) in *Silpha obscura*, have no relation to the original metamerism.

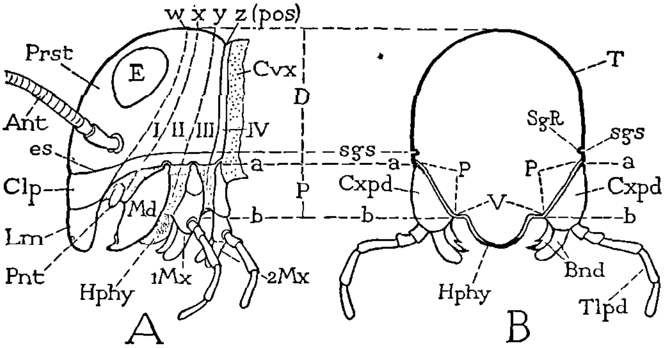

FIG. 54.—Diagrams illustrating the fundamental structure of the insect head. A, the composite definitive head formed by the union of at least four postoral somites (*I*, *II*. *III*, *IV*) with a preoral region derived from the cephalic lobes of the embryo (Fig. 23, *Prc*) including the prostomium and perhaps one or two (preantennal and antennal) somites (Fig. 244). B, relation of the head appendages to the head wall as shown in cross section,

Since the gnathal section of the definitive head is derived from the anterior part of the primitive segmented body of the insect, its surface regions must be homodynamous with those of the thoracic segments, and the parts of its appendages with those of the legs. The segment structure of the head is best seen in a cross section (Fig. 54 B). The line on each side of the head through the articulations of the appendages with the lower edge of the cranium (*a-a*) clearly represents the dorso-pleural line of a more generalized part of the body (Fig. 35 C, *a-a*), and the lower ends of the appendage bases (*b, b*) mark the pleuro-ventral line (*b-b*). The arch of the cranium, therefore, is the dorsum of the head (Fig. 54, *D*), and its posterior sclerotization represents the fused terga of the gnathal segments. The true pleural areas of the head are the lateroventral membranous parts (B, *P, P*) in which are implanted the broad bases of the appendages (*Cxpd*). The venter is the lower wall of the head (*V*) between the appendage bases, including the hypopharynx (*Hphy*). The principal parts of the gnathal appendages are the limb bases (*Cxpd*), which in the two pairs of maxillae bear each a pair of endite lobes (*Bnd*), and a segmented palpus, which is the telopodite (*Tlpd*).

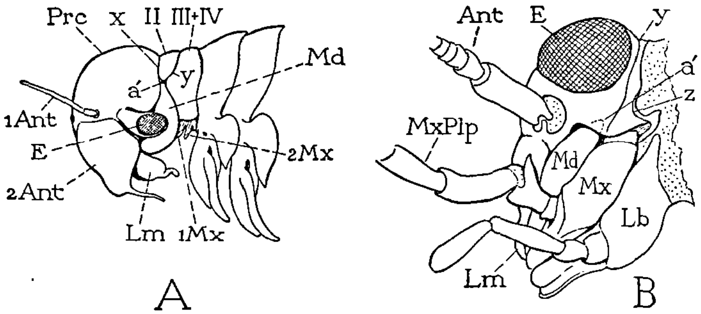

FIG. 55.—Head of a primitive crustacean compared with that of an apterygote insect. A, *Eubranchipus*, showing gnathal segments (*II, III, IV*) distinct from the protocephalon (*Prc*). B, *Machilis*, with procephalic and gnathal regions combined.

On the inner surfaces of the head walls there are developed various apodemal inflections of the cuticula, taking the form of ridges and arms, which together constitute the endoskeleton of the head. The most important endoskeletal feature consists of two pairs of apophyses that unite in pterygote insects to form the structure known as the *tentorium*, upon which arise the ventral muscles of the gnathal appendages and usually the muscles of the antennae.

2. STRUCTURE OF THE DEFINITIVE INSECT HEAD

The mature insect head, as we have seen, is a capsule in which all semblance of a segmented structure has been lost. Most of its sutures are secondary developments, being merely lines of cuticular inflections that form endoskeletal ridges. The dorsal, anterior, lateral, and posterior walls of the head are continuously sclerotized, forming a caplike *cranium*. The antennae in most adult insects occupy a lateral or anterior position on the cranial wall, but the gnathal appendages in the more generalized insects preserve their primitive lateroventral positions and articulate with the lower lateral margins of the cranium.

According to the position of the mouth parts the head may assume one of three types of structure. If the gnathal appendages are directed downward, and the cranium corresponds in position to the body segments (Fig. 66 A), the head is said to be *hypognathous*. In many insects, however, the cranium is turned upward on the neck so that the mouth parts are directed forward (B) and the head becomes *prognathous*. The hypognathous condition is the more primitive in the sense that it preserves the ventrolateral position of the appendages typical of ambulatory limbs, but it is possible, as claimed by Walker (1932), that the early insects were prognathous. The third, or *opisthognathous*, type results from a deflection of the facial region, giving the mouth parts a posterior ventral position, as in certain Homoptera. The three types of head structure relative to the position of the mouth are adaptations to different habitats or ways of feeding, and all may occur among closely related insects.

General External Structure of the Head.—In an adult insect that preserves the hypognathous condition of the head, the facial area is directed forward (Fig. 56 B), the mandibles, maxillae, and labium project downward, and the labrum (*Lm*) hangs as a free lobe before the mouth from the ventral edge of the face. A pair of *compound eyes* (*E*) is located on the lateral or dorsolateral walls of the cranium, and usually three *ocelli* (A, *O*) occur between them on the facial or dorsal area. Two of the ocelli are symmetrically placed laterad of the midline, the third is median and ventral or anterior to the others. The *antennae* (*Ant*) vary in their location from lateral points near the bases of the mandibles (Figs. 55 B, 63 A, 64 A) to a more median site on the upper part of the face (Figs. 58, 63 C, D). The posterior surface of the head (Fig. 56 C) is occupied by the opening from the head into the neck, usually a large aperture (Figs. 59 B, 65 A), but sometimes much reduced by the encroachment of the posterior cranial walls (Fig. 65 B, C). The aperture is properly the *foramen magnum* by analogy with vertebrate anatomy, but in entomology it is commonly termed the "occipital" foramen.

On the under surface of the head (Fig. 56 D) the areas occupied by the bases of the mandibles and the maxillae (*MdC*, *MxC*) take up the lateral regions; the labrum (*Lm*) projects from the anterior margin of the cranium, and the base of the labium (*Lb*) lies transversely below the foramen magnum. The true ventral area is that between the bases of the lateral appendages, the median part of which forms the variously modified lobe known as the *hypopharynx* (*Hphy*). Anterior to the hypopharynx and immediately behind the base of the labrum is the *mouth* (*Mth*). The posterior surface of the labrum sometimes bears a small median lobe called the *epipharynx*. It is clear that neither the epipharynx nor the hypopharynx has any relation to the pharynx, which is a part of the stomodaeal section of the alimentary canal. The two lobes are external head structures, but since their names have been handed down from earlier days in entomology they have become a part of our accepted vocabulary. The space enclosed by the labrum and the mouth appendages is sometimes called the "mouth cavity," but inasmuch as it lies entirely outside the body it is merely an intergnathal space and should be termed the *preoral*, or *extraoral*, *cavity* (Figs. 60, 155, *PrC*).

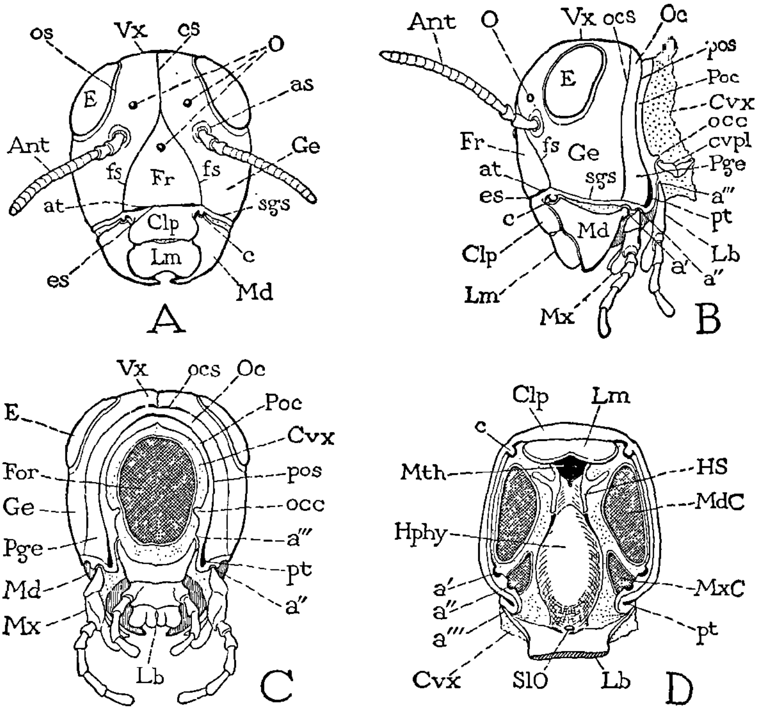

FIG. 56.—Typical structure of the head of a pterygote insect, showing potential sutures and intersutural areas. A, anterior. B, lateral. C, posterior. D, ventral, appendages removed. *a'*, *a''*, *a'''*, primary cranial articulations of mandible, maxilla, and labium; *Ant*, antenna; *as*, antennal suture; *at*, anterior tentorial pit; *c*, secondary anterior articulation of mandible; *Clp*, clypeus; *cs*, coronal suture; *cvpl*, cervical plates; *Cvx*, neck (cervix); *E*, compound eye; *es*, epistomal suture; *For*, foramen magnum; *Fr*, frons; *fs*, frontal suture; *Ge*, gena; *Hphy*, hypopharynx; *HS*, hypopharyngeal suspensorium; *Lb*, labium; *Lm*, labrum; *Md*, mandible; *MdC*, mandibular cavity; *Mx*, maxilla; *MxC*, maxillary cavity; *O*, ocelli; *Oc*, occiput; *occ*, occipital condyle; *ocs*, occipital suture; *os*, ocular suture; *Pge*, postgena; *Poc*, postocciput; *pos*, postoccipital suture; *SlO*, orifice of salivary duct; *sgs*, subgenal suture; *Vx*, vertex.

Sutures of the Cranium.—The endoskeletal ridges of the head are marked on the surface of the cranium by grooves which are known as the head "sutures." One of these grooves, the postoccipital suture, lying close to the posterior margin of the head (Fig. 56 B, C, *pos*), probably marks the intersegmental line between the primitive first and second maxillary segments. The other head sutures commonly present in pterygote insects are all apparently secondary inflections of the cuticula. Some of them form apodemal ridges of functional importance but having no segmental significance.

The Epicranial Suture.—This suture is a distinctive feature of the insect head, though it is not fully developed in Apterygota and is more or less suppressed in many Pterygota. Typically it has the form of an inverted Y with the stem placed medially on the top of the head, and the arms diverging downward on the face. The dorsal part is known as the *coronal*, or *metopic, suture* (Figs. 56 A, 57 B, *cs*). The facial arms branching from the coronal suture are apparently not homologous in all cases. Those more usually present diverge above the median ocellus and proceed ventrally on the face *mesad* of the antennal bases toward the anterior articulations of the mandibles. These sutures may be defined as the true *frontal sutures* (*fs*). In most insects, however, the frontal sutures are incomplete (Figs. 58 A, 59 A), and often they are entirely absent. In certain orthopteroid insects two sutures diverge from the coronal suture above the lateral ocelli and extend a varying distance laterally and ventrally on the face *laterad* of the antennal bases. These sutures are the *postfrontal* sutures (Fig. 57 B, *pfs*). They are particularly prominent in some Dermaptera but are present in Plecoptera, especially in larval stages, and they are weakly developed in Phasmidae and Mantidae. In some of these insects there is also a suggestion of the frontal sutures (*fs*). Since generally, however, the two pairs of sutures do not occur in the same

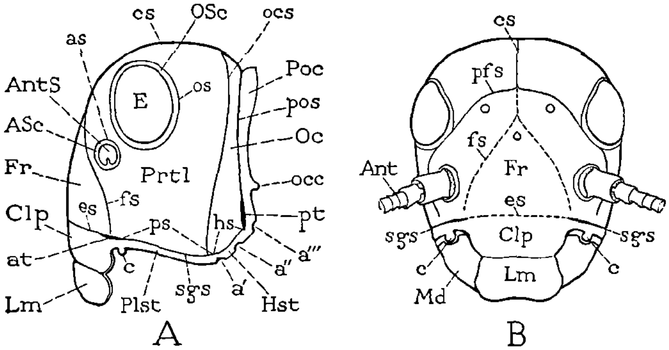

FIG. 57.—Diagrams illustrating the principal sutures and areas of the insect cranium, and two potential sutures in the frontal region. *AntS*, antennal socket; *ASc*, antennal sclerite; *hs*, hypostomal suture (postmandibular part of subgenal suture); *Hst*, hypostoma; *Oc*, occipital arch (occiput and postgena); *OSc*, ocular sclerite; *pfs*, postfrontal suture; *Plst*, pleurostoma; *Prtl*, parietal; *ps*, pleurostomal suture (supramandibular part of subgenal suture). (Fig. 56.)

species, the postfrontal sutures have often been confused with the frontal sutures, but their independence has been clearly shown by Crampton (1932).

The Occipital Suture.—A suture of the head developed particularly in orthopteroid insects is the occipital suture (Figs. 56 B, C, 57 A, *ocs*). This suture crosses the back of the head and suggests the posterior head suture of *Machilis* (Fig. 55 B, *y*), but it ends ventrally on each side of the epicranium *before* the posterior articulations of the mandibles (*a'*). The occipital suture forms internally a ridge which serves probably to strengthen the posterior parts of the epicranial walls.

The Postoccipital Suture.—This suture lies on the extreme posterior part of the cranium where it closely surrounds the foramen magnum dorsally and laterally (Figs. 56 B, C, 57 A, *pos*). Internally the postoccipital suture forms a strong *postoccipital ridge* (Figs. 58 B, 59 B, *PoR*), often produced into apodemal plates, upon which are attached the anterior ends of the prothoracic and neck muscles that move the head. The posterior arms of the tentorium arise from the ventral ends of the postoccipital ridge, and the points of their invagination appear externally as pits in the lower ends of the postoccipital suture (Figs. 56 B, C, 57 A, 58 B, 59 B, *pt*).

The Subgenal Sutures.—On each side of the head close to the lower edge of the lateral cranial wall is a subgenal suture (Figs. 56 A, B, 57 A, 58 B, *sgs*). It usually follows the contour of the cranial margin, but in some insects it is arched upward over the mandible (Fig. 58 A). On the inner surface of the cranium this suture forms a submarginal *subgenal ridge* (Figs. 54 B, 58 B, *SgR*), which usually extends from the posterior tentorial pit (Fig. 56 B, *pt*) to a point just above the anterior articulation of the mandible (*c*). The two subgenal ridges strengthen the cranial walls along the lines of attachment of the gnathal appendages. For descriptive purposes the part of the subgenal suture lying above the mandible is sometimes distinguished as the *pleurostomal suture* (Fig. 57 A, *ps*), and the part posterior to the mandible as the *hypostomal suture* (*hs*).

The Epistomal Suture.—In many pterygote insects the anterior ends of the subgenal sutures are connected across the lower part of the face by an *epistomal suture* (Figs. 56 A, B, 57, *es*). This suture is often a deep inflection producing internally a strong *epistomal ridge* (Figs. 58 B, 76 A, B, C, *ER*), which typically forms a brace in the region between the anterior mandibular articulations. As we shall later see, however, the epistomal suture and its ridge are subject to much variation in position. In pterygote insects the anterior arms of the tentorium usually arise from the epistomal ridge, and their external pits (*at*), lying in the epistomal suture, serve to identify this suture when the latter is likely to be confused with neighboring sutures.

The Ocular Sutures.—These sutures are grooves which frequently surround the compound eyes (Figs. 56 A, 57, *os*), each forming internally a skeletal ridge around the edge of the retina.

The Antennal Sutures.—Each antenna is set in a membranous area of the cranial wall, known as the *antennal socket,* the rim of which is reinforced by a submarginal ridge. The external groove of this ridge is the so-called *antennal suture* (Figs. 56 A, 57, *as*).

Other Head Sutures.—In addition to the sutures described above, other grooves of less constant occurrence may occur on the head wall. In the cockroach, for example (Fig. 58 A), a prominent *subantennal suture* (*sas*) extends downward from each antennal suture to the subgenal suture. It is sometimes called the "frontogenal suture," but its lateral position makes it doubtful if it defines the lateral limits of the region of the true frons (*Fr*). In the cricket (Fig. 59 A) a *subocular suture* (*sos*) extends from the lower angle of each compound eye to the subgenal suture above the anterior mandibular articulation. In the higher Diptera a *ptilinal suture* cuts across the region of the frons just above the bases of the antennae, which marks the groove where the pupal ptilinum was permanently withdrawn. Still other grooves frequently appear in the cranial walls but they are too variable to be included in a general account of the head sutures.

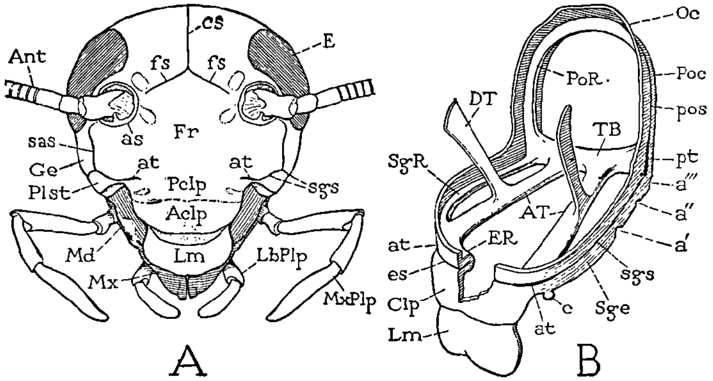

FIG. 58.—External and internal structures of the insect cranium. A, head of *Blatta orientalis* (note absence of epistomal suture, B, *es*) between anterior tentorial pits. B, diagram of relation of endoskeletal structures of head to the cranial sutures. *AT*, *at*, anterior tentorial arm and pit; *DT*, dorsal tentorial arm; *ER*, *es*, epistomal ridge and suture; *PoR*, *pos*, postoccipital ridge and suture; *SgR*, *sgs*, subgenal ridge and suture; *TB*, *pt*, tentorial bridge and posterior tentorial pit.

The Tentorial Pits.—The four points on the cranial wall where the arms of the tentorium are invaginated are never entirely closed, and the external depressions at the tentorial roots are such important landmarks in the head structure that they deserve special consideration. The depressions are conveniently called "pits" since they are usually pitlike in form, but frequently they are elongate slits, and sometimes suture-like grooves.

The Anterior Tentorial Pits.—The anterior arms of the tentorium in pterygote insects always arise from some part of the subgenal or epistomal ridges, and their roots appear externally as depressions in the corresponding sutures. In the more generalized pterygote insects the anterior tentorial pits or fossae lie in the subgenal sutures above the bases of the mandibles or above the anterior mandibular articulation (Figs. 58, 59 A, *at*); but in the majority of cases they are contained in the epistomal suture (Figs. 56 A, 57, *at*), though their position in the latter is subject to much variation. A facial suture that contains the tentorial pits, therefore, is usually to be identified as the epistomal suture. If the bases of the anterior tentorial arms are broad, the pits are correspondingly elongate, as in the cricket, where each anterior "pit" is a long slit (Fig. 59 A, *at*) contained in both the subgenal and epistomal sutures.

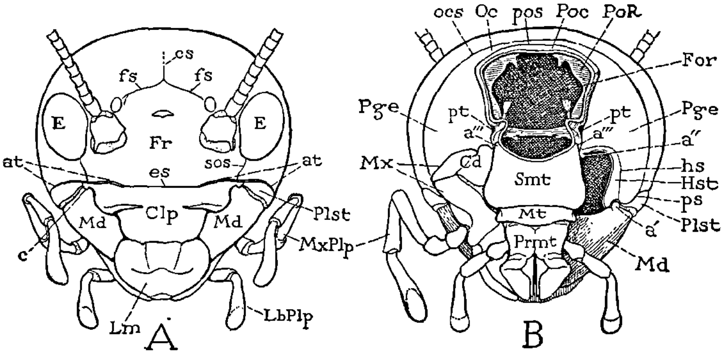

FIG. 59.—Head of a cricket, *Gryllus assimilis.*

The Posterior Tentorial Pits.—The posterior arms of the tentorium arise from the ventral ends of the postoccipital ridge, and their pits lie in the lower extremities of the postoccipital suture (Figs. 56 B, C, 57 A, 59 B, *pt*). If the head is of the prognathous type, the posterior pits are usually drawn forward on the ventral side of the head (Fig. 66 B, *pt*), and the lower ends of the postoccipital suture (*pos*) are correspondingly lengthened behind them. The posterior pits also may take the form of slits or grooves. In the soldier termites the sutural lines at the sides of the elongate base of the labium (Fig. 69 A, *pt, pt*) are the roots of the extended posterior arms of the tentorium (C, *PT*).

The dorsal arms of the tentorium, when present, are often united with the epicranial wall in the neighborhood of the antennae, and the points of union are sometimes marked by depressions or dark spots (Fig. 63 B, C, *dt*), which may be distinguished as *tentorial maculae*, since they are usually not true invagination pits.

The Areas of the Cranium.—The cranial areas set off by the head sutures are quite definite features of the head structure when the sutures are complete, and are given distinctive names, but their limits become obscure when the sutures are obsolete or suppressed. The cranial areas, in themselves, probably have little or no significance; their demarkation is incidental to the presence of the sutures, which in turn are but the external grooves of endoskeletal ridges, which are the important structural features. The intersutural areas, however, sometimes called the head "sclerites," serve as convenient characters for descriptive purposes. The principal areas of the cranium are the median facial *frontoclypeal* area, the lateral *parietals,* the *occipital arch,* the *postocciput,* and the narrow *subgenal areas* above the bases of the gnathal appendages.

The Frontoclypeal Area.—This area of the head is typically the facial region between the antennae, or between the frontal sutures when the latter are present, and the base of the labrum. When the epistomal suture is present the frontoclypeal area is divided into a dorsal or posterior *frons* (Figs. 56 A, 57, *Fr*), and a ventral or anterior *clypeus* (*Clp*). The frons bears the median ocellus on its upper part and is the area of the head on which the muscles of the labrum, when present, with rare exceptions (Diptera), take their origin. When the frontal sutures are complete, as in many coleopterous larvae, the frons is a well-defined sclerite. The antennae are never located on the true frontal area, but their bases may become approximated medially and constrict the frons between them. In some insects the frons is greatly reduced by an upward extension of the clypeus. The clypeus is the region of the cranial wall on which the dorsal dilator muscles of the extraoral "mouth cavity" (cibarium) take their origin, and in general it varies in size according to the size of these muscles, being greatly enlarged in some of the sucking insects (Fig. 177), but in the caterpillars also it becomes extended dorsally as a prominent triangular plate (Fig. 64 A, *Clp*). The clypeus is often subdivided into a *postclypeus* and an *anteclypeus,* even though the postclypeal part, as in the cockroach (Fig. 58 A), may not be separated from the frons.

The Parietals.—The lateral areas of the cranium, separated above by the coronal suture, are the *parietals* (Fig. 57 A, *Prtl*). They are bounded anteriorly and posteriorly by the frontal and occipital sutures, respectively, when these sutures are present. Each parietal area bears an antenna, one of the lateral ocelli, and a compound eye. The dorsal surfaces of the two parietals forming the top of the head constitute the *vertex* (Fig. 56 A, B, *Vx*). In some insects there is a prominent angle, the *fastigium,* between the vertex and the face. The lateral parts of the parietals beneath or behind the eyes are the *genae* (*Ge*). The narrow bands encircling the compound eyes within the ocular sutures (*os*) are known as the *ocular sclerites* (*OSc*), and the marginal areas of the antennal sockets, defined by the antennal sutures (*as*), are termed the *antennal sclerites* (*ASc*).

The Occipital Arch.—On the posterior surface of the head (Fig. 56 C) the horseshoe-shaped band between the occipital and the postoccipital sutures (*ocs*, *pos*) is the *occipital arch* (*Oc*, *Pge*). Generally the term *occiput* (*Oc*) is given to the dorsal part of this area, and the lateral parts, lying posterior to the genae, are called the *postgenae* (B, C, *Pge*). Rarely the occiput and the postgenae are separated by a suture on each side of the foramen magnum. Since the occipital suture is frequently imperfect or absent, the occipital and postgenal areas can generally be defined only as the posterior region of the cranium.

The Postocciput.—This is the narrow posterior rim of the epicranium (Figs. 56 C, 57 A, *Poc*) set off from the occipital arch by the postoccipital suture (*pos*), and to which the neck membrane is attached. Ventrolaterally the posterior margin of the postocciput may be produced on each side in a small process, the *occipital condyle* (*occ*), to which is articulated the anterior cervical sclerite (Fig. 56 B, *cvpl*). The postocciput probably is a sclerotic remnant of the labial segment. It is often so narrow as to be scarcely perceptible, and sometimes it is nothing more than the posterior lip of the inflection forming the postoccipital ridge.

The Subgenal Areas.—The narrow marginal areas on the sides of the cranium below the subgenal sutures (Fig. 57 A), on which the gnathal appendages are articulated, are important though often inconspicuous features of the cranium, and their modifications have a distinctive character in many groups of insects. The part of each subgenal area above the mandible is distinguished as the *pleurostoma* (*Plst*), and the part behind the mandible as the *hypostoma* (*Hst*). The hypostomal areas, set off by the hypostomal sutures (*hs*), are sometimes extended mesally on the ventral side of the head, forming, as in the caterpillars (Fig. 164 C, *Hst*), a pair of hypostomal lobes of the cranium cutting into the base of the labium. In other cases, as in adult Hymenoptera (Fig. 65, B, C), Diptera, and Heteroptera, they may be approximated or completely united in a *hypostomal bridge* closing the ventral end of the foramen magnum behind or above the base of the labium. The pleurostoma is sometimes enlarged by an arching of the pleurostomal suture above the base of the mandible. When the subgenal sutures are connected across the face by an epistomal suture (Figs. 56 A, 57, *es*), there is set off a ventral marginal rim of the epicranium known as the *peristome.* In some of the higher Diptera the peristome surrounds a ventral depression of the head into which the proboscis is retractile. The clypeus, or its upper part, considered as a part of the peristome, is sometimes called the *epistoma*, though this term is applied also to the epistomal ridge, especially when the latter appears as a conspicuous dark band on an otherwise weakly sclerotized cranium (Fig. 161 E, H, *Est*).

The Labrum.—The labrum of generalized insects is usually a broad flat lobe of the head (Fig. 59 A, *Lm*) that hangs downward before the mandibles and forms the anterior wall of the intergnathal preoral cavity. Its external surface is attached proximally to the lower margin of the clypeus by the clypeolabral suture, which gives mobility to the labrum. Its inner surface is continuous with the membranous inner surface of the clypeal region of the head (Fig. 60 A), the two forming the so-called epipharyngeal wall of the preoral cavity, which ends proximally at the mouth aperture (*Mth*). A median lobe sometimes developed on the epipharyngeal wall may form a more or less distinct *epipharynx* (Fig. 163 B, *Ephy*). In the lateral angles between the labrum and the clypeus there is generally present a pair of small sclerites, the *tormae*, which usually extend into the epipharyngeal surface of the clypeus. The form of the labrum varies much in insects with specialized mouth parts, but the organ seldom loses its essential structure of a movable preoral lobe of the head.

The musculature of the labrum includes muscles situated within the labrum itself, and cranial muscles inserted on its base. Within the labrum is a single or paired median muscle, the *compressor of the labrum* (Fig. 60 A, *cplr*), attached on the anterior and posterior walls. The labrum is movable usually by two pairs of long muscles taking their origins on the upper part of the frons. One pair, the *anterior labral muscles* (*mlra*), is inserted on the anterior margin of the labral base, sometimes laterally, sometimes medially; the other pair, the *posterior labral muscles* (*mlrp*), is inserted posteriorly, usually on the epipharyngeal processes of the tormae. The labrum, therefore, is variously movable, its potential motions being those of retraction, production and reduction, and of lateral movements. Either pair of labral muscles may be absent, and in some cases both pairs are absent; in adult Diptera the labral muscles are exceptional in that they take their origins on the clypeus.

The Hypopharynx.—The ventral wall of the gnathal region of the head in the more generalized insects is mostly occupied by the large median lobe known as the *hypopharynx* (Figs. 54 B, 56 D, *Hphy*). The mouth (Fig. 56 D, *Mth*) lies between the base of the clypeus and the hypopharynx, and usually the opening of the salivary duct (*SlO*) is situated in a pocket between the hypopharynx and the base of the labium (*Lb*), but in some insects the salivary orifice is placed on the hypopharynx, as in adult Hemiptera and Diptera, in which the hypopharynx is traversed by a salivary canal. In many insects, especially the more generalized forms, the hypopharynx includes a pair of lateral lobes known as the *superlinguae* (Fig. 77 C, D, *Slin*), which have united with the median part of the hypopharynx, or *lingua* (*Lin*), to form the definitive organ. The superlinguae in some of the Apterygota arise in the embryo separate from the median lingua (A) in a position close to the bases of the mandibles (*Md*).

The usual form of the hypopharynx in orthopteroid insects is that of a thick, sometimes irregular lobe (Fig. 60 A, *Hphy*), lying like a tongue in the preoral cavity, where it is attached to the head between the mouth and the labium. Its posterior wall is reflected into the adoral wall of the labium usually at the base of the prementum, and there is formed here a small salivary pocket, or *salivarium* (Figs. 60 A, 155, *Slv*), into which opens the duct of the labial glands (*SlD*). The lateral walls of the hypopharynx contain a pair of basal plates or bars (*w*), the posterior ends of which may extend to the salivarium. On these sclerites are inserted the retractor muscles of the hypopharynx (*rhphy*), which take their origins on the tentorium. The adoral surface of the hypopharynx is differentiated into a distal sclerotized area and a proximal more membranous part. The latter presents a median depression, the floor of which is directly continuous through the mouth with the ventral wall of the stomodaeum and itself forms the floor of a special preoral food chamber, the *cibarium* (*Cb*), beneath the opposing epipharyngeal wall of the clypeus.

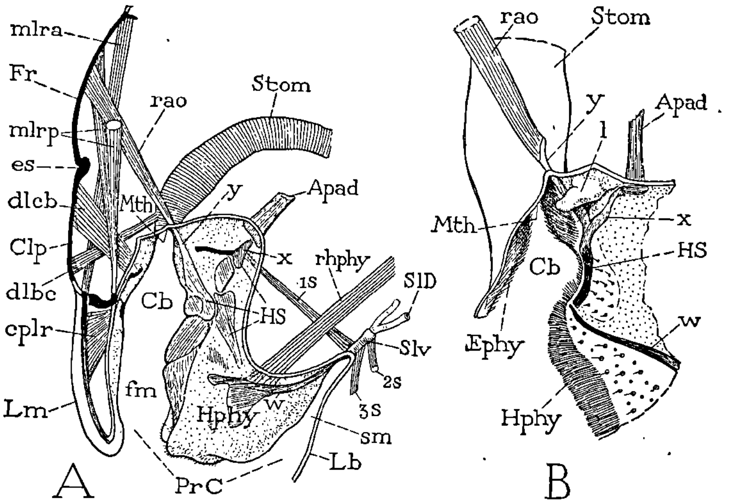

FIG. 60.—The preoral cavity and the hypopharynx. A, section through region of labrum, hypopharynx, mouth, and salivary orifice of *Gryllus*, showing the food pocket (cibarium, *Cb*) and the salivary pocket (salivarium, *Slv*) of the preoral cavity and their related muscles. B, base of hypopharynx, cibarium, and mouth of *Dissosteira*.

The adoral area of the hypopharynx is flanked on each side by a sclerite (Fig. 60 B, *HS*) or a group of sclerites (A, *HS*), the pair or paired groups of which constitute the *suspensoria* of the hypopharynx (*fulturae, Zungenstäbchen*). Each suspensorium in its simpler form of a single sclerite (B, *HS*) articulates distally with the anterior end of the lateral sclerite (*w*) of the hypopharynx, and the proximal end (*y*) enters the lateral angle of the mouth where it ends in the stomodaeal wall and gives insertion to the retractor muscle of the mouth angle (*rao*), which takes its origin on the frons (A). The suspensorial sclerites are subject to much variation in form in different insects, and they may be entirely absent. In *Dissosteira* (B) each suspensorial rod has a proximal branch (*x*) that extends laterally to the base of the adductor apodeme of the mandible, and a similar mandibular branch is present in *Blatta*, but in the cricket (A) the suspensorial apparatus consists of a group of sclerites (*HS*) on each side.

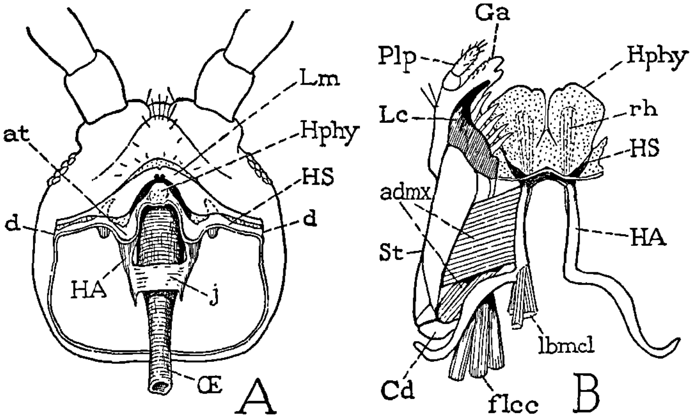

Fig. 61.—Examples of the presence of ventral hypopharyngeal apodemes (*HA*) in a centipede and an apterygote insect, which evidently represent the anterior arms of the usual insect tentorium. A, under surface of head of *Lithobius*, mouth appendages removed, showing hypopharyngeal suspensorium (*HS*) and apodemes (*HA*). B, hypopharynx and right maxilla of *Heterojapyx*, ventral view, showing long hypopharyngeal apodemes on which are attached muscles of maxillae and labium.

It is possible that the suspensorial area of the hypopharynx should not be regarded as a part of the true hypopharynx. Morphologically it lies between the mouth and the bases of the mandibles, and hence it may represent the venter of the postoral tritocerebral somite of the head. In the acridid *Dissosteira* (Fig. 60 B) there project from its walls between the forks of the suspensorial rods (*HS*) of the hypopharynx, anterior to the mandibles, a pair of small lobes (*l*), which are suggestive of being remnants of the postantennal appendages.

In the Chilopoda the hypopharynx is a small postoral lobe of the ventral head wall (Fig. 61 A, *Hphy*), but it is supported by a pair of large suspensorial plates (*HS*) that extend laterally and are connected with the ventral edges of the cranium at points (*d*, *d*) before the bases of the mandibles. From each plate there is given off posteriorly an apodemal process (*HA*) into the head cavity at the side of the stomodaeum. It is possible, as we shall see presently, that these hypopharyngeal apophyses of the chilopods are related to the anterior tentorial arms of insects.

The Tentorium.—In pterygote insects the lower edges of the epicranial walls are braced by an endoskeletal structure known as the *tentorium.* The tentorium is formed by two pairs of cuticular invaginations that unite within the head to compose a framework arching over the ventral nerve cord, but passing beneath the stomodaeum and supporting the latter. The component invaginations are the *anterior tentorial arms* and the *posterior tentorial arms.* The first arise from the anterior tentorial pits in the subgenal sutures or in the epistomal suture; the second take their origins from the posterior tentorial pits in the lower ends of the postoccipital suture. Very commonly the tentorium includes also a pair of *dorsal arms* (Figs. 58 B, 62 B, *DT*) extending from the anterior arms to the head wall near the bases of the antennae. The dorsal arms appear to be secondary outgrowths of the anterior arms, since, though sometimes firmly united with the cranial cuticula, they are often attached only to the epidermis, and their origin as external ingrowths has not been demonstrated.

In orthopteroid insects the tentorial arms unite in the middle of the back part of the head cavity to form an X-shaped structure (Fig. 76 B), the central part of which may become expanded, and in such cases the shape of the tentorium suggests a tent, as the name implies, or a canopy braced by four stays. In many other insects, however, the tentorial structure has the form of the Greek letter π, inverted when seen from behind (Fig. 62 A), the posterior arms being continuous in a transverse bar, or *tentorial bridge* (*TB*), through the back of the head, with the anterior arms (*AT*) attached to it near its outer ends. A study of the apparent origin of the tentorium in the Apterygota suggests that the π-form, rather than the X-form, is the more primitive type of tentorial structure (Fig. 58 B).

The shape of the pterygote tentorium is subject to numerous modifications. The central part of the structure may be enlarged to form a broad plate, the so-called "corporotentorium" (Fig. 62 C, *CT*). In some of the Orthoptera a pair of median processes arises at the bases of the anterior arms (C, *a*); in Blattidae these processes are united in an anterior bridge before the circumoesophageal connectives, which thus pass through an aperture in the central plate of the tentorium. The bridge composed of the posterior arms attains an excessive development in the termite soldier (Fig. 69 B, C), where it forms a long rooflike structure (*PT*) over the basal plate of the labium (*Pmt*), enclosing a triangular channel traversed by the ventral nerve connectives and the salivary ducts extending from the thorax into the head; from its anterior end the narrow anterior arms (*AT*) diverge to the facial wall of the head in the usual manner. The relative size of the anterior arms and the bridge varies much in different insects. In some the anterior arms form strong braces expanded against the subgenal or epistomal sutures, and in such cases the bridge may be reduced to a narrow bar (Fig. 62 D, *TB*) between the posterior tentorial pits; but, again, the anterior arms are slender rods or are reduced to mere threads (E, F), especially when the posterior bridge is large, and not unfrequently in such cases they appear to be entirely suppressed or represented only by a pair of spurs on the anterior margin of the bridge. Finally, the bridge itself may be incomplete and the posterior arms reduced to a pair of small processes (F, *PT*), either in conjunction with well-developed anterior arms or entirely isolated by the suppression of the latter. In rare cases there is no trace of a tentorial structure.

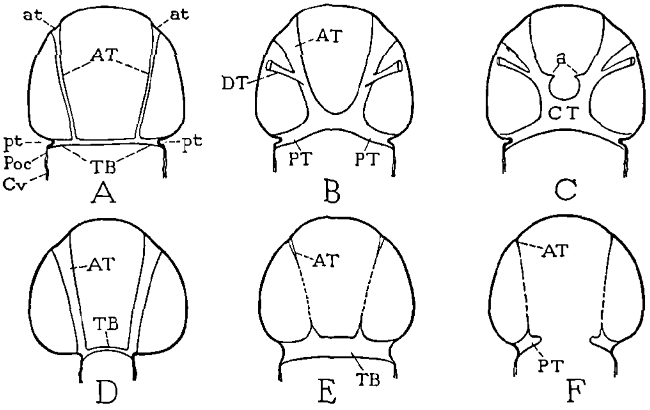

FIG. 62.—Various modifications of the tentorium. *AT*, anterior tentorial arms; *CT*, corporotentorium; *DT*, dorsal arms; *PT*, posterior arms; *TB*, tentorial bridge.

Besides bracing the cranial walls, the tentorium gives attachment to the ventral adductor muscles of the mandibles, maxillae, and labium, to the retractors of the hypopharynx, and to the ventral dilators of the stomodaeum. All these muscles are muscles that, it would seem, should take their origins on the sterna of the gnathal segments or on apodemal processes of the sterna, and yet the tentorium *appears* to be a tergal structure, since its arms in pterygote insects arise from the cranial walls dorsal to the bases of the gnathal appendages. In most insects the antennal muscles also arise on the tentorium, particularly on the dorsal arms.

A study of the Apterygota and Chilopoda suggests an explanation of the seeming anomaly in the relation of the pterygote tentorium to the ventral head muscles. In the Japygidae (Fig. 61 B) the ventral muscles of the gnathal appendages arise upon two long endoskeletal arms (*HA*) that spring from the base of the hypopharynx, where they are supported by two short divergent bars (*HS*). A similar structure, as we have seen, exists in the Chilopoda (A), but here the suspensoria of the apodemal arms (*HA*) are long sclerites (*HS*) that extend laterally to the ventral edges of the cranium, to which they are attached at points (*d, d*) anterior to the bases of the mandibles. In some of the Apterygota and in the Chilopoda, therefore, the ventral muscles of the gnathal appendages arise from a pair of endoskeletal processes that are clearly *sternal* apophyses of the gnathal region of the head. We can scarcely avoid the conclusion, then, that these sternal apophyses are in some way homologous with the anterior arms of the pterygote tentorium.

Sufficient evidence is not yet at hand to show the exact manner by which the hypopharyngeal sternal apophyses, which retain their primitive ventral position in some of the Apterygota, may have been transposed in the Pterygota to the facial region of the cranium, where evidently they have become the anterior arms of the tentorium. But the fact that in many of the lower Pterygota the anterior tentorial arms take their origins laterally in the subgenal sutures, and not in the epistomal suture, suggests that the apophyses have migrated first to this position, and subsequently to that in the epistomal suture. In the larvae of Ephemerida the anterior tentorial arms arise from deep lateral grooves of the head wall just above the bases of the mandibles; these grooves evidently represent the subgenal sutures of higher insects; but in *Lepisma* the anterior tentorial roots lie in the membranous areas between the bases of the mandibles and the lateral margins of the clypeus.

The pterygote tentorium, it thus appears, is a composite structure formed of tergal and sternal elements. Its anterior arms, bearing the attachments of the ventral muscles of the head appendages, are primitively sternal apophyses, analogous to the sternal apophyses of the thorax, that have secondarily migrated to the lateral or facial walls of the head; the posterior bridge is formed by a pair of tergal apodemes arising in the suture between the maxillary and labial segments. After the union of the anterior arms with the posterior bridge, the muscles of the former have migrated to all parts of the tentorium, and even in some cases to the adjoining cranial walls. The muscles of the antennae evidently have gained access to the tentorium by way of the secondary dorsal arms. In the more generalized condition found in some insect larvae the antennal muscles arise on the dorsal walls of the cranium.

3. SPECIAL MODIFICATIONS IN THE STRUCTURE OF THE HEAD

The important structural modifications of the head affect principally the frontoclypeal area and the posterior lateral and ventral regions.

Modifications in the facial plates are often correlated with variations in the relative size of the buccal and pharyngeal parts of the stomodaeum or with the special development of the cibarium as an organ of sucking. Modifications in the posterior ventral parts of the head are associated with a flattening and elongation of the cranial capsule, usually resulting from an upward revolution of the head on the neck by which the mouth parts become directed forward, and, in certain orders, are accompanied by an elongation of the base of the labium or the addition of a *gula* to its proximal part.

Modifications in the Frontoclypeal Region of the Head.—The frons and the clypeus, as we have seen, are not always clearly defined or delimited cranial areas, since the epistomal suture is frequently absent, as in the head of the cockroach (Fig. 58 A), and the frontal sutures themselves are generally obsolete or suppressed. Moreover, even when the facial sutures are present they may depart so widely from their typical positions that they cannot readily be identified. In such cases the student must consult other characters than the sutures for determining the true frontal and clypeal areas.

When the epistomal suture is absent, the anterior tentorial pits lie in the anterior ends of the subgenal sutures (Fig. 58, *sgs*); but when the epistomal suture is present, the pits are usually in this suture (Fig. 63 A, *at, at*) regardless of its displacement. The epistomal suture, when present, therefore, is to be identified as the suture of the face containing the anterior tentorial pits. Additional evidence of the identity of the clypeal and frontal areas, especially valuable when the epistomal suture is absent, may be deduced from the attachments of certain muscles on the cranium. The clypeus is the area upon which arise the dilator muscles of the cibarium and the dorsal muscles of the buccal cavity, or that part of the stomodaeum just within the mouth (Fig. 60 A, *dlcb, dlbc*). These muscles lie anterior to the frontal ganglion (Fig. 155, *FrGng*). The frons gives attachment to the muscles of the labrum (Fig. 60, *mlra, mlrp*) and to stomodaeal dilators lying posterior to the frontal ganglion (Fig. 155). The frons also bears, usually in its upper angle, the median ocellus (Fig. 56 A) when the latter is present. By following these principles a consistent identification of the facial cranial areas becomes possible in most cases.

As long as the epistomal suture maintains its direct course across the face (Fig. 63 A), no complications arise; but the suture is frequently arched upward, and this change in the position of the suture extends the clypeus into the facial region and reduces the area of the frons. A modification of this kind has taken place in the Hymenoptera, as seen in the larval head of *Vespa* (B), in the adult of the currant sawfly (*C*), and in the honey bee (D), where the clypeus extends upward almost to the bases of the antennae. The arched epistomal suture (*es*) is to be identified by the tentorial pits (*at*, *at*) in its course. In the caterpillars the clypeus takes on a triangular form (Fig. 64 A) and has generally been mistaken for the frons. That the triangular plate of the caterpillar's face is the clypeus, however, is attested by the facts that the anterior tentorial arms arise from its lateral sutures (B, *AT*) and that the dorsal dilator muscles of the mouth cavity have their origins on its inner surface. The labral muscles (*mlrp*), on the other hand, arise as usual on the true frontal area, which in the caterpillar is invaginated above the apex of the clypeus (*Fr*). The clypeus attains its greatest development in some of the Hemiptera (Fig. 177), where it often forms a large bulging plate of the face, which accommodates the huge dilator muscles of the sucking pump.

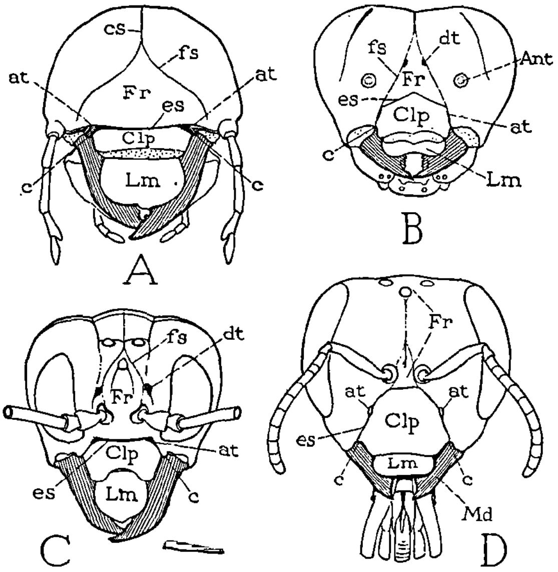

FIG. 63.—Various types of heads showing modification and suppression of the frontal sutures. A, larva of *Popillia japonica*. B, larva of *Vespa*. C, adult of *Pteronidea ribesii*. D, adult of *Apis mellifica*.

The frons is typically a triangular area narrowed dorsally between the converging frontal sutures (Fig. 63 A, *Fr*), and it usually preserves its triangular shape, but its limits are generally obscured by a partial or complete suppression of the frontal sutures. The true frontal region, however, is to be identified by the location of the median ocellus and the origins of the labral muscles upon it. It always lies between the antennae, though it may be greatly narrowed or constricted by the approximation of the bases of these appendages. In the larval head of *Vespa* (B) the frons is distinct (*Fr*), but it is reduced in size by the upward extension of the clypeus. In the adult head of *Pteronidea* (C) the frontal sutures are obsolete ventrally where the frontal region is narrowed between the approximated bases of the antennae. In the adult honey bee (D) the frontal sutures are obliterated, but the frontal region (*Fr*) must extend upward from the clypeus to include the median ocellus, and upon this region, just above the bases of the antennae, are attached the muscles of the labrum. In the Hemiptera the frons may be apparent as a small triangular area upon which is located the median ocellus (Fig. 177 B, *Fr*), but usually it is not defined from the vertex, though the latter may be greatly enlarged (F, H) or greatly reduced (J).

The frons suffers an extreme modification in the caterpillar head. It is here transformed into the shape of an inverted Y by the upward growth of the clypeus into its ventral part. The stem of the Y, moreover, has sunken into the head by a median invagination of the head wall above the apex of the clypeus. The dorsal part of the frons, therefore, is to be seen internally as a deep fold or ridge (Fig. 64 B, *Fr*) upon which arise the labral muscles (*mlrp*). The ventral parts, or arms of the frontal Y, are apparently the narrow strips between the clypeus and the parietals, which entomologists usually term the "adfrontals" (A, *fr*). The true vertex of the caterpillar's head is cut out by the posterior emargination of the dorsal wall of the cranium.

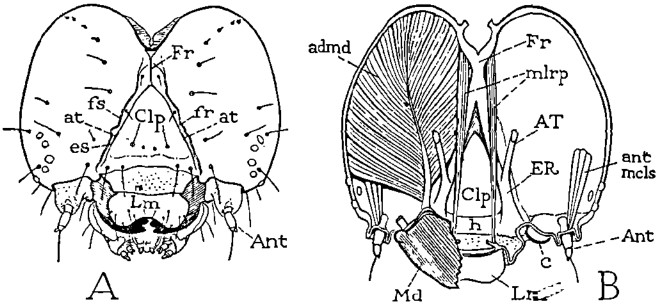

FIG. 64.—Head of a caterpillar. A, *Lycophotia margaritosa*, anterior view. B, *Prionoxystus robiniae*, interior of the head from behind, showing invaginated frons (*Fr*) on which the labral muscles (*mlrp*) are attached.

Modifications in the Posterior Ventral Region of the Head.—In the more generalized type of cranial structure, as in the Orthoptera (Fig. 59 B), there is no ventral sclerotization of the head wall between the foramen magnum and the base of the labium, the submentum (*Smt*) being directly continuous with the neck membrane between its lateral attachments to the cranial margins just behind the posterior tentorial pits. In many insects, however, the postgenal regions of the cranium are greatly lengthened anteroposteriorly, and a long space intervenes between the foramen magnum and the mandibles. Two different types of structure are developed upon this modification, both of which involve a sclerotic separation of the true base of the labium from the foramen magnum. In one type the separation is formed by the mesal extension of hypostomal lobes of the cranial walls forming a more or less complete ventral *hypostomal bridge* proximal to the labium; in the other a sclerotization of the gular region of the neck, uniting the ventral margins of the cranium proximal to the posterior tentorial pits, is added to the base of the labium and constitutes a ventral plate of the head wall known as the *gula*.

The Hypostomal Bridge.—Mesal extensions of the hypostomal areas of the cranium are a characteristic feature of the head of lepidopterous larvae; in adult Hymenoptera, Diptera, Heteroptera, and certain other insects the hypostomal lobes are united in a complete bridge closing the foramen magnum ventrally.

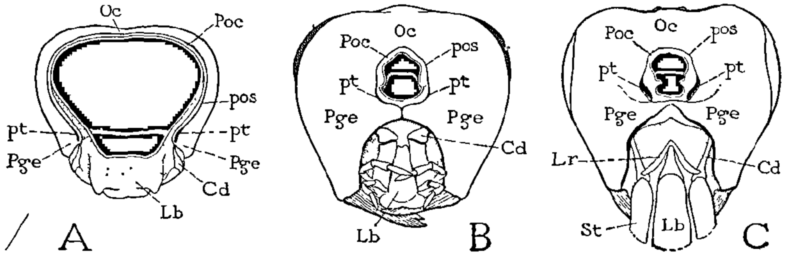

FIG. 65.—Heads of Hymenoptera, showing evolution of the hypostomal bridge formed by united median lobes of the postgenal regions. A, larva of *Vespa*. B, adult of *Vespa*. C, adult of *Apis mellifica*.

On the ventral side of a caterpillar's head (Fig. 164 C) it will be seen that the base of the labiomaxillary complex is separated from the neck by two sclerotic lobes (*Hst*) extending mesally from the lateral walls of the cranium. These lobes are expansions of the hypostomal parts of the subgenal margin of the cranium, and each is separated from the corresponding postgenal region by a distinct hypostomal suture (*hs*), which extends posteriorly to the root of the posterior arm of the tentorium concealed in the deep inflection at the base of the neck. The hypostomal lobes vary in size in different groups of caterpillars, but they do not unite to form a complete hypostomal bridge.

A structural condition in the back of the head very similar to that of the caterpillars is found again in adult Tenthredinidae, which leads to a further specialization in the higher Hymenoptera. In *Pteronidea*, for example, the labium is displaced ventrally and united with the maxillae, and the base of the labiomaxillary complex is separated from the foramen magnum by two approximated hypostomal lobes of the cranial wall. In the adult of *Vespa* (Fig. 65 B) the hypostomal lobes are contiguous and united, forming thus a sclerotic bridge between the postgenal areas of the cranium (*Pge*), completely separating the foramen magnum from the fossa containing the labium and maxillae. The hypostomal sutures are here absent, and the hypostomal lobes are continuous with the postgenae. The evolution of the hypostomal bridge in the Hymenoptera reaches its final stage in the bees (C), where the line of union between the two hypostomal lobes is obliterated, and the posterior surface of the head presents a wide, continuous occipito-postgenal-hypostomal area in the center of which is the greatly reduced foramen magnum. A similar condition is found in the higher Diptera.

It is important to note that in adult Hymenoptera and Diptera, as in the larvae of Lepidoptera, the posterior pits of the tentorium (Fig. 65 B, C, *pt*) retain their primary positions in the lower parts of the postoccipital suture (*pos*) close to the foramen magnum and thus preserve in this respect the more primitive larval condition (A).

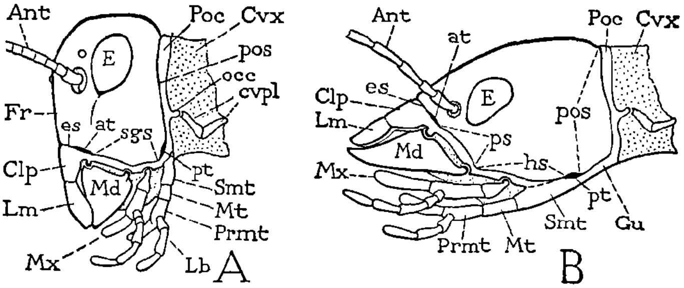

Fig. 66.—Diagrams illustrating the hypognathous (A) and prognathous (B) types of head structure.

The Gula.—The modifications in the posterior ventral parts of the head of insects in which a gula is developed are generally associated with a prognathous condition; the head, usually more or less flattened, is turned upward on the neck (Fig. 66 B), causing the true anterior surface to become dorsal, and the mouth parts to be directed forward. In insects of this type the under side of the head, which morphologically is the posterior surface, is lengthened by an expansion of the postgenal areas of the cranium; the bases of the maxillae lie far in advance of the foramen magnum, the hypostomal parts of the subgenal sutures (*hs*) are extended, and the basal region of the labium is correspondingly elongated. In many prognathous insects, particularly in Coleoptera, a part of the ventral extension of the head lies posterior to the tentorial pits (*pt*), and in such cases the lower ends of the postoccipital suture (*pos*), which terminate in the pits, appear to be drawn forward on the lower wall of the cranium. In the space between the ventral parts of the postoccipital suture, proximal to the tentorial pits, is formed the gula (*Gu*).

In studying the modifications of the head that have produced the gula of Coleoptera it is possible to start with forms that preserve the generalized or orthopteroid type of structure. The posterior surface of the head of a scolytid or scarabaeid larva (Fig. 67 A), for example, differs in no essential respect from that of *Gryllus* (Fig. 59 B). The labium of the scarabaeid larva is suspended from the neck membrane by a basal plate (*Pmt*), which is attached laterally to the postoccipital margins of the head (*Poc*) at points (a''', a''') just behind the tentorial pits (*pt, pt*) exactly as in the labium of the cricket. There is no sclerotization in the scarabaeid larva that might be regarded as a gula.

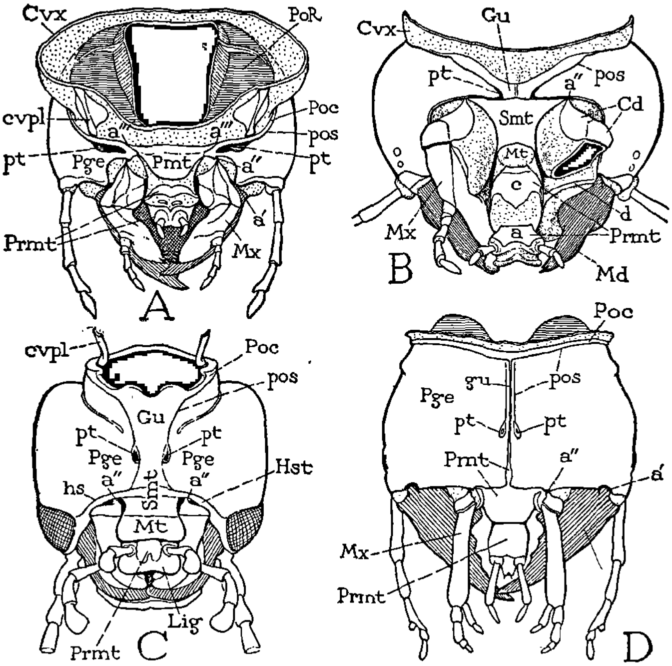

FIG. 67.—Heads of Coleoptera showing evolution of the gula. A, *Popillia japonica* larva; gula absent. B, *Silpha* larva; short gula (*Gu*) proximal to posterior tentorial pits (*pt*). C, *Epicauta* adult; gula typically developed. D, *Scarites* larva; gula obliterated, the gular area (*gu*) reduced to a median "suture."

The head of a silphid beetle larva (Fig. 67 B) has in general the same structure as that of the scarabaeid larva (A), though it is somewhat more elongate; but proximal to the tentorial pits (*pt*) there is here a short median sclerotic area, or gula (*Gu*), lying proximal to the basal plate of the labium (*Smt*) and continuous laterally with the postoccipital rim of the cranium behind the postoccipital suture (*pos*).

With the elongation of the postgenal areas of the cranium proximal to the tentorial pits, the gular plate becomes correspondingly lengthened.

The characteristic structure of a coleopterous head having a well-developed gula is shown in the adult head of a meloid beetle (Fig. 67 C). The form of the cranium here differs from that of the scarabaeid or silphid larva principally in the lengthening of the postgenal regions to accommodate the head to a more horizontal position. The general extension of the posterior part of the cranium has been accompanied by an elongation of the gula (*Gu*), so that the tentorial pits (*pt, pt*) now lie a considerable distance anterior to the foramen magnum, and the lower ends of the postoccipital suture (*pos*) appear to be drawn forward behind the pits.

In certain coleopterous larvae the region occupied by the gula of the adult insect is entirely membranous (Fig. 160 A, *gu*), being merely an extension of the neck membrane in a ventral emargination of the head wall extending forward to the base of the labium. This region becomes sclerotized in the adult as a gular plate (B, *Gu*) continuous proximally with the postoccipital rim of the foramen magnum (*Poc*), and distally with the basal plate of the labium (*Smt*). Since the gula seldom has a median suture, it is apparently formed in most cases by a uniform sclerotization of the region primarily belonging to the neck between the lower ends of the postoccipital margins proximal to the tentorial pits. The parts of the postoccipital suture separating the gula from the postgenae are commonly termed the "gular sutures." The gula varies in length according to the position of the tentorial pits, and it is sometimes narrowed, or almost obliterated, by a median approximation of the postgenal margins of the cranium (Fig. 68 A). A well-developed gula occurs also in some Neuroptera (Fig. 68 B).

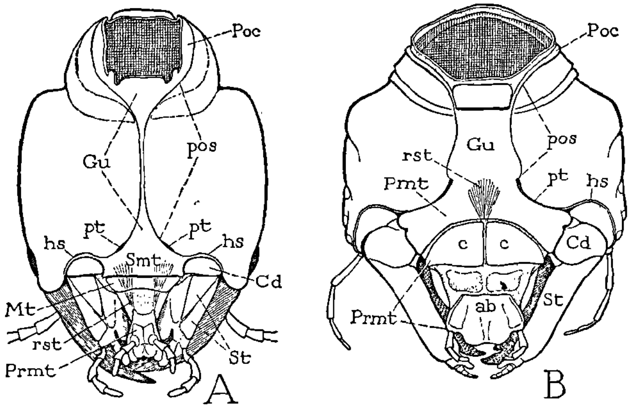

FIG. 68.—Types of gular and labial structures in Coleoptera and Neuroptera. A, *Staphylinus cinnamopterus* adult: gula narrow; postmentum subdivided into mentum (*Mt*) and submentum (*Smt*); prementum (*Prmt*) simple. B, *Corydalus* larva: gula broad; postmentum (*Pmt*) undivided; prementum (*Prmt*) subdivided.

In many Coleoptera, especially in larval forms, there is no gula though the head may be elongate and the posterior tentorial pits may have an anterior position on the ventral side of the head. We have just noted, for example, that the gular area of the adult (Fig. 160 B) may be represented in the larva (A) by a wide membranous area of the neck (*gu*) proximal to the tentorial pits. In the larvae of *Scarites* (Fig. 67 D), *Thinopinus* (Fig. 160 C), *Staphylinus* (D), and many other beetles, the gular region is narrowed to a median line or "suture" (*gu*) between the approximated postgenal areas of the cranium.

Among the Isoptera the head of the soldier caste is often greatly lengthened posteriorly to accommodate the muscles of the huge mandibles (Fig. 69 A). The single proximal plate of the labium (*Pmt*) is in such cases correspondingly lengthened between the long postgenal regions of the cranium (*Pge*) and is sometimes called the "gula." The apparent "gular sutures" (*pt, pt*) separating it from the postgenae, however, are found by examining the interior of the head (B) to be the lines of inflections that form the broad, plate-like posterior arms of the tentorium (B, C, *PT*). In the termite soldier, therefore, the grooves at the sides of the "gular" region of the labium (A, B, C, *pt, pt*) are the greatly lengthened posterior tentorial pits, and the structure of this part of the termite head, while similar to that in the Coleoptera, is not identical with the usual gular structure in this order, though in some of the Scarabaeidae the gula is likewise demarked by the greatly elongate tentorial pits (Fig. 159 D, *pt*).

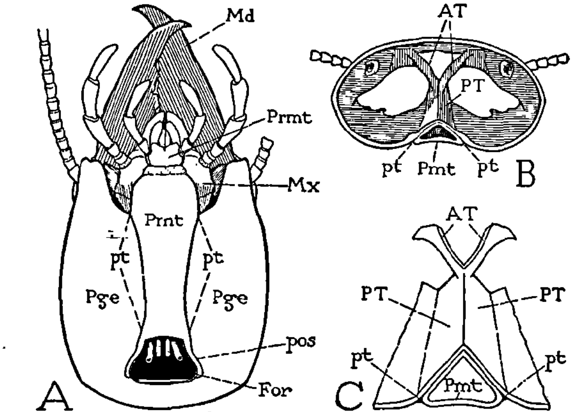

Fig. 69.—Head of *Termopsis*, soldier form. A, under surface of head showing long postmentum bounded by elongate posterior tentorial pits (*pt*). B, cross section of head showing tentorium. C, diagram of tentorium, seen from behind, showing posterior arms (*PT*) united to form the roof of a long ventral channel above the postmentum (*Pmt*).

GLOSSARY OF TERMS APPLIED TO THE HEAD

Antennal Sclerite (*ASc*).—The sclerotic rim of the antennal socket within the antennal suture.

Antennal Suture (*as*).—The line of inflection in the cranial wall surrounding the antennal socket.

Cibarium (*Cb*).—The food pocket of the extraoral or preoral mouth cavity between the base of the hypopharynx and the under surface of the clypeus.

Clypeus (*Clp*).—The facial area of the cranium just above the labrum, usually separated from the frons by an epistomal suture, and sometimes divided into an *anteclypeus* (*AClp*) and a *postclypeus* (*Pclp*); the dilator muscles of the cibarium are attached on its inner surface.

Coronal, or Metopic, Suture (*cs*).—The median dorsal arm of the epicranial suture.

Cranium.—The sclerotic, skull-like part of the head.

Epicranial Suture.—The dorsal Y-shaped suture of the cranium, including the median *coronal suture* (*cs*) of the vertex, and the divergent *frontal sutures* (*fs*) of the facial region.

Epicranium.—A term variously applied to the entire cranium, to the cranium exclusive of the frons, or preferably to the upper part of the cranium.

Epipharynx (*Ephy*).—A median lobe sometimes present on the posterior (or ventral) surface of the labrum or clypeus.

Epistomal Suture (*es*).—The frontoclypeal suture; a groove uniting the anterior ends of the subgenal sutures across the face, forming internally a strong *epistomal ridge* (*ER*), typically straight, but often arched upward, sometimes absent.

Foramen Magnum (*For*).—The opening from the head into the neck, usually called the *occipital foramen*.

Frons (*Fr*).—The facial area of the cranium between the frontal and epistomal sutures, or the corresponding area when the sutures are absent, bearing the median ocellus and the origins of the labral muscles.

Frontal Sutures (*fs*).—The arms of the epicranial suture diverging ventrally (or anteriorly) from the coronal suture *between* the antennal bases toward the anterior articulations of the mandibles.

Fulturae.—See *suspensorium of hypopharynx*.

Genae (*Ge*).—The lateral parts of the parietals, generally the areas behind and beneath the eyes.

Gnathocephalon (*Gnc*).—The part of the head formed by the gnathal segments, bearing the mandibles and the first and second maxillae.

Gula (*Gu*).—A median ventral plate of the head in some prognathous insects formed by a sclerotization of the neck region proximal to the posterior tentorial pits, continuous with the postmentum or submentum.

Gular Sutures.—The ventral ends of the postoccipital suture extended forward on the under side of the head in some prognathous insects.

Hypopharynx (*Hphy*).—The median postoral lobe of the ventral wall of the gnathal region of the head anterior to the labium.

Hypostoma (*Hst*).—The part of the subgenal margin of the cranium posterior to the mandible, usually narrow, but sometimes extended mesally as a hypostomal plate or as a hypostomal bridge in the ventral wall of the head.

Hypostomal Suture (*hs*).—The part of the subgenal suture posterior to the mandible, often obsolete or suppressed.

Labrum (*Lm*).—The preoral lobe of the head suspended from the clypeus, with muscles arising on the frons.

Mouth (*Mth*).—The external opening of the stomodaeum, situated in the ventral wall of the head between the labrum and the hypopharynx.

Occipital Arch.—The area of the cranium between the occipital and postoccipital sutures; its dorsal part is the *occiput* proper (*Oc*), its lateral parts the *postgenae* (*Pge*).

Occipital Condyles (*occ*).—Processes on the margin of the postocciput to which the lateral neck plates are articulated.

Occipital Suture (*ocs*).—A transverse groove sometimes present on the back of the head ending ventrally anterior to the posterior articulations of the mandibles.

Occiput (*Oc*).—The dorsal part of the occipital arch, or also the entire arch including the postgenae.

Ocular Sclerite (*OSc*).—A narrow band of the cranial wall encircling the compound eye within the ocular suture.

Ocular Suture (*os*).—The line of inflection in the cranial wall around the compound eye, forming internally a circumocular ridge.

Parietals (*Prtl*).—The lateral areas of the cranium between the frontal and occipital areas, separated above by the coronal suture.

Peristome.—The ventral marginal part of the cranium formed by the clypeus, or epistoma, the pleurostomata, and the hypostomata.

Pleurostoma (*Plst*).—The subgenal margin of the cranium bordering the mandible.

Pleurostomal Suture (*ps*).—The part of the subgenal suture above the mandible.

Postfrontal Sutures (*pfs*).—Facial sutures present in some insects diverging from the coronal suture *laterad* of the antennal bases.

Postgenae (*Pge*).—The lateral and ventral parts of the occipital arch, or areas of the cranium posterior to the genae.

Postoccipital Suture (*pos*).—The posterior submarginal groove of the cranium having the posterior tentorial pits in its lower ends; internally it forms the *postoccipital ridge* (*PoR*) on which are attached the dorsal prothoracic and neck muscles of the head.

Postocciput (*Poc*).—The extreme posterior rim of the cranium behind the postoccipital suture, probably a sclerotic remnant of the labial somite.

Procephalon (*Prc*).—The region of the definitive head anterior to that of the gnathal segments, representing the primitive protocephalon, formed in the embryo from the cephalic lobes and the tritocerebral segment; bearing the labrum, the mouth, the eyes, the first antennae, and the second antennae when the last are present.

Ptilinal Suture.—The crescentic groove cutting across the frons above the antennal bases in Diptera where the ptilinum has been withdrawn.

Ptilinum.—An eversible sac of the frons in dipterous pupae used for rupturing the puparium.

Salivarium (*Slv*).—The pocket between the base of the hypopharynx and the labium into which opens the salivary duct; in higher insects converted into a salivary pump or a spinning apparatus.

Subgenal Areas (*Sge*).—The usually narrow lateral marginal areas of the cranium set off by the subgenal sutures above the gnathal appendages, including the pleurostomata and hypostomata.

Subgenal Sutures (*sgs*).—The lateral submarginal grooves of the cranium just above the bases of the gnathal appendages, forming internally a subgenal ridge (*SgR*) on each side, continuous anteriorly with the epistomal suture when the latter is present.

Suspensorium of the Hypopharynx.—A pair of bars or groups of sclerites in the lateral walls of the adoral surface of the base of the hypopharynx. (*Fulturae.*)

Tentorial Pits.—The external depressions in the cranial wall at the roots of the tentorial arms; the *anterior tentorial pits* (*at*) located in the subgenal sutures or usually in the epistomal suture, the *posterior tentorial pits* (*pt*) in the lower ends of the postoccipital suture.

Tentorium (*Tnt*).—The endoskeletal brace of the cranium formed of united anterior and posterior pairs of arms, bearing primarily the origins of the ventral muscles of the gnathal appendages, and usually giving attachment secondarily, on a pair of dorsal arms, to the antennal muscles.

Vertex (*Vx*).—The top of the cranium between and behind the compound eyes.

CHAPTER VII

THE HEAD APPENDAGES

The usual appendages of the insect head include a pair of *antennae*, a pair of *mandibles*, a pair of *maxillae*, and the *labium*, the last representing a pair of united second maxillae. In the embryo of the walkingstick insect, however, there has been observed a pair of lobes lying anterior to the antennae, which possibly are rudiments of a pair of *preantennae*, and in the embryonic stages of various insects there are rudiments of *postantennal appendages.* The series of cephalic appendages appears to be the same in Crustacea and Myriapoda as in insects, except that the postantennal appendages are usually highly developed as the second antennae in Crustacea and appear to be entirely absent, even as embryonic vestiges, in Chilopoda. The homologies of the head appendages in the several mandibulate groups are established by their innervation from corresponding cerebral and postcerebral nerve centers. In many Crustacea a pair of ventral head lobes known as the *paragnatha* occurs between the mandibles and the first maxillae, and a similar pair of lobes, the *superlinguae,* is present in some insects as lateral parts of the hypopharynx. Since the superlinguae of insects have been supposed to represent a pair of head appendages, they will be discussed in the present chapter, though it now seems probable that neither the paragnatha nor the superlinguae have the status of segmental limbs.

Associated with the head appendages is a series of paired glands, which appropriately may be described in connection with the appendages.

1. PREANTENNAL APPENDAGES

The existence of preantennal appendages in the Arthropoda cannot as yet be regarded as established. Heymons (1901), however, has described and figured a pair of evanescent appendage-like lobes in the embryo of *Scolopendra* lying anterior to the antennae (Fig. 70 A, *Prnt*), and Wiesmann (1926) reports the presence of a pair of similar preantennal rudiments in the embryo of a phasmid insect, *Dixippus morosus* (B, *Prnt*). The stalks bearing the compound eyes in certain Crustacea have an appendage-like structure, since they are movable, segmented, and amply provided with muscles; but since the compound eyes certainly belong to the prostomium, it seems most probable that the crustacean eye stalks are of the nature of the sensory tentacular organs of the prostomium in Annelida.

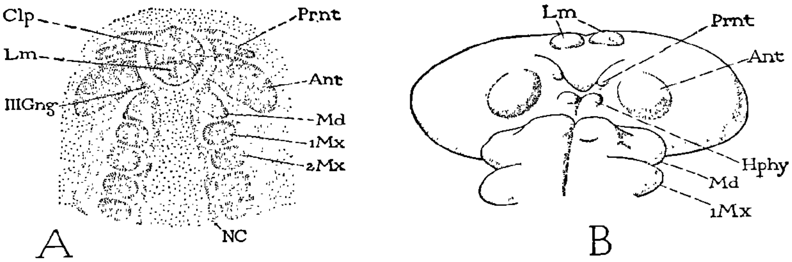

Fig. 70.—Examples of the presence of apparent rudiments of preantennal appendages (*Prnt*) in arthropod embryos. A, *Scolopendra*. (*From Heymons*, 1901.) B, *Dixippus* (*Carausius*) *morosus*. (*From Wiesmann*, 1926.)

2. THE ANTENNAE

The antennae are the first of the appendicular organs of the head present in the adult insect. They are innervated from the deutocerebral lobes of the brain and generally have been regarded as the appendages of a corresponding antennal segment. Neither in their segmentation nor in their musculature, however, do the insect antennae resemble the limbs of the postoral somites, and the homologous organs of the Crustacea, the first antennae, or antennules, are never biramous in the manner characteristic of the second antennae and the succeeding appendages. If the antennae are not true segmental limbs, they must be regarded as organs analogous to the prostomial tentacles of the annelid worms. Though in the embryos of some of the lower insects the antennal rudiments arise at the sides of the mouth, or even behind the latter, the morphologically preoral position of their nerve centers in the brain suggests that the antennae belong to the preoral part of the head. In adult insects the antennae are situated on the anterior parts of the parietal regions of the cranium, usually on the facial aspect, but in many larvae and in some adults they are placed laterally just above the bases of the mandibles. Antennae are absent in the Protura, and they are practically absent in most larvae of the higher Hymenoptera, where the position of each is indicated only by a disc or a slight swelling over the tip of the imaginal organ developing beneath the larval cuticula.

The typical insect antenna is a many-jointed filament, but generally three principal parts may be distinguished in its shaft (Fig. 71 A). The first part, by which the antenna is attached to the head, is usually larger than the others and constitutes a basal stalk of the appendage, termed the *scape* (*Scp*). The second part, or *pedicel* (*Pdc*), is short and in nearly all insects contains a special sensory apparatus known as the organ of Johnston. The part of the antenna beyond the pedicel is the *flagellum, or clavola (Fl).* The flagellum is usually long and made up of many small subsegments, but it may be abbreviated or reduced to a single piece. Since the flagellar divisions in orthopteroid insects increase in number from one instar to the next, they appear to be secondary subdivisions of one primary antennal segment. The antennae are subject to many variations in form, giving rise to the several distinct types recognized in descriptive entomology, but the basic structure of the appendages is remarkably uniform.

The base of the antenna is set into a small membranous area of the head called the *antennal socket.* The rim of the socket is often strengthened by an internal submarginal ridge formed by an external inflection, the *antennal suture* (Fig. 71 A, *as*). Usually a pivotlike process on the rim of the antennal socket (*n*) forms a special support and articular point for the base of the scape, allowing the antenna a free motion in all directions. The pivot, or *antennifer,* is generally ventral but is not always so, and in some cases it is obsolete or absent.

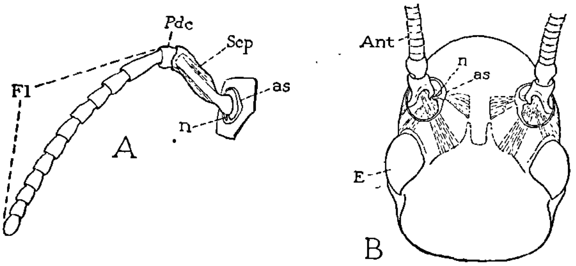

FIG. 71.—Structure of the antenna. A, diagram showing the typical segmentation of an insect antenna. B, head of a chilopod, *Scutigera forceps,* with antennal muscles arising on the cranium. *as,* antennal suture; *Fl,* flagellum; *n,* articular point (antennifer); *Pdc,* pedicel; *Scp,* scape.

Each antenna is moved as a whole by muscles inserted on the base of the scape. The origin of the antennal muscles in adult pterygote insects is commonly on the dorsal or anterior arms of the tentorium, but in some larval insects the muscles arise on the walls of the cranium (Fig. 64 B), as they do in the chilopods (Fig. 71 B). The attachment of the antennal muscles on the tentorium, therefore, is probably a secondary condition resulting from a migration of the cranial ends of the muscles to the dorsal tentorial arms after the latter have made connections with the head wall. The pedicel and the flagellum together are moved by muscles arising in the scape and inserted on the base of the pedicel (Fig. 71 A), but the flagellum and its subsegments, so far as observed by the writer, are never provided with muscles in insects.

3. THE POSTANTENNAL APPENDAGES

The appendages of the tritocerebral segment of the arthropods undoubtedly belong to the series of true limbs, and it seems very probable that they represent the first pair of appendages in this series. Morphologically the postantennal appendages are postoral, since they are innervated from the tritocerebral lobes of the brain, which are unquestionably postoral ganglia, since they preserve their ventral connections by a substomodaeal commissure. The postantennal appendages occur as functional adult organs only in Chelicerata and Crustacea. In the first group they form the chelicerae (Fig. 72 A); in the second they are the highly developed second antennae (B), which have distinctly the biramous leg type of structure, segmentation, and musculature.

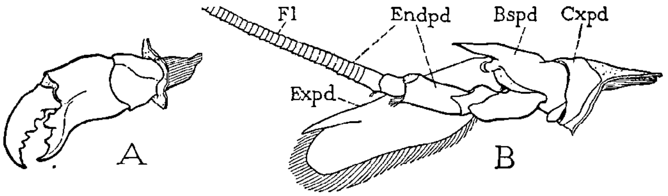

FIG. 72.—Types of functional postantennal appendages. A, chelicera of a scorpion. B, second antenna of a decapod crustacean, *Spirontocharis*, with biramous structure like that of following appendages.

The postantennal appendages are at best rudimentary in all insects. Embryonic vestiges of them occur in representatives of several orders and are usually called "second antennal," "intercalary," or "premandibular" appendages (Fig. 23 B, *Pnt*). In a few adult insects (*Campodea, Machilis heteropus, Dissosteira*) small lobes have been observed before the mandibles, which may possibly be persisting rudiments of the postantennal appendages (Fig. 60 B, *l*). The occurrence of corresponding structures has not been recorded in any stage of the myriapods. We have no evidence to suggest what the form of the postantennal appendages may have been when they were functional organs in insects, but it is perhaps reasonable to suppose that in terrestrial arthropods, in which the gnathal appendages were not yet added to the head, the tritocerebral appendages served in some capacity connected with feeding.

4. THE MANDIBLES

The mandibles are the appendages of the first gnathal segment and are undoubtedly homologous organs in all the mandibulate arthropods. The corresponding appendages of the Chelicerata are the pedipalps.

The typical mandible of pterygote insects is a strong biting jaw hinged to the head by anterior and posterior articulations, and having a transverse movement of abduction and adduction produced by abductor and adductor muscles arising on the dorsal wall of the cranium. In most of the apterygote insects, however, and in the Mandibulata generally, the mandible has a single point of articulation, and dorsal and ventral muscles, suggesting that it has been evolved from the basis of a leglike appendage provided with the usual tergal and sternal promotor and remotor muscles. The presence of a well-developed telopodite in the form of a segmented palpus on the mandible of many Crustacea, and the limblike structure of the corresponding appendage in certain Arachnida amply confirm the leg origin of the arthropod jaw.

To understand the more specialized, though simpler, mandible of the Pterygota, we must first study the structure and musculature of the organ as found in apterygote insects and in other mandibulate arthropods. The leglike form of the appendage is well shown in the pedipalp of a phalangid (Fig. 47, B), which consists of a basis (*Cxpd*) provided with a large endite lobe (*Bnd*), and a long telopodite of six segments that are clearly identical with the segments of the legs. Among the Mandibulata, the mandible appears to be in some respects most generalized in the Diplopoda, since in this group it has certain features suggestive of the structure of an insect maxilla. The jaw of the Chilopoda is evidently derived from an organ similar to the diplopod mandible. In the more generalized Crustacea and Hexapoda the appendage is more generalized in certain ways, though it is only in the Crustacea that it retains the telopodite; but in the higher forms of these groups the mandible presents numerous specializations in its structure, musculature, and mechanism.

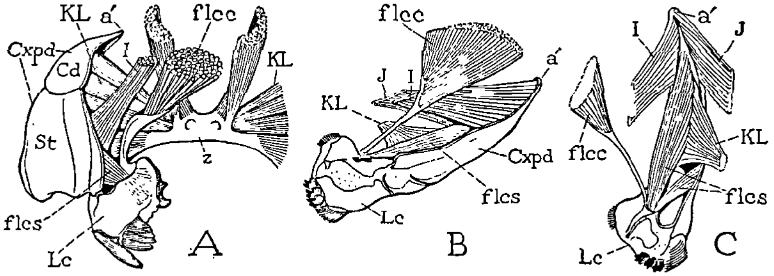

FIG. 73.—Mandibles and mandibular musculature of Myriapoda. A, right mandible of a diplopod, anterior view. B, left mandible of *Scutigera*, anterior view. C, right mandible of same, dorsal view.

The Mandibles of Diplopoda.—The diplopod mandible (Fig. 73 A) consists of a large basal part (*Cxpd*) and a movable terminal lobe (*Lc*). The sclerotic wall of the basis is distinctly divided into a proximal plate, or *cardo* (*Cd*), and a distal plate, or *stipes* (*St*). The musculature of the basis consists of two groups of fibers. The fibers of one group form a single anterior muscle (*I*) arising dorsally on the head wall and inserted on the upper (anterior) margin of the stipes. The fibers of the second group (*KL*) form numerous muscle bundles connected with each mandible, those from opposite sides taking their origins on a thick median ligament (*z*) from which they diverge into the cardo and stipes of each mandible, the two sets forming thus a strong *zygomatic adductor* between the two jaws. The median ligament is supported from the dorsal wall of the head by two large vertical muscles.

The movable distal lobe of the diplopod mandible (Fig. 73 A, *Lc*) is of particular interest because of its resemblance to the lacinia of an insect maxilla (Fig. 78, *Lc*). The lobe is hinged to the inner distal angle of the stipes and is provided with a short *stipital flexor* muscle (*flcs*) arising within the stipes, and with a large *cranial flexor* (*flcc*) arising on the head wall and inserted on a strong apodeme of the inner basal angle of the lobe.

The Mandibles of Chilopoda.—The chilopod mandible (Fig. 73 B, C) is similar to the jaw of the diplopod, but the basis (B, *Cxpd*) is not subdivided, and the distal lobe (*Lc*) is less movable, since it has no true articulation with the basis, though it is flexible on the latter and is provided with both stipital and cranial flexor muscles (*flcs*, *flcc*). The basis is rotated on its long axis by an anterior dorsal muscle (*I*) and a posterior dorsal muscle (*J*); and it is provided with a ventral adductor (*KL*), the fibers of which take their origin on a median ligament supported on a pair of ventral apophyses arising at the base of the hypopharynx (Fig. 61 A, *HA*).

The Mandibles of Crustacea.—The crustacean mandibles present a great variety of forms, with many types of mechanism resulting from the different ways in which the organs are articulated to the head or the mandibular segment. In the more generalized groups of both the Entomostraca and the Malacostraca, however, they have a type of structure very similar to that of the chilopod jaws. The mandibles of *Apus* and *Anaspides* are good representatives of this apparently generalized type of structure.

The mandible of *Anaspides* (Fig. 74 A) consists of an elongate basis (*Cxpd*) with a large endite lobe (*Bnd*) and of a small three-segmented telopodite, or palpus (*Tlpd*). The basis is broadly implanted by its entire inner surface on the membranous lateral wall of the mandibular segment and is provided with a single dorsal point of articulation (*a'*) with the tergum. The broad terminal lobe (*Bnd*) is entirely immovable on the basis, but it is differentiated into incisor and molar areas. The musculature of the *Anaspides* mandibles is very simple. Each jaw is provided with an anterior rotator muscle (*I*) and a posterior rotator (*J*), both arising on the dorsal wall of the mandibular segment, and with strong ventral adductor muscles (*KL*). The fibers of the adductors are separated into two groups; those of one group take their origin on a median ligament (*k*) arising from the ventral body wall, those of the other group are continuous from one jaw to the other and form a zygomatic adductor.

The mandibles of *Apus* are similar to those of *Anaspides*, but they lack palpi, and the adductor apparatus consists only of a large, dumbbell-shaped zygomatic muscle between the two jaws. This same type of mandible is found in many other crustaceans and is evidently the one from which the more specialized types have been evolved.

The Mandibles of Apterygote Insects.—Among the Apterygota the mandibles resemble those of the Chilopoda and the simpler Crustacea in all groups except Lepismatidae, in which they take on special features characteristic of the mandibles of Pterygota. In all insects the mandibular telopodite is entirely absent.

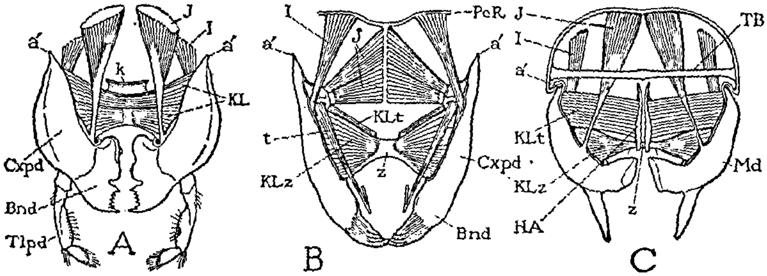

FIG. 74.—Generalized type of mandible in Crustacea and Hexapoda. A, *Anaspides tasmaniae*, posterior view. B, *Heterojapyx gallardi*, dorsal view. C, *Nesomachilis maoricus*, posterior view.

In the Japygidae the mandibles are deeply retracted into the head, but each consists of a slender basis (Fig. 74, B, *Cxpd*) articulated to the head by a single point of articulation (*a'*), and ending distally in an elongate terminal lobe (*Bnd*). The appendage is provided with anterior and posterior rotator muscles (*I*, *J*) arising on the dorsal wall of the head and is equipped with two ventral adductor muscles (*KL*). The fibers of one pair of adductor muscles from the two mandibles (*KLt*) arise medially on a pair of sternal apophyses of the head springing from the base of the hypopharynx (Fig. 61 B, *HA*). These apophyses, as we have seen (page 118), are evidently the prototypes of the anterior tentorial arms in the Pterygota. The fibers of the other pair of muscles (*KLz*) from the opposite jaws are united upon a median ligament (*z*) and constitute a common zygomatic adductor.

In the Machilidae the mandibles (Fig. 74 C) are exserted, but they have the same essential structure as in Japygidae. The free distal lobe of each is differentiated into a slender incisor point and a thick molar process. The muscle fibers of the adductor apparatus are disposed in two distinct groups, those of one group (*KLt*) forming a wide flat muscle attached medially on the corresponding hypopharyngeal apophysis (*HA*), those of the other (*KLz*) converging upon a narrow median ligament (*z*) to form, with the corresponding group from the opposite jaw, a zygomatic adductor between the two mandibles.

Morphology of the Arthropod Mandibles.—From the brief review just given of the basic structure of the mandibles in the principal groups of mandibulate arthropods, it is evident that the mandible has been evolved from a limb of the ambulatory type, and that the modifications that have produced the more generalized forms of the jaw are of a comparatively simple nature.

The body of the mandible corresponds to the coxopodite of a generalized appendage; the telopodite is retained as a palpus in many of the Crustacea, but in other groups it has been completely suppressed. The projecting terminal lobe is an endite of the basis; in the Diplopoda this lobe is freely movable, and in both the diplopods and the chilopods it is provided with muscles corresponding to the muscles of the lacinia of a generalized insect maxilla. In other groups the terminal lobe loses its mobility and becomes solidly fused with the basis, in consequence of which its muscles have disappeared. The anterior and posterior dorsal muscles of the mandibular base correspond to the dorsal promotor and dorsal remotor of a generalized appendage (Fig. 41, *I*, *J*). The ventral muscles evidently represent the ventral promotors and remotors (*K*, *L*), which, being grouped together, become functionally the adductors (*KL*) of the generalized mandible. The somatic ends of the adductors are usually supported on sternal apophyses of the ventral head wall or on a membranous fold of the latter or of the apophyses. The membrane between the ends of some of the fibers from opposite jaws may become detached and form a ligament uniting the opposing fibers, thus producing a zygomatic adductor between the mandibles having no connection with the body wall.

The Mandibles of Pterygote Insects.—The typical mandible of the biting type in pterygote insects is quite different in both its mechanism and musculature from the mandible of most Apterygota and other arthropods. The pterygote type of mandible, however, is found in Lepismatidae, and a similar form of mandibular mechanism has been developed in some of the higher Crustacea.

The jaw of the more generalized mandibulate arthropods, as we have seen, is hinged to the lower edge of the cranium, or the mandibular segment of the body, by a single point of articulation (Fig. 75 A, *a′*), which evidently corresponds to the dorsal articulation of the basis of an ambulatory limb (Fig. 43 A, B, *a*). The mandible of Lepismatidae and Pterygota differs from a generalized mandible in that it has a secondary anterior dorsal articulation on the head (Fig. 75 B, *c*) and thus acquires a long axis of attachment (*a′-c*) with a definitely limited transverse movement of abduction and adduction. By this change from a pivotal to a dicondylic hinge articulation, the primitively anterior and posterior dorsal muscles of the jaw (*A*, *I*, *J*) become respectively a *dorsal abductor* (B, *I*) and a *dorsal adductor* (*J*). The ventral muscles remain unaltered in function, but, with the increasing size of the dorsal adductors, they become of secondary importance and are usually reduced (B, *KL*) or absent in higher forms. In many of the lower Pterygota and in Lepismatidae, however, the ventral adductors persist; they are highly developed in the larvae of Ephemerida and Odonata, where they arise on the anterior arms of the tentorium, and they are represented in the adult Isoptera and most Orthoptera, except Acrididae.

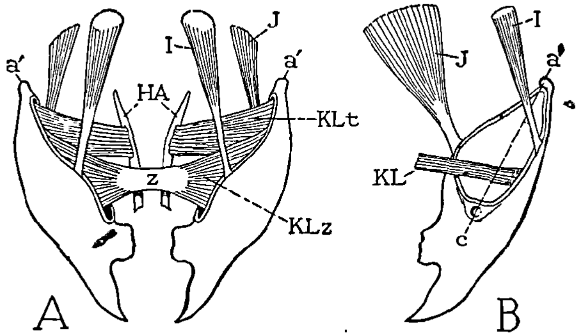

Fig. 75.—Diagrams of types of insect mandibles. A, apterygote type with one articulation (*a′*). B, pterygote type with two articulations (*a′*, *c*).

The typical biting jaw of pterygote insects, therefore, by the acquisition of a long hinge line on the head, with anterior and posterior articulations, comes to have a transverse movement of abduction and adduction (Fig. 75 B), and the primitive dorsal promotor and remotor muscles (*I*, *J*) come to be, respectively, dorsal abductors and adductors. The dorsal adductor increases in size, while the ventral adductors (*KL*) are reduced, and finally, with the disappearance of the ventral muscles, the adductor function is taken over entirely by the dorsal muscle. In addition to these changes in the motor apparatus, the action of the mandible undergoes an alteration by a change in the slope of its axis. In the more primitive condition, retained in Lepismatidae, the axis of the jaw slopes downward from the posterior articulation to the anterior articulation; in most Pterygota it is oblique in the opposite direction, thus giving the tip of the jaw a posterior motion accompanying the movement of adduction.

The structure and mechanism of the biting type of mandibles in the Pterygota are well represented by the mandibles of an acridid grasshopper (Fig. 76). Each mandible (D) is a thick, strong appendage with a broad triangular base, having its mesal surface differentiated into a distal toothed incisor lobe (*o*) and a proximal molar lobe (*p*). The jaw is broadly hinged to the pleurostomal margin of the cranium by the outer edge of its triangular base and has a strong articulation with the head at each end of the hinge line (A, C, *c*, *a'*). It should be observed that the articular surfaces of the mandible lie outside the basal membranous connection of the jaw with the head; they are merely specialized points of contact between the mandible and the cranium (Fig. 27 D). The musculature of the grasshopper mandible consists only of a dorsal abductor and a dorsal adductor. The abductor is relatively small; it arises on the lateral wall of the cranium and is inserted on a small apodeme (Fig. 76 D, 8*Ap*) attached to a flange of the outer margin of the mandibular base sufficiently far outside the axis line to give effectiveness to the muscle. The adductor is a huge muscle composed of several bundles of fibers (C, 9*a*, 9*b*) arising on the dorsal and lateral walls of the cranium, and inserted on a large apodeme (D, 9*Ap*) attached at the inner angle of the mandibular base. The width of the mandible between the hinge line and the point of attachment of the adductor apodeme gives great power to the adductor muscle in closing the jaw.

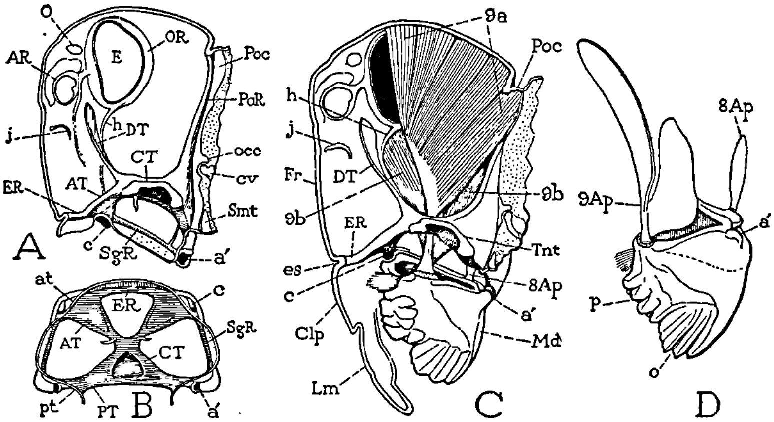

Fig. 76.—Endoskeletal structures of the cranium, and mandibles of a grasshopper, *Dissosteira carolina*. A, interior view of right half of cranium. B, the tentorium, ventral view. C, same as A, but with clypeus, labrum, and right mandible and muscles in place. D, right mandible and its apodemes, posterior view.

Further modifications of the pterygote mandible by which it becomes adapted to various specialized modes of feeding will be described in Chap. XII.

5. THE SUPERLINGUAE

The paired ventral lobes of the head known as the superlinguae (or "paraglossae") are best developed in apterygote insects and in some of the lower members of the Pterygota. In adult insects the superlinguae, if discernible as such, always appear as lateral lobes of the hypopharynx (Fig. 77 C, D, *Slin*), the median part of which (*Lin*) is designated the lingua (or "glossa"). In embryonic stages of apterygote insects, however, the superlinguae arise as independent lobes of the ventral wall of the head in the neighborhood of the mandibles (A, *Slin*), and for this reason they have been regarded by some writers as representing a pair of postmandibular appendages, equivalent to the first maxillae (maxillulae) of Crustacea, that have secondarily united with the median lingua to form the definitive hypopharynx. The shape of the superlinguae in certain apterygote insects is somewhat suggestive of a rudimentary limb appendage (D, E), but in others the form is so variable that little significance can be attached to it in any case. The embryonic superlinguae of Collembola have been said to be innervated from special centers in the suboesophageal ganglion, but different claimants disagree as to the position of the alleged centers, and most investigators find no evidence of the presence either of such nerve centers or of a corresponding head somite. According to Hoffmann (1911) the superlinguae of *Tomocerus* arise as lobes at the bases of the mandibles (B. *Slin*), and Silvestri (1933), in a study of the development of the head appendages of *Japyx*, shows conclusively that the superlinguae are formed in connection with the median part of the hypopharynx as lobes of the mandibular somite.

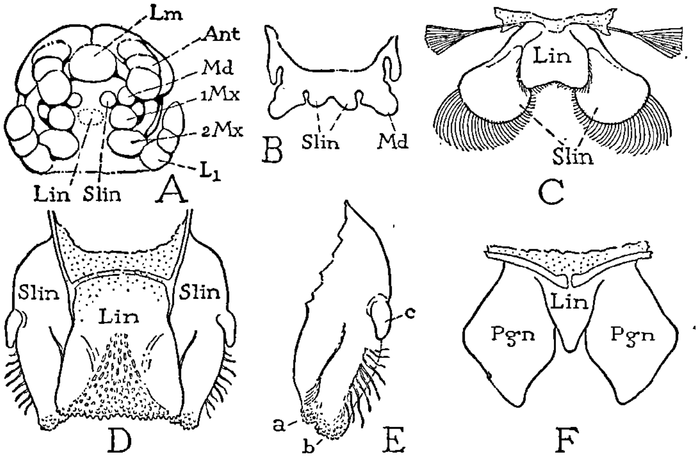

FIG. 77.—The hypopharynx of insects and a crustacean. A, ventral view of head of embryo of *Anurida maritima*, showing rudiments of lingua (*Lin*) and superlinguae (*Slin*). (*From Folsom*, 1900.) B, embryonic superlinguae of *Tomocerus*. (*From Hoffmann*, 1911.) C, hypopharynx of ephemerid nymph. D, hypopharynx of *Nesomachilis*, posterior view. E, detached superlingua of same. F, hypopharynx of an isopod crustacean, composed of median lingua and lateral paragnatha (*Pgn*), posterior view.

The superlinguae of some adult insects have a close resemblance to the paragnatha of certain Crustacea (Fig. 77 F, *Pgn*), and, when the paragnatha are united with a median lingua (*Lin*), the resulting structure is very similar to the insect hypopharynx (C). The paragnatha are said to be innervated by branches of the mandibular nerve trunks, and there is no evidence that the organs are other than secondary lobes of the head. If the paragnatha and the superlinguae are not homologous, they are entirely analogous structures developed in crustaceans and insects, but not in the myriapods.

6. THE MAXILLAE

The maxilla of insects having typical biting mouth parts closely preserves the structure of a limb that may be supposed to have *two* movable basal endites provided with muscles arising in the basis. The telopodite is relatively small and palpiform, but it has the essential structure of the shaft of a leg beyond the coxa both in its segmentation and in its basal musculature.

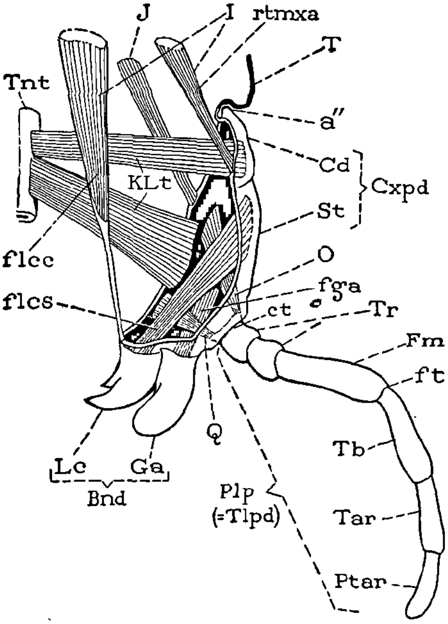

FIG. 78.—Diagram of the structure and musculature of a typical insect maxilla, suggesting that the cardo and stipes represent the coxopodite (*Cxpd*) and the palpus the telopodite (*Tlpd*) of a leg.

General Structure of a Maxilla.—The maxillary basis is typically elongate (Fig. 78, *Cxpd*) and is implanted by its entire inner surface on the pleural region of the head (Fig. 54 B) just behind the mandible. On its dorsal extremity it bears a single condyle (Fig. 78, *a''*) by which it articulates with the lower lateral margin of the tergal region of the cranium (*T*). A line of flexure in the upper part of the outer wall divides the basis into a proximal *cardo* (*Cd*) and a distal *stipes* (*St*). Usually the cardo is flexed mesally on the upper end of the stipes (Fig. 80 A, C). At its ventral extremity the stipes bears two endite lobes. The mesal lobe is the *lacinia* (Fig. 78, *Lc*), the outer lobe the *galea* (*Ga*). Laterad of the galea arises the *palpus* (*Plp*), or telopodite. The relative size and the segmentation of the palpus vary much in different insects. In many orthopteroid forms there are two small segments in the base of the palpus which appear to be trochanters (*Tr*), the second followed by a longer femurlike segment (*Fm*), which is separated by a characteristic femoro-tibial joint (*ft*) with a ventral flexure from a distal part containing two or three segments. The proximal articulation of the palpus on the basis (*ct*) has a dorsoventral movement suggestive of that of the coxotrochanteral joint of a leg. The region of the stipes supporting the palpus is sometimes differentiated as a *palpifer*, but the musculature of the palpus gives no reason for believing that the palpifer in any way represents a primitive segment of the maxillary limb.

The Muscles of the Maxilla.—The musculature of a typical maxilla in biting insects comprises muscles of the basis that move the appendage as a whole, muscles arising within the basis that move the terminal lobes and the palpus, and muscles of the palpus segments.

The basal musculature of the maxilla in all biting pterygote insects (Fig. 78) is very similar to the musculature of the mandible in apterygote insects and other arthropods. It includes anterior and posterior dorsal muscles (*I*, *J*) taking their origins on the tergal wall of the head, and ventral adductors (*KL*) arising on the tentorium (*Tnt*) in pterygote insects, or on the hypopharyngeal apophyses in apterygote insects (Fig. 79 B). The dorsal muscles may comprise an *anterior rotator* (Fig. 78, *rtmxa*) and a *posterior rotator* (*J*) attached on the cardo, though usually the second is absent; but nearly always there is a large anterior muscle (*flcc*) inserted on the inner angle of the base of the lacinia, which is thus a *cranial flexor of the lacinia*, resembling in every way the similar muscle of the mandible in the diplopods and chilopods (Fig. 73, *flcc*). The fibers of the ventral adductor muscles (Fig. 78, *KLt*), taking their origin on the tentorium (*Tnt*), are usually separated into two groups, those of one group being inserted in the cardo, those of the other on the posterior margin of the stipes. These muscles are here termed "adductors" because morphologically they correspond to the ventral adductors of a primitive appendage; in function, however, they may produce various movements of the maxilla.

The muscles of the terminal lobes of the maxilla always have their origin in the stipes. A *stipital flexor of the lacinia* (Fig. 78, *flcs*) is inserted on the basis of the lacinia, and a *flexor of the galea* (*fga*) on the base of the galea. The lobe muscles may be branched, but they never occur in antagonistic pairs.

The palpus is moved by a *levator muscle* (Fig. 78, *O*) and a *depressor* (*Q*), both arising in the stipes, but never in the palpifer. These muscles are evidently homologues of the levator and depressor of the telopodite of a leg that arises in the coxa and are inserted on the trochanter; the depressor of the palpus, however, never has a branch corresponding to the body muscle of the leg trochanter. The segments of the palpus have usually each a single muscle inserted on its base (Fig. 80 C).

Structural Variations of the Maxillae.—The maxillae may become variously reduced in different groups of insects, particularly in larval forms, by a suppression of one or both of the terminal lobes or by the loss of the palpus; but other than this, except in the Hemiptera and Diptera and certain other piercing or sucking insects, they do not depart radically from the generalized type of structure, and they are fundamentally alike in both Apterygota and Pterygota. The crustacean maxillae are in general almost rudimentary appendages by comparison with the typical insect maxilla, but a study of such forms as *Anaspides* brings out a fundamental similarity in the basal structure. The postmandibular appendages of the Chilopoda are small leglike structures, each composed of a large basis and a reduced telopodite, but endite lobes may be present on the bases of the first pair.

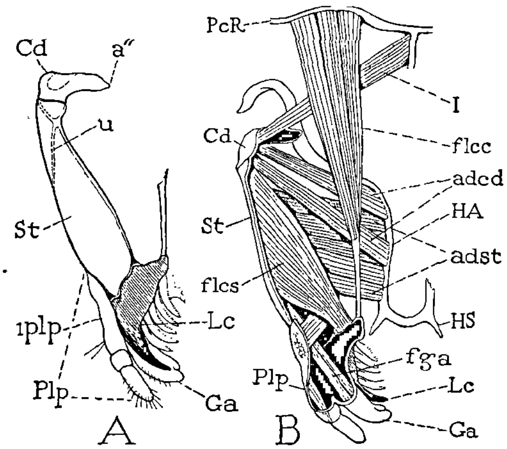

FIG. 79.—Maxilla of an apterygote insect, *Heterojapyx gallardi*. A, ventral (posterior) view. B, dorsal (anterior) view.

The apterygote maxilla is scarcely more primitive than that of the lower Pterygota. In the Thysanura the maxillae are suspended from the hypostomal margins of the cranium (Fig. 82 A, *Mx*) and have the usual maxillary structure. In Japygidae the maxillae are mostly concealed with the mandibles in deep pouches above the labium in which they have a horizontal position. The basis of each appendage, however, is composed of a small cardo (Fig. 79 A, *Cd*) and a long stipes (*St*). The stipes bears a short palpus (*Plp*), a strongly sclerotized lacinia (*Lc*), and a weak galea (*Ga*). The palpus and galea are somewhat separated from the stipes and connected with the base of the hypopharynx; this condition has given rise to the idea that they are not parts of the maxilla but represent the superlinguae. The fact, however, that both structures are well provided with the usual muscles *arising in the stipes* (B) shows conclusively that they belong to the maxilla. The lacinia is equipped with a broad stipital flexor (*flcs*) and a large cranial flexor (*flcc*) arising on the back of the head. The basal musculature of the appendage consists of an anterior dorsal muscle (*I*) and of two groups of ventral adductors (*adcd, adst*) arising on the hypopharyngeal apophysis (*HA*).

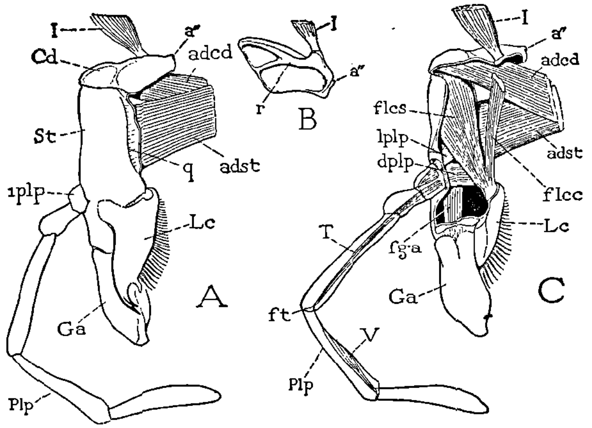

FIG. 80.—Maxillae of *Periplaneta americana*. A, left maxilla, posterior view. B, inner surface of cardo. C, right maxilla, anterior view.

The generalized structure of the pterygote maxilla is well exemplified in the maxilla of the cockroach (Fig. 80). The cardo and the stipes (A, *Cd, St*) are flexible on each other by a distinct hinge, and their planes form an abrupt angle at the union. The cardo is articulated to the cranium by a basal condyle (a''); its surface is marked by the line of an internal ridge (B, *r*), but it is not otherwise "divided" as it is sometimes said to be. The elongate stipes has a sutural groove (A, *q*) near its inner edge which forms internally a submarginal ridge on which muscles are attached. In some insects the surface of the stipes is marked by other ridge-forming grooves or by-sutures, but, as with the cardo, these features are not evidence that the stipes is a composite sclerite.

The large terminal lobes of the cockroach maxilla arise from the distal end of the stipes, the galea (*Ga*) being external and the lacinia (*Lc*) mesal, but the galea also partly overlaps the lacinia anteriorly. The galea is a broad, soft lobe, widened distally; the lacinia is more strongly sclerotized and ends in an incisor point provided with two apical teeth curved inward, and its inner margin is fringed with long hairs. Both lobes are movable on the end of the stipes; the galea can be deflexed, the lacinia can be flexed mesally. The galea has a single muscle (C, *fga*) arising in the stipes. The lacinia has both a stipital flexor (*flcs*) and a cranial flexor (*flcc*), but the two are united with each other at their insertion on the lacinia. In some insects the area of the stipes supporting the galea is differentiated as a distinct lobe called the *subgalea*, but the base of the true galea is to be determined by the point of attachment of its muscle.

The long maxillary palpus of the roach is composed of five segments (Fig. 80 A, B, *Plp*). There is no palpifer lobe differentiated in the stipes, and the small basal segment of the palpus cannot be mistaken for a palpifer, since the palpus muscles (C, *lplp*, *dplp*) are inserted upon it. There are only three muscles within the palpus, the first being a muscle of the second trochanteral segment arising in the first trochanter, the second a long ventral muscle (*T*) of the tibial segment arising also in the first trochanter, and the third (*V*) a muscle of the terminal segment having its origin in the tibia. Between the third and fourth segments there is a characteristic femoro-tibial flexure (*ft*).

The basal musculature of the roach maxilla (Fig. 80 C) is of the usual type. There is but a single anterior dorsal muscle (*I*) inserted on the cardo. The ventral muscles arising on the tentorium consist of two large groups of fibers, one (*adcd*) inserted in the cardo, the other (*adst*) on the mesal ridge of the posterior surface of the stipes (A, *q*). These muscles, though they are evidently the primary sternal adductors of the appendage, give a movement of protraction to the maxilla because of the angulation between the cardo and stipes, and because the stipes rests and moves against the side of the hypopharynx.

7. THE LABIUM

The insect labium is a composite structure. Its major part is formed by the union of a pair of gnathal appendages closely resembling the maxillae, but the organ perhaps includes in its base a part of the sternal region of the labial somite. The component labial appendages are termed the *second maxillae* of insects, and there is little doubt that they correspond to the second maxillary appendages of Crustacea. In certain

Crustacea the first maxillipeds are united in a labiumlike organ attached to the head.

In its generalized form, the labium (Fig. 81 A) consists of a flat median part, of two lateral segmented palpi (*Plp*), and of four unsegmented terminal lobes (*Gl, Pgl*). Structurally the organ is divisible into a free distal *prelabium* (*Prlb*) bearing the palpi and the terminal lobes, and a proximal *postlabium* (*Plb*) largely or entirely adnate on the posterior or ventral wall of the head. The line of flexibility between the two parts may be termed the *labial suture* (*lbs*). All the proximal muscles of the labium are inserted on the movable prelabium.

The body of the prelabium is commonly termed the *prementum* (*Prmt*); the postlabium, therefore, may be called the *postmentum* (*Pmt*). Some writers designate the two primary parts of the labium "mentum" and "submentum," respectively, but more generally these names are given to subdivisions or sclerites of the postlabium. Unfortunately the current terms given to the parts of the labium cannot be made to fit consistently with the morphology of the organ. The prelabium functionally is the under lip of the insect, and it has been termed the "eulabium" by Crampton (1928); but commonly the name "labium" applies to the entire organ, and terms composed with "mentum" are given to its several parts or sclerites. Only by a radical change in the labial nomenclature could its numerous inconsistencies be eliminated (see Walker, 1931).

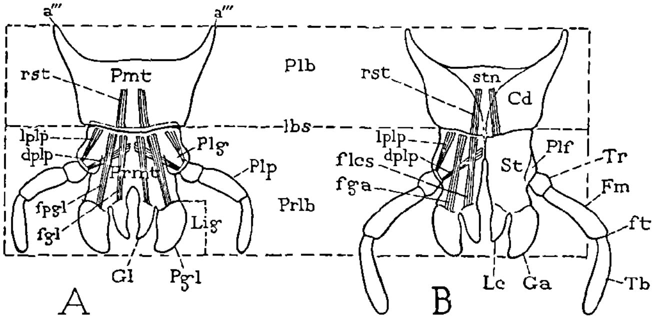

FIG. 81.—Diagrams illustrating the fundamental structure of the insect labium, and the correspondence of its parts with those of a pair of united maxillae. *Plb*, postlabium, consisting of the postmentum (*Pmt*); *Prlb*, prelabium, including the prementum, or labiostipites (*Prmt*), palpi (*Plp*), and terminal lobes (*Gl, Pgl*).

The Prelabium.—The prelabium (Fig. 81 A, *Prlb*) is the movable distal part of the labium. It is composed of a central body, the *prementum* (*Prmt*), of the labial *palpi* (*Plp*), and of the *terminal lobes* (*Gl, Pgl*), the last collectively constituting the *ligula* (*Lig*).

The Prementum.—When the labium is compared with a pair of maxillae, it becomes evident that the prementum (Fig. 81 A, *Prmt*) represents the united stipites of a pair of maxilla-like appendages (B, *St*), since it is the part of the labium in which arise the muscles of the palpi and the ligular lobes. The prementum, therefore, is appropriately designated *pars stipitalis labii*, or *labiostipites.* The paired origin of the prementum is suggested often by a distal cleft between its stipital components (Fig. 83) or by the presence of paired sclerites in its ventral wall (Fig. 158 C). Lateral lobes of the prementum bearing the palpi are frequently differentiated from the median area and are termed the *palpigers* (Fig. 81 A, *Plg*), since they are analogous with the palpifers of the maxillae (B, *Plf*). The size of the prementum varies much in different groups of insects. In adult Coleoptera, for example, it is often a relatively small part of the labium (Figs. 67 C, 68 A, 158 C, 160 B, *Prmt*), while in the higher Hymenoptera it becomes the major piece of the appendage (Fig. 158 F), and in the prehensile labium of odonate larvae it is a large spatulate lobe (E) bearing the clawlike palpi (*Plp*) on its distal angles. There has been much confusion as to the identity of the prementum in comparative studies of the labium, but an examination of the labial musculature will seldom fail to give a positive determination of the limits of the stipital region of the labium, which is the prementum.

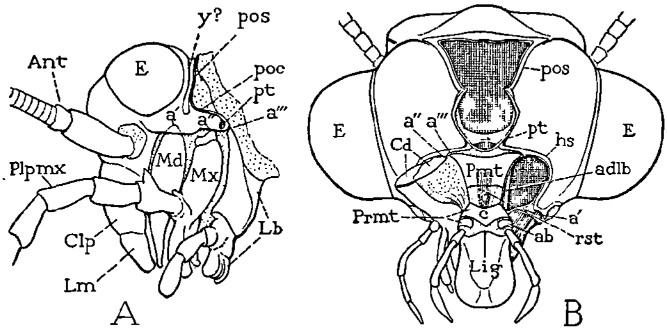

FIG. 82.—Articulation of the gnathal appendages on the cranium. A, an apterygote insect, *Nesomachilis*, with single mandibular (a'), maxillary (a''), and labial (a''') articulation on each side. B, head of a myrmeleonid, posterior view.

The muscles inserted on the prementum comprise two pairs of cranial adductors arising on the tentorium (Fig. 84 A, *1adlb, 2adlb*), and a pair of median retractors (or flexors) arising on the postmentum (Figs. 81 A, 84 A, *rst*). The muscles that take their origin within the prementum include the muscles of the palpi (*lplp, dplp*) and the muscles of the terminal lobes (*fgl, fpgl*), together usually with muscles associated with the duct of the labial glands (Fig. 84 A, 1*s*, 2*s*).

The sclerotization of the ventral wall of the prementum is highly variable. Typically it forms a single premental plate (Figs. 59 B, 83 B, 158 E, F, *Prmt*), but often it is broken up into two or more sclerites.

In some adult Coleoptera there is present a pair of lateral premental sclerites (Fig. 158 C, *Prmt*), while in adult Neuroptera and many larval Coleoptera the premental sclerotization is characteristically subdivided into a distal plate or group of sclerites (Figs. 67 B, 68 B, 82 B, 158 A, B, 159 A, B, *ab*, or *a*, *b*), giving insertion to the tentorial adductor muscles (Fig. 159 B), and into a proximal plate or pair of sclerites (*c*), on which are inserted the median retractor muscles (*rst*) from the postmentum. The surface of the prementum, again, is sometimes entirely membranous.

The Labial Palpi.—The palpi of the labium are usually shorter than the maxillary palpi and are commonly three segmented (Fig. 83). Each is provided with levator and depressor muscles taking their origins in the prementum (Figs. 81 A, 83 B, 84 A, *lplp*, *dplp*). Generally, therefore, the palpi can be distinguished from the terminal lobes of the labium by their provision with antagonistic muscles. In some cases, as in odonate larvae, and possibly in adult Diptera, the ligular lobes are suppressed and the palpi become the movable terminal appendages of the labium (Fig. 158 E, *Plp*).

The Ligula.—The terminal lobes of the labium vary much in relative size and shape in different insects (Fig. 83) and are sometimes subdivided (A); rarely they are absent, but they may be variously united. Collectively the lobes (or the distal part of the labium including the lobes) constitute the ligula (Fig. 81 A, *Lig*).

The labium typically has four terminal lobes borne on the distal margin of the prementum (Fig. 81 A). The median pair are the *glossae* (*Gl*), the lateral pair the *paraglossae* (*Pgl*). The labial lobes are clearly the laciniae and galeae of the united labial appendages (B, *Lc*, *Ga*). They have the same type of musculature as the lobes of the maxillae, each being provided with a single or branched flexor arising in the prementum (Figs. 81 A, 83 B, 84 A), but never having a pair of antagonistic muscles. The ligular lobes are sometimes confluent at their bases, sometimes the pair on each side are united, or, again, the two glossae are combined to form a single median lobe (Fig. 158 D, *Gl*), which, as in the bees, may be prolonged in a slender tongue-like organ (F, *Gl*), and, finally, the four lobes may be fused in a single ligular flap terminating the labium (Figs. 82 B, 158 B, *Lig*). On the other hand, the labial lobes are often reduced, and one or both pairs may be absent. In many holometabolous larvae having the hypopharynx adnate upon the anterior (or dorsal) surface of the prementum, the ligula is fused with the end of the hypopharynx in a composite terminal lobe bearing the orifice of the labial glands at its extremity (Figs. 161 B, 164 C).

The Postlabium.—Since the postlabium (Fig. 81 A, *Plb*) has no appendicular parts, it consists entirely of the proximal region of the body of the labium. To preserve uniformity in the nomenclature of the labial regions, therefore, the surface of the postlabium, as distinguished from the distal prementum of the prelabium, may be termed the *postmentum* (*Pmt*). The postlabial sclerotization is so variable that the limits of the postmentum cannot be determined by a study of the labial sclerites alone. In practice the postmentum is to be identified as that part of the labium lying proximal to the *insertions* of *all* the labial muscles. The only muscles having their origins on the postmentum are the median muscles of the labium (*rst*) that extend from the postmentum to the prementum.

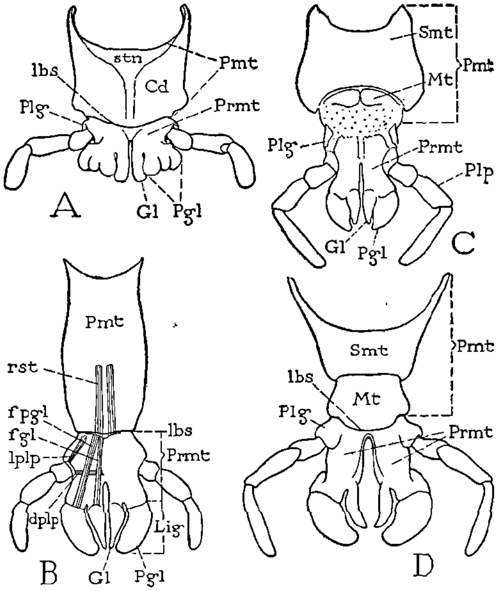

FIG. 83.—Types of generalized structure of the labium. A, *Machilis*. B, *Termopsis*, soldier form: body of labium composed of prementum (*Prmt*) and postmentum (*Pmt*) only. C, *Blatta orientalis*, with small mental sclerites (*Mt*) in distal part of postmental region. D, *Scudderia*, with well-developed mentum (*Mt*) and submentum (*Smt*).

Though the postmentum is usually broadly adnate on the posterior, or ventral, wall of the head, its distal part sometimes projects to give support to the movable prelabium. In the larvae of Odonata the basal stalk of the labium (Fig. 158 E) appears superficially to be the postmentum, but the musculature and mechanism of the organ are here so different from those in a labium of typical structure that the homologies of its parts become questionable. A recent paper by Munscheid (1933) gives a good account of the musculature of the odonate labium, but the mechanism of the larval organ is not satisfactorily explained.

In the more generalized insects, the labium joins the neck membrane on a line between the posterior tentorial pits (Figs. 59 B, 82 A), and the proximal angles of its basal plate (a''') are attached to the postoccipital rim of the head just behind or below the tentorial pits, in line with the articulations of the maxillae and mandibles on the subgenal margins of the cranium (*a''*, *a'*). The postmentum thus corresponds in position to the cardines of the maxillae and would appear, therefore, to include in its composition the cardines of the primitive labial appendages (Fig. 81 B, *Cd*). Since, however, the secondary median orifice of the labial glands, which belongs to the venter of the labial somite, moves forward during development until it comes to lie anterior (or dorsal) to the bases of the labial appendages (Fig. 155, *SlO*), it seems probable that the postmentum contains in its median part also an element derived from the venter of the labial segment. The postmentum thus may be regarded as a composite structure formed by the union of the cardinal parts of the labial appendages with the primitive sternum of the labial segment, in which character it would resemble the definitive sterna of most of the succeeding body segments. Some writers regard the entire postmentum as a sternal derivative, but in this case it must be assumed that the labial cardines are absent, and that the sternum of the labial segment has become interposed between the tergum and the appendages in such a way that the latter are supported by the sternum alone. In the Machilidae the lateral areas of the postmentum (Fig. 83 A, *Cd*) are separated by faint lines from a triangular median area (*stn*) in a manner suggestive that the postmentum (*Pmt*) has a cardinosternal composition.

The sclerotization of the postlabium forms in many insects a single postmental plate (Fig. 81 A, *Pmt*). This plate may cover the entire area of the postmentum, as in Apterygota (Fig. 83 A), termites (B), and some Neuroptera (Fig. 158 B), though again it may occupy only the basal part of the postmentum (Fig. 82 B), or, as in most caterpillars, it may be reduced to a small sclerite (Fig. 164 C, *pmt*) in the otherwise membranous postmental wall. On the other hand, the postmental area of the labium may be entirely membranous, as in hymenopterous larvae (Fig. 161, B, D, F, *Pmt*).

In the majority of Orthoptera and adult Coleoptera the postlabial area, or postmentum, contains two distinct plates. The distal plate in such cases is generally called the *mentum* (Figs. 59 B, 67 C, 83 D, *Mt*), the proximal one the *submentum* (*Smt*). The mentum always lies proximal to the insertions of the median muscles of the prementum, which arise on the submentum when the postmentum contains two plates (Fig. 84 A, *rst*). The mentum and submentum in some insects appear to be differentiations of a more primitive postmental plate; in others the mentum is evidently a secondary sclerotization in the membranous distal part of the postmentum. In adult Coleoptera the mentum is typically large and conspicuous (Fig. 158 C, *Mt*), but in the Orthoptera it is often reduced (Fig. 83 C) and is entirely absent in Mantidae and Acrididae.

The proximal angles of the postmentum (or of the submentum) generally preserve the primitive close association of the labial base with the posterior tentorial pits; but they may become far removed from the foramen magnum if the postgenal regions of the cranium are elongate, or especially when a gular plate bridges the space between the postoccipital margins proximal to the labium (Figs. 67 C, 68, *Gu*). The base of the labium loses its association with the posterior tentorial pits only when mesal lobes of the hypostomal areas of the cranium are developed proximal to its base (Fig. 164 C, *Hst*) or form a complete bridge between the labium and the foramen magnum (Fig. 65 B, C).

Musculature of the Labium.—The muscles of the labium may be divided into four groups. Those of the first group are the muscles of the palpi and the terminal lobes; those of the second include several pairs of muscles inserted near the orifice of the duct of the labial glands; those of the third group are the median muscles extending from the postmentum to the prementum; and those of the fourth are the extrinsic muscles of the labium arising on the tentorium and inserted on the prementum.

The muscles of the palpi and the terminal lobes of the labium (Fig. 81 A) correspond to muscles of the palpi, laciniae, and galeae of a pair of maxillae (B). Each labial palpus is provided with a levator and a depressor muscle arising in the prementum (Fig. 84 A, *lplp, dplp*). The glossae and paraglossae have each a flexor muscle taking its origin in the prementum (*fgl, fpgl*), but the glossae have no muscles arising on the head wall corresponding to the cranial flexors of the maxillary laciniae (Fig. 78, *flcc*).

The labial muscles associated with the orifice of the labial, or salivary, glands have no homologues in the maxillae, and they are not always present in the labium. Generally there are two pairs of them, which arise in the prementum and converge to the labial wall of the salivary pocket formed at the junction of the hypopharynx with the prementum, into which opens the salivary duct (Fig. 84 A, B, *2s*, *3s*). These labial "salivary muscles" and the pair of opposing muscles from the hypopharynx (*1s*) will be more fully described in Chap. XII.

The median muscles of the labium that extend from the postmentum to the prementum also have no homologues in the maxillae, and they are not always present in the labium. They arise on the postmentum, or on the submentum when there are two plates in the postlabial region, and are always inserted on the prementum (Fig. 84 A, B, *rst*). They are, therefore, possibly sternostipital muscles, since there are never cardinostipital muscles in the maxillae. Usually these muscles are retractors of the prementum, but in some cases they serve to flex the prementum on the postmentum (Fig. 159 E).

The extrinsic muscles of the labium comprise two pairs of muscles having their origins on the tentorium and their insertions on the prementum (Fig. 84 A, B, 1*adlb*, 2*adlb*). These muscles clearly correspond to the tentorial adductors of the maxillae, and in a morphological sense, therefore, they may be termed the *labial adductors*, though in their actual function it is probable that they produce various movements of the labium besides that of adduction. One pair of the adductors is inserted anteriorly, or dorsally, on the prementum (1*adlb*), the other posteriorly, or ventrally (2*adlb*). In some of the higher insects, as in the bees (Fig. 163 C), the labial adductors may take their origin on the cranium, but this condition is evidently a secondary one resulting from a migration of the muscle bases from the tentorial arms to the adjacent cranial walls in order to give the fibers greater length and increased effectiveness. There are no head muscles inserted on the postmentum corresponding to either the cranial muscles or the tentorial adductors of the maxillary cardines, but the absence of these muscles in the labium is evidently consequent upon the usual immobility of the postmentum.

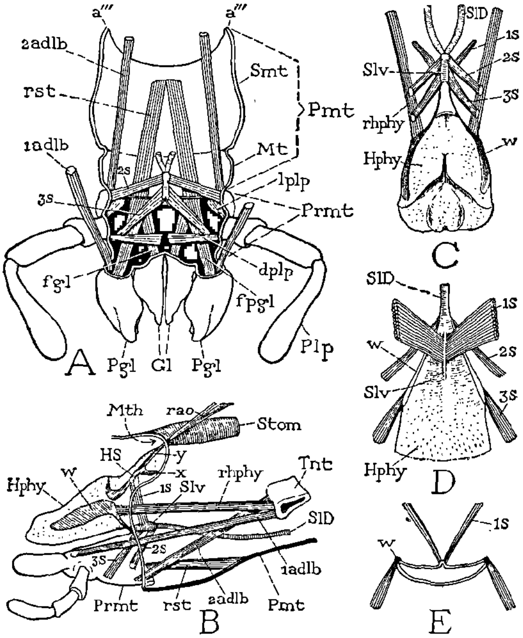

FIG. 84.—The labium and associated structures of Orthoptera. A, labial musculature of *Gryllus assimilis*, dorsal (anterior) view. B, diagram of orthopteroid hypopharynx, salivarium, and labium, lateral view. C, salivarium and under surface of hypopharynx of *Gryllus*. D, salivarium and base of hypopharynx of a mantis, *Paratenodera cinensis*, dorsal view. E, diagrammatic section of salivarium of *Paratenodera*.

Associated with the anterior (or dorsal) adductors of the labium there is usually present in generalized insects a pair of *retractors of the hypopharynx* (Fig. 84 B, *rhphy*). These muscles take their origins on the posterior bridge of the tentorium (*Tnt*) and are inserted laterally on the base of the hypopharynx (*Hphy*), where they are attached to the plates (*w*) of the latter, when these plates are present.

8. GLANDS OF THE HEAD APPENDAGES

Associated with the mouth parts of insects is a series of paired glands, which perhaps are coxal glands of the gnathal appendages. Some writers have attempted to correlate these glands with the nephridial glands of Crustacea, but the head glands of insects appear to be entirely of ectodermal origin. Glands occur also in connection with the antennae, but it is doubtful if they belong to the series of gnathal glands.

Antennal Glands.—Glands connected with the antennae, so far as observed, are not of common occurrence in insects. In an ant, *Myrmica rubra*, however, Janet (1894, 1898) has described a group of one-celled antennal glands, the ducts of which open separately in a small pit on the rim of the antennal socket. In the roach *Periplaneta americana* a small coiled tubular gland, mentioned by Bugnion (1921), opens at the base of each antenna. Perhaps a further search will show that antennal glands are more generally present in insects than the few records of their occurrence would indicate.

Mandibular Glands.—Glands associated with the mandibles are known to occur in Apterygota, Isoptera, Orthoptera, Coleoptera, Trichoptera, larval Lepidoptera, and Hymenoptera. In the Apterygota, Willem (1900) reports the presence of head glands in *Orchesella* opening on each side of the hypopharynx near the bases of the mandibles, and Bruntz (1908) describes mandibular glands in *Machilis maritima* as "anterior cephalic glands," each of which consists of a large racemose glandular mass with a principal lobe in the head and a smaller one in the thorax, the duct extending ventrally from the former to its opening in the preoral cavity at the base of the mandible. In the Orthoptera, Suslov (1912) found mandibular glands in Mantidae and Blattidae but discovered none in Gryllidae, Tettigoniidae, or Acrididae. The glands of *Mantis religiosa*, he says, consist each of a thick-walled glandular sac and a thin-walled reservoir, the second opening to the exterior mesad of the posterior angle of the mandible. In the Hymenoptera also the glands of the mandibles are saclike with thick cellular walls. The mandibular glands attain their highest development in certain lepidopterous larvae, in which they have the form of long tubes extending often far back into the body cavity. The secretion of the mandibular glands probably has a "salivary" function in most cases; the size of the glands in some caterpillars may be correlated with the transformation of the ordinary salivary glands (labial glands) into silk-forming organs.

Maxillary Glands.—The presence of maxillary glands has been reported in Protura, Collembola, Heteroptera, the larvae of some Neuroptera and Trichoptera, and Hymenoptera; they occur also in some *coleopterous larvae.* The maxillary glands are usually small and inconspicuous, but in certain prionid larvae (*Orthosoma*) they consist of long convoluted tubes opening mesad of the maxillary bases and extending far back in the body cavity.

Labial Glands.—The glands of the head appendages generally most highly developed in insects are those of the second maxillae, the ducts of which are united in a common median outlet tube (Fig. 84 B, *SlD*) that opens typically in the pocket of the ventral wall of the head between the base of the free part of the labium and the base of the hypopharynx (*Slv*). These glands are commonly known as the "salivary glands"; but since their function is variable and has not been definitely determined in many cases, they are better termed the *labial glands.*

In the embryo the labial glands originate as paired invaginations of the ectoderm just behind the bases of the rudiments of the second maxillary appendages. As development proceeds, the two orifices approach each other and unite medially on the venter of the second maxillary segment. At the same time, the appendages of this segment also come together and unite by their mesal edges. Meanwhile, however, the median aperture of the glands has moved forward, so that, when the labium is formed by the fusion of the second maxillary appendages, the outlet of the glands lies in the ventral wall of the head anterior to the base of the labium. Labial glands are present in all the principal orders of insects except Coleoptera.

The size and shape of the labial glands are highly variable in different insects. Usually the glands lie in the thorax, but they may have a part in the head, and they often extend into the abdomen. Typically they are simple or convoluted tubes, but they may be branched or take on the form of dense racemose masses. A part of each lateral duct is sometimes enlarged to form a reservoir. The secretion of the labial glands generally has some function connected with feeding, though not necessarily that of a digestive fluid, for in blood-sucking insects it may have inflammatory and anticoagulatory properties. In lepidopterous and hymenopterous larvae the labial glands are silk-producing organs. Several writers have attributed an excretory function to the labial glands of Apterygota based on their reaction to ammoniacarmine and indigocarmine injected into the body, but as in the case of the so-called "nephrocytes" (see page 415) this test perhaps does not necessarily indicate an excretory function.

The salivary pocket, or salivarium (Fig. 84 B, *Slv*), at the base of the hypopharynx in generalized insects, into which opens the duct of the labial glands, is of much interest because of its various modifications in the higher order to form an organ for actively expelling the secretion of the glands. It becomes the "salivary syringe" of Hymenoptera, Diptera, and Hemiptera, and the "silk press" of lepidopterous larvae. The salivarium in both its generalized and its specialized forms will be more particularly described in Chap. XII.

GLOSSARY OF TERMS APPLIED TO THE HEAD APPENDAGES

Antennae (*Ant*).—The appendicular organs of the procephalic region of the head innervated from the deutocerebral lobes of the brain; called *first antennae*, or *antennules*, in Crustacea; absent in Chelicerata.

Cardo (*Cd*).—The proximal subdivision of a maxillary appendage.

Chelicerae.—The first pair of appendages of adult Chelicerata, innervated from the tritocerebral ganglia of the brain; equivalent to the second antennae of Crustacea.

First Maxillae (1*Mx*).—The second pair of appendages of the gnathal region of the head; in insects called simply "the maxillae."

Flagellum (*Fl*).—The part of the antenna distal to the pedicel, typically filamentous, but of various forms, usually subsegmented or multiarticulate.

Galea (*Ga*).—The outer endite lobe of a maxilla, provided with a muscle arising in the stipes.

Glossae (*Gl*).—The two median ligular lobes of the labium, each provided with a muscle arising in the prementum.

Gula (*Gu*).—A median ventral plate of the head of some insects, developed as a sclerotization of the gular region of the neck proximal to the posterior tentorial pits, continuous with the basal plate of the labium.

Labial Glands (*SlGl*).—The usual "salivary glands" of insects, opening by a median duct between the base of the hypopharynx and the labium, or on the hypopharynx.

Labial Suture (*lbs*).—The suture of the labium between the prementum and the postmentum, always distal to the mentum when the latter is present.

Labiostipites (*Lst*).—The prementum, or that part of the labium formed by the stipites of the component labial (second maxillary) appendages.

Labium (*Lb*).—The posterior median appendage of the insect head formed by the union of the second maxillae.

Lacinia (*Lc*).—The inner endite lobe of a maxilla, provided with a muscle arising in the stipes, and often with a second muscle arising on the cranial wall.

Ligula (*Lig*).—The terminal lobes of the labium collectively, or a terminal part of the labium formed by the union of the lobes.

Mandibles (*Md*).—The first pair of appendages of the gnathal region of the head in the Mandibulata; biting jawlike organs in their generalized form.

Mandibular Glands.—A pair of glands often present in insects opening mesally at the bases of the mandibles.

Maxillae (*Mx*).—The first and second maxillary appendages, or specifically in insects the first maxillae.

Maxillary Glands.—Glands present in some insects opening mesally at the bases of the maxillae.

Maxillipeds.—The three pairs of appendages in Crustacea following the second maxillae; the first pair sometimes (Amphipoda) united to form a labiumlike structure attached to the head.

Maxillulae.—The first maxillae of Crustacea.

Mentum (*Mt*).—A distal plate of the postlabium between the prementum and the submentum. (*Secondary submental plate,* Walker, 1931.)

Palpifer (*Plf*).—A lobe of the maxillary stipes bearing the palpus.

Palpiger (*Plg*).—A lobe of the stipital region of the labium, or prementum, bearing the palpus.

Palpus (*Plp*).—The telopodite of a gnathal appendage.

Paraglossae (*Pgl*). The lateral ligular lobes of the labium, each with a muscle arising in the prementum.

Paragnatha (*Pgn*).—A pair of lobes of the gnathal region of Crustacea situated between the mandibles and the first maxillae.

Pedicel (*Pdc*).—The second segment of the insect antenna, containing a special sense organ, the organ of Johnston.

Pedipalps.—The second appendages of adult Chelicerata, corresponding to the mandibles of Mandibulata.

Postantennal Appendages (*Pnt*).—The appendages of the tritocerebral somite: the chelicerae of Chelicerata, the second antennae of Crustacea, embryonic rudiments in some Hexapoda, absent in Myriapoda.

Postmentum (*Pmt*).—The postlabium, or basal part of the labium proximal to the stipital region, or prementum; when sclerotized, containing either a single postmental plate, or a distal mental plate and a proximal submental plate. (*Submentum,* Walker, 1931.)

Preantennae (*Prnt*).—Theoretically a pair of primitive procephalic appendages anterior to the antennae; possibly represented in *Scolopendra* and *Dixippus* by a pair of embryonic preantennal lobes; absent in all adult arthropods.

Prelabium (*Prlb*).—The distal part of the labium, comprising the prementum, the ligula, and the palpi. (*Eulabium.*)

Prementum (*Prmt*).—The stipital region of the labium, containing the muscles of the palpi and the ligular lobes, and giving insertion to the cranial muscles of the labium. (*Mentum,* Walker, 1931.)

Salivary Glands (*SlGl*).—See *labial glands.*

Scape (*Scp*).—The basal segment or stalk of the insect antenna.

Second Antennae.—The appendages of the tritocerebral somite of Crustacea. (See *postantennal appendages.*)

Second Maxillae (*2Mx*).—The third pair of gnathal appendages; in insects united in the labium.

Stipes (*St*).—The distal subdivision of a maxilla, bearing the endite lobes and the palpus, and containing the palpal and lobe muscles. (Plural *stipites.*)

Subgalea (*Sga*).—A lobe or subdivision of the maxillary stipes bearing the galea.

Submentum (*Smt*).—A proximal plate of the postlabium; when continuous with a gular plate the submentum lies distal to the posterior tentorial pits. (*Primary submental plate,* Walker, 1931.)

Superlinguae (*Slin*).—A pair of ventral lobes of the insect head similar in some respects to the paragnatha of Crustacea, developed from the mandibular somite and united with the lingua in the hypopharynx of adult insects.

CHAPTER VIII

THE THORAX

The thorax of a winged insect is a highly perfected bit of animal machinery. Insects are unsurpassed flyers, and few other creatures can make more effective and diversified uses of their legs. A thorax of the insect type is exclusively a hexapod structure; it distinguishes the insects and proturans from all their relatives. Other members of the Arthropoda may have a body section called the "thorax," but its segments do not correspond to those of the insect thorax, and its functions are by no means as centralized or specialized. The thorax of the Hexapoda consists of the three body segments following the gnathal segments (Fig. 23 C, *Th*), which are designated, respectively, the *prothorax* (Fig. 85, Th_1), the *mesothorax* (Th_2), and the *metathorax* (Th_3). Each segment bears a pair of legs (*L*), and the second and third segments carry the wings (W_2, W_3) in alate Pterygota. The thorax contains the muscles of the legs and wings, and the thoracic ganglia are the chief centers of control for both sets of appendages.

Between the thorax and the head is a narrowed, mostly membranous part of the trunk forming the neck, or *cervix* (*Cvx*). Though the neck is probably a composite region formed from the labial and the prothoracic segments, it is more conveniently treated as a part of the thorax.

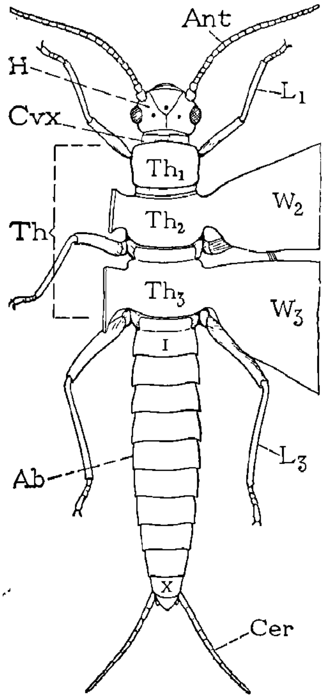

FIG. 85.—Diagram showing the contiguity of the tergal sclerites in the dorsum of the wing-bearing region of the body to prevent longitudinal movement of the back plates.

1. EVOLUTION OF THE THORAX

The thorax must have been evolved very early in the phylogenetic history of the Hexapoda as a locomotor section of the body through the specialization of its appendages for more active progression. In the Apterygota as well as the Pterygota the thorax is distinctly differentiated from the abdomen in the structure of its segments, showing that the inception of the thorax as a body region long antedated the acquisition of wings. The thoracic region of the embryo (Fig. 23 C, *Th*) is well developed as the leg-bearing part of the body at a stage when the gnathal segments (*Gn*) are yet distinct and show no evidence of their future union with the procephalic lobes (*Prc*). Concurrent with the specialization of the thoracic appendages as organs of locomotion, the abdominal appendages were lost (Fig. 24 D), and the future gnathal appendages assumed functions accessory to feeding. When the gnathal segments were then finally combined with the protocephalon to become a part of the definitive head (E, *H*), the hexapods appeared in their modern three-part form.

The wings are acquisitions developed comparatively late in the evolution of insects, though they are fully formed in the earliest known fossil forms. The wings are flat folds of the body wall extended from the lateral parts of the dorsum of the mesothorax and metathorax; they are thus in a sense homodynamous with laterotergal lobes that may occur on any of the body segments in both insects and other arthropods. That the wings belong to the dorsum is shown by the fact that the thoracic spiracles always lie below their bases.

There is no evidence that true wings were ever present on the prothorax, but in many of the earlier fossil insects small lateral lobes project from the margins of the prothoracic tergum (Fig. 119, *pnl*), suggesting that similar lobes on the mesothorax and metathorax were the precursors of the wings. The immediate ancestors of the flying insects, therefore, probably had three pairs of laterodorsal, or paranotal, flaps on the thorax, together forming broad extensions from the dorsum at the sides of the body. Evidently, then, in a second stage of their evolution, insects were enabled to depart from a strictly terrestrial or arboreal life by using their paranotal lobes as gliders on which they could launch themselves into the air from some elevation or sustain themselves after a preliminary leap from the ground. Later, a third stage was inaugurated with the transformation of the paranotal lobes of the mesothorax and the metathorax into movable organs of true flight.

Each of the three stages in the evolution of modern insects from their generalized polypod ancestors has left its separate impression on the structure of the thorax. Hence, in a study of the thorax, we may observe three groups of characters, aside from the presence of the legs and wings, that distinguish the thorax from the other body regions. First, there are features common to the thorax of apterygote and pterygote insects that were probably evolved as direct adaptations to a more efficient use of the legs when the function of locomotion became localized in the thorax. Second, there are characters distinctive of the pterygote thorax not evidently related to the legs, but which are repeated in each segment, and which, therefore, may be supposed to be correlated in their origin with the equal development of paranotal lobes on the prothorax, mesothorax, and metathorax to form a glider apparatus. Third, there are characters peculiar to the mesothorax and metathorax of pterygote insects which undoubtedly have been acquired in connection with the evolution of the paranotal lobes of these segments into organs of flight.

2. THE NECK

The neck, or *cervix*, of insects is a narrowed membranous region of the trunk between the head and the thorax (Fig. 85, *Cvx*). It is usually short and mostly concealed within overlapping parts of the prothorax (Fig. 87, *Cvx*), but it is generally of greater length than it appears to be and is sometimes elongate and exposed (Fig. 99, *Cvx*). Some writers have regarded the neck as a reduced body segment ("microthorax"), but no conclusive evidence has been adduced in favor of this view; others have regarded it as a posterior part of the labial segment, and still others as an anterior part of the prothorax. The true morphology of the cervix is still obscure, but many structural features associated with the neck suggest that it includes parts of both the labial and the prothoracic segments (Fig. 87), and that it contains the primary intersegmental line between these segments (*1Isg*). This view is in part substantiated by Smreczynski (1932), who says that in the embryonic development of *Silpha obscura* most of the second maxillary segment enters into the formation of the neck.

Both the dorsal and the ventral series of longitudinal trunk muscles arise on the back of the head and extend through the neck. The principal dorsal muscles (Fig. 87, *DMcl*) are attached anteriorly on the postoccipital ridge of the cranium (*PoR*) and posteriorly on the antecosta, or phragma (*1Ph*), of the mesothorax. The ventral muscles (*VMcl*) extend from the postoccipital ridge or the tentorial bridge (*PT*) to the apophyses of the prosternum. Neither the dorsal nor the ventral muscles, therefore, have connections in the prothorax corresponding to the usual antecostal attachments of intersegmental muscles. We have seen that the postoccipital ridge of the head most probably represents the intersegmental fold between the maxillary and labial segments. It is evident, therefore, that the intersegmental line between the labial segment and the prothorax lies somewhere in the membranous neck (*1Isg*), and that the dorsal and ventral muscles of the neck and prothorax include the fibers normal to two segments; that is, the muscles of the labial segment have become continuous with the muscles of the prothorax through the loss of their attachments on the intersegmental fold between these two segments. It is quite obvious that some such structural modification as this is necessary to give freedom of movement to the head;

otherwise the activities of the head on the prothorax would be limited to the restricted movements of the ordinary intersegmental mechanism.

On each side of the neck there is typically a pair of lateral *cervical sclerites* (Fig. 87, *1cv*, *2cv*). The two sclerites of each pair are hinged to each other, the first articulates anteriorly with the back of the head, the second posteriorly on the prothoracic episternum. The lateral neck plates not only link the head to the thorax, but the anterior ends of the first in each pair form two fulcral points on which the head can be tilted up and down by the dorsal and ventral muscles attached to it. There are muscles also inserted on the neck sclerites, some arising on the back of the head, others on the pronotum. The cervical plates and their muscles, therefore, when typically developed, constitute a protractor apparatus of the head, for the head is protruded when the angle between the plates is straightened by the contraction of the muscles. Either one or both of the lateral cervical sclerites may be absent, however, and when only one is present it is sometimes fused with the episternum (Fig. 99, *cv*). In some insects there are also dorsal, lateral, and ventral cervical sclerites, but these usually have no muscles connected with them. The general mechanism of the insect neck has been but little investigated; a review of the structure of the cervical sclerites may be found in several papers by Crampton (1917, 1926) and in one by Martin (1916).

3. GENERAL STRUCTURE OF THE THORAX

The thorax of an adult insect is in general easily recognized, since it is the section of the trunk bearing the legs, and the wings when wings are present. Ordinarily the thorax consists of the three body segments following the head, but in most of the Hymenoptera the fourth segment is so intimately associated with the third that it virtually becomes a thoracic rather than an abdominal segment. On the other hand, the thorax is often distinctly divided between its first two segments into a prothoracic part and a meso-metathoracic part. The second part, composed of the wing-bearing segments more or less closely united with each other, may be termed the *pterothorax.*

In the present section we shall consider only those more fundamental features of the thoracic structure that presumably were developed before the paranotal lobes evolved into movable organs of flight; the structural modifications by which the pterothorax has been evolved into a mechanism of wing movement will be discussed separately.

The Thoracic Terga.—The tergal plates of the thorax are usually modified in various ways, but the generalized structure is preserved in the mesothorax and metathorax of wingless insects. In the Apterygota and in nymphal and many larval Pterygota, the terga of these segments are simple back plates similar to those of the abdomen where a typical secondary segmentation has been established (Fig. 37). Each plate comprises the primary segmental sclerotization of the dorsum and the preceding intersegmental sclerotization (Fig. 86 A). The definitive tergum, therefore, is crossed anteriorly by the line of the primary intersegmental groove, which forms the antecostal suture (*acs*) externally and a submarginal antecosta (B, *Ac*) internally, and is thus divided into a narrow precostal acrotergite (*atg*) and a long postcostal area ending at the secondary intersegmental membrane following (*Mb*). The tergal antecostae of generalized thoracic segments give attachment to the dorsal longitudinal muscles in the usual manner (Fig. 86 B, *DMcl*). In most winged insects, however, these muscles are greatly enlarged in the wing-bearing segments, and to accommodate them there are developed plate-like apodemal lobes from the antecostae of the mesotergum, the metatergum, and the first abdominal tergum. These antecostal apodemes, which are usually paired but sometimes single, are known as the *phragmata*. Since there are typically three of them, the phragmata may be distinguished as the *first phragma* (Fig. 98, *1Ph*), the second *phragma* (*2Ph*), and the *third phragma* (*3Ph*).

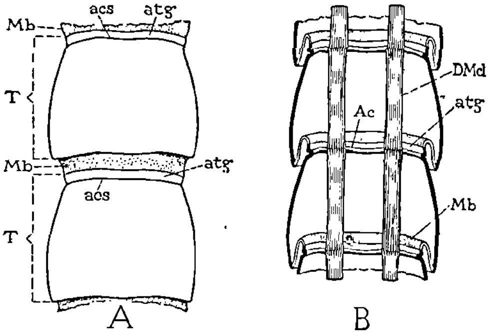

FIG. 86.—Diagrams illustrating intersegmental relations between the tergal plates of generalized segments.

The thoracic spiracles are generally situated on the sides of the segments, but the areas occupied by them must be supposed to belong to the dorsum, though they are beneath the wing bases in alate segments (Fig. 88, *Sp*). In Protura the spiracles are located in the lateral margins of the mesothoracic and metathoracic terga. Because of the dorsal extension of the thoracic pleura in insects, the thoracic spiracles are sometimes enclosed between the successive pleural plates. The first spiracle is mesothoracic, but it is often displaced anteriorly on the prothorax; the second is metathoracic and is also subject to an anterior migration.

The Thoracic Pleura.—The insects resemble the chilopods in that there are associated with the functional leg bases one or more sclerites in the lateral walls of the leg-bearing segments. Evidence from ontogeny suggests that these so-called *pleural sclerites* belong to primitive subcoxal parts of the leg bases, and the fact that in both the chilopods and the insects some of the body muscles of the legs may be inserted on the pleural areas gives a further reason for believing that the primary limb bases included not only the coxae but also the subcoxal areas of the body wall containing the pleural sclerites. In most other arthropods the coxopodites, or basal limb segments, are implanted in the pleural walls of the body segments between the tergal and sternal plates, and thus not only does each coxopodite include the coxa of the leg but its base occupies the area of the subcoxa of chilopods and insects. The legs of many larval insects are borne on distinct subcoxal lobes of the thoracic body

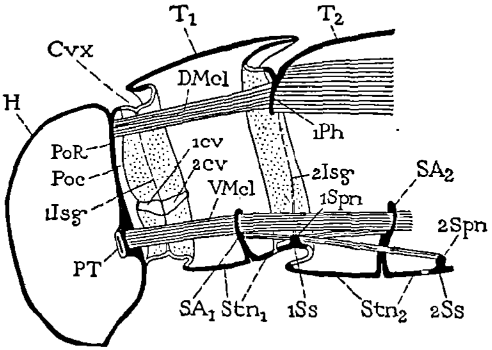

FIG. 87.—Diagram of intersegmental relations between the head and the prothorax, and between the prothorax and the mesothorax.

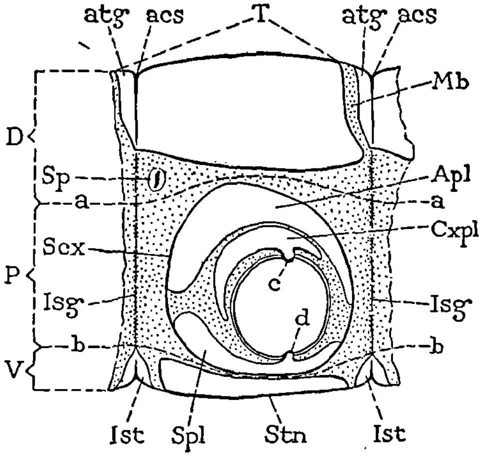

FIG. 88.—Diagram of the theoretically primitive sclerotic elements of a thoracic segment, in which the subcoxal part of the limb basis (*Scx*) includes two supracoxal sclerotic arches, the *anapleurite* (*Apl*) and *coxopleurite* (*Cxpl*), and an infracoxal arc, or *sternopleurite* (*Spl*).

segments, which contain the pleural sclerites in their dorsal walls (Figs. 152 A, 153 A, *Scx*).

The primitive subcoxal part of a thoracic leg probably formed a complete annulus proximal to the coxa (Fig. 88, *Scx*), which became flattened out in the pleural area of the body wall (*P*) to form a support for the rest of the limb. The entire subcoxal element in the body wall, therefore, includes not only the region of the pleural sclerites above the base of the coxa but also a ventral arc below the coxa.

The subcoxal sclerotization becomes variously broken up into sclerites, but a study of the more primitive insects and the chilopods suggests that there were primarily three major sclerotic areas surrounding the base of the coxa, two concentrically placed above the coxa, and one below it. These are respectively the *anapleurite* (Fig. 88, *Apl*) situated dorsally, the *coxopleurite* (*Cxpl*) closely associated with the upper rim of the coxa, and the *sternopleurite* (*Spl*) adjoining the sternum. The coxa is articulated between the coxopleurite and the sternopleurite (*c*, *d*). In most pterygote insects the two supracoxal arches unite to form the so-called pleuron, but they remain quite distinct in many Apterygota; the infracoxal arc usually becomes a lateral element of the definitive sternum (Fig. 91 B, *Ls*). The pleuro-ventral line of a thoracic segment (Fig. 88, *b-b*), therefore, generally runs through the lateral part of the definitive sternal plate.

The Apterygote Pleurites.—In the Apterygota the subcoxal sclerites of the thorax are small and variable and do not form definite pleural structures. A primitive condition in which each subcoxal area contains two distinct supracoxal sclerotic arches is well shown in some of the Protura and Collembola (Fig. 89, *Apl, Cxpl*). If the coxa has a definite dorsal articulation in these forms it is with the coxopleurite (C, *c*). The presence of a ventral articulation (*d*) probably means that the sternopleurite is contained in the definitive sternal plate. In Diplura and Thysanura the pleurites are variable and more or less degenerate, but in many cases there are distinct remnants of both the anapleural and the coxopleural arches. The ventral arc of the subcoxa more commonly preserves its independence from the sternum in the chilopods (Fig. 52 A, *Spl*) than it does in the insects. The thoracic pleurites of the Apterygota in many ways resemble the pleurites of the Chilopoda, and it is evident that in both groups the sclerites are in a degenerative state, since they have no very important function to perform. The highly developed pterygote pleuron, however, as we shall presently see, has apparently been derived from a more primitive pleural structure resembling that of the Apterygota and Chilopoda.

The Pterygote Pleuron.—In the Pterygota the progressive evolution of the supracoxal part of the subcoxa into an important skeletal part of the body segment, and the union of the infracoxal arc with the sternum have largely obscured the more primitive subcoxal structure exhibited by the Apterygota. It is only in the prothorax of Plecoptera that the pterygote pleuron retains the apterygote condition in which the anapleurite and the coxopleurite are distinct sclerites (Fig. 90, *Apl*, *Cxpl*). In all other cases these sclerites apparently are united in the single lateral plate supporting the coxa (Fig. 91 A, B). The prearticular part of the coxopleurite, however, generally remains as a partly or entirely free sclerite, the *trochantin* (*Tn*), the ventral extremity of which usually acquires an articulation with the anterior margin of the coxa (*e*).

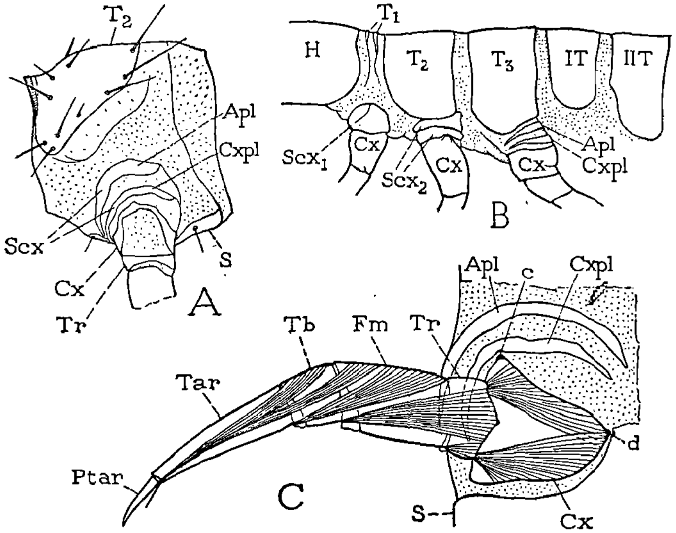

FIG. 89.—Examples of the presence of two supracoxal arches in the thoracic subcoxal region, as shown in Fig. 88. A, mesothorax of *Acerentomon doderoi*. (*From Berlese*, 1910.) B, *Isotoma*. C, mesothorax of *Acerentulus barberi*. (*B, C from H. E. Ewing*, 1928.)

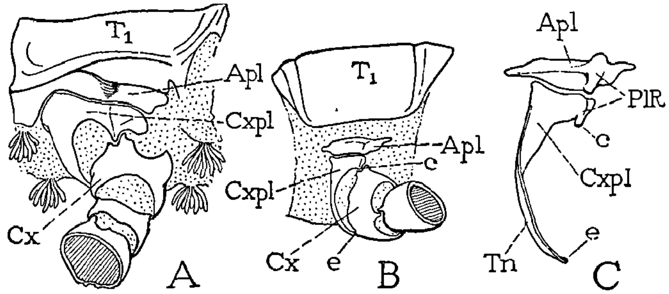

FIG. 90.—Examples of the retention of a distinct anapleurite and coxopleurite in the prothorax of pterygote insects (Plecoptera). A, larva of *Pteronarcys*. B, larva of *Perla*, external view. C, same, internal view.

The usual pterygote thoracic pleuron, formed by the union of the two supracoxal arches of the subcoxa, is typically a more or less continuous sclerotic area in the lateral wall of the body segment, surrounding the base of the coxa dorsally, anteriorly, and posteriorly (Fig. 91, A, B). Above the coxa the pleuron is reinforced by a strong internal *pleural ridge* (Fig. 92 A, *PlR*) extending upward from the coxal articulation (*CxP*), which is formed by a linear inflection of the outer wall, known as the *pleural suture* (Fig. 91, *PlS*). In a wing-bearing segment both the pleural ridge and its suture are carried upward into the pleural wing process (B, *WP*), and in such cases the ridge braces the pleural wall between the wing support and the coxal articulation. From each pleural ridge there projects inward and downward an apodemal arm, the *pleural apophysis* (Fig. 92 A, *PlA*), which is usually associated with a corresponding sternal apophysis (*SA*).

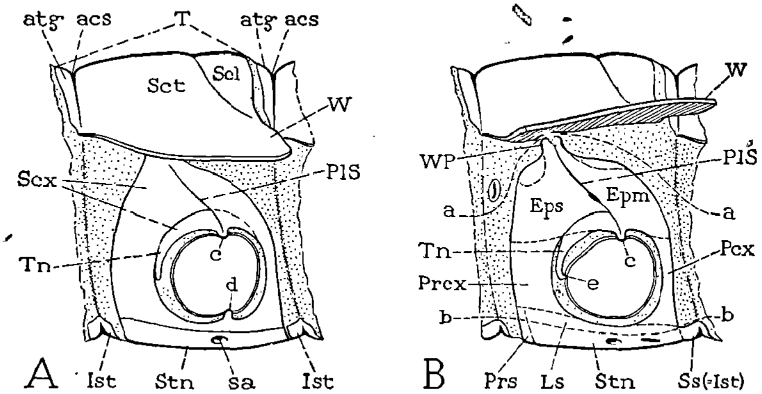

FIG. 91.—Diagrams illustrating the apparent evolution of the pleural and sternopleural sclerotization of a wing-bearing segment from the subcoxa. (Compare with Fig. 88.) The anapleurite and its ventral extensions become the *episternum* (B, *Eps*), the *epimeron* (*Epm*), the *precoxale* (*Prcx*), and the *postcoxale* (*Pcx*); the anterior part of the coxopleurite forms the trochantin (*Tn*); the sternopleurite unites with the primitive sternum (*Stn*) and becomes a laterosternal element (*Ls*) of the definitive sternum.

The pleural suture divides the upper part of the pleuron into a presutural *episternum* (Fig. 91 B, *Eps*) and a postsutural *epimeron* (*Epm*). The region of the pleuron extending downward from the episternum anterior to the coxa and the trochantin is the *precoxal bridge*, or *precoxale* (*Prcx*), generally united ventrally with the sternum; that behind the coxa, continuous from the epimeron and frequently united below with the sternum, is the *postcoxal bridge*, or *postcoxale* (*Pcx*). The precoxal and postcoxal sclerotizations may end ventrally in an infracoxal fold, evidently the infracoxal arc of the subcoxa (*A*); when they are united with the sternum it would appear probable that the ventral subcoxal arc has fused with the primary sternum (*Stn*) and forms a lateral part of the definitive sternum (B, *Ls*). The precoxal region sometimes forms a distinct sclerite separated from both the episternum and the sternum (Fig. 102 B, *Prcx*). The postcoxal sclerotization is seldom an independent sclerite, but it is often suppressed.

The anterior remnant of the coxopleurite, known as the *trochantin* (Fig. 91 A, *Tn*), is best preserved in the more generalized pterygote insects. When well developed it bears at its anterior or ventral end the anterior trochantinal articulation of the coxa (B, *e*); and usually the tergal promotor muscle of the leg is inserted on it. In the higher insects the trochantin becomes reduced or obliterated, or it may be united with the lower margin of the episternum in such a way that its limits are often difficult to determine.

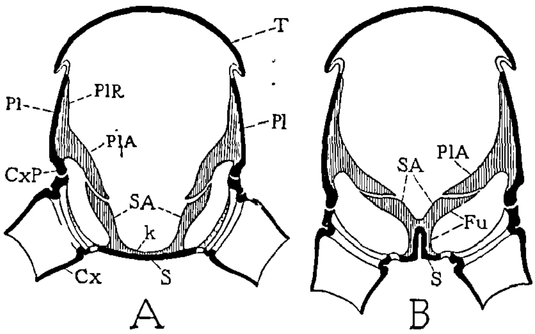

Fig. 92.—Diagrammatic cross section of thoracic segments illustrating the evolution of the furca (B, *Fu*) from the sternal apophyses (A, *SA*) and the inflected median part of the sternum (*S*).

The thoracic pleuron of the Pterygota is thus seen to differ consistently from the variable and weakly developed pleural parts of Apterygota in that it forms, in the adult stage of the insect, a definite and elaborate structure in the lateral wall of the body segment between the coxa and the tergum. Moreover, the basic features of the pterygote pleuron are the same in the wingless prothorax as in the alate mesothorax and metathorax. We cannot, therefore, attribute the characteristic structure of the pterygote pleuron to the development of the wings. On the other hand, we may suppose that the thoracic pleura of winged insects acquired their fundamental characters in correlation with the development of paranotal lobes on *all* the thoracic segments in the preflying glider stage of insect evolution.

The Thoracic Sterna.—The degree of sclerotization in the ventral walls of the body segments varies much in different arthropods; in some the venter is entirely membranous, in others it is occupied by definite sternal plates. Though a typical sternum (Fig. 36 B, *Stn*) includes the preceding intersegmental fold (*Ac*) on which the principal ventral body muscles are attached, the venter may be occupied by a series of alternating segmental and intersegmental sclerites, as in some of the chilopods (Fig. 38).

The sternal plates of the thorax in adult insects differ generally in three respects from those of the abdomen: first, in the independence of the primary segmental and intersegmental sclerotizations, or in the opposite relation of the second to the first when the two are united; second, in the reversed overlapping of the plates at the secondary intersegmental lines; and, third, in a transposition of the attachments of most of the ventral muscles from the intersegmental to the segmental sclerites.

Basic Structure of the Thoracic Sterna.—In the thorax the intersegmental sclerites of the venter between the prothorax and the mesothorax and between the mesothorax and the metathorax are never united with the segmental plates following; either they remain as free intersternites (Fig. 37, *1Ist*, *2Ist*) or they unite with the segmental sterna preceding. The primary intersegmental sclerotization behind the metasternum is generally lost or is united with the abdominal sternum following.

The segmental plate of the venter of a thoracic segment may be designated the *eusternum* (Figs. 93 A, B, *Stn*, 96, *ES*). The intersternites of the thorax (Fig. 93 A, *Ist*) are commonly termed *spinasterna* (Figs. 93 B, 96, *Ss*), because each usually bears a median apodemal process called the *spina* (Fig. 87, *Spn*).

Since both the first and the second spinasterna may be free intersternal sclerites, or the second, or also the first, may unite with the eusternum preceding, we usually encounter one of the following three series of sclerites in a study of the thoracic sterna, except when the eusternum itself is secondarily subdivided: (1) eusternum of prothorax, first spinasternum, eusternum of mesathorax, second spinasternum, eusternum of metathorax; (2) eusternum of prothorax, first spinasternum, composite mesosternum, eusternum of metathorax; (3) composite prosternum, composite mesosternum, eusternum of metathorax. A fourth condition may arise when the sternal plates of the wing-bearing segments are all united in a large pterothoracic plastron. It should be observed that the metasternum never has a spinasternite, because the third intersternite either is suppressed or becomes the acrosternite of the first abdominal sternum.

The eusternum of a thoracic segment, as we have observed, usually comprises the primary sternal plate and the subcoxal sternopleurites, the latter constituting the *laterosternites*, or *pleurosternites*, of the definitive sternum (Fig. 93 D, *Ls*). In some insects the thoracic sterna are bordered by distinct subcoxal folds continuous with the pleura before and behind the coxae (Fig. 95 A); in others the limits of the laterosternites are suggested by submarginal sutures; but in general the presence of lateral subcoxal derivatives is not evident in the definitive sternal plates of adult insects (Fig. 96, *ES*) and is only to be inferred from the continuity of the sternum with the precoxal and postcoxal bridges of the pleuron or from the presence of a ventral articulation of the coxa with the sternum, though the latter probably is secondary in some cases.

The Reversed Overlapping of the Thoracic Sterna.—The sternal plates of the thorax characteristically overlap each other *anteriorly* (Fig. 37) and thus present a relation just the opposite from that prevailing in the dorsum, and in the venter of the abdomen. This reversed overlapping of the thoracic sterna is particularly striking in some of the Apterygota and in the more generalized Pterygota, but it is evident wherever the successive sternal plates are not united with each other. It is apparently correlated with the reversed relations of the intersegmental spinasterna to the eusternal plates, and, while the reason for this peculiarly thoracic modification is not clear, it must have some important significance in the mechanism of the thorax not connected with the wings. As a consequence, the sternum of the metathorax (Fig. 37, Stn_3) stands usually as a dividing plate overlapping in both directions between the mesothorax and the abdomen, though sometimes it also is overlapped by the first abdominal sternum.

The Transposition of the Ventral Thoracic Muscles.—Associated with the reversed overlapping of the thoracic sterna, but not necessarily correlated with it, there occurs a partial or complete transfer of the attachments of the longitudinal sternal muscles from the intersternites to the preceding segmental parts of the definitive sterna. Theoretically we must assume that both the dorsal and the ventral muscles were originally attached on the lines of the primary intersegmental folds, which are preserved as the antecostae of the terga and of the abdominal sterna, but which are reduced in the sternal region of the thorax to the small, median, spinal processes of the spinasternites (Fig. 87, *Spn*). In adult pterygote insects the principal groups of ventral muscle fibers in the thorax extend between paired apophyses arising on the eusternal plates (SA_1, SA_2), though a few fibers usually preserve the original connections with the spinae (*Spn*). In most holometabolous larva, on the other hand, the principal ventral muscles throughout the length of the body are regularly attached on the intersegmental folds. The adult condition, then, is evidently a secondary one.

The Thoracic Sterna of Apterygota.—The sternal sclerotizations of the thorax in the Apterygota are variously developed and show no progressive evolution within the group. In the Protura and in *Japyx* the principal sternal plate in each segment bears an internal median ridge which may be forked anteriorly, with the arms extending to the ventral articulations of the coxae. Endosternal structures are absent in Lepismatidae, where each sternum is produced posteriorly into a large, scale-like lobe. In Machilidae the thoracic sterna are weakly developed areas of sclerotization between the leg bases, separated by ample intersegmental spaces. From each intersternal area a pair of delicate apodemal arms projects inward from a common median base, forming thus a series of furca-like structures. The intersegmental position of their bases, however, allies these apodemal structures with the median processes of the spinasternites in the Pterygota rather than with the true sternal apophyses.

The Thoracic Sterna of Pterygota.—The sterna of pterygote insects are characterized by the possession of paired apophyses arising from the eusternal plates. The *sternal apophyses* (Fig. 92 A, *SA*) are often

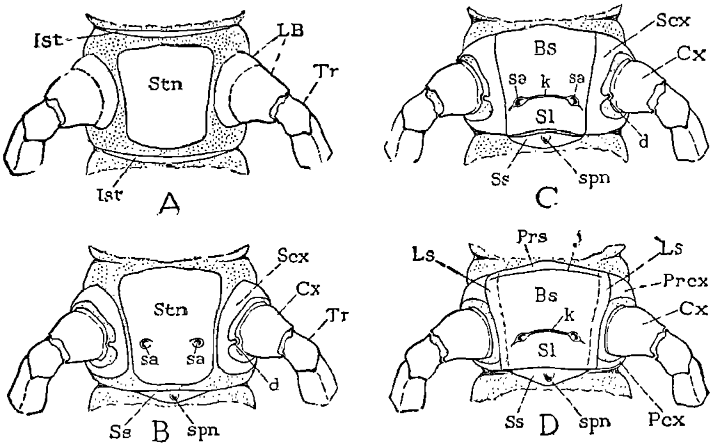

FIG. 93.—Diagrams suggesting the evolution of a generalized definitive thoracic sternum (D) by union of the primitive sternum (A, *Stn*) with the infracoxal arcs of the subcoxae (B, C, *Scx*), and with the following intersternite (A, *Ist*), which becomes the spinasternum (B, C, D, *Ss*). The definitive eusternum is finally divided by the sternacostal suture (C, D, *k*) into *basisternum* (*Bs*) and *sternellum* (*Sl*), and may have a narrow *presternum* (*Prs*) set off by an anterior submarginal suture (*j*).

called the *furcal arms*, because in the higher pterygote orders the two apophyses in each segment are supported on a median inflection of the sternum and thus become the divergent prongs of a forked endoskeletal structure known as the *furca* (B, *Fu*). The outer ends of the sternal apophyses are closely associated with the inner ends of the pleural arms (*PlA*) of the same segment, the two pairs of processes being usually connected by short muscle fibers, or in some cases fused with each other. When the pleural and sternal processes are united on each side of the segment, they form a buttresslike arch across the coxal cavity from the sternum to the pleuron.

The sternal apophyses support the principal longitudinal ventral muscles of the thorax, and they give attachment to some of the ventral muscles of the legs. Externally their roots are marked by a pair of pits in the sternum between the coxae (Fig. 93 B, *sa*, *sa*). The primitive position of the apophyses is doubtful; according to Weber (1928, 1928*a*), the processes are invaginations between the lateral edges of the primary sternum and the subcoxal laterosternites, but the location of the external pits of the apophyses does not always conform with this view.

In the more generalized Pterygota, the bases of the sternal apophyses are often connected by an internal transverse ridge, the *sternacosta* (Fig. 92 A, *k*), the line of which appears externally as a *sternacostal suture* through the apophyseal pits (Fig. 93 C, D, *k*). The sternal suture divides the surface of the eusternum into a presutural area, or *basisternum* (*Bs*), and a postsutural area, the *sternellum* (*Sl*), or "furcasternum." When the anterior part of the eusternum is reinforced by an internal submarginal ridge, there is formed externally a *presternal suture* (D, *j*), which sets off a narrow marginal area of the sternum, called the *presternum* (*Prs*). Muscles are never attached on the presternal ridge, and the latter should not be mistaken for a true antecosta; the sternal antecostae of the thorax are represented by the spinae of the spinasternites.

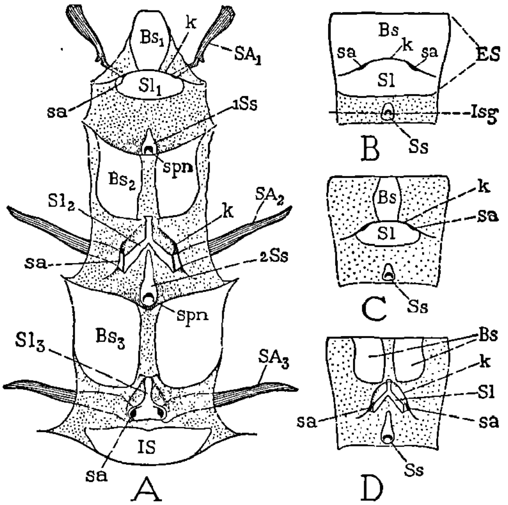

FIG. 94.—An example of desclerotization in the venter of the thorax. A, thoracic sterna of *Blatta orientalis*. B, diagram of the typical sternal sclerotization of a thoracic segment. C, result of desclerotization in the prothorax of *Blatta*. D, result of extreme desclerotization as in the mesothorax or metathorax of *Blatta*.

In its surface structure the thoracic sternum departs in many ways from the simple divisional pattern shown at D of Fig. 93. The sternacostal suture is subject to variations in form, being often produced forward and variously branched, giving rise to an endoskeletal structure of diversified form. In some cases also convergent ridges extend posteriorly from the bases of the apophyses and may unite in a median ridge, thus forming a Y-shaped endosternal ridge (*Y-Leiste* of Weber, 1933), the external sutures of which cut the sternellum into median and lateral areas. Or, again, a confusing condition may arise from a partial desclerotization of the sternal plates, as in the mesothorax and metathorax of Blattidae (Fig. 94 A), where the eusternum in each of these segments is divided into one or two anterior basisternal sclerites (*Bs*) and a posterior sternellar sclerite (*Sl*) supporting the long apophyses. The prosternum of the roach (C), however, retains more nearly the generalized sternal structure (B), and it is not difficult to see how the sclerite pattern of the mesosternum (D) or of the metasternum has been derived from the former (B) by a loss of sclerotic continuity.

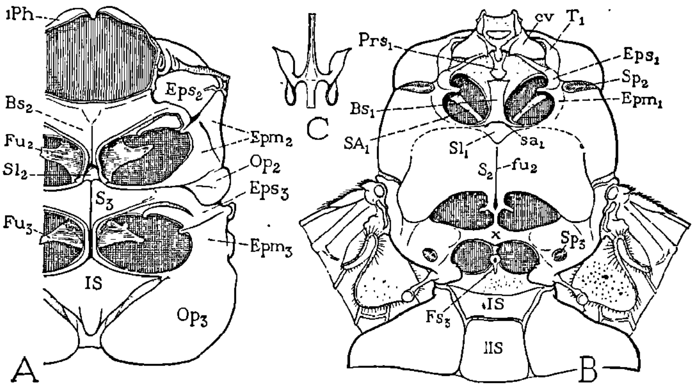

Fig. 95.—Examples of highly modified sternal sclerotization in the thorax. A, pterothorax of *Magicicada septendecim*, ventral view. B, thorax of *Calliphora*, ventral view. C, mesothoracic furca of *Calliphora*, dorsal view.

In the higher pterygote orders the sternal apophyses are carried inward upon a median inflection of the sternum to form the Y-shaped endosternal apodeme known as the *furca* (Fig. 92 B, *Fu*). The stalk of the furca may arise from a definite pit marking the division between the basisternal and sternellar regions of the sternum (Fig. 95 A, Bs_2, Sl_2), or the part of the sternum bearing the furca may become detached as a distinct *furcasternum* (B, Fs_3). In many insects, however, the base of the furca is extended forward as a long median ridge through the whole length of the sternum (C), the site of which is marked externally by a median sternal groove (B, fu_2). In this case there is no distinction between basisternum and sternellum or furcasternum, and it is impossible to say how much of the true sternum has been inflected to form the furcal base.

In a study of the thoracic sterna of the higher insects it seems more advisable to accept the facts as they are, unless identities with the sternal regions of more generalized insects can be traced through a series of families. In the pterothorax of the higher Diptera, for example (Fig. 95 B), the more primitive sutures of the sternal as well as the pleural areas have become almost wholly obliterated, and secondary grooves appear which divide the skeletal surface into parts that have little relation to those in more generalized orders. The large ventral plate of the mesothorax of *Calliphora* (Fig. 95 B) is evidently composed of the sternum, the precoxal bridges, and parts of the episterna; the bridge (*x*) separating the middle and hind coxae must include the postcoxalia of the mesothorax, the precoxalia of the metathorax, and the metathoracic basisternum. The small sclerite (Fs_3) between the hind coxae is a detached furcasternum, though the furca is supported also on the plate (*x*) before it. The prosternum, on the other hand, retains the more generalized structure in that the bases of the sternal apophyses (sa_1) separate a long basisternal sclerite (Bs_1) from a small sternellar region (Sl_1), which is united with the mesosternum. A presternal sclerite (Prs_1) is here entirely cut off from the basisternum.

4. THE PROTHORAX

The prothorax differs consistently from the other body segments in that its tergum and sternum always lack the antecostal and precostal elements of typical segmental plates, these parts apparently having been lost by membranization in the neck. The prothoracic tergum is a plate of the primary segmental region only (Fig. 87, T_1). It never bears a phragma, since the first phragma (*1Ph*) is never detached from the mesotergum, and the acrotergite of the mesotergum is not sufficiently enlarged to constitute a postnotum of the prothorax. The principal dorsal muscles of the prothorax (*DMcl*) extend through the segment from the postoccipital ridge of the head (*PoR*) to the antecosta, or phragma (*1Ph*), of the mesotergum, but shorter muscles may connect the head with the protergum or the latter with the mesotergum. The size and form of the prothoracic tergum are highly variable. In some insects, as in Orthoptera, Hemiptera, and Coleoptera, the protergum may be a large plate, sometimes greatly expanded; but since, in general, the back plate of the prothorax has little specific function aside from giving attachment to the dorsal muscles of the legs, it frequently assumes strange and fantastic shapes, or, on the other hand, it is reduced in size and may be but a narrow band between the head and the mesothorax. In some of the Hymenoptera the protergum is so intimately associated with the mesotergum that the isolated pleurosternal parts of its segment form a free suspensorium for the first pair of legs. When the protergum is well developed its surface may be marked by sutures, which form ridges on the inner surface of the plate; but the resulting "divisions" of the protergum have no relation to those characteristic of the wing-bearing terga. The internal ridges are usually found to have an intimate relation to muscle attachments.

The prothoracic sternum has the same fundamental structure as the sterna of the pterothorax but is commonly more generalized than the latter. The eusternum bears a pair of apodemal apophyses (Fig. 87, SA_1), and the spinasternum (*1Ss*), which may be widely separated from the eusternum or fused with it, bears a median spina. The true intersegmental line between the prothorax and the mesothorax (*2Isg*) runs through the spinasternite ventrally and the base of the first phragma dorsally, but usually a wide membranous area constitutes the functional intersegmental conjunctiva.

The pleuron of the adult prothorax resembles the pleural sclerotization of the pterothorax of nymphal and larval insects in that it lacks the alar development characteristic of the adult pterothoracic pleuron. In its general features it has the same type of structure as the pleura of the wing-bearing segments, and only in the Plecoptera (Fig. 90) does it show any suggestion of the more primitive structure of the apterygote pleuron. The episternum and epimeron are always well separated by a pleural suture and ridge, though the epimeron is often much reduced or fused with the margin of the tergum. In some Orthoptera the episternum is largely concealed within a lateral fold of the protergum, but, since it gives origin to the abductor muscle of the coxa, it is seldom reduced in proportion to the reduction of the epimeron. The lateral sclerites of the neck usually articulate with the prothoracic episterna, but they may be fused with the latter to form a pair of arms projecting from the propleura to support the head. Precoxal and postcoxal extensions of the supracoxal pleurites, of which one or both may be continuous with the sternum, are commonly present in the prothorax as in the pterothorax. The entire structure of the prothoracic pleuron suggests an evolution homodynamous with that of the pleura of the wing-bearing segments to a point where the latter became specialized as parts of the wing mechanism.

5. THE PTEROTHORAX

The wing-bearing segments differ structurally from the prothorax only in details that are clearly adaptations to the function of movement in the wings. The modifications affect chiefly the terga, in a lesser degree the pleura, and least the sterna.

General Structure of the Wing-bearing Segments.—The typical structure of a wing-bearing segment is shown diagrammatically in Fig. 96. The dorsum of the segment may be occupied entirely by a single tergal plate (*AN*), which bears the wings; but usually the segment in which the wings are better developed contains also a second, posterior plate (*PN*), which carries a phragma (*Pph*). Since entomologists generally prefer the term *notum* for the tergal plates of the thorax, we may designate the wing-bearing plate in the dorsum of a pterothoracic segment the *alinotum* (*AN*), and the phragma-bearing plate the *phragmanotum*, or *postnotum* (*PN*). The alinotum is often supported on the pleura by prealar arms (*Pra*) extending laterally or downward from its anterior angles to the episterna; the postnotum is generally firmly braced upon the pleura by lateral postalar extensions (*Pa*) united with the epimera.

Since the phragmata are inflections of the integument on the primary intersegmental grooves (Fig. 96, *acs*), the phragma-bearing postnotal plates of the dorsum are in every way comparable with the spinasterna of the venter (*Ss*). The true intersegmental lines of the thorax (*Isg*) run dorsally through the bases of the phragmata, and ventrally through the bases of the spinae. The phragma-bearing plates of the dorsum, however, differ from the spina-bearing plates of the venter in that they may be more closely associated or united with the segmental plate either before or behind them. Thus the segment carrying the principal pair of wings may have a phragma at each end of its tergal region. The anterior phragma in this case may be distinguished as a *prephragma* (*Aph*), and the posterior one as a *postphragma* (*Pph*).

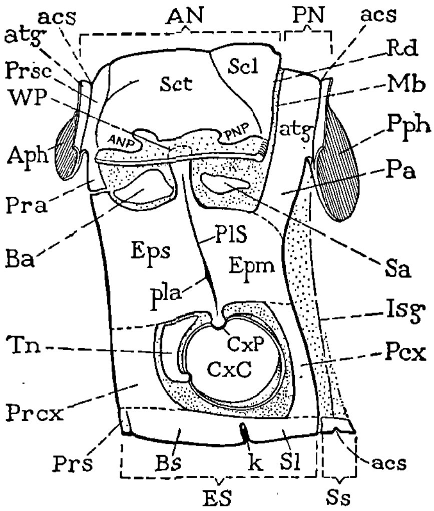

FIG. 96.—Diagram of the typical sclerites of a wing-bearing thoracic segment, and their subdivisions, lateral view. *acs*, antecostal suture; *AN*, alinotum; *ANP*, anterior notal wing process; *Aph*, anterior phragma, prephragma; *atg*, acrotergite; *Ba*, basalare; *Bs*, basisternum; *CxC*, coxal cavity; *CxP*, pleural coxal process; *Epm*, epimeron; *Eps*, episternum; *ES*, eusternum; *Isg*, primary intersegmental line; *k*, sternacostal suture; *Mb*, conjunctiva, secondary intersegmental membrane; *Pa*, postalare; *Pcx*, postcoxale; *pla*, root of pleural apophysis; *PlS*, pleural suture; *PN*, postnotum, phragmanotum; *PNP*, posterior notal wing process; *Pph*, posterior phragma, postphragma; *Pra*, prealare; *Prcx*, precoxale; *Prs*, presternum; *Prsc*, prescutum; *Rd*, posterior fold or reduplication of alinotum; *Sa*, subalare; *Scl*, scutellum; *Sct*, scutum; *Sl*, sternellum; *Ss*, spinasternum; *Tn*, trochantin; *WP*, pleural wing process.

The wings are flat folds of the body wall extending laterally from the edges of the alinotal plates (Fig. 85, W_2, W_3), their upper membranes being continuous with the dorsal integument, their ventral membranes reflected into the lateral walls of the segments. The posterior border of each wing is continuous with the posterior marginal fold of the alinotum

(Fig. 96, *Rd*), but anteriorly the wing base ends behind the prealar arm of the notum.

The pleural sclerotization of a wing-bearing segment is usually well developed and is almost always divided by a pleural suture (Fig. 96, *PlS*) into an episternum (*Eps*) and epimeron (*Epm*). At the upper end of the suture the dorsal margin of the pleuron is produced into a *pleural wing process* (*WP*), which serves as a fulcrum for the movement of the wing. Before and behind the wing process in the upper membranous parts of the pleural wall, there are situated two or more *epipleurites* (*Ba, Sa*), usually small plates upon which are inserted important muscles of the wings. Ventrally the pleuron is generally supported on the sternum by the precoxal and postcoxal bridges (*Prcx, Pcx*). The trochantin (*Tn*) is variable and is usually suppressed in the higher orders.

The sterna of the pterothoracic segments have no special features to distinguish them from the prothoracic sternum, except for the size of the basisternal regions, which are usually enlarged to accommodate the ventral ends of the tergosternal wing muscles, representatives of which are absent in the prothorax.

The Tergal Plates of the Pterothorax.—The terga of the wing-bearing segments not only support the wings but are themselves important elements in the mechanism for moving the wings, since each acts as an intermediary between the indirect wing muscles of its segment and the bases of the wings. The tergum plays its part in the production of wing movement by responding to the contraction of the longitudinal dorsal muscles with an upward curvature between its two ends, and by a reverse action to the downward pull of the antagonistic tergosternal muscles. The depression of the tergum causes the upstroke of the wings; the dorsal flexure assists in the downstroke. It is evident that the effect of the dorsal muscles on the pterothoracic terga must depend on a close connection between the mesotergum and the metatergum and between the metatergum and the first abdominal tergum; otherwise there would be much lost motion, since, with the usual intersegmental relations, the contraction of the dorsal muscles simply pulls the tergal plates together.

To accommodate them to their parts in the wing mechanism, the alate terga have been modified in three principal ways. In the first place, in order that the tergal plates may respond by changes in their dorsal curvature to the action of the longitudinal muscles attached on them, the intersegmental membranes have been reduced or eliminated, usually by a redistribution of the intersegmental sclerotization between the mesotergum and metatergum and between the metatergum and the first abdominal tergum, which has given rise to the so-called postnotal plates. In the second place, the wing-bearing plates have been strengthened, in order to withstand the strain of work imposed upon them, by the development of various ridges on their inner surfaces. These ridges are formed by linear inflections, or "sutures," of the outer surfaces. Consequently, a wing-bearing tergum is subdivided by its ridges and their sutures into several distinct areas characteristic of the terga of the pterothorax, but having no morphological counterparts in the tergal plates of other segments. Finally, since the wings are movable by definite articulations on the supporting back plates, the lateral margins of the mesotergum and the metatergum present structural features precisely adapted to the hinging of the wing bases on the dorsum.

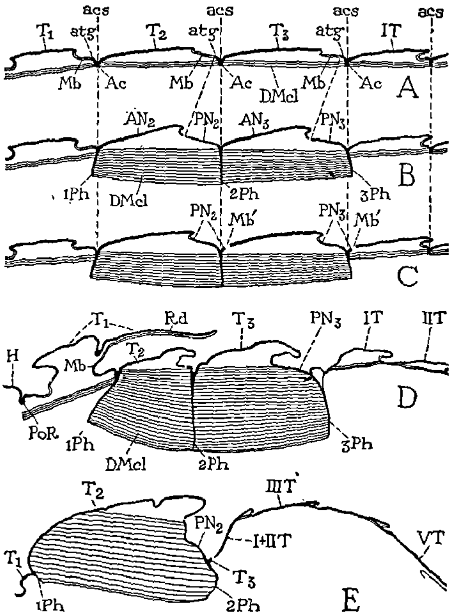

FIG. 97.—Evolution of the postnotal plates of the mesothorax and metathorax from the acrotergites of the segments following, and the development of the phragmata and dorsal muscles. A, generalized condition. B, postnotal plates formed as extensions of the acrotergites. C, postnotal plates with phragmata cut off by secondary membranes (*Mb'*) from tergal plates following. D, section of *Dissosteira*, showing postnotum developed only in metathorax. E, section of *Calliphora*, showing postnotum in mesothorax, and metathoracic tergum almost obliterated on median line.

Redistribution of the Intertergal Sclerotization in the Wing-bearing Segments.—The mesothoracic and metathoracic terga of apterygote insects and of nymphal and larval forms of pterygote insects having a well-developed thoracic sclerotization are the same as the abdominal terga in that each tergal plate comprises the segmental and preceding intersegmental sclerotization and is crossed anteriorly by a submarginal antecostal suture (Fig. 86). It is evident, therefore, that the immediate ancestors of the winged insects had a typical secondary segmentation throughout the dorsum of the thorax and abdomen (Fig. 97 A). This structure is retained in the mesothoracic and metathoracic terga of some adult winged insects, such as the Isoptera, in which the dorsal thoracic muscles are small and weak and probably have little to do with moving the wings. The pterothoracic and first abdominal terga of the Isoptera, however, are closely attached to each other. A similar structure occurs in the Blattidae, in which also the small dorsal muscles are relatively unimportant elements in the wing mechanism by comparison with those of most insects. The successive terga in the wing region of Blattidae are connected by lateral expansions of the acrotergites of the metatergum and the first abdominal tergum. In both Isoptera and Blattidae there may be small phragmatal lobes on the antecostae of the mesotergum and metatergum.

With the majority of winged insects the dorsal muscles of the pterothoracic segments are greatly enlarged, and their ends are attached on well-developed phragmata depending from the antecostae of the mesotergum, the metatergum, and the first abdominal tergum (Fig. 97 B). The phragmata, as we have seen, are intersegmental inflections, and the external grooves, or antecostal sutures (*acs*), through their bases mark the primary intersegmental lines. The acrotergite (*atg*) of the mesotergum (T_2) retains the usual form of a narrow flange before the antecostal suture (A, B); but the acrotergite of the metatergum and the acrotergite of the first abdominal tergum (B) are each enlarged and extended forward to the posterior margin of the tergum preceding in each case. In this way the dorsal intersegmental membranes (A, *Mb*) are practically eliminated between the mesotergum and the metatergum, and between the latter and the first abdominal tergum, and are replaced by the expanded acrotergites, which become postnotal plates of the mesothorax and the metathorax, respectively (B, PN_2, PN_3).

The obliteration of the dorsal intersegmental membranes by the development of acrotergal postnotal plates produces a continuous sclerotization in the dorsum of the pterothorax (Fig. 85) from the base of the first phragma (Fig. 97 B, *1Ph*) to that of the third (*3Ph*). The contractile force of the dorsal muscles is thus prevented from pulling the successive terga together and is therefore expended against the tergal plates themselves, which may now respond by an upward curvature, producing a depression of the wings on the pleural fulcra. The elimination of the secondary intersegmental membranes by the enlargement of the acrotergites virtually restores the pterothoracic dorsum to a condition of primary segmentation, since the functional segmental limits are now marked by the primarily intersegmental phragmata. The postnotal plates are thus seen to belong morphologically each to the segment of the tergal plate preceding it.

If the hind wings are the principal organs of flight, as in Orthoptera and Coleoptera, a postnotum is developed in the metathorax only (Fig. 97 D, PN_3). With most of the higher insects, however, in which the fore wings are large and the hind wings small, there is usually present a postnotal plate in each of the alate segments, though the second is generally reduced in size, as is also the alinotum of the same segment. An extreme adaptation to the two-winged condition occurs in the higher Diptera (E), in which the metatergum is a scarcely perceptible rudiment (T_3), and practically the entire dorsum of the thorax is formed of the alinotum and postnotum of the mesothorax, between which, or their respective phragmata (*1Ph*, *2Ph*), extend the great dorsal muscles of the mesothorax.

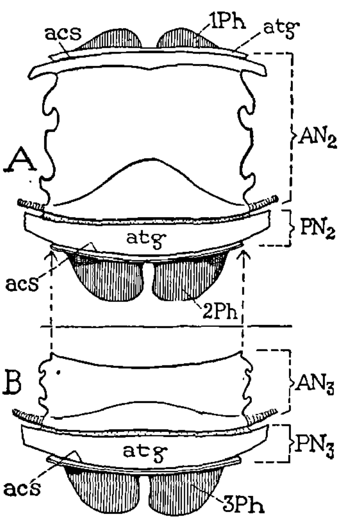

Fig. 98.—Diagrams showing the derivation of the phragma-bearing postnotal plate (*PN*), associated with each wing-bearing alinotal plate (*AN*), from the tergum following in each case.

In many of the higher insects the base of each phragma becomes separated from the tergum behind it by a transverse line of membranization (Fig. 97 C, *Mb′*), and in such cases the postnotum (Fig. 98, PN_2, PN_3) includes not only the acrotergite (*atg*) but also the narrow posterior lip of the phragmatal inflection behind the antecostal suture. With insects having this type of structure, the functional conjunctivae on the dorsum are the membranes (*Mb′*) *behind* the bases of the phragmata, and the tergal plates of the metathorax and first abdominal segments are incomplete by the lack of their usual anterior phragma-bearing parts. Generally the posterior lip of a detached postnotum is very narrow or scarcely apparent, but in some cases it is large, as in the metathorax of *Panorpa* (Fig. 99, PN_3), where it includes the major part of the first abdominal tergum (*IT*).

Each phragma consists typically of a pair of thin, plate-like apodemal lobes (Fig. 98, *Ph*) separated by a median notch giving passage to the dorsal blood vessel; but in some cases the two lobes are united in a single broad plate, and the blood vessel then dips beneath the latter. In certain Hymenoptera the median part of the second phragma is membranous, giving the phragma the appearance of being connected with the tergum only by its lateral angles.

The Sutures, Ridges, and Surface Areas of the Alinotum.—The surfaces of the alinotal plates are greatly diversified in different insects by topographical irregularities and by sutures. The so-called sutures are mostly the external grooves of internal ridges, which are the important mechanical features of the notum, but the sutures are the characters more generally used in descriptive works. The principal alinotal sutures and the areas they define may be described as follows:

The *antecostal suture* is the groove through the base of a phragma which marks the line of the antecosta (Fig. 100 A, *acs*). The acrotergite before the antecostal suture is usually a very narrow anterior lip of the alinotum (*atg*), except when it is enlarged to form the postnotal plate of the preceding segment (Figs. 96, 98).

The *scutoscutellar*, or *V-shaped, suture* (Fig. 100 A, *vs*) lies in the posterior part of the alinotum with its apex directed forward; it divides the notum into an anterior *scutum* (*Sct*) and a posterior *scutellum* (*Scl*). Internally this suture forms usually a strong *V-shaped ridge* (B, *VR*), which not only strengthens the notum but probably, in its typical form, serves also as a gradient device to bring the peak of the upward flexure of the notum during flight on a line between the bases of the wings. The scutoscutellar ridge and its suture, however, are subject to much variation in form and degree of development, and they are sometimes obsolete or absent; but in general the V-shaped ridge and its suture are the most constant features of the wing-bearing plates and are present in some form in nearly all winged insects (Fig. 101, *vs*).

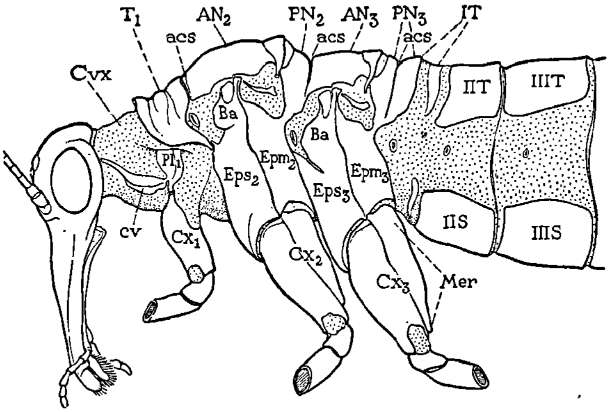

FIG. 99.—Head, thorax, and base of abdomen of *Panorpa consuetudinis*.

A *reversed notal suture* occurs in some insects in which the true scutoscutellar suture is obsolete or absent. In the Acrididae, for example, the usual V-ridge and its suture are partially suppressed (Fig. 101 C, *vs*), and the posterior part of the alinotum is marked by the line of a secondary ridge (*rvs*) of similar shape but having the apex directed posteriorly. The true scutellar region is thus divided into a median elevated shield-shaped area (*Scl*) and two lateral depressed areas (*scl*, *scl*). A similar topographical condition is even more strongly pronounced in the mesothorax of Hemiptera and Coleoptera.

A *transverse*, or *prescutal*, *suture* (Fig. 100 A, *ts*), with its corresponding internal ridge (B, *TR*), is of frequent recurrence in many groups of insects. It lies in the anterior part of the alinotum and sets off a *prescutum* (*Prsc*) in the area immediately behind the antecostal suture. The prescutum is variable in size and shape. It is well developed in Plecoptera, in some Orthoptera (Fig. 101 B, C), and in the mesothorax of Lepidoptera (G) and Coleoptera (H), but in other insects it is frequently very narrow (D, E, I); in Diptera it ends in a small lobe on each side of the notum before the wing base (D, E, *e*). Since the prescutal suture is often obsolete or absent, however, the prescutum may be but weakly defined or not distinguishable from the scutum (F, J).

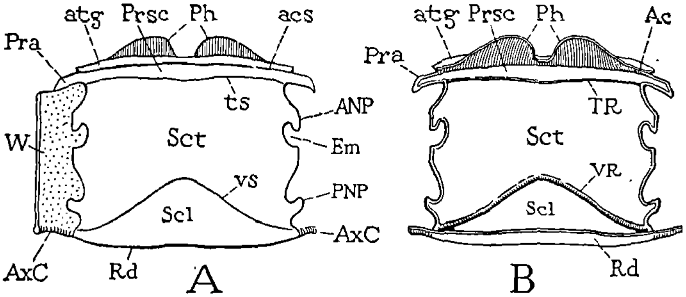

FIG. 100.—Diagrams showing the principal features of a generalized wing-bearing tergal plate. A, dorsal surface with sutures. B, ventral surface with corresponding ridges. *Ac*, antecosta; *acs*, antecostal suture; *ANP*, anterior notal wing process; *atg*, acrotergite; *AxC*, axillary "cord"; *Em*, lateral emargination; *Ph*, phragma; *PNP*, posterior notal wing process; *Pra*, prealare; *Prsc*, prescutum; *Rd*, posterior marginal fold of alinotum continuous with wing margins; *Scl*, scutellum; *Sct*, scutum; *TR*, transverse notal ridge; *ts*, transverse notal suture; *VR*, V-shaped, or scutoscutellar, ridge; *vs*, suture of V-shaped ridge; *W*, base of wing.

A pair of *convergent sutures*, or *notaulices*, sometimes occurs in the anterior part of the alinotum. These sutures arise anterolaterally and extend posteriorly a varying distance, usually converging toward the median line of the back (Fig. 101 I, *no*); but the same sutures apparently, in some cases, may continue posteriorly to the transscutal suture (F, *no*) and thus divide the scutum into a median area (*g*) and two lateral areas (*h*, *h*). The convergent sutures are generally known as the "notauli" to systematists in Hymenoptera, which term is evidently a misspelling for *notaulices* (from *aulix*, *aulicis*, a furrow), but the same sutures are often called "parapsidal furrows," and, again, many entomologists have regarded them as discontinuous median parts of the transverse prescutal suture turned posteriorly. If the convergent sutures are parts of the prescutal suture, the area between them is the prescutum, but in some insects, as in Tenthredinidae (Fig. 101 I), both the transverse prescutal suture (*ts*) and the convergent sutures (*no*) are present, showing that the area between the latter belongs to the scutum. The development of the convergent sutures and their internal ridges is correlated with the posterior extension of the attachments of the dorsal wing muscles on the scutum (Fig. 128 B).

A pair of *lateral sutures,* or *parapsidal furrows,* occurs frequently in the scutum of the mesothorax of Hymenoptera; the sutures begin posteriorly usually at the transscutal suture and diverge forward a varying distance in the lateral areas of the scutum (Fig. 101 F, *pf*). These sutures, according to Tulloch (1929), are the sutures properly termed parapsidal furrows. The parts of the scutum lying laterad of them are the *parapsides.* In common practice, however, the anterior convergent sutures of Hymenoptera are often called the parapsidal furrows, and the

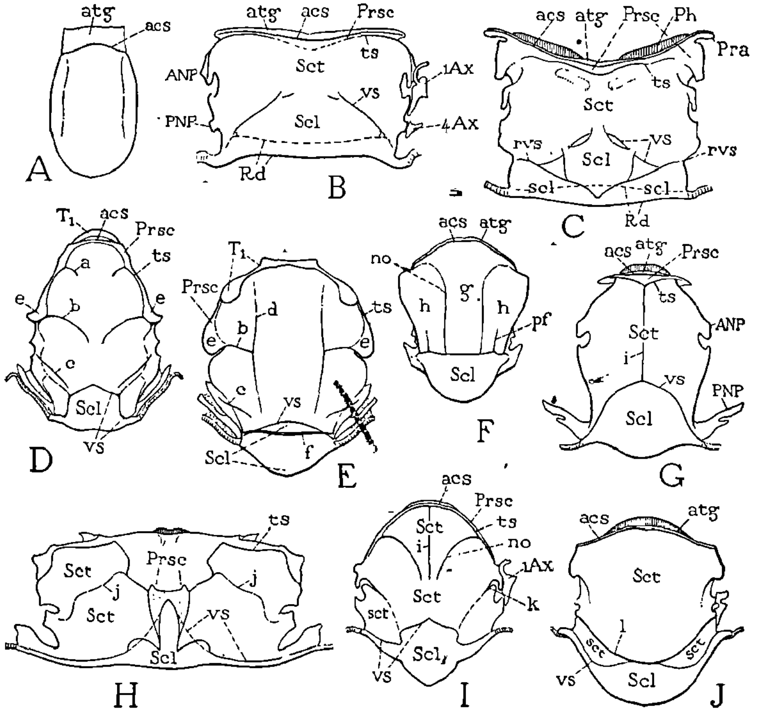

FIG. 101.—Examples of various sutural patterns in the tergal plates of the thorax. A, mesonotum of *Japyx.* B, metathoracic alinotum of *Gryllus.* C, mesonotum of *Melanoplus.* D, pronotum (T_1) and mesothoracic alinotum of *Holorusia.* E, pronotum and mesothoracic alinotum of *Tabanus.* F, mesothoracic alinotum of *Cynips.* G, mesothoracic alinotum of *Phassus.* H, mesothoracic alinotum of *Calosoma.* I, mesothoracic alinotum of *Pteronidea.* J, mesothoracic alinotum of *Apis.* (For principal sutures see Fig. 100.) *a, b, c, d,* intrascutal sutures of Diptera; *e,* prescutal lobe; *f,* trans scutellar suture; *g,* median scutal area; *h, h,* lateral scutal areas; *i,* median notal suture; *j, j,* transverse intrascutal sutures of Coleoptera; *k,* posterior intrascutal groove; *l,* trans scutal suture; *no,* notaulix; *pf,* parapsidal furrow.

areas laterad of them in Cynipoidea and Chalcidoidea are then designated the parapsides. In general usage the two terms, notaulices and parapsidal sutures, therefore, are usually synonymous since each may refer to the anterior convergent sutures.

A *median suture* of the notum sometimes occurs in the anterior part of the scutum (Fig. 101 I, *i*) or extends through the entire length of the scutum (G, *i*). Internally it forms a median carina, which, when fully developed, extends like a ridgepole from the prescutum to the apex of the scutellum.

A *transscutal suture* in most of the clistogastrous Hymenoptera, as in the honey bee (Fig. 101 J, *l*), cuts completely through the posterior part of the scutum, setting off two posterolateral areas of the latter (*sct, sct*) from the major scutal area (*Sct*). The parts of the alinotum separated by this suture are commonly termed "scutum" and "scutellum" by students of Hymenoptera, but it is clear that these areas are not identical with the scutum and scutellum of more generalized insects. The true scutoscutellar suture is well preserved in the Tenthredinidae (Fig. 101 I, *vs*) and may be present also in the higher Hymenoptera (J, *vs*) in conjunction with the transscutal suture (*l*).

A *transscutellar suture* cuts through the anterior part of the scutellum in higher Diptera (Fig. 101 E, *f*) between the lateral extremities of the scutoscutellar suture (*vs*).

Various other sutures may occur in the alinotum, which are often characteristic of different orders, but which can be given no general names. In the metathorax of Coleoptera, for example, the lateral areas of the irregular scutum are partially divided by oblique sutures (Fig. 101 H, *j, j*) into anterior and posterior parts (*Sct, Sct*). In the Diptera short lateral sutures or also longitudinal sutures occur in the mesoscutum (*D, E, a, b, c, d*), which give the sectional pattern characteristic of the wing-bearing notum in this order.

A comparative study of the sutures and subdivisions of the alinotum brings out so many differences in these features between different orders that it becomes questionable if many of them are truly homologous structures. Aside from the antecostal suture, the only fairly constant character of a wing-bearing tergum is its division into two major parts by the suture of the V-shaped endotergal ridge, and even this feature is often obscured by a partial suppression of the ridge. The other ridges and sutures, producing various tergal subdivisions, are local adaptations to mechanical stresses and demands for flexibility in the wing-bearing plate, and a careful study of the wing mechanism would probably reveal the reason for them in each particular case. The structure of the tergum is often quite different in the two segments of the pterothorax according to the relative development of the two pairs of wings, and in most insects with small or rudimentary hind wings the metatergum becomes much reduced.

The Alar Margins of the Alinotum.—The lateral margins of the alinotum are specifically modified in adaptation to the complex articular and flexor mechanisms of the wing bases. Very frequently each anterior lateral angle of the postcostal region of the notum is produced in a prealar bridge, or *prealare* (Fig. 96, *Pra*), that extends laterad or ventrad to the episternum (*Eps*) and thus supports the notum anteriorly on the pleural wall of the segment. The wings arise from the scutoscutellar margins of the alinotum (Fig. 100 A, *W*), which may be long or much shortened, and the posterior thickened edges, or "axillary cords" (*AxC*), of the basal wing membranes are always continuous with the posterior marginal fold of the scutellum (*Rd*).

Each alar margin of the scutum presents typically an *anterior notal wing process* (Figs. 96, 100 A, *ANP*) and a *posterior notal wing process* (*PNP*). The anterior notal wing process is almost always present and supports the neck of the first axillary sclerite of the wing base (Fig. 101 B, I, 1*Ax*). Immediately behind it is a deep emargination in the edge of the scutum (Fig. 100 A, *Em*). The posterior wing process usually gives support to the third axillary of the wing base (Fig. 122, 3*Ax*), but sometimes a fourth axillary intervenes between the third axillary and the notal margin, and in such cases a posterior wing process is usually absent. In the metathorax of some Orthoptera a special arm of the alinotum supports the vannal veins of the wings.

The Pleuron of a Winged Segment.—The pleura of the wing-bearing segments do not differ fundamentally from the prothoracic pleura, but secondary differences between the two may be considerable on account of the degenerative tendency of the prothoracic pleura, and because of the special developments that take place in the pterothoracic pleura. The pleura of the pterothorax are important elements of the wing mechanism, though, for the most part, their role is a passive one. The pleura show many minor variations in structure, and their areas may be variously broken up into secondary sclerites. In most cases it is difficult to discover the mechanical significance of these modifications, but their progressive development within a family or order often furnishes a valuable clue to the relationships of genera and families.

The principal alar functions of the pleuron in a winged segment are to furnish a fulcrum for the wing and to give attachment to the pleural wing muscles, though usually, as already observed, the pleuron also supports the tergal plates on the prealar and postalar arms of the latter (Fig. 96, *Pra, Pa*). The wing fulcrum, or *pleural wing process* (*WP*), typically has the form of a short, thick arm arising from the dorsal margin of the pleuron. The wing process is braced internally by the pleural ridge, which in the adult insect extends dorsally or obliquely from the coxal process of the pleuron to the wing process. The pleural suture is thus to be identified as the groove on the external wall of the pleuron (*PlS*) that extends between the articular processes of the wing and the leg. Usually the pleural suture takes a direct course between these two points (Fig. 102 D, PlS_2), but it may be irregular or angularly bent (E, PlS_2).

The episternum and epimeron of the wing-bearing segments exhibit numerous variations in form and undergo various subdivisions into secondary sclerites, but their modifications are in general easy to follow. The most frequent type of subdivision divides the episternal and epimeral regions into dorsal and ventral areas. These are distinguished as the *supraepisternum*, or *anepisternum*, the *infraepisternum*, or *katepisternum*, the *supraepimeron*, or *anepimeron*, and the *infraepimeron*, or *katepimeron*. An anterior subdivision of the episternum is a *preepisternum;* if it is continuous with the presternum, the anterior pleurosternal piece thus set off is termed the *prepectus*. The precoxal and postcoxal areas of the pleuron (Fig. 96, *Prcx*, *Pcx*) are usually sclerotized in the wing-bearing segments, forming precoxal and postcoxal bridges to the sternum. Sometimes they are separated from the episternal and epimeral regions, but usually in adult insects they are united with the sternum. The postcoxal bridge is generally narrower than the precoxal bridge and is more frequently absent.

The trochantin of the pterothoracic segments (Fig. 96, *Tn*) is best developed in the more generalized Pterygota, but it always shows a tendency toward reduction and is lost in the higher orders.

The Epipleurites.—The chief distinctive feature of the pterothoracic pleura, aside from the presence of the wing processes, is the development and individualization of small sclerites beneath the wing bases, on which important muscles of the wings are inserted. These plates may be termed the *epipleurites*, since they lie above the principal pleurites from which they are derived, though they have often been called the "paraptera." The anterior, or episternal, epipleurites are the *basalares;* the posterior, or epimeral, epipleurites are the *subalares*. Generally there is but one basalare in each segment (Fig. 96, *Ba*) and one subalare (*Sa*), though each is sometimes double.

The epipleurites appear to be derived by a secondary separation from the upper edges of the episternum and the epimeron. While the subalare is nearly always a distinct sclerite in adult insects, the basalare is frequently but an imperfectly separated lobe of the episternum (Fig. 99, *Ba*) or merely an area of the latter on which the anterior pleural wing muscles are attached. In nymphal Orthoptera neither the basalare nor the subalare is yet differentiated from the rest of the pleuron (Fig. 102 A, B), and both the anterior and posterior pleural wing muscles arise from the upper edges of the latter, the first on the episternum, the second on the epimeron (C, $3E'$, $3E''$).

The Mesopleuron of Diptera.—In the higher Diptera the structure of the pleuron of the mesothorax becomes complicated by several unusual modifications. In the Tipulidae, however, the mesopleural elements are relatively simple and easy to identify. In *Holorusia* (Fig. 102 D), for example, the pleural suture (PlS_2) takes the ordinary straight course from the base of the coxa to the wing process, and the only unusual features of the pleuron are the presence of an incomplete suture (*a*) separating the episternal region (Eps_2) from the precoxal region (*Prcx*),

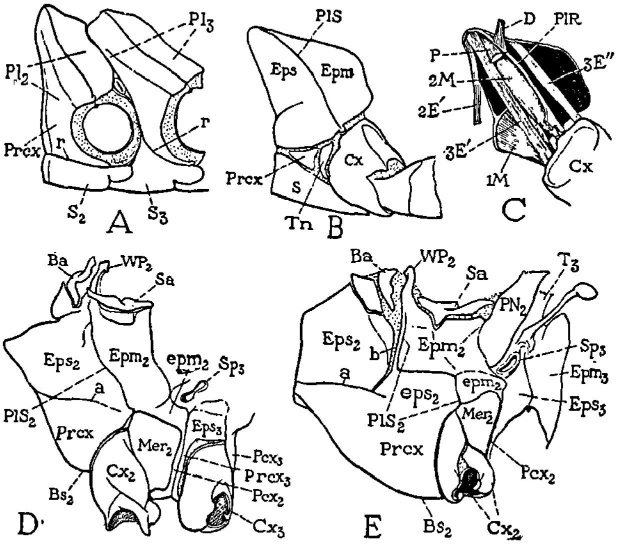

FIG. 102.—Examples of simple and highly modified patterns of the pleural sclerites of wing-bearing segments. A, nymph of *Melanoplus*. B, nymph of *Gryllus*, mesopleuron. C, inner view of same showing muscles. D, *Holorusia grandis*, mesopleuron. E, *Tabanus atratus*, mesopleuron and metapleuron.

and the partial separation of the lower part of the epimeron (epm_2) from the principal epimeral area (Epm_2) above it. The meron of the middle coxa (Mer_2) is conspicuous by its size, but it is not detached from the rest of the coxa.

In the higher Diptera, as exemplified by *Tabanus* (Fig. 102 E), the pleural suture of the mesothorax (PlS_2) is sharply flexed in two rectangular bends, and a long, membranous cleft (*b*) extends downward in the episternum, before the dorsal part of the pleural suture, from the wing process (WP_2) to a horizontal episternoprecoxal suture (*a*). The episternal area is divided by this cleft (*b*) into a large anterior region (Eps_2) separated from the precoxal area by the suture *a*, and into a smaller posterior region (eps_2), most of which is ventral to the horizontal part of the pleural suture and continuous with the precoxal area (*Prcx*). The epimeron is also divided into a large supraepimeron (Epm_2) and a smaller infraepimeron (epm_2). Finally, the meron of the mesocoxa (Mer_2) is completely detached from the rest of the coxa and is solidly incorporated into the pleural wall, being united both with the epimeral plate above it and with the narrow postcoxal bridge (Pcx_2) behind it. The ventral end of the subalar muscle of the wing, normally attached on the meron, as it is in Tipulidae, has migrated upward to the horizontal part of the pleural suture; but the remotor muscle of the coxa retains its attachment on the meron and becomes an adjunct to the indirect elevators of the wings. These complex changes in the mesopleuron, together with the reduction of the metapleuron and the unusual modifications of the sterna (Fig. 95 B), give the thorax of the higher Diptera a very specialized type of structure.

The Sternum of a Winged Segment.—The sterna of the wing-bearing segments show fewer special modifications than do either the terga or the pleura of these segments; their essential structure has been sufficiently described in the general discussion of the thoracic sterna (pages 166 to 172). While the pterothoracic sterna differ in no important respect from the sternum of the prothorax, peculiarities of structure are likely to be more accentuated in them. Each is characterized principally by the greater size of the basisternal region on which the tergosternal muscles are attached. In the higher orders the second spinasternum is usually consolidated with the eusternum of the mesothorax and may become indistinguishable from the latter.

6. THE THORACIC MUSCLES

The thoracic muscles of all pterygote insects, excepting perhaps the Odonata, conform closely to one general plan of arrangement. The potential number of muscles in each segment appears to be limited, or, at least, the maximum number of muscles or of functional units of fiber bundles can be pretty definitely stated according to our present knowledge of the thoracic musculature in the principal orders of pterygote insects, though the full complement does not occur in any one group. Variations in the muscle pattern, therefore, are the result principally of the absence of certain muscles, though a single muscle in one species may be represented in another by two or more bundles of fibers having a common point of insertion. The leg musculature varies according to the different types of movement in the coxae resulting from alterations in the coxal articulation on the body, the simpler types of leg musculature being evidently secondary modifications correlated with a limitation of the coxal movement.

Morphologically the usual thoracic muscles, as represented in an alate segment, may be classed as (1) dorsal muscles, (2) tergopleural muscles, (3) tergosternal muscles, (4) tergocoxal muscles, (5) pleurosternal muscles, (6) pleurocoxal muscles, (7) ventral muscles, (8) sternocoxal muscles, (9) lateral intersegmental muscles, and (10) spiracular muscles. The musculature of the prothorax differs from that of a winged segment chiefly in the lack of the tergosternal muscles and of muscles in other groups that function principally in connection with the movement of the wings in the pterothoracic segments.

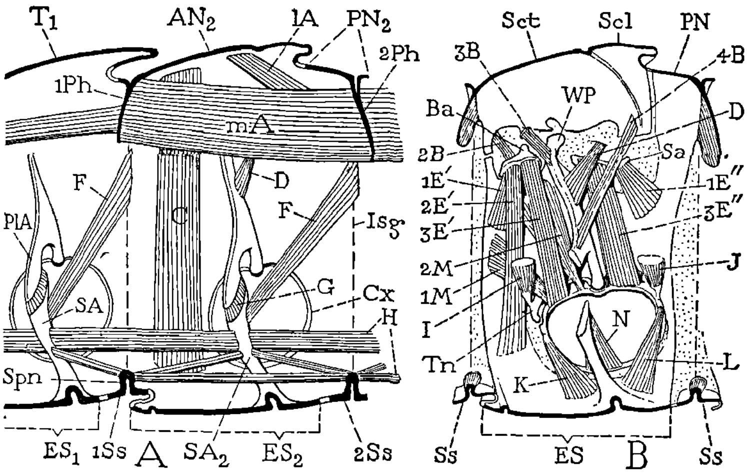

FIG. 103.—The thoracic musculature, diagrammatic, showing most of the muscles known to occur in a wing-bearing segment. A, dorsal, ventral, tergosternal, and oblique muscles of right side, inner view. B, lateral and leg muscles of right side. *A*, dorsal muscles (*lA*, oblique lateral dorsals; *mA*, longitudinal median dorsals); *B*, tergopleural muscles; *C*, tergosternal muscle; *D*, the wing flexor; *E′*, basalar muscles (*1E′*, pleurobasalar; *2E′*, sternobasalar; *3E′*, coxobasalar); *E″*, subalar muscles (*1E″*, pleurosubalar; *3E″*, coxosubalar); *F*, oblique intersegmental muscle; *G*, pleurosternal muscle; *H*, ventral muscles; *I*, *J*, tergal promotor and remotor of coxa (upper parts cut off); *K*, *L*, sternal promotor and remotor of coxa; *M*, abductors of coxa; *N*, adductor of coxa.

For a practical study of the thoracic musculature it will be found more convenient to classify the muscles in the following groups, the individual muscles of which are shown diagrammatically in Fig. 103, the more median muscles on the right side at A, the lateral muscles at B. The spiracular muscles, omitted here, will be described in connection with the spiracles.

A. Dorsal Muscles.—The muscles of this group comprise longitudinal median muscles and oblique lateral muscles (Fig. 103 A, *mA*, *lA*). In the prothorax the principal dorsal muscles extend from the first phragma to the postoccipital ridge of the head (Fig. 87, *DMcl*), though others may go from the tergum to the head or from the tergum to the first phragma. In the pterothorax the median dorsals are usually highly developed (Figs. 97 D, *DMcl*, 103 A, *mA*), at least in the segment bearing the principal pair of wings (Fig. 97 E), and are attached on the phragmata or also on the alinotal and postnotal plates. They are reduced in wingless insects, or in insects with weak powers of flight, as in Isoptera, Blattidae, and Gryllidae. The oblique lateral dorsals, when present (Fig. 103A, *lA*), extend from the posterior part of the scutum to the following phragma. Though usually relatively small, these muscles are highly developed in the mesothorax of higher Diptera and are large and powerful, almost vertical, muscles in the mesothorax of some Homoptera (Fig. 128 B, *lA*).

B. Tergopleural Muscles.—These muscles, found principally in the wing-bearing segments, are highly variable in their development, and some or all of them may be absent. Four muscles of this group have been recorded in the mesothorax of different insects. One goes from the prealar arm of the tergum to the episternum (not shown in the figure), another (Fig. 103 B, *2B*) from the lateral tergal margin to the basalare, a third (*3B*) from the tergum to the wing process. The fourth muscle (*4B*) extends from the posterior part of the scutum to the base of the pleural arm or the lower part of the pleural ridge. The last is an important muscle in Ephemerida, Plecoptera, Sialidae, Mecoptera, Trichoptera, Aphididae and is often two branched.

C. Tergosternal Muscles.—Generally large muscles of the pterothorax in flying insects; attached above on the scutum, below on the basisternum anterior to the coxae (Figs. 103 A, 128 B, 130). Absent in weak-flying insects, and not represented in the prothorax. These muscles are the principal levators of the wings, being functionally antagonistic to the dorsal muscles in their action on the tergum.

D. Axillary Muscles.—The muscles of the axillary sclerites of the wing base arise on the pleuron and are probably in origin tergopleural muscles since the wings are expansions of the dorsum. Two muscles occur in this group. One, known only in Diptera, is inserted on the first axillary. The other, present in all winged insects (Fig. 103 B, *D*), is inserted on the third axillary and is the usual flexor of the wing (Fig. 128 C, *D*); it is a simple or branched muscle arising on the upper part of the pleuron.

E. Epipleural Muscles.—The muscles comprised in this group are the lateral muscles of the mesothorax and metathorax attached dorsally on the epipleural sclerites (basalare and subalare). In the adult they are important muscles of the wings, but in nymphal stages they arise on the upper margins of the pleura, and two of them appear to be primarily coxal muscles (Fig. 102 C). The basalar muscles (Fig. 103 B, *E′*) include a muscle from the episternum (*1E′*), a muscle from the sternum before the coxa (*2E′*), and a large muscle (*3E′*) attached below on the outer margin of the coxa before the pleural articulation of the latter. The first two of these muscles are variable in occurrence, either one or both being often absent; the third is a constant feature of the thoracic musculature of winged insects. The subalar muscles (E'') duplicate the basalar muscles in reverse order, one arising on the epimeron ($1E''$), another on the sternum, and the third ($3E''$) on the coxa behind the pleural articulation. The coxosubalar muscle is an important element of the wing mechanism; the postcoxal sternosubalar is highly developed in Ephemerida but has not been observed in other orders; the epimerosubalar muscle appears occasionally in various insects.

F. Lateral Intersegmental Muscle.—An oblique muscle attached below on the sternal apophysis, dorsally on the anterior margin of the following pleuron or tergum (Fig. 103 A, *F*). This muscle is more commonly present in generalized insects and in larval forms; in adults it usually occurs only between the prothorax and the mesothorax, but a corresponding muscle is sometimes present between the mesothorax and the metathorax.

G. Pleurosternal Muscles.—The muscle most commonly present in this group consists of short fibers connecting the opposed ends of the pleural and sternal apophyses on each side of the segment (Fig. 103 A, *G*); absent when the apophyses are united. In rare cases a muscle extends from the lower end of the pleural ridge to the sternal apophysis.

H. Ventral Muscles.—Longitudinal or oblique horizontal muscles stretched between the eusternal apophyses, between the spinasternal spinae, and between the apophyses and the spinae (Fig. 103 A). The prothoracic muscles of this group are attached anteriorly on the head, usually on the tentorial bridge, or some of them on the cervical sclerites (Fig. 87).

I. Tergal Promotor of the Leg.—Usually a single large muscle, sometimes double, arising dorsally on the tergum, inserted below on the ventral end of the trochantin (Fig. 103 B, *I*) or on the anterior angle of the coxa if the trochantin is absent.

J. Tergal Remotor of the Leg.—A single muscle, or a group of muscles, arising dorsally on the posterior part of the tergum, inserted ventrally on the posterior rim of the coxa (Fig. 103 B, *J*).

K. Sternal Promotor of the Leg.—Origin on the sternum; insertion on the anterior part of the coxal base (Fig. 103 B, *K*). If the coxa turns on the pleural articulation alone, this muscle is an anterior rotator of the coxa.

L. Sternal Remotor of the Leg.—Origin on the sternum, the sternal apophysis, or the spina; insertion on the posterior part of the coxal base (Fig. 103 B, *L*). This muscle, as the last, is a rotator of the coxa if the latter has a free movement on the pleuron only.

M. Pleurocoxal Muscles.—Usually two muscles, arising on the episternum, inserted on the coxal base anterior to the pleural articulation (Fig. 103 B, 1*M*, 2*M*). These muscles appear to be abductors of the coxa if the coxa has no sternal articulation; otherwise they are coxal promotors.

N. Adductor Muscle of the Coxa.—A muscle present in insects lacking a sternal articulation of the coxa, arising on the sternal apophysis, inserted on the mesal margin of the coxa (Fig. 103 B, *N*).

P. Extracoxal Depressor of the Trochanter.—The depressor of the trochanter usually has one or more branches arising in the body segment bearing the leg (Fig. 117); generally there is a branch from the tergum (Fig. 115 A, 133*c*), another from the sternal apophysis (133*d*), and sometimes one from the pleuron (Fig. 102 C, *P*).

GLOSSARY OF TERMS APPLIED TO THE THORAX

Names used in the present chapter, but not given in the following list, may be found in the glossaries of Chaps. III, V, IX, and X.

Alinotum (*AN*).—The wing-bearing plate of the dorsum of the mesothorax or metathorax of pterygote insects.

Anapleurite (*Apl*).—The dorsal supracoxal sclerotization of a generalized thoracic pleuron. (*Eupleuron.*)

Anterior Notal Wing Process (*ANP*).—The anterior lobe of the lateral margin of the alinotum supporting the neck of the first axillary. (*Vorderer Tergalhebel.*)

Basalare (*Ba*).—The episternal epipleurite (sometimes double) giving insertion to the anterior pleural muscles of the wing; often represented by an undetached or partially detached lobe of the episternum before the pleural wing process. (*Episternalgelenkstück, preparapteron.*)

Basisternum (*Bs*).—The principal area of the sternum anterior to the roots of the sternal apophyses or the sternacostal suture. (*Sternannum.*)

Cervical Sclerites, Cervicalia (*cv*).—The sclerites of the neck, particularly one or two pairs of lateral neck plates (*Kehlplatten*) joining the head to the prothoracic episterna.

Cervix (*Cvx*).—The neck; including probably the posterior nonsclerotized part of the labial somite and the anterior part of the prothorax.

Coxopleurite (*Cxpl*).—The sclerite of a generalized thoracic pleuron adjacent to the dorsal margin of the coxa, bearing the dorsal coxal articulation; its anterior part becomes the definitive trochantin. (*Eutrochantin, Trochantinopleura.*)

Epimeron (*Epm*).—The area of the pleuron posterior to the pleural suture, sometimes divided horizontally into a *supraepimeron*, or *anepimeron*, and an *infraepimeron*, or *katepimeron.*

Epipleurites (*Ba, Sa*).—The basalar (*Ba*) and subalar (*Sa*) sclerites of a wing-bearing segment differentiated from the upper ends of the episternum and epimeron, respectively. (*Paraptera, Pleuralgelenkstücke.*)

Episternum (*Eps*).—The area of the pleuron before the pleural suture and above the trochantin, sometimes divided horizontally into a *supraepisternum*, or *anepisternum*, and an *infraepisternum*, or *katepisternum.*

Eupleuron (*Apl*).—See *anapleurite.*

Eusternum (*ES*).—The intrasegmental ventral plate of a thoracic segment, exclusive of the spinasternum, but usually including the sternopleurites.

Eutrochantin.—See *coxopleurite.*

First Thoracic Spiracle (*Sp_2*).—The spiracle of the mesothorax, often displaced into the posterior part of the prothorax.

Furca (*Fu*).—The forked endosternal process of higher insects, formed of the sternal apophyses supported on a median inflection of the sternum.

Furcasternum.—A distinct part of the sternum in some insects bearing the furca. (The term generally applied to the sternellum.)

Intersternites (*Ist*).—Primary intersegmental sclerites of the venter, becoming the spinasterna of the thorax.

Laterosternite (*Ls*).—The lateral part of a definitive thoracic sternum apparently derived from the ventral arc (sternopleurite) of the subcoxa.

Mesothorax (*Th_2*).—The second segment of the thorax; bearing the first pair of wings in winged insects.

Metathorax (*Th_3*).—The third segment of the thorax; bearing the second pair of wings in winged insects.

Notaulices (*no*).—Longitudinal furrows convergent posteriorly in the anterior part of the mesonotum of some insects. (Incorrectly spelled "notauli," and sometimes mistaken for the parapsidal furrows. Singular, *notaulix.*)

Notum (*T*).—The tergum, or particularly the tergum of a thoracic segment.

Parapsidal Furrows (*pf*).—Lateral grooves divergent anteriorly in the posterior part of the scutum of the mesothorax of some Hymenoptera.

Parapsides.—Lateral areas of the mesoscutum in some Hymenoptera laterad of the parapsidal furrows. (Singular, *parapsis.*)

Paraptera.—See *epipleurites.*

Phragmanotum (*PN*).—See *postnotum.*

Phragmata (*Ph*).—Plate-like apodemal lobes of the antecostae of the mesonotum, metanotum, and first abdominal tergum; the second and third carried by the postnotal plates of the pterothorax when the latter are separated from the following terga to which they normally belong. (Singular *phragma.*)

Pleural Apophysis (*PlA*).—The internal arm of the pleural ridge.

Pleural Ridge (*PlR*).—The endopleural ridge formed by the pleural suture, bracing the pleuron above the leg, or between the coxal articulation and the wing support.

Pleural Suture (*PlS*).—The external groove of the pleural ridge, separating the episternum from the epimeron.

Pleural Wing Process (*WP*).—The wing support of the pleuron at the upper end of the pleural ridge.

Pleuron (*Pl*).—The sclerotization of the pleural area of a body segment, probably derived from the subcoxal part of the primitive limb basis.

Postalar Bridge, Postalare (*Pa*).—A lateral extension of the postnotum of a wing-bearing segment behind the wing base, generally united with the epimeron. (*Lateropostnotum.*)

Postcoxal Bridge, Postcoxale (*Pc*).—The postcoxal part of the pleuron, often united with the sternum behind the coxa.

Posterior Notal Wing Process (*PNP*).—A posterior lobe of the lateral margin of the alinotum supporting the third axillary sclerite of the wing base. (*Hinterer Gelenkfortsatz.*)

Postnotum, Phragmanotum (*PN*).—The postscutellar, phragma-bearing plate often present in the dorsum of an alate segment, derived from the anterior part of the following tergum. (*Postscutellum.*)

Prealar Bridge, Prealare (*Pra*).—A lateral extension of the prescutal area of the alinotum before the wing base, sometimes connected with the episternum.

Precoxal Bridge, Precoxale (*Prcx*).—The precoxal part of the pleuron anterior to the trochantin, usually continuous with the episternum, frequently united with the sternum, sometimes a distinct sclerite.

Prepectus (*Prp*).—An anterior marginal sclerite of the sternopleural areas of a segment, set off by a transverse suture continuous through the sternum and episterna.

Prescutal Suture (*ts*).—A transverse groove of the mesonotum or metanotum behind the antecostal suture, setting off a prescutum from the scutum, and forming internally a *prescutal ridge* (*TR*).

Prescutum (*Prsc*).—The anterior area of the mesonotum or metanotum between the antecostal suture and the prescutal suture, when the latter is present.

Presternum (*Prs*).—A narrow anterior area of the sternum sometimes set off from the basisternum by a submarginal suture of the eusternum. (Not the acrosternite.)

Propodeum.—The first abdominal segment of clistogastrous Hymenoptera incorporated into the thorax. (*Median segment.*)

Prothorax (Th_1).—The first segment of the thorax.

Pterothorax.—The two wing-bearing segments, often closely connected or united with each other.

Scutellum (*Scl*).—The area of the alinotum posterior to the suture of the V-shaped notal ridge, or the corresponding area when the ridge is incomplete or absent.

Scutoscutellar Suture (*vs*).—The external suture of the V-shaped notal ridge of the alinotum, the arms divergent posteriorly, dividing the notum into scutum and scutellum.

Scutum (*Sct*).—The area of the alinotum anterior to the suture of the V-shaped notal ridge, or between this suture and the prescutal suture if the latter is present.

Second Spiracle (Sp_3).—The metathoracic spiracle, located near the anterior margin of the metapleuron, between the mesopleuron and the metapleuron, or in the posterior margin of the mesopleuron.

Spina (*Spn*).—The median apodemal process of a spinasternum.

Spinasternum (*Ss*).—One of the spina-bearing intersegmental sclerites of the thoracic venter, associated, or united, with the sternum preceding; a spinasternum may become a part of the definitive prosternum or mesosternum, but not of the metasternum.

Sternacosta.—The transverse internal ridge of the sternal suture through the bases of the sternal apophyses.

Sternacostal Suture.—The external suture of the sternacosta, separating the basisternum from the sternellum.

Sternal Apophyses (*SA*).—The lateral apodemal arms of the eusternum; in higher insects united on a median base, the whole structure forming the *furca.*

Sternellum (*Sl*).—The area of the eusternum posterior to the bases of the sternal apophyses or the sternacostal suture.

Sternopleurite (*Spl*).—The infracoxal sclerotization of a generalized thoracic pleuron, generally united with the primary sternum in the definitive eusternal plate.

Sternum (*S*, *Stn*).—Primarily the *primitive sternum* (*Stn*), or sclerotization of the true venter of a segment; secondarily the *definitive sternum* (*S*), which in the thorax usually includes the sternopleurites and may include the following intersegmental spinasternum.

Subalare (*Sa*).—The epimeral epipleurite giving insertion to the posterior pleural muscle of the wing. (*Epimeralgelenkstück, postparapteron.*)

Trochantin (*Tn*).—The precoxal sclerite of a thoracic pleuron derived from the anterior part of the primitive coxopleurite; usually articulated at its ventral end to the anterior margin of the coxa, and giving insertion to the tergal promotor muscle of the leg.

V-shaped Notal Ridge (*VR*).—The V-shaped endoskeletal ridge of the mesonotum or metanotum, its arms divergent posteriorly, marked externally by the scutoscutellar suture. (*V-Leiste.*)

CHAPTER IX

THE THORACIC LEGS

The appendages of insects that ordinarily serve as organs of terrestrial locomotion are the appendages of the three thoracic segments; but in some Apterygota and in the larvae of various pterygote insects the abdominal appendages also play a part in the locomotor function. In the present chapter only the general structure and the musculature of the thoracic legs will be considered; the legs of many insects assume various other functions than that of locomotion and are structurally modified accordingly.

1. STRUCTURE OF THE LEGS

In describing the structure and mechanism of the legs we shall limit the term "leg" to the free part of the appendage having the coxa as its base, since we need not be concerned here with the question of the subcoxal origin of the pleuron. The surfaces of the legs are oriented for descriptive purposes when the limb is extended at right angles to the body; the preaxial surface is then anterior, the postaxial surface posterior, the outer surface dorsal, and the inner surface ventral.

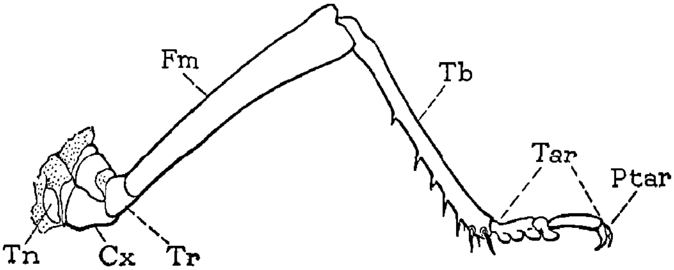

Fig. 104.—Middle leg of a grasshopper, anterior view.

The Leg Segments.—The typical and usual segments of the insect leg (Fig. 104) are the *coxa* (*Cx*), one *trochanter* (*Tr*), the *femur* (*Fm*), the *tibia* (*Tb*), the *tarsus* (*Tar*), and the *pretarsus* (*Ptar*). In the Odonata two trochanteral segments are present (Fig. 109 C, 1 *Tr*, 2 *Tr*), but they are not movable on each other.

The Leg Joints.—The joints of the legs are membranous rings of the leg wall between the cylindrical sclerotized areas that constitute the segments. The membrane of the joint is the *articular corium.* Sometimes there are no contiguous points of articulation between adjoining segments; but usually one or two pairs of opposed articular surfaces limit the movement of the joint to that of a hinge. Hinged joints are therefore either monocondylic (Fig. 105 A) or dicondylic (B). A single articulation is typically dorsal; in dicondylic joints one articulation is anterior and the other posterior, except at the trochantero-femoral joint where the articulations if present are usually dorsal and ventral. The coxotrochanteral hinge is always dicondylic with an anteroposterior axis. In the telopodite, dicondylic hinges are characteristic of the legs of adult insects; monocondylic hinges are usual in the legs of larvae (Fig. 106), but in the larvae of Neuroptera and Trichoptera the femoro-tibial joint is dicondylic.

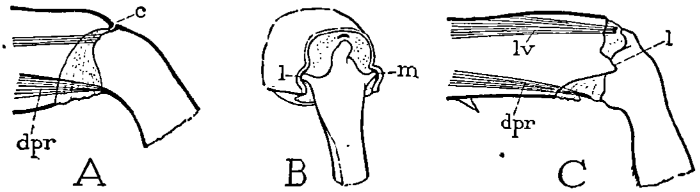

FIG. 105.—Diagrams of articular mechanisms at the femoro-tibial joint of a leg. A, monocondylic joint. B, C, dicondylic joint, end view and side view with levator and depressor muscles.

The structure of the articulations between the leg segments varies much at different joints and at corresponding joints in different insects. Sometimes the opposing surfaces simply touch at their points. In other cases the articulation is of the ball-and-socket type, a condyle on one surface fitting into a socket on the other. In dicondylic hinges of this kind the two articulations are frequently reversed in structure. An occasional, perhaps generalized, type of articulation consists of a flexible sclerotic bar continuous from one segment to the other through the articular membrane.

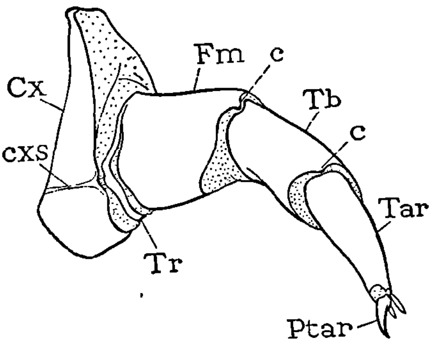

FIG. 106.—Thoracic leg of a caterpillar, anterior view.

The Coxa.—In its more symmetrical form the coxa has the shape of a short cylinder or truncate cone (Figs. 104, *Cx*, 107 A), though commonly it is ovate and may be almost spherical. The proximal end of the coxa is girdled by a submarginal *basicostal suture* (Fig. 107 A, *bcs*), which forms internally a ridge, or *basicosta* (*Bc*), and sets off a marginal flange, the *coxomarginale*, or *basicoxite* (*Bcx*). The basicosta strengthens the base of the coxa and is commonly enlarged on the outer wall to give insertion to muscles (B, C); on the mesal half of the coxa, however, it is usually weak and often confluent with the coxal margin. The trochanteral muscles that take their origin in the coxa are always attached distal to the basicosta.

The coxa is attached to the body by an articular membrane, the *coxal corium,* which surrounds its base. It has almost always an outer articulation with the pleuron of its segment, and it may have an inner articulation with the sternum or with a laterosternal sclerite, as was observed in Chap. VIII. These two articulations are perhaps the primary dorsal

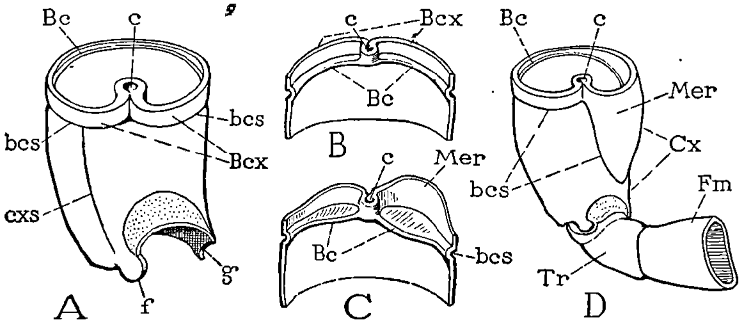

FIG. 107.—Diagrams illustrating structural details of the coxa. A, lateral view of coxa. B, C, inner view of outer wall of basicoxal region. D, a coxa with the meron extended distally. *Bc,* basicosta; *bcs,* basicostal suture; *Bcx,* basicoxite; *c,* pleural articular socket; *Cx,* coxa; *cxs,* coxal suture; *f,* anterior coxotrochanteral articulation; *Fm,* femur; *g,* posterior coxotrochanteral articulation; *Mer,* meron; *Tr,* trochanter.

and ventral articular points of the subcoxo-coxal hinge (Fig. 88, *c, d*). In addition, the insect coxa has often an anterior articulation with the anterior, ventral end of the trochantin (Fig. 91 B, *e*), but the trochantinal articulation does not coexist with a sternal articulation (A). The pleural articular surface of the coxa is borne on a mesal inflection of the coxal wall (Fig. 107 A, *c*). If the coxa is movable on the pleural articulation alone, the coxal articular surface is usually inflected to a sufficient depth to give a leverage to the abductor muscles (Fig. 114, *M*) inserted on the outer rim of the coxal base. Distally the coxa bears an anterior and a posterior articulation with the trochanter (Fig. 107 A, *f, g*).

The outer wall of the coxa is often marked by a suture extending from the base to the anterior trochanteral articulation (Figs. 106, 107 A, 108 A, *cxs*). In some insects the coxal suture falls in line with the pleural suture (Fig. 108 B), and in such cases the coxa appears to be divided into two parts corresponding to the episternum and epimeron of the pleuron. The coxal suture is absent in many insects (Fig. 108 C).

The inflection of the coxal wall bearing the pleural articular surface divides the lateral wall of the basicoxite into a prearticular part and a postarticular part, and the two areas often appear as two marginal lobes on the base of the coxa. The posterior lobe is usually the larger and is termed the *meron* (Fig. 107 C, *Mer*).

The meron may be greatly enlarged by an extension distally in the posterior wall of the coxa (Fig. 107 D, *Mer*); in the Neuroptera, Mecoptera (Fig. 99), Trichoptera, and Lepidoptera, the meron is so large that the coxa appears to be divided into an anterior piece, the so-called "coxa genuina," and the meron (*Mer*), but the meron never includes the region of the posterior trochanteral articulation, and the groove delimiting it is always a part of the basicostal suture (Fig. 107 D, *bcs*). A coxa with an enlarged meron has an appearance similar to one divided by a coxal suture falling in line with the pleural suture (Fig. 108 B), but the two conditions are fundamentally quite different and should not be confused.

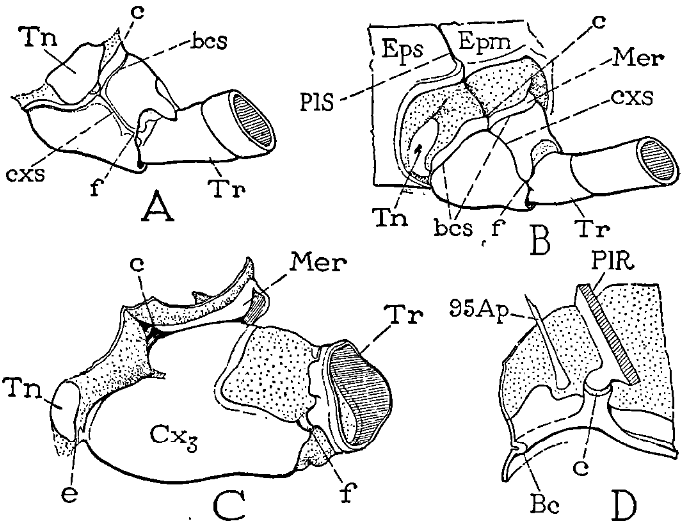

FIG. 108.—Coxal structures of a grasshopper, *Dissosteira carolina*. A, coxa and trochanter of first leg, anterior view. B, same of middle leg, with adjoining part of pleuron. C, coxa and reduced trochanter of hind leg, anterior view. D, inner view of articulation of middle coxa with pleuron.

The meron reaches the extreme of its departure from the usual condition in the Diptera. In some of the more generalized flies, as in the Tipulidae, the meron of the middle leg appears as a large lobe of the coxa projecting upward and posteriorly from the coxal base (Fig. 102 D, *Mer*); in higher members of the order it becomes completely separated from the coxa and forms a plate of the lateral wall of the mesothorax (E, *Mer*). By this transposition of the meron, the remotor muscle of the coxa attached on it loses its function as a leg muscle and serves as a depressor of the tergum, thereby becoming an adjunct to the usual elevators of the wings. The meral plate in the thorax of the Diptera was long a puzzle to entomologists until its true nature was shown by Crampton and Hasey (1915) and by Crampton (1925, 1925*a*).

The Trochanter.—The trochanter (Fig. 104, *Tr*) is the basal segment of the telopodite; it is always a small segment in the insect leg, freely movable by a horizontal hinge on the coxa, but more or less fixed to the base of the femur. When movable on the femur the trochanterofemoral hinge is usually vertical or oblique in a vertical plane, giving a slight movement of production and reduction at the joint, though only a reductor muscle is present (Fig. 109 A, *R*). In the Odonata, both nymphs and adults, there are two trochanteral segments (C, 1*Tr*, 2*Tr*), but they are not movable on each other; the second contains the reductor muscle of the femur (*R*). The usual single trochanteral segment of insects, therefore, probably represents the two trochanters of other arthropods fused into one apparent segment, since it is not likely that the primary coxotrochanteral hinge has been lost from the leg. In some of the Hymenoptera a basal subdivision of the femur simulates a second trochanter (Fig. 109 B, *fm*), but the insertion of the reductor muscle (*R*) on its base attests that it belongs to the femoral segment, since as shown in the odonate leg (C), the reductor has its origin in the true second trochanter.

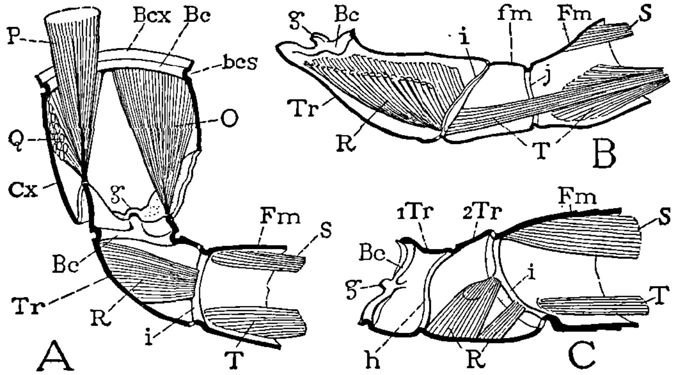

Fig. 109.—The coxal and trochanteral musculature. A, diagram of inner view of posterior wall of coxa, trochanter, and base of femur, with typical musculature. B, trochanter and base of femur of an ichneumoid, *Megarhyssa*, showing basal subdivision (*fm*) of femur. C, corresponding part of the leg of a dragonfly larva, showing divided trochanter (*1Tr*, *2Tr*) with reductor muscles of femur (*R*) in second segment.

The Femur.—This, the third segment of the insect leg (Fig. 104, *Fm*), is usually the longest and strongest part of the limb, but it varies in size from the huge hind femur of leaping Orthoptera (Fig. 116, *Fm*) to a very small segment such as is present in many larval forms. The volume of the femur is generally correlated with the size of the tibial muscles contained within it, but it is sometimes enlarged and modified in shape for other purposes than that of accommodating the tibial muscles.

The Tibia.—The tibia (Fig. 104, *Tb*) is characteristically a slender segment in adult insects, only a little shorter than the femur or the combined femur and trochanter. Its proximal end forms a more or less distinct head bent toward the femur, a device allowing the tibia to be flexed close against the under surface of the femur.

The Tarsus.—The tarsus of insects corresponds to the penultimate segment of a generalized arthropod limb, which is the segment called the propodite in Crustacea (Fig. 50 A, *Tar*). In adult insects it is commonly subdivided into from two to five subsegments, or *tarsomeres* (Fig. 104, *Tar*), but in the Protura (Fig. 53A), some Collembola, and most holometabolous insect larvae (Fig. 106) it preserves the primitive form of a simple segment. The subsegments of the adult insect tarsus are usually freely movable on one another by inflected connecting membranes, but the tarsus never has intrinsic muscles. The tarsus of adult pterygote insects having fewer than five subsegments is probably specialized by the loss of one or more subsegments or by a fusion of adjoining subsegments. In the tarsi of Acrididae the long basal piece is evidently composed of three united tarsomeres, leaving the fourth and the fifth free (Fig. 118 A). The basal tarsomere is sometimes conspicuously enlarged and is distinguished as the *basitarsus.* On the under surfaces of the tarsal subsegments in certain Orthoptera there are small pads, the *tarsal pulvilli,* or *euplantulae* (Fig. 118 A, *a*). The tarsus is occasionally fused with the tibia in larval insects, forming a tibiotarsal segment; in some cases it appears to be eliminated or reduced to a rudiment between the tibia and the pretarsus.

The Pretarsus.—The terminal part of the insect leg in its usual form departs so far from the simple structure of a primitive end segment of the limb that entomologists generally have not understood its nature, though its morphological status has long been clear from the work of de Meijere (1901).

In the majority of arthropods the leg ends in a simple clawlike segment, which in the Crustacea is known as the *dactylopodite* (Fig. 50 A, *Ptar*). The crustacean dactylopodite is provided with two muscles, a levator and a depressor, both arising in the tarsus, or propodite. In the Hexapoda, a simple dactylopodite-like end segment of the leg occurs in the Protura, in some Collembola, in the larvae of many Coleoptera, and in the larvae of Lepidoptera and Tenthredinidae (Fig. 106, *Ptar*). In these forms it differs from the crustacean dactylopodite only in lacking a levator muscle and in having the fibers of the depressor muscle distributed in the tibia and the femur.

In most other adult, nymphal, and larval insects, the pretarsus bears a pair of movable lateral claws situated upon its base and articulated dorsally to the end of the tarsus, and the body of the segment is reduced to a small median claw or a lobe-like structure. The median claw is well preserved in the Lepismatidae (Fig. 110, C, D, *dac*) and the tendon of the depressor muscle arises from the ventral lip of its base (C, E, *x*). In *Japyx* the base of the pretarsus forms a large plate ventrally (B, *Utr*) upon which is attached the depressor "tendon" (*x*), while its tip is reduced to a minute median claw (A, *dac*) lying dorsally between the bases of the lateral claws (*Un*). In the so-called triungulin larvae of meloid beetles the apparent "lateral claws" of the feet are probably spines arising from the base of the median pretarsal claw, as are also the "lateral claws" of certain lampyrid larvae.

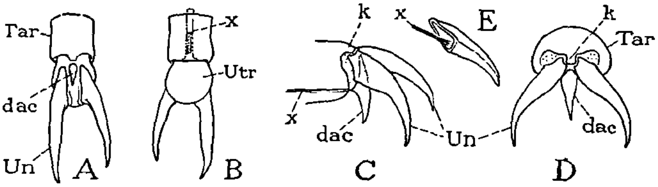

FIG. 110.—Examples of the retention of the median pretarsal claw (*dac*) in insects. A, pretarsus of *Japyx*, dorsal view. B, same, ventral view. C, pretarsus and end of tarsus of *Lepisma*, lateral view. D, same, end view. E, median claw, or rudimentary dactylopodite of *Lepisma*, with "tendon" (*x*) of depressor muscle attached ventrally.

The typical pretarsus, or terminal foot structure, in insects having true lateral claws (Fig. 111 A, B) arises from the end of the tarsus by a membranous base, upon which are supported the pair of *lateral claws* (*Un*) and a median lobe, the *arolium* (*Ar*). The claws are hollow multicellular organs and their cavities are continuous with the lumen of the pretarsus. Each claw is articulated dorsally to the *unguifer* (A, *k*), a median process of the distal end of the last tarsomere (*Tar*). The arolium, likewise a hollow lobe, is a direct continuation of the median part of the pretarsal base; it may be entirely membranous, or its walls may be partly sclerotized. On the ventral surface of the pretarsus is a median basal plate, the *unguitractor* (B, *Utr*), which is partly invaginated into the end of the tarsus (*Tar*). To its proximal end is attached the tendon-like apodeme (*x*) of the depressor muscle of the pretarsus, usually called the *retractor of the claws*. The unguitractor plate may be divided into two sclerites (C, *Utr*), or sometimes there is a sclerite distal to it distinguished as the *planta* (Fig. 118 C, *Pln*). Lateral plates beneath the bases of the claws are termed *auxiliae* (Fig. 111 B, E, *l*). In the Diptera two large lateral lobes of the foot, known as the *pulvilli* (D, E, *Pv*), arise from the auxiliary plates, one beneath the base of each claw, and there is commonly also present a median process, or *empodium* (*Emp*), arising from the distal end of the unguitractor plate. The empodium may have the form of a spine, or it may be lobe-like and similar in form to the pulvilli. The arolium is rudimentary or absent in most Diptera except Tipulidae.

All parts of the pretarsus are subject to much variation. The lateral claws are sometimes of unequal size, one becoming reduced or occasionally obliterated, the result being a one-clawed foot, as in the Coccidae, Pediculidae, and mammal-infesting Mallophaga. Again, both claws may become very small, and both may be lacking. In the Thysanoptera the claws are minute and the foot consists principally of the bladderlike arolium. In some insects the arolium is hollowed beneath and acts as a vacuum cup to enable the insect to walk on surfaces too smooth or too hard for the claws to grasp. Other insects cling to such surfaces by means of a gummy liquid exuded from the ventral side of the foot.

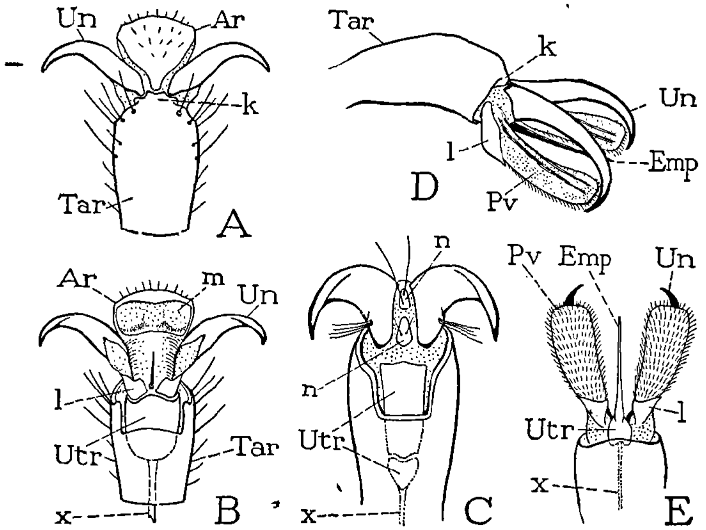

FIG. 111.—Examples of "foot" structures of insects. A, *Periplaneta americana*, dorsal view. B, same, ventral view. C, *Magicicada septendecim*, ventral view. D, asilid fly, lateral view. E, same, ventral view. *Ar*, arolium (dorsal lobe); *Emp*, empodium (median ventral process or lobe); *k*, unguifer process of tarsus; *l*, auxilia; *m*, aroliar pad; *n*, accessory sclerites between claws; *Pv*, pulvillus (lateral ventral lobe); *Tar*, tarsus; *Un*, ungues (lateral pretarsal claws); *Utr*, ungitractor plate; *x*, "tendon" of depressor muscle of pretarsus (retractor of claws).

2. MUSCLES AND MECHANISM OF THE LEGS

The muscles of the legs, as of any segmented appendage, are comprised in two sets, namely, (1) muscles of the limb basis, or those that move the appendage as a whole, and (2) muscles of the telopodite segments, or those that move individual parts of the limb. Muscles of the second class are usually named according to the limb segment on which they have their insertions, though they may be motors of the entire part of the appendage distal to the insertions. Most of the muscles of the leg segments of insects take their origin in the segment immediately proximal to the one on which they are inserted, but some of them arise in the second or third segment removed from the point of insertion.

Mechanism of the Leg Base.—The possible movements of the coxa depend upon the nature of the coxal articulation with the body, which may have any one of three types of structure (Fig. 112). If the coxa is articulated to the pleuron only (A, *c*), it is free to make any movements that its musculature will impart to it; if, however, it is hinged between pleural and trochantinal articulations (B, *c*, *e*), its movements may be more limited, though the flexibility of the trochantin usually does not impose a rigid hinge motion on the coxa; but if the coxa is articulated to the pleuron dorsally and to the sternum ventrally (C, *c*, *d*), its movements are strictly limited to those of a hinge with the axis in a transverse plane.

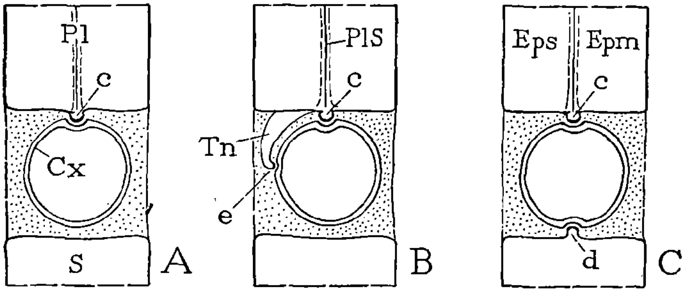

FIG. 112.—Diagrams illustrating three types of coxal articulation. A, with pleural articulation (*c*) only. B, with pleural (*c*) and trochantinal (*e*) articulations. C, with pleural (*c*) and sternal (*d*) articulations.

A typical insect coxa of the first or second types, having only a pleural articulation with the body or both pleural and trochantinal articulations (Fig. 113 A, *c*, *e*), is provided with muscles that arise on the tergum, muscles that arise on the sternum, and muscles having their origin on the pleuron. The dorsal muscles include *tergal promotors* (*I*) and *tergal remotors* (*J*). The sternal muscles comprise *sternal promotors* and *remotors*, or, functionally, *anterior* and *posterior rotators* (*K*, *L*), and also an *adductor* (*N*). The pleural muscles include functional *abductors* (*M*) and, in the wing-bearing segments of adult insects, the muscles of the basalar and subalar sclerites (3E′, 3E″), which serve as wing muscles.

The muscles of the leg base are not necessarily inserted directly on the coxa itself. The tergal promotor, for example, is always inserted on the trochantin (Fig. 113 A, *Tn*), except when this sclerite is much reduced or is absent. Some of the other muscles are frequently inserted on apodemes that arise in the articular membrane between the coxa and the pleuron. In special cases, certain muscles inserted on the pleuron are evidently coxal muscles that have been transferred to the pleural wall. The presence of an articulation between the trochantin and the coxa does not usually result in an alteration of the coxal musculature.

A coxa of the third type (Fig. 112 C), having its movements limited to those of a hinge on a transverse or transversely inclined axis by articulations with both the pleuron (*c*) and the sternum (*d*), is likely to have a more simple musculature than that of a coxa of the first or second type. In the middle leg of a bee, for example (Fig. 113 B), the usual tergal musculature of the coxa is absent, though the coxa has anterior and posterior sternal muscles (*K*, *L*), a large two-branched pleural muscle (*M*), and a subalar muscle (3E″). This form of reduced coxal musculature is probably a specialized condition in the higher insects, since the primitive musculature of the leg base appears to comprise both tergal and sternal muscles. In the prothorax of the bee a posterior tergocoxal muscle (tergal remotor, *J*) is present.

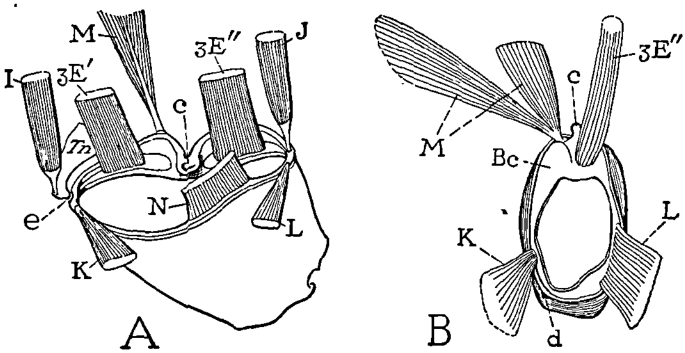

FIG. 113.—The coxal musculature. A, diagram of typical musculature of a coxa with pleural and trochantinal articulations. B, muscles of the mesothoracic leg of a bee with pleural and sternal articulations. (See Fig. 103 B.)

If the coxa has no sternal articulation, the pleural articular surface on its base is usually more or less inflected mesally from the outer wall (Fig. 114, *c*), occupying thus a point approximately central in the plane of the leg base. By this device a leverage is given to muscles inserted to any side of the articular point. The attachments of the coxal muscles occur approximately at the opposite ends of two axial lines through the articulation, one longitudinal (*b-b*), the other transverse (*c-c*). The coxa, therefore, has movements of *promotion* and *remotion* on a transverse axis, and movements of *abduction* and *adduction* on a longitudinal axis;

while furthermore, because of the single point of articulation, it is capable also of a *partial rotation* on a vertical axis (*d-d*) through the articular point (*c*).

In comparative studies of insect musculature we must consider muscles as functional groups of fibers rather than as individual fiber bundles, for it is often found that a single muscle in one species is represented by several muscles in another, and that, even in the same species, the number of muscles in a functional group varies in the different segments of the thorax. Thus while the coxal musculature may be represented diagrammatically in a simplified form, as in Fig. 113 A, it must be borne in mind that at each cardinal point of the coxal base there may be attached several distinct fiber groups constituting a functional unity. There can be little doubt also that between different species, or between different segments of the same species, homologous muscles may have quite different functions owing to differences in the relations between the skeletal parts on which they are inserted. For this reason it is impossible to name insect muscles consistently in all cases on a basis of their functions.

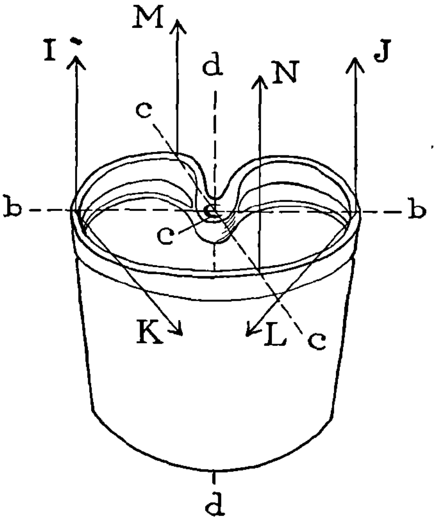

FIG. 114.—Diagram of the possible axes of movement of a coxa having only a pleural point of articulation (*c*). *b-b*, axis of abduction and adduction (muscles *M* and *N*); *c-c*, axis of promotion and remotion (muscles *I* and *J*); *d-d*, axis of partial rotation (muscles *K* and *L*).

For an elementary study of the insect leg muscles it will be best to examine some particular species, and the leg musculature of the acridid *Dissosteira carolina* is here given as fairly representative of the more generalized type of leg musculature in insects. The muscles of the legs of the grasshopper are essentially the same in each segment, with the difference only that a single group of fibers in one leg may be represented by two or more groups in another, and that the anterior rotator is absent in the prothoracic leg. The following descriptions are based specifically on the musculature of the hind leg.

Muscles of the Leg Base of Dissosteira.—The coxae of the grasshopper are attached to the body by the pleural articulations only (Fig. 108 D, *c*), though a small trochantinal plate is present at the base of each leg, the sclerite being best developed in the fore leg (A, *Tn*) and becoming successively smaller in the other two (B, C, *Tn*).

Tergal Promotor of the Coxa (Fig. 115 A, *118*).—A large muscle of the hind leg lying immediately posterior to the tergosternal muscle of the metathorax. Origin dorsally on the lateral area of the scutum; insertion ventrally on a stalked apodemal disc of the anterior angle of the coxa (D, F). In the prothorax this muscle is inserted on the ventral end of the trochantin, as it is in most cases in which the trochantin is not rudimentary.

Tergal Remotors of the Coxa (Fig. 115 A, *119*, *120*).—Two bundles of fibers attached on the posterior part of the coxa. The larger anterior one (*119*) arises on the posterior margin of the scutal area of the metatergum and is inserted on an apodemal disc of the posterior inner angle of the coxal base (D, F, *119*). The smaller posterior muscle (A, *120*) lies close behind *119* and is inserted on a slender apodeme attached to the extreme posterior angle of the coxa (B, D, F, *120*).

The tergal promotor and remotors are clearly antagonists to each other because of their opposite relations to the pleural fulcrum of the coxa.

Anterior Rotator of the Coxa (Fig. 115 D, E, F, *121*).—A large muscle with fibers arising in two groups, one from the lateral part of the sternum before the base of the sternal apophysis, the other from the sternellar lobe behind the apophysis (E, *121*); all fibers converging to a common point of insertion on the mesal side of the anterior angle of the coxal base (D, E, *121*).

Posterior Rotators of the Coxa (Fig. 115 D, E, *122*, *123*, *124*).—A group of three muscles arising on the posterior surface of the lateral arm of the metasternal apophysis (E); all inserted posteriorly on the base of the coxa (D, E).

In the mesothorax there is but a single anterior rotator and a single posterior rotator, the first arising on the sternellar lobe, the second on the mesosternal spina. In the prothorax the anterior rotator is absent, and the posterior rotator includes two muscles, one from the sternal apophysis, the other from the spina. Since the rotators lie approximately in the plane of the coxal base, it is clear that they must serve to give the coxa a partial rotation on the pleural articulation.

Abductors of the Coxa (Fig. 115 C, *125*, *126*).—Two muscles arising on the episternum of the metathorax and inserted on the outer rim of the coxal base appear to belong to the abductor system of the hind leg. The first, however, a very small muscle (*125*), is inserted so far forward on the coxa that it probably functions as an accessory to the tergal promotor (A, *118*). The second (C, *126*) covers most of the inner face of the episternum and its fibers converge upon a slender apodemal stalk arising in the articular membrane at the base of the coxa close before the pleural articulation (C, D, F, *126*). Because of the mesal inflection of the articular surface on the base of the coxa (F, *c*) this muscle is enabled to function as an abductor of the leg.

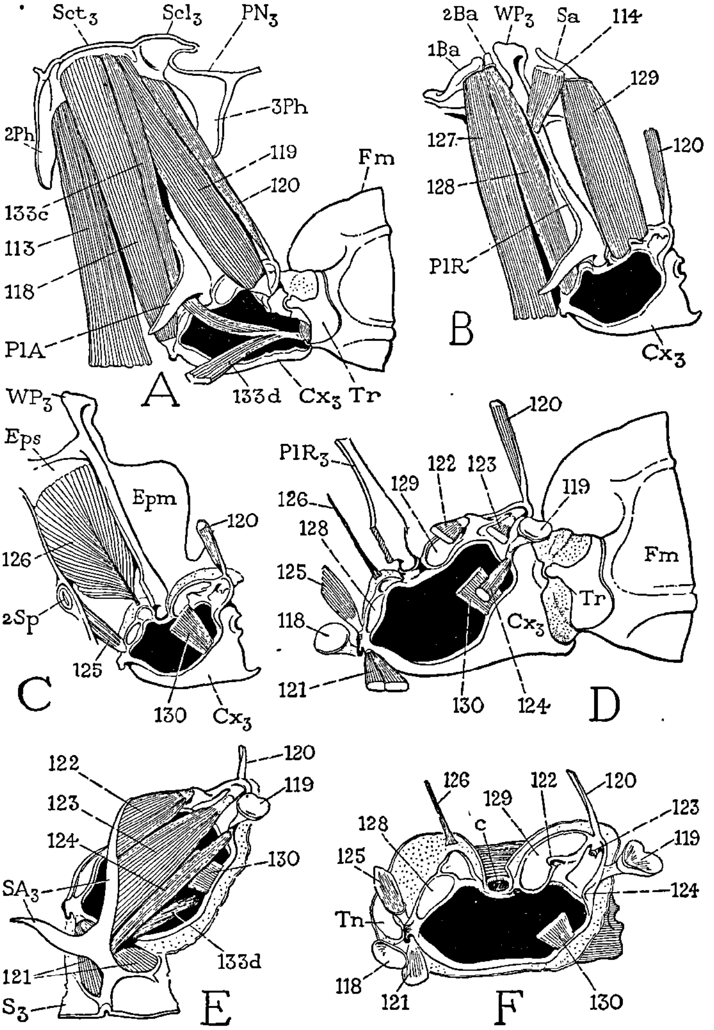

FIG. 115.—Musculature of the hind coxa of a grasshopper, *Dissosteira carolina*. *113*, tergosternal muscle; *114*, wing flexor; *118*, tergal promotor of coxa; *119*, *120*, tergal remotors of coxa; *121*, sternal promotor (anterior rotator) of coxa; *122*, *123*, *124*, sternal remotors (posterior rotators) of coxa; *125*, *126*, abductors of coxa; *127*, basalar-sternal muscle; *128*, basalar-coxal muscle; *129*, subalar-coxal muscle; *130*, sternal adductor of coxa; *133c*, *133d*, body branches of depressor of trochanter.

Adductor of the Coxa (Fig. 115 C, D, E, F, *130*).—A flat muscle taking its origin on the posterior surface of the metasternal apophysis beneath the posterior rotators (E), and extending posteriorly and ventrally to the inner margin of the coxal base (C, D, E, F, *130*). This muscle is evidently antagonistic to the abductor (*126*) since the two are inserted at opposite ends of a transverse axial line through the pleural articulation (C, D, F).

Two other muscles attached on the outer rim of the coxa, present in the mesothorax and metathorax but absent in the prothorax, are muscles of the epipleurites and function as wing muscles in the adult. These muscles in the metathorax are the following:

Second Pronator-extensor of the Hind Wing (Fig. 115 B, *128*).—A large muscle attached dorsally on the second basalar sclerite (*2Ba*) and ventrally on the base of the coxa anterior to the pleural fulcrum (D, F, *128*).

Depressor-extensor of the Hind Wing (Fig. 115 B, *129*).—A very thick muscle attached dorsally on the subalar sclerite (*Sa*) and ventrally on the coxal base posterior to the pleural articulation (D, F, *129*).

In the nymph the last two muscles take their origin on the dorsal edge of the pleuron, one on the episternum (Fig. 102 C, $3E'$), the other ($3E''$) on the epimeron, and they here evidently belong to the abductor system of the coxa.

Muscles of the Telopodite.—The part of the leg beyond the coxa is the principal movable part of the limb. The coxo-trochanteral joint at its base is almost universally a dicondylic hinge with articulations anterior and posterior relative to the normal vertical plane of the shaft of the limb. Its musculature, therefore, consists of levator and depressor muscles inserted on the basal segment, which is the trochanter. The levator fibers arise entirely within the coxa (Fig. 109 A, *O*); the depressor fibers include a coxal group (*Q*) and usually one or more groups (*P*) arising in the body segment supporting the leg (Fig. 117).

Muscles of the Trochanter.—In the hind leg of *Dissosteira* there are two levator muscles of the trochanter (Fig. 116 A, *131*, *132*) arising dorsally in the base of the coxa and inserted on the dorsal lip of the base of the trochanter. The depressor muscles include two groups of fibers arising ventrally in the base of the coxa (*133a*), and three groups taking their origin in the body of the metathorax. Of the latter, two arise on the tergum (Fig. 115 A, *133c*, the second not shown), and the third (*133d*) on the sternal apophysis (E, *133d*). The fibers of all groups are inserted on the ventral lip of the trochanter and together constitute a powerful depressor of the telopodite (Fig. 117, *P*, *Q*).

Muscles of the Femur.—In the hind leg of *Dissosteira* there is no movement between the small trochanter (Fig. 115 D, *Tr*) and the femur (*Fm*), and consequently the femur has no muscles. When the femur is movable on the trochanter, it is provided with a short *reductor* muscle arising in the trochanter and inserted on the posterior edge of the femoral base (Fig. 109 A, *R*). This muscle is present in the first and second legs of *Dissosteira* and imparts a slight rearward flexion to the femur on the dorsoventral trochantero-femoral hinge.

Muscles of the Tibia.—The tibial muscles are the most important muscles of the hind legs in the Acrididae, since it is the strong and sudden movement of the hind tibiae on the femora that gives the grasshopper its power of leaping. The muscles occupy almost the entire cavity of each femur (Fig. 116) and determine the size and shape of the latter; they comprise *levator* and *depressor* groups of fibers. Most of the levator muscle consists of two large masses of short overlapping fiber bundles occupying the dorsal three-fourths of the femoral cavity (A, B, *135a*, *135b*). They are attached to the lateral femoral walls on the spaces between the "fishbone" ridges that form the external sculptured pattern of the outer and inner faces of the femur; they are inserted on a flat apodeme that tapers distally to a thick stalk arising from the dorsal margin of the tibial base (A, *135Ap*). Two small branches of the levator muscle arise in the distal part of the femur from the dorsal wall and are inserted on the base of the apodeme (A, *135c*, the other not shown).

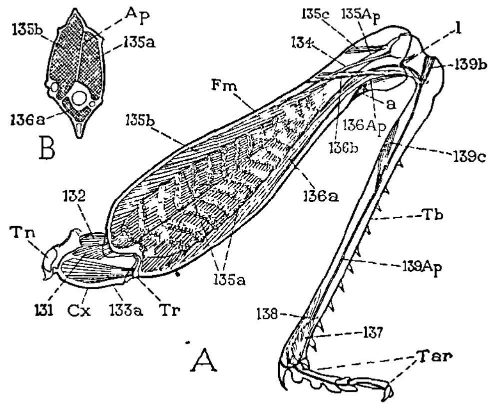

Fig. 116.—Muscles of the hind leg of a grasshopper, *Dissosteira carolina*. *131*, *132*, levators of trochanter; *133a*, coxal branch of depressor of trochanter; *134*, *135*, levators of tibia; *136*, depressor of tibia; *137*, *138*, levator and depressor of tarsus; *139*, depressor of pretarsus (retractor of claws).

The depressor of the hind tibia is a relatively small muscle with long, slender fibers arising in the ventral part of the femur (Fig. 116 A, B, *136a*) and converging to the sides of a tapering apodeme arising in the ventral membrane of the knee joint. The terminal straplike part of this apodeme slides over a strong internal process (A, *a*) near the end of the ventral wall of the femur. Two small accessory bands of depressor fibers arise distally from the dorsal wall of the femur and are inserted on the base of the depressor apodeme (*136b,* the posterior one not shown).

In the fore- and middle legs of *Dissosteira* the relative size of the tibial muscles is the reverse of that in the hind leg, the depressor being the stronger of the two. In these legs there is also a very small anterior levator, which is reduced to a fibrous strand in the hind leg (Fig. 116 A, *134*). The mechanism of the tibial muscles of the hind leg is shown in Fig. 117.

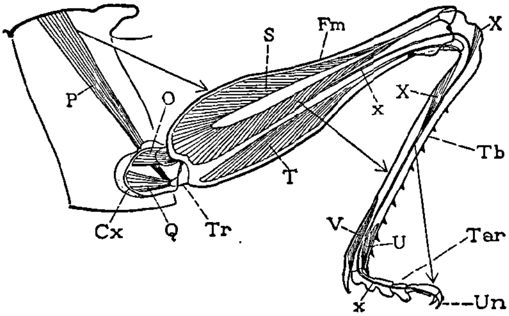

Fig. 117.—Mechanism of the hind leg of a grasshopper. *O*, levator of trochanter and femur; *P*, *Q*, depressors of trochanter and femur; *S*, *T*, levator and depressor of tibia; *U*, *V*, levator and depressor of tarsus; *X*, depressor of pretarsus.

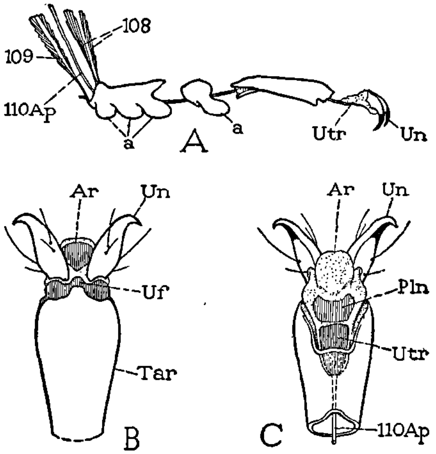

Fig. 118.—Pretarsus of a grasshopper, *Dissosteira carolina.* A, tarsus and pretarsus disjointed, showing tendonlike apodeme (*110Ap*) of depressor of pretarsus. B, pretarsus and end of tarsus, dorsal view. C, same, ventral view. *Ar*, arolium; *Pln*, planta; *Tar*, tarsus; *Uf*, unguifer; *Un*, ungues; *Utr*, unguitractor plate.

Muscles of the Tarsus.—The tarsal muscles, a *levator* and a *depressor,* are both small and lie in the distal part of the long slender tibia, (Fig. 116 A, *137*, *138*), the first inserted on the dorsal lip of the first tarsomere, the second on the ventral lip. The other subsegments of the tarsus are never provided with muscles and are consequently not independently movable.

Muscles of the Pretarsus.—The pretarsus of insects, as in the Chilopoda and Diplopoda, always lacks a levator muscle. The depressor forms the flexor, or retractor, of the claws, so called because it serves to flex the claws ventrally and proximally on the dorsal articulations of the latter with the distal end of the tarsus. Its fibers arise in the tibia and the femur and are inserted on a long tendonlike apodeme (Fig. 118 C, *110Ap*) arising from the unguitractor plate (*Utr*) in the base of the pretarsus, and extending through the tarsus and tibia (A) into the femur. In each leg of *Dissosteira* the first branch of the flexor of the claws arises posteriorly in the basal part of the femur; the second arises in the proximal bend of the tibia (Fig. 116 A, *139b*); the third (*139c*) on the inner wall of the basal third of the tibia. The extension of the claws is caused by the elasticity of the basal parts of the pretarsus supporting them.

GLOSSARY OF TERMS APPLIED TO THE PARTS OF AN INSECT'S LEG

The following terms are here defined as they are used in entomology; more general terms applied to the appendages are given in the Glossary of Chap. V.

Arolium (*Ar*).—The usual median lobe of the pretarsus, arising between the bases of the claws.

Auxiliae.—Small plates beneath the bases of the pretarsal claws, bearing the pulvilli when the latter are present.

Basicosta (*Bc*).—The proximal submarginal ridge of the inner wall of a leg segment.

Basicostal Suture (*bcs*).—The external groove of a leg segment forming the basicosta.

Basicoxite (*Bcx*).—The usually narrow basal rim of the coxa proximal to the basicostal suture and its internal ridge. (*Coxomarginale.*)

Basitarsus.—The proximal segment of the tarsus.

Coxa (*Cx*).—The basal segment of the leg articulating with the pleuron, or also with the sternum.

Coxal Corium.—The articular membrane surrounding the base of the coxa.

Coxomarginale (*Bcx*).—See *basicoxite.*

Dicondylic Joint.—A joint with two points of articulation between the adjacent leg segments.

Empodium (*Emp*).—A median lobe or spine-like process arising ventrally between the bases of the pretarsal claws, usually from the unguitractor plate.

Euplantulae.—Padlike structures on the ventral surfaces of the tarsal subsegments. (*Tarsal pulvilli.*)

Femur (*Fm*).—The third and usually the largest segment of the insect leg.

Meron (*Mer*).—The lateral postarticular area of the base of the coxa, in some insects greatly enlarged and extended distally in the posterior part of the coxa, but always proximal to the basicostal suture.

Monocondylic Joint.—A joint with a single point of articulation between the adjacent leg segments.

Planta.—A median ventral sclerite of the pretarsus distal to the unguitractor plate.

Pretarsus (*Ptar*).—The terminal parts of the leg distal to the tarsus, including median remnants of the dactylopodite, and the lateral claws, or ungues; in most larvae a simple clawlike segment.

Pulvilli (*Pv*).—Lateral lobes of the pretarsus arising beneath the bases of the claws. Ventral lobes of the tarsal subsegments (euplantulae) are sometimes called *tarsal pulvilli*.

Tarsus (*Tar*).—The fifth segment of the leg, usually divided into from two to five subsegments, or tarsomeres.

Tibia (*Tb*).—The fourth segment of the leg.

Trochanter (*Tr*).—The usual second segment of the insect leg, probably composed of two united trochanteral segments; in some cases (Odonata) showing a division between its component segments.

Ungues (*Un*).—The lateral claws of the pretarsus; usually called "tarsal" claws.

Unguifer.—The median dorsal process on the end of the tarsus to which the pretarsal claws are articulated.

Unguitractor Plate (*Utr*).—The ventral sclerite of the pretarsus from which arises the tendonlike apodeme of the retractor muscle of the claws.

CHAPTER X

THE WINGS

Insects differ from the other flying animals in that their wings are structures superadded to the primitive motor equipment of their ancestors. The birds and the bats, in acquiring the power of flight, have lost the use of a pair of limbs for other modes of locomotion, since their wings are the forelegs made over for purposes of flying. Insects thus seem related to the winged creatures of fiction, though the latter, it must be observed, are given wings quite irrespective of their anatomical possibilities of using them. And yet the wings of insects, as we shall presently see, when first acquired were probably outgrowths of the back incapable of movement. Certainly their evolution into organs of flight has involved much reconstruction in the thoracic segments to contrive a motor mechanism for them.

1. ORIGIN AND EVOLUTION OF THE WINGS

The oldest insects known from the fossil records lived in Carboniferous times, their remains being found in the lower beds of the Upper Carboniferous or Pennsylvanian period. These ancient insects had two pairs of fully developed wings, which differed but little in structure from the wings of modern insects (Fig. 119). Many of the Carboniferous insects, however, had in addition to the wings a pair of small, flat lobes (*pnl*) projecting laterally from the tergum of the prothorax, and these lobes

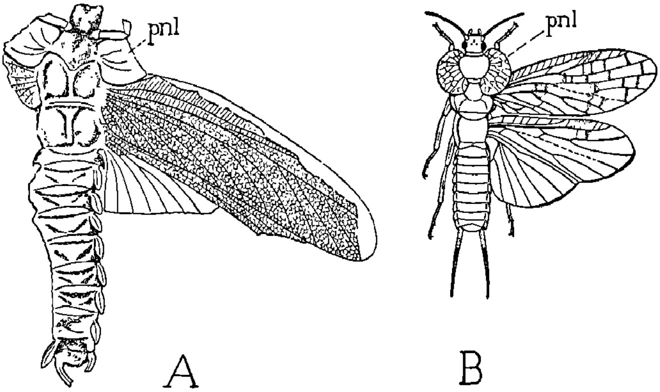

FIG. 119.—Examples of fossil insects with paranotal lobes on the prothorax. A, *Stenodictya lobata*. (*From Brongniart*, 1890.) B, *Lemmatophora typica*. (*From Tillyard*, 1928.)

suggest that at an earlier period the wings themselves were developed from similar tergal lobes of the mesothorax and the metathorax. We may visualize the immediate ancestors of the winged insects, therefore, as creatures having the body already differentiated into head, thorax, and abdomen and characterized by the possession of a series of three partly overlapping, fanlike extensions, or *paranotal lobes,* projecting on each side of the body from the thoracic terga. If the paranotal lobes, then, were the precursors of the wings, it seems most probable that they served as gliding organs, allowing their possessors to launch themselves into the air from an elevation and to sail off to some more distant objective.

The structure and development of the wings of modern insects attest the origin of the wings from lateral folds of the tergal margins, for each wing is essentially a hollow extension of the body wall, the dorsal lamina of which is directly continuous with the tergal plate supporting it, while the ventral lamina is reflected into the lateral wall of the segment (Fig. 120). The pleural plates of the thoracic segments must have been evolved for the purpose of supporting the bases of the paranotal lobes from below. We can thereby understand why the pleura of adult pterygote insects have the same essential structure in all the thoracic segments, and why they differ so characteristically from the primitive pleurites of the Apterygota. The special features of the pleura in the wing-bearing segments are final adaptations to the later-developed mechanism for moving the wings.

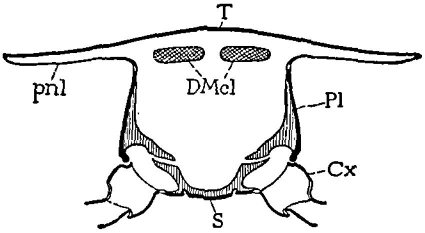

Fig. 120.—Diagrammatic cross section of a thoracic segment with paranotal extensions of the tergum.

The first step in the evolution of the paranotal lobes into organs of flight must have consisted in the acquisition of a line of flexibility in the base of each lobe. The longitudinal dorsal muscles (Fig. 103 A, *A*) could then, by arching the terga upward between the ends of the segments, throw the wing flaps downward, since the latter, in their recent capacity of glider lobes, were already substantially supported from below on the pleura. In order to give mechanical efficiency to the muscles in arching the terga, however, movement between the tergal plates had first to be eliminated. Sclerotic continuity in the dorsum of the wing-bearing region has been acquired either by a union of the successive terga or by a forward extension of the acrotergal lips of the metatergum and first abdominal tergum into the regions of the intersegmental membranes (Fig. 85).

With the downstroke of the wings produced by an upward bend of the tergum, the upstroke must depend on some antagonistic force that will flatten the tergum. It is possible that, in the first place, the elasticity of the tergal plates sufficed to restore the normal contour of the latter; but most modern insects have special tergal depressor muscles in the two wing-bearing segments. These muscles lie laterad of the longitudinal muscles; they are attached dorsally on the anterior lateral parts of the tergum and ventrally on the sternum before the coxae (Fig. 103 A, *C*). They are perhaps derived from the primitive lateral body muscles.

The wings of insects are thus movable up and down by a relatively simple mechanism. Flight, however, is not to be achieved by the mere flapping of a pair of flat appendages. Forward motion in the air depends upon a more complex movement in the motor organs, involving a slight forward and rearward action of the wings and a partial rotation on their long axes. With the wings sufficiently flexible at their bases, and of a proper structure in their distal parts, these movements may result from the changing air pressure on their surfaces when they are vibrated in a vertical direction. The stiffening of the anterior parts of the wings by a forward crowding of the veins (Fig. 131), and the flexibility of the more weakly supported posterior areas, automatically gives a torsion to the wing planes in motion. But if the wings had to depend upon air pressure alone for the slant of their planes that gives the forward impulse to the insect in the air, it is evident that the wings on opposite sides of the body would have always approximately the same degree of movement. Controlled or differential action in the two wings of a pair would then be impossible, and the insect would have no power of directing its flight or of changing its course. Most modern insects, however, do control efficiently their motions on the wing, and many of them, besides being well able to direct their forward flight, can also fly sidewise and backward without changing the position of the body, or they can hover at one point in the air. It is possible that some insects may shift their course by altering the posture while flying, but it has been shown that steering, for the most part, is a function of the wings.

The rotary movement of the wings is produced chiefly by powerful muscles lying against the pleural walls of the wing-bearing segments (Fig. 129, *E′*, *E″*). These muscles are inserted usually on small sclerites situated immediately beneath the wings, respectively before and behind the wing fulcrum (*WP*), or in some cases on lobes of the dorsal margin of the pleuron. The principal pair of these so-called "direct wing muscles" in each side of the segment take their origins ventrally on the coxa (*Cx*), showing that they are primarily leg muscles that have been given over to the service of the wings. When insects in this way acquired the direct action of muscles on the wing bases, they possessed a mechanism capable of controlling the movements of each wing separately and thus became endowed with the power of directive flight.

2. DEVELOPMENT OF THE WINGS

Since the insect wing is a flattened, double-layered expansion of the body wall, its own walls consist of the same elements as the body wall, namely, cuticula, epidermis, and basement membrane, and its lumen contains nerves, tracheae, and the body fluid, or blood.

The wings of insects with incomplete metamorphosis grow externally in the same manner as do the legs, the mouth parts, and other appendicular organs. The wing buds appear first in the second or third instar of the nymph as hollow, flattened outgrowths of the body wall along the lateral margins of the dorsum in the mesothorax and metathorax. They increase in size at each moult, without much change in structure until they assume the adult form at the transformation to the imago. In insects with complete metamorphosis the wings develop during the larval stage beneath the outer cuticula, usually within pouches of the epidermis. The time of their first formation varies in different insects from a late embryonic period to the last larval instar. The internal wing buds are normally everted from their pouches during the prepupal period of the last larval stage, but they are then still covered by the loosened cuticula of the larva. When this last larval skin is shed, and the insect enters the pupal stage, the wings are first exposed as external organs. During the pupal stage they develop rapidly and then quickly take their final form when the insect issues as an imago from the pupal skin.

In the very young wing bud the epidermis consists of upper and lower layers corresponding to the dorsal and ventral surface of the wing fold; but very soon the epidermal cells become elongate, and the inner ends of those in the opposing layers meet and unite. The fused basement membranes then become the so-called *middle membrane* of the wing. Along certain lines, however, the basement membranes do not come together; the channels thus left open, which are remnants of the primitive wing cavity, determine the courses of the future veins of the wing. The channels contain the wing nerves, tracheae, and blood. In later stages of development, the epidermal cells condense along the vein channels and form here the thick cuticular layers that are to constitute the walls of the wing veins. When the wing development is completed, the epidermis has largely disappeared, and the mature wing is almost entirely a cuticular structure. Nevertheless, an active circulation of blood persists in the adult wing, observed in insects of most of the principal orders, and sense organs are of frequent occurrence on the wing surfaces.

The histological changes in the growth of the wing are somewhat more complicated in the Holometabola, but the developmental processes are essentially the same as in insects with a simpler metamorphosis. The most important accounts of the development of the wings will be found in the papers by Weismann (1864), Gonin (1894), Mayer (1896), Comstock and Needham (1898–1899), Mercer (1900), W. L. Tower (1903), Powell (1903), Marshall (1915), Comstock (1918), and Köhler (1932).

The origin and growth of the tracheae of the wings are of much importance in the study of the wing venation, because, in many cases, the tracheation of the young wing serves as a key to the homology of the veins of the adult wing. The wing tracheae arise from a basal trachea, or two united tracheae, at the base of the wing bud, and in general are given off into the latter in two groups, one anterior, the other posterior. In insects with incomplete metamorphosis the tracheae take their places in the wings before the veins are formed and thus appear to determine the courses of the veins. In the Holometabola, however, the vein channels may be formed in advance of the tracheae, and, though in the Coleoptera, Neuroptera, and Lepidoptera each trachea is said to penetrate the vein corresponding to the one its homologue occupies in insects with incomplete metamorphosis, in the Trichoptera, Hymenoptera, and Diptera the relations between the tracheae and the veins are not so clearly preserved.

The internal wing buds of holometabolous larvae are aerated first by a few simple tracheae, but in the later larval stages they are supplied with numerous bundles of tracheoles that grow directly from the walls of the primary wing trachea. The definitive wing tracheae are finally formed during the last larval stage and become functional in the pupal stage, when the earlier tracheae and tracheoles degenerate. From the walls of the definitive tracheae, finally, a second set of tracheoles is developed, and these tracheoles become functional at the change to the imago.

The development of the wing tracheoles and tracheae was first studied by Gonin (1894); the details of the origin of the wing trachea from the basal trachea or tracheae of the wing in the principal groups of insects have been described by Chapman (1918), and the development of the wing veins of a cockroach by Beck (1920).

3. THE STRUCTURE OF THE WINGS

In studying the wings of insects we must give special attention to three features of their structure, namely, the *articulation* to the body, the *veins*, and the differentiation of the alar surface into *wing regions*. The veins serve to strengthen the wing and to adapt it to the movements demanded of an organ of flight. The articular parts furnish the basal structure in the wing necessary for the movements of flight in the distal area and constitute also the flexor apparatus in the wing-flexing insects.

The wing regions are local differentiations of the wing area partly subserving the function of flight, but largely accessory to the act of flexion.

The principal veins of the wings spring from the wing base, and most of them, except those of the posterior area, branch in varying degrees in

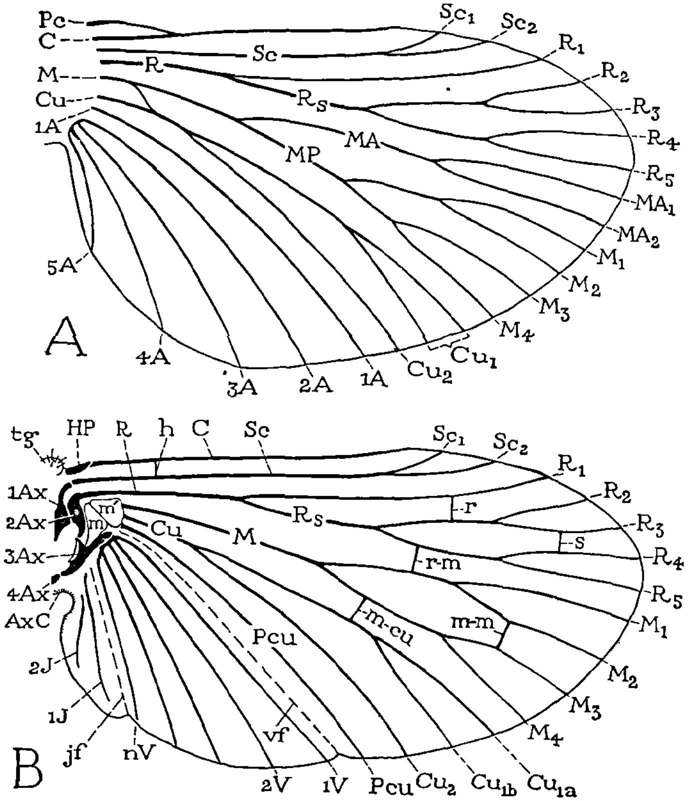

Fig. 121.—Diagrams of wing venation. A, the archetype venation, with veins named according to the Comstock-Needham system. (*Adapted from Bradley*, 1931, *to include three branches of cubitus.*) B, the usual wing veins and axillaries as designated in the accompanying text. *A*, anal veins; *Ax*, axillary sclerites (first, second, third, and fourth); *AxC*, axillary cord; *C*, costa; *Cu*, cubitus; *h*, humeral cross-vein; *HP*, humeral plate; *J*, jugal veins; *jf*, jugal fold; *M*, media; *m*, *m'*, median plates; *MA*, media anterior; *m-m*, median cross-vein; *m-cu*, mediocubital cross-vein; *MP*, media posterior; *Pc*, precosta; *Pcu*, postcubitus (first anal); *R*, radius; *r*, radial cross-vein; *Rs*, radial sector; *s*, sectorial cross-vein; *tg*, rudiment of tegula; *V*, vannal veins (anal veins except the first); *vf*, vannal fold.

the distal part of the wing. It is probable that all the diverse patterns of wing venation found in living and extinct insects have been derived from a single type of primitive venation; but the true primitive venation is not actually known, because the oldest fossil insects yet discovered have a highly complex system of wing veins. The venation pattern given in Fig. 121 A represents the plan of venation which students of the wing veins of insects regard as an ancient type from which the venation of modern insects has been derived, and it is therefore termed the *archetype* venation.

The theoretically complete archetype venation (Fig. 121 A) includes the following veins, named according to the Comstock-Needham system of vein nomenclature: first, a small *precosta* (*Pc*) at the base of the wing; second, a *costa* (*C*), which is usually marginal in modern insects; third, a two-branched *subcosta* (*Sc*); fourth, a five-branched *radius* (*R*); fifth, a six-branched *media* (*M*); sixth, a three-branched *cubitus* (*Cu*); and, finally, a varying number of *anal veins* (*A*).

The vein nomenclature given above is adopted in the present text with the exception that the anal veins are not recognized as a homogeneous group. The first anal vein (Fig. 121 A, *1A*) in more generalized insects is always associated at its base with the cubitus, and in the wings of many nymphal insects it is represented by a distinct trachea (Fig. 125 A, *Pcu*). The independence of the first anal from the other anals becomes an important feature in a study of the mechanism of the wings. For this reason it is here designated the *postcubitus* (Fig. 121 B, *Pcu*). The rest of the anals, which constitute a definite functional group of veins in generalized insects, associated with the flexor sclerite (*3Ax*) of the wing base, are distinguished as *vannal veins* (*V*) because the wing region containing them often forms a large fanlike expansion (vannus) of the posterior part of the wing. At the base of the wing, proximal to the vannal region, there is usually a small but variously developed lobe, the jugum, which may contain one or two *jugal veins* (B, *J*). The second principal branch of cubitus, the postcubitus, and the vena dividens sometimes present in the fold between the postcubital and vannal veins are the first, second, and third plical veins of Forbes (1933).

In the wings of modern insects (Fig. 121 B) the precosta does not appear, and the anterior fork of media (A, *MA*) is usually absent. The remaining veins in the wing are subject to many modifications in different groups of insects by the union of adjacent veins or by a partial or even complete suppression of certain veins, and the venational pattern may be further complicated by the addition of secondary veins. It often becomes, therefore, a difficult matter to identify with certainty the veins that are present, and the problem of determining the wing-vein homologies in the various orders of insects has been a major subject in entomology. A help in the study of the venation of adult insects may be derived from an examination of the basal connections or association of the veins with small sclerites in the articular region of the wing. These sclerites, the pteralia, are present in the wings of all insects, but they are particularly developed in insects that flex the wings over the back when at rest. The sclerites have definite and constant relations both to one another and to the bases of the veins. This fact has long been known, but for some reason students of wing venation have made little use of the basal connections of the veins in adult insects for determining vein homologies.

The Articulation of the Wings.—The various movements of the wings, especially in insects that flex the wings horizontally over the back when at rest, demand a more complicated articular structure at the wing base than a mere hinge of the wing with the body. Each wing is attached to the body by a membranous basal area, but the articular membrane contains a number of small articular sclerites, collectively known as the *pteralia* (Fig. 121 B). The pteralia include an anterior *humeral plate* (*HP*) at the base of the costal vein, a group of *axillaries* (*Ax*) associated with the subcostal, radial, and vannal veins, and two less definite *median plates* (*m, m′*) at the base of the mediocubital area. The axillaries are specifically developed only in the wing-flexing insects, where they constitute the flexor mechanism of the wing operated by the flexor muscle arising on the pleuron (Fig. 128 C, *D*). Characteristic of the wing base is also a small lobe on the anterior margin of the articular area proximal to the humeral plate (Fig. 121 B, *tg*), which, in the forewing of some insects, is developed into a large, flat, scale-like flap, the *tegula*, overlapping the base of the wing. Posteriorly the articular membrane often forms an ample lobe between the wing and the body, and its margin is generally thickened and corrugated, giving the appearance of a ligament, the so-called *axillary cord* (Fig. 122, *AxC*), continuous mesally with the posterior marginal scutellar fold of the tergal plate bearing the wing.

The articular sclerites, or pteralia, of the wing base of the wing-flexing insects and their relations to the body and the wing veins, shown diagrammatically in Fig. 122, are as follows:

The Humeral Plate (*HP*).—Usually a small sclerite on the anterior margin of the wing base, movably articulated with the base of the costal vein; greatly enlarged in Odonata (Fig. 123 B).

The First Axillary (1*Ax*).—This sclerite is the anterior hinge plate of the wing base. Its anterior part is supported on the anterior notal wing process of the tergum (*ANP*); its posterior part articulates with the tergal margin. The anterior end of the sclerite is generally produced as a slender arm, the apex of which (*e*) is always associated with the base of the subcostal vein (*Sc*), though it is not united with the latter. The body of the sclerite articulates laterally with the second axillary.

The Second Axillary (2*Ax*).—This sclerite is more variable in form than the first axillary, but its mechanical relations are no less definite. It is obliquely hinged to the outer margin of the body of the first axillary, and the radial vein (*R*) is always flexibly attached to its anterior end (*d*). The second axillary presents both a dorsal and a ventral sclerotization in the wing base; its ventral surface rests upon the fulcral wing process of the pleuron (Figs. 128 C, 129, 2*Ax*). The second axillary, therefore, is the pivotal sclerite of the wing base, and it specifically manipulates the radial vein.

The Third Axillary (3*Ax*).—The third axillary sclerite lies in the posterior part of the articular region of the wing. Its form is highly variable and often irregular, but the third axillary is the sclerite on which is inserted the flexor muscle of the wing (*D*). Mesally it articulates anteriorly (*f*) with the posterior end of the second axillary, and posteriorly (*b*) with the posterior wing process of the tergum (*PNP*), or with a small fourth axillary when the latter is present (Fig. 121 B, 4*Ax*). Distally the third axillary is prolonged in a process which is always associated with the bases of the group of veins in the anal region of the wing here termed the vannal veins (*V*). The third axillary, therefore, is usually the posterior hinge plate of the wing base and is the active sclerite of the flexor mechanism, which directly manipulates the vannal veins. The contraction of the flexor muscle (*D*) revolves the third axillary on its mesal articulations (*b*, *f*) and thereby lifts its distal arm; this movement produces the flexion of the wing.

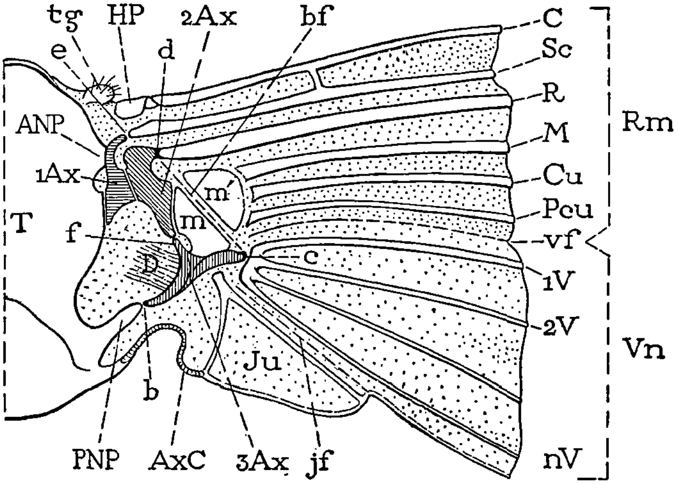

Fig. 122.—Diagram showing the articulation of the wing with the alinotum, and the basal relations of the veins to the humeral plate and the axillary sclerites. (Lettering as on Fig. 121.)

The Fourth Axillary (Fig. 121 B, 4*Ax*).—This sclerite is not a constant element of the wing base. When present it is usually a small plate intervening between the third axillary and the posterior notal wing process and is probably a detached piece of the latter.

The Median Plates (*m*, *m′*).—These sclerites are not so definitely differentiated as specific plates as are the three principal axillaries, but nevertheless they are important elements of the flexor apparatus. They lie in the median area of the wing base distal to the second and third axillaries and are separated from each other by an oblique line (*bf*) which forms a prominent convex fold during flexion of the wing. The proximal plate (*m*) is usually attached to the distal arm of the third axillary and perhaps should be regarded as a part of the latter. The distal plate (*m'*) is less constantly present as a distinct sclerite and may be represented by a general sclerotization of the base of the mediocubital field of the wing. When the veins of this region are distinct at their bases, they are associated with the outer median plate.

The Wing Base of Ephemerida.—The mayflies, when at rest, bring the wings together vertically over the back, but they do not flex the wings in the sense of folding them horizontally. A flexor mechanism, therefore, is not developed in the bases of the wings; and yet the structure of the articular areas of the wings (Fig. 123 A) is not radically different from that of the wing-folding insects. At the base of each wing of the mayfly there is a small humeral plate (*HP*) intermediating between the head of the costal vein (*C*) and a small tergal lobe of the body segment supporting the wing. In the axillary region there is a group of weakly defined sclerites (*Ax*), which in their arrangement and relations to the vein bases give a suggestion of the axillaries of the wing-folding insects. The posterior part of the axillary membrane in the mayfly has the usual form of a fold bordered by a corrugated thickening, or axillary cord (*AxC*), continuous with the posterior margin of the tergum.

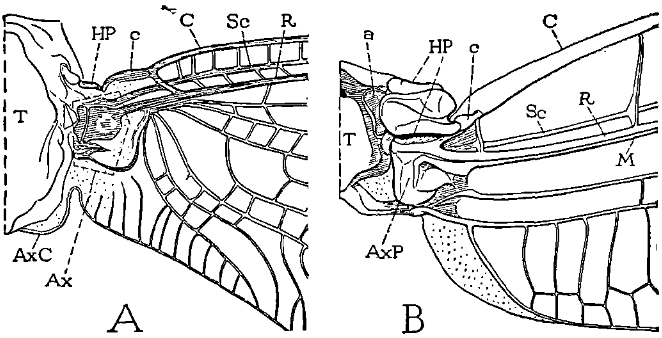

FIG. 123.—The wing articulation in insects that do not flex the wings. A, wing base of a mayfly. B, wing base of a dragonfly. *Ax*, axillary region; *AxP*, axillary plate; *HP*, humeral plate.

The Wing Base of Odonata.—The articular region of the wing of a dragonfly contains two large, strongly sclerotized plates (Fig. 123 B). The anterior plate (*HP*) supports the costal vein by a small intermediate sclerite (*c*) at the base of the latter and thus corresponds to the humeral plate of Ephemerida (A) and the wing-flexing insects (Fig. 121 B, *HP*). The great enlargement of the humeral plate in Odonata is evidently a specialized feature of the flight mechanism in this group. The posterior plate of the dragonfly wing (Fig. 123 B, *AxP*) carries the four basal shafts of the postcostal veins and hence may be termed the *axillary plate,* since it corresponds in position to the group of sclerites in the ephemerid wing (A, *Ax*) that appear to represent the axillaries of the wing-flexing insects. The humeral plate of the odonate wing is hinged to the anterior half of the lateral edge of the tergum (*T*) of the segment supporting the wing, or in some species to a distinct sclerite (*a*) of the tergum. The axillary plate is articulated to the posterior half of the lateral tergal margin opposite a deep membranous area of the latter. The pleural wing process supporting the wing has two arms, one applied to the humeral plate, the other to the axillary plate. The basal plates of the dragonfly's wing turn up and down on the fulcral arms when the wings are lifted or depressed. The two plates, however, are slightly movable on each other, and, since the costal vein (*C*) is doubly hinged to the humeral plate by a small intermediary piece (*c*) at its base, the costal area of the wing can be quite freely deflected independent of the rest of the wing area, which is solidly supported on the axillary plate by the veins attached to the latter.

The flight mechanism of the Odonata, including the structure of the wing bases and the attachments of the wing muscles, appears to be a special development of a more generalized structure, retained by the Ephemerida, from which the wing mechanism of other insects has been evolved.

The Wing Veins.—The usual veins of the wing, omitting the precosta of certain fossil insects, are shown diagrammatically at B of Fig. 121. Their characteristic features and basal connections are as follows:

Costa (*C*).—The usual first vein of the wing, commonly marginal, but sometimes submarginal; associated at its base with the humeral plate (*HP*). The trachea of the costal vein is perhaps a branch of the subcostal trachea.

Subcosta (*Sc*).—The second vein of the wing, typically forked distally into two short branches (Sc_1, Sc_2); associated at its base with the distal end of the neck of the first axillary ($1Ax$).

Radius (*R*).—The third and generally the strongest vein of the wing. Toward the middle of the wing it forks into a first undivided branch (R_1) and a second branch, called the *radial sector* (R_s), which subdivides dichotomously into four distal branches (R_2, R_3, R_4, R_5). Basally the radius is flexibly united with the anterior end of the second axillary ($2Ax$).

Media (*M*).—The fourth vein of the wing. In the archetype pattern (A) the media forks into two main branches, a *media anterior* (*MA*), which divides into two distal branches (MA_1, MA_2), and a *median sector,* or *media posterior* (*MP*), which has four terminal branches (M_1, M_2,

M_3, M_4). In most modern insects (B) the media anterior has been lost, and the usual "media" is the four-branched media posterior with the common basal stem. In the Ephemerida, according to present interpretations of the wing venation, both branches of the media are retained, while in Odonata the persisting media is the primitive anterior branch. The stem of the media is often united with the radius, but when it occurs as a distinct vein its base is associated with the distal median plate (m') or is continuously sclerotized with the latter.

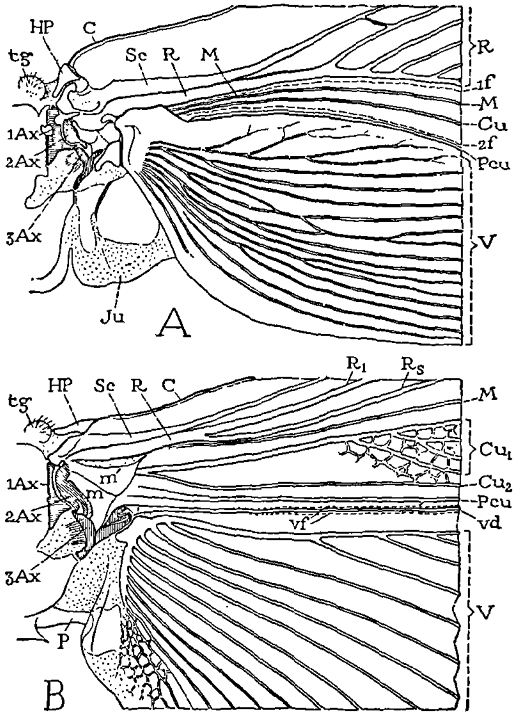

FIG. 124.—Bases of the fore and hind wings of *Periplaneta americana*.

Cubitus (*Cu*).—The fifth vein of the wing, primarily two branched. The primary forking of the cubitus takes place near the base of the wing (Figs. 124 B, 125 A, B, C), forming the two principal branches (Cu_1, Cu_2). The anterior branch may break up into a number of secondary branches (Figs. 124 B, 125 B), but commonly it forks into two distal branches (Fig. 121 B, Cu_{1a}, Cu_{1b}). The second branch of the cubitus (Cu_2) in Hymenoptera, Trichoptera, and Lepidoptera was mistaken by Comstock and Needham for the first anal, as has been shown by Tillyard (1919), Lameere (1922), Tanaka (1926), Imms (1931*a*, 1934), and others. Proximally the main stem of the cubitus is associated with the distal median plate (m') of the wing base.

Postcubitus (*Pcu*).—This vein is the *first anal* of Comstock and Needham (Fig. 121 A, 1*A*), except where these writers wrongly identified the second branch of cubitus as the "first anal." The postcubitus, however, has the status of an independent wing vein (B, *Pcu*) and should be recognized as such. In nymphal wings, as amply shown by Comstock (1918), its trachea arises between the cubital trachea and the group of vannal tracheae (Fig. 125 A, *Pcu*). In the mature wings of more generalized insects the postcubitus is always associated proximally with the cubitus (Fig. 124 B) and is never intimately connected with the flexor sclerite (3*Ax*) of the wing base. In Neuroptera, Mecoptera, and Trichoptera the postcubitus may be more closely associated with the vannal veins (Fig. 125 C, *Pcu*), but its base is always free from the latter. The postcubitus is usually unbranched; according to Lameere (1922) it is primitively two branched. In a former paper the writer (1930) called this vein "second cubitus (2*Cu*)" and mistakenly regarded it as representing the second branch of cubitus in Orthoptera.

Vena Dividens.—This is apparently a secondary vein present in the hind wing of some Orthoptera (Figs. 124 B, 134 B, *vd*), developed in the fold (*vf*) that sets off the vannal region from the wing region before it.

Vannal Veins (1*V to nV*).—The vannal veins are the anal veins that are immediately associated with the third axillary, and which are directly affected by the movement of this sclerite that brings about the flexion of the wings. In number the vannal veins vary from 1 to 12, according to the expansion of the vannal area of the wing. The vannal tracheae usually arise from a common tracheal stem in nymphal insects (Fig. 125 A, *V*), and the veins are regarded by Lameere (1922) and Tanaka (1926) as branches of a single anal vein. Distally the vannal veins are either simple or branched.

Jugal Veins (*J*).—The jugal lobe of the wing is often occupied by a network of irregular veins, or it may be entirely membranous; but sometimes it contains one or two distinct small veins, the *first jugal vein*, or *vena arcuata* (Fig. 121 *B*, 1*J*), and the *second jugal vein*, or *vena cardinalis* (2*J*).

Cross-veins.—All the veins of the wing are subject to secondary forking and to union by cross-veins. In some orders of insects the cross-veins are so numerous that the whole venational pattern becomes a close network of branching veins and cross-veins. Ordinarily, however, there is a definite number of cross-veins having specific locations as indicated at B of Fig. 121. The more constant cross-veins are the *humeral cross-vein* (*h*) between costa and subcosta, the *radial cross-vein* (*r*) between R_1 and the first fork of R_s, the *sectorial cross-vein* (*s*) between the two forks of R_s, the *median cross-vein* (*m-m*) between M_2 and M_3, and the *medio-cubital cross-vein* (*m-cu*) between media and cubitus.

The veins of the wing appear to fall into an undulating series of *convex veins* and *concave veins,* according to whether they have a tendency to fold up or down when the wing is relaxed. The basal shafts of the veins are convex, but according to Lameere (1922) each vein forks distally into an anterior convex branch and a posterior concave branch. Thus the costa and subcosta are regarded as convex and concave branches of a primary first vein, R_s is the concave branch of the radius, *MP* the concave branch of the media, Cu_1 and Cu_2 are respectively convex and concave, while the primitive postcubitus and the first vannal have each an anterior convex branch and a posterior concave branch. The convex or concave nature of the veins has been used as evidence in determining the identities of the persisting distal branches of the veins of modern insects, but it has not been demonstrated to be consistent for all wings.

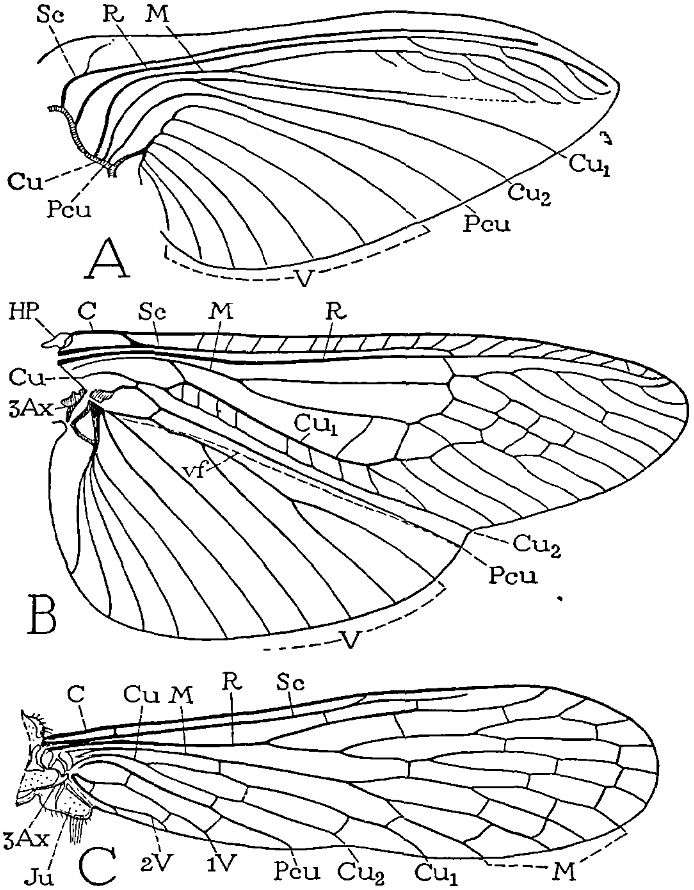

FIG. 125.—Examples of wing venation. A, hind wing of nymph of *Scudderia.* (*From Comstock,* 1918.) B, hind wing of a plecopteron, *Isogenus.* C, forewing of *Panorpa.*

The Wing Regions.—In the wings of all insects we must distinguish a basal *articular area* from the true *ala*, or distal expanse of the wing containing the veins. The wing base of Odonata, as we have observed, contains two large plates: an anterior humeral plate (Fig. 123 B, *HP*) supporting the costal vein, and a posterior axillary plate (*AxP*) supporting the other veins. The structure here is probably a specialized development of a more generalized structure of the wing base in primitive insects. In the Ephemerida (A) the humeral plate is small, as it is in insects generally, and the axillary region (*Ax*) contains a group of indistinctly differentiated sclerites. In the wing-flexing insects the axillary sclerites are well defined and individualized; the area containing them is a definite feature of the wing base and may be termed the *axillary region* of the wing (Fig. 126, *Ax*).

The true alar area of the wing is always more or less asymmetrical in form. The contour of the front margin is different from that of the hind margin, and the pattern of the anterior venation never matches with that of the venation in the posterior part of the wing. There is a tendency for the anterior veins to become thickened and crowded toward the forward margin in such a manner as to give greater rigidity to the front half of the wing, while the weaker posterior veins are more widely spaced and give flexibility to the rear half. The alar area thus becomes differentiated into an anterior region (Fig. 126, *Rm*), which is actively effective in flight, and a posterior more passive region (*Vn*). The anterior rigid part of the wing may be termed the *remigium* (from Latin, an *oar*). In more generalized slow-flying insects, the posterior flexible part of the wing is often enlarged to form a fanlike expansion of the wing and hence may be termed the *vannus* (from Latin, a *fan*). In the more specialized swift-flying insects the vannus is reduced; but since it contains the veins connected with the flexor sclerite of the wing base and is therefore an essential part of the flexor apparatus, the vannus is seldom entirely obliterated. Finally there is often developed at the base of the wing proximal to the vannus a membranous lobe of the wing, the *neala* of Martynov (1925), commonly called the *jugum* (Fig. 126, *Ju*) because that of the forewing in some insects serves to yoke the two wings on each side with each other. At the posterior angle of the wing base there sometimes occurs a membranous lobe, or pair of lobes, known as the *alula*, or *calypter*.

The three regions of the alar surface are commonly separated by lines of folding in the wing membrane. This is true particularly when the wings are wide and cannot be placed flat over the body in the flexed position. There occurs then between the remigium and the vannus, or approximately separating these regions, a *plica vannalis*, or *vannal fold* (Fig. 126, *vf*). This fold either allows the vannus to take a horizontal position over the back, while the remigium slopes downward on the side, or it enables the vannus to be folded beneath the remigium in the flexed wing. The jugum, when well developed, is likewise separated from the vannus by a line of folding, the *plica jugalis*, or *jugal fold* (*jf*), and in the flexed wing the jugum is usually turned up or down on the inner edge of the vannus. The vannal fold, called also the "anal furrow," does not occur at exactly the same place in the wings of all insects, as will be noted in special examples to be described later, and in narrow-winged insects it may be eliminated. The wing regions are particularly distinct in insects having a large vannus, and especially in those that plait the vannus when the wing is flexed.

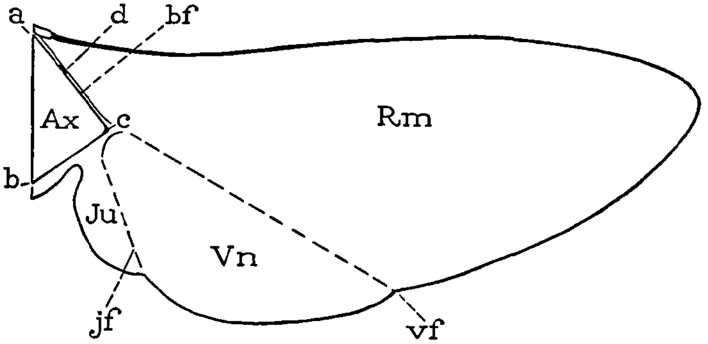

FIG. 126.—Diagram of the wing regions in wing-flexing insects. *Ax*, axillary region; *bf*, basal fold; *jf*, jugal fold; *Ju*, jugum; *Rm*, remigium; *Vn*, vannus; *vf*, vannal fold.

The Axillary Region.—The region containing the axillary sclerites (Fig. 122) has in general the form of a scalene triangle (Fig. 126, *Ax*). The base of the triangle (*a-b*) is the hinge of the wing with the body; the apex (*c*) is the distal end of the third axillary sclerite (Fig. 122, *c*); the longer side (Fig. 126, *a-c*) is anterior to the apex. The point *d* on the anterior side of the triangle marks the articulation of the radial vein with the second axillary sclerite (Fig. 122, *d*). The line between *d* and *c* (Fig. 126) is the *plica basalis* (*bf*), or fold of the wing at the base of the mediocubital field (Fig. 122, *bf*).

The Remigium.—The wing region anterior to the vannal fold (Fig. 126, *Rm*) is the part of the wing chiefly productive of the movements of flight, since it is directly affected by the motor muscles of the wing. When the vannal fold has the usual position anterior to the group of vannal veins (Fig. 121 B, *vf*), the remigium contains the costal, subcostal, radial, medial, cubital, and postcubital veins. In the flexed wing the remigium turns posteriorly on the flexible basal connection of the radius with the second axillary (Fig. 122, *d*), and the base of the mediocubital field is folded medially on the axillary region along the plica basalis (*bf*) between the median plates (*m*, *m'*) of the wing base.

The Vannus.—The vannal fold typically occurs between the postcubitus and the first vannal vein (Figs. 121 B, 122, *vf*). In Orthoptera it usually has this position (Fig. 124 B, 134 A, B, *vf*). In the forewing of Blattidae, however, the only fold in this part of the wing lies immediately before the postcubitus (Fig. 124 A, *2f*). In Plecoptera the vannal fold is posterior to the postcubitus (Fig. 125 B, *vf*), but proximally it crosses the base of the first vannal vein. In the cicada (Fig. 127 A) the vannal fold lies immediately behind the first vannal vein (*1V*). These small variations in the actual position of the vannal fold, however, do not affect the unity of action of the vannal veins, controlled by the flexor sclerite (*3Ax*), in the flexion of the wing. In the hind wings of most Orthoptera a secondary vena dividens forms a rib in the vannal fold (Figs. 124 B, 134 B, D, *vd*).

The vannus is usually triangular in shape (Fig. 126, *Vn*), and its veins typically spread out from the third axillary like the ribs of a fan. Some of the vannal veins may be branched, and secondary veins may alternate with the primary veins (Fig. 134 B, *a*, *b*, *c*). The vannal region is usually best developed in the hind wing, in which it may be enlarged to form a sustaining surface, as in Plecoptera and Orthoptera. The great fanlike expansions of the hind wings of Acrididae (Fig. 134 B) are clearly the vannal regions, since their veins are all supported on the third axillary sclerites of the wing bases, though Martynov (1925) ascribes most of the fan areas in Acrididae to the jugal regions of the wings. The true jugum of the acridid wing is represented only by the small membrane (*Ju*) mesad of the last vannal vein. The jugum is more highly developed in some other Orthoptera, as in the Mantidae. In most of the higher insects with narrow wings the vannus becomes reduced (Figs. 125 C, 127 C), and the vannal fold is lost, but even in such cases the flexed wing may bend along a line between the postcubitus and the first vannal vein.

The Jugal Region, or Neala.—The jugal region of the wing (Fig. 126, *Ju*) is usually a small membranous area proximal to the base of the vannus strengthened by a few small, irregular veinlike thickenings; but when well developed it is a distinct section of the wing (Figs. 124 A, 125 C, 127 A, D, *Ju*) and may contain one or two jugal veins (Figs. 121 B, 127 D, *1J*, *2J*). When the jugal area of the forewing is developed as a free lobe, it projects beneath the humeral angle of the hind wing and thus serves to yoke the two wings together. In the Jugatae group of Lepidoptera it bears a long fingerlike lobe. The jugal region is termed the *neala* ("new wing") by Martynov (1925), because it is evidently a secondary and recently developed part of the wing.

The Alula.—At the posterior angle of the wing base in some Diptera there is a pair of membranous lobes (*squamae*, or *calypteres*) known as the *alula*. The alula is well developed in the house fly (Fig. 127 C, *c*, *d*).

The outer squama (*c*) arises from the wing base behind the third axillary sclerite (3*Ax*) and evidently represents the jugal lobe of other insects (A, D); the larger inner squama (*d*) arises from the posterior scutellar margin of the tergum of the wing-bearing segment and forms a protective, hoodlike canopy over the halter. In the flexed wing the outer squama of the alula is turned upside down above the inner squama, the latter not being affected by the movement of the wing. In many Diptera a deep incision of the anal area of the wing membrane behind the single vannal vein sets off a proximal alar lobe distal to the outer squama of the alula.

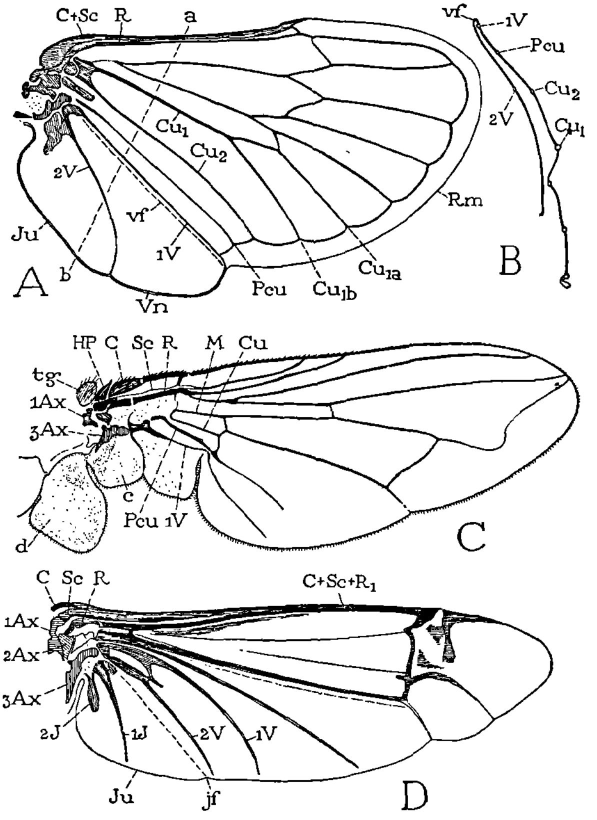

FIG. 127.—Examples of wing venation. A, *Magicicada septendecim*, hind wing, extended. B, section of same along line *a-b* when folded. C, *Musca domestica*, wing and calypteres. D, *Epicauta pennsylvanica*.

4. THE WING MUSCLES

The movements of the wings in the majority of insects are accomplished by five pairs or paired sets of muscles in each alate segment. These muscles are the *dorsal muscles* (Fig. 103, *A*), the *tergosternal muscles*

(*C*), the *axillary muscles* (*D*), the *basalar muscles* (*E′*), and the *subalar muscles* (*E″*). The dorsal and tergosternal muscles are often called the "indirect wing muscles," and the axillary and epipleural muscles the "direct wing muscles," but, strictly speaking, only the axillary muscles in most insects are attached directly on the wing bases.

In addition to the muscles listed above as specific wing muscles, it is probable that most of the segmental and intersegmental muscles of the pterothorax that are not leg muscles have some action in relation to the wing movements. Particularly the tergopleural muscles (Fig. 103 B, *B*), which extend from the tergum to the basalare, to the wing process, or to the epimeron, must exert some controlling influence on the movement of the tergum. Those inserted on the basalare undoubtedly have a direct action on the wings; a large tergobasalar muscle present in some Diptera sharply extends the wing in a horizontal plane. Since however, the tergopleural muscles are highly variable and are not constantly present in the wing-bearing segments, they will not be considered in the following general discussion of the wing muscles.

The Dorsal Muscles.—These muscles are the ordinary longitudinal muscles of the back, which, in the usual secondary segmentation of the body (Fig. 37), extend from the antecosta of one tergum to that of the next. In the wing-bearing segments of most insects the dorsal muscles are differentiated into *median longitudinal muscles* (Fig. 128 A, *mA*) and *lateral oblique muscles* (*lA*).

The median dorsal muscles are usually greatly enlarged in the wing-bearing segments, and their expansion is accommodated by the development of phragmatal lobes on the antecostae of the mesotergum, the metatergum, and the first abdominal tergum, but frequently also their dorsal fibers encroach upon the postcostal surface of the alinotum and on the precostal surface of the postnotum (Fig. 128 A). The longitudinal dorsal muscles are the principal depressors of the wings, since, by their contraction, they arch the wing-bearing terga upward between the ends of the segments and thus deflect the wings on the pleural fulcra (Fig. 131 C). The action of the dorsal muscles as wing depressors, however, depends on an obliteration of the dorsal intersegmental membranes, a condition that has been brought about either by a fusion of the consecutive terga or by a forward extension of the precostal lips of the metathoracic and first abdominal terga (Fig. 85) to form the phragma-bearing postnotal plates of the mesothorax and metathorax, respectively. The dorsal muscles are most highly developed in the segment bearing the principal pair of wings; they are usually reduced or absent in a segment of which the wings are small or are used for other purposes than that of flight. With insects such as Isoptera, Blattidae, and Gryllidae having weak powers of flight, the dorsal muscles are very small in both segments of the pterothorax, but they are also reduced in the strong-flying Odonata, in which the wings are moved by the lateral thoracic muscles.

The lateral oblique dorsal muscles (Fig. 128 A, *lA*) arise on the posterior part of the scutum and are inserted posteriorly on the succeeding phragma laterad of the bases of the median dorsals. Usually these muscles are relatively small, and they are not always present; in function they probably supplement the tergosternals in their downward pull on the tergum. In the mesothorax of the cicada and in the Diptera the oblique dorsal muscles are unusually large (B, *lA*) and assume a position so nearly vertical, by reason of the great size of the second phragma (*2Ph*), that they become powerful adjuncts of the tergosternal muscles (*C*) as depressors of the tergum.

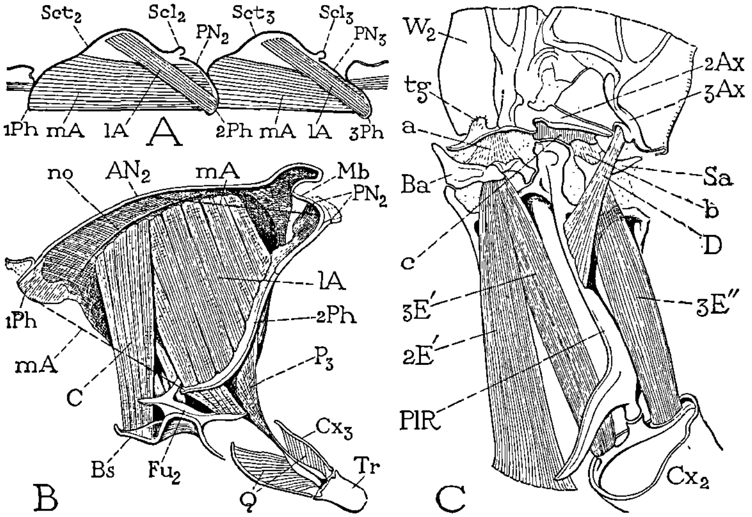

FIG. 128.—The wing muscles. A, dorsal muscles of pterothorax of *Panorpa*, lateral view. B, mesothorax of *Magicicada*, median dorsals (*mA*) removed, showing almost vertical position of large lateral dorsals (*lA*). C, mesothorax of *Dissosteira* with basalar (*E′*), subalar (*E″*), and wing flexor muscles (*D*) of right side, mesal view.

The Tergosternal Muscles.—These muscles lie to the sides of the median dorsal muscles in the anterior part of the segment (Figs. 103 A, 128 B, *C*). They are attached dorsally on the anterior lateral areas of the tergum, and ventrally on the basisternum before the coxae. There may be one or several pairs of them in each segment. Functionally the tergosternal muscles are antagonists of the longitudinal dorsals, since by contraction they depress the tergum and thereby elevate the wings on the pleural fulcra (Fig. 131 A). These muscles have no representatives in the prothorax, and they may be absent in the pterothorax of insects of weak flight.

In the Diptera a third pair of muscles, lying between the anterior tergosternals and the posterior oblique dorsals, becomes secondarily levators of the wings. The muscles of this pair are the normal tergal remotors of the middle legs inserted on the meral lobes of the coxae. In the higher Diptera; however, the mesothoracic meron is detached from the rest of the coxa and becomes solidly incorporated into the lateral wall of the thorax (Fig. 102 E, *Mer*). The tergal remotor of the coxa is thus anatomically transferred from the leg and given over functionally to the service of the wing, since, by the loss of movement at its lower end, it becomes a depressor of the tergum.

The Axillary Muscles.—The only muscles attached directly on the wing bases, in insects other than Odonata, are muscles arising on the pleuron and inserted on the first and third axillary sclerites.

A muscle of the first axillary is known to occur only in Diptera. In a syrphid fly this muscle consists of two parts, one arising on the episternum, the other behind the pleural ridge, both inserted on the inner margin of the first axillary. A pull on the muscle turns the axillary upward on its tergal articulations, which is the usual action of the first axillary during flexion of the wings.

The muscle of the third axillary (Fig. 103 B, *D*) is present in all the wing-flexing insects, since it is the effector of the flexion movements of the wing. The muscle arises on the pleuron, but it is variable in size and distribution. Typically it consists of a single bundle of fibers attached on the pleural ridge (Fig. 128 C, *D*), but it may comprise several branches arising on the episternum, the pleural ridge, and the epimeron. Distally the flexor muscle is inserted on the base of the third axillary sclerite (Fig. 122, *3Ax*). Its contraction revolves the third axillary dorsally and inward on the proximal articulations of the latter (*b, f*) and thus turns the alar area of the wing posteriorly on the axillary region by a flexure along the line of the plica basalis (*bf*).

A muscle corresponding to the wing flexor is well developed in each wing-bearing segment of zygopterous Odonata. It arises on the pleural ridge and is inserted posteriorly on the axillary plate.

The Basalar Muscles.—The muscles of the basalar sclerites, or of the basalar lobe of the episternum, usually include two muscles on each side, but sometimes three are present, or again only one. The first of the potential three muscles of this group arises on the episternum (Fig. 103 B, *1E′*), the second (*2E′*) arises on the sternum or the precoxal bridge of the pleuron or occasionally on the trochantin (*Gryllus*), the third (*3E′*) arises on the outer rim of the coxa anterior to the pleural coxal articulation. The last muscle appears to be a pleural leg muscle that has secondarily become a wing muscle in the adult by reason of the intimate connection of the basalare with the humeral angle of the wing

(Figs. 128 C, 129, 130, *a*). The basalar muscles of the adult winged insect function as depressors of the costal margin of the wing during flight and as extensors of the flexed wing, for which reasons they may be termed the *pronator-extensor* muscles of the wing.

In Odonata there are two anterior wing muscles arising on the lower edge of the episternum and inserted by long tendons directly on the large humeral plate of the wing base (Fig. 123 B, *HP*). There are no epipleural sclerites in the dragonflies, and no pleurocoxal muscles are associated with the wing mechanism.

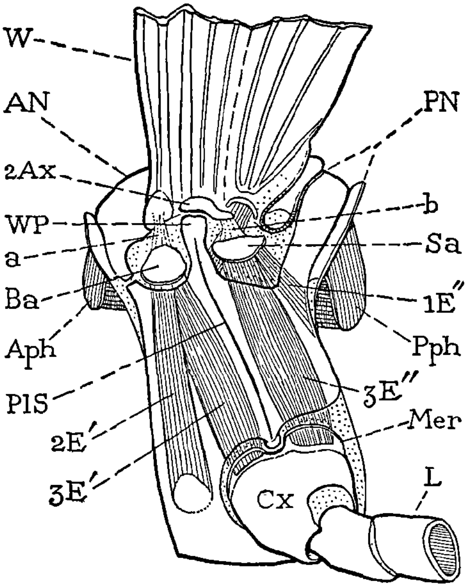

FIG. 129.—Diagram of the pleural mechanisms of the wing.

The Subalar Muscles.—In most insects there is but a single subalar muscle, usually of large size (Fig. 128 C, $3E''$), lying against the epimeral wall of the pleuron on each side of each wing-bearing segment, which is attached ventrally on the meron of the coxa. Associated with this muscle, however, there is sometimes, as in Gryllidae, Trichoptera, and Lepidoptera, a second muscle (Figs. 103 B, 129 $1E''$) arising on the epimeron and inserted on the posterior part of the subalare or on a distinct second subalar sclerite (*Gryllus*). This muscle is a counterpart of the first basalar muscle (Fig. 103, $1E'$) arising on the episternum. A subalar muscle corresponding to the sternal muscle of the basalare ($2E'$) is known to occur only in Ephemerida; it is here a large muscle of the mesothorax arising medially on the sternum behind the coxae and inserted dorsally on the subalar region of the pleuron. In the mesothorax of the higher Diptera the single large subalar muscle arises on the lower part of the epimeron dorsal to the meron, but this muscle is probably the usual subalar-coxal muscle transposed from the displaced meron to the pleural wall. The subalar muscles serve to extend and to depress the wing because of the close connection of the subalar sclerite with the second axillary sclerite of the wing base (Figs. 128 C, 129, *b*). They may be called, therefore, the *depressor-extensor* muscles of the wing.

In the Odonata two posterior pleural wing muscles take their origins on the ventral edge of the epimeron in each alate segment and are inserted directly on the axillary plate of the wing base (Fig. 123 B, *AxP*).

5. THE WING MOVEMENTS

The insect wing is movable on the body by the flexibility of its basal connections with the tergal plate and with the pleural wall of the segment, but it is definitely hinged to the tergum by the first and third axillary sclerites (Fig. 122, 1*Ax*, 3*Ax*) or by the first and fourth (Fig. 121 B, 1*Ax*, 4*Ax*) if a fourth axillary is present. The wing, therefore, is capable of responding only to the up-and-down movements of flight on its extreme base line. Most of the other movements of flight, as well as the movements of flexion and extension, depend on the flexible connections of the veins with the articular sclerites, and on the interaction of the articular sclerites themselves. The motions of insects' wings fall into two distinct categories; those of one include the *movements of flight,* those of the second embrace the *movements of flexion and extension.*

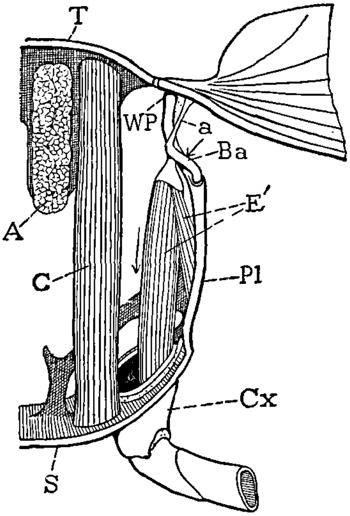

FIG. 130.—Diagrammatic cross section of a winged segment, anterior view, showing basalar mechanism of extension and anterior deflection of the wing.

The Movements of Flight.—The movements of the wing that make flight possible consist of an *upstroke,* a *downstroke,* a *forward movement,* a *rearward movement,* and a *partial rotation* of each wing on its long axis.

The Upstroke of the Wings.—The elevation of the wings in flight is produced, as we have seen, by the simple device of depressing the tergum of the segment bearing the wings (Fig. 131 A), the action being the result of a contraction of the vertical tergosternal muscles (*C*), assisted in some cases by the oblique dorsal muscles and in Diptera by the remotors of the coxae. The mechanism of the upstroke, therefore, is simply that of a lever of the first order, the fulcrum being the pleural wing process (*WP*) upon which the base of the wing rests. The tergosternal muscles are often large and powerful, suggesting that the upstroke of the wings is an important contributant to the force of flight.

The Downstroke of the Wings.—The depression of the wings is not the work of a single set of muscles. It results in part from the restoration of the dorsal curvature of the back by the contraction of the longitudinal dorsal muscles (Fig. 131 C, *A*), which are the segmental antagonists of the tergosternal muscles; but probably an important effector of the wing depression in most insects is the posterior pleural muscle or muscles (Figs. 128 C, 129 $3E''$) inserted on the subalar sclerite (*Sa*). The subalar sclerite being in immediate connection (*b*) with the second axillary of the wing base (*2Ax*), a pull upon the subalar muscle strongly depresses the wing.

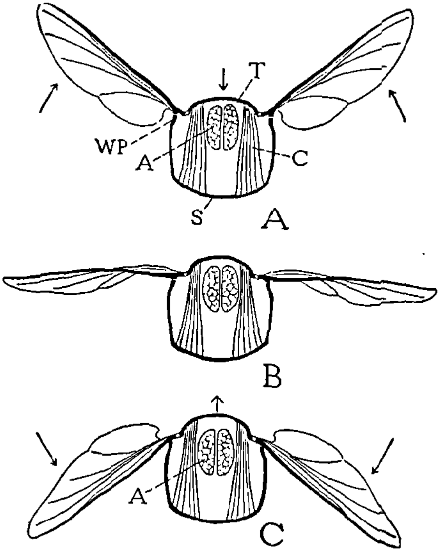

Fig. 131.—Diagrams of successive positions of the wings in flight and the corresponding movements of the tergum.

The Anteroposterior and Rotary Movements of the Wings.—The partial rotation of each wing on its long axis is a part of the anterior and posterior movements and is accompanied by changes in the position of the plane of the wing surface during the upstroke and the downstroke caused by pressure of the air. It was formerly supposed that the torsion of the wings, including the horizontal and rotary movements, is entirely the result of changing air pressure on the flexible posterior areas of the wings as the latter are vibrated in a vertical direction. There is no doubt that the wings do respond by a differential action in their planes to air pressure alone, but it is also true that each wing is partially revolved at the base by the muscles of its motor mechanism. The muscles that produce this movement are undoubtedly the muscles of the basalar and subalar sclerites. The first (Fig. 130, E'), pulling downward on the basalare (*Ba*), turn this sclerite inward on the upper edge of the episternum (*Pl*), and the connection (*a*) of the basalare with the humeral angle of the wing base deflects the anterior part of the wing as it turns it slightly forward. The mechanism of anterior deflection, including the basalar sclerite and its muscle or muscles, has been called the *pronator apparatus* of the wing. The movement of anterior deflection accompanies the depression of the wing (Fig. 131 C).

The reverse movement, or the combined rearward motion and posterior deflection of the wing accompanying the upstroke (Fig. 131 A), is probably caused largely by air pressure on the expanded, flexible posterior area of the wing surface; but it is likely that the tension of the subalar muscles (Figs. 128 C, 129, E''), exerted on the second axillary sclerite (*2Ax*) posterior to the pleural fulcrum, contributes to the posterior deflection of the wing during the upstroke.

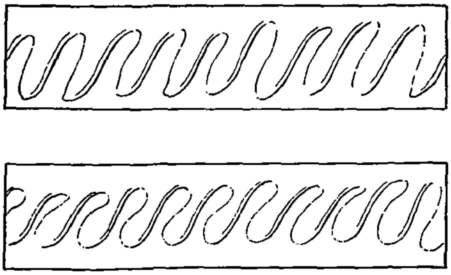

FIG. 132.—Curves described on a moving recorder by the wing tip of a stationary blow fly making the wing movements of flight. (*From Ritter*, 1911.)

The Wing Motion in Flight.—The motion of each wing in flight is the resultant of its several elemental movements. During the downstroke, the wing goes from above downward and forward; its anterior margin is deflected and its posterior area turns upward (Fig. 131 C). During the upstroke, the wing goes upward and relatively backward, and its posterior surface is deflected (A).

As a result of the compound motion of the vibrating insect wing, the tip of the wing, if the insect is held stationary, describes a curve having the form of a figure 8. This fact has long been known from direct observation on insects in which the figure described by the vibrating wings is made visible in strong light by bits of gold leaf attached to the wing tips (Marey, 1869, 1874). The wing motion, however, has been studied more accurately by mechanical devices in which a graphic record of the wing movements is obtained, as in the experiments of Marey (1869*a*) and of Ritter (1911), showing that the wings of an insect in motion describe a series of open loops (Fig. 132), the distance between the loops depending on the speed at which the insect flies. The wing movements have also been recorded by cinematographic methods (see Marey, 1901; von Lendenfeld, 1903; Bull 1904; Voss, 1913, 1914). The rotary movement of the wings is most accentuated in swift-flying insects, such as the dragonflies, bees, and flies, which have relatively narrow wings; in slower flying insects with broad wings, such as the grasshoppers and butterflies, the up-and-down movement is the principal one.

The Rate of the Wing Vibration.—The rapidity of the wing motion varies much in different species of insects. Landois (1867) deduced from the pitch of the sound made by insects in flight that the house fly makes 352 wing strokes a second, a bumble bee 220, and the honey bee, when at its best, 440, though when tired its hum indicates a speed of only 330 beats a second. Marey (1869*a*) obtained graphic records of the wing beats on a revolving cylinder, and he gives 330 wing strokes a second for the house fly, 240 for a bumble bee, 190 for the honey bee, 110 for a wasp, 28 for a libellulid, and 9 for the cabbage butterfly. Voss (1914), however, calculating the rate of the wing motion from series of moving picture photographs, obtained in most cases lower figures; the honey bee, by his test, making 180 to 203 wing strokes a second, the house fly from 180 to 197, the mosquito from 278 to 307, while various other insects have mostly a slower rate. In general it may be said the flies and bees have the highest speed of wing movement, other insects, by comparison, being slow of flight and correspondingly slow in wing motion. The lowest records of speed are obtained from the butterflies and moths, the cabbage butterfly making at best about 9 strokes a second, some of the noctuid moths about 40, though the sphinx moths, on the other hand, are swift fliers and move the wings at a high rate of speed. The student will find summarized statements of the recorded rates of the wing strokes in insects given by Voss (1914) and by Prochnow (1924, 1925). It must be recognized, however, that experimentally obtained records at best tell only what the insects did under the conditions of the experiment.

The Movements of Flexion and Extension.—The movements by which the wings are folded after flight, or extended preliminary to flight, are executed too rapidly to be observed closely in a living insect; but the action of a wing and the operation of the flexor mechanism can be well studied in freshly killed specimens. A grasshopper, a bee, a fly, or almost any insect sufficiently large will answer the purpose, but the grasshopper, or particularly the scorpionfly *Panorpa,* will be found to be a very suitable subject. If the wing of a fresh specimen is slowly folded posteriorly over the back and then brought forward into the position of flight, the accompanying movements of the vein bases on the articular sclerites and the movements of the sclerites on one another can be observed. From the action of the parts in a dead specimen the probable working of the flexor mechanism in the living insect can be deduced.

We have seen that the axillary sclerites are contained in an axillary region of the wing base, which is approximately triangular (Fig. 133 A, *Ax*), the apex of the triangle (*c*) being formed by the outer end of the third axillary sclerite (Fig. 122, 3*Ax*). The costal vein (*C*) alone has no connection with the axillary triangle, its base being associated with the humeral plate (*HP*). The subcosta (*Sc*) has a loose attachment (*e*) with the head of the first axillary, and the radius (*R*) is flexibly continuous by its base (*d*) with the second axillary. The vannal veins (1*V*-*nV*) are closely associated with the outer end of the third axillary. The median and cubital veins (*M*, *Cu*, *Pcu*) have no direct connection with the axillary sclerites, but their bases, when distinct, are either associated with the second median plate (*m′*) or more or less united in the corresponding area of the wing when this plate is absent. The base of the mediocubital field, therefore, abuts upon the basal fold of the wing, or plica basalis (*bf*), which forms the hinge line between the two median plates (*m*, *m′*) when these plates are present as distinct sclerotizations.

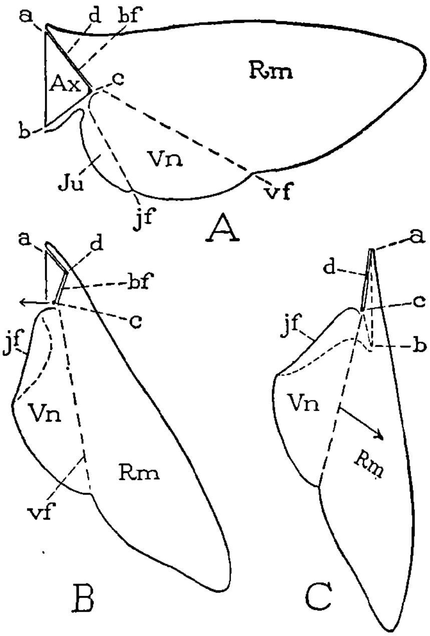

FIG. 133.—Diagrams of the typical folding of a wing during flexion. A, the wing extended and flat. B, the wing partly flexed by dorsal revolution of axillary area on its base (*a-b*). C, the fully flexed wing. (For lettering see Fig. 126.)

The essential skeletal element of the flexor mechanism is the third axillary. This sclerite is typically Y-shaped in form (Fig. 122, 3*Ax*) inasmuch as it consists of a distal stalk, the outer end of which (*c*) is associated with the bases of the vannal veins, and presents two proximal arms, the posterior one of which articulates with the tergum (*b*), while the anterior usually articulates with the posterior end of the second axillary sclerite (*f*). The flexor muscle of the wing (*D*) is inserted on the base of the third axillary in the crotch between the two basal arms of the latter.

Flexion of the Wings.—Flexion begins with a relaxation of the extensor muscles, which allows each wing to turn a little posteriorly. This automatic preliminary movement of the wing produces a strong convex fold at the base of the mediocubital field along the line of the plica basalis (Fig. 122, *bf*), which is between the two median plates (*m, m′*) if these plates are present. At the same time, the movement revolves the third axillary sclerite (3*Ax*) upward on its basal articulations (*b, f*). The insertion point of the flexor muscle (*D*) on the third axillary is thus turned dorsad and mesad of the axis of the basal hinge line of the sclerite, and the muscle, having now gained a purchase on the latter, is able by contraction to continue the revolution of the sclerite, turning it dorsally and mesally until it is completely inverted and reversed in position. The movement of the third axillary brings with it directly the vannal region of the wing (Fig. 133 A, *Vn*), the base of which is lifted and carried horizontally against the side of the back (B), while indirectly also it turns the remigial region (*Rm*) posteriorly on the articulations of the subcostal and radial veins with the first and second axillaries, producing a convex fold along the plica basalis (Fig. 122, *bf*), at the base of the mediocubital field.

Since the first median sclerite of the wing base (Fig. 122, *m*) is usually attached to the distal arm of the third axillary, the rotation of the flexor sclerite (3*Ax*) has also a direct effect on the mediocubital field and brings about the folding along the plica basalis (*bf*) between the two median plates. With insects in which the vannal area of the wing is reduced, the action of the third axillary is principally on the mediocubital field through the first median plate. By the revolution of the third axillary, the fold of the plica basalis is accentuated as the first median plate (*m*) is turned vertically on its hinge with the second axillary and is finally tilted mesally. The plica basalis now crosses the wing base obliquely from in front posteriorly and mesally (Fig. 133 B, *bf*).

The final pull of the flexor muscle apparently is expended on the general wing base, for, in many insects, when the wing is fully flexed, the first axillary is revolved into a vertical plane on its hinge with the tergum, and the second axillary is thereby lifted, turned into a nearly longitudinal position, and brought close against the side of the back. A movement of the first and second axillaries, however, does not always accompany the wing flexion, the essential changes in the basal region being the revolution of the third axillary and the folding along the line of the plica basalis at the bases of the median and cubital veins.

As the posterior edge of the flexing wing comes against the side of the body, the jugal lobe (Fig. 133 A, *Ju*) is deflected and turned beneath the vannus along the line of the plica jugalis (B). If a plica vannalis (*vf*) is present, the remigial region (*Rm*) may be turned downward (C) during the flexion of the wing though many insects, such as the flies and bees, keep both the remigium and the vannus in a horizontal plane. If the vannus is large it also may be deflected beneath the remigium, as in the hind wing of the cicada (Fig. 127 B) in which both the jugum and the vannus are turned downward against the side of the abdomen beneath the sloping remigium. In some Lepidoptera the flexed hind wing folds also along supplementary lines of plication in the rear part of the wing.

The flexing of the wing becomes a still more complicated process if the vannal region is particularly enlarged, as in Plecoptera, Orthoptera, and Dermaptera. In most of the Orthoptera the vannus of each hind

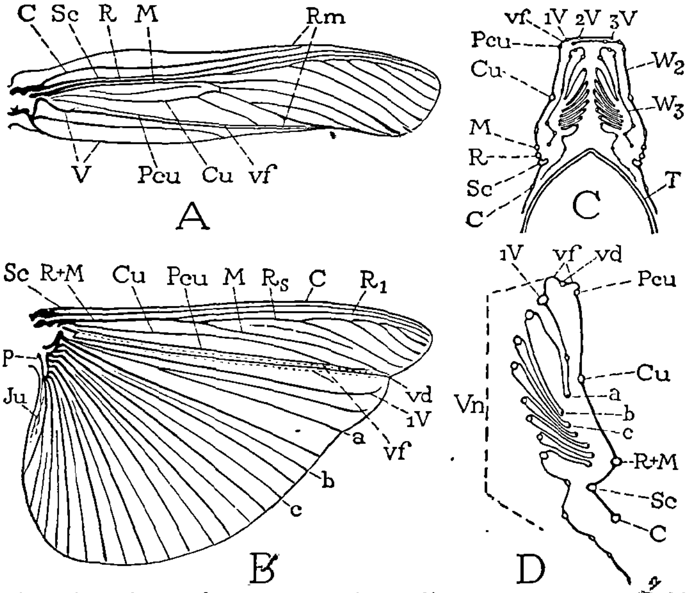

FIG. 134.—Wings of a grasshopper, *Dissosteira carolina*. A, forewing. B, hind wing. C, position and plication of wings folded over the body as shown in transverse section. D, plications of flexed and folded right hind wing in section, more enlarged.

wing is so greatly expanded (Fig. 134 B) that, when the wing is flexed, it must be plaited and folded together like a fan in order to give space for the rest of the wing. The folding and plaiting of the fully flexed wings of a grasshopper are shown at C and D of Fig. 134. The narrower forewings, or tegmina (C, W_2), overlap each other to form a rooflike covering with steeply sloping sides completely enclosing the more delicate hind wings (W_3) folded beneath them. The membrane of most of the vannal region of each hind wing is deeply inflected between the primary vannal veins (D), and the secondary veins (*a*, *b*, *c*) lie in the troughs of the folds. In most of the Orthoptera the vannal fold of the hind wing lies between the postcubitus and the first vannal vein; the fold usually contains a secondary vein, the vena dividens (Figs. 124 B, 134 B, D, *vd*).

The hind wings of Dermaptera and Coleoptera when flexed are shortened by folds across the veins in order that they may be covered by the protective forewings, or elytra. The fanlike hind wings of the Dermaptera consist principally of the expanded vannal regions. When flexed, the fans are plaited between the veins and then folded twice across the veins. In the Coleoptera the large jugum (Fig. 127 D, *Ju*) is folded in the usual manner beneath the vannus, and the transverse plications take place in the distal part of the wing. The transverse folding results automatically from the structure and flexibility of the veins.

Extension of the Wings.—Extension involves a reversal of the movements of flexion. The flexor muscles must first relax. It is probable, then, that a contraction of the basalar muscles (Figs. 128 C, 129, *E'*), pulling on the humeral angle of the wing base, extends the wing directly in most insects, though the action of these muscles in this capacity is often difficult to demonstrate in a dead specimen. On the other hand, with insects in which the second axillary sclerite is elevated on the outer edge of the upturned first axillary in the fully flexed wing, it is clear that the wing may be extended by the downward pull of the subalar muscles (*E''*) on the second axillary, for a pressure on this sclerite from above at once restores all the axillary elements to a horizontal plane and thereby spreads the wing. Some insects may be seen to extend the wings deliberately before taking flight, but with most species flight is practically simultaneous with the wing expansion.

6. INSECT FLIGHT

An object self-moved through the air must be able to create a difference in the density, or pressure, of the air on opposite sides of it; motion takes place toward the region of lowered pressure. Flight by any heavier than air animal or machine that does not depend upon rising columns of air for its support must have a mechanism capable not only of producing horizontal motion but also of creating a lifting force sufficient to overcome the pull of gravity. Most flying machines are so constructed that the force of the propeller gives only a forward drive, the lifting force in horizontal flight being the result of decreased pressure above the wings created secondarily by the motion of the plane. The wings of insects, on the other hand, furnish directly not only the driving power but the lifting force as well; that is to say, the movement of the wings creates a region of lowered pressure both before and above the body of the insect.

The possibilities of a motor mechanism for aerial locomotion can be judged by studying the air currents the motor will produce if it is itself held stationary. The nature of the air currents produced by the wing vibrations of insects, when the insects are secured by the body in such a manner that the wing movements will not be hindered, has been studied by Demoll (1918). By means of a simple apparatus consisting of a frame with horizontal bars on which were suspended fine owl feathers, Demoll, by observing the deflection of the feathers when an insect with its wings in rapid vibration was brought near them, was able to determine the direction of the air currents created by the wing movements.

Experimenting in this way with insects of different orders, Demoll found that the air currents drawn toward the stationary insect by the vibrating wings come from in front, from above, from the sides, and from below, while the currents given off are all thrown out to the rear (Fig. 135). The strength of the currents, however, is not the same from all directions, as is indicated by the relative thickness of the arrows in the diagrams. The air is drawn toward the insect most strongly from before and above the anterior part of the body; the outgoing currents are strongest in a horizontal or slightly downward direction. Most of the oncoming currents, therefore, are turned to the rear in the neighborhood of the insect's body and are condensed in a small region behind it.

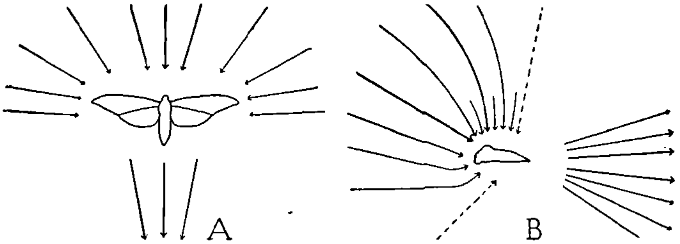

Fig. 135.—Diagram showing direction and relative strength of air currents produced by the vibrating wings of a stationary insect. (*From Demoll*, 1918.)

If the insect is free to move, the mechanical effect of the vibrating wings on the air will be the same as when the insect is held stationary; but, instead of moving the air, or instead of moving the air to the same extent as before, the greater part of the wing force will propel the insect through the air opposite the direction of the air currents created when the insect is secured. In terms of mechanics, the direction from which a current is drawn by a stationary object is the direction of lowered pressure, while the opposite is that of increased pressure. According to the observations of Demoll, therefore, when an insect launches itself into the air and sets up a vibration of its wings, there is at once created before it and above it a region of decreased pressure, and the convergence of all the currents behind produces here a region of greatly increased pressure. The lowered pressure above counteracts the weight of the insect; the increased pressure behind drives the insect forward into the low-pressure region in front.

The driving force of the insect's wing movements probably depends upon the angle at which the wing surfaces cut the air. Slow-flying insects with broad wings, such as the butterflies and grasshoppers, keep the wing surfaces almost horizontal and fly more in the manner of small birds with comparatively few strokes of the wings in any unit of time; some of the large swallowtail butterflies even soar for short distances with the wings held stationary. The more swiftly flying insects, however, having narrow wings, turn the wing surface more nearly vertical with each stroke, whether up or down, and, as Ritter (1911) says, "the insect flies fastest when the downstroke approaches a vertical direction," because the curve of the upstroke is drawn forward in the direction of flight.

The speed of insect flight may be very high considering the small size of insects, but it varies greatly with different species. Demoll (1918) has computed the flying rate of various species from the time in which individuals traversed a room, going direct from the dark side to the light. The hawk moths (Sphingidae) he found are the swiftest flyers, making a speed up to 15 meters a second. A tabanid fly (*Tabanus bovinus*), however, is a close second, going at a rate of 14 meters. A dragonfly (*Libellula depressa*), doing ordinarily 4 meters a second, is capable of 6 to 10 meters in the same length of time. A house fly travels from 2 to 2.3 meters a second; a bumble bee (*Bombus*) from 3 to 5; the honey bee, unladen, has a speed of 3.7 meters a second, but when weighted with pollen it makes only 2.5 meters in the same unit of time.

Insects appear to have no steering apparatus other than the wings themselves. Ordinary observation, as well as the experimental tests made by Stellwaag (1916) on the steering powers of insects, show that little or no compensatory movements of the body or legs are made during flight. Stellwaag showed that living insects impaled on pins turn themselves to the right or left by a differential action of the wings when the latter are rapidly vibrating with the movements of flight. The muscles concerned in the differential, or steering, action of the wings must be the lateral muscles of the alar segments, which are those of the basalar and subalar sclerites (Fig. 129, *E′*, *E″*), since these muscles alone have specific connections with the wings. The longitudinal and vertical muscles of the wing-bearing segments, though potent effectors of wing movements, can not unequally distribute their influence between the two sides of the segment.

Not only can most insects guide their course adroitly in forward flight, but many of them are able to fly directly backward or sidewise without altering the position of the body. The dragonflies are particularly adept in these modes of flight, but many of the smaller insects, such as the flies and bees, are quite equal to the dragonflies in their ability to dart suddenly to one side or rearward, while the head still points in the direction of the arrested forward flight. Reversed and lateral flying is probably controlled also by the lateral muscles of the flight mechanism, but it is remarkable that organs so evidently fashioned for forward flight, as are the wings of insects, can function efficiently for producing motion in other directions.

Still another feat that many insects perform on the wing with apparent ease is *hovering*. Presumably, in maintaining one position in the air, the wings are vibrated approximately in a horizontal plane, thus creating a region of decreased air pressure above the body of the insect, but none before it. The rate of the wing movements then must be just sufficient to create a balance with the force of gravity.

GLOSSARY OF TERMS APPLIED TO THE WINGS

Alula, or Calypter.—A pair of membranous lobes at the posterior angle of the wing base, particularly developed in some Diptera.

Anal Fold (*vf*).—See *plica vannalis.*

Anal Veins (*A*).—All the veins between the cubitus and the jugal region, including, according to the Comstock-Needham system, the veins here called postcubitus and vannals.

Arcuate Vein (1*J*).—See *vena arcuata.*

Axillary Cord (*AxC*).—The thickened, corrugated posterior edge of the articular membrane of the wing base, continuous with the posterior marginal fold of the alinotum.

Axillary Plate (*AxP*).—The posterior sclerite of the wing base in Odonata, supporting the subcostal, radial, medial, cubital, and vannal veins.

Axillary Region (*Ax*).—The region of the wing base containing the axillary sclerites.

Axillary Sclerites.—The sclerites of the axillary region in the wing-flexing insects, partly differentiated in Ephemerida, represented by the axillary plate in Odonata.

Basal Fold (*bf*).—See *plica basalis.*

Cells.—The areas of the wing membrane between the veins and cross-veins.

Costa (*C*).—The usual first vein of the wing, typically marginal, connected basally with the humeral plate.

Cross-veins.—Short veins between the lengthwise veins and their branches; numerous in net-veined wings, in others generally few and located in definite positions.

Cubitus (*Cu*).—The usual fifth vein of the wing.

First Axillary (1*Ax*).—The anterior hinge plate of the wing base, associated with the base of the subcostal vein. (*Vordere Tergalgelenkplatte.*)

First Median Plate (*m*).—A small sclerite of variable shape lying in the angle between the second axillary and the distal arm of the third axillary at the base of the mediocubital field; accessory to the third axillary in function, and usually attached to it.

Fourth Axillary (4*Ax*).—A posterior hinge plate of the wing base present in some insects, intervening between the third axillary and the posterior wing process of the tergum. (*Hintere Tergalgelenkplatte.*)

Frenulum.—The spine or group of bristles arising on the humeral angle of the hind wing of most moths, projecting beneath the forewing, and often held here in a *frenulum hook.*

Humeral Plate (*HP*).—The anterior preaxillary sclerite of the wing base supporting the costal vein; very large in Odonata.

Jugal Region (*Ju*).—A posterior basal lobe or area of the wing set off from the vannal region by the plica jugalis, containing the vena arcuata and vena cardinalis when these veins are present.

Media (*M*).—The usual fourth vein of the wing; its base, when not united with radius, associated with the median plates of the wing base along the fold of the plica basalis.

Median Plates.—See *first median plate* and *second median plate.*

Paranotal Lobes (*pnl*).—Lateral lobes of the pronotum in certain fossil insects, and theoretical lobes of the mesonotum and metanotum supposed to be the precursors of the wings.

Plica basalis (*bf*).—The basal fold of the wing, or line of flection between the base of the mediocubital field and the axillary region, forming a prominent convex fold in the flexed wing extending between the median plates from the articulation of radius with the second axillary to the articulation of the vannal veins with the third axillary.

Plica jugalis (*jf*).—The jugal fold of the wing of some insects, or radial line of folding setting off the jugal region from the vannal region. (*Axillary furrow, plica ano-jugalis.*)

Plica vannalis (*vf*).—The vannal fold of the wing, or radial line of folding usually between the cubital field and the first vannal vein, but somewhat variable in position (*Anal furrow, plica analis.*)

Postcubitus (*Pcu*).—The usual sixth vein of the wing, represented by an independent trachea in most nymphal wings, associated basally with the cubitus in the adult. (*First anal* of Comstock and Needham in most cases.)

Precosta (*Pc*).—A small first vein of the wing in certain fossil insects.

Pteralia.—The articular sclerites of the wing base, including the humeral plate and the axillary plate or axillary sclerites.

Radius (*R*).—The third vein of the wing; its base flexibly attached to the second axillary.

Remigial Region, or Remigium (*Rm*).—The wing area anterior to the vannal fold, containing the costal, subcostal, radial, medial, cubital, and postcubital veins. (*Preanal region, preclavus.*)

Second Axillary (*2Ax*).—The pivotal plate of the wing base resting on the pleural wing process, connected with the base of the radial vein.

Second Median Plate (*m'*).—A variable sclerotization at the base of the mediocubital field, folding convexly on the outer edge of the first median plate along the plica basalis; often absent, or represented by the united bases of the medial and cubital veins.

Subcosta (*Sc*).—The usual second vein of the wing, associated basally with the anterior end of the first axillary sclerite.

Tegula (*Tg*).—A large, scale-like lobe overlapping the base of the forewing in some insects; usually represented by a small setigerous pad or lobe (*tg*) at the anterior root of the wing base.

Third Axillary (*3Ax*).—The flexor sclerite of the wing base; the sclerite on which the flexor muscle is inserted.

Vannal Region, or Vannus (*Vn*).—The wing area containing the vannal veins, or veins directly associated with the third axillary; when large, usually separated from the remigium by the plica vannalis; often forming an expanded fanlike area of the wing.

Vannal Veins (*1V*, *2V*, etc.).—The veins associated at their bases with the third axillary sclerite, and occupying the vannal region of the wing. (The "anal" veins except the first, or postcubitus.)

Veins.—The tubular thickenings of the wings springing from the wing base and branching distally.

Vena arcuata (*1J*).—The first jugal vein.

Vena cardinalis (*2J*).—The second jugal vein, usually appearing as a basal branch of the vena arcuata.

Vena dividens (*vd*).—A secondary vein present in some Orthoptera lying in the fold between the remigium and vannus.

Wing Base.—The proximal part of the wing between the bases of the veins and the body, containing the humeral and axillary sclerites.

Wing Regions.—The principal areas of the wings differentiated in the wing-flexing insects, and often separated by distinct lines of folding, including the axillary, remigial, vannal, and jugal regions.

CHAPTER XI

THE ABDOMEN

The third division of the insect trunk, the abdomen, differs characteristically from the head and the thorax by its simplicity of structure and general lack of segmented appendages. The union with the thorax may be broad or constricted, but, except in the aculeate Hymenoptera, there is seldom any question as to the line of separation between the thoracic and abdominal regions of the body. The abdomen varies much in form in different insects. Its segments usually remain distinct, though some of the posterior segments are commonly reduced or absent. In certain aberrant species, however, the entire abdomen may be greatly reduced in size.

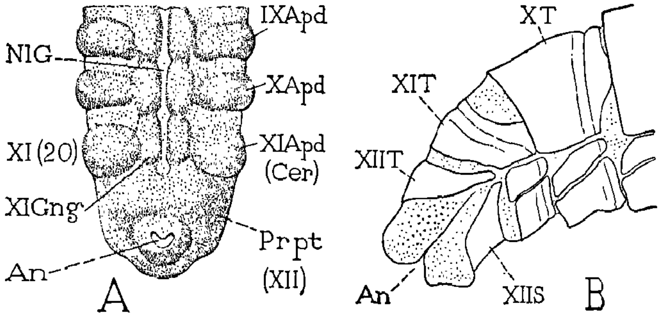

Fig. 136.—Examples of the presence of twelve segments in the hexapod abdomen. A, end of abdomen of embryo of *Gryllotalpa*. (*From Heymons*, 1895.) B, terminal segments of abdomen of an adult proturan, *Acerentulus confinis*. (*From Berlese*, 1910.)

The usual number of segments in the abdomen of adult insects is 10 or 11, and from embryological evidence it appears that the primitive number was no greater than 12. Twelve segments are well developed in adult Protura (Fig. 136 B), and the same number occurs in embryos of certain generalized insects (A), but in postembryonic stages possible remnants of a twelfth segment are rare. The twelfth segment of the Hexapoda appears to be the periproct, that is, the primitive endpiece of the body anterior to which the true somites are formed. In the Protura the tenth and eleventh segments are said to be differentiated during postembryonic development; but in all the true Insecta the definitive segmentation of the body is established before hatching.

A reduction in the number of abdominal segments is the rule in both immature and adult insects generally. Eleven segments are distinct in many of the more generalized insects, but in the higher orders not more than 10 segments are usually present, and sometimes only 9 are distinct. In the Collembola the number is reduced to six and the limits of some of these are obscured in certain forms. Generally reduction takes place at the posterior end of the body, but in many of the higher insects there is a tendency toward elimination of the first abdominal segment.

In general the abdomen serves as a container of the principal viscera of the insect and is the chief part of the body that produces movements of respiration. On the ventral surface of its posterior part are situated the apertures of the genital ducts, with which are associated the organs of copulation and oviposition; the alimentary canal opens at the end of its terminal segment. The median female genital aperture varies in position; in a few insects it is located just behind the seventh abdominal sternum, in others it is on or behind the eighth sternum, and in still others it is on or behind the venter of the ninth segment. The male aperture appears to be always on the posterior part of the ninth segment, except in Collembola, in which the gonopore in each sex is between the fifth and sixth segments.

For convenience of study the segments of the abdomen may be grouped into *pregenital,* or *visceral, segments, genital segments,* and *postgenital segments.* The genital segments are primarily the eighth and the ninth in the female, and the ninth in the male, since it is the appendages or other outgrowths of these segments that form the principal parts of the external genitalia. One or more segments preceding and following the primary genital segments, however, are frequently involved in the genital modifications of the abdomen, and it is often found more expedient to divide the abdomen accordingly into a *preabdomen* and a *postabdomen.* In the higher Diptera, for example, the first five segments form a distinct preabdomen, while the remaining segments are more or less modified as a part of the genital apparatus, including the long telescopic "ovipositor" of the female (Fig. 312 B, C).

Notwithstanding the simplicity of appearance in the structure of the abdomen and the retention of individuality of its segments, the abdomen is in many respects a highly modified and specialized region of the body. Though its sclerotized areas have usually the form of simple segmental plates, the sterna at least are evidently composite structures; and, while segmental appendages are characteristically absent, such rudiments of them as do persist raise questions in morphology that are difficult to settle.

1. GENERAL STRUCTURE OF THE ABDOMINAL SEGMENTS

The abdominal segments of adult insects for the most part are typical secondary segments, the functional conjunctivae being the membranous posterior parts of the primitive somites. The primary intersegmental folds usually form internally submarginal antecostae on the definitive tergal and sternal plates, to which the longitudinal muscles are attached, and they are marked externally by corresponding antecostal sutures. The terga and sterna regularly overlap posteriorly (Fig. 37). In soft-bodied larval insects the abdominal segmentation is more nearly of the primary type, though in holometabolous larvae there is a tendency for the longitudinal muscles to become separated into groups of fibers that do not all have intersegmental attachments.

The generalized form of an abdominal segment is approximately retained in larval insects that preserve rudiments of the abdominal appendages. In an ephemerid larva, for example (Fig. 150 A, B), each gill-bearing segment is distinctly divided into a dorsum and a venter by large lateroventral lobes (*Cxpd*) supporting the gills, which evidently represent the bases of abdominal appendages. Generally, however, the limb bases are more or less united with the venter, and in the adult insect the sternal plate of each segment is usually a continuous sclerotization of the ventral and pleural regions.

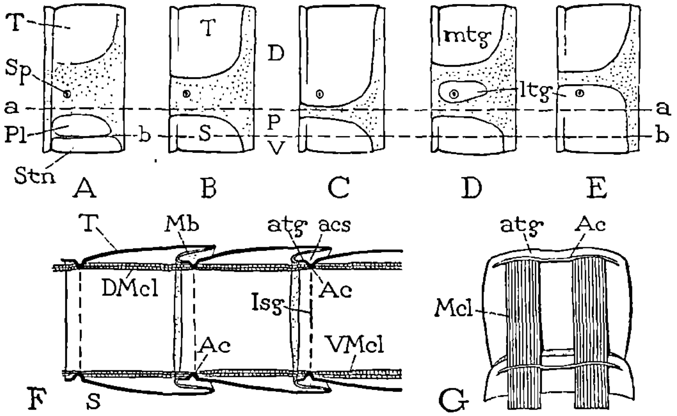

FIG. 137.—Sclerotization of the abdomen. A–E, examples of variation in the abdominal sclerotization above and below the dorso-pleural line (*a-a*). F, typical secondary segmentation of the abdomen. G, inner view of consecutive tergal plates, with muscle attachments.

The Abdominal Sclerotization.—The sclerotized parts of the abdominal integument usually take the form of dorsal and ventral segmental plates, separated by membranous areas on the sides (Fig. 139 A). In certain larval and adult insects, however, there are four distinct series of abdominal plates, namely, dorsal tergal sclerites, lateral pleural sclerites, and ventral sternal sclerites. Thus in some of the Thysanura (Fig. 138 A) each abdominal segment presents a broad tergal plate (*T*) above, a small median sternal plate (*Stn*) below, and, flanking the latter, a pair of large pleural plates (*Cxpd*). The pleural plates of the Thysanura, it is generally conceded, represent the bases of abdominal limbs. A generalized abdominal segment, therefore, we may assume, had a tergum occupying at least the major part of the dorsum (Fig. 137 A, *T*), a pleuron (*Pl*), or a group of pleurites, on each side situated in the area of the limb base (*P*), and a sternum (*Stn*) in the venter. In modern insects, however, the relation of the definitive abdominal sclerotization to the morphological regions of the body is highly variable, and the numerous anatomical inconsistencies that arise create many difficulties in nomenclature.

In the usual condition found in adult and nymphal insects the primitive pleura and sternum of each segment (Fig. 137 A, *Pl*, *Stn*) are united in a continuously sclerotized *definitive sternal plate* (B, *S*) opposed to the tergum. If the tergal sclerotization extends downward on the sides of the dorsum so far as to include the spiracular areas, the spiracles will be enclosed in the lateral parts of the tergum (C). In many cases, however, the dorsum contains lateral tergal sclerites, or *laterotergites* (D, *ltg*), quite distinct from the principal median tergite (*mtg*). The laterotergites often contain the spiracles, but the spiracles may be located in the membrane above or below the laterotergites. With some insects, again, the spiracles occur in lateral parts of the ventral plates (E), and in such cases it is evident that the definitive sterna are continuous sclerotizations of the primary sternal, pleural, and laterotergal areas. Finally, as in the larvae of Plecoptera and in the male genital segment of many adult insects, the tergal, pleural, and sternal plates may become confluent in a continuously sclerotized annulus.

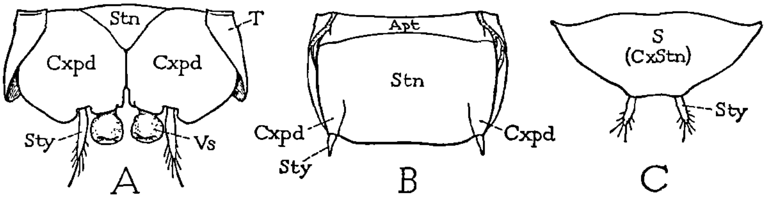

FIG. 138.—Pleurosternal plates of the abdomen. A, under surface of abdominal segment of *Nesomachilis*, showing true sternum (*Stn*) and plates of limb bases (*Cxpd*). B, abdominal sternum of *Heterojapyx*, with limb bases united with sternum, and a sternal apotome (*Apt*) separated from the latter. C, definitive sternal plate, or coxosternum, of ninth abdominal segment of male termite, *Termopsis*.

The Abdominal Terga.—The dorsal sclerotization of an abdominal segment usually has the form characteristic of a secondary segmental plate (Fig. 137 F). A typical abdominal tergum (*T*), therefore, presents anteriorly a marginal or submarginal ridge, the antecosta (F, G, *Ac*), on which the principal longitudinal muscles usually have their attachments. The antecostal suture (F, *acs*) is generally but faintly marked, and the precostal acrotergite (*atg*) varies from a scarcely perceptible marginal rim to a fairly wide flange extending anterior to the muscle attachments (G).

In some cases, however, the antecosta and acrotergite are lost and the muscles attach simply on the anterior edge of the tergum. Apodemal arms are sometimes developed from the anterior margins of the abdominal terga, which give effectiveness particularly to protractor muscles inserted upon them. Behind the tergum is the conjunctival membrane (F, *Mb*), and the abdominal terga regularly overlap posteriorly, except where successive segmental plates are united.

In many insects, particularly in larval forms, the dorsal sclerotization of the abdomen may be broken up into groups of segmental tergites. In simple cases we may distinguish in each segment a median tergite (Fig. 139 B, *mtg*) and one or more laterotergites (*ltg*); but often the sclerotization of the median area is again subdivided into smaller sclerites. The lower limit of the dorsum must be determined by discovering, where possible, the position of the dorso-pleural line (*a-a*), which is often marked by a lateral groove extending into the thorax above the subcoxal pleurites (*Scx*).

Abdominal Pleurites.—Strictly defined, an abdominal plate properly called a pleural sclerite is a sclerotization in the region of the abdomen corresponding to that of the subcoxal pleural plates of the thorax. An abdominal pleurite, therefore, is presumably a derivative of the primitive basis of an abdominal appendage. The stylus-bearing plates of the abdomen of some Thysanura (Fig. 138 A), the gill-bearing lobes of ephemerid larvae (Fig. 150), the basal plates of the ovipositor (Fig. 35 C), or the lateral sclerites in the abdomen of many holometabolous larvae (Fig. 139 B, *pl*), lying between the dorso-pleural and pleuro-ventral grooves, are examples of abdominal plates that may very evidently be referred to the true pleural region. But, again, it is undoubtedly true in many cases that small sclerites occurring in the pleural region of the abdomen are secondary sclerotizations, or lateral subdivisions of the definitive pleurosterna, and thus cannot be supposed to represent literally the bases of abdominal limbs. Such sclerites are sometimes designated *laterosternites*, though they are pleurites in the sense that they lie in the pleural region. The term "pleurite," however, should not be given to laterotergites or sclerites that lie clearly above the dorso-pleural line (Fig. 139 B, *ltg*), such as those often called "epipleurites" in descriptive entomology. In many species of lepidopterous larvae the serial identity of the thoracic and abdominal areas or their sclerites is shown by corresponding setae or groups of setae located on them (Fig. 153 A).

The Abdominal Sterna.—The definitive sternal plates of the abdomen of adult insects are in general similar to the tergal plates, each including a primary intersegmental area in its anterior part (Fig. 137 F). The antecostae (*Ac*) may be coincident with the anterior margins of the plates or preceded by distinct acrosternal flanges. The sterna of most adult insects, however, as we have seen, are evidently composite plates (Fig. 137 B, *S*), each formed by a union of the primary sternum (A, *Stn*) with the regions of the primitive limb bases (*Pl*). The frequent occurrence of styli on the ninth abdominal sternum of the male in more generalized pterygote insects (Fig. 138 C) attests the triple composition of the sternal plate, since in some of the apterygote insects the stylus-bearing plates are either only partially fused with the sternum (B, *Cxpd*) or entirely free from it (A). A definitive sternal plate that includes the areas of the limb bases is morphologically a *coxosternum*, or *pleurosternum*. The limb base elements of such a sternum (commonly called "coxites") are *coxosternites*, or *pleurosternites*.

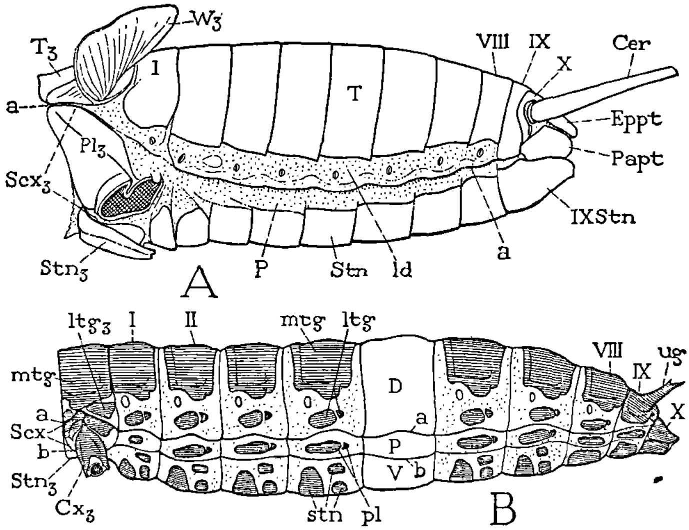

FIG. 139.—Examples of abdominal sclerotization with reference to the dorso-pleural line (*a-a*) and the pleuro-ventral line (*b-b*). A, metathorax and abdomen of adult male *Gryllus*. B, metathorax and abdomen of larva of *Calosoma*. *ltg*, laterotergites; *mtg*, mediotergite; *pl*, pleurites; *stn*, sternites.

The ventral sclerotization of the abdomen, as that of the dorsum, may be broken up into a group of sternites, as in various holometabolous larvae (Fig. 139 B, *stn*). In the Japygidae a short anterior subdivision of each abdominal sternum is separated by a membranous fold from the rest of the plate, forming a distinct sternal *apotome* (Fig. 138 B, *Apt*).

Characteristics of the Abdominal Segments.—Adult insects having well-developed organs of copulation and egg laying usually show a distinct differentiation in the structure of the segments of the visceral, genital, and postgenital abdominal regions. The modifications affect principally the genital segments, which are structurally adapted to their special functions, and the postgenital segments, which generally suffer reduction in proportion to the hyperdevelopment of the genital segments.

The Visceral Segments.—The segments of the visceral region of the abdomen are usually of simple structure and differ but little from one another. In adult pterygote insects they never bear appendicular organs. The first segment is either broadly joined to the thorax or separated from it by a constriction. In winged insects the antecosta of the first abdominal tergum bears the third pair of phragmatal lobes (Fig. 97 D, 3*Ph*), and the acrotergite is usually much enlarged, forming the postnotal plate of the metathorax (PN_3), which, together with the base of the phragma, is frequently detached from the rest of the first abdominal tergum and becomes virtually a part of the metathorax. The rest of the first segment is often reduced or fused with the second, and the sternal sclerotization is sometimes obliterated. In the clistogastrous Hymenoptera the entire first abdominal segment is so intimately united with the metathorax that it forms anatomically a part of the thorax, termed the *propodeum.* In these insects the constriction between the apparent thoracic and abdominal sections of the body occurs between the first and second segments of the abdomen. In some of the ants the second segment is small and a second constriction occurs between it and the third segment.

The Genital Segments.—In some of the simpler insects there is no modification of the segments associated with the genital apertures to distinguish them as genital segments; but usually the ninth segment in the male, and the eighth and ninth in the female show some structural adaptation to the genital functions.

Modifications of the eighth segment occur principally in female insects having a well-developed ovipositor, since the first valvulae of the ovipositor are developed from this segment. The valvulae are borne directly by small pleural plates, the *first valvifers* (Fig. 314 A, B, 1*Vlf*), which correspond to the stylus-bearing plates of the Thysanura, though styli themselves are absent from the eighth segment in all pterygote insects. The sternum of the eighth segment may be a simple plate resembling the sterna preceding it, but often it is enlarged and produced posteriorly beneath the base of the ovipositor. In such cases it forms the *female subgenital plate.* On the other hand, the eighth sternum is sometimes reduced, and in some insects it is practically obliterated. This condition is usually accompanied by an enlargement of the seventh sternum, which then becomes the subgenital plate.

The second genital segment usually has less of the typical segmental form than does the first. It is the segment of the second and third valvulae of the ovipositor in the female. These valvulae are borne by pleural sclerites of the ninth segment (Fig. 314 A, B, 2*Vlf*), the *second valvifers* (commonly called "coxites"), which correspond to the valvifers of the eighth segment. Rudimentary styli occur on the second valvifers in nymphal and adult forms of some of the lower Pterygota (E, *Sty*), but generally they are absent from the ninth segment of the female, except in Thysanura. The venter of the ninth segment in the female is usually inconspicuous, and, where an ovipositor is present, it is reduced to a narrow membranous space between the valvulae, but it may contain intervalvular sclerotic remnants of the ninth sternum.

In the male the ninth segment retains a generalized structure in the Thysanura, but in pterygote insects it is subject to many modifications and takes on a great variety of forms. The dorsal and ventral areas are usually sclerotized and form definite tergal and sternal arcs of the segment. In some insects the bases of the male gonopods are distinct plates having a normal pleural position on the sides of the ninth segment between the tergum and the sternum, and in such cases they usually bear movable lobes, serving generally as claspers, which apparently represent the styli of generalized insects. The gonopod bases, however, may be united with the sternum, and the resulting coxosternal plate then carries the styli, if the styli are preserved, which retain a typical styliform shape in some Orthoptera and Isoptera. On the other hand, the basal plates of the gonopods may be displaced posteriorly as free lobes bearing the claspers, or, again, they become fused with both the tergum and the sternum in a continuous segmental annulus.

The modifications of the genital segments and the structure of the organs of copulation and egg laying will be more fully described in Chap. XIX.

The Tenth Segment.—The tenth segment is present in the abdomen of nearly all insects, but its limits are often difficult to determine because of the frequent union between the tenth and eleventh segments. When only one postgenital segment is retained, as in the majority of holometabolous insects, both larval and adult, this segment is presumably the tenth. It sometimes bears a pair of appendicular processes, such as the socii of adult Trichoptera and Lepidoptera, the cercuslike appendages of adult Tenthredinidae, and the postpedes of larval Neuroptera, Trichoptera, Lepidoptera, and Tenthredinidae. The tenth segment appendages may be termed collectively the *pygopods,* since the tenth segment is the pygidial, or "rump," segment. The tenth segment sometimes bears lobes or processes that clearly have no relation to appendages.

When two postgenital segments are present, as in many of the more generalized insects, the tenth segment is frequently reduced and more or less united with the ninth or the eleventh segment. In none of the exopterygote insects does it have appendages in postembryonic stages, though rudiments of limbs may be present on it in the embryo (Fig. 136 A, *XApd*). The tenth segment, accompanied by the eleventh, occurs as a complete and independent annulus among the Thysanura (Fig. 140

A, *X*), Odonata (C), Ephemerida (D), Dermaptera (I), Homoptera (L), and in females of Panorpidae. In the Ephemerida its tergal plate (D, *XT*) is produced posteriorly in a small truncate lobe between the bases of the cerci and thus resembles the supra-anal plate of some other insects formed of the eleventh tergum, but in the ephemerid the dorsal part of the eleventh segment, or true epiproct, lies beneath the lobe of the tenth tergum and carries the median caudal filament (*cf*). Likewise, in the Plecoptera (E), Embiidae (F), and Blattidae (J), the tenth tergum (*XT*) is the terminal dorsal plate of the abdomen; the epiproct in these insects is reduced to a supra-anal pad or membrane beneath the end of the tenth tergum. In the Orthoptera the ventral part of the tenth segment is mostly membranous and usually does not appear in the adult as a definitely defined segmental region, though it sometimes contains a small sternal sclerotization. The tergum of the segment is generally a distinct plate, as in Acrididae (K), but sometimes it is more or less united with the

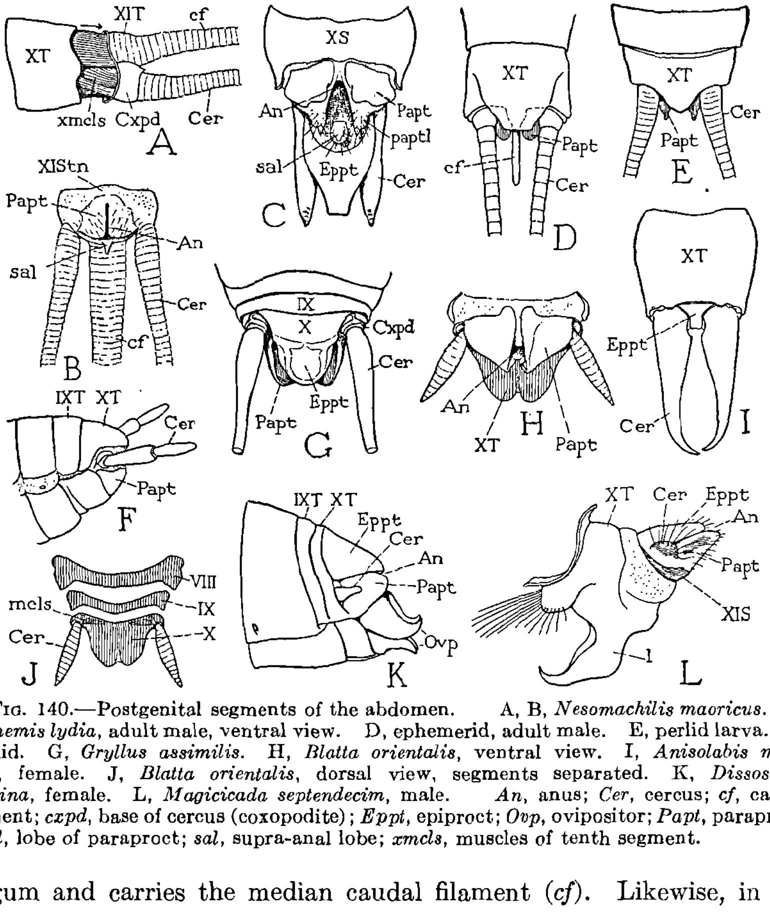

FIG. 140.—Postgenital segments of the abdomen. A, B, *Nesomachilis maoricus*. C, *Plathemis lydia*, adult male, ventral view. D, ephemerid, adult male. E, perlid larva. F, embiid. G, *Gryllus assimilis*. H, *Blatta orientalis*, ventral view. I, *Anisolabis maritima*, female. J, *Blatta orientalis*, dorsal view, segments separated. K, *Dissosteira carolina*, female. L, *Magicicada septendecim*, male. *An*, anus; *Cer*, cercus; *cf*, caudal filament; *cxpd*, base of cercus (coxopodite); *Eppt*, epiproct; *Ovp*, ovipositor; *Papt*, paraproct; *paptl*, lobe of paraproct; *sal*, supra-anal lobe; *xmcls*, muscles of tenth segment.

epiproct to form a composite supra-anal plate, though the division between the two parts may remain quite evident, as in *Gryllus* (G).

The Eleventh Segment.—The eleventh segment of the abdomen represents the last true somite of the body. It is present in the embryos of lower insects as a well-developed metamere bearing the rudiments of the terminal pair of appendages, which are the cerci of the imago (Fig. 136 A, *XI*). In adult Protura (B) it is a normal annulus with tergal and sternal plates; but in all the true Insecta the eleventh segment is more or less reduced, and its individuality is often lost by union with the tenth segment. In most of the Holometabola it is suppressed entirely, and the body ends with the tenth segment.

To generalize on the structure of the eleventh segment, we may say that, when present, it forms a conical endpiece of the body, bearing the cerci laterally and the anus at its apex; its dorsal surface is covered by a triangular or shield-shaped tergal plate, the *epiproct* (Fig. 140 K, *Eppt*), and its ventrolateral parts form two lobes, the *paraprocts* (*Papt*). The ventral margins of the paraprocts are usually connected basally by a median membranous area (C, H), and the posterior margin of the latter is sometimes produced in a small subanal lobe, or *hypoproct*. Occasionally the paraprocts bear terminal lobes, such as the small, soft, apical parts in some adult Odonata (C, *paptl*), the stylus-like processes of the paraprocts in tridactylid Orthoptera, or the broad, tracheated plates forming the lateral gills of zygopterous odonate larvae (Fig. 141 C, *paptl*).

The cerci are implanted typically in membranous areas between the bases of the epiproct and the paraprocts behind the tenth tergum (Fig. 140 K, *Cer*). Though they are generally closely associated with the tenth segment, embryologists mostly agree that they arise in the embryo as limb rudiments on the eleventh segment (Fig. 136 A, *XIApd*). Their connection with the tenth segment becomes more pronounced with the reduction of the eleventh segment or its union with the tenth. In Campodeidae and Japygidae the abdominal segments beyond the tenth are obliterated, but the cerci are retained and are necessarily borne directly on the end of the tenth segment. In Machilidae each cercus is supported on a large pleural lobe of the eleventh segment (Fig. 140 A, *Cxpd*), and in many of the more generalized Pterygota the appendage has a small, usually imperfect basal segment (G, *Cxpd*). The shaft of the cercus is sometimes distinctly divided into segmentlike sections (D, F), but it never contains muscles. Most of the muscles that move the cerci, which are inserted on or near the cercal bases, take their origins on the tenth tergum and are probably muscles of the tenth segment (A, *xmcls*). In some insects one muscle of each cercus arises on the epiproct, but the cerci never have muscles from the paraprocts. The latter, therefore, do not have the relation of limb bases to the cerci.

The cerci of insects apparently correspond to the *uropods* of malacostracan Crustacea. They are usually simple processes, conical or filamentous in form, and of a sensory function, but sometimes they are modified to serve as clasping organs.

The generalized structure of the eleventh segment is perhaps most fully retained in the Machilidae. In *Nesomachilis*, for example (Fig. 140 A), the eleventh segment, though normally concealed within the tenth, has the form of a complete ring with distinct tergal and sternal regions separated on the sides by the large lateral lobes (*Cxpd*) bearing the cerci (*Cer*). The tergal region (*XIT*) is produced into the median caudal filament (*cf*). The ventral region presents anteriorly a narrow sternal bridge (B, *XIStn*) between the lateral cercus-bearing lobes, and posteriorly a pair of broad paraprocts (*Papt*) at the sides of the anus.

Among the lower Pterygota, the parts of the eleventh segment are *entirely distinct from the tenth segment in Odonata. In an adult* dragonfly (Fig. 140 C) the epiproct (*Eppt*) is a large free median lobe tapering to a truncate point. The cerci arise laterad of the epiproct and are broadly hinged to the posterior margin of the tenth tergum. The ·paraprocts (*Papt*) are wide triangular ventral lobes at the sides of the anus; each contains a large basal plate and terminates in a small fleshy process (*paptl*). In the larvae of anisopterous Odonata the epiproct and paraprocts form the three tapering valvular processes that close the large anal opening (Fig. 141 A, B). In zygopterous larvae each lobe of the eleventh segment bears a gill plate (C), the median gill (*cf*) being a process of the epiproct, and the lateral gills (*paptl*) processes of the paraprocts. The small cerci (*Cer*) arise in the usual position. In the Ephemerida (Fig. 140 D) the reduced epiproct bearing the caudal filament (*cf*) is concealed beneath the overhanging median lobe of the tenth tergum; and in the Plecoptera (E) and Embiidae (F) the epiproct is reduced to a supra-anal pad adnate to the ventral surface of the tenth tergum. In Dermaptera (I), however, the epiproct (*Eppt*) is a distinct plate between the bases of the cerci, movably hinged to the posterior margin of the tenth tergum. In most orthopteroid insects the eleventh segment is distinct, though often closely united with the tenth (K), and the epiproct may be fused with the tenth tergum (G); but in Blattidae (H, J) the epiproct is practically obliterated except for a membranous fold beneath the tenth tergum on which the muscles of the paraprocts (H, *Papt*) are attached.

The Twelfth Segment.—The primitive terminal segment of the arthropod trunk is the periproct, or endpiece of the body containing the anus, anterior to which the true appendage-bearing somites are formed. In the malacostracan Crustacea the periproct forms the *telson,* typically a broad terminal lobe of the abdomen having the anus situated in the basal part of its ventral surface. The periproct appears to be represented in the embryos of some insects by a terminal twelfth segment of the abdomen (Fig. 136 A, *Prpt*), which never has appendages; but among adult hexapods a twelfth abdominal segment with tergal and sternal plates occurs only in the Protura (B). In most insects no trace of a twelfth segment is to be found, and the periproct must be supposed to be represented, if at all, only by the circumanal membrane at the end of the eleventh segment.

The best example of the possible retention of a twelfth abdominal segment in postembryonic stages of insects is furnished by the larvae of anisopterous Odonata, in which the anus is contained in a small circular fold (Fig. 141 A, *Prpt*) ordinarily concealed between the bases of the epiproct (*Eppt*) and the paraprocts (*Papt*). In the walls of this fold there is a small dorsal sclerite, or *lamina supra-analis* (*sal*), and two lateroventral sclerites, or *laminae infra-anales* (*lal*). These sclerites are lost in adult Odonata, but a small supra-anal lobe, apparently a remnant of the lamina supra-analis, projects from beneath the epiproct (Fig. 140 C, *sal*). A similar lobe occurs in larva of Ephemerida and in some adult Thysanura (B, *sal*). The supra-anal lobe of these insects, therefore, might be regarded as a dorsal remnant of the telson.

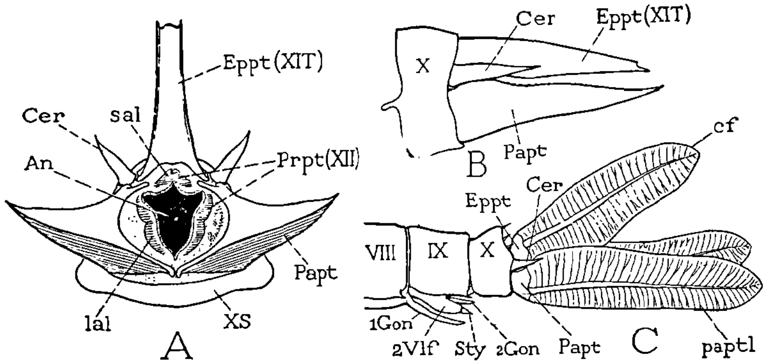

FIG. 141.—Terminal segments of Odonata. A, aeschnid larva, end view of abdomen showing possible rudiment of twelfth segment, or periproct (*Prpt*). B, same, lateral view, with parts in usual position. C, *Archilestes grandis* larva.

2. THE ABDOMINAL MUSCULATURE

The abdominal musculature of adult and larval insects in general conforms to a rather simple fundamental pattern, which is repeated with only minor variations in each of the pregenital segments; in the genital and postgenital segments the basic plan of musculature is more or less obscured by special modifications. In some of the Apterygota, however, and in larval forms of holometabolous insects the body musculature may be highly complex. Some writers have regarded the complex types of muscle arrangement as representing a primitive condition; but since these types have no conformity among one another, and since the musculature of holometabolous larvae shows in all orders a progressive evolution away from the simple adult type, it would seem that the latter must be more nearly representative of the muscle pattern of primitive insects. The abdominal musculature of adult insects is more elaborate than the body musculature of the thorax, but on the whole it is simpler than the thoracic musculature because of the absence of leg muscles.

Since the muscles are derived from the walls of the embryonic coelomic sacs, or at least from the metameric divisions of the mesoderm, we may assume that the primitive somatic fibers of arthropods were all intrasegmental in arrangement (Fig. 35 A), as they are in the Annelida; but with the acquisition of secondary segmentation, consequent upon the development of sclerotic plates in the body wall, the longitudinal fibers become functionally intersegmental (B). The body of the animal can thus be shortened by a telescoping of its segments (C) brought about by contraction of the longitudinal muscles, and it can be compressed by contraction of the lateral dorsoventral muscles. The opposite movements may result either from the elasticity of the body wall or from pressure generated by contraction in one part of the body transmitted to another through the medium of the body liquid and the visceral organs; but in the abdomen of the higher arthropods protractor and dilator apparatus are developed in which certain muscles become antagonistic to the retractors and compressors.

General Plan of the Abdominal Musculature.—The muscles of the insect abdomen may in general be classed in three groups, namely, *dorsal muscles*, *ventral muscles*, and *lateral muscles*. The dorsal muscles include *longitudinal dorsals* and *transverse dorsals;* the ventral muscles are similarly divided into *longitudinal ventrals* and *transverse ventrals;* the lateral muscles comprise *lateral muscles of the body wall* and *spiracular muscles*. Each of these sets of muscles is again often subdivided into two or more minor groups. The naming of the muscles according to this classification would, in a final analysis, lead to the compounding of terms of unwieldy length. Hence the writer (1931) has proposed a scheme for simplifying the nomenclature by limiting the terms "dorsal" and "ventral" to the longitudinal dorsal and ventral muscles only, and dividing the transverse muscles into dorsal and ventral sets. According to this plan the major groups of muscles are as follows:

I. **Dorsal muscles** (Fig. 142 A, *d*), the fibers of which are typically longitudinal and attached on the intersegmental folds or on the antecostae of successive terga.

II. **Ventral muscles** (*v*), resembling the dorsal muscles in that their fibers are typically longitudinal and attached on the intersegmental folds or on the antecostae of successive sterna.

III. Lateral muscles (*l*), typically dorsoventral, and both intrasegmental (*le*) and intersegmental (*li*) in position.

IV. Transverse muscles (*C*, *t*), lying internal to the longitudinals, including *dorsal transverse muscles* (*td*) and *ventral transverse muscles* (*tv*).

V. Spiracular muscles, generally not more than two connected with each spiracle, one an *occlusor*, the other a *dilator*.

Each of the first three of these primary groups of muscles may undergo an endless diversification resulting from a multiplication of fibers in the group, a separation of the fibers into subgroups, or a rearrangement of the fibers brought about by changes in the points of attachment.

With respect to the dorsal and ventral muscles the most general departure from the simple plan, in which the fibers all lie in a single plane against the body wall, consists of a differentiation of the fibers in each group into *external* muscles and *internal* muscles. Thus it is found in nearly all insects that the dorsal and ventral muscles comprise each two layers, there being, namely, *internal dorsals* (*di*) and *external dorsals* (*de*), and *internal ventrals* (*vi*) and *external ventrals* (*ve*). A second form of diversification affecting the same muscles consists of a more or less distinct grouping of the fibers into *median* and *lateral* sets. In most insects, therefore, we may distinguish four sets of dorsal fibers, and four sets of ventral fibers. The several resulting muscles or sets of fiber bundles then may be designated as follows: *median* and *lateral internal dorsals* (Fig. 143 A, *dim*, *dil*), *median* and *lateral external dorsals* (*dem*, *del*), *median* and *lateral internal ventrals* (*vim*, *vil*), and *median* and *lateral external ventrals* (*vem*, *vel*).

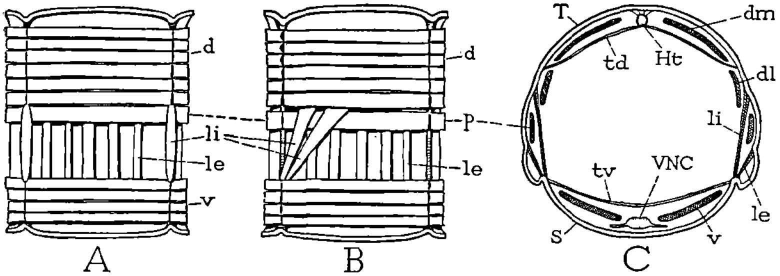

FIG. 142.—Diagrams of abdominal musculature. A, B, simple types of musculature, right half of a segment, inner view. C, cross section of a segment. (For lettering see page 260.)

In some insects there is a longitudinal muscle or group of longitudinal fibers situated on the lateral part of the dorsum above the line of the spiracles, external to the upper ends of the internal lateral muscles. This muscle is sometimes called a "pleural" muscle, but since it evidently belongs to the dorsum it is more properly termed a *paradorsal muscle* (Figs. 142 B, C, 143 B, *p*).

The lateral muscles are more subject to irregularities of position than are the dorsal and ventral muscles, but they likewise are often divided into *internal laterals* (Fig. 142, *li*) and *external laterals* (*le*).

To express more concisely the major groups of abdominal muscles and their principal subdivisions, we may tabulate the several sets of fiber bundles enumerated above as follows:

I. **Musculi dorsales** (*d*).
  1. M. dorsales interni (*di*).
    a. M. dorsales interni mediales (*dim*).
    b. M. dorsales interni laterales (*dil*).
  2. M. dorsales externi (*de*).
    a. M. dorsales externi mediales (*dem*).
    b. M. dorsales externi laterales (*del*).
  3. M. paratergales (*p*).
II. **Musculi ventrales** (*v*).
  1. M. ventrales interni (*vi*).
    a. M. ventrales interni mediales (*vim*).
    b. M. ventrales interni laterales (*vil*).
  2. M. ventrales externi (*ve*).
    a. M. ventrales externi mediales (*vem*).
    b. M. ventrales externi laterales (*vel*).
III. **Musculi laterales** (*l*).
  1. M. laterales interni (*li*).
  2. M. laterales externi (*le*).
IV. **Musculi transversales** (*t*).
  1. M. transversi dorsales (*td*).
  2. M. transversi ventrales (*tv*).
V. **Musculi spiraculorum**
  1. M. occlusores spiraculorum (*osp*).
  2. M. dilatores spiraculorum (*dlsp*).

It is often difficult to define individual muscles of the body wall of insects because the fiber bundles are not surrounded by a common sheath; but generally the muscles are distinct because of the grouping of the fibers and may be given individual names. For reference purposes, however, it will be found more practical to indicate individual muscles on drawings with Arabic numerals, since it is often difficult or impossible to identify corresponding muscles throughout the series of segments. Though in the visceral region of the abdomen the muscles may be segmentally repeated with fair regularity, the arrangement is usually so distorted in the genital and postgenital regions that the muscle homologies become very doubtful.

We may now give a brief summary of the principal modifications in the arrangement of the muscles of the several principal muscle groups in the visceral segments of the abdomen. The musculature of the genital and postgenital segments requires a special study and will not be considered here.

The Dorsal Abdominal Muscles.—The muscles of the dorsum are composed primarily of longitudinal fibers of segmental length attached on the intersegmental folds (Fig. 142 A, *d*). In many larvae the principal dorsal fibers retain this primitive condition; but in insects having fully developed tergal plates the dorsal muscles become functionally intersegmental because the folds on which they are attached become the antecostae of the definitive terga (Fig. 143 C). Since the segmental plates are pulled forward by the contraction of the longitudinal muscles, the anterior end of a longitudinal abdominal muscle may be termed its *origin*, and the posterior end its *insertion*.

The internal dorsals commonly retain their longitudinal position and their segmental length (Fig. 143 C, D, *di*); but they undergo many departures from this generalized condition through becoming oblique or by a shift in their origins to the postcostal regions of the terga. The external dorsals, on the other hand, are seldom of segmental length; typically they are short muscles lying in the posterior parts of the segments (C, *de*), and often they become strongly oblique, sometimes actually transverse, giving a movement of torsion to the segments they connect. Finally, their origins may become transposed to the posterior margins of the terga, in which case the external dorsals are reversed in position (D, *de*); functionally they then become antagonistic to the internal dorsals (*di*) and act as abdominal *protractors*, since their contraction lengthens the abdomen by decreasing the overlap of the segments. In some cases the anterior ends of the protractors are attached on apodemal arms of the anterior margins of the terga, thus increasing the effectiveness of the muscles. The dorsal muscles are often variously reduced, and some of the principal groups of fibers may be entirely suppressed.

The paradorsal muscle (Figs. 142 B, C, 143 B, *p*) is not commonly present in adult insects, or, at least, its fibers are not generally separated from those of the other lateral dorsal muscles. It is well shown in the Acrididae as a distinct muscle (Fig. 144 A, *169*), and it is a characteristic feature of the musculature of some larval insects.

The Ventral Abdominal Muscles.—The ventral muscles of the abdomen undergo an evolution parallel in most respects to that of the dorsal muscles. The fibers of the internal layer are typically intersegmental wherever complete sternal plates are present and serve as *retractors* of the ventral arcs of the segments. The external ventrals are usually short and take their origins on the posterior parts of the sterna. Frequently they become sternal *protractors* by a reversal in position, and commonly their anterior ends are then carried forward on anterior apodemal arms of the sterna (Fig. 144 A, *174*). The ventral muscles, as the dorsal muscles, however, are sometimes reduced, and one or more of the principal groups may be lost.

The Lateral Abdominal Muscles.—The lateral muscles of the abdomen do not conform so closely to a general plan of arrangement as do the dorsal and ventral muscles. Most of them are intrasegmental in position, and tergosternal in their attachments (Fig. 142 A, *le*); but some of them may lie on the intersegmental folds (*li*), and frequently some of them are intersegmental in the sense that they cross obliquely from one segment to the next. Furthermore, the lateral muscles are not always strictly tergosternal in their attachments, for some of them may be attached at one end on small sclerites located in the pleural areas of the lateral integument between the tergal and sternal plates. Such muscles, therefore, may be termed tergopleural, or pleurosternal. A division of the lateral muscles into *internal laterals* and *external laterals* (Fig. 142 C, *li, le*) is not always apparent, often because of the absence of an internal group, but it is of common occurrence.

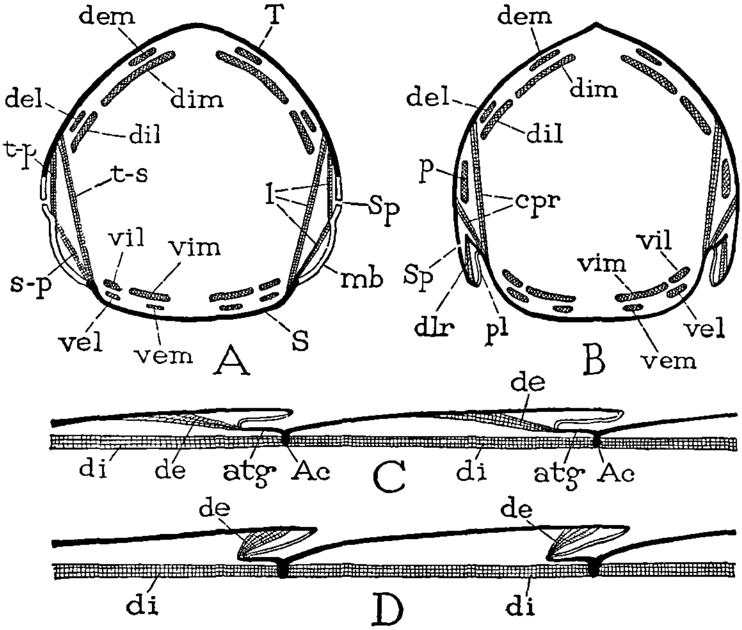

FIG. 143.—Diagrams of abdominal musculature. A, cross section, showing principal muscles differentiated into distinct groups of fibers, with lateral muscles comprising tergosternal (*t-s*), tergopleural (*t-p*), and sternopleural (*s-p*) muscles. B, illustrating lateral muscles differentiated into compressors (*cpr*) and dilators (*dlr*). C, longitudinal section through consecutive terga, showing usual position of external dorsals (*de*) and internal dorsals (*di*), which are both retractors. D, same, with outer dorsals (*de*) reversed in position to function as protractors. (For other lettering see page 260.)

In some insects there is a well-defined internal set of lateral muscles lying mesad of the lateral longitudinal tracheal trunk, having the upper attachments on the dorsum above the paradorsal muscle (Fig. 142 C, *li*), when the latter muscle is present. The internal laterals may be distributed along the length of each segment, but in some cases they are limited to the extreme anterior parts of the segments, and in certain holometabolous larvae they lie on the intersegmental folds (A, *li*). The external laterals (C, *le*) arise dorsally below the paradorsal muscle (*p*), when this muscle is present. Frequently some of them cross each other obliquely, and in their attachments they are often diversified into tergosternal, tergopleural, and pleurosternal groups.

Functionally, most of the lateral muscles are *compressors* of the abdomen (Fig. 143 B, *cpr*), since their contraction approximates the tergal and sternal plates. With some insects, however, in which the lateral parts of the abdominal terga overlap the edges of the sterna, certain of the lateral muscles are so situated as to be antagonistic to the others. These muscles, therefore, become *dilators* of the abdomen (B, *dlr*). Their dilator action results from the fact that their tergal attachments are on the lower edges of the terga ventral to their sternal attachments. By contraction, therefore, they separate the tergal and sternal plates. The effectiveness of these muscles is usually increased by the elevation of their sternal ends on lateral apodemal arms of the sternal margins (Fig. 144 A, *177*). The contraction of the lateral abdominal muscles most frequently produces a movement of the sternal plates; but if the sternal arcs are larger and more rigid than the tergal plates, it is the latter that respond to the action of the lateral muscles. When a dilator mechanism is absent, the expansion of the abdomen following contraction results from the general elasticity of the abdominal integument. Soft-skinned larval insects usually contract only a small part of the body at one time, and this part is then expanded by pressure resulting from contraction in some other part.

The Transverse Abdominal Muscles.—The transverse muscles of the abdomen are best known as the muscles of the dorsal and ventral diaphragms (Fig. 142 C, *td*, *tv*). The fibers of the dorsal diaphragm arise typically in groups on the anterior edges of the lateral parts of the abdominal terga and spread mesally to their attachments along the ventral wall of the heart. In a few insects they are evenly distributed along the entire length of each tergum or collected into anterior and posterior groups. The ventral transverse muscles in some insects, as in Acrididae and Hymenoptera, form a continuous sheet of weblike tissue throughout most of the length of the visceral region of the abdomen, which constitutes a ventral diaphragm stretched between the edges of the sterna over the ventral nerve cord; in others, however, as in Tettigoniidae and most Gryllidae, the ventral fibers are aggregated to form widely separated compact muscles crossing the anterior parts of the abdominal sterna. Not only are the ventral transverse muscles more variable in their arrangement than are their dorsal counterparts, but they are of less constant occurrence and are generally absent in holometabolous larvae.

The Spiracular Muscles of the Abdomen.—The regulator mechanism at the entrance to the abdominal tracheae usually includes one or two muscles associated with each spiracle. The muscle most generally present is an occlusor. This is a short muscle usually attached at both ends on apodemal processes of the spiracular atrium, where its contraction compresses the inner end of the atrium and so closes the entrance to the trachea; in the Acrididae the occlusor muscle arises dorsally on the tergum close behind the spiracle. An antagonistic muscle, or dilator of the spiracle, is absent in many insects; when present it arises ventral to the spiracle, on either the tergum or the sternum, and is inserted on one of the processes of the atrium in line with the occlusor. The regulator mechanism of the spiracles will be more fully described in Chap. XV on the respiratory system.

The Abdominal Musculature of a Grasshopper.—The abdominal musculature will be best understood by studying the muscles of some fairly generalized insect, and any of the larger grasshoppers will serve as a good subject for laboratory work.

The abdominal muscles are well developed in the Acrididae, since the grasshoppers make dorsoventral expansions and contractions of the abdomen during breathing and execute strong movements in this part of the body during the acts of copulation and oviposition. The great extension of the female abdomen during oviposition, however, is apparently caused by the action of the muscles connected with the ovipositor; as the latter organ automatically digs into the earth, it stretches the visceral region of the abdomen far beyond the capacity of the protractor muscles. The muscular activities of the abdomen are all accomplished by the abdominal muscles, there being no muscles in the grasshopper extending from the thorax into the abdomen. The abdominal musculature shows little variation in the several segments of the visceral region, except in the first and second segments (Fig. 144 B). The muscle pattern in the third segment (A) may be taken as typical of the general segmental plan of the abdominal musculature; but in the genital segments the musculature is highly modified, and in the terminal segments it is reduced. For a general review of the abdominal musculature in orthopteroid insects the student is referred to the work of Ford (1923). The following specific descriptions are based on *Dissosteira carolina,* the abdominal muscles of which the writer has fully described elsewhere (1935).

The Dorsal Muscles.—The dorsal muscles of the grasshopper occupy the lateral areas of the abdominal terga, but they do not entirely cover the tergal surfaces. The internal dorsals form several broad bands of fibers in each side of the body (Fig. 144 A, *167, 168, 169*) and are in general longitudinal though they have a tendency to obliquity, which is accentuated in the more posterior segments (B). The most lateral group of dorsal fibers on each side (A, *169*) is a paradorsal muscle, since it is separated from the others by the upper ends of the internal lateral muscles (*175*, *176*). The others, again, are divided by the attachments of the muscles of the dorsal diaphragm on the body wall (A, *td*) into a median intrapericardial group of three or four flat bands of fibers (*167a*, *b*, *c*, *d*,), and into a broad, lateral extrapericardial muscle (*168*). The intrapericardial fibers are attached anteriorly on a secondary tergal ridge (*tr*); posteriorly all the dorsal muscles are inserted on the anterior margin of the following tergum (*IVT*). The internal dorsal muscles are thus retractors of the terga. The wide separation of the ends of corresponding groups of the longitudinal fibers in consecutive segments of the grasshopper presents an atypical condition.

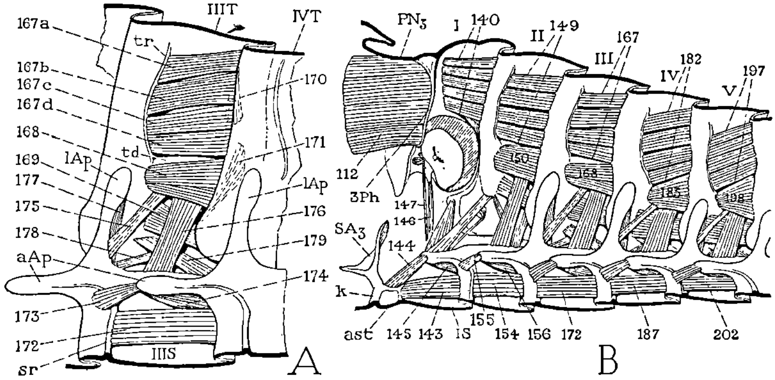

FIG. 144.—Abdominal musculature of a grasshopper, *Dissosteira carolina*. A, muscles of right half of third segment. B, muscles of right half of segments *I* to *V*.

The external dorsals comprise two muscles in each segment, one median (Fig. 144 A, *170*), the other lateral (*171*), which assume oblique or transverse positions. In the third segment each of the external dorsals arises on the posterior part of the tergum, the median one (*170*) extending dorsally to its insertion on the anterior edge of the following tergum, the lateral one ventrally (*171*). In the more posterior segments the corresponding muscles are longer and cross each other on the side of the tergum. The external dorsals of the grasshopper are thus torsion muscles serving to give a partial transverse rotation of the abdominal segments on each other.

The Ventral Muscles.—The ventral muscles form a uniform series in the first seven segments of the female and in the first eight segments of the male. The internal ventrals are distinctly divided in each segment into a broad median band of longitudinal fibers (Fig. 144 A, *172*) reaching from a submarginal sternal ridge (*sr*) to the anterior edge of the following sternum, and into a smaller bundle of lateral fibers (*173*) extending from the anterior lateral area of the sternum to the anterior end of the anterior apophysis (*aAp*) of the following sternum. Both sets of internal ventrals are sternal retractors.

The external ventral muscles consist of a single bundle of fibers on each side of each segment (Fig. 144 A, *174*). Each muscle arises on the posterior lateral area of the sternum of its segment and extends anteriorly to its insertion on the overlapping under surface of the anterior apophysis (*aAp*) of the succeeding sternum. The external ventrals are thus protractor muscles inasmuch as their contraction serves to separate the sternal plates. Since there are no tergal protractors, the sternal protractors evidently may give an upward flexure to the extended abdomen or serve to counteract a deflexed condition produced by the internal ventrals in opposition to the internal dorsals.

The Lateral Muscles.—The arrangement of the lateral muscles forms the same pattern in segments III to VII (Fig. 144 B), in which all the lateral muscles are tergosternal in their attachments. There are two internal laterals in each side of each of these segments (A, *175*, *176*), both arising on the tergum beneath the ventral edge of the lateral dorsal muscle (*168*); the first (*175*) is inserted on the base of the lateral sternal apodeme (*lAp*), the second (*176*) on the lateral margin of the sternum. External to the second internal lateral are two oblique outer laterals (*178*, *179*) having their origins on the tergum ventral to the paradorsal muscle (*169*); the two cross each other, going respectively posteriorly and anteriorly to their insertions on the lateral edge of the sternum. The internal laterals and the two oblique external laterals are all compressors of the abdomen and are therefore expiratory muscles in respiration. A third external lateral arises from the lower anterior angle of the tergum (A, *177*) and extends dorsally to its insertion on the upper outer surface of the lateral sternal apodeme (*lAp*). This reversed lateral is antagonistic in its action to the other laterals; it is therefore a dilator of the abdomen and an inspiratory muscle in respiration.

In the first abdominal segment the lateral musculature is reduced to a single slender muscle (Fig. 144 B, *146*), which is apparently a tensor of the tympanum of the "auditory" organ. In the second segment the lateral muscles do not entirely conform with those of the segments following, and in addition to the tergosternal muscles there are a pair of tergopleural muscles and a single short sternopleural muscle; these lie external to the tergosternal laterals and are therefore not seen in the figure.

The Complex Types of Abdominal Musculature.—The musculature of apterygote hexapods is not well known in all the several groups, but it has been carefully studied in Protura and Japygidae. The abdominal musculature of Protura, as described by Berlese (1910), is somewhat more complex than that of adult pterygotes. In the Japygidae the musculature throughout the body presents a highly complicated pattern; in each of the first eight abdominal segments of *Heterojapyx*, for example, there are at least 40 pairs of muscles having a most intricate arrangement, which, except that the fibers are comprised in dorsal, ventral, and lateral sets, shows little to suggest that the muscle pattern of adult pterygote insects has been derived from it. The multiplicity of muscles in *Heterojapyx* would appear to be a specialized condition. Among holometabolous larvae the body musculature is elaborate in the maggots of higher Diptera, but it reaches its greatest degree of complexity in the caterpillars (Fig. 145). In more generalized forms, however, the abdominal musculature of the larva is not essentially different from that of the adult.

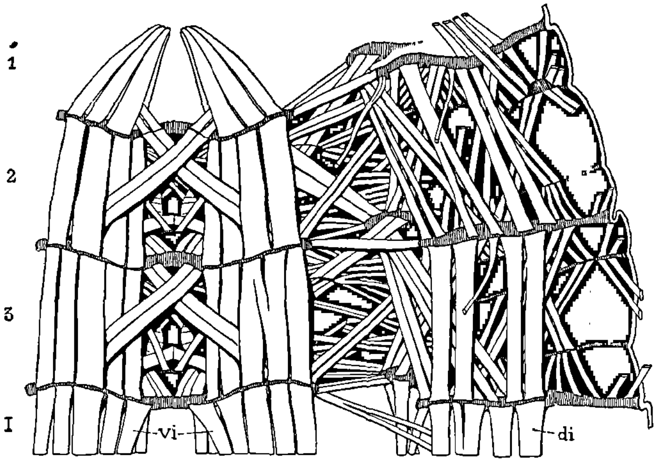

FIG. 145.—Ventral muscles and muscles of right half of the mesothorax and metathorax of a caterpillar, *Malacosoma americana*, inner view.

3. THE ABDOMINAL APPENDAGES

The usual abdominal appendages of adult insects are the gonopods of the genital segments and the uropods, or cerci, of the eleventh segment. In some of the Apterygota, however, appendages occur also on the pregenital segments, and the larvae of Pterygota present numerous varieties of appendicular structures on the abdomen, many of which appear to be rudiments of true segmental limbs. The cerci have already been described in connection with the eleventh segment (page 255), the gonopods will be discussed in Chap. XIX on the external genital organs; the present section, therefore, is limited to a brief review of the pregenital appendages of the Apterygota and the appendicular organs of pterygote larvae.

Abdominal Appendages of Protura.—A pair of short cylindrical appendages is present on each of the first three abdominal segments of adult Protura, arising from the membranous parts of these segments between the posterior angles of the tergal and sternal plates. The appendages are best developed in Eosentomidae, where the three pairs are alike in size and structure; each organ consists of two segments (Fig. 146) and a small terminal vesicle (*v*), which is eversible and retractile. In Acerentomidae the appendages of the first pair are like those of the Eosentomidae, but the second and third pairs are very small, simple tuberculiform protuberances, unsegmented and lacking the vesicle. Each appendage of the larger type in the two families, as described by Berlese (1910), is movable by two tergal muscles (B, *I*, *J*) inserted on the basal segment, one anteriorly, the other posteriorly. The second segment is provided likewise with two muscles, one arising anteriorly, the other posteriorly in the proximal segment, the two crossing each other medially to be inserted on opposite sides of the base of the distal segment. The terminal vesicle is retracted by a single large muscle (*rv*), which takes its origin mesally in the base of the first segment and is inserted on a central depression of the ventral face of the vesicle. The extrusion of the vesicle is evidently brought about by blood pressure from within the body.

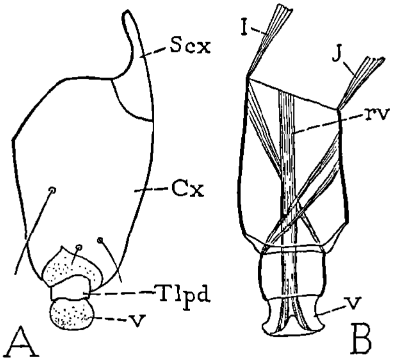

Fig. 146.—Abdominal appendages of Protura. A, abdominal leg of *Eosentomon germanicum*. (*From Prell*, 1913.) B, musculature of first abdominal leg of *Acerentomon doderoi*. (*From Berlese*, 1910.)

Abdominal Appendages of Collembola.—The Collembola have three characteristic appendicular organs on the abdomen, which, though unpaired at least basally in the adult stage and located medially on the ventral side of the body, are said to be formed in the embryo from paired rudiments. Each retains in its adult structure evidence of its double origin. The first appendage is carried by the first abdominal segment and is known as the *ventral tube*, or *collophore* (Fig. 147 A, *Coll*); the second is the clasp, or *tenaculum* (C), of the third segment; the third is the spring, called the *furcula* (A, *Fur*), apparently arising from the fifth abdominal segment, though its muscles take their origin in the fourth.

The Collophore.—The ventral tube, or collophore, is a large, thick cylindrical pouch of the body wall projecting ventrally and somewhat anteriorly from the sternal region of the first abdominal segment (Fig. 147 A, *Coll*). In most species the tube ends in a bilobed terminal vesicle

(B, *v*), which is ordinarily retracted but is capable of being protruded by blood pressure. A pair of large lateral retractor muscles (*rv*), arising within the body, traverse the collophore to be inserted on the lobes of the terminal vesicle. The structure of the collophore thus suggests that the organ is formed by the fusion of a pair of abdominal appendages resembling those of the Protura (Fig. 146), though in the latter the retractor muscle of the vesicle (*rv*) is said to arise in the base of the appendage, while the appendage itself is movable by two muscles (*I*, *J*) arising in the body and inserted on its base. In some of the Collembola, as in Sminthuridae, each lobe of the vesicle is produced into a long eversible tube.

The anterior surface of the collophore presents a median vertical groove continuous ventrally with the depression between the lobes of the terminal vesicle and communicating dorsally with a median channel of the ventral wall of the thorax. Anteriorly the thoracic channel is continued upon the outer face of the rudimentary labium as far as the distal cleft of the latter, where there open into it the ducts of two pairs of head glands. It has been suggested by Willem and Sabbe (1897) that the secretion of the head glands is conveyed to the collophore through the ventral thoracic channel and, when collected between the lobes of the terminal vesicle, enables the tube to function as an adhesive organ. Hence the name *collophore* ("glue bearer"). An elaborate description of the histology of the collophore, the head glands, and the connecting channel is given by Hoffmann (1905), who concurs with Willem and Sabbe as to the function of the tube. An adhesive function of the organ, however, has apparently not been demonstrated, and it is quite possible that the channel between the vesicle and the labium might convey liquid from the former to the mouth; and yet, though the Collembola inhabit moist places, most of them do not ordinarily come in contact with water.

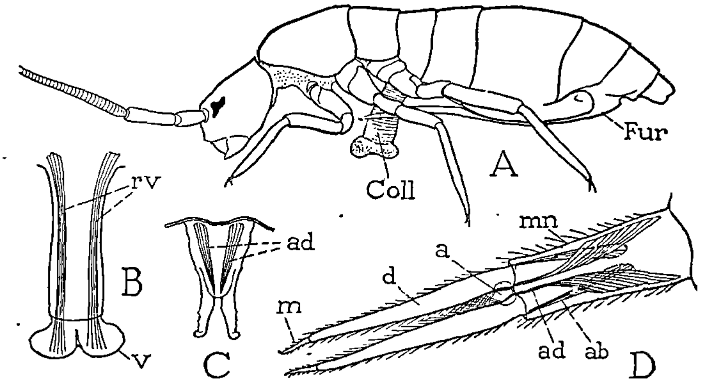

FIG. 147.—Abdominal appendages of a collembolan, *Tomocerus vulgaris*. A, entire insect with furcula in flexed position. B, collophore. C, tenaculum. D, furcula.

The Tenaculum.—The tenaculum, or clasp, is a minute organ situated medially on the concave ventral surface of the third abdominal segment. It consists of a conical base and of two laterally divergent distal prongs toothed on their outer margins (Fig. 147 C). Each prong is provided with an adductor muscle (*ad*). The tenaculum serves to hold the furcula in place when the latter is flexed against the ventral side of the body, the prongs projecting between the bases of the furcular arms.

The Furcula.—The furcula is the leaping organ of the Collembola and is the feature from which the insects get their common name of "springtails." The furcula consists of a large median base, the *manubrium* (Fig. 147 D, *mn*), and of two slender arms, each of which is subdivided into a long proximal segment, the *dens* (*d*), and a short terminal segment, or *mucro* (*m*). On the base of the manubrium are inserted a pair of flexor and a pair of extensor muscles arising in the fourth abdominal segment. In *Tomocerus vulgaris* each of the arms is provided with an abductor muscle (*ab*) and an adductor muscle (*ad*) having their origins in the manubrium. When the furcula is flexed in the position of repose (A), its proximal half is concealed in a ventral concavity of the abdomen, and the arms are closed upon the tenaculum, which fits into an oval space between the bases of the dentes (D, *a*) having thin, hard edges that are held by the teeth on the outer margins of the tenacular prongs (C). The spring evidently is released by the contraction of the adductor muscles of the prongs (C, *ad*). At the same time the furcular arms are spread and the entire organ is forcibly extended, throwing the insect upward and forward.

The furcula varies much in length in different species of Collembola, and it is absent in the genera *Neanura* and *Anurida*. In some species of *Sminthurus* that live on the surface of water the spring has a fanlike structure, the divergent arms being fringed with long, stiff hairs.

Abdominal Appendages of Thysanura.—The abdominal appendages of Thysanura are of particular interest because they have been taken as a starting point for the study of the structure of the genital appendages of adult pterygote insects, and they appear also to retain the basic structure of the abdominal appendages of pterygote larvae.

The thysanuran abdominal appendages, not including the cerci, best preserve their individuality in Machilidae, where they are present on each of the first nine segments of the abdomen except the first. Each of the pregenital appendages in this family consists of a large lateroventral basal plate, or rather of a flat basal lobe having a wide plate in its ventral wall (Fig. 148 B, *Cxpd*), and of a distal tapering process, termed the *stylus* (*Sty*), which is freely movable on the basis. The basal plates of each segment are intercalated proximally between the deflected lateral edges of the tergum (Fig. 138 A, *T*) and the small triangular median sternum (*Stn*); they are united with the sternum, and ankylosed with each other medially behind the sternum. Each plate is provided with muscles arising on the tergum and has all the aspects of being the enlarged basis of an otherwise rudimentary limb.

The abdominal styli of Thysanura are equipped with muscles arising proximally in the basal plates (Fig. 148 B, *smcls*). They would appear, therefore, to be the rudimentary telopodites of the abdominal appendages. In the Machilidae, however, similar styliform processes occur on the coxae of the second and third thoracic legs (A), which, though they lack muscles, suggest by their form that they are serially homologous with the abdominal styli. It is possible, therefore, that both the thoracic and abdominal styli are *coxal epipodites;* they are not "exopodites," as they are often supposed to be, since the true exopodite of Crustacea (Fig. 44 C) arises from the first trochanter (basipodite). The abdominal styli of Thysanura support the abdomen of the insect in life and play an active part in locomotion. Whatever may be their morphological nature, the styli appear to be represented in various forms on the abdominal segments of pterygote larvae and on the male genital segment of many adult insects.

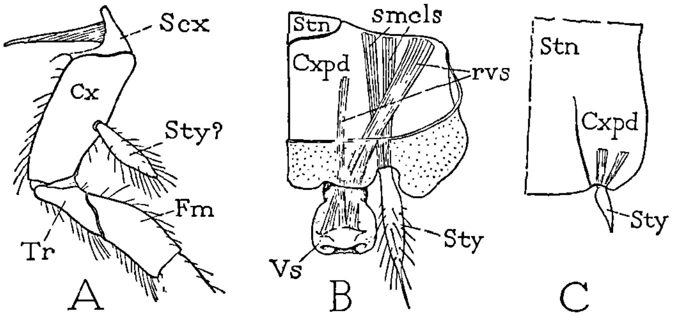

Fig. 148.—Appendages of Apterygota. A, metathoracic leg of *Nesomachilis* with coxal stylus. B, abdominal appendage of *Nesomachilis* bearing a stylus (*Sty*) and retractile vesicle (*Vs*). C, abdominal appendage of *Heterojapyx* with base (*Cxpd*) united with sternum.

Styli are present on the posterior segments of some Thysanura in which the limb bases are fused with the sterna, and they occur likewise on lateral lobes of the definitive pleurosternal plates of Diplura (Fig. 148 C). There can be little question that the styli present on the ninth sternum of certain male Pterygota, such as Ephemeridae, Termitidae, Blattidae, Grylloblattidae, and Tettigoniidae (Fig. 138 C), are homologues of the thysanuran styli, and it seems equally certain that the movable genital claspers of male holometabolous insects are organs equivalent to the more typical styli of these less specialized pterygote insects.

A second distal structure of the pregenital appendages, present in most of the Thysanura, has the form of a small eversible and retractile *vesicle* (Fig. 148 B, *Vs*) located mesad of the base of the stylus, and provided with strong retractor muscles (*rvs*) arising proximally on the basal plate. In some species there is a pair of vesicles on each appendage. The function of these organs is not known. Their structure suggests that they represent the terminal vesicles of the proturan abdominal appendages (Fig. 146, *v*); but the presence of two sacs on each appendage in some species of Thysanura precludes the idea that they may be rudiments of the distal parts of the abdominal limbs. The gill-bearing tubercles on the bases of the abdominal limbs of the larva of the neuropteron *Corydalus* and the terminal lobes of the abdominal legs of caterpillars have a structure very similar to that of the retractile vesicles of the Thysanura.

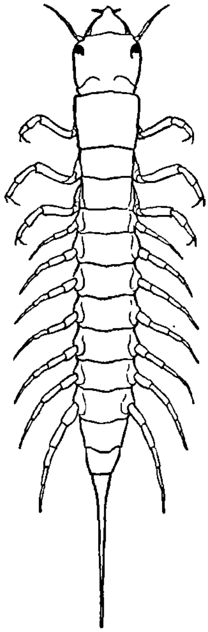

FIG. 149.—Larva of *Sialis*, showing leg-like appendages of the abdomen.

The gonopods of Machilidae and Lepismatidae differ from the pre genital appendages in that each may be provided with a gonapophysis and always lacks a retractile vesicle (Fig. 313 A, B, C). The gonapophysis (B, C, *Gon*) is a slender process arising from the mesal proximal angle of the coxopodite and is provided with short muscles arising in the latter (*gmcl*). Its proximal position on the coxopodite shows that it has no relation to the vesicles of the pregenital appendages and also does not favor the idea that the gonapophyses are the telopodites of the genital appendages. The four gonapophyses form the ovipositor of the female. The first pair is usually absent in the male, and in some species neither pair is present.

Abdominal Appendages of Pterygote Larvae.—The larvae of pterygote insects are remarkable for the variety of appendicular organs they have on the abdomen. Morphologists have not given much attention to these structures because it has been supposed that they are special developments serving the needs of the larvae; but there is no question as to the origin of some of them from the limblike rudiments of the embryo, and nearly all of them suggest by their structure and musculature that they are parts at least of true segmental appendages.

The most leglike in form of the larval abdominal appendages occur in the neuropterous genus *Sialis* and on certain aquatic coleopterous larvae, especially in the families Dytiscidae and Gyrinidae. The larva of *Sialis* (Fig. 149) has on each of the first seven segments of the abdomen a pair of long, tapering, six-segmented appendages projecting laterally from the sides of the body. Each appendage (Fig. 151 D) is supported on a lateral lobe (*Cxpd*) of the body wall of its segment, and within this lobe there arise muscles inserted anteriorly and posteriorly on the base of the movable shaft of the appendage. More than this, there are muscles within the proximal part of the appendage itself. The development of these organs in the embryo has not been studied, so far as the writer is aware. The abdominal appendages of the coleopterous larvae mentioned above are very similar to those of *Sialis*. The appendages in all cases are penetrated by tracheae and are supposed to function as gills, but this assumption needs experimental evidence.

The well-known gills of ephemerid larvae are borne on lobes on the sides of the abdominal segments (Fig. 150 A, B, *Cxpd*) situated between the terga and the sterna, and each gill is provided with muscles inserted on its base which arise in the ventral part of the supporting lobe (B, *bmcls*). There is little doubt, therefore, that the gills are appendicular parts of abdominal limbs, of which the supporting lobes are the bases. The gill stalk or gill plate, by its position on the basis and its basal musculature, suggests that it is a homologue of the stylus of the thysanuran abdominal appendages. The gill basis is very evidently the equivalent of the stylus-bearing plates of Machilidae, though, since it is immovable, there are no body muscles inserted upon it.

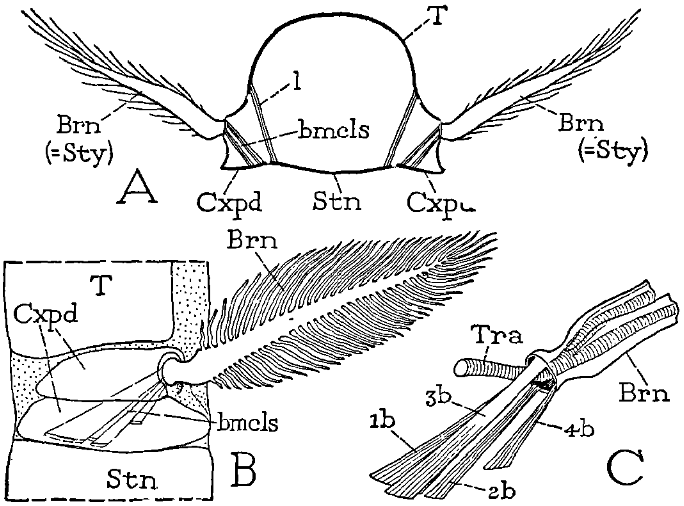

FIG. 150.—Abdominal appendages of an ephemerid larva. A, diagrammatic cross section of an abdominal segment, showing pleural lobes (*Cxpd*) of the body bearing the gills (*Brn*). B, a gill and its basis (*Cxpd*) in the pleural wall of the body. C, the gill muscles.

Returning again to the neuropterous family Sialidae, we find in the genera *Chauliodes* and *Corydalus* long tapering appendages on the sides of the first eight abdominal segments, and a terminal pair (pygopods) on the tenth segment (Fig. 151 A, B, C). Each appendage is a hollow process of the integument and is supported on a lateral lobe of the body wall (C, E, *Cxpd*). The appendage bases fall in line with the thoracic subcoxae, and within them arise muscles inserted on the bases of the movable parts of the appendages (F, *smcls*). It would appear, therefore, that we have here also a reduced and modified limb consisting of the coxopodite (*Cxpd*) and a distal part (*Sty*), the latter representing the ephemerid gill, or the thysanuran stylus. In *Corydalus* the basis of each of the first seven pairs of appendages supports ventrally a large tubercle bearing a thick tuft of gill filaments (C, E, *Vs*). A long muscle (E, F, *rvs*) arising on the dorsum of the body segment is inserted by three branches in the distal end of the tubercle and evidently serves to retract the latter. The gill-bearing tubercles of sialid larvae thus recall, in their structure and musculature, the retractile vesicles of the abdominal limbs of Thysanura, though in the sialid the tubercle muscles arise on the dorsum of the body and not in the appendage bases.

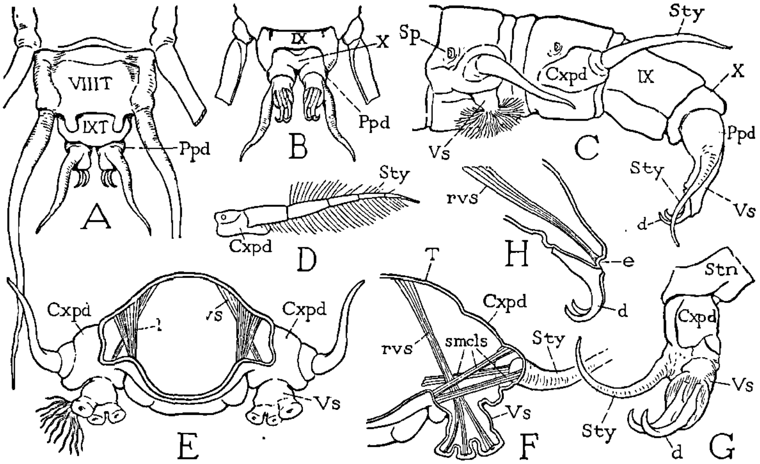

FIG. 151.—Abdominal appendages of larvae of Neuroptera. A, end of abdomen of *Chauliodes*, dorsal view. B, same, ventral view. C, *Corydalus cornutus*, segments *VII–X* and appendages. D, appendage of *Sialis*. E, an abdominal segment of *Corydalus*, posterior view. F, right half of same in section showing muscles of appendage. G, tenth segment appendage (pygopod) of *Corydalus*, right, anteromesal view. H, claws of terminal appendage of *Corydalus* and their retractor muscle.

The appendages of the tenth larval segment, or pygopods, in both *Chauliodes* and *Corydalus*, differ from those of the preceding segments in that the basis of each projects from the body as a short, free cylindrical lobe (Fig. 151 A, B, C, *Ppd*, G) bearing the stylus laterally (C, G, *Sty*), and the tubercle is provided with two large curved claws (*d*) instead of gills. The claws are set on the flat distal end of the tubercle by long, parallel bases, and the retractor muscle (H, *rvs*) is inserted posteriorly at the proximal ends of the convex margins of the claws.

The larvae of Trichoptera likewise have a pair of large claw-bearing pygopods on the tenth abdominal segment, though they have no appendages on the other segments of the abdomen. In some forms these terminal appendages are short, each consisting of a decurved distal claw arising from two basal plates implanted on the side of the tenth segment (Fig. 152 B, *Ppd*, C). In others the appendages are long, freely movable, cylindrical organs, projecting posteriorly, each bearing a large decurved claw on its distal end (E, F). Neither the structure nor the musculature (D, E) of the pygopods of trichopterous larvae in any way resembles that of the terminal appendages of the sialid larvae, nor do they have any similarity to the terminal legs of lepidopterous larvae; this fact is somewhat surprising considering that in many respects the Trichoptera and Lepidoptera appear to be related orders. Clawlike appendages are present on the tenth segment of certain coleopterous larvae, as in the family Helmidae, but the morphological status of such structures is doubtful.

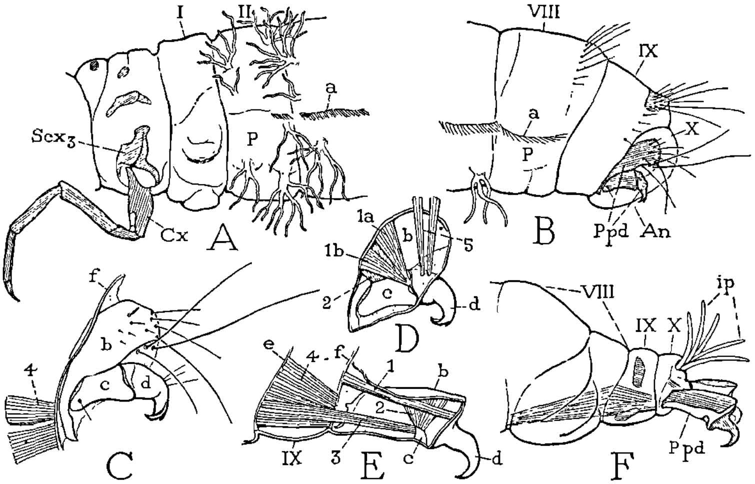

FIG. 152.—Abdomen and appendages of larvae of Trichoptera. A, *Platyphylax designatus*, metathorax and base of abdomen. B, end of abdomen. C, same, left pygopod of tenth segment. D, same, right pygopod and muscles. E, *Hydropsyche*, right pygopod and muscles. F, same, end of abdomen, with pygopods, and intestinal filaments protruded from the anus.

The abdominal legs of lepidopterous larvae are said by students of embryology to be developed from limb rudiments in the embryo that correspond to the rudiments of the thoracic legs. They appear, therefore, to be true segmental appendages. Most caterpillars have five pairs of these abdominal legs (Fig. 153 A), four pairs being on segments *III* to

VI, inclusive, the fifth on segment *X*; but the number is sometimes reduced, as in the loopers, and in some forms all the appendages are suppressed.

A typical abdominal leg of a caterpillar consists of three parts (Fig. 153 F). Proximally there is a ring of flexible integument (*mb*); beyond this is a longer cylindrical section (*Cx*) forming the greater part of the appendage, and usually having a sclerotic plate in its outer wall, often marked by a distinctive group of setae (A); distally the leg ends in a retractile lobe (F, *Vs*), called the *planta*, which bears the claws, or *crochets* (*d*).

Functionally the planta is the most important part of the abdominal leg of the caterpillar, and structurally it is the most variable. In its more generalized condition the planta is a short circular pad (Fig. 153 B, *Vs*) with a central depression (*e*) on which is inserted a group of retractor muscle fibers (*rvs*). In such cases the crochets (*d*) may be arranged in a complete circle around the periphery of the distal plantar surface, with their recurved points turned outward and upward. With most caterpillars, however, the claws are limited to a semicircle or a small arc usually on the inner margin of the planta (C, D), and in such cases the planta itself (*Vs*) generally becomes asymmetrical by a reduction or obliteration of its outer half. The planta then assumes the form of a lobe projecting to the mesal side of the limb axis, the latter being marked by the insertion point of the retractor muscle (*e*), and the crochets curve mesally and upward when the planta is protracted in the usual position (H).

Immediately above each abdominal leg of the caterpillar there is usually a prominent lobe or swelling of the body wall (Fig. 153 A, F, *Scx*), limited above by a groove marking the dorso-pleural line (*a-a*) of the abdomen. Corresponding lobes are present on the legless segments of the abdomen, and also on the thorax above the bases of the legs. The series of suprapedal lobes, therefore, appears to represent the lateral parts of the subcoxae on both the thorax and the abdomen (A, *Scx*).

The musculature of an abdominal leg of a caterpillar consists of two sets of fibers (Fig. 153 I), those of one set being inserted on the base of the principal part of the leg (*Cx*), those of the other on the distal surface of the planta (*Vs*). The plantar muscles, in the species figured, consist of four fibers, three of which (*5*, *6*) arise in the upper part of the subcoxal lobe, while the fourth (*4*) arises on the lateral wall of the body segment. The insertion of the other muscles (*1*, *2*, *3*) on the base of the principal segment of the leg (*Cx*) suggests that the latter is the coxa; the musculature of the planta leaves little doubt that the planta is a structure equivalent to the gill-bearing tubercles of the neuropterous larvae above described (Fig. 151 F), and that it is therefore analogous at least to the retractile vesicles of Thysanura. In the caterpillars most of the plantar muscles arise in the limb base, but there is always a long fiber from the body wall; the plantar musculature is thus intermediate between that of the vesicles of Thysanura and the gill tubercles of Neuroptera. Representatives of styli are not present in any lepidopterous larvae.

The appendages of the tenth abdominal segment of the caterpillar, known as the *anal legs*, or *postpedes*, resemble the appendages of the preceding segments in structure; their musculature differs from that of the others in that the basal muscles are largely eliminated, while the muscles of the planta are much larger and include both dorsal and ventral groups of fibers.

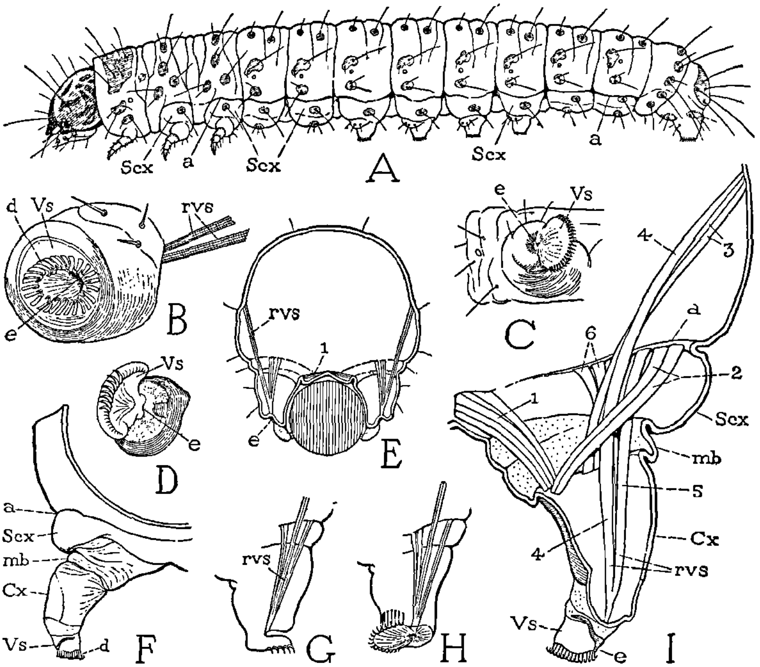

FIG. 153.—Abdominal appendages of larvae of Lepidoptera. A, *Carpocapsa pomonella.* B, same, left abdominal leg, ventral view. C, *Hyphantria cunea,* left leg, ventral view. D, *Xylina,* right leg, ventral view. E, diagrammatic section of caterpillar grasping a twig. F, *Malacosoma americana,* left leg, posterior view. G, diagram of position of planta on a rough surface. H, same on a smooth surface. I, *Malacosoma americana,* right leg and muscles, posterior view.

When a caterpillar with lobate plantae clings to a small twig or plant stem, the abdominal feet are turned mesally and clasp the support with the incurved claws (Fig. 153 E). The closure of each pair of legs on the support must be caused by the contraction of the median muscles (*1*) inserted on their bases, for the plantar muscles (*rvs*) evidently serve to release the grasp of the claws. If the caterpillar walks on a flat but rough surface, the plantar lobes are turned outward by their muscles (G) and their inner surfaces are applied to the support with the claws directed downward. If, however, the caterpillar finds itself on a smooth, hard surface, such as that of glass, the soles of the plantae are pressed flat against it (H), with the claws turned upward, and apparently a tension of the plantar muscles converts the soft end walls of the plantae into vacuum cups by which the caterpillar maintains its foothold.

The caterpillars do not move either their abdominal or their thoracic appendages in the way that adult insects move their thoracic legs. In regular forward progression the last pair of abdominal legs are first released from the support and brought forward by a contraction and slight humping of the posterior part of the body. Then in turn the other abdominal legs are lifted and advanced in the same manner, as the wave of body contraction runs forward through the segments. Finally, the movement affects the thoracic segments and their appendages. Thus the crawling caterpillar moves forward with each successive wave of contraction that runs through its body. If the caterpillar is a "looper," the posterior group of appendage-bearing segments is brought forward together and the body is stretched out for a new grasp by the thoracic legs.

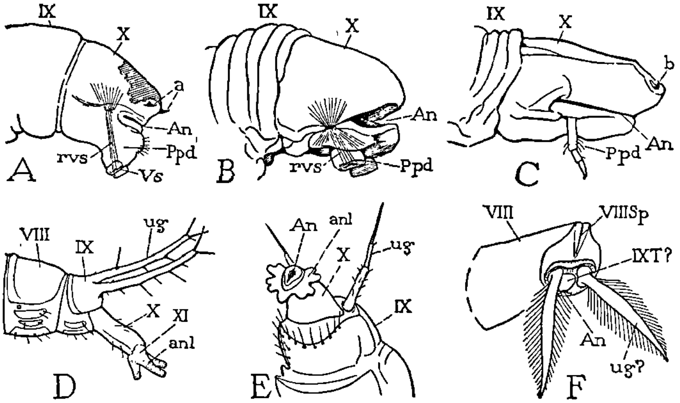

Fig. 154.—Terminal abdominal appendages and other appendicular processes of larvae of Hymenoptera and Coleoptera. A, *Pteronidea ribesii*, end of abdomen with pygopods. B, *Cimbex americana*. C, *Cephaleia*. D, *Oodes helopiodes*, end of abdomen with urogomphi. (*From Kemner*, 1918.) E, *Thanatophilus*. (*From Kemner*, 1918.) F, *Dytiscus circumcinctus*, end of abdomen with appendicular processes.

The larvae of the sawflies (Tenthredinidae and related families) resemble caterpillars in the possession of appendages on the abdomen, which are similar to those of the caterpillars but not so highly organized. The appendages of the tenth segment, however, differ in different forms. Those of species living in the open (Fig. 154 A, B) are much the same as the anal legs of lepidopterous larvae and are adapted to grasping the edges of leaves; species that bore into the stems of plants or that live in the protection of web nests or curled leaves, however, such as the Cephidae and Pamphiliidae, have slender, jointed appendages on the tenth segment (C, *Ppd*). Abdominal appendages similar in appearance to those of lepidopterous and tenthredinid larvae occur also on some larvae of Coleoptera.

Finally, we may mention, in connection with the study of abdominal appendages, certain fixed or mobile processes found on the terminal segments of certain larvae. Such structures are of frequent occurrence on the dorsum of the ninth segment in the larvae of Coleoptera and have been variously called styli, cerci, pseudocerci, and corniculi, but the term *urogomphi* (Böving and Craighead, 1932) is more specific and descriptive. The urogomphi vary much in size and shape from short spine-like points to long, thick processes or multiarticulate filaments, and they are sometimes distinctly jointed (Fig. 154 D, E, *ug*). In some species they are fixed outgrowths of the posterior end of the ninth tergum; in others they arise from the membrane behind the tergal plate and are then flexible at their bases. Evidently the urogomphi are simply cuticular outgrowths of the dorsum of the ninth segment having no relation to segmental appendages. The terminal appendages of the larva of *Dytiscus* (F, *ug?*), however, are of a more problematical nature; they appear to belong to the ninth segment and are provided with muscles arising on the tergum of the eighth segment (Speyer, 1922; Korschelt, 1924); but it is possible that these appendages also are urogomphi, and that the muscles that move them are the intersegmental muscles between the eighth and ninth segments.

The larvae of some chalastogastrous Hymenoptera have a pair of small processes arising on the tergum of the tenth segment (Fig. 154 A, *a*) which have sometimes been regarded as rudimentary cerci, but which are evidently mere cuticular processes comparable with the urogomphi of coleopterous larvae. In certain forms there is only a single median process (C, *b*). The caudal horn of sphingid caterpillars is an analogous structure.

CHAPTER XII

THE ORGANS OF INGESTION

The organs primarily concerned with the intake of food are the gnathal appendages and lobes of the head surrounding the oral aperture of the alimentary canal, known collectively as the mouth parts. But the mouth parts do not constitute the entire apparatus of ingestion, for when the food has been delivered into the mouth cavity it must yet be passed on to the section of the alimentary canal where digestion takes place. The anterior part of the stomodaeum, then, is always an important part of the ingestive system. In the sucking insects, whose food consists mainly of plant and animal juices, the pumping apparatus associated with the mouth is principally a highly specialized development of the preoral cibarium; but, in its anatomical continuity, the pump becomes virtually a part of the alimentary tract and is usually called the "pharynx." In order to understand the true morphology of the ingestive organs, therefore, it will be necessary to refer back, on the one hand, to the contents of Chap. VII for the basic structure of the mouth parts, and, on the other, to anticipate something from the subject matter of the following chapter on the alimentary canal.

So diverse in form are the feeding organs in the various groups of insects specialized for obtaining particular kinds of food that the study of the mouth parts becomes a major subject in any course in entomology. A good system for classifying the leading types of mouth-part structure, therefore, will be of much assistance in understanding the various functional adaptations of the organs, and the student is referred to the tabulation of insect mouth parts on a functional basis given by Metcalf and Flint (1928), and more fully elaborated by Metcalf (1929). For morphological purposes, however, the mouth parts cannot be studied from a physiological standpoint, since very different types of structure are often adapted to similar modes of feeding, and great discrepancies in both structure and function have been independently evolved in adult and larval forms of the same orders. Hence, in the following discussion of the more specialized feeding organs of insects, the leading types of structure will be described as they occur in the ordinal groups.

Since all the more generalized forms of modern insects have the mouth parts constructed for feeding on so-called solid substances, that is, on the whole tissues of plants and animals rather than on their juices or liquid products, there is no question that the "orthopteroid," or biting and chewing, type of mouth parts is the one from which the other types have been derived, as the more specialized forms clearly show in most cases by their own structure and development. The fundamental structure of mouth parts of the biting type, having been fully described and illustrated in Chap. VII, need be given little attention in the present chapter, wherein will be discussed the more important modifications characteristic of the principal orders.

1. THE PREORAL CAVITY

Since the mouth parts of insects are closely assembled in their attachments on the head, they enclose between them a space which is often called the "mouth cavity," and which functionally deserves this name; but inasmuch as this region lies entirely outside the oral aperture, it is more appropriately termed the *preoral cavity* (Fig. 155, *Prc*). In a strict sense, of course, it is not a cavity at all but merely an external space bounded anteriorly by the epipharyngeal wall of the labrum and clypeus, posteriorly by the labium, and laterally by the mandibles and maxillae. Within the preoral cavity lies the tongue-like hypopharynx (*Hphy*), which morphologically is a median lobe of the ventral wall of the gnathal region of the head. The true *mouth* of the insect is the anterior opening of the stomodaeum (*Mth*), which is located in the ventral wall of the head (in hypognathous insects) immediately behind the clypeus and in front of the hypopharynx, where it is normally concealed between the bases of the mandibles. Correspondingly situated at the posterior end of the hypopharynx, between the latter and the base of the prementum, is the opening of the salivary duct (*SlO*).

In the orthopteroid insects the preoral cavity is largely occupied by the hypopharynx (Figs. 60 A, 155, *Hphy*). Anteriorly, however, there is an open *food meatus* (*fm*) between the hypopharynx and the epipharyngeal wall of the labrum and clypeus, which leads up to the mouth (*Mth*); and posteriorly there is a broad *salivary meatus* (*sm*) between the hypopharynx and the labium, at the inner end of which is the opening of the salivary duct (*SlO*). The food passage is closed laterally by the mandibles, and its upper or inner part, lying proximal to the molar surfaces of the closed jaws, forms the preoral food chamber here named the *cibarium* (*Cb*). The salivary channel (*sm*) terminates in the salivary pocket, or *salivarium* (*Slv*), between the base of the hypopharynx and the base of the labial prementum. The cibarium and the salivarium are important elements in the feeding mechanism of nearly all insects; in the higher orders they are variously modified to form specialized organs for the ingestion of liquid food and for the ejection of saliva or other products of the labial glands.

The Cibarium.—The cibarium of generalized insects (Fig. 155, *Cb*) is a part of the intergnathal preoral cavity (*PrC*) of the feeding apparatus. Morphologically it lies outside the true mouth (*Mth*), but functionally it is the "mouth cavity" of the insect and is so defined (*Mundhöhle*) by Weber (1933). Its concave floor is formed by the adoral surface of the base of the hypopharynx, flanked by the suspensorial sclerites of the latter (Figs. 60, 155, *HS*); its roof, or anterior wall, is the epipharyngeal surface of the clypeus. The cibarium, in chewing insects, serves as a chamber in which the food material, pushed upward through the food meatus by the adduction of the jaws, is held at the base of the hypopharynx preparatory to being passed into the mouth. If a partially narcotized cockroach is offered a bit of moistened bread, a particle is seized between the mandibles; after a few movements of the jaws the particle may be seen neatly stowed in the cibarial pocket at the base of the hypopharynx, from which it presently disappears into the mouth. During feeding, a copious flow of saliva issues from the salivary channel on the labium and floods the tips of the mouth parts.

On the inner surface of the epipharyngeal wall of the cibarium is inserted a pair of dilator muscles (Figs. 60 A, 155, *dlcb*) taking their origin on the clypeus. The cibarium is compressed by the contraction of the retractor muscles of the mouth angles (*rao*), which arise on the frons and are inserted on the oral branches of the suspensorial bars of the hypopharynx (*HS*). The contraction of these muscles accompanying the adduction of the mandibles pulls the hypopharynx forward and upward, and it is this movement of the hypopharynx apparently that forces the food from the cibarial chamber through the mouth into the buccal region of the stomodaeum, whence it is carried along by the peristalsis of the stomodaeal wall. The opposite movement of the hypopharynx is produced by the contraction of the retractor muscles (Figs. 60 A, 84 B, 155, *rhphy*) arising on the tentorium and inserted on the lateral sclerites (*w*) of the hypopharyngeal base.

In most of the sucking insects, particularly in Dytiscidae, Thysanoptera, Hemiptera, and Diptera, the cibarium undergoes a remarkable transformation by which it is converted into the *sucking pump* of the feeding mechanism. By an extension and closure of the lateral lips of the true mouth aperture, the cibarium becomes a chamber partly or entirely enclosed within the head cavity; its distal opening into the food meatus (Fig. 155, *fm*) is then the *functional mouth.* The dilator muscles of the cibarial pump are always the epipharyngeal muscles arising on the clypeus (*dlcb*). On the other hand, in Lepidoptera and Hymenoptera the sucking pump includes the pharynx, and its dilator muscles arise on the clypeal, frontal, and postfrontal regions of the cranium. The relation of the muscles to the parts of the ingestive tract will be shown in a following section.

The Salivarium.—In its simplest form the salivarium is merely the pocket where the posterior or ventral wall of the hypopharynx is reflected into the anterior or dorsal wall of the labial prementum (Fig. 155, *Slv*), into which opens the duct of the salivary glands (*SlD*). On its dorsal wall is inserted a pair of dorsal salivary muscles (1*s*) taking their origins on the suspensorial sclerites (*HS*) of the hypopharynx or on the lateral walls of the hypopharynx when these sclerites are absent. On its ventral wall are inserted the salivary muscles of the labium, usually two pairs (2*s*, 3*s*) arising in the prementum.

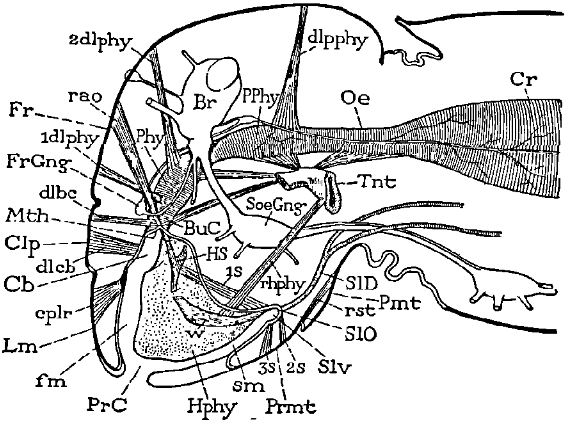

Fig. 155.—Sectional diagram of the head of an orthopteroid insect showing the generalized stomodaeal and hypopharyngeal musculature. *Br*, brain; *BuC*, buccal cavity; *Cb*, Cibarium; *Clp*, clypeus; *cplr*, compressor labri; *Cr*, crop; *dlbc*, dilator buccalis; *dlcb*, dilator cibarii; *1dlphy*, *2dlphy*, first and second dilatores pharyngium; *dlpphy*, dilator postpharyngialis; *fm*, food meatus; *Fr*, frons; *FrGng*, frontal ganglion; *Hphy*, hypopharynx; *HS*, hypopharyngeal suspensorium; *Lm*, labrum; *Mth*, mouth; *Oe*, oesophagus; *Phy*, pharynx; *Pmt*, postmentum; *PPhy*, posteriorpharynx; *PrC*, preoral (mouth) cavity; *Prmt*, prementum; *rao*, retractor anguli oris; *rhphy*, retractor hypopharyngis; *1s*, *2s*, *3s*, muscles of salivarium; *SlD*, salivary duct; *SlO*, salivary orifice; *Slv*, salivarium; *sm*, salivary meatus; *SoeGng*, suboesophageal ganglion; *Tnt*, tentorium; *w*, basal sclerite of hypopharynx.

The primitive form of the salivarium is well shown in some of the Orthoptera. In the Acrididae, for example, the organ is a simple salivary cup on the base of the prementum, into which fits a prominent knob on the base of the hypopharynx. In the mantis the pocket is produced into a long, flat, triangular pouch (Fig. 84 D, *Slv*) with the orifice of the salivary duct at its apex. The lateral margins of the pouch are strengthened by two weakly sclerotic bars (*w*) connected distally with the basal angles of the hypopharynx. On these bars are inserted the two pairs of salivary muscles from the labium (2*s*, 3*s*). The dorsal, or hypopharyngeal, wall of the pouch is somewhat concave (E), with a median fold on which is inserted a pair of wide dilator muscles (D, E, 1*s*) that converge from the lateral walls of the hypopharynx. A similar structure is described by Walker (1931) in *Grylloblatta,* including the three pairs of muscles. In *Gryllus* the salivarium is narrowed to a short rigid tube (Fig. 84 C, *Slv*), with both the hypopharyngeal and labial salivary muscles inserted upon it. The basal bars of the hypopharynx (*w*) diverge from the mouth of the tube into the lateral walls of the hypopharynx, where, as in most Orthoptera (Fig. 60), they give attachment to the tentorial retractor muscles of the hypopharynx (*rhphy*).

The salivary ejection apparatus becomes highly developed in the larvae of Lepidoptera as the *silk press* (Fig. 165, *Pr*). In the caterpillar, however, the hypopharynx and the prementum are united in a median lobe supported by the postmentum and the maxillary stipites, on the extremity of which the duct of the silk glands opens through a hollow spine, the *spinneret* (*Sr*). It is evident, therefore, that the silk press is the salivarium enclosed by the complete union of the hypopharynx with the prementum. Both dorsal and ventral salivary muscles are present in the caterpillar (Fig. 165 E) as in Orthoptera. In the higher Hymenoptera the salivary duct terminates in a cylindrical pouch opening above the distal part of the prementum (Fig. 163 C, *Syr*) just before the base of the rudimentary hypopharynx (*Hphy*). This pouch, known as the *salivary syringe,* has two pairs of muscles inserted on it. In the honey bee one pair arises on the hypopharyngeal region covering the oral surface of the prementum, but in *Xylocopa* these muscles (Fig. 163 C, 1*s*) have migrated to the wall of the prementum. The other muscles (3*s*) arise ventrally in the prementum and are inserted on the sides of the syringe.

The salivary syringe of Diptera (Fig. 172 D, *Syr*) and of Hemiptera (Fig. 179, *Syr*) is evidently also a derivative of the salivarium, though in these orders it has a terminal outlet duct (*sm*) that traverses the hypopharynx and opens on the tip of this organ. The ventral labial muscles are absent in both cases, but the dorsal dilators are present. In the Hemiptera the dilator muscles (*dlsyr*) arise on the inner faces of long basal plates of the hypopharynx (Fig. 180 B, *hpl*); in the Diptera they take their origin on the posterior wall of the sucking pump of the feeding apparatus (Fig. 172 D), but the pump chamber is evidently the cibarium, the floor of which is formed by the basal part of the hypopharynx.

2. THE CEPHALIC STOMODAEM

The stomodaeum in its generalized form is a simple tube extending from the mouth to the mesenteron (Fig. 189, *Stom*). In most insects, however, it is differentiated into several more or less distinct regions distinguished by variations in the diameter of the tube, accompanied by differences in the intima and in the muscular sheath (Fig. 190, *Stom*). The stomodaeal regions are structural adaptations to functional differences in various sections of the tube, and they are not strictly homologous in all insects.

The part of the stomodaeum contained in the head lies above the transverse bar of the tentorium and passes into the thorax through the upper part of the foramen magnum (Fig. 155). It is embraced by the nerve connectives from the brain (*Br*) to the suboesophageal ganglion (*SoeGng*); the frontal ganglion (*FrGng*) lies on its dorsal wall anterior to the brain. The first part of the stomodaeum lies immediately within the mouth and may be termed the *buccal cavity* (*BuC*). Following the buccal cavity is the region of the *pharynx* (*Phy*), usually apparent as a dilatation of the stomodaeum between the frontal ganglion and the cerebral nerve connectives. Posterior to the brain the stomodaeum may take the form of a simple oesophageal tube, but in Orthoptera, Coleoptera, and some other insects it is here differentiated into a second pharyngeal region, or *posterior pharynx* (*PPhy*). The precerebral pharynx must then be distinguished as the *anterior pharynx* (Eidmann, 1925). Following the posterior pharynx there may be an *oesophagus* (*Oe*), which generally enlarges into the *crop*, or *ingluvies* (*Cr*).

All parts of the head stomodaeum, as well as the preoral epipharyngeal surface of the clypeus and labrum, are provided with dilator muscles arising on the head walls and on the tentorium (Fig. 155). The number of these muscles is not the same in all insects, but those that arise on the head wall maintain definite relations in their points of origin and insertion. They are therefore of much value for determining homologies both in the cranial areas of their attachments, and in the parts on which they are inserted. The dorsal series of these muscles is consistently divided by the frontal ganglion connectives into an anterior set of muscles arising on the clypeus and labrum, and a posterior set arising on the frontal and parietal areas of the cranium. The following anterior and dorsal muscles are regularly present in orthopteroid insects, and representative muscles recur in most of the other orders.

Compressores labri (Fig. 155, *cplr*).—A group of fibers within the labrum, attached on its anterior and posterior surfaces.

Dilatores cibarii (*dlcb*).—A pair of muscles within the clypeus, arising on its anterior wall and inserted on the epipharyngeal surface of the cibarium. These muscles become the principal dilators of the sucking pump in Dytiscidae, Thysanoptera, Hemiptera, and Diptera.

Dilatores buccales (*dlbc*).—A pair of muscles arising on the clypeus and inserted on the stomodaeum just within the mouth.

The foregoing muscles lie *anterior* to the nerve connectives of the frontal ganglion (*FrGng*); the following are inserted *posterior* to the connectives.

Retractores angulorum oris (*rao*).—A pair of large muscles arising dorsally on the frons, inserted on the oral branches of the suspensorial sclerites of the hypopharynx.

Dilatores pharyngis frontales (1*dlphy*).—One or more pairs of slender muscles arising on the frons, inserted on the anterior part of the pharynx.

Dilatores pharyngis postfrontales (2*dlphy*).—One or more pairs of muscles arising on the postfrontal region of the cranium, inserted on the pharynx before the brain.

Dilatores postpharyngeales (*dlpphy*).—One or more pairs of muscles arising on the vertex, inserted on the stomodaeum behind the brain.

Besides these muscles there are also lateral and ventral dilators of the stomodaeum arising on the head walls and on the tentorium, but they are not so constant as the dorsal muscles, and their diagnostic value is less important.

From the foregoing review we should note particularly the following points: (1) The muscles of the clypeus are distributed to the cibarium and to the buccal cavity; (2) the frontal ganglion lies over the anterior end of the pharynx, and its connectives go anterior to the retractor muscles of the mouth angles and the first pharyngeal dilators; (3) the dorsal dilators of the pharynx arise on the frontal and postfrontal regions of the cranium.

3. THE FEEDING MECHANISM OF NEUROPTERA AND COLEOPTERA

The feeding organs of Neuroptera and Coleoptera are in general of the orthopteroid type of structure, but in some members of each order they are specially modified for other purposes than those of biting and chewing, such as those of grasping, injecting, and sucking. In certain features, particularly in the structure of the labium, an interesting interrelationship is found between larval and adult forms. The labium of adult Coleoptera, for example, is a three-part structure resembling that of many Orthoptera in that the postlabium contains a distinct mentum and a submentum. In the Neuroptera, however, a true mentum is apparently never present, and some larval Coleoptera resemble Neuroptera in the structure of the labium, while others have a labium like that of the adults of their own order.

The Mandibles.—The jaws are the most important members of the feeding organs in biting insects, and in the Neuroptera and Coleoptera they usually preserve the orthopteroid structure. With phytophagous species there is generally a well-marked differentiation in each mandible between a distal incisor lobe with cutting edges (Fig. 156 A, *in*) and a basal molar lobe (*mol*) provided with an irregular masticatory surface. In predacious species, however, the grasping function of the jaws is more important than that of chewing, and in such species the mandibles are usually simple biting organs with strong incisor points (B, E), which may be notched or toothed, but in which effective molar surfaces are generally absent. In some forms with greatly enlarged jaws, as the male stage beetles (Lucanidae), the huge mandibles have no function in connection with feeding and are used for holding the female at the time of mating.

Among both the Neuroptera and the Coleoptera, predacious larvae of certain species feed only on the juices or liquefied body contents of their prey as they hold the latter in their jaws, and some of these larvae, by a special modification of the feeding mechanism, become true sucking insects.

The most familiar insects having the grasping-sucking type of mouth parts are the larvae of the diving water beetles, *Dytiscus* and related genera. The mandibles of the *Dytiscus* larva are long, curved fangs

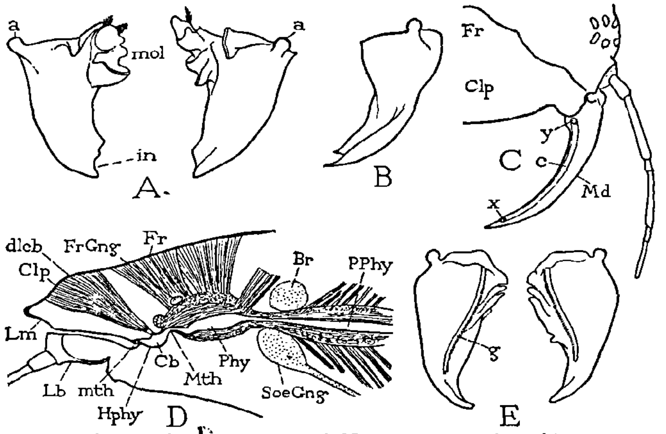

Fig. 156.—Mandibles of Coleoptera and Neuroptera, and sucking apparatus of the larva of *Dytiscus*. A, mandibles of scarabaeid larva, posterior view. B, right mandible of adult *Chrysopa*. C, left mandible of *Dytiscus* larva, dorsal view, showing inner canal. D, section of head of *Dytiscus* larva showing cibarial (*Cb*) and pharyngeal (*Phy*) pumps. (*From Burgess*, 1883.) E, mandibles of adult *Pterosticus*, posterior view, showing grooves.

(Fig. 156 C, *Md*) hinged to the anterior lateral angles of the head by dorsal and ventral articulations so that they work in a horizontal plane. Each mandible is traversed by a tubular canal (*c*), really a groove on the inner face of the appendage with confluent edges, opening distally near the tip (*x*) and proximally near the base of the jaw (*y*). The labrum (D, *Lm*) is sharply deflected against the base of the labium (*Lb*), where a marginal ridge of the former is securely held in a transverse groove of the labial surface. Just behind the closure thus formed is a transverse preoral chamber (*Cb*), which is evidently the cibarium (Fig. 155, *Cb*), its floor being the dorsal surface of the hypopharynx (*Hphy*). The lateral extremities of the cibarial chamber, or "mouth cavity," extend to the bases of the mandibles, where, on each side, there is a small aperture to the exterior. When the mandibles are flexed, the proximal openings of their canals come into contact with the lateral apertures of the cibarium and thus establish continuous passages into the latter from the tips of the fangs. The dorsal wall of the cibarium is provided with strong dilator muscles (Fig. 156 D, *dlcb*) arising on the clypeal region (*Clp*) of the frontoclypeal plate of the cranium (*C*). By the action of these muscles the closed cibarial chamber becomes a preoral pump. The true mouth of the *Dytiscus* larva (D, *Mth*) lies in the posterior wall of the cibarium. It leads into a large, strongly musculated anterior pharynx (*Phy*), which also apparently is a part of the pumping apparatus.

When the *Dytiscus* larva closes its mandibles in the body of its prey, a poisonous and digestive fluid discharged from the stomach is ejected from the cibarium through the mandibular canals, which, as described by Blunck (1916*a*), spreads quickly through the body of the victim and rapidly dissolves the softer tissues. The liquefied material is then, by a reversal in the action of the pumping mechanism, sucked back into the pharynx and passed on to the stomach. Detailed descriptions of the feeding apparatus and the method of feeding of the *Dytiscus* larva are given by Burgess (1883), Rungius (1911), Blunck (1916*a*, 1918), Korschelt (1924), and Weber (1933).

The occurrence of grooves on the mandibles is not unusual in Coleoptera (Fig. 156 E, *g*); and other predacious species have taken advantage of their presence in much the same way as has the *Dytiscus* larva. In the larvae of certain Lampyridae, for example, the mandibles are perforated by channels opening at their bases, through which a liquid is injected into the body of the prey. This liquid, according to Bugnion (1929*a*), comes from the stomach and converts the tissues of the recipient into a "bouillon nutritif"; but in the case of the lampyrids, Bugnion observes, ingestion takes place directly through the mouth and not by way of the mandibular canals. In some other lampyrid larvae the mandibles are simply grooved, but the grooves are converted into tubes by long accessory lobes applied against them. In still other species the accessory lobes are short and the mandibular grooves are open canals. The sucking apparatus of the lampyrid larvae, as illustrated by Bugnion (1929*a*, Fig. 21), appears to be principally, as in the *Dytiscus* larva, the cibarial chamber of the preoral cavity, with its dorsal dilator muscles arising on the clypeal area of the head wall.

A grasping-sucking feeding mechanism occurs also in many predacious larvae of the Neuroptera that have long, fanglike jaws. The mandibles of such species are deeply grooved on their ventral surfaces, but here the closing lobes are long blades of the maxillae, which fit into the mandibular grooves and thus form tubular channels between the two appendages, through which the larva sucks out the juices of its victims. Familiar examples of neuropterous larvae thus equipped are the aphislions and antlions. Lozínski (1908), in his study of the latter, describes a group of glandular cells in the wall of each maxillary blade, which discharge into a cuticular canal opening at the tip of the organ. The secretion from these cells, he believes, is poisonous and accounts for the ease with which the larva overcomes a struggling ant held in its fangs.

The Maxillae.—It is seldom that any difficulty is encountered in a study of the maxilla in adult Neuroptera and Coleoptera, since the appendage usually preserves the typical generalized form and musculature (Fig. 157 A, B). The posterior surfaces of both the cardo and stipes may be conspicuously marked by the lines of internal ridges, which give them a "divided" appearance, but each part preserves its unity, and the stipes may always be identified as such by the origin of the muscles of the palpi and terminal lobes within it (A). The galea sometimes appears to be two segmented, but the true galea is to be determined by the point of insertion of its flexor muscles (A, *fga*). In larval forms the maxilla often suffers a reduction, especially in its appendicular parts (C, D), and in such cases it is only by a comparative study of serially related species that the persisting lobes can be identified (see Blunck, 1918; Korschelt, 1924).

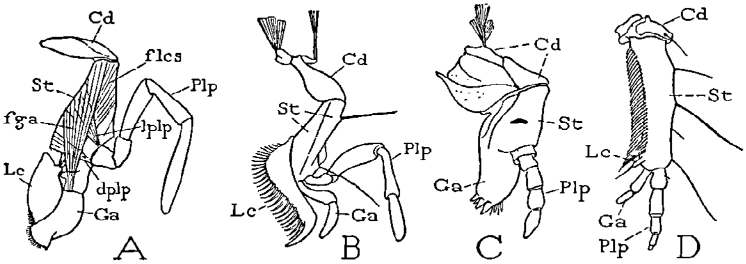

FIG. 157.—Maxillae of Coleoptera and Neuroptera. A, *Chrysopa* adult. B, *Pterosticus* adult. C, scarabaeid larva. D, carabid larva, *Scarites*.

The Labium.—It is in the study of the labium that students of Neuroptera and Coleoptera find themselves most often confronted with problems concerning the identities of the parts, and with difficulties in making satisfactory comparisons between divergent forms. Discrepancies of interpretation are in part merely the use of common terms in different senses by different writers, but in a larger measure they are the result of a failure to determine the fundamental morphology of the labium, which in most cases is readily disclosed by a study of the labial musculature.

Neuroptera.—The parts of the labium in Neuroptera are likely to be misinterpreted because, in both larval and adult forms (Figs. 68, B, 82 B, 158 B), the labium contains a middle plate (*c*), which at first sight appears to be a mental sclerite. An examination of the labial musculature, however, reveals that the median muscles (*rst*) are inserted on this plate, which is thus shown to belong to the prementum. The tentorial adductor muscles of the labium are inserted on the distal part of the prementum. The postmentum varies in size, but it consists of only one sclerite (*Pmt*). The labium of Neuroptera, therefore, is characterized by a differentiation of the premental sclerotization into a distal plate, or plates, bearing the insertions of the tentorial adductor muscles of the labium, and into a proximal plate giving insertion to the median retractor muscles. The postlabial sclerotization is not divided into a mentum and a submentum, as in adult Coleoptera, but there may be a wide membranous area distal to the single postlabial plate.

The labium of an adult myrmeleonid (Fig. 82 B) shows well the typical structure of the neuropterous labium. The postlabium contains a large proximal sclerite (*Pmt*), but its distal part is membranous and is traversed by the retractor muscles (*rst*) extending from the postmentum to the proximal sclerite (*c*) of the prementum. The sclerotization of the prementum is differentiated into a pair of anterior sclerites (*ab*) giving insertion to the tentorial adductors (*adlb*), and into the large proximal plate (*c*) on which the median retractors (*rst*) are inserted. Each of the anterior sclerites (*ab*) is expanded on the lateral wall of the prementum in a triangular plate supporting the hypopharynx. The labium of *Chrysopa* (Fig. 158 B) is structurally the same as that of the myrmeleonid, but the postmental plate (*Pmt*) is very long, and the proximal sclerite (*c*) of the prementum (*Prmt*) is a narrow transverse bar giving attachment to the retractor muscles (*rst*). The distal sclerotization of the prementum (*ab*), on which are inserted the tentorial adductors of the labium (*adlb*), is continuous with that of the broad spatulate ligula (*Lig*).

In the Sialidae the prementum is relatively large. In the larva of *Corydalus* (Fig. 68 B, *Prmt*) its sclerotization includes a distal plate (*ab*) supporting the palpi and giving attachment to the tentorial adductor muscles, and a pair of proximal plates (*c*, *c*) on which the median muscles (*rst*) are inserted. The postmentum (*Pmt*) is broad but short and is continuous proximally with a well-developed gula (*Gu*) posterior to the tentorial pits (*pt*).

Larval Coleoptera.—The labium of many coleopterous larvae has a structure very similar to that of the labium of larval and adult Neuroptera. In a silphid larva, for example (Fig. 158 A), the prementum (*Prmt*) contains two principal sclerites (*a*, *c*), on the proximal one of which (*c*) are inserted the median retractor muscles (*rst*), and on the distal one (*a*) the dorsal adductors. A pair of very small intermediate sclerites (*b*) is here present, however, which give insertion to the ventral adductors (*2adlb*). The proximal premental sclerite of coleopterous larvae (*c*) is commonly mistaken for the mentum, but the attachment of the retractor uscles (*rst*) on its base shows clearly that it is not the homologue of the entum of an adult beetle (C, *Mt*), which always lies proximal to the sertions of the median muscles (D). The plate in question, on the other and, corresponds exactly to the proximal premental sclerite in the labium *Chrysopa* (Fig. 158 B, *c*). The basal region of the silphid labium, lying roximal to the labial suture (A, *lbs*), contains a well-developed postental plate (*Smt*), which here evidently corresponds to the submentum the adult, since there is a distinct though weakly sclerotized area istal to it (*Mt*) in the position of the mentum of an adult beetle (C, *Mt*). many coleopterous larvae, however, the mentum is either entirely

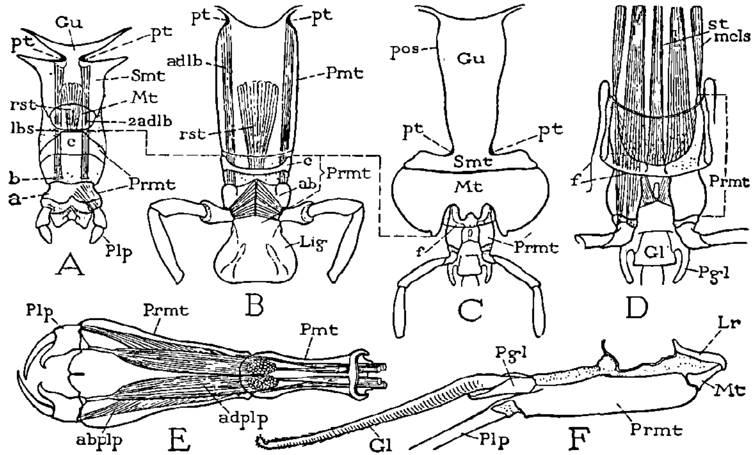

FIG. 158.—Various types of labial structure. A, B, C, larva of *Silpha*, adult *Chry- pa*, and adult *Pterosticus*, showing corresponding division between prementum (*Prmt*) d postmentum (*Pmt*) as determined by the musculature. D, prementum and ligula of ult *Pterosticus*. E, labium of larval dragonfly. F, labium of adult *Bremus*, lateral view.

nrepresented, or its area is included in that of the single postmental late.

A simple condition of this type of structure in the coleopterous rval labium is shown in the Scarabaeidae (Fig. 159 A, B). The body the labium here consists of a movable prementum (A, B, *Prmt*) having e hypopharynx (B, *Hphy*) adnate on its dorsal surface, and of a broad stmental plate (*Pmt*) in the ventral wall of the head. The median tractor muscles of the prementum (A, B, *rst*) arise on the proximal argin of the postmentum. The ventral wall of the prementum conins a distal sclerite (*a*) surrounding the bases of the palpi, two small termediate sclerites (*b*) on which are inserted the ventral adductor uscles (B, 2*adlb*), and a large proximal plate (*c*) giving insertion to the tractor muscles (*rst*). The proximal plate is reflected dorsally on the sides of the prementum to the base of the irregular hypopharynx (B, C, *Hphy*). Various other coelopterous larvae are found to have this same type of structure in the labium, but an extensive comparative study of the labial musculature will be necessary to determine its prevalence. The median muscles of the labium (*rst*) function as retractors of the prementum when the prementum and postmentum are separated by a membranous area, but if the adjacent plates are hinged to each other the muscles become flexors (adductors) of the prementum. The second function is well exemplified in the larva of *Dermestes*.

A second type of labial structure, which is identical with that of the adult, also occurs in the larvae of Coleoptera. In the melandryid larva

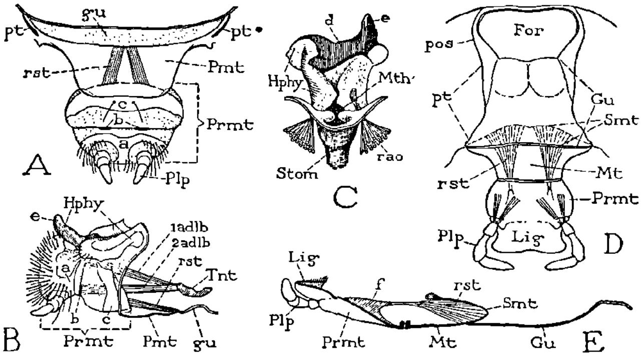

Fig. 159.—Labium of Coleoptera. A, scarabaeid larva, *Ochrosidia villosa*, ventral view. B, same, labium and hypopharynx, lateral view. C, same, hypopharynx and mouth, dorsal view. D, labium of adult *Phyllophaga*, showing submentum invaginated between mentum and gula. E, same, longitudinal section.

(Fig. 160 A) the middle part of the labium (*Mt*), though weakly sclerotized, is a rigid extension from the submentum (*Smt*) and has no muscles inserted upon it. This part of the larval labium evidently becomes the mentum of the adult (B, *Mt*). The prementum is the small terminal part of the labium (A, *Prmt*) retractile within the mentum. The same type of structure occurs likewise in some larval Staphylinidae (C, D), in which the mental region (*Mt*) may be largely membranous, but it is the area of the labium containing the mentum of the adult beetle (Fig. 68 A). In carabid larvae (Fig. 67 D) the labial plate lying between the maxillary cardines is a part of the postmentum (*Pmt*), and apparently its distal part is separated in the adult (Fig. 158 C) from the proximal submental area to form the mentum (*Mt*).

A gular plate is either present or absent in the larvae of Coleoptera and when present is variously developed. Frequently, however, the gular region is entirely membranous (Fig. 160 A, *gu*), and it is often almost obliterated by an approximation of the postgenal areas of the cranium, being reduced in such cases to a median membranous line, or "suture," proximal to the tentorial pits (D, *gu*). In certain coleopterous larvae, especially in the Prionidae, the base of the labium is separated from the neck by a sclerotization uniting the postgenal areas of the cranium, which appears to be a hypostomal bridge. In these larvae there is no true gula, since the tentorial pits remain at the posterior margin of the head.

Associated with the labium in many coleopterous larvae is a pair of bars extending outward from the sides of the prementum or the hypopharynx to the posterior articulations of the mandibles or to the distal extremities of the hypostomal margins of the cranium (Fig. 67 B, *d*). These bars, often called "bracons," lie in the membranous ventral wall of the head between the bases of the mandibles and the maxillae.

Adult Coleoptera.—The labium of adult Coleoptera is typically a three-part structure (Fig. 158 C), there being in its ventral wall a well-defined middle plate (*Mt*) which lies proximal to the insertions of all the labial muscles and is, therefore, a true mentum, that is, a distal plate of the postlabium. The prementum (*Prmt*) is usually small, and its sclerotization is variable, but it always bears the insertions of all the stipital muscles of the labium (D, *stmcls*). Generally the prementum is retractile into the mental region, since the base of the prementum is usually attached to the mentum by an infolded membrane (C, D, *f*); but in some cases the prementum is hinged to the distal margin of the mentum, and its movement is then one of flexion on the latter (Fig. 159 E).

The ligula is generally a distinct part of the adult coleopterous labium, with the glossae and paraglossae more or less separated (Fig. 158 D, *Gl*, *Pgl*), though the glossae are usually united in a median lobe; but the entire ligula may be a single broad terminal flap between the palpi (Fig. 159 D, *Lig*). The muscles of the ligula, when present, as well as those of the palpi arise in the prementum (Fig. 158 D).

The basal region of the adult coleopterous labium generally contains a mentum and a submentum (Fig. 158 C, *Mt*, *Smt*), though the respective areas of the two plates are sometimes confluent or are separated only by a groove or a transverse depression (Fig. 67 C). The wide anterior part of the submentum lies between the maxillary cardines (Figs. 67 C, 68 A); proximally the submentum extends to the posterior tentorial pits (*pt*), and its length, therefore, varies according to the position of the pits. Proximal to the pits it is continuous with the gula (*Gu*). The mentum projects forward from the distal margin of the submentum between the bases of the maxillary stipites and supports the prementum. It is usually a well-developed plate, but its size is variable (Figs. 67 C, 68 A, 158 C, 160 B, *Mt*). When the entire postlabium is sclerotized in the larva, the mentum and submentum of the adult are to be regarded as subdivisions of the postmental plate; if only the proximal part of the larval postlabium is sclerotized, the mentum appears to be developed in the distal membranous part.

An unusual labial structure is found in some adult Scarabaeidae, as in *Phyllophaga* (Fig. 159 D), in which the labium appears to consist only of a prementum (*Prmt*) and a mentum (*Mt*), projecting beyond the large gula (*Gu*). An examination of the inner surface of the labium (E), however, shows that the submentum is represented by an internal recurved plate (*Smt*) deeply inflected between the mentum and the gula, on which arise the median muscles of the prementum (D, E, *rst*). These muscles here act as flexors of the prementum, since the prementum has a definite hinge on the distal margin of the mentum.

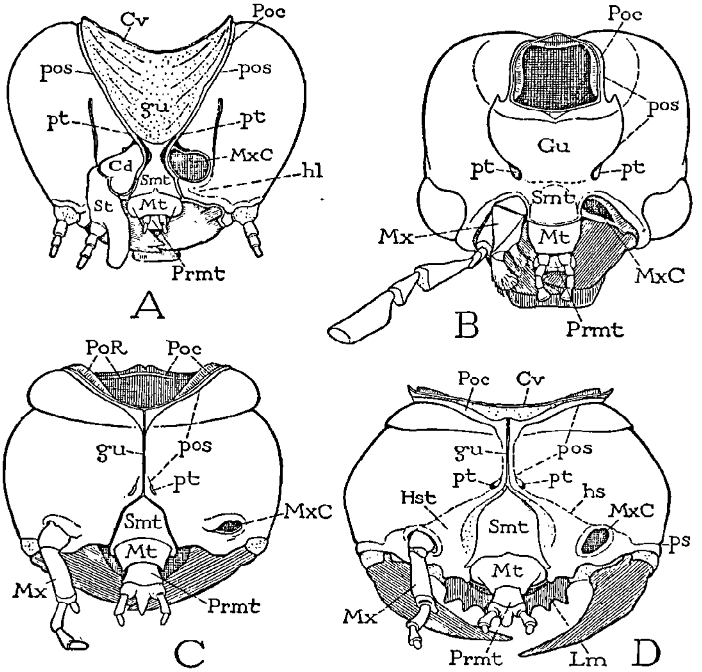

Fig. 160.—Head and mouth parts of Coleoptera. A, larva of *Melandrya* with membranous gular region (*gu*). B, adult *M striata* with well-developed gula (*Gu*). C, larva of *Staphylinus* with gular area represented by a median suture (*gu*). D, adult staphylinid, *Thinopinus pictus*, with same type of structure, but retaining hypostomal sutures (*hs*). *Cv*, neck; *Gu*, gula; *gu*, gular area, either wide or reduced to a median "suture"; *hl*, hypostomal lobe; *hs*, hypostomal suture; *Hst*, hypostoma. *Poc*, postocciput; *PoR*, postoccipital ridge; *pos*, postoccipital suture; *ps*, pleurostomal suture.

4. THE FEEDING MECHANISM OF HYMENOPTERA

The Hymenoptera in classification are usually assigned a place near the top of the series of insect orders, but their structural attainments seem scarcely to warrant so high a rank, and the hymenopterous mouth parts, though adapted in the adult stage for feeding on liquids, are never so highly modified to this end as are the organs of Lepidoptera, Diptera, and Hemiptera. The essential features in the sucking mechanism of the higher hymenopterous families are present likewise in the lower members of the group, showing that the basic structure formed in the latter has been evolved into the specialized structure of the former, and suggesting also that the fundamental mechanism of the mouth parts must have been acquired in the first place as an adaptation to the feeding habits of ancestral forms resembling the modern sawflies, or members of the chalastogastrous families.

The Larval Mouth Parts.—The mouth parts of all hymenopterous larvae are in some respects degenerate, and in parasitic species the reduction is usually carried much further than in others; but in all forms the basic structure of the mouth parts is the same. The feature characteristic of them is a close association or union of the maxillae, the labium, and the hypopharynx to form an under-lip complex, in which the ligula and the hypopharynx are combined in a median lobe on which opens the duct of the labial glands. These glands, at least in the mature stage of the larva, produce the silklike material from which the fabric of the cocoon is spun. The composite feeding and spinning organ of hymenopterous larvae is in many respects identical with the similar organ of lepidopterous larvae, and the likeness in the mouth parts only accentuates the general resemblance between the larvae of the two groups, so conspicuous in the body form of a sawfly larva and a caterpillar.

The hymenopterous larval mouth parts preserve a more generalized condition in the chalastogastrous families, as shown in the larva of *Cimbex* (Fig. 161 A, B, C). The mandibles (A) are strong biting jaws of the ordinary type of structure. The maxillae are united basally with the labium (B), but each consists of a cardo and a stipes (C), with two terminal lobes and a segmented palpus. The labium is distinctly divided into a wide, membranous postmentum (B, *Pmt*) and a distal prementum (*Prmt*) bearing a pair of palpi (*LbPlp*). The ligula (*Lig*) and the hypopharynx (*Hphy*) are united in a median distal lobe, on the apex of which is the spinneret (*Sr*) containing the orifice of the labial glands.

In the aculeate Hymenoptera the larval mouth parts become more simplified, and in some respects more specialized. In Apidae and Vespidae (Fig. 161 D) the mandibles retain the ordinary form and position, but the maxillae and labium are reduced. Each maxilla may consist of a distinct cardo and stipes (*Cd*, *St*), but it always terminates in a single small lobe, which, by comparison with *Cimbex* (C), is apparently the galea, at the base of which is a small papilla possibly representing the palpus. The labium is a simple structure, composed of a basal postmentum (*Pmt*) and a distal prementum (*Prmt*), but its wall contains no distinct sclerites.

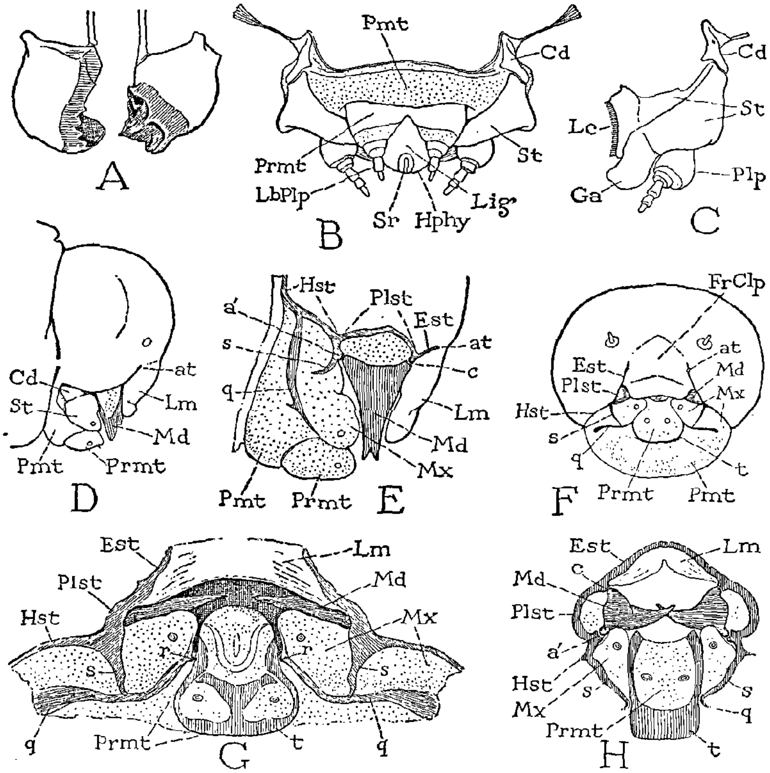

Fig. 161.—Mouth parts of larval Hymenoptera. A, *Cimbex americana*, mandibles. B, same, labium, hypopharynx, and maxillae, ventral view. C, same, left maxilla. D, *Vespa maculata*, head and mouth parts, lateral view. E, *Chrysis*, mouth parts, lateral view. F, *Sphecophaga*, head and mouth parts, anterior view. G, *Exetastes*, mouth parts, ventral view. H, *Itoplectis*, mouth parts, ventral view.

It is in parasitic species that the mouth parts of larval Hymenoptera become most specialized and acquire a distinctive structure. The weakly sclerotized head capsule is generally strengthened along its subgenal regions by strong marginal ridges (Fig. 161 E), forming a prominent bar on each side, differentiated into a hypostoma (*Hst*) supporting the labium and maxillae, and a pleurostoma (*Plst*) bearing the mandibular articulations. Anterior to the mandibles the lateral ridges are usually produced as a pair of epistomal bars (E, F, G, *Est*) extending to the anterior tentorial pits (*at*), but generally the bars are not connected between the pits, the frons and clypeus being thus continuous (F, *FrClp*). In some cases the epistomal bars are united by a transverse ridge at the base of the labrum (H).

The mandibles of more generalized parasitic species have the usual form and position (Fig. 161 E, *Md*); but very commonly they assume a horizontal position and become more or less concealed behind the labrum (F, G, H). In some forms they are very small or rudimentary.

The maxillae in most parasitic species are simple elongate lobes with no demarkation into cardo and stipes (Fig. 161 E, *Mx*). Very commonly, however, a sclerotic spur (*s*) from the hypostoma just behind the mandible extends into the wall of the maxilla, and it may completely divide the maxilla into a proximal part, united with the postmentum, and a free distal part (F, G, *Mx*). Generally the posterior (or ventral) margin of the maxilla is reinforced by a sclerotic bar (*q*), which is sometimes united proximally with the hypostoma (E), but which more commonly ends in a free basal expansion (F, G), though it may be more or less reduced or almost completely suppressed (H, *q*).

The labium preserves its division into postmentum and prementum (Fig. 161 E, F, *Pmt*, *Prmt*). The first is always membranous, but the prementum usually contains a marginal sclerotization, with sometimes a central expansion. The shape of the premental sclerite is highly variable (F, G, H, *t*), but its general form is often characteristic of genera or groups of genera. In some species the premental sclerite articulates laterally with the distal extremities of the maxillary sclerites (G, *r*), on which the prementum apparently is movable. The structure is then very similar to that characteristic of the spinning apparatus of lepidopterous larvae (Fig. 165 D, E). A curious conformation in the mouth region sometimes results from a suppression of the hypostomal ridges and the proximal parts of the maxillary sclerites, accompanied by a strong development of the pleurostomal and epistomal ridges and the spurs (*s*) of the maxillary sclerites to form an oral framework (*H*) supporting the labrum, the mandibles, the maxillary lobes, and the prementum.

The Feeding Mechanism of Adult Hymenoptera.—The mouth parts of adult Hymenoptera have the same fundamental characteristic as those of the larva, namely, the union of the maxillae with the labium, but the terminal parts of the appendages are better developed in the imago and are readily identified in the more generalized forms, while the secretion of the labial glands has the usual "salivary" function.

The Mouth Parts of a Sawfly.—The basic structure of the mouth parts of adult Hymenoptera is well shown in the Tenthredinidae. The mandibles here have the form of typical biting jaws (Fig. 162 B). The maxillae and labium are united in a composite structure (A) suspended from the postgenal margins of the cranium by the basal articulations of the maxillary cardines. Each maxilla (C) is composed of a triangular cardo (*Cd*) and an elongate stipes (*St*); the stipes bears a five-segmented palpus, a broad galea (*Ga*), and a small lacinia (*Lc*). The labium is somewhat compressed between the maxillary stipites and cardines (A), to which it is attached by membrane. The body of the labium consists of a sclerotized prementum (*Prmt*) and of a large, mostly membranous postmentum (*Pmt*) containing a small proximal sclerite (*Smt*). The prementum (*Prmt*) is reinforced by a median internal ridge continued forward from a thickening of its posterior margin and thus appears to be composed of a pair of united sclerites. The muscles of the palpi arise on its inner surface, and the cranial muscles of the labium are inserted upon it. The proximal sclerite of the postmentum (*Smt*) has the position of a submentum and apparently is to be identified with the lorum of the Apidae (Figs. 162 D, 163 A, *Lr*), since it has the relation of the lorum in the basal mechanism of the maxillolabial complex, though it is not connected with the cardines. The terminal lobes of the tenthredinid labium include a pair of free lateral paraglossae (Fig. 162 A, *Pgl*) and a narrow median lobe (*Gl*), which is evidently the united glossae. Arising from the dorsal surface of the labium is a median elevation which is probably the hypopharynx.

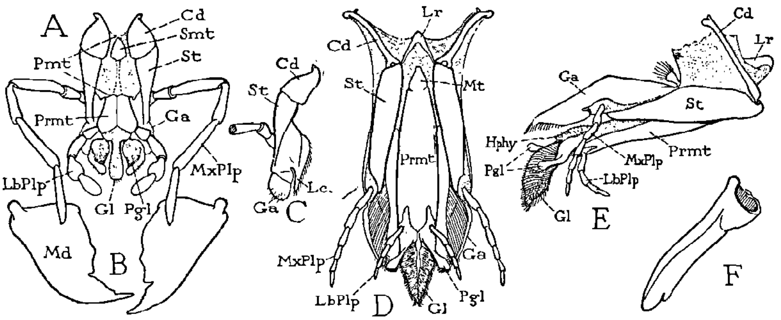

FIG. 162.—Mouth parts of adult Hymenoptera. A, *Pteronidea ribesii*, labium and maxillae. B, same, mandibles. C, same, maxilla detached. D, *Andrena carlini*, labium and maxillae, posterior view. E, same, lateral view. F, mandible of *Andrena*.

The maxillolabial complex of Tenthredinidae is attached to the posterior wall of the head between the postgenal margins of the epicranium by ample membranes, which allow it a free movement on the suspensoria formed of the maxillary cardines. A line of flexure crosses the posterior part of the organ through the stipitocardinal sutures of the maxillae laterally, curving anterior to the submental plate of the labium.

In the usual position, the part distal to this fold lies parallel with the under surface of the head, while the cardosubmental part is bent abruptly toward the head, where it is attached. The entire organ can thus be extended by swinging distally on the maxillary cardines. The distal parts of the maxillae lie dorsal (anterior) to the bases of the labial palpi, and the maxillary lobes are turned in a plane vertical to the surface of the ligula, so that the terminal parts of the labium and maxillae form the floor and sides of a wide troughlike channel leading upward to the mouth over the dorsal surface of the labium.

The maxillolabial organ thus simply formed in the Tenthredinidae from the usual parts of the maxillary and labial appendages is retained with but slight modifications in the majority of adult Hymenoptera, as shown in the series of studies by Bugnion (1925, 1927, 1929, 1930), and it furnishes the basis of the more specialized lapping and sucking apparatus of the bees. The structure and mechanism of the mouth parts of Sphecidae are elaborately described by Ulrich (1924).

The Feeding Mechanism of Bees.—In the bees the mandibles lose the typical biting form and become more or less flattened or spoon shaped to form tools that may be used for a variety of purposes (Fig. 162 F). The maxillolabial complex is lengthened (D, E), and its free parts become modified as accessories to a sucking pump developed from the buccopharyngeal region of the stomodaeum.

A generalized condition of the apoid type of mouth parts is found in some of the solitary bees, such as *Andrena* (Fig. 162 D, E). The prementum (*Prmt*) is here elongate, and the median glossal lobe (*Gl*) forms a short, conical, hairy "tongue," with the paraglossae (*Pgl*) diverging from its base. In the maxillae the laciniae are lost, but the galeae (*Ga*) are enlarged; the palpi (*MxPlp*) are reduced in size, though they retain a distinct segmentation. The cardines (*Cd*) are long, rodlike suspensoria of the maxillolabial complex, articulated with the postgenae, which are united in a median hypostomal bridge behind the base of the labium, as in the honey bee (Fig. 65 C). Between the cardines is a small V-shaped sclerite (Fig. 162 D, *Lr*) articulating laterally with the distal ends of the cardines and supporting the base of the labium. This sclerite, known as the *lorum*, lies proximal to the transverse line of flexion passing through the stipitocardinal joints and thus corresponds in position to the submental sclerite of *Pteronidea* (A, *Smt*). A small triangular plate in *Andrena* united with the base of the prementum (D, *Mt*) is possibly a mentum.

In the higher bees, such as *Xylocopa*, *Bombus*, and *Apis*, still further modifications have taken place in the maxillolabial apparatus. The galeae are large flat blades (Fig. 163 A, *Ga*) much longer than the maxillary stipites; the laciniae are rudimentary or absent; the maxillary palpi, though long in *Xylocopa*, are reduced to small pegs in *Apis* (A, *MxPlp*). The glossal tongue of the labium (*Gl*) is greatly lengthened and highly mobile, being flexible in all directions and capable of an active movement of protraction and retraction. Its base is closely embraced by the relatively small paraglossae (*Pgl*). The labial palpi are long and four segmented (*LbPlp*), the two basal segments of each forming a large flat blade tapering distally to the two small distal segments. The region of the long labial stipites, or prementum (*Prmt*), contains a large, strongly sclerotized plate (commonly called the "mentum" by students of Hymenoptera). The membranous palpigers and the base of the ligula are partly retractile into the anterior end of the stipital region. At the base of the prementum is a small triangular sclerite

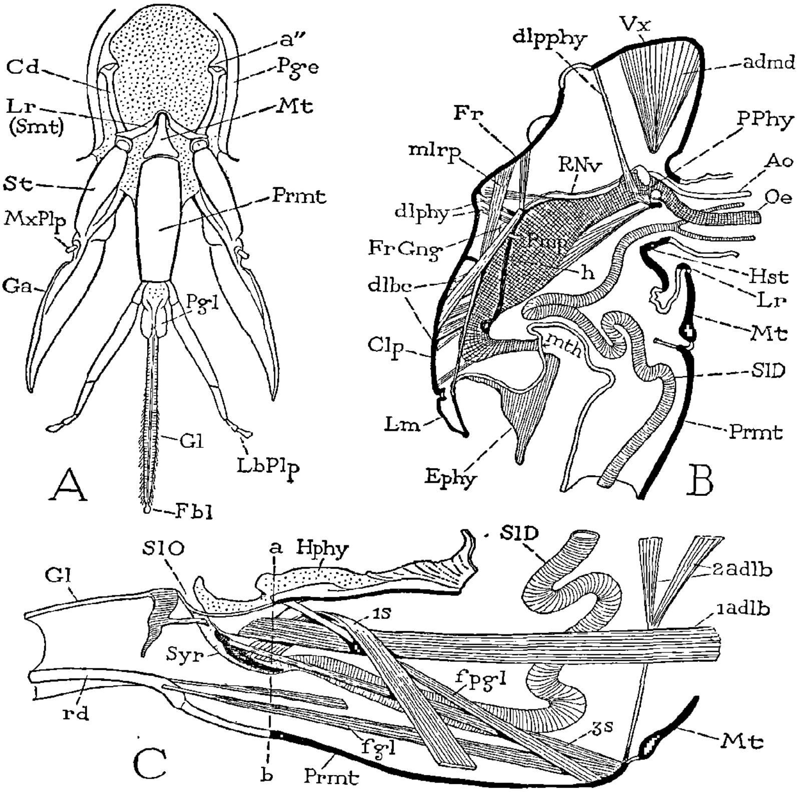

FIG. 163.—Feeding mechanism of adult bees. A, *Apis unicolor*, worker, labium and maxillae with attachment to head. B, section of head of *Xylocopa virginica*, showing sucking pump (*Pmp*). C, section of basal part of labium of *Xylocopa*, showing salivary syringe (*Syr*) and muscles of the prementum.

(*Mt*), which appears to belong to the postlabium, since it lies proximal to the insertions of the posterior cranial muscles of the labium (C, *2adlb*), and may therefore be termed the mentum. The apex of this sclerite fits into the concave angle of the lorum (A, *Lr*), which, as in *Andrena* (Fig. 162 D), articulates by its lateral extremities with the distal ends of the maxillary cardines. Retractor muscles of the prementum are absent in Hymenoptera.

The long glossal tongue of the bees is an organ of particular importance in the feeding mechanism. It is densely clothed with hairs except at its base and terminates in a small lobe called the "spoon," or *flabellum* (Fig. 163 A, *Fbl*). When the bee feeds on a liquid easily accessible, the broad maxillary galeae and the labial palpi are brought together over the tongue, thus improvising a tubular proboscis, the end of which is thrust into the food liquid. By a rapid back-and-forth movement of the tongue the liquid is drawn up into the tube, and from the latter it is sucked up to the mouth by the stomodaeal pump. If the food liquid is confined in a narrow space, as in the corolla of a flower, however, the tongue may be thrust out far beyond the ends of the maxillae in order to obtain it. Both the tongue and the paraglossae are deeply retractile into the distal part of the prementum by an infolding of the membrane at their bases caused by a contraction of the glossal muscles (C, *fgl*). In some of the shorter tongued bees the maxillary galeae are stiff, sharp-pointed blades and are used for cutting through the outer wall of a corolla in order to gain access to the nectar within.

The posterior surface of the glossal tongue is excavated by a deep channel which extends from the flabellum to the base of the tongue, where the latter is closely embraced by the paraglossal lobes. Dorsally, the paraglossae cover the salivary orifice located on the oral surface of the labium at the distal end of the prementum (Fig. 163 C, *SlO*). The paraglossae thus evidently serve to conduct the salivary secretion around the base of the tongue into the channel on the ventral side of the organ, through which it is conveyed to the tip of the latter to be mixed with the food during ingestion.

The salivary duct (Fig. 163 C, *SlD*) opens into the lumen of an expulsive apparatus known as the *salivary syringe* (*Syr*). This organ consists of an elongate pouch with two pairs of muscles inserted on its walls. Its outlet is the functional salivary orifice (*SlO*) located on the distal extremity of the prementum between the base of the glossal tongue and the rudimentary hypopharynx (*Hphy*). There can be no doubt, therefore, that the syringe is a development of the salivarium, which in its primitive form is a simple salivary pocket at the junction of the hypopharynx with the oral surface of the labium (Fig. 155, *Slv*). In *Xylocopa* the syringe is provided with two pairs of long muscles arising in the prementum (Fig. 163 C, 1*s*, 3*s*), but in *Apis* the dorsal pair (1*s*) have their origin on the lateral margins of the hypopharyngeal surface (*Hphy*) and thus correspond to the usual hypopharyngeal dilators of the salivarium (Fig. 155, 1*s*).

The sucking pump of the bees is a large muscular sac lying entirely within the head anterior to the brain (Fig. 163 B, *Pmp*). The morphology of the organ is not entirely clear, but, judging from its musculature, it includes without doubt the pharynx and the buccal cavity and perhaps the cibarium. Its dorsal dilator muscles are separated into two groups inserted anterior and posterior to the frontal ganglion (*FrGng*) and its connectives. Those of the first group (*dlbc*) arise on the clypeus; those of the second group (*dlphy*) take their origin on the frons. On the floor of the pump, just within the mouth, is a broad sclerotic plate, from which a long arm (*h*) extends posteriorly and dorsally on each side in the lateral wall of the organ and gives insertion to a pair of convergent muscles, one arising on the clypeus, the other on the frons. It is perhaps possible that these bars represent the oral arms of the hypopharyngeal suspensoria of more generalized insects (Fig. 60, *y*). A pair of large ventral dilator muscles of the pump arise on the transverse bar of the tentorium. The posterior end of the pump narrows to a more slender tube, which passes between the brain and the suboesophageal ganglion, and enlarges again in a small posterior pharynx (*PPhy*) lying in the rear part of the head behind the brain. The posterior pharynx is provided with a pair of long slender dorsal dilator muscles (*dlpphy*), and a pair of short ventral dilators arising on the tentorium.

5. THE FEEDING MECHANISM OF LEPIDOPTERA

In the Lepidoptera the structural divergence between the mouth parts of the larva and those of the adult has been carried to a still greater degree than in the Hymenoptera. The mouth parts of a caterpillar show a general resemblance to those of the larvae of Hymenoptera, and in each group the salivary glands secrete a substance that becomes silky when extruded and which may be used for constructing a cocoon. The mouth parts of a moth or butterfly, on the other hand, have little to suggest a common origin with the mouth parts of a wasp or bee, since in the majority of Lepidoptera the mandibles are rudimentary or absent and the labium is eliminated from the feeding mechanism. In all but certain generalized forms the maxillae remain as the only appendages involved in the apparatus of ingestion, and they are greatly modified by a reduction of the palpi, the loss of the laciniae, and the elongation of the galeae to form a tubular *proboscis*. The sucking pump of the Lepidoptera, as in the Hymenoptera, is formed largely of the precerebral pharyngeal region of the stomodaeum, but it appears to include the cibarium. Its dorsal dilator muscles take their origin on the frontoclypeal plate of the head wall.

THE FEEDING AND SPINNING ORGANS OF A CATERPILLAR

The mouth parts of a caterpillar are of the biting and chewing type of structure as far as the function of feeding is concerned, but they are used for various purposes other than that of taking food. The mandibles, for example, serve with many species as implements for gnawing and tunneling, while the maxillae, labium, and hypopharynx are always united in a large under-lip complex on which opens the duct of the silk-forming labial glands, and its activities, therefore, mostly pertain to the function of "spinning."

The Mandibles.—The caterpillar's mandibles are jaws of the ordinary biting and chewing form (Fig. 164 B). Each is hinged to the head by posterior and anterior articulations (*a′*, *c*) of the usual type of structure. The abductor muscles are relatively small, but the great adductors (Fig. 64 B, *admd*) occupy most of the lateral parts of the head cavity and appear to determine the size and form of the lateral hemispheres of the cranium. Some species of caterpillars are provided with a pair of large tubular mandibular glands reaching often far back into the thorax and abdomen, the duct of each extending down to the inner edge of the base of the mandible close to the apodeme of the adductor muscle.

The Maxillolabial-hypopharyngeal Complex.—The maxillae, the labium, and the hypopharynx in the caterpillars, as in hymenopterous larvae, are united to form a large composite structure that projects like a thick under lip behind the mouth and bears the spinneret at its tip (Fig. 164 C). Basally the organ is supported on the hypostomal lobes (*Hst*, *Hst*) of the postgenae, which are approximated medially between the neck and the base of the labium.

The walls of the under-lip complex (Fig. 164 C) may be largely membranous, the sclerotization being usually broken up into various small plates; but by observing certain landmarks the components of the organ can be pretty well defined. Two lateral lobes, representing the maxillae, are more or less distinct from a median lobe formed of the labium and hypopharynx. A small plate (*Cd*) at the base of each lateral lobe is evidently the cardo, since it articulates (*a″*) with the hypostoma (*Hst*) and bears the insertions of the tentorial cardinal muscles. On the mesal border of each lateral lobe is the line of a strong internal ridge (Fig. 164 C, *q*) upon which are inserted the usual stipital muscles of the maxilla. The areas laterad of the ridges, therefore, are the maxillary stipites (*St*). Each stipital area ends distally in a membranous lobe (*Lo*), usually having small sclerites in its walls and bearing terminal papillae provided with sense organs. Three muscles are inserted on the base of the lobe, two arising in the stipes and one on the hypostoma, but the homology of the lobe is difficult to determine in the ordinary caterpillar structure. In the micropterygid *Sabatinca*, however, the larval maxilla, as shown by Tillyard (1922), ends with a three-segmented palpus and a distinct lacinia and galea (Fig. 167 A).

The median component of the under-lip complex of the caterpillar consists of the labium and the hypopharynx. Its proximal part is the postmentum (Fig. 164 C, *Pmt*), which may be an entirely membranous area, though it frequently contains a postmental sclerite (Fig. 164 C, *pmt*). The distal part, which forms a free median lobe between the terminal lobes of the maxillae (*Lo*), is the prementum (*Prmt*) with the hypopharynx (*Hphy*) adnate upon its anterior surface. It bears distally the spinneret (*Sr*), a hollow spine having the orifice of the silk duct at its extremity. Labial palpi are absent, unless they are represented by the pair of small papillae located at the sides of the spinneret.

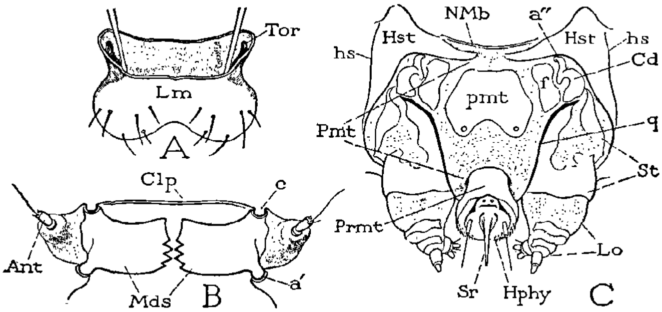

FIG. 164.—Mouth parts of larval Lepidoptera. A, *Lycophotia margaritosa*, labrum, anterior view. B, *Estigmene acrea*, mandibles, ventral view. C, same, labium, hypopharynx, and maxillae united and suspended from hypostomal lobes of cranium.

The mouth parts of larval Trichoptera are structurally identical with those of the caterpillars. The maxillae and labium are united in the same manner, and the hypopharynx is fused with the small prementum. The postmentum, however, is elongate and contains a relatively large plate included between the elongate postgenal areas of the cranium. In some species the postmental plate simulates a gula, but the posterior tentorial pits are always at the neck margin of the head. All the labial muscles are inserted on the prementum, but the median retractors are absent, as they are in the caterpillars. The maxillary musculature is the same as that of a caterpillar.

The Spinning Apparatus.—The material of the silk threads spun by caterpillars is secreted by the labial glands, which consist of a pair of greatly elongate tubes lying in the body cavity at the sides of the alimentary canal (Fig. 196, *SkGl*). The ducts of these *silk glands*, after receiving the ducts of a pair of small accessory acinous glands, sometimes called the *glands of Filippi*, unite in a short median conduit that opens into the base of an organ known as the *silk press* (Fig. 165, A, B, E, *Pr*). The press lies in the median lobe of the mouth parts formed of the united hypopharynx and prementum (A, C). It discharges through a narrow terminal duct that opens on the tip of the spinneret (*Sr*) located on the distal surface of the hypopharyngeal-premental lobe. The dorsal wall of the press is deeply invaginated into the lumen of the organ (F) and contains a median sclerotic bar, or raphe (*Rph*), on which are inserted two or three pairs of muscles (A, B, C, E, F, *17*, *18*) having their origins on the dorsolateral parts of the spinneret-bearing lobe. Another pair of muscles (*19*) arising ventrally in the premental part of the lobe is inserted on the lateral walls of the press (E, F). Both sets of muscles apparently are dilators of the press lumen, the antagonistic force being the elasticity of the infolded dorsal wall of the organ.

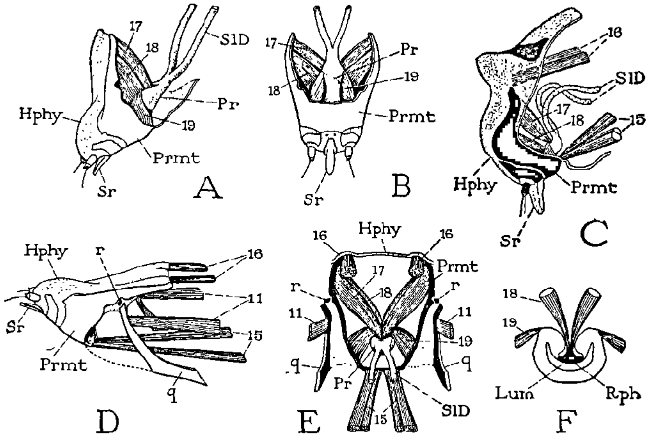

FIG. 165.—Spinning apparatus of caterpillars. A, premento-hypopharyngeal lobe of a noctuid caterpillar, with silk press and spinneret, lateral view. B, same, ventral view. C, same of *Malacosoma americana*, lateral view. D, premento-hypopharyngeal lobe of a noctuid, showing support on maxillary arms (*q*), and muscles, lateral view. E, same in cross-section, posterior view. F, diagrammatic cross-section of silk press.

Morphologically the silk press of the caterpillars is a highly specialized development of the salivarium of more generalized insects (Fig. 155, *Slv*). By the complete union of the hypopharynx with the prementum the press has become entirely enclosed between the component elements of the hypopharyngeal-premental lobe, and its outlet duct represents the persisting remnant of the salivary passage (*sm*) between the hypopharynx and the labium. Its dorsal muscles are the hypopharyngeal dilators of the salivarium (1*s*), its ventral muscles are those normally arising in the prementum (2*s*, 3*s*).

The spinneret-bearing lobe of the caterpillar is supported laterally at its base on two sclerotic bars (Fig. 165 D, E, *q*), which are the distal arms of the mesal ridges of the maxillary stipites (Fig. 164 C, *q*), articulated by their extremities (Fig. 165 D, E, *r*) with the sides of the prementum. Upon these fulcra the entire spinning apparatus can be swung up and down, or anteriorly and posteriorly, by muscles inserted upon its base. The spinning muscles comprise a pair of ventral labial muscles (*15*) inserted on the base of the prementum, and a pair of dorsal hypopharyngeal muscles (*16*) inserted on the base of the hypopharyngeal surface, both pairs taking their origin on the tentorium. The fulcral arms (*q*) give insertion to a pair of maxillary adductors (*11*). The numerous other movements made by the caterpillar in the act of spinning are produced by the elaborate musculature of the back of the head and the anterior part of the body.

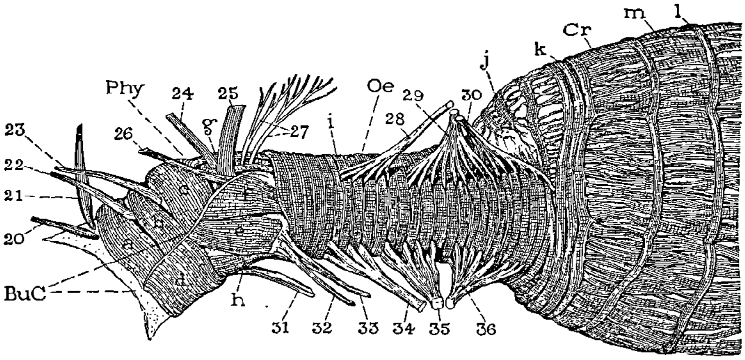

Fig. 166.—Anterior part of the stomodaeum of a noctuid caterpillar. *20–23*, dilator muscles of buccal cavity arising on clypeal triangle of cranium; *24–27*, precerebral dorsal dilators of pharynx; *28–30*, postcerebral dorsal dilators of oesophagus; *31–36*, ventral dilators of pharynx and oesophagus.

The Head Stomodaeum.—The mouth of the caterpillar opens into a wide stomodaeal chamber, covered externally by broad plaques of muscle fibers, lying anterior to the nerve ring of the head (Fig. 166, *BuC*, *Phy*). The chamber is evidently the buccopharyngeal region of the stomodaeum, since its dorsal dilator muscles are separated into two groups by the frontal ganglion and its connectives, those of one group (*22*, *23*) arising on the triangular clypeus, while those of the other group (*24*, *25*, *26*, *27*) arise on the postclypeal areas of the head. A third anterior set of muscles (*20*, *21*), arising also on the clypeus, is inserted just before the first transverse muscles (*a*) of the stomodaeal wall. These muscles are clearly cibarial muscles. The part of the stomodaeum lying in the head behind the nerve ring is merely a wide cylindrical oesophagus (*Oe*) with strong circular muscles. The dilator muscles inserted upon it, however, show that this part of the stomodaeum in the caterpillar corresponds to the posterior pharynx in Orthoptera and Coleoptera (Fig. 156 D 192, 193, *PPhy*).

THE FEEDING ORGANS OF ADULT LEPIDOPTERA

With most of the Lepidoptera the mouth parts undergo a radical change in structure during the metamorphosis from the larva to the imago. The mandibles become rudimentary or are entirely suppressed; the terminal parts of the maxillae are transformed into long half tubes, which, together, form the characteristic coiled proboscis of the imago (Fig. 168, *Prb*); the labium is reduced to little more than a flap, but it acquires a pair of large palpi (*LbPlp*); the anterior part of the stomodaeum is developed into an efficient sucking pump (Fig. 169 F, *Pmp*). In the primitive family Micropterygidae the adult mouth parts have a more generalized structure, and one which clearly demonstrates the evolution of the sucking apparatus of the Lepidoptera from mouth parts of the usual biting type, and not from a mouth-part structure of the larval type. The feeding and spinning mouth parts of the caterpillar, therefore, appear to represent a specialized larval condition adaptive to the needs of the caterpillar.

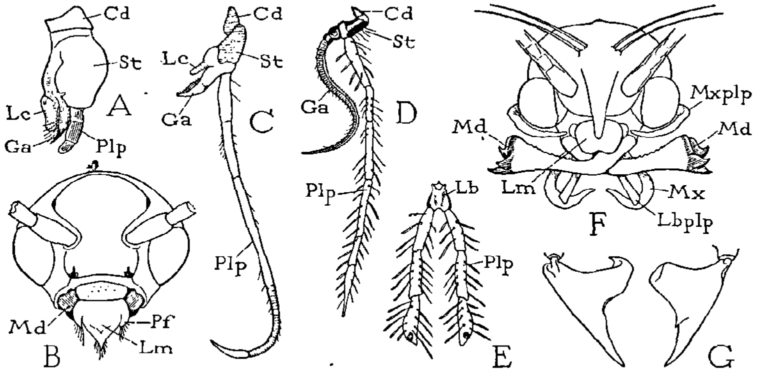

FIG. 167.—Mouth parts of Micropterygidae. A, *Sabatinca barbarica*, larval maxilla. B, *Micropteryx ammanella*, head of adult. C, *Micropteryx aruncella*, maxilla of adult. D, *Mnemonica auricyanea*, maxilla of adult. E, same, labium of adult. F, same, head of pupa. G, *Sabatinca incongruella*, mandibles of pupa. (A, C, G *from Tillyard*, 1922, 1923; B, D, E, F *from Busck and Böving*, 1914.)

Generalized Lepidopterous Mouth Parts.—The members of the Micropterygidae are moths in every essential respect, but they have mandibulate mouth parts in the larval, pupal, and adult stages. The mandibles of the pupa and imago are typical functional jaws (Fig. 167

B, G). Those of the adult are said by Tillyard (1923) to work in conjunction with brushes of the epipharynx and hypopharynx and a basket-like structure on the hypopharynx "as grinders of the minute pollen grains or other fine vegetable matter which forms the food of the imago." The maxillae have a typical generalized structure, each being composed of a basis formed of a cardo and stipes (C, *Cd*, *St*) and provided with a long palpus (*Plp*) and two terminal lobes (*Ga*, *Lc*). The lacinia (*Lc*), however, is much smaller than the galea (*Ga*). The labium is rudimentary in that its median part is reduced to a simple lobe, but it bears two large three-segmented palpi.

In the Eriocranidae, a related family, the mouth parts show their origin from the micropterygid type of structure, but they take on the peculiarities of the typical lepidopterous feeding organs. Mandibles are present in the adult stage, though they are very small and probably functionless. In the pupa, however, they are extraordinarily large (Fig. 167 F, *Md*) and are so constructed that they open forcibly outward, thus enabling the pupa to use its jaws for liberating itself from its tough underground cocoon and for digging upward to the surface of the earth. The maxilla of the adult (D) has a large six-segmented palpus (*Plp*) and a long slender galea (*Ga*), but the lacinia is absent. The galeae of the two maxillae are grooved on their opposing surfaces, which are joined to form a curved proboscis capable of being partly coiled. The labium is a simple lobe with long three-segmented palpi (E).

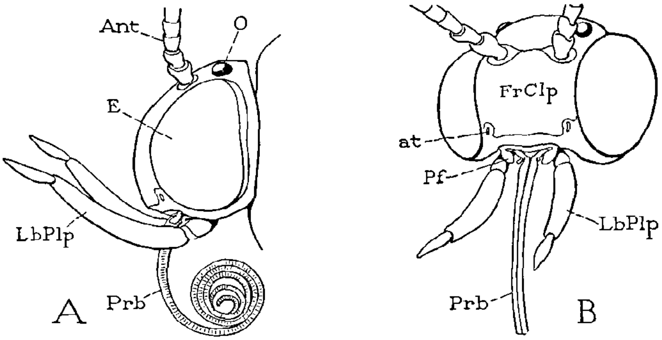

Fig. 168.—Head of peach-tree borer moth, *Synanthedon exitiosa*.

The Typical Feeding Mechanism of Moths and Butterflies.—The feeding mechanism characteristic of the Lepidoptera is a simple device for extracting nectar from the depths of flower corollas. It consists essentially of a long tube, the proboscis (Fig. 168 A, B, *Prb*), arising from the oral region of the head, where its lumen opens into the mouth (Fig. 169 F, *mth*), and of a pumping organ (*Pmp*) formed of the anterior part of the stomodaeum. Though nectar is the principal food of adult moths and butterflies, the feeding apparatus serves as well for imbibing exposed liquids, such as water and the juices of fruits. Many species, however, take no food of any kind, and in such species the mouth parts are usually reduced, in some they are rudimentary and functionless, and the mouth pump is entirely absent, the stomodaeum being reduced in the head to a threadlike tube.

The Labrum.—The labrum is never large; usually it is a narrow transverse band at the lower edge of the large clypeal region of the face (Fig. 169 A, C, D, *Lm*). On its lateral extremities it bears a pair of small, hairy lobes, the *pilifers* (A, *Pf*), which are present likewise in the Micropterygidae (Fig. 167 B, *Pf*).

The Mandibles.—Rudiments of the mandibles occur in some macrolepidopterous moths as small immovable lobes projecting from the cranial walls at the sides of the labrum (Fig. 169 D, *Md*). The reduction of the jaws from the larval size takes place at the transformation from the caterpillar to the pupa, and again at the change from the pupa to the moth. In most species the mandibles are entirely obliterated in the adult.

The Proboscis.—The essential external part of the sucking apparatus is the proboscis. This organ is formed of the greatly elongate terminal lobes of the maxillae, which, as we have seen, are probably the galeae, the laciniae being reduced and suppressed. The proboscis is thus composed of two lateral pieces, which are held together by interlocking grooves and ridges (Fig. 169 E). The opposed walls are thickened and concave and enclose between them a canal (*fc*) through which the liquid food or drink of the insect is drawn up to the mouth by the stomodaeal pump (F, *Pmp*). The basal part of each maxilla usually shows a division into a small cardo (B, *Cd*) and a larger stipes (*St*), the latter bearing a rudimentary palpus (*Plp*) and the elongate galea (*Ga*).

When the proboscis is not in use it is tightly coiled beneath the head, but it can be completely extended in response to a food stimulus. The mechanism of extension and coiling, however, is not well understood. The outer wall of each half of the proboscis shows a closely ringed structure produced by a succession of sclerotic arcs alternating with narrow membranous spaces. This structure probably allows the coiling of the tube. Within each half of the latter there is a series of short muscle fibers arising near the middle of the outer wall (Fig. 169 G, *mcls*) and extending obliquely distad and toward the inner edge of the concave side of the organ, on which they have their insertions. The muscles occupy the entire length of each half of the proboscis, and their arrangement suggests that they serve to coil the proboscis. Unless there is some mechanical principle here involved that is not yet understood, we must assume, then, that the proboscis is extended by blood pressure, in the same way that a toy paper "snake" is unrolled by inflating it, and it must be observed that the natural uncoiling of the lepidopterous proboscis, beginning at the base and progressing toward the tip, has a striking resemblance to the unrolling of the inflated "snake." The mechanism for creating the assumed blood pressure, however, is not evident.

With species that do not feed in the adult stage the proboscis is usually short and weak, and in some forms the entire maxillae are reduced to small lobes projecting at the sides of the mouth (Fig. 169 C, *Mx*).

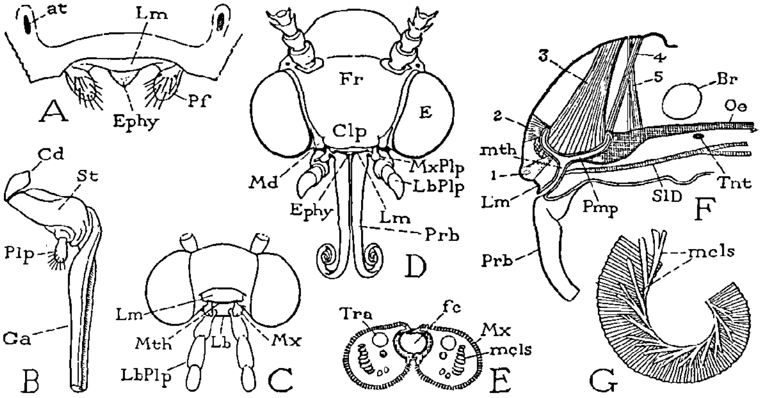

FIG. 169.—Mouth parts and sucking apparatus of adult Lepidoptera. A, *Synanthedon exitiosa*, labrum, epipharynx, and pilifers. B, same, base of maxilla. C, *Malacosoma americana*, showing rudimentary maxillae. D, *Hyphantria cunea*, head and proboscis. E, cross section of proboscis of *Danais archippus*. (*From Burgess*, 1880.) F, section of head of sphinx moth, showing sucking pump, diagrammatic. G, diagram of part of proboscis and its muscles.

The Labium.—In all adult Lepidoptera the labium has the simple form it has in the Micropterygidae and Eriocranidae (Fig. 167 E), being at most a small lobe or flap, but often it is reduced to a mere membranous area behind the base of the proboscis supported posteriorly on a hypostomal bar uniting the postgenal areas of the epicranium. The three-segmented labial palpi, however, are usually well developed and covered with long hairlike scales, forming thus two conspicuous brushes projecting upward at the sides of the proboscis.

The Sucking Pump.—A sucking organ is highly developed in adult Lepidoptera having functional mouth parts; but with species in which the proboscis is rudimentary or absent, the pump is likewise rudimentary, the mouth opening into a small funnel leading into the simple slender stomodaeum. The functionally developed pump of the Lepidoptera includes the buccopharyngeal region of the stomodaeum, as it does in Hymenoptera, since the frontal ganglion lies on its dorsal wall, and the dorsal dilator muscles are inserted before and behind the connectives of the ganglion; but it is to be suspected that the anterior part of the organ may be formed by the cibarium. The sucking pump of the Lepidoptera, however, has been but little studied, and no definite statement can be made as to its morphology until we have more comparative information on its structure and the relation of its muscles to the head wall.

In the sphinx moth the sucking pump is a large bulblike structure with strongly muscular walls lying in the anterior part of the head (Fig. 169 F, *Pmp*). It opens on the base of the proboscis through a narrow neck and tapers posteriorly into the oesophageal tube. The first dilator muscle (*1*) consists of a transverse sheet of fibers arising on the lower edge of the clypeal region of the head wall and inserted on the neck of the pump. Above these muscles is a median mass of fibers (*2*) inserted on the anterior end of the bulbous part of the pump. The principal dilators, however, comprise two thick, paired bundles of fibers (*3*) arising on the upper part of the facial region of the head and inserted laterally on the dorsal wall of the pump anterior to the frontal ganglion and its connectives. Posterior to the frontal ganglion are a pair of smaller muscles (*4*) and a single median muscle (*5*), the insertions of which show that the rear part of the sucking organ at least is the pharynx, as it is in Hymenoptera.

6. THE FEEDING MECHANISM OF DIPTERA

The differentiation between larval and imaginal structures in insects has reached its highest degree in the mouth parts of the Diptera, for here both adults and larvae have widely diverged from the ancestral norm, and in the higher families the maggots have outdone the flies. In fact, in the Cyclorrhapha it appears that the larvae have developed not only a feeding mechanism but also a functional head and mouth that have little relation to the cephalic structures of the imago. The true mouth parts of the fly are entirely suppressed during the whole larval period, the major part of the head is invaginated into the body, and a new set of organs is developed to serve the purposes of the maggot. The imaginal parts are restored during the pupal transformation and then developed directly into the specialized form characteristic of the adult. In the more generalized Orthorrhapha, however, the larva retains the usual head structure and a feeding mechanism that clearly demonstrates the origin of the Diptera from insects having typical biting mouth parts.

Mouth Parts of Dipterous Larvae

Only the extreme types of dipterous larval mouth parts will be described here, one representing the most generalized form, occurring in the Orthorrhapha, the other the highly specialized structure developed in the muscoid maggot. The intermediate stages between these extremes are still not well understood and offer an inviting field for further exploration.

The Orthorrhaphous Type of Larval Mouth Parts.—In the larvae of Tipulidae or Tabanidae and related families the head is an elongate oval capsule with strong sclerotic walls, but it is almost completely retracted into the anterior part of the thorax (Fig. 170 A), where it is enclosed in a membranous sheath formed by an inflection of the neck membrane (*Cv*). The dorsal wall of the head, however, is much longer than the lateroventral walls, which taper anteriorly and are united below in a small, toothed, triangular hypostomal lobe (*Hst*) projecting beneath the mouth (*Mth*) and the rudimentary labium (*Lb*). The brain and the suboesophageal ganglion are withdrawn from the head and lie in the middle of the thoracic region of the body, but long nerve trunks extend forward from them to the organs of the head normally innervated by these ganglia.

The mandibles in the tipulid larva are strongly musculated jaws of the generalized biting type of structure (Fig. 170 B). In the tabanid larva the mandibles are rudimentary, but in various other families of the more generalized flies, as in the Chironomidae and Culicidae, the larval mandibles are also jawlike in form.

The maxillae of the tipulid larva are small flat lobes (Fig. 170 C), in which the usual parts of a maxilla are somewhat indefinitely separated. In the larva of *Tabanus*, however, the maxillae have a more generalized structure, each organ (D) comprising a basal lobe (*Cd*), which is apparently the cardo, and a larger stipes (*St*) bearing a distinct galea (*Ga*) and a lacinia (*Lc*), but the palpus is absent.

The labium is rudimentary in all fly larvae, and the hypostomal lobe of the ventral head wall is frequently mistaken for it. In the larva of *Tipula* the labium is a small median projection beneath the mouth (Fig. 170 A, *Lb*), but it is concealed above the hypostoma (*Hst*). United with the labium is a small hypopharyngeal lobe (*Hphy*), and between the latter and the labium opens the duct of the salivary glands (*SlD*).

The head stomodaeum of the tipulid larva is a straight tube (Fig. 170 A, *Stom*), slightly widened anteriorly, but showing no structural differentiation into buccal, pharyngeal, and oesophageal regions. On its dorsal wall are inserted three groups of dilator muscles. The fibers of the first group (*dlcb, dlbc*) belong to the cibariobuccal region; those of the second and third groups (*dlphy*) correspond to the dilators of the anterior pharyngeal region in other insects (Fig. 155, *Phy*), since they are inserted posterior to the connectives of the frontal ganglion (*FrGng*) and are precerebral in position, the brain being withdrawn into the thorax.

The Muscoid Type of Larval Mouth Parts.—In the higher cyclorrhaphous Diptera the usual mouth parts are entirely suppressed in the larval stage, and the only external feeding organs of the maggot are a pair of strong mouth hooks movable in a vertical plane. Moreover, the entire facial region of the head posterior to the clypeus, including the area of the frons and that of the imaginal antennae and compound eyes, is invaginated (not merely retracted) into the thorax, and a circular fold of the neck projects beyond the mouth to form a conical snout, which is the functional "head" of the maggot.

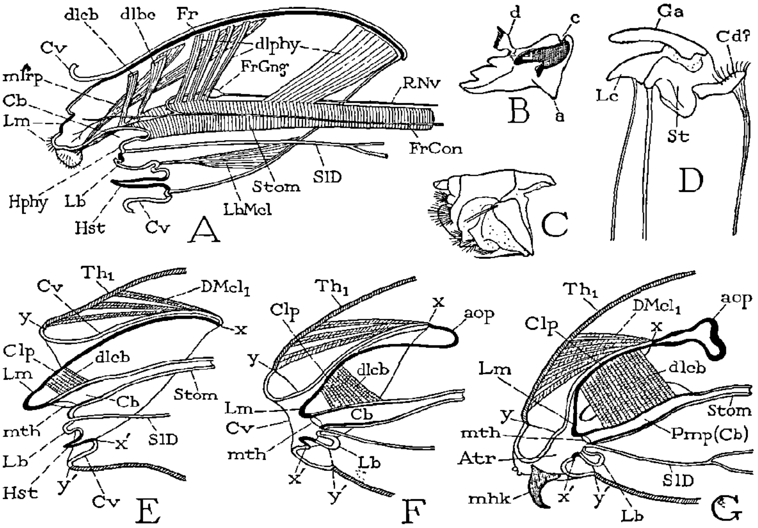

FIG. 170.—Head and mouth parts of larval Diptera. A, *Tipula abdominalis*, diagrammatic section of retracted head. B, same, right mandible, mesal view. C, same, left maxilla, outer view. D, *Tabanus punctifer*, left maxilla, outer view. E, F, G, diagrams illustrating stages in the invagination of the head of a muscoid maggot.

To understand the morphology of the extraordinary head structure of the cyclorrhaphous maggot, we must trace its evolution from the head structure of a simpler type, possibly from an invaginated head of the tipulid or tabanid variety (Fig. 170 E). First, we must assume that the neck membrane (*Cv*), between the points x and y above, and x' and y' below, has been extended in a fold (F, *Cv*) somewhat beyond the mouth (*mth*) of the retracted head, while, at the same time, the areas of the dorsal wall of the head on which the antennae and compound eyes of the adult are to be formed have become invaginated posterior to the clypeus (F, *Clp*) as a pair of lateral pouches (*aop*, only the right pouch shown in the figure), which contain the histoblastic rudiments of the antennae and compound eyes. Next, apparently, the cleft between the two antenno-ocular pouches has been extended forward through the clypeal region, dividing the latter mesally into two lateral plates covered by the closely appressed neck membrane, forming thus two flat, double-walled wings on which the clypeal muscles (*dlcb*) take their origin, and from the posterior ends of which the antenno-ocular pouches (*aop*) extend into the thorax. Finally, by a further extension of the neck fold, there is established within the latter a preoral cavity, known as the *atrium* (G, *Atr*). The functional mouth (*mth*) is thus situated at the inner end of the atrium, and the closed passages from the antenno-ocular pouches over the wings of the clypeus are confluent at the labrum (*Lm*) in a dorsal diverticulum of the atrium just before the mouth. The neck fold enclosing the atrium now becomes the apparent larval head. Below the oral aperture is a pair of very small ectodermal pouches said to contain the histoblasts of the imaginal labium (*Lb*), the labium being suppressed as an external organ in the larva in the same way as are the thoracic appendages. Just within the lips of the atrial opening there project, one on each side, the two mouth hooks (*mhk*), the substitute jaws of the maggot.

Along with the numerous transpositions that so alter the cephalic structure of the cyclorrhaphous larva, the ingestive apparatus becomes highly developed and specialized. In the tipulid larva (Fig. 170 A) it is to be observed that the cibarium (*Cb*) has a typically orthopteroid position and structure, and that the cibarial and buccal dilators (*dlcb, dlbc*) form a distinct group of muscles separated from the true pharyngeal dilators (*dlphy*) by the frontal ganglion connectives. In the cyclorrhaphous larva (G) the cibarium is transformed into a large sucking pump (*Pmp*), with its great mass of dilator muscles (*dlcb*) arising on the invaginated clypeal surface of the head (*Clp*). The orifice of the pump (*mth*) is the functional mouth, but the true mouth is the opening from the pump lumen into the stomodaeum (*Stom*). The floor of the pump is the base of the hypopharynx, and the salivary duct (*SlD*) opens in the normal position between the hypopharynx and the labial rudiment (*Lb*). The lateral walls of the pump and the walls of the clypeal wings leading back to the antenno-ocular pouches (*aop*) become strongly sclerotized, forming the conspicuous sclerotic structure lying in the anterior end of the maggot, commonly known as the "pharyngeal skeleton" or "bucco-pharyngeal armature."

The mouth hooks of the cyclorrhaphous larva (Fig. 170 G, *mhk*) are often called "mandibles," but since they are solid cuticular structures, shed with each moult, arising from the lips of the atrial cavity (*Atr*), which is evidently derived from the infolded neck membrane, it is not clear how the larval jaws can have any relation whatever to true mandibles. Furthermore they lie in vertical planes and are moved by muscles taking their origins on the lateral walls of the cibarial pump. The mouth hooks thus appear to be secondary cuticular structures developed for the purposes of the maggot. After the third moult they are not renewed.

The accompanying diagrams (Fig. 170 E, F, G) perhaps do not express accurately all the relations in the larval head structures, since there are still certain points that are obscure, but the known facts of development and of comparative anatomy demonstrate that in some such way as that indicated the peculiar structures of the cyclorrhaphous maggot have been evolved from the more usual type of head structure. Essentially, the condition is one in which not only the appendages but a large part of the head as well have been reduced to histoblastic rudiments and withdrawn into the body during the larval stage, to be everted later during the pupal transformation in order to complete their development into the imaginal parts. In most insects the invaginations that contain the imaginal histoblasts do not appear until the last larval stage; in the higher Diptera they are formed in the embryo and thus become a part of the larval structure. A much more primitive condition occurs in some of the lower Diptera, as in *Chironomus* and *Psychoda,* in which the antenno-ocular pouches are formed only in the pupal integument developed in the last larval instar, while the other features of the cyclorrhaphous larva do not appear at all.

THE FEEDING MECHANISM OF ADULT DIPTERA

No adult dipteron has mouth parts of the typical biting type of structure. Though certain flies are said to "bite," the effect is the result of a puncture and not of a pinch. The majority of flies are incapable of inflicting any kind of wound. The familiar "biting flies" belong to two groups; in one group the mandibles are the piercing organs, in the other the labium is the effective instrument. Mandibles occur only in a few of the more generalized families of Diptera, being present in the females of *Phlebotomus* (Psychodidae), Dixidae, *Culicoides* (Chironomidae), Culicidae, various species of Simuliidae, and in Tabanidae. Among male flies mandibles are said to occur only in certain species of *Simulium.* Flies having a piercing labium include principally the tsetse fly, stable fly, and horn fly of the family Muscidae. The robber flies (Asilidae) also should be included among the biting flies, though they confine their attacks to other insects. The piercing organ of the robber flies, however, appears to be the hypopharynx, which is long, sharp pointed, and protractile. The only truly biting flies are certain species of Dolichopodidae, in which the terminal lobes of the labium are strongly sclerotized and jawlike in form and action.

The best known of the mandibulate piercing flies are the female horse flies (Tabanidae), and female mosquitoes. The mouth parts of a horse fly may be studied as an example of the more generalized condition of the mouth parts as it occurs in adult Diptera. To understand the entire feeding mechanism, however, it will be necessary to know also something of the structure of the clypeal region of the head.

The Feeding Organs of a Horse Fly.—The mouth parts of the horse fly form a compact group of organs projecting downward from the peristomal margin of the head (Fig. 171 A). In the female fly there are nine pieces included in the group, three of which are median and unpaired, while the other six represent three pairs of lateral organs. The most anterior of the median organs is the broad, dagger-shaped labrum (*Lm*). Its lateral edges are overlapped in the usual position by a pair of large two-segmented palpi (*MxPlp*), which belong to the maxillae. Posterior to the labrum are two pairs of long, slender, tapering blades, the anterior of which are the mandibles (*Md*), the posterior the lobes of the maxillae (*Mx*). Posterior to the mandibles and between the maxillae is a second median piece resembling the labrum but slenderer. This is the hypopharynx. Behind and partly enclosing all these parts in the normal position is the large median labium (*Lb*) ending in two broad lobes.

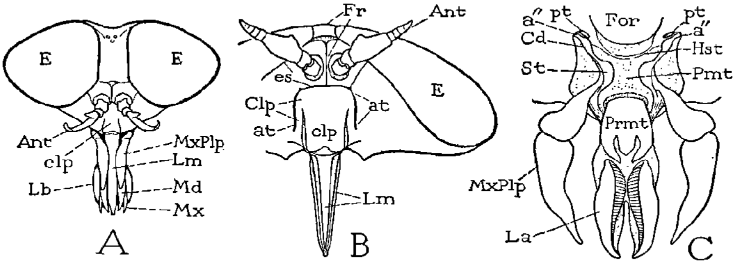

FIG. 171.—Head and mouth parts of an adult horse fly, *Tabanus atratus*. A, anterior view. B, details of clypeus and labrum. C, labium and maxillae, posterior view.

The Labrum and the Clypeus.—The labrum of the horse fly, as noted above, is shaped like the blade of a dagger, but it is not particularly rigid, and its point is blunt (Figs. 171 A, B, 172 A, *Lm*). Proximally it is attached to the lower margin of the facial area of the head by a median membranous area and two divergent lateral arms. A short median apodeme projects dorsally into the head cavity from the anterior wall of the labrum and gives insertion to a fan-shaped muscle arising on the clypeal plate of the head (Fig. 171 B, *clp*). This muscle serves apparently to keep the labrum in close contact with the other pieces of the mouth parts. The presence of a clypeolabral muscle is a special feature of the Diptera and constitutes an exception to the general rule that the labral muscles take their origin on the frons. The posterior, or epipharyngeal, wall of the labrum is excavated by a median channel continued proximally into the small mouth aperture located behind the base of the labrum (Fig. 172 A, *mth*).

When the mouth parts of the female horse fly are in the normal position, the labral groove is closed posteriorly by the broad, overlapping mandibles, and there is thus formed a tubular passage leading up to the mouth. This conduit is the *food meatus*, which, in female Tabanidae, as pointed out by Vogel (1921), lies thus between the labrum and the mandibles. In the female mosquito, however, Vogel shows, the labrum itself forms the food canal since its concavity is closed posteriorly by the approximation or overlapping of its incurved lateral margins.

In many of the Dolichopodidae the epipharyngeal wall of the labrum bears an armature of spines or movable teeth, the latter being highly developed in the genus *Melanderia;* but since, in general, the posterior surface of the dipterous labrum is smooth and presents no structure of any kind to be specifically termed an epipharynx, the writer sees no reason for following the usual custom of calling the elongate labral lobe of the Diptera a "labrum-epipharynx."

The area of the head wall in *Tabanus* from which the labrum is suspended is a median part of the clypeus (Fig. 171 B, *clp*) separated from the lateral parts of the clypeal area by a membranous fold on each side. The lateral limits of the true clypeus (*Clp*) are marked by the long slitlike anterior tentorial pits (*at, at*), from which the epistomal suture (*es*) is arched upward and crosses the lower part of the face beneath the bases of the antennae: Upon the median clypeal plate (*clp*), as we shall presently see, the dilator muscles of the sucking pump take their origin. In the Tipulidae the clypeal area forms the upper wall of a snoutlike projection of the head extending anterior to the eyes, and in some species bearing a strong spine-like process near its distal end. In the higher Diptera the median part of the clypeus becomes an independent sclerite, but the dilator muscles of the pump retain their attachments upon it.

The Mandibles.—The mandibles of the horse fly are long, flattened, sharp-pointed blades, their tips reaching to the apex of the labrum (Fig. 171 A, *Md*). Each is articulated by an expanded base (Fig. 172 B) to the lower edge of the head at the sides of the mouth and is provided with antagonistic muscles that take their origin on the head wall. The mandibles of the fly are thus, as in biting insects, capable of being moved in a transverse plane, but they have no movements of protraction or retraction. The thrust of the piercing mandibles is made by a forceful action of the head and body of the fly.

The Maxillae.—Each maxilla consists of a basal part evidently composed of the cardo and stipes (Fig. 172, C, *Cd, St*), of a large, thick, two-segmented palpus (*Plp*), and a long, slender, tapering blade (*Ga*). The maxillary bases underlap the proximal part of the labium (Fig. 171 C, *Pmt*) and are articulated by their cardinal extremities to the lower edges of the postgenae (*a''*) just below the posterior tentorial pits (*pt, pt*). The palpus (*MxPlp*) arises by a narrow stalk from the outer edge of the stipes. Beyond the base of the palpus the stipes is continued into the long blade-like maxillary lobe. The latter (Fig. 172 C, *Ga*) may be regarded as the galea, since it appears to correspond to the principal lobe of the maxilla in Hymenoptera and Lepidoptera. Near its base it gives off a small strip (*a*) that connects mesally with the head wall. Patten and Evans (1929) regard this small lobe in *Haematopota* as the lacinia, but its origin from the base of the larger lobe makes this interpretation seem doubtful. The maxillae are well developed in many orthorrhaphous flies that lack mandibles.

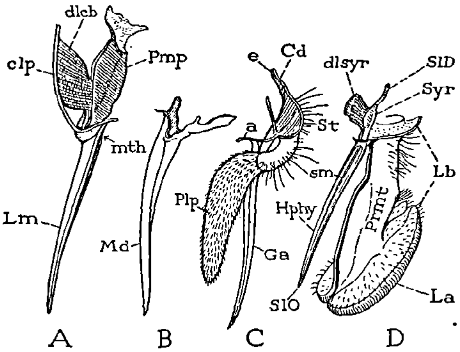

FIG. 172.—Mouth parts of *Tabanus atratus*, separated, lateral view. A, labrum and sucking pump (cibarium) with dilator muscles arising on clypeus. B, left mandible. C, left maxilla. D, labium, hypopharynx, and salivary syringe.

The Hypopharynx and the Salivary Syringe.—The hypopharynx is a long, narrow, tapering stylet (Fig. 172 D, *Hphy*) arising from the ventral wall of the head just behind the mouth aperture. Normally it lies in the deep groove of the anterior face of the labium. It is traversed by the outlet duct of the salivary glands (*sm*), which opens by an aperture on its tip (*Slo*). Just proximal to the base of the hypopharynx the duct is enlarged to form a syringe-like apparatus (*Syr*), the anterior wall of which is inflected into the lumen and is provided with dilator muscles (*dlsyr*) arising on the posterior surface of the sucking pump of the feeding apparatus (A, *Pmp*). Since the food pump of Diptera represents the cibarium of orthopteroid insects (Fig. 155, *Cb*), its floor is formed by the adoral surface of the hypopharynx. The dilator muscles of the salivary syringe, therefore, are the usual hypopharyngeal muscles (1*s*) of the salivarium; the ventral, or labial, muscles are absent. Just how the syringe and the salivary channel have become enclosed within the hypopharynx cannot be explained. The salivary glands of the Tabanidae are long, simple, tubular organs; their secretion is said to contain a powerful blood anticoagulin (see Patten and Evans, 1929).

The Labium.—The labium of the horse fly is a large, thick, elongate appendage (Fig. 172 D, *Lb*) ending in two broad lobes known as the *labella* (*La*). It is suspended from the posterior part of the head by a membranous basal region (Fig. 171 C, *Pmt*) lying between the maxillary stipites and is separated from the foramen magnum (*For*) by a narrow hypostomal bridge (*Hst*) connecting the posterior angles of the postgenae. The stalk of the free part of the organ is the stipital region of the appendage and is therefore the prementum (Figs. 171 C, 172 D, *Prmt*). It is deeply evacated longitudinally on its anterior surface. In the normal position of the mouth parts, the labrum, the mandibles, the hypopharynx, and the maxillae all lie within the cavity of the labium, the hypopharynx immediately behind the mandibles, with the maxillae to either side of it but posterior to its broad lateral margins. The relations of the several elements of the mouth parts to one another are best seen in a cross section (see Vogel, 1921).

The terminal lobes of the labium, or labella, are large soft pads capable of being spread outward from the end of the stipital stalk (Fig. 172 D) to form a broad disc, sometimes called the "oral sucker." The posterior halves of the labella are united, but their anterior parts are separated by a deep median cleft. The under surface of each lobe is marked by the lines of numerous close-set, transverse channels in its membranous wall, called *pseudotracheae* from their superficial resemblance to half-open tracheal tubes. The mesal ends of the canals lead to the base of the cleft between the labellar lobes, at which point normally lies the apex of the labrum. In the feeding fly, the blood collected by the labellar channels is here taken into the food canal between the labrum and the mandibles.

In the genus *Melanderia* of the Dolichopodidae the labella have a very unusual development (see Aldrich, 1922; Snodgrass, 1922). Each labellum has a strongly sclerotized movable lobe with the free, sharp apical part turned inward. The two lobes give the appearance of a pair of mandibles, and they are provided with muscles arising in the prementum so attached on the lobes that the latter apparently can be opened and closed in the manner of a pair of jaws. Since the Dolichopodidae are predacious, it is highly probable that the labellar lobes of *Melanderia* serve to grasp and hold the living prey on which the insects feed.

The labella of the fly labium have been generally regarded as the paraglossae, apparent rudiments of the glossae being sometimes present between them; but Crampton (1923, 1925*b*), from a comparative study of the labium in Diptera and related insects, has given reasons for believing that the labellar lobes are the labial palpi. Palpi, however, are typically provided with antagonistic muscles; the lobes of the fly labium have usually each only one muscle inserted directly upon it. The term "labella" is used by some writers in a singular sense, but it is properly the plural of *labellum* (diminutive of "lip"), which is the Latin form of the singular.

The Sucking Pump.—The sucking apparatus of the horse fly is a small chamber which extends upward in the lower part of the head from the functional mouth (Fig. 172 A, *Pmp*). The posterior and wide lateral walls of the organ are strongly sclerotized and fixed to the upper end of the labrum. The anterior wall, on the other hand, is thin and flexible and is ordinarily deeply invaginated into the lumen of the pump, but it is provided with two large groups of muscle fibers taking their origin on the median clypeal plate of the head wall (Fig. 171 B, *clp*) and is thus capable of exerting a sucking action on the liquid food ascending to the mouth through the food canal of the mouth parts. The origin of the dilator muscle of the pump on the median plate of the clypeus shows that the sucking apparatus of the Diptera is the cibarium of orthopteroid insects, together with its dilator muscles and the clypeal plate on which these muscles take their origin. The functional mouth aperture (*mth*) leading into the pump chamber, therefore, is not the true mouth, the latter being the opening into the stomodaeum at the inner end of the pump.

The Muscoid Types of Mouth Parts.—In the higher Diptera the external feeding apparatus of the adult fly consists of a *proboscis.* The proboscis is a composite structure formed of the labrum, the hypopharynx, and the labium, all supported on a membranous base that contains in its anterior wall the median clypeal plate on which arise the dilator muscles of the sucking pump. The proboscis supports a pair of palpi, which are probably the maxillary palpi, and it terminates in a pair of labellar lobes. Two functional types of structure are distinguishable in the proboscis, depending on the nature of the labellar lobes. In most of the muscoid flies the labella are broad, soft pads resembling those of the horse fly, and such species are incapable of biting, though some are provided with small labellar teeth that enable them to rasp the food substances. Flies having mouth parts of this kind are designated by Metcalf and Flint (1928) as the *sponging type* of Diptera. With these flies the proboscis is usually flexible and extensible and when not in use is folded against the lower part of the head or retracted into a ventral cavity of the head wall surrounded by the projecting margins of the peristome. In a few species of the family Muscidae the proboscis is rigid, and the labellar lobes are small, cutting plates. These species constitute the so-called "biting" muscoid flies.

The Nonpiercing, or Sponging, Type of Muscoid Mouth Parts.—The typical muscoid proboscis, as seen in the blow fly or house fly (Fig. 173 A, *Prb*), consists of three parts: first, a large *basiproboscis*, or *rostrum* (*Rst*);

second, a *mediproboscis*, or *haustellum* (*Hstl*); and, third, a *distiproboscis*, formed of the labella (*La*), or lobes of the so-called "oral sucker."

The rostrum is a broad inverted cone having for the most part flexible membranous walls. On the upper part of its anterior surface, however, there are usually two median plates (Fig. 174, C, *c*, *clp*). The more ventral of these plates (*clp*), having the form of an inverted V, is a constant feature of the rostrum in the muscoid proboscis; the upper plate (*c*) is a weaker sclerotization hinging the V-shaped plate to the lower edge of the cranial capsule. On the lower part of the anterior face of the rostrum are two small lateral sclerites (*mxpl*), which support the pair of long palpi (*MxPlp*).

The cylindrical haustellum projects downward and somewhat forward from the end of the rostrum when the proboscis is protracted; in the retracted condition it folds upon the anterior surface of the rostrum. The posterior wall of the haustellum is occupied by a prominent plate known to students of Diptera as the *thyroid* or "mentum." The anterior surface is covered by a long, tapering, strongly sclerotized flap (Figs. 173 A, 174 C, *Lm*), which arises from the distal margin of the rostrum and is partly overlapped by lateral folds of the haustellum. This flap is the labrum. By lifting its distal end (Fig. 173 B, *Lm*) there is exposed in the anterior part of the haustellum a deep, lengthwise cavity in which lies the blade-like hypopharynx (*Hphy*). Between the labrum and the hypopharynx is the food canal (*fm*) of the proboscis, which leads up to the functional mouth situated behind the base of the labrum as in the horse fly (Fig. 172 A, *mth*).

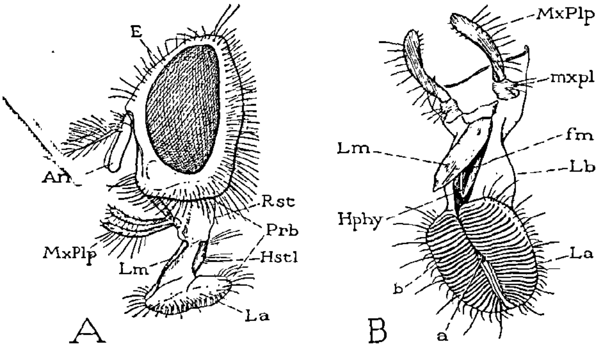

FIG. 173.—Head and proboscis of the house fly, *Musca domestica*. A, lateral view of head with proboscis extended. B, anterodistal view of extended proboscis, showing ventral surfaces of labella with aperture (*a*) leading into food meatus (*fm*) between labrum and hypopharynx.

The labellar lobes (Fig. 173, *La*) terminating the proboscis in the nonpiercing, or sponging, type of muscoid mouth parts are broad pads