SMITHSONIAN MISCELLANEOUS COLLECTIONS
VOLUME 138, NUMBER 2

EVOLUTION OF ARTHROPOD MECHANISMS

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R. E. SNODGRASS
Research Associate of the Smithsonian Institution
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(Publication 4347)

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THE LORD BALTIMORE PRESS, INC.
BALTIMORE, MD., U. S. A.

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INTRODUCTION

Any study of evolution necessarily involves theories, but if we stopped short with known facts our phylogenetic trees would wither at the roots. Particularly when we attempt to reconstruct events that took place in remote Precambrian times we can have recourse only to our imagination. Where connecting links between modern animals cannot be known, we must invent them; at least, if evolution is true, we can feel sure that connecting links really did exist. Imagination, of course, must be controlled by reasoning from the known to the unknown, but unfortunately our brains do not all reason in the same way and often produce very different concepts from the same set of facts. Yet some ideas should be more plausible than others.

Though many zoologists hold that the arthropods have been evolved from polychaete annelids, the following discussions are based on the belief that the Polychaeta, having lateral swimming appendages, or parapodia, are a branch of the chaetopod annelids descended from some remote, simple segmented worm (fig. 1 A), and that the Onychophora and Arthropoda are derived from the same ancestral worm stock, but from forms that developed lateroventral lobelike appendages (B) and became crawling or walking animals. They presumably lived in shallow water where they crawled on the bottom, over rocks, or on water plants. The theoretical phylogenetic stage represented at B is literally reproduced in an early embryonic stage of the Onychophora, and is approximately recapitulated in the ontogeny of various arthropods. From their common lobopod ancestors the Onychophora and the Arthropoda diverged as two separate lines of descent, the onychophorans retaining a flexible integument, the arthropods acquiring a sclerotization of the cuticle, which allowed the legs to become longer (C), and finally jointed (D). The difference in the nature of the body wall thus accounts primarily for other differences in the organization of these two related groups of walking animals.

That the modern terrestrial Onychophora have descended from

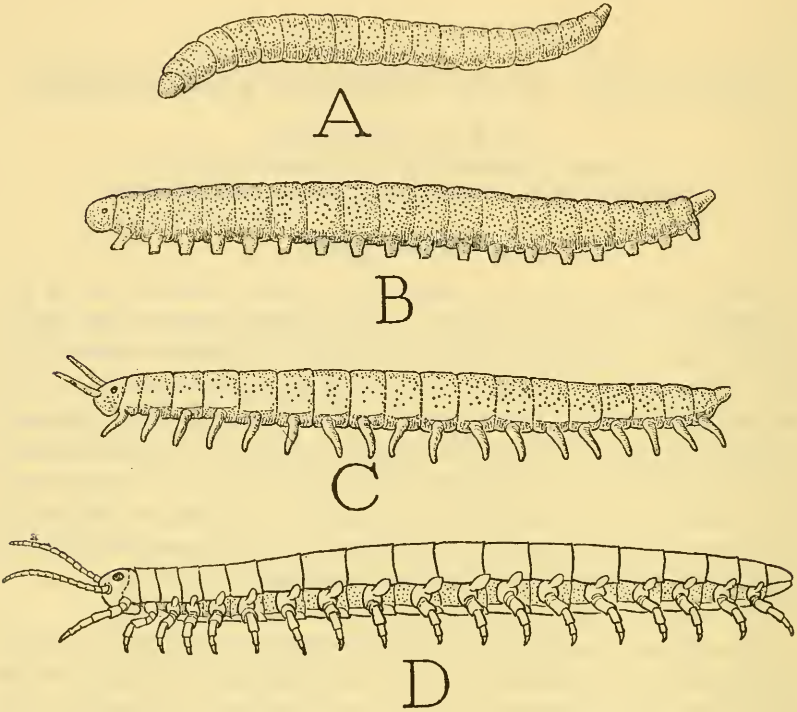

Fig. 1.—Theoretical evolutionary stages from a simple segmented worm to a primitive arthropod.

A, A primitive segmented Precambrian worm without bristles or appendages, from which may have been derived the chaetopods on one evolutionary line, and the lobopods on another. B, A crawling derivative of A with small lateroventral lobelike outgrowths of the segments (repeated in the embryogeny of Onychophora and all arthropods) from which might have been evolved directly the soft-skinned Onychophora. C, A walking form derived from B by sclerotization of the integument, allowing the limbs to become longer and slenderer. D, A primitive arthropod derived from C, with jointed appendages.

very ancient aquatic ancestors is attested by the presence of the genus *Aysheaia* in the middle Cambrian. There can be little doubt that *Aysheaia* (fig. 2 E) is an onychophoran, though it differs externally in some ways from any modern form. It has been depicted by Hutchinson (1931) as having a pair of branched appendages arising dorsally at the back of the head. An examination of the specimens in the U. S. National Museum, however, shows clearly that the branched appendages are the first pair of legs. In two specimens, including the type (D) described by Walcott (1911) as *Aysheaia pedunculata,* the

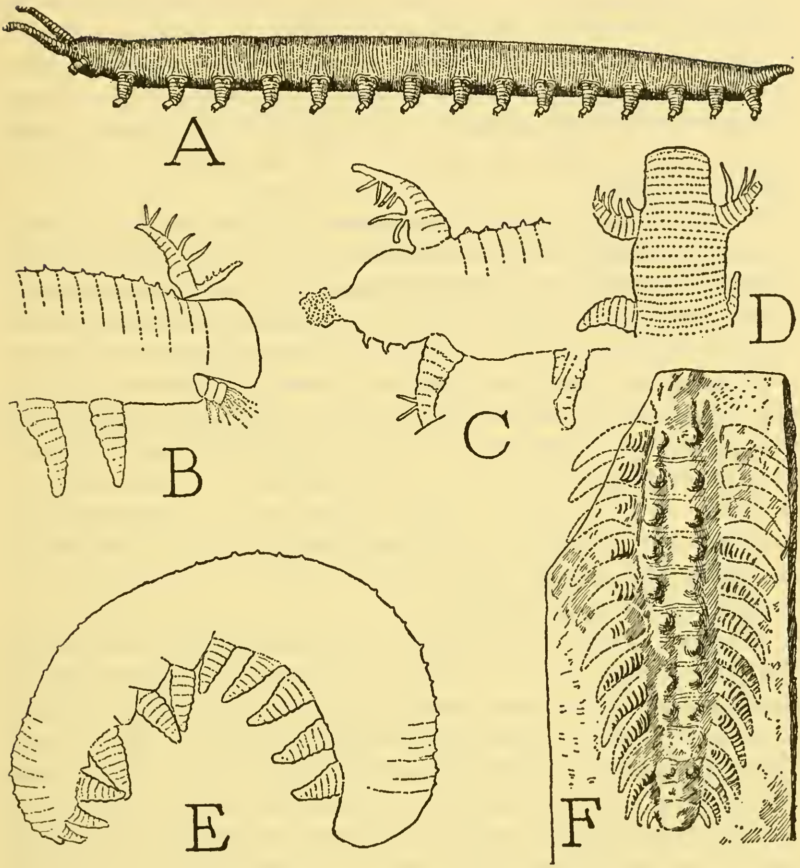

Fig. 2.—Onychophora, modern and ancient.

A, *Peripatoides novae-zealandiae*, modern. B, C, D, E, *Aysheaia pedunculata*, Cambrian (from specimens in U. S. Nat. Mus.). F, *Xenusion auerswaldae*, Algonkian (from Heymons, 1928).

branched first legs are spread out symmetrically on opposite sides. In the specimen studied by Hutchinson (B) one appendage is fully preserved and is dorsal, but it is evidently detached from the body of the animal and displaced dorsally; the other appears to be the stump of an annulated limb frayed out distally into irregular strands of an uncertain nature. On a fourth specimen (C), in which the anterior end of the body is twisted to the left and the head somewhat mashed, the first legs are extended laterally; the right one is fully branched, the left shows at least two small spikelike branches. All specimens sufficiently well preserved show the presence of 11 pairs of legs, including the branched first legs. The general similarity of the head region of *Aysheaia* (E) to that of a modern onychophoran is suggestive that *Aysheaia* had a pair of concealed jaws. The specimens do not have a sufficiently primitive, or "embryonic," appearance to support Hutchinson's suggestion that the second pair of legs become the jaws of modern species.

The largest and best-preserved specimen of *Aysheaia* in the Museum collection (fig. 2 E) shows no branches on the front legs, though they might be concealed on the mesal surfaces; or perhaps there were different species of *Aysheaia*. The most striking difference between modern Onychophora and the Cambrian fossils is the entire lack of any remnant or trace of antennae on the head of the latter. Hutchinson suggested that the branched appendages, which he thought were dorsal, become the antennae in modern Onychophora, but the migration of these appendages to the front of the head seems very improbable. Walcott (1911), taking *Aysheaia* to be a polychaete, interpreted a very indistinct formation in the shale seen at the anterior end of the type specimen (but not shown at D) as a head and minute tentacles of the supposed worm.

Inasmuch as there is no evidence of the presence of antennae in the Cambrian Onychophora, it might appear that these appendages of modern forms are a more recent acquisition. Five hundred million years is a rather long time, and probably sufficient for the development of a pair of tentacular appendages from the front of the head, as well as a primitive tracheal system for life on land, considering what other animals have accomplished in the same time. Unfortunately there is no evidence as to the antiquity of the terrestrial onychophorans. In the other direction, *Aysheaia* is preceded by the Algonkian *Xenusion* (fig. 2 F), which, as figured by Heymons (1928), appears to belong to the onychophoran line of lobopod evolution. In any case, it seems that the Onychophora have given rise to nothing but forms of their own kind.

On the other hand, that the Onychophora and the Arthropoda are fundamentally related through some remote lobopod ancestor is attested by the following characters they have in common: (1) The lateroventral position of their appendages, which develop alike in the embryo from simple, lobelike outgrowths of the body wall; (2) the undivided body cavity (mixocoele) in the adult stage; (3) the presence of coelomic excretory organs with simple coelomic exit ducts; (4) a single pair of coelomic gonadial sacs, which in the arthropods may be branched, within which the germ cells are developed, and are discharged through a pair of coelomic ducts, which may unite in a common ectodermal exit duct; (5) the origin of the nerve cords from "ventral organs" of the ectoderm, characteristic of the Onychophora and retained in Symphyla and Pauropoda among the arthropods. In one important respect the Onychophora differ from adult arthropods, namely, in the wide separation of the nerve cords.

The ancient onychophorans undoubtedly were aquatic, and their modern terrestrial descendants must still live in permanently damp places. The rate of water loss from the body of *Peripatopsis,* as determined by Manton and Ramsay (1937), is twice that of an earthworm and 80 times that of a cockroach. Water loss probably is due mainly to the large number of spiracles scattered over the body, which have no closing apparatus. The primitive open tracheal system alone, Manton and Ramsey suggest, may have been responsible for the onychophorans not becoming a widely spread or diversified group of modern animals. The Onychophora are poor relations of the arthropods, and not their ancestors.

The terrestrial arthropods having a sclerotized integument, and especially the insects with closing valves on their spiracles, have not been handicapped for living in dry environments. The contrast between the simple, soft-skinned onychophorans, and the structurally highly diversified, hard-shelled arthropods, however, has resulted largely from the ease with which skeletomuscular mechanisms can be evolved from a sclerotized integument on which the somatic muscles are attached. The modern arthropods, therefore, are noted for the number of anatomical tools and mechanisms they possess, and for the great variety of forms into which they have developed.

Students of evolution do not ordinarily consider the fact that with each new mechanical device an animal acquires, the animal must know how to use it. The animal's "know how" is instinctive, that is, automatic, and this presumably implies that a new sensory-motor system has been at the same time developed in the nervous system. The copulatory genital structures of insects, for example, are often highly complex, so complex that taxonomists who study them intensively for specific characters do not know in most cases how the insect uses them. The insect knows exactly how to use each part, but we at present know nothing of the nervous apparatus by which the mechanism is instinctively operated.

The problem becomes still more complicated where arthropods acquire different mechanisms in different stages of their life histories. The caterpillar or the larva of a fly or bee, for example, has a relatively simple feeding apparatus that responds to the stimulus of food, but the adult acquires a very different kind of mechanism adapted to feeding in a different way on a different kind of food. The feeding apparatus of an adult bee is so complicated that understanding its physical structure requires a painstaking study on the part of the anatomist, but the bee operates this intricate mechanism without giving it a thought (since it can't think). During the transformation of the bee from the larva, therefore, there must have been developed in the feeding center of the nervous system a whole new complex of sensory and motor fibers, as well as new sense organs responsive to the stimulus of a new kind of food. The task of natural selection has then been a double one of bringing into correlation a skeletomuscular mechanism and a neural mechanism—if natural selection alone accounts for evolution.

The term "instinct" covers a vast field of ignorance. If automatic behavior has a specific structural basis in the nervous system, activated by sensory stimuli, a desideratum for the future is a treatise on "The Anatomy of Instinct."

I. ARTHROPOD INTERRELATIONSHIPS

Now that we have differentiated the arthropods from the onychophorans, after deriving both from a lobe-footed worm, something should be said about the relationships of the arthropods to one another. The theme is really not worth the space of a full discussion, since the subject is not one of known facts, and the connecting links are entirely missing. However, it will clarify some of the following discussions to give here a brief outline of the scheme of relationships adopted in this paper.

If we reduce the arthropods to a common plan of structure the primitive arthropod must have been an elongate, segmented animal (fig. 1 D), with a head represented by the cephalic lobe in a modern embryo, and a pair of jointed appendages on each body segment. The trilobites retained a primitive condition only in their limbs, which were all uniformly segmented walking legs. Otherwise, the trilobites in their body structure were already highly specialized by early Cambrian times. The Xiphosurida resemble the trilobites so much in the structure of the prosoma that they must have had a remote connection with the trilobite ancestors, but their prosomatic appendages are literally those of the arachnids, so evidently these latter two groups are somehow related. The Eurypterida, Xiphosurida, Pycnogonida, and Arachnida constitute the Chelicerata, so named because their principal feeding organs are the chelicerate first pair of postoral appendages; they have no true masticatory jaws, and lack antennae.

The rest of the arthropods, including the crustaceans, the myriapods, and the insects, are known as the Mandibulata because they have mandibles, but in other respects also they so consistently differ from the Chelicerata as to leave no doubt that the two groups represent distinct lines of arthropod evolution. Within the Mandibulata, however, the relationship of the component groups is obscure. The crustaceans are the earliest mandibulates known in the fossil record, but there is no evidence whatever yet found as to when or where the ancestral myriapods and insects originated. The crustaceans appear to be an independent branch of the mandibulate line; they are the only mandibulates that preserve functional second antennae and retain both the dorsal and the ventral muscle of the dactylopodite.

The myriapods and the insects are themselves distinct groups, but they have in common enough characters to separate them as a group from the Crustacea. They lack second antennae, except as embryonic vestiges, and they consistently lack the dorsal (levator) muscle of the pretarsus (dactylopodite). A centipede in its general form and number of unmodified legs might appear to be closest to a primitive arthropod, but nothing is known of its ancestry. It has been argued that the insects were derived from crustaceans, but their affinities with the myriapods, perhaps through symphylan progenitors, is too close to allow them an independent status. The evidence of relationship of the insects to the myriapods rather than with the Crustacea has been well discussed by Tiegs (1949). Remington (1955) also contends that the available evidence leads to the conclusion that the myriapods and hexapods are a series of forms with a common ancestor. Some writers have proposed a separate origin of the myriapods from primitive Onychophora, but the mandibulate arthropods are too evidently a monophyletic group not to have had a single origin.

Though it is to be assumed that all the arthropods came from aquatic stock, we have no evidence as to how or when the terrestrial myriapods and insects came out of the water. It has been suggested by Ghilarov (1956) that the primitive insects on leaving the water penetrated the earth along the shore and were at first soil dwellers. The same even more probably might have been true of the myriapods. In this case, the transition from water to air would have been less abrupt, though still it was necessary to develop a tracheal respiratory system before life on dry land could be practical.

The myriapods differ from the insects in having seven segments in the legs, the insects having only six. The insect mandible maintains a unit structure whatever form it may take. In the chilopods the gnathal lobe is flexible on the mandibular base; in the diplopods and symphylans the lobe itself becomes the functional jaw independently movable on the base of the mandible. The diplopods are the most specialized of the myriapods. The insects owe their body structure first to having become hexapods through the elimination of all body appendages except the first three pairs, next to the specialization of the thorax as the locomotor center of the body, and finally to the development of wings. With the acquisition of organs of flight they left their crawling relatives behind and assumed the leading role in arthropod evolution. They have overpopulated the earth with their progeny, who have come into competition with the descendants of *Homo sapiens,* and have thereby raised the profession of entomology to a high rank.

II. BODY SEGMENTATION

Body segmentation, or metamerism, is characteristic of the Annelida and the Arthropoda, and is an adaptation to body movement, but the segmental mechanism is not the same in these two groups of segmented animals. The Onychophora also are fundamentally segmented, though in the adult stage the segmentation of the body wall is suppressed; their body mechanism again differs from both that of the annelids and that of the arthropods.

The phylogenetic origin of metamerism is usually deduced theoretically from embryonic development, because the embryo has been said to repeat the history of its race. An embryo shut up in an egg, however, lives under conditions that are very different from those of its free-living ancestors, and for this reason its developmental story cannot be taken too literally as a repetition of its adult race history. It is confusing also to find that embryos of related species often differ much in their methods of development, and arrive at the same end results in quite different ways. Moreover, the embryo may develop into a highly metamorphosed larva adapted to a different way of living from that of its parents. In such cases the larval form and structure may be in no sense ancestral, and the larva must undergo a second metamorphic transformation to get back into the adult form of its species.

The embryonic origin of body segmentation is much better shown in the polychaete annelids and the Onychophora than in the development of the arthropods and may be taken to repeat more nearly the origin of segmentation in the ancestors of these three groups. The polychaete larva, known as a trochophore, is a minute top-shaped creature designed for floating upright in the water and for swimming by means of circles of vibratile cilia in order to distribute the members of its species before they take on the worm form and habits. The trochophore, therefore, has to undergo a metamorphosis to become a worm, and neither the trochophore itself nor its metamorphosis recapitulates anything in the history of its adult ancestors, any more than does the caterpillar and its change into a butterfly represent anything in the adult history of the Lepidoptera. The trochophore becomes a worm through elongation of its postoral part by teloblastic generation of new tissues in a subterminal zone of growth. The newly formed body becomes segmented as coelomic cavities are formed in its mesoderm bands, but the way segments are formed by growth from the rear end of the body is a metamorphic process.

We had better turn to the Onychophora then for a more reliable picture of the primitive beginning of body segmentation. The Onychophora have no differentiated larval stage; the embryo in the egg develops directly into a miniature segmented adult, and its early embryogeny has been fully described by Manton (1949) and others. The mesoderm grows forward from the region of the blastopore as two lateral bands that extend to the mouth. The bands then become divided from before backward into solid blocks, which immediately are excavated by coelomic cavities. The first cavities converge in front of the mouth and become the coelomic cavities of the antennal region.

Most embryologists call the coelomic sacs "the somites," but the term *somite* should be synonymous with "body segment." However, the segmentation of the mesoderm is unquestionably preliminary to body segmentation, since, Manton says, there is no ectodermal segmentation until after the mesodermal somites are completed. The outer walls of the coelomic sacs in the annelids, onychophorans, and arthropods give rise to the somatic muscles, and it is the muscles that mechanize the body for locomotion and make the segments functional motor units, except where external segmentation is later suppressed as in the Onychophora. It might thus appear that the whole future organization of the segmented animal is determined by the formation of two rows of holes in the mesoderm. However, in evolution structures do not arise for what they may later become, and hence there must have been some independent functional reason for the first formation of the mesodermal cavities, the presence of which in itself can hardly be regarded as a segmentation of the body. Two principal theories have been proposed to explain the origin of the coelomic cavities, one is the *nephrocoele* theory, the other the *gonocoele* theory, but neither need concern us here in a study of the later-developed skeletomuscular mechanisms that owe their inception to the coelomic sacs.

The somatic musculature of the annelids consists of an outer layer of circular fibers and an inner layer or bands of longitudinal fibers. In their origin the longitudinal muscles are said to be perfectly metameric, but later their metamerism is entirely effaced (Dawydoff, 1928). In the adult of *Nereis* or an earthworm these muscles are composed of fine, threadlike fibers that are continuous through the segments. The fiber bundles of *Nereis* are bound to the body wall at the intersegmental grooves, but the fibers have no attachment on the cuticle. In the earthworm the longitudinal fibers form a layer surrounding the entire body cavity, except along the middorsal line and at the insertions of the setae; they have no attachments on the body wall. The parapodia of the polychaetes have their own muscles arising on the body wall.

The locomotor movements of *Nereis,* as analyzed by Gray (1939), are very complex whether for crawling on the ground or for swimming, and involve coordinated action of both the body musculature and the muscles of the parapodia. The locomotor mechanism of the earthworm is more simple. As shown by Chapman (1950) it is the antagonistic action of the circular and longitudinal somatic muscles on a fluid-filled body that gives the earthworm its principal means of locomotion by contracting the rear part of the body and pushing out the front.

The onychophoran body musculature is highly complex; it covers the whole inner surface of the body wall, and the fibers have no segmental attachments. It includes an external layer of circular muscles, a double layer of oblique fibers crossing in opposite directions, dorsoventral lateral fibers, and bands of internal longitudinal fibers. Unlike the worms, the onychophoran is a walking animal; its legs have a strong extrinsic and intrinsic musculature. The body is a relatively rigid cylinder and takes no part in the progressive movement of locomotion. As observed by Manton (1950), however, "the movements of *Peripatus* are much more varied than they are in terrestrial Arthropoda provided with an exoskeleton." The head end of the body anterior to the second or third pair of legs is turned to right or left as the animal goes forward, and "the head and antennae may be raised and lowered with an irregular rhythm."

When we turn to the arthropods we encounter an entirely different kind of mechanical organization from that of either the Annelida or the Onychophora. Of prime importance is the sclerotization of the arthropod cuticle; second, the direct attachment of the somatic muscles on the cuticle by means of cuticular tonofibrillae; and third, the breaking up of the longitudinal muscle fibers into bundles of segmental length. The general plan of the arthropod body musculature is much simplified as compared with that of an onychophoran. It consists essentially of dorsal and ventral bands of longitudinal fibers, and dorsoventral lateral muscles, which latter perhaps are remnants of primitive circular muscles. In contrast to the reduction of the body musculature, there is a strongly developed musculature of the appendages, befitting a walking animal. As Manton (1950) has noted, "a reduction of the propulsive force provided by the longitudinal body muscles and an increase in that supplied by the extrinsic muscles of the limbs must have been an important step in the evolution of limbs for terrestrial locomotion." The same, of course, might be said of adaptation to locomotion by legs in an aquatic environment. The first arthropods were inhabitants of the water and had fully developed legs (as the trilobites), but having learned to walk under water, it was a simple matter for some of their descendants to walk on land.

The principal longitudinal muscles of the arthropods, except where segments are united or otherwise modified, are firmly attached to the cuticle on the primary intersegmental grooves, which are sclerotized to form anterior marginal or submarginal internal ridges (antecostae) on the tergal and sternal plates. There are, therefore, no true intersegmental lines of movement in the skeleton, and this condition involves another essential modification of the body wall to allow the segmental plates to be movable on each other. The so-called "intersegmental" membranes are not intersegmental; they are the unsclerotized posterior parts of the primary segments. The functional "segments," or the segmental plates, are merely the sclerotized parts of the primary segments, including the intersegmental ridges, or antecostae, on or near their anterior margins. The functional segmentation of the arthropod, therefore, is a secondary segmentation, and does not correspond with the polychaete segmentation defined by the flexible primary intersegmental grooves. Without this adaptation in the arthropod skeleton, a wholly sclerotized integument would encase the animal in an inflexible tube.

While it is probable that body segmentation of the Annelida, Onychophora, and Arthropoda had its origin in some simple wormlike common ancestor, the locomotor mechanism has been differently developed in each group. The arthropods attained the most efficient mechanical organization, but considering the many essential adaptive modifications of structure that were necessary, it is evident that the transformation of a simple segmented worm into an arthropod involved a long and complex evolutionary process. Once the arthropods attained the essential features of their organization, however, they were endowed with unlimited possibilities for further development and differentiation.

III. SCLEROTIZATION AND SCLERITES

The primitive cuticle of the annulate animals was probably a proteinaceous product of the epidermis; in modern arthropods and onychophorans it is more or less impregnated with chitin. The cuticle of most adult arthropods is hardened, or sclerotized, in definite areas to form *sclerites.*

Typically the arthropod cuticle consists of two principal layers, a thicker, inner chitin-containing layer, the *procuticle* of Richards (1951), and a very thin, nonchitinous surface layer, or *epicuticle.* Cuticular sclerotization among the arthropods in general may result either from the deposit of calcium salts in the inner part of the cuticle, or from a hardening of the protein constituent. Calcium sclerotization occurs principally in the Crustacea and Diplopoda, probably in combination with protein sclerotization; portein sclerotization is characteristic of the insects. Sclerotization of the insect cuticle, when present, affects the epicuticle and the outer part of the procuticle, differentiating the latter into an outer dense *exocuticle* and a softer, inner *endocuticle.* The protein sclerotization in the insect cuticle, as described in a recent review by Wigglesworth (1957), is a very complex chemical process. As deduced from a study of fly puparia (see Richards, 1951), there is first an oxidase given off from the blood through the epidermis that penetrates the cuticle into the epicuticle. Then tyrosine, or some oxidative product of it in the blood, goes through the epidermis and the procuticle and is tanned by the oxidase in the epicuticle to an O-quinone, which then diffuses inward and tans the outer part of the procuticle into a hard exocuticular layer. The endocuticle appears to be immune to the tanning process.

The remarkable feature about cuticular sclerotization is that it results in the formation of definitely limited *sclerites* separated by nonsclerotized areas of the cuticle, commonly called membranes. If the sclerotizing elements come from the blood, it is difficult to understand why they do not penetrate the entire cuticle. The pattern of sclerotization is distinctive of species, and must be determined by hereditary factors. The various sclerotic patterns, moreover, are intimately adapted to the skeletal mechanism of the animal. Evidently there must be some preliminary differentiation in the epidermis that determines the pattern of sclerotization.

Though the sclerites in general have definite limits, sclerotization may be continuous from one part of a segment to another, as in insects where the pleural and ventral sclerotization of a thoracic segment may not be separated. In such cases it is often assumed that the pleuron has extended ventrally and crowded out the sternum. If there is truly a replacement of the skeleton of one body region by extension from that of another, there should be a corresponding extension of the epidermis. Otherwise, the condition of sclerotic continuity may be merely a confluence of sclerotization, as when an entire segment becomes a continuously sclerotized annulus.

Then finally, there is the question of how it came about in the first place that sclerites were laid down in conformity with the mechanical needs of the animal. Was sclerotization at first a haphazard process, from which proper sclerites were evolved by trial and error, with errors eliminated by natural selection, until the animal became a working mechanism? If so the arthropods must have had a hard time getting a practical start. Unfortunately the fossil record gives us no information on the early evolutionary stages of the arthropods, when they might be called "Proarthropoda."

It is clear that arthropod sclerites are in no way equivalent to the bones of a vertebrate animal. Primitive sclerotized areas can be broken up into smaller parts or fused into a larger unit. On the other hand, secondary desclerotization often occurs, as in the abdomen of a hermit crab. Leg segments can be eliminated, or divided into subsegments. The vertebrate animal is limited by its bones to a certain form; the skeleton has little plasticity, except for the increase of vertebrae and ribs or the reduction and loss of appendages. The difference between a man and a snake is insignificant compared with that between a crab and a *Sacculina* parasitic within it.

IV. SCLEROTIZATION OF THE BODY SEGMENTS

The body segments of an annelid worm without appendages are mere integumental rings limited by circular grooves. In an animal having lateroventral appendages (fig. 3 A), however, the periphery of a segment is divided into a *dorsum* (*D*) above the limb bases, and a *venter* (*V*) between them. It is with the development of sclerotization that complexities arise in the segment structure, since the pattern of sclerotization may be very different in different arthropods, or even on different body segments in any one species.

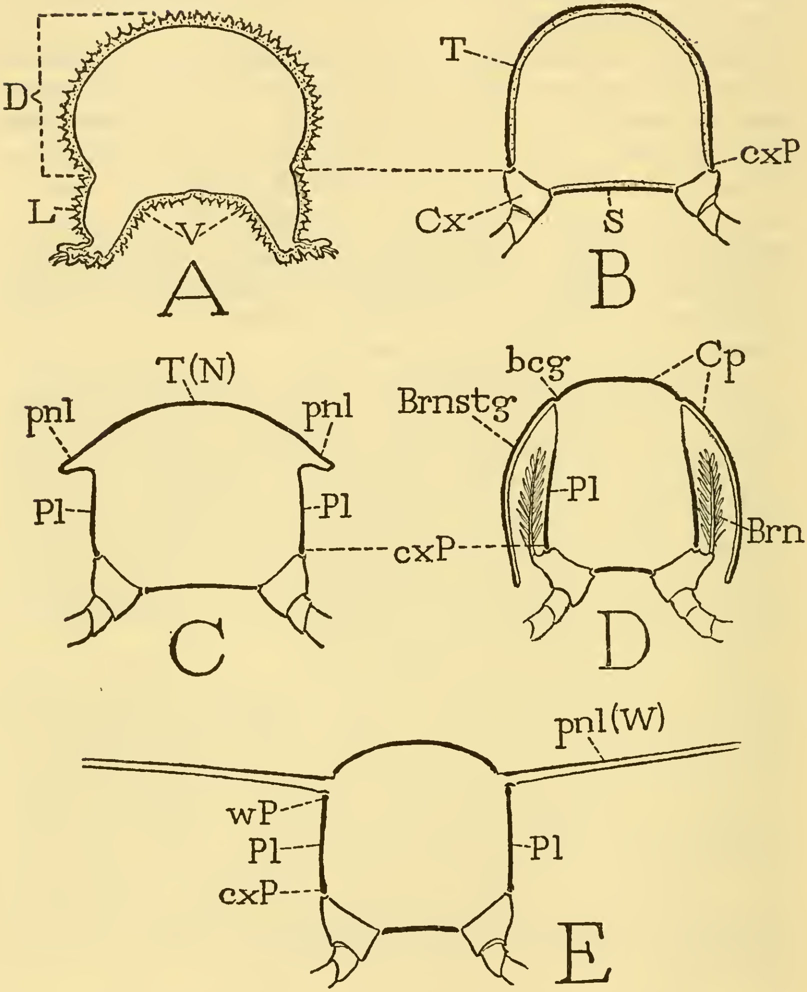

FIG. 3.—Diagrammatic cross sections of body segments, showing differentiation of surface areas.

A, Cuticle unsclerotized. B, Sclerotization forms a tergal and a sternal plate. C, Dorsal sclerotization differentiated into tergum, or notum, and pleura by paranotal lobes. D, Tergum replaced by a carapace (*Cp*) produced into gill covers (*Brnstg*), pleural areas become inner walls of gill chambers. E, Paranotal lobes produced into wings.

Though there can be no doubt that integumental sclerotization is the basis of modern arthropod structure and mechanisms, we have no evidence as to the pattern it first assumed. It seems reasonable that sclerotization was primarily developed for protection, but it is improbable that the body segments of a soft-skinned wormlike ancestral form became at once hard rings. Perhaps there was first formed in each segment a tergal plate on the back and a sternal plate on the venter, leaving the lateral areas soft and flexible. With such a structure the early arthropods could preserve something of the hydraulic motor mechanism of their vermiform progenitors, which is still operative in some soft-skinned larvae. With the development of limbs, however, body movements became less important in locomotion, and in most adult modern arthropods the side walls of the segments are sclerotized to support the appendages.

When we turn to modern arthropods, it is only a matter of opinion as to which retain a primitive type of sclerotization, and which are specialized. Among the crustaceans and diplopods the entire dorsum of a segment may be continuously sclerotized (fig. 3 B), in which case the name tergum (*T*) must apply to the whole back plate. In the crustacean *Anaspides* (fig. 4 B), for example, the dorsal plates of the thoracic segments continue down on the sides and support the legs on their lower ends, though each is cut by a slight groove near the lower margin that demarks a small laterotergite (*ltg*). A similar condition is shown in a cross section of the head of an insect (A), in which the mouth parts are suspended directly from the ventral edges of the cranial walls. Likewise in malacostracan crustaceans in which the carapace is short or attached on only a few thoracic segments, as in Mysidacea (fig. 6 B, C), Cumacea, and Stomatopoda, the terga of the free segments are simple dorsal arcs carrying the legs on their lower margins (G). In all these forms there is no anatomical distinction between tergum and pleura.

The legs of an isopod (fig. 5) are suspended from lateral lobes or plates (*Cx*) of the dorsal walls of the thoracic segments. These plates, usually called "epimera" by carcinologists, look like laterotergites, but according to Gruner (1954) they are formed in the embryo from the coxae of the legs; in some forms, as in *Porcellio* (A), they have become continuous with the terga. Corresponding plates in the amphipods (fig. 13 D, *Lcx*) are freely suspended from the tergal margins. If these plates on the leg bases are truly coxal, there is no part of the skeleton in the isopods and amphipods intervening between the terga and the coxae that can be regarded as pleural; the legs are here again carried directly on the tergal margins.

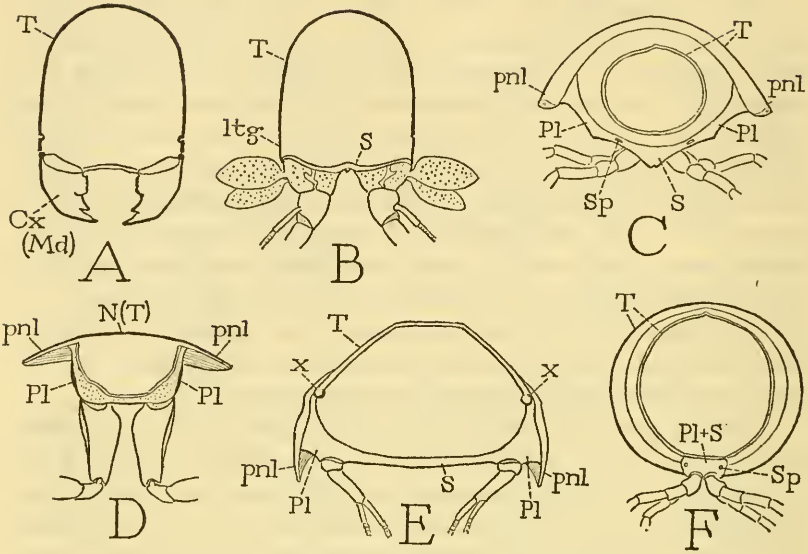

Fig. 4.—Examples of segment modifications.

A, Vertical section of head of an orthopteroid insect. B, Vertical section of thoracic segment of crustacean *Anaspides*. C, Segment of a polydesmoid diplopod, anterior. D, Prothorax of a cockroach, *Periplaneta*, posterior. E, Abdominal segment of female crayfish, anterior. F, Segment of a juliform diplopod, anterior.

x,x, articular condyles.

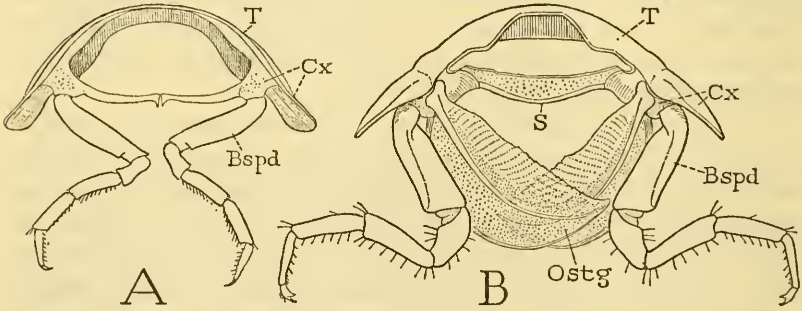

Fig. 5.—Thoracic segments of isopods.

A, *Porcellio laevis*, male, anterior. B, *Ligyda exotica*, female, posterior.

Where the dorsum of a segment is continuously sclerotized, it is only when some structural feature, such as paranotal lobes (fig. 3 C, *pnl*), separates the back from the sides of the segment that we arbitrarily restrict the term tergum (*T*) to the back, and call the lateral areas below the lobes *pleura* (*Pl*). Thus in a polydesmoid diplopod (fig. 4 C) or the abdomen of a decapod (E), in which the segments are wholly sclerotized annuli, the lateral areas between the paranotal lobes and the limb bases are conventionally designated pleura (*Pl*). In the cylindrical juliform diplopods, which have no paranotal lobes, each tergum (F, *T*) is continued downward on the sides to a small ventral plate (*Pl+S*) that contains the spiracles (*Sp*) and supports the legs. Since the spiracles of the polydesmoid are in the pleural areas, the ventral plate of the julid is evidently a pleurosternum, in which the pleural components are greatly reduced and separated from the tergum. The wings of insects (fig. 3 E) appear to have been evolved by a great extension of paranotal lobes; the lateral areas below them by definition are pleural (fig. 3 E).

It might be supposed that the gill covers, or branchiostegites, of the decapod crustaceans (fig. 3 D, *Brnstg*) are structures analogous to insect wings developed from paranotal lobes of the thoracic terga. The decapod structure as seen in cross section, however, is misleading. The carapace is *not* the united terga of the segments it covers; it is a posterior fold from the maxillary region of the "head shield," which has extended through the thoracic dorsum as far as the last segment and replaced the median parts of the invaded terga. The branchiostegites are lateral folds of the carapace.

A halfway stage in the replacement of the thoracic terga by the maxillary carapace is well shown in the Mysidacea, in which only three or four thoracic segments have been invaded by the carapace, though the latter may cover the entire thorax (fig. 6 A). When the carapace is removed from the thorax there is exposed a large V-shaped hole in the dorsum of the first three segments (B, C), on the margins of which is attached the inner lamella of the carapace. The dorsal parts of the thoracic terga in this region have been obliterated by the invasion of the carapace, and the lateral parts have been pushed back dorsally and drawn out into tapering tongues converging toward the end of the carapace attachment. In the decapods then, the attachment of the carapace has been extended from the maxillary region through the first seven thoracic segments, and has completely replaced the true tergal wall of these segments between the branchiocardiac grooves (fig. 3 D, *bcg*).

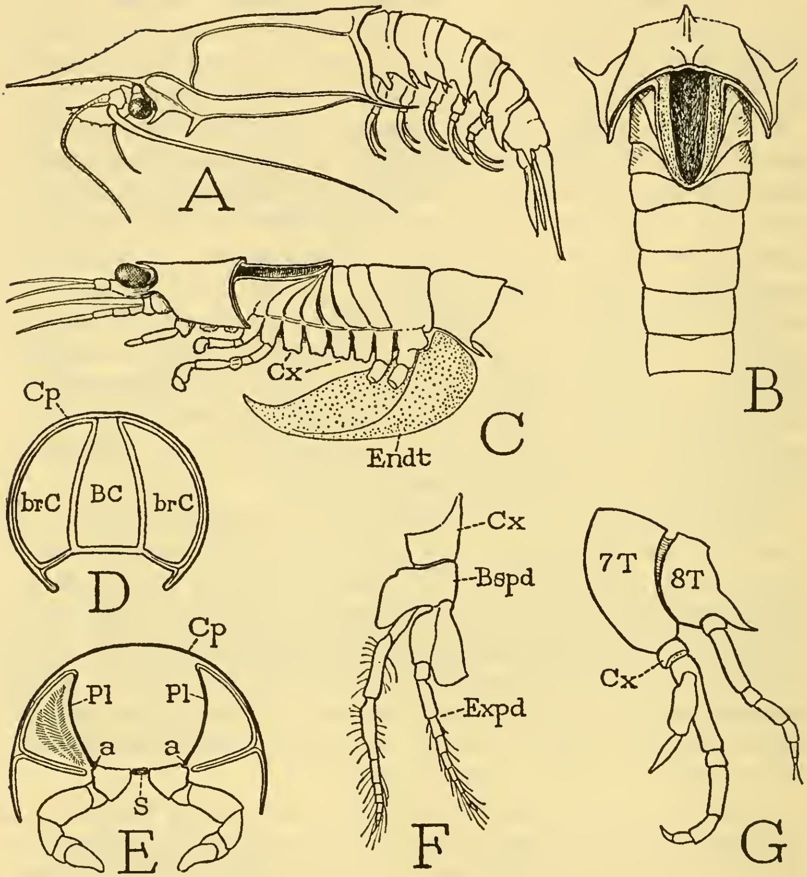

FIG. 6.—Formation of malacostracan carapace by extension from maxillary region, with conversion of lateral tergal areas of invaded segments into so-called epimeral, or pleural, plates carrying the legs.

A, *Gnathophausia calcarata bengalensis,* Mysidacea. B, Same, carapace cut off anteriorly, exposing its attachment by under lamella on back of thorax. C, *Acanthomysis dyboskii,* Mysidacea, carapace cut off behind maxillary segment, showing attachment on anterior thoracic segments. D, *Diastylis glabra,* Cumacea, section of second thoracic segment. E, *Emerita talpoida,* Decapoda, section of thoracic segment. F, *Acanthomysis dyboskii,* thoracic leg. G, *Diastylis glabra,* last two thoracic segments, showing direct suspension of legs from the terga.

The carapace of Cumacea commonly covers the first three, but sometimes more, of the thoracic segments. In *Diastylis* the carapace is attached by its inner lamella along only a narrow median strip of the back (fig. 6 D). Ventrally its wide lateral wings are connected by median submarginal flanges with the lower edges of the lateral body walls. The voluminous branchial chambers (*brC*) are thus entirely closed except anteriorly where the huge gill-bearing epipodites of the first maxillipeds project backward within them. The very short carapace of the stomatopods, likewise a fold from the maxillary segment, covers four of the thoracic segments, but it is attached on the back of only the first two segments, and the terga of these segments are cut by the carapace into lateral plates.

The malacostracan carapace is thus seen to be equivalent to that of the Notostraca and of *Nebalia;* but, instead of extending as a free fold over the thorax from the maxillary segment, it has united by its under lamella with the back of a varying number of thoracic segments, and has replaced the dorsal parts of their terga.

As an inference from the fact that the malacostracan carapace cuts through the back of the thoracic terga, it is clear that the plates on the inner walls of the gill chambers, still carrying the legs, though commonly termed "pleura" or "epimera," are actually the lateral parts of the severed terga. The concept that these plates represent "subcoxal" segments of the legs, therefore, has no foundation in crustacean anatomy. That the so-called pleural plates are tergal remnants is confirmed on finding that in the decapods there are no dorsal muscles of the thoracic limbs or longitudinal body muscles attached on the back behind the second maxillary segment. All these muscles retain their primitive tergal attachments on the "pleura." (See Schmidt, 1915; Berkeley, 1928; Cochran, 1935).

In contrast to the condition found among the Diplopoda and in those Crustacea that have free thoracic segments, in which the pleural areas of the segments are sclerotized in continuity with the back, the pleural regions of the leg-bearing segments in various other arthropods may be largely membranous, or occupied by discrete pleural plates. In *Limulus,* for example, the wide membranous pleural regions of the prosoma contain only small Y-shaped sclerites on which the legs are articulated. In the Arachnida integumental folds between the carapace and the leg bases are all that can be regarded as pleural. The thoracic pleurites of apterygote hexapods are two small sclerites in the otherwise membranous pleural wall concentrically arched over the coxae (fig. 9 A, B, C). The thoracic pleural plates of pterygote insects are always separate from the notum, but may be continuous with the sternum by precoxal or postcoxal bridges; they carry the legs and on the alate segments support the wings. In the chilopods the pleural areas of the segments are variously sclerotized, but the principal sclerites are closely associated with the coxae of the legs (fig. 8 H, K).

A very unusual pleural structure occurs among the diplopods in the Oniscomporpha. Two small spiracle-bearing plates on each side of the venter of each double segment (fig. 7 B, *pl*) intervene between the legs and a broad lateral lobe (*ltg*) inflected mesally from the lower margin of the tergum. Inasmuch as the coxae articulate by their lateral basal angles on these spiracle plates (B, C) the latter can hardly be anything other than pleural sclerites, and the fact that they contain the spiracles is in harmony with the pleural position of the spiracles in the Polydesmoidea (fig. 4 C). The plates are termed "laminae pedigerae" by Silvestri (1903) and "Stigmenplatten" by Gruner (1953), but Manton (1954) calls them "sternites." A true segmental sternum should lie between the coxae, but in the Oniscomorpha the coxae of each pair of legs are contiguous (fig. 7 A) leaving no space for a sternal sclerotization between them. In

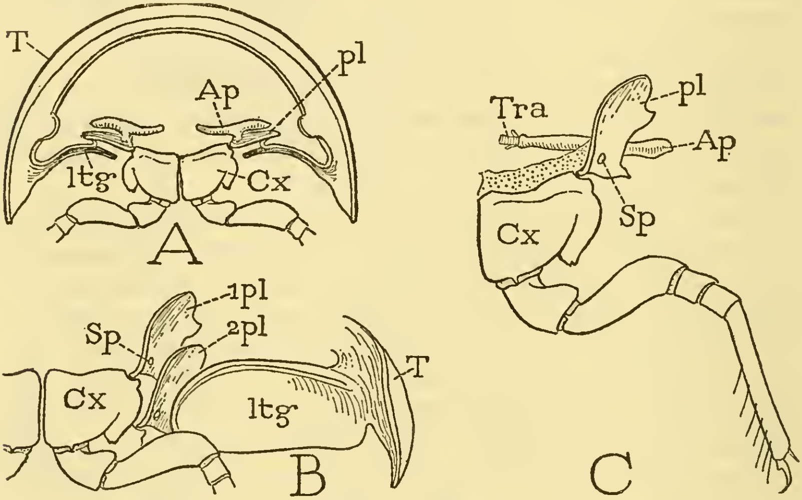

FIG. 7.—*Sphacropoeus* sp., oniscomorph diplopod.

A, Section of body segment with leg attachments. B, Ventral view of left half of a segment, showing base of anterior leg, spiracle-bearing pleurites (*pl*), and laterotergite (*ltg*). C, A left leg, showing articulation on pleurite, and spiracular apodeme (*Ap*).

Sphaeropoeus the thickened mesal margins of the spiracle plates stand out as free folds, so that successive plates overlap each other (B). Laterally each plate is connected by membrane with the lobe (A, *ltg*) inflected from the tergum. While there are two pairs of spiracle plates for each double segment, there is only one pair of lateral tergal lobes.

According to a rather widely accepted theory, the pleural plates have been derived from the leg bases and represent primitive "subcoxal," or "precoxal," segments of the limbs. As already shown, the theory receives no support from the diplopods or crustaceans; the alleged evidence in its favor has been deduced principally from a study of the chilopods and insects.

In the chilopod *Scutigera* the lateral areas of the anterior body segments contain each a large supracoxal plate (fig. 8 H, *Scx*) marked by a median spiny ridge and scarcely separated from the coxa (*Cx*). On the posterior segments these plates are successively smaller (I), until on the last segment (J) the remnant of the plate is fully united with the coxa in a single basal segment of the leg. In a geophilid (K) a circular fold (*Scx*) completely surrounds the base of the much reduced coxa (*Cx*), and, though it is not completely sclerotized, it might well be imagined to be a basal segment of the leg. Yet here again, on the last body segment there is only a single basal plate supporting the rest of the leg. The supracoxal pleural plates of the chilopods, therefore, are evidently secondary derivatives of the coxae, and there is no evidence that they represent basal segments of the legs. In *Scutigera* they carry with them some of the body muscles of the coxae.

The pleural sclerites of some insect larvae lie in ventrolateral lobes of the thoracic segments (fig. 8 F, G), but nothing in the development of the larva suggests that these lobes are basal segments of the legs. Eventually the small pleural sclerites of the larva expand upward to form the pleural plates of the adult.

A subcoxal origin of the thoracic pleura of insects has been claimed by Heymons (1899) and by Roonwal (1937, 1939) to be shown in the embryonic development of Hemiptera and Acrididae. According to Heymons the primary basal segment of the embryonic leg in Hemiptera divides into a proximal subcoxa and a distal coxa. The subcoxa flattens out and forms the part of the thoracic wall on which the definitive leg articulates, and from which leg muscles arise. In the embryo of *Locusta,* as described by Roonwal, the primary leg bases divide each into a subcoxal segment (fig. 8 A, *Scx*), and a coxotrochanteral segment (*Cx*+*Tr*) that later separates into coxa

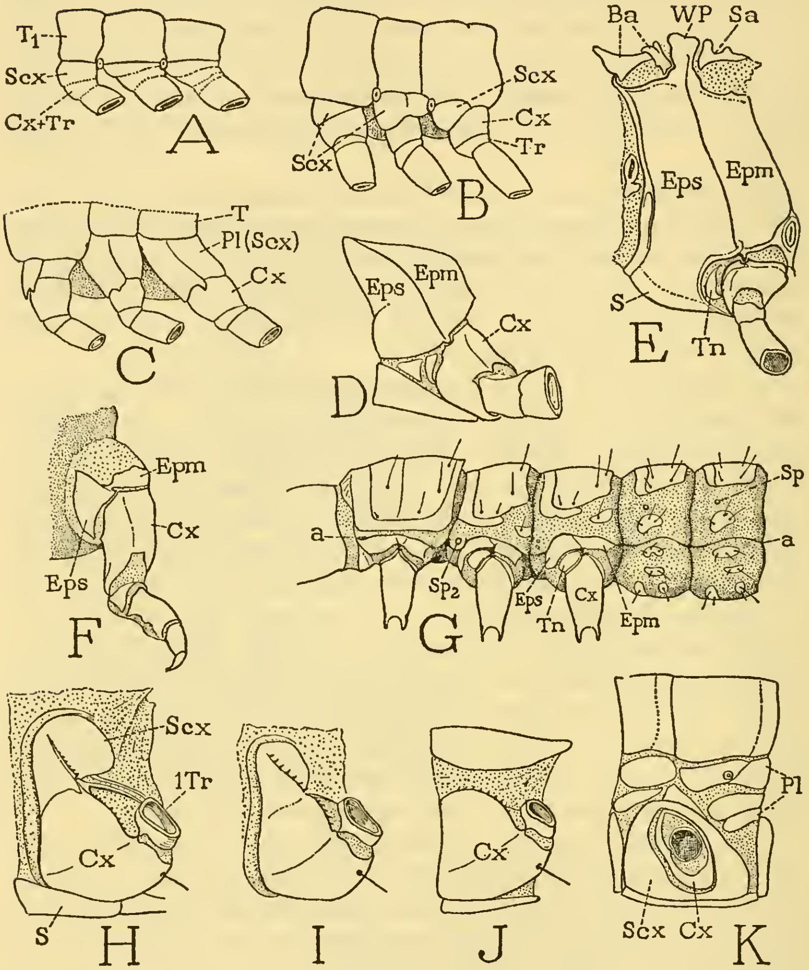

FIG. 8.—Features that have been interpreted as evidence of a subcoxal origin of the pleural plates. (A, B, C from Roonwal, 1937.)

A, Thorax and leg bases of young embryo of *Locusta*. B, Same, later stage. C, Same, newly hatched nymph. D, *Acheta assimilis*, mesothoracic pleuron and leg base of young nymph. E, *Dissosteira carolina*, mesopleuron and leg base of adult. F, *Pteronidia ribesii*, pleural sclerites and leg of larva. G, *Scarites* sp., carabid beetle larva, thorax and part of abdomen. H, *Scutigera* sp., centipede, leg base and "subcoxal" plate of eleventh leg-bearing segment. I, Same, thirteenth leg-bearing segment. J, Same, last leg-bearing segment. K, *Strigamia bothriopa*, geophilid centipede, middle body segment and leg base.

a-a, dorso-pleural line

and trochanter (B). The subcoxae then expand upward and become the pleura of the adult (C, *Pl*).

This evidence of subcoxal origin of the pleural plates as presented by Heymons and by Roonwal does not necessarily, as Heymons admits, substantiate the idea that the subcoxal elements were once the functional basal segments of the legs, though Heymons contends that the embryological evidence is in favor of the theory. However, since in isopods, amphipods, and chilopods plates in a pleural position are evidently formed from the coxae, it is quite possible that a mistaken significance may be given to the observed facts of embryonic development. The development of arthropod limbs in general gives little support to the theory of the derivation of the pleural sclerotization from a subcoxal leg segment.

The pleural sclerotization of a wing-bearing thoracic segment of adult insects generally covers most of the side wall of the segment (fig. 8 E). Characteristically it is marked by a median vertical or inclined groove that forms internally a strengthening ridge from the coxa to the wing, ending below in a coxal articular process, and above in a fulcral arm (*WP*) that supports the base of the wing. The pleural areas respectively before and behind the coxo-alar sulcus are the so-called *episternum* (*Eps*) and *epimeron* (*Epm*). Detached from the lower end of the episternum is usually a precoxal *trochantin* (*Tn*), which makes a secondary anterior articulation with the coxa. One or two *basalar* sclerites (*Ba*) lie in the subalar membrane before the wing fulcrum, and behind the latter is a subalar sclerite (*Sa*). These epipleural sclerites have an important function in the movement of the wing. A thoracic pleuron of this type is clearly constructed primarily for giving a strong support for the leg, and secondarily has been modified in the alate segments in adaptation to its relation to the wing and wing movements. The pleuron of the wingless prothorax, or that of a prospective alate segment of the nymph (fig. 8 D) or larva (F, G) bears a coxal articular process, but lacks the special features related to the wing.

The pleural sclerotization of the thorax in adult insects, however, undergoes various modifications in the different orders, and may be broken up into subsidiary parts, or reduced where the wings are small or suppressed. In a male scale insect, in which the hind wings have been reduced to a pair of small halterlike appendages, the metathoracic pleura, as shown by Ezzat (1956), are slender rods extending from the halteres to the coxae.

When we turn from the pterygote insects to the apterygotes we find an entirely different type of sclerotization in the thoracic pleural regions (fig. 9 A, B, C). The pleural areas are here largely membranous, but in each segment are two narrow sclerites concentrically arched over the base of the coxa, a dorsal *anapleurite* (*Apl*) and a ventral *catapleurite* (*Cpl*). In the Lepismatidae (C) a third sclerite intervenes between the catapleurite and the coxa, which some writers regard as a trochantin, but it has the appearance of a basicoxite. Though the apterygote Protura, Collembola, and Diplura have no close relation to the rest of the hexapods, the Thysanura undoubtedly

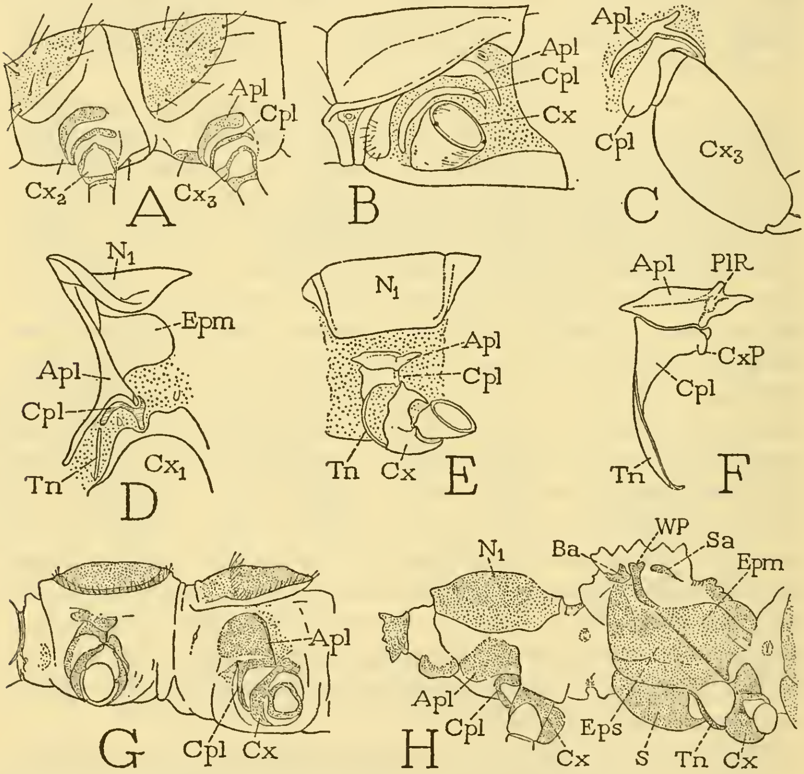

Fig. 9.—Thoracic pleura of insects: apterygotes, termite, and stonefly.

A, *Acerentomon doderoi,* mesothorax and metathorax (from Berlese, 1910). B, *Heterojapyx gallardi,* metathorax. *C, Ctenolepisma urbana,* metathoracic pleurites and coxa. D, Prothoracic pleuron of a winged termite (from Fuller, 1924). E, *Perla* sp., larva, prothorax. F, Same, right propleuron, internal. G, *Chloroperla grammatica,* prothorax and mesothorax of larva (from Grandi, 1950). H, *Protonemura* sp., prothorax and mesothorax of adult (from Grandi, 1950).

are preliminary to the pterygote line of evolution. It might be inferred, therefore, that the apterygote type of pleural sclerotization is primitive, the Collembola being the oldest known hexapods, and that from it has been derived the thoracic pleuron of the Pterygota.

Evidence of the derivation of the pterygote pleuron from two supracoxal sclerotic arches may be deduced from a comparative study of larval and adult Plecoptera. In the larva of *Perla* (fig. 9 E), for example, the membranous pleural area of the prothorax contains a typical anapleurite and a catapleurite. The catapleurite is articulated with the coxa, and from its anterior ventral angle a trochantinal bar (*Tn*) extends down to the lower angle of the coxa. The inner surface of the anapleurite (F) is crossed by a ridge (*PlR*) in line with the coxal process (*CxP*) of the catapleurite. The same pleural structure, as shown by Marta Grandi (1950), may be present on the other thoracic segments of the larva (G) and on the prothorax of the adult (H). In the winged segments of the adult, however, the pleuron has the typical pterygote structure (H, right), including basalar and subalar sclerites (*Ba, Sa*).

During development of the plecopteron from larva to adult, according to Grandi, the anapleurite of the larva unites with the posterior dorsal part of the catapleurite to form the adult episternum (fig. 9 H, *Eps*), and the ventral arm of the catapleurite becomes the trochantin (*Tn*). The epimeron (*Epm*), however, is mostly a secondary sclerotization not derived from the larval plates. The pleural sclerotization of larval Plecoptera, Grandi says, thus undergoes a gradual transition to that of the typical adult pleuron of the Pterygota.

The prothorax of a winged termite (fig. 9 D), as figured by Fuller (1924), also suggests the evolution of the pterothoracic pleuron from two supracoxal arches (*Apl, Cpl*), though Fuller did not so interpret it. Verhoeff (1902) analyzed the pleuron of the other pterygote insects into similar anapleural and catapleural components, which he homologized with supracoxal sclerites of *Lithobius forficatus.* It must be noted, however, that the pleural sclerotization is highly variable in different groups of chilopods, and, as has been shown, the principal plates appear to be derivaties of the coxae.

Convincing evidence of a primitive subcoxal limb segment would be the finding of an arthropod, modern or fossil, with a functional leg segment proximal to the coxa. It is true that a "subcoxa," or "precoxa," has often been described and figured in illustrations, but the segment becomes subcoxal by shifting the name "coxa" to the next segment or giving it to an imaginary segment. Since the coxa is usually the functional basal segment of the limb on which most of the body muscles of the appendage are attached, if there was primarily a functional subcoxa, it should be explained how the muscles became transferred from the subcoxa to the coxa.

The writer himself formerly (1927) advocated and elaborated the subcoxal theory of the origin of the thoracic pleura, and devised a set of diagrams purporting to show the evolution of the insect pleuron from a subcoxal segment of the leg. Hansen (1930, pp. 75, 76) made some pungent remarks about the writer's subcoxal diagrams, and expressed it as his opinion that they "belong to fiction or poetry." The author of the diagrams makes no claim to being a poet, but does admit that he may sometimes have had uncontrolled flights of imagination.

A general survey of the pleural sclerotization in the several arthropod groups shows that there is no common pleural structure, and suggests that the various types of sclerotization in the lateral walls of the body segments are specific adaptations to the structural needs of each kind of animal. While the term *pleuron,* meaning the lateral sclerotization of a body segment, therefore, has no specific morphological significance, it is nevertheless by definition a convenient and useful name to retain for descriptive purposes.

The major segment plates of the arthropod skeleton—*tergum, pleura, and sternum*—are subject to subdivision into *tergites, pleurites,* and *sternites.* The subdivisions may be separated by membranous lines or areas in the integument. More often, however, they are demarked by grooves, commonly known as "sutures," which form internal sclerotic ridges to strengthen the skeleton or to give attachment to muscles. Clearly, neither membranous lines of the integument nor ridge-forming grooves are sutures in a literal sense of the term, which should imply lines along which originally distinct sclerites have secondarily united (*sutura,* a seam). A better term for such impressed lines is *sulcus* (a groove, or furrow), reserving the term *suture* for lines or grooves that can be demonstrated to be formed by the union of sclerites. The skeleton of arthropods, especially that of the insects, has been studied too much as a map, without giving attention to the mechanical significance of its structural features. On the other hand, arthropod morphology is becoming overloaded with theories.

V. INTERSEGMENTAL MECHANISMS

Since the arthropod body wall is continuous, it is not truly "divided" into segments. The functional body segments of the adult animal.

as already explained (p. 11), are merely the sclerotized parts of the primary segments separated by unsclerotized membranous areas. These so-called "intersegmental" membranes are the posterior parts of the primary segments, and each is generally folded into the preceding segment to allow movement of consecutive segments on each other. Particular types of structure, however, may limit the intersegmental movement to the horizontal or the vertical plane, and devices are sometimes present for separating the segments as far as the intersegmental membranes will allow.

Chilopoda.—The centipedes differ from most of the other arthropods in that they make lateral undulatory movements of the body as they run around objects obstructing their paths. This facility is owing in part to the fact that the tergal plates are limited to the back and do not curve downward on the sides. The intersegmental structure between the terga and sterna differs in the several chilopod groups.

A simple intertergal condition is seen in the agile lithobiids. The tergal plates overlap from before backward (fig. 10 A) and are connected by the infolded intersegmental membranes. When the terga are pulled apart and viewed from the inner surface (B), the membranes (*isMb*) are seen to be relatively narrow medially and expanded laterally where they merge into the pleural membranes (*plMb*). This arrangement allows the terga to be freely movable on each other in the transverse plane. The posteriorly overlapping sternal plates are connected by deeply inflected membranes, which also widen laterally. The body is traversed by longitudinal muscles that pull the segments together, and produce also the lateral movements, but there is no specific mechanism for pushing the segments apart. The intersegmental structure of *Scutigera* is essentially the same as in *Lithobius*. Manton (1952b) notes that "in the anamorphic Chilopoda, *Lithobius* and *Scutigera,* the length of the body in resting and running animals does not differ materially."

In a scolopendrid the tergal plates seen from above (fig. 10 C) overlap and seem to be the same as in *Lithobius*. A lengthwise section through the overlap (D), however, shows that it is the posterior part of the tergum itself (*Rd*) that is underfolded, and is attached to the anterior margin of the next tergum by only an extremely narrow connecting membrane (*isMb*). The reduplication, or infolded part of the tergum (E, *Rd*), is flexible, being somewhat thinner than the exposed part, and is marked by a fine transverse striation, which is weakly visible also on the rest of the plate. The narrow connective strip of membrane between the margins of the terga abruptly widens

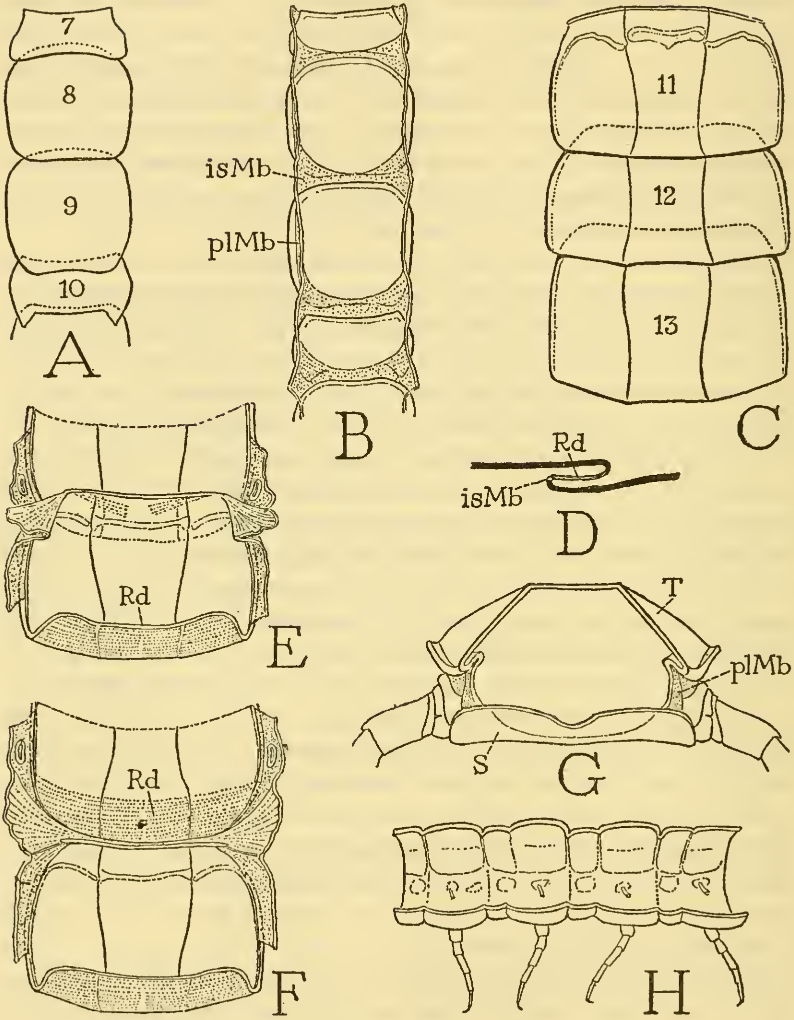

FIG. 10.—Intersegmental mechanisms, Chilopoda.

A, *Lithobius* sp., tergal plates in normal position, dorsal. B, Same, plates pulled apart, ventral, showing intersegmental membranes. C, *Scolopendra heros castaneiceps,* tergal plates normally overlapping. D, Same, section of adjoining parts of two terga. E, Same, inner surfaces of adjoining terga in normal position. F, Same, plates forcibly pulled apart. G, Same, fourteenth segment, anterior. H, *Arenophilus bipuncticeps,* right half of segments, mesal.

on each side and is folded in a pocket where it joins the pleural membrane. When two consecutive terga are forcibly pulled apart (F) the lateral folds are flattened out and are seen in their full extent. It is evident that here sidewise movements of the segments on each other must depend largely on the flexibility of the posterior infolded parts of the terga. Within each fold are two small transverse muscles (E) arising medially on the anterior tergum and attached laterally on the margin of the posterior tergum. The pleural areas of *Scolopendra* (G) are mostly occupied by sclerites surrounding the bases of the coxae. The sternal plates (*S*) are separated by deep infolds of the integument, in which is a pair of small lateral sclerites that appear to belong to the segment following. *Scolopendra* has a strong and elaborate body musculature.

According to Manton (1952b) the body of a scolopendrid running at a fast gait may lengthen as much as 5 percent of its normal length. Since there is no protractor mechanism between the segments, the stretching of the body must result from a drag by the posterior legs exerted on the flexible tergal reduplications.

The geophilomorph chilopods present an intersegmental condition that is quite different again from that of either *Lithobius* or *Scolopendra*. A longitudinal section of the body of a species of *Arenophilus* (fig. 10 H) shows that there is no overlapping of the segmental plates, the segments being separated only by shallow indentations of the integument. The whole body is soft and flexible; a dead specimen can be stretched slightly by a flattening of the segmental plates. Manton (1952b) says that an individual running at a fast gait is only 3-6 percent longer than one going slowly. According to Dr. R. E. Crabill of the U. S. National Museum, *Arenophilus bipuncticeps* is adept at going either forward or backward. The movements of the legs and the accompanying undulations of the body by the chilopods are fully described and illustrated by Manton (1952b).

Insects.—Among the insects, particularly those that make respiratory movements of the abdomen, the abdominal segments in some species can be muscularly protracted as well as retracted. More commonly the respiratory movements consist of dorsoventral dilations and compressions of the segments, but both longitudinal and vertical movements may take place at the same time, as in the bees.

The typical longitudinal muscles of the insect abdomen (fig. 11 A, *rmcl*) retract the segments in the usual manner. The opposite movement of protraction is produced by short muscles (*pmcl*) lying in the intersegmental folds between successive terga and sterna. They take their origins on the posterior parts of the segment plates and are inserted on apodemes (*Ap*) of the plate following that project forward into the preceding segment. Contraction of these muscles pushes the segments apart (B) as the connecting membranes become folded. Inasmuch as the retractors and protractors are both longitudinal muscles, which typically are of segmental length, it might be supposed that the protractors have shifted their origins to the rear parts of the terga and sterna, while their insertions have been carried forward on the apodemes. However, this imaginary simultaneous migration of four muscles until their function becomes reversed is difficult to visualize; it would be more simple if we might assume that special muscles can be formed during evolution to operate a new mechanism.

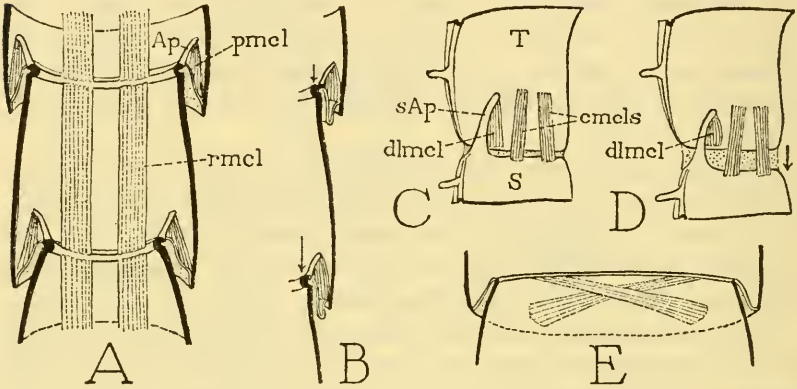

FIG. 11.—Abdominal mechanisms of insects, diagrammatic.

A, Consecutive terga in state of retraction, inner surface. B, Section of same protracted. C, Right half of segment, mesal, sternum elevated by compressor muscles (*cmcls*). D, Same, sternum depressed by dilator muscle (*dlmcl*). E, Oblique intertergal muscles of an acridid, giving movement of transverse torsion.

A mechanism of partial torsion of the abdominal segments on each other is present at least in the Acrididae. Two intersegmental transverse muscles in the fold between two terga (fig. 11 E) cross each other from one side to the other, and evidently by antagonistic action give the adjoining segments a sidewise or rotary movement on each other.

The mechanism of dorsoventral dilation and compression works in the same way as that of protraction and retraction, but the operative muscles are antagonistic sets of vertical lateral muscles. The compressors are typical lateral tergosternal muscles (fig. 11 C, *cmcls*). Dilation is produced by a reversed muscle on each side (*dlmcl*) arising on the lower edge of the tergum and inserted on the upper end of a long marginal apodeme of the sternum (*sAp*); by contraction it pushes the sternum downward (D).

Diplopoda.—The diplopods are so named because all their functional segments, except the first four or five bear each two pairs of legs. This fact is taken to mean that these four-legged segments are composed each of two wholly consolidated primitive segments. The doubling of the segments is explained by Manton (1954) as an adaptation to the habit of most diplopods of pushing into debris or under objects that obstruct their path, instead of running around such impediments as do the more flexible centipedes. "A marked ability to push," she says, "is as diagnostic of the Diplopoda as is the possession of diplo-segments." The union of the segments strengthens the body without the loss of legs, and is thus more effective for pushing or burrowing than would be twice the number of segments with the same number of legs. Manton tested the pushing ability of different species by harnessing them to flat-bottomed pans loaded with measured weights, assuming that the animals could push with a force equal to that with which they can pull. Members of the Polydesmoidea and Nematophora were found to be the strongest pushers among the diplopods.

The diplopods are noted for their ability to flex or coil the body ventrally by movement of the segments on each other. There is no protractor mechanism between the segments such as that found in the abdomen of some insects, and there are no intersegmental points of articulation. In the Proterandria the segments are solid rings connected by flexible membranes, and are shorter ventrally than dorsally. Ventral flexion and straightening are effected by the opposing action of antagonistic sets of body muscles.

The body segments of the Polydesmoidea are each distinctly differentiated into an anterior prozonite and a posterior metazonite (fig. 12 A, B). The longer metazonite is produced laterally into a pair of paranotal lobes (fig. 4 C). The prozonite is a simple ring with a smooth, polished surface, and is somewhat incurved anteriorly to fit into the preceding segment. In the extended position of the animal (fig. 12 A) the metazonite overlaps the prozonite of the following segment. The infolded connective membrane arises from the anterior margin of a posterior reduplication (*Rd*) of the tergum, which extends almost to the middle of the metazonite. Ventrally (B), however, the short sterna are entirely separated by wide, flat membranes connecting the upcurved posterior margin of each sternum with the sternal prozonite of the next segment. In the flexed condition (B) the dorsal intertergal membranes are stretched out flat, and are just long enough to prevent a complete separation of the terga, so that the back of the animal makes an even curve. The sterna, on the other hand, come together, the prozonites overlapping internally the preceding sterna, and the connective membranes are deeply infolded.

The long cylindrical Juliformia have numerous short segments, which are only a little longer dorsally than ventrally. The anterior margin of each segment (fig. 12 C) is thickened to form a strong internal ridge, the antecosta (*Ac*) or prophragma, for muscle attachments. The free posterior margin is a very narrow, rimlike reduplication (*Rd*) from the base of which arises the intersegmental membrane (*Mb*). In the straight condition (D) the metazonite widely overlaps the following prozonite.

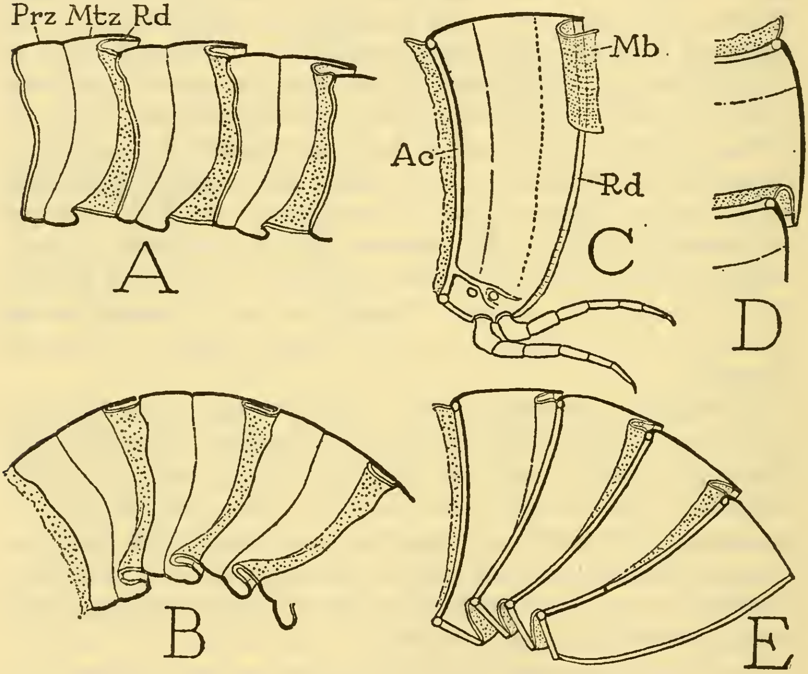

FIG. 12.—Intersegmental mechanisms, Diplopoda.

A, *Apheloria trimaculata,* Polydesmoidea, segments in straight position, mesal view of right side. B, Same, segments deflexed. C, *Narceus* sp., Juliformia, inner view of right side of a segment. D, Same, intertergal connection. E, Same, segments deflexed, diagrammatic.

Ventral flexion of the julid diplopod involves principally a compression and infolding of the ventral parts of the segments (fig. 12 E), which are pulled tight together. The terga are not separated enough to expose the intersegmental membranes, but the sterna are sharply tilted upward so that their anterior ends deeply overlap internally the depressed posterior ends of the preceding sterna. The segments are thus turned downward posteriorly. Though there is only a relatively small amount of movement between successive segments, the julids are able to curve themselves into a spiral because of the large number of short segments. The ball-and-socket nature of the intersegmental joints allows also a small degree of transverse rotation of the segments on each other. The body musculature and the function of the various sets of muscles concerned in the flexion of the diplopods has been fully described by Manton (1954).

Among the opisthandrious diplopods, members of the Oniscomorpha are noted for their ability to roll themselves up in a tight ball. A representative of this group will be described in the next section.

Crustacea.—The principal body movements of the malacostracan Crustacea are dorsoventral flexions of the abdomen on the thorax, and of the abdominal segments on each other. In the crayfish, for example, the successive segments of the abdomen are definitely hinged to each other by articular knobs on the posterior segmental margins at the bases of the lateral lobes of the terga (fig. 4 E, *x*, *x*). Movements of the segments on each other, therefore, are restricted to flexion and extension in a vertical plane. Dorsally each tergum widely overlaps the one behind it, and the two are connected by an ample infolded membrane. The narrow sternal plates by contrast, are separated by wide, flat conjunctivae that simply fold upward between the sterna when the abdomen is flexed. Owing to this intersegmental structure the animal is able to drive itself backward in the water by sudden, strong downward and forward strokes of the broad tail fan, as do also the shrimps and the lobsters. To accomplish this action the whole abdomen is filled with a great, complex mass of muscles, including bands of longitudinal fibers, segmental transverse muscles, and huge pleurisegmental oblique muscles, as shown by Schmidt (1915) in the crayfish *Astacus,* and by Berkeley (1928) in the shrimp *Pandalus.*

The ability of these crustaceans while peacefully swimming forward with the pleopods to suddenly dash backward on the appearance of danger is evidently of great importance to them for escaping from enemies in the water. The very musculature that enables them to escape from aquatic enemies, however, has made them victims in greater numbers to a more ingenious terrestrial predator, on whose menus they have become favorite items.

The beach-living amphipods known as "sandfleas" are notorious jumpers. The abdomen (fig. 13 A, B) is differentiated into a larger anterior part of three ordinary segments (*1, 2, 3*) bearing typical pleopods, and into a smaller posterior part of three condensed segments (B, *4, 5, 6*) and a small conical telson (*Tel*). The limbs of these posterior segments are thick, two-pronged appendages projecting backward and decreasing in length from the first to the third. The terminal part of the abdomen is the jumping organ of the sandflea. Its base is hinged dorsally to the large third tergum allowing the whole tail structure to be flexed downward and forward (A). With the prongs of the appendages braced against the beach sand, by a sudden straightening of the abdomen the amphipod makes a spring of remarkable distance, sometimes more than a meter.

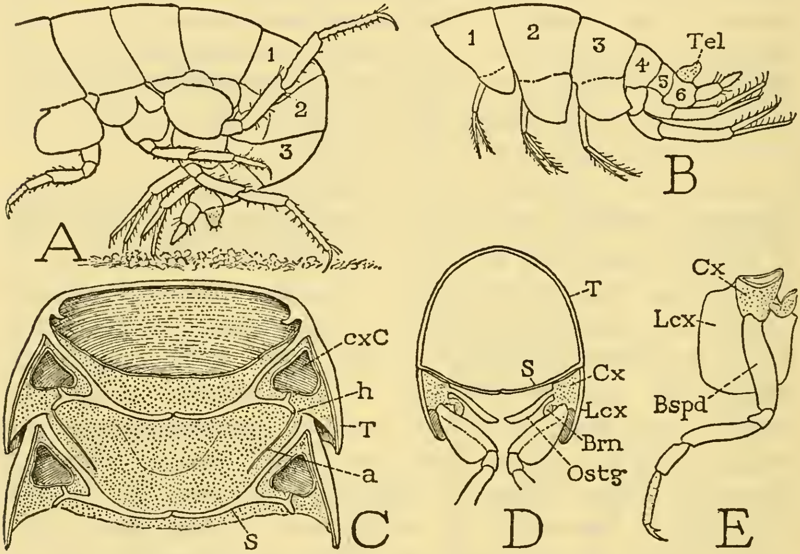

FIG. 13.—*Talorchestia longicornis,* Amphipoda.

A, Posterior thoracic segments and abdomen in flexed jumping position. B, Abdomen extended. C, Under surface of fifth and six thoracic segments, legs and coxal plates removed. D, Section of sixth thoracic segment of female, anterior. E, A right thoracic leg, mesal.

h, angle of flexion.

The tergal plates of the thorax and the anterior three abdominal segments are strongly arched and overlap each other from before backward. The under surface in *Talorchestia* (fig. 13 C) is weakly membranous except for a pair of narrow, delicate sternal bars (*S*) joined in the middle of each segment. The outer ends of the bars are widely forked into two arms that embrace the coxal cavities (*cxC*). The longer anterior arm on each side goes forward and upward to join the margin of the tergum at the base of the lateral coxal plate (removed in the figure). The shorter posterior arm ends behind the coxa, and gives attachment to a slender bar (*a*) that turns mesally at a sharp angle and runs along the anterior sternal arm of the following segment. The consecutive segments are thus connected by V-shaped links, the apices of which (*h*) are the turning points of the segments on each other. Long bands of dorsal and ventral muscles run through the entire length of the thorax and abdomen, but the dorsal muscles are much larger than the ventrals. The weak, delicately membranous venter of the body allows a large degree of ventral flexion by the ventral muscles. The large dorsal muscles are the effectors of the backward stroke of the flexed posterior part of the abdomen by which the amphipod springs forward.

VI. FOLDING AND ROLLING ARTHROPODS

The device of flexing the body in a U-shaped fold or of rolling up in a ball to protect the soft under surface has been made use of by arthropods of several groups, as well as by such mammals as the hedgehog and some armadillos.

The first arthropods that practiced folding, bringing the venter of the posterior half of the body close against that of the anterior half, were the trilobites (fig. 14 A). The species of *Phacops* shown in the figure is a Devonian trilobite, but many of the earlier forms did the same thing. Among modern arthropods folding and rolling occur among the isopods, the diplopods, and the Acarina.

Most of the land isopods are adept in ventral flexion of the body. Some fold the body together in the manner of the trilobite; others such as *Armadillo* and *Armadillidium* roll themselves into a ball, and have thereby acquired the name of "pillbugs." A folding species is *Cylisticus convexus* (fig. 14 B), described by Gruner (1953) as a "Halbkugler." A detailed description of the skeleton and musculature of this isopod, with comparative studies on other species, is given by Gruner, from whose paper the following extract is taken.

The thoracic terga of *Cylisticus* are strongly calcified and widely overlap posteriorly. Transversely they are arched, more so than in such forms as *Porcellio* (fig. 5 A), but less than are the terga of *Armadillidium* (fig. 14 D). The sterna by contrast are flatly convex, weak, and but little calcified. The ventral intersternal membranes are folded posteriorly so that each overlaps internally the following sternum. This feature, Gruner points out, is of much importance for ventral flexion and folding of the body. Where the terga and sterna come together the sternum has a notch on its posterior border that receives the margin of the following tergum. The segments are thus articulated on each other in a manner to allow of only an up-and-down movement.

Members of the genus *Armadillidium* (fig. 14 C) give a good ex-

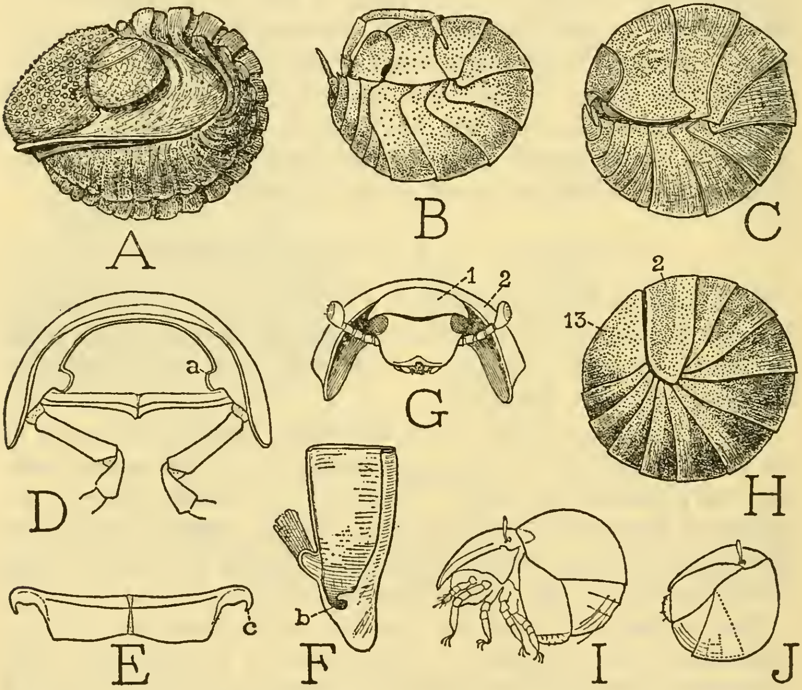

Fig. 14.—Folding and rolling arthropods.

A, *Phacops* sp., a folded Devonian trilobite. B, *Cyclisticus convexus,* a folded isopod (from Gruner, 1953). C, *Armadillidium vulgare,* a rolled isopod. D, Same, a thoracic segment, anterior. E, Same, a thoracic sternum. F, Same, lower end of a thoracic tergum, inner surface. G, *Sphaeropoeus* sp., head, collum (*1*), and second tergum (*2*). H, Same, completely rolled. I, *Aedeloplophora glomerata,* a water mite (from Grandjean, 1932). J, Same, rolled by compression (from Grandjean, 1932).

ample of isopods that roll themselves up in a spherical ball. In the rolled condition of *Armadillidium* the uropods cover the antennae and the mouth parts, but the top of the head is fully exposed. The thoracic terga are strongly arched transversely (D) and connected by deeply infolded membranes. The anterior tergal margin is produced into a small apodemal lobe on each side (D, *a*) on which is inserted a thick, transversely oblique muscle from the preceding tergum. The thoracic sterna (D, E) are thin, weakly sclerotized plates, each of which is divided into lateral halves by a hinge joint in the middle. The ends of the sternal plates are produced into lobes before the leg bases, each of which terminates in a recurved hook (E, *c*) inserted into a notch on the inner face of the lower part of the tergum (F, *b*).

The isopod body musculature includes dorsal and ventral longitudinal muscles, and dorsoventral muscles, and has been described by Gruner (1953) for *Cyclisticus* and *Armadillidium.* The dorsal muscles are mostly of segmental length and straighten the body after flexion, but in such forms as *Porcellio,* according to Gruner, some of the dorsal muscles extend through two segments, and these nonrolling species can bend the body upward. The ventral muscles of the isopods are two long lateral bands extending from the head to the telson. The dorsoventral muscles serve to lift the weak sterna, and thereby elevate the whole ventral body wall. When the ventral and the dorsoventral muscles contract at the same time, the under side of the body is both shortened and lifted, resulting in a ventral flexion of the body, or in the rolling of those species that curve into a ball.

Various other adaptive modifications of the skeleton are shown by Gruner to be correlated with rolling. In *Porcellio,* for example, the terga are of equal size and the lateral margins form an even ventral line. In *Armadillidium,* however, the third and fourth terga are not so deep as the others, leaving a notch in the lateral margins that facilitates rolling.

Ventral flexion of the body has been carried farthest in the oniscomorph diplopods, which roll up to such an extent that not only the mouth parts and antennae, but also the head and the collum are all completely concealed beneath the large, hoodlike last dorsal plate (fig. 14 H, *13*). This plate is the tergum of the thirteenth body segment, counting the collum (G, *1*) as the first. It covers the membranous terminal segment that carries the two pairs of gonopods and the anus-bearing telson, and in the rolled condition its free posterior part overlaps the head and collum. The enclosure of the head and collum, however, is due not so much to the degree of rolling as to the fact that these parts hang down from beneath the front margin of the large second segmental tergum (G) instead of projecting forward.

The Oniscomorpha differ from the proterandrious diplopods and resemble the isopods in the flatness of the under surface of the body, which, including the laterotergites, is arched upward (fig. 7 A), a feature necessary for rolling. The unusual structure of the under surface of the oniscomorphs, in which the pleura are small, independent spiracle-bearing plates, has been described in connection with the general discussion of the pleural modifications (p. 20). The structure, body musculature, and rolling mechanism of *Glomeris* have been fully described by Gruner (1953), and Manton (1954) has exhaustively analyzed the rolling mechanisms of *Sphaerotherium* and *Glomeris,* as well as the flexing and locomotor mechanism of the other diplopods. In Manton's discussions the identification of the spiracular plates of the Oniscomorpha (fig. 7 B, *pl*) as "sterna" is confusing. As already pointed out, the articulation of these plates with the lateral basal angles of the coxae can scarcely leave any doubt that the plates are anything else than pleural, except by changing the definition of pleuron.

Finally, there are the oribatid mites of the family Protoplophoridae that compress themselves into a compact ball. The dorsal skeleton of one of these mites (fig. 14 I), as described by Grandjean (1932), is divided into five plates. The first is a shieldlike lobe, the *aspis,* covering the gnathosoma, the genital region, and the legs. The second and third are strongly convex, segmentlike dorsal plates connected by an infolded membrane. The other two are lateral plates depending from the edges of the first dorsal plate. In the "rolled" condition (J) the mite assumes a spherical form quite as complete as that of the isopod (C) or the diplopod (H), but its manner of doing so is different. Instead of rolling, accompanied by a separation of the dorsal parts of the back plates, the mite becomes a ball by collapsing. The aspis is brought down tight between the lateral plates (J), concealing the gnathosoma and the legs, and the second dorsal plate slides *forward* within the first dorsal plate. Thus, while the trilobite, the isopod, and the diplopod take the spherical form by folding or rolling the body upon itself, the mite accomplishes the same thing by compressing the body into a ball.

VII. TAGMOSIS

There is no known adult arthropod, living or fossil, in which all the primitive trunk segments are distinct annuli. The union of segments into functional groups is called *tagmosis.* Examples of tagmata are the head, thorax, and abdomen of the Mandibulata, the prosoma and opisthosoma of the Chelicerata.

The head tagma of the mandibulate arthropods varies much in its segmental composition. The simplest embryonic head is a large cephalic lobe (fig. 15 A, B, C, F, *emH*) on which the eyes and first antennae are developed. Later there are added to this embryonic head and consolidated with it from one to six primary body segments to form the head of the adult. The embryonic cephalic lobe is regarded by most arthropod morphologists as being originally itself a segmented part of the trunk, but the alleged segments are differently identified by different writers, resulting in much confusion in the literature on "head segmentation."

A body segment, according to most students of arthropod embryogeny, is to be identified as such by the presence of a pair of coelomic sacs in the embryonic mesoderm. In the adult animal, however, a segment is an independently musculated and movable section of the trunk, unless secondarily combined with other segments. The question, therefore, is: was there ever any such segmentation in the embryonic cephalic lobe—did it ever consist of independently movable sections with a segmental musculature? If so, no evidence of tagmosis remains either in the head of the embryo, or in the structure and musculature of the corresponding part of the adult cranium of modern arthropods. Convincing evidence of former segmentation in this part of the head must await the finding of an embryo with a segmented cephalic lobe, or the discovery of a fossil arthropod with independent segments before the segment of the second antennae.

Only by definition does the presence of cavities in the mesoderm constitute body segmentation. For this reason some writers have regarded the cephalic lobe of the arthropod embryo as the equivalent of the annelid prostomium, since each structure contains the primitive brain. In either case, whether the primary arthropod head was prostomial or a segmental tagma, it was a purely sensory structure in which were developed the ocular and antennal centers that became the major parts of the modern brain. Later, the segment of the second antennae, or also the segments of the feeding appendages, were added to it to form the definitive head.

The adult head of modern arthropods occurs in its simplest form among the Crustacea, and is best seen in the anostracan branchiopods, where it is not covered by a carapace. The head of *Eubranchipus* (fig. 15 H), for example, is a distinct cephalic capsule (*Prtc*) bearing the eyes and both pairs of antennae. It is therefore a tagma com-

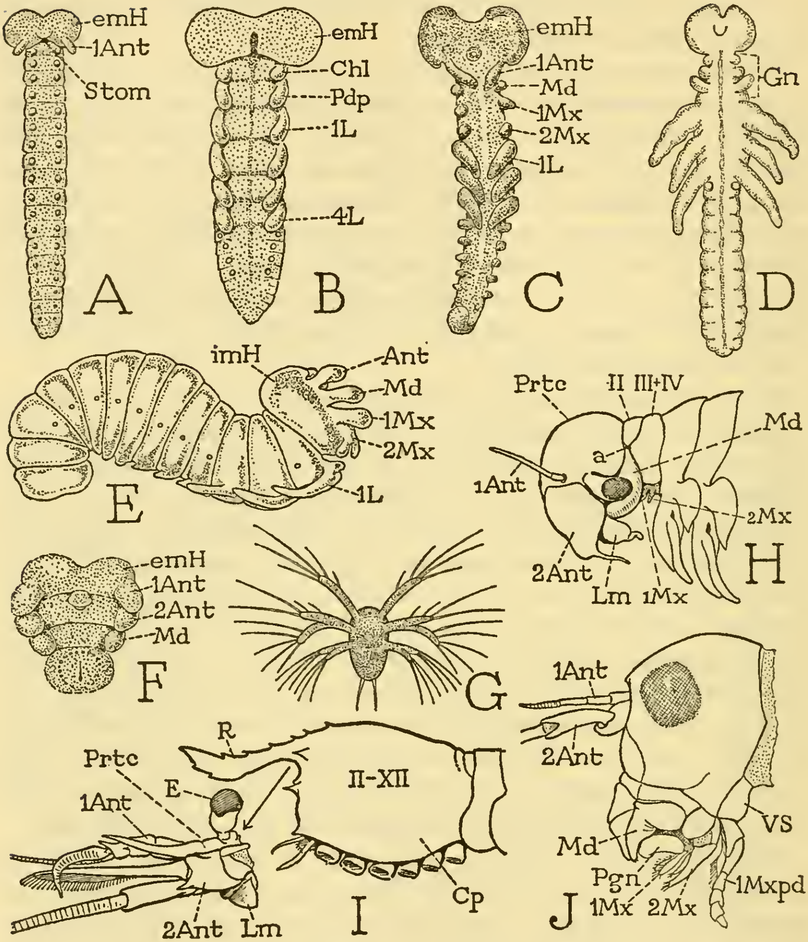

Fig. 15.—Tagmosis of the head.

A, Diagram of a fully segmented arthropod embryo. B, Embryo of a spider, *Agelena labyrinthica* (from Balfour, 1880). C, Embryo of a mantid, *Paratenodera sinensis* (from Hagan, 1917). D, Embryo of an hemipteron, *Ranatra fusca,* with differentiated thorax (from Hussey, 1926). E, An embryonic caterpillar, *Pieris rapae,* with imaginal head formed (from Eastham, 1930). F, Early stage of a crustacean embryo, *Leander serratus,* that develops in the egg (from Sollaud, 1923). G, A crustacean trochophore larva, *Penaeus sertiferus,* that hatches at a stage corresponding with F (from Pearson, 1939). H, Head and anterior body segments of an anostracan crustacean, *Eubranchipus vernalis.* I, Protocephalon of a decapod crustacean, *Spirontocaris polaris,* detached from beneath rostrum of carapace. J, Head of an amphipod crustacean, *Talorchestia longicornis.*

posed of the embryonic head lobe and the second antennal segment. Being the first step in the further evolution of the arthropod head, it may be termed a *protocephalon* (*Prtc*). In the anostracan the head is followed by a small independent mandibular segment (*II*) and the united segments (*III*+*IV*) of the greatly reduced first and second maxillae. In the other branchiopods all these segments are combined with the protocephalon in a composite head, which is covered by a head shield. In the primitive, newly discovered *Hutchinsoniella macracantha* (fig. 16 C, D) described by Sanders (1957), the shield covers only the head; in the Notostraca it is extended as a free fold over the anterior part of the body.

The protocephalon is again a discrete head unit in *Anaspides* and in most of the Malacostra having a carapace (fig. 15 I); though normally hidden under the front of the carapace, it is easily detached as represented in the figure (*Prtc*). In these crustaceans the mandibular and maxillary segments are united with the thorax in a gnathothoracic tagma mostly covered by the carapace.

On the other hand, in the isopods and the amphipods the three gnathal segments and the first maxilliped segment have united with the protocephalon to form a composite adult head (fig. 15 J), which strikingly resembles the head of an insect, while the following thoracic segments remain free. Some entomologists, in fact, have regarded the isopods as possible ancestors of the insects, but the last segment of the insect head is that of the second maxillae, and in some of the isopods even the second maxilliped segment has been added to the head. The isopods and amphipods demonstrate, however, that within a single arthropod class, the embryonic gnathal segments may become either a part of the body or a part of the head. The union of the gnathal segments with the protocephalon seems to form the more efficient kind of head, since it combines the feeding organs with the major sensory organs of the animal, as in the vertebrate head, and has been adopted by all mandibulate arthropods other than crustaceans. In the diplopods and pauropods, however, the head appears to contain only two gnathal segments, the segment corresponding with that of the second maxillae being the first body segment.

The most uniform type of head among the mandibulate arthropods is that of the symphylans, the chilopods, and the insects, in which the mandibular segment and both maxillary segments are entirely incorporated in the adult cranium. In the early insect embryo, however, these segments are a part of the body behind the cephalic lobe (fig. 15 C), or they are condensed in a gnathal tagma (D, *Gn*) between the embryonic head and the thorax. Finally, they completely unite with the embryonic head to form the imaginal head in the larva (E, *imH*) and the adult.

The insect embryo with well-developed legs (fig. 15 C), or with the thorax already differentiated from the abdomen (D), might suggest that in the evolution of the insects the thorax was developed as the locomotor center before the gnathal segments were added to the head. We cannot be sure, however, that the embryo follows the phylogenetic timetable. With insects that develop first into a larva, the differentiation of the thorax may be delayed to the pupal stage. A caterpillar (E) has short legs, but no differentiated thorax, and in legless larvae the legs are suppressed as external growths in the embryo. The structure of the embryo, therefore, does not necessarily reproduce the form or appearance of a primitive insect; it is only in its fundamental organization that the embryo can be taken to repeat evolutionary development. The large size of the head in the early arthropod embryo is due presumably to precocious growth expediting the development of the brain and optic lobes, just as the head of a vertebrate embryo is out of proportion to the size of the body, and does not mean that the early vertebrates were big-headed animals.

If the embryo leaves the egg at a very early stage of development, as with most of the Crustacea, it must be equipped at once for living an independent life. The course of its development in the egg, therefore, is directed to fitting the young animal on hatching for an active life. The crustacean nauplius larva (fig. 15 G) is equivalent to the early stage of an embryo that completes its development inside the egg (F), but the nauplius shows no division into head and body and no external segmentation; though it has first and second antennae and mandibles, these appendages have been modified to form swimming organs. In its later development the nauplius takes on the adult structure, either gradually or by assuming several successive metamorphic forms.

The Trilobita and the Chelicerata have no distinct head in the adult stage, because the head region is combined with the thorax in a cephalothoracic tagma, or prosoma; but still the arachnid embryo (fig. 15 B) may have a typical head lobe followed by distinct body segments, indicative that the embryonic cephalic lobe represents the primitive head of all the arthropods.

It is clear from these few examples of the structure of the head, that there is no standardized arthropod head with a uniform composition. The statement frequently made that the head of the mandibulate arthropods is composed of six segments is contrary to the evidence from plainly visible facts, as shown by the writer (1951) in a comparative study of the head in the Mandibulata.

Tagmosis of the body segments is likewise variable. The centipede with its uniformly segmented body does very well in its special habitat, which it never leaves; but the centipedes have attained no such diversity of form as have the arachnids, the crustaceans, and the insects, in which the body structure is characterized by the association of segments to form distinct body regions with different functions. The diplopods might be said to have a multiple tagmosis in the union of the segments into double segments.

Since the arthropods are endowed with a superabundance of segmental appendages, it would appear that tagmosis primarily was an adaptation to limiting the walking appendages to a consolidated section of the body, commonly termed the thorax, leaving the postthoracic section, or abdomen, freely movable. The thoracic limbs, however, may be secondarily modified for swimming if the animal has given up walking for swimming. The abdominal appendages in all cases except that of the myriapods have lost their leg structure, and are generally modified for special purposes, such as swimming, copulation, egg laying, respiration, and silk spinning. By this division of labor among the appendages the animal retains its locomotor power, and at the same time acquires tools for a variety of other uses. The three segments of the insect thorax became differentiated as a tagma when the legs of these segments took over the locomotor function, and those of the following segments were suppressed. With the thorax established as the locomotor center of the body, it later served as the basis for the development of wings.

Tagmosis is carried farthest in the Chelicerata, in which the primitive head (fig. 15 B) and the following six or seven segments are combined in a single body unit, the prosoma, carrying the eyes, the feeding appendages, and the legs, while the posterior segments constitute an opisthosoma, or abdomen. In *Limulus* and the scorpion the abdomen remains fully segmented, and *Limulus* retains the abdominal appendages in a modified form. In most of the spiders, however, external segmentation of the abdomen has been entirely suppressed, but the two parts of the body are separated by a narrow constriction, which gives freedom of movement to the abdomen. This is necessary to the spinning spiders, but seems an inconvenience to the ground-living species.

Finally, the ticks and most of the mites have attained the ultimate in tagmosis by a union of all the body segments in a one-piece body. Only a small head structure, the capitulum, or gnathosoma, carrying the feeding organs remains free, but since no other arachnid has a similar headpiece, the capitulum is evidently a special development of the Acarina to facilitate their feeding habits.

The prevalence of tagmosis among the arthropods would indicate that, while body segmentation is the fundamental feature of arthropod organization, inherited from remote wormlike ancestors, modern arthropods have made their chief structural advances by partially suppressing it.

VIII. THE SEGMENTAL APPENDAGES

The arthropods stand apart from other animals by reason of the number of segmental appendages they possess, and it is very probable that primarily all their limbs were jointed legs, as are those of the trilobites (fig. 16 A), and served for walking. In the evolution of the arthropods, however, it was soon found that fewer appendages could serve as well for locomotion, and that the others could advantageously be converted into organs for grasping, feeding, swimming, copulation, egg laying, and numerous other purposes. Thus, to their polypod ancestors the modern arthropods owe their equipment with a great variety of anatomical tools, and the fact that they have thereby become the most diversified animals on the earth today. The quadripeds, the bipeds, and the apodous creatures had no such evolutionary possibilities.

The arthropod appendages, regardless of their adult form, all have the same origin in the embryo, namely, from paired, lateroventral, budlike lobes of the body segments (figs. 15 A, 17 A). Though "recapitulation" does not hold so prominent a place in zoological thought as it once did, it can hardly be renounced completely. The embryonic development of the arthropod appendages would seem to be a case in which recapitulation can be safely invoked in support of the idea that the embryonic origin and growth of the appendages repeats their phylogenetic history. As illustrated by Roonwal (1937) in *Locusta* (fig. 17 A-F) the legs develop from primary budlike rudiments by lengthening and becoming segmented until they attain the adult structure.

The legs of the Onychophora likewise begin in the embryo as simple buds (fig. 17 G), but since the onychophoran ancestors did not acquire a sclerotization of the cuticle, their legs of necessity remained short, thick, and unsegmented. However, the lateroventral position of the

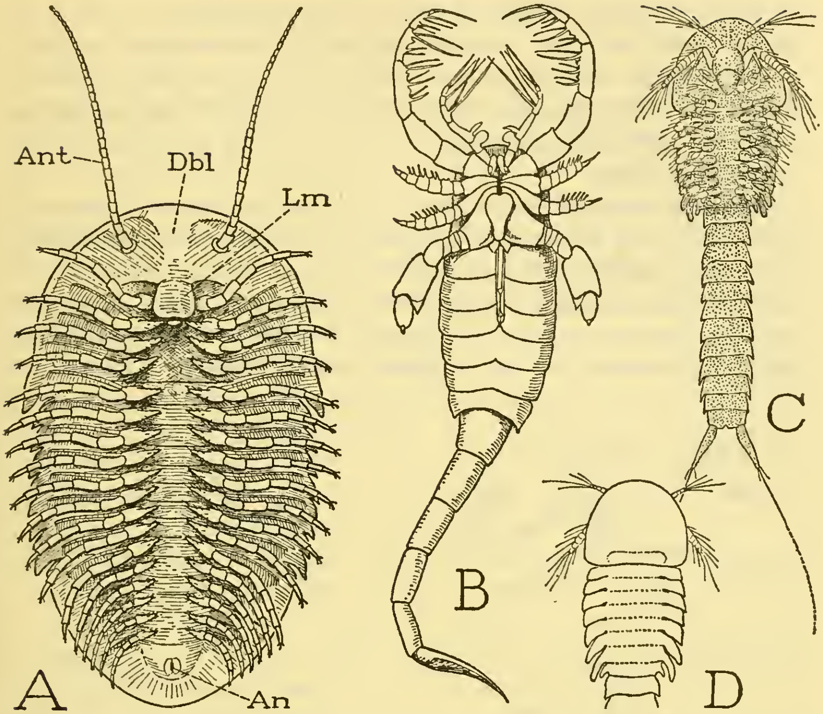

FIG. 16.—Examples of specialized palaeozoic arthropods, and a primitive modern crustacean.

A, Diagram of a trilobite, ventral surface and legs. B, A scorpionlike eurypterid, *Mixopterus kiaeri* (outline from Störmer, 1934). C, *Hutchinsoniella macracantha,* a primitive modern crustacean. D, Same, head and thorax, dorsal.

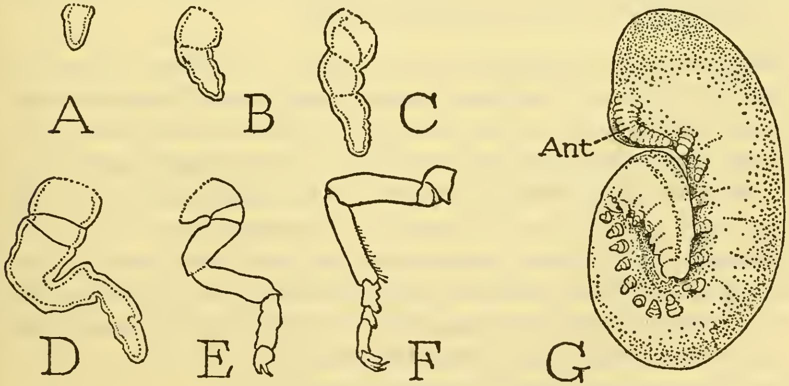

FIG. 17.—Embryonic development of legs.

A-F, Developmental stages of middle leg of a locust, from 70-hour embryo to newly hatched nymph (from Roonwal, 1937). G, Embryo of an onychophoran, *Peripatopsis moseleyi,* with appendage rudiments (outline from Manton, 1949).

onychophoran and arthropod limbs, their embryonic origin from simple lobes, and their musculature are all features that have no counterparts in the parapodia of the Polychaeta, and this fact discredits the often-expressed opinion that the limbs of the onychophorans and arthropods have been evolved from the parapodia of ancestral polychaetes.

Inasmuch as an arthropod limb is a tubular outgrowth of the body wall, its movable sections, or *podomeres,* are merely sclerotized parts of the tube, and the *joints* are short unsclerotized parts between them. The embryonic limbs are penetrated by mesoderm, which forms the intrinsic limb musculature, the fibers of which become attached on specific podomeres, but not necessarily on all of them. The musculated podomeres constitute the true *segments,* or *podites,* of the limbs (fig. 18 A, *Seg*). A segment, however, may be subdivided into nonmusculated subsegments, and in the joints there are sometimes present small rings without muscle attachments. These minor parts of the limbs have been counted as "segments" by some writers, who thus confuse the true segmentation and the segment nomenclature. Subdivisions of the tarsus, for example, are tarsomeres, but are commonly called "tarsal segments" by taxonomists. The only known case of tarsomeres being individually musculated is in the ovigerous legs of a male pycnogonid. Finally, the term "joint" should not be used for a leg segment, though it often is so used.

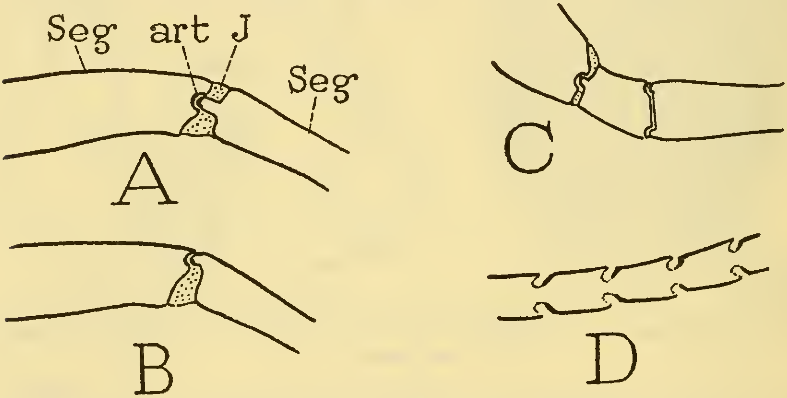

FIG. 18.—Limb segments, joints, and articulations.

A, Adjoining parts of two leg segments with articulated joint. B, Joint with single dorsal articulations. C, Double articulations, horizontal and vertical. D, Unarticulated joints of an antennal flagellum.

In order to limit the movement at intersegmental limb joints, the ends of the adjoining segments are specifically articulated on each other. An *articulation* is usually formed by the extension of an articular process from the base of the distal segment through the joint membrane received in a socket on the end of the proximal segment (fig. 18 A, *art*). There may be only one articulation at a joint (B), or two articulations. The hinge of a double articulation is sometimes horizontal, sometimes vertical (C). Since different types of articulations are usually present at different joints of the same leg, the leg as a whole is capable of varied movement. Articulations are generally absent at joints between nonmusculated subsegments (D), allowing free movement in any direction.

Failure to recognize that a musculated limb segment may be divided into nonmusculated subsegments has led to confusion in comparative studies on the arthropod antennae. It was shown by Imms (1939) that the antennae of most arthropods, including Collembola and Diplura among the hexapods, are composed of musculated segments, while those of thysanuran and pterygote insects have muscles only in the basal segment. On this apparent difference in the antennae, the tracheate mandibulate arthropods have been classed by Remington (1955) into Myocerata and Amyocerata. The actual difference between the two types of antennae, however, is not in the musculature, but in the number of segments. The basal stalk, or scape, of the insect antenna contains muscles inserted on the pedicel, and is a true segment. The pedicel may be a basal part of the flagellum, but more probably it is a segment from which muscles to the flagellum have been removed to make space for the organ of Johnston. The flagellum, having no intrinsic muscles, is a *single segment* usually subdivided into short rings, as are the flagella of crustacean limbs. The insect antenna, therefore, contains at most only *three* segments. The antennae of coleopterous and lepidopterous larvae (see Dethier, 1941) are usually composed of three simple segments, and even in adult brachycerous Diptera the antennae are clearly three-segmented, with the apical segment subdivided or not. It has furthermore been shown by Imms (1940) that true antennal segments are generated by subdivision of the apical segment, but that the flagellum grows from its base, as described also by Lhoste (1942) in *Forficula*.

The evolution of the limbs into jointed legs must have taken place in Precambrian times, since the limbs of the trilobites and their relatives were already fully segmented legs in the early Cambrian. If all the podomeres of a trilobite leg were true musculated segments, discounting the segmental nature of a small basal ring that Störmer

(1939) regarded as a "precoxa," the trilobites had eight-segmented legs (fig. 19 A). In the later evolution of the arthropods some of the original segments were lost, united, or subdivided, leading to confusion in attempts to name the segments consistently. However, we have long-established names for eight segments that can be consistently applied if we assume that the basal segment is the same in all groups and that segmentation in the telopodite is variable.

The basal limb segment, *coxa,* or *coxopodite,* gives attachment to the body muscles that move the limb as a whole, and therefore should be homologous in all the arthropods. Yet, when the limb contains eight segments, some writers have regarded the functional basal segment as a "precoxa," or "subcoxa," without explaining how the muscles become transferred to the coxa in a seven-segmented limb. In a few cases the coxa is immovably attached to the body, and the second segment then becomes the functional base of the limb, but it does not take over the coxal muscles.

The eight apparent segments of the trilobite leg (fig. 19 A) are subequal in length, except for the very small, three-clawed apical pretarsus. In the eurypterids (B) the last two legs appear to be nine-segmented, but two short rings following the coxa may be subdivisions of a segment since there is only one segment here in the other legs. In the legs of a modern pycnogonid (C) eight segments are typically differentiated. Following the coxa are two short trochanteral segments (*1Tr, 2Tr*), a long femur (*Fm*), a patella (*Pat*), a slender tibia (*Tb*), a subdivided tarsus (*Tar*) of two tarsomeres, and a three-clawed pretarsus. These same eight segments are present in some of the legs of solpugid arachnids (D) and in the Acarina, though in the latter the second trochanter is much reduced in size. The scorpion (E) and most of the other arachnids have only seven leg segments by elimination of one trochanter, but the tarsus is divided into two subsegments. The patella is characteristically present in all the Chelicerata, including the Xiphosurida, which also have but one trochanter. In the trilobite leg (A) the fifth segment (*Pat*), therefore, is to be identified with the patella of the chelicerates.

The legs of the mandibulate arthropods (fig. 19 F-J) consistently lack a patellar segment. The malacostracan Crustacea (F) and the myriapods (G, H, I) have seven-segmented legs, there being two segments in the trochanteral region. The segments, however, differ much in relative size, showing that the size of a segment is no criterion of its identity. The apical segment is a simple, clawlike dactylopodite, or pretarsus. Finally the typical insect leg (J) is

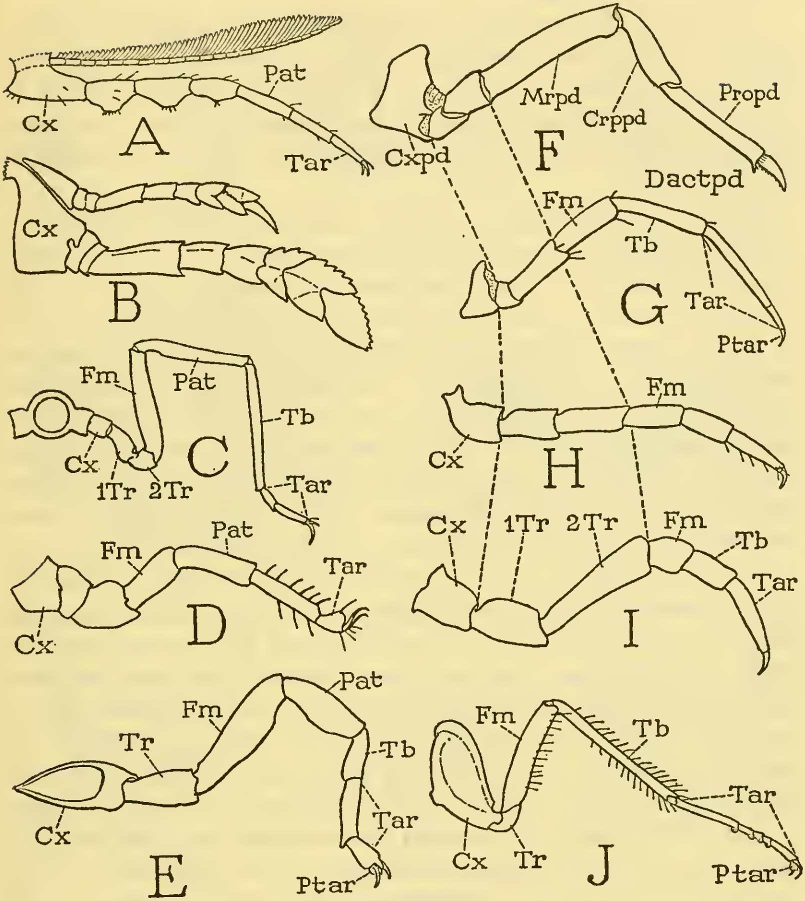

FIG. 19.—Comparative leg segmentation.

A, Leg of a trilobite, apparently 8-segmented, with coxal epipodite (from Störmer, 1939). B, Fifth and sixth legs of a eurypterid, apparently 9-segmented (from Clarke and Ruedemann, 1912). C, 8-segmented leg of a pycnogonid. D, 8-segmented leg of a solpugid arachnid. E, 7-segmented leg of a scorpion. F, 7-segmented leg of a crustacean, *Cambarus*. G, 7-segmented leg of a chilopod, *Lithobius*. H, Leg of a julid diplopod, 7 subequal segments. I, Leg of a polydesmoid diplopod, 7 segments of unequal length. J, Typical 6-segmented insect leg, *Periplaneta*.

six-segmented, having only one trochanter, a subdivided tarsus, and a two-clawed pretarsus.

It is evident that the different leg segmentation among the arthropods has come about principally by the elimination of segments, either of one of the trochanters or of the patella, or both. Rarely it is apparent that adjoining segments have united, but there is no clear case of a segment having been divided into two true musculated segments.

The end segment, dactylopodite, or pretarsus, of the walking legs undergoes numerous modifications to give it a more efficient grasping or clinging function. In the crustaceans and myriapods this segment is a simple claw. In the pycnogonids, arachnids, and insects a pair of accessory lateral claws arises from the base of the dactylopodite, forming thus a three-clawed foot, or a two-clawed foot if the median dactyl is suppressed. The typical pretarsus of adult insects is two-clawed, but in some of the apterygote insects the median dactyl is retained. Generally the body of the insect pretarsus is produced as an adhesive lobe or pad, the *arolium,* projecting between or below the claws, which enables the insect to walk on vertical surfaces.

A similar adhesive pad is present on the feet of ticks and on the feet of the pselaphognathous diplopod *Polyxenus* (the latter described by Manton, 1956). Though it cannot be supposed that the adhesive pads in these forms are homologous with the insect arolium, their presence gives an interesting example of the independent development of similar structures for the same purpose. *Polyxenus* is exceptional among the diplopods in being able to walk on smooth vertical surfaces and even on the under sides of horizontal objects.

In the Chelicerata and Crustacea the pretarsus (dactylopodite) has both a levator and a depressor muscle. In the hexapods and the myriapods there is only a depressor muscle. Both muscles of the pretarsus in *Limulus,* Pycnogonida, and Crustacea arise in the tarsus (propodite), but in the other arthropods there is a tendency for one or both muscles to be extended into the more proximal segments of the legs. The persistent absence of the dorsal muscle in the myriapods and insects is difficult to explain functionally, but it should be a phylogenetic link between these two mandibulate groups.

The basal segment of a leg, the *coxa,* or *coxopodite,* is usually articulated on the body in such a manner that the whole appendage turns forward and backward on a transverse or transversely oblique axis. The primitive leg probably had dorsal promotor and remotor muscles arising on the segmental tergum and corresponding ventral muscles arising on the sternum (fig. 20 A). The sternal muscles

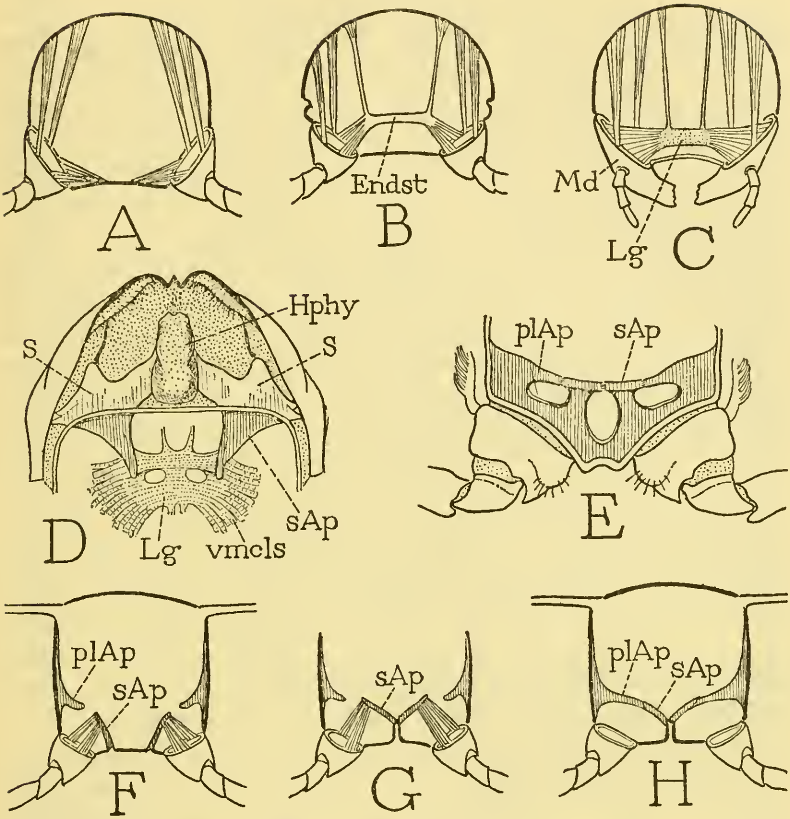

FIG. 20.—Illustrating various attachments of ventral limb muscles, mostly diagrammatic.

A, Probable primitive limb musculature. B, Ventral leg muscles of Chelicerata arising on a noncuticular "endosternum." C, Mandibles of a lower crustacean with ventral muscles arising from an intergnathal ligament. D, Ventral muscles of mouth parts of a chilopod arising from an intergnathal ligament supported on apodemes from premandibular sternal sclerites of head. E, Cross section of lower part of thorax of a decapod crustacean, *Cambarus,* showing united intersegmental pleural and sternal apodemes. F, Thoracic segment of a lower insect, ventral muscles of legs attached on intrasegmental sternal apodemes. G, Thoracic sternal apodemes of a higher insect elevated on a median sternal inflection. H, Union of pleural and sternal apodemes in thorax of an insect.

being practically horizontal were at a mechanical disadvantage, and in most modern arthropods their mesal attachments have been elevated. In most of the Chelicerata the ventral muscles of all the appendages arise from a platform, the so-called endosternum (fig. 20 B, *Endst*), suspended in the body by branches attached on the back. A similar structure is present in the gnathal region of some lower Crustacea, but usually it is contracted to the form of a thick transverse ligament uniting the inner ends of the opposing muscles of the mandibles (C, *Lg*). An intergnathal ligament of the same kind is present in the Diplopoda. Among the chilopods a broad, flat ligamentous plate in the head of Scutigeromorpha (D, *Lg*) gives off the ventral muscles of the mouth parts, but it is supported on a pair of anterior ventral cuticular apodemes (*sAp*). In the other chilopods and in the symphylans the muscles have been taken over by the apodemes and the ligament disappears. In the insects the anterior, originally ventral, apodemes have united with a bar through the back of the head forming the endoskeletal structure known as the tentorium, on which the ventral muscles of the mouth parts are attached.

In the macruran Crustacea the ventral muscles of the thoracic appendages arise on an elaborate endoskeletal structure (fig. 20 E) composed of a series of united pleural and sternal apodemes (*plAp, sAp*) inflected from the intersegmental grooves between successive segments. All the muscles of the thoracic appendages in the crayfish arise on this structure and on the pleural plates; only the mandibles and the first maxillae have dorsal muscles from the carapace.

In some of the lower pterygote insects most of the ventral muscles of the legs take their origin on a pair of lateral sternal apodemes (fig. 20 F, *sAp*). In the higher orders, however, the two apodemes are approximated and are carried inward on a median inflection of the sternum (G), forming a Y-shaped structure known as the *furca.* The arms of the furca are often connected by muscles with pleural apodemes, but the pleural and sternal apodemes of each side are sometimes united (H), forming thus a weak imitation of the pleurosternal endoskeleton of the decapod (E). It must be noted, however, that the insect differs from the crustacean in that both the pleural and the sternal apodemes are *intrasegmental* and not intersegmental. A similar structure for the same mechanical purpose has thus been formed in different ways in the two groups.

Though the ventral muscles of the appendages are primarily productors and reductors, when the sternal articulation of the limb is eliminated these muscles become adductors. This change of function occurs particularly with the ventral muscles of the gnathal appendages, in which adduction is the important movement.

The segmental appendages of the arthropods were developed in the first place for locomotion, and, though a variable number of them have been modified for other purposes, in each major arthropod group some of the limbs have retained the primitive leg structure and are still used for walking, except where all the legs have been converted into swimming organs. In a series of papers on "The Evolution of Arthropodan Locomotory Mechanisms," Manton (1950, 1952a, 1952b, 1953, 1954, 1956) has described the skeletomuscular mechanism of locomotion and the leg movements of an onychophoran and representatives of the various groups of walking arthropods. "The locomotory mechanism shown by *Peripatus*," she says, "provides a key to the understanding of the evolution of the various mechanisms found in the higher Arthropoda." This fact, perhaps, may be taken to mean that locomotion by walking was first developed by common ancestors of the two groups.

The differentiation of the primitive arthropod legs into organs for purposes other than walking or running has been due in large part to the development of outgrowths of various kinds from the outer and inner surfaces of the limb segments. Such structures are known as *exites* and *endites* respectively.

Exites in the form of long, pectinate branches that perhaps served as gills were present on the basal leg segments of such Cambrian arthropods as *Marella, Burgessia,* and the trilobites (fig. 21 B, *Eppd*). In modern Crustacea branchial exites are commonly borne on the leg bases. A coxal exite is designated an *epipodite* regardless of its function.

Many of the Crustacea, particularly larval forms, have a variously developed exite on the second limb segment, or basipodite, which is known as an *exopodite* (fig. 21 A, *Expd*) because it gives the appendage the appearance of being two-branched. The trilobite epipodite has often been mistaken for an exopodite, but these two limb branches, being on different segments, are clearly not homologous. The trilobite leg, therefore, is not "biramous" in the manner of a crustacean limb, and does not relate the trilobites to the Crustacea. It is not clear what the primary function of the exopodites may have been, but in many crustacean larvae these branches on the cephalic and thoracic appendages bear brushes of long setae that facilitate the temporary use of these limbs as swimming organs. The exopodites may then be reduced or lost when the pleopods of the adult assume

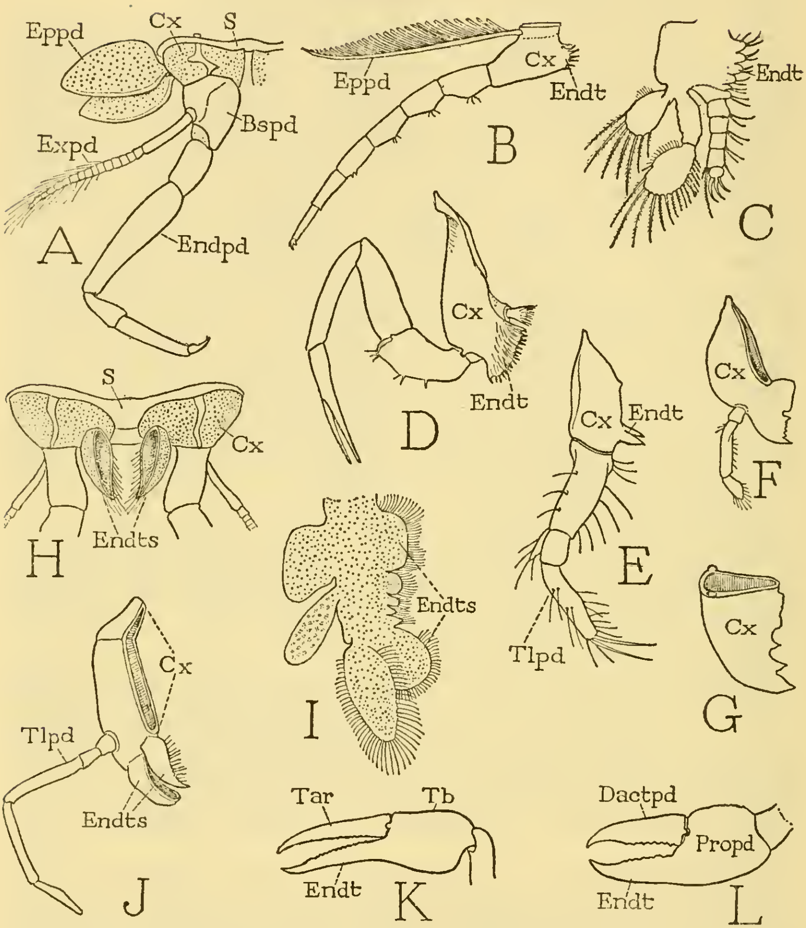

FIG. 21.—Development of exites and endites on arthropod limbs.

A, A biramous crustacean limb, left pereiopod of *Anaspides,* posterior. B, A uniramous trilobite leg with coxal exite and endite (from Störmer, 1939). C, Thoracic limb of the primitive crustacean *Hutchinsoniella.* D, Fourth leg of *Limulus.* E, Leglike mandible of an ostracod, *Philomedes.* F, A crustacean mandible with reduced telopodite. G, An insect mandible, telopodite eliminated. H, Bases of sixth or seventh thoracic limbs of *Anaspides* with coxal endites. I, A phyllopodial branchiopod limb with segmental endites, segmentation suppressed. J, An insect maxilla. K, Pedipalp chela of a scorpion. L, Chela of a decapod crustacean.

the swimming function. The pleopods, on the other hand, usually retain the biramous form, but they never have the structure or segmentation of functional legs, suggesting that their growth is arrested at an early stage of development—if they ever were functional legs.

The development of endites, particularly on the coxal segments of the limbs, has been of great importance in the later evolution of all the arthropods. The coxae of the trilobite legs are produced mesally into spiny lobes directed somewhat forward (fig. 16 A), which evidently served for securing food and passing it along to the mouth by the action of the legs. The legs of *Limulus* are equipped with similar spiniferous coxal processes (fig. 21 D), but none of the Chelicerata has developed true masticatory jaws. Coxal endites play only a subsidiary feeding role in the arachnids by enclosing a preoral food cavity.

A particularly important result of the development of coxal endites was the evolution of a specific pair of appendages as jaws, or *mandibles,* that became distinctive of the mandibulate branch of the arthropods. The mandibles are simply the coxae of a pair of primitive legs associated with the mouth having strongly developed gnathal endites opposed to each other. The distal part of the limb is retained in some Crustacea (fig. 21 E, F) as a palpus, but in the other mandibulates it has been discarded as useless (G). The gnathal endite of the mandible is usually a solid outgrowth of the coxa, but in the diplopods and symphylans it has become an independently movable lobe, which is itself the functional jaw. Though the mandibles are generally biting and chewing organs, they may be prolonged into a pair of grasping fangs, or drawn out into slender piercing stylets.

To be effective as jaws the mandibles have lost the primitive leg articulation on the sternum so that they swing transversely on the lateral hinges; the ventral muscles then become adductors. A mandible of the primitive type has thus only a single lateral articulation on the head or the mandibular segment, but in some of the higher crustaceans and in most of the biting insects they have acquired a secondary anterior articulation on the epistome or the clypeus, so that they swing more effectively on fixed horizontal axes close to their outer margins. In most of the insects the primitive adductor ventral muscles have been eliminated, and the operation of the mandibles is taken over entirely by the dorsal muscles.

The maxillae also owe much of their function as food manipulators to the presence of coxal endites, which, however, are highly diverse in form, as are the maxillae themselves. The insect maxilla (fig. 21 J) usually retains the telopodite as a segmented palpus, and bears two endite lobes on the end of the coxa. The most leglike maxillae are those of the second pair in the chilopod *Scutigera,* which are simple, segmented appendages with a slender endite on the coxa. Crustacean maxillae retain so little of the leg structure and are so various in form that it is often difficult to identify their parts.

Endites are not commonly present on the legs of mandibulate arthropods, except in the branchiopods. The flattened, unsegmented thoracic limbs of these crustaceans may have as many as six lobes on the inner margin, together with an apical lobe (fig. 21 I), suggesting the usual seven segments of a walking leg. The development of these appendages shows, in fact, that they begin as slender leglike limbs, and later take on the flattened, lobulated phyllopodial form. In the amphipods and isopods coxal endites are highly developed on the thoracic legs of the female to form a brood chamber in which the eggs and the young are carried (fig. 5 B, *Ostg*). In the crustacean *Anaspides* membranous, scoop-shaped, setigerous endite lobes with concave surfaces toward each other (fig. 21 H, *Endts*) are borne on the mesal surfaces of the coxae of the sixth and seventh thoracic appendages of the female. When the body is flexed ventrally the endites come together and apparently form a passageway for the eggs from the openings of the oviducts to the spermatheca on the venter of the eighth segment.

The egg-laying apparatus, or ovipositor, of female insects has usually been regarded as formed of coxal endites on the appendages of the eighth and ninth abdominal segments, but recently Matsuda (1958) has contended that the ovipositor blades (valvulae) are secondary outgrowths of the sterna, as claimed formerly by Heymons (1899). Likewise the complex external genital structures of male insects have commonly been interpreted as modified segmental appendages, but evidence against their leg origin has been presented by the writer (1957) and independently by Matsuda (1958).

On the distal parts of the limbs the development of endites has enabled various arthropods to be equipped with grasping organs, or chelae. In the Crustacea (fig. 21 L) a chela is formed by an endite process of the propodite opposed to the movable dactylopodite. In the scorpion (K), on the other hand, the movable member of the chela is the tarsus, or the fused tarsus and pretarsus, and the fixed claw is an endite of the tibia. The same is true of the leg pincers of *Limulus,* except those of the last legs. Various other implements have been fashioned on the legs, such as the pollen brushes, the antenna cleaners, and the pollen-collecting apparatus of the bees.

If we had lived in the time of the lobopod ancestors of the arthropods, we should never have suspected the potentiality that lay in their simple feet, which has led to the future development and diversification of the modern arthropod appendages. But who, also, would have supposed that the fins of the coelacanth fishes 300 million years ago would ever develop into the legs of mammals or the human arm and hand? It is only in retrospect that we can believe in evolution.

IX. THE INSECT WINGS

The highest mechanical achievement of the arthropods is the power of flight, and the credit for this goes entirely to the pterygote insects. As flying animals the insects surpass both the birds and the bats, and in some ways they are superior to any flying machine yet invented.

Since the wings were already fully developed in the earliest winged insects of the fossil record, we do not know when or how the insects acquired their organs of flight, and hence we must be content with theories. There are at least three theories that we can choose from concerning the origin of insect wings. An idea once proposed is that the wings being flat folds of the body wall amply supplied with tracheae, were derived from tracheal gills, but this theory involves a too roundabout way of wing development. The presence of a tracheal respiratory system implies that the insects first lived on land and breathed air; then to acquire tracheal gills they had to live for a while in the water; and finally to convert the gills into wings they returned to the land.

According to another theory, that of Goldschmidt (1945), based on wing deformities in the fly *Drosophila,* the wings are homodynamous with legs. The front part of a wing, Goldschmidt says, is a leg, and the entire wing has been evolved from the dorsal and ventral lobes of a polychaete parapodium. Raw (1956) limits the wing origin to the dorsal lobe of the parapodium. This theory still invokes the old belief that the arthropods are descended from polychaete annelids, and it would seem to imply also that the insects are a direct offspring from the polychaetes, rather than a final product of arthropod evolution. Raw (1956) says of the parapodia "it is improbable that between the ancestral Polychaete and the Insect they ever ceased to be appendages moved by muscles." It must be observed, however, that the musculature of the worm moves the parapodia forward and backward, and that the up-and-down movement of an insect's wings involves an entirely different type of musculation. Certainly the oldest known insects, which were Collembola, and the modern apterygotes are wingless, and there is no evidence that they ever possessed wings, though the parapodial theory of wing origin requires the assumption that the first insects were winged and that the modern apterygotes have secondarily lost their wings. In any case it is too great a strain on the imagination to visualize a worm flopping along out of the water with its parapodia until it was able to fly and become an insect. If such a thing happened once, why has it not recurred again during the last 200 million years, since polychaetes are still abundant?

The simplest and most reasonable theory of the origin of insect wings is that the wings were developed from paranotal lobes of the thorax after the insects, whatever their previous history, became terrestrial hexapods. Paranotal lobes are not hypothetical structures, since, as already shown, they occur in various modern arthropods, and in nonholometabolous insects the wings appear first on the nymph as lobelike extensions from the margins of the back plates of the mesothorax and metathorax. Presumably when paranotal lobes became sufficiently large in the primitive insects they first served as gliders (fig. 22). If the at first rigid paranotal lobes became flexible at their bases, they could then by action of thoracic muscles be flapped up and down and thus enable the gliding insect to sustain itself longer in the air. Even this simple wing movement, however, involved adaptive modifications of the thoracic skeleton, and some degree of adaptation in the musculature.

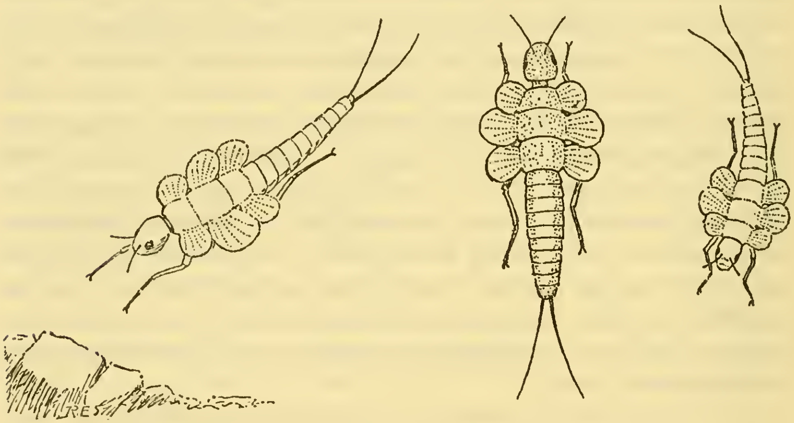

FIG. 22.—Insects in the glider stage of wing evolution.

When the progenitors of the insects became hexapods by the elimination of functional legs from all but the first three segments behind the head, the thorax was thereby differentiated from the abdomen as the locomotor center of the body, and when wings were developed it is natural that they should be on the thorax alone.

As a prerequisite of wing movement by paranotal lobes, the thoracic walls, particularly the pleural areas, had to be strengthened to resist the stress of muscles that might operate the wings. Since evolution is not forward looking, it is not to be supposed that the thorax was prepared in advance for the role it was later to play in the wing mechanism. More probably, therefore, the pleural sclerotization of the thorax of winged insects was developed in the preglider stage to give stronger support to the legs. Before the insects could launch themselves as gliders from elevated positions they must have developed the habit of climbing, and for this they needed strong and well-supported legs. Later, the pleural plates gave support also to the paranotal lobes and finally to the wings. Hocking (1957) has made the interesting observation that, geologically speaking, the first winged insects appeared almost immediately with the appearance of tall plants growing from the swamps.

Clearly the development of wings from paranotal lobes was not a simple process of expanding the lobes, since it depended on previous modifications of the thoracic skeleton. The presence of strong pleural plates on the wingless prothorax of modern insects is further evidence that the thoracic pleura were first developed as leg supports. Since the development of wings took place after the insects became hexapods there is no reason to suppose that the abdominal segments ever had pleural plates like those of the thorax. The presence of well-sclerotized pleura on a winged segment, however, is essential to the wing mechanism. The pleural plates strengthen the side walls of the segment against the downward pull of vertical wing muscles, and each culminates in a fulcral process on which the wing rests and turns.

A paranotal lobe in order to become movable in the manner of a wing had to become first flexible on the notum mesad of its pleural support. It would thus be free to turn up and down on the pleural fulcrum. There would then be two principal ways in which the lobe or its wing derivative might be moved. The simplest method would be by the attachment of lateral body muscles on the wing base at opposite sides of the fulcrum. Muscles so attached acting as antagonists would elevate and depress the wings (fig. 23 B, C). This *direct* method of wing movement has been most efficiently developed by the modern dragonflies. On the other hand, with the wings flexibly attached on the supporting notal plates mesad of the pleural fulcra, downward and upward movement of the notal plates (D, E) would give the wings the converse movements of elevation and depression. This *indirect* method of wing movement has been adopted by nearly all the flying insects except Odonata, but to give proper action to the wing-bearing nota has involved reconstructive modifications in the thoracic skeleton and the development of an appropriate musculature. The wing mechanism of both the direct and indirect type will be more fully discussed later, but we should note here that the cockroaches and their relatives fly, rather inefficiently, by a mechanism somewhat intermediate between the other two.

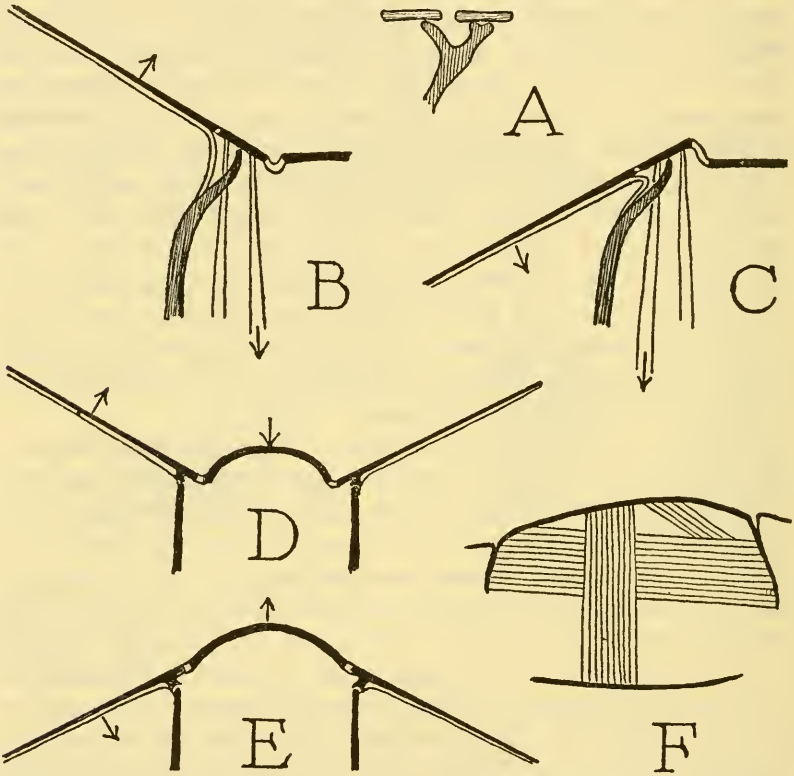

FIG. 23.—Diagrams of direct and indirect types of insect wing mechanism.

A, Forked pleural wing process of a dragonfly. B, C, Wing movements of a dragonfly by muscles attached on wing base at opposite sides of pleural fulcrum. D, E, Indirect type of wing beat by vertical movements of wing-supporting notal plate. F, The indirect flight muscles of a thoracic segment.

The thoracic musculature of modern pterygote insects is so thoroughly adapted to the wing mechanism that it is difficult to visualize what may have been the pattern of the somatic musculature in primitive wingless insects. If the arthropods have been derived from annelid forebears, they probably, while still in a wormlike stage, had an outer layer of circular body muscles and inner bands of longitudinal muscles. With sclerotization of the back and venter, however, the segments could no longer be constricted, and the circular muscles were reduced to lateral muscles only. The somatic musculature of modern adult insects consists principally of longitudinal dorsal and ventral muscles and dorsoventral lateral muscles. In the thorax the lateral muscles have become diversified in their attachments, some being notosternal muscles, others notopleural, and still others notal or pleural leg muscles. When wings were developed, any of these muscles could serve as wing motors.

We might look to the modern apterygote insects for the primitive type of insect thoracic musculature. The apterygotes, as shown by Barlet (1950, 1953, 1954), have an elaborate thoracic musculature including dorsal muscles and numerous lateral muscles. In *Lepisma saccharina,* Barlet (1954) enumerates four muscles from the notum to the anapleurite in the mesothorax and five in the metathorax. In each of these segments he finds six notal muscles going to the catapleurite, and four to the trochanter. Pleural leg muscles include in each segment two muscles from the anapleurite to the coxa, and one to the trochanter, while another trochanteral muscle arises on the catapleurite. Likewise in a machilid Barlet (1950) shows that in the mesothorax numerous muscles arise on the notum and have various ventral attachments. It is clear, however, that the thoracic musculature of the apterygotes is adapted to the needs of these insects and could hardly serve as the basis for the wing musculature of the pterygotes. No apterygote could fly even if it had wings.

The dragonflies have made use of the lateral thoracic muscles for moving the wings. Since the dorsal walls of the paranotal lobes or the wing bases are lateral extensions of the notum, muscles here attached have simply retained their original notal connections. The problem of the early dragonflies then was to divide these muscles into two functional groups pulling on opposite sides of the wing fulcrum. The problem was readily solved by curving the wing fulcrum inward until it supported the wing base between lateral and mesal groups of the muscles (fig. 23 B). The muscles attached mesad of the fulcrum thus became wing elevators (B) and those laterad of it became wing depressors (C).

In modern Odonata the base of each wing contains two large sclerites that support the veins, an anterior *humeral plate* and a posterior *axillary plate*. The wing fulcrum, arising from a strong pleural ridge, bends inward, not into the thoracic cavity but in a fold of the subalar membrane, and forks into two arms, one to the humeral plate, the other to the axillary plate (fig. 23 A). Thus the muscles pulling alternately on opposite sides of the fulcral arms rock the wings up and down.

The thoracic musculature of the dragonflies has been described by Clark (1940), Marta Grandi (1947b), and several earlier writers. Most of the wing muscles are thick cylinders of fibers attached on the wing bases by stalked cup tendons. The odonate wing muscles are said by Clark to be individually comparable to those of other insects. This may be so, but certainly they are quite different in their relative development and in the part they play in the wing mechanism from those of any other modern insects. Dorsal longitudinal muscles are relatively small in the thorax of all Odonata; according to Grandi they are absent in the metathorax of Libellulidae. The horizontal or partial rotary component of the wing movements necessary to give forward flight is probably produced by anterior and posterior muscles attached on very small sclerites imbedded in the membranous pleural wall beneath the wings, which, as pointed out by Chao (1953), evidently represent the basalar and subalar sclerites of other insects. The mechanism of the dragonfly wings, however, has been less studied than the musculature. The thoracic structure has been modified in ways characteristic of the Odonata; the pleural sclerotization of the alate segments is confluent, producing a strong lateral wall on each side. The pleural ridges are greatly strengthened to withstand the double pull of the muscles on the wing bases. A comparative study of them made by Sargent (1937) shows that in the Aeschnidae the ridges are deep folds, which, particularly in the Gomphinae, take on a scalariform structure by the development of crossbars in the posterior walls.

It is clear that even in the dragonflies the paranotal lobes were not converted directly into organs of efficient flight; adaptational adjustments of the thorax, and reorganization of the muscles had to be evolved. Yet the thoracic structure of the dragonflies is simpler than that of insects with an indirect wing mechanism. If Lemche's (1940) classification of the Odonata and the extinct Protodonata with the Megasecoptera and Palaeodictyoptera is well founded, the direct method of wing movement may have been that of all these early insects, and probably was the first to be evolved.

Another insect group of ancient origin includes the cockroaches, the mantids, the termites, and probably the zorapterans, classed by Chopard (1949) as a superorder, the Blattopteroidea. These insects also make use of the dorsoventral muscles for wing motors, but not in the same way as do the dragonflies. The thoracic musculature of the cockroaches has been described by Carbonell (1947) in *Periplaneta* and by Tiegs (1955) in *Blattella,* that of the mantis by Levereault (1938), LaGreca and Raucci (1949), and Tiegs (1955), that of a winged termite by Fuller (1924). In these insects the dorsal longitudinal muscles are either absent or are too small to have any indirect action on the wings. The dorsal muscles are fairly large in Zoraptera, but have nothing like the size of the dorsal muscles of insects with an indirect flight mechanism. A relation of the Zoraptera to the Blattopteroidea, however, may be inferred from the thoracic structure, which, according to Adam and Lepointe (1948), is that of the cockroaches and mantids.

The method by which the blattopteroids move their wings is not well understood. Arising on the notum of each alate segment, however, are numerous muscles which are mostly leg muscles, though in the termites there are large notosternal and notopleural muscles. These muscles by depressing the notum might elevate the wings in the manner of the notosternal muscles of insects with a typical indirect flight mechanism. The downstroke of the wings, on the other hand, is probably produced by lateral muscles attached on basalar and subalar sclerites. The blattopteroids are relatively weak flyers, but they have advanced beyond the dragonflies in one respect, which is the development of a flexor apparatus in the base of each wing, by which the wings are folded horizontally backward when at rest.

Tiegs (1955) says of the Orthoptera that they are of primary importance in the evolution of the wing mechanism for the light they "can still throw on the initial adaptation of the thoracic musculature to flight." However, it is evident that the members of the blattopteroid group have made little progress, if any, toward the development of an indirect type of wing mechanism; rather, they seem to have a not very efficient type of mechanism of their own based somewhat on the dragonfly scheme of direct wing movement. There is no evidence that the dorsal musculature has been secondarily reduced, since structural features of the thorax that are essential to the indirect type of wing mechanism, such as postnotal plates between the wing-bearing plates and intersegmental phragmata, are entirely undeveloped. The cockroaches and the mantids very probably never flew better than they do today. The Blattopteroidea, on the basis of their wing musculature and thoracic structure, are appropriately separated in classification from the rest of the orthopteroid insects.

The indirect mechanism of wing movement in which the up-and-down strokes are imparted to the wings by vibrations of the supporting notal plates is that made use of by all the winged insects except the Odonata and the Blattopteroidea. The upstroke results from the depression of the notum by notosternal or other vertical muscles; the downstroke is produced by the lengthwise compression and arching of the notum by contraction of the longitudinal dorsal muscles. Before this mechanism could be operative, however, several adaptative modifications had to be made in the thoracic skeleton, and the muscles involved had to be sufficiently enlarged to be effective.

The indirect elevator muscles of the wings are principally large notosternal muscles (fig. 23 F), though some of the dorsal muscles may become so oblique that they probably contribute to the depression of the notum. Comparable notosternal muscles are not generally present in insects having a direct wing mechanism. The notosternal muscles have been shown by Kelsey (1957) in the megalopteron *Corydalus* to originate in the pupa, having no counterparts in the larva. Holometabolous larvae, however, are metamorphosed forms, and their musculature, which usually is either reduced or elaborated, serves their own needs. The normal adult musculature is restored in the pupa.

The notal plates of wingless segments are ordinarily connected by so-called "intersegmental" membranes, and the dorsal muscles are attached on the intersegmental antecostae of the notal plates (fig. 24 A). To utilize these muscles as wing depressors, therefore, the membranous conjunctivae between the mesonotum and the metanotum, and between the metanotum and the first abdominal tergum had to be eliminated, otherwise the contraction of the muscles would simply pull the wing-bearing plates together without producing any deformation of these plates. To obviate this action, the intersegmental membranes behind the wing-bearing nota have become sclerotized, forming plates that brace each wing-bearing plate against the one behind it (B). The dorsum of each winged segment thus typically contains an anterior wing-bearing *notal plate* (*N*) and a posterior *postnotal plate* (*PN*). The contraction of the dorsal muscles can now arch the nota upward and thus deflect the wings on the pleural fulcra. To accomplish this effect, however, the dorsal muscles must be greatly enlarged, and to accommodate their increase in size the antecostae (*Ac*) on which they are attached have been produced into deep sclerotic folds, or *phragmata* (C, *Ph*). Most insects that fly with both pairs of wings have a prophragma on the anterior margin of the mesonotum, a middle phragma on the mesothoracic postnotum, and a posterior phragma on the metathoracic postnotum. The three phragmata, however, are actually intersegmental in position.

Finally, the indirect flight muscles themselves have undergone a structural change in the higher insects to give them increased strength and speed of contraction. The ordinary muscles of insects have the usual muscle structure in which the fibers are composed of extremely fine fibrillae less than half a micron in section. In the higher orders the fibrils of the indirect flight muscles are greatly thickened, distinctly striated sarcostyles that may be as much as five microns in diameter. The sarcostyles are separated by spaces containing numerous large mitochondrial bodies known as *sarcosomes,* and are readily teased apart by ordinary dissection. The number and size of the

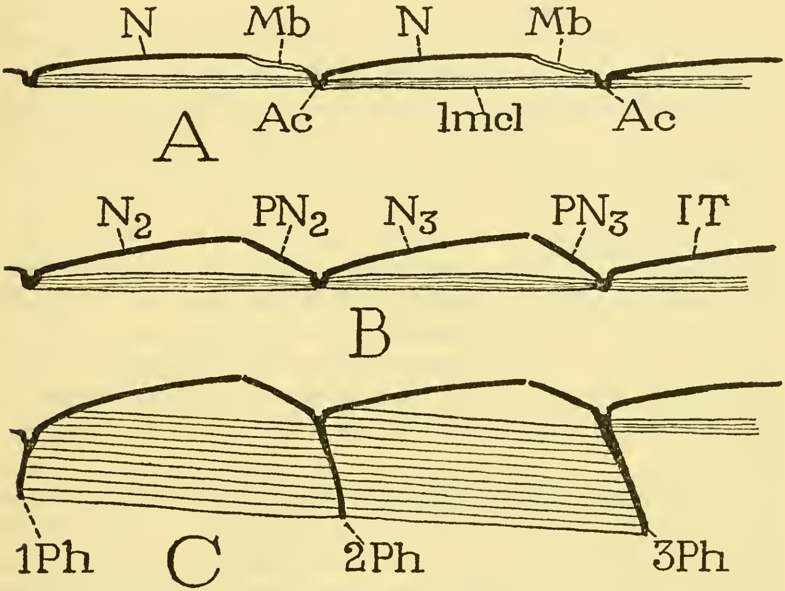

FIG. 24.—Development of postnotal plates and phragmata in the evolution of the indirect type of insect wing mechanism.

A, Section through consecutive notal plates with generalized structure, nota connected by infolding membranes. B, Internotal membranes of winged segments replaced by sclerotized postnotal plates. C, Development of phragmata from the intersegmental antecostae to accommodate increased size of dorsal muscles.

sarcosomes is closely related to the increased physiological activity of the flight muscles.

The first efforts of the insects to fly by flapping the primitive wings up and down could have accomplished little more than a lifting of the insects in the air. To give forward or directed flight the wings must have a partial rotary motion on their long axes accompanying the vertical movements. Probably some rotary movement resulted automatically from air pressure and the nature of the wing articulation on the body, but it became mechanically controlled with the attachment of strong lateral muscles on movable epipleural basalar and subalar sclerites in the membrane beneath the wing bases before and behind the wing fulcra. That the basalar and subalar sclerites are secondary differentiations of the upper part of the pleuron is clear from the work of Kelsey (1957) on *Corydalus.* Most insects with an indirect flight mechanism have a wing-flexing apparatus like that of the Blattopteroidea.

It is evident that the acquisition of an efficient indirect flight mechanism has not been a simple matter of direct evolution of paranotal lobes into wings. As finally developed, however, it has made the insects unsurpassed flying machines. According to the records of Sotavalta (1947) certain dipterous midges have a wing-beat rate of 800 to 1,000 per second. By contrast, the strong-flying dragonflies with their direct wing mechanism make only 35 to 52 wing beats per second.

In some of the higher insects there are a number of small muscles attached on the axillary sclerites of the wing base. Such muscles have been described by Williams and Williams (1943) and by Zalokar (1947) in *Drosophila,* in which muscles from the pleuron go to the first, third, and fourth axillaries. These muscles are termed "wing adjustors" by Tiegs (1955), their function being to adjust the position of the axillaries to steering movements of the wings. In a tipulid he finds three small muscles attached on the axillaries and other parts of the wing base, besides four from the pleural arm and the episternum attached on the notum and two below the wing. Observations on the presence of these muscles in other insects are not extensive. Ritter (1911) describes a pleural muscle of the first axillary, and two others attached on the anal ligament in the wing of a blow fly; Mihalyi (1935-36) mentions no axillary muscles in the house fly.

Among the axillary muscles the most important is the pleural muscle of the third axillary that operates the flexing apparatus by which the wing of most insects with an indirect motor mechanism is turned horizontally backward over the abdomen when not in use.

The first insects to adopt the indirect mechanism of wing movement must have been the ancestors of the modern Ephemeroptera, or mayflies. The thoracic pleural sclerotization is yet imperfectly developed in the mayflies, but it includes a wing fulcrum and differentiated basalar and subalar plates. In the axillary region of the wing are several small sclerites termed by Grandi (1947a) pseudopteralia, but Matsuda (1956) says the wing-base sclerites of *Siphlonurus* closely correspond with the usual three axillaries of other insects. There is, however, no wing-flexing apparatus, the wings being usually held vertically over the back when at rest. Both Grandi and Matsuda have fully described the wing musculature of the Ephemeroptera; discrepancies in the two accounts are unimportant. The wing motors include large longitudinal and oblique dorsal muscles, a pair of thick notosternal muscles, and perhaps a nototrochantinal muscle. The wing mechanism of the mayflies is thus clearly of the indirect type, in striking contrast to that of the dragonflies. The Ephemeroptera and the Odonata, therefore, are not related insects; they represent two early lines of pterygote evolution differentiated by the method adopted for moving the wings.

The flight of the mayflies is weak and the principal movements of the wings are up and down. Since adult mayflies have no functional feeding organs, as noted by Edmunds and Traver (1954), they have no concern with food finding, and the only use of their wings is for mating flight. "The nuptial flight of most mayflies," these writers say, "consists of flying upward and then passively coasting or leisurely flying downward." The mayflies, both larvae and adults, show by many structural features that they are relatively primitive pterygotes, but their relation to the higher insects with an indirect wing mechanism is not clear.

The Plecoptera have a strongly developed indirect wing mechanism. In *Perla,* as described by Grandi (1948) and by Wittig (1955), there are huge longitudinal and oblique dorsal muscles in each winged segment, and a pair of large notosternal muscles. Other notal muscles include muscles from the pleuron, the furcisternum, and the coxae.

Among the orthopteroid insects the wing mechanism of Gryllidae, Tettigoniidae, and Acrididae is of the indirect type. The flight muscles are relatively weak in the first two families, but they attain a high degree of development in the strong-flying acridids (see Snodgrass, 1929; Misra, 1947; Albrecht, 1953; Tiegs, 1955). In short-winged or wingless species the musculature evidently has undergone a secondary reduction. *Grylloblatta* is an entirely wingless insect, but its relation to winged Orthoptera leaves little doubt that it once had wings. It still retains relatively large longitudinal and oblique dorsal muscles in both the mesothorax and the metathorax, but the size of these muscles, Walker (1938) points out, is related to the free mobility of the thoracic segments on each other. With the absence of wings, however, is associated a complete absence of notosternal muscles. In orders in which all species are wingless, as Mallophaga (Mayer, 1954) and Siphonaptera, the dorsal muscles are small.

From the Orthoptera on through all the higher orders of insects that have functional wings, including Megaloptera (Kelsey, 1957), Neuroptera (Czihak, 1956), Psocoptera (Badonnel, 1934, fig. 45), the standard wing mechanism is that of the indirect type, which clearly has proved to be highly efficient for swift and controlled flight. The direct mechanism as developed by the dragonflies, however, is hardly to be rated as inferior to the indirect mechanism. The two ways of flying were not evolved by competition; they were simply adopted from the beginning as two possible ways of moving the wings. The dragonflies came from a group of primitive insects that have left no descendants other than modern dragonflies; the inventors of the indirect flight mechanism account for most of the other insects in the world today. As noted by Hocking (1957) the insects during their experimental and developmental stages of wing evolution for nearly 100 million years had the air to themselves free from attack by other flying creatures. Then when the birds and the bats came along the poorer models were the first to be eliminated.

Even after the indirect wing mechanism had attained a high degree of efficiency for flight, certain other improvements and accessories have been added. Most insects move the two wings on each side in unison, and in general it seems there is a tendency to reduce the size of the hind wings. Unity of movement has been better secured in some cases by linking the smaller hind wings to the fore wings, as in Lepidoptera and bees. This has resulted in an economy in the motor apparatus by allowing a reduction of the metathorax and its muscles as the mesothorax takes over the chief function of moving both pairs of connected wings. The Diptera have attained the ultimate in two-winged flight by completely eliminating the hind wings as organs of flight and highly developing the mesothorax and its muscles to motorize the single pair of wings.

The hind wings of the Diptera, however, have not been discarded as useless, but have been converted into important regulatory organs of the flight mechanism. They are reduced to club-shaped or capitate rods with enlarged bases, and during flight they vibrate in a vertical plane at the same speed as the wings but in opposite phase. The organs are called *halteres* because they were formerly regarded as balancers, but to express their function as it is now known Fraenkel and Pringle (1938) have termed them "gyroscopic organs of equilibrium." Removal of the halteres from a live fly results in a complete loss of flight control, particularly when the fly attempts to rotate about a vertical axis.

The base of each halter is equipped with numerous proprioceptive sense organs, including several groups of campaniform organs and chordotonal organs. The sensilla on the halteres of Diptera were minutely studied by Pflugstaedt (1912), and his account has been fully verified by Pringle (1948), who closely analyzed the operation of the halteres as flight stabilizers. When the insect on the wing alters the direction of its flight, the change produces stresses in the bases of the vibrating halteres, which will be registered in one group or another of the basal sense organs. Specific nerve impulses are thus delivered to the nerve centers of flight, which enable the insect to give the proper motor response to maintain its equilibrium in the air.

There is little question that the ancestors of the Diptera were four-winged insects, and there must have been some advantage in the change to the two-wing condition by reducing the hind wings. It is evident, however, that during the change the flies were not able to adapt to two-wing flight without a stabilizer apparatus. It therefore poses a problem in evolution to understand how the hind wings were reduced to halteres and at the same time became instruments for stabilizing flight by the fore wings. It is to be noted, however, that the wing bases themselves contain the same kind of sense organs as those of the halteres; the regulatory action of these sense organs, therefore, is not a newly acquired function.

Finally, there are the so-called veins of the wings, which, being strengthening ribs, must be of importance in the wing mechanism. The vein arrangement is characteristic of orders and differs even among genera and species, and a study of wing venation has been a major part of the work of insect taxonomists. On the other hand, little attention has been given to the functional significance of the numerous venational patterns.

ABBREVIATIONS ON THE FIGURES

Ac, antecosta.
An, anus.
Ant, antenna (*1Ant,* first antenna, *2Ant,* second antenna).
Ap, apodeme.
Apl, anapleurite.
art, articulation.

Ba, basalare.
BC, body cavity.
bcg, branchiocardiac groove.
brc, branchial chamber.
Brn, branchia (gill).
Brnstg, branchiostegite.
Bspd, basipodite.

Chl, chelicera.
cmcls, compressor muscles.
Cp, carapace.
Cpl, catapleurite.
Crppd, carpopodite.
Cx, coxa.
CxC, coxal cavity.
CxP, pleural coxal process.
Cxpd, coxopodite (coxa).

D, dorsum.
Dactpd, dactylopodite.
Dbl, doublure.
dlmcl, dilator muscle.

E, compound eye.
emH, embryonic head (cephalic lobe).
Endpd, endopodite.
Endst, endosternum.
Endt, endite.
Epm, epimeron.
Eppd, epipodite.
Eps, episternum.
Expd, exopodite.

Fm, femur (meropodite).

Gn, gnathal tagma.

Hphy, hypopharynx.

imH, imaginal head.
isMb, intersegmental membrane.

J, leg joint.

L. leg.
Lcx, lamina coxalis.
Lg, intergnathal ligament.
Lm, labrum.
lmcl, longitudinal muscle.
ltg, laterotergite.

Mb, "intersegmental" membrane.
Md, mandible.
Mrpd, meropodite (femur).
Mtz, metazonite.
Mxpd, maxilliped.

N, notum (N_1 pronotum; N_2, mesonotum; N_3, metanotum).

Ostg, oostegite.

Pat, patella.
Pdp, pedipalp.
Pgn, paragnath.
Ph, phragma (*1Ph, 2Ph, 3Ph,* first, second, third phragma).
Pl, pleuron.
pl, pleurite.
plAp, pleural apodeme.
plMb, pleural membrane.
PlR, pleural ridge.
pmcl, protractor muscle.
PN, postnotum.
pnl, paranotal lobe.
Propd, propodite.
Prtc, protocephalon.
Prz, prozonite.
Ptar, pretarsus (dactylopodite).

R, rostrum.
Rd, posterior reduplication.
rmcl, retractor muscle.

S, sternum.
Sa, subalare.
sAp, sternal apodeme.
Scx, subcoxa.

Seg, leg segment.
Sp, spiracle.
Stom, stomodaeum.

T, tergum (notum).
Tar, tarsus.
Tb, tibia.
Tlpd, telopodite.
Tn, trochantin.
Tr, trochanter (*1Tr,* first trochanter *2Tr,* second trochanter, or prefemur).
Tra, trachea.

V, venter.
vmcls, ventral muscles.

WP, wP, pleural wing process.

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