ARTHROPOD ANATOMY

A TEXTBOOK OF ARTHROPOD ANATOMY

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PREFACE

THE arthropods are a group of related invertebrates; arthropodists, for the most part, are a group of unrelated vertebrates. Each specialist, whether an entomologist, a myriapodist, a carcinologist, or an arachnologist, works in his own particular field and gives little thought to the work of specialists in other fields. As a result, the relationships of the various kinds of arthropods to one another are by some ignored, while others propose theories of arthropod phylogeny based on an insufficient knowledge of the anatomy of the arthropods in general. Since the insects are conceded to be at the top of the arthropod line of evolution, entomologists in particular have been concerned with the ancestry of insects. Some have sought to derive the insects from myriapods, others from symphylans, others from crustaceans, while some would carry the insects back to the trilobites, or even in a direct line of descent to the annelid worms. Clearly, all these claims of insect ancestry cannot be true. The writer, therefore, himself for many years an entomologist, has attempted to evaluate the various theories of insect origin by browsing around in the fields of other specialists. The final result has been the disconcerting conclusion that the facts of arthropod structure are not consistent with any proposed theory of arthropod interrelationships. The investigation, however, has added much to the writer's own information about the comparative anatomy of the arthropods, and this information is set forth in the following chapters in the hope of making a general knowledge of the arthropods more readily available to students who expect to be specialists in one arthropod group or another. Just as a cone sits best on its base, so specialization should taper upward from a broad foundation.

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INTRODUCTION

IN THEIR fundamental organization the arthropods show that they are segmented animals related to the segmented annelid worms and the Onychophora. Though the body of the onychophoran is not segmented in the adult stage, it is fully segmented during embryonic development, and in many respects the structure of the mature animal retains clear evidence of its primitive metamerism. The Annelida, the Onychophora, and the Arthropoda, therefore, may rightly be classed together as members of the superphylum Annulata (Articulata of Cuvier). The interrelationships of the three groups, however, is a matter on which there is no specific evidence, though plenty of theoretical opinion.

The arthropods, the onychophorans, and the polychaetes among the annelids have segmental locomotor appendages. The appendages of the aquatic polychaetes are bilobed, chaeta-bearing flaps along the sides of the body, known as *parapodia*, which normally serve for swimming, but can be used for progression on solid surfaces when the worms are taken out of the water. The polychaete parapodium, therefore, has been much exploited as the prototype of the arthropod leg. A parapodium, however, is a lateral appendage having no resemblance to the jointed limbs of the arthropods, and moreover, the Polychaeta are a specialized group of annelids, so highly individualized, in fact, that it is hardly to be supposed they have ever produced anything else than polychaete worms. Furthermore, since the antiquity of the polychaetes is not known, it is quite possible that the arthropod progenitors antedated them.

The locomotor appendages of the terrestrial Onychophora are short legs in the position on the body of arthropod legs; they are not truly jointed, but they are transversely ringed, and some of the distal rings are individually musculated, so that the leg might be said to have an incipient segmentation. In its embryonic origin the onychophoran leg and the leg rudiment of an arthropod are both mere lobelike outgrowths of the body wall. The arthropod leg, therefore, would seem to be much more probably related in its origin to the onychophoran leg than to the annelid parapodium, and neither the structure nor the development of the parapodium gives any reason for believing that the onychophoran leg originated from a parapodium. In other respects also the Arthropoda have characters that are more onychophoran than annelidan. The excretory organs of the Onychophera are direct derivations of the segmental coelomic sacs, and the coelomic excretory organs of the arthropods have essentially the same structure. The onychophoran reproductive organs are composite coelomic sacs with a single pair of coelomic exit ducts, and furnish the basic pattern of structure for the reproductive system of the arthropods. On the whole, therefore, the arthropods appear to be much more closely related to the Onychophora than to the Polychaeta. The annelid connections of the two groups, then, must be with some primitive member of the Annelida, far more generalized than the modern polychaetes or their immediate ancestors.

The oldest known arthropods are the fossil trilobites, but certainly a trilobite has little resemblance to any wormlike animal, either an onychophoran or an annelid. Its appendages are fully segmented ambulatory legs; the body is flattened, the integument shell-like, the body segments are grouped in well-defined tagmata, in the first of which the component segments are highly integrated, and the animal has filamentous antennae and compound eyes. To believe that a trilobite is a direct descendant from a polychaete worm requires much faith in a theory, and it is not any easier to visualize the descent of a trilobite from an onychophoran. In short, the only logical concept of annulate interrelationships is that, from some primitive, segmented wormlike animal, there evolved, on the one hand, a branch culminating in the parapodia-bearing polychaetes and, on the other, a lobe-legged form (lobopod) with coelomic excretory and reproductive organs discharging through coelomaducts, which soon split into the progenitors of the Onychophora and the Arthropoda, the one developing a sclerotized integument and jointed legs, the other remaining soft-skinned and wormlike, and sufficiently accommodated for locomotion by its primitive leg stumps.

Modern Onychophora are all terrestrial animals, but there are fossils of onychophoralike forms from Cambrian and Pre-Cambrian times that must have been aquatic. A wormlike animal with legs would be much better fitted for crawling out of the water and becoming a land animal than would a parapodia-bearing polychaete, but probably no animals were able to live on land before the Devonian, and the trilobites were fully developed at the beginning of the Cambrian. Hence, a terrestrial onychophoran was not the ancestor of the arthropods. Whenever an aquatic onychophoran did take to the land, it acquired tracheal organs of a simple kind for the respiration of air. The terrestrial Onychophora, therefore, might be said to have invented the mode of breathing by means of ingrowths of the integument; the idea was adopted by later land arthropods, but was applied in different ways, so that the presence of tracheae is no evidence of close relationship between different tracheate forms. The pretrilobite history of the arthropods probably never will be known, since it has been erased from the records of Pre-Cambrian time, but there can be little doubt that arthropod forms were already well differentiated before the Cambrian, since the trilobites ended their career in the Permian as trilobites, and among modern arthropods only the horseshoe crab has any resemblance to them.

The arthropods are so named because they have jointed legs, a feature clearly not distinctive of them, but the segmentation of the legs taken in combination with segmentation of the body might serve as a definition for any arthropod that preserves its ancestral form. Body segmentation is fundamentally muscle segmentation (i.e., mesoderm segmentation) with correlated segmentation of the nervous system, giving a more efficient mechanism for bodily movement than that possessed by an unsegmented animal; legs are adjuncts adding further locomotor efficiency. Body segmentation is practical in a soft-skinned animal, but elongate flexible legs would be of little use as locomotor organs. The arthropod type of limb, therefore, must have been developed in an animal with a hard integument, since the jointing of the appendages into individually musculated segments thus became possible and followed as a mechanical necessity. Since the segmentation of the legs is essentially the same in all the arthropods, from trilobites to insects, the form and segmentation of the limb must have been established in some early ancestor of the group.

The principal evolutionary changes in the body of the arthropods have been a grouping of the segments into different body regions, or *tagmata*, accompanied often by a fusion of the grouped segments, or of some of them. Thus there have been produced the characteristic features of the several arthropod classes, as the trilobites, the arachnids, the crustaceans, the myriapods, and the insects. It is to their numerous jointed limbs, however, that the arthropods owe the major part of their evolution and the multitude of activities of which they are capable. The large number of legs were at first all ambulatory in function, but it was soon found that they were not all needed for locomotion. Hence the great structural and functional diversification of the limbs in modern arthropods; no other animals carry on their bodies such an assortment of tools. The possession of tools implies the ability to use them, and their use involves a high degree of development in the nervous system, which, in the arthropods, is expressed in a marvelous development of instinctive intelligence.

Taxonomically the arthropods are divisible into eleven well-defined classes, namely, the Trilobita, the Xiphosurida, the Eurypterida, the Pycnogonida, the Arachnida, the Crustacea, the Chilopoda, the Diplopoda, the Pauropoda, the Symphyla, and the Hexapoda, representatives of which will be the subjects of the following chapters. In a larger way the classes are separated into three major groups: the Trilobita, the Chelicerata, and the Mandibulata. The Trilobita have filamentous antennules, but their distinguishing feature is the uniformity in structure of the other appendages, which are all ambulatory legs. The Chelicerata lack antennules, and take their name from the pincerlike structure of the first pair of ventral appendages, known as *chelicerae;* they include the Xiphosurida, Eurypterida, Pycnogonida, and Arachnida. The Mandibulata have antennules, but their important feeding organs are the jawlike second pair of ventral appendages, the *mandibles.* The first pair are suppressed except in Crustacea. The mandibulate arthropods are the Crustacea, Chilopoda, Diplopoda, Pauropoda, Symphyla, and Hexapoda. Again, the Xiphosurida and Eurypterida are generally classed together as Merostomata or, together with the Trilobita, Pycnogonida, and Arachnida, as Arachnomorpha. The chilopods, diplopods, pauropods, and symphylans were formerly combined in the Myriapoda, but modern zoologists do not generally recognize the myriapods as a natural group, though the chilopods are often termed the Myriapoda opisthogoneata, and the other three the Myriapoda progoneata, because of the different position of the genital opening.

Finally there are two small groups of animals, the minute Tardigrada and the parasitic Pentastomida, that are often classed with the arthropods, or thought to be somehow related to them, because they have short stumps of legs. However, since the taxonomic affinities of these creatures are very uncertain, they will not be included in the present text.

I

THE TRILOBITA

THE trilobites (fig. 1) are arthropods of particular interest because of their great antiquity. They appear on the geological scene at the very beginning of the Paleozoic already fully developed as trilobites; they flourished during the Cambrian and Silurian periods, and continued in diminishing numbers through the Carboniferous into the Permian. Several thousand species have been described, referred to numerous genera and many families in four recognized orders. Such highly organized and diversified animals, therefore, must have had a long evolutionary history in Pre-Cambrian times, though the rocks of this period have so far furnished no evidence of their existence. The trilobites may truly be said to be the oldest of known arthropods, and in some respects they are the most generalized of known arthropods, but if the arthropods have been developed from a segmented, wormlike progenitor provided with jointed legs, there is a vast gap between the trilobites and their vermiform ancestors. A trilobite is in no sense a primitive arthropod, and, notwithstanding all the claims that have been made in favor of a trilobite ancestry for the other arthropods, it is not probable that any other group of arthropods was derived directly from the trilobites. Any specialized form of animal produces only more specialized and diversified forms of its own kind.

Very soon after the beginning of the Cambrian the trilobites are accompanied in the geologic record by representatives of the Crustacea, the Eurypterida, and the Xiphosurida, but also there are various fossil arthropods found in the Cambrian rocks that cannot accurately be classified in these groups, but which appear to be related to them.

Hence, it is to be supposed that the arthropods present in Cambrian and Ordovician periods represent lines of descent from common progenitors that lived far back in the immeasurable period before the Cambrian, and which, therefore, have little chance of ever being known. It is curious, however, that in the later Paleozoic rocks arachnids, myriapods, and insects appear as fully formed animals

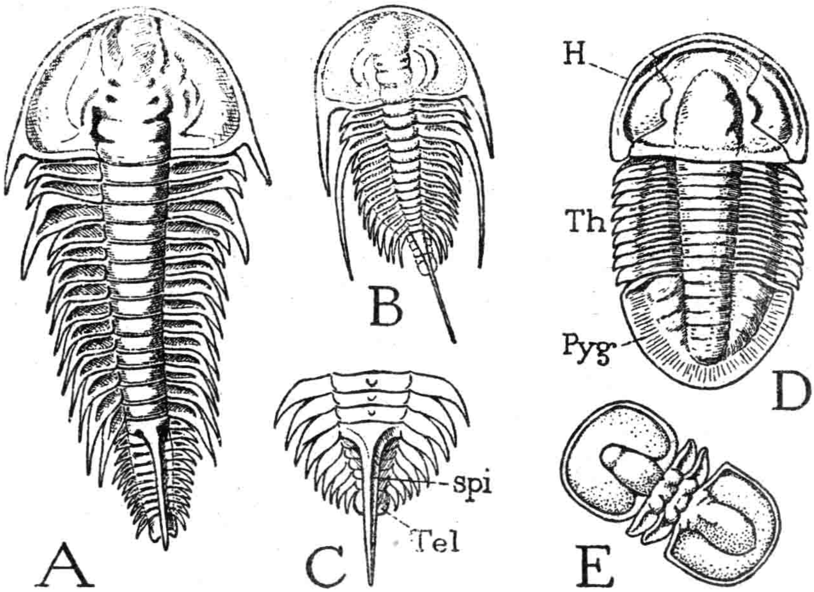

Fig. 1. Trilobita. Examples of trilobite forms.

A, *Olenellus vermontanus* Hall (from Walcott, 1910). B, *Olenellus gilberti* Meek (from Walcott, 1910). C, *Schmidtiellus mickwitzi* Schmidt (from Walcott, 1910). D, *Asaphiscus wheeleri* Meek (from Walcott, 1916). E, *Peronopsis montis* (Matthew) (from Walcott, 1908).

H, head, or prosoma; *Pyg*, pygidium; *spi*, spine; *Tel*, telson; *Th*, thorax.

of their kinds, while there is nothing to show from what they came during the earlier Devonian, Ordovician, and Cambrian times, when trilobites, eurypterids, xiphosurids, and crustaceans were well preserved. Fossilization, however, depends largely on the presence of a hard skeleton, so that it is likely that animals first appear as fossils only when they have acquired a sufficiently resistant integument, and even then they must meet with favorable external conditions for fossilization, while, finally, fossils themselves may be utterly destroyed by subsequent metamorphosis of the containing rocks.

The form and structure of the trilobites (fig. 2) show clearly that in these ancient animals the fundamental arthropod organization was already fully developed and had attained a specific type of specialization. Only in the lack of differentiation in the postoral appendages are the trilobites generalized, but their specialization is of a relatively simple kind that fitted them for life on the ocean bottom in shallow water along the shore, where most of them lived probably in the manner of the modern *Limulus*, though some species are thought to have been pelagic, or even deepwater inhabitants. Lacking jaws or grasping organs of any kind other than the legs, the trilobites could not have obtained active prey by raptatory methods, and it has been thought that probably they were mud feeders, but animals with long filamentous antennae can hardly be supposed to have made a practice of burrowing in mud or sand. In some species the projecting mesal ends of the coxae (fig. 2 B) are armed with spines, which fact suggests that the coxal lobes had some use in the obtaining of food; Raymond (1920) says, "The primary function of these spiny lobes of the coxa was doubtless the gathering and preparation of food, and carrying it to the mouth by passing it forward from one to the next." On the other hand, since the coxal lobes do not meet in the middle line, and the spines are not well developed in all species, Störmer (1944) thinks it unlikely that they functioned as jaws. In any case, whatever may have been the food of the trilobites, and however they obtained it, the great numbers of the animals would indicate that they had an ample food supply within their reach. Certainly worms of various kinds as well as other soft-bodied creatures living in the mud or sand along the ocean shores were abundant in both Cambrian and Pre-Cambrian times. It would seem, in fact, that a trilobite should be quite fit to live under modern conditions, and paleontologists have no positive evidence to account for their early extinction.

General Structure of a Trilobite

Since few perfectly preserved specimens of trilobites are known, it is not possible to give a full description of the trilobite structure in any one species, but inasmuch as the details of structure have been carefully studied in different species, we can reconstruct diagrammatically, as given in figure 2, the general form and make-up of a typical representative of the group.

The body of a simple trilobite of usual form is oval and dorsoventrally flattened (figs. 1 D, 2 A); it is divided transversely into three parts known as the *head* (H), the *thorax* (*Th*), and the *pygidium* (*Pyg*). The thorax and pygidium together, however, may be said to constitute the *body* as distinguished from the *head*, but,

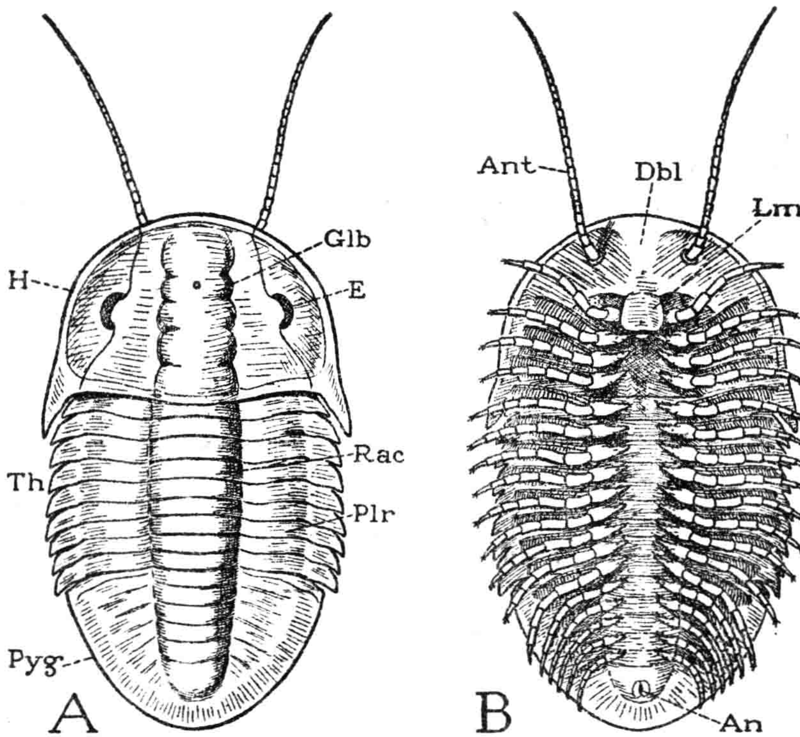

Fig. 2. Trilobita. Diagrams showing the structure of a generalized trilobite. A, dorsal. B, ventral.

An, anus; *Ant*, antenna; *Dbl*, doublure; *E*, compound eye; *Glb*, glabella; *H*, head or prosoma; *Lm*, labrum or hypostome; *Plr*, pleura (not the pleuron of other arthropods): *Pyg*, pygidium; *Rac*, rachis or axis; *Th*, thorax.

since the so-called head bears the first four pairs of legs, the terms *prosoma* and *opisthosoma* are preferable names for the two principal parts of the animal. The prosomatic head is unsegmented in the adult, though it may show evidence of coalesced segments; the thorax is completely segmented; and the pygidium is clearly composed of united segments. In the earlier trilobites the pygidial region is fully segmented (fig. 1 A, B, C). Extending lengthwise usually through the three parts is a rounded, median elevation, which is flanked by wide, flattened or decurved lateral areas. On the head the median elevation is known as the *glabella* (fig. 2 A, *Glb*), the lateral parts as the *cheeks,* or *genae;* on the body the median elevation is termed the *axis,* or *rachis* (*Rac*), the lateral parts the *pleurae* (*Plr*). These terms and others to be introduced later are those current in trilobite taxonomy, and the parts they connote have no necessary relation to those similarly named in other arthropod groups. The name *trilobite* is derived from the apparent *lengthwise* division of the animal into three parts.

Though the trilobite as seen from above (fig. 2 A) looks like no other animal with which we are familiar, the undersurface (B) at once shows that the trilobite is an arthropod; on each side is a long row of jointed *legs,* and from the anterior part of the head there projects forward a pair of slender, filamentous *antennae* (*Ant*). Behind the bases of the antennae and extended over the mouth is a median lobe (*Lm*), such as all arthropods have and which is commonly known as the *labrum*, though students of trilobites have generally called it the *hypostome.* The mouth presumably is covered by the labrum, and behind it is a small metastomal lobe. Of the legs, the first four pairs pertain to the head, the others to the thorax and pygidium, there being a pair for each body segment except the last. It will be noted that the legs are attached to the body at each side of a narrow median space, and that the pleural areas of the dorsum (fig. 4 A, *D*) are inflected on the undersurface to the bases of the legs. The inflected ventral surfaces laterad of the leg bases constitute the *doublure* (*Dbl*), which includes also the inflected undersurface of the head (figs. 2 B, 3 K).

A cross section through the thorax of a trilobite (fig. 4 A) clearly shows that the principal body cavity of the animal is in the median part, or rachis (*Rac*), which is strongly convex on the back, and that the so-called pleurae are merely flat hollow extensions of the body segments over the appendages. Since various other flattened arthropods have a similar structure, the "three-lobed" character is not distinctive of the trilobites. The special feature of the trilobites is the uniform, leglike structure of all the appendages except the antennae, in which respect the trilobites are more generalized than any modern arthropods, since in all of the latter at least some of the appendages are modified and specialized for purposes other than that of locomotion; the trilobites apparently did not even have appendages that served specifically as jaws. Details of the leg structure will be described in a later section.

The Head, or Prosoma

The head section, or prosoma, of a typical adult trilobite (fig. 2 A, *H*) is usually somewhat semicircular in outline, with its rounded anterior and lateral margins produced posteriorly in a pair of large *genal spines*. Between the bases of the spines the head is directly attached to the body by its transverse posterior margin, without the intervention of a neck. The dorsal surface of the head, as already noted, generally presents a median, elevated glabellar area (*Glb*) and broad, lateral genal areas, but in many species the head is covered by a perfectly smooth, rounded, shieldlike plate. The features of the head given in the following description, and illustrated diagrammatically in figure 3 L, have been made out from a study of many specimens of more generalized trilobites; the beginning student, however, is likely to see little trace of them in ordinary museum examples, owing partly to the imperfection or corrosion of the specimens, but also to the fact that the characters themselves were suppressed in the later evolution of the trilobites.

The grooves that separate the glabella from the genae are known as the *dorsal furrows* (fig. 3 L, *df*). A subdivision of the glabella into five successive parts, of which the first is the *frontal lobe* (*frl*), may be indicated by lateral notches in the dorsal furrows, or by imperfect transverse grooves in the glabellar surface. Each genal area is divided lengthwise by a *facial sulcus*, or "suture," before and behind the eye (*afs*, *pfs*), which separates it into a median part called the *fixed cheek*, or *fixigene* (*Fg*), and a lateral part distinguished as the *free cheek*, or *libragene* (*Lg*). The free cheeks are produced posteriorly into the genal spines (*gspi*). An *ocular ridge* (*er*) goes from each side of the frontal lobe to the eye. The entire median part of the head shield between the facial sulci, including the glabella and the fixed cheeks, is termed the *cranidium* (*Crn*). A *marginal furrow* (*mf*) surrounds the head inside a narrow *border area* (*b*). Most trilobites have a pair of large, lateral *compound eyes* (*E*) on the mesal parts of the free cheeks, and above each eye a protective *palpebral lobe* (*pbl*) on the edge of the fixed cheek. On the anterior part of the glabella in some species there is present a small tubercle, which has been regarded as a median eye, but its ocular nature is questionable. A complete terminology for all parts of the trilobite is given by Howell, Frederickson, Lochman, Raasch, and Rasetti (1947).

Inasmuch as the trilobite head carries the first four pairs of legs, it must include at least four primitive postoral somites, and the glabellar grooves of the adult evidently represent the primary intersegmental lines of the head segments. The best understanding of the adult head has been derived from studies, such as those of Raw (1925), Warburg (1925), Lalicker (1935), Störmer (1942, 1944), and others, on specimens of very young trilobites in successive stages of development. All writers are in close agreement as to the visible facts, though they differ somewhat in their interpretations.

The youngest-known developmental stage of a trilobite is a minute oval thing, from half a millimeter to a millimeter and a half in length, and is termed the *protaspis* (fig. 3 A, E). The major part of the protaspis represents only the head of the adult trilobite. On the back of the youngest specimens a median glabellar elevation is already differentiated from wide lateral genal areas and very soon becomes divided transversely into five primary subdivisions, of which the last four (*I–IV*) represent the somites of the four pairs of legs carried by the adult head; faint intersegmental lines may be seen extending laterally in the genal areas (E). The first glabellar subdivision of the protaspis includes the area of the frontal lobe of the adult (J, *frl*) and its lateral extensions curving posteriorly around the anterior margin, which eventually become the free cheeks bearing the compound eyes. This anterior, or acronal, section of the larva may be termed the *acron* (A, *Acr*), though the term has been used with various other applications. Its underfolded anterior part forms the doublure of the head, on which the antennae and labrum of the adult are situated (fig. 2 B).

The preoral antennae of the trilobites are clearly the first antennae, or antennules, of other arthropods. The four postoral pairs of legs on the head, then, should reasonably be supposed to correspond with the first four postantennular appendages of other arthropods, which primarily arise behind the mouth, these appendages being the chelicerae, the pedipalps, and the first two pairs of legs in the Chelicerata, or the second antennae, the mandibles, and the two pairs of maxillae in the Mandibulata. If the acron of the trilobite