

SMITHSONIAN MISCELLANEOUS COLLECTIONS

VOLUME 97 NUMBER 6

EVOLUTION OF THE ANNELIDA, ONYCHOPHORA,
AND ARTHROPODA

BY

R. E. SNODGRASS

Bureau of Entomology and Plant Quarantine
U. S. Department of Agriculture



(PUBLICATION 3483)

CITY OF WASHINGTON
PUBLISHED BY THE SMITHSONIAN INSTITUTION
AUGUST 23, 1938

SMITHSONIAN MISCELLANEOUS COLLECTIONS

VOLUME 97, NUMBER 6

EVOLUTION OF THE ANNELIDA, ONYCHOPHORA,
AND ARTHROPODA

BY

R. E. SNODGRASS

Bureau of Entomology and Plant Quarantine
U. S. Department of Agriculture



(PUBLICATION 3483)

CITY OF WASHINGTON
PUBLISHED BY THE SMITHSONIAN INSTITUTION
AUGUST 23, 1938

The Lord Baltimore Press
BALTIMORE, MD., U. S. A.

EVOLUTION OF THE ANNELIDA, ONYCHOPHORA, AND ARTHROPODA

BY R. E. SNODGRASS

Bureau of Entomology and Plant Quarantine, U. S. Department of Agriculture

CONTENTS

	PAGE
I. The hypothetical annelid ancestors.....	1
II. The mesoderm and the beginning of metamerism.....	9
III. Development of the annelid nervous system.....	21
IV. The adult annelid.....	26
The teloblastic, or postlarval, somites.....	26
The prostomium and its appendages.....	32
The body and its appendages.....	34
The nervous system.....	39
The eyes	45
The nephridia and the genital ducts.....	45
V. The Onychophora	50
Early stages of development.....	52
The nervous system.....	55
The eyes	62
Later history of the mesoderm and the coelomic sacs.....	62
The somatic musculature.....	64
The segmental appendages.....	67
The respiratory organs.....	70
The circulatory system.....	70
The nephridia	72
The organs of reproduction.....	74
VI. The Arthropoda	76
Early embryonic development.....	80
Primary and secondary somites.....	82
The cephalic segmentation and the development of the brain.....	89
Evolution of the head.....	107
Coelomic organs of adult arthropods.....	126
The genital ducts.....	131
VII. Phylogenetic conclusions	132
References	149

I. THE HYPOTHETICAL ANNELID ANCESTORS

Among the simplest of the metazoic animals that lead an active, free existence is the planula larva of the Coelenterata. The planula develops into a polyp or a medusa because it is a young coelenterate, but, so far as its structure goes, it contains the fundamental building

elements that, with the appropriate hereditary influences, might be fashioned into a flatworm, an annelid, an arthropod, a mollusk, or a vertebrate.

The typical planula is a minute oval or elongate creature (fig. 1 A, C) consisting of an outer layer of ectoderm cells, and an inner mass of endoderm cells. The planula, therefore, represents the gastrula stage of embryonic development, though it may have no enteric cavity and no blastopore. Its motor mechanism is a covering

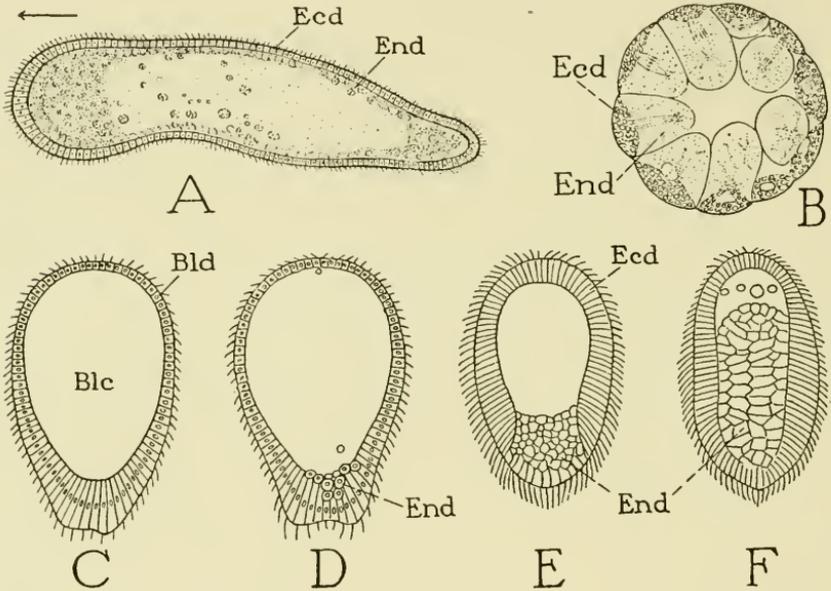


FIG. 1.—The coelenterate planula, and two methods of endoderm formation.

A, planula of *Sympodium coralloides* (from Kowalevsky and Marion, 1883). B, blastula of *Carmarina fungiformis*, showing differentiation of endoderm from ectoderm by delamination of blastoderm cells (from Metschnikoff, 1882). C-F, formation of endoderm by internal proliferation from posterior pole of planula (from Hatschek, 1888, after Claus).

Blc, blastocoele; *Bld*, blastoderm; *Ecd*, ectoderm; *End*, endoderm.

of vibratile cilia. The embryology of the planula is very simple. The cleavage of the coelenterate egg produces a morula, and the morula becomes a blastula. In the succeeding planula stage the inner endodermal cell mass is formed, but it is not certain that gastrulation takes place by simple invagination in any of the coelenterates. With some forms the endoderm arises as an inward migration of scattered cells from the blastoderm; in others the blastomeres divide regularly each into an outer ectoderm cell and an inner endoderm cell (fig. 1 B): but the most common method of endoderm formation is the internal

proliferation of cells from the posterior pole of the blastula (D, E, F), and this last process suggests that it is an embryonic modification of gastrulation by invagination. When, shortly, the planula settles to the bottom of the water and becomes attached preparatory to its metamorphosis into a polyp, a stomach cavity appears in the endoderm, and a mouth cavity breaks through at the free pole.

The development of the planula shows clearly that there is in ontogeny no fixed method for the formation even of so important an organ as the stomach. The effective thing in embryonic development is the inherited organizing property resident in the egg that converts a mass of cells, however formed, into a definite functional structure. The same principle, as we shall see later, applies also to the development of the annelids and the arthropods, for in these animals there is so much apparent irregularity in the formation of the germ layers that attempts to interpret all observed facts in terms of cell genealogy lead only to confusion. Ontogeny and phylogeny, therefore, while they produce the same end results, may follow quite different methods of procedure. In phylogeny we must visualize the successive stages in the evolution of an animal as free-living adult forms, each structurally adapted for performing the functions of an independent animal.

If the coelenterate planula were an adult animal instead of a temporary larval form, or if it had to maintain itself for any considerable length of time, it almost certainly would have a stomach cavity and a mouth. Thus modified, as it is later in its own development, the planula would be an independent, motile gastrula, having a stomach in the form of an open pocket of the blastoderm for the retention of food particles (fig. 2 A). An animal of this simple type of structure, we must suppose, was the actual ancestor of the polyp and medusa forms of the Coelenterata; but equally well it might have been the progenitor of the annelids, and through the latter of the arthropods. Various writers on phylogeny have proposed an origin of the segmented worms direct from a coelenterate polyp, but it should be recognized as a fundamental principle in evolution that a specialized type of animal does not give rise to another specialized type—if two forms are related, they are related through some simple common ancestor. This principle as applied to the coelenterate derivatives is expressed by Ziegler (1898), who says:

It is to be supposed that the higher animals derived from coelenterate stock took their origin not from the highly specialized forms of the Coelenterata, such as the anthozoans and ctenophores, but from a planula-like or gastrula-like ancestral form of the coelenterates.

The theoretical planulalike gastrula postulated above as the common ancestor of the Coelenterata and the Annelida (fig. 2A) presumably swam habitually in one direction by means of a covering of cilia, and the mouth, or blastopore, was at the posterior pole where food particles might be swept into the stomach with the eddy of currents converging to the rear.

In the ontogenetic development of the annelids, gastrulation generally takes place by epiboly, which is the overgrowth of the endoderm by the ectoderm, and the primary open blastopore is at the posterior pole of the embryo. There is no reason why this ontogenetic stage should not represent an early phylogenetic stage, and one identical with the gastrula ancestor of the Coelenterata (fig. 2 A). With the further development of the annelid embryo, however, the blastopore elongates forward on the ventral surface of the gastrula (fig. 2 F) until its anterior end comes to be near the anterior pole (G); but, at the same time, the lips of the blastopore grow together from behind forward, leaving finally only the anterior end open into the archenteron, and this opening is the primitive mouth (H, *Mth*). Secondly, an anal aperture (*An*) is formed later at the original posterior end of the blastopore on the caudal extremity of the embryo. The endodermal archenteron of the annelid thus becomes a simple alimentary canal having the oral aperture located *ventrally near the anterior end of the body*, and the anal aperture situated *terminally at the posterior end*.

If we visualize the change in the position of the blastopore as an event in the phylogenetic history of the annelids, we must see a correlated change in the habits of the animal. The actively swimming gastrula (fig. 2 A) in its search for food, we may suppose, took to brushing over the surfaces of stones or aquatic plants (B), where food particles were more numerous and more easily obtained. For this manner of feeding, a ventrally placed blastopore would be a distinct advantage, or, even more efficient, a blastopore drawn out lengthwise on the under surface (C). With a form thus modified in habits and structure, there may easily have developed a creeping habit, and an adaptation of the ventral cilia for progression on solid surfaces (D). Finally, then, came a more complete adaptation to feeding on a subsurface, resulting in an elongate flattened body, and the establishment of an alimentary canal with a ventral mouth and a terminal anus (E) produced by the closure of the intermediate part of the blastoporic slit.

A creeping mode of locomotion may be subserved entirely by a ciliary coating of the body wall, as is shown in the Platyhelminthes,

but a creeping animal encounters irregularities and obstructions. A provision for body movements, therefore, becomes an advantageous adjunct to the motor mechanism, and such movements can be produced only by an internal muscular system. Hence, the next stage in evolution, recorded in both the flat worms and the annelids, was

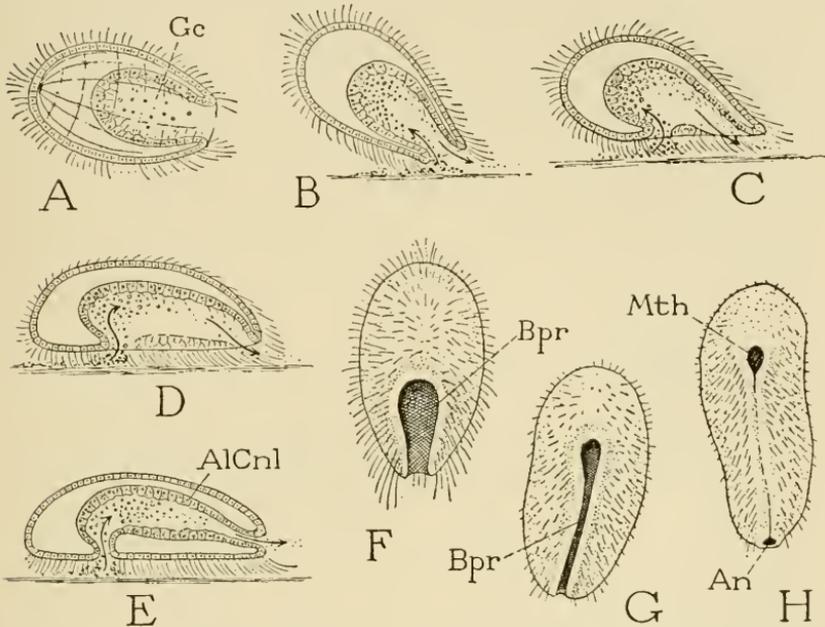


FIG. 2.—Hypothetical evolution of a swimming planularlike creature with an open gastrocoele into a creeping wormlike animal with a simple alimentary canal, a subsapical ventral mouth, and a terminal anus.

A, primitive swimming form with posterior blastopore. B, the same having acquired the habit of sweeping up food particles from a solid surface. C, blastopore elongated forward on surface of contact to accommodate the feeding habit. D, the same more fully adapted to subsurface feeding. E, final development of alimentary canal, with ventral mouth and terminal anus, formed by closure of intermediate part of blastopore, creeping habit fully established. F-H, three stages of elongation and closure of the blastopore, ventral view.

AlCnl, alimentary canal; *An*, anus; *Bpr*, blastopore; *Gc*, gastrocoele, or archenteron; *Mth*, mouth.

the development of contractile tissue that conferred the power of diversified adjustive movements on the body itself. Muscles, however, are not generally automatically active, as are cilia, and hence the development of muscle tissue is usually accompanied by the development of a mechanism for its activation. Furthermore, since a muscular system is a provision for adjustment to external conditions, the source of its stimulus must come from the environment. The sponges are said to have a primitive contractile tissue that is

stimulated directly by environmental changes; in all other animals there is intimately associated with the contractile muscle tissue a specifically receptive and conductive nerve tissue, through which environmental stimuli become effective on the muscles. Finally, the high metabolic rate of muscular activity creates the need of special excretory organs for the removal of waste products from the body.

The genesis of contractile and conductive tissues, and their integration into a neuromuscular system are best seen in the Coelenterata. Contractility, being a common property of protoplasm, may become localized and specially developed in a particular part of any cell of the body in a primitive animal. In the coelenterates fingerlike muscle processes are produced from the inner ends of cells in both the ectodermal and the endodermal epithelium, those of the ectoderm (fig. 3, *mp*) taking a longitudinal course, those of the endoderm a

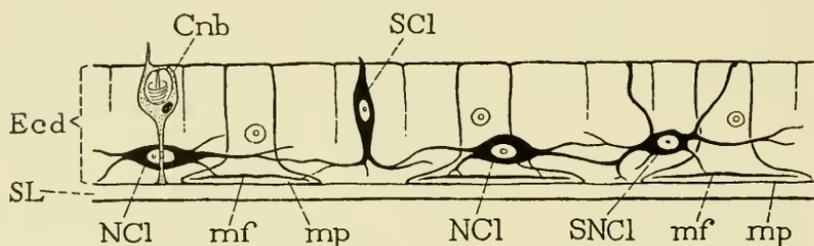


FIG. 3.—Diagram of the ectodermal neural and muscular elements of *Hydra*. (From Curtis and Guthrie, 1927.)

Cnb, cnidoblast; *Ecd*, ectoderm; *mf*, muscle fiber; *mp*, muscle process of epithelial cell; *NCl*, neural cell; *SNCl*, neurosensory cell; *SCl*, sensory cell; *SL*, supporting lamella.

transversely circular course. Fibrils of contractile tissue (*mf*) become differentiated in these processes. In the hydra, the body of the muscle cell remains as a part of the epithelial layer, but in some of the other coelenterates the entire cell may be withdrawn beneath the surface and converted into a muscle fiber. A primitive nerve cell is an epithelial cell in which the common protoplasmic properties of irritability and conductivity are specially developed both in the cell body and in branching processes given off from the latter, but the nerve cells become differentiated into superficial receptive cells and deeper-lying conductive cells. In the hydra the receptive cells (fig. 3, *SCl*) and the sensory cells (*SNCl*) contained in the ectoderm have connections, on the one hand, with the surface of the body, and, on the other, send branches to the strictly neural cells (*NCl*), which are distributed through the inner parts of the ectoderm, and in turn send branches to the muscle processes of the muscle cells. The endo-

derm of the coelenterates, though its cells have numerous muscle processes, contains relatively few sensory and neural cells, and fibrous branches of these cells are but little developed.

The polychaete annelid larva of the trochophore type (fig. 8) has a muscular system of which the elements appear to be quite analogous to the ectodermal muscles of the coelenterates, though the system itself is carried to a higher degree of development. Furthermore, the larval muscles are parts of a neuromuscular system, since generally they follow the inner surfaces of nerve tracts in the ectoderm. The muscle fibers are formed from cells derived directly from the larval ectoderm, along with numerous small undifferentiated cells that constitute a loose layer of mesenchyme distributed through the haemocoel. The fibers are arranged principally in longitudinal and circular tracts, though some of them extend from the body wall to the alimentary canal. The endoderm of the larva does not produce directly either muscular or neural cells. The nervous system of the polychaete larva, when best developed, consists of longitudinal and circular strands of ectodermal nerve cells and fibers following the muscle tracts, and of ganglionic groups of nerve cells developed particularly in connection with sensory organs on the preoral part of the body. The larval elaboration of the neuromuscular system is largely a temporary adaptation to the specialized form and habits of the trochophore, for most of it is lost when the larva undergoes its metamorphosis into the definitive worm form; but the preoral part of the larval nervous system forms the brain of the adult, and some of the larval muscle fibers are taken over into the definitive muscular system.

If now we endow our hypothetical annelid ancestor (fig. 2 E) with a primitive neuromuscular system derived from the ectoderm, and provide it with a pair of primitive nephridia, it will have reached an evolutionary stage entirely comparable in structure with that of an annelid in the ontogenetic stage of the young polychaete larva. The usual trochophore larva of the Polychaeta (fig. 4 A), however, leads a purely pelagic life; it floats upright in the water and swims by means of bands of cilia that encircle the body. Its radial and circular neuromuscular system appears to be entirely adapted to its upright position, and many zoologists have regarded the trochophore as the ancestral form of the annelids as well as of various other invertebrates. The lateral position of the mouth, however, just below the principal circle of cilia (*Mth*), gives us good reason for suspecting that the shape of the trochophore and the position assumed in the water are secondary adaptations to a brief swimming existence;

in fact, the later horizontal development of the worm form along the vertical axis of the larva shows clearly that the trochophoral position is one quite out of harmony with the general organization of a worm.

The trochophore, therefore, is to be regarded as a temporary, specialized larval form in polychaete ontogeny, adapted to a free pelagic life for the purpose of disseminating the individuals of its species. The metamorphic alterations that it undergoes at its transformation to the worm are changes of a nature that could not have been a part of the phylogenetic evolution of any animal. On the

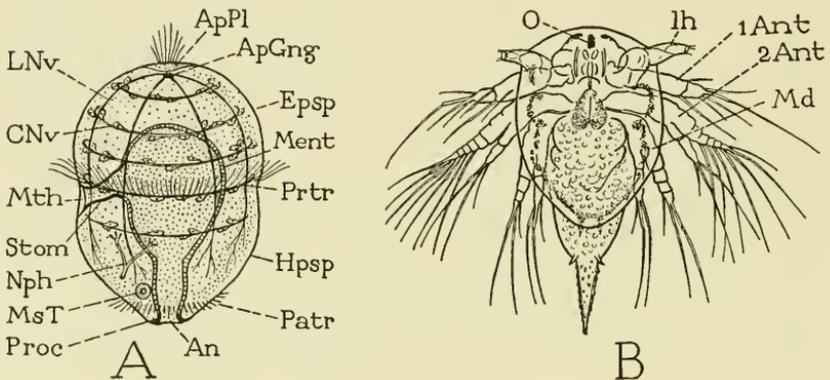


FIG. 4.—The polychaete trochophore and the crustacean nauplius, two specialized larval forms of an early ontogenetic stage, having, therefore, primitive characters, but no phylogenetic significance in their shape or general structure.

A, typical structure of a trochophore, diagrammatic. B, nauplius of a cirriped, *Alcippe lampas* Hancock, dorsal surface (from Kühnert, 1935).

An, anus; 1Ant, first antenna; 2Ant, second antenna; ApGng, apical ganglion; ApPl, apical plate; CNv, circular nerve; EpSp, episphaere; HpSp, hyposphaere; lh, lateral horn; LNv, longitudinal (radial) nerve; Md, mandible; Ment, mesenteron; MsT, mesodermal teloblast; Mth, mouth; Nph, nephridium; O, naupliar ocellus; Patr, paratroch; Proc, proctodaeum; Prtr, prototroch; Stom, stomodaeum.

other hand, inasmuch as the trochophore is an early ontogenetic stage, its general organization is primitive, and is repeated in the ontogenetic development of many other invertebrates besides the annelids. It should be noted, furthermore, that the trochophore is not a universal larval form even among the annelids, for most of the archannelids, some of the polychaetes, and all the oligochaetes have a direct development, in which either there is no suggestion of the trochophore form, or a remnant of it is preserved from ancestors that had a typical swimming larva.

The presence of a mesoblastic muscle system and of a mesenchyme, or parenchymatous layer between the ectoderm and the endoderm, gives the annelid larva, or the platyhelminth adult, the status of a triploblastic animal; but the middle layer is here only an elaboration of elements present also in the so-called diploblastic coelenterates. The young annelid larva, however, is endowed from its parents with hereditary influences that will mold its growing tissues into structures never attained by the coelenterates or flat worms. Particularly affected are two individualized groups of mesoblast cells, which, though they may be set apart in the platyhelminths, will give rise in the annelids to special bands of mesoblastic tissue, known as the *mesoderm*. Within the mesoderm will be formed a new body cavity, the *coelom*, and from the walls of the latter will be produced a new muscular system, a more efficient excretory system, a circulatory system, and various tissues of special functions, to all of which is added an extension and elaboration of the nervous system. With the formation of the mesodermal cavities the triploblastic annelid larva becomes a coelomate animal, but, shortly before the appearance of the coelom, there takes place a segmentation of the body affecting the ectoderm and the mesoderm, so that the young annelid worm is almost at once a segmented and a coelomate animal.

II. THE MESODERM AND THE BEGINNING OF METAMERISM

In the ontogeny of the articulate animals, the formation of the coelomic cavities in the mesoderm is so closely associated with the appearance of body segmentation as to give the impression that the two are intimately related developmental processes, and since the segmentation of the mesoderm is usually more conspicuous than the segmentation of the body, embryologists often describe metamerism in terms of mesoderm segmentation, as if the formation of "mesoderm somites" were equivalent to body segmentation. Closer attention recently given to the sequence of events in the development of the Polychaeta, however, shows that metamerism begins in the ectoderm and the primary ectodermal musculature, and that it secondarily effects a division of the coelomic mesoblast into segmental sections. Subsequently, the coelomic cavities are formed in the segmented mesoderm. That coelomic sacs do not determine metamerism is shown also by the formation of paired coelomic cavities in the preoral cephalic mesoderm of the Onychophora and Arthropoda, in which there is no corresponding external segmentation.

Metamerism, therefore, probably took its origin in a subdivision of the primary somatic musculature into successive sections (myo-

tomes) to give greater efficiency to body movement. The segmentation of the ectoderm and the mesoderm then followed as a result of the segmentation of the muscular system. The primitive coelomic cavities were probably spaces formed in the mesoderm for the accumulation of waste products in the body fluid, to be discharged through primitive nephridial tubules. The coelomic mesoblast, however, formed also a secondary musculature that reinforced the primary musculature, and which, in the higher arthropods, has completely replaced the latter. Evidence that such has been the course of evolution in the Articulata will be shown in the following discussion of the early stages in annelid ontogeny; but there still remains the question as to the origin and nature of the primitive mesoderm, which antedates metamerism.

A study of the growth and differentiation of the annelid mesoderm takes us into the later part of larval development, but to obtain light on the origin of the middle germ layer we must go back to an earlier ontogenetic stage. During cleavage of the annelid egg most of the yolk remains consistently in the blastomeres situated on the vegetative surface of the blastula (fig. 5 A), with the result that, in the 64-cell stage, there are 8 large, yolk-filled blastomeres at the posterior pole (B). These cells are designated by embryologists *4A*, *4B*, *4C*, *4D*, and *4a*, *4b*, *4c*, *4d*, since they comprise the so-called macromeres of the fourth generation and the fourth quartet of micromeres. All of them at this stage would appear to be endodermal, and at the time of gastrulation they all become internal, owing to their overgrowth by the ectoderm. Seven of them, in fact, give rise to purely endodermal progeny, but the *4d* cell will form in most cases both endoderm and mesoderm. The first cleavage of *4d* produces two bilaterally symmetrical cells, *4d*¹ and *4d*² (C), and these cells, in their immediately following divisions, give rise to a few very small cells (D, *end*), usually regarded as endoderm cells, and a pair of large cells (*MsT*) that are destined to produce the coelomic mesoblast, and hence constitute the *mesodermal teloblasts*. (It is perhaps possible that the small "endoderm" cells of this generation are the primary germ cells.)

The common occurrence in the annelids of mesodermal teloblasts derived from cells closely associated with the endoderm has given rise to the idea that the coelomic mesoblast is of endodermal origin, and for this reason it is often called the "endodermal mesoblast" to distinguish it from the larval mesoblast, which is derived from the ectoderm. In most animals the mesoderm is, one way or another, associated in its origin with the endoderm, but among the annelids there are many cases where its endodermal connection is not evident.

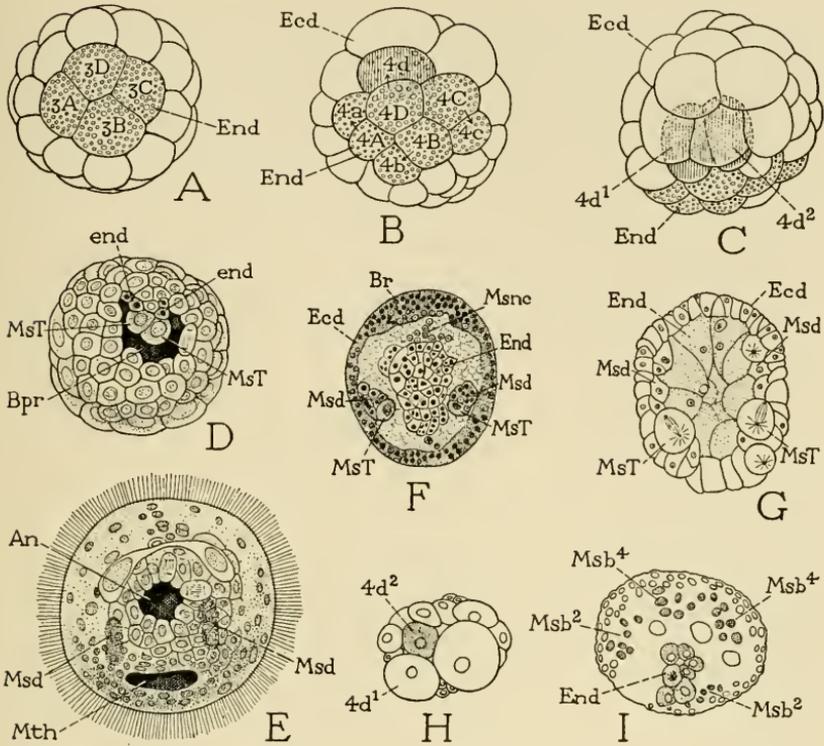


FIG. 5.—Late cleavage stages and mesoderm formation in Annelida and Platyhelminthes.

A, diagram of posterior pole of annelid blastula showing four yolk-filled "macromeres" of third generation. B, posterior pole of blastula of *Arenicola cristata* Stimpson after next cleavage forming fourth quartet of "micromeres," showing differentiation of *4d* blastomere (adapted from Child, 1900). C, same, after cleavage of *4d* into *4d*¹ and *4d*² (adapted from Child, 1900). D, blastula of *Podarke obscura* Ehlers, showing mesodermal teloblasts (*MsT*) derived from blastomeres *4d*¹ and *4d*² (C) after separation of small endoderm cells (from Treadwell, 1901). E, posteroventral view of 40-hour embryo of *Podarke obscura* with mouth and anus, showing position of mesoderm bands (*Msd*) in body (from Treadwell, 1901). F, optical frontal section of embryo of *Capitella capitata* Fabr., showing mesodermal teloblasts and rudiments of mesoderm bands (from Eisig, 1890). G, optical section of embryo of *Dinophilus* sp., with mesoderm bands (*Msd*) extending forward from teloblasts (from Nelson, 1904). H, optical section of blastula of *Planocera inquilina* Wheeler (Polycladia) from right side just after division of *4d*, producing *4d*¹ that will form endoderm, and *4d*² that will form mesoblast (from Surface, 1907). I, same, later stage seen from posterior pole, showing mesoblast (*Msb*¹) derived from *4d*², and mesoblast (*Msb*²) derived from second quartet of ectodermal blastomeres (from Surface, 1907).

3A-3D, *4A-4D*, "macromeres" of third and fourth generations; *4a-4d*, "micromeres" of fourth quartet; *An*, anus; *Bpr*, blastopore; *Br*, brain; *4d*¹, *4d*², daughter cells of *4d* blastomere; *Ecd*, ectoderm; *End*, endoderm; *end*, endoderm derived from *4d*¹ and *4d*² blastomeres; *Msb*², mesoblast derived from second quartet of micromeres; *Msb*⁴, mesoblast derived from *4d* cell of fourth quartet; *Msd*, mesoderm; *Msnc*, mesenchyme; *MsT*, mesodermal teloblast; *Mth*, mouth.

It is claimed by both Kleinenberg (1886) and E. Meyer (1901), for example, that in the larva of *Lopadorhynchus* the mesoderm arises from the ectoderm, and in *Capitella*, according to Eisig (1899), the coelomic mesoblast is produced from blastomeres other than *4d*. Furthermore, the mesoderm of the postlarval somites is said by Iwanoff (1928) to be formed in many polychaetes directly from the ectoderm, and the same is probably true in cases of regeneration. The mesoderm of certain other coelomate invertebrates also may have no genetic relation to the endoderm, as in the gastropod *Paludina*, in which the embryonic mesoblast that gives rise to the usual mesodermal organs is generated directly from cells of the ventral ectoderm (see Dautert, 1929).

During larval life, or at the transformation of the larva to the worm, the annelid mesodermal teloblasts, however formed, proliferate within the haemocoel two masses of mesoderm cells (fig. 5 E, F, G, *Msd*), which eventually take the form of ventrolateral bands extending forward at least as far as the sides of the mouth (fig. 6 F). These primary mesoderm bands are solid cell masses; they are never observed at this early stage to contain cavities, and there is no evidence from annelid embryology to suggest that they represent phylogenetically a pair of open pouches. Later, with body segmentation, the bands are broken up into solid segmental blocks (G), and finally the blocks are excavated by coelomic cavities (H). The nature of the mesoderm and the primitive function of the coelomic cavities can be better discussed after we have examined the known facts concerning the beginning of metamerism, but it should be noted here that the formation of the mesoderm bands precedes body segmentation.

Metamerism in the polychaete larva becomes first evident as a subdivision of the body region between the mouth and the pygidium into a small number of somites (fig. 7 A, I, II, III). There is ample reason to believe, as Iwanoff (1928) claims, that the formation of these *primary somites*, or *larval segments* of ontogeny, represents the beginning of metamerism in phylogeny, and, as we shall see, the same phenomenon of direct segmentation in the body of the embryo or young larva recurs in various arthropods. The primary somites are thus to be distinguished from the *secondary somites* later added by teloblastic growth in a subterminal generative zone, and which will constitute the major part of the adult animal. The larval somites of the Polychaeta, Iwanoff shows, are formed approximately simultaneously in contrast with the successive, individual generation of the teloblastic somites. E. Meyer (1901) observes that in *Lopadorhynchus* metamerism takes place so rapidly as to give the impres-

sion that a relatively large number of somites are formed all at once, but Sokolow (1911) says that in *Ctenodrilus* the intermediate somites or the more anterior ones are first differentiated and the series then completed anteriorly and posteriorly. Segmentation may be delayed until the beginning of metamorphosis, as in *Polygordius*, or it may take place while the larva is still in the swimming trochophore stage.

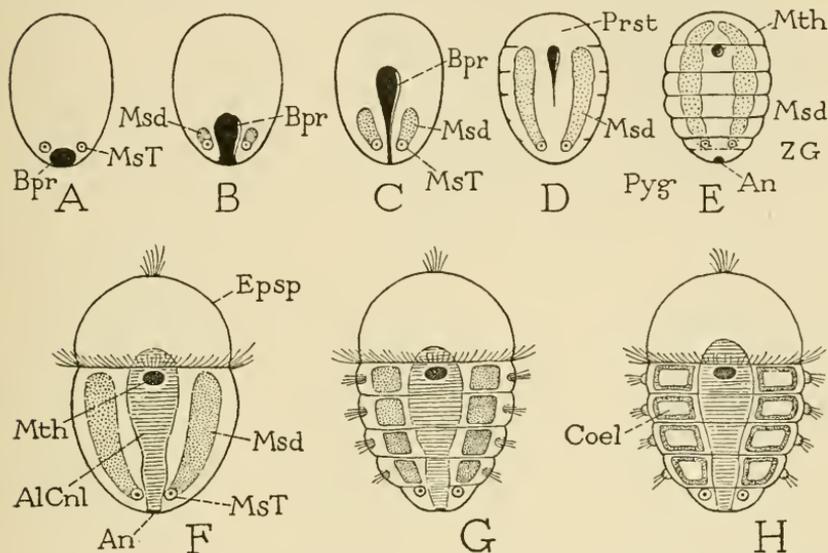


FIG. 6.—Transformation of the annelid blastopore, primary segmentation of the body, growth and segmentation of the mesoderm bands, and formation of the coelomic sacs, diagrammatic.

A, blastopore and mesodermal teloblasts at posterior pole of embryo. B, blastopore elongating forward on ventral surface; rudiments of mesoderm generated from teloblasts. C, blastopore still more elongate, closing posteriorly; mesoderm growing forward. D, blastopore closed posteriorly; mesoderm bands extended to prostomium. E, blastopore obliterated except for mouth opening at anterior end; anus formed secondarily at posterior end; mesoderm segmented following metamerism of body, and extended into prostomium. F, polychaete trochophore before segmentation. G, same after segmentation, mesoderm cut into solid segmental blocks. H, same, mesoderm blocks excavated by coelomic cavities.

AlCnl, alimentary canal; *An*, anus; *Bpr*, blastopore; *Coel*, coelomic cavity; *Episp*, episphere; *Msd*, mesoderm; *MsT*, mesodermal teloblast; *Mth*, mouth; *Prst*, prostomium; *Pyg*, pygidium; *ZG*, zone of growth.

In *Polynoë*, as described by Hacker (1895), seven somites are first marked out in the body of the trochophore, which is transformed while still active into a swimming "nectochaete" larva with seven segments and corresponding chaeta-bearing parapodia. The number of larval somites is always small, three or four being usual (fig. 7 A, B, C), the maximum not more than 13. Completion of larval metamerism is followed by a pause in development.

Observations on the beginning of embryonic segmentation in the annelids differ somewhat as to whether the intersegmental divisions appear first in the ectoderm or in the mesoderm, but most students of annelid development find either that the ectoderm and the meso-

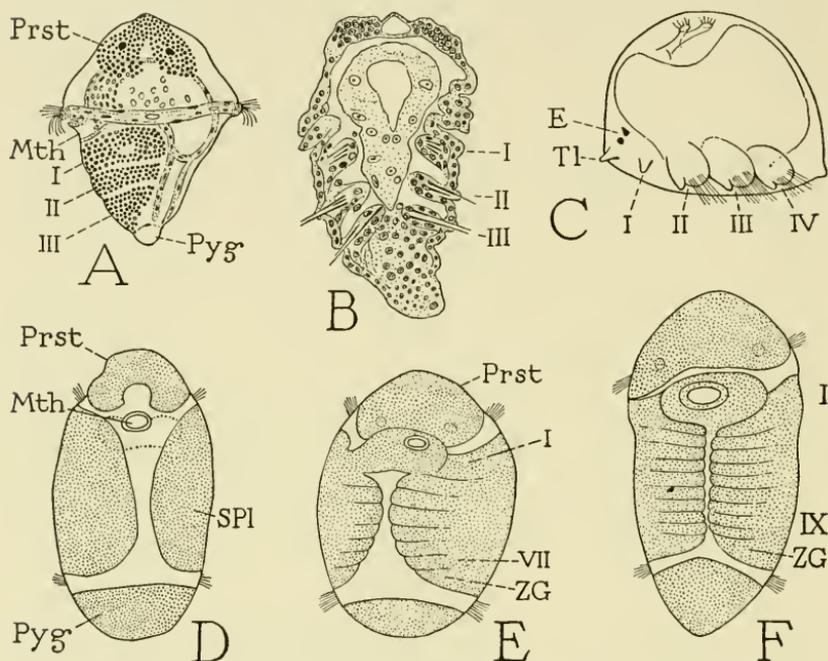


FIG. 7.—Examples of primary segmentation in polychaete larvae.

A, *Eupomatus uncinatus*, trochophore showing primary segmentation of the mesoderm (from Iwanoff, 1928). B, same, later larval stage, horizontal section showing development of chaetal sacs in primary somites, and extension of posterior part of body (from Iwanoff, 1928). C, *Platynereis dumerilii* Aud. & Milne-Edw., nereidogen larva just out of egg, with four primary somites (from Hempelmann, 1911). D, *Capitella capitata* Fabr., embryo before segmentation, ventral view (from Eisig, 1899). E, same, embryo with seven somites and zone of growth formed directly in primary body region (from Eisig, 1899). F, same, later stage with two additional somites formed from zone of growth (from Eisig, 1899).

E, eye; I-IX, somites; Mth, mouth; Prst, prostomium; Pyg, pygidium; SPI, somatic plate; Tl, tentacle; ZG, zone of growth.

derm are segmented at the same time, or that the first signs of metamorphism are to be seen in the ectoderm.

In the development of the polychaete *Capitella*, according to Eisig (1899), on the sixth day after fertilization of the egg, the cells of the ventral somatic plates of the larva (fig. 7 D, SPI) become arranged in transverse rows, and on the sixth day seven or eight somites are already demarcated by transverse lines in the ectoderm of the larval

body region between the mouth and the pygidium (E). On the same day, however, the mesodermal bands also become divided into segmental sections. At first the ectodermal and mesodermal somites of *Capitella* do not entirely correspond, there being several supernumerary mesodermal divisions in the mouth region, but by the twelfth or thirteenth day the larva has 13 somites with coincident limits in both the ectoderm and the mesoderm.

The segmentation of the mesoderm bands as described by E. Meyer (1901) in *Psymobranthus*, *Polygordius*, and *Lopadorhynchus* appears to be determined by elements of the mesenchymatic primary mesoblast in the form of spindle-shaped cells that penetrate into the mesoderm bands at the intersegmental lines and cut the bands into a series of segmental sections. From the penetrating mesenchyme cells are later formed, according to Meyer, the muscles of the intersegmental dissepiments. Similarly in the Serpulidae and Spionidae the larval segmentation is said by Iwanoff (1928) to be secondarily imposed upon the mesoderm bands by metamerism in other parts of the body, as by the ectodermal segmentation, the ingrowth of the chaetal sacs (fig. 7 B), the penetration into the mesoderm of mesenchymatous muscle elements, or by the segmental formation of blood lacunae in the general mesoderm mass.

The primary larval segments are seldom as fully developed in the adult worm as are the teloblastic segments, and both the segment limits and the differentiation of ganglia on the nerve cords may remain obscure. In the Spionidae, Iwanoff (1928) says, the trochophoral mesoderm is very weakly developed, the dissepiments are only imperfectly formed, often absent, and in some species a segmentation of the mesoderm in the primary segments is absent even in the adult. Chlorogogen cells are not developed in the coelomic walls of the larval segments, and in these segments *germ cells are never present*.

As a result of body metamerism, the mesoderm bands are divided each into a series of segmental sections, and these sections, as the bands themselves, are at first solid blocks of cells (fig. 6 G). Later the coelomic cavities appear as cleavage spaces within the cell blocks (H). Hence, just as there is no evidence that the primary mesoderm bands represent primitive sacs, so there is no evidence from ontogeny that the coelomic cavities of the annelids took their origin as a series of separate mesodermal pouches. The facts of development suggest only that the primitive mesoderm bands were continuous tracts of cells, and that the formation of cavities within them was a secondary process, subsequent to segmentation.

With the formation of the coelomic cavities in the mesoderm, the young annelid becomes a coelomate animal. Before the appearance

of the coelom, however, it might pass for the ancestor of a flatworm, for even in the Platyhelminthes there is a teloblastic proliferation of cells that appear to correspond with the mesoderm cells of the annelids, though the cells thus produced soon disperse and become a part of the parenchyma. It is in the development and elaboration of the mesoderm, or teloblastic mesoblast, therefore, that the Coelomata depart from the Platyhelminthes. Segmentation is a feature superimposed upon the mesoderm in the Annelida as a result of body metamerism, in which apparently the ingrowth of the septal muscles plays an important part.

The mesoderm of the adult annelid or arthropod gives rise to a large variety of tissues and organs, but most of the specialized derivatives of the mesoderm are formed in the secondary segments of the adult animal. The principal products of the primary mesoderm are muscle and connective tissues, and an epithelial lining of the coelomic cavities.

According to E. Meyer (1901), the mesodermal myoblasts of the polychaete larva are not recognizable as such until the mesoderm bands have become broken up into segmental sections, and the transformation of the myoblasts into functional muscle fibers is not evident until after the appearance of the coelomic cavities. The myoblasts of each mesodermal segment, Meyer says, consist of four large cells on each side, two dorsal and two ventral, lying along the lines of the larval longitudinal muscles of mesenchymatic origin already present. The mesoderm fibers finally replace the mesenchyme fibers and become the definitive longitudinal muscles of the worm. The coelomic myoblasts, Meyer shows, are true epithelial muscle cells that form muscle processes from their outer surfaces, while the plasmatic bodies of the cells retain their places for some time in the coelomic walls. The parts of the coelomic walls not involved in muscle formation become thinner, and finally transform into typical peritoneal epithelium.

The important part that the mesoderm plays in the development of the coelomate animals is entirely clear; but what the mesoderm becomes in the course of evolution does not explain what it was in its beginning. Most of the theories that have been proposed to account for the primitive mesoderm, it will be found, are attempts to explain the functional nature of the coelomic sacs rather than the origin of the mesoderm itself.

The theory most widely accepted at one time as to the origin of the mesoderm is the *enterocoele theory* (Hertwigs, 1882, Sedgwick, 1884), by which the coelomic sacs are explained as diverticula of the archenteron. In some animals the coelomic sacs are thus formed in

the embryo, and the enterocoele theory has some plausibility as a wide generalization, considering the very common early association of the coelomic mesoderm rudiments with the endoderm; but, as applied to the annelids and arthropods, the theory must entirely discard the direct evidence from embryology that the mesoderm first appears as solid proliferations of cells, which only in a purely hypothetical manner could be interpreted as representing pouches of the archenteron. The only known case of the formation of the mesoderm from enteric pouches that might be referred to the articulates occurs in the Tardigrada (see Marcus, 1929), but there is much uncertainty concerning the relationships of the tardigrades.

A second mesoderm theory is the *gonocoele theory*, based on the almost universal association of the germ cells with the coelomic mesoderm in the coelomate animals. Hatschek (1877, 1894) believed that the mesodermal teloblasts of the annelid larva are themselves germ cells, and Rabl (1879, 1889) adopted this view. The gonocoele theory of the origin of the coelomic sacs, however, was principally elaborated by E. Meyer (1891, 1901). Meyer contended that the primitive coelomic sacs were muscular pouches, from the epithelial walls of which the germ cells are generated, and that, as these gonadial sacs expanded to increase the reproductive function, they finally preempted the haemocoele, and their muscles were transferred to the body wall. The gonocoele theory loses much of its support now that the old belief that the germ cells are direct products of the coelomic epithelium is no longer tenable, and, moreover, it entirely breaks down in view of the fact that the primary larval somites of the annelids do not contain germ cells. In the primitive annelids, as will be shown later, the germ cells probably were located in the zone of undifferentiated tissue behind the last primary somite. If so, the reproductive function had nothing to do with the origin of the mesoderm or the formation of the coelomic sacs.

A third theory, concerned principally with the function of the coelomic sacs, is the *nephrocoele theory* (Ziegler, 1898; Faussek, 1899, 1901). According to Ziegler, the primitive coelomic cavities were open pouches for the accumulation of waste products; they were not diverticula of the archenteron, but were, perhaps, of the nature of protonephridia. The nephrocoele theory as modified by Faussek holds that the excretory coelomic sacs are not primitive structures in a phylogenetic sense, but that they have been developed for excretory purposes in the embryo, and are hence purely ontogenetic organs. Faussek supports his theory with the generalization that the open metanephridia constitute exits from the coelom, while the closed

protonephridia serve for removal of waste products from the haemocoel. This statement, however, is not entirely true, for in some of the Polychaeta protonephridia are associated with coelomic sacs, and the primary larval somites of the annelids do not have metanephridia. On the other hand, there can be no question that the coelomic fluid does contain waste products of metabolism.

A fourth theory, that of Kleinenberg (1886), identifies the primitive mesoderm with muscle tissue, and is thus more satisfactory than the other theories because it deals with the beginning of the mesoderm as a functional tissue. Kleinenberg attributes the idea of a muscle origin for the mesoderm to Rabl, who later discarded it, but the theory rests principally on Kleinenberg's studies of the development of *Lopadorhynchus*. Kleinenberg claimed that in the larva of *Lopadorhynchus* the mesoderm is derived directly from the ectoderm at the posterior end of the body, and that the ectodermal myoblasts, and the neuroblasts of the ventral nerve cords, arise from a common neuromuscular rudiment. The mesoderm bands, or "muscle plates," become divided into segmental myotomes consequent on metamerism of the body, and the myotomes give rise to the body musculature, including, according to Kleinenberg, the dorsal and ventral longitudinal muscles, the parapodial muscles, and the circular muscles of the body wall. Then follows a separation of the muscle plates into parietal and visceral layers in each somite, producing thus the paired coelomic cavities, the peritoneal linings of which are formed by the inner cells of the myotomes. Kleinenberg's theory of the origin of the mesoderm thus gives to metamerism a mechanical significance, since it explains body segmentation as an adaptation to more efficient locomotion. Certainly, when once established, the chief function of metamerism is effective movement of the body, and to this feature the segmented annelids owe their superiority over the unsegmented flatworms. A serious weakness of the muscle theory of the origin of the coelomic mesoblast, however, is found in the fact that so many tissues other than muscle are evolved from it. Muscle fiber is a highly specialized tissue, and it seems hardly likely that epithelial tissue, for example, would be formed from muscle cells, since ordinarily it is epithelial tissue that gives rise to muscle fibers and to the various other specialized tissues of the body. Furthermore, as shown by Meyer (1901), muscle is not formed from the coelomic mesoblast of *Lopadorhynchus* until after the segmentation of the mesoderm bands and the formation of the coelomic cavities.

The literature of annelid morphology is replete with discussions on the nature and difference of the "two kinds of mesoblast"; but

the facts concerning the ontogenetic origin of the annelid mesoblast apparently can be expressed in the simple statement that *mesoblastic tissue may be formed by internal proliferation from any part of the blastoderm*, and may, therefore, be both "ectodermal" and "endodermal." The mesoblast of the first three quartets of the blastula (see Torrey, 1903) gives rise to the so-called larval mesoblast, or mesenchyme; from the fourth quartet ordinarily arises the coelomic mesoblast, or mesoderm. That these two groups of mesoblast cells primarily have the same morphological status is indicated by the fact that in the Platyhelminthes they do not become differentiated into separate tissues. Surface (1907), who first followed the divisions of the $4d$ cell in a flatworm, shows that in *Planocera* the $4d$ blastomere gives rise to both endoderm and mesoblast as it does in the annelids, since, of the two cells of the first division, $4d^1$ (fig. 5 H) forms the endoderm (I, *End*), and $4d^2$ gives rise to two lateral groups of scattered mesoblast cells (I, *Msb*⁴), which are at first quite distinct from the mesoblast of the second quartet (*Msb*²), though eventually they intermingle with the latter to form the parenchymatous tissue of the adult. In *Planocera* the usual endodermal "macromeres" degenerate and almost the entire endoderm proceeds from the $4d^1$ cell. Finally, we may correlate the "double origin" of the annelid mesoblast with the production of muscle tissue from both the ectoderm and the endoderm in the Coelenterata.

From the condition in the Platyhelminthes, it becomes evident that the primitive mesoblast was a parenchymatous mass of undifferentiated cells occupying the haemocoel, which had been proliferated internally from both the ectoderm and the endoderm. In the unsegmented ancestors of the annelids, the ectodermal mesoblast must have formed a primary somatic muscular system, represented by the larval musculature of modern annelids, which is derived from the ectodermal quartets of the blastula. The principal part of the parenchyma, therefore, came to be that part of the mesoblast proliferated in the posterior part of the body, chiefly, or usually, from the $4d$ cell of the fourth quartet. The persistent parenchyma thus became the embryonic middle layer known specifically as the mesoderm.

Since the most important result of metamerism is the production of a mechanism of movement based on the division of the body into consecutive motor units, it can scarcely be questioned that metamerism had its origin as an adaptation to more effective body movement. Inasmuch as the evidence from embryonic development shows that metamerism originates ontogenetically in the ectoderm and its derivatives, and is secondarily imposed upon the mesoderm, we may

suppose that it took its inception phylogenetically from an attachment of the primary (ectodermal) longitudinal somatic muscles at consecutive rings on the body wall, and from the accompanying ingrowth of fibers that formed contractile dissepiments between the myotomes. The ingrowth of the septal muscles cut the parenchymatous mesodermal bands into segmental blocks. This modification and elaboration of the primitive muscular system, and the consequent segmental division of the mesoderm bands, give at once the essential quality of metamerism, and from it there follows as a necessary result the metamerization of other organs, such as external ectodermal structures, the ventral nerve cords, and all structures of mesodermal origin.

The coelomic cavities first appear in the annelid embryo or larva as cleavage spaces in the segmental mesoderm blocks. Since the unsegmented Platyhelminthes have nephridial organs, it may be assumed that the primitive annelids possessed simple segmental nephridia in the form of internally closed tubules extending into the haemocoel. The primitive coelomic cavities, therefore, were probably spaces formed in the segmented parenchyma for the accumulation of body fluid charged with excretory products. The inner cells of the parenchyma now formed epithelial walls about the nephric cavities, which became the coelomic sacs; the outer cells were converted largely into muscles and connective tissue. The muscle cells gave rise to fibers that reinforced the somatic musculature, and eventually came to be its principal constituents. The definitive musculature of modern annelids, therefore, is a composite of fibers derived from the larval ectoderm and of fibers formed from the coelomic mesoblast, but in the Onychophora and the Arthropoda the entire musculature appears to be now a coelomic product. There is no reason necessarily for supposing that the primitive mesodermal muscles were functional elements of the coelomic sacs, for, though in ontogeny the mesoderm usually takes the form of two-layered bands of cells, within which the coelomic cavities are formed, it would seem probable that the primitive mesoderm was a loose parenchymatous tissue. The coelomic sacs are specifically the epithelial walls formed about the nephric cavities; the surrounding muscles were probably generated from the outer undifferentiated cells of the original parenchyma.

With the later development of the teloblastic somites, into which the germ cells were distributed from their posterior source of proliferation, the reproductive products were discharged into the coelomic sacs of these somites, which thus became gonocoelic as well as nephrocoelic in function. Open nephridia or coelomoducts now connected the coelomic cavities with the exterior and served both as excretory

and as genital outlets. Finally, in the Onychophora and the Arthropoda, the coelomic sacs have been divided into gonadial compartments and nephridial compartments, which have become reduced in size and limited to restricted parts of the body, with the result that the haemocoel is restored as the functional body cavity.

III. DEVELOPMENT OF THE ANNELID NERVOUS SYSTEM

The annelids and the arthropods undoubtedly have a closer bond of union in the structure of the nervous system than in any other feature of their organization, except metamerism itself. The definitive central nervous system of the polychaete annelids is developed from two distinct sources, one located in the prostomium, or episphere of the trochophoral larva, the other in the somatic region, or hyposphere of the larva. From the first is produced the brain; from the second, the ventral nerve cords. The nervous system of the trochophore consists of ganglionic centers in the prostomium connected by circular and radial nerve tracts, from which trunks proceed into the hyposphere (fig. 4 A). This primary system centering in the prostomium must represent the primitive neural system of the unsegmented ancestors of the annelids, adapted to the structure of the trochophoral larva, and is probably congenetic in its origin with the nervous system of the Platyhelminthes. The segmentally ganglionated ventral nerve cords of the postoral region of the trunk are correlated in their development with the development of body metamerism; they pertain, therefore, to a later stage of evolution, and have no homologues in the unsegmented worms. The definitive connection between the prostomial and somatic parts of the nervous system is established secondarily in the ontogeny of the polychaetes, but in the oligochaetes the two parts are said to be continuous from their inception. The fundamental structure of the somatic nervous system of the articulate animals is an adaptation to the function of regulating the muscular mechanism of metameric body movement; the prostomial system is primarily sensory in function, except insofar as it controls the movements of prostomial appendages.

The phylogenetic origin of the articulate nervous system can probably be interpreted very closely from the development of the neural elements in the trochophore larva of the polychaete annelids, and must have been about as follows: The primary neurocytes were probably sensory cells of the ectoderm closely associated with the primary myocytes, and were thus, at first, both receptive and motor in function. As the muscular system became elaborated, however, the primary neurocytes were withdrawn to the inner surface of the ectoderm,

while other superficial cells assumed the receptive function and transmitted secondarily the impulses from external stimuli to the first set of cells, which now became purely motor neurones. Finally, still other neurocytes gave rise to a subepidermal plexus of fibrous tracts that formed lines of intercommunication between the scattered motor and sensory elements, and thus unified and coordinated the entire nervous system. Then the nerve cells of the prostomial region became aggregated into a number of ganglionic centers, principally associated with groups of receptive cells in primitive sensory organs, and the nerve

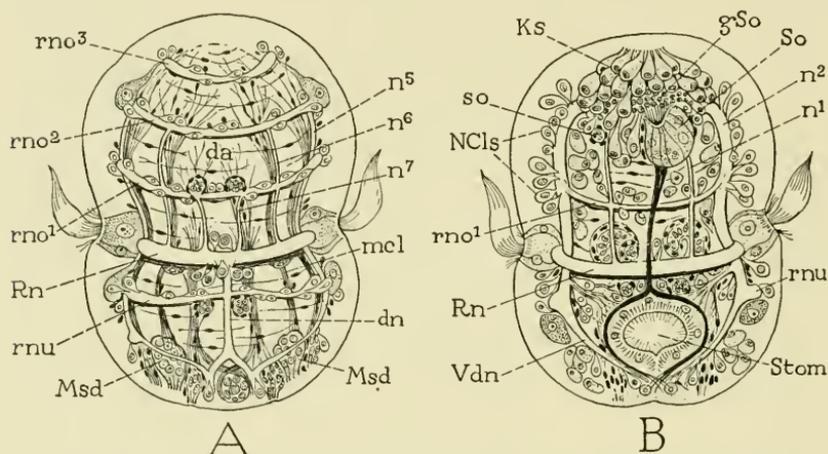


FIG. 8.—The nervous and muscular elements of a young trochophore larva of *Lopadorhynchus*, nerve tissue represented in white, muscle tissue in black. (From E. Meyer, 1901.)

A, aboral surface of larva. B, oral surface.

da, rudiments of so-called dorsal antennae; *dn*, median dorsal nerve of hyposphere; *gSo*, ganglion of left ciliary organ; *Ks*, apical plate; *mcl*, muscle fibers; *Msd*, mesoderm; *n*, longitudinal nerves (seven pairs in episphere); *NCl's*, nerve cells; *Rn*, circular nerve of prototroch; *rno*¹, *rno*², *rno*³, circular nerves of episphere; *rnu*, circular nerve of hyposphere; *So*, left ciliary organ; *so*, rudimentary right ciliary organ; *Stom*, stomodaeum; *Vdn*, larval stomodaeal nerve.

tracts assumed definite courses. Thus was evolved the primary nervous system of the polychaete larva. The prostomial ganglia of this system later coalesce to form the definitive brain. The somatic nervous system, subsequently developed in correlation with metamerism, took its origin from restricted ventrolateral tracts of the somatic ectoderm, became connected with the brain, and finally replaced the primary system in the body region.

The most primitive nerve center of the annelids probably is represented by the apical ganglion of the polychaete trochophore (fig. 4 A, *ApGng*) situated beneath the ectodermal apical plate (*ApPl*), which

usually bears a tuft of cilia, and with which there may be associated a pair of small larval tentacles, and sometimes a pair of "eye spots." From the apical ganglion, nerves radiate posteriorly (*LNv*) on the inner surface of the epidermis, and these longitudinal radial nerves are connected by bands of circular fibers (*CNv*), chief of which is the nerve ring of the prototroch (*Prtr*). The nerve tracts, both radial and circular, closely follow the peripheral muscle bands of the larva (fig. 8), thus attesting that the nervous and contractile elements arose from common ectodermal neuromuscular rudiments. The nerve tissue is situated between the muscle fibers and the epidermis, the nerve cells being scattered individually, or condensed in small ganglionic groups.

The nervous system of the polychaete trochophore is best known from the elaborate studies of Kleinenberg (1886) and of E. Meyer (1901) on the larval development of *Lopadorhynchus*, a small errant polychaete of the family Phyllodocidae (fig. 13 D) having two pairs of prostomial tentacles but no palpi. The larva of *Lopadorhynchus* is a typical trochophore (fig. 8) with an equatorial band of cilia, the prototroch, just above the mouth. The apical ciliary organ, however, does not have the usual form and position; it is transposed to the anterior ventral surface, and is divided into a well-developed organ on the left (*B, So*), and a rudimentary organ on the right (*so*). The episphere contains seven pairs of longitudinal nerves (n^1-n^7), and is encircled by three nerve rings (rno^1-rno^3) above that of the prototroch (*Rn*). In the hyposphere there is but a single nerve ring (*A, rnu*). The largest of the longitudinal nerves are two thick lateroventral nerve tracts (*B, n^2*), which anteriorly (apically) are continuous with each other in a wide transverse commissural arch within the episphere, and posteriorly are extended into the hyposphere as a pair of large lateral trunks (*Vdn*) that break up into smaller branching nerves.

The neural cells of the *Lopadorhynchus* larva are described in great detail by Meyer. In general they lie along the fiber tracts (fig. 8 B, *NCl's*), where many of them are aggregated into small ganglionic clumps, particularly in the episphere. In the early stages of development, according to both Meyer and Kleinenberg, the neurocytes are generated from the ectoderm in association with muscle cells, and the principal neuromuscular rudiments of the episphere represent larval sensory organs (fig. 16 A), of which the nerve cells (*n*) form small ganglionic centers. The scattered neurocytes are probably the generative cells of the fibers in the nerve tracts. The ganglionic centers of the larva pertain to the apical ciliary organs, a pair of transient larval antennae, the two pairs of persistent tentacles, which are dorsal and ventral in the adult (fig. 13 D), and the nuchal organs, but include

also two cell groups of unknown significance situated on the dorsal surface of the episphere (fig. 8 A, *da*). From some of the ganglion cells nerve processes go to the muscles, and from others fibers penetrate centrally into the nerve tracts.

Before the beginning of larval metamorphosis, Meyer says, the production of myocytes ceases in the larval neuromuscular centers, and during metamorphosis a large part of the larval musculature is

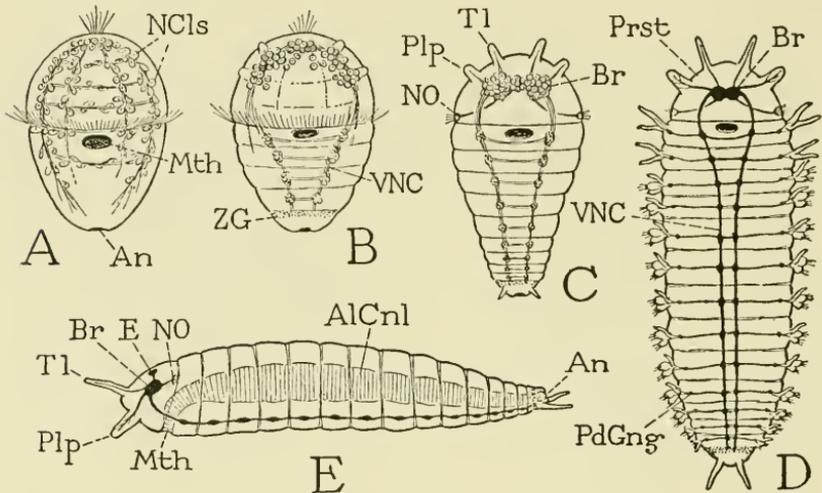


FIG. 9.—Theoretical evolution of the annelid nervous system, diagrammatically following Kleinenberg's and Meyer's accounts of the development of the nervous system in the larva of *Lopadorhynchus*.

A, early trochophore with diffuse nerve cells (*NCl's*) along the radial and circular nerve tracts. B, nerve cells of episphere concentrated in incipient ganglia connected with ectodermal sensory organs along lateral radial nerves; ventral nerve cords (*VNC*) developed from ectoderm of hyposphere. C, scattered ganglia of episphere condensed into a cerebral mass (*Br*); cerebral connectives united with ventral nerve cords. D, generalized adult nervous system; podial ganglia developed at bases of body appendages. E, nervous system of adult polychaete, lateral view.

AlCnl, alimentary canal; *An*, anus; *Br*, brain; *E*, eye; *Mth*, mouth; *NCl's*, nerve cells; *NO*, nuchal organ; *PdGng*, podial ganglion; *Plp*, palpus; *Prst*, prostomium; *Tl*, tentacle; *VNC*, ventral nerve cord; *ZG*, zone of growth.

lost. Many of the primary muscles, however, remain, including those of the persistent tentacles and nuchal organs, and certain other muscles of the prostomium. The neural cells of the various ganglionic centers of the larval episphere, on the other hand, increase in number until they become so crowded that details of their further development cannot be followed. The cells thus generated, however, are massed upon the large lateral nerve trunks of the episphere (fig. 8 B, *n*²) and their anterior commissure. In this manner there is formed from

numerous agglomerated centers in the larval episphere (fig. 9 A, B) a compact cellular and fibrous body of nerve tissue (C, Br), which becomes the brain of the adult worm (D). Hence, as Kleinenberg remarks, the developmental history of the brain in *Lopadorhynchus* shows how extraordinarily complicated in its origin is the cephalic ganglion even in the annelids. However, that details in the probable phylogenetic history of the nervous system are not necessarily recapitulated in ontogeny is shown in many annelids having a direct development, or one in which the trochophoral stage is passed within the egg, for in such forms the brain is differentiated from the

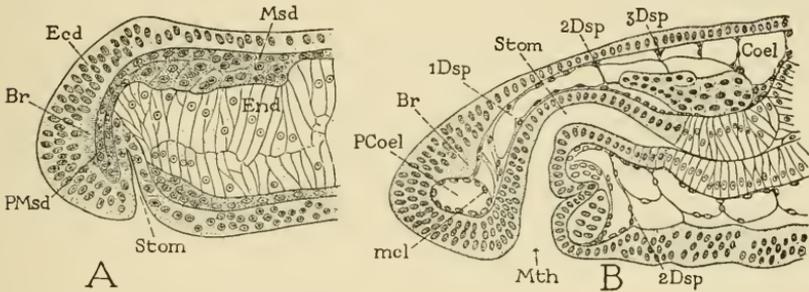


FIG. 10.—Median vertical sections of the anterior end of an embryo of the viviparous polychaete *Ctenodrilus branchiatus* Sokolow (Cirratulidae), showing extension of the mesoderm into the prostomium, and the direct development of the brain from the prostomial ectoderm. (From Sokolow, 1911.)

A, embryo before appearance of coelom, with mesoderm (*Msd*) extended into prostomium (*PMsd*). B, full-grown embryo, with coelom and dissepiments, coelomic cavity of prostomium (*PCoel*) continuous with coelomic cavity of first postoral somite (metastomium), which in the embryo is separated from second somite by a temporary dissepiment (*1Dsp*).

Br, brain; *Coel*, coelom; *1Dsp*, first (temporary) dissepiment, behind first postoral somite; *2Dsp*, *3Dsp*, second and third (permanent) dissepiments; *Ecd*, ectoderm; *mcl*, muscles; *Msd*, mesoderm; *Mth*, mouth; *PCoel*, prostomial coelom; *PMsd*, prostomial mesoderm; *Stom*, stomodaeum.

prostomial ectoderm as a single, compact mass of neural cells (fig. 10, *Br*).

The larval innervation of the hyposphere gives way during metamorphosis to the definitive body nervous system, consisting of the ganglionated ventral nerve cords and their peripheral nerves. The rudiments of this system appear first in the embryo as continuous strands of neurocytes proliferated in the ventral parts of the ectodermal somatic plate as the median edges of the latter unite to close the blastopore. The cords later become ganglionated by the segmental aggregation of their cells. The neuroblasts of the somatic nerve cords, Meyer believes, represent the nerve cells of a series of primitive ectodermal sense organs. Though there are no persistent remnants of

such sensory organs in the annelids, the so-called "ventral organs" of the Onychophora, from which the nerve cords are differentiated, suggest that the latter took their origin from ectodermal structures of some kind.

The final connection between the brain and the ventral nerve cords, according to Kleinenberg and Meyer, is established by fibers that grow forward from the first ventral ganglia (fig. 9 B) and unite with the lateral nerve trunks (fig. 8 B, *Vdn*) extending posteriorly from the arms (n^2) of the cerebral commissure. The union thus formed produces the stomodaeal (circumoesophageal) connectives, through which the prostomial and somatic nerve centers are unified in the definitive nervous system.

The peripheral subcutaneous nervous system of the adult worm is developed directly from scattered neurocytes of the ectoderm. To this system Kleinenberg ascribes the parapodial ganglia (fig. 9 D, *PdGng*), which, he says, are formed quite independently of the central system by groups of ectodermal neurocytes situated mesad of the parapodial bases. Secondarily, the parapodial ganglia send connecting nerves to the ventral nerve cords.

IV. THE ADULT ANNELID

The final development of the adult polychaete annelid from the larva depends upon the histogenic activity in the zone of undifferentiated cells situated between the last larval somite and the pygidium (fig. 11 B, *ZG*). Within this *zone of growth* is generated anteriorly a series of secondary postlarval somites (C, D), which does not represent an extension of the body, but an expansion of a small part of it, since the new somites are interpolated between the primarily segmented larval body and the pygidium. The more anterior somites of the new series, being those first formed, are the first to acquire the mature structure. The teloblastic growth-process is the same whether the larva is a typical trochophore (fig. 12 B, D), or one more nearly resembling the adult worm (E, F, G), but in the first case a greater degree of metamorphosis accompanies the formation of the new somites. Hence, though we may eliminate the trochophore from our concept of the primitive annelid, we cannot dismiss the secondary formation of the teloblastic somites as a purely ontogenetic process—it must be explained in terms of phylogeny.

THE TELEBLASTIC, OR POSTLARVAL, SOMITES

The zone of growth, as described by Lillie (1906) in *Arenicola cristata*, is a mass of large clear mesodermal and ectodermal cells,

which are frequently to be seen in the process of mitosis. Posteriorly the growing zone is sharply defined from the pygidial region, but anteriorly it passes by gradual transition into the more fully differentiated region in front. Its ectodermal cells, Lillie says, must be derived from the last transverse row of cells in the ectodermal somatic plate produced from the *2d* cell of the embryo. The space between the ectoderm and the endoderm is filled with a mass of mesoderm cells very probably generated from the mesodermal teloblasts. Anteriorly the mesoderm of the growing zone is shut off by a roughly defined

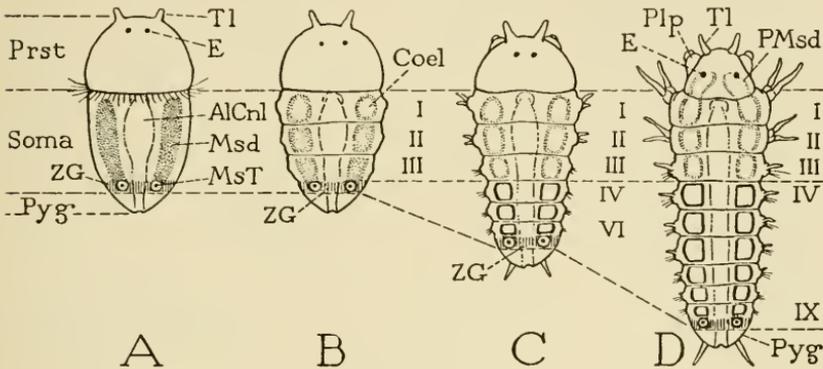


FIG. 11.—Diagrams illustrating the direct primary segmentation of the body of a larval polychaete, and the growth of the worm by successive addition of secondary teloblastic somites generated in the subterminal zone of growth.

A, larva with unsegmented soma and mesoderm bands. B, larval soma and mesoderm directly segmented. C, D, successive formation, from subterminal zone of growth, of teloblastic somites interpolated between primary larval somites and terminal pygidium.

AlCnl, alimentary canal; *Coel*, coelomic cavity; *E*, eye; *I-III*, primary larval somites; *IV-IX*, secondary teloblastic somites; *Msd*, mesoderm; *MsT*, mesodermal teloblast; *Plp*, palpus; *PMsd*, prostomial mesoderm; *Prst*, prostomium; *Pyg*, pygidium; *Soma*, body region between prostomium and pygidium in which somites are formed; *Tl*, tentacle; *ZG*, zone of growth at end of soma.

transverse partition from the coelomic cavity of the somite before it. The first evidence of new somite formation is the appearance of an irregular space in the mesodermal mass of the zone of growth, which enlarges upward around the alimentary canal and becomes the coelomic cavity of the new somite. (*Arenicola* has a dorsal mesentery but none beneath the alimentary canal.) The anterior coelomic wall is pressed against the preceding partition and becomes the posterior lamella of the dissepiment thus formed. Longitudinal muscle fibers make their appearance at an early period in the somatic layers of the mesoderm, but the circular muscles, Lillie claims, appear much later, and evidently, as described by Meyer (1901), are derived from

the inner surface of the ectoderm. According to Iwanoff (1928) the mesoderm of the postlarval somites is formed in *Polygordius*, *Aricia*, *Arenicola*, and the Oligochaeta from the mesodermal teloblasts that generate the larval bands of mesoderm, but in the rest of the Polychaeta the postlarval mesoderm is proliferated from the ectoderm of the zone of growth.

The pygidial region posterior to the zone of growth retains its primitive characters throughout the course of development, and is carried continuously backward as the number of somites increases. When the definitive number of somites has been formed, the growing zone loses its distinctive features and becomes indistinguishable as such. Structurally the secondary, or teloblastic, somites are modeled according to the general plan of the primary somites before them; but, though they may differ in various structural details from the latter, they have one distinctive feature, which is that they alone contain the germ cells. Germinal centers ("gonads") may occur in all the teloblastic segments, but in most of the polychaetes they are limited to a definite part of the body (the epitoke), and in the oligochaetes they are usually restricted to a few segments.

The ancestral annelids necessarily were reproductive as adults in all their evolutionary stages, but phylogenetic forms recapitulated in ontogeny are generally not reproductive. Hence, it is difficult to study the evolution of the reproductive system from ontogenetic development. The germ cells of the annelids usually are not recognizable as such in the larva, and little is known of their embryonic origin. It is claimed by Malaquin (1925), however, that in the serpulid *Salmacina dysteri* the sex elements first appear as differentiated cells in the gastrula, and that later (Malaquin, 1924) these cells become localized immediately before the zone of growth in the posterior segments of the young larva, where they lie ventral to the rectum, and are distinguishable from the surrounding cells by their large, clear, spherical nuclei containing numerous small chromatic masses. In the oligochaete *Pachydrilus*, Penners (1930) claims the germ cells arise directly from the mesodermal teloblasts, and are the first cells formed by the latter. The germ cells, as shown also by Penners and Stäblein (1930) in Tubificidae, appear prior to the formation of the definitive gonad somites, and migrate in the haemocoel to these somites, where they penetrate the mesoderm and finally take their definitive positions in the dissepiments. It seems highly probable, therefore, that the primitive annelids, at a phylogenetic stage before the teloblastic somites were formed, carried the germ cells in the undifferentiated posterior part of the body behind the last primary

somite. From this point the germ cells must have been distributed to the secondary somites when the latter began to be developed during the course of evolution. Hence, primarily, the entire series of teloblastic somites would appear to have been genital segments.

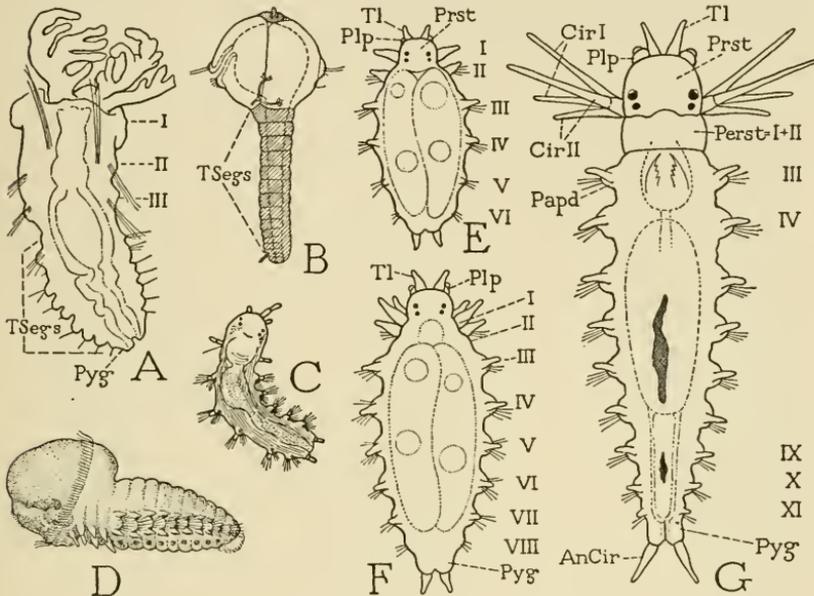


FIG. 12.—Examples of the growth of larval Archiannelida and Polychaeta by proliferation in a subterminal zone of growth of teloblastic segments added to the primary larval body.

A, larva of *Eupomatus uncinatus* with series of teloblastic, or "postlarval," segments (*TSegs*) interpolated between the three primary larval somites (*I*, *II*, *III*, see fig. 7 A, B) and the terminal pygidium (simplified from Iwanoff, 1928). B, larva of *Polygordius neapolitanus* Fraipont during metamorphosis, with series of teloblastic segments added to the trochophoral body, which is itself unsegmented and contains no primary mesoderm (from Woltereck, 1905). C, half-grown young of *Nerilla antennata* Schmidt (from Schlieper, 1925). D, larva of *Lopadorhynchus brevis* Grube with series of teloblastic segments (from Kleinenberg, 1886). E-G, growth stages of "nereidogen" larva of *Platynereis dumerilii* Aud. & Milne-Edw. (from Hempelmann, 1911, see also fig. 7 C, first stage larva).

AnCir, anal cirrus; *CirI*, *CirII*, tentacular cirri of first two somites, united in peristomium; *I-XI*, somites; *Papd*, parapodium; *Perst*, peristomium; *Plp*, palpus; *Prst*, prostomium; *Pyg*, pygidium; *Tl*, prostomial tentacle; *TSegs*, teloblastic segments.

A condition similar at least to that which we should expect to find in the primitive annelids is seen in the archiannelid *Dinophilus* (fig. 13 A). The body of *Dinophilus* consists of six or seven somites clearly defined externally between the prostomium and the pygidium, but there are no coelomic cavities in the diffuse mesoderm of the

somites anterior to the last one, though each of these somites has a pair of simple protonephridia. In the terminal somite are formed the reproductive organs, which, in the female, consist of a delicate gonadial sac, either single or double, extending forward in the body, and opening posteriorly by a median pore, at least at the time of egg laying. The gonadial sac appears to represent the coelom of the last segment, though, as Iwanoff (1928) points out, it may be simply a space accommodating the germ cells in the undifferentiated tissue near the end of the body. Hence, the apparent last somite is either a single teloblastic genital somite, or a region corresponding with the zone of growth of the polymerous annelids.

A concrete example of the secondary distribution of the germ cells in a polymerous annelid is given by Malaquin (1924 a) in his study of the development of *Salmacina dysteri*. The germ cells, as we have seen, are first localized in the growing zone of the young larva. When the formation of the postlarval segments begins, Malaquin says, the germ cells multiply, and three, four, or five of the resulting gonocytes become adherent to the outer wall of each new coelomic sac. Thus the germ cells, proliferated from a constant source, are distributed to the newly forming somites, and are extracoelomic both in their origin and in their secondary segmental positions. After a period of inactivity the segmentally distributed gonocytes begin to multiply in the coelomic walls, and here form the small masses of germinal cells ensheathed in peritoneal folds that are known as the "gonads."

If, now, the ontogenetic facts of annelid growth are given a phylogenetic significance, it becomes evident, as claimed by Iwanoff (1928), that the extension of the worm by the teloblastic generation of new somites, in which are apportioned groups of the multiplying germ cells, was primarily a means of amplifying the reproductive function. In the course of evolution it gave rise to a type of animal from which have been derived the modern Annelida, the Onychophora, and the Arthropoda.

The teloblastic genital segments are in many respects mechanical improvements over the primary segments; their muscular equipment is stronger, the parapodia better constructed for locomotion, the dissepiments usually more complete, and the nephridia more efficient for excretory purposes. Hence, the whole worm is clearly a stronger and a more active animal by reason of the addition of the well-organized reproductive somites. At the bottom of the water the creeping worm is better able to force its way under stones or into crevices, or to burrow into sand or mud; but at the breeding season

its new powers of locomotion come into effective service, for now many modern species that habitually live at the bottom rise to the surface in swarms of energetically swimming individuals, both males and females, and here discharge the matured gametes.

That the genital segments may be of no special physiological importance to the worm, except for carrying, maturing, and distrib-

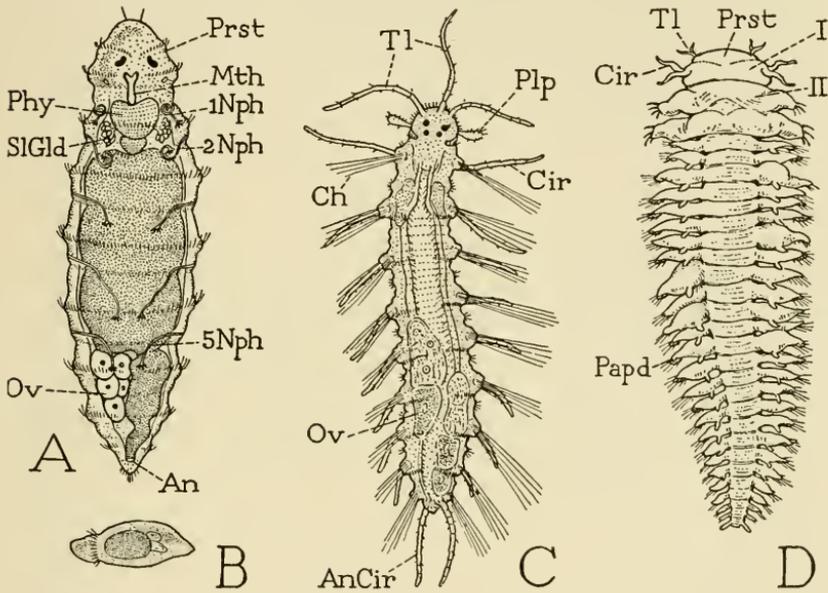


FIG. 13.—Examples of annelid types.

A, B, *Dinophilus*, a very simple archiannelid, perhaps a primitive form, lacking teloblastic somites, tentacles, cirri, chaetae, parapodia, and coelomic sacs; with five pairs of protonephridia, reproductive organs in posterior part of body (A, *D. gyrocoliatius* Schmidt, adult female; B, adult male, from Shearer, 1912). C, *Nerilla*, an archiannelid with polychaete characters, perhaps a degenerate form, having a coelom, open metanephridia, and direct development (fig. 12 C) (*N. antennata* Schmidt, from Goodrich, 1912). D, *Lopadorhynchus*, an errant polychaete (Phyllodocidae), having typical trochophoral development (fig. 8) with metamorphosis (fig. 12 D) producing long series of teloblastic somites (*L. uncinatus* Fauvel).

An, anus; AnCir, anal cirrus; Ch, chaetae; Cir, cirrus; I, II, first two somites; Mth, mouth; Nph, nephridium; Ov, ovary; Papd, parapodium; Phy, pharynx; Plp, palpus; Prst, prostomium; SIGld, salivary gland; Tl, tentacles.

uting the reproductive elements, is shown by the various ways in which the annelids can dispose of these segments without otherwise impairing their functional integrity. There is the well-known case of the palolo worms, *Eunice fucata* and *E. viridis*, for example, which live in crevices of rocks at the bottom of the water, and at the time for spawning detach the rear parts of their bodies, already

loaded with the mature generative elements. The reproductive tail-ends (epitokes) then actively swim to the surface, where myriads of them congregate to liberate the gametes. In their accustomed haunts the anterior nonreproductive sections (atokes) regenerate the discarded epitokes in preparation for next year's consignment to the breeding grounds. Various other species of Polychaeta have similar habits. The Syllidae are famous for the many forms of schizogenesis, strobilation, and budding that take place among them, but here the detached piece, either before or after separation, generates a new head and becomes a complete worm except perhaps for the lack of an alimentary canal and a few other unimportant structures. Again, in some of the Ctenodrilidae the worm breaks up by constriction into several pieces of a few segments each, and the middle pieces regenerate both a head and a tail.

The periodic fragmentation of the body for reproductive purposes, however, cannot lead to anything in the way of constructive evolution, and, with the annelids in general, the tendency has been to integrate the entire series of somites into a mechanical and physiological unit, in which the reproductive cells are assigned to definite segments. In the Arthropoda, though the body may still be composed of freely movable segments, the process of integration has been carried so far, and the various organs so interdependently distributed, that fission becomes impossible without fatal results. It would seem, therefore, that the teloblastic somites, first added apparently for reproductive efficiency, have been found so useful in other ways that they have come to constitute not only the largest part of the body in all the articulate animals, but its most important part, except for the primary sensory and nervous elements contained in the head.

A structural differentiation between groups of somites, forming distinct body regions, or tagmata, has taken place in many of the polychaetes, particularly in the Sedentaria, and is a characteristic feature of all the Arthropoda. The zone of growth, therefore, which presumably at first gave rise to a series of identical somites, has acquired the remarkable faculty of differential activity, producing successively, at definite segment intervals, two or more series of somites having often a strongly contrasting structure, while minor differences may be distributed throughout the entire series of segments.

THE PROSTOMIUM AND ITS APPENDAGES

The annelid prostomium is the part of the trunk that is not invaded by the blastopore as the latter elongates forward on the ventral sur-

face of the embryo (fig. 6 D, *Prst*); in the adult it is reduced to a small lobe overhanging the mouth (fig. 14, *Prst*). Appendages of the prostomium are best developed in the errant polychaetes, where typically they include a pair of anterior tentacles, or "antennae" (*Tl*), with frequently a median tentacle between them, and a pair of more posterior and ventral palpi (*Plp*). The prostomial appendages are clearly not equivalent to the parapodia of the postoral body somites, but they have the same development in the larva as the parapodial cirri (cf. fig. 16, A and B). Since the prostomium usually contains the brain and bears the apical sense organs, it constitutes the "head" of the worm. In the absence of prostomial appendages and sense

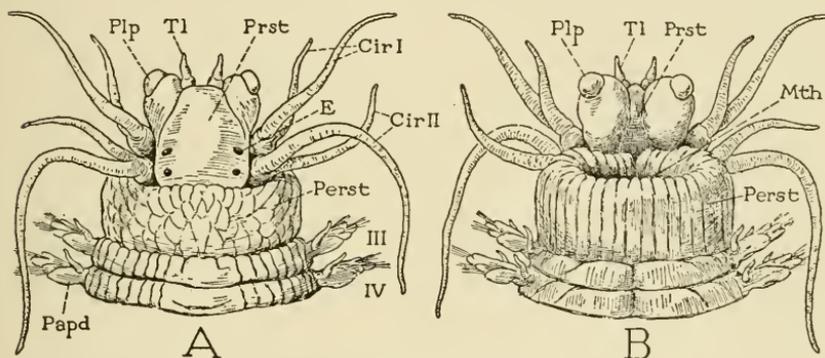


FIG. 14.—Head and anterior body segments of *Nereis virens* Sars. A, dorsal; B, ventral.

Cir I, *Cir II*, tentacular cirri of first and second somites united in peristomium; *E*, eye; *III*, *IV*, third and fourth somites; *Papd*, parapodium; *Perst*, peristomium (somites I and II); *Plp*, palpus; *Prst*, prostomium; *Tl*, prostomial tentacle.

organs, however, the brain may be secondarily withdrawn into the body, as in the earthworms (fig. 17 C, D, *Br*).

The prostomium is not affected by the process of metamerism that cuts the postoral body region into a series of somites. Since the mesoderm bands of the larva do not proceed anterior to the mouth (fig. 6 F), the larval prostomium does not contain mesoderm; but in later stages the mesoderm of the first somite may be extended into the prostomium (fig. 10 A) and give rise to a cephalic coelom and peritoneum (B, *PCoel*). Ordinarily the cephalic mesoderm is not segmented, but according to Binard and Jeener (1928) there is present in the prostomium of the spionid *Scolecopsis fuliginosa* a pair of distinct coelomic sacs, which are continuous with the cavities of the palpi, and have no connection with the coelomic sacs of the first postoral somite. This fact, the authors point out, gives a new argu-

ment in favor of the homology of the polychaete palpi with the tentaclelike antennae of the Onychophora; but evidently it does not prove their further contention (1929) that the palpi are appendages of a secondarily "cephalized" somite, since it must first be demonstrated that coelomic cavities may not pertain to the preoral mesoderm itself.

THE BODY AND ITS APPENDAGES

The body of the annelid is the segmented part of the trunk posterior to the acronal prostomium, including the region of the true somites, the zone of growth, and the pygidium; but the term *soma*, in a restricted sense, would apply literally only to the region of the *somites* between the prostomium and the zone of growth or the pygidium. In the Polychaeta the first two somites are generally united with each other in a double segment known as the *peristomium* (fig. 14, *Perst*), the tentaclelike cirri of which (*CirI*, *CirII*) take an anterior position closely associated with the prostomium. The "cephalization" of the anterior segments in the polychaetes, therefore, contrasts with that in the arthropods, since, with the latter, the first stage of cephalization is a union of the first somite with the prostomium. In the oligochaetes, however, the first somite and the prostomium may unite to form a composite head as in the arthropods.

The fundamental demarcation of the annelid somites is the attachment of the longitudinal muscle fibers of the body wall and the muscles of the dissepiments on transverse circular grooves of the integument; but the coelomic sacs when present are strictly intra-segmental, and most of the ectodermal and mesodermal organs are segmentally repeated. The locomotor mechanism of the annelids consists primarily of the somatic musculature and the regulating nerve ganglia, which give movement to the body wall, but it usually includes external adjuncts in the form of bristles or chaetae, and, in the Polychaeta, lobelike segmental appendages, the parapodia. The annelid body musculature should be the basis of the derived arthropod musculature, but there is reason to doubt that the polychaete parapodia are prototypes of the arthropod legs.

The somatic musculature of the annelids includes the muscles of the body wall, the muscles of the chaetal sacs, and the muscles of the parapodia. The muscle fibers, with possibly rare exceptions, are of the nonstriated type. The musculature of the body wall is of a very simple pattern, so far as the arrangement of the fibers is concerned, but it may attain a strong development in the rapacious polychaetes and the burrowing oligochaetes. The longitudinal muscles

can produce only contraction or lateral undulatory movements of the body; the circular muscles are constrictors producing peristaltic waves of body compression, and longitudinal extension of the body by the creation of internal pressure. The arthropod type of body mechanism, involving intersegmental movement of integumental plates, can be derived from the intrasegmental annelid mechanism only by the establishment of new intersegmental divisions.

The polychaete somatic musculature is well developed in the Nereidae, of which *Nereis virens* may be taken as an example (fig. 15). The outermost layers of body wall muscles consist of fine circular fibers closely adherent to the integument (A, D, 1). Internal to these there may be bands of oblique fibers (D, 2) crossing each other in opposite directions. The largest of the somatic muscles, however, are four thick bundles of longitudinal fibers (A, 3, 4) lying internal to the others, two dorsal and two ventral, the fibers of which are attached on deeply inflected intersegmented folds of the integument (D, *isf*). The longitudinal muscles of the terrestrial oligochaetes are continuous in a thick layer around the entire circumference of each somite, except where they are interrupted by the intrusion of the four chaetal sacs. Besides the muscles of the body wall there is in *Nereis* a double series of paired, obliquely transverse ventral muscles, one pair anterior and the other posterior in each segment (D, 5, 6), which extend outward and upward from the median ventral fold of the body wall (A) to the lateral intersegmental folds between the parapodial bases. The intersegmental folds give attachment also to the transverse or radial muscles of the intercoelomic dissepiments. Most of the other muscles of the body pertain to the chaetal sacs and the parapodia, and will be described in connection with the parapodia.

A typical polychaete parapodium is a lateral outgrowth of the body wall (fig. 15 A, *Papd*), flattened antero-posteriorly, and usually divided into a dorsal lobe and a ventral lobe, which again may be subdivided into secondary lobules. Each major lobe bears distally a fan-shaped group of long chaetae (B, *Ch*), and on its base a slender cirrus (*dCir*, *vCir*). The chaetae arise from the inner walls of chaetal sacs (C, *chS*), from each of which a long rod, the acicula (*Acic*), extends inward to give attachment to protractor and retractor muscles.

The larval rudiments of the parapodia represent the cirri and the chaetal sacs, and are differentiated as cellular bodies within the ectoderm. The rudiments of the cirri, as described by Kleinenberg (1886) and by Meyer (1901) in the larva of *Lopadorhynchus* (fig. 16 B, *dcR*, *vcR*), consist each of an outer layer of myoblasts (*m*) and an inner core of sensory nerve cells (*n*). The cirri in their origin,

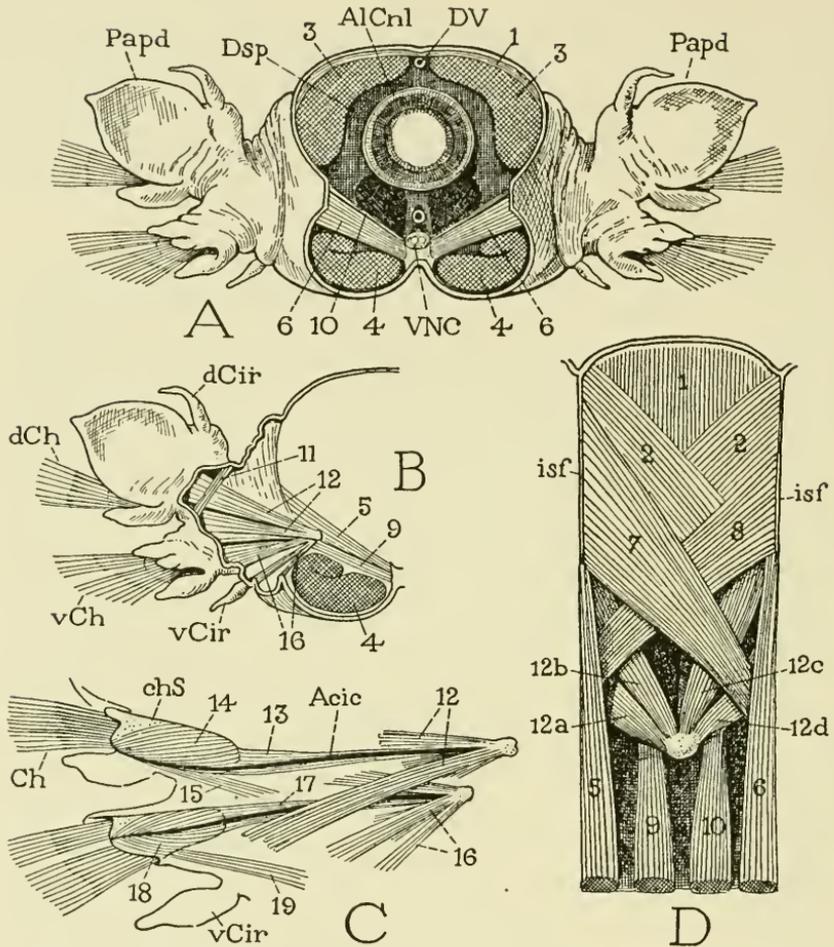


FIG. 15.—The polychaete locomotor mechanism: parapodia, and somatic and parapodial muscles of *Nereis virens* Sars.

A, transverse section of a body segment, posterior view, somewhat diagrammatic. B, a parapodium and its muscles, posterior view. C, chaetal apparatus of a parapodium. D, muscles of right half of a body segment, inner view.

Acic, acicula; *AlCnl*, alimentary canal; *Ch*, chaetae; *chS*, chaetal sac; *Cir*, cirrus; *dCh*, dorsal chaetae; *dCir*, dorsal cirrus; *Dsp*, intersegmental dissepiment; *DV*, dorsal blood vessel; *isf*, intersegmental fold of integument; *Papd*, parapodium; *vCh*, ventral chaetae; *vCir*, ventral cirrus; *VNC*, ventral nerve cord.

1, circular muscles of body wall; 2, oblique muscles of body wall; 3, dorsal longitudinal muscles; 4, ventral longitudinal muscles; 5, 6, anterior and posterior lateroventral, obliquely transverse muscles; 7, 8, dorsal motors of parapodium; 9, 10, ventral motors of parapodium; 11, intrinsic muscle of parapodium between dorsal and ventral lobes; 12, protractors of dorsal acicula and chaetal sac; 13, 14, retractor and protractor of dorsal chaetae; 15, retractor of dorsal chaetal sac and acicula; 16, protractors of ventral acicula and chaetal sac; 17, 18, retractor and protractor of ventral chaetae; 19, retractor of ventral chaetal sac.

therefore, resemble the tentacular rudiments of the prostomium (A), and later they grow out as tentaclelike processes. The bristle sacs are formed as ectodermal cell masses between the cirri (B, *chS*), the outer cells of which become myoblasts, while some of the inner cells enlarge and produce the chaetae; a lumen then appears in the cell mass, and the latter becomes an open eversible sac from which the chaetae protrude. Finally the cirri and the chaetal pouches are carried outward on an outgrowth of the body wall that becomes the principal part of the appendage. The mature parapodia of *Lopadorhynchus* are not of typical form in that each consists of a single lobe (fig. 16 C) with both chaetal sacs at its extremity.

In some of the polychaetes, particularly in the Sedentaria, there are two rows of podial organs on each side of the body (fig. 16 F), those of one series, the notopodia (*dPd*), being situated dorso-laterally, those of the other, the neuropodia (*vPd*), ventrolaterally. Each organ includes a cirrus (*Cir*) and a chaetal sac (*chS*), and is innervated separately from the corresponding podial ganglion (*PdGng*). In the Oligochaeta the podial organs are represented only by the chaetae, which usually are arranged in two separated rows on each side of the body. It is possible, therefore, that the usual two-branched parapodium of the Polychaeta (fig. 15 B) has been formed by the union of a notopodium and a neuropodium. Furthermore, the double composition of each notopodium and neuropodium suggests that the primitive polychaetes had dorsolateral and ventrolateral rows of cirri, and between them on each side two series of chaetal sacs. On the peristomial segments of adult polychaetes generally only the cirri are present (fig. 14 A, *CirI*, *CirII*), but on the rest of the body segments the chaetae-bearing lobes are usually the more important podial elements.

The musculature of a parapodium is somewhat complex: it includes extrinsic muscles that move the appendage as a whole, and intrinsic muscles concerned principally with the movement of the chaetae. In *Nereis virens* there are four extrinsic muscles for each parapodium, two dorsal (fig. 15 D, 7, 8), and two ventral (9, 10). The dorsal muscles arise anteriorly and posteriorly on the body wall, but cross each other obliquely to opposite margins of the parapodial base. The ventral muscles take their origins on the median infold of the ventral wall of the body segment (A), and extend laterally and dorsally, above the ventral longitudinal body muscles (4), to the anterior and posterior margins of the base of the parapodium. If the dorsal and ventral muscles inserted anteriorly act in opposition to those inserted posteriorly, the parapodium is moved anteriorly and posteriorly on

the vertical axis of its base, and this is the usual motion of the appendage; but the latter can also be lifted and depressed, and the up-and-down motion evidently results from an antagonistic action

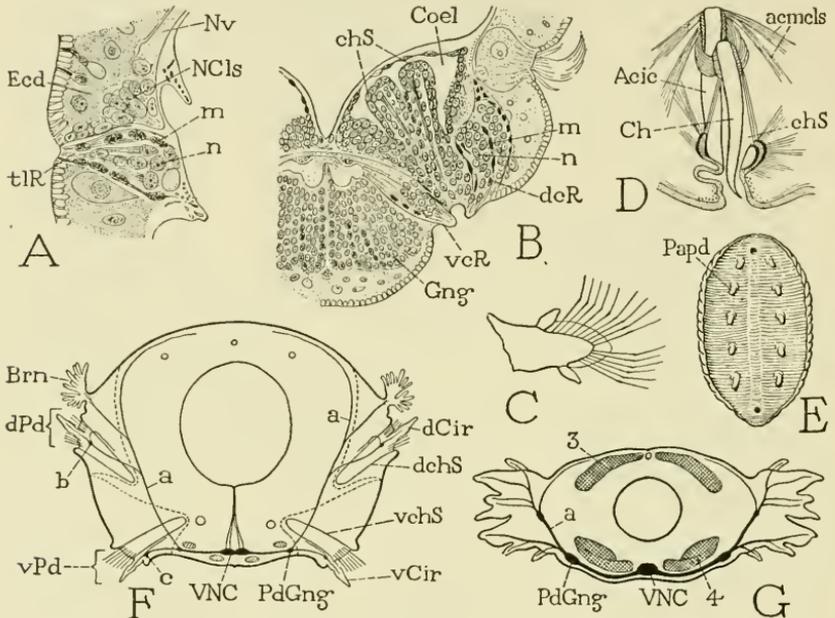


FIG. 16.—Development, structure, and innervation of the polychaete appendages.

A, section through larval rudiment of persistent dorsal tentacle (*tlR*) of trochophore of *Lopadorhynchus* (from E. Meyer, 1901). B, transverse section of larva of *Lopadorhynchus* through rudiments of a pair of chaetal sacs (*chS*) and associated cirri (from Meyer, 1901). C, parapodium of adult *Lopadorhynchus*. D, structure of the armature of a parapodium of *Myzostomum asteriae* Marinzeller, diagrammatic (from Stummer-Traunfels, 1903). E, a myzostomid, ventral view, showing parapodia. F, diagrammatic section of an amphinomid, *Hermodice carunculata* Pallas, showing widely separated notopodia (*dPd*) and neuropodia (*vPd*) and their innervation (from Storch, 1913). G, section of *Nereis virens* Sars, showing innervation of parapodia (from Hamaker, 1898).

a, lateral nerve from podial ganglion; *Acic*, acicula; *acmcls*, acicular muscles; *b*, notopodial ganglion; *Brn*, branchia; *c*, neuropodial ganglion; *Ch*, chaeta or chaetae; *chS*, chaetal sac; *Coel*, coelom; *dCir*, dorsal cirrus; *dcR*, dorsal cirrus rudiment; *dPd*, notopodium; *Ecd*, ectoderm; *Gng*, ventral ganglion; *m*, primary muscle cell; *n*, primary neural cell; *NCLs*, nerve cells; *Nv*, nerve; *Papd*, parapodium; *PdGng*, podial ganglion; *tlR*, rudiment of tentacle; *vcR*, ventral cirrus; *vcR*, ventral cirrus rudiment; *VNC*, ventral nerve cord; *vPd*, neuropodium; *3*, dorsal muscles; *4*, ventral muscles.

between the dorsal and ventral muscles. The intrinsic muscles of the parapodium include protractors and retractors of the chaetal sacs. The principal protractors (B, C, 12, 16) converge from the parapodial walls upon the inner ends of the acicular processes of the sacs (B,

C, D), but the sacs themselves are eversible by muscles in their own walls (C, 14, 18). A retractor (15, 19) arising within the parapodium is inserted on the distal part of each chaetal sac, and a muscle (13, 17) from the acicula, attached on the base of the sac, opposes the muscles (14, 18) that evert the sac itself.

The parapodia are subject to numerous structural modifications in the different groups of Polychaeta, and among the specialized types the small leglike parapodia of the Myzostomidae (fig. 16 E) are of particular interest because of their resemblance to the legs of Onychophora. Each myzostomid appendage, as described by Stummer-Traunfels (1903), contains a deep apical pouch (D, *chs*), from the inner end of which a large hooked process (*Ch*) projects outward, while from its distal wall a thick rod (*Acic*) extends inward and gives attachment to protractor muscles (*acmcls*) and muscles inserted on the base of the hook. It is evident that the hook is a single, greatly enlarged chaeta, and the internal arm an acicula. The myzostomid "leg," therefore, is only a modified parapodium adapted for clinging to the crinoid hosts on which the Myzostomidae live, and has only a superficial likeness to the appendages of Onychophora (fig. 31).

THE NERVOUS SYSTEM

The central nervous system of the Polychaeta, as shown in the larval development, is produced from separate prostomial and somatic rudiments, which secondarily become united (fig. 9); in the Oligochaeta the two parts are said to be continuous from their inception. The definitive brain, whether formed from discrete ganglionic centers, as in *Lopadorhynchus*, or from a single generative zone of the prostomial ectoderm (fig. 10 A, B, *Br*), is always a compact organ, though it is generally bilobed (fig. 17 A) or differentiated into several consecutive parts (fig. 18 C). The ventral nerve cords in the more primitive condition found in most of the archiannelids and in various polychaete and oligochaete families are entirely separate, except for their connection by commissures (fig. 19 A, B), and in such cases the nerve tissue usually preserves a close contact with the ectoderm from which it is derived (C). More commonly, however, the paired ganglia of the cords are united in single median ganglia (fig. 17 C, D), giving the cords themselves a median position; but even in such cases the ganglia of one or more pairs carried by the divergent anterior ends of the cords may remain widely separated. The first pair of united ganglia on the cords constitutes the so-called "suboesophageal ganglion," but it is evident that this ganglion does not belong always

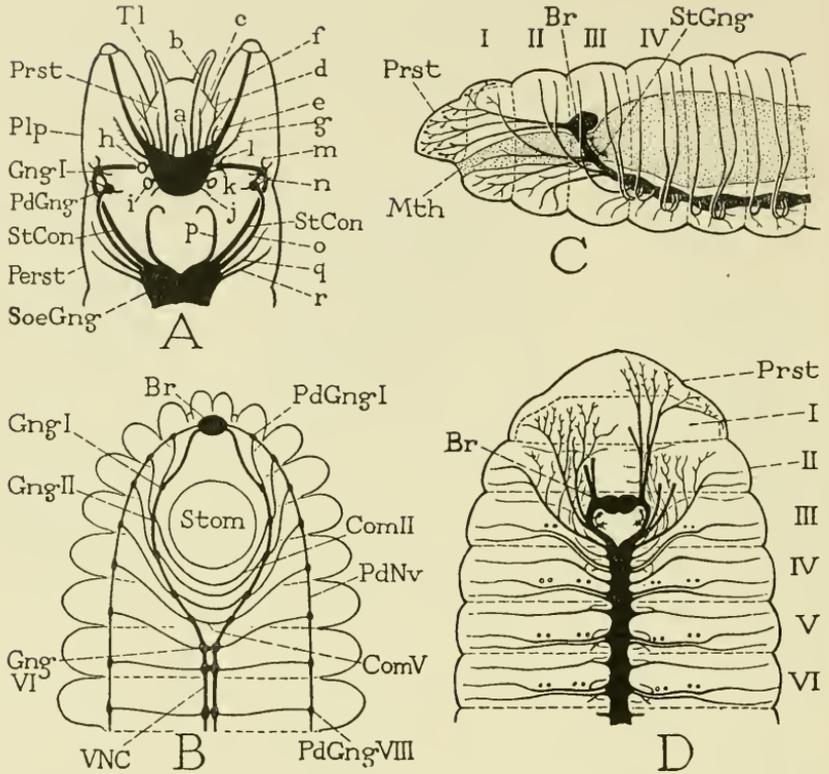


FIG. 17.—Nervous system of Annelida.

A, anterior nervous system of *Nereis virens* Sars, diagrammatic, showing nerves of cerebral and suboesophageal ganglia (adapted from Hamaker, 1898). B, anterior nervous system of an amphinomid, *Hermodice carunculata* Pallas, showing podial nerves (*PdNv*) from brain connecting the podial ganglia, and divergence of ventral nerve cords (*VNC*) through several somites around stomodaeum (from Gustafson, 1930). C, anterior nervous system of *Lumbricus terrestris* Linn., lateral view, showing retraction of brain into third somite (simplified from Hess, 1925). D, same, dorsal view (from Hess, 1925).

Br, brain; *ComII*, *ComV*, commissures of second and fifth somites; *GngI-GngVI*, central ganglion of first to sixth somites; *I-VIII*, first to eighth somites; *Mth*, mouth; *PdGng*, podial ganglion of second peristomial cirri; *PdGngI*, *PdGngVIII*, podial ganglia of first and eighth somites; *PdNv*, podial nerve; *Perst*, peristomium; *Plp*, palpus; *Prst*, prostomium; *SoeGng*, suboesophageal ganglion; *StCon*, stomodaeal nerve connective; *StGng*, stomodaeal ganglion; *Stom*, stomodaeum; *Tl*, tentacle.

Nerves of Nereis (fig. A): *a*, nerve to stomodaeum; *b*, tentacle nerve; *c*, *d*, nerves to muscles and prostomial integument; *e*, nerve to proboscis; *f*, palpus nerve; *g*, tegumentary nerve; *h*, *i*, ocular nerves; *j*, nerve to nuchal organ; *k*, commissural ganglion; *l*, *m*, nerves to proboscis; *n*, connective between peristomial ganglia; *o*, nerve to second peristomial ganglion (podial ganglion, *PdGng*); *p*, nerve to proboscis; *q*, *r*, nerves to muscles and integument of peristomium.

to the same somite, and, furthermore, it sometimes contains the ganglia of more than one somite. In the polychaete family Amphinomidae there is, in addition to the median nerve cords, a pair of lateral cords extending posteriorly from the brain (fig. 17 B, *PdNv*), which unite the series of podial ganglia (*PdGng*) lying at the bases of the parapodia (see Storch, 1912, 1913, Gustafson, 1930). The tetra-neurous structure is regarded by Storch as representing the more primitive condition of the annelid nervous system, though Gustafson contends that it is probably secondary. According to a theory proposed by Jeener (1928) the lateral line system represents a primitive series of neuromuscular sensory organs, from which there has been preserved and developed in the Sedentaria the sensorial elements, in the Errantia the ganglionic elements, and in the Oligochaeta the muscular elements.

The annelid brain in its simplest form probably consists of a homogeneous mass of neurocytes aggregated upon a fibrous commissure continuous on each side with the stomodaeal connectives, and through the latter with the ventral nerve cords (fig. 19 A, B, *Br*). With higher development, however, specialized groups of cells appear in the cortex, and specific tracts of fibers are individualized in the neuropile. A very simple brain structure occurs in the archiannelid *Polygordius* (fig. 18 A), in which, according to Hanström (1929), a pair of glomerulous association centers (*PlpGlm*) receive the roots of the palpal nerves and are connected by a palpal commissure (*PlpCom*). The peripheral sense cells of the palpi form ganglionlike masses (*SCLs*) at the bases of the appendages. Two posterior lobes of the brain (*NL*) are connected with the nuchal organs, but eyes and anterior tentacles are absent in *Polygordius*.

In the active polychaetes, in which cephalic tentacles, palpi, eyes, and nuchal organs are well developed, the brain takes on a more complex form and may acquire a high degree of differentiation in its internal organization. Particularly conspicuous are the paired cellular and fibrous masses known as corpora pedunculata. Each of these bodies consists of a cap of small chromatic cells lying in the upper anterior part of the cortex (fig. 18 B, E, *Gb*), and of a stalk, or pedunculus (*Ped*), composed of the neurites of the cap cells, which penetrate the central part of the brain. Within the stalks the terminals of the neurites (*B, d*) form synaptic associations between fibers from all other parts of the brain and from the ventral nerve cords (*a, b, c*). A simple development of the corpora pedunculata is shown by Hanström (1927) to occur in the Hesionidae (fig. 18 D), in which the caps consist each of a single globulus of cells, and the stalks are

connected by a fibrous commissure. In most of the other errant polychaetes the corpora pedunculata are more highly developed, and the cap cells become segregated into two or three distinct globuli (E, F). On the other hand, in the sedentary polychaetes with reduced cephalic

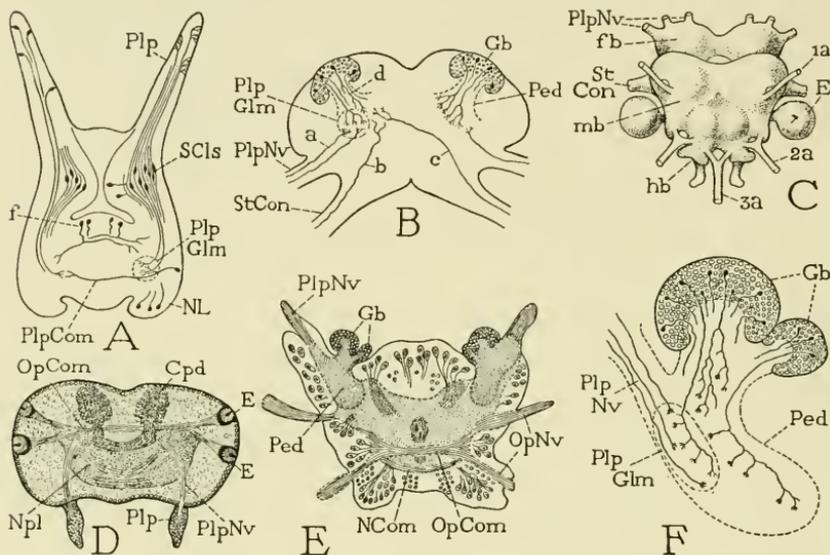


FIG. 18.—Structure of the brain in Archiannelida and Polychaeta.

A, outline of head and diagram of simple brain structure in *Polygordius* (from Hanström, 1929). B, horizontal section of brain of *Sthenelais picta* Verrill (*Aphroditidae*), diagrammatic (from Hanström, 1927). C, brain of *Eunice punctata* Risso (*Eunicidae*), showing high degree of external differentiation (from Heider, 1925). D, transverse section of brain of *Podarke obscura* Ehlers (*Hesionidae*) through corpora pedunculata (from Hanström, 1927). E, horizontal section of brain of *Nereis virens* Sars (*Nereidae*) showing internal structure (from Hanström, 1927). F, diagram of a corpus pedunculatum of *Nereis virens* (from Hanström, 1927).

a, sensory fibers of palpus nerve; 1a, 2a, 3a, nerves of lateral and median prostomial tentacles; b, c, fibers of stomodaeal connectives; d, axons of globuli cells of corpus pedunculatum; E, eye; f, central neurocytes in anterior part of brain; fb, forebrain; Gb, globulus of corpus pedunculatum; hb, hindbrain; mb, midbrain; NL, nuchal lobe; NCom, nuchal commissure; OpCom, optic commissure; OpNv, optic nerve; Ped, pedunculus of corpus pedunculatum; Plp, palpus; PlpCom, palpal commissure; PlpGlm, palpal glomeruli; PlpNv, palpal nerve; SCLs, sense cells of palpus; StCon, stomodaeal connective.

sense organs, the corpora pedunculata are correspondingly reduced or are vestigial, and in the Oligochaeta they are absent.

The development of the corpora pedunculata in the Polychaeta is clearly correlated with the development of the prostomial sense organs, but the particular relationships of the bodies are with the sensory nerves of the palpi. It is shown by Hanström (1927, 1928, 1929) in

the Hesionidae (fig. 18 D), the Aphroditidae (B), the Nereidae (E, F) and other errant families, that the roots of the palpal nerves are closely associated in glomerulous bodies with the stalks of the corpora pedunculata, which fact, Hanström points out, clearly suggests that the corpora pedunculata had their inception as association centers for the sensory nerves of the palpi. Much importance attaches to a study of the corpora pedunculata in connection with annelid and arthropod phylogeny, because bodies very similar in position, structure, and variations are characteristic features also of the brain of Onychophora and Arthropoda.

The relative positions of the principal internal structures of the polychaete brain, it should be noted for later comparison with the onychophoran and arthropod brain, are as follows: Anteriorly and dorsally are the corpora pedunculata (fig. 18 B, D, E); closely associated with the stalks of the latter are the palpal glomeruli (A, B, F, *PlpGlm*), and the glomeruli are connected by a palpal commissure; behind the corpora pedunculata is the optic commissure (D, E, *OpCom*); and in the posterior part of the brain are the nerve centers of the nuchal organs and a nuchal commissure (E, *NCom*). The stomodaeal connectives attach to the ventral surface of the brain.

The number of nerves given off from the brain is highly variable according to the development of prostomial sense organs. In *Polygordius* (fig. 18 A) there is but a single pair of cerebral nerves, which innervate the tentaclelike palpi, while in such forms as *Nereis* (fig. 17 A) an elaborate innervation of the prostomial walls, the sense organs, and the stomodaeum proceeds from the brain.

The principal stomodaeal nerves of the Polychaeta arise in some families from the first ganglia of the ventral nerve cords, or from the brain connectives near these ganglia, while in others they come from the upper parts of the connectives or from the back of the brain. It is contended by Hanström (1927, 1928), therefore, that in the second case the primitive first ganglia of the cords have been drawn forward and united with the brain, forming thus in certain polychaete families a posterior part of the definitive brain corresponding with the tritocerebral lobes of the arthropod brain, which always have connections at least with the stomodaeal (stomatogastric) system of nerves.

The stomodaeal innervation of the Polychaeta is most elaborate in those forms that have a large and eversible stomodaeal proboscis, and in such cases the innervation of the organ may be derived from so many sources that the evidence adduced in favor of Hanström's theory is not convincing. In *Nereis*, for example, Hamaker (1898) describes

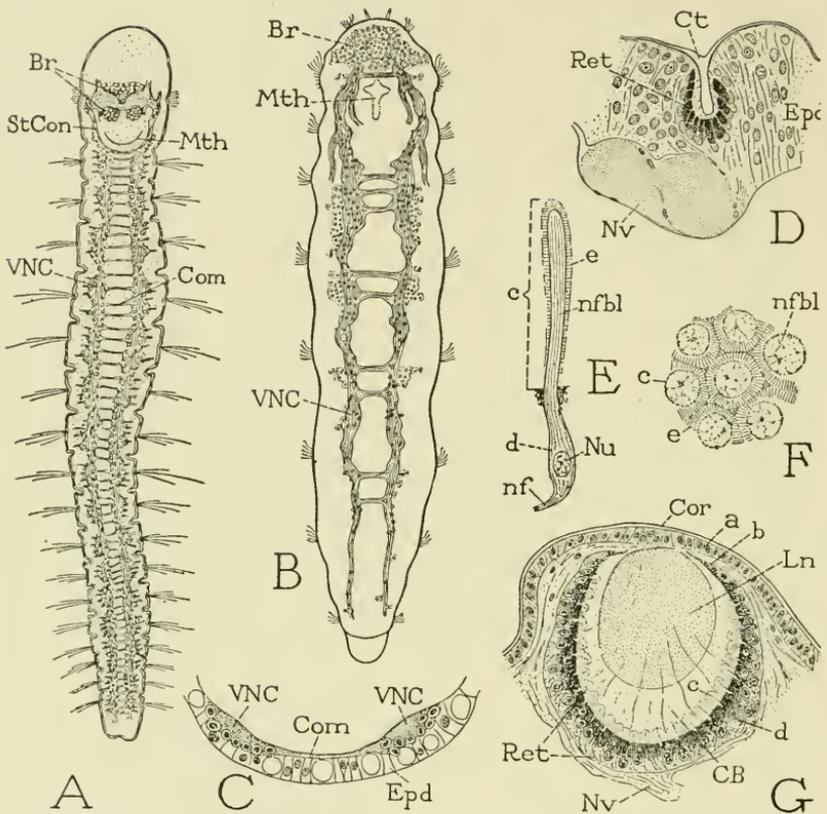


FIG 19.—Examples of generalized structure in the annelid nervous system, and the structure of the annelid eye.

A, the "rope-ladder" type of nervous system in an oligochaete, *Acolosoma tenebrarum* (from Brace, 1901). B, same in an archiannelid, *Dinophilus conklini* Nelson (from Nelson, 1907). C, cross-section of ventral body wall of *Acolosoma tenebrarum*, showing nerve cords not separated from epidermis (from Brace, 1901). D, vertical section of an eye of primitive structure in a chaetopterid, *Ranzania sagittaria* Claparède (from Hesse, 1899). E, diagram of a typical annelid retinal cell (based on Pflugfelder, 1932). F, cross-section of optic rods of retina of *Heteronereis* sp. (from Pflugfelder, 1932). G, vertical section of eye of a nereid, *Lycastis* sp. (from Pflugfelder, 1932).

a, outer layer of epidermis over eye; b, inner layer of epidermis forming ocular vesicle (see fig. 28 C, D, E); Br, brain; c, optic rod of sensory retinal cell; CB, crystalline body; Com, nerve commissure; Cor, cornea; Ct, cuticula; d, cell body of sensory retinal cell; e, striated border of retinal optic rod; Epd, epidermis; Ln, lens; Mth, mouth; nf, nerve fiber; nfbl, neurofibrillae; Nu, nucleus; Nv, nerve trunk; Ret, retina (including sensory and supporting cells); StCom, stomodaeal connective; VNC, ventral nerve cord.

five pairs of stomodaeal nerves, two pairs of which proceed from the anterior part of the brain (fig. 17 A, *a*, *c*), a third pair (*l*) from small ganglia on the upper ends of the stomodaeal connectives, a fourth (*m*) from the ganglia of the first peristomial cirri, and a fifth (*p*) from the suboesophageal ganglion. In the earthworm, *Lumbricus*, the stomodaeal innervation arises from the connectives between the brain and the first ganglia of the cords (fig. 17 C, *StGng*). Other examples would only show further inconsistencies in the origin of the nerves that supply the annelid stomodaeum. We can, therefore, most readily agree with Gustafson (1930), who concludes that no homology exists between the stomodaeal nervous system of the Annelida and that of the Arthropoda. Gustafson points out, furthermore, in reference to Hanström's theory of transposed ganglia, that there is no concrete evidence of the transfer of a pair of ventral ganglia to the brain in any of the annelids, whereas in the arthropods there is conclusive proof that the tritocerebral ganglia have been secondarily united with the brain. In the higher arthropods, moreover, the ganglia of the stomodaeal nervous system are derived directly from the ectodermal wall of the stomodaeum itself, and their definitive nerve connections with the central system appear to be secondary.

THE EYES

Light-receptive organs in the form of eyes are widely present in the Polychaeta. The polychaete type of eye is fundamentally a vesicular ingrowth of the integument (fig. 28 C, D, E), the retinal cells being epithelial cells of the vesicle wall converted into primary sense cells by the extension of their inner ends as nerve fibers. In the simpler forms of eyes the cuticula may form a mere plug in the cavity of the retinal sac (fig. 19 D), but usually the ingrown part of the cuticula is enlarged and becomes a lenslike body, either connected with the surface by a cuticular strand, or entirely shut in by the union of the lips of the retinal sac (G, *Ln*). The outer ends of the retinal cells form optic rods, converging upon the inner surface of the lens (E, G, *c*), which contain the distal parts of the neural fibrillae (E, *nfb*), but the apposed surfaces of adjacent rods do not form rhabdoms (F), as they do in the Arthropoda.

THE NEPHRIDIA AND THE GENITAL DUCTS

The most primitive excretory organs of the annelids are the *protonephridia* of trochophore larvae. These are minute tubes, one or two pairs, extending from the body wall into the haemocoel, where they

end blindly, but may be branched; each tube or each branch terminates with a cell that sends a long vibratile flagellum into the lumen of the tube. The larval protonephridia are apparently of ectodermal origin, being said to be formed from primary nephroblasts derived from cells of the third quartet of blastomeres; their structure is essentially that of the "flame cell" tubes of the excretory canals of the Platyhelminthes. Since the larval nephridia are present before the coelomic sacs are formed, they lie within the primary body cavity, which later becomes the haemocoel.

A type of closed nephridium resembling the larval nephridia, and therefore often called a protonephridium, occurs in the five pregenital somites of the archiannelid *Dinophilus* (fig. 13 A), and in the post-larval somites of several families of Polychaeta. The closed nephridia of the adult worm, however, are more highly developed excretory structures than the larval organs, and usually have a more complex end apparatus of tube-cells (solenocytes), which contain long filaments resembling the flagella of the larval nephridia, but said to be nonmotile. The nephridial canal has a simple structure, and its lumen is ciliated. These nephridia project into the coelomic cavities, but, inasmuch as they are ensheathed in folds of the peritoneum, they lie morphologically in the haemocoel. Because of the similarity of their structure to that of the larval nephridia, the closed nephridia of the adult are supposed also to be of ectodermal origin, but their development apparently has not been studied.

The usual adult excretory organ, occurring in most Archiannelida and Polychaeta, and in all Oligochaeta, is of the type called a *metanephridium*. The characteristic feature of a metanephridium is the presence of an inner opening, or nephrostome, by which the nephridial canal communicates with the coelom. Solenocytes in this case are absent. The nephrostome may be a simple ciliated aperture, as in the archiannelids, but more commonly it has the form of a wide, open, ciliated funnel. Unless coelomic dissepiments are absent, the nephrostome always lies in the anterior lamella of the dissepiment before the somite in which the canal opens to the exterior. The canal thus appears to traverse the coelomic cavity behind the funnel, but morphologically it is extracoelomic, since it is ensheathed in a peritoneal fold produced from the posterior lamella of the dissepiment bearing its funnel. A closed nephridium is without doubt strictly an excretory organ, but an open nephridium may serve both for the removal of excretory products and for the discharge of the gametes from the coelom.

The reproductive elements of the annelids are liberated in various ways. In some of the Archannelida and Polychaeta there is no anatomical provision for the discharge of the sex products from the coelomic sacs, and in such cases the gametes escape by a rupture of the body wall or by fission of the rear part of the body. With certain polychaetes having closed nephridia, a funnel-shaped structure is developed in the genital somites on the anterior surface of the septum, which at maturity opens into the canal of the nephridium, and serves as an outlet for the gametes; but again in others the funnel, though present, is a mere "ciliated organ" of the coelomic peritoneum, not known to acquire an opening. Special genital ducts with an internal funnel and an external aperture are present in only a few Polychaeta, as in some of the Capitellidae, but they are characteristic features of the genital segments of Oligochaeta and Hirudinea. In most of the Polychaeta the nephridial funnels serve for the discharge of the gametes.

The relationship of the various types of annelid excretory organs and genital ducts to one another is difficult to understand. According to the well-known theory of Goodrich (1898-1900), nephridia and genital ducts, or coelomoducts, originally formed two separate series of segmental organs, and are still retained as such in Oligochaeta, Hirudinea, and certain Capitellidae. In the majority of the Polychaeta, however, Goodrich claimed, the genital funnel has lost its own duct and its funnel has united with the mouth of the nephridium, intermediate stages being suggested in some forms where there is a partial fusion between the funnel and the nephrostome.

The study of the development of the open nephridia has given rise to much difference of opinion as to the origin of the nephridial rudiments. The earlier investigators, such as Hatschek and Vejdovsky, regarded the nephridial funnels and canals as mesodermal structures, but Whitman (1886) claimed that the nephridia of the leech *Clepsine* are entirely of ectodermal origin. Wilson (1889), in his work on the development of *Lumbricus*, described the nephridial canals as being apparently ectodermal structures, developed from continuous rudiments formed from the second and third rows of ectodermal cells of the germ band, though he admitted they might be mesodermal; the funnels, however, he said are derived separately from the anterior walls of the coelomic septa. Staff (1910) asserted also that the nephridial canals are ectodermal products in *Criodrilus*, but are formed from only the second row of cells in the germ band; and Tannreuther (1915) claimed the nephridia of *Bdellodrilus* have the same origin, though he did not follow their complete development.

On the contrary, nearly all other investigators have stoutly maintained that both the funnels and the canals are mesodermal, though some regard these two parts as derived from separate rudiments. In this class may be mentioned E. Meyer (1887, *Psymobranchnus*), Bergh (1888, *Criodrilus*, 1890, *Lumbricus*, 1899, *Rhynchelmis*), Bürger (1891, *Nephelis*, 1894, *Hirudo*, *Aulastomum*), Michel (1898, *Allolobophora*), Lillie (1906, *Arenicola*), Bychowsky (1921, *Clepsine*), Penners (1924, *Tubifex*), and A. Meyer (1929, *Tubifex*). Only Bergh is insistent that the entire nephridium is mesodermal; most of the others admit that a terminal part, perhaps including the reservoir, may be formed from the ectoderm.

According to Lillie, the nephridia of the polychaete *Arenicola cristata* are gradually differentiated in the somatic mesoderm, starting from the posterior angles between the septa and the body wall, but the mesoderm in early stages of somite formation presents no cell boundaries. The lumen of each organ appears as a minute intracellular canal, which from its inception opens through the dissepiment into the preceding coelomic cavity. Later, as the nephridial cells divide, the lumen becomes intercellular, and finally it opens posteriorly through the ectoderm. Lillie says, however, that there is no invagination of the ectoderm, and no specific evidence that the reservoir is an ectodermal formation.

Those writers who claim that the nephridia of the Oligochaeta and Hirudinea are of mesodermal origin agree essentially with Bergh that each organ is formed from a single cell of the anterior lamella of an intersegmental septum. According to A. Meyer (1929), for example, the nephridioblasts of *Tubifex* are early differentiated from the other cells of the septa by their large size (fig. 20 A, *Npbl*). By successive divisions of the nephridioblast a column of cells is formed that pushes backward within a sheath of ordinary epithelial cells derived from the posterior lamella of the septum (B-E). The young nephridium extends in a space between the somatopleure and the longitudinal muscles, and is thus *extracoelomic*. The lumen appears first as an intracellular canal, which later becomes intercellular by a radial division of the cells; it is ciliated from an early stage. Posteriorly the canal ends against an epidermal cell (G), through which it eventually opens to the exterior, and from which is later generated the reservoir. The coelomic funnel is formed by the original teloblast, the nucleus of which divides into four nuclei, one taking a position in the dorsal lip of the funnel, the other three in the ventral lip (H, I). According to Bergh (1899) only the lower lip of the funnel in *Rhynchelmis* is derived from the nephridioblast, the upper

lip being formed from a neighboring group of septal cells. In *Clepsine*, Bychowsky (1921) says, the first division of the nephridioblast is in the plane of the dissepiment, and gives rise to an anterior cell that forms the funnel and the adjacent part of the canal, and a posterior cell that generates the rest of the canal. The latter opens finally to the exterior through an ectodermal invagination. Bergh

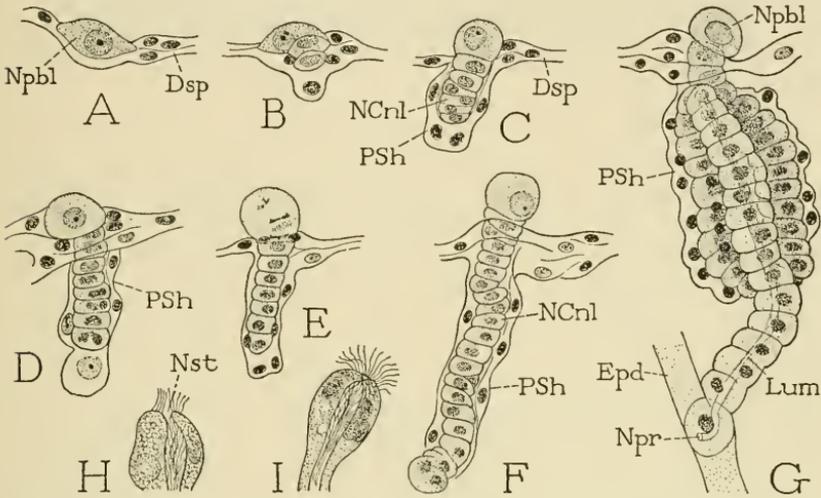


FIG. 20.—Successive early stages in the development of the posterior nephridia of the oligochaete *Tubifex rivulorum* Lam. (From A. Meyer, 1929.)

A, a primary nephridioblast developed from a cell of the anterior lamella of a dissepiment. B, proliferation of nephridial cells by transverse division of the nephridioblast. C-F, successive extensions of the nephridial canal within a peritoneal sheath derived from the posterior lamella of the dissepiment; the canal acquires first an intracellular lumen. G, the canal still more elongate and looped upon itself, attached posteriorly to an epidermal cell, through which the lumen penetrates to the exterior, and which later forms the nephridial bladder. H, I, two stages in the final development of the nephrostome in the primary nephridioblast by radial division of the nucleus.

Dsp, dissepiment; *Lum*, lumen; *NCnl*, nephridial canal; *Npbl*, nephridioblast; *Npr*, nephropore; *Nst*, nephrostome; *PSh*, peritoneal sheath.

claims that there is no ectodermal element in the nephridium of *Criodrilus*, *Rhynchelmis*, or *Lumbricus*.

It thus appears to be now well established that the metanephridia of the annelids in general are structures of the nature of coelomoducts, formed principally as outgrowths of the posterior walls of the coelomic sacs, but perhaps including a terminal part of variable extent derived from the ectoderm. They are extracoelomic, inasmuch as each nephridial canal is invested in a fold of the coelomic peritoneum. The nephridial organs have always been important subjects in dis-

cussions of relationships between the Annelida, the Onychophora, and the Arthropoda. The onychophoran nephridia, however, are developed as simple diverticula of the ventral walls of the coelomic sacs, which connect with short ectodermal ingrowths of the same segments situated mesad of the leg bases, and the nephridial organs of the arthropods most probably have had the same genesis as the onychophoran organs. Hence, it is possible that the coelomic exits have had an independent origin in the higher Annelida on the one hand, and in the common ancestors of the Onychophora and Arthropoda on the other.

V. THE ONYCHOPHORA

Somewhere from a generalized annelid stock there must have branched off in remote pre-Cambrian time the ancestors of the group of animals that includes the modern Onychophora (fig. 21 A), the Cambrian *Aysheaia* (B), and the pre-Cambrian *Xenusion* (C). The primitive onychophorons undoubtedly were segmented, wormlike creatures, in which coelomic sacs and the basic features of the annelid muscular and nervous systems had long been established, and in which the body had been lengthened by the addition of a series of reproductive somites generated from the posterior zone of growth. A distinctive feature of the Protonychophora, however, was the possession of movable locomotor appendages having the form of small lobelike outgrowths of the body wall along the lateroventral lines of the segments. The ancestors of the lobopod Onychophora, and the ancestors of the chaetopod Annelida, therefore, probably constituted two divergent branches from a generalized annelid stock. The primitive chaetopods were creeping worms that progressed by the usual vermiform movements of the body, produced by the body musculature with the aid of integumental chaetae. The primitive onychophorons became distinguished as walking worms, a character well expressed in the name *Peripatus* (Guilding, 1826) given to the first-described modern form. The walking habit led to the adaptation of the modern Onychophora to life on land, but the older forms, such as *Aysheaia* and *Xenusion*, may have been inhabitants of the ocean.

A typical onychophoron is a slender wormlike creature with a pair of tentacular antennae at the anterior end of the trunk, and a double row of short, conical, lateroventral legs along the length of the body (fig. 21 A). The trunk is cylindrical or somewhat depressed, blunt anteriorly, and tapering posteriorly. The rough integument is closely ringed, but there is no external sign of segmentation except for the series of appendages. The animal has no distinct head; the anterior

part of the trunk, however, forms a cephalic lobe (D, E) bearing the antennae, a pair of small dorsal eyes (E, E) just behind the antennal bases, and on the ventral surface the mouth (D). The mouth, which is a triangular opening into the stomodaeum, is sunken into a preoral cavity surrounded by an integumental circumoral fold

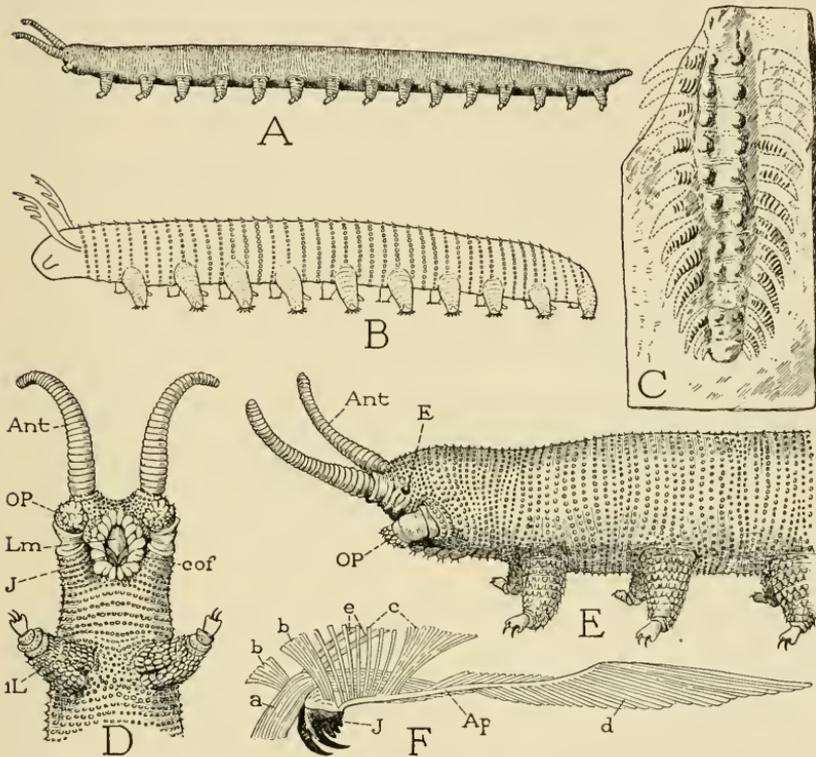


FIG. 21.—Onychophora, ancient and modern.

A, *Peripatoides novae-zealandiae* Hutton. B, *Aysheia pedunculata* Walcott (1911), of Middle Cambrian, British Columbia, "conjectural restoration" (from Hutchinson, 1930). C, *Xenusion auerswaldi* Pompeckj (1927), of Algonkian, proterozoic pre-Cambrian (from Heymons, 1928, broken lines hypothetically completing lacking parts). D, *Peripatoides novae-zealandiae*, anterior part of trunk, ventral view. E, same, head and anterior part of body, lateral view. F, same, right jaw, dorsal view, with muscles.

a-d, jaw muscles; Ant, antenna; Ap, apodeme of jaw muscles; cof, circumoral fold; E, eye; J, jaw; iL, first leg; Lm, labrum; OP, oral papilla.

(cof). Within the preoral cavity is a small anterior labral lobe (Lm), and a pair of flat, two-hooked jaws (J) that converge posteriorly at the sides of the mouth. On the sides of the head, laterad of the mouth, is a pair of oral papillae (E, D, Op) that give vent to a pair of large, many-branched slime glands widely spread in the

body cavity (fig. 32 A, *SlmGld*). The following appendages are the legs, varying in number with different species from a minimum of 13 pairs to an average of perhaps 25 or 30 pairs, though some species have 40 or more. Behind the last legs the body tapers to a terminal cone on which is situated the anus. The genital aperture in each sex is a median ventral opening lying either between the legs of the last pair, or behind the last pair present in species having one or two of the posterior pairs of legs absent.

EARLY STAGES OF DEVELOPMENT

Were it not for the evidence of annelid relationships shown in the adult structure of the Onychophora, we should have little reason for believing that the onychophorans are descended from Annelida, for in their ontogeny we encounter none of the familiar early phases of development so characteristic of the annelids. Most of the Onychophora are viviparous, the embryos developing to maturity in uterine chambers of the oviducts (fig. 32 A, *Utrs*); only a few species are known to be oviparous. Eggs supplied with a large quantity of deutoplasm complete their development from their own store of yolk, but the embryos of viviparous species with small eggs receive nourishment from the uterine walls, and in some cases a placentalike growth of the blastoderm forms a large vesicular trophoblast applied to the walls of the uterus.

The early stages of onychophoran development are so variable in different species that it is impossible to give any general account of the processes of cleavage and germ-layer formation. Cleavage in some species with small eggs is holoblastic, producing first a solid morula and then a hollow blastula (see Sclater, 1888). Contrary to what we might expect, however, gastrulation in such cases does not take place by invagination. In *Peripatus imthurni*, as described by Sclater, an internal proliferation of cells proceeds from a definite point on the blastula, and the cells thus produced become differentiated into endoderm and mesoderm. A similar method of endoderm-mesoderm formation is described by Kennel (1888) in *Peripatus edwardsi*, there being here a blastoporic depression of the blastoderm from which an internal proliferation gives rise to endoderm and to ventrolateral bands of mesoderm. With eggs having much yolk, meroblastic cleavage is the rule. The egg nucleus divides within the yolk, and the cleavage nuclei enclosed in small masses of cytoplasm migrate to the surface and form a blastoderm. In *Peripatooides novaezealandiac*, however, according to Sheldon (1888), the blastoderm

lies beneath a superficial layer of yolk, the early embryo in this case being a sac not only containing yolk, but also surrounded by it. The outer yolk is later absorbed. In this species the manner of germ-layer formation has not been definitely determined, but the endoderm cells appear within the yolk, and the mesoderm takes the form of two widely separated bands along the sides of the embryo, in which the coelomic sacs are formed.

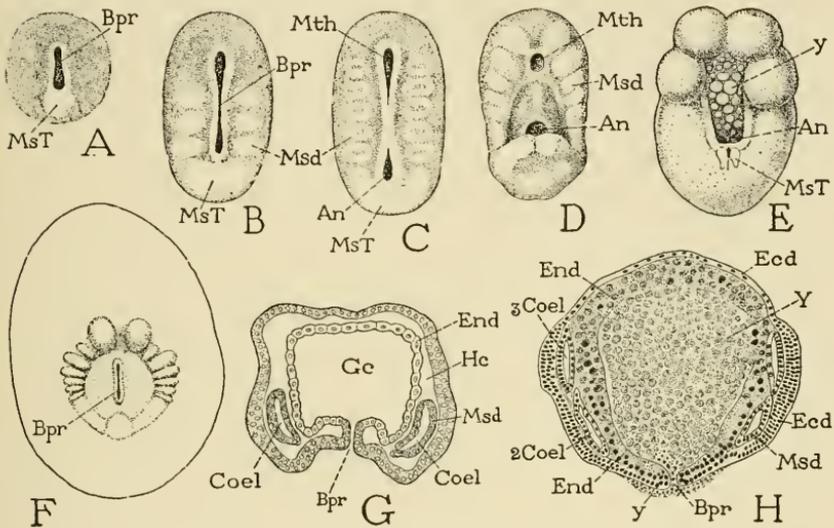


FIG. 22.—Early developmental stages of Onychophora.

A-D, successive embryonic stages of *Peripatopsis capensis* Grube, showing elongation and closure of the blastopore except at oral and anal extremities, and forward growth and segmentation of mesoderm bands (from Balfour, 1883). E, young embryo of *Eoperipatus weldoni* Evans, ventral view, mouth covered by external yolk (from Evans, 1902). F, young embryo of *Peripatopsis moseleyi* Wood-Mason with open blastopore (from Bouvier, 1905). G, cross-section of embryo of *Peripatopsis capensis* through open blastopore (from Balfour, 1883). H, cross-section of embryo of *Eoperipatus weldoni*, blastopore covered with yolk (from Evans, 1902).

An, anus; Bpr, blastopore; Coel, coelomic cavity; 2Coel, 3Coel, second and third coelomic cavities; Ecd, ectoderm; End, endoderm; Gc, gastrocoele; Hc, haemocoel; Msd, mesoderm; MsT, mesodermal teloblast ("primitive streak"); Mth, mouth; Y, internal yolk; y, external yolk.

In *Peripatopsis capensis*, Sedgwick (1885) says, cleavage is complete but unequal, the blastomeres being differentiated into four small, dark ectodermal cells at the animal pole of the egg, and four large, clear endodermal cells at the vegetative pole. Subsequent divisions proceed in each group separately. The endoderm cells soon draw together into the center of the egg, and are here overgrown by the ectoderm until completely enclosed by the latter, except at one point where

the endoderm remains exposed on the surface. A cavity now appears in the endodermal mass, and opens externally where the endoderm is not covered by the ectoderm. The opening is the blastopore (fig. 22 A, *Bpr*). With the growth of the embryo, the blastopore lengthens to an elongate slit on the ventral surface (B). The first observations on the development of *Peripatopsis capensis* were made by Balfour (1883), who believed that the mesoderm arises in the form of paired coelomic pouches along the edges of the elongate blastopore where the ectoderm and endoderm are confluent. From the subsequent work of Sedgwick, however, it appears that the mesoderm in *P. capensis* is generated from an opaque area of the blastoderm situated behind the posterior end of the blastopore (A, B, C, *MsT*). From this area, or "primitive streak," there takes place an internal proliferation of cells, which, migrating forward in each side of the embryo, produce two ventrolateral mesoderm bands along the margins of the blastopore (B). The bands then break up into sections that mark the primitive somites of the embryo, and later are excavated by the coelomic cavities (G, *Coel*). The elongate blastopore finally closes by the fusion of its lips, except at the two ends, which become the primary mouth and the primary anus (D, *Mth, An*).

The development of the endoderm of *Eoperipatus weldoni*, as described by Evans (1902), is again different from that of *Peripatopsis capensis*. "The endodermal elements," Evans says, "are derived from the lips of the blastopore and travel inward along the outer layers of the yolk, which is at first devoid of nuclei." Here, evidently, is a process suggesting invagination. On the surface of the yolk the endoderm cells form a complete investing layer, but later some of them invade the yolk, probably bringing about its partial digestion, and then again most of these cells return to the surface, where they reconstruct a permanent endodermal sac containing the yolk (fig. 22 H, *End*). A few endodermal cells, however, remain within the yolk. The mesoderm of *Eoperipatus weldoni*, according to Evans, is formed in the same way as described by Sedgwick for *Peripatopsis capensis*, that is, from a proliferating area of the blastoderm situated immediately behind the blastopore (E, *MsT*).

Considering the various processes by which the organization of the onychophoron is accomplished in the embryo, it would appear that the manner of development has little significance. In extreme cases the assembling of the germ layers seems to be almost haphazard. Sheldon (1888) observes of *Peripatoides novae-zealandiae* that the embryo might be said to be formed "by a process of crystallizing out *in situ* from a mass of yolk, which is a protoplasmic reticulum con-

taining nuclei." Among the early developmental phases of the Onychophora, however, we cannot fail to note two important likenesses to annelid development. The first is the elongation of the blastopore on the ventral surface of the embryo as it occurs in *Peripatopsis capensis* (fig. 22 A, B), followed by the closure of its median part (C), finally leaving only the persistent oral and anal apertures at the two extremities (D). We have here evidently a condition even more generalized than in the annelids, in which the anus is usually a secondary perforation. The second suggestion of annelid development, shown in several onychophoran species, is the forward growth of the mesoderm as bands of cells generated from a proliferating area of the blastoderm situated behind the blastopore (fig. 22 A, B, C, E, *MsT*). The mesoderm is, therefore, a teloblastic product, though it is not possible to identify in the generative area a primary pair of teloblastomeres. It would appear, however, that the onychophoran mesoderm may not be entirely of teloblastic origin, for Sedgwick (1887) finds that the forwardly growing bands in *Peripatopsis capensis* are augmented by cells proliferated from the lips of the blastopore along the lines where ectoderm and endoderm meet. The later development of the mesoderm is unquestionably a strictly homologous process in both the Annelida and the Onychophora, for in the latter, as in the annelids, the primarily solid mesoderm bands are first segmented corresponding with the body somites (fig. 22 B), and then excavated by coelomic cavities (C, G).

Beyond the early stages of cleavage and germ-layer formation the course of onychophoran ontogeny is well standardized and gives a good basis for comparison of the Onychophora with the Annelida on the one hand, and with the Arthropoda on the other. It will be found, however, that many of the irregular earlier processes of onychophoran development are duplicated among the Arthropoda.

THE NERVOUS SYSTEM

The onychophoran nervous system includes a brain situated in the head above and before the decurved anterior end of the stomodaeum (fig. 32 A, *Br*), and two long, widely separated nerve cords (*NC*) extending from the brain to the posterior end of the body, where they appear to be continuous in an arc above the rectum. The cords are connected by numerous ventral commissures (*Com*), and they give off in each segment a series of dorsal nerves against the body wall (fig. 24 B) and ventral nerves that go downward to the legs and other ventral parts. Opposite the legs the nerve cords are slightly

thickened, but they have no differentiated ganglia, since the neurocytes are scattered along their lengths. The brain, on the other hand, is a well-developed, bilobed cerebral body (fig. 25 A, B) extending horizontally forward from the anterior ends of the nerve cords (C). It bears anteriorly the large antennal nerves (*AntNv*), laterally a pair of small optic lobes supporting the eyes (E), and ventrally a pair of small pear-shaped bodies (B. C. *IVO*). Numerous other

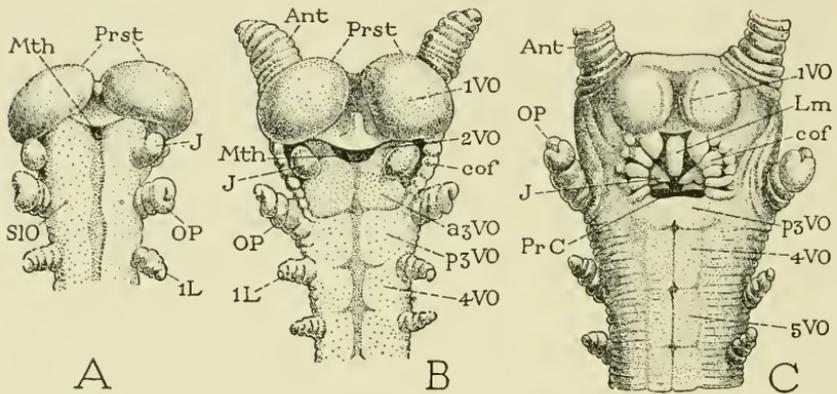


FIG. 23.—Development of the onychophoran head and anterior body region as shown in three embryonic stages of *Peripatus edwardsi* Blanchard, ventral view. (From Kennel, 1888.)

A, young embryo with large prostomial cephalic lobes, postoral jaw appendages (*J*) and oral papillae (*OP*) resembling legs. B, older embryo with prostomial antennal rudiments, jaws approaching mouth and surrounded by circumoral fold (*cof*), ventral organs (*VO*) becoming differentiated. C, still older embryo; jaws with definitive form, retracted into preoral cavity, ventral organs more distinct; head region composed of procephalic lobes, jaw somite, and somite of oral papillae.

a3VO, anterior ventral organ of papillar somite; *cof*, circumoral fold; *J*, jaw; *L*, leg; *Lm*, labrum; *Mth*, mouth; *OP*, oral papilla; *PrC*, preoral mouth cavity; *Prst*, prostomium; *p3VO*, posterior ventral organ of papillar somite; *SIO*, orifice of salivary gland; *1VO*, ventral organ of preoral cephalic lobe; *2VO*, ventral organ of jaw somite; *3VO*, ventral organ of somite of oral papillae (subdivided into anterior and posterior parts); *4VO*, *5VO*, ventral organs of first and second leg somites.

small nerves are given off from the brain (fig. 24 A), among which are anterior ventral nerves that go to the mouth and the circumoral fold, a dorsal median nerve (*f*) that turns downward and posteriorly on the dorsal surface of the stomodaeum, a pair of posterior stomodaeal nerves (*i*), and the nerves of the jaws (*j*), which arise from the nerve cords just behind the brain.

The entire central nervous system of the Onychophora is developed in the embryo from a series of paired ventral thickenings of the ectoderm known as the "ventral organs" (fig. 23 B, C, *VO*), which

correspond with the embryonic somites, except that the first pair (*IVO*) lies on the preoral head region. Whether these thickenings represent primitive organs or are merely embryonic structures is open to question, but they suggest the paired tubercles on what may be the ventral surface of *Xenusion* (fig. 21 C). From the inner surfaces of the ventral organs of the body are differentiated the

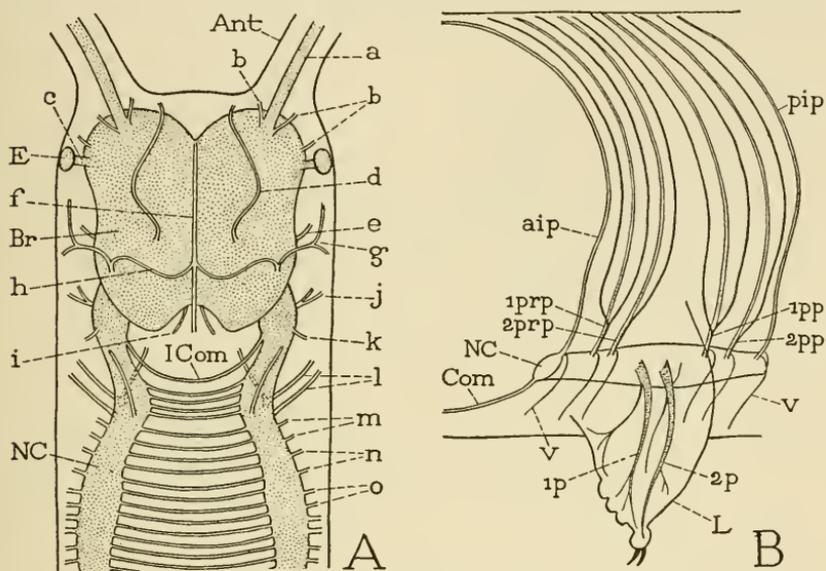


FIG. 24.—Nervous system of the head and of a body segment of *Peripatus tholloni* Bouvier. (From Fedorow, 1926, 1929.)

A, diagram of brain and anterior parts of nerve cords, with bases of nerves, dorsal view. B, nerve cord and peripheral nerves of left side of a body segment, lateral view.

a, sensory antennal nerve; *aip*, anterior interpedal nerve; *Ant*, antenna; *b*, motor nerves of antenna; *Br*, brain; *c*, optic nerve; *Com*, nerve commissure; *d*, lateral dorsal nerve; *E*, eye; *e*, nerve to circumoral fold; *f*, median dorsal nerve; *g*, nerve to dorsal muscles of head; *h*, commissural nerve from *f* to *g*; *i*, stomodaeal nerve; *ICom*, first ventral commissure; *j*, *k*, nerves of jaw; *L*, leg; *l*, nerves of oral papilla; *m*, *n*, *o*, nerves of first leg segment; *1p*, *2p*, first and second pedal nerves; *1pp*, *2pp*, first and second postpedal nerves; *pip*, posterior interpedal nerve; *1prp*, *2prp*, first and second prepedal nerves; *v*, ventral nerves.

ventral nerve cords; the outer parts are then gradually reduced in size until finally they disappear as distinct areas of the epidermis. When the nerve strands become free cords within the body they do not approach each other or unite as do the nerve cords of most annelids or arthropods; on the contrary they *move farther apart* until they take positions along the sides of the body on a level with the leg bases (fig. 29, *NC*). The definitive cords, moreover, lie laterad of

series of dorsoventral lateral muscles (*dvm*) attached dorsally and ventrally on the body wall. A condition thus arises in the Onychophora that has no counterpart in the annelids or arthropods, for in the latter the nerve cords, even when laterally situated, have no barrier to a median approximation or union.

The major part of the brain, from which arise the antennal and optic nerves, is shown by Sedgwick (1888), Kennel (1888), and Evans (1902) to be generated from the paired ventral organs of

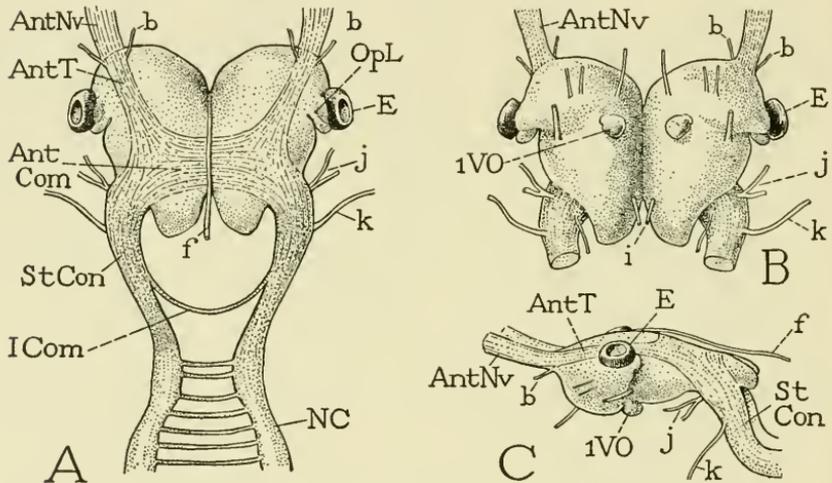


FIG. 25.—Brain of *Peripatoides novae-zealandiae* Hutton.

A, dorsal surface of brain and anterior parts of nerve cords, showing posterior antennal commissure and dorsal position of antennal tracts. B, ventral surface of brain, with remnants of ventral organs. C, lateral view of brain and stomodaeal connectives.

AntCom, antennal commissure; *AntNv*, antennal nerve; *AntT*, antennal tract; *b*, motor nerves of antenna; *E*, eye; *f*, median dorsal nerve; *i*, stomodaeal nerves; *ICom*, first ventral commissure; *j*, *k*, nerves of jaw; *NC*, nerve cord; *OpL*, optic lobe; *StCon*, stomodaeal connective; *iVO*, remnant of first ventral organ.

the head (figs. 23 B, 27 B, *iVO*). Evans says that the brain includes also a pair of anterior "archicerebral lobes" belonging to the apical part of the head, but in his account of the embryonic development of *Eoperipatus weldoni* he makes no mention of observing a separate origin of such lobes, and attributes the entire brain, except a posterior part, to the neural elements derived from the cephalic ventral organs. The ventral organs of the head, unlike those of the body, are finally invaginated as vesicles connected with the nerve tissue; eventually they are reduced, but persist as the small bodies attached to the ventral side of the brain (fig. 25 B, C, *iVO*).

The small posterior lobes of the brain from which arise the posterior stomodaeal nerves (fig. 25 B, *i*), together with the adjoining parts of the nerve cords that give off the nerves of the jaws (A, B, C, *j*), are said by Evans to be secondarily added to the antenno-ocular lobes from the ventral organs of the postoral jaw somite (fig. 23 B, *zVO*), and Kennel clearly shows in a head section (fig. 27 A) the inclusion in the brain of a mass of neural cells given off from these generative centers (*zVO*). The definitive onychophoran brain, therefore, as

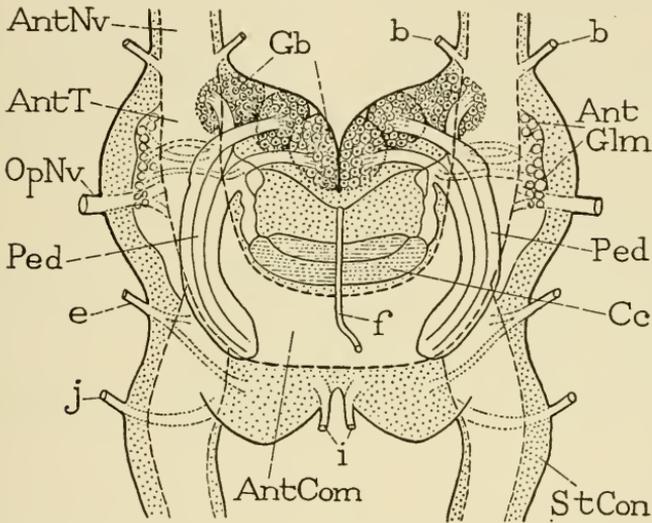


FIG. 26.—Internal structure of the brain of *Peripatopsis capensis* Grube. (From Holmgren, 1916.)

AntCom, antennal commissure; *AntGlm*, antennal glomeruli; *AntNv*, sensory antennal nerve; *AntT*, antennal tract; *b*, motor nerves of antenna; *Cc*, corpus centrale; *e*, nerve to circumoral fold; *f*, median dorsal nerve; *Gb*, globuli of corpus pedunculatum; *i*, stomodaeal nerves; *j*, nerve of jaw; *OpNv*, optic nerve; *Ped*, peduncle of corpus pedunculatum; *StCon*, stomodaeal connective.

shown by the records of its development, and as claimed by Holmgren (1916) and by Hanström (1928, 1935) from histological evidence, would appear to be a syncerebrum composed of a prostomial fore-brain including the ocular and antennal centers, and of a postoral hindbrain containing the centers of the posterior stomodaeal nerves and the nerves of the jaw appendages.

A quite different concept of the composition of the onychophoran brain is deduced by Fedorow (1929) from a study of *Peripatus tholloni*, in which he attempts to correlate the cerebral nerves with the nerves of a series of body segments (fig. 24 A, B). Fedorow

concludes that the anterior part of the brain, lying before the antennal commissure and bearing the optic lobes, represents the prostomial archicerebrum of the annelids, and that the rest of the brain is of postoral origin, being formed of the united anterior ends of the nerve cords extended secondarily in front of the stomodaeum. This alleged postoral part of the definitive brain, Fedorow believes, includes the ganglionic centers of the antennal somite, and the ganglia of a reduced premandibular somite that has lost its appendages. The jaw centers, he contends, are contained in the parts of the nerve cords immediately behind the brain, from which arise the nerves of the jaw muscles (*j*), and which are connected by the first postoral commissure (*1Com*). Fedorow's elaborate analysis of the brain structure and nerves would be more convincing if it took into account the embryonic development of the brain; his results are entirely unsupported by ontogenetic evidence, and are mostly at variance with observations on the brain development reported by other investigators.

The internal structure of the onychophoran brain (fig. 26) shows fundamental characters of the polychaete brain, and contains certain arthropod features, but it presents also special modifications that are not found in either the annelids or the arthropods. Corpora pedunculata are well developed, each consisting of a cap of three globuli (*Gb*) of small chromatic cells lying in the anterior part of the brain, and of a large pedunculus (*Ped*) composed of three confluent groups of fibers springing from the globuli cells. The sensory antennal nerves (*AntNv*) coming into the anterior angles of the brain traverse the upper part of the cerebrum in distinct antennal tracts (*AntT*), which are united posteriorly in a broad antennal commissure (*AntCom*). The association centers of the antennal nerve fibers, called by Holmgren (1916) and Hanström (1928, 1935) the *antennal glomeruli* (*AntGlm*), lie laterad of the anterior ends of the corpora pedunculata, and are said by Hanström to be closely connected with neurites of the globuli cells. In this feature, Hanström points out, the Onychophora have a distinctly polychaete character in the brain structure, since the antennal glomeruli of the onychophoran brain evidently correspond with the palpal glomeruli of the polychaete brain (fig. 18 B, F, *PlpGlm*). On the other hand, the onychophoran brain shows arthropodan characters in the presence of a well-developed central body (*Cc*) and an antennal commissure (*AntCom*). But again, the small optic lobes of the eyes (fig. 25 A, *OpL*) contain each only a single ganglionic center, while all arthropods have at least two. The optic ganglia are connected with the corpora pedunculata and with the central body.

The onychophoran brain thus appears to contain, as Hanström (1935) has shown, a mixture of polychaetous and arthropodan characters. Its origin must be found in the annelid brain; but certain peculiar features of the onychophoran brain would seem to preclude

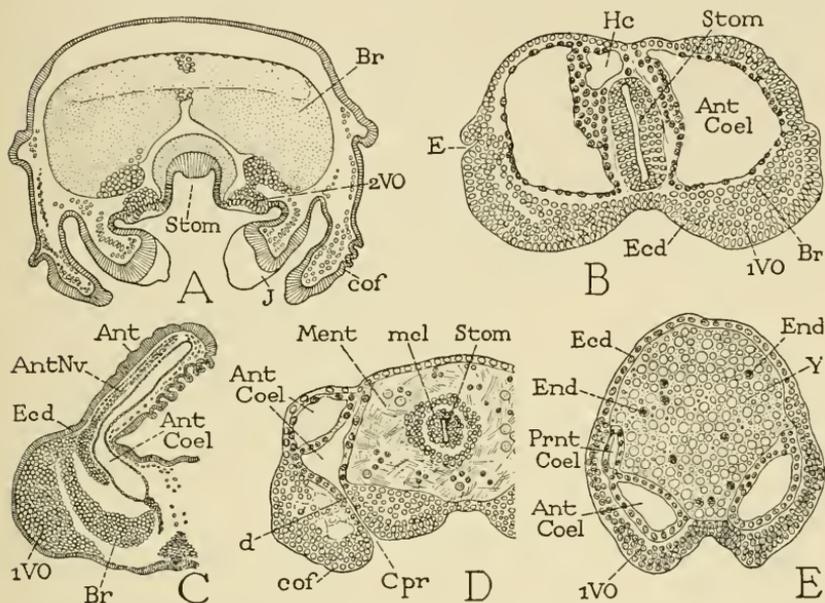


FIG. 27.—Developmental stages of various head structures of Onychophora. (A, C from Kennel, 1888; B, D, E from Evans, 1902.)

A, cross-section of head of embryo of *Peripatus edwardsi* Blanchard through jaws (*J*), showing groups of brain cells proliferated from ventral organs (*2VO*) of jaw somite. B, cross-section of embryonic head of *Eoperipatus weldoni* Evans, showing coelomic sacs of antenna embracing the stomodaeum, and generation of brain (*Br*) from cephalic ventral organs (*iVO*). C, section through anterior part of head of embryo of *Peripatus edwardsi*, showing antennal coelomic sac extending into antenna. D, section of embryonic head of *Eoperipatus weldoni* with canal (*d*) from antennal coelom opening mesad of circumoral fold (*cof*). E, same, more anterior section, showing antennal coelomic sacs, and a preantennal sac on left side.

Ant, antenna; *AntCoel*, coelomic sac of antenna; *AntNv*, antennal nerve; *Br*, brain; *cof*, circumoral fold; *Cpr*, coelomopore of antennal coelom; *E*, pit of developing eye; *Ecd*, ectoderm; *End*, endoderm; *Hc*, haemocoel; *J*, jaw; *mcl*, muscles of stomodaeum; *Ment*, mesenteron (folded forward on stomodaeum); *PrntCoel*, preantennal coelom; *Stom*, stomodaeum; *iVO*, preoral cephalic ventral organ; *2VO*, ventral organ of postoral jaw somite; *Y*, yolk.

the possibility of its having given rise to the arthropod brain. The superficial position of the antennal nerve tracts (fig. 25 A, C, *AntT*), which traverse the forebrain dorsal to the optic lobes (A, *OpL*), constitutes a condition quite at variance with that in any arthropod, for in all the Arthropoda the antennal nerves issue from antennal lobes

that lie ventral to the optic lobes, showing that the antennae have migrated forward beneath the eyes, and not above them as in the Onychophora. Moreover, in the arthropod brain the antennal glomeruli are not immediately connected with the corpora pedunculata. The onychophoran brain in its modern form, therefore, could not have given rise to a brain of arthropod structure, and we can assume only that the two types of cerebral structure have taken their origins separately from some common progenitor not far removed from a generalized annelid. Even the inclusion of the nerve centers of the first postoral somite in the onychophoran brain cannot be taken as evidence that the Onychophora are ancestral to the Arthropoda, for in some of the lower members of the second group the first postoral (tritocerebral) ganglia are not united with the brain.

THE EYES

The eyes of the Onychophora resemble the eyes of annelids in structure and development. An eye of the annelid-onychophoran type is formed from an invagination of the body wall (fig. 28 C), which becomes closed by an approximation or union of its lips (D, E), thus producing an inner optic vesicle (*OpV*) beneath an outer layer of epidermis and corneal cuticula (*Cor*). The cavity of the vesicle is occupied by a crystalline lens (*Lu*), probably of a cuticular nature, and its inner wall becomes the retina (*Ret*). In the onychophoran eye (A), as described by Dakin (1921), the lens is strongly convex outwardly and rests on the thick retina (*Ret*). Each retinal cell (B) is differentiated into a distal cylindrical rod (*c*) and a basal pigmented part (*d*), which contains the nucleus (*Nu*), and is prolonged proximally as a nerve fiber (*nf*) that enters the optic lobe of the brain. The rods appear to have peripheral striations (*e*), but, as shown in cross-section (F), they do not form structures between them corresponding with the rhabdoms of arthropod eyes.

LATER HISTORY OF THE MESODERM AND THE COELOMIC SACS

The mesoderm bands of the Onychophora in their forward growth (fig. 22 B, C) continue into the head, where they form a pair of distinct coelomic sacs in the antennal region diverging anteriorly from the mouth (D). The cephalic coelomic sacs are described by Sedgwick (1887) in *Peripatopsis capensis*, by Kennel (1888) in *Peripatus edwardsi*, and by Evans (1902) in *Eoperipatus weldoni*. The sacs are at first of large size (fig. 27 B); posteriorly their splanchnic walls embrace the stomodaeum (*Stom*) and give rise to a part of the

stomodaeal musculature; anteriorly they extend into the antennae (*C, AntCoel*), and thus show their relation to these appendages. According to Evans, the antennal sacs acquire temporary coelomoducts (*D, d*) opening ventrally to the exterior (*Cpr*) within the circumoral fold (*cof*). With the increase in the size of the brain,

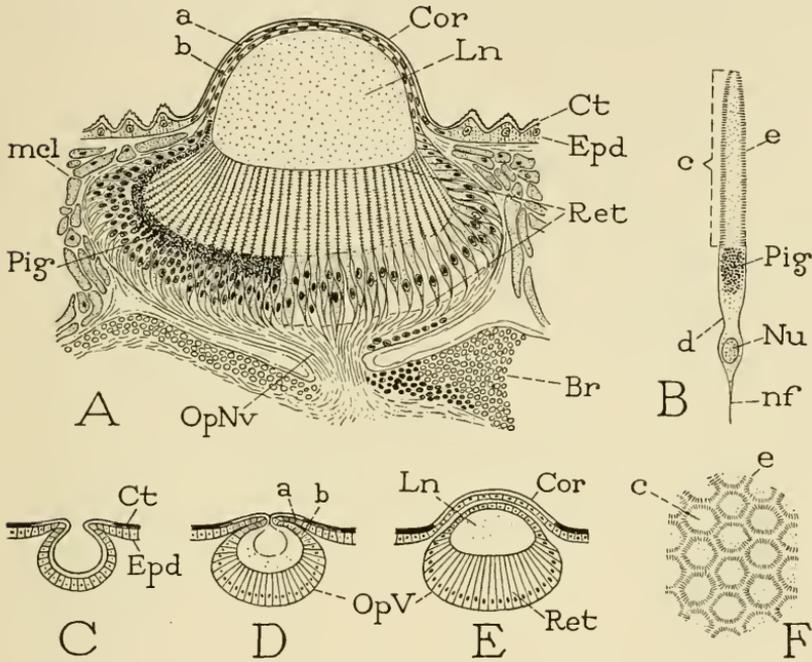


FIG. 28.—Structure of the onychophoran eye. (A, B, F from Dakin, 1921.)

A, vertical longitudinal section of eye of *Peripatoides occidentalis* Fletcher, right half of retina depigmented. B, a retinal cell, differentiated into basal plasmatic part (*d*) and distal optic rod (*c*). C, D, E, diagrams of development of an eye of the vesicular type (see also fig. 19 G). F, tangential section through optic rods of retina.

a, b, outer and inner layers of corneal epidermis; *Br*, brain; *c*, optic rod of retinal cell; *Cor*, cornea; *Ct*, cuticula; *d*, basal plasmatic part of retinal cell; *e*, striated border of optic rod; *Epd*, epidermis; *Ln*, lens; *mcl*, muscle fibers; *nf*, nerve fiber; *Nu*, nucleus; *OpNv*, optic nerve; *OpV*, optic vesicle; *Pig*, pigment; *Ret*, retina.

the antennal sacs become reduced until finally, Evans says, they appear only as two small spaces situated above the brain in front of the eyes.

A pair of small mesoderm masses observed by Evans in an embryo of *Eoperipatus weldoni*, lying above and before the antennal sacs, in one of which a cavity was present (fig. 27 E, *PrntCoel*), are regarded by Evans as representing a pair of preantennal coelomic sacs, possibly

corresponding with a pair of transient rudiments of preantennal appendages mentioned by Kennel in *Peripatus edwardsi*.

The coelomic sacs of the body region conform with the series of postoral somites. The sacs of the jaw somite soon disappear. Those of the following somites attain a high state of development during the early embryonic period, leaving thus no doubt that the Onychophora are descended from typically metameric ancestors. The coelomic cavities become connected with the exterior by ventral diverticula from the mesodermal walls of the sacs (fig. 32 C, *c*) that unite with ectodermal invaginations (*d*), and thus form ducts opening on the mesal aspects of the bases of the legs (D). These outlet ducts of the coelomic sacs (coelomoducts) probably served primarily in the early history of the Onychophora for the discharge of excretory products and the gametes (fig. 34 A); but the coelomic sacs of the somites anterior to the somite of the definitive genital outlets become differentiated into dorsal gonadial and ventral nephridial compartments (B, C, *a, b*). The gonadial compartments eventually disappear except in a few posterior segments where they unite to form the gonads; the nephridial compartments are reduced to the form of delicate vesicles at the inner ends of the coelomoducts (D, *b*), and thus persist as end-sacs of the definitive nephridia. In the somite of the genital outlet the entire coelomic sacs (figs. 32 E, 34 E, *a, b*) with their coelomoducts (*d*) are converted into the lateral genital ducts. The sacs of the second postoral somite become the salivary glands that open into the preoral mouth cavity. Derivation products of the coelomic walls include the entire muscular system, the dorsal pulsating blood vessel (fig. 29, *DV*), and a muscular dorsal diaphragm (*DDph*) beneath the blood vessel.

THE SOMATIC MUSCULATURE

The body musculature of the Onychophora is in general similar to that of the annelids in so far as it consists mostly of flat sheets or bands of circular, oblique, and longitudinal fibers closely applied to the integument throughout the length of the animal (fig. 29), but it includes a series of lateral dorsoventral fibers (*dvm*) along each side of the body cavity, which have no representatives in annelid musculature. These lateral muscles divide the body cavity into a median compartment (*mBC*) containing the alimentary canal (*AlCnl*) and the slime glands (*SlmGld*), and lateral compartments (*lBC*) enclosing the salivary glands (*SlGld*), the nephridia (*Nph*), and the nerve cords (*NC*). The muscle fibers are all very slender, and for the

most part are not closely grouped into bundles forming specific muscles as in the arthropods. Each fiber is invested in a delicate sarcolemma, the nuclei are superficial, and the axis is distinctly fibrillated but shows no trace of cross striation (see Camerano, 1897).

The following account of the onychophoran body musculature is based on a study of *Peripatoides novae-zealandiae*. When the body is laid open from above there are exposed on each side three sets of

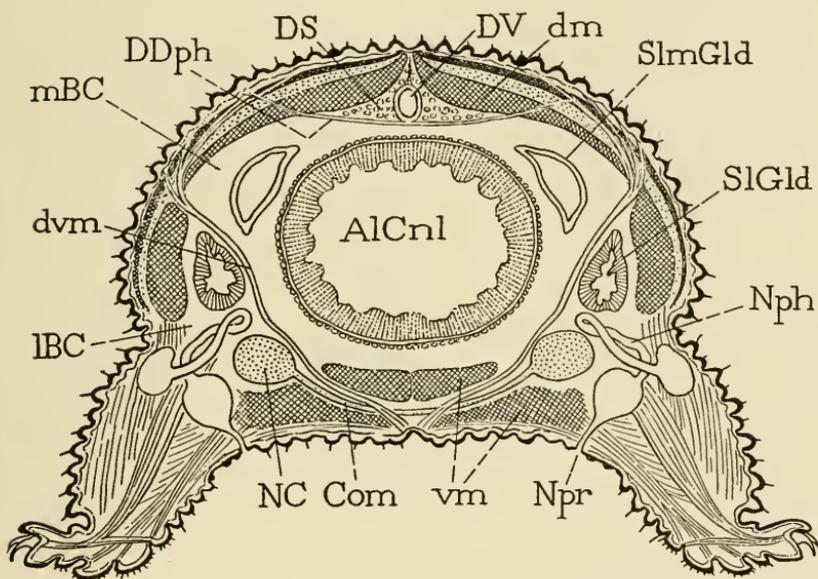


FIG. 29.—Cross-section of middle body region of *Peripatoides novae-zealandiae* Hutton, showing position of principal organs, diagrammatic.

AlCnl, alimentary canal; *Com*, commissure of nerve cords; *DDph*, dorsal diaphragm; *dm*, dorsal muscles; *DS*, dorsal sinus; *DV*, dorsal blood vessel; *dvm*, dorsoventral lateral muscles; *IBC*, lateral compartment of body cavity; *mBC*, median compartment of body cavity; *NC*, nerve cord; *Nph*, nephridium; *Npr*, nephropore, *SlGld*, salivary gland; *SImGld*, slime gland (reservoir); *vm*, ventral muscles.

fibers. Dorsally is a broad, thin band of internal *dorsal longitudinal fibers* (fig. 30, 1), the more median fibers beginning anteriorly at the bases of the antennae, the more lateral ones behind the bases of the oral papillae. Ventrally is a much narrower band of *ventral longitudinal fibers* (2) lying along the midventral line. Between the dorsal and ventral longitudinal muscles is a series of flat, closely adjacent, straplike lateral *dorsoventral muscles* (fig. 29, *dvm*, fig. 30, 3), beginning anteriorly midway between the oral papillae and the first legs. When fully exposed, however, these lateral muscles are seen to be

nearly semicircular in extent (fig. 29), since they are attached dorsally high up on the back external to the dorsal muscles, and ventrally along the midline of the body external to the median ventral muscles.

By removing a section of the lateral muscles and the more lateral fibers of the dorsal muscles (fig. 30, left), there will be exposed two flat *external laterodorsal longitudinal muscles* (4, 5) lying above the leg base, an *external lateroventral longitudinal muscle* (6) mesad of the leg base, two dorsal muscles of the leg (7, 8), and a layer of

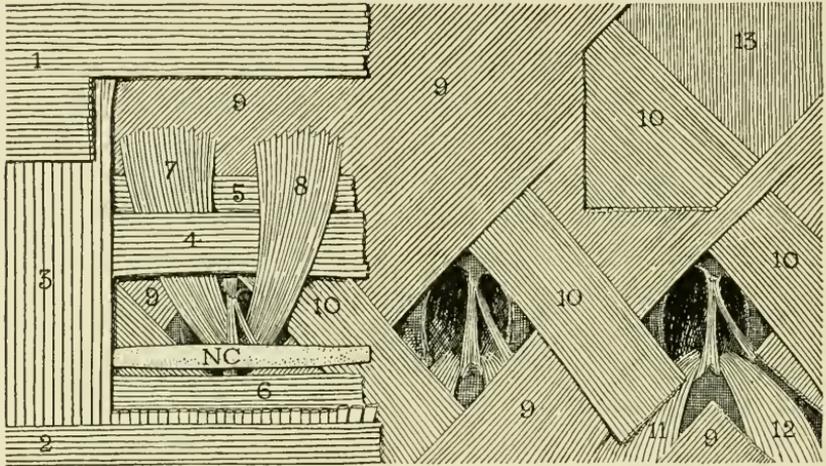


FIG. 30.—Muscles of body wall of *Peripatoides novae-zealandiae* Hutton. The various muscle layers exposed on right side of three successive segmental areas.

1, dorsal longitudinal muscles; 2, ventral longitudinal muscles; 3, dorsoventral lateral muscles; 4, 5, internal and external laterodorsal longitudinal muscles; 6, lateroventral longitudinal muscles; 7, dorsal promotor of leg; 8, dorsal remotor of leg; 9, internal oblique muscles; 10, external oblique muscles (9 and 10, reversed in position between legs); 11, ventral promotor of leg; 12, ventral remotor of leg; 13, circular muscles.

oblique muscles (9, 10). The fibers of the leg muscles penetrate between the oblique fibers to make attachments on the body wall.

The *oblique muscles* (fig. 30, 9, 10) lie external to all the other muscles thus far described. They consist of two thin sheets of fibers crossing each other at right angles in opposite directions. The fibers that are internal on the back (9) go from above downward and forward; those that are external dorsally (10) go downward and posteriorly. Just above each leg, however, a broad band of the external fibers becomes internal by crossing over a similar band of the otherwise internal fibers (9) going below the leg from behind. Between

each two successive legs, therefore, the relation of the two sets of oblique fibers is reversed. On the venter all the fibers again take the same relative position that they have on the back. The two sets of oblique fibers arise on the integument close to the middorsal and midventral lines, and are hence not continuous from one side to the other. External to the oblique fibers may be seen the anterior and posterior ventral muscles of the legs (fig. 30, right, *11*, *12*).

Finally, outside all the other muscles of the body wall, are the *circular muscles* (fig. 30, *13*). They consist of extremely fine fibers closely adherent to the inner surface of the integument, and are apparently continuous across the middorsal and midventral lines.

A few other body muscles occur in the region of the mouth, and the jaws have an elaborate musculature quite different from the musculature of the legs (fig. 21 F).

THE SEGMENTAL APPENDAGES

The appendages of the Onychophora include the antennae, the jaws, the oral papillae, and the legs. Their rudiments appear in the embryo as conical outgrowths of the body wall (fig. 23). The antennae arise from the anterior angles of the cephalic lobes (B, *Ant*) and retain this position. The jaws, which are the appendages of the first postoral somite, arise posterior to the mouth (A, *J*), but later they migrate mesally and forward (B), and are finally buried in the preoral mouth cavity (C), where they become reduced to a pair of double flattened hooks (fig. 21 F) converging in a horizontal plane beneath the mouth (D, *J*). The oral papillae are the appendages of the second postoral somite (fig. 23 A, *OP*), but in the definitive state they take a more anterior position at the sides of the mouth (fig. 21 D, E, *OP*). The legs retain their primary lateroventral positions (fig. 23 B, C), and show but little variation in their final structure.

The onychophoran appendages in their development give no evidence of having been derived from polychaete parapodia; they have no cirri or bristle sacs, and nothing suggests that they are composite organs formed of notopodial and neuropodial elements. The terminal claws of the onychophoran leg in no way resemble parapodial chaetae, and the general structure and musculature of the leg has little in common with a parapodium, except features that adapt each appendage to forward and backward movement on its base. On the other hand, the segmental appendages of the Onychophora and the Arthropoda have the same manner of origin and growth in the embryo, the organs in each case being hollow muscled lobes of the body wall,

and it is only in their later development that they assume the structure characteristic of the adult appendages in each group.

An onychophoran leg (fig. 31 A) is a hollow, conical outgrowth of the body wall terminating in a small pedal lobe bearing a pair of decurved claws. The leg integument is thrown into permanent circular folds, which on the thick basal part of the limb are covered with

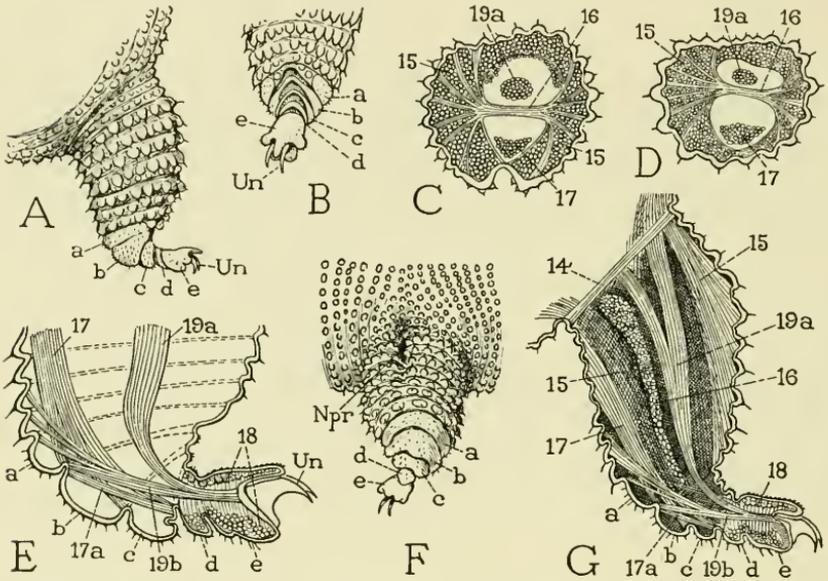


FIG. 31.—Structure and musculature of an onychophoran leg, *Peripatoides novae-zealandiae* Hutton.

A, anterior view of a leg. B, lateral view of distal part of leg. C, horizontal section of basal part of leg. D, section of more distal part of leg. E, diagrammatic vertical section of distal part of leg. F, mesal view of leg. G, section of entire leg in transverse plane of body.

a, b, c, d, distal nontuberculate rings of leg; e, claw-bearing pedal lobe; *Npr*, nephropore; *Un*, claws; 14, transverse muscle of leg base; 15, peripheral muscles of basal part of leg; 16, anteroposterior septal muscles of leg; 17, flexor muscle of leg; 17a, flexor of distal leg rings; 18, circular muscles of foot; 19a, 19b, two-branched retractor of claws.

bristle-bearing tubercles. The distal folds, however, form distinct segmentlike rings (A, B, a, b, c, d) and are devoid of tubercles. The pedal lobe (e) appears to be a larger terminal ring bearing the claws (*Un*).

The leg is movable anteriorly and posteriorly on the obliquely transverse axis of its base by the four somatic muscles (fig. 30, 7, 8, 11, 12) that converge from the body wall into its basal opening. These muscles undoubtedly serve principally as promotors and re-

motors, but are probably also levators and depressors of the leg as a whole. Within the leg the fibers of the four somatic muscles spread out into a thick peripheral layer of intrinsic leg fibers (fig. 31 C, D, G, 15) attached on the successive rings of the thick basal part of the appendage. Running through the narrow axial cavity of the leg is an antero-posterior muscular septum (16), the fibers of which diverge among those of the peripheral layer to the anterior and posterior walls of the leg (C, D). The rest of the leg muscles, except a slender transverse basal muscle (G, 14), are motors of the distal rings and of the claws. The former include a bundle of fibers (17) arising mesally in the leg base (G), with its fibers distributed to the ventral walls of the distal rings (E, G), and a series of strong circular muscles (18) in the pedal lobe. The claws are provided with a large two-branched muscle (E, G, 19), the larger branch arising in the base of the leg (G, 19a), the other in the distal part (E, G, 19b); the short common terminal part is inserted dorsally between the bases of the claws. The claw muscle is, therefore, a levator, or extensor, of the claws and has no antagonist.

It is quite reasonable to suppose that the onychophoran leg is a prototype of the arthropod limb, but if we look for structural resemblances in these two sets of locomotor organs we find few such, if any at all. The differentiation of the onychophoran leg into a thick basal part and a slenderer distal part, and the individualization of the distal rings, on which muscle branches are separately inserted, might be seen as an incipient segmentation. There is, however, no actual parallelism between the structure of the onychophoran leg and that of any arthropod leg, so that all we can say of the former is that it suggests a mode by which segmentation might arise in an ambulatory appendage. We may conclude, therefore, that the appendages of the Onychophora and the appendages of Arthropoda have had a common origin as lobiform outgrowths of the body wall containing extensions of the somatic muscles. The common need of a mechanism for anterior and posterior movement of each appendage on its base then brought about a differentiation of the extrinsic parts of the limb muscles into promoters and remoters, while the parts of the muscles within the leg were elaborated to give greater efficiency to movements of the leg itself. The further course of evolution producing segmentation and correlated musculation in the limb evidently has proceeded independently in the Onychophora and the Arthropoda from a very primitive common beginning, and has gone much farther in the Arthropoda than in the Onychophora.

THE RESPIRATORY ORGANS

The Onychophora are provided with numerous fine tubular ingrowths from the body wall, which undoubtedly serve for respiration, and are therefore termed tracheae, though it is possible that anatomically they are more of the nature of insect tracheoles. The tubules, which are only one to three microns in diameter, arise in dense bundles (fig. 32 B, *Tra*) from small flask-shaped pits (*tp*) of the integument, and extend long distances into the body cavity. The tracheal pits may be very numerous; they occur on all parts of the body, on the head, and around the mouth, but they are most abundant on the back, where several may occupy the space of a square millimeter. For the most part the pits are irregularly distributed, but in some species they are arranged in longitudinal rows. The tracheal bundles issuing from the inner ends of the pits contain large, conspicuous nuclei in their basal parts (*Nu*), which probably pertain to the matrix cells, but the tubes themselves diverge and extend far beyond these nuclei. According to Dakin (1920), the tracheal walls are strengthened by excessively minute but perfect spiral fibers visible in fresh material. In their distal parts the tracheae are branched and go to practically all the internal organs, but their final terminations have not been observed.

Since tracheal invaginations of the body wall are developed for respiratory purposes in nearly all groups of terrestrial arthropods, the mere presence of such organs can have no taxonomic significance, any more than has the presence of gills in diverse groups of aquatic animals. Inasmuch as invertebrates breathe through the skin in any case, evaginations or invaginations of the integument are about the only devices they can develop for improving their respiratory functions.

THE CIRCULATORY SYSTEM

The blood vascular system of the Onychophora consists only of a tubular dorsal vessel (fig. 29, *DV*) extending the entire length of the body, said to be open anteriorly and posteriorly. The walls of the vessel consist of circular muscle fibers, and are perforated dorsally in each segment by a pair of ostia. The tube is suspended from the body wall by connective tissue strands, and is supported on a membranous and muscular dorsal diaphragm (*DDph*). The diaphragm muscles are fine, regularly transverse fibers medially attached on the ventral wall of the blood vessel; laterally they penetrate between the fibers of the dorsal somatic muscles and are apparently attached on

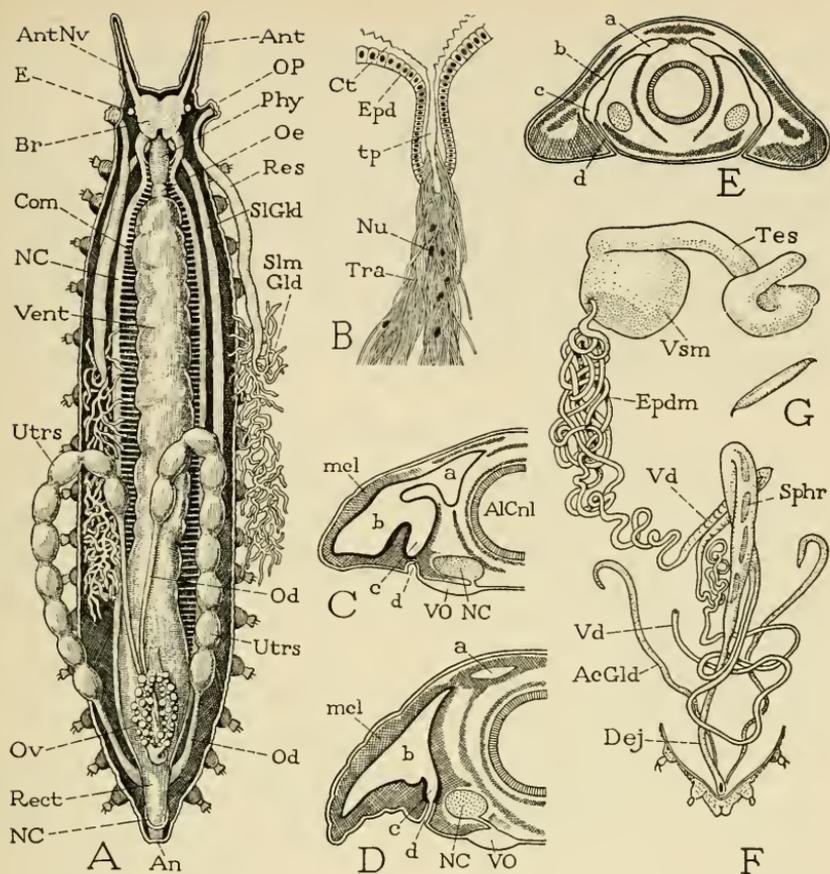


FIG. 32.—Internal structure of Onychophora, and later development of the coelomic sacs.

A, general view of internal anatomy of *Peripatoides novae-zealandiae* Hutton, female, dorsal view; muscles, nephridia, peripheral nerves, and dorsal blood vessel omitted. B, tracheal pit of *Peripatopsis capensis* Grube and respiratory tubules extending inward from it (from Schneider, 1902). C, section of embryo of *Peripatus edwardsi* Blanchard, showing constriction of coelomic cavity into dorsal gonadial compartment (*a*) and lateral nephridial compartment (*b*); rudiments of coelomoduct (*c, d*) not yet united (from Kennel, 1888). D, same, later stage, dorsal compartment (*a*) of coelomic sac (which later disappears except in genital somites) and nephridial compartment (*b*) entirely separated, coelomoduct (*c, d*) open to exterior (from Kennel, 1888). E, section of embryonic somite of genital outlets, coelomic sacs narrowed but not divided as in other segments (C, D), continuous from gonads (*a*) through coelomoducts (*d*) to exterior (from Kennel, 1888). F, male reproductive organs of *Peripatopsis blainvillei* Gay-Gervais (from Bouvier, 1902, with accessories omitted). G, spermatophore of same (from Bouvier, 1902).

a, dorsal gonadial compartment of coelomic sac; *AcGld*, genital accessory gland; *AlCnl*, alimentary canal; *Ant*, antenna; *AntNv*, antennal nerve; *b*, nephridial compartment of coelomic sac; *Br*, brain; *c*, mesodermal component of coelomoduct; *Com*, nerve commissures; *Ct*, cuticula; *d*, ectodermal component of coelomoduct; *Dej*, ductus ejaculatorius; *E*, eye; *Epd*, epidermis; *Epdm*, epididymis; *mcl*, muscle; *NC*, nerve cord; *Nu*, nucleus; *Od*, oviduct; *Oe*, oesophagus; *OP*, oral papilla; *Ov*, ovary; *Phy*, pharynx; *Res*, reservoir of slime gland; *Rect*, rectum; *SlGld*, salivary gland; *SlmGld*, slime gland; *Sphr*, spermatophore; *Tes*, testis; *tp*, tracheal pit; *Tra*, tracheal tubules; *Utrs*, uteri; *Vd*, vas deferens; *Vent*, ventriculus; *VO*, ventral "organ"; *Vsm*, vesicula seminalis.

the body wall. Above the diaphragm on each side of the blood vessel are masses of small individual cells, probably "nephrocytes." The circulatory system of the Onychophora thus resembles that of the Chilopoda and the Hexapoda in the simplicity of its structure. Since many of the arthropods, in common with the annelids, have a highly developed blood vascular system, it would seem probable that the simpler forms represent reductions from a more elaborate primitive system such as that of the Annelida.

THE NEPHRIDIA

The nephridiallike excretory organs of the Onychophora are paired segmental structures usually present in all the somites between the somite of the oral papillae and that of the genital ducts, though they may differ much in size and in the relative development of their parts. They lie in the lateral compartments of the definitive body cavity at the bases of the legs (fig. 29, *Nph*), and open externally in grooves on the ventral surfaces of the leg bases (figs. 29, 31 F, 33 A, *Npr*), except those of the fourth and fifth pairs, which in most species open at the bases of the distal rings of the legs (fig. 33 C).

A well-developed onychophoran nephridium consists of five distinct parts (fig. 33 A): First, beginning externally, is a short outlet duct (*Nd*); second, a bladderlike enlargement, or reservoir (*Bl*); third, a tubular canal (*Cnl*) varying in length and usually coiled; fourth, a funnel-shaped enlargement of the inner end of the canal (*Fun*); and fifth, a thin-walled end-sac (*ESc*). The walls of the funnel (*B*) are relatively thick and are histologically different from the rest of the canal; they are clothed with long vibratile cilia directed toward the nephridial exit (see Dakin, 1920, Cuénot, 1926, Zilch, 1936).

The funnel and the canal of an adult onychophoran nephridium are comparable with an entire metanephridium of the annelids; the end-sac is a remnant of the coelomic sac of the embryonic somite. The opening of the nephridial funnel into the end-sac, therefore, is the nephrostome (fig. 33 B, *Nst*). The canal is developed in the embryo as an exit duct of the coelomic sac, formed by the union of a ventral diverticulum of the sac (fig. 32 C, *c*) with a tubular ingrowth (*d*) from the ectoderm of the same segment mesad of the leg rudiment (*D*). The primitive function of the coelomoducts undoubtedly was the discharge of excretory products and, in the genital segments, of the gametes. Embryonic coelomoducts occur, according to Evans (1902), in connection with the coelomic sacs of the antennae (fig. 27 D, *d*), and in all the postoral somites except

the somite of the jaws. During embryonic development the coelomic sacs of those segments that eventually contain nephridia become each constricted into a dorsal section (fig. 32 C, *a*) and a ventral section (*b*), which soon become entirely separate compartments (D). Except in the genital region the dorsal compartments disappear; in the nephridial somites the ventral compartments become much reduced, but they retain their open connections with the coelomoducts, and persist as the delicate end-sacs of the nephridia (fig. 33, *ESc*).

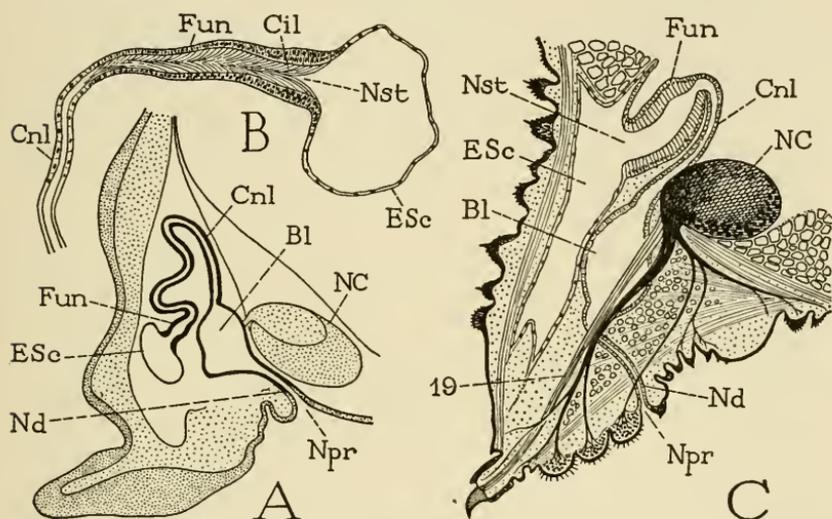


FIG. 33.—Structure of onychophoran nephridia.

A, diagrammatic transverse section of leg and nephridium of mature embryo of *Peripatopsis capensis* Grube (from Sedgwick, 1888). B, inner part of nephridium of *Peripatoides* sp., showing ciliated funnel (*Fun*) with nephrostome opening into coelomic end-sac (from Dakin, 1920). C, diagrammatic transverse section of leg and nephridium of adult *Peripatus tholloni* Bouvier (from Fedorow, 1926).

Bl, nephridial bladder; *Cil*, cilia; *Cnl*, nephridial canal; *ESc*, coelomic end-sac of nephridium; *Fun*, nephridial funnel; *NC*, nerve cord; *Nd*, nephridial duct; *Npr*, nephropore; *Nst*, nephrostome.

It is commonly held that the excretory organs of the Onychophora are homologous with the annelid metanephridia (see Glen, 1919). The simple development of the canals as open ventral diverticula of the coelomic walls (not of the septa), the direct opening of the canals to the exterior on the same segment, and the occurrence of embryonic coelomic ducts in the head, however, are all features distinctive of the Onychophora. Considering, therefore, that there is little probability on other grounds that the Onychophora have been derived from annelids having metanephridia, we may conclude that the open

nephridia of the higher Annelida and the coelomic exits of the Onychophora have been separately acquired and developed in each group. On the other hand, there can be little doubt that the nephridial organs of Arthropoda (antennal, maxillary, and coxal glands) are entirely comparable with the onychophoran nephridia.

THE ORGANS OF REPRODUCTION

In the evolution of specific reproductive organs the Onychophora are far in advance of any of the polychaete or oligochaete annelids; but the development and the definitive structure of the genital organs are so closely parallel in the Onychophora and the Arthropoda that we can scarcely question the probability of the genital systems in these two groups having had a common origin. In fact, it is the fundamental similarity in the genital system that would appear to constitute the closest bond of union between the Onychophora and the Arthropoda, and which most strongly suggests that the two groups have been derived from a common progenitor. The germinal centers of the Onychophora, as in the arthropods, are entirely enclosed in gonadial sacs of coelomic derivation, and the gametes are discharged through ducts whose lumina are continuous with those of the gonads. An approach to a closed genital system is seen in the Oligochaeta in the development of coelomic seminal vesicles containing the genital outlet funnels, and a system as completely closed as that of the Onychophora and Arthropoda is perfected in the Hirudinea; but the ontogeny of the organs in these several groups shows that there is no possibility of the onychophoran-arthropod reproductive system having been evolved from that of the higher annelids.

The primary germ cells of the Onychophora become localized at an early stage of embryonic development in the median dorsal parts of the splanchnic walls of one or several posterior pairs of coelomic sacs (fig. 34 A, *Grm*). According to Evans (1902) there are four embryonic genital somites in *Eoperipatus weldoni*, while Kennel (1888) says the germ cells of *Peripatus edwardsi* occur in but one somite. Whatever the number of genital segments may be in modern forms, we must suppose that the germ cells once occupied most of the somites, for the early embryonic relation of the germinal centers to the coelomic sacs is identical with the adult condition in the Polychaeta, and undoubtedly means that in the primitive Onychophora the gametes were discharged into the coelomic sacs (*A*, *Spz*), and were liberated from the latter through the coelomoducts (*d*). As we have seen, the upper parts of all the coelomic sacs between

the somite of the oral papillae and the somite of the genital ducts become constricted from the ventral parts (fig. 32 C, *a*), and then separated as independent dorsal compartments (D, *a*). In the pre-genital somites the dorsal compartments disappear, but in the definitive genital somites they persist as gonadial sacs containing the germaria (fig. 34 C, *G*). The gonadial sacs of each lateral series,

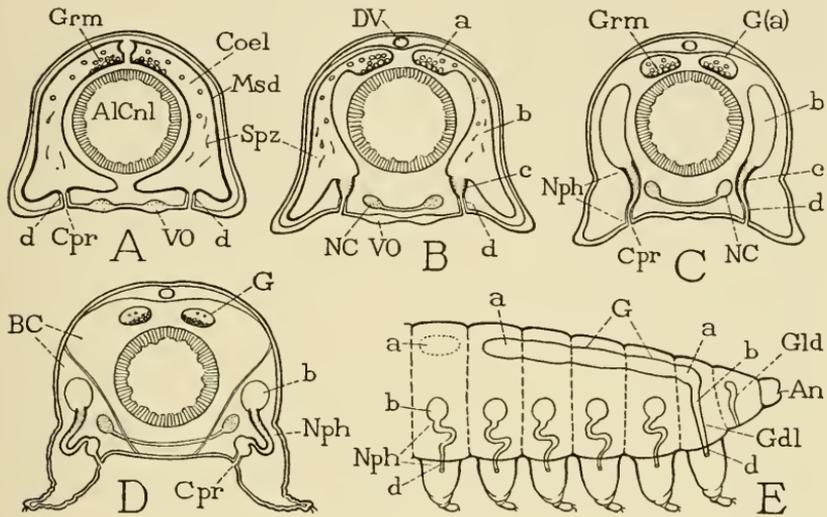


FIG. 34.—Diagrams showing the transformation of the onychophoran coelomic sacs and coelomoducts into genital organs and nephridia. (From Snodgrass, 1936, based on Sedgwick, 1885, Kennel, 1888, and Evans, 1902.)

A, theoretical primitive stage in which excretory products and the gametes were discharged from the coelomic sacs through coelomoducts. B, C, D, differentiation and division of the coelomic sacs into dorsal gonadial sacs (*a*) and ventral nephric sacs (*b*), the last finally reduced (D) to end-sacs of the nephridia. E, gonadial sacs of definitive genital segments united on each side in a gonadial tube (*G*) opening through undivided coelomic sac of penultimate somite.

a, gonadial compartment of primitive coelomic sac; *AlCnl*, alimentary canal; *An*, anus; *b*, nephric compartment of coelomic sac; *BC*, definitive body cavity (haemocoelae); *c*, nephridial diverticulum of coelomic sac; *Coel*, coelomic cavity; *Cpr*, coelomopore; *d*, ectodermal part of coelomoduct; *DV*, dorsal blood vessel; *G*, gonad; *Gdl*, lateral gonoduct; *Gld*, accessory genital gland; *Grm*, germarium; *Msd*, mesoderm; *NC*, nerve cord; *Nph*, nephridium; *Spz*, spermatozoa; *VO*, ventral "organ" of ectoderm.

however, unite in a continuous tube (E, *G*), which becomes the definitive gonad with a germinal band in its ventral wall (C, D, *G*). Furthermore, the posterior ends of the gonadial tubes open into the coelomic sacs of the following somite, and these sacs, which maintain their integrity, and their continuity with the coelomoducts (fig. 32 E, *a, b, c, d*), become the lateral genital ducts (fig. 34 E, *Gdl*). Eventu-

ally the apertures of the lateral ducts come together on the midline of the venter, where they are carried inward at the end of an ectodermal invagination that forms a common definitive exit tube, the ejaculatory duct or median oviduct.

The adult reproductive organs of the Onychophora are strikingly arthropodan in character. In the male, the testes retain the tubular embryonic form (fig. 32 F, *Tes*); each discharges into a seminal vesicle (*Vsm*) from which proceeds a long tubular vas deferens (*Vd*), the anterior part of which is thrown into an epididymislike mass of coils (*Epdm*). The ejaculatory duct (*Dej*) is usually long and irregularly looped; its opening is on the region of the penultimate somite. Associated with the gonopore is a pair of tubular accessory glands (*AcGld*), said to be the reduced coelomic sacs of the last somite (fig. 34 E, *Gld*). In the female, the tubular ovaries are united at their extremities and lie on the dorsal surface of the alimentary canal in the posterior part of the body (fig. 32 A, *Ov*). The oviducts (*Od*) proceed first forward from the posterior ends of the ovaries, and then turn backward to unite beneath the rectum (*Rect*) in a very short terminal atrium, or common oviduct, opening in the same position as the gonopore of the male. In viviparous species the intermediate parts of the oviducts are enlarged in a series of uterine chambers (*Utrs*) containing the embryos. Sperm receptacles usually occur on the lateral oviducts near their ovarian ends.

VI. THE ARTHROPODA

The fundamental characters of the arthropods are those of the Onychophora and the Annelida. The three groups have in common the following features: (1) The ventral elongation of the blastopore and the closure of its intermediate part, resulting in the formation of a tubular enteron with a ventral subapical mouth and a terminal anus, and in the conversion of the preblastoporic region of the trunk into a prostomial cephalic lobe; (2) a definitive tripartite alimentary canal composed of the primitive endodermal enteron, and of a secondary ectodermal stomodaeum and proctodaeum; (3) the differentiation of a part of the mesoblast, originally formed in the posterior end of the body, into a specific mesoderm taking the form of ventrolateral bands that extend forward through the entire length of the body and penetrate into the prostomium; (4) metamerism of the somatic ectoderm and mesoderm, involving a segmental repetition of organs derived from these germ layers; (5) the continuity of the acronal centers of the primary nervous system with the somatic centers

secondarily developed in connection with metamerism; (6) internal cleavage of the mesoderm segments to form paired coelomic cavities; (7) a somatic muscular system applied against the body wall, consisting primarily of an outer set of constrictor fibers running in transverse planes, and of an inner set of contractor fibers taking a longitudinal course, each of which may be variously amplified or reduced; (8) the development of a blood vascular system from the mesoderm, composed essentially of a dorsal and a ventral longitudinal vessel connected by lateral vessels, but often reduced to a dorsal vessel and more or less well-defined sinuses; (9) the association of the germ cells with the walls of the coelomic sacs, and their discharge into the coelom.

The common basic features of organization above enumerated attest the origin of the Arthropoda, the Onychophora, and the higher Annelida from a common ancestral form, which itself must necessarily be visualized as a generalized annelid. It is to be assumed that the progenitors of the three groups had already acquired a lengthened body by the addition of secondary genital somites proliferated from a subterminal zone of growth. Though teloblastic growth does not appear in the ontogeny of the Onychophora, it is quite as characteristic of certain arthropods as of the annelids.

The Arthropoda have in common with the Onychophora the following nonannelid characters: (1) A chitinous ectodermal cuticula; (2) segmental ambulatory appendages formed as simple outgrowths of the body wall, which in their structure and development give no suggestion of a community of origin with the composite parapodia of the Polychaeta; (3) segmental excretory organs (antennal, maxillary, and coxal glands) that resemble the nephridia of Onychophora in being remnants of coelomic sacs connected with the exterior by simple coelomoducts, but which have neither the anatomical position nor the development of annelid metanephridia; and (4) closed gonadal sacs of coelomic origin, containing the germinal centers in their walls, and connected with the exterior by a pair of coelomic sacs set apart to serve as genital ducts. A feature characteristic of both the Arthropoda and the Onychophora is the restoration of the haemocoel as the definitive body cavity, resulting from the reduction of the coelom to the cavities of gonadal and nephridial sacs, but it is not distinctive of them because an obliteration of the coelom occurs also in certain annelids.

The small but important assemblage of characters given above as common to the Onychophora and the Arthropoda would seem to indicate that the two groups have been evolved from the same ancestral

stock, which arose from some generalized nonchaetopodous annelid; but since none of the modern annelids has these characters it is evident that the annelidan progenitors of the Protonychophora-arthropoda have left no direct descendents. The Arthropoda differ in so many respects from present-day Onychophora that it is certain they must have branched off from the common onychophoran-arthropod trunk before the latter had gone far in the onychophoran direction. Arthropod forms were highly developed and differentiated in the early Cambrian period of geological history, and must, therefore, have had their origin in remote pre-Cambrian times, though in the rocks of this period there is no specific evidence of their existence.

As an individualized group, the Arthropoda are characterized particularly by the development of hard plates in the cuticular layer of the integument, separated by areas of flexibility. In the Mandibulata sclerotization results from the presence of nonchitinous substances in the otherwise chitinous cuticula; in the Trilobita and Chelicerata sclerotization may be due to a structural differentiation of the chitin itself, though apparently little attention has been given to the chemical composition of the cuticular skeleton in these groups. Ruser (1933) describes the physical structure of "hard chitin" and "elastic chitin" in the Ixodidae, but makes no determination of their chemical nature.

Since the muscles are primarily attached on the body wall, the differentiation of the latter into hard and flexible areas at once created a possibility for unlimited development of skeletomuscular mechanisms, and it is through the elaboration of such mechanisms that the arthropods have attained their exalted position among the articulates, and their wonderful diversity of structure. It is true, of course, that some of them, particularly those that have taken up parasitic habits, have renounced their birthright, and among the latter we find examples of physical degeneration carried to such an extent that every semblance of arthropod structure may be lost.

Sclerotization of the integument involved first a complete change in the mechanism of body movement, for if the rings of flexibility between segmental plates remained at the primary intersegmental grooves, on which the longitudinal muscles are attached, there would be little if any possibility of movement. Hence, each dorsal and ventral plate includes the primary intersegmental groove in front, while the areas of flexibility occupy the posterior parts of the segmental regions. The sclerotized parts of the primary intersegmental grooves, carrying the muscle attachments, thus come to form internal ridges, or antecostae, on or near the anterior margins of the definitive

tergal and sternal plates, and the primary intersegmental grooves become the submarginal antecostal sutures. As a consequence, a new, *secondary* type of segmentation has been established, in which the functional intersegmental rings are the membranous posterior parts of the primary segments, and the action of the longitudinal muscles becomes intersegmental instead of intrasegmental. A body mechanism of this kind is typical of all the arthropods, but still it is by no means fixed, for innumerable modifications of it have been introduced in adaptation to the development of special structures for specific purposes.

The acquisition of an exoskeleton necessarily limits freedom of body movement, such as that possessed by the highly flexible annelids, but at the same time it furnishes a mechanism by which movements may become more specific, since the development of definite hinge joints becomes possible, and muscles can assume more effective antagonistic relations to each other. The longitudinal muscles lose nothing of their efficiency, but their contraction now results in a telescoping of the body segments. The presence of dorsal and ventral plates, however, necessarily eliminates the constrictor effect of the primitive circular or semicircular muscles; the latter, therefore, have become reduced to lateral tergo-sternal muscles, the contraction of which produces a flattening of the body. The primitive mechanism of dilation and extension by unequal distribution of internal pressure is still operative; but the potentiality of developing endoskeletal structures gives the possibility of a new mechanism of expansion, for the ingrowth of apodemal arms from tergal or sternal areas, on which primarily compressor muscles are attached, may reverse the position of such muscles to the extent that they become dilators. A separation of contiguous plates, however, may be brought about also by the contraction of intersegmental muscles that have been reversed by the overlapping of the plates. All these mechanical devices and many others are variously and often highly developed in the different arthropod groups, and their elaboration has set the arthropods far above the annelids and onychophorons in the power of performing definite and specific acts. Even the wing mechanism of pterygote insects has been built up from little more than the skeletal parts and musculature common to the body segments. It should be observed, however, that although the musculature of the body segments and the appendages is fairly definite and fixed within the major arthropod groups, there seems to be no limit to the potential genesis of new muscles in connection with special organs, such as the male genitalia of insects, and, furthermore, that the entire body musculature is

subject to adaptive changes, which may be very extensive, as in certain holometabolous insect larvae.

Sclerotization of the integument has affected not only the wall of the body, but also the walls of the tubular segmental appendages, and the latter are jointed by definite rings of flexible membrane interposed between the resulting limb segments, or podomeres. Hence, the arthropod limb itself has possibilities of much variety and specificity of action. As a consequence, while probably the appendages in the first place were all simple locomotor organs, many of them have been converted into instruments adapted to various purposes, and those that still subserve the locomotor function are capable of all the kinds of mechanical progression except flying known among animals.

Concomitant with the evolution of the skeletomuscular mechanisms, the nervous system and the sense organs have necessarily acquired a high state of development, and the elaboration of most intricate instincts has been possible because of the facility with which tools may be produced and adapted to their ends.

The primitive arthropods, being closely related to the primitive onychophorons, and together with the latter derived from generalized annelids, must have been slender, many-segmented, polypodous creatures resembling modern centipedes. They differed from their contemporaneous onychophoran relatives in having dorsal and ventral segmental plates and specifically jointed appendages. The Protarthropoda were early differentiated into primitive trilobites and primitive mandibulate forms. From the primitive trilobites were evolved the later Trilobita, Xiphosurida, Eurypterida, and Arachnida, while the Protomandibulata gave rise to the Crustacea, the Diplopoda, the Chilopoda, and the Hexapoda.

EARLY EMBRYONIC DEVELOPMENT

The processes of cleavage and germ-layer formation are so variable among the arthropods that they can have little value in a phylogenetic study of arthropod relationships. Cleavage, whether total or partial, results usually in the formation of a superficial blastoderm, and the embryo appears as a germ band on the ventral side of the egg. Gastrulation in some of the Crustacea takes place by invagination, but more commonly both the endoderm and the mesoderm are formed by delamination or by proliferation from the blastoderm or the germ band. Manton (1928) gives a precise account of the proliferation of the germ layers and the primary germ cells from the blastoporic region in the crustacean *Hemimysis*, the cells of the several groups

being first differentiated on the surface of the germinal disk. The first endoderm cells in many of the arthropods scatter through the yolk as independent trophocytes (vitellophags) and the definitive enteron may then be formed either by a reassembling of the cells about the yolk, or by regeneration from intact endodermal rudiments.

The mesoderm in some of the Crustacea, Chilopoda, and Chelicerata is proliferated forward from a posterior generative zone very much in the manner of the onychophoran mesoderm, and suggestive of the teloblastic origin of the coeloblast in the Annelida. Among the Crustacea there are in fact a few cases in which the mesoderm takes its origin, at least in part, from a single pair of teloblastomeres derived from the endoderm, as in the cirriped *Lepas*. The mesodermal telo-

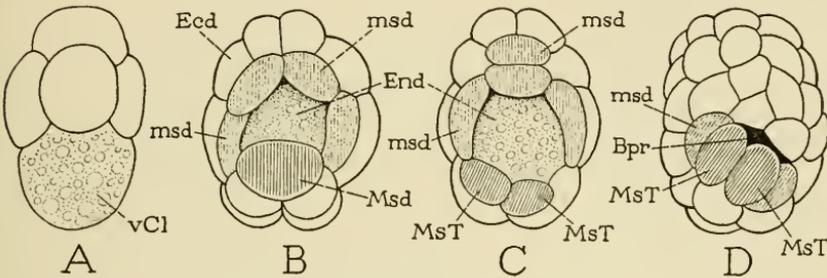


FIG. 35.—Early stages in the development of a cirriped, *Lepas*. (Simplified from Bigelow, 1902.)

A, 8-cell stage, with large yolk-filled posterior cell. B, 30-cell stage, endoderm surrounded by mesoderm comprising a posterior cell (*Msd*) of endodermal origin, and four cells (*msd*) of ectodermal origin. C, the posterior mesoblast cell divided into mesodermal teloblasts (*MsT*). D, near close of gastrulation, but with mesoderm cells still exposed.

Bpr, blastopore; *Ecd*, ectoderm; *End*, endoderm; *Msd*, endodermal mesoderm; *msd*, ectodermal mesoderm; *MsT*, mesodermal teloblast; *vCl*, yolk-filled cell at vegetative pole of morula.

blasts of *Lepas*, according to Bigelow (1902), appear in the 32-cell stage on the posterior lip of the blastopore (fig. 35 C, *Mst*), and are produced from a single mesoblast cell (B, *Msd*) that results from the division of a primary yolk-filled blastomere (A, *vCl*) at the posterior pole of the morula. Four other mesoblast cells, however, are formed in *Lepas* from the ectodermal lips of the blastopore (B, C, *msd*), and eventually the entire mesoblast sinks into the blastopore (D). A separate destiny of the mesoblast from the two sources, entoblastic and ectoblastic, has not been distinguished in *Lepas*, but it is a point of much interest to note that here the mesoblast *completely surrounds the open blastopore* between the ectoderm and the endoderm, a part of it being of endodermal and a part of it of ectodermal

derivation. It is not difficult, then, to understand from this condition how, in forms having a *closed* blastopore, the coelomic mesoblast may arise from the entire length of the linear blastoporic area, and we may further see some significance in the statement by Sedgwick (1887) that in the onychophoron *Peripatopsis* the mesoderm bands in their forward growth are augmented by cells derived from the lips of the blastopore. In the more specialized types of arthropod development evidence of teloblastic generation of the mesoderm is entirely lost, or at least obscured, and the whole of the mesoderm appears to be a direct product of the germ band closely associated with the endoderm. In its full development the arthropod mesoderm surrounds the blastopore anteriorly, since in the adult the lateral bands of the cephalic mesoderm may be continuous from side to side in front of the mouth.

Segmentation of the mesoderm and the subsequent formation of coelomic sacs take place in the early embryonic stages of many Crustacea and Arachnida almost as completely as in the Onychophora and Annelida, but in the myriapods the coelomic sacs are small, and in the insects they are for the most part represented only by cleavage spaces in the lateral parts of the mesoderm. In all cases, however, the walls of the sacs break down, except such parts of them as are retained in the formation of certain organs of coelomic origin, and the haemocoel is restored as the definitive body cavity. Probably all muscle tissue of the arthropods is produced from the coelomic mesoblast; though some writers have claimed that certain muscles are produced directly from the ectoderm, the evidence is open to question and needs closer scrutiny (see Needham, 1937).

PRIMARY AND SECONDARY SOMITES

There is ample reason from arthropod ontogeny for believing that the arthropods have been derived, as have the annelids, from primitively unsegmented ancestral forms in which metamerism first appeared as a direct subdivision of the primary body region into a small number of somites, and that the subsequent increase in the number of somites proceeded secondarily from growth in a subterminal zone of undifferentiated cells. This dual method of somite production is recapitulated in the embryogeny of some of the arthropods, and teloblastic growth is of frequent occurrence in postembryonic development.

In the Trilobita it seems very probable, as contended by Iwanoff (1933) and Schulze (1936), that the so-called head represents the

area of primary segmentation, for there is no doubt that the post-cephalic segments are produced by teloblastic growth. The youngest trilobite larvae known give no evidence of metamerism (fig. 46 A), but there soon appears in the glabellar region four pairs of lateral impressions or transverse grooves that divide the glabella into five consecutive lobes (fig. 36 A). These depressions produce internal

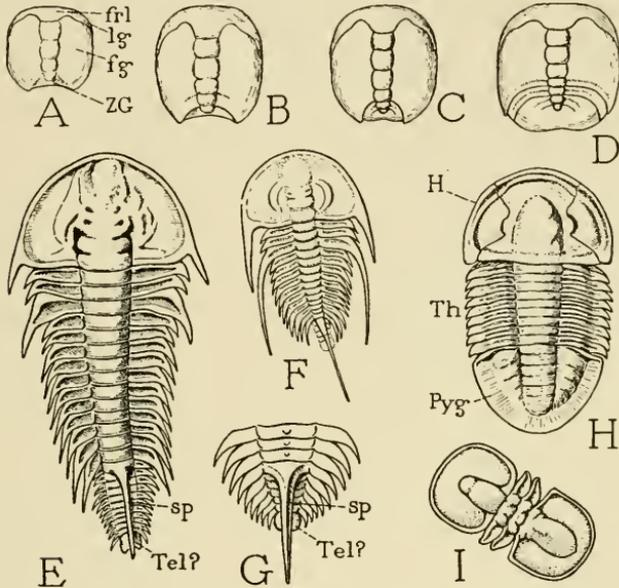


FIG. 36.—Segmentation and tagmosis of Trilobita.

A-D, four successive stages in larval development of *Liostracus linnarssoni* Brögger (from Warburg, 1925). E, *Olenellus vermontanus* Hall (from Walcott, 1910). F, *Olenellus gilberti* Meek (from Walcott, 1910). G, *Schmidtiellus nickwitzii* Schmidt, distal body segments (from Walcott, 1910). H, *Asaphiscus wheeleri* Meek, example of a trilobite with distal segments united in a caudal fan, or pygidium (from Walcott, 1916). I, *Agnostis montis* Matthew, example of the group Agnostia having only two free segments between head and pygidium (from Walcott, 1908).

fg, fixed cheek, or fixigene; *frl*, frontal lobe; *H*, head; *lg*, free cheek, or librigenae; *Pyg*, pygidium; *sp*, spine; *Tel?*, terminal lobe of body, probably the telson; *Th*, thorax; *ZG*, zone of growth.

ridges or apodemes most probably for muscle attachments, and their formation, therefore, does not represent the process of segmentation itself, but unquestionably they mark the primary intersegmental lines of the segments united in the larval body. The first glabellar division, known as the frontal lobe (A, *frl*), is continuous with a pair of lateral areas (*lg*) that become the "free cheeks" of the adult bearing the compound eyes (fig. 46 E, *lg*). The frontal lobe, therefore, may

be regarded as a part of the eye segment, or acron, and further reasons for so regarding it will be given later. The other four glabellar lobes must then represent four primary larval somites, the intersegmental lines of which should, theoretically, have extended to the lateral margins of the simple oval body before segmentation in the latter was suppressed. The postlarval somites of the adult trilobite are generated teloblastically (fig. 36 B, C, D) from a small region of the larva behind the glabella (A, ZG), and are, therefore, clearly secondary somites. The definitive segments of the postcephalic series remain distinct in some of the trilobites to the end of the body (E, F), where there is a small terminal lobe (E, G, *Tel?*) that may be the telson; in others the posterior segments are united in a tail-fan, or pygidium (H, *Pyg*), and in the *Agnostia* (I) only two segments retain their independence between the head and the pygidium.

The Xiphosurida in the adult stage resemble the Trilobita in so many respects that we should expect to find an even closer approach to the trilobite structure in their developmental stages; and, in fact, it has been shown by Iwanoff (1933) that the primary segmentation in the embryo of *Limulus moluccanus* produces four somites (fig. 37 A, I-IV), those of the chelicerae, the pedipalps, and the first two pairs of legs, which evidently represent the four postacronal head somites of a trilobite. Because of the large amount of yolk in the ectoderm, embryonic metamerism appears first in the mesoderm, which is early divided almost simultaneously into four sections corresponding with the four primary somites. The preoral cephalic region of *L. moluccanus*, Iwanoff says, is at first not distinctly differentiated from the surrounding blastoderm, but later it becomes apparent as a preoral head segment without appendages, and in an older embryo it forms a pair of definite cephalic lobes (B, *Prc*). Behind the fourth somite there is in the young embryo (A) only an unsegmented tail piece, but at the base of this region are later generated consecutively (B) the remaining segments of the adult, which are thus typically teloblastic in the manner of their formation.

It would thus appear that the primary segmentation of the ancestors both of the trilobites and the xiphosurids produced only four somites. These four primary somites, united with one another and with the cephalic lobe, or acron, constitute the "head" in the Trilobita (fig. 36 H, *H*); in the Xiphosurida they form the anterior part of the prosoma, for in this group three following somites and part of a fourth are combined with the four primitive somites in the anterior section of the body (fig. 47 E). Moreover, in the Xiphosurida a union has taken place between all the opisthosomatic somites, so that

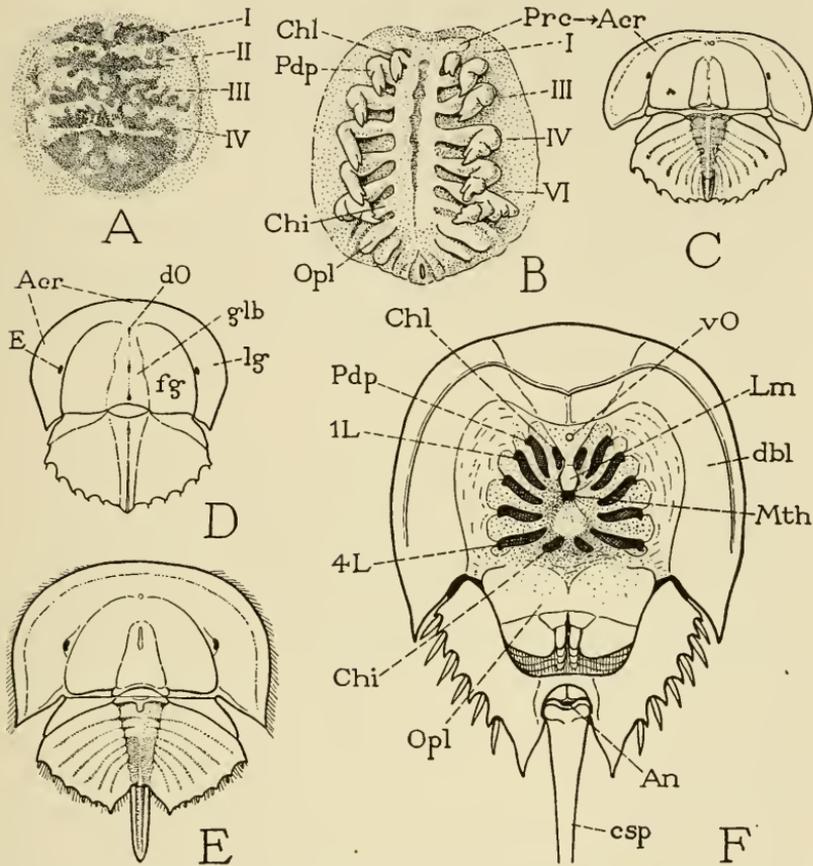


FIG. 37.—Embryonic and adult segmentation of *Limulus*. (A-E from Iwanoff, 1933.)

A, *Limulus moluccanus* Linn., germ band with mesoderm divided into four postoral somites, cephalic lobes not yet differentiated from blastoderm. B, same, embryo with nine pairs of appendages, cephalic lobes (*Prc*) present. C, first instar larva, segments of opisthosoma indicated by internal mesoderm bands before moulting. D, first instar larva before moulting stage. E, second instar larva. F, *Limulus polyphemus* Linn., young adult, ventral view, prosomatic appendages removed, showing radial position of their bases around the central mouth.

Acr, acron, derived from procephalic lobes of embryo; *An*, anus; *Chi*, chilarium; *Chl*, chelicera; *csp*, caudal spine; *dbl*, doublure; *dO*, dorsal ocellus; *E*, compound eye; *fg*, fixigene; *glb*, glabella; *I-VI*, first six somites; *L*, leg; *lg*, librigenae; *Lm*, labrum; *Mth*, mouth; *Opl*, genital operculum; *Pdp*, pedipalp; *Prc*, procephalic lobe; *vO*, ventral ocellus.

there is no intermediate region of free somites as in the Trilobita and Agnostia (fig. 36 H, I).

The adult structure of *Limulus* contains evidence of the presence of 14 postoral somites, the last somite being behind the last gill-bearing segment (fig. 47 D, XIV); but Iwanoff (1933) says that in the embryo rudiments of three somites appear in the postbranchial region, giving thus a total of 16 somites anterior to the caudal spine. The caudal spine of the Xiphosurida is often called the "telson," but, as shown by Schulze (1936), a comparison with the subterminal spine of such trilobites as *Mesonacis* and *Olenellus* (fig. 36 E, F, G), which arises from a segment some distance from the end of the body, suggests that the caudal spine of the xiphosurids may not be a true terminal structure, and that several primitive somites beyond it may have been lost.

Studies on the embryogeny of Arachnida have not brought out any distinction between primary and secondary somites, and the arachnids have no postembryonic teloblastic growth. Schulze (1936), however, has pointed out many features in the adult structure of the arachnids, especially in the Acarina, that suggest the trilobite type of segmentation. The area of the four primary somites, he shows, is often evident as a differentiated anterior region of the prosoma, and in the segmentation and body form of such acarinids as *Oxypleurites* there may be seen a striking general resemblance to a mesonacid trilobite. The arachnid prosoma contains six postacronal somites, and in this respect, therefore, is intermediate between the trilobite "head" and the xiphosurid prosoma.

The embryonic development of segmentation in the Crustacea has been particularly studied by Sollaud (1923) in the palaemonid *Leander*. The germ band of *Leander* is at first V-shaped (fig. 38 A), its two arms diverging forward on the blastoderm from a posterior area of proliferation (*GD*) in the region of the blastopore, whence also are proliferated forward two corresponding bands of mesoderm. Each mesoderm band soon becomes divided into four consecutive parts, which appear as four lobes on the surface (B). The germ bands themselves gradually become less divergent, and finally their anterior ends curve mesally and unite by a bridge between their anterior lobes (C). At the same time the rudiments of three pairs of appendages appear on the second, third, and fourth lobes, which are respectively the first antennae (B, D, *1Ant*), the second antennae (*2Ant*), and the mandibles (*Md*). The first lobes (*Prc*) have no appendages, but they give rise to the compound eyes and the optic ganglia. There now appear in the ectoderm of the young embryo,

Sollaud says, three transverse grooves which define the first segmentation (D). The most anterior groove runs between the first and second pairs of antennae, the next between the second antennae and the mandibles, and the third behind the mandibles. The body of the embryo is thus divided into an anterior prostomial head segment

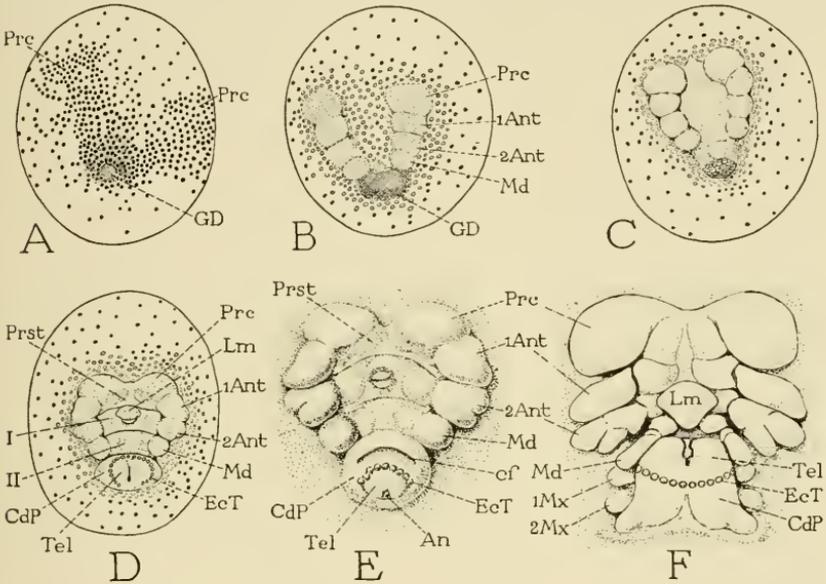


FIG. 38.—Early embryonic stages of a palaemonid crustacean, showing the development of the procephalic lobes and the antennules from the unsegmented prostomial region, and the formation of four primary body somites. (From Sollaud, 1923.) A, *Leander squilla* Linn. B-F, *L. serratus* Pennant.

A, ventral surface of egg showing germinal disk and anterior proliferation of germ bands. B, early nauplius stage with first appearance of appendages. C, later stage with germ bands united anteriorly. D, nauplius stage, with caudal papilla (CdP) differentiated, but circle of ectodermal teloblasts (EcT) yet incomplete. E, older nauplius embryo with ventral groove (cf) in caudal papilla. F, metanauplius stage, with rudiments of first and second maxillae formed on posterior part of nauplius body before generation of teloblastic somites has begun.

1Ant, first antenna; 2Ant, second antenna; CdP, caudal papilla; EcT, ectodermal teloblasts; GD, germinal disk; I, II, first two somites; Lm, labrum; Md, mandible; 1Mx, 2Mx, first and second maxillae; Prc, procephalic lobe; Prst, prostomium; Tel, telson.

(Prst) bearing the procephalic lobes and the first antennae, a second segment (I) bearing the second antennae, a third segment (II) bearing the mandibles, and a terminal unsegmented piece (CdP), which is the caudal papilla. The embryo is now in the nauplius stage. The first segment, bearing the optic lobes and first antennae, Sollaud

claims, is the prostomium, the other two segments being the first and second true somites (*I, II*). (See also Sollaud, 1933.)

The caudal papilla of the malacostracan embryo (fig. 38 D, E, *CdP*) projects from the blastoderm. In its distal part is a circle of undifferentiated cells, ectodermal (*EcT*) and mesodermal, which are the teloblasts that will generate the postnaupliar somites. Beyond the teloblasts is the region of the telson (*Tel*) containing the anus (*An*). In its development the caudal papilla bends forward (*F*) beneath the part of the embryo contained in the blastoderm.

When the malacostracan embryo reaches the metanauplius stage there appear at the base of the caudal papilla the two maxillary somites and their appendages (fig. 38 F, *1Mx*, *2Mx*). In a study of the development of *Hemimysis*, Manton (1928) includes the two maxillary somites in the part of the body produced from the teloblasts. Sollaud (1923), however, asserts that in *Leander* both maxillary somites arise from the base of the caudal papilla before the beginning of activity in the teloblast, and that the first somite of the teloblastic series is that of the first maxillipeds. According to Sollaud, therefore, the four somites of the metanauplius (*F*), namely, those of the second antennae, the mandibles, the first maxillae, and the second maxillae, are primary somites formed directly in the primitive embryonic body between the acronal prostomium and the caudal papilla. If so, it would seem to be more than a coincidence that the same number of primary somites occurs in Malacostraca, Xiphosurida, and Trilobita.

In most of the entomostracan Crustacea the embryo hatches in the nauplius stage when only three pairs of appendages are present (fig. 4 B). The trunk is not yet distinctly segmented, but it consists of three regions. The first region is a preoral cephalic lobe bearing a median eye, the first antennae (*1Ant*), and the labrum; the second carries anteriorly the second antennae (*2Ant*) and the mandibles (*Md*), and includes posteriorly the area on which the first and second maxillae will be formed; the third region is a terminal unsegmented lobe, the telson, at the base of which is the generative zone from which will be formed the teloblastic somites. The nauplius, therefore, represents an ontogenetic stage in which the body region of the four primary somites is present, though the appendages of the posterior two of these somites are as yet undeveloped.

The crustacean nauplius has often been likened to the trochophore larva of the Polychaeta (fig. 4 A), and the two forms are comparable in so far as each represents an early stage of ontogenetic development. We cannot suppose, however, that the arthropods and the annelids

are separately derived from an ancestral form represented by the polychaete trochophore, since the adult arthropods have too many features in common with adult annelids that are not yet present in the trochophore. The common ancestor of the two groups, therefore, is to be found in a much later stage of annelid development than that of the trochophore. The trochophore and the nauplius are specialized larval forms, adapted in their general shape and structure to a temporary pelagic life; but, since they represent an early stage of phylogenetic development, and probably originated as larvae at an early phylogenetic period of evolution in their respective groups, they necessarily show primitive characters in their basic organization.

THE CEPHALIC SEGMENTATION AND THE DEVELOPMENT OF THE BRAIN

The question of the number of segments that enters into the composition of the arthropod "head" has been widely investigated and discussed, but with such lack of uniformity in the results as to lead to the suspicion that interpretation of the observed facts has been too much influenced by theoretical considerations. The writer believes that a more literal acceptance of the known facts of embryonic development in the case of the arthropod head will give a simpler and more satisfactory concept of the fundamental cephalic structure than that which has been current for several decades.

In the first place, it should be understood that there is no specific "arthropod head." The cephalic structure is a variable combination of segments, and the number of cephalized segments may be quite different in different arthropod groups, or even within a single major group. The more complex types of head, such as occur in the Mandibulata, include an anterior procephalic region bearing the labrum, the eyes, and two pairs of antennae, and a posterior gnathal region bearing the mandibles, the first and second maxillae, and in some forms the first maxillipeds or also the second maxillipeds. In the Trilobita the so-called "head" is a combination of at least four postoral somites with the prostomial acron, and the "prosoma" of the Chelicerata is a similar composite structure, except that it contains six or eight somites. On the other hand, in many of the Crustacea, the true head is a primitive structure corresponding with the procephalic part of the head in other mandibulate groups. However, differences of opinion as to the number of somites involved in the head composition pertain chiefly to the procephalic region, since the segments of the gnathal region are usually distinct in the embryo, and are readily identified by their appendages.

On the assumption that the Arthropoda and the Onychophora are derived from generalized annelids, the primary head of the onychophoran-arthropod ancestors must have been the prostomium. The prostomium, therefore, constitutes the *archicephalon* in the series of articulate animals. In the polychaete annelids the prostomium (fig. 39 A, *Prst*) supports two pairs of sensory appendages, the tentacles (*Tl*) and the palpi (*Plp*), and often a median anterior tentacle, and bears dorsally the eyes and the nuchal organs, while between it and the first somite (*I*) is situated ventrally the mouth (*Mth*). The neural elements of the prostomium, probably including originally a median apical ganglion and several paired ganglia developed in connection with the sensory organs (fig. 9 B), unite to form the composite suprastomodaeal nerve mass known as the brain, or archicerebrum (*C*, *D*, *Br*).

The young arthropod embryo characteristically has at the anterior end of the body a large cephalic lobe (fig. 39 B, *Acr*). On this head lobe are developed the eyes, both simple and compound (*E*), the first antennae (*IAnt*), in some cases a pair of transient preantennal rudiments (*Prnt*), and the labrum (*Lm*). The neural elements of the embryonic head, which may include an anterior median ganglionic rudiment and as many as four paired lateral rudiments, soon unite to form the suprastomodaeal brain. The exact parallelism in structure and development between the cephalic lobe of the arthropod embryo and the prostomium of the polychaete worm (A) certainly suggests a morphological identity between the two organs. In neither is there ever any external mark of segmentation, or direct evidence of the confluence of more primitive segments.

Sollaud (1923, 1933), from his study of the development of the crustacean *Leander*, contends that the embryonic head region (fig. 38 D, E, *Prst*) on which are developed the procephalic (ocular) lobes (*Prc*) and the first antennae (*IAnt*) must represent the annelid prostomium, since the first intersegmental groove runs behind the first antennae, and there is no external evidence of segmentation before it. Moreover, in the procephalic nerve ganglia, he says, only a slight constriction occurs at an early stage between the ocular, or protocerebral, parts and the antennal, or deutocerebral, parts. Sollaud asserts, therefore, that there is no valid reason for the commonly accepted view that the first antennae are homodynamous with the following appendages in the sense that they are the appendages of a primarily postoral somite that has been secondarily incorporated with the prostomium. The first antennae of *Leander*, he shows, remain uniramous, while almost from the beginning the second antennae

(D, E, *2Ant*) take on the biramous structure characteristic of the following somatic appendages. The postoral segment of the second antennae is thus, according to Sollaud's interpretation, the first true somite. The same view is strongly advocated by Holmgren (1916) and Hanström (1928) from a comparative study of the annelid and arthropod brain, but, as will be shown later, the evidence adduced by these authors from the brain structure must be qualified by facts of development.

The principal ground for the generally accepted belief that the acronal region of the arthropod embryo contains one or more "ceph-

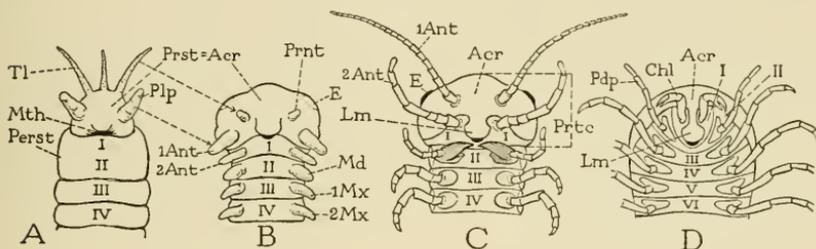


FIG. 39.—Diagrams of cephalization in the Polychaeta and Arthropoda, showing the relation of the annelid prostomium to the arthropod head on the assumption that the first antennae are prostomial appendages.

A, an adult polychaete with prostomial tentacles and palpi, first two somites united in the peristomium. B, an insect embryo in which the head (acron) is an archicephalon representing the annelid prostomium, and may bear two pairs of appendages. C, a theoretical protomandibulate arthropod, in which the head is a protocephalon (*Prtc*) composed of the acron and one somite. D, a chelicerate arthropod, in which the acron is extended laterally and dorsally over several somites united in the prosoma.

Acr, acron (arthropod prostomium); *1Ant*, first antenna (acronal appendage); *2Ant*, second antenna (appendage of first somite); *Chl*, chelicera (equivalent to second antenna); *E*, lateral eye; *I-VI*, first six somites; *Lm*, labrum; *Md*, mandible; *Mth*, mouth; *1Mx*, *2Mx*, first and second maxillae; *Pdp*, pedipalp; *Perst*, peristomium; *Plp*, palpus; *Prnt*, preantenna; *Prst*, prostomium; *Prtc*, protocephalon; *Tl*, tentacle.

lized somites" is the occurrence of temporary coelomic sacs in this region. However, it has not been shown that the presence of cavities in the cephalic mesoderm is necessarily indicative of somites, and it would seem that the burden of proof should be on the positive side of this question.

The mesoderm bands of the annelids, as shown in an earlier part of this paper, extend forward in the sides of the body from their posterior centers of propagation. In the trochophore larva the mesoderm is arrested at the mouth, but in the later development of the worm the bands extend into the prostomium and may here contain a pair of coelomic cavities. While it is usually observed that the pro-

stomial coelom of the annelids is a continuation from the coelomic cavities of the first somite, it is claimed by Binard and Jeener (1928) that the prostomial cavities of the spionid *Scolecopsis fuliginosa* belong to a distinct pair of mesodermal sacs associated with the palpi. In the Onychophora and Arthropoda the mesoderm likewise extends into the head region at the sides of, or before, the stomodaeum (fig. 41 A), and is usually excavated by a pair of well-developed coelomic sacs pertaining to the antennae (C, *AntCS*); but in the arthropods there may be formed also a pair of sacs pertaining to transitory preantennal appendages (fig. 42 B, *PrntCS*), and even a third pair in the labral region (D, *LmCS*). The position of the antennal sacs, as that of the antennal rudiments themselves, is somewhat variable in different arthropods, both structures being in some cases postoral, in others adoral, and again preoral; in the Onychophora the antennal sacs are decidedly preoral, though their posterior mesal ends embrace the stomodaeum and give rise to some of the stomodaeal muscles. The preantennal sacs are usually slightly preoral; the labral sacs lie directly before the mouth.

When we consider that the forwardly growing mesoderm bands, in their fullest development, should finally meet in front of the blastopore, it is evident that coelomic cavities formed in the cephalic region must assume adoral and preoral positions with their axes centering in the mouth (fig. 40 B). Being thus *radial* in position, the cephalic coelomic sacs cannot represent "somites" in the manner of the paired sacs lying posterior to the mouth, which are transversely opposed to each other. Hence, the assumption that these anterior sacs represent "cephalized somites" is inconsistent with the anatomical conditions that arise in the acronal region of the trunk. Moreover, as we have seen in a study of the annelids, the coelomic sacs themselves do not determine metamerism; the segmentation of the postoral parts of the mesoderm bands is secondary to metamerization of the primary somatic muscular system, and the coelomic cavities are later formed probably for physiological purposes. The coelomic sacs, therefore, correspond with the somites in the segmented part of the trunk, but similar mesodermal cavities might be formed for the accumulation of waste products in an unsegmented region such as the prostomium. The usual absence of well-differentiated coelomic sacs in the annelid prostomium, and the fact that the fullest development of the head sacs is found in the higher arthropods indicate that the formation of cavities in the cephalic mesoderm is a secondary accompaniment of advancing organization in the prostomial lobe; but the temporary

nature of the head cavities might equally suggest that they are purely ontogenetic structures, as claimed by Faussek (1899, 1901), for coelomic cavities in general.

The association of the antennal coelomic sacs with the antennae and the association of the preantennal sacs with preantennal appendicular rudiments suggest that in a primitive stage there may have

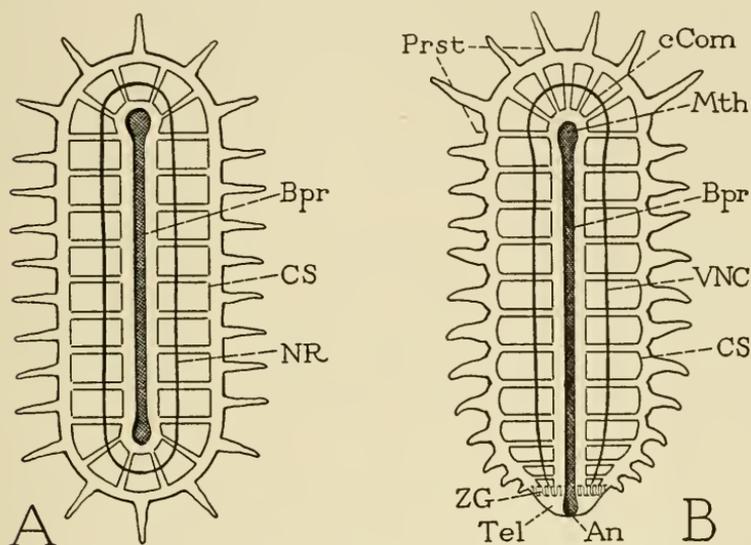


FIG. 40.—Diagrams illustrating two theories of the fundamental structure of the Articulata.

A, the theory of radial structure, based on a supposed origin of the articulata from a zoantharian polyp, according to which the coelomic sacs represent radial pouches of the enteron, and the nervous system a circumoral nerve ring, segmentation of the body being determined by the enteric pouches.

B, the theory adopted in this paper, which assumes an origin of the articulata from a creeping wormlike ancestor, based on the facts that, though the mouth is subapical, the anus is terminal, and that in embryonic development segmentation precedes the formation of the coelomic sacs, which have no connection with the enteron; the mesoderm, being teloblastic, grows forward, and, in its fullest development, may surround the mouth anteriorly, and thus give rise to a secondary radial symmetry in the prostomial region.

Bpr, blastopore; *cCom*, cerebral commissure; *CS*, coelomic sac; *Mth*, mouth; *NR*, nerve ring; *Prst*, prostomium; *VNC*, ventral nerve cord.

been a pair of appendages in the labral region corresponding with the labral sacs. Some writers have contended that the labrum itself represents a pair of united appendages, but since the labrum is immediately preoral, a pair of "labral" appendages in an annelid would arise from the base of the prostomium. Perhaps, by a long stretch of the imagination, the labral sacs might better be correlated with a hypothetical pair of primitive apical prostomial tentacles (fig. 40 B),

possibly represented by the median tentacle of certain Polychaeta (fig. 13 C), which, having a double nerve root in the brain (fig. 45 B, C, *ITINv*), might be supposed to have had itself a double origin. However, the possibility of the median polychaete tentacle having been formed by the union of a pair of apical tentacles is denied by Binard and Jeener (1928).

The theory here proposed to explain the occurrence of coelomic sacs in the prostomial region of the articulate animals has no relation whatever to the theory of Sedgwick (1884), Lameere (1926), and Binard and Jeener (1928) that the annelids and arthropods are derived from a coelenterate polyp form, and therefore have fundamentally a radial organization (fig. 40 A). A radial structure secondarily affects the anterior end of the articulate trunk because of the subapical position of the mouth (B); but the terminal position of the anus creates a quite different structure at the posterior end.

The term *acron* (Janet, 1899) is frequently used by students of arthropod embryology to designate the apical part of the arthropod head that lies anterior to the first true somite; its exact application, therefore, differs according to each writer's interpretation of the head segmentation. Janet defined the acron as the preantennal part of the head. As the term is used in the present paper, the arthropod acron is equivalent to the annelid prostomium, and is represented in the arthropod embryo by the cephalic lobe (or lobes) bearing the eyes, the labrum, the preantennae, and the first antennae. The prostomium is primarily the anterior part of the trunk not invaded by the blastopore (fig. 6 D, *Prst*); the median part of the arthropod acron is always preoral, but its lateral parts may lap backward and extend even a considerable distance behind the mouth. The *telson* at the posterior end of the trunk is not morphologically equivalent to the acron. It is traversed by the alimentary canal, and has the anus at its extremity; it does not contain coelomic sacs, but its representative in the annelids, the so-called pygidium, may support a pair of tentaclelike appendages.

The principal reasons for regarding the oculo-antennal region of the arthropod head, here defined as the acron, as representing a primarily unsegmented archicephalon corresponding with the annelid prostomium may be summarized as follows: (1) There is never any external division of the acronal region into segmental areas; (2) there is no specific evidence of the cephalization of primarily postoral somites, except in the case of the tritocerebral somite; (3) the embryonic coelomic sacs of the first antennae, the preantennae, and the labrum are formed directly where they occur in the cephalic meso-

derm, and give no evidence of having been drawn forward from behind the mouth; (4) coelomic sacs of the acronal region, so far as known, are best developed in the higher arthropods, and thus do not appear to be primitive structures; (5) the protocerebral and deutocerebral parts of the brain are always connected by preoral commissures, the only postoral cerebral commissure being that of the cephalized tritocerebral ganglia; (6) the mouth and labrum are innervated from the tritocerebral ganglia, which would not likely be the case if several other postoral ganglia preceded the tritocerebral ganglia; (7) paired appendages, sense organs, and primarily discrete nerve centers pertain both to the annelid prostomium and to the arthropod acron; (8) the first antennae of the arthropods never have

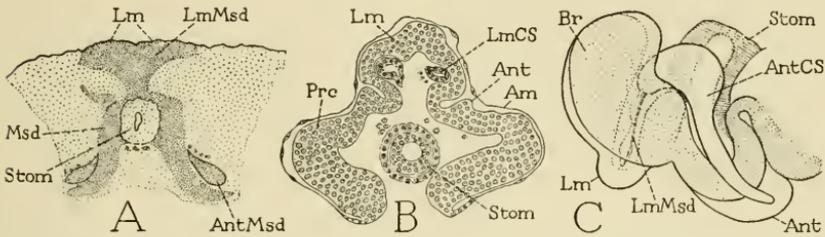


FIG. 41.—Development of the procephalic mesoderm in Orthoptera. (A, B from Roonwal, 1937; C from Wiesmann, 1926.)

A, horizontal section of anterior end of 52-hour embryo of *Locusta migratoria* Linn. showing cephalic mesoderm extending to labrum anterior to stomodaeum. B, same of 56½-hour embryo, with coelomic cavities in labral mesoderm. C, reconstruction of head of embryo of *Carausius morosus* Brunner, lateral view, with developing antennal coelom, and mesoderm extending into clypeolabral region.

Am, annion; *Ant*, antenna; *AntCS*, antennal coelomic sac; *AntMsd*, antennal mesoderm; *Br*, brain; *Lm*, labrum; *LmCS*, coelomic sac of labrum; *LmMsd*, labral mesoderm; *Msd*, mesoderm; *Prc*, cephalic lobe; *Stom*, stomodaeum.

the structure or musculature of the following appendages; in the Crustacea they are never truly biramous.

A brief review of the facts now known concerning the development of the procephalic mesoderm and nervous system of the arthropods will show that the facts are not inconsistent with the idea that both coelomic sacs and multiple nerve centers may be formed directly in the otherwise unsegmented acronal region, and that the phenomena of embryonic development pertaining to the head are most easily understood if they are taken approximately at their face value for phylogenetic recapitulations.

The cephalic mesoderm of the arthropods is usually continuous with the mesoderm bands of the anterior somites. In a 52-hour embryo of *Locusta*, Roonwal (1937) says, "it is seen that a pair of

mesoderm bands extends upward from the junction of the head-lobe with the trunk and meet over the stomodaeum" (fig. 41 A, *Msd*). The same is true of *Carausius* (B), as shown by Wiesmann (1926), but in the crustacean *Hemimysis*, according to Manton (1928), a part of the preoral mesoderm has an independent origin from the germ band.

Among the Chelicerata the cephalic mesoderm is less developed or differentiated than in the Mandibulata. In *Limulus longispina*, as described by Kishinouye (1893), the first pair of coelomic sacs in the embryo occupies both the cephalic lobe and the cheliceral somite. Later these sacs become partially divided by an incomplete septum into a pair of cephalic sacs and a pair of cheliceral sacs, but the latter soon disappear. In the scorpion, according to Brauer (1895), the cephalic coelom is an extension of the coelomic cavities of the cheliceral somite, and is never shut off from the latter in a pair of specific head sacs. Likewise in the Pedipalpida (*Thelyphonus*) Schimkewitsch (1906) says the coelomic sacs of the head segment are continuous with those of the cheliceral segment. Kishinouye (1894) finds, on the other hand, in the Araneida (*Lycosa* and *Agelena*) a pair of coelomic sacs in the cephalic lobe that are entirely separate from the sacs of the cheliceral somite. The cephalic sacs are later divided each into two parts; the ventral sections disappear, the dorsal sections elongate upward and form between them the cephalic aorta.

In the Mandibulata coelomic cavities associated with the first antennae are of common occurrence in the cephalic mesoderm. A diverticulum from each antennal sac extends into the corresponding antenna (fig. 41 C, *AntCS*) and gives rise to the antennal musculature. The inner dorsal parts of the sacs, as observed by the majority of investigators (see Wiesmann, 1926, Roonwal, 1937), grow mesally into the space between the stomodaeum and the brain, where they extend anteriorly and posteriorly and form the cephalic part of the aorta, including the anterior end of the tubular aorta proper, and an open distributing section that extends from beneath the brain to the clypeal region. The cephalic aorta of the crustacean *Hemimysis*, however, is said by Manton (1928) to be a product of the preantennal mesoderm.

The presence of preantennal coelomic sacs associated with small evanescent rudiments of preantennal appendages (figs. 42 A, 43 A, *Prnt*) is recorded by Heymons (1901) in *Scolopendra* (fig. 42 B, *PrntCS*), and by Wiesmann (1926) in *Carausius* (F, *PrntCS*), and the occurrence of coelomic cavities in the preantennal mesoderm of *Hemimysis* is reported by Manton (1928), though vestiges of pre-

antennal appendages are not known in the Crustacea. In the diplopod *Platyrhacus amauros*, Pflugfelder (1932a) shows that a pair of coelomic sacs is formed in the cephalic lobes of the embryo in con-

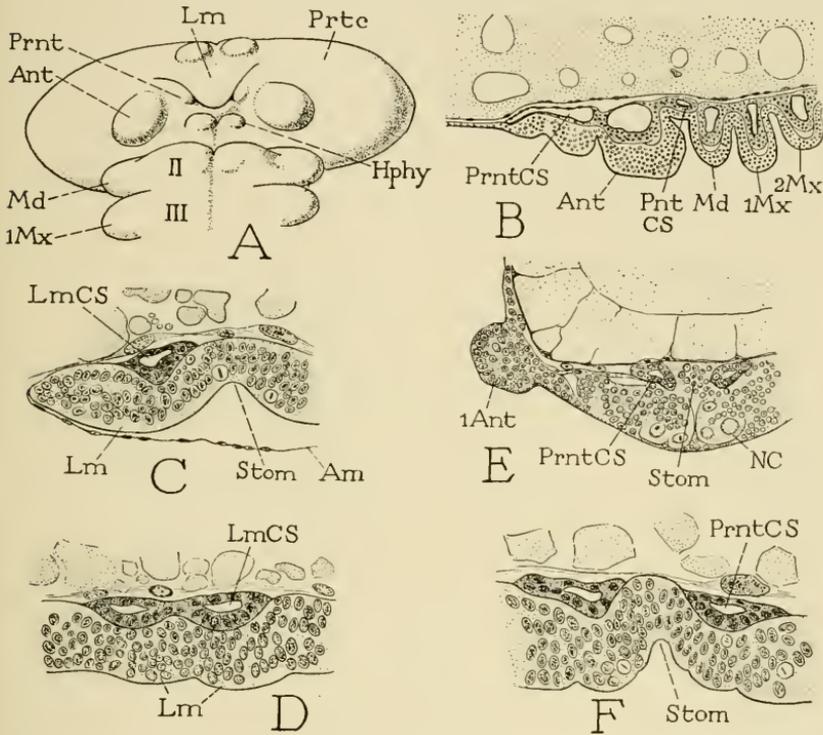


FIG. 42.—Embryonic appendages and coelomic sacs of the procephalic region of an insect, a chilopod, and a crustacean.

A, head (protocephalon) and two following somites of young embryo of *Carausius morosus* Brunner, ventral view (from Wiesmann, 1926). B, lengthwise section through cephalic appendages and coelomic sacs of embryo of *Scolopendra* (from Heymons, 1901). C, lengthwise section through a coelomic sac of the embryonic labral rudiment of *Carausius* (from Wiesmann, 1926). D, cross-section of same through labral coelomic sacs (from Wiesmann, 1926). E, cross-section through preantennular coelomic sacs of embryo of *Hemimysis lamornae* (from Manton, 1928). F, cross-section through preantennular coelomic sacs of embryo of *Carausius* (from Wiesmann, 1926).

Am, amnion; Ant, 1Ant, first antenna; Lm, labrum; LmCS, labral coelomic sac; Md, mandible; 1Mx, 2Mx, first and second maxillae; PntCS, postantennular coelomic sac; Prnt, preantenna (preantennule); PrntCS, preantennal (preantennular) coelomic sac; Prtc, protocephalon (acron and first somite); Stom, stomodaeum.

nection with the protocerebral lobes of the brain (fig. 44 D, *Pcr*), and a second pair in connection with the deutocerebral lobes (*Dcr*). Hence, if there is any necessary homology between the cavities of the cephalic mesoderm in different arthropods, the "protocerebral"

sacs of *Platyrrhacus* should represent the preantennal sacs of *Scolopendra*, *Carausius*, and *Hemimysis*, though there are in the diplopod, as in the crustacean, no corresponding appendage rudiments. While, in most cases observed, the preantennal mesoderm is a part of the general mesoderm, the preantennal mesoderm of *Hemimysis* is said by Manton (1928) to have an independent origin from the germ band just behind the optic lobes. When the arms of the V-shaped germ band of *Hemimysis* later come together, the preantennal mesoderm rudiments are approximated immediately before the mouth. In their growth, Manton says, they extend posteriorly and embrace the lateral and dorsal walls of the stomodaeum, their cavities entirely disappear, and their walls give rise to a part of the stomodaeal ("stomach") muscles, and to the cephalic aorta.

Coelomic sacs of the labral region of the embryonic head were first described by Wiesmann (1926) in the stick insect, *Carausius morosus*, and have since been observed by Mellanby (1936) in the hemipteron *Rhodnius*, and by Roonwal (1937) in a grasshopper, *Locusta migratoria*. Pflugfelder (1932a) describes in the diplopod *Platyrrhacus* a pair of mesodermal cavities in the "clypeus" (fig. 44 D, *Clp*), but since these cavities lie immediately before the mouth, they evidently correspond with those called "labral" in the insects. In both *Locusta* (fig. 41 A) and *Carausius* (C) the head mesoderm extends into the labrum (*LmMsd*) anterior to the stomodaeum (*Stom*), and the cavities formed in it are thus literally preoral in position (fig. 42 C, *LmCS*); the mesal walls of the labral sacs of *Carausius* are united before the mouth (D). In *Locusta*, Roonwal says, the labral and stomodaeal mesoderm is loosely continuous prior to the appearance of the labral cavities (fig. 41 A), but when the sacs are formed the latter are independent structures (B, *LmCS*). After the disappearance of the cavities the coelomic cells remain as two bodies of mesoderm that suggest similar mesodermal masses found in the labrum of certain other insects in which corresponding cavities are not known to occur.

The definitive brain of the mandibulate arthropods consists of an anterior bilobed part, including the protocerebrum and the deutocerebrum, which innervate respectively the eyes and the first antennae, and of a pair of posterior lobes, the tritocerebrum, which innervate the second antennae when these appendages are present. The proto-deutocerebral lobes are always united above the stomodaeum, and thus appear to belong to the prostomial part of the head; the tritocerebral lobes, on the other hand, are unquestionably derived from the postoral somite of the second antennae, and are connected by a

postoral commissure. In many cases the dorsal lobes are developed in the embryo from a single pair of generative centers in the ectoderm, just as are the corresponding lobes of the brain in the Onychophora and in some of the Annelida. Considering, however, that the annelid brain, as shown in the larva of *Lopadorhynchus*, has probably taken its origin from a number of discrete prostomial ganglionic centers corresponding with the sensory organs of the prostomium, we should expect that a more primitive condition in the arthropods would show that the definitive brain of these animals is likewise a composite structure formed by the union of primarily

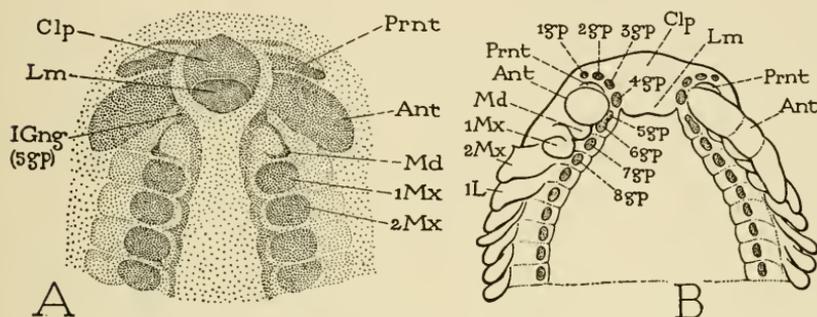


FIG. 43.—Embryonic development of the cephalic appendages and nerve ganglia of a chilopod, *Scolopendra*. (From Heymons, 1901.)

A, anterior end of germ band with rudiments of appendages, including preantennal, antennal, mandibular, and maxillary lobes, but no rudiments of postantennal (intercalary) appendages, though postantennal (triticerebral) somite marked by a pair of ganglia (*IGng*). B, same, later stage (antenna removed on left), showing ganglionic pits (*gp*) of ectoderm from which ganglia are developed.

Ant, antenna; *Clp*, clypeus; *1gp*, generative pit of optic ganglion; *2gp*, pit of protocerebral ganglion; *3gp*, pit of preantennal ganglion; *4gp*, pit of antennal ganglion; *5gp*, pit of triticerebral ganglion; *6gp-8gp*, pits of mandibular and maxillary ganglia; *IGng*, triticerebral ganglion; *1L*, first leg; *Lm*, labrum; *Md*, mandible; *1Mx*, *2Mx*, first and second maxillae; *Prnt*, preantenna.

separate ganglia. Various studies on the development of the arthropod brain, in fact, demonstrate its diffuse origin.

The best-known example of the development of the arthropod brain from diffuse ganglionic centers is that described by Heymons (1901) in *Scolopendra*. The embryonic cephalic appendages of *Scolopendra* that correspond with cerebral rudiments include the persistent antennae (fig. 43 A, *Ant*) and a pair of transient preantennae (*Prnt*), appendages of the postantennal "intercalary," or triticerebral, somite being absent. The definitive brain of *Scolopendra*, according to Heymons, is formed by the coalescence of an anterior unpaired ganglionic rudiment and five paired rudiments. The unpaired rudiment arises

directly from the ectoderm of the clypeal region of the cephalic lobes (fig. 43 B, *Clp*), and appears before any of the appendages except the antennae are formed. The paired rudiments are groups of ganglionic cells proliferated from the inner ends of small ectodermal pits (*1gp-5gp*). The first of these rudiments to be formed (*2gp*) lie at the extremities of the median rudiment, and their cells become closely associated with the latter to produce a cellular mass that becomes the lamina dorsalis of the definitive protocerebrum. Laterad of these rudiments are formed a pair of pits (*1gp*) that furnish principally the cells of the definitive frontal lobes of the brain, and later when the eyes appear give rise also apparently to the small optic lobes. Following the lateral rudiments of the lamina dorsalis on each side are formed in series three other cephalic pits, which generate respectively the primitive ganglionic centers of the preantennae (*3gp*), of the antennae (*4gp*), and of the appendageless tritocerebral somite (*5gp*). The two series of neurogenic pits are continued posteriorly on the mandibular, the maxillary, and the leg somites.

Heymons regards the median unpaired brain rudiment as the equivalent of the annelid "archicerebrum," but it would seem rather to correspond with the ganglion of the apical plate of the polychaete larva. The two paired rudiments that combine with the median rudiment to form the definitive protocerebrum he refers also to the "acronal," or prostomial, part of the head, but the preantennal, antennal, and tritocerebral rudiments he claims represent postoral somites. The preantennal ganglia constitute at first a connection between the protocerebrum and the deutocerebrum, but later they merge so completely into the brain that their identity is lost in the definitive brain structure. The deutocerebral lobes formed of the antennal ganglia lie primarily behind the protocerebrum, but with the forward migration of the antennae they become transposed to a position anterior to the protocephalon and take on a conical form with the antennal nerves issuing from their distal ends. The tritocerebral lobes lie beneath the deutocerebral lobes and are continuous with the stomodaeal connectives.

The claim of Heymons that the preantennal and antennal ganglia represent postoral somites is not substantiated by any external evidence of segmentation in the corresponding cephalic region of the scolopendrid embryo, and as represented in Heymons' figure (fig. 43 B) these ganglia appear to be actually preoral in position. In none of the arthropods do the true cerebral ganglia have postoral commissures, but the preoral position of their commissures in the brain mass, Heymons says, is to be explained ontogenetically by the

fact that the commissures are not formed until after the respective ganglia have taken a preoral position. This proposed explanation, however, is merely the statement of a fact that can as well be taken as evidence that the ganglia themselves are morphologically preoral.

In the Diplopoda the embryonic rudiments of the nervous system appear to be completely double, for no median ganglionic center has been observed corresponding with the "archicerebral" rudiment described by Heymons in *Scolopendra*. Preantennal appendages are absent so far as known, and the tritocerebral somite always lacks appendages, as in the Chilopoda. According to Robinson (1907) the nervous system of a 16-day-old embryo of *Archispirostreptus* consists of a pair of trilobed "archicerebral" rudiments situated before the mouth (fig. 44 E, *Arc*), and of two ganglionated nerve cords proceeding posteriorly from the latter around the stomodaeum. The first ganglia of the cords (*AntGng*), which are distinctly postoral, Robinson claims are the antennal ganglia. The next pair, she says, are the ganglia of the tritocerebral somite (*TcrGng*), which has no appendages, and the next pair (*MdGng*) belong to the mandibles. At a later stage (F), just before hatching, the "antennal ganglia" (*AntGng*), to which Robinson says the tritocerebral ganglia are now joined, still lie behind the mouth and are approximated to the median line. It is very surprising, however, that antennal ganglia should be postoral at such a late stage of development, and not yet united with the protocerebrum, so much so, in fact, that the relation of these alleged "antennal" ganglia to the antennae becomes questionable. Robinson gives no evidence of any nerve connection between the ganglia and the antennae (*Ant*); hence we might suspect that the antennae are innervated from the posterior ganglia of the "archicerebral" groups (*Arc*), and that the first postoral ganglia are the tritocerebral ganglia.

Heymons (1897) gives a brief description of the embryo of *Glomeris* (fig. 44 C), in which the antennae (*Ant*) appear as adoral appendages of the cephalic lobes (*Prc*), whence presumably they derive their innervation.

A more detailed account of the cephalic and cerebral segmentation of a diplopod is given by Pflugfelder (1932 a) for *Platyrrhacus amauros*, but it only adds to the difficulties of understanding the development and morphology of the diplopod head. According to Pflugfelder, the protocerebral and deutocerebral elements of the brain appear on the surface of the young embryo of *Platyrrhacus* as a single pair of preoral cephalic lobes (fig. 44 A, *Prc*). Just behind the mouth is the somite of the antennae (*Ant*), and the latter is

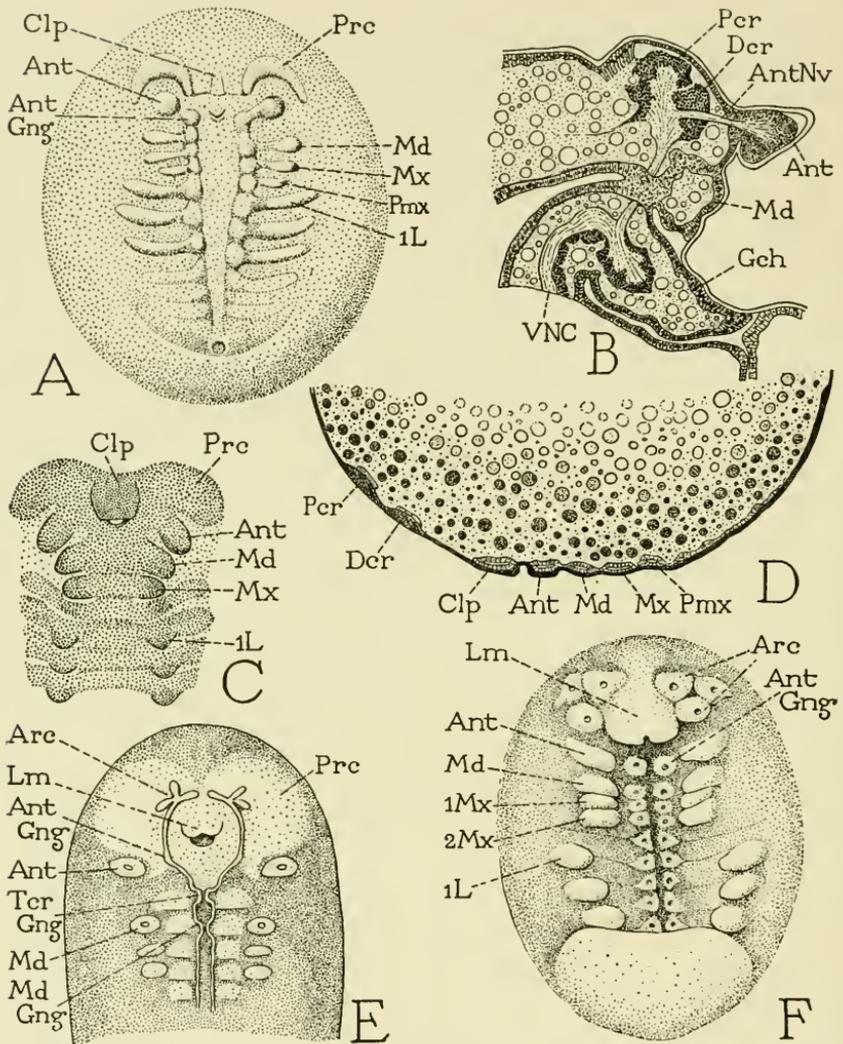


FIG. 44.—Embryonic segmentation of the head of Diplopoda as interpreted by different investigators.

A, germ band of *Platyrrhacus amauros* Attems before invagination (from Pflugfelder, 1932 a). B, longitudinal section of head of embryo of *Platyrrhacus amauros* shortly before hatching (adapted from Pflugfelder, 1932 a). C, young embryo of *Glomeris* (from Heymons, 1897). D, longitudinal section of germ band of *Platyrrhacus amauros* just before invagination, showing preoral coelomic sac of clypeal region and sacs of four postoral somites (from Pflugfelder, 1932 a). E, embryo of *Archispirostreptus* sp., about four days before hatching (from Robinson, 1907). F, same, one day before hatching (from Robinson, 1907).

Ant, antenna; *AntGng*, antennal ganglion; *AntNv*, antennal nerve; *Arc*, archicerebrum; *Clp*, clypeus (labrum); *Dcr*, deutocerebrum; *Gch*, gnathochilarium; *1L*, first leg; *Md*, mandible; *MdGng*, mandibular ganglion; *Mx*, maxilla; *1Mx*, *2Mx*, first and second maxillae; *Per*, protocerebrum; *Pmx*, postmaxillary appendage, or somite; *Prc*, procephalic lobe; *TcrGng*, tritocerebral ganglion; *VNC*, ventral nerve cord.

followed directly by the mandibular (*Md*) and two maxillary somites (*Mx*, *Pmx*), there being no evidence of a tritocerebral somite. In sections the cephalic lobes show internally a distinct division into a protocerebral rudiment (*D*, *Pcr*) and a deutocerebral rudiment (*Dcr*), each later accompanied by a coelomic sac. It would seem to be inferred from Pflugfelder's description, though not so stated, that the primary antennal ganglia lie in the postoral "antennal somite" (*Ant*), and yet he says, "das Deutocerebrum tritt sehr früh mit den Antennen in Verbindung durch den Antennennerv," and he clearly shows the antennal nerve connection with the preoral deutocerebrum (*B*,

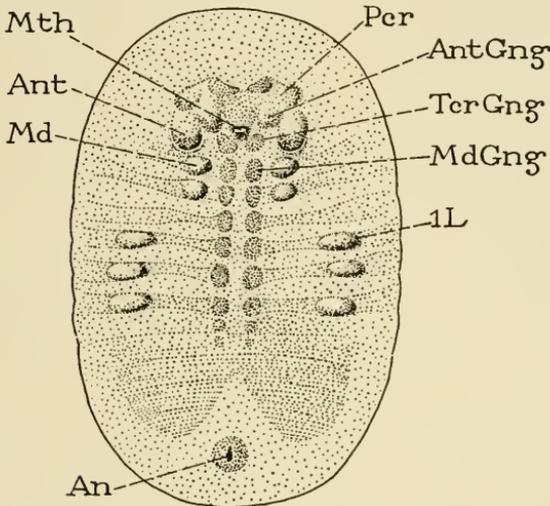


FIG. 44 G.—Germ band of a diplopod, *Archispirostreptus gigas* Peters, showing rudiments of appendages and ganglia. (From Silvestri, 1933.)

An, anus; *Ant*, antenna; *AntGng*, antennal ganglion; *1L*, first leg; *Md*, mandible; *MdGng*, mandibular ganglion; *Mth*, mouth; *Pcr*, protocerebrum; *TcrGng*, tritocerebral ganglion.

AntNv). The anatomical evidence here would seem to show that the true morphological relations of the antennae are with the deutocerebral ganglia, and we can only suppose, therefore, as in the case of Robinson's account of *Archispirostreptus*, that the postoral so-called "antennal" ganglia are the tritocerebral ganglia. In any event, the implication from Pflugfelder's statements that the antennae are appendages of a postoral somite, but are finally innervated from the preoral deutocerebrum gives the impression that there is some error involved.

The interpretation of the anterior cephalic ganglia of the diplopod embryo given by Silvestri (1933), illustrated in *Archispirostreptus gigas* (fig. 44 G), unquestionably presents the most reasonable view

that can be taken concerning the homologies of the ganglionic rudiments, since it disposes of the latter in a manner entirely consistent with the evident facts in other arthropods. According to Silvestri the ganglia of the antennae (*AntGng*) are neural masses situated mesad of the antennal bases, and the first pair of postoral ganglia (*TcrGng*) are the tritocerebral ganglia (ganglia of the intercalary somite). It should be observed that the antennal ganglia, as shown by Silvestri, have a preoral position and are not separated from the protocerebral lobes of the brain (*Pcr*).

Among the higher arthropods the more primitive stages in the brain development are generally not shown in embryonic recapitulation, for the proto-deutocerebral centers are usually proliferated from the ectoderm as a unified ganglionic cell mass, just as in the Onychophora and in many of the Annelida. It is observed by Baden (1936) and by Roonwal (1937), however, that the brain of the grasshopper (*Melanoplus*, *Locusta*) is formed from five pairs of ganglionic centers, three of which give rise to the protocerebrum and the optic lobes, and the other two to the deutocerebrum and the tritocerebrum, respectively. On the other hand, Nelson (1915) finds that in the honey bee the lateral surfaces of the primarily undivided cephalic lobes of the embryo become directly differentiated into three areas from which are proliferated the neural centers of the protocerebrum, the deutocerebrum, and the tritocerebrum.

In view of the well-authenticated examples of a diffuse origin of the cerebral ganglionic centers in the arthropods, the theory of Holmgren (1916) and of Hanström (1928) that the protocerebrum and the deutocerebrum are secondarily differentiated parts of a primitive, undivided archicerebrum does not appear to be substantiated by the facts of embryogeny. However, since the definitive brain is evidently a conglomerate of primitively separate ganglionic centers in the Annelida as well as in the Arthropoda, the general contention of these authors is not invalidated, namely, that both the protocerebral and the deutocerebral parts of the arthropod brain belong to the preoral prostomial region of the head, and, therefore, together represent the annelid archicerebrum.

The concept that all coelomic sacs and corresponding nerve centers represent postoral somites seemed reasonable enough, as applied to the arthropod head, when only antennal sacs were known; it was somewhat stretched, though still acceptable, when preantennal sacs were discovered; but now that we must add a third pair of cephalic sacs lying directly before the mouth in the labral region it begins to look farfetched. The theory here proposed, illustrated at D of

figure 45, accepts the embryonic facts more literally. It assumes that the archicephalic nervous system of the arthropods, as that of the annelids, has been built up from groups of ganglionic cells centering

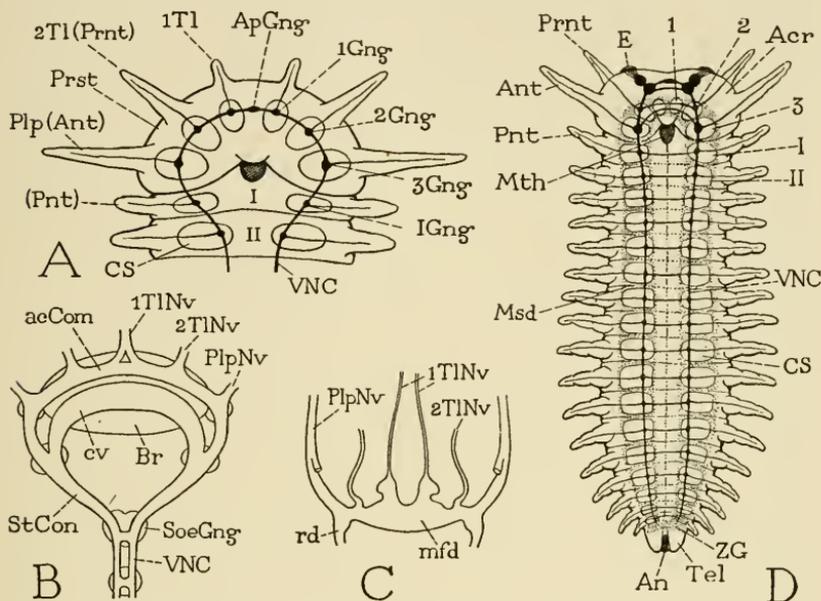


FIG. 45.—Suggestions of homologies between the prostomium of the annelids and the acronal region of the arthropod head.

A, diagram of the anterior segments of a theoretical "lobopod" annelid, with elemental ganglia corresponding with those of the arthropod cerebrum distributed on a preoral commissural arch of the nerve cords, and the potential number of coelomic sacs of the arthropod acron shown in their possible relation to the prostomial appendages. B, diagram of the fundamental structure of the prostomial nervous system of a polychaete annelid (from Binard and Jeener, 1928). C, reconstructed frontal section of dorsal fibrillar mass of brain and nerves arising from it in a sedentary polychaete, *Sabellaria spinulosa* Leuckart (from Binard and Jeener, 1928). D, analytical diagram of the relation of the coelomic sacs of an arthropod to the central nerve ganglia and the associated appendages.

acCom, anterior cerebral commissure; *Acr*, acron (prostomium); *An*, anus; *Ant*, antenna; *ApGng*, apical ganglion; *Br*, brain; *CS*, coelomic sac; *cv*, ventral fibrillar mass of brain; *E*, lateral eye; *1Gng*, protocerebral ganglion; *2Gng*, preantennal ganglion; *3Gng*, antennal ganglion; *I*, *II*, first and second somites; *IGng*, first somatic (triticerebral) ganglion; *mfd*, dorsal fibrillar mass of brain; *Msd*, mesoderm; *Mth*, mouth; *Plp*, palpus; *PlpNv*, palpal nerve; *Pnt*, postantennal appendage; *Pnt*, preantenna; *Prst*, prostomium; *rd*, dorsal root of stomodaeal connective; *SoeGng*, suboesophageal ganglion; *StCon*, stomodaeal connective; *Tel*, telson; *1Tl*, first tentacle; *2Tl*, second tentacle; *1TINv*, nerve roots of median tentacle; *2TINv*, nerve of second tentacle; *VNC*, ventral nerve cord; *ZG*, zone of growth; *1*, labral coelomic sac; *2*, preantennal coelomic sac; *3*, antennal coelomic sac.

upon a fibrous commissural tract arched forward around the mouth and continuous posteriorly with the ventral nerve cords of the somatic system. The primary cephalic ganglia included a median anterior

ganglion, paired protocerebral and optic ganglia, paired preantennal ganglia, and paired first antennal ganglia. That these ganglia belong to the preoral acron (*Acr*) is shown by the fact that the paired ganglia are always connected by preoral commissures. The cephalic mesoderm extends forward from the somatic mesoderm bands, and, in its fullest development, surrounds the mouth anteriorly; it may become excavated by cavities corresponding with the first antennae (3), the preantennae (2), and the labrum (1). The development of the prostomial nerve ganglia and mesodermal cavities is determined probably in all cases by external structures (appendages or sense organs), but the acronal neuromeres and coelomic sacs, because of their radial position around the mouth, cannot have the same relation in the body structure as have their postoral counterparts that are transversely opposed to each other. For a like reason there is no prostomial metamerism of the muscular system. The same concept may be applied to the preoral lobe of the polychaete annelids (*A*), assuming that potentially the annelid prostomium might have a full quota of coelomic sacs corresponding with its appendages, which actually it does not have. The tritocerebral somite of the arthropods thus represents the first postoral somite of the annelids. The tritocerebral ganglia are secondarily united with the preoral cerebrum in the Onychophora and in most of the Arthropoda, and always have a postoral commissure; the corresponding appendages are the jaws of the Onychophora, the chelicerae of the Chelicerata, and the second antennae of the Mandibulata.

The definitive arthropod brain more closely resembles the brain of the Polychaeta than that of the Onychophora. Its principal part is the protocerebrum, formed of a median apical ganglion and the first pair of lateral ganglia, with which are connected the optic ganglia. The preantennal ganglia lose their individuality in the general cerebral mass. The antennal ganglia form the deutocerebral lobes, but the latter take a forward position beneath the protocerebrum, with the result that, in the definitive condition, the antennal nerves arise anteriorly *below* the optic lobes. In the Onychophora, on the other hand, though the antennae are anterior, the brain maintains a horizontal position (fig. 25 A, C) with the antennal commissure behind the optic region, and the antennal tracts (*AntT*) traverse the dorsal part of the brain *above* the optic lobes. The tritocerebral ganglia are united with the primary cerebrum in the Onychophora and in nearly all the Arthropoda, but the union would seem to have taken place separately in the two groups, since in some of the lower Crustacea the corresponding centers are independent ganglia on the nerve cords, as they are in most of the Annelida.

EVOLUTION OF THE HEAD

The prostomial acron does not constitute the definitive head of any known arthropod; there is always added to the acron at least one postoral somite, and generally the definitive head includes from four to six somites. A head composed of the acron and one somite, however, recurs so frequently, either in the adult stage or in ontogenetic development, as to suggest that a simple head structure of this kind (fig. 39 C, *Prtc*) represents the earliest stage in the evolution of the more complex types of arthropod head. It may hence be termed the *protocephalon*. The best example of a functional protocephalon is to be seen in the anostracan Branchiopoda (fig. 50 A), in which the definitive head is a large cephalic lobe (*Prtc*) bearing the eyes, both pairs of antennae, and the labrum. The protocephalon is unquestionably the primitive head of all the mandibulate arthropods. There is no direct evidence, however, that it ever occurred as a specific stage in the evolution of the Trilobita or the Chelicerata, and hence, in the ancestors of these groups, and in the protarthropods generally, the primitive head may have been merely the prostomial acron.

Crampton (1928) applies the term "archicephalon" to a supposed stage in the cephalic evolution of the arthropods when the head consisted of the procephalic region and the mandibular somite. That such a stage occurred relatively late in the phylogenetic history of the head, however, is clearly shown in the ontogeny of the Mandibulata, in which the primitive embryonic head is always a cephalic lobe bearing the first antennae and usually including the second antennal somite, while the gnathal somites are still a part of the body region. Antedating this protocephalic stage, however, there must theoretically have been a truly primitive stage when there was no head structure other than the prostomium. The prostomium, therefore, which becomes the acronal region of the definitive head, is the only stage in the evolution of the arthropod head that might properly be termed the "archicephalon."

The trilobite branch of the protarthropods is characterized by a lateral expansion of the body, produced by an extension of the lateral margins of the tergal plates into long flat lobes (fig. 36 E, 48 D). The dorsal surface of the body thus presents a median elevated area (rhachis) accommodating the alimentary canal, and broad depressed lateral areas (pleurae). On the under surface the true venter (fig. 48 D, *V*) is the area between the leg bases, the areas laterad of the legs being the ventral doublure (*dbl*) of the dorsum. The appendages bear long coxal epipodites (*Eppd*) supporting branchial lamellae or filaments.

The so-called "head" of an adult trilobite (fig. 36 H, *H*), as we have seen, represents the 5-segmented body of the larva (*A*), the "body" segments of the adult being formed secondarily of a series of teloblastic somites generated from a subterminal zone of growth (*ZG*). The very young larva (fig. 46 *A*) presents a broad anterior acronal region (*Acr*), and a postacronal region in which are already differentiated the elevated median glabella (*glb*), which is the cephalic part of the rhachis, and the broad lateral areas (*fg*) that become the fixed cheeks of the adult (*E*). When the glabellar impressions appear (*B*, *C*) the glabella is cut into five consecutive divisions, but it is evident that the first division, or frontal lobe (*C*, *frl*), is derived from the acron, and that the following four divisions represent the first four postacronal somites (*I-IV*). With successive stages of development (*B*, *C*, *D*), the lateral wings of the acron (*lg*) extend posteriorly along the sides of the somites and eventually form the so-called free cheeks of the adult (*E*, *lg*), on which are located the compound eyes (*E*). The cephalic segmentation of the trilobite larva, therefore, may be represented as at *I* of figure 46, in which the intersegmental lines (*Is-As*) are theoretically extended to the lateral margins of the body. A median dorsal ocellus, when present, is always situated on the glabella, but since it must belong to the acron, it is placed on the frontal lobe in the diagram (*I*, *dO*).

In the mature trilobite head of typical structure (fig. 46 *E*), the preocular part of the acronal suture (*I*, *Is*) has disappeared, but the postocular parts become the posterior parts of the sutures known as the "facial sutures" (*fsp*), the preocular parts of which (*fsa*) are probably secondary lines of cleavage developed to facilitate moulting. In some forms the facial sutures end on the lateral margins of the head; in others they go to the posterior margin (*E*), and in such cases the genal spines are continuations of the free cheeks. On the ventral surface of the head (*F*) the acronal surface is broadly inflected to form the doublure (*dbl*), which carries the labrum (*Lm*), or "hypostome," on its preoral margin. The probable dorsal segmentation of the adult trilobite head, therefore, may be represented diagrammatically as shown at *J* of figure 46. The acron (*Acr*) clearly forms an extensive part of the mature cephalic structure, since it must include the frontal lobe of the glabella (*frl*), the free cheeks (*lg*) with the compound eyes (*E*), and the doublure (*F*, *dbl*) with the labrum (*Lm*). Furthermore, since the dorsal ocellus often occurs far back on the glabella (*J*, *dO*), we must assume that it is contained in a median tongue of the frontal lobe extended posteriorly into the glabellar somites, because the simple eyes as well as the compound eyes always belong to the acronal segment.

The antennal appendages of the trilobites, judging from their filamentous form in contrast with the segmented structure of the following appendages, evidently represent the first antennae (anten-

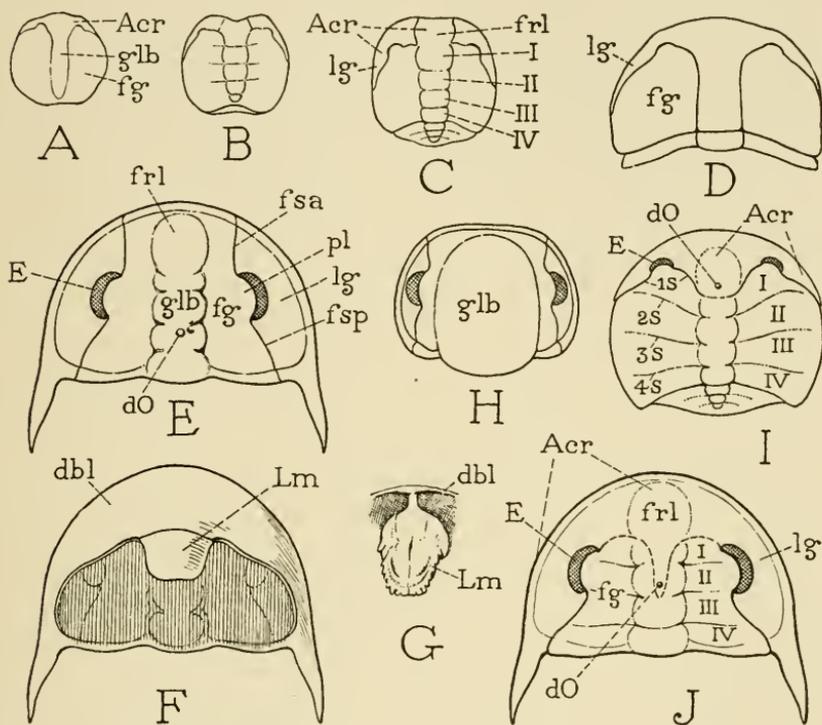


FIG. 46.—Segmentation of the trilobite "head," or prosoma.

A-D, four consecutive stages in the larval development of *Blaimia gregaria* Walcott, showing gradual posterior extension of lateral wings (free cheeks) of acron against sides of anterior somites, and division of glabella (C) into four segmental areas behind frontal lobe of acron (from Lalicker, 1935). E, diagram of typical trilobite head, dorsal surface. F, diagram of ventral surface of trilobite head, showing labrum attached to margin of doublure. G, labrum of *Paedeumias transitans* Walcott, example of a stalked labrum (from Walcott, 1910). H, head of *Holotrachelus punctillosus*, with segmentation obliterated in the large swollen glabella (from Warburg, 1925). I, diagram of larval trilobite, with head segmentation indicated. J, head of adult trilobite with probable segmentation deduced from the larval structure (I).

Acr, acron; *dbl*, doublure; *dO*, dorsal ocellus; *E*, compound eye; *fg*, fixigene (fixed cheek); *frl*, frontal lobe (of acron); *fsa*, anterior part of facial suture; *fsp*, posterior part of facial suture; *glb*, glabella; *I-IV*, cephalic somites; *lg*, libragene (free cheek); *Lm*, labrum; *pl*, palpebral lobe; *1s-4s*, intersegmental sutures of head.

nules) of other arthropods; if so, according to the theory here followed, they should belong to the acron, and perhaps had their muscle attachments on the frontal lobe. The position of the antennal

bases is not exactly known, but the antennal appendages are generally represented as arising at the sides of the labrum. The four following segmented, leglike appendages of the head clearly pertain to the four postfrontal somites of the dorsal shield.

Henriksen (1926), in his analysis of the segmentation of the trilobite head, convincingly argues that the free cheeks bearing the compound eyes must belong to the "eye segment" (acron), and that the preocular parts of the facial sutures are secondary lines of cleavage to facilitate moulting; but the median part of the eye segment he believes is represented only by the narrow anterior marginal rim of the dorsal shield before the frontal lobe. Henriksen notes, however, the anomalous position of the median eye far back on the glabella, and it is not clear why the reasoning by which he assigns the free cheeks to the eye segment does not demand that the eye segment include also the area of the median eye. The antennae, Henriksen contends, belong to a separate postoral somite, represented dorsally by the frontal lobe of the glabella. Furthermore, since he believes that the trilobite head must have the same segmentation as the head of certain Crustacea, Henriksen concludes that a second antennal somite has been lost by the trilobites. To the writer this theoretical elaboration of the trilobite head to give conformity with crustacean structure appears quite unnecessary, since the trilobites are non-mandibulate arthropods having no immediate relations with the Crustacea, and their structure clearly leads into that of the Chelicerata.

The Xiphosurida, in the structure of the prosoma, show unmistakably their trilobite derivation, for the trilobite head is carried over into the xiphosurid prosoma with few changes other than the inclusion of a few extra segments, the loss of the antennae, and a differentiation of the other appendages.

A comparison of figure 47 A with figure 46 E will show at once the likeness of the prosomatic carapace of *Limulus* to the typical head shield of a trilobite. The segmentation of the xiphosurid prosoma is evident from the position of the limb bases on the ventral surface (fig. 47 C), where it is seen that the anterior somites lap forward at the sides of the labrum from behind the central mouth, while the posterior somites curve somewhat backward. The chelicerae (*Chl*) thus come to have anatomically a preoral position at the sides of the labrum, though their somite (*I*) is morphologically postoral, and the same is true of the pedipalps (*Pdp*) and the first legs (*1L*). On the inner surface of the prosomatic carapace the attachments of the limb muscles (fig. 47 B), as depicted by Benham (1885), follow the segmentation indicated ventrally by the limb bases. The chelical

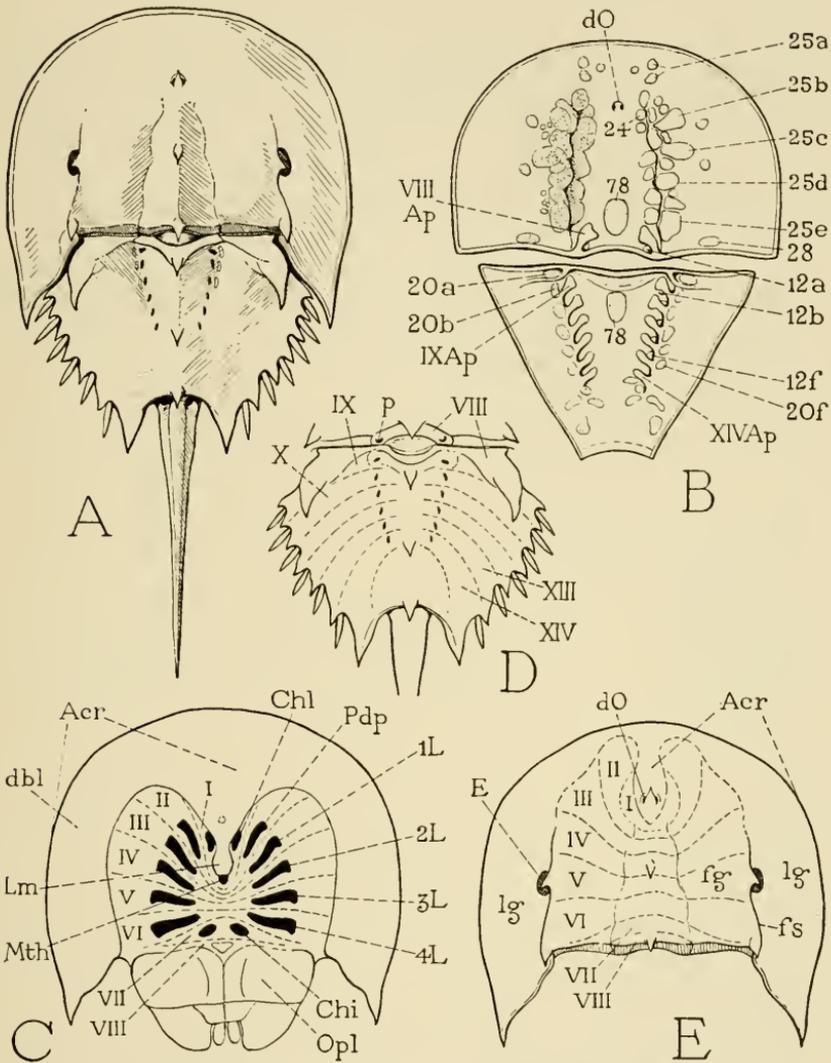


FIG. 47.—Segmental analysis of Xiphosurida (*Limulus polyphemus* Linn.).

A, young adult, dorsal surface. B, ventral surface of dorsal carapace, showing muscle attachments and series of dorsal apodemes, or entapophyses (from Benham, 1885, with dorsal ocelli added). C, ventral surface of prosoma, showing segmentation as indicated by position of leg bases. D, dorsal surface of opisthosoma, with segmentation indicated. E, theoretical approximate segmentation of prosoma.

Acr, acron; *Ap*, tergal apodemes (entapophyses); *Chi*, chilarium; *Chl*, chelicera; *dbl*, doublure (ventrally inflected part of acron); *dO*, dorsal ocellus; *E*, compound eye; *fg*, fixigene; *fs*, facial suture; *I-XIV*, postoral somites; *L*, leg; *lg*, librigenae; *Lm*, labrum; *Mth*, mouth; *Opl*, genital operculum; *p*, external pits of tergal apodemes; *12a, b, f*, dorsal attachments of tergo-sternal muscles of opercular and gill somites; *20a, b, f*, dorsal attachments of anterior muscles of opercular and gill appendages; *25a-e, 28*, dorsal attachments of tergo-coxal muscles of prosomatic appendages.

muscles (24) arise near the midline just behind the dorsal eyes; the muscles of the pedipalps (25a) take their origins farthest forward; and the muscles of the other appendages (25b-25c) are distributed on the following areas of the "fixed cheeks." Diagrammatically, therefore, we may represent the segmentation of the prosomatic carapace as given at E of figure 47. The horseshoe-shaped acron (*Acr*) bearing the eyes encloses the region of the prosomatic somites (*I-VIII*), and sends posteriorly, between the lobes of the anteriorly curved cheliceral and pedipalp somites, a median tongue bearing the dorsal ocelli (*dO*). The structural conformity with the trilobite head (fig. 46 J) is exact, except for the greater number of somites included in the xiphosurid prosoma.

Students of the embryology of *Limulus* (Kishinouye, 1893, Iwanoff, 1933) have indicated the segmental divisions of the prosoma as subtending the lateral areas of the carapace bearing the compound eyes. Branches of the segmental nerves, the "haemal nerves" of Patten and Redenbaugh (1900), extend into these parts, but, as in the case of the trilobites, the location of the compound eyes on the lateral plates of the prosoma is sufficient proof that these plates belong to the eye segment, or acron. Hence, they cannot be lateral extensions of the median somites.

The gills of the trilobite legs, borne on coxal epipodites (fig. 48 D, *Eppd*), have not been retained on the prosomatic appendages of Xiphosurida, though an epipodite is present on the fourth leg (E, *Eppd*), but gill-bearing epipodites are highly developed on the opisthosomatic appendages, which are otherwise much reduced.

The prosomatic appendages of *Limulus*, except the chelicerae, as shown by Benham (1885), have the typical arthropod coxal musculature, consisting of dorsal promotor and remotor muscles (fig. 48 F, *I, J*), and ventral muscles (*K, L*). Of the latter, two (33, 34) are promotors and remotors, but two others (32m, 32n) are united proximally and evidently function as adductors. The dorsal muscles arise on the tergal carapace (C). The ventral muscles, however, are attached on an internal plate, or "entochondrite" (*k*), suspended in the ventral part of the body by dorsal muscles (*t-s*). The same structure (B) is characteristic of most of the Chelicerata, and a similar structure occurs in the gnathal segments of many of the Mandibulata (figs. 50 E, H, 51 B, *k*). Since the ventral muscles of the appendages should primarily arise on the ventral body wall, the "entochondrite" might be supposed to be a sternal derivative, but Schimkewitsch (1895, 1906) claims that in the Arachnida it is produced from transformed muscle tissue. In various mandibulate

arthropods some of the adductor fibers of the mandibles go continuously from one appendage to the other.

That the prosoma of *Limulus* contains at least a part of the eighth somite is evident from several structural features, but the writer's

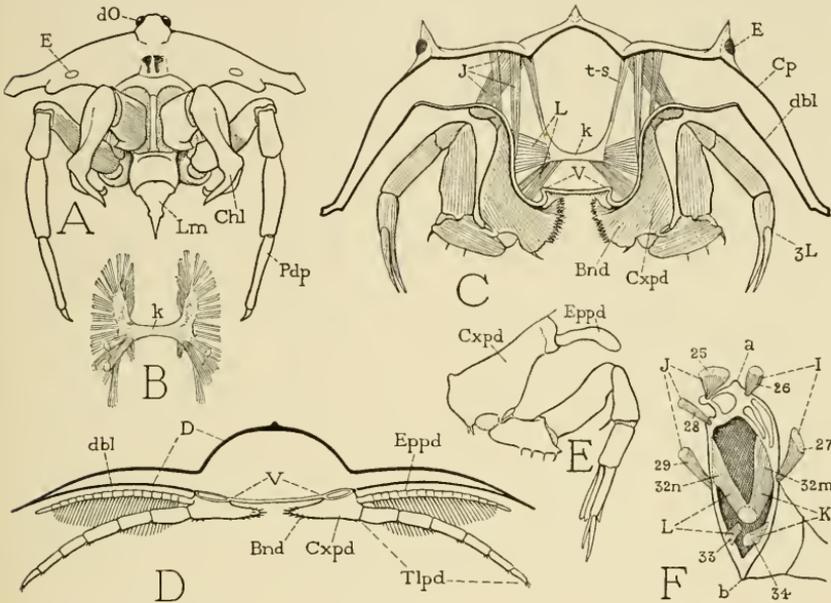


FIG. 48.—Structure of Chelicerata and Trilobita.

A, *Liobunum* sp. (Phalangida), anterior view of body, showing secondary preoral position of chelicerae above base of labrum. B, same, "endosternite" of prosoma with adductor leg muscles (suspensory dorsal muscle not shown). C, *Limulus polyphemus* Linn. (Xiphosurida), section of prosoma behind third legs, leg muscles somewhat diagrammatic. D, diagrammatic cross-section of a trilobite. E, *Limulus polyphemus*, fourth leg, with coxal epipodite. F, same, base of a left leg, mesal view, with muscle insertions (from Benham, 1885).

a, dorsal articulation of coxopodite; b, ventral end of coxal axis; Bnd, basen-dite; Chl, chelicera; Cp, carapace; Cxpd, coxopodite; D, dorsum; dbl, doublure; dO, dorsal ocellus; E, lateral eye; Eppd, epipodite; I, tergal promotor muscles of coxopodite; J, tergal remotors of coxopodite; K, anterior ventral muscles of coxopodite; k, ligamentous "endosternite" on which ventral leg muscles are attached; L, posterior ventral muscles of coxopodite; 3L, third leg; Lm, labrum; Pdp, pedipalp; Tlpd, telopodite; t-s, tergal suspensory muscle of "endosternite"; V, venter; 26, 27, dorsal promotor muscles of coxopodite arising on carapace; 25, 28, 29, dorsal remotor muscles arising on carapace; 32m, 32n, anterior and posterior branches of coxal adductor arising on "endosternite"; 33, 34, ventral remotor and promotor muscles arising on "endosternite".

former statement (1936) that the prosoma and opisthosoma of *Limulus* are separated between segments VIII and IX is not strictly correct. The attachment of the muscles and the distribution of the nerves in this region demonstrate that the dorsal hinge between the prosomatic carapace and the opisthosomatic carapace lies within the

eighth segment itself, and not behind it, a narrow anterior median part of this segment being incorporated into the posterior margin of the prosoma, while lateral parts of it form the anterior lateral lobes of the opisthosomatic carapace (fig. 47 D, *VIII*). Six following segments of the opisthosoma are marked by the six pairs of impressions bordering the median elevation of the carapace, and by the six pairs of marginal spines. The intrasegmental division of the body into movable parts is not an anomalous condition; it occurs between the thorax and the abdomen of many insects, and is a necessary mechanical adaptation resulting from the primarily intersegmental attachments of the longitudinal muscles.

The six pairs of dorsal impressions on the opisthosoma of *Limulus* (fig. 47 D) and a pair of similar impressions on the posterior margin of the prosomatic carapace (*p*) form internally (B) a double series of tergal apodemes, the "entapophyses" of Benham (1885), of which the larger first pair (*VIII Ap*) is on the prosoma, and the other six pairs (*IX Ap-XIV Ap*) are on the opisthosoma. The tergo-sternal muscles of the five gill-bearing segments are shown by Benham to have their dorsal attachments (*12b-12f*) at the bases of the first five opisthosomatic apodemes, while the corresponding muscles of the opercular segment (*VIII*) arise at the bases of the corresponding prosomatic apodemes (*12a*). On the other hand, while the "external branchial muscles" of the gill segments have their dorsal attachments (*20b-20f*) just laterad of the first five opisthosomatic apodemes, the corresponding muscles of the operculum take their origins also on the opisthosomatic shield, but more laterally on the anterior lateral lobes. The muscle attachments, therefore, show that the dorsal part of the eighth segment has been divided between the prosoma and the opisthosoma, or, as Benham says, the first pair of tergal apophyses has been transferred from the opisthosoma to the prosoma. The dorsal longitudinal muscles between the prosoma and the opisthosoma of *Limulus* have been condensed into a single large bundle of fibers, the "arthrotergal muscle" of Benham, and the attachments of this muscle (fig. 47 B, 78) have extended somewhat anteriorly and posteriorly on the two body regions to acquire greater efficiency as a flexor of the opisthosoma.

The innervation of the hinge region of the carapace gives the same evidence of division within the eighth segment as that furnished by the musculature. As shown by Patten and Redenbaugh (1900), the nerves of the genital operculum proceed from the composite ventral ganglion of the prosoma, while the corresponding somatic nerves ("haemal nerves" of segment *VIII*) are distributed to the anterior

lateral lobes of the opisthosoma. From a comparative study of the position of the cardio-aortic valve in the Chelicerata, Petrunkevitch (1922) found that the valve is always between segments *VIII* and *IX*, and he therefore claimed that segment *VIII* is included in the prosoma of *Limulus*. His contention is but little affected by the modified view here shown to be in better accord with the facts. The operculum is anatomically more closely connected with the prosoma, from which it derives its innervation, than with the opisthosoma, and the partition of the tergum of its segment between the prosoma and the opisthosoma, as above noted, is but a necessary adaptation to give intersegmental action to primarily intrasegmental muscles.

The Eurypterida and Arachnida differ from the Xiphosurida in that the prosoma includes only six somites, and in this respect they are nearer to the Trilobita, which have only four prosomatic somites. The eurypterids and arachnids, however, lack the lateral expansions of the prosomatic carapace characteristic of the trilobites and xiphosurids, and, judging from the more anterior position of the lateral eyes (fig. 49 E, *E*), it seems probable that the acronal element of the prosoma is less extensive on the marginal areas of the latter, though medially it must include the region of the dorsal eyes (*dO*).

In a typical arachnid embryo (fig. 49 A) the somites are regular transverse sections of the trunk behind the large prostomial acron (*Acr*), which is produced laterally into a pair of cephalic lobes. Ordinarily there are no appendages on the acron, but Jaworowski (1891) has described a pair of apparent antennal rudiments in a species of *Trochosa* (*C, b*), and Pokrowsky (1899) found two pairs of transient precheliceral lobes in an embryo of *Pholcus opilionides* (*B, a, b*), the second of which, he says, correspond in position with the "antennal" rudiments described by Jaworowski. The nature of these embryonic lobes may be doubtful, but since the trilobites have well-developed antennae, there is no reason why embryonic vestiges of acronal appendages might not recur in some chelicerate forms. In adult Solpugida there is a pair of small appendages (fig. 49 F, *Ant?*) arising at the sides of the epistomal lobe, which are movable by muscles (*G, mcl*), and are, therefore, suggestive of being antennal remnants.

The cheliceral somite of the arachnid embryo (fig. 49 A, *I*) lies transversely immediately behind the acronal lobes; but in the adult this somite curves forward around the sides of the labrum from behind the mouth as in *Limulus*, so that the chelicerae come to have a preoral position above the labrum (fig. 48 A, *Chl*), though usually they are separated by a median epistomal bar extending downward

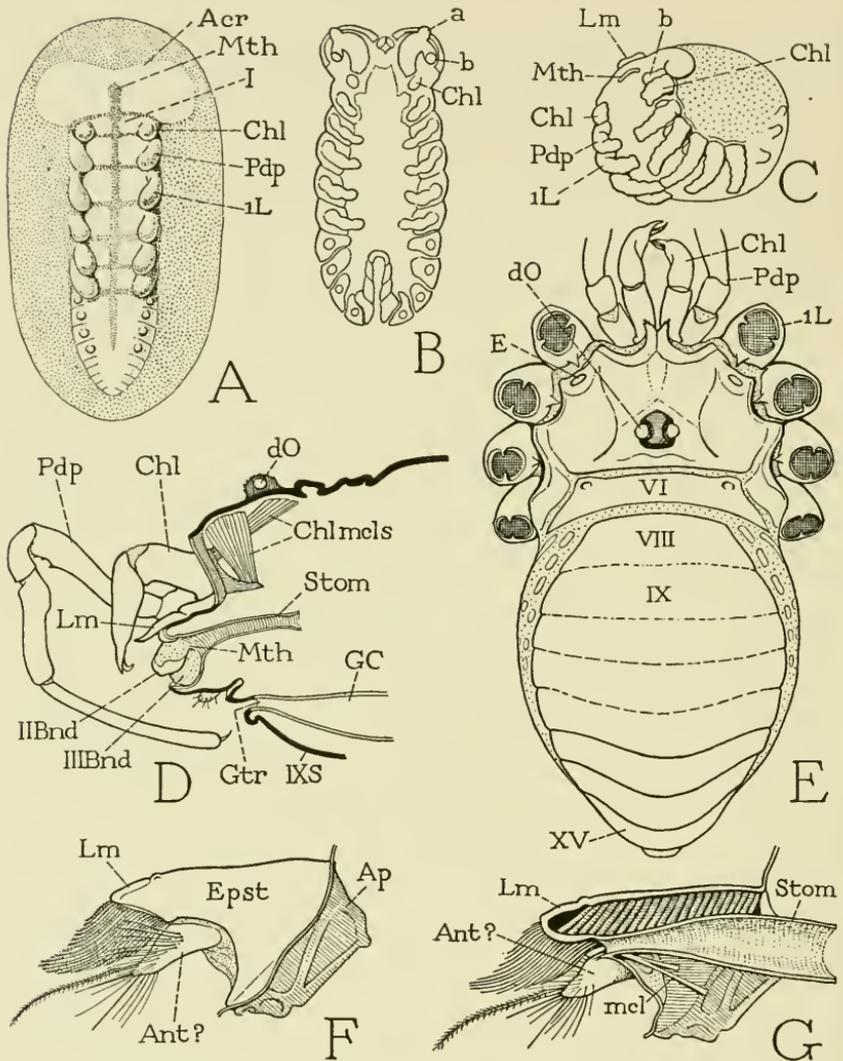


FIG. 49.—Embryonic and adult structures of Arachnida.

A, embryo of *Agelena labyrinthica* (from Balfour, 1880). B, embryo of *Pholcus opilionides* Schrank with two lateral lobes (*a*, *b*) on acron (from Pokrowsky, 1899). C, embryo of *Trochosa singoriensis* Laxm., with possible antennal rudiments (from Jaworowski, 1891). D, longitudinal section through anterior end of prosoma of a phalangid (*Liobunum*), showing anterior tergal attachments of cheliceral muscles. E, dorsal surface of phalangid (*Liobunum*), legs removed from coxopodites. F, epistomal lobe and labrum of a solpugid, lateral view, showing movable appendage (*Ant?*) at side of epistoma. G, same, longitudinal section, showing muscles of epistomal appendage.

a, possible preantennal rudiment of embryo; *Acr*, acron (cephalic lobe of embryo); *Ant?*, adoral (possibly antennal) appendage of adult solpugid; *b*, possible antennal rudiment of embryo; *Ap*, apodeme; *Chl*, chelicera; *Chlmcls*, cheliceral muscles; *dO*, dorsal ocellus; *E*, lateral eye; *Epst*, epistoma; *GC*, genital chamber; *Gtr*, gonotreme; *II Bnd*, *III Bnd*, basendites of second and third appendages; *IXS*, sternum of ninth somite; *1L*, first leg; *Lm*, labrum; *mcl*, muscles; *Mth*, mouth; *Pdp*, pedipalp; *Stom*, stomodaeum; *I-XV*, postoral somites.

to the labrum from the frontal region of the carapace. As in *Limulus* again, the chelicerae have only dorsal muscles, which arise on the anterior part of the carapace (fig. 49 D, *Chlmcls*).

The ancestors of the modern Mandibulata were represented in the more generalized members of the Protarthropoda that persisted after the trilobite-chelicerate branch had been given off from the main stem (fig. 54). The Protomandibulata undoubtedly retained the primitive centipedelike form of the protarthropods, but, as shown in the embryology of modern Mandibulata, the head at this stage must have been a composite protocephalon (fig. 39 C, *Prtc*) formed by an intimate union of the first somite (*I*) with the highly developed prostomial acron (*Acr*). It carried, therefore, the eyes (*E*), the labrum (*Lm*), the acronal appendages, or first antennae (*1Ant*), and the appendages of the included somite, which became a second pair of antennal organs (*2Ant*). The distinctive feature of the early mandibulates, however, was the presence of a pair of jaws, the mandibles (*Md*), developed from the bases of the appendages of the first postcephalic somite. Probably also the appendages of the following two somites were reduced in size and modified in a manner suggestive of their future transformation into maxillae; and perhaps a pair of paragnathal lobes was developed between the mandibles and the first maxillary appendages, since these structures are not present in the chelicerate branch.

The Crustacea represent the first offshoot from the mandibulate section of the arthropod stem that has given rise to a specialized group of modern forms (fig. 54). The wide recurrence among the Crustacea of cursorial appendages identical in segmentation with the legs of the trilobites can leave little doubt that the primitive crustaceans were polypodous walking animals, living on the bottom of the water or on aquatic plants along the ocean shores, and adapted to life in the water, as were the trilobites, by the development of branchial organs on exite lobes of the coxopodites. According to this view, the natatory appendages of swimming or purely pelagic Crustacea are legs that have been modified secondarily for swimming purposes, just as the gnathal appendages have been modified for feeding. It is a sound principle of ecology that pelagic forms in all cases have been derived from benthonic forms (see Hesse, Allee, and Schmidt, 1937, p. 179), and the fact that many of the more generalized modern Crustacea are pelagic is no argument that such forms are ancestral. The frequent biramous structure of crustacean appendages is entirely a crustacean feature, since the exopodite is a specially developed outer branch of the basipodite, and therefore has no counterpart in the Trilobita or in any other arthropod group.

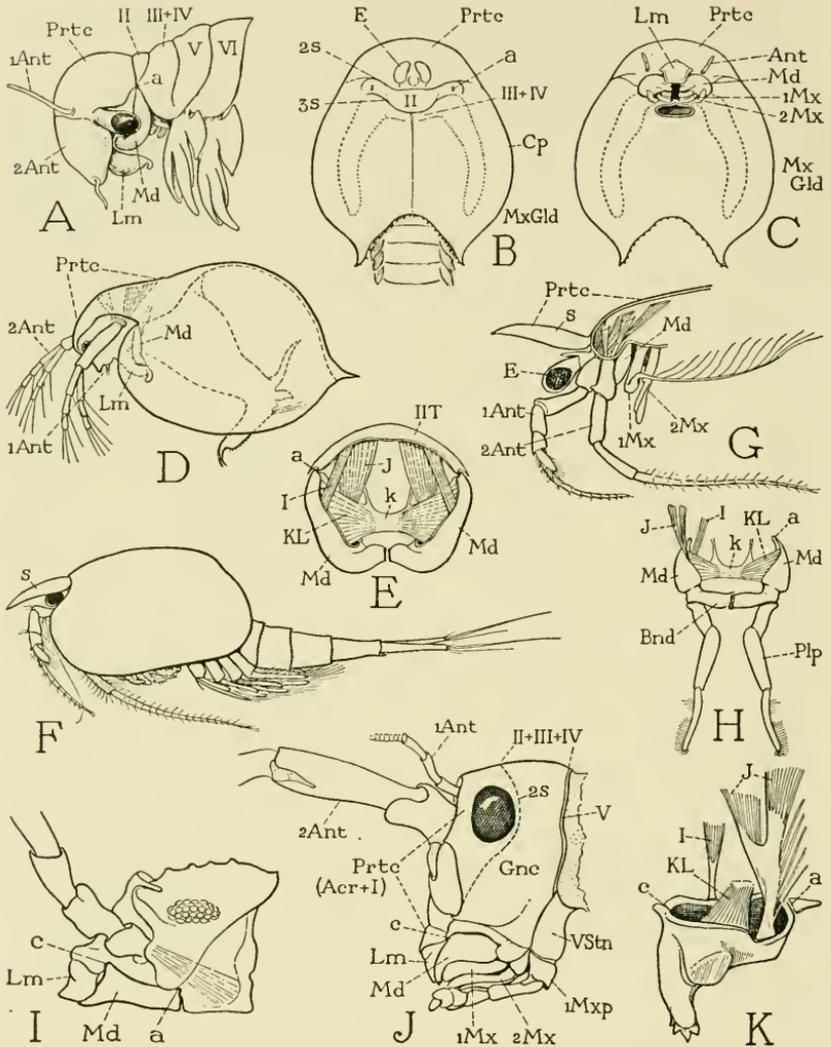


FIG. 50.—Cephalic structures of Crustacea in which the protocephalon (acron and first somite) is either the definitive head, or is united with several following somites to form a more extensive syncephalon.

A, *Eubranchipus vernalis* Hay (Anostraca): protocephalon a distinct head lobe (*Prtc*) separate from mandibular somite (*II*); maxillary somites (*III*, *IV*) united with each other. B, *Apus longicaudatus* Le Conte (Notostraca), dorsal view: mandibular and maxillary somites united with protocephalon, maxillary tergum produced in large cephalic carapace (*Cp*). C, same, ventral view of head, showing labrum, antennules, mandibles, and maxillae. D, *Daphnia pulex* Degeer (Cladocera): head structure as in *Apus*, body covered by bivalved maxillary carapace. E, *Eubranchipus vernalis*, detached mandibular segment, anterior view, showing mandibles suspended from tergum, and mandibular musculature. F, *Nebalia bipes* Fabr. (Leptostraca): bivalved carapace has same composition as in *Apus* and *Daphnia*. G, section of head of *Nebalia* showing muscle attachments of protocephalic appendages. H, mandibles of *Nebalia*,

The crustacean head is variable in structure according to the number of somites it contains. The most primitive crustacean head, as already noted, is a simple protocephalon formed by the union of the tritocerebral somite with the prostomial acron. A head of this type occurs in some of the Branchiopoda, and in all the Malacostraca except Leptostraca, Amphipoda, and Isopoda.

The best example of a protocephalic head is seen in the anostracan branchiopods. The head of *Eubranchipus*, for example (fig. 50 A, *Prtc*), is a large cephalic capsule bearing only the eyes, both pairs of antennae, and the labrum. Behind it is the small but distinct tergum of the mandibular somite (*II*), which supports the large mandibles (*Md*). The next following segment is evidently the two maxillary somites united (*III + IV*), since it carries the vestigial first and second maxillae. The muscles of the head appendages, including those of the eye stalks, the antennules, the second antennae (in the male), and the labrum, all take their origins on the walls of the head capsule. The mandibular muscles, on the other hand, arise on the mandibular tergum (*E*), except the adductors (*KL*), which are united on a median ligament (*k*) and thus form a zygomatic muscle between the two jaws.

The head of most of the other Entomostraca and of Leptostraca is a more extensive structure than that of the Anostraca, since it includes the mandibular and maxillary somites united with the protocephalon. The maxillary region of the head is often expanded to form a large cephalic shield, or bivalved shell, covering the anterior part of the body. In *Apus* (fig. 50 B) the region of the protocephalon (*Prtc*) forms a distinct anterior part of the definitive head bearing the eyes dorsally and the antennae and labrum ventrally (*C*). Behind the protocephalon the limits of the mandibular tergum (*B, II*) are clearly marked, but the maxillary terga (*III + IV*) are confluent as in

posterior view. I, *Porcellio* sp. (Isopoda), head, composed of protocephalon and four following somites (maxillae and maxillipeds removed). J, *Orchestoidea californica* Brandt (Amphipoda), head, same composition as in *Porcellio*, approximate division between protocephalic and gnathal regions indicated by broken line (*zs*). K, *Talorchestia longicornis* Say (Amphipoda), right mandible, mesal view.

a, primary (dorsal) articulation of mandible; *1Ant*, first antenna (antennule); *2Ant*, second antenna; *Bnd*, basendite; *c*, secondary (anterior) articulation of mandible; *Cp*, carapace; *E*, compound eye; *I*, tergal promotor muscles of mandible; *II-VI*, second to sixth somites; *III*, mandibular tergum; *J*, tergal remotor of mandible; *k*, ligament uniting ventral adductors of mandibles; *KL*, ventral adductor muscles of mandible; *Lm*, labrum; *Md*, mandible; *1Mx*, *2Mx*, first and second maxillae; *MxGld*, maxillary gland; *1Mxp*, first maxilliped; *Plp*, palpus; *Prtc*, protocephalon (acron + somite *I*); *zs*, suture between protocephalon and mandibular somite (*B*), or theoretical line of division between protocephalic and gnathal regions of head (*J*); *3s*, suture between mandibular and maxillary somites; *VStn*, sternum of first maxilliped somite.

Eubbranchipus (A). In the Cladocera (D) the general head structure and composition is the same as in *Apus*, except for the lateral compression of the maxillary shield, which gives the latter its "bivalved" form, but the intersegmental lines are lost, and the limits of the protocephalon (*Prtc*) are marked only by the attachments of the antennal muscles. The Leptostraca (F) have the cladoceran type of head and bivalved maxillary shield, but are distinguished by the presence of a large frontal lobe (*s*) projecting above the bases of the eye stalks. Here again the protocephalic area of the composite head is marked only by the origins of the muscles of the protocephalic appendages (G), including those of the eye stalks and the two pairs of antennae. The mandibles of the Leptostraca (*Nebalia*) retain the palpi (H, *Plp*), but their basal structure and musculature is the same as those of *Eubbranchipus* (E) and other Entomostraca.

The Malacostraca, other than Amphipoda and Isopoda, are commonly said to have a "cephalothorax," which includes the gnathal somites and a number of following somites up to a maximum of 12 in all. Most of this composite structure, however, which in its fullest development is covered by the carapace (fig. 51 C, *Cp*), is more truly a *gnathothorax*, since the true head is always a distinct though small protocephalic lobe more or less concealed beneath the overhanging rostrum (*r*) of the mandibular somite. When the protocephalon is detached, as shown in the figure (C), it is seen to be a distinct cephalic structure bearing the stalked eyes, both pairs of antennae, and the labrum. The typical malacostracan head is thus identical with the protocephalic head of the Anostraca (fig. 50 A, *Prtc*). Even in the Brachyura (fig. 51 D, E) the protocephalon is readily identified as such, though dorsally (D) it is much reduced, and is concealed in a pocket beneath the anterior margin of the carapace; ventrally (E) it carries a large epistomal plate and a small labrum. In the Stomatopoda, on the other hand, the protocephalon is highly developed (fig. 51 F, G), and its integumental sclerotization is broken up into several distinct plates (*d, e, f, g*), which, however, can in no sense be regarded as representing a "segmentation" of the head. The mandibles of the more generalized type found in the Malacostraca (B) are identical in their structure and musculature with the mandibles of Entomostraca (fig. 50 E, H).

The Amphipoda and the Isopoda (including Apseudidae), with regard to the structure of the head, do not appear to be properly classed with the rest of the Malacostraca, since the head (fig. 50 I, J) is an intimate combination of the gnathal somites (*II+III+IV*) with the protocephalon (*Prtc*), and thus resembles in its composition

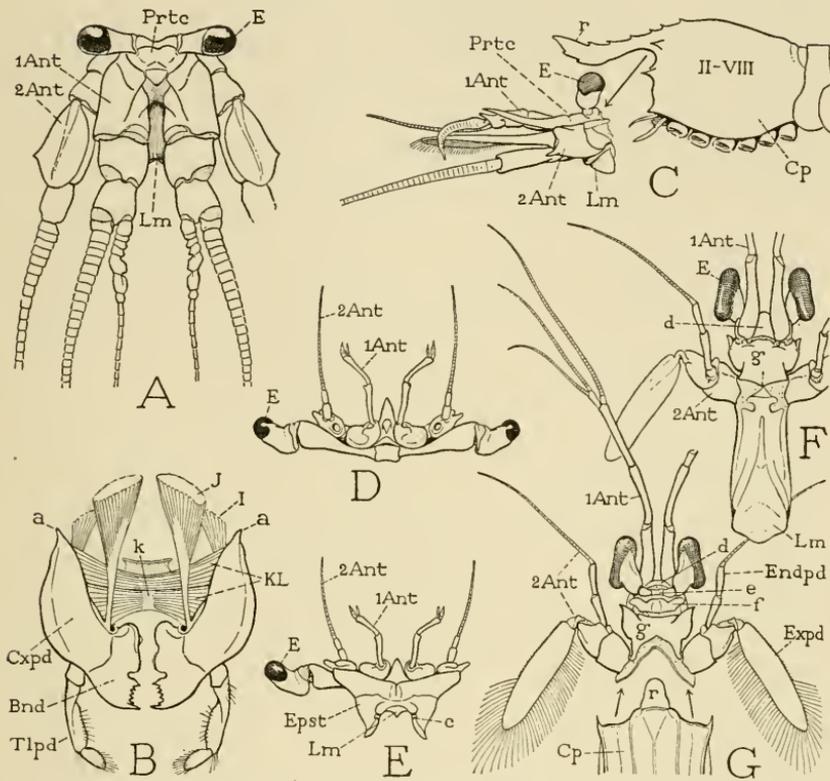


FIG. 51.—Cephalic structures of malacostracan Crustacea in which the definitive head is the protocephalon, as in Anostraca (fig. 50 A).

A, *Anaspides tasmaniae* Thomson (Syncarida), protocephalon and appendages, anterior view. B, same, mandibles and muscles, posterior view. C, *Spirontocaris polaris* (Decapoda-Macrura), showing protocephalon (*Prtc*) detached from carapace. D, *Callinectes sapidus* Rathbun (Decapoda-Brachyura) protocephalon and appendages, dorsal view. E, same, protocephalon and appendages, ventral view. F, *Chloridella panamensis* Bigelow (Stomatopoda), protocephalon and appendages, anterior view. G, same, protocephalon detached from carapace (*Cp*), dorsal view.

a, primary (dorsal) articulation of mandible; *1Ant*, first antenna (antennule); *2Ant*, second antenna; *Bnd*, basendite; *c*, secondary (anterior) articulation of mandible; *Cp*, carapace; *Cxp*, coxopodite; *d*, anterior (ocular) division of protocephalon; *E*, compound eye; *e*, ocular plate of protocephalon; *Epst*, epistoma; *Expd*, exopodite; *f*, postocular dorsal plate of protocephalon; *g*, posterior (antennular) division of protocephalon; *I, J*, dorsal promotor and retractor muscles of mandibles; *II-VIII*, second to eighth somites; *k*, adductor ligament of mandibles; *KL*, adductor muscles of mandibles; *Lm*, labrum; *Prtc*, protocephalon; *r*, rostrum of mandibular somite; *Tlp*, telopodite (palpus).

the head of *Nebalia* and of such entomostracan forms as *Apus*, *Daphnia*, and others, though in form it often has a striking resemblance to the head of a hexapod mandibulate. However, in both the amphipods and the isopods the head usually includes also the first maxilliped somite and its appendages (fig. 50 J, *IMxp*), and may in addition bear the second maxillipeds. The mandible acquires a secondary anterior articulation with the cranium (I, J, K, *c*), by which its action is limited to a hinge movement on a horizontal axis between its two articular points (K, *a*, *c*). The same mandibular mechanism has been independently developed in the decapod Crustacea and in the pterygote Hexapoda. While the head structure of the Amphipoda and Isopoda sets these groups apart from other Malacostraca, it does not necessarily relate them to any other group.

The final type of head developed in the Arthropoda is that characteristic of the myriapods and hexapods, and must have evolved in the common ancestors of these groups represented in the post-crustacean, protomyriapodan section of the main arthropod stem (fig. 54). The head of all the myriapod and hexapod groups is a highly standardized structure, composed of the protocephalon and the three gnathal somites, so closely united that little evidence of the original segmentation remains, except in the presence of the appendages (fig. 53 A), and even here the evidence is obscured by the loss of the second antennae. In early ontogenetic stages, however, the gnathal somites are entirely distinct from a large anterior cephalic lobe that usually includes the second antennal somite, which may bear vestiges of its former appendages. The Protomyriapoda must have had compound eyes, since eyes of the compound type recur finally in the Hexapoda; they likewise must have carried paragnathal lobes of the head from the Crustacea to the Hexapoda, though these organs have disappeared in the modern myriapodous forms. The maxillary appendages probably were no more specialized in the protomyriapods than in modern Chilopoda (fig. 53 A, C). The mandibles lost the telopodites, but they developed a special feature of which no suggestion is to be found in the Crustacea, namely, a mobile gnathal lobe, the lacinia, movable by muscles arising in the mandibular base and on the walls of the cranium. The mandibular lacinia is retained as a movable lobe in modern Symphyla (fig. 52 E, *Lc*) and Diplopoda; in the Chilopoda it is not separated from the stipital region of the mandible (fig. 53 E, F), though it is provided with strong stipital and cranial muscles (F, *I3*, *I0*); in the Pauropoda and Hexapoda (fig. 52 F) apparently it has united with the stipes (*St*), producing a solid jaw of the crustacean type, and its muscles have disappeared.

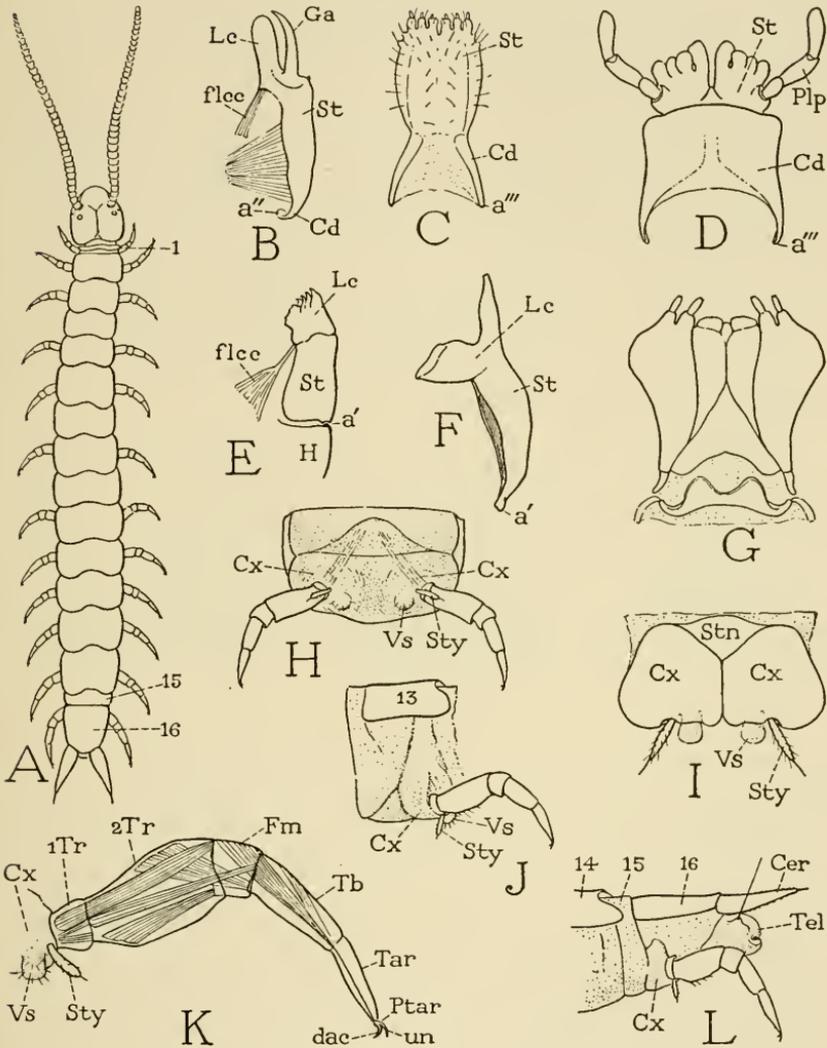


FIG. 52.—Symphyla, Diplopoda, and Thysanura.

A, *Scutigerebella immaculata* Newport (Symphyla). B, same, maxilla. C, same, labium. D, labium of *Machilis* sp. (Thysanura). E, mandible of *Scutigerebella*. F, mandible of *Machilis*. G, gnathochilarium of *Fontaria virginiana* (Drury) (Diplopoda). H, thirteenth body segment of *Scutigerebella*, ventral view. I, seventh abdominal segment of *Machilis*, ventral view. J, thirteenth body segment of *Scutigerebella*, lateral view. K, last leg of *Scutigerebella*, posterior view. L, terminal segments of *Scutigerebella*, lateral view.

a', a'', a''', cranial articulations of mandible, maxilla, and labium; Cd, cardo; Cer, cercus; Cx, coxa; dac, dactyl (clawlike remnant of dactylopodite); floc, cranial flexor muscle of lacinia; Fm, femur; Ga, galea; H, head; Lc, lacinia; Plp, palpus; Ptar, pretarsus; St, stipes; Stn, sternum; Sty, stylus; Tar, tarsus; Tb, tibia; Tel, telson; 1Tr, first trochanter; 2Tr, second trochanter (prefemur); un, lateral claw (unguis) of pretarsus; Vs, eversible vesicle; 1-16, body segments.

The maxillary appendages in Symphyla and Hexapoda have acquired two endite lobes of the stipes (lacinia and galea), but the palpi have been lost in Symphyla (B).

The last important event in the evolution of arthropod head appendages was the union of the bases of the second maxillae to form a single median organ, the so-called labium. The labium took its origin in the common ancestors of the Symphyla, Diplopoda, Pauropoda, and Hexapoda, which constituted the third and most prolific branch of the arthropod stock (fig. 54). The primitive structure of the labium is best preserved in the more generalized hexapods (fig. 52 D); in the Symphyla (C), Pauropoda, and Diplopoda (G) it has lost the telopodites, or palpi, and in the diplopods it forms at least a part of the complex gnathochilarium (G).

Crampton's (1928) phylogenetic conclusions drawn from comparative studies of the arthropod head differ radically in some respects from the concept of arthropod relationships here deduced from the same source. Crampton believes that the first arthropods derived from annelid precursors were probably prototrilobites, and that from the latter were evolved in one direction the Trilobita and Chelicerata, in another the Protocrustacea, which last in turn produced the higher Crustacea, while finally, from the malacostracan Crustacea were evolved the Myriapoda and Hexapoda.

To the writer it would seem that if the Protarthropoda are conceded to have been derived from wormlike ancestors, whether annelidan or protoonychophoran, by a sclerotization of the integument and a jointing of the appendages, they must have taken on at once a centipedelike form. According to the theory here proposed, therefore, a long, unbroken line of slender polypodous arthropods has persisted from the ancient protoonychophoran progenitors to the modern chilopods. Along this line have been carried the features common to all the arthropods, while new characters evolved in the main line itself have been distributed to subsequent lateral branches, where in some cases they have persisted in their original state, in others they have still further evolved, and in still others they have been lost.

The first lateral branch from the arthropod stem was that of the Prototrilobita (fig. 54), which produced the Trilobita and the Chelicerata. In this branch cephalization united the first four somites with the acron to form the trilobite "head," and continued in the Chelicerata until the "prosoma" contained six and eight somites. Meanwhile, in the main protarthropod stem, cephalization produced a more simple head (protocephalon) consisting of the acron and only the first somite, but the appendages of the second somite were converted into a pair

of jaws. The protarthropods thus developed into Protomandibulata. At this point arose the crustacean branch, in which the simple protocephalon is still the definitive head in a large number of forms, though

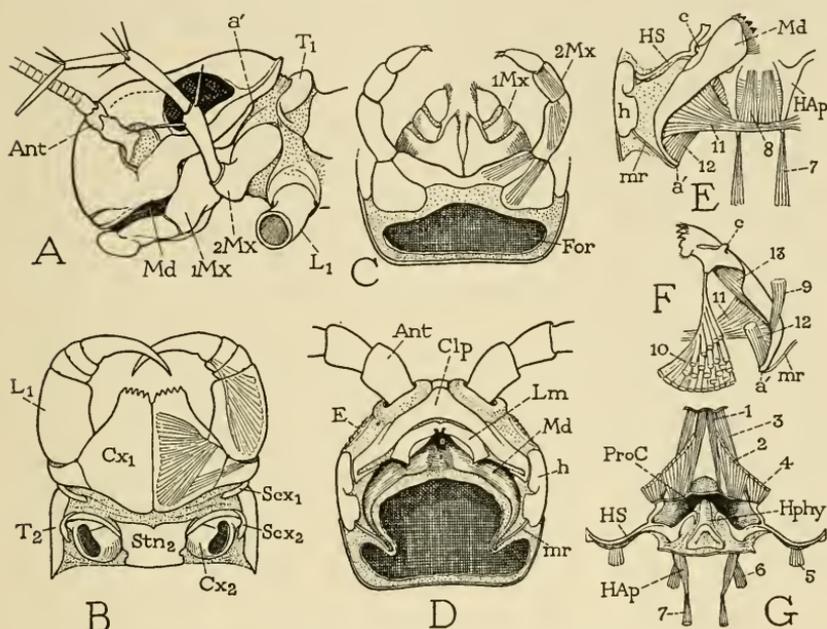


FIG. 53.—Head and mouth parts of Chilopoda.

A, head of *Scutigera forceps* Raf. B, poison claws (first legs) and second body segment of *Lithobius* sp., ventral view. C, first and second maxillae of *Lithobius*, ventral view. D, head of *Lithobius* with maxillae removed, ventral view. E, right mandible and associated head structures of *Lithobius*, ventral view. F, right mandible of *Lithobius*, dorsal view. G, hypopharynx, hypopharyngeal suspensoria, and preoral mouth cavity of *Lithobius*, ventral view (labrum and clypeus removed).

a', primary posterior articulation of mandible; *Ant*, antenna; *c*, secondary anterior articulation of mandible; *Clp*, clypeus; *Cx*, coxa; *E*, eye; *For*, foramen magnum; *h*, ventral inflexion of cranium; *HAp*, hypopharyngeal apodeme; *Hphy*, hypopharynx (metastoma); *HS*, hypopharyngeal suspensorium (fulcrum); *L*, leg; *Lm*, labrum; *Md*, mandible; *mr*, mandibular rod; *1Mx*, *2Mx*, first and second maxillae; *ProC*, preoral mouth cavity; *Scx*, subcoxa; *Stn*, sternum; *T*, tergum; *1*, *2*, frontal and clypeal muscles of labrum; *3*, *4*, frontal and clypeal muscles of hypopharyngeal suspensorium; *5*, *6*, *7*, cranial muscles of same; *8*, ventral dilator muscles of pharynx; *9*, cranial muscle of mandibular stipes; *10*, cranial flexor of mandibular lacinia (origin lateral on cranium); *11*, adductor muscle of mandible; *12*, protractor muscle of mandible; *13*, stipital flexor of mandibular lacinia.

in several groups a more extensive head has been evolved by adding to the protocephalon the following three, four, or five somites. Cephalization, however, continued also in the main protomandibulate line, and produced here a composite head of standardized structure in

which the three gnathal somites were intimately combined with the protocephalon, while the appendages of the protocephalic somite (second antennae) were suppressed. The Protomandibulata now became Protomyriapoda. A composite head has thus been produced along three separate lines of arthropod evolution, but in each case with characteristic differences.

The Protomyriapoda had all the characters common to the several groups of arthropods finally derived from them, and also older characters earlier transmitted to the Crustacea, which later appear in one or more descendent groups, and are lost in others. From the protomyriapods there arose the final persistent arthropod branch, the Protosymphyla, while the main stem continued into the relatively generalized modern Chilopoda (fig. 54). The Protosymphyla developed a labium by the union of the bases of the second maxillary appendages, and so characteristic is this feature of all their descendants, including the modern Symphyla, Diplopoda, Pauropoda, and Hexapoda, that this group as a whole might be distinguished as the *Arthropoda labiata*. The chilopods have developed few special features other than the conversion of the first legs into a pair of poison claws, but they have lost certain features of the protomyriapods.

COELOMIC ORGANS OF ADULT ARTHROPODS

In no modern adult arthropod is there retained a complete series of coelomic sacs, but remnants of the coelom are preserved as the lumina of the gonads and genital ducts, of various glands having an excretory or accessory genital function, and perhaps of other glandular structures. The embryonic development of the coelomic sacs of the Onychophora very probably recapitulates fairly closely the phylogenetic history of the coelomic sacs in both the Onychophora and the Arthropoda. The primitive coelom of these animals undoubtedly consisted of a full series of paired segmental cavities, each opening to the exterior through a ventral diverticulum of the coelomic wall connected with the ectoderm mesad of the base of the corresponding appendage. The cavities must have served for the accumulation of excretory products, and for the retention of the developing germ cells, and the outlets gave vent to both the excreta and the gametes (fig. 34 A). The more primitive annelids do not have permanent coelomic openings, and it seems doubtful that the simple coelomoducts of the Onychophora had a common origin with the metanephridia of the higher Annelida, since the metanephridia are outgrowths of the posterior walls of the coelomic sacs and each opens through the segment following.

Early in the evolution of the common ancestors of the Onychophora and Arthropoda, judging from the embryonic development of modern Onychophora, the coelomic cavities were differentiated into dorsal compartments (fig. 34 B, *a*) containing the proliferation centers of the germ cells in their walls, and into ventral compartments (*b*) opening through the coelomoducts (*c*, *d*). With the complete separation of the two series of compartments (C), the dorsal compartments became gonadial sacs (*G*) and the ventral compartments (*b*) became nephridial sacs. The gonadial sacs, being deprived of outlets, united with one another on each side and formed a pair of longitudinal gonadial tubes (E, *G*), which retained exit passages through one pair of coelomic sacs that maintained their integrity and served as genital ducts. The ventral sacs and their respective coelomoducts were transformed into specific segmental excretory organs, or nephridia. It is thus clear that the genital ducts are not "modified nephridia," as they are often said to be, but that the genital ducts and the nephridia are separate products of the primitive open coelomic sacs, and hence, when once individually established, cannot be interchangeable in function. However, because of the variable position of the genital ducts in the Arthropoda, it is evident that a different pair of coelomic sacs has been retained in different groups to serve as genital outlets.

Excretory organs of coelomic origin in the Arthropoda are represented by the coxal glands of Chelicerata and the nephridial head glands of Crustacea, and perhaps also by certain head glands of Diplopoda, Chilopoda, and apterygote Hexapoda. The coxal glands of the Chelicerata, with one exception, consist of a single pair of excretory organs situated in the prosoma and opening at the bases of the appendages. Each gland in its fullest development is a composite structure composed of several lobes or saccules derived from coelomic sacs and united upon a common tubular base, the so-called "stolon," or "labyrinth," composed of glandular cells and tubules, and is connected with the exterior by one or two segmental ducts. The organ is, therefore, variable in features that might be supposed to vary in a composite structure of such a nature, as in the number of coelomic sacs involved, the number of segmental openings, and the position of the openings. The excretory head glands of Crustacea include a pair of antennal glands ("green glands") and a pair of maxillary glands ("shell glands"). The first are present in the adult stage only in the Malacostraca; the second occur in the Entomostraca and in some Malacostraca; both pairs are present in *Nebalia* (Manton,

1934). The maxillary glands are usually simple tubes or sacs, but the antennal glands may take on a highly complex structure.

The coxal glands of *Limulus* are a pair of large brick-red organs lying in the sides of the prosoma. Each organ consists of four successive glandular lobes arising from a common longitudinal stolon composed of numerous connecting tubules, and of a long coiled duct that proceeds from an end-sac in the fourth lobe and opens behind the base of the fifth appendage (third leg). According to Patten and Hazen (1900) the nephridial lobes are developed from masses of mesodermal cells derived apparently from the somatic walls of the coelomic sacs of the second, third, fourth, and fifth somites. Similar masses of cells in the first and sixth somites degenerate and disappear. The duct arises as a tubular diverticulum of the fifth coelomic sac, which latter becomes the fourth nephridial lobe. A short terminal part of the definitive duct is formed as an ectodermal invagination at the external orifice of the mesodermal duct.

The coxal glands of Arachnida are best known from the work of Buxton (1913, 1917, see also Petrunkevitch, 1933, and Chickering, 1937). A relatively primitive condition is found in the araneid groups Liphistiomorphae and Mygalomorphae, in which each gland has two saccules, one in the third, the other in the fifth segment, both connected with a long convoluted tubular labyrinth, from which two outlet ducts proceed to the exterior, one opening behind the third appendage, the other behind the fifth. Such an organ would appear to be a composite structure formed by the union of three consecutive segmental glands. In certain genera of the Amblypygi group of the Pedipalpida the gland of the fifth segment is shown by Buxton (1917) to be an independent organ opening separately on the fifth segment. In the Uropygi each gland has two saccules but only a single opening, which is on the third segment. All other Arachnida have but a single saccule for each lateral gland and a single outlet, but the opening is at the base of the second appendage (pedipalp) in Solpugida and Palpigradida, at the base of the third appendage (first leg) in Araneida, excepting the two groups above mentioned, and at the base of the fifth appendage (third leg) in Scorpionida and Phalangida, as in *Limulus*. Buxton calls attention to the correspondence of the coxal glands of Solpugida and Palpigradida with the salivary glands of Onychophora, the organs in each case having their opening on the second postoral body somite.

Studies on the development of the arachnid coxal gland appear to leave no doubt that the organs are derivatives of coelomic sacs with coelomoducts formed as direct diverticula from the sacs as are the

coelomic ducts of Onychophora. Brauer (1895) has shown that in the embryonic development of the scorpion there are formed five pairs of diverticula from the coelomic sacs of somites *III*, *IV*, *V*, *VI*, and *VIII*, respectively, of which those of the fifth and eighth somites acquire openings to the exterior. The coelomic sacs and their diverticula in the fifth somite develop into the definitive coxal glands, the coelomic diverticula of the eighth somite become the genital ducts, and the sacs and diverticula of the other segments disappear. According to Kishinouye (1894) the development of the coxal glands in the araneid genera *Lycosa* and *Agelena* shows that each organ is a composite structure formed of small parts of the coelomic sacs of somites *III*, *IV*, and *V*, but only the first acquires an opening to the exterior.

The nephridial glands of the Crustacea, being individual organs, resemble the simple nephridia of the Onychophora rather than the composite coxal glands of the Chelicerata. Each organ consists of a mesodermal end-sac, a mesodermal canal, which may become highly complex in form, and a short exit duct of ectodermal origin (see Cannon and Manton, 1927, and Manton, 1930). The embryogeny of the crustacean excretory glands, however, is in some cases complicated by an indirect course of development.

The antennal gland of *Hemimysis lamornae* is said by Manton (1928) to be formed from two masses of cells derived from the antennal mesoderm, one of which produces the end-sac, the other the canal. The canal becomes attached distally to the ectoderm, and a small ingrowth from the latter forms a short ectodermal exit duct. Where the canal touches the wall of the sac, a compact group of 7 or 8 cells bulges into the lumen of the canal, and at this point the sac and the canal become united, but the only visible communication between them, Manton says, is by fine rather vague channels passing through the nephrostome cells. According to Vogt (1935) the antennal mesoderm of *Mysis relicta* produces only the canal and a sheet of connective tissue membrane in the base of the antenna, to which the canal becomes attached. A group of 8 cells in this membrane then forms the nephrostome. The true end-sac, Vogt claims, is constructed from adventitious connective tissue cells that wander into the antenna from the thoracic segments and form the end-sac beneath the nephrostome membrane. Vogt contends that the development of the antennal gland of *Mysis relicta* so closely resembles the development of an annelid nephridium that the two organs must be homologous structures, the nephrostome membrane of *Mysis* representing a dissepiment in the annelid. To the writer a parallelism in the two

cases is far from evident, and the development of the mysid antennal gland seems better explained as a secondary modification of the developmental processes that give rise to the coxal glands of Arachnida and the nephridia of Onychophora.

Most of the tracheate Mandibulata have a series of head glands pertaining to the gnathal somites, the openings of which lie mesad of the appendage bases, or are displaced anteriorly or posteriorly when the bases of the two appendages of a pair are united. Some of these glands have been shown to have an apparent excretory function, because of their property of eliminating from the blood particles of carmine injected into the body of the animal, and such glands also have a complex structure, usually described as consisting of a sacculle, a labyrinth, and a duct. Hence, various writers have claimed that glands of this type represent nephridial organs corresponding with the excretory head glands of Crustacea, though little evidence as to their embryonic origin has been produced.

The gnathochilarial glands of the Diplopoda have been shown by Bruntz (1903) to collect injected carmine from the blood, and they are said by Heathcote (1886) to be derived from the mesoderm in embryonic development. Likewise, according to Bruntz (1908) and Philiptschenko (1928), a pair of labial glands of apterygote insects have an excretory function and a nephridialike structure. These glands open either separately (*Campodea*, *Japyx*) between the hypopharynx and the labium, or (*Machilis*, *Lepisma*) their ducts unite in a common median duct, and are joined by the ducts of a pair of "posterior salivary glands." The labial glands of the apterygote insects, particularly those of Thysanura, would so evidently seem to be the same as the labial glands of pterygote insects, which are commonly found to be ectodermal organs, that it is difficult to believe they are not homologous structures, regardless of their function. In the Chilopoda, according to Fahlander (1938), there are present generally three pairs of head glands associated with the bases of the gnathal appendages, but in addition there is another pair having a complex structure suggesting an excretory function. These glands have each two openings, one mesad of the base of the first maxilla, the other behind the base of the second maxilla. Fahlander contends, therefore, that each gland has been formed by the union of two nephridial organs pertaining to the maxillary somites. The morphological status of all such glands must yet be determined by a study of the embryonic development.

THE GENITAL DUCTS

The student of arthropod phylogeny is confronted at every turn with the vexing problem that arises from the different position of the genital outlets in the various arthropod groups, and in recent years much discussion has been given to the question as to how the heterogoneate condition came about (see Tillyard, 1930, 1932, 1935, Snodgrass, 1933, 1936, Reynolds, 1935, Imms, 1936). Two phases of the problem have been somewhat confused, namely, that pertaining to the position of the openings of primary lateral ducts, and that pertaining to the position of secondary median ducts. The opening of a median duct is subject to migration, usually in a posterior direction; the openings of lateral ducts are closely associated with particular segments, since the lateral ducts themselves represent specific pairs of segmental coelomic sacs.

The possible migration of lateral genital ducts is narrowly restricted because of the limitations imposed by the transverse segmental nerve trunks; a secondary median duct formed by invagination of the ventral wall of the body, however, lies beneath the ventral nerve cords, and may, therefore, become lengthened from one segment to another by an extension of its connection with the body wall. There is no evidence to support Tillyard's (1930) contention that segmental gonads were once connected by a common duct, which has retained a single definitive opening on different segments in different arthropods, because when the germaria were segmentally arranged they were contained in the dorsal parts of segmental coelomic sacs with individual openings to the exterior, and the serial union of the dorsal parts of the coelomic sacs has produced the definitive tubular gonads opening through a single pair of coelomic sacs, while the ventral parts of the other sacs discharging through the coelomoducts became nephridial sacs. Likewise, Tillyard's (1935) second proposal that a heterogoneate condition has arisen by a variation in the number of somites formed before or behind the primary genital somite cannot be accepted for the reason that somite formation in the genital region is primitively teloblastic.

Inasmuch as the primary lateral genital ducts represent specific coelomic sacs that have been retained to serve as genital outlets, a segmental difference in the position of the genital openings is to be explained only as the result of mutations that have been effective in the organizer of the zone of teloblastic growth, which determines what particular pair of coelomic sacs shall be utilized as genital exits. A branching of the embryonic lateral ducts has been observed by

Heymons and by Wheeler in Dermaptera, and, according to Heymons (1901), the definitive ducts of *Scolopendra* are formed from two united pairs of coelomic sacs. In such cases we have, perhaps, examples of the supplanting of one pair of exit sacs by another pair.

The heterogoneate condition of modern arthropods, therefore, must be the result of mutations that occurred among ancestral forms. The faculty of mutation affecting the position of the genital ducts was carried over into the entomostracan branch of the Crustacea, and was not entirely extinct in the early forms of the Hexapoda. Moreover, in the Chilopoda, as in the Onychophora, there still exists a variability as to the segment of the genital ducts, for, though the genital outlet is always on the subterminal segment in Chilopoda and on the antepenultimate segment in Onychophora, the genital segment is not morphologically the same somite in all cases, since the number of somites preceding it may be quite different in different genera. In the Geophilomorpha, furthermore, the number of pregenital somites is said to vary even among individuals of the same species.

VII. PHYLOGENETIC CONCLUSIONS

1.—A planulalike creature with an open posterior blastopore was probably the ancestor of the Metazoa. A creeping form adapted to feeding on a subsurface by the forward elongation of the blastopore on the under side of the body might readily have evolved into a worm by the partial closure of the blastopore, producing thus an alimentary canal with a ventral subapical mouth and a terminal anus. The subapical position of the mouth differentiated the animal into an acronal sensory region, or *prostomium*, and a postoral visceral and motor region, the body, or *soma* in a restricted sense.

2.—The unsegmented progenitors of the annelids were probably small, creeping, wormlike creatures having a simple alimentary canal, a mouth on the anterior part of the under surface of the body, and a terminal anus. Locomotion on solid surfaces was effected by a ventral clothing of cilia, and body movements were produced by a system of muscle fibers on the inner surface of the body wall, derived from the ectoderm. The body cavity was a blastocoelic haemocoel, and was largely occupied by lateral bands of a mesoblastic parenchyma proliferated in the gastrula stage from endodermal or ectodermal teloblastomeres. The nervous system consisted of longitudinal and circular nerve tracts centering in ganglionic cell groups of the prostomium, which latter eventually united to form a "brain." Sensory organs may have included tactile tentacles and photoreceptive "eye spots" located on the prostomium.

3.—The annelidan progenitors acquired a more effective body movement by the attachment of the longitudinal somatic muscle fibers at several successive rings on the body wall, and by the accompanying formation of transverse muscular septa at the resulting integumental grooves. The body region of the wormlike animal in this way became differentiated into a small number of consecutive motor units, the *primary somites*. To regulate the new muscular mechanism of metameric movement, there was developed from the body surface of contact with the substratum a new somatic nervous system in the form of ventral nerve cords with ganglia corresponding with the myotomes. The primary and secondary nervous systems were then unified by a connection of the ventral nerve cords with the brain, and the somatic elements of the primary system disappeared. The ingrowth of the septal muscles cut the parenchymatous mesoblast bands into segmental blocks, and the latter became excavated by cleavage spaces (primitive coelomic cavities) for the accumulation of body fluid containing waste products. Excretory organs, if present at this stage, were simple nephridial tubules extending from the ectoderm into the haemocoel, where they were associated with the mesoblast cavities. The inner parenchymal cells lining the cavities formed epithelial coelomic sacs, but the outer cells, being still an undifferentiated tissue, were converted into muscle fibers and connective tissue. The secondary muscles thus formed reinforced the primary somatic muscles already present, and eventually became the major part of the muscular system. The germ cells remained in a mass of undifferentiated tissue near the posterior end of the body, and the gametes were liberated probably through a pore or temporary rupture of the body wall. The primitive segmented worms evolved in this manner from unsegmented progenitors were the ancestors of the annelids.

4.—To increase the reproductive function, the subterminal genital region of the primitive oligomerous annelids was enlarged by the successive generation of new somites from its undifferentiated tissue. A series of secondary *teloblastic somites* duplicating the structure of the primary somites was thus interpolated between the primitive body of the worm and a small postgenital terminal cone containing the anus. The multiplying germ cells spread into the haemocoel of the new somites, and groups of them became lodged in the walls of the coelomic sacs. The ripening germ cells were now discharged into the coelomic cavities, which latter thus became gonadial as well as nephric in function. Since the coelomic sacs as yet probably had no permanent openings, the gametes must have been liberated through temporary pores of the body wall, through secondary genital openings

into the nephridia, or by the autotomous separation of the genital somites. At this stage the generalized annelids had acquired the fundamental characters common to the higher Annelida, the Onychophora, and the Arthropoda.

5.—The increase in the size of the body by the addition of the teloblastic genital somites created a demand for a still greater efficiency of locomotion, and, according to the nature of the response to this demand, two divergent groups of worms were evolved from the generalized annelids. The members of one group acquired segmental clusters of eversible and retractile chaetae serving as adjuncts to the somatic muscular system by maintaining a hold on surfaces of contact; the members of the other group developed segmental pairs of lobelike outgrowths of the body wall containing extensions of the somatic muscles, which served as primitive legs. The chaetae-bearing forms gave rise to the Chaetopoda; the lobopod forms were the ancestors of the walking Onychophora and Arthropoda.

6.—From the primitive chaetopods were evolved the several groups of modern annelids. By the extension of open tubes from the posterior walls of the coelomic cavities to the exterior, a more efficient type of excretory organ (metanephridium) was developed, which could serve also for the liberation of the gametes. The Polychaeta are distinguished particularly by the elaboration of external structures of various kinds, while the Oligochaeta and Hirudinea have achieved a higher development of internal organs and functions. The locomotor powers of the Polychaeta were increased by the development of lateral lobes of the body wall supporting the segmental groups of chaetae, and in most forms each lateral pair of chaetigerous lobes eventually combined to produce a single locomotor organ, the parapodium. The parapodia served for progression on solid surfaces, and became also effective adjuncts to the undulatory motion of the body during swimming.

7.—The lobopod annelids became further differentiated from their chaetopod relatives by a chitinization of the entire cuticula, and by the suppression of all the cephalic tentacles except one pair probably corresponding with the palpi of the Polychaeta. They also acquired outlets from the coelomic sacs to the exterior, but the exit ducts were formed as diverticula from the ventral walls of the sacs and opened each on the segment of its sac mesad of the base of the corresponding leg. The germ cells were located in the walls of the dorsal parts of the coelomic sacs, and the primitive coelomoducts discharged both excretory matter and the gametes. The coelomic sacs, however, soon became divided into dorsal gonadial compartments and ventral nephric

compartments. The gonadial sacs of each lateral series united with each other, forming thus a pair of tubular gonads, which opened to the exterior through one pair of undivided coelomic sacs and their outlet ducts. The ventral nephric sacs now became exclusively excretory reservoirs, and, with the coelomoducts, formed a series of nephridial organs along each side of the body. As a result of the conversion of the original coelomic sacs into gonadial sacs and nephridial sacs, the haemocoel was restored as the definitive body cavity.

At this stage of their evolution, the lobopod annelids assumed the status of Protonychophora. Some of the protonychophorons retained the flexible integument of the worms; others developed a sclerotization in the cuticula, and thus acquired an external skeleton of cuticular plates. The soft-skinned forms, preserving some of the general aspects of their annelidan ancestors, evolved into the modern Onychophora; the armored forms gave rise to the Protarthropoda. Since the members of both groups were well adapted by their leglike appendages to a walking mode of progression, many of their descendants found an advantageous habitat on land.

8.—The Onychophora retained the cylindrical wormlike form, but they lost the segmented structure in the integument and musculature. The lobiform appendages became more efficient locomotor organs through the development of an incipient segmentation, and the acquisition of terminal claws, but the first postoral appendages were converted into a pair of jaws. The single pair of prostomial tentacles took an apical position by migrating forward on the dorsal surface of the head, but their nerve tracts were united by a commissure in the posterior part of the brain. The eyes retained the annelid type of structure. The somatic nerve cords, which presumably must have been ganglionated in the segmented generalized annelids, became simplified by a redistribution of the neurocytes, and took widely separated positions along the sides of the body. The ganglia of the jaw somite, however, united with the cerebral ganglion of the prostomium and became posterior lobes of the brain. The coelomic sacs of the penultimate somite, regardless of the total number of somites in the body, were retained intact to serve as genital outlets; the persisting remnants of most of the other coelomic sacs became small end-vesicles of the coelomoducts, which formed nephridial excretory organs.

9.—The Protarthropoda, because of the hardening of the integumental cuticula, lost the flexibility and contractility of their annelidan ancestors and onychophoran relatives, and, to compensate, developed

a mechanism of telescopic movement between successive body segments by the simple device of retaining nonsclerotized areas in the posterior parts of the primary segments, thus establishing a secondary segmentation in which the longitudinal muscles became intersegmental instead of intrasegmental in action. The sclerotized appendages necessarily became segmented into individually movable parts, and their movements became more specifically controlled by body muscles inserted on their bases. The protarthropods retained the annelid structure of the nervous system, and the independence of the first postoral ganglia of the ventral nerve cords. The prostomial appendages (antennules) assumed an anterior position by a forward migration below the eyes, with the result that in the arthropod brain the antennal lobes lie beneath the optic lobes, and the brain takes a vertical position by contrast with the horizontal position of the onychophoran brain. Lateral eyes of the compound type were first developed in the Protarthropoda. Because of the origin of the Protarthropoda from Protonychophora, the protarthropods were equipped with a series of nephridial organs like those of the Onychophora, and their internal reproductive organs were of the onychophoran type. The segmental relations of the genital ducts, however, were subject to mutation, and the position of the gonopores was, therefore, different in different forms, as shown by the highly variable position of the genital outlets in modern arthropods.

The Protarthropoda, having an annelid ancestry, and being directly derived from wormlike protonychophorons by a sclerotization of the integument and a jointing of the appendages, could scarcely take on other than a centipedelike form and structure, though they did not, of course, have the composite head and other specialized features of present-day myriapods. The number of body segments was variable, and potentially large, since the production of new somites in the zone of growth was not limited. The cephalic appendages (antennules) were filamentous, the lateral eyes primitively compound. The body appendages were probably all ambulatory legs with little differentiation among them, each composed of seven segments. The dactylopodites were provided with extensor and flexor muscles arising in the propodites. Aquatic forms probably had branchial epipodites on the coxopodites. Perhaps the majority of the protarthropods lived in shallow water near the ocean shore, where they inhabited the bottom or aquatic plants, but probably also they occurred abundantly in débris along the beach, and very likely some of them were to be found in damp places on the land. The genital openings being on specific body segments, propagation took place by sex mating, though

fertilization of the eggs was probably external. Postembryonic development was anamorphic. The first major diversification of the Protarthropoda gave rise to the ancestors of the Trilobita and the ancestors of the Mandibulata (fig. 54).

10.—The Trilobita preserved the uniform, generalized structure and segmentation of the protarthropod appendages, but otherwise they became highly specialized by a lateral extension of the margins of the body segments, taking on thus a broad, flattened form except for a median elevation giving passage to the alimentary canal. Furthermore, the first four postoral segments became intimately united with one another and with the prostomial acron to form a solid anterior body section, or prosoma, the so-called "head," bearing the labrum, the eyes, the antennules, and four pairs of postoral ambulatory appendages. Basal endites of the anterior appendages may have served as feeding adjuncts, but the trilobites, so far as known, developed no specific jaws. The Trilobita were entirely marine animals, but they lived at the bottom of the water, and their legs show few deviations from the ambulatory type of structure, except for the high development of branchial lobes from the lateral surfaces of the coxopodites. The extended tergal margins covering the gills probably formed respiratory chambers. The position of the genital openings in the trilobites has not been discovered, but, because of the close relation between the Trilobita and the Chelicerata, the genital apertures may be expected to be found on the fourth postcephalic segment. The Trilobita became extinct by the end of the Paleozoic period of geological history, but from a branch of the primitive pre-Cambrian prototrilobites were evolved the Chelicerata.

11.—The Chelicerata are distinguished from the Trilobita by the union of several additional somites with the head to form a more extensive prosoma, by the loss of the acronal appendages (antennules), by a greater differentiation among the somatic appendages, and by the forcipate structure of the reduced first appendages. Very commonly, also, there is an extra podomere in at least some of the legs, the patella, interpolated between the femur and the tibia. In modern forms the nephridial organs are suppressed in most of the somites, but some of them are retained as coxal glands, and (except in Pycnogonida and some Acarinida) the genital openings occur always on the eighth postoral somite. The Chelicerata have become the most specialized of all the arthropods, there being little in their body form and general organization suggestive of the ancestral centipede type of structure, which is so evident throughout the mandibulate

branch. The Chelicerata include the Xiphosurida, the Eurypterida, the Arachnida, the Acarinida, and very probably the Pycnogonida.

12.—The Xiphosurida are undoubtedly the closest living representatives of the Trilobita. The xiphosurid prosoma has the same structure as the trilobite head, and the same composition except for the addition of three extra somites and a part of the eighth somite. Likewise, the opisthosoma corresponds with the trilobite pygidium extended forward to include all the somites behind the prosoma, so that in the Xiphosurida there is no intermediate "thoracic" region of free segments. Such fossil forms as *Belinurus* and *Prestwichia* would appear to be intermediate between modern Xiphosurida and Trilobita, and the Middle Cambrian *Naraoia* (see Walcott, 1931, fig. 1) must be related to the xiphosurid line somewhere close to the trilobites. The first six prosomatic appendages retain the leg type of structure, except for the reduction and chelicerate form of the first pair. The seventh appendages are reduced to a pair of small lobes, the chilaria, and the following six have the form of broad plates formed chiefly by epipodite lobes, those of the last five bearing lamellate gills. The genital openings in both sexes are on a median ventral fold of the eighth segment united with the bases of the opercular appendages of this segment.

13.—The Pycnogonida, judging from some of their structural features, such as the union of the anterior body segments, the posterior position of the dorsal eyes between the bases of the third pair of appendages, the presence of a patellar segment in the legs, and the chelicerate structure of the first appendages, are to be classed with the Chelicerata; but because of their many unique characters, including the occurrence of multiple genital openings, it is impossible to connect them closely with any other of the chelicerate groups. It may be noted, however, that species with eight pairs of legs have presumably the same number of somites in the prosoma as have the Xiphosurida.

14.—The Eurypterida and the Arachnida differ from the xiphosurids in having only six segments in the prosoma, and this character together with various other features of their organization shows that these two groups are more closely related to each other than is either group to the Xiphosurida. On the other hand, the Eurypterida have certain characters of the xiphosurids that leave little doubt of their common ancestry with the latter, and their descent from trilobite stock. The general resemblance of the eurypterids to scorpions suggests a relationship between the two, but the theory of Versluys and Demoll (1920, 1923) that the Eurypterida and Xiphosurida are

derived from primitive aquatic scorpions cannot be maintained against the evidence of close relationship between the Xiphosurida and the Trilobita. The Arachnida, as invaders of the land, had to evolve organs for aerial respiration, and the lamellate gills of their aquatic progenitors borne on the abdominal appendages were structures readily convertible into "lung books" by invagination into pockets of the integument (see Lankester, 1885). In addition, however, tracheal ingrowths of the body wall were developed in the Arachnida, as they have been in nearly all the other terrestrial arthropods.

15.—The Protomandibulata preserved the slender, polypodous, centipedelike form of the primitive protarthropods, but they acquired as a distinctive character a pair of jawlike feeding organs, the *mandibles*, developed from the bases of the second postoral appendages. Probably long before the evolution of the mandibles, the first somite had been united with the prostomial acron to form a primitive composite head, or protocephalon, bearing the acronal sensory organs, the mouth, and the first pair of postoral appendages, which last became a second pair of antennae. The two pairs of appendages following the mandibles were reduced and modified to serve as accessory feeding organs. The other appendages were probably all leglike in form, as in modern centipedes, and were 7-segmented, since a patella does not occur in the mandibulate branch of the arthropods. The circulatory system still retained the basic structure of that of the generalized annelids; respiration probably was branchial, the gills being carried on epipodite lobes of the coxopodites, as in the Trilobita; the nephridial organs were perhaps suppressed in most of the body segments, but those that remained were of the onychophoran type of structure. The reproductive organs were closed gonadial tubes opening in each sex through a single pair of ducts formed from a pair of coelomic sacs, but the segmental position of the genital openings varied in different forms according to what particular pair of coelomic sacs served as gonadial outlets.

The primitive Protomandibulata probably inhabited both the water and the land, since from them were early evolved the aquatic Crustacea, while the main branch developed into the terrestrial Protomyriapoda, from which have descended the modern myriapods and the Hexapoda.

16.—That the Crustacea are derived from crawling, centipedelike protomandibulate ancestors is attested by the retention in all the higher forms of ambulatory appendages having the same structure as the limbs of terrestrial arthropods. Many forms, however, have become adapted in part or entirely to swimming by a modification of the

appendages, and the special development of an exite lobe of the basipodites has given rise to a characteristic biramous structure of the limbs. The primitive protocephalon is retained as the definitive head in the Anostraca and in most of the Malacostraca, but in the majority of the Entomostraca and in the Leptostraca, Amphipoda, and Isopoda from three to five gnathal somites have been united with the protocephalon to form a more extensive cephalic structure. A carapace is variously developed in many groups, either from the cephalognathal region, or from the gnathothoracic region, but there is no true cephalothorax formed by an intimate union of cephalic and thoracic somites as in the Chelicerata. The mandibles have no movable lobes such as those of the myriapods; in most forms the jaws preserve the primitive monocondylic articulation with the head, but in the higher Malacostraca they are secondarily dicondylic. The genital openings are variable in position in the Entomostraca, but are fixed with respect to a specific segment in the Malacostraca. The hatching of the young at an early embryonic stage has resulted in the development of specialized swimming larval forms representing more primitive ancestral stages in their general structure than the immediate protarthropod ancestors of the crustaceans. The great antiquity of the Crustacea is shown by the occurrence of highly evolved forms in the Cambrian period contemporaneous with the oldest known trilobites.

17.—The Protomyriapoda, being the direct descendants of the protarthropods, perpetuated the generalized arthropod form after the trilobites, the chelicerates, and the crustaceans had branched off as side issues and taken on variously specialized forms. During their evolution the protomyriapods acquired the structures characteristic of their descendants, which include the modern Symphyla, Diplopoda, Hexapoda, and Chilopoda. The three gnathal somites became intimately united with one another and with the protocephalon, forming the standardized head of the above-mentioned groups, composed of the acron and four postoral segments. The compound eyes and the first antennae of the Protomandibulata were retained, but the second antennae became reduced and eventually were lost, though their ganglia were preserved as tritocerebral lobes of the brain. The mandibles lost the telopodites, but each had a strong gnathal lobe (lacinia) movable by a muscle arising within the coxopodite and by another arising on the cranial wall. The two postmandibular maxillary appendages were modified by a reduction of the telopodites and by other adaptations to serve as accessory feeding organs. Since the Symphyla and some of the more generalized Hexapoda have lateral hypopharyngeal lobes (superlinguae) resembling the paragnatha of

Crustacea, it is possible that these structures were transmitted from the Crustacea to the symphylids and hexapods through the Protomyriapoda, though they have been lost in modern Diplopoda and Chilopoda. The legs of the protomyriapods were all alike and retained the generalized 7-segmented structure, but the extensor muscle of the pretarsus was lost, leaving only the flexor muscle, which, for more effective action, shifted its origin from the tarsus into more proximal segments of the leg. This last feature is a distinctive character of all the descendants of the Protomyriapoda. Nephridial excretory organs were supplemented or replaced functionally by Malpighian tubules of the proctodaeum. The position of the genital openings was probably in general posterior, but variable. Postembryonic development was anamorphic, the young being hatched with a small number of segments, and the full number acquired by teloblastic generation in the subterminal zone of growth.

The Protomyriapoda undoubtedly were terrestrial, and the larger forms may have developed tracheal invaginations on various parts of the body for respiration, but there was no definitely established tracheal system transmitted alike to all the descendent groups of terrestrial mandibulates. The probable characters of the Protomyriapoda are summarized as follows by Imms (1936):

(1) The head bore a single pair of antennae and two pairs of jaws, viz. mandibles and maxillae: the second maxillae were probably a subsequent acquisition. (2) The trunk was composed of a variable and indefinite number of sub-equal segments, each bearing a pair of legs. It is probable that anamorphosis was universal and was continued throughout the life of the animal. (3) The gonads opened to the exterior by paired apertures, and the segmental disposition of the orifices probably varied in different families and depended upon that of the coelomoducts involved. . . . (4) The alimentary canal was probably a simple straight tube, while the excretory organs were little more than proctodaeal outgrowths or pockets; an accessory excretory function was probably performed by the fat-body. (5) Respiration was probably cutaneous in many forms and partially tracheate in others. The tracheae were presumably in the form of groups of unbranched tubuli devoid of taenidia and bearing a general resemblance to those of Diplopoda. Each group of tracheae opened laterally by means of simple cryptlike, segmentally arranged spiracles: in some forms a pair of spiracles was probably located also on the head.

From the Protomyriapoda there emerged a specialized lateral branch, the Protosymphyla, from which have been evolved in one direction the progoneate modern Symphyla, Pauropoda, and Diplopoda, in another the opisthogoneate Hexapoda, while the generalized myriapodan stock has more directly continued into the modern Chilopoda.

18.—Since modern Symphyla combine features of the progoneate Diplopoda and Pauropoda on the one hand, and of the opisthgoneate Hexapoda on the other, there can be little question that they are direct descendants of common ancestors of these two groups. Modern Symphyla, however, are linked more closely with the progoneate forms by the anterior position of the gonopore, the segmentation and structure of the legs, and the retention of the movable laciniae of the mandibles. The Protosymphyla, therefore, gave rise to an opisthgoneate branch that became the Protohexapoda.

In general appearance the Protosymphyla probably resembled their modern representatives, but retained certain features of the Protonomyriapoda that have been transmitted to the hexapod line, though lost in the progoneate descendants. The legs were all alike and had the 7-segmented protonomyriapod type of structure, but the coxopodites bore each, mesad of the telopodite base, a small stylus and an eversible vesicle, as in modern Symphyla (fig. 52 H), which structures are preserved also on the abdomen of some of the apterygote insects (I). The appendages of the last body somite became reduced to styliform cerci. The head appendages included a pair of antennae, a pair of mandibles, and two pairs of maxillae. The lateral eyes must have been compound, because compound eyes have been transmitted along the arthropod line from the Trilobita to the Xiphosurida, the Crustacea, and through the Protosymphyla to the Hexapoda. The protosymphylan mandibles had the protonomyriapodan structure, movable laciniae being well developed, and palpi absent. The first and second maxillae retained the palpi and each acquired two basal lobes (lacinia and galea), features transmitted to the hexapods, though the palpi have been lost in the progoneate branch. The bases of the second maxillae, however, became united to form a single appendage, the *labium*, an organ so characteristic of all the descendants of the Protosymphyla that the group as a whole, including Symphyla, Pauropoda, Diplopoda, and Hexapoda, might well be designated the "Labiata" (fig. 54).

19.—The direct descendants of the progoneate branch of the protosymphylids are the modern Symphyla, but at an early period there were evolved from the symphyliid line the common ancestors of the Diplopoda and Pauropoda. The Symphyla retain the generalized structure of the body and appendages (fig. 52 A), but of the 16 body segments evident in the dorsum of most forms, 3 are without appendages. The legs (K) show the diplopod type of structure in the relatively large size of the second trochanter (*2Tr*) and the smallness of the femur (*Fm*), but the coxae do not appear as typical leg segments, since each pair apparently is confluent in a large posterior division of

the venter of the body segment (H, *Cr*), carrying mesad of the base of each telopodite a small stylus (*Sty*) and an eversible vesicle (*Vs*). The end segments of the legs are reduced to small dactyls (K, *dac*), but each has an accessory claw (*un*) arising from its base. The first legs are usually reduced in size and lack tibiae. The last body segment bears a pair of cerci (L, *Cer*), which presumably are homologues of the legs or possibly of the styli of the preceding segments. Compound eyes are absent. The mandibles preserve the movable laciniae (E, *Lc*); the maxillae have both laciniae and galeae (B), but the palpi are small or vestigial; the labium (C) is a simple flap without palpi. Lateral lobes of the hypopharynx (superlinguae) are present at least in *Scutigerebella*, as shown by Hansen (1930), and a pair of slender apodemal arms extend into the head from the hypopharyngeal base. The single median genital aperture is situated on the anterior part of the venter of the fourth body segment, but since the paired gonopores of Pauropoda and Diplopoda are on the third body segment, the median genital outlet of the symphylids might be supposed to have migrated secondarily into the fourth segment.

20.—The Diplopoda are a specialized branch of the early Symphyla, in which the somites back of the fourth postcephalic somite are united in pairs to form double segments. The mandibles are well developed and have strong movable lacinial lobes, but there is only one post-mandibular appendage of the head, the gnathochilarium (fig. 52 G), the morphology of which is uncertain, though the organ is probably either a combination of the maxillae with the labium, or the labium alone. The legs of the first body segment are absent, and there are no cerci on the last somite. Body segments are numerous in most forms, and all but the first few are generated teloblastically in pairs during postembryonic development. The paired gonopores are on the third postcephalic somite at the bases of the second pair of legs. The Pauropoda are probably an early branch of the Diplopoda, in which a union of the somites in pairs had already taken place, and the first legs had been much reduced but not yet obliterated. Special characters of the pauropods are the lack of movable laciniae on the mandibles, a weak development of the gnathochilarium, and a branching of the antennae beyond the fourth segments.

21.—The Hexapoda resemble more closely the Symphyla than any other of the modern arthropods, a fact recognized by several of the earlier writers, and Packard (1898) first formulated a definite theory of the origin of insects from symphylid ancestors. Recently the evidence in favor of this theory has been more thoroughly reviewed in the light of present-day knowledge of the apterygote hexapods by

Inms (1936), who shows that the most plausible concept of the ancestry of insects is that of symphylid derivation. The important difference between modern Hexapoda and Symphyla is in the position of the genital openings, the symphylids being progoneate, the hexapods opisthgoneate. It is necessary to assume, therefore, that the Protohexapoda were evolved from an opisthgoneate branch of the Protosymphyla.

The Protohexapoda became differentiated as a hexapod group through the concentration of the locomotor function in the first three postcephalic segments, with the consequent division of the body into a motor thorax and a visceral abdomen. The abdominal appendages were reduced, modified for purposes other than locomotion, or suppressed, but in most cases the abdominal coxal remnants united with the sternal plates of the segments and preserved the styli and eversible vesicles inherited from the Protosymphyla, though on the thorax these structures were lost. The number of body segments was limited to 14 somites and a simple terminal lobe (telson) containing the anus. The persistent appendicular organs of the last somite were styluslike cerci, as in Symphyla. It is probable that the true telopodites of all the abdominal segments were absent. The mandibles became solid jaws by a complete fusion of the lacinial lobes with the coxopodites, and thus came to resemble the mandibles of Crustacea, but the maxillae and labium retained the generalized protosymphylan structure. The hypopharynx consisted of a median lobe and two lateral lobes, as in Symphyla, and had a pair of basal apodemes giving attachment to muscles of the gnathal appendages. The eyes were compound. The protohexapods were opisthgoneate insofar as the paired genital apertures were located on the posterior part of the abdomen, but the exact position of the ducts and their outlets was still subject to mutation, as shown in the variable position of the genital outlets in modern forms.

The discrepancy in the position of the genital openings as between Symphyla and Hexapoda raises the chief difficulty in relating the hexapods directly to the symphylids. The opisthgoneatism of the Hexapoda, however, is more truly a heterogoneate condition, which in a broad sense applies to the entire group of labiate mandibulates, for the primary genital ducts open on the third postcephalic somite in Diplopoda and Pauropoda, on the eighth in Collembola, on the tenth in female Pterygota, on the thirteenth (primitively) in male Pterygota, and on the fourteenth in Protura. Since the primary gonopores of the hexapods are always fixed with specific segments, as in Symphyla, Pauropoda, and Diplopoda, the opisthgoneate con-

dition in the Hexapoda is not comparable with that in the Chilopoda, in which the genital outlet, though always subterminal, may be on a quite different somite in different forms because of the variable number of somites that may precede it. There is reason for believing, therefore, that the opisthogoneate condition of the Hexapoda has been acquired secondarily, and that it is a derivative from the progoneatism of Symphyla and Diplopoda, rather than from the opisthogoneatism of Protomyriapoda represented in modern Chilopoda. The establishment of the genital openings on the posterior part of the body in the Hexapoda was very probably an adaptation correlated with the concentration of the locomotor function in the thorax.

22.—An early specialization among the Protohexapoda gave rise to the modern entognathous Diplura, Protura, and Collembola, small hexapods characterized by a retraction of the mandibles and maxillae into pouches of the head wall closed ventrally by the labium. The identity in the structure of the mouth parts would alone suggest a phylogenetic unity among the above-mentioned groups, but the latter show also a peculiarity in the development of the hypopharyngeal apodemes, which structures, instead of projecting as free arms into the head, as in myriapods and Machilidae, take the form of long internal ridges that, in Diplura and Collembola, diverge posteriorly from the base of the hypopharynx as sclerotic linear inflections of the membranous integument along the folds between the gnathal pouches and the inner surface of the labium. In Protura the two rods are united for a part of their length. These superficial apodemes give attachment to the same muscles as do the internal apodemes of other forms, and in Collembola they support an elaborate "tentorial" superstructure. In many other respects the entognathous hexapods are widely different from one another, and their inter-relationships are by no means clear. Except for the common characters above mentioned, they might be supposed to have had quite separate origins from protosymphylan or protohexapod ancestors (see Imms, 1936, fig. 11). They represent abortive lines of evolution that have not led to higher forms.

The Diplura depart least from the thysanuran branch that has given rise to the winged insects, since they retain the abdominal styli and cerci, and have the usual hexapod position of the genital openings. The Protura preserve a remnant of the primitive anamorphism of the hexapod ancestors, inasmuch as the last two somites are formed during postembryonic development, but they lack antennae, styli, and cerci; the small appendicular organs on the first three abdominal segments may be coxal remnants of limbs, with eversible vesicles in

one family. The paired genital ducts in both sexes open on the eleventh abdominal segment. The Collembola are the most aberrant of all the hexapods, and in some ways the most primitive. They have only nine body segments, and the single genital opening is on the fifth abdominal segment. There can be no question that the Collembola are derived from more generalized ancestors having a greater number of segments, but since, in their phylogenetic history, segment formation in the zone of growth has ceased after the establishment of the genital ducts in the eighth somite, it is fruitless to look for evidence of the ancestral segmentation in the embryogeny of present-day Collembola. The three pairs of appendicular organs on the collembolan abdomen are unique in structure, and give little suggestion of homology with the abdominal appendages of Symphyla, Diplura, and Thysanura, though it may be supposed that the colophore is a pair of united eversible vesicles, and that the two paired appendages are highly developed styli. (For a fuller discussion of the special features of the Collembola, see Imms, 1936.)

23.—The main evolutionary line of the early hexapods led from the opisthogoneate branch of the Protosymphyla directly into the Machilidae, since in this family are best preserved the coxal accessory structures of the symphylids (fig. 52 I) along with the normal ectognathous mouth parts. Moreover, it was in the ancestors of the Machilidae that the characteristic ovipositor of the hexapods had its inception, and, therefore, from the machilid line have been evolved the Lepismatidae and the Pterygota. The common ancestors of these last two groups developed two special features in the head structure. One was the acquisition of a secondary anterior articulation of the mandible on the cranium, giving the jaw a hinge movement on a longitudinal axis, which brought about a reorganization of the mandibular musculature, giving the principal function of abduction and adduction to the dorsal muscles, and reducing the ventral muscles to a condition of such little importance that they have completely disappeared in the higher Pterygota. The other feature was the development of the endocranial framework known as the tentorium, characteristically present in Lepismatidae and Pterygota, but foretokened in Machilidae. The tentorium is evidently a product of the hypopharyngeal apodemes and of a transverse bar developed in the back of the head from lateral invaginations. Both structures are present in Machilidae, but are not united. In Lepismatidae the anterior apodemes are reflected directly from the cranial margins and are united posteriorly with the transverse bar, producing a typical tentorium. In the Pterygota the roots of the anterior arms take a submarginal position on the cranium, and in higher forms they have migrated to the facial aspect of the head.

The hexapod structure, with the locomotor function centered in the thorax, apparently gave little if any advantage over the polypod structure for ordinary terrestrial life, but it furnished a condition particularly fitted for the development of wings. Hence, with the appearance of alar lobes on the thorax, the evolution of these lobes into organs of flight was readily accomplished, and the pterygote insects quickly achieved a great superiority over the other arthropods. While there is much to suggest that the winged insects are most closely related to the apterygote thysanurans, their direct origin from the latter is questionable. It is difficult to explain, for example, how it comes about that the pterygote Ephemeroptera and Dermaptera have paired genital openings while secondary median ducts are already established in the Thysanura, with openings on the same segments as in the higher Pterygota.

24.—The Chilopoda are the conservatives among the arthropods; they are the least-modified descendants of the Protomyriapoda, and in certain phases of their embryogeny they still follow the course of development in the Onychophora. The gnathal appendages are probably more generalized than in any other of the Mandibulata; though the bases of the mandibles are deeply sunken into pouches of the head wall, they have strongly muscled lacinial lobes (fig. 53 E, F), and the two maxillary appendages (C) are but little modified except by reduction of the telopodites and a partial union of the coxopodites. The suspensorial sclerites of the hypopharynx maintain connections with the cranial margins, and bear the apodemes on which the ventral muscles of the gnathal appendages are attached. The characteristic specialization of the chilopods is the conversion of the first legs into a pair of poison claws (B). Most of the other body appendages retain the structure of simple 7-segmented legs, though at the base of each is an extensive subcoxal sclerotization suggestive of that in the insect thorax. The last two pairs of legs are reduced and modified to serve as genital accessories, and consequently there are no terminal cerci. Styli and eversible vesicles are absent. The genital opening is always on the last somite before the telson, but since the total number of somites is variable, the genital segment may be a quite different somite in different chilopod groups. Anamorphic postembryonic development persists in some forms, while in others segmentation is complete at hatching.

25.—Evolution may be accepted as a fact, but the true history of phylogeny can never be demonstrated. Though the main branches of the genealogic tree of any major group of animals are fairly evident, an endeavor to follow in detail the phylogenetic connections between more closely related forms invariably leads into a maze of difficulties,

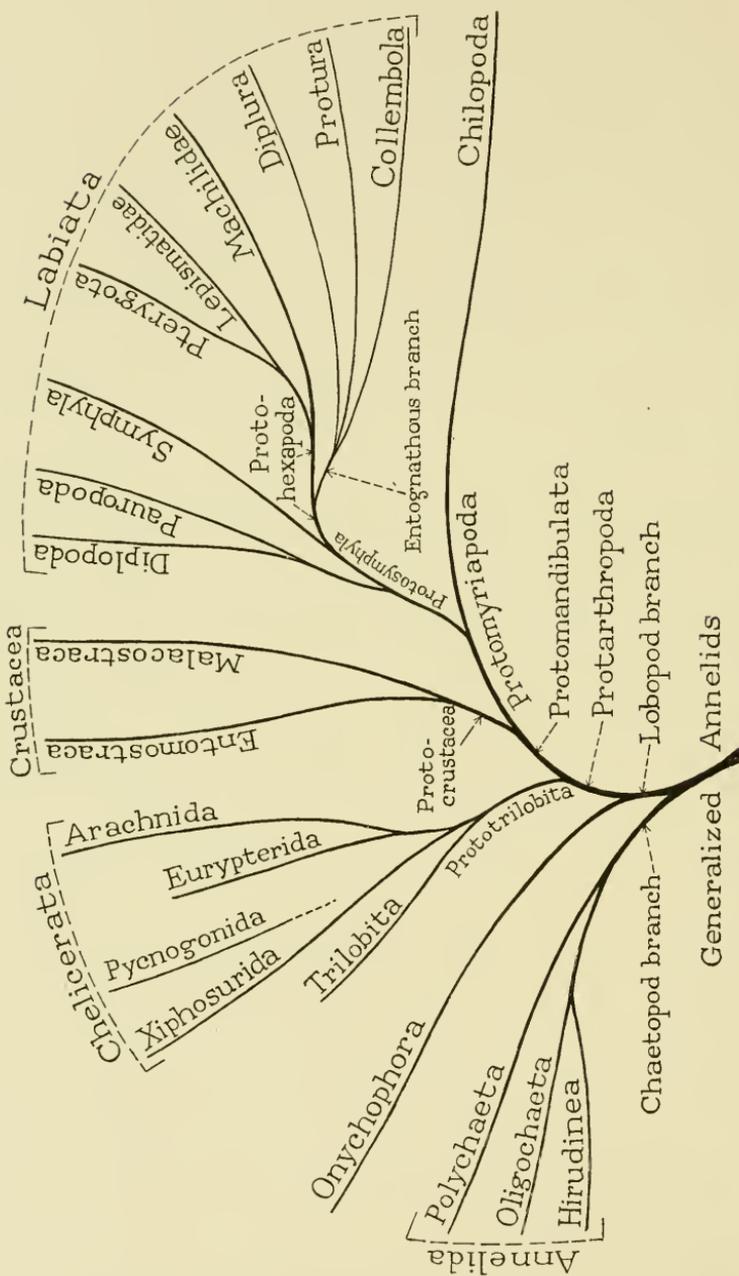


FIG. 54.—Diagram illustrating the phylogenetic relationships of the Annelida, Onychophora, and Arthropoda proposed in the text.

for it is seldom found that all characters will fit into a scheme of relationship that attempts to relate every feature in one form with a similar feature in another. It must be recognized that various structural adaptations have been often independently developed in approximately the same way. A successful adaptation will be equally valuable in many groups, and it is, therefore, not surprising that an adaptive structure should independently recur either in distantly related or in closely related groups. To distinguish between such structures and those that have had an identical origin, however, is one of the most uncertain tasks of the phylogeneticist, but the very condition of uncertainty injects into the study of phylogeny the element of personal opinion which gives to phylogeny that controversial status by which it never lacks in interest. Every biologist must have a working creed of phylogeny, but he should not too implicitly believe its tenets.

REFERENCES

BADEN, V.

1936. Embryology of the nervous system in the grasshopper, *Melanoplus differentialis* (Acrididae; Orthoptera). *Journ. Morph.*, vol. 60, pp. 159-188, 4 pls.

BALFOUR, F. M.

1880. Notes on the development of the Araneina. *Quart. Journ. Micr. Sci.*, vol. 20, pp. 1-23, pls. 19-21.
1883. The anatomy and development of *Peripatus capensis*. *Quart. Journ. Micr. Sci.*, vol. 23, pp. 213-259, pls. 13-20.

BENHAM, W. B. S.

1885. Description of the muscular and endoskeletal systems of *Limulus*. *Trans. Zool. Soc. London*, vol. 11, pp. 314-338, pls. 72-76. (See Lankester, Benham, and Beck, 1885.)

BERGH, R. S.

1888. Zur Bildungsgeschichte der Excretionsorgane bei *Criodrilus*. *Arb. Zool.-Zoot. Inst. Würzburg*, vol. 8, pp. 223-248, pls. 13, 14.
1890. Neue Beiträge zur Embryologie der Anneliden. I. Zur Entwicklung und Differenzierung des Keimstreifens von *Lumbricus*. *Zeitschr. wiss. Zool.*, vol. 50, pp. 469-526, pls. 19-21.
1899. Nochmals über die Entwicklung der Segmentalorgane. *Zeitschr. wiss. Zool.*, vol. 66, pp. 435-449, pl. 30.

BIGELOW, M. A.

1902. The early development of *Lepas*. A study of cell-lineage and germ-layers. *Bull. Mus. Comp. Zoöl.*, vol. 40, pp. 61-144, 12 pls.

BINARD, ALICE, and JEENER, R.

1926. Recherches sur la morphologie du système nerveux des Annélides. I. *Nereis*. *Bull. Acad. R. Belgique, Classe Sci.*, ser. 5, vol. 12, pp. 437-448, 6 figs.
1928. Sur l'existence de cavités coelomiques dans le segment palpaire des Polychètes. *Recueil Inst. Zool. Torley-Rousseau*, vol. 1, pp. 173-178, 1 fig.
1929. Morphologie du lobe préoral des Polychètes. *Recueil Inst. Zool. Torley-Rousseau*, vol. 2, pp. 117-240, 45 text figs., pls. 5-12.

BOUVIER, E. L.

1902. Sur l'organisation, le développement et les affinités du *Peripatopsis Blainvillei* Gay-Gervais. Zool. Jahrb., Suppl. vol. 5 (Fauna Chilensis, vol. 2), pp. 675-730, pls. 20-22.
- 1905, 1907. Monographie des Onychophores. Ann. Sci. Nat., Zool. sér. 9, vol. 2, pp. 1-383, pls. 1-13; vol. 5, pp. 61-318, 191 figs.

BRACE, EDITH M.

1901. Notes on *Aeolosoma tenebrarum*. Journ. Morph., vol. 17, pp. 177-184, pl. 21.

BRAUER, A.

1895. Beiträge zur Kenntnis der Entwicklungsgeschichte des Skorpions. II. Zeitschr. wiss. Zool., vol. 59, pp. 351-435, 20 text figs., pls. 21-25.

BRUNTZ, L.

1903. Sur la présence des reins labiaux et d'un organ phagocytaire chez les Diplopodes. C. R. Acad. Sci. Paris, vol. 136, pp. 57-59.
1908. Les reins labiaux et les glandes céphaliques des Thysanoures. Arch. Zool. Exp. Gén., vol. 9, pp. 195-238, pls. 2, 3.

BÜRGER, O.

1891. Beiträge zur Entwicklungsgeschichte der Hirudineen. Zur Embryologie von *Nepheleis*. Zool. Jahrb., Anat., vol. 4, pp. 697-738, pls. 41-43.
1894. Neue Beiträge zur Entwicklungsgeschichte der Hirudineen. (*Hirudo* and *Aulastomum*). Zeitschr. wiss. Zool., vol. 58, pp. 440-459, pls. 26-28.

BUXTON, B. H.

1913. Coxal glands of the arachnids. Zool. Jahrb., Suppl. 14, pp. 231-282, pls. 1-43.
1917. Notes on the anatomy of arachnids. Journ. Morph., vol. 29, pp. 1-31, 8 text figs., 3 pls.

BYCHOWSKY, A.

1921. Über die Entwicklung der Nephridien von *Clepsine sexoculata* Bergmann. Rev. Suisse Zool., vol. 29, pp. 41-131, 16 text figs., pls. 1-5.

CAMERANO, L.

1897. Sulla striatura trasversale dei muscoli delle mandibole negli Onicofori. Atti R. Accad. Sci. Torino, vol. 33, pp. 589-593.

CANNON, H. G., and MANTON, S. M.

1927. Notes on the segmental excretory organs of Crustacea. I-IV. Journ. Linn. Soc. London, vol. 36, pp. 439-456, 7 figs.

CHICKERING, A. M.

1937. Evolution in spiders. 38th Ann. Rep., Michigan Acad. Sci., Arts, Lett., pp. 22-51.

CHILD, C. M.

1900. The early development of *Arenicola* and *Sternaspis*. Arch. Entwicklmech., vol. 9, pp. 587-723, pls. 21-25.

CRAMPTON, G. C.

1928. The evolution of insects, chilopods, diplopods, Crustacea, and other arthropods indicated by a study of the head capsule. Canadian Ent., vol. 60, pp. 129-141, pls. 8-12.
1928. The evolution of the head region in lower arthropods and its bearing upon the origin and relationships of the arthropodan groups. Canadian Ent., vol. 60, pp. 284-301, pls. 20, 21, 22.

CUÉNOT, L.

1926. L'entonnoir vibratile de la néphridie des Péripatés. Ann. Soc. R. Zool. Belgique, vol. 56, pp. 13-17.

CURTIS, W. C., and GUTHRIE, MARY J.

1927. Textbook of general zoology. New York and London.

DAKIN, W. J.

1920. Fauna of Western Australia. III. Further contributions to the study of the Onychophora. Proc. Zool. Soc. London, vol. for 1920, pp. 367-389, 5 pls.
1921. The eye of Peripatus. Quart. Journ. Micr. Sci., vol. 65, pp. 163-171, 3 text figs., pl. 7.

DAUTERT, E.

1929. Die Bildung der Keimblätter von Paludina vivipara. Zool. Jahrb., Anat., vol. 50, pp. 433-496, 33 figs.

EISIG, H.

1899. Zur Entwicklungsgeschichte der Capitelliden. Mitt. Zool. Sta. Neapel, vol. 13, pp. 1-292, pls. 1-9.

EVANS, R.

1902. On the Malayan species of Onychophora. Part II. The development of Eoperipatus weldoni. Quart. Journ. Micr. Sci., vol. 45, pp. 41-88, pls. 5-9.

FAHLANDER, K.

1938. Beiträge zur Anatomie und Systematischen Einteilung der Chilopoden. Zool. Bidrag Uppsala, vol. 17, pp. 1-148, 36 text figs., 18 pls.

FAUSSEK, V.

1899. Über die physiologische Bedeutung des Coeloms. Trav. Soc. Imp. Nat. St. Petersburg, vol. 30, Livr. 1, pp. 40-57 (in Russian), 83-84 (résumé in German).
1901. Untersuchungen über die Entwicklung der Cephalopoden (VII, Was ist das Cölom?). Mitt. Zool. Station Neapel, vol. 14, pp. 83-237, pls. 6-10.

FEDOROW, B.

1926. Zur Anatomie des Nervensystems von Peripatus. I. Das Neurosomit von Peripatus tholloni Bouv. Zool. Jahrb., Anat., vol. 48, pp. 273-310, 4 text figs., pls. 10, 11.
1929. Zur Anatomie des Nervensystems von Peripatus. II. Das Nervensystem des vorderen Körperendes und seine Metamerie. Zool. Jahrb., Anat., vol. 50, pp. 279-332, pls. 6, 7.

GLEN, EDITH H.

1919. A revision of certain points in the early development of Peripatus capensis. Quart. Journ. Micr. Sci., vol. 63, pp. 283-292, pl. 20.

GOODRICH, E. S.

- 1898-1900. On the nephridia of the Polychaeta. Parts I-III. Quart. Journ. Micr. Sci., vol. 40, pp. 185-195, pls. 6-9; vol. 41, pp. 439-457, pls. 32-35; vol. 43, pp. 699-748, pls. 37-42.
1912. Nerilla an archianellid. Quart. Journ. Micr. Sci., vol. 57, pp. 397-425, pls. 38-41.

GUILDING, L.

1826. Molusca Carribeana. 2. An account of a new genus of Mollusca. Zool. Journ., vol. 2, pp. 437-444, pl. 14.

GUSTAFSON, G.

1930. Anatomische Studien über die Polychäten-Familien Amphinomidae und Euphrosynidae. Zool. Bidrag Uppsala, vol. 12, pp. 305-471, 64 text figs., 36 pls.

HACKER, V.

1895. Die spätere Entwicklung der Polynoë-Larve. Zool. Jahrb., Anat., vol. 8, pp. 245-288, pls. 14-17.

HAMAKER, J. I.

1898. The nervous system of *Nereis virens* Sars. Bull. Mus. Comp. Zoöl., vol. 32, pp. 89-124, 5 pls.

HANSEN, H. J.

1930. Studies on Arthropoda III. Copenhagen.

HANSTRÖM, B.

1926. Eine genetische Studie über die Augen und Sehzentren von Turbellarien, Anneliden und Arthropoden. K. Svenska Vetenskapskad. Handl., 3d ser., vol. 4, no. 1, 176 pp., 80 figs.
1927. Das zentrale und periphere Nervensystem des Kopfappens einiger Polychäten. Zeitschr. Morph. Ökol. Tiere, vol. 7, pp. 543-596, 27 figs.
1928. Vergleichende Anatomie des Nervensystems der wirbellosen Tiere. Berlin.
1929. Weitere Beiträge zur Kenntnis des Gehirns und der Sinnesorgane der Polychäten. Zeitschr. Morph. Ökol. Tiere, vol. 13, pp. 329-358, 27 figs.
1935. Bemerkungen über das Gehirn und die Sinnesorgane der Onychophoren. Lunds Univ. Årssk. N. F. Avd. 2, vol. 31, no. 5, 38 pp., 22 figs.

HATSCHEK, B.

1877. Die Embryonalentwicklung und Knospung von *Pedicellina echinata*. Zeitschr. wiss. Zool., vol. 29, pp. 502-549, pls. 28-30.
- 1888-91. Lehrbuch der Zoologie. Jena.
1894. Über den gegenwärtigen Stand der Keimblättertheorie. Verh. Deutschen Zool. Ges. 3d Jahresvers., pp. 11-23.

HEATHCOTE, F. G.

1886. The early development of *Julus terrestris*. Quart. Journ. Micr. Sci., vol. 26, pp. 449-470, pls. 23, 24.

HEIDER, K.

1925. Über Eunice. Systematisches, Kiefersack, Nervensystem. Zeitschr. wiss. Zool., vol. 125, pp. 55-90, 16 figs.

HEMPELMANN, F.

1911. Zur Naturgeschichte von *Nereis dumerilii* Aud. et Edw. Zoologica. Orig.-Abhandl. Gesamtg. Zool., vol. 62, 135 pp., 4 pls.
1931. Archannelida and Polychaeta. Kükenthal and Krumbach's Handbuch der Zoologie, vol. 2, 2d half.

HENRIKSEN, K. L.

1926. The segmentation of the trilobite's head. Saert. Meddel. Dansk Geol. For., vol. 7, pp. 1-32, 27 figs.
1929. Contribution to the interpretation of the cephalic segments of Arthropoda. Trans. 4th Internat. Congr. Ent. (Ithaca, N. Y.), pp. 589-594.

HERTWIG, O. and R.

1882. Die Cölontheorie, Versuch einer Erklärung des mittleren Keimblattes. *Jenaische Zeitschr. Naturwiss.*, vol. 15 (N. F. vol. 8), pp. 1-150, 3 pls.

HESS, W. N.

1925. Nervous system of the earthworm, *Lumbricus terrestris* L. *Journ. Morph.*, vol. 40, pp. 235-259, 7 figs.

HESSE, R.

1899. Untersuchungen über die Organe der Lichtempfindung bei niederen Thieren. V. Die Augen der polychäten Anneliden. *Zeitschr. wiss. Zool.*, vol. 65, pp. 446-516, pls. 22-26.

HESSE, R., ALLEE, W. C. and SCHMIDT, K. P.

1937. *Ecological animal geography*. New York and London.

HEYMONS, R.

1897. Mittheilungen über Segmentirung und den Körperbau der Myriapoden. *Sitzungsbr. K. Preuss. Akad. Wiss. Berlin*, vol. for 1897, pp. 915-923, 2 figs.

1901. Die Entwicklungsgeschichte der Scolopender. *Zoologica. Orig.-Abhandl. Gesammtg. Zool.*, vol. 33, 244 pp., 42 text figs., 8 pls.

1928. Über Morphologie und verwandtschaftliche Beziehungen des *Xenusion auerswaldae* Pomp. aus dem Algonkium. *Zeitschr. Morph. Ökol. Tiere*, vol. 10, pp. 307-329, 7 figs.

HOLMGREN, N.

1916. Zur vergleichenden Anatomie des Gehirns von Polychaeten, Onychophoren, Xiphosuren, Arachniden, Crustaceen, Myriopoden und Insekten. *K. Svenska Vetenskapsakad. Handl.*, vol. 56, no. 1, 303 pp., 12 pls.

HUTCHINSON, G. E.

1930. Restudy of some Burgess shale fossils. *Proc. U. S. Nat. Mus.*, vol. 78, pp. 1-24, pl. 1.

IMMS, A. D.

1936. The ancestry of insects. *Trans. Soc. British Ent.*, vol. 3, pp. 1-32, 11 figs.

IWANOFF, P. P.

1928. Die Entwicklung der Larvalsegmente bei den Anneliden. *Zeitschr. Morph. Ökol. Tiere*, vol. 10, pp. 62-161, 40 text figs., pls. 1-7.

1933. Die embryonale Entwicklung von *Limulus moluccanus*. *Zool. Jahrb., Anat.*, vol. 56, pp. 163-348, 78 text figs., pls. 1-3.

JANET, C.

1899. *Essai sur la constitution morphologique de la tête de l'insecte*, 74 pp., 7 pls. Paris.

JAWOROWSKI, A.

1891. Über die Extremitäten bei den Embryonen der Arachniden und Insekten. *Zool. Anz.*, vol. 14, pp. 164-169, 173-176, 4 figs.

JEENER, R.

1928. *Recherches sur le système neuromusculaire latéral des Annélides*. *Recueil Inst. Zool. Torley-Rousseau*, vol. 1, pp. 99-121, pl. 3.

KENNEL, J. VON

- 1884, 1888. *Entwicklungsgeschichte von Peripatus Edwardsii* Blanch. und *Peripatus torquatus* n. sp. *Arb. Zool.-Zootom. Inst. Würzburg*, vol. 7, pp. 95-229, pls. 5-11; vol. 8, pp. 1-93, pls. 1-6.

KISHINOUE, K.

1893. On the development of *Limulus longispina*. Journ. Coll. Sci. Imp. Univ. Japan, vol. 5, pp. 53-100, pls. 5-11.

1894. Note on the coelomic cavity of a spider. Journ. Coll. Sci. Imp. Univ. Japan, vol. 6, pp. 287-296, pl. 10.

KLEINENBERG, N.

1886. Die Entstehung des Annelids aus der Larve von *Lopadorhynchus*. Zeitschr. wiss. Zool., vol. 44, pp. 1-227, pls. 1-16.

KOWALEVSKY, A., and MARION, A. F.

1883. Documents pour l'histoire embryogénique des Alcyonaires. Ann. Mus. Hist. Nat. Marseille, Zool., vol. 1, no. 4, 50 pp., 5 pls.

KÜHNERT, L.

1935. Beitrag zur Entwicklungsgeschichte von *Alcippe lampas* Hancock. Zeitschr. Morph. Ökol. Tiere, vol. 29, pp. 45-78, 24 figs.

LALICKER, C. G.

1935. Larval stages of trilobites from the Middle Cambrian of Alabama. Journ. Paleontol., vol. 9, pp. 394-399, pl. 47.

LAMEERE, A.

1926. Les organes segmentaires des Polychètes. Ann. Soc. R. Zool. Belgique, vol. 56, pp. 113-119.

LANKESTER, E. R., BENHAM, W. B. S., and BECK, E. J.

1885. On the muscular and endoskeletal systems of *Limulus* and *Scorpio*, with some notes on the anatomy and generic characters of scorpions. Trans. Zool. Soc. London, vol. 11, pp. 311-384, pls. 72-83.

LILLIE, R. S.

1906. The structure and development of the nephridia of *Arenicola cristata* Stimpson. Mitt. Zool. Sta. Neapel, vol. 17, pp. 341-405, pls. 22-25.

MALAQUIN, A.

1924. Les glandes génitales et les cellules sexuelles primordiales chez l'Annélide *Salmacina Dysteri* (Huxley). La genèse des ébauches génitales par des gonocytes extracoelomiques. C. R. Acad. Sci. Paris, vol. 179, pp. 1348-1351.

1924 a. Les glandes génitales et les cellules sexuelles primordiales chez l'Annélide *Salmacina Dysteri* (Huxley). La filiation des cellules sexuelles (gonocytes); leur origine dans le bourgeon caudal. C. R. Acad. Sci. Paris, vol. 179, pp. 1636-1639.

1925. La ségrégation, au cours de l'ontogénèse, de deux cellules sexuelles primordiales, souches de la lignée germinale, chez *Salmacina Dysteri* (Huxley). C. R. Acad. Sci. Paris, vol. 180, pp. 324-327, 1 fig.

MANTON, S. M.

1928. On the embryology of a mysid crustacean, *Hemimysis lamornae*. Philos. Trans. R. Soc. London, ser. B, vol. 216, pp. 363-463, 32 text figs., pls. 21-25.

1930. Notes on the segmental excretory organs of Crustacea. V. On the maxillary glands of the Syncarida. Journ. Linn. Soc. London, Zool., vol. 37, pp. 467-472, 9 figs.

1934. On the embryology of the crustacean *Nebalia bipes*. Philos. Trans. R. Soc. London, ser. B, vol. 223, pp. 163-238, 17 text figs., pls. 20-28.

MARCUS, E.

1929. Zur Embryologie der Tardigraden. Zool. Jahrb., Anat., vol. 50, pp. 333-384, 31 text figs., pl. 8.

MELLANBY, HELEN

1936. The later embryology of *Rhodnius prolixus*. *Quart. Journ. Micr. Sci.*, vol. 79, pp. 1-42, 22 text figs.

METSCHNIKOFF, E.

1882. Vergleichend-embryologische Studien. *Zeitschr. wiss. Zool.*, vol. 36, pp. 432-444, pl. 28.

MEYER, A.

1929. Die Entwicklung der Nephridien und Gonoblasten bei *Tubifex rivulorum* Lam. nebst Bemerkungen zum natürlichen System der Oligochäten. *Zeitschr. wiss. Zool.*, vol. 133, pp. 517-562, 31 figs.

MEYER, E.

1887. Studien über den Körperbau der Anneliden. I-III. *Mitt. Zool. Sta. Neapel*, vol. 7, pp. 592-741, pls. 22-27.
 1891. Die Abstammung der Anneliden. Der Ausprung der Metamerie und die Bildung des Mesoderms. *Biol. Centralbl.*, vol. 10, pp. 296-308.
 1901. Studien über den Körperbau der Anneliden. V. *Mitt. Zool. Sta. Neapel*, vol. 14, pp. 247-585, pls. 12-17.

MICHAELSEN, W.

1928. Oligochaeta. Kükenthal and Krumbach's *Handbuch der Zoologie*, vol. 2, 2d half.

MICHEL, A.

1898. Recherches sur la régénération chez les Annélides. *Bull. Sci. France et Belgique*, vol. 31, pp. 245-417, pls. 13-19.

NEEDHAM, A. E.

1937. Some points in the development of *Neomysis vulgaris*. *Quart. Journ. Micr. Sci.*, vol. 79, pp. 559-588, pls. 23, 24.

NELSON, J. A.

1904. The early development of *Dinophilus*: a study in cell-lineage. *Proc. Acad. Nat. Sci. Philadelphia*, vol. 56, pp. 687-737, pls. 43-48.
 1907. The morphology of *Dinophilus conklini* n. sp. *Proc. Acad. Nat. Sci. Philadelphia*, vol. 59, pp. 82-143, pls. 12, 13.
 1915. The embryology of the honey bee. *Princeton Univ. Press*.

PACKARD, A. S.

1898. A text-book of entomology. New York.

PATTEN, W., and HAZEN, A. P.

1900. The development of the coxal gland, branchial cartilages, and genital ducts of *Limulus polyphemus*. *Journ. Morph.*, vol. 16, pp. 459-502, pls. 22-28.

PATTEN, W., and REDENBAUGH, W. A.

1900. Studies on *Limulus*. I. The endocrania of *Limulus*, *Apus*, and *Mygale*. *Journ. Morph.*, vol. 16, pp. 1-26, pls. 1, 2.

PENNSERS, A.

1924. Die Entwicklung des Keimstreifs und die Organbildung bei *Tubifex rivulorum* Lam. *Zool. Jarb., Anat.*, vol. 45, pp. 251-308, 32 text figs., pls. 12-14.
 1930. Entwicklungsgeschichtliche Untersuchungen an marinen Oligochäten. II. Furchung, Keimstreif und Keimbahn von *Pachydriilus (Lumbri-cillus) lineatus* Müll. *Zeitschr. wiss. Zool.*, vol. 137, pp. 55-119, 40 figs.

PENNERS, A., and STÄBLEIN, A.

1930. Über die Urkeimzellen bei Tubificiden (*Tubifex rivulorum* Lam. und *Limnodrilus udekemianus* Claparède). Zeitschr. wiss. Zool., vol. 137, pp. 606-626, 13 figs.

PETRUNKEVITCH, A.

1922. The circulatory system and segmentation in Arachnida. Journ. Morph., vol. 36, pp. 157-188, pls. 1, 2.
1933. An inquiry into the natural classification of spiders, based on a study of their internal anatomy. Trans. Connecticut Acad. Arts Sci., vol. 31, pp. 299-389, 13 pls.

PFLUGFELDER, O.

1932. Über den feineren Bau der Augen freilebender Polychäten. Zeitschr. wiss. Zool., vol. 142, pp. 540-586, 24 figs.
1932 a. Über den Mechanismus der Segmentbildung bei der Embryonalentwicklung und Anamorphose von *Platyrrhacus amauros* Attems. Zeitschr. wiss. Zool., vol. 140, pp. 650-723, 40 figs.

PHILIPTSCHENKO, J.

1908. Beiträge zur Kenntnis der Apterygoten. II. Über die Kopfdrüsen der Thysanuren. Zeitschr. wiss. Zool., vol. 91, pp. 93-111, pls. 5, 6.

POKROWSKY, S.

1899. Noch ein Paar Kopfhöcker bei den Spinnembryonen. Zool. Anz., vol. 22, pp. 272-273, 1 fig.

POMPECKJ, J. F.

1927. Ein neues Zeugnis uralten Lebens. Paläontol. Zeitschr., vol. 9, pp. 287-313, pl. 5.

RABL, C.

1879. Über die Entwicklung der Tellerschnecke. Morph. Jahrb., vol. 5, pp. 562-660, pls. 32-38.
1889. Theorie des Mesoderms. Morph. Jahrb., vol. 15, pp. 113-252, pls. 7-10.

REYNOLDS, J. M.

1935. A new contribution to the problem of segmentation in the Arthropoda. Amer. Journ. Sci., vol. 30, pp. 373-382.

ROBINSON, MARGARET

1907. On the segmentation of the head of Diplopoda. Quart. Journ. Micr. Sci., vol. 51, pp. 607-624, pl. 37.

ROONWAL, M. L.

1937. Studies on the embryology of the African migratory locust, *Locusta migratoria migratorioides* Reiche and Frm. II. Organogeny. Philos. Trans. R. Soc. London, ser. B, vol. 227, pp. 175-244, pls. 1-7.

RUSER, MAGDALENE

1933. Beiträge zur Kenntnis des Chitins und der Muskulatur des Zicken (*Ixodidae*). Zeitschr. Morph. Ökol. Tiere., vol. 27, pp. 199-261, 39 figs.

SCHIMKEWITSCH, W.

1895. Über Bau und Entwicklung des Endosternits der Arachniden. Zool. Jahrb., Anat., vol. 8, pp. 191-216, pls. 10, 11.
1906. Über die Entwicklung von *Thelyphonus caudatus* (L.), vergleichen mit derjenigen einiger anderer Arachniden. Zeitschr. wiss. Zool., vol. 81, pp. 1-95, pls. 1-8.

SCHLIEPER, C.

1925. Zur Systematik der Gattung *Nerilla*. Zool. Anz., vol. 62, pp. 229-234, 4 figs.

SCHNEIDER, K. C.

1902. Lehrbuch der vergleichenden Histologie. Jena.

SCHULZE, P.

1936. Trilobita, Xiphosura, Acarina. Eine morphologische Untersuchungen über Plangleichheit zwischen Trilobiten und Spinnentieren. Zeitschr. Morph. Ökol. Tiere, vol. 32, pp. 181-226, 39 figs.
1938. Über rein glabellare Karapaxbildungen bei Milben und über die Umgestaltung des Vorderkörpers der Ixodidea als Folge der Gnathosomaentstehung. Zeitschr. Morph. Ökol. Tiere, vol. 34, pp. 135-149, 18 figs.

SCLATER, W. L.

1888. On the early stages of the development of a South American species of *Peripatus*. Quart. Journ. Micr. Sci., vol. 28, pp. 343-363, pl. 24.

SEDGWICK, A.

1884. On the origin of metameric segmentation and some other morphological questions. Quart. Journ. Micr. Sci., vol. 24, pp. 43-82, pls. 2, 3.
1885. The development of *Peripatus capensis*. Part I. Quart. Journ. Micr. Sci., vol. 25, pp. 449-468, pls. 31, 32.
1886. The development of the cape species of *Peripatus*. Part II. Segmentation of the ovum and formation of the layers. Quart. Journ. Micr. Sci., vol. 26, pp. 175-212, pls. 12-14.
1887. The development of the cape species of *Peripatus*. Part III. The changes from stage A to stage F. Quart. Journ. Micr. Sci., vol. 27, pp. 467-550, pls. 34-37.
1888. The development of the cape species of *Peripatus*. Part IV. The changes from stage G to birth. Quart. Journ. Micr. Sci., vol. 28, pp. 373-396, pls. 26-29.

SHEARER, C.

1912. The problem of sex determination in *Dinophilus gyrotiliatus*. Quart. Journ. Micr. Sci., vol. 57, pp. 329-371, pls. 30-34.

SHELDON, LILIAN

- 1888, 1889. On the development of *Peripatus Novae-Zealandiae*. Quart. Journ. Micr. Sci., vol. 28, pp. 205-237, pls. 12-16; vol. 29, pp. 283-293, pls. 25, 26.

SILVESTRI, F.

1933. Sulle appendici del capo degli "Japygidae" (*Thysanura entotropha*) e rispettivo confronto con quelle dei Chilopodi, dei Diplopodi e dei Crostacei. 5th Congr. Internat. Entom., Paris, 1932, pp. 329-343, 7 figs.

SNODGRASS, R. E.

1933. Morphology of the insect abdomen. Part II. The genital ducts and the ovipositor. Smithsonian Misc. Coll., vol. 89, no. 8, 148 pp., 58 figs.
1936. Morphology of the insect abdomen. Part III. The male genitalia. (Including arthropods other than insects). Smithsonian Misc. Coll., vol. 95, no. 14, 96 pp., 29 figs.

SOKOLOV, I.

1911. Über eine neue Ctenodrilusart und ihre Vermehrung. Zeitschr. wiss. Zool., vol. 97, pp. 547-603, pls. 27-29.

SOLLAUD, E.

1923. Recherches sur l'embryogénie des Crustacés décapodes de la sous-famille des "Palemoninae." Bull. Biol. France et Belgique, Suppl., vol. 5, 234 pp., 5 pls.
1933. Le blastopore et la question du "prostomium" chez les Crustacés. Assoc. Française Avanc. Sci., 57th Sess., Chambéry, pp. 321-327, 2 figs.

STAFF, F.

1910. Organogenetische Untersuchungen über Criodrilus lacuum (Hoffmstr.). Arb. zool. Inst. Wien, vol. 18, pp. 227-256, 2 pls.

STEPHENSON, J.

1930. The Oligochaeta. Oxford.

STORCH, O.

1912. Zur vergleichenden Anatomie der Polychäten. Verhandl. zool.-botan. Ges. Wien, vol. 62, pp. 81-97, 4 figs.
1913. Vergleichend-anatomische Polychätenstudien. Sitzungsber. Akad. wiss. Wien, Math.-natur. Kl., vol. 122, Ab. 1, pp. 877-988, 3 pls.

STUMMER-TRAUNFELS, v. R. R.

1903. Beiträge zur Anatomie und Histologie der Myzostomen. I. Myzostoma asteriae Marenz. Zeitschr. wiss. Zool., vol. 75, pp. 495-595, pls. 34-38.

SURFACE, F. M.

1907. The early development of a polyclad Planocera inquilina Wh. Proc. Acad. Nat. Sci. Philadelphia, vol. 59, pp. 514-559, pls. 35-40.

TANNREUTHER, G. W.

1915. The embryology of Bdelodrilus philadelphicus. Journ. Morph., vol. 26, pp. 143-216, 26 text figs., 8 pls.

TILLYARD, R. J.

1930. The evolution of the class Insecta. Roy. Soc. Tasmania, Papers and Proc., 1930, 89 pp., 19 figs.
1932. The evolution of the class Insecta. Amer. Journ. Sci., vol. 23, pp. 529-539.
1935. Evolution of progoneate and opisthogoneate types in the myriapod-hexapod group of terrestrial Arthropoda. Amer. Journ. Sci., vol. 30, pp. 438-449.

TORREY, J. C.

1903. The early embryology of Thalassema mellita (Conn.) Ann. New York Acad. Sci., vol. 14, pp. 165-246, 2 pls.

TREADWELL, A. L.

1901. The cytogeny of Podarke obscura Verrill. Journ. Morph., vol. 17, pp. 399-486, pls. 36-40.

VERSLUYS, J., and DEMOLL, R.

1920. Die Verwandtschaft der Merostomata mit den Arachnida und den anderen Abteilungen der Arthropoda. Proc. K. Akad. Wetens. Amsterdam, vol. 23, pp. 739-765.
1923. Das Limulus-Problem. Die Verwandtschaftsbeziehungen der Merostomen u. Arachnoideen unter sich u. mit anderen Arthropoden. Ergebnisse u. Fortschritte der Zoologie, vol. 5, pp. 67-388, 123 figs.

VOGT, W.

1935. Die Entwicklung der Antennendrüse der Mysideen. *Zeitschr. Morph. Ökol. Tiere.*, vol. 29, pp. 481-506, 20 figs.

WALCOTT, C. D.

1908. Mount Stephen rocks and fossils. *Canadian Alpine Journ.*, vol. 1, no. 2, pp. 232-248, 4 pls.
1910. Olenellus and other genera of the Mesonacidae. *Smithsonian Misc. Coll.*, vol. 53, no. 6, pp. 231-422, 22 pls.
1911. Cambrian geology and paleontology. II. No. 5. Middle Cambrian annelids. *Smithsonian Misc. Coll.*, vol. 57, no. 5, pp. 110-144, pls. 18-23.
1916. Cambrian geology and paleontology. III. No. 5, Cambrian trilobites. *Smithsonian Misc. Coll.*, vol. 64, no. 5, pp. 303-456, pls. 45-67.
1931. Addenda to descriptions of Burgess shale fossils. *Smithsonian Misc. Coll.*, vol. 85, no. 3, 46 pp., 23 pls.

WARBURG, ELSA.

1925. The trilobites of the Leptaena limestone in Dalarne. *Bull. Geol. Inst. Univ. Uppsala*, vol. 17, pp. 1-450, 11 pls.

WHITMAN, C. O.

1886. The germ-layers of Clepsine. *Zool. Anz.*, vol. 9, pp. 171-176, 1 fig.

WIESMANN, R.

1926. Zur Kenntnis der Anatomie und Entwicklungsgeschichte der Stabheuschrecke *Carausius morosus* Br. III. Entwicklung und Organogenese der Cölombläsen, 206 pp., 86 figs. *Zool.-vergl. anat. Inst. Univ. Zürich*.

WILSON, E. B.

1889. The embryology of the earthworm. *Journ. Morph.*, vol. 3, pp. 387-462, pls. 16-22.

WOLTERECK, R.

1905. Wurm "kopf," Wurmrumpf und Trochophora. Bemerkungen zur Entwicklung und Ableitung der Anneliden. *Zool. Anz.*, vol. 28, pp. 273-322, 24 figs.

ZACHER, F.

1933. Onychophora. Kükenthal and Krumbach's *Handbuch der Zoologie*, vol. 3, 2d half, pp. 79-138, figs. 57-122.

ZIEGLER, E.

1898. Über den derzeitigen Stand der Cölomfrage. *Verh. Deutschen Zool. Ges.*, 8th Jahresvers., pp. 14-78, 15 figs.

ZILCH, A.

1936. Zur Frage des Flimmerepithels bei Arthropoden. *Zeitschr. wiss. Zool.*, vol. 148, pp. 89-132, 11 figs.