The Development and Affinities of the Pauropoda, based on a Study of *Pauropus silvaticus*

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PART II

With 2 Plates and 7 Text-figures

CONTENTS

OBSERVATIONS ON POST-EMBRYONIC DEVELOPMENT

THE following is not intended as an exhaustive description of the whole larval development, but is restricted to those aspects of it to which special significance attaches.

### 1. *External Characters of Larvae*

(a) First Instar Larva. A description of this has already been given (section 6, iv).

(b) Second Instar Larva (Text-fig. 23 A). Length about 0·4 mm.

On the antenna three basal segments are now present, the new segment having been generated from thickened epidermis at the base of the antenna, and not at the tip. In each flagellum the number of rings has increased.

In the abdomen only one additional segment is present, i.e. eight in all. As will be seen in section 2, the new segment is the seventh abdominal, which has become interpolated between the sixth and anal segments of the previous instar, whose fifth and sixth segments have enlarged and acquired each a pair of legs. The sixth segment, like the fourth, is wedge-shaped with reduced tergal wall, the third tergal shield being the product of the fifth
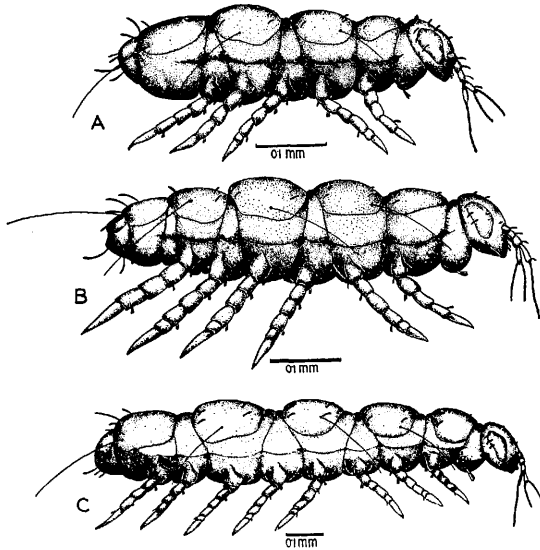
TEXT-FIG. 23. Larvae; A second, B third, C fourth instars.

segment alone. The new (seventh) segment is large and has a tergal shield bearing a pair of trichobothria.

The two newly formed legs are five-segmented, their tarsi being undivided. In the second and third legs, on the other hand, the hitherto unsegmented tarsi have divided into two segments. The first leg remains permanently with unsegmented tarsus. The legs progressively increase in length towards the hinder end of the abdomen.

(c) *Third Instar Larva* (Text-fig. 23 B). Length about 0·5 mm.

In the abdomen there are ten segments, two additional segments having been acquired, viz. the eighth and ninth. The eighth segment, like the sixth and fourth, is a wedge-shaped segment, without a tergal shield. The ninth, like the seventh and fifth, is a large segment, with tergal shield, and it bears the new (fourth) trichobothrium. Neither segment bears legs in this instar.

On the seventh segment the sixth pair of legs has formed, its tarsi being unsegmented. The tarsi of the fourth and fifth legs have become bi-seg-mented.

(*d*) *Fourth Instar Larva* (Text-fig. 23 c). Length about 0·7–0·8 mm. Within the antenna the fourth (and last) basal segment has appeared.

In the abdomen there are eleven segments, one additional segment having been acquired, namely, the tenth. This segment, like the alternate segments that precede it, is a wedge-shaped segment, without a tergal shield, and remains permanently without one. It does not yet bear legs.

On the eighth and ninth segments, which were the new segments of the previous instar, the seventh and eighth legs have formed, their tarsi being unsegmented. The tarsi of the sixth legs have become bisegmented.

(*e*) *Adult Animal* (Text-fig. 24). Length 1–1·2 mm.

In the abdomen there are twelve segments, the newly acquired segment being the eleventh or permanent pre-anal segment. Like the alternate seg-ments that precede it, it is a large segment, with a tergal shield (sixth of the series) and bears a pair of long trichobothria, but it is, and remains, devoid of legs. Its sternal wall is markedly reduced, and, like the anal segment, bears a well-sclerotized sternite.

On the wedge-shaped tenth segment, which was the new segment of the previous instar, a pair of legs has formed. Being the last of the series of en-larging legs, they are the most strongly developed of all; nevertheless they follow the general rule of first appearing with unsegmented tarsi, and since there is no further ecdysis, remain permanently in this state. The two pre-ceding pairs of legs have now acquired bisegmented tarsi.

The fact that the last leg, though the largest of the series, should remain permanently in this incompletely differentiated condition, suggests that ad-ditional ecdyses may have been suppressed in *Pauropus*, and points even to the possibility that further teloblastic segmentation may have been arrested. This conclusion is supported by the discovery of *Decapauropus*, in which an additional segment (twelfth) is present between the anal and eleventh seg-ments, the latter bearing an additional pair of legs (Remy, 1931).

2. *The Formation of New Segments and their Ganglia*

In the following account it will suffice to describe in detail the develop-ment of the teloblastic segments during the first larval stadium. According to Silvestri (1902) 'the formation of new segments takes place between the last segment of the trunk, which always remains small during the entire larval period, and the one preceding it'; opposed to this is Harrison's state-ment that the new segments appear between the last leg-bearing and 'pre-anal' segments. To examine the teloblastic growth of segments in the larva, it is necessary to look beneath the chitin, for a bare inspection of the external characters of successive larval instars does not suffice to reveal its nature.

The segmental muscles are a particularly useful guide, and they at once show that the fifth and sixth segments of the future second instar larva are the fifth and sixth of the first instar, which need mainly the legs to com-
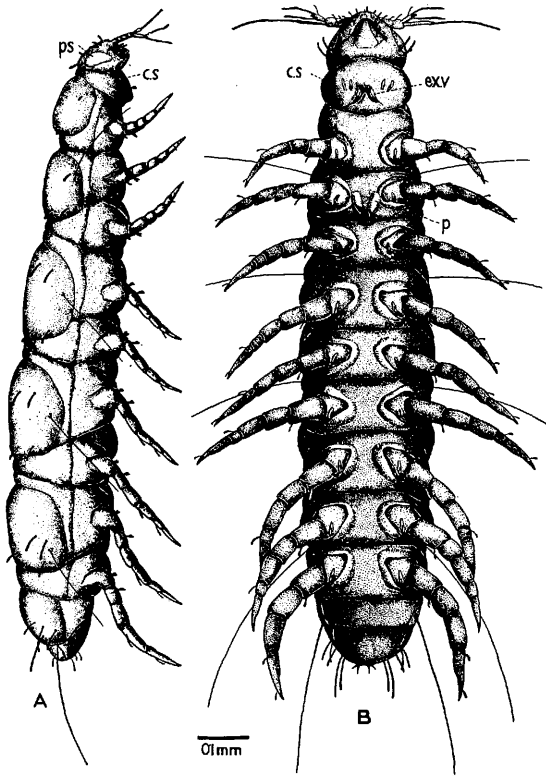
TEXT-FIG. 24. Adult.
A. Lateral view of a fully extended animal. B. Ventral view of a male.
Lettering. c.s collum segment; *ex.v* 'exsertile vesicle'; *p* penis; *ps* pseudoculus.

plete their development. The new segments, as Silvestri observed, must therefore develop in front of the anal segment, and the supposed stationary 'pre-anal segment' of Harrison is an error of observation.

The muscles of the first instar larva are shown in Text-fig. 25. By comparison with Text-fig. 22 C it will at once be seen that the tergal muscles

of the third leg, which in the adult are connected above to the second and third tergal shields, arise in the larva from the second and third shields respectively. Similarly, the second oblique muscle (*obl.b*) of the larva, which is attached above to the hinder end of the third shield, is attached in the adult also to the hind end of the third shield. It is clear, therefore, that the third shield of the first instar larva must become the third abdominal shield of the next and all later instars. That its sensory seta (trichobothrium) must become the second of the series is proved by the fact that when the fifth
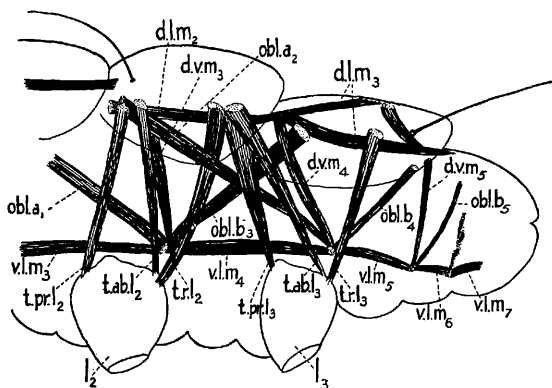
TEXT-FIG. 25. Hinder end of trunk of a first instar larva, drawn to show muscles. The drawing should be compared with Text-fig. 22 C, in which the same muscles are identified by attached numerals.

Lettering. d.l.m dorsal longitudinal muscle; *d.v.m* dorso-ventral muscle; $l_{2}, _{3}$ second and third legs; *obl.a, obl.b* two sets of oblique muscles; *t.ab.l* tergal abductor of leg; *t.pr.l* tergal promotor of leg; *t.r.l* tergal remotor of leg; *v.l.m* ventral longitudinal muscle.

abdominal ganglion becomes defined in the first instar larva, the nerve to the trichobothrium is found to arise from it, and not from the teloblastic ganglion. The clue to the sternal parts of the new segments is given by the ventral longitudinal muscles, those of the fifth and sixth segments being already present in the newly emerged first instar larva.

Turning now to the actual process of formation of new segments, it will be well to begin with the advanced embryo, in which the demarcation of the fifth abdominal segment from the anal takes place (cf. section 6, ii, A). In the 9-day embryo intersegmental lines appear in the abdomen, but behind the fourth abdominal segment the development of such lines is delayed, and it is not until a little before the pupa forms that an indication of the line between the fifth abdominal and anal segments is seen (fig. 31, Pl. III). Yet when the pupa is set free, there is already a deep groove in the epidermis between these segments (fig. 32 A, Pl. III). The larva, when this in turn

emerges, displays yet another new segment; it is the sixth abdominal segment, i.e. a wedge-shaped segment with reduced tergal wall, and is interpolated between the fifth and anal segments (fig. 34, Pl. III). How has this new segment arisen?

It may have arisen by division of the original fifth segment; or it may have developed out of cells which spread forward from a zone of proliferation in the anal segment. That the latter is the case is shown by examining the ventral longitudinal muscles. In the terminal segments the development of the muscles takes place much later than in the leg-bearing segments, the fifth muscle not appearing until about the time that the pupa is due to leave the egg. This muscle is attached behind, at the intersegmental line between the fifth and anal segments. It is readily identified in the first instar larva, where it is still the ventral longitudinal muscle of the fifth segment; the new (sixth) segment could therefore not have arisen by division of the original fifth segment, but must have been generated from behind. The process of teloblastic growth therefore actually begins in the pupa.

In the newly emerged larva the terminal segments present the following features (fig. 34, Pl. III; Text-fig. 26 A): within the anal segment the epidermal cells, though seldom more than one deep, lie closely crowded, this crowding of cells involving all its lateral walls, and the hinder part of the roof of the segment, together with most of the floor anterior to the line of attachment of the occlusor ani muscles. The attachment of these muscles behind the zone of proliferation ensures that they remain fixed as the proliferating epidermal cells spread forward. In the fifth and sixth segments the epidermis is for the most part thin; the floor of the segments is, however, greatly thickened, owing to the presence of the developing ganglia, while to the side ·there is also a thickening, though less pronounced, in the region of impending leg-formation (fig. 127, Pl. X). In these terminal segments there are still only two ganglia (Text-fig. 26 A), as in the advanced embryo and pupa (cf. Text-figs. 8, 9). Of these the more anterior is the fifth abdominal, now sharply delimited, but still in course of enlargement, for mitoses are often seen in its cells, and its 'ventral organs' are still present. With it is connected the nerve from the second trichobothrium. Behind the fifth ganglion, on the floor of the sixth segment, is the teloblastic ganglion, but the future sixth ganglion has not yet become demarcated from it. With the teloblastic ganglion is merged the vestigial anal ganglion, and from it arises also the caudal visceral ganglion. The presence of the latter gives clear *a priori* evidence that· growth of the nerve-cord must proceed sub-terminally, and not terminally. Of the ventral longitudinal muscles the fifth has already been referred to; the sixth begins to form in the early pupa, and is therefore already well defined on the floor of the sixth segment of the first instar larva. Behind the sixth the seventh has already appeared, its formation taking place in the advanced pupa; this muscle, as Text-fig. 25 shows, intrudes well into the anal segment, and is a specially useful guide in following the development of the seventh segment during the first larval stadium.

Early in this stadium the epidermis of the anal segment and of the floor of the fifth and sixth segments undergoes intensive cell-proliferation, in consequence of which it grows still more in thickness, its cells becoming even more densely crowded, and imparting to the epithelium a markedly embryonic appearance; cf. fig. 131, Pl. X, with fig. 132, Pl. X (anal segment), and figs. 127 and 128, Pl. X (sixth abdominal segment). On the fifth and sixth segments the fourth and fifth pairs of legs now appear (fig. 35, Pl. III), and as these enlarge they soon become bent on themselves. The ganglion of the fifth segment meanwhile becomes separated from the epidermis, the vestiges of its 'ventral organs' being absorbed into it (Text-fig. 26 B). From the now greatly enlarged teloblastic ganglion a new ganglion has in turn been generated. It is the sixth abdominal. It is still in process of growth, for mitoses are encountered among its cells, and moreover, it is still connected with the sternal epidermis by the dwindling remnant of its 'ventral organ'.

While the fifth and sixth segments have thus been maturing, the seventh has begun to make its appearance (fig. 35, Pl. III). The intersegmental line delimiting it behind from the anal segment is already present, and on its tergal wall may be seen the initial thickening associated with the development of its trichobothrium. That the new segment has, like the sixth that preceded it, arisen out of cells that have proliferated from the anal segment, is proved by examining its ventral longitudinal muscle, for the muscle of the new segment (seventh ventral longitudinal) is already definable in newly emerged larvae, where its hinder end has attachment to the epidermis within the anal segment (Text-fig. 25). For the tergal wall of the segment the trichobothria give equally conclusive evidence, the new (third) trichobothrium taking origin within the limits of the anal segment (fig. 36, Pl. III; fig. 132, Pl. X).

In late first instar larvae terminal enlargement has proceeded to such an extent that there is much stretching of the chitin at the intersegments. The fourth and fifth legs have attained full segmentation, and the seventh segment has become much enlarged (fig. 37, Pl. III). The already existing (second) trichobothrium of the fifth segment has lost connexion with the cells that generated it, and a new second trichobothrium is in process of forming; and behind this, on the new seventh segment, the new (third) trichobothrium is growing out. Shortly before the first larval moult this trichobothrium acquires connexion with the teloblastic ganglion, into which the neuropilem has now extended. The ganglion of the sixth segment has meanwhile taken its place in the series of ganglia, having lost connexion with the sternal epidermis (Text-fig. 26 c).

Behind the ventral longitudinal muscle of the seventh segment another such muscle has appeared in late first instar larvae; as usual, it has its posterior attachment well within the anal segment, and thereby gives the first indication of the production of the eighth segment, which will, however, not be fulfilled until after the first moult.
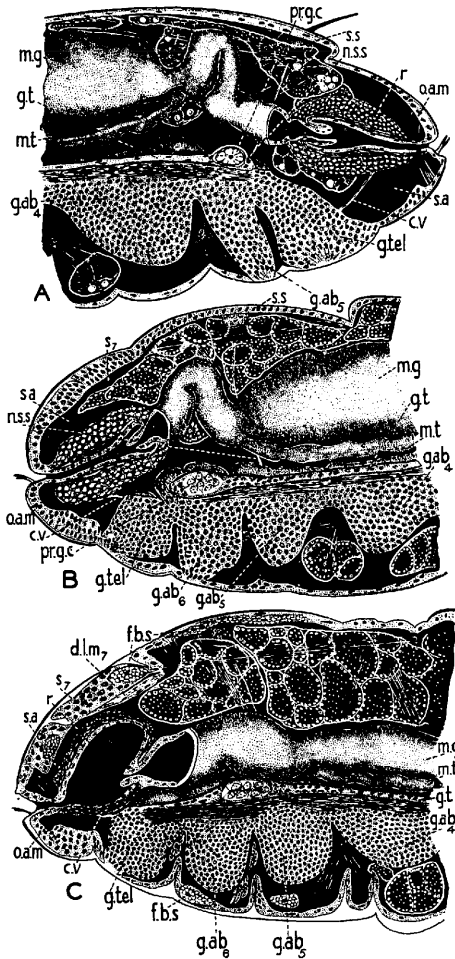
TEXT-FIG. 26. Internal views of hinder ends of the three first instar larvae shown in figs. 34, 35, 37, Pl. III.

A. Newly emerged larva. B, about half through first larval stadium. C, near end of first larval stadium. In A the new (fifth) ganglion has appeared; in B the sixth has formed, but is still in course of enlargement; in C the sixth has separated from the sternal epidermis. Fat-body is indicated as a transparent body; in A the large spherical inclu-

It is evident from the above description that two already formed segments have completed their development in the first larval stadium, while a single additional segment (seventh) has been added to the series. The ganglion of the latter is, in the early second instar larva, the teloblastic ganglion, which then again enlarges, thereby giving origin to the eighth ganglion. Rudiments of the new (sixth) legs also soon appear in the second larval stadium.

In the fourth instar larva the teloblastic ganglion still occupies the floor of the sub-terminal (now tenth) segment. No new ganglion is released from it, but it remains as the ganglion of the tenth segment. The new segment, which is produced after the moult (i.e. legless eleventh segment of the adult animal), is therefore devoid of a ganglion, its muscles, like those of the anal segment, being innervated from the preceding ganglion.

From the foregoing account it is evident that teloblastic segment formation in *Pauropus* proceeds in a much simpler manner than in Symphyla (Tiegs, 1945). Specially noteworthy is the evidence which it affords against the supposed bisegmental origin of the tergal shields. It has already been shown above (section 6, ii, A) that the second tergal shield of the first instar larva is the product of a single segment, and this now clearly holds for the new shields that develop in the larva. The fourth shield, for example, must be the product of the seventh segment alone, for the future eighth segment does not even exist in the second instar larva; and the fifth shield must clearly be the product of the ninth segment alone, for the future tenth segment has not yet appeared in the third instar.

3. *The Mesoderm*

In the advanced embryo the 'teloblastic mesoderm', whose formation has already been described in section 8 (viii), may be seen as two small clumps of cells that lie against the lateral body-wall behind the mesoderm of the fifth abdominal segment, i.e. within the limits of the anal segment. It is shown in fig. 87, Pl. 7. Out of this mesoderm is generated the musculature of the sixth and succeeding abdominal segments that develop in the larva; out of it develops also the median septum of neuroglia cells of the new nerve-ganglion; and finally it yields a small contribution of cells to the hinder end of the growing genital tube (see below, section 6).

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sions in the fat-body are residual yolk from the embryo; in B and C they have disappeared and smaller reserve granules are accumulating in great number. In C new (secondary) fat-body is arising from the epidermis. Note progressive development of the genital tube.

Lettering. c.v caudal visceral nerve; *d.l.m$_7$* developing seventh dorsal longitudinal muscle; *f.b.s* secondary fat-body arising from epidermis; *g.ab$_4$, $_5$, $_6$* fourth, fifth, and sixth abdominal ganglia; *g.t* rudiment of genital tube; *g.tel* teloblastic ganglion; *m.g* mid-gut; *m.t* Malpighian tube; *n.s.s* nerve from the second sensory seta (trichobothrium), passing to fifth abdominal ganglion; *o.a.m* occlusor ani muscle; *pr.g.c* primordial germ-cells; *r* rectum, cavity exposed; *s$_7$* developing seventh segment; *s.a* anal segment; *s.s* second sensory seta (trichobothrium); the labelling line is directed to the clump of sense-cells at its base.

The development of the teloblastic mesoderm takes place along unexpectedly simple lines, without the production of somites. It begins in the early pupa; that this must be so is shown by the fact that the ventral longitudinal muscles and second oblique muscles of the future sixth and seventh segments are already present in the newly emerged larva (Text-fig. 25).

The early phases in the development of the teloblastic mesoderm consist merely of an enlargement of its mass, its proliferating cells becoming heaped up, in the young pupa, along the lateral wall of the anal segment, just behind the mesoderm of the fifth segment. From here the cells now spread backwards to form a complete lining to the floor of the anal segment, and also upward on to the roof of the segment, to form the Anlage of the new dorsal longitudinal muscle. These early phases will be understood by reference to fig. 129, Pl. X, and fig. 125 A and B, Pl. X; for orientation of the sections reference should be made to Text-fig. 9. Fig. 129 shows the position of the teloblastic mesoderm in relation to the mesoderm of the fifth segment; it represents one of the hindermost sections of a transversely cut young pupa, so that the hinder segments are necessarily cut 'horizontally' (cf. Text-fig. 9 for orientation). Figs. 125 A and B, on the other hand, are from a 'horizontally' cut series, the terminal segments being therefore transversely cut; the sections are immediately adjacent to one another, B being nearer the anus than A. In A note the lateral heaping up of the enlarging teloblastic mesoderm, and the development of some median mesoderm; in B note the complete lining of the floor of the anal segment by mesoderm.

The first muscle-Anlage to form out of the teloblastic mesoderm is the ventral longitudinal muscle of the developing sixth segment; it is present in 2-day pupae, and is first seen as a short column of cells that lies immediately behind the fifth similar muscle, and it intrudes into the anal segment. It may be seen in fig. 130, Pl. X, which should be compared with fig. 129, Pl. X; note that in the more advanced pupa shown in fig. 130 the fifth ganglion has become delimited from the teloblastic ganglion. In transverse sections the differentiating mesoderm may also soon be seen spreading down over the lateral wall of the enlarging sixth abdominal ganglion (still part of teloblastic ganglion); this is shown in fig. 126, Pl. X (the drawing should be compared with the right side of fig. 125 A, Pl. X, which is at exactly the same level, but from an early pupa). The vestige of teloblastic mesoderm that is not absorbed into the new segment remains as a conspicuous clump of cells on the floor of the anal segment (fig. 130, Pl. X), where it may also be seen in early first instar larvae (fig. 131, Pl. X). As described in the previous section, the epidermis of the anal segment again becomes, in the early first instar larva, a locus of intense cell-proliferation; the teloblastic mesoderm also again enlarges, and the above-described processes are repeated; cf. fig. 132, Pl. X, with fig. 131, Pl. X, and note in fig. 132 the Anlage of the new dorsal longitudinal muscle.

Only brief reference need be made to the further differentiation of the mesoderm allotted to the newly forming segments. That of the sixth segment

may serve as example. Figs. 125 A (right side), 126, 127, 128, Pl. X, represent this segment in successive stages of development, the sections being respectively from an early pupa, a late pupa, an early first instar larva, and a late first instar larva. In fig. 125 A, Pl. X, the mesoderm of the sixth segment is still part of the teloblastic mesoderm. In fig. 126, Pl. X, the Anlage of the ventral longitudinal muscle has appeared, and the mesoderm is spreading down the side of the ganglion to provide myoblasts for the sternal musculature, while other cells are beginning to spread a little way up the lateral body-wall to form the dorso-ventral muscles. In fig. 127, Pl. X, the ventral longitudinal muscle has completed its development (cf. Text-fig. 25), and a clump of myoblasts has become applied to the appendage Anlage; some of the dorso-ventral muscles are already in course of formation, and the dorsal longitudinal muscle is distinguishable. Finally in fig. 128, Pl. X, in which the fifth leg is forming, a great proliferation of the associated myoblasts has taken place, and these are being drawn into the cavity of the leg. In this figure the median mesoderm is no longer distinguishable, having become incorporated, in the usual way, into the new ganglion.

Specially noteworthy in the development of the teloblastic mesoderm is the complete absence of somites, in which respect *Pauropus* differs from *Hanseniella*, where even well-developed coelomic sacs are present in each developing teloblastic segment (Tiegs, 1945). As in *Hanseniella*, the larval mesoderm arises exclusively from the already formed mesoderm of the embryo; I have not been able to see any evidence that the new mesoderm arises directly from the epidermis of the growing zone, as described by Pflugfelder (1932) for the diplopod *Platyrrhacus*. Such formation of new mesoderm from the epidermis has been described for some annelids (*Lopadorhynchus*—Kleinenberg, 1886; *Spio*—Iwanoff, 1928); but in others (*Polygordius*—Woltereck, 1902; *Arenicola*—Lillie, 1905; *Aricia*—Iwanoff, 1928) it seems to arise exclusively from the embryonic mesoderm.

4. *The Alimentary Canal and Malpighian Tubes*

Both in the growing larva and in the adult animal an occasional dislodged mid-gut cell, with or without excretory content, may be seen within the mid-gut lumen. Beyond this there is no indication of any destruction of mid-gut epithelium, there being nothing comparable with the periodical renovation that is so striking a feature of the growing mid-gut of Symphyla and many insects.

Frequently, both in larvae and in adult animals, intestines are met that are entirely free from excretory substance; it would seem that, apart from its continuous slow ejection, this waste material may undergo a periodic but complete discharge from the mid-gut wall. In intestines which are thus freed of their stored excretion products, mitoses are occasionally seen among the epithelial cells, not only of the mid-gut itself, but also of the fore- and hind-gut (fig. 138, Pl. X). Actual cell counts in first instar and adult animals show a five- to sevenfold increase in the number of mid-gut cells. It is

probable that the cell-division which underlies this increase proceeds in sporadic outbursts, rather than continuously, for in those rare instances in which mitoses do occur they are present in relative abundance (e.g. a third instar larva with 180 mid-gut cells showed eleven in some phase of mitosis).

During the first larval stadium the Malpighian tubes enlarge considerably; their elongation does not, however, keep pace with that of the entire larva, so that, by the end of the stadium, their anterior ends, hitherto well within the second abdominal segment, have become withdrawn to the third. The distinction between the three regions, already indicated in the pupa (see above, section 9 (*b*) iv), is now very pronounced (fig. 134, Pl. X). These are: (i) a short proximal region of embryonic cells, enclosing a lumen that opens into the hind-gut; (ii) a longer median part of large pale and already markedly vacuolated cells; (iii) a shorter terminal portion of cells that present the appearance of gland-cells.

Throughout the larval period mitoses may be encountered in the growing zone at the base of each tube (fig. 135, Pl. X). The new cells, of course, become incorporated into the hinder end of the tube only, and there is no proliferation of cells within the terminal glandular part. The entire Malpighian tube of a late second instar larva is shown in fig. 135, Pl. X.

The Malpighian tube preserves this character until the adult condition is attained. Thereafter the already pale and weakly staining character of the main part of the tube becomes accentuated, and spreads into the terminal glandular portion. I have not been able to observe the time of closure of the bases of the tubes.

5. *The Fat-body*

In the embryo, as described above (section 12), the fat-body develops out of the yolk-cells. By the time the larva is ready to emerge this fat-body has become depleted of most of its reserves. In the newly emerged larva it is therefore found as a loose and irregular reticulum of cytoplasm, with scattered nuclei that display each an exceptionally large nucleolus, but without any sign of demarcation into separate cells. Unabsorbed yolk-grains, that have survived from the egg, are scattered rather sparsely throughout the fat-body (a few may be seen in Text-fig. 26 A).

As the larva begins to feed, reserve products start to accumulate again in the fat-body. These comprise the usual albuminoid grains and large spheres of fat. The fat-body thereby comes to acquire a much firmer texture than in the early larva (cf. figs. 127, 128, Pl. X). There is, however, never a sign of mitosis amongst its nuclei throughout the whole larval period, nor do any recognizable cell-partitions arise to break up the syncytial mass.

In newly emerged larvae about eighty nuclei can be counted in the fat-body; in the adult animal these have increased about fourfold. What is the source of this nuclear increase? In Symphyla there is ample evidence of mitosis in the fat-body of the growing larva (Tiegs, 1945); but in *Pauropus* I have not met it among several thousand nuclei examined. The possibility of

nuclear increase by amitosis cannot be excluded; there is, however, ample evidence of the formation of new fat-body from a quite unexpected source, namely the epidermis of the growing larva.

In newly emerged larvae the epidermis is, on the whole, rather thin, and is composed of cells with comparatively small nuclei (fig. 127, Pl. X). I can find no evidence of associated mesodermal cells, the formation of new fat-body from which might lead to the false impression of its derivation directly from the epidermis. During the first larval stadium some of the epidermal cells begin to enlarge, acquire bigger nuclei and clear cytoplasm, and are now in the first phase of differentiation into fat-cells (fig. 128, Pl. X). They are found mainly along the tergal body-wall, though a few are also present below the nerve-cord. A rather more advanced phase in the development of the new fat-body is shown in fig. 136, Pl. X. The enlarging epidermal cells have now acquired a highly alveolar cytoplasm, while the adjacent small epidermal cells are beginning to close in over them. The developing fat-cells thereby become pressed out of the epidermis; it is, however, noteworthy that at this phase of their development they are still part of the epidermis itself, for they lie external to the basement membrane.

There follows upon this the condition shown in figs. 137 and 138, Pl. X. The newly forming fat-body, easily distinguishable by its delicate lace-like reticulum and absence of reserve material, has grown in bulk, and has begun to assume a syncytial character, while renovation of the epidermis above it is almost complete.

Finally, the new fat-body separates from the epidermis; large fat-vacuoles appear within it and the albuminoid reserves become more abundant. The already formed fat-body thereby becomes displaced to the sides of the enlarging abdominal cavity, the new fat-body occupying the space between the alimentary canal and the dorsal body-wall, while there is also a smaller amount under the nerve-cord. In larvae in which the old fat-body contains ample reserves, the contrast between it and the new fat-body is very marked (fig. 145, Pl. XI). But as reserve material begins to accumulate in the new fat-body, the distinction between the two is gradually lost.

The above-described formation of new fat-body from epidermis was quite unexpected. In insects and in Symphyla growth of the fat-body in the larva may be attended by mitosis in already formed fat-body, or new fat-cells may arise from dormant mesodermal cells. As far as I know the only record of new fat-body formation out of epidermis is that of Rössig (1904) for certain gall-forming wasps (Cynipidae).

6. *The Reproductive Organs*

(*a*) *Anatomy of Adult Organs.* The structure of the reproductive organs has already been described by Schmidt (*1895*), Kenyon (*1895*), and Silvestri (1902); there is, however, considerable lack of agreement, particularly for the male organs. The accounts of Schmidt and Kenyon refer to *Pauropus huxleyi*, that of Silvestri to *Allopauropus brevisetus*.

(i) *Female* (Text-fig. 27). The ovary is a very thin-walled unpaired sac, lying between the nerve-cord and the intestine; it extends throughout the fifth to eighth segments, and, when replete with eggs, even into the tenth. The statement by Schmidt that the eggs probably develop from the epithelial wall of the ovary is incorrect, for a localized germarium is present. The latter is unpaired, and is situated on the floor of the ovarian tube near its middle. (This is not general for Pauropoda; in an undescribed species which I have the germarium occupies the hindermost end of the ovary.) It is more conspicuous in animals with eight leg-pairs than in adults, and in the latter tends to disappear with advancing age (see Text-fig. 27 A). The eggs do not lie loose within the cavity of the ovary, but are contained within a very thin follicular membrane, by which they are attached to the ovarian wall. From four to six eggs may simultaneously undergo enlargement by accumulation of yolk, the expanding ovary pressing upon the adjacent organs. Between the enlarging eggs there may be abundant smaller eggs in which yolk has not yet begun to accumulate.

At its anterior end the ovary passes into a remarkable thick-walled cylindrical glandular duct, through which the eggs must pass on their way to the oviduct. I shall speak of it as the 'ductus glandularis'. It extends from the fifth to the third abdominal segment. It is composed of tall columnar gland-cells, and is invested externally by a strongly developed layer of circular muscle-fibres. When empty its cavity is, except for a narrow median channel, hardly visible; closer inspection reveals, however, an almost completely collapsed triradiate lumen between its thick epithelial walls (Text-fig. 27 C). Whether its function is to secrete the egg-shell, as Schmidt has suggested, is uncertain; in none of the females, with large eggs in the ovary, that I have examined are the eggs provided with a shell.

There is only a single oviduct and it may lie either to right or to left of the nerve-cord, around which it bends on its way to the genital atrium. It is much thinner than the ductus glandularis, and provides a surprisingly narrow channel for the passage of the large eggs. Its walls, evidently highly distensible, are lined by cubical epithelium, but are not glandular in character (Text-fig. 27 B).

The oviduct opens into the side of the genital atrium. This is merely a slight depression in the floor of the third segment, just behind the second legs, there being no genital sclerites associated with it. I have sections from one animal in which the genital atrium, distended with some glandular material, presumably from the ductus glandularis, is invaginated deeply into the floor of the segment.

Into the genital atrium, immediately above the orifice of the oviduct, opens a single receptaculum seminis, a short, thick-walled, flask-shaped organ, lined by cubical epithelium, and often filled with sperms (Text-fig. 27 B).

(ii) *Male* (Text-fig. 28). There are four large rounded testes lying, one behind the other, above the alimentary canal below the fourth to sixth tergal
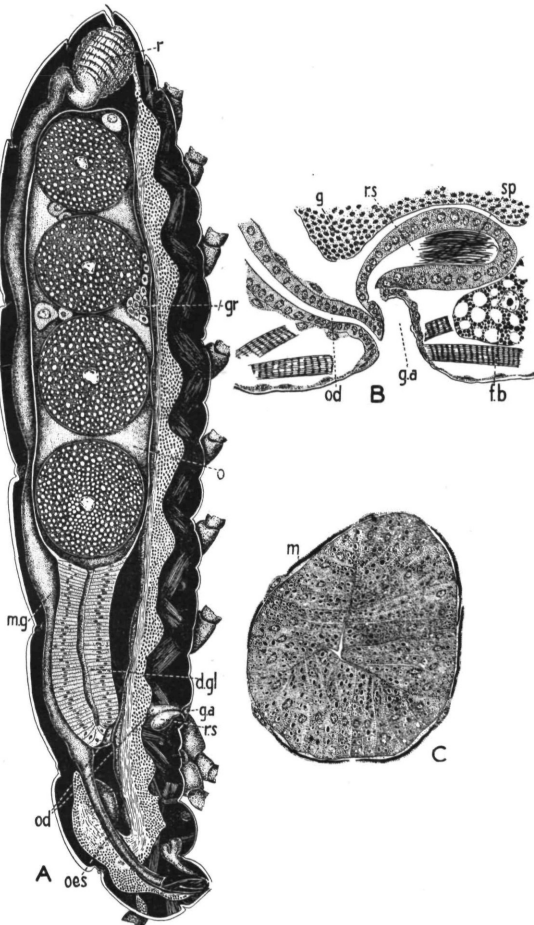
TEXT-FIG. 27. Structure of adult female reproductive organs; from an animal in which the germarium has almost disappeared.

A. Internal view of adult female. B. Transverse section through floor of genital segment, showing genital atrium, and the openings into it of the receptaculum seminis and oviduct. C. Approximately transverse section through ductus glandularis.

Lettering. *d.gl* ductus glandularis; *f.b* fat-body; *g* ganglion; *g.a* genital atrium; *gr* vestige of germarium; *m* muscle sheath; *m.g* mid-gut; *o* ovarian tube; *od* oviduct; *oes* oesophagus; *r* rectum; *r.s* receptaculum seminis; *sp* sperms in receptaculum.

shields. Each testis is a hollow sac, completely enclosed by germinal epithelium, and the interior is filled with masses of developing sperms. Investing the germinal epithelium is a thin, almost imperceptible, membrane, which is the wall of the genital tube itself. The four vasa deferentia that arise from the four testes pass down, two on either side, below the intestine, where they continue forward as four vesiculae seminales.

The vasa deferentia are easily distinguishable from the vesiculae by the orientation of their sperm content, whereas in the vesiculae the sperms are disposed quite at random (Text-fig. 28 c, b). The walls of the vasa deferentia are composed of very large flattened cells, while externally there is a thin investing sheath. The vesiculae, whose walls are markedly glandular, are often distended with sperms. Within the sixth segment the four vesiculae become confluent at their tips, and from the common chamber the two exit channels arise. Developmentally the latter are found to form from the epidermis alone, and though differentiated into three distinct regions, may therefore conveniently be spoken of as the ejaculatory ducts. Following Kenyon (1895) we may refer to the three regions as the posterior, glandular, and anterior ejaculatory ducts respectively. The posterior ducts are quite short and narrow. The glandular section of the ducts are not unlike the unpaired 'ductus glandularis' of the female; they are, however, rather thinner, the nuclei lie at the bases of the cells, and an investing muscle sheath is absent. The narrow lumen of each lodges a long structureless filament of unknown meaning (Text-fig. 28 b). It is probable that the function of the glandular ducts is to secrete a viscous matrix in which the sperms are transferred to the female, for sperms within the receptaculum seminis of the female are always enveloped in a thick secretion which is not visible in the vesiculae. The anterior ejaculatory ducts pass to right and left of the nerve-cord to the penes, which lie just median to the second coxae (Text-fig. 24 b).

(b) Development. In the pupa the reproductive organs are still in a very rudimentary condition (cf. above, section 11). The future genital tube consists of a narrow string of cells, resting in a median groove along the roof of the nerve-cord, and extending from the fifth abdominal segment a short distance into the third (Text-fig. 9). Not more than about a dozen cells are present, and of these most are aggregated around the single primordial germ-cell (or exceptionally two germ-cells) located within its hinder end (fig. 139,· Pl. XI). Behind the germ-cell the cells of the genital tube merge with the median mesoderm of the developing new segments. Sexual distinctions are not yet evident.

In this condition the reproductive organs are found even in newly emerged larvae. During the course of the first larval stadium the primordial germ-cells and cells of the genital tube begin to divide. In consequence the future genital tube grows in thickness. In late first instar larvae from four to six primordial germ-cells are present within it, forming a bulge at its hinder end, but of a lumen there is yet no sign (Text-fig. 26).
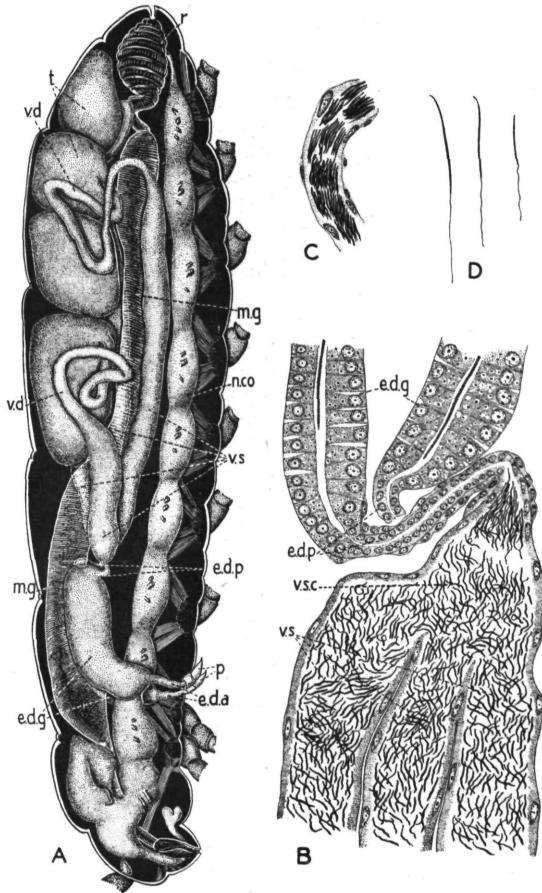
TEXT-FIG. 28. Structure of male reproductive organs.

A. Internal view of adult male to show general plan of reproductive system. B. Fragment from a 'horizontally' sectioned adult male, showing vesiculae seminales and portion of ejaculatory ducts; only three of the four vesiculae are present in the section. C. Fragment of vas deferens. D. Mature sperms.

Lettering. e.d.a, e.d.g, e.d.p anterior, glandular, and posterior portions respectively of the ejaculatory ducts; *m.g* mid-gut; *n.co* nerve-cord; *p* penis; *r* rectum; *t* testis; *v.d* vas deferens; *v.s* vesicula seminalis; *v.s.c* common chamber formed by fusion of vesiculae seminales.

Connexion with the exterior is established by the ingrowth of a pair of ducts from the epidermis a little postero-medial to the bases of the second legs. The development of the ducts often takes place in first instar larvae, though in many cases it is delayed till well into the second larval stadium. They first become apparent as a pair of small epidermal thickenings out of which arise a pair of ingrowing cords of cells (fig. 140, Pl. XI), which, passing upward and a little backward, bend medially round the ventral longitudinal muscle, and fuse with the anterior tip of the genital tube over the roof of the nerve-cord. The genital tube has, by this time, grown markedly in thickness, but even now does not display a lumen.

Even well into the second, and often third, larval stadia, no sexual distinction is evident; it is particularly noteworthy that the epidermal exit ducts do not give the expected clue, for in these earlier larvae they are paired in both sexes, though, in the adult female, only one of the two ducts survives. The structure of the gonad prior to the onset of sexual differentiation is shown in fig. 138, Pl. X, the drawing being from a sagittal section of a second instar larva. The genital tube, still devoid of a lumen, is now a compact cord of cells. The germ-cells, much increased in number, form a bulge at its hinder end, and have now moved back into the sixth abdominal segment. It is evident from the position of these cells that the genital tube must have become elongated behind; and this terminal elongation seems to be still in progress, for posterior to the germ-cells the genital tube passes directly into the undifferentiated median mesoderm of the developing new (seventh and eighth) abdominal segments. As far as I have been able to observe, terminal growth of the genital tube ceases after the second larval moult.

Sexual differentiation becomes apparent first in the gonad itself; and since the testis departs more than the ovary from the primitive condition, it is the males that are at first distinguishable with certainty.

(i) *Male.* In some larvae differentiation of the gonad-rudiment into the four testes is already in progress before the end of the second larval stadium, though generally it is deferred till well into the third. The earliest phase in the differentiation of the testes that I have obtained is shown in Text-fig. 29 A; a section taken through its hinder portion is drawn in fig. 145, Pl. XI. It is taken from a late second instar larva, and shows the developing testes arising as two pairs of lateral thickenings that are growing up to the side of the mid-gut from the anterior and the posterior ends respectively of the gonad rudiment, which itself now lies mainly in the sixth segment. In transverse section the wall of the gonad displays an epithelial character, with much mitosis amongst its cells. Within the four developing testes germ-cells are plainly distinguishable by their large nuclei; the intervening region, with relatively small nuclei, evidently represents the wall of the genital tube itself, and out of it the vasa deferentia will eventually form; but as fig. 145, Pl. XI, shows clearly, its epithelium merges into the developing germinal epithelium of the testis Anlage itself.

A later phase in the differentiation of the male gonad, taken from a third instar larva, is shown in Text-fig. 29 B; a section through the anterior, middle, and hinder regions respectively is depicted in fig. 146, A, B, and C, Pl. XI. The anterior pair of testes have grown high up around the mid-gut, and extend almost to the dorsal body-wall (fig. 146 A). The hinder pair of testes are also markedly enlarged, but their dorsal displacement is not very advanced, for they still lie to the side of the intestine (fig. 146 C). Between the anterior and posterior pair of testes the genital tube is reduced to a comparatively narrow band of cells, with just perceptible lumen (fig. 146 B). Within the testes the germ-cells have greatly increased in number, and among these a few (indicated by x in fig. 146, Pl. XI) are already in meiotic prophase.

In fourth instar larvae development of the testes proceeds apace. The anterior pair has become much enlarged (Text-fig. 29 C), sections through them (fig. 147, Pl. XI) showing that the enlargement is due to distension of their cavities. The testicular cavity is lined by germinal epithelium, external to which is a thin membrane, often recognizable only by its flattened nuclei, and presumably the product of the original sheath of mesoderm (genital tube) which invested the primordial germ-cells. Within the germinal epithelium mitoses are abundant, and many spermatocytes, with nuclei in meiotic prophase, have been released into the cavity of the testis. The posterior pair of testes have also much enlarged, and within them also spermatogenesis is proceeding; they still lie, however, to the side of the intestine.

The vasa deferentia have now also appeared, and the vesiculae seminales are in course of formation. The vasa deferentia arise from that part of the genital tube which originally included the germ-cells. As the latter become concentrated within the four enlarging testes, the intervening part of the genital tube, now freed from germ-cells, becomes reduced in thickness. The displacement of the anterior pair of testes into a position above the intestine has the effect of drawing out the adjoining part of the genital tube into the anterior pair of vasa deferentia, which, however, remain connected with the genital tube below the intestine; this will readily be seen in fig. 146 A, Pl. XI. That portion of the genital tube which still joins the anterior pair of testes with the posterior pair has now become reduced to a narrow strip with just-perceptible lumen (fig. 146 B, Pl. XI; Text-fig. 29 B). In fourth instar larvae this median band is seen to have divided longitudinally into the two vasa deferentia of the hinder pair of testes, and these soon become widely separated from one another (Text-fig. 29 C; fig. 147, Pl. XI).

Anterior to the region of the gonad, i.e. in the fourth and fifth abdominal segments, the genital tube has grown markedly in width. As the four vasa deferentia become better defined, the whole of this widened part of the genital tube proceeds to divide into four separate tubes that lie side by side above the nerve-cord. The splitting spreads from behind forwards; fig. 148, Pl. XI, is drawn from the actual region of division. In these four separate tubes we have the rudiments of the vesiculae seminales; the outer pair is
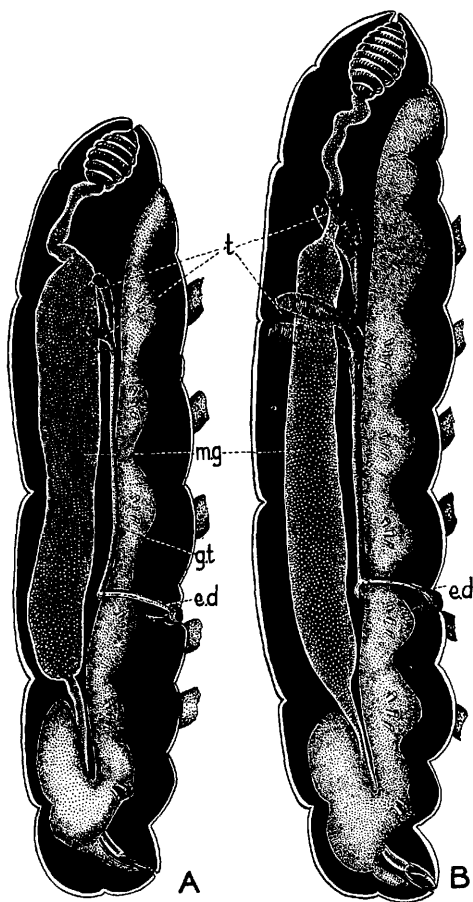
TEXT-FIG. 29. Differentiation of male reproductive organs.

A. Initial phase (from a late second instar larva) showing the four rudimentary testes develop-
ing out of the genital rudiment. The epidermal exit ducts have already become associated
with the anterior end of the genital tube. Sections through such a larva are shown in
figs. 141, 145, Pl. XI.   B. Later phase (from a third instar larva). For section see figs. 145
A, B, C, Pl. XI.   C. From a fourth instar larva, showing later phase in differentiation of the
vasa deferentia, and the beginning of splitting of the genital tube into the four vesiculae
seminales. For section see fig. 147, Pl. XI.   D. From a fourth instar larva, showing still
later phase of development. The anterior pair of testes is completely dorsal in position,
the posterior pair in process of becoming so, but alinement of the testes has hardly begun.
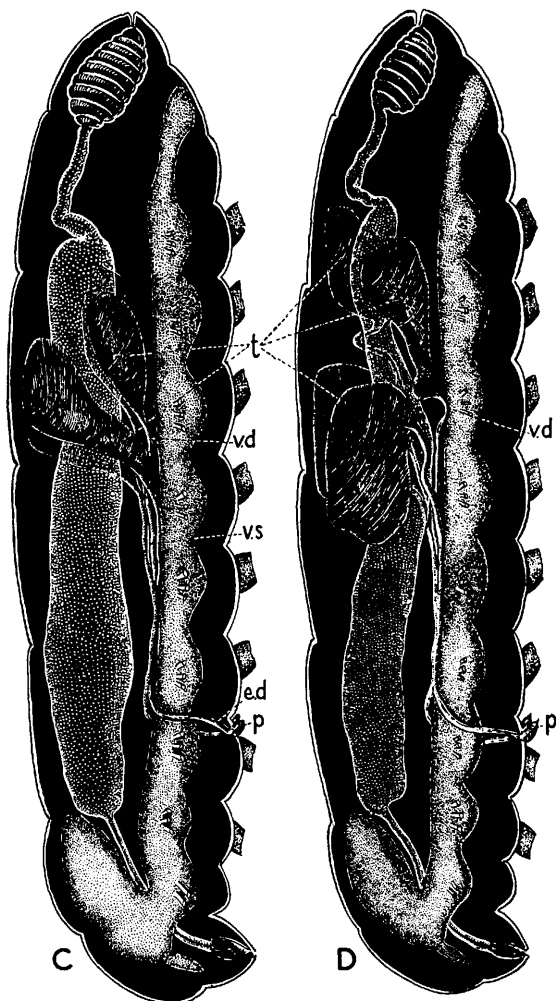
Differentiation of the epidermal exit ducts into the ejaculatory ducts has also not yet started.

All four figures drawn to scale.

Lettering. *e.d* undifferentiated exit ducts (rudimentary ejaculatory ducts); *g.t* genital tube; *m.g* mid-gut; *p* penis; *t* testes; *v.d* vasa deferentia; *v.s* vesiculae seminales.

connected, through the anterior pair of vasa deferentia, with the anterior pair of testes, the median pair with the hinder pair of testes.

A still later phase in the development of the testes is shown in Text-fig. 29 D. The testes have enlarged further, and the anterior pair has begun to assume its definitive form, with the vasa deferentia arising from their postero-lateral walls. Twisting of the vasa deferentia is now also beginning. In this larva the final alinement of the four testes, one behind the other, has hardly begun; nevertheless even before the final larval moult this alinement is attained.

Late in the fourth larval stadium spermatogenesis becomes accelerated, and all phases from early spermatocytes to apparently mature spermatozoa are visible within the cavities of the enlarging testes. A testis from such a larva, cut in sagittal section, is shown in fig. 150, Pl. XI. The vesiculae seminales have now also begun to increase in thickness, their cells enlarging and acquiring an obviously glandular texture of cytoplasm (fig. 149, Pl. XI); but in none of the fourth instar larvae that I have examined do they ever show any sperm-content.

The ejaculatory ducts alone are of epidermal origin, for they develop out of the paired ingrowing cords of cells whose formation in an earlier larval instar has already been described above. Throughout the second and third larval stadia they undergo considerable thickening, there being much evidence of mitosis among their cells; but a lumen is not distinguishable except perhaps near their epidermal attachments (fig. 141, Pl. XI). Not till late in the fourth larval instar does structural differentiation set in. By separation of cells each now develops a lumen throughout its length. The inferior portions of the ducts remain rather thin-walled, and so form the 'anterior ejaculatory ducts'. The middle part becomes markedly thickened, and out of this forms the glandular portion of the ejaculatory ducts (fig. 142, Pl. XI). I have not been able to make direct observations on the development of the short thin posterior ejaculatory ducts, but as they participate in the terminal bifurcation of the genital ducts, it is probable that they too must be assigned to the epidermal portion.

The two penes are already present in fourth instar larvae (Text-fig. 29 C and D; fig. 142, Pl. XI). This points to the possibility of a precocious sexual maturity in some males, as in Symphyla; but although apparently fully mature sperms are present in the testes of some fourth instar larvae, I have never seen any that have been released into the vesiculae seminales. The penes develop, in third instar larvae, by thickening of the epidermis around the bases of the ejaculatory ducts. Just prior to the next moult they begin to protrude from the surrounding epidermis, and so become prominent in fourth instar larvae.

(ii) *The Female.* In its development this departs much less from the condition of the gonad-Anlage than is the case for the male, and consequently females are not distinguishable as early as the latter; in no instance have I been able to recognize the female before the third larval stadium. In such larvae the gonad-Anlage has somewhat thickened, but otherwise retains its

earlier features except that, among the nuclei of the germ-cells, we can occasionally recognize prophase stages of meiosis (fig. 151, Pl. XI). Later, during the third larval stadium, these meiotic prophases become much more abundant, while at the same time a number of cells with small nuclei appear among the germ-cells (fig. 152, Pl. XI). It is from these cells that the future follicles, within which the eggs are held in the ovary, are developed. It is most unlikely that they can have arisen from the germ-cells; it is much more probable that they grow into the ovary from the ovarian wall, for they are connected with the latter, and have nuclei of similar appearance.

The ovary in such larvae lies within the sixth and seventh abdominal segments. As in the male the genital tube has now lost all connexion with the median mesoderm of the developing hinder end of the larva, so that it does not acquire any additional cells from this source. In front of the ovary the genital tube has markedly thickened, but does not, at this period, show any noteworthy difference from that of the male. The entire ovary, together with proximal part of the genital tube, from a larva cut in 'horizontal' section, is shown in fig. 153, Pl. XI.

During the following larval stadium enlargement of certain oocytes begins. Therewith the ovary itself grows still more in size, its most anterior tip lying well within the fifth segment, while its hinder end may intrude a little into the eighth. The enlarging oocytes lie in two rows along the lateral walls of the ovary, and may even bend up a little to envelop the lateral walls of the intestine, giving to the ovary the false appearance of a paired organ. Between the two rows of enlarging oocytes, on the floor of the ovary, and within the sixth and seventh segments, lies the mass of unenlarged germ-cells, some in mitosis, others in various prophases of meiosis; we may now speak of this as the germarium (fig. 154, Pl. XI).

In the adult animal the ovary enlarges still further, as the number of enlarging oocytes increases, and may extend almost into the fourth segment. The germarium, on the other hand, decreases in size as its cells are gradually released into the cavity of the ovary, and eventually disappears. Text-fig. 27 shows an adult female with dwindling germarium.

The ductus glandularis develops from that portion of the genital tube that lies in the fourth and fifth segments, anterior to the ovary, and is wholly mesodermal. Its rudiment, from a fourth instar larva, is shown in fig. 155, Pl. XI, its point of junction with the epidermal exit duct being very clearly seen. Already in this undeveloped condition it displays an outer thin investment of flattened cells, from which presumably the muscle-coat later develops. Sometimes the transformation of this rudiment into the fully formed duct is complete even before the final moult; on the other hand, I have often seen 'adult' animals, with nine leg-pairs, in which the duct is still imperfectly developed. The expectation that the ductus glandularis might have a similar origin to the glandular ejaculatory duct of the male, which it closely resembles, has not been fulfilled; the ductus glandularis is rather the equivalent of the vesiculae seminales.

Of the two epidermal exit ducts which are present in earlier larval instars, only one survives, and this may be either the left or the right duct. Degeneration and final disappearance of the opposite exit duct takes place in fourth instar larvae (fig. 143, Pl. XI). There is no evidence that the receptaculum seminis is a vestige of the degenerated exit-duct, for fourth instar larvae are sometimes encountered in which the second duct has completely disappeared, before there is even a sign of the receptaculum. The latter arises as a thickening of the base of the surviving exit duct (oviduct)—fig. 143, Pl. XI, but later acquires an opening into the genital atrium, close beside that of the oviduct, but quite distinct from it (fig. 144, Pl. XI). The atrium is merely a depression of the epidermis between the bases of the second coxae.

(*c*) *Gametogenesis*. This will be treated only very briefly, since a detailed consideration of the nuclear phenomena is not within the scope of this work.

(i) *Spermatogenesis*. Throughout the later larval instars, and particularly in the fourth, mitoses appear in great abundance in the germinal epithelium, and this has the effect of further enlarging the testes and of replacing cells that have been liberated into their cavities. In adult animals the frequency of mitosis declines.

When we examine the contents of the testes, we see all phases in the development of sperms, from early meiotic prophases to the completed gamete. These are not scattered singly through the testes, but lie in clumps, and within these clumps the progress of spermatogenesis is markedly synchronized (fig. 150, Pl. XI). This appears to be due to the fact that patches of germinal epithelium, and not individual cells, are released into the testicular cavities. Especially in fourth instar larvae is this release of masses of spermatocytes, with nuclei in early meiotic prophase, met with; it is evidently in progress in the upper part of the testis shown in fig. 150, Pl. XI.

After release from the testes, the mature sperms are stored in the vesiculae, which may be distended with them. The heads of the sperms (Text-fig. 28 D) are rod-shaped bodies, often with a slight bend at the tip, and range in length from 13μ to 24μ. (The above measurements are of the same order as those given by Schmidt (1895) for *Pauropus huxleyi*. In *Allopauropus brevisetus*, according to Silvestri (1902), the sperms are many times this size. In an undetermined Australian species, to which I have referred several times above, similar enormous sperms are present.) The tail is about the length of the head, but can be seen only in sharply stained preparations. Living sperms examined in saline often display typical swimming movements, but even in such active forms the tail is quite invisible.

(ii) *Oogenesis*. In the third instar larva a considerable proportion of the germ-cells in the ovary are in some recognizable prophase of meiosis. In many others the nuclei are in a resting condition. Occasionally a true mitosis is seen. Between the germ-cells are the future follicular cells, easily distinguishable by their small size (fig. 152, Pl. XI).

In the following larval stadium, as already described, the more laterally situated germ-cells begin to enlarge, each being now enclosed within its

own sheath of follicular cells (fig. 154, Pl. XI). Their nuclei are in the germinal vesicle condition. The median row of smaller germ-cells may be regarded as germarium. But after the last larval moult an increasing proportion of its cells, also, are found in the germinal vesicle condition, even though the phase of enlargement has not yet set in. Early phases of meiosis are now scarce, and true mitoses very rare (fig. 1, Pl. I).

In certain of the enlarged oocytes yolk then begins to accumulate, smaller oocytes, still without yolk, lying singly or in small groups between the enlarging cells (fig. 2, Pl. I; Text-fig. 27). Prior to the laying down of yolk, a deeply staining body, presumably a 'yolk-nucleus', may be met with in the oocytes (fig. 2, Pl. I).

After the discharge of the egg from the ovary, other laterally placed germ-cells within the 'germarium' begin to enlarge, to repeat the process. Eventually the whole germarium disappears.

The nuclear phenomena which follow upon the germinal vesicle phase have been described above (see Part 1, Emb. Dev., section 1).

I have not been able to make any observations on the development of the chorion. The fact that none of the ovarian eggs which I have seen showed even a rudiment of a chorion supports the suggestion made by Schmidt (1895) that the chorion may be secreted on to the eggs as they pass along the ductus glandularis.

AFFINITIES OF THE PAUROPODA

Although taxonomic work on these minute and fragile creatures has brought to light peculiar genera like *Eurypauropus*, *Brachypauropus*, and *Decapauropus*, the group still remains a singularly homogeneous one, whose members reveal no clear indication of close affinity with any of the other forms of myriapods. Lubbock (1868), who looked upon paucity of appendages as a primitive and ancestral feature, regarded the Pauropoda as 'a link not only connecting the chilopods and diplopods together, but also bridging over to a certain extent the great chasm that separates these forms from other articulates'; and when, in 1879, Ryder discovered the remarkable *Eurypauropus*, he, too, emphasized the annectant character of the group, for it seemed to him to link the diplopods, chilopods, hexapods, and even, owing to the branching antenna, the crustaceans.

Adopting the position of the gonopore as the basis of classification, Kennel (1891) was the first to suggest a dichotomous line of descent of the tracheate arthropods, in which either an anteriorly situated, or a posteriorly situated pair of segmental organs of some primitive *Peripatus*-like ancestor had become utilized as the exit ducts of the reproductive organs; the one line of descent gave origin to the Pauropoda, Symphyla, Diplopoda, and Arachnida, the other to the Chilopoda and Insecta. Pocock (1893) proposed a similar scheme, but wisely excluded the Arachnida, and his classification of the 'tracheate arthropods' into Progoneata and Opisthogoneata is now generally accepted. The affinities of the Pauropoda within the Progoneata have,

however, remained uncertain. Schmidt (1895) correctly recognized the evidence of structural simplification in their minute bodies, and regarded the Pauropoda and Symphyla as simplified offshoots of the 'protodiplopod' stem. (I have shown in a previous paper (Tiegs, 1940) that the evidence for vestigial diplopody in Symphyla is invalid.)   Kenyon (1895) united the Pauropoda and Pselaphognatha as sub-orders in the order Protodiplopoda. In Lankester's (1904) classification the Symphyla and Pauropoda are included in the Diplopoda.

If current notions on the heterogeneous character of the 'Myriapoda' are well founded, comparison of *Pauropus* with any but the progoneate forms must be futile. Thus in Lankester's classification (1904) the Onychophora, Diplopoda (including Pauropoda and Symphyla), and Arachnida are conceived as 'terrestrial offshoots of successive lower grades of primitive aquatic Arthropoda which are extinct', while 'the Hexapoda, and with them, at no distant point, the Chilopoda, have branched off from the Crustacean main stem as specialized terrestrial lines of descent'. Even the more conservative schemes of Kennel and Pocock can leave no room for comparison with opisthogoneate groups. There is, however, little doubt that the remarkable anatomical characters of the Symphyla invalidate these classifications; for our present knowledge seems to justify Ryder's (1800) original contention that the Symphyla are an annectant group, which weld together the Insecta, Diplopoda, and Pauropoda into a group of relatively closely related Arthropoda. Into the evidence for their insectan affinities it is not necessary here to enter, as this has recently been reviewed by Calman (1936), Imms (1936), and Tiegs (1940); but I would, as newer evidence, point to the remarkable embryonic 'dorsal organ' common to Symphyla, Collembola, and *Campodea* (Tiegs, 1942a, 1942b), and not known, so far, in any other arthropod. Their diplopod affinities are perhaps less striking, for their embryology does not support Schmidt's (1895) contention, accepted by several authorities, that their abdominal segments present a vestigial diplopody; but the manner of segmentation of the egg and of mesoderm formation, and the presence of such organs as the exsertile vesicles and spinning glands (both present in the diplopod order Nematophora), segmented mandibles, organs of Tömösvary, fat-body, proctodaeal Malpighian tubes, as well as peculiarities in structure of the brain and gonads, are features which point to more than a merely general relationship with Diplopoda.

In view of these facts it is surprising that a single character of uncertain morphological value should, as a criterion of classification, be held to outweigh so much evidence of affinity between the progoneate and opisthogoneate groups. Does the position of the gonopore really have the great significance that is generally assigned to it? It is, of course, true, that within the various natural groups of myriapods its position is constant. The notion at the bottom of the classification is, however, the retention of a forwardly situated pair of ancestral coelomoducts to serve as gonoducts in the Progoneata, and of a posteriorly situated pair in the Opisthogoneata. For the latter the scheme seems to be well justified; for in *Scolopendra* (Heymons,

1901) and in various Orthoptera and Dermaptera (Wheeler, 1893; Heymons, 1895; Wiesmann, 1926; Roonwal, 1937) the gonoducts do indeed develop, in the embryo, out of mesodermal coelomoducts. This seems to hold also for *Peripatus* (Sedgwick, 1887), though Kennel (1886) asserts that here the ducts are chiefly ectodermal. In the Progoneata, on the other hand, in which evidence from the Symphyla and Pauropoda is now available, it is plain that the exit ducts from the genital tubes are not coelomoducts at all, as had been assumed, but are ectodermal ingrowths. For the Diplopoda evidence on this point is not yet available.

The gonopore of Progoneata seems, therefore, in contrast to that of Opisthogoneata, to have the status of a secondary opening, and it is not unlikely that it was acquired as an adaptation to their anamorphosis; for if the genital segment has become involved in teloblastic growth, the need has arisen for the formation of a new gonopore, remote from the zone of growth, unless its formation may be deferred till after the completion of anamorphosis. As long ago as 1895 Kenyon, recognizing the anomalous position of *Scolopendrella* (Symphyla), wrote: 'The animal truly shows many chilopod and some thysanuran features, but until it can be shown from a study of its ontogeny that the genital ducts are already fairly well formed before the posterior segments, it is safe to conclude that the position of the genital opening on the fourth body-segment, together with other characters, indicates an affinity nearer the Diplopoda than to any other group of Arthropods.' Actually, not only are the genital ducts of Symphyla 'already fairly well formed before the more posterior segments', but they may even be functioning (Tiegs, 1944). In *Pauropus*, also, they arise long before the hinder end of the animal has completed its development, but there is no evidence in this case that the gonads are functioning before the completion of anamorphosis. For the Diplopoda no observations on the development of the genital ducts seem to have been made; the remarkable observations of Verhoeff (1926) on 'intercalated males' (Schaltmännchen) of Julidae (with indefinite segment number) have shown, however, that terminal accretion of segments does indeed continue after sexual maturity, though this does not hold for species with definite segment number. The existence of anamorphic chilopods, with terminal genital opening, does not invalidate this line of argument, for at least five instars intervene between completion of anamorphosis and the attainment of sexual maturity, and it is in these instars that the genital segment and external genitalia develop (hemianamorphosis of Verhoeff, 1902–25). For the Protura, in which three new segments are added behind during anamorphosis, no relevant observations seem to have been made.

It would appear, then, that at present the classification of 'tracheate arthropods' into Progoneata and Opisthogoneata, implying as it does two independent lines of descent from an ancestor with multiple gonoducts, is not sufficiently well founded to invalidate a comparison of *Pauropus* with other than progoneate forms. In the following discussion a more general comparison will therefore be drawn.

(*a*) *General Features of Development.* The segmentation of the egg recalls that of Symphyla and most Diplopoda and Collembola. In the phases which ensue—a blastoderm, within which a germ-band becomes defined, from which, in turn, scattered cells separate away to form the mesoderm—we see the distinctive features of myriapod-insect ontogeny. There can, indeed, be no question of the ingrowth of mesoderm at a blastopore, as in *Peripatus* or Crustacea. Yet in *Pauropus* a modified gastrula can be distinguished preceding the blastoderm, but with characters which give a possible clue to the path of evolution of the more specialized ontogeny without a gastrula that prevails in other myriapods and insects. This question has already been discussed (see Emb. Dev., section 5).

If there is any close affinity between myriapods and higher Crustacea, as some authors contend, these early developmental phases might be expected to reflect it. That the segmentation of the egg may at times be very similar, as in *Scolopendra* and *Astacus*, must be conceded; such resemblances are, however, largely governed by the yolk-content of the egg. On the other hand, the peculiar manner in which the ectoderm and mesoderm develop in higher Crustacea, from ectodermal and mesodermal teloblasts, is never encountered in any myriapod or insect embryo. Moreover, in Crustacean embryos there seems to be an almost total suppression of coelomic sacs, only a few well-attested cases of diminutive coelomic sacs having been recorded (*Estheria*, Cannon, 1924; *Hemimysis*, Manton, 1928). It is true that in *Pauropus* the coelomic sacs are also not well developed; but this is almost certainly a simplification, associated with the absence of a cardiac Anlage (see Emb. Dev., section 8, ix). In the embryos of all other myriapods and primitive insects so far examined, we find very complete series of coelomic sacs, which in size rival even those of *Peripatus*.

The presence of a gastrula in *Pauropus*, even though it be a much modified gastrula, must be adjudged a primitive feature. The failure to develop completely specialized vitellophages is also primitive, for, as in the yolked species of *Peripatus* (Sheldon, 1887–8; Evans, 1901) and in Symphyla, all its 'yolk-cells' are subsequently used in the formation of adult tissues. These tissues in *Pauropus* are the mid-gut epithelium and fat-body. The development of the fat-body out of 'yolk-cells' is particularly significant; it arises in a similar way in Symphyla and probably Diplopoda, but in chilopods and insects is derived from the mesodermal somites.

The absence of a ventral flexure in the germ-band is noteworthy. In all other myriapods and in insects a ventral flexure appears, being sometimes precocious (Symphyla, Diplopoda) or delayed (Chilopoda, Insecta).

The absence of embryonic membranes is not unexpected, for they are not found in any other myriapod, and are a product of evolution within the class Insecta.

The 'dorsal organ' of the embryo is not the highly specialized organ of Collembola, Symphyla, and *Campodea*, but is a smaller and simpler structure, recalling rather the 'dorsal organ' of Crustacea (see Emb. Dev., section 14, vii).

(*b*) *Post-embryonic Development.* The most striking feature of the post-embryonic development of Pauropoda is the anamorphosis, which they have in common with Diplopoda, Symphyla, Protura, and some Chilopoda. What significance attaches to it?

It is probable that precocious emergence from the egg, with deficient segmentation, is merely an adaptation to the deficiency of yolk available to the growing embryo. Some authors contend that the ensuing anamorphosis is a repetition of ancestral history, in which a line of few-segmented ancestors grew in length by the sub-terminal acquisition of new segments; this is, indeed, the central idea in Tillyard's (1930) theory of the evolution of myriapods and insects. The laws of metamerism are, however, too insufficiently known to permit any such deduction; what significance can attach to the condition of the larva at eclosion, when within the single family Scutigerellidae, some species emerge with six pairs of legs, others with seven? There is, in fact, no sure evidence as to whether the ancestor of myriapods was a few-segmented (Tillyard), or, as Lankester (1904) urges, a multi-segmented arthropod; probability favours the latter view, since paucity of segments, both in extinct and surviving arthropods, is quite exceptional. The deficient abdominal segmentation of Collembola is almost certainly a case of arrested development (Imms, 1936); that of Pauropoda is probably the same (see Post-emb. Dev., section 1).

Since two orders of chilopods, and all insects except Protura, develop without anamorphosis, is the latter to be adjudged a secondary acquisition of those myriapods that display it, or is the reverse the case? The occurrence of anamorphosis in all the primitive surviving myriapods points to the likelihood of its being an archaic feature, and not a secondary acquisition. (According to recent studies by Fahlander (1938) the multi-segmented chilopods without anamorphosis are the least primitive members of the group.) But this evidence can hardly be regarded as conclusive; in particular it throws no light on the question whether the anamorphosis was complete, or a 'hemianamorphosis' of the chilopod type. It is important in this connexion to observe that emergence from the egg in a partially developed condition is not confined to the anamorphic myriapods; its prevalence throughout the metabolic insects is the basis of Berlese's theory of larval forms (see Imms, 1937). It is reasonable to expect that a larva, forced to precocious emergence through lack of nutriment in the egg, should find it advantageous to have well-developed anterior parts, on which the sense and feeding organs are borne, and relegate the completion of its hinder end to the post-embryonic phase; but it is disconcerting to find that the metabolic insects, confronted with the same problem, have adopted the alternative of emerging with a complete outfit of imperfectly developed segments. Possibly the difference has been imposed by the character of the ontogeny: in the embryo of *Hanseniella agilis* the germ-band divides into a head and five abdominal segments, to which four additional segments are successively added by sub-terminal growth before eclosion, and judging by Silvestri's (1903) figures, this type of

development characterizes also the diplopods (*Pachyjulus*). This can also be recognized in *Pauropus*, though here the teloblastic growth in the embryo is limited to one segment; and it is clearly also the case in *Peripatus*, as the figures of Sedgwick and Kennel show. In *Scolopendra* (Heymons, 1901) and insects, on the other hand, segmentation of the germ-band proceeds along different lines; the latter attains its full length, after which segmentation spreads along it, but there is no teloblastic growth of segments in the egg. The extreme of precocious emergence in the first type of ontogeny is provided by *Pauropus* and some diplopods; for the second type of ontogeny it is found in the remarkable 'protopod' larvae of some parasitic Hymenoptera, in which even external segmentation of the abdomen is suppressed.

(*c*) *The Head*. The structure of the head-capsule and its appendages is of special importance for the assessment of affinities.

In the head of *Pauropus* specialized features are easily recognized, such as the peculiar branched antennae with their globuli and flagella, the deeply embedded unsegmented mandibles adapted to a semi-fluid diet, and the suctorial mouth-parts and oesophagus. But beneath these specializations there is evidence of a very primitive construction of the head; for while in Chilopoda, Symphyla, and Insecta the head-capsule is composed of a procephalon to which have been added a mandibular, maxillary, and second maxillary segment, in the Pauropoda the latter segment has not been cephalized, but remains distinct from the head as the collum segment.

In *Peripatus* the 'head' consists of three segments, each furnished with a pair of large coelomic sacs and segmental organs in the embryo, and with a pair of ganglia (Kennel, 1886; Sedgwick, 1887; Evans, 1901); the acron, equivalent of the annelid prostomium, is not separately demarcated, but the 'frontal processes' may perhaps represent its antennae (Korschelt and Heider, 1899). Following Heymons (1901) most morphologists are agreed that the procephalon of myriapods and insects is formed by the welding together of an acron and three segments (pre-antennary, antennary, and pre-mandibular), and it would therefore appear to be the equivalent of the 'head' of *Peripatus*. Snodgrass (1938) has recently proposed a radical change in our conception of head-segmentation in myriapods and insects, the pre-mandibular segment being regarded as the first true segment, and the whole region anterior to this as acron. The absence of any trace of intersegmental grooves in the entire procephalon is held to outweigh the doubtful testimony for segmentation which the coelomic sacs and ganglia offer. It must be acknowledged that in insect embryos the delineation of the segments, and particularly of the acron, is largely conjectural; on the other hand, Heymons (1901, pp. 34, 37) states quite explicitly that in *Scolopendra* intersegmental grooves are present delimiting not only the gnathal segments, but also the antennary and pre-antennary segments and acron. To regard the coelomic sacs of the procephalon as 'ontogenetic structures' for the accumulation of waste products is probably to under-estimate their real significance; in a generalized myriapod like *Hanseniella* both pre-antennary and antennary coelomic sacs perform

a normal role in developmental processes, in that both play an essential part in the development of the dorsal blood-vessel, and even in insects the antennary coelomic sac plays this role, though the pre-antennary is usually reduced to a vestige. The hope that so primitive a myriapod as *Pauropus* might throw some light on this question has not been fulfilled, for inter-segmental grooves appear too late, and all the somites are vestigial. Ferris (1942), on the other hand, believes that the component segments of the heads of insects can be identified by sutures even in the adult head-capsule; but since intersegmental lines are not present in the procephalon of the embryo, it is surprising, though perhaps not impossible, that they should be present in the adult. It is noteworthy that these adult sutures transect a region of the head from which the protocerebral ganglion develops. In *Scolopendra*, where the evidence seems to be clear, this ganglion develops from the acron (Hey-mons, 1901), in which case the sutures cannot possibly be true intersegmental lines. A re-examination of the development of a chilopod head is very desirable, as it seems to offer the best chance for deciding these questions.

Evolution in the Myriapoda has been attended by the successive merging of three gnathal segments with the procephalon. In *Pauropus* we seem to have a very specialized descendant of a primitive stock of myriapods with only two gnathal segments, the 'lower lip' protruding from between the maxillae. We may speak of these as DIGNATHA. (The name has already been used by Lankester (1904) though with a different implication. It is noteworthy that Imms (1936) assigned only two gnathal segments to the hypothetical 'Proto-myriapoda'.) In the Chilopoda, Symphyla, and Insecta cephalization has proceded a segment further, and they may be spoken of as TRIGNATHA. In the embryology of Symphyla we have evidence of the relatively recent incorporation of the third gnathal segment (second maxillary) into the head, for that segment appears first as part of the abdomen, being separated from the head by a deep intersegmental groove; and even in insects the abdominal character of the mesoderm of this segment has long been recognized (Wies-mann, 1926). In the Chilopoda the maxillae, especially the second maxillae, still retain, to a surprising degree, the character of ambulatory appendages, and it is the appendages of the first abdominal segment (poison jaws) which have undergone the greatest specialization. The lower lip of the pre-oral cavity in Chilopoda is formed by the first maxillae, fused, as Heymons (1901) has shown, with a diminutive maxillary sternite, the fused bases of the second maxillae (sterno-costal plate) lying well behind the pre-oral cavity. In Sym-phyla and Insecta, on the other hand, the first maxillae operate within an enlarged pre-oral cavity, a new 'lower lip' being formed by the fusion of the second maxillae (labium). This is the highest grade of elaboration undergone by the gnathocephalon in the Myriapoda–Insecta; following Snodgrass (1938), we may speak of its members as LABIATA.

The position of the Diplopoda is still uncertain. The lower lip is here formed by the gnathochilarium. It has at times been claimed (e.g. Carpenter, 1905) that two pairs of maxillae can be distinguished in the adult organ. But

embryology alone can provide the clue to its composition; yet there is a complete lack of unanimity amongst embryologists as to its manner of formation. The contradictory accounts of its development have already been set out (Emb. Dev., section 6, v); it will suffice here to repeat that while the most recent work, that of Pflugfelder, contends that it develops by a fusion of first and second maxillae, most writers (Metchnikoff, Heymons, Silvestri, Lignau) state that only the first maxillae enter into its formation. Heymons does not even refer to an incorporation of the post-maxillary segment into the head, but Silvestri and Lignau agree that the sternum of that segment becomes the 'hypostome' of the gnathochilarium. Snodgrass (1938) includes the Diplopoda in the Labiata, and in my earlier paper on the development of Symphyla (Tiegs, 1940) I expressed a similar view. Experience of the development of *Pauropus*, the germ-band of which is almost identical with that figured by Silvestri (1933) for the diplopod *Archispirostreptus*, leads me to suspect that this view is wrong, and that the Diplopoda are in reality Dignatha; for the possible incorporation of a post-maxillary sternite, without appendages, into the head, is not comparable with the cephalization of a whole segment as in Chilopoda, much less still with the formation of a true labium. (In the only Palaeozoic diplopod whose mouth appendages have been described (the Permian *Acantherpestes*) there is apparently no gnathochilarium, but a pair of mandibles and a single pair of maxillae (Fritsch, 1901).) But if Pflugfelder's observations should eventually prove correct, then the case for the inclusion of Diplopoda among the Labiata will have been proved. A really critical investigation of the development of Diplopoda is much needed.

The primitive organization of the head of *Pauropus* is expressed also in its musculature. Snodgrass (1928), in discussing the problem of the insect tentorium, has shown how the sternal adductor muscles must, in the first instance, have arisen from the hypopharyngeal apophyses, but that in Chilopoda the muscles of the mandibles have secondarily taken origin from a ligamentous bridge between the apophyses, while 'in Diplopoda, Crustacea, and Apterygota groups of the adductor fibres from the mandibles have lost their sternal connexions, and have united with each other by a median ligament to form a dumb-bell muscle between the two jaws'. In Symphyla I have found (1940) that the primitive condition postulated by Snodgrass has survived in the mandibular musculature; and this proves to be the case also in *Pauropus* (see Emb. Dev., section 15). On the other hand, in the great development of the oesophageal dilator muscles that take origin from the apophyses, we have one of those remarkable specializations that are so frequent in *Pauropus*.

In the primitively constructed head of *Pauropus* we seem to have the clue to some hitherto-unsolved problems in the morphology of the mouth-parts of other myriapods and insects. The maxillae, as we have seen (Emb. Dev., section 6, ii, B), are more generalized appendages than was formerly thought; for a lacinia, stipes, and cardo are distinguishable, even though a palp and galea are lacking. The cardo in this case is not provided with muscles, and

may therefore be looked upon, not as a part of the appendage itself, but as a pleural sclerite; and it is not unlikely that this homology may be extended to cardines in general. Snodgrass (1928), it may be recalled, has already pointed to the difficulty of seeing in the cardo a distinct basal segment of the appendage. It is probable, also, that in the maxillae with their associated intermaxillary plate, we have the forerunner of the complex gnathochilarium of diplopods; for the lateral parts of the gnathochilarium show an unmistakable resemblance to maxillae, in which cardo and stipes are distinguishable, while the central part may well be derived from the intermaxillary plate, the hypostome alone being of post-maxillary origin. In the gnathochilarium of *Polyxenus* these components are especially evident. In this primitive diplopod, according to Carpenter (1905), superlinguae (maxillulae) are also present, but these seem to be unknown in other diplopods.

It would also appear that with the formation of a new 'lower lip' in the Labiata, the primitive 'lower lip' of Dignatha, as exemplified in *Pauropus*, has survived as the hypopharyngeal apparatus; superlinguae are common to both, being derived in both cases from the mandibular epidermis, and the median lobe (hypopharynx proper, lingua) is formed in Labiata mainly from the maxillary sternite, though there is evidence that the mandibular and even labial sternite may contribute to its formation.

(d) *The Abdomen.* The chief problem in the abdomen relates to the nature of the segments: are they simple segments or diplosegments? Kenyon long ago observed that while in *Eurypauropus* 'the diplopod condition is indubitable', on the other hand, in *Pauropus* alternate legs seem 'to come between the dorsal plates, thus much less clearly bearing evidence of a diplopodial segmentation'. Attems (1926) nevertheless writes 'there is recognisable a developmental tendency for two segments to be united into double segments by a common tergite', and this view may fairly be said to express current opinion. Verhoeff (1934) makes the extraordinary assertion that the segments of *Pauropus* are quadruplosegments, produced by a fusion of two diplosegments, which have each been reduced beyond the stage of reduction attained by Symphyla; but I have shown in a previous paper (Tiegs, 1940) that the embryology of Symphyla does not support the view that the abdominal segments of these animals are reduced diplosegments, and there is certainly nothing in the embryology of *Pauropus* from which Verhoeff's statement can gain any support.

In *Brachypauropus* each leg-bearing segment, except the first, is said to have one tergal scute, and a diplopod condition is therefore excluded in this genus. But in the remaining genera of Pauropoda there is only one such tergal shield for every two leg-bearing segments. If animals are examined that have died in a contracted condition, the impression is undoubtedly given that the tergal shields are diplotergites that cover two separate segments; but if the animals have died in an extended condition, then the tergal shields seem to be the products of alternate segments only (Text-fig. 24 A). Embryology, which alone can decide the question, confirms this latter interpretation

(see above, Emb. Dev., section 6, ii, A; Post-emb. Dev., section 2). The commonly accepted opinion that we have in the abdomen of *Pauropus* an incipient diplopody proves therefore to be an error; the condition of the segments may be compared rather with that of some chilopods (*Lithobius* and especially *Scutigera*) in which there is a tendency for reduction in the tergal region of alternate segments. In the oldest-known myriapod, the Silurian and Devonian *Archidesmus* (Peach, 1882, 1889), a similar reduction in the tergites of alternate segments is found. In the Diplopoda, on the other hand, the segments are welded together in couples, which have a common tergite. This remarkable condition may have been brought about either by the duplication of parts within single segments, or by the coupling of segments; the presence of two separate sternites in the diplosegments of the extinct and primitive Palaeozoic Macrosterna (Fritsch, 1901) is suggestive of an incomplete fusion of simple segments.

In one important respect, however, the Pauropoda seem to show affinity with the Diplopoda. In both groups the post-maxillary segment appears to be a legless collum segment. In Pauropoda the evidence is very clear; here the collum segment is a complete ring, and even in the embryo is devoid of any rudiments of appendages (the so-called vestigial legs of the collum segment of *Pauropus* are not developed from appendage rudiments in the embryo—see Emb. Dev., sections 6, ii, A; 14, v). In Diplopoda, also, the post-maxillary segment seems to be devoid of any rudiments of appendages in the embryo (Heymons, Silvestri), Pflugfelder's statement to the contrary standing in need of confirmation; but the collum segment, which develops out of the post-maxillary segment of the embryo, is not in diplopods a complete ring, for its sternite seems to become incorporated into the head as the hypostome. In this respect the collum segment of Diplopoda shows an advance in specialization over that of *Pauropus*. Should the legless post-maxillary segment prove to be a general feature of all Diplopoda, it will provide most weighty evidence of affinity of these animals with Pauropoda; for in no other myriapod is this peculiar condition found (the so-called collum segment of some Symphyla is a post-labial segment). In the primitive diplopod *Polyxenus*, according to Reinecke (1910), a collum segment is not present; but the interpretation of adult segments in diplopods is notoriously uncertain, and needs the support of embryological evidence. .

The legs, on the other hand, except for the smaller trochanter and the jointed tarsus, resemble those of Symphyla rather than of Diplopoda; for the pre-femur of Diplopoda is not present, nor do we find the close approximation of opposite coxae that is so characteristic of these myriapods (Text-fig. 24 B). But with Diplopoda and Symphyla the legs of Pauropoda share one primitive feature: opposite legs move in unison, whereas in chilopods and insects their action is alternating.

Exsertile vesicles (coxal sacs) have not hitherto been described for Pauropoda. The small papillae on the collum segment, commonly regarded as reduced legs, are, however, probably organs of this type (cf. Emb. Dev.,

section 14, v); and, like the exsertile vesicles of Symphyla, they develop from the remains of the 'ventral organs'. In Diplopoda true exsertile vesicles are met with; from Scudder's (1882) drawing it is evident that they were well formed in the huge Carboniferous *Euphoberia*, and amongst surviving groups they are prevalent in the orders Nematophora and Cholobognatha. They have not been found in any chilopod, but occur throughout the Symphyla, and, amongst primitive insects, in Diplura as well as in *Machilis*. The supposed abdominal appendages of Protura have, at their ends, a form of exsertile vesicle, and such a vesicle is also present on the ventral tube of Collembola. Whether the vesicles of Protura and Collembola, situated, as they are, at the ends of what seem to be appendages, are comparable with exsertile vesicles that arise from the abdominal wall, is uncertain; but apart from these doubtful cases, the widespread occurrence of exsertile vesicles in other myriapods and primitive insects points to the essential unity of these groups.

The function of these organs is unknown. They have been variously regarded as adhesive, water-absorbing, or even excretory; current opinion favours the view that they are respiratory, though there is no real experimental evidence for this. It is stated that in *Machilis* they are extruded in a warm damp atmosphere (Haase, 1889), but whether to absorb moisture or oxygen is uncertain. Nutman (1941) has shown that in Collembola the vesicle at the end of the ventral tube has a water-absorbing function. The exsertile vesicles of Symphyla seem to have a similar function, as the following observations on *Hanseniella agilis* show. A batch of sixteen animals were placed overnight in a petri dish on soil that had been moistened with water containing a little dissolved 'light green' dye. The following morning the animals were anaesthetized and examined with a binocular microscope. In eight animals the entire series of vesicles was coloured bright green; in one animal only a few were coloured. The coloration was quite selective for the exsertile vesicles, except for an occasional discoloration of the chitin of the distal leg-joint. It is therefore evident that the animals had been applying the opened vesicles to the moistened soil. Many of the animals had also succeeded in taking moisture into the alimentary canal. In four, both alimentary canal and exsertile vesicles were coloured; in five, only the latter; three had used only the alimentary canal, while in the remaining four there was no evidence of any water-intake at all. In *Campodea fragilis* I have never obtained any discoloration of the vesicles, though the alimentary canal in all cases soon became green. In *Pauropus*, also, the 'exsertile vesicle' of the collum segment was never found discoloured; in this animal there is evidence for direct absorption of water through the general chitin, for the interior of the distal leg-segments is commonly discoloured. Judging by the work of Oudemans (1888), the exsertile vesicles of *Machilis*, also, are not used for the absorption of water.

(e) *The Glands.* For purposes of phylogenetic discussion, interest centres chiefly in those salivary glands that are of mesodermal origin. These are

generally regarded as derivatives of segmental organs, after the manner of the great salivary glands of *Peripatus*. Of these glands there are two in *Pauropus*, the pre-mandibular and the maxillary glands.

The presence of a functional pre-mandibular gland in the remote ancestors of insects and chilopods had been suspected by Wheeler (1893) and Heymons (1901), and its actual occurrence in *Pauropus* does not, therefore, come as a surprise. Its presence on the third cephalic segment suggests, indeed, a direct affinity with the salivary gland of *Peripatus*. In *Pauropus* the adult gland shows no vestige of its original tubular character, and the absence of an end-sac is particularly noteworthy. The survival of this gland in *Pauropus* is probably correlated with the inturning of the lateral margin of the clypeus (cf. section 6, ii, B), by which means the orifice of the gland has become enclosed within the enlarged pre-oral cavity. In the Symphyla pre-mandibular glands, complete with end-sacs, are present up to the time that the larva leaves the egg, after which they degenerate, the end-sacs alone surviving as the great tubular nephrocytic organs (Tiegs, 1940). It will be recalled, in this connexion, that the end-sacs of the nephridia of *Peripatus* have a nephrocytic function (Bruntz, 1904a). In chilopods the 'lymphoid tissue' of the pre-mandibular segment, and, in insect embryos, the sub-oesophageal bodies, nephrocytic in appearance, and also derived from the pre-mandibular mesoderm, seem to be the vestiges of this organ; it was indeed these tissues which first suggested to Wheeler and Heymons the former existence of a pre-mandibular segmental organ. In the weevil *Calandra* the sub-oesophageal body survives even in the adult insect, and here its nephrocytic action in response to injected ammonia carmine is readily displayed (see Emb. Dev., section 10, ii). In Collembola the 'head-kidney' described by Hoffman (1908) seems to be a related body.

The presence, in *Pauropus*, of a mesodermal maxillary gland, furnished with a nephrocytic end-sac, is also not unexpected, for such a gland is present in Symphyla. In the diplopod *Julus*, also, the tubular maxillary gland is of mesodermal origin (Heathcote, 1888); in *Glomeris* the nephrocytic character of the end-sac of the maxillary gland has been shown by Bruntz. Among chilopods, *Scolopendra* seems to be lacking in mesodermal glands (Heymons), but in *Scutigera* and *Lithobius* there is present a maxillary gland whose structure recalls a segmental organ (Fahlander, 1938), but its development still needs elucidation. Most of the other cephalic glands of chilopods are epidermal ingrowths (Heymons, 1901), in which respect they resemble the cephalic glands of pterygote insects.

Amongst Collembola and Thysanura we find the remarkable tubular glands whose development from mesoderm has in one case, *Isotoma*, been proved (Philiptschenko, 1912). These glands have end-sacs, which display a nephrocytic action towards injected ammonia carmine (Bruntz, 1904b; Philiptschenko, 1908). But it is noteworthy that they are not maxillary but labial glands, and as such are not present in *Pauropus*. According to Fahlander (1938) labial glands occur also in certain chilopods and in the symphylid

Scutigerella immaculata; but in *Hanseniella agilis*, which I have examined carefully, they are not present.

As the labial glands are mesodermal and are furnished with typical end-sacs, they are regarded as surviving archaic segmental organs. That they should be present in the labial rather than maxillary segment is surprising, for the labial segment is looked upon, with good reason, as a recent addition to the head, and can therefore hardly be expected to have retained its segmental organ. Have we here, perhaps, an instance of Lankester's 'seventh law' of metamerism (translation of heterosis)?

(*f*) *The Alimentary Canal.* In the simplicity of its structure, the alimentary canal of *Pauropus* resembles that of other myriapods, of primitive insects and of *Peripatus*, and differs most markedly from the specialized gut of most Crustacea, with its cephalic 'stomach' and associated 'liver' and (in Malacostraca) complex fore-gut.

The presence of Malpighian tubes, associated with the hind-gut, is also a myriapod feature; similarly named tubes from a group of Crustacea (Amphipoda) are hardly comparable with them, for they are mid-gut derivatives.

The Malpighian tubes present us with a peculiar problem. In *Peripatus* they are not present, the most effective organ of excretion being the mid-gut epithelium (Manton, 1937). They are found in most myriapods and insects; and even in myriapods there seems no reason to doubt their excretory function (Plateau, 1876). Yet we find a recurring tendency for these organs to degenerate again and even disappear, the mid-gut epithelium or even fat-body assuming the role of excretory organ. In *Pauropus*, for example, it is clear that the mid-gut epithelium is the principal excretory organ, as in *Peripatus*; in *Pauropus huxleyi* Malpighian tubes are said to be absent (Schmidt, 1895); in *P. silvaticus* they are markedly degenerate and do not open into the hind-gut; in *Allopauropus brevisetus*, according to Silvestri (1902), they are present but small, and only in *Eurypauropus* do well-formed tubes occur (Kenyon, 1895). Again, in Symphyla a pair of well-formed tubes is present, and these show at least some evidence of excretory function, for they eliminate indigo-carmine when this is injected into the blood (Tiegs, 1944); yet urate concretions are quite absent in their lumen, but accumulate in great quantity in the fat-body. In the chilopod *Lithobius* the mid-gut epithelium seems to eliminate waste products, even though Malpighian tubes are present (Manton, 1937). In Collembola, where Malpighian tubes are absent, special 'urate cells' are present in the fat-body, and the mid-gut epithelium also seems to exercise an excretory function (Folsom and Welles, 1906). In *Campodea*, where sixteen very diminutive Malpighian tubes are said to be present, urates accumulate in great quantity in the fat-body, as is the case also in *Japyx*, where Malpighian tubes are apparently absent. The meaning of these facts is not clear.

(*g*) *Blood and Respiratory System; Fat-body.* The absence of a heart and of blood-vessels in *Pauropus* must clearly be attributed to degeneration, and

is presumably correlated with dwarfing of the body. The little movement that the blood is capable of is probably imparted to it chiefly by peristalsis of the intestine.

The absence of tracheae is probably also a simplification, cutaneous respiration sufficing in so small a body. Collembola, which rival *Pauropus* in minuteness, also rely upon cutaneous respiration, only one family (Sminthuridae) having tracheae. In the minute Protura the tracheal system is also, when present at all, greatly reduced.

The presence of fat-body is a feature which *Pauropus* shares with all other myriapods and with insects; it is not found in Crustacea. In all insects so far examined, and in chilopods, it develops from cells which separate from the mesodermal somites. Its development in *Pauropus* out of 'yolk-cells' in the embryo is, however, not unexpected, for it has a similar origin in Symphyla (Tiegs, 1940), while Heathcote's rather meagre description for *Julus* points to a similar origin. But the development of secondary larval fat-body out of epidermis (Post-emb. Dev., section 5) seems to be without parallel in myriapods.

The phylogenetic origin of fat-body in myriapods is unknown, there being no comparable tissue in *Peripatus*. Its development out of yolk-cells in primitive myriapods suggests that it may have arisen by the persistence of yolk-bearing vitellophages beyond the egg and pupoid phases into the larva.

(*h*) *Reproductive Organs.* Here interest centres chiefly in the evaluation of the progoneate condition as a criterion of classification. The manner of development of the gonoducts does not support the view that they are, as in *Peripatus*, chilopods, and insects, the remains of segmental organs; and since they arise long before the hinder end of the abdomen has completed its development, it is not unlikely that their position remote from the zone of growth, is a secondary adaptation to anamorphosis. This question has already been discussed.

It remains only to refer briefly to the gonads themselves. The unpaired condition of the gonad-Anlage is surprising, as is also the failure of the coelomic sacs to participate directly in its development. It is impossible to assess the meaning of this beyond suspecting that it is bound up with the general decline of the coelomic sacs in *Pauropus*.

The structure of the ovary, with its parietal[1] germarium and scattered oocytes, each encased in a follicular epithelium, recalls that of other myriapods (*Lithobius*, Tönniges, 1902; *Polydesmus*, Effenberger, 1909; *Hanseniella*, Tiegs, 1945) and of Collembola (Willem, 1900; Imms, 1906), but is wholly unlike that of all true insects.

The location of the testes dorsal to the alimentary canal is quite different from that of diplopods and Symphyla, and resembles rather that of *Peripatus* and chilopods; the resemblance is, however, misleading, for both in *Peripatus* and chilopods the testes develop from the dorso-lateral lobes of the coelomic

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[1] This is not general for Pauropoda; reference has already been made above (Post-emb. Dev., section 6) to a species of *Pauropus* with terminal germarium in the ovary.

sacs, while in *Pauropus* they migrate into this position from below the alimentary canal.

(*i*) *The Nervous System and Sense Organs.* Beyond the presence of only two component ganglia in the sub-oesophageal ganglion (dependent upon the occurrence of only two gnathal segments in the head), the fully formed nerve-cord of *Pauropus* does not display any features worthy of note.

In the embryo, however, the developing ganglia are associated with 'ventral organs'. These peculiar structures were first described and named by Kennel (1886) from the embryo of *Peripatus*, where they were later also observed by Sedgwick (1888). In *Peripatus* the 'ventral organs' are bulging thickenings of the ectoderm below the developing ganglia; they present, in their middle, a gentle depression, from which the nuclei recede, but toward which they are orientated. These features also distinguish the 'ventral organs' of *Pauropus* and Symphyla (Tiegs, 1940). In Symphyla they are not themselves an important source of ganglion-cell formation; they later completely separate from the ganglia, and out of their remains the exsertile vesicles form. In *Pauropus*, on the other hand, the ganglia undoubtedly undergo enlargement at the expense of cells which arise from the 'ventral organs', and in the abdominal segments the remains of the 'ventral organs' are themselves finally incorporated into the ganglia; in the collum segment alone do vestiges of the 'ventral organs' remain to produce an organ comparable with the exsertile vesicles of Symphyla. In the embryo of *Scolopendra*, as shown by Heymons (1901), the ganglia arise from epidermal pits, with orientated cells recalling those of 'ventral organs', but these pits later invaginate below the surface and become part of the ganglia. Yet the developing nerve-cord of *Scolopendra* displays, in common with *Peripatus*, one important feature which has so far not been found in any other myriapod or insect embryo: in *Peripatus* the dwindling 'ventral organs', as they approach one another before fusing in the mid-line, remain connected with the widely separated ganglion-halves by a peculiar string of cells (Kennel, 1886; Sedgwick, 1888); in *Scolopendra* a similar string of cells (Mittelstrang) is present, but in this myriapod the two ganglion-halves become drawn together, and the cells of the 'Mittelstrang' remain to form a median band of neuroglia tissue within the completed ganglion. In Diplopoda, also, according to Pflugfelder (1932), the ganglia arise by invagination of pits of orientated cells; but a detailed account of the development of these ganglia has not yet been given.

The debatable question of the significance of these peculiar structures has been discussed above (Emb. Dev., section 13 (*b*) i). They are not found in insects, nor in any other arthropod hitherto examined. Their prevalence in the myriapods seems therefore to point to a closer affinity of the latter with *Peripatus*, than with any other surviving arthropod.

The brain, in its external form, displays some features unexpected in a myriapod. From the descriptions of Saint Remy (1887), Holmgren (1916), Fahlander (1938), and others, it is known that the three component ganglia

of the brain are, in most myriapods, imperfectly fused paired lobes, the antennary lobes (deutocerebrum) lying beneath the protocerebral lobes, and the tritocerebral lobes, in turn, beneath the deutocerebrum. But in *Pauropus* the deutocerebrum gives no external evidence of its originally paired condition, and is so intimately merged with the protocerebrum, that there is scarcely any external demarcation between the two. The tritocerebral ganglia are small, as in other myriapods, in which respect they differ from those of Crustacea. They remain as separate lobes, and display, moreover, one primitive feature, in that they merge below into the sub-oesophageal ganglion, without the intervention of a free connective. Such a condition is found also in some chilopods (*Scutigera*, *Lithobius*), but in other chilopods and in those diplopods that have been examined the tritocerebral ganglia are drawn up near the brain, thereby exposing the connectives which are free from nerve-cells. In insects, as is well known, a still greater specialization is attained, the tritocerebrum merging so closely into the contour of the brain as to become almost obscured. In one respect, however, the tritocerebrum of *Pauropus* shows a surprising specialization: the upper ends of the paired ganglia fuse above the oesophagus, with the formation of a second commissure and an unpaired connective with the frontal ganglion, there ·being nothing comparable with the 'stomatogastric bridge' of other myriapods.

In the deutocerebrum the presence of separate motor and sensory nerves to the antenna is noteworthy; this condition seems to be general for myriapods.

The presence of what seems to be a vestigial pre-antennary ganglion, or ganglion of the hypothetical pre-antennary segment, is also noteworthy. Such a ganglion was first observed by Heymons (1901) for the embryo of *Scolopendra*, and is known also in Symphyla (Tiegs, 1940). It is not known in insects nor in diplopods, though its discovery in the latter, and perhaps in primitive insects also, would not cause surprise.

The protocerebrum is distinguished, even among myriapods, by the relative simplicity of its structure. As in other blind members of the group, 'visual masses' are not developed. Globuli cells, also, are absent, as in Symphyla, Collembola (*Tomocerus*), and the chilopod *Geophilus*. Yet peduncles are recognizable; but, as in *Julus*, they are related to a 'medial body', and not to a corpus centrale, the latter being much reduced. A 'medial body', it may be observed, is found also in some Chilopoda, and in the Diplura, but is quite unknown in Crustacea. On the whole, the protocerebrum seems to display a simplified diplopod character; but in the absence of adequate data both for *Pauropus* and for other myriapods a more searching comparison cannot be made. In its development out of three separate ganglion masses, the protocerebrum of *Pauropus* resembles that of *Scolopendra*, Symphyla, and insects (the diplopods have not been properly examined on this point).

It is evident, from the foregoing discussion, that the brain of *Pauropus*, despite some singular features, conforms to the myriapod type. In what relation does the latter stand to that of *Peripatus*? According to Holmgren's description the brain of *Peripatus* consists of a central portion containing

the corpora pedunculata, of a pair of lateral ganglia associated with the antennae, and of a hinder part, from which the nerves to the mandibles arise. The presence of corpora pedunculata in the central portion seems to identify this region with the archicerebrum (ganglion of prostomium) of annelids, and with the more highly developed protocerebrum of myriapods and insects, of which it is probably the forerunner. On the view here adopted the lateral ganglion masses from which the nerves to the antennae originate would be the equivalent of the much-reduced pre-antennary ganglia of myriapods, i.e. ganglia of the first segment. It seems difficult to avoid this conclusion; for the first segment of *Peripatus* must have the status of a true segment and not of an acron, since it contains in the embryo a well-developed coelome, and, as all writers agree, a pair of vestigial segmental organs (Kennel, 1886; Sedgwick, 1887; Sheldon, 1888; Evans, 1901). Yet in Kennel's clear description of the developing brain the entire ganglionic mass of the first segment is shown to originate from a single pair of invaginating 'ventral organs'. Evans, indeed, later sought to demarcate an archicerebrum within the mass of developing ganglionic tissue, but the evidence for this is not clear. A renewed investigation on this point is needed; it is perhaps significant that in *Pauropus* the Anlage of the pre-antennary ganglia is at first confluent with that of the protocerebrum, and only later becomes separately defined.

The presence, both in Diplopoda and Chilopoda, of eyes consisting of aggregations of ocelli points to their probable occurrence also in the forerunners of the Pauropoda. But in all the members of this group that have so far been discovered eyes are absent, as they are also in Symphyla, Diplura, and various diplopods that habitually live in the dark. For purposes of phylogenetic discussion the chief problem concerns the compound eye. No theory which presents the Myriapoda-Insecta as a continuous line of evolution of terrestrial arthropods, and excludes the Crustacea, may ignore this remarkable organ, for there can be no denying its almost complete identity in Crustacea and higher Insecta. That the compound eye has evolved from a simple aggregation of ocelli is now generally agreed; for there is much similarity in structure of an ommatidium and an ocellus, and moreover, in the larvae of many holometabolous insects, as well as in adult fleas and Strepsiptera, the eye is found in this condition. It is only by multiplication and aggregation into a compound eye that groups of ocelli could achieve even such moderate resolution as the insect eye is capable of. Korschelt and Heider, who support the theory of a myriapod origin of insects, point out that a compound eye must have appeared in this way at least four times in arthropods, namely, in scorpions, Crustacea, *Scutigera*, and insects, the organ of insects and Crustacea being almost indistinguishable. Hesse (1901), on the other hand, regards the possibility of convergence as too remote to consider. Yet he has himself provided the evidence that the compound eye of higher insects has probably evolved within the class Insecta itself; for in *Lepisma* the compound eye is of the bilaminate type found in *Scutigera*, a vestige of this being recognizable even in the eye of *Periplaneta*. If the remarkable similarity

between the eyes of higher insects and Crustacea be accepted as evidence of affinity, then it must be of the most immediate affinity; but this is hardly compatible with the many deep-seated differences between the two groups.

Of the sense-organs of *Pauropus*, the most remarkable are the pseudoculi and the strange tactile flagella of the antennae. The latter, as Verhoeff has already observed, seem to be modifications of the peculiar clubbed 'hairs' which abound on the chitin of *Pauropus*, and seem to be quite unique. The pseudoculi are also very specialized organs, apparently unknown in other myriapods. Whether there is any affinity between them and the widely distributed organs of Tömösvary is uncertain.

EVOLUTION OF THE MYRIAPODA AND INSECTA, AND THEIR RELATION TO OTHER ARTHROPODA

Any theory of the evolution of the myriapods, and their derivatives the insects, must embrace the wider problem of their ultimate origin. But on this question the greatest perplexity still prevails, for the fossil evidence has not proved helpful, and both embryology and morphology speak with an uncertain voice.

The Myriapoda may have arisen from the Crustacea, or from the Trilobita, or from some extinct *Peripatus*-like ancestor. But it is also possible that they may have sprung from an extinct type of arthropod that cannot be assigned to any of these groups, as in Tillyard's (1930) 'Protaptera' theory.

In theories of the last-named type, in which the hypothetical ancestor is conceived to embody a combination of characters requisite to the particular case, conviction must depend ultimately on the discovery of such an ancestor as a fossil. Here the actual evidence for the existence of such an ancestor, in the form of the supposed pre-Cambrian *Proadelaidea* (David and Tillyard, 1936), seems much too meagre to justify the important conclusions that have been drawn from it. For the present, therefore, we can turn only to known forms of arthropod.

In the Crustacea we have a sharply delimited group of already markedly specialized and primarily aquatic arthropods, whose most primitive members, the Branchiopoda, seem to show evidence of near-annelid affinity. In the theories of Carpenter (1903), Börner (1909), and Crampton (1919, 1928) the higher Crustacea are conceived as the ancestors of Myriapoda and Insecta, the arguments being variously based on such external characters as structure of mandibles and of head-capsule, and the supposed identity in segment number. It is the already high specialization of the Crustacea which presents the main difficulty for these theories. In no myriapod or insect is there any true biramous appendage of the crustacean type, nor is it ever met in the embryo. The post-cephalic region of Crustacea, already differentiated into thorax and abdomen, with diversified forms of appendages, is in marked contrast to the undifferentiated post-cephalic region of myriapods, with its serially uniform walking-legs. The specialized alimentary canal, with cephalic 'stomach' and 'liver', and, in higher Crustacea, diminutive mid-gut,

is also quite different from the thoroughly simple type of gut that prevails throughout the myriapods and primitive insects, while the pronounced shortening of the heart in the higher Crustacea is never met with in any myriapod or insect, though in the more primitive Crustacea an elongate heart of the myriapod-insect type is found. The remarkable ectodermal and mesodermal teloblasts of crustacean embryos are never encountered in the ontogeny of myriapods or insects, while the marked suppression of coelomic sacs is in contrast to their strong development in most myriapods and primitive insects. There is, moreover, never an indication of a nauplius phase in the development of any myriapod or insect, yet it is of universal occurrence in Crustacea. In thus rejecting the crustacean theory one must, however, fairly face the evidence from the compound eye; this question has already been discussed, the resemblance being attributed to convergence. The retention of segmental organs in the head of Crustacea and some myriapods is also difficult to assess; it is noteworthy that in Crustacea they are excretory organs and in myriapods salivary glands. The problem of the mandibles, which Börner in particular has stressed, does not seem a serious one, for similar feeding habits may well be expected to engender similar feeding organs.

The Trilobita are the most primitive and generalized of all known Arthropoda, unless *Peripatus* be admitted to the phylum. Formerly regarded as Arachnida, they are now, following the discovery of their biramous appendages, usually ranked with the Crustacea. Of their internal anatomy nothing is known beyond the fact that they had a straight intestine with cephalic stomach and probably liver (Raymond, 1920), features which they share with Arachnida and Crustacea, but not with myriapods and insects. The appendages were, except for the simple antennules, serially similar biramous structures, there being four such appendages on the cephalon. The terms 'antennae', 'mandibles', &c., that are sometimes applied to the cephalic appendages cannot therefore be used with strict propriety. In the most recent work of Walcott (1918, 1921) the trilobite appendage is described as consisting of a coxopodite (always with gnathobase), an endopodite (walking-leg), an exopodite (which may be a broad setiferous swimming (?) blade or a spiral filament fringed with delicate branchiae), and a blade-like epipodite.[1] Since chelicerae are absent, the Trilobita cannot be Arachnida. But there are also strong grounds for excluding them from the Crustacea: (*a*) from their appearance early in the Cambrian to their extinction in the Permian, they preserve a remarkably stereotyped body-form, differing from that of any known crustacean; (*b*) there is no diversity of appendages, which is so characteristic of Crustacea; (*c*) the larva in all known cases is a 'protaspis' and not a crustacean nauplius. Yet in the wonderful mid-Cambrian marine fauna discovered by Walcott the trilobite affinities of the Crustacea are clearly brought out. *Burgessia*, *Waptia*, and *Yohoia* were Branchiopoda, but,

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[1] Störmer (1933), who has since re-examined Walcott's material, agrees with Raymond that there is no real evidence of an epipodite.

as Raymond (1920)[1] has shown, with strong evidence of trilobite affinity in their appendages, and this is especially clear in the later restorations given by Walcott (1931); particularly noteworthy are the mouth-appendages, which were walking-legs without differentiation into mandibles and maxillae. In the remarkable *Cheloniellon* described by Broili (1933) we have evidence for the survival of such primitive Crustacea even into the lower Devonian. Yet this can hardly be construed as valid evidence for the derivation of these primitive Crustacea from trilobites. Of the long pre-Cambrian ancestry of the trilobites from annelids nothing whatever is known; but we may presume that it was from some pro-Trilobite Arthropod that the primitive Crustacea, with their more worm-like body, arose. The affinity between Trilobita and Arachnida seems to be even closer than with Crustacea. Whether the 'trilobite larva' of *Limulus*, with its chelate appendages and unsegmented abdomen, but otherwise very trilobite-like body, implies such affinity may perhaps be doubted. On the other hand, there seems to be good evidence for a 'protaspis' stage in the embryo of *Limulus* (Iwanoff, 1933). The recent work of Raasch (1939) on the Aglaspida has brought out the merestome nature of these Cambrian arthropods, for in one genus chelicerae have been revealed; yet, except for their long articulated telson spine, they show a most remarkable resemblance to trilobites, and especially is this the case for the mid-Cambrian *Beckwithia* described by Resser (1931). This would seem to imply the former existence of even more primitive types derived either from the trilobites or from the base of the trilobite stem: Their distinguishing features would be a general resemblance to trilobites, the presence of trilobite appendages (including simple antennules), and the occurrence of an articulated telson spine. It is quite possible that the remarkable mid-Cambrian genera *Molaria*, *Habelia*, and *Emeraldella* described by Walcott (1912), but referred by him to the merestomes, fulfil these conditions.

From the presence of chelicerae and uniramous appendages in Aglaspida, Raasch has argued against any close affinity between them and trilobites. Exopodites are, however, notoriously difficult to detect except in the most perfect material; in any case, the appendages of the mesosoma of *Limulus* are biramous. Moreover, Störmer (1933), who has re-examined the remarkable trilobite material of Beecher, Raymond, and Walcott, declares that in *Limulus* 'the exopodite is much more like that of the trilobite than is that of any Crustacean'.

Such being the affinities of the Trilobita, is there any reason to suppose, as Handlirsch (1925) and Raymond (1920) do, that the Myriapoda may have arisen from them? The already stereotyped body-form of the Trilobita is in marked contrast to its simplicity in the generalized myriapods, and throughout the whole range of known trilobites there is not a single form that shows

In a more recent paper Raymond (*Bull. Mus. Comp. Zool. Harvard*, 1935, **76**, no. 7) considers it necessary 'to remove the Mid-Cambrian forms from the sub-class Branchiopoda, although still considering them as belonging to the stock from which the modern groups were derived'.

even a passing resemblance to a known myriapod. This may perhaps be attributed to the adoption of a terrestrial habitat by the latter; but terrestrial adaptation in other groups of arthropods has not so completely obscured all trace of affinity with related aquatic groups (e.g. scorpions and their aquatic Silurian ancestors), and even the most ancient myriapods, the Silurian and Devonian *Archidesmus* (Peach, 1882, 1889), give no sign of it. It must however be acknowledged that the nature and diversity of the terrestrial fauna of the Silurian and Ordovician are almost completely unknown, and that some fortunate discovery, such as the Rynie chert of a later period, may yet reveal an unexpected terrestrial myriapod fauna with trilobite affinities. Yet, on the whole, the evidence suggests that this will not be the case: neither in the adult nor embryonic condition of any myriapod do we meet with appendages of the trilobite type, the supposed biramous character of the head-appendages of chilopods (Tothill, 1916) being a misconception. The simple alimentary canal of myriapods is also in contrast to that of trilobites, with its cephalic 'stomach' and digestive glands of the crustacean type; nor do we ever encounter in myriapods, as we do in *Limulus*, an embryonic phase comparable to the 'protaspis' of trilobites. The embryonic development of trilobites can never be known; but if that of *Limulus* may serve as a guide, it would seem that nerve-ganglia developed without the formation of 'ventral organs', which are so characteristic of primitive myriapods.

The possibility of seeing in some ancient *Peripatus*-like form the actual ancestor of myriapods and insects is no new idea. It is stated, for example, by Sedgwick (1909) in the following words, which seem to express most clearly the real affinities of these terrestrial arthropods: 'The classes Insecta, Onychophora and Myriapoda are the survival of a once great and continuous group of land Arthropods, a large number of which have become extinct, leaving two groups, Insecta and Onychophora, each fairly compact and showing but little variation of organization, and one, the Myriapoda, loose and heterogeneous, and with considerable gaps between the orders.'

Not the least surprising of the many remarkable features of *Peripatus* is the fact that it is terrestrial, even though it stands nearer to the annelids than do any of the true Arthropoda. But the mid-Cambrian *Peripatus*-like *Aysheaia* (Walcott, 1911b, 1931) is found in association with the remains of marine animals, and was therefore itself of marine or at least littoral habitat. But even the recent *Peripatus* gives ample evidence of primitive adaptation to its terrestrial environment: one might point to its low capacity to resist desiccation; to its retention of ineffective 'nephridia', whose use as excretory organs would entail a drain on its water economy (Manton, 1937); to the crude device for achieving internal fertilization, consistent with a terrestrial habitat (Manton, 1938); and finally, to the widespread prevalence of viviparity as a means of protecting the eggs not yet fully adapted to the land. Has this migration to the land been without further issue, a kind of evolutionary cul-de-sac? Or has it set in train the evolution of the great terrestrial groups of myriapods and insects? Should the latter be

the case, then it will have been one of the most momentous events in the whole Palaeozoic age.

In the general form of the body and its appendages, *Peripatus* is devoid of those specializations which distinguish the Trilobita and Crustacea. Except for the presence of a rudimentary head, composed of the three most anterior segments, there is no demarcation of the body into regions. The alimentary canal, quite unlike that of Crustacea, is simple and closely resembles that of myriapods, and its mid-gut epithelium has, as in some myriapods, an excretory function. The heart also is similar to that of myriapods, and quite unlike that of higher Crustacea. In the embryo a succession of strongly developed coelomic vesicles develops, vestiges of which persist in the segmental organs; in myriapods and primitive insects, also, the coelomic vesicles are strongly developed, and there is a recurring tendency for authors to compare them with those of *Peripatus* and not of Crustacea. Segmental excretory organs, it is true, do not develop in myriapods and primitive insects, but there is often a marked development of coelomoducts in the embryo, and these rudiments are not met in Crustacea. The pre-mandibular salivary gland of *Pauropus* and Symphyla is a derivative of such a segmental organ, and it is probably no mere coincidence that the salivary gland of *Peripatus* is the segmental organ of the same (third) segment. The segmental organs of the penultimate segment of *Peripatus* become the exit ducts for the gonads; this holds also for the opisthogoneate myriapods, and there is reason to believe that, for myriapods, this is the more primitive condition, since in the opisthogoneate forms alone do the gonoducts develop out of embryonic coelomoducts. Finally, the nerve-ganglia of *Peripatus* develop in association with 'ventral organs', and these remarkable structures are also present in myriapods but in no other arthropod (the supposed 'ventral organs' of Pycnogonida are, according to Dogiel (1913), not comparable with those of *Peripatus*).

These facts, unless they are quite misleading, seem to point to the Onychophora as the not very distant progenitors of Myriapoda. The evolution of the latter must have taken place upon a background of increasing adaptation to the terrestrial environment, and this must have involved not only the freely living animals, but also their eggs.

The evolution of the 'closed box' type of terrestrial egg (cleidoic egg of Needham, 1931) presents special problems, to evade which the device of viviparity may, as in *Peripatus*, have been temporarily resorted to. In its most highly developed form (in birds) the cleidoic egg contains its own water requirements, and relies on the environment only for its supply of oxygen. In most myriapods and primitive insects this degree of independence has not been attained; the yolk is inadequately supplied with water, which must be supplemented by absorption from without, and oviposition is therefore restricted to damp localities. Although remarkable adaptations to dry conditions may at times have been evolved (e.g. *Sminthurus*), there seem to be few exceptions to the rule that the eggs depend for their development on an

external supply of water. The developing embryo therefore soon outgrows the available space within the chorion, which is stretched and usually ruptured. This is probably the explanation of the widespread occurrence of pupoid phases in myriapods. In many higher insects, also, swelling of the egg occurs as development proceeds (see review by Buxton, 1932), and special water-absorbing organs, as in *Melanoplus* (Slifer, 1938), may be present. Yet in its most perfected form, the land-adapted insect egg is often found, encased in a thick, firm, and indistensible chorion, exposed to the most adverse climatic conditions. The nature of these adaptations does not seem to have been adequately investigated.

Upon leaving the egg, water conservation remains one of the chief problems of the small terrestrial animal. The myriapods have largely evaded this problem by restricting their habitat to moist localities. Most small myriapods and primitive insects desiccate rapidly in dry air, and only occasionally do we meet well-adapted land forms, such as *Scutigera* and *Lepisma*. Early in the evolution of the myriapods, we may suspect, an increasing impermeability of the chitin to water developed; but physiological studies on water-conservation in myriapods have lagged far behind the illuminating work on insects. As the external chitin of the soft-bodied *Peripatus*-like animal acquired greater rigidity, this must have led to an accentuation of the body-segments, and the jointing of appendages. To compensate for the loss of flexibility there was 'developed a mechanism of telescopic movement between successive body segments, by the simple device of retaining non-sclerotized areas in the posterior parts of the primitive segments, thus establishing a secondary segmentation in which the longitudinal muscles become intersegmental instead of intrasegmental in action' (Snodgrass, 1938). The hardened exoskeleton must, in its turn, have produced the conditions for the development of rapidly moving striated muscle, and for the eventual evolution of those mechanical contrivances to which the arthropods owe their immeasurable superiority over the annelids.

Except for the simplicity of its head, such an animal would differ but little, in external appearance, from a generalized myriapod. The myriapod head-capsule may be presumed to have arisen by the incorporation of two, and later a third abdominal segment, into the primitive head, the latter having become stabilized as the three-segmented procephalon of myriapod-insect embryos. (This would necessarily entail the conversion of the mandibular appendage of the *Peripatus*-like ancestor into an antenna. It is not necessary to discuss the possible difficulty that might arise from the transformation of the mandibles, i.e. enlarged claws, of a recent *Peripatus* into antennae, since in the only Palaeozoic onychophoran of which we have any information (*Aysheaia*, see Hutchinson, 1930), the 'mandibular' appendage is an undifferentiated ambulatory leg, no true jaws being present.) *Pauropus* is to be looked upon as a dwarfed and simplified, but also in some respects very specialized, survivor of a primitive stock of myriapods, in which only two such segments have been added to the procephalon (DIGNATHA); and it is

probable that, when their development is better known, the diplopods also will be found to be members of this group, though specialization in another direction, with the formation of diplosegments, has here taken place. The presence of a limbless collum segment in Diplopoda and Pauropoda even suggests a community of origin for these two groups of Dignatha.

With the incorporation of the second maxillary segment into the head there arose the Trignatha. These comprise the Chilopoda, Symphyla, and Insecta. Within the Trignatha, by further specialization, arose the Labiata, in which the second maxillae fused to form a new lower lip to the pre-oral cavity, within which the first maxillae operated, the lower lip of the Dignatha apparently remaining as 'hypopharynx'. They comprise the Symphyla and Insecta. Their great antiquity is attested by the recent discovery of Collembola in the middle Devonian (Tillyard, 1928; Scourfield, 1940).

This classification, based on the structure of the head-capsule, does not necessarily imply any close affinity between chilopods and insects. The chilopods remain, indeed, a puzzling group. In their early development they display features reminiscent of *Peripatus*. The mesodermal somites are also extremely generalized, in one respect even more so than in *Peripatus*, for both dorsal and ventral blood-vessels arise by apposition of the somitic walls, as in annelids. In the development of the nerve-cord, as described by Heymons, there is a marked resemblance to *Peripatus*, and this applies also to the development of the gonads. On the other hand, the conversion of the first pair of abdominal legs into poison jaws is a specialization which we find in no other myriapod. Their fossil record is not helpful: whereas diplopod remains are abundant in Carboniferous and later formations, there are only a few disputed chilopod remains earlier than the Tertiary, Scudder (1890) having attributed to the Chilopoda some rather nondescript remains from the Carboniferous of North America.

Of all the Myriapoda the Symphyla, being alone Labiata, must stand nearest the insects. In this connexion the Collembola present a special problem; for while, among insects, *Campodea* and its allies seem to be the most nearly related to the Symphyla, it is actually in the Collembola that myriapod features to the greatest extent prevail. Their early developmental processes are quite non-insectan in character, and are of the Diplopoda-Symphyla type. The reproductive organs are, except for the terminal genital opening, also quite unlike those of any insect, and resemble those of Diplopoda and Symphyla. The visual organs are aggregates of ocelli; such ocelli are characteristic of myriapods, and occur only rarely in adult insects, and then probably in consequence of degeneration. Organs of Tömösvary, prevalent in the Myriapoda, are found also in Collembola, but not in true insects. They differ, moreover, from all insects, by the presence of never more than nine post-cephalic segments in the embryo. The presence of three pairs of walking-legs is, on the other hand, an insectan character; but as evidence for their inclusion in the Hexapoda this is offset by the presence of two more abdominal appendages (in addition to the 'ventral tube'), which also play

an important role in their locomotion. Minor insectan characters, which are, however, difficult to evaluate, are the unsegmented mandibles, and the development of the ganglion cells of the embryo from 'neuroblasts' (Claypole, 1898; Philiptschenko, 1912), which are general throughout insects, but quite unknown in myriapods. As Imms (1936) has convincingly shown, there can be little ground for including Collembola among the insects; the available evidence is consistent with the hypothesis that they constitute an independent group within the Labiata, in which anamorphosis has been suppressed, and in which consequently a progoneate condition has not supervened, and that specialization has taken the form of elaboration of the springing apparatus.

It is not unlikely that when the development of the Protura becomes known, they will be found to form a fourth group within the Labiata.

From time to time remains of ancient and extinct myriapods have been discovered which cannot be accommodated within any of the existing groups: *Archidesmus* (Silurian, Devonian), *Kampecaris* (Devonian), Peach, 1882, 1889; *Palaeocampa* (Carboniferous), Meek and Worthen, 1865, Scudder, 1884; *Latzelia* (Carboniferous), Scudder, 1890. In these scanty remains we have the only real evidence of a former line of myriapod descent, from which the present rather isolated groups may be supposed separately to have arisen. The state of preservation does not, however, suffice to determine the all-important character of the head-capsule. In particular, there is no known example of the hypothetical MONOGNATHA, which may be supposed to have bridged the gap between the Onychophora and the Dignatha.

The scheme of affinities which the foregoing discussion suggests may be put thus:
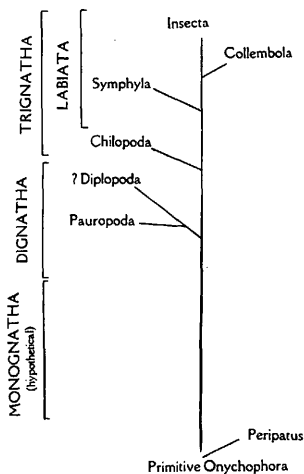
The Myriapoda, we may suppose, were, like the Onychophora, primarily opisthogoneate, for in the opisthogoneate groups alone do the gonoducts develop out of coelomoducts in the embryo. From the prevalence of ana-morphosis in recent myriapods we may suspect that some form of ana-morphosis, the consequence of deficient yolk in the egg, was prevalent also in primitive myriapods; but whenever conditions favoured the development of the reproductive ducts before the completion of anamorphosis, it must have led to the formation of a new gonopore, remote from the zone of growth. Thus arose the progoneate groups. (Even in insects secondary genital openings, remote from the terminal genital opening, may at times appear (cf. Imms, 1936).)

We may further suppose that, in adaptation to a terrestrial existence, the segmental organs were soon discarded, for already in *Peripatus* they have been functionally superseded as excretory organs by the mid-gut epithelium, and only in the head were some retained as salivary glands. It is probable that the mid-gut epithelium, as well as fat-body, which seems to have arisen by retention of embryonic vitellophages, assumed the role of excretory organs. But from the presence of Malpighian tubes throughout the Myriapoda it would seem that these organs soon arose to meet the special needs of an excretion consistent with a stringent water economy. Yet it is surprising to see how often these organs have again been discarded, as effective excretory organs (*Pauropus*, Collembola, Symphyla, *Japyx*, *Campodea*), in favour of excretion by the fat-body or mid-gut wall.

Terrestrial adaptation of the respiratory organs involved the development of the tracheal system. Tracheae are present in such diverse forms in different myriapods and insects that a polyphyletic origin is commonly ascribed to them; yet it is difficult to concede that an effective tracheal system, like that of most chilopods, should be completely discarded in favour of a wholly new system, as in *Scutigera*. It seems more likely that there was evolved a general tendency to develop tracheae, and that, in consequence of mutation, the development of these tracheae became localized in different areas of epidermis. The evolution of tracheae was of the greatest importance, not only in pro-moting enlargement of the body, but in resolving the dilemma between the need for a cutaneous respiration and the inevitable water-loss through a thin chitin that it entailed; for in the better land-adapted types the investing chitin becomes increasingly impermeable to water, while evaporation through the tracheae is subject to control by temporary closure of the spiracles. It is noteworthy that among Collembola *Sminthurus*, which alone possesses tracheae, is alone resistant to desiccation.

The greater freedom of movement that had its origin in the development of mechanical devices in the hardening exoskeleton must have profoundly affected, and in turn been conditioned by, the elaboration of the nervous system and sense-organs. For swiftly moving animals the tactile and olfactory senses must become subordinated to the visual sense; and accordingly we find, in passing from the myriapods to the insects, a great relative increase

in the visual centres of the brain, and a retrogression in the olfactory centres (cf. Hanström, 1928). Amongst myriapods the eyes have remained mere aggregates of ocelli, and only in the swiftly moving *Scutigera* have large compound eyes developed. In insects the conversion of these aggregates of ocelli into compound eyes, with their enhanced resolving power, is almost certainly correlated with their greater freedom and speed of movement.

In thus deriving the Myriapoda directly from some ancient terrestrial *Peripatus*-like ancestor, and excluding from the line of descent the great Trilobite-Crustacean-Arachnid branch of the phylum, it is possible, though not inevitable, that we are committed to a polyphyletic origin of the Arthropoda. Many years ago this very question was discussed by a group of writers, with singular lack of unanimity (see Hutton and others, 1897); yet so distinguished a student of arthropod morphology as Lankester could still declare (1904) that it was 'impossible to conceive of them as having a polyphyletic origin'. That the development of heavy plating in the outer chitin, necessitating the production of segmented appendages and of striated muscle, might arise repeatedly as a specialization in soft-bodied annelids, could be conceded; but there are other basic features of arthropod structure—the haemocoele and ostiate heart, the appendicular jaws, and the cephalization of segments—for which this might less readily be granted; and these features are all displayed, in some measure, by *Peripatus*. A haemocoele is, however, not a unique character restricted to arthropods, for it is encountered also in Mollusca and in some annelids, and the jaws of arthropods are gnathobases, while those of *Peripatus* are enlarged claws, and 'the whole musculature and movement of the jaws ... contrasts absolutely with the Myriapoda, Crustacea and Insecta' (Manton, 1937). It is therefore possible that, if the fossil record ever discloses the ancestry of Crustacea and Trilobita, it may reveal a descent from annelid ancestors quite unlike the Onychophora. The enormous assemblage of animals embraced by Cuvier's ARTICULATA will then comprise a single phylum, distinguished from the other phyla by its own peculiar plan of organization; and within this great phylum there will have arisen, by specialization, and with much convergence, two separate lines of descent, of which one is constituted by the Crustacea, Trilobita, and Arachnida, the other by the Myriapoda and Insecta.

Summary

1. The minute egg is heavily yolked, and is devoid of periplasm or vitelline membrane. Shortly before laying, the germinal vesicle phase gives way to one in which the chromosomes reappear as thirteen 'tetrads' in a central clump of cytoplasm. The latter moves to the periphery, and in this first meiotic prophase the egg is laid. The 'polar bodies' do not separate from the egg. In most eggs they degenerate very rapidly. Male and female pro-nuclei fuse in the centre of the egg to form a resting nucleus.

2. Cleavage is total and unsynchronized, the cleavage-cells becoming arranged as yolk-pyramids around a central blastocoele. This blastula per-

sists up to about the eighty-cell stage, when a gastrula is formed by migration of one, or at most two cells, from the layer of yolk-pyramids into the blastocoele to form the endoderm.

3. The gastrula is succeeded by a blastoderm of the familiar myriapod-insect type; the cleavage nuclei, except those of the endoderm, move into the peripheral layer of accumulating cytoplasm, while the internal cell-partitions break down. Total cleavage is thereby replaced by a superficial cleavage within the blastoderm. A blastodermic cuticle is secreted.

4. Out of the blastoderm there now differentiates the germ-band; it is of the usual elongate myriapod type, and extends over the anterior and posterior poles of the egg on to its upper half. At no time does a ventral flexure form. The rest of the blastoderm becomes much thinned out and is a provisional body-wall.

5. From the inner surface of the blastoderm isolated cells with enlarging nuclei have meantime migrated as yolk-cells into the yolk; from them will eventually form the fat-body of the larva.

6. During the development of the germ-band the latter becomes the source of the developing mesoderm, cells separating from it in great numbers along its length, and so coming to form a second, and at first very irregular layer, internal to the ectoderm.

7. The early developmental processes are of the usual myriapod type, except for the presence of an easily recognized gastrula. The survival of the latter is of importance for the interpretation of the specialized myriapod-insect type of ontogeny; in particular, the blastoderm phase is found to be a post-gastrula stage, and not a blastula as commonly believed.

8. Stomodaeum and proctodaeum are the first structures to appear in the germ-band. The formation of the head-lobes soon follows. Then the Anlagen of the antennae arise, being at first post-oral in position; and after them appear the Anlagen of the mandibles and maxillae. The premandibular segment does not bear even the rudiments of appendages. The segment behind the maxillary segment is the collum segment, without appendage-Anlagen, and it remains part of the abdomen; there is, therefore, no second maxillary segment. The Anlagen of the first, second, and third legs then appear in succession. Intersegmental lines form only in the advanced embryo; when these eventually appear, they reveal two segments behind the fourth abdominal (third leg-bearing), namely the fifth abdominal and anal segments. The fifth segment of the embryo becomes the fifth of the adult animal, so that the teloblastic formation of new segments must proceed by the budding off of new segments from the stationary anal segment.

9. The embryo now slowly swells, presumably owing to absorption of water, and so outgrows the available space within the egg. A gradually enlarging rent appears in the egg-shell, and after several days the embryo emerges from it in a quiescent 'pupoid' phase. Unlike the 'pupa' of other myriapods, it shows but little resemblance to the future larva. Within the pupa the first teloblastic segment (sixth abdominal) appears.

10. The development of the abdominal segments, both in the embryo and in the pupa and larva, shows that there are no 'diplosegments' in *Pauropus*; the tergites are derivatives of simple segments, and the apparent 'diplopody' arises from the presence of a wedge-shaped segment, with reduced tergal wall, behind the tergite-bearing segments.

11. The differentiation of the head-capsule out of the primitive head-segments is attended by the familiar inturning of the sternal wall of the post-oral segments to form the floor of the pre-oral cavity; and by the curving forward of the more lateral parts of the segments towards the front of the head. The antennae are thereby carried into a completely pre-oral position. The pre-mandibular epidermis becomes rolled under to form the roof of the pre-oral cavity (inferior surface of clypeus).

12. The head is composed of a procephalon, in which pre-antennary, antennary, and pre-mandibular segments are represented; and of a gnatho-cephalon, consisting of only two segments, the mandibular and maxillary. Superlinguae, derived from the mandibular epidermis, are present. The mandibles are closed in by the inturned margins of the clypeus; they are unsegmented and adapted to a diet of semi-fluid food. The maxillae display a cardo, a stipes, and a lacinia. Between them is the intermaxillary plate (sternite of maxillary segment).

13. At no time does the germ-band display a ventral flexure. Embryonic membranes are absent. An embryonic 'dorsal organ' appears, but it is not of the type found in Symphyla, Collembola, and *Campodea*.

14. In the early germ-band the mesoderm tends to aggregate laterally into two bands of cells, from which the succession of somites arises. Although many of the somites soon display very small coelomic cavities, they remain poorly developed, and coelomoducts do not appear. Since there are no blood-vessels in *Pauropus*, they do not contain any vasoblasts; they are, more-over, quite unique in that they do not even contribute any mesoderm to the mid-gut wall, the splanchnic mesoderm arising entirely from the mesoderm of the stomodaeum. Nor do they participate in the formation of the genital rudiment. The dorso-lateral muscles also are not derived from the somites.

15. Between the rows of somites is a layer of unsegmented 'median meso-derm'; out of it develops the genital tube, as well as a median band of neuro-glia (?) tissue in the nerve-cord.

16. Although the somites are diminutive, a complete set is present. They are the pre-antennary (vestigial), antennary, pre-mandibular, mandibular, maxillary, collum, second, third, and fourth abdominal somites; a fifth abdominal and very small anal somite form in the more advanced embryo. In addition to these there is also a small clump of 'teloblastic mesoderm' arising in the late embryo from the mesoderm that is heaped up in front of the proctodaeum; from it is generated the mesoderm of the larva.

17. From the pre-antennary somite arise the buccal dilator muscles; from the antennary and mandibular somites arise the muscles of the antennae and mandibles respectively.

18. From the pre-mandibular somite arises the large pre-mandibular gland; it opens to the side of the mandibles and is evidently a salivary gland. Its duct seems to be of ectodermal origin. There is no associated 'end-sac'. In Symphyla a pre-mandibular gland is present up to the time the larva leaves the egg, when it degenerates, leaving only its nephrocytes; in *Pauropus* alone among myriapods is it known to survive, though vestiges of it are found both in chilopods ('lymphoid tissue') and insects (sub-oesophageal bodies).

19. From the maxillary somite there develops, in addition to the muscles of the maxilla, the maxillary gland. The latter has an 'end-sac', which displays nephrocytic action to trypan blue injected into the blood.

20. The somites of the collum and other abdominal segments, as well as the anal segment, give origin to nothing but myoblasts from which most of the muscles of the respective segments develop.

21. In addition to the glands already referred to, there are present: (*a*) clypeal glands, that arise from the epidermis of the clypeus; (*b*) pseudocular glands, lying adjacent to the pseudoculi, and derived from the epithelium of the latter; (*c*) large intermaxillary glands, derived from the maxillary sternum.

22. The mid-gut epithelium is formed from the endoderm of the gastrula, the cells gradually losing their yolk and slowly increasing in number. The mesoderm of the mid-gut is derived from the mesoderm that is heaped up along the stomodaeum, whence it spreads back as an arching roof to the endoderm, the immediately underlying cells of which become arranged into an epithelium, within which excretory concretions, similar to those of the adult mid-gut, soon appear. The floor of the mid-gut remains for long free from any mesoderm; from it develops a ventral band of enlarged mid-gut cells, permanently free from excretory concretions. The hindermost tip of the mid-gut is of proctodaeal origin. The lumen of the mid-gut does not communicate with those of the stomodaeum and proctodaeum till shortly before the larva emerges.

23. The two Malpighian tubes arise from the anterior tip of the proctodaeum; they do not seem to be functional excretory tubes, since in the growing larva they begin to display a markedly degenerate character.

24. The genital rudiment does not arise out of the somites, but from the 'median mesoderm' of the fifth abdominal segment, i.e. from the vestige of the mesoderm that remains in front of the proctodaeum after the fifth somites and teloblastic mesoderm have separated from it. Embedded in it is a single primordial germ-cell. A string of cells spreads forward from this mesoderm along the roof of the nerve-cord into the third abdominal segment, thus forming the genital rudiment.

25. The fat-body does not develop out of the somites, as in insects and chilopods, but out of the embryonic yolk-cells, as in Symphyla. It is phagocytic towards injected Indian ink. The haemocoele arises from spaces left by shrinkage and withdrawal of fat-body.

26. The ganglia of the nerve-cord develop in association with 'ventral organs', of which there is a single pair in each segment, except the anal segment. In the abdominal segments the 'ventral organs' become incorporated into the ganglia. The 'median mesoderm' plays an unusual role, in that it gives origin to a median band of neuroglia (?) cells, within the chain of ganglia; there is no incorporation of 'median cord' ectoderm into the ganglia.

27. The ventral nerve-cord of the embryo comprises a mandibular and maxillary ganglion (fused into one), followed, in the abdomen, by the ganglia of the collum, second, third, and fourth abdominal (leg-bearing) segments, fifth segment, and a vestigial anal ganglion. The ganglion of the fifth, or penultimate segment, is in reality a teloblastic ganglion, which enlarges, and from which the fifth ganglion proper is separated off in the pupa, the rest remaining as teloblastic ganglion, from which, in the larva, the sixth and remaining ganglia in turn arise.

28. The brain develops out of: (*a*) a trilobed protocerebral Anlage, whose posterior lobes invaginate below the surface, but whose lateral and frontal lobes do not invaginate but display 'ventral organ' cell-disposition; (*b*) a pair of diminutive pre-antennary (?) ganglia, which give origin to a definite part of the brain between the protocerebrum and deutocerebrum; (*c*) a pair of antennary ganglia, from which the deutocerebrum will arise; (*d*) a pair of pre-mandibular ganglia, from which will form the tritocerebrum. The last three all develop in association with 'ventral organs'.

29. A detailed account of the morphology of the brain and of the cerebral nerves is given.

30. The visceral nervous system consists of: (*a*) a frontal ganglion, derived from the roof of the oesophagus; (*b*) a pair of 'oesophageal ganglia' (?), which develop in a most unexpected way, for they arise from the inner ends of the mandibular apodemes; (*c*) a stomachic ganglion, formed from the hinder end of the oesophagus; (*d*) a 'caudal' visceral ganglion, which is apparently the hind end of the last abdominal ganglion.

31. The structure and development of certain epidermal organs (trichobothria, basal antennal sense organs, pseudoculi) is described. The supposed vestigial appendages of the collum segment are not appendages at all, but seem to be related to exsertile vesicles; they develop from vestiges of the 'ventral organs' of the collum segment. The hypopharyngeal apophyses are epidermal ingrowths that arise a little in front of, and median to, the mandibles.

32. The greater part of the muscular system is derived from cells that are set free by the break-down of the somites. The dorsal longitudinal muscles are exceptional.

33. Four larval instars precede the adult animal with 9 leg-pairs. These instars have 3, 5, 6, and 8 leg-pairs respectively. The adult animal does not moult.

34. The new segments arise by proliferation of epidermal cells within the anal segment.

35. The mesoderm of the growing zone is generated entirely from the 'teloblastic mesoderm', located in the anal segment, successive clumps of mesoderm being allotted to the new segments as these successively develop. The ventral longitudinal muscles always develop precociously. Somites do not form in the mesoderm of the new segments.

36. There is no periodic renovation of mid-gut epithelium in the growing larva, such as is encountered frequently in insects; nevertheless there is considerable cell-proliferation, both in the mid-gut and in the fore- and hind-gut. The Malpighian tubes gradually degenerate, but do not disappear.

37. The fat-body of the larva is supplemented by new fat-body that develops unexpectedly from the epidermis.

38. In the newly emerged larva the genital rudiment, still sexually indeterminate, consists of a narrow string of cells lying between the intestine and the nerve-cord, and extending forward just into the third abdominal segment. Posteriorly it merges with the 'median mesoderm' of the growing zone. Its further development in the larva involves (*a*) slow multiplication of the primordial germ-cells located at its hinder end; (*b*) posterior elongation of the genital rudiment at the expense of 'median mesoderm' cells in the growing zone; (*c*) thickening of the anterior part of the genital tube. The exit ducts arise as a pair of epidermal ingrowths just behind the second legs, which grow round the nerve-cord and join the anterior tip of the genital rudiment. In the female one only survives, and forms the oviduct and receptaculum seminis; in the male both are retained as ejaculatory ducts. The ovary remains in its primitive position below the intestine, the oocytes arising from laterally placed germ-cells in the median germarium; the anterior end of the original genital rudiment survives in the female as the 'ductus glandularis'. In the male the gonad-Anlage bends up dorsally to either side of the mid-gut, and divides into four testes; the anterior end of the genital rudiment then splits longitudinally into the four vesiculae seminales. In fourth instar larvae the reproductive organs are often almost mature, but there is no evidence for precocious sexual functioning.

39. The classification of Myriapoda into Progoneata and Opisthogoneata does not seem to reflect the real affinities of the component groups, and in particular it fails badly for the Symphyla which are undoubtedly closely related to the Insecta. In Pauropoda and Symphyla the exit ducts from the gonads are not surviving coelomoducts, as assumed, but epidermal ingrowths, new gonopores having apparently arisen, in adaptation to anamorphosis, remote from the zone of growth. A new classification is proposed, based on the degree of cephalization and specialization of originally abdominal segments: the lowest grade of surviving myriapods are the DIGNATHA (Pauropoda and probably Diplopoda); the Chilopoda, Symphyla, Collembola, and Insecta are TRIGNATHA, and of these the Symphyla, Collembola, and Insecta are united as LABIATA by the common possession of a labium. The Myriapoda seem to have arisen, independently of the other great groups of Arthropoda, from some ancient stock of *Peripatus*-like ancestors.

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DESCRIPTION OF PLATES

PLATE X

Fig. 116, A and B. Drawings of two immediately adjacent sections (A the more anterior) from an embryo a little more advanced than that shown in the previous figure; in A only part of the section is drawn. The plane of section is only approximately frontal, the right half being a little posterior to the left.

A. The section shows the neuropilem passing between protocerebrum, deutocerebrum, and tritocerebrum and mandibular ganglion; note the pre-antennary ganglion lying median to the neuropilem. Below the oesophagus the inferior tritocerebral commissure has formed. Between the tritocerebrum and mandibular ganglion the hypopharyngeal apophysis may be seen, from which a string of cells is growing up along the side of the brain (ascending arm of apophysis). To the right side of the mandibular ganglion is the transected hind end of the mandibular apodeme.

B. On the left the section passes along the mandibular apodeme; on the right the hindermost end of the apodeme is seen. A continuous band of cells now unites them, and out of this will form the oesophageal ganglia. The deutocerebrum and a fragment of the tritocerebrum intrude from in front into the section. The protocerebral commissure is forming. The hindermost ends of the hypopharyngeal apophyses appear in the section; they have become connected with mesoderm from the oesophagus, thereby initiating the formation of the oesophageal dilator muscles. On the left side is seen part of the pre-mandibular gland. × 780.

Fig. 117. Drawing of a section approximately similar to that shown in Fig. 116 B, but from a still later embryo. The section is taken a little anterior to the protocerebral commissure,

and shows the developing septal (pre-antennary) ganglia, with the epidermal septum growing down between them. The oesophageal ganglia are now becoming recognizable, but are still connected with the tips of the mandibular apodemes. A connexion has been established between the hypopharyngeal apophyses and the mandibular apodemes (median ligament of latter). A portion of the maxillary gland with end-sac is present in the section. The two round clumps of cells just median to the hypopharyngeal apophyses are fragments of trito-cerebrum that intrude from in front into the section (cf. Fig. 116 B), and must not be confused with the oesophageal ganglia. × 780.

Fig. 118. Drawing of part of a section through anterior end of a very advanced embryo, to show the oesophageal ganglia. The latter have become completely detached from the mandibular apodemes (present in the immediately preceding section), but have not yet become associated with the oesophagus. × 780.

Fig. 119. Approximately 'horizontal' section through head of a young pupa. The asymmetry of the section is illustrated by the difference in the mandibles, and the almost complete absence of clypeal fold on the left. This asymmetry has the advantage of bringing out the configuration of the hypopharyngeal apophyses; on the right side the base of the developing right apophysis is seen, while on the left is seen its more distal end curving round the trito-cerebral ganglion and thereby making connexion with the developing oesophageal dilator muscle. In the premandibular gland a distinction between the two kinds of nuclei has become apparent, but the backward movement of the gland has not yet begun; nor has the duct started to form. × 780.

Fig. 120. 'Horizontal' section through head-end of a 2-day pupa, to show hypopharyngeal apophyses and related structures. Fusion of right and left apophyses has taken place under the oesophagus. In the pre-oral cavity the future suspensorium for the hypopharyngeal apophyses has become defined. The pre-mandibular gland is in process of moving backward into the abdomen. × 780.

Fig. 121. Fragment of a 'horizontal' section along head of a young pupa, to show develop-ing left pre-mandibular gland. The position of the fragment will at once be understood by reference to Fig. 119 or 120. The mandibular apodeme is not present in this section, but the section passes exactly along the epidermal attachment of the gland (indicated by *x*). × 780.

Fig. 122. Similar section, from right side of head of a more advanced pupa, to show pre-mandibular gland in a later phase of development, and with its duct in course of formation. × 780.

Fig. 123. Fragment of a section cut 'horizontally' through head of a young pupa, showing epidermal attachment (*x*) of the maxillary gland. The section grazes the anterior surface of the left maxilla, and passes just under the mandible, which is therefore not present in the section. The rounded clump of cells to the right of the maxillary gland is a fragment of the mandi-bular apodeme, which intrudes from above into the section. Note also the developing inter-maxillary glands. × 650.

Fig. 124. Approximately similar section, from an advanced pupa; the orientation is not exactly the same, for the maxilla is not present, while the base of the mandible intrudes from above into the section. Note the developing exit duct of the maxillary gland. The maxillary gland has receded into the collum segment. × 650.

Fig. 125, A and B. Two immediately adjacent sections, cut transversely through the hinder-most segments of a young pupa, to show the disposition of the teloblastic mesoderm. The sections are from a 'horizontally' cut pupa (for orientation cf. Text-fig. 9). Section B is 'above', i.e. morphologically posterior to A, and is taken just in front of the anal opening. In section A the last 'ventral organ' is seen on the right side; on the left the section is a little to the rear of it, i.e. it must transect the anal segment itself. In B the section is entirely through the anal segment. In both sections the roof of the fifth abdominal segment is necessarily present in the section. × 780.

Fig. 126. Section through developing sixth abdominal segment of a late pupa; the section is taken at the same level as that shown in Fig. 125 A (right side), the latter section being from an early pupa. Note that the ganglion has begun to enlarge, and that mesoderm cells have spread down the lateral wall of the enlarging ganglion. The small clump of mesoderm cells along the upper margin of the ganglion is the first recognizable sign of the sixth ventral longitudinal muscle. × 780.

Fig. 127. Transverse section through sixth abdominal segment of a very young first instar larva. The drawing is to be compared with Figs. 125 A and 126. Reserve products have not yet appeared in the fat-body. × 780.

Fig. 128. Similar section, but from an advanced first instar larva (cf. Fig. 35). The fifth leg is now developing. Note that the epidermis of the body-wall has grown in thickness, and that along the dorsal surface some of the cells are enlarging, thereby giving the first indication of the development of secondary fat-body. In the old fat-body reserves have appeared in quantity. ×780.

Fig. 129. Section through hinder tip of a young pupa, to show the teloblastic mesoderm. Owing to the fact that the hinder end of the pupa curves upward (cf. Text-fig. 9), the section, whilst transecting the anal segment, must necessarily pass 'horizontally' along the fifth segment. The fifth and teloblastic ganglia, not yet delimited from one another, are therefore cut horizontally, and below this even the hinder tip of the fourth ganglion enters the section. Fragments of the last pair of legs are present. Note also developing fifth ventral longitudinal muscle. ×780.

Fig. 130. Portion of a section through hind end of an advanced pupa. The orientation is about the same as in the previous figure, but development is more advanced. The terminal ganglion has much enlarged, and the fifth abdominal ganglion has partially separated from it. Note, in the anal segment, that the Anlage of the sixth ventral longitudinal muscle has now appeared, behind that of the fifth, having separated away from the clump of teloblastic mesoderm. ×780.

Fig. 131. Transverse section through anal segment of a newly emerged larva, to show teloblastic mesoderm. ×780.

Fig. 132. Similar section, from a later first instar larva. Note pronounced thickening of epidermis, and enlargement of teloblastic mesoderm. Note developing third trichobothrium. ×780.

Fig. 133. Entire Malpighian tube, from a late pupa. ×780.

Fig. 134. The same, from a late first instar larva. ×780.

Fig. 135. The same, from an advanced second instar larva; a fragment of intestine is included at left end of drawing. Note mitosis in one of the cells at base of tube. ×780.

Fig. 136. Transverse section through roof of fifth abdominal segment of an advanced first instar larva, to show an early phase in development of secondary fat-body from the epidermis. ×650.

Fig. 137. Section through roof of one of the hinder segments of a third instar larva, showing development of secondary fat-body from epidermis. The new fat-body is completely closed in above by renovated epidermis. N.B.: this is not a later phase in the development of the part shown in the previous figure, but is from a wholly new part of the larva. ×650.

Fig. 138. Sagittal section of hinder half of a second instar larva. The genital rudiment, with primordial germ-cells located in the sixth abdominal segment, is still in the sexually indifferent condition; the future genital tube is in process of thickening, and is also undergoing terminal elongation at the expense of median mesoderm cells in the growing zone. In the hind-gut note mitosis (indicated by *x*) in one of its epithelial cells. Secondary fat-body is developing, especially along the tergal body-wall. ×385.

PLATE XI

Fig. 139. Portion of a 'horizontal' section of a pupa, to show the genital rudiment. The section passes along the roof of the nerve-cord, and extends from the fifth segment into the hinder end of the third, and therefore includes the genital rudiment for its entire length. Note that behind the primordial germ-cell the genital rudiment merges with the median mesoderm of the growing zone. ×780.

Fig. 140. Section through floor of third abdominal segment of a late first instar larva, showing ingrowing cords of epidermal cells, from which will develop the exit-ducts of the gonads. ×780.

Fig. 141. Similar section from a late second instar larva, showing enlargement of the developing exit-ducts from the gonads. The section is from a larva in which the gonads are already recognizable as male (Fig. 145 is from the same larva). ×650.

Fig. 142. Similar section, from an advanced fourth instar male larva, showing differentiation of the genital ducts. The section is not truly transverse, the left side being a little posterior to the right. Note differentiation of the glandular and anterior portion of ejaculatory ducts. ×650.

Fig. 143. Similar section, from fourth instar female larva, showing degeneration of the left epidermal exit duct, and enlargement of the right duct. Note initial phase in development of recentaculum seminis. ×650.

Fig. 144. Similar section, from a more advanced fourth instar female larva, showing enlargement of the right exit duct (oviduct), formation of receptaculum seminis, and complete disappearance of left exit duct. × 650.

Fig. 145. Transverse section through second instar male larva, taken at the level of the developing hinder pair of testes; cf. Text-fig. 29 A (Fig. 141 is from the same larva). It shows a very early phase in the differentiation of the testes. Note also the distinction between original and secondary fat-body. × 650.

Fig. 146, A, B, C. Three sections through a third instar male larva, to show a more advanced phase in the differentiation of the testes. The gonads of this larva are shown diagrammatically in Text-fig. 29 B.

Fig. A, which represents an almost complete transverse section through the sixth abdominal segment, shows the developing anterior two testes bending dorsally round the mid-gut. In Fig. C, which is taken through the seventh segment, we see the third and fourth testes, only the relevant part of the section having been drawn. In Fig. B, which is a little behind A, and in which again only the relevant fragment has been drawn, we see the narrow strip of genital tube connecting the anterior and posterior pairs of testes. In A and C two cells in meiotic prophase (indicated by x) are present. In B the section passes through the bases of the Malpighian tubes; in C it is well behind them. × 650.

Fig. 147. Section through the upper half of a fourth instar larva, showing later phase in differentiation of testes. The two vasa deferentia are those of the hinder pair of testes. × 650.

Fig. 148. Fragment of a transverse section through the fifth segment of a fourth instar larva, showing splitting of the widened genital tube into the four vesiculae seminales. The section is taken exactly at the point of splitting, which is progressing from behind forwards. × 650.

Fig. 149. Similar section from a more advanced fourth instar larva, showing enlargement of the four vesiculae. × 650.

Fig. 150. One of the hinder testes of an advanced fourth instar larva, cut in sagittal section, and showing spermatogenesis. × 540.

Fig. 151. Transverse section through genital rudiment of a third instar larva, showing the earliest recognizable phase of differentiation of an ovary. Note, on the left, three meiotic prophases. × 780.

Fig. 152. Similar section, from a more advanced third instar larva; prophases of meiosis numerous; follicle cells now present in ovary. × 780.

Fig. 153. Entire ovary and proximal end of genital tube, from a 'horizontally' cut third instar larva. In the ovary we see the first enlarging oocytes. × 780.

Fig. 154. Transverse section through an ovary of a fourth instar larva; enlarging oocytes at the side; germarium in the middle. × 780.

Fig. 155. Parasagittal section along floor of abdomen of a fourth instar female larva, to show condition of the developing reproductive organs. The genital tube is evidently rather asymmetrically placed, for it is contained for its entire length in a section that simultaneously grazes the lateral walls of the chain of nerve-ganglia. On the extreme left is seen the epidermal exit duct, whose connexion with the epidermis, however, lies medial to the section. Then follows the genital tube, with the reproductive cells confined to the sixth and seventh segments. × 385.

The abbreviations used in the Plates are given on pp. 266–7 of Part 1 of this paper (*Quart. J. micr. Sci.*, vol. 88, part 2 (1947)).

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PLATE X

PLATE XI