THE EMBRYOLOGY OF THE JUMPING BRISTLETAIL *PEDETONTUS UNIMACULATUS* MACHIDA (INSECTA, MICROCORYPHIA, MACHILIDAE)

BY

RYUICHIRO MACHIDA

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CONTENTS

INTRODUCTION

On the morphological bases, a close affinity between the Microcoryphia, Thysanura s. str., and lower Pterygota seems to be clear in many resembrances of the general organization of the body, and it seems that the Microcoryphia and Thysanura possess the primitive characters that the pterygotan ancestors may have had. Making a comparison between the Microcoryphia and Thysanura, there seems no doubt that the Microcoryphia is less specialized or probably more primitive, because the former does not possess any specialized features shared with the latter and the pterygote insects: such as 1) presence of two mandibular articulations (one articulation in the former), 2) presence of a gonangulum, 3)origin of ventral mandibular stipital adductors on the tentorium, and 4) presence of longitudinal and transverse tracheal trunks.

The machilids and lepismatids are often treated simply as the divisions constituting a single order, the Thysanura s. lat., but the present author takes the position that they represent each independent order, the Microcoryphia and the Thysanura s. str. throughout the present study.

Embryological studies of the Microcoryphia and Thysanura are of great value, since they are regarded as probably taking such phylogenetical positions as just mentioned. Relatively many such studies on the

Thysanura have appeared (Heymons, 1897a; Uzel, 1898; Sharov, 1953; Sahrhage, 1953; Wellhouse, 1954; Woodland, 1957; Yashika, 1960; Larink, 1970; Klag, 1977a, b, 1978). On the other hand, for the Microcoryphia, we have only the brief study on the formation of embryonic membranes of Machilis alternata (=Trigoniophthalmus alternatus) by Heymons and Heymons (1905), Larink's (1969) study that deals with the embryonic development of Petrobius brevistylis, and also his papers (1972, 1979) concerning the blastoderm cuticle formation in several microcoryphian species. These papers, especially Larink's of 1969, indeed provide us with many valuable data, but they are rather fragmentary. Therefore, also from the interesting characteristics that the Microcoryphia may possess, the more detailed embryological studies throughout all the course of their embryogenesis have been earnestly expected.

For these reasons, the author set about the embryological investigation on a machilid, Pedetontus* unimaculatus Machida (Machilidae, Petrobiinae). The concrete objects of this investigation are summarized as follows: i) describing and discussing carefully the developmental process of this insect, 2) examining the affinities of

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* Although Silvestri (1911) regarded Pedetontus Silv. as one of the subgenera of the genus Petrobius, it is now regarded as an independent genus (cf. Paclt, 1972).

the Microcoryphia to the other insects and the myriapods, based on only the embryological data, 3) providing some ground for the systematical treatment of the machilids and lepismatids in higher level, which is at the present much controversial, from the comparative embryological views, and 4) describing the morphogenetical processes and origins of each structure to tender some valid data for the comparative morphology.

In the present paper, the developmental process of Pedetontus unimaculatus during the whole embryonic stages and in some cases also the early-instar-larval will be described, and the results obtained will be discussed and compared with previous works.

MATERIALS AND METHODS

Specimens were collected at Shimoda, Shizuoka Prefecture, Japan.

A pair of the insects was kept at room temperature in a plastic case with a plaster bottom. Moistened stones or bark coated with unicellular green algae were provided as food. The female laid her eggs mainly under stones, under bark, and in crevices. These were transferred to other humid cases and kept at room temperature. The oviposition of Pedetontus unimaculatus lasted from March to September, and the larvae hatched out the following spring. The embryos in each stage, from the germ disc to the full-grown embryo, and early instar larvae, formed the main material of this investigation.

The materials for the observations of external features were prepared as following. In Pedetontus unimaculatus, the outer dark and inner transparent blastoderm cuticles are formed just beneath the chorion, as in the other machilids (Larink, 1969, 1972, 1979). Eggs were dechorionated with fine forceps, and the dark outer blastoderm cuticle was soaked in 4 % antiformin. After this treatment, it was possible to see inside the egg through the transparent blastoderm cuticle. The eggs were then transferred to Ringer's solution. Embryos were removed from the eggs with forceps and washed several times in the latter solution.

These embryos were fixed with Bouin's fluid for several hours and stored in 70 % ethyl alcohol. This method is favorable for observation because the embryos which are flexed in ovo become somewhat straightened, and lack coagulated material on the surface. Advance embryos with developed musculature often change their form during fixation: therefore, prior to fixation a few drops of Ringer's solution mixed with chloroform were added to the Ringer's solution containing living embryos. Larvae were anesthetized with ethyl ether vapor for several minutes prior to fixation and then fixed with alcoholic Bouin's fluid overnight. Materials were stained with Mayer's acid hemalum. In order to stain larvae or embryos possessing a larval cuticle it was necessary to perforate the body wall with a fine needle.

The whole eggs were used for sectioning, other than the embryos and larvae prepared or fixed in the same way as previously mentioned. The egg membranes of whole eggs should be perforated with a fine needle in fixatives, for the purpose of accelerating fixation. Prior to perforation, some of the eggs were dechorionated, or further their outer blastoderm cuticle was resolved with antiformin. The alcoholic Bouin's fluid was used for the fixation of the eggs. The usual paraffin embedding method was mainly employed. The materials were dehydrated and cleared through an ethyl alcohol – butyl alcohol series or an ethyl alcohol – methylbenzoate –

butyl alcohol series. The celloidin-paraffin double embedding method was also employed. Sections, six to ten-μm thick, were stained with Delafield's hematoxylin or Mayer's acid hemalum and eosin G, and Masson's one-step triple stain modified by Gomori.

Drawings were made with the aid of Abbe's camera lucida.

OBSERVATIONS

The egg-period of Pedetontus unimaculatus varies from 230 to 380 days at room temperature. Considerable individual differences in the period were observed. The eggs and embryos in each stage, from the germ disc to the full-grown embryo, and the first three instar larvae, formed the main material of this investigation. In this study, the developmental process from the germ disc to the full-grown embryo is divided into fourteen stages, according to the external features (see Chapter D).

A. Egg and egg membranes

The newly laid eggs of Pedetontus unimaculatus assume orange color, and are covered with only the chorion and gelatinous layer (Fig. 1a). The chorion is initially so soft that the eggs display various shapes as in the case for other machilid eggs (Wygodzinsky, 1941; Delany, 1959; Larink, 1968). The chorion, however, soon hardens. The ellipsoidal eggs of Pedetontus unimaculatus are about 1.3 mm long, and 0.8 mm wide. The gelatinous layer of eggs is about 1.5 μm thick, and the chorion is composed of two layers, exochorion and endochorion. The exochorion, ca. 1.5 μm thick, is darker than the endochorion, ca. 2 μm thick. At about the time of cleavage, the exochorion and endochorion become uniformly darker, to be undistinguishable with each other.

With the progression of development, the blastoderm forms just beneath the chorion. It secretes a blackish cuticle layer between the blastoderm and chorion (Fig. 1b). This layer becomes thicker upto ca. 4.5 μm during the formation of the germ disc (Stage 1), and is provided with many spinules, ca. 2 μm tall, on its outer surface (Fig. 1c). This blackish cuticle layer with the spinules is designated as 'blastoderm cuticle 1'.

From the germ disc stage (Stage 1) to the early stage of germ band (early in Stage 2), two additional blastoderm cuticles successively appears. First, a eosinophilic cuticular layer, ca. 6 μm thick, (blastoderm cuticle 2) is formed just beneath the blastoderm cuticle 1 (Fig. 1d). Then, the blastoderm cuticle 3, ca. 7 μm thick and unstainable with any of hematoxylin, eosin, chromotrope 2R and light green, appears between the blastoderm cuticle 2 and blastoderm (Fig. 1e). The longitudinal lines are observed in the blastoderm cuticle 3. The boundary between the blastoderm cuticles 2 and 3 is more or less obscure, and the transient region of them assumes a characteristic stainability against light green. During the formation of blastoderm cuticles, the blastoderm is folded beneath the germ disc (Fig. 5). The blastoderm cuticles secreted by the folded part of the blastoderm assumes the peculiar spine-like shape.

The chorion parts from the egg proper by the formation of blastoderm cuticles mentioned above. With the enlargement of egg, the chorion cracks, and becomes to be helpless for the protection of egg. Now, the blastoderm cuticles fulfill this function, instead of the chorion. The blastoderm cuticles are considerably thicker than the chorion, and are responsible for the toughness of the egg of this species. Larink (1969, 1972, 1979) studied the formation of egg membranes of several species of machilids*. The egg membranes of them acquire a complex structure similar to those of Pedetontus unimaculatus, and this seems the characteristic of machilid eggs.

The blastoderm cuticles completed in Stage 2 are in the same condition as they are, until Stage 13. Near the hatching, the blastoderm cuticles become thinner. In the egg ready to hatching, the blastoderm cuticle 3 disappears, the blastoderm cuticle 2 is also much reduced, and only the blastoderm cuticle 1 remains intact. Although it is clear that the blastoderm cuticles are digested by a kind of hatching enzymes, the origin of it is obscure. It is, however, noteworthy, concerning this matter, that embryos of this species have well-developed pleuropodia.

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* Larink called the blastoderm cuticle "Blastodermmembran" in his paper of 1969.

The cuticles secreted by the embryonic membranes have been reported in many insects, such as the thysanuran Thermobia domestica (Woodland, 1957), Odonata (Ando, 1962), the orthopteran Melanoplus differentialis (Slifer, 1937) and the plecopteran Pteronarcys proteus (Miller, 1940). These cuticular egg membranes are secreted by the blastoderm or the serosa, which the blastoderm develops into. Slifer clearly demonstrated in her experimental embryological studies (1937, 1938) that the enzyme secreted by the pleuropodia is responsible for the thinning of the white cuticular membrane of Melanoplus differentialis near the hatching.

B. Blastokinesis

The small germ disc is first observed at the posterior end of the egg (Stage 1: Fig. 2a). The embryo then begins to grow anteriorly on the surface of the yolk (Stages 2, 3 and 4: Fig. 2b, c). Next, the abdominal region of the embryo begins to sink into the yolk slightly, but the head and thoracic regions still remain on the surface. At about the same time, small yolk folds form on both sides of the embryo (Stages 5 and 6: Fig. 2d).

Subsequently the embryo moves further forward and becomes located in the center of the surface of the yolk. The yolk folds increase in size, and a new fold appears in front of the embryo. As the yolk folds enlarge, the embryo begins to invaginate between them

(Stage 7: Fig. 2e). At the posterior part of the dorsal surface of the embryo a new yolk bulge also occurs, but it is less well developed than in Petrobius brevistylis (Larink, 1969).

With further development, the yolk folds and yolk bulge grow and cover the embryo (Stages 8, 9 and 10: Fig. 2f, f´), so that only part of the abdomen and the caudal filament can be seen through the cleft between the folds and the bulge (Fig. 2f´). The embryo continues to develop enclosed within them.

As embryonic development progresses, the yolk folds begin to decrease in size, since yolk is rapidly consumed, and the yolk bulge becomes enclosed as the dorsal closure proceeds (Stages 11 and 12: Fig. 2g). The frontal yolk fold disappears first, but the lateral folds still remain at the back of the thorax before the formation of the larval cuticle in Pedetontus unimaculatus (early Stage 13), while in Machilis alternata of a comparable stage (Heymons and Heymons, 1905) only the horn-shaped yolk sac is left at the anterior end of the embryo. Up to this time the embryo completely fills its shell.

Finally, however, these lateral yolk folds become completely incorporated into the embryo and the dorsal closure is complete (Stage 13). At this point, the chorion becomes loose and the egg begins to swell, becoming almost spherical (Fig. 48). The additional

space thus provided gives the embryo room for further development (Fig. 49).

In Stage 14 the egg swells further. The embryo grows further, and again comes to occupy the egg-shell completely (Fig. 50). Shortly thereafter the first instar larva hatches.

C. Early development and formation of germ rudiment

On the very early development of Pedetontus unimaculatus, the available data are not sufficient to warrant any descriptions and conclusions. The earliest-stage-eggs that are possible to furnish some available data already attained the stage with several cleavage nuclei.

Each of the cleavage nuclei is surrounded by a large amount of plasm. At about the time when these nuclei commence to migrate centrifugally to the periphery of the egg, the yolk mass is divided into large yolk blocks (Fig. 3). The secondary yolk cleavage of Pedetontus unimaculatus is ephemeral, and breaks down at the time of the completion of blastoderm. The appearance and breakdown of yolk cleavage of this species occur exceptionally in earlier stages, comparing with those of the other insects (cf. Johannsen and Butt, 1941). In Petrobius brevistylis, no yolk cleavage is observed throughout the whole developmental stages (Larink, 1969).

The cleavage nuclei finally arrive at the thin

periplasm, to form the blastoderm. Initial stages of development of Pedetontus unimaculatus are broadly similar to those in the majority of insects: it may be concluded, although the insufficiency of data on earlier development, that the type of cleavage of this species is a typical superficial one. The manner of cleavage in Pedetontus unimaculatus is fundamentally different from the total cleavage found in myriapods and collembolans.

When the completion of blastoderm, many yolk cells stay in the yolk, and they are regarded as the primary yolk cells. The plasm surrounding each of them gradually diminishes in quantity, and finally becomes undiscernible at all. The nuclei of blastoderm undergo the multinucleation, as is the case for Petrobius brevistylis (Larink, 1969). Judging from this, Larink (1969) suggested the presence of secondary yolk cells.

Parallel with the blastoderm formation, a loosely aggregated cellular mass, about 70 μm in diameter, is formed at the posterior pole of the egg (Fig. 4). This mass is the germ rudiment, and many mitotic figures are observed. The large dorsal part of the germ rudiment is the future germ disc. The small lower part differentiates into the embryonic membrane*, to form

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* In this paper, the term 'embryonic membrane' also implies the blastoderm, other than the serosa and amnion.

the folded structures (cf. Fig. 5). The cell arrangement of the lower part of the germ rudiment represents the rudimentary condition of the folded part of embryonic membrane. Here, it is notable that the nuclei of the fold assume the similar morphological characteristics to those of blastoderm: i) size, ii) stainability and iii) multinucleation. The folds should be, therefore, regarded as the blastoderm in nature. The folds are stretched and thinned, with the enlargement of germ disc.

D. Embryonic membranes and dorsal organ

The folds of blastoderm situated under the germ disc is unfolded and stretched in Stages 2 to 4. The blastoderm begins to be concentrated towards the anterior, and then the ring-shaped thickening, the secondary dorsal organ, is produced (Fig. 6). Parallel with this, a area of the embryonic membrane, which is scantly cellulated, appears between the secondary dosal organ and embryo (Fig. 7). The embryonic membrane newly formed is proliferated at the margin of embryo, and is undoubtedly embryonic in origin. It is, therefore, homologized with the amnion of the higher insects. A part of the embryonic membrane other than the secondary dorsal organ and amnion is, now, regarded as the serosa. The nuclei of amnion is flattened and relatively small. The serosa is more densely cellulated than the amnion, and the cells of serosa are with large and flattened

nuclei. They tend to undergo the multinucleation as in the other insects, in contrast to those of the amnion.

The concentration of embryonic membrane and the replacement of the serosa with the amnion are more progressive in the dorsal region of egg (Fig. 9). In Stage 7, the serosa is at last concentrated up in front of the embryo, and it remains as the small secondary dorsal organ. At least by Stage 9, however, the secondary dorsal organ is completely absorbed into the yolk. The tightly packed columnar cells of secondary dorsal organ are unexceptionally multinucleated, and resemble the glandular cells. These cells of secondary dorsal organ, as if they were holocrine cells, separate into the yolk, and are absorbed there (Fig. 8). Such a separation and absorption process of the cells of secondary dorsal organ has been reported in many other insects. The secondary dorsal organ is considered and defined as the structure that is produced accompanyingly with the concentration and degeneration of the embryonic membrane. Therefore, it stands to reason that the secondary dorsal organ of Pedetontus unimaculatus should be homologized with ones of the other insects, although the ring-shaped dorsal organ of this species appears to be very different from the typical ones.

After the disappearance of the secondary dorsal organ, the amnion represents the embryonic membrane.

The yolk folds and bulges mentioned previously are formed at the area of amnion. With the extension of the developing terga, the dorsal closure is near its completion. The amniotic cells, with the nuclei heavily stained with hematoxylin, is concentrated in the dorsal region of embryo (Fig. 83). They are replaced with the newly formed terga and degenerate. However, some amniotic cells are left just above the heart, and are taken into the body of full-grown embryo (Fig. 84). The similar condition of amniotic cells has been reported in Locusta migratoria migratorioides (Roonwal, 1937). In Pedetontus unimaculatus, the amniotic cells taken into the body are also observed in the early instar larvae.

In Pedetontus unimaculatus, the primary dorsal organ, found in the myriapods (Tiegs, 1940; Seifert, 1960; Dohle, 1964), collembolans (Claypole, 1898; Philiptschenko, 1912; Tiegs, 1941; Jura, 1965, 1967a, b) and diplurans (Uzel, 1898; Tiegs, 1944; Asaba, unpublished), is not observed throughout the whole developmental stages. In Thermobia domestica, Woodland (1957) observed a group of six to ten closely packed cells at the extreme anterior end of the egg. According to him, it represents the primary dorsal organ. If true, his observations are extremely interesting in view of the phylogenetic significance which has been attached to this embryonic structure. However, on the identifi-

cation of this group of cells, he took no account of the other possible interpretations, even such as concerning the hydropylar and aeropylar apparatuses as observed in some pterygote insects. Reexaminations on Woodland's observations are earnestly expected.

E. External features of embryogenesis

The external morphology of the embryo and the first instar larva is described. The embryonic developmental process is divided into fourteen stages.

Stage 1 (Figs. 10 and 11)

A circular germ disc about 100 μm in diameter forms. With development, the germ disc becomes triangular, and begins to differentiate into a protocephalon and a protocorm.

Stage 2 (Fig. 12)

The triangular germ disc elongates to become a pear-shaped germ band. Segmentation of the embryo is not yet evident.

Stage 3 (Figs. 13 – 15)

Segmentation of the embryo is first visible at this stage. First, the antennal, mandibular, and maxillary segments and the neural groove appear (Fig. 13). As these structures become more distinct, the labial and thoracic segments appear successively (Figs. 14 and 15). Just anterior to the mandibular segment a pair of flat bulges becomes visible. They are thought to represent the developing intercalary segment. The

shallow stomodaeal notch forms at the extreme anterior end of the neural groove. In front of the notch a small bulge, thought to be the clypeolabral anlage, is found (Fig. 14), and in several cases a pair of anlagen was observed.

Stage 4 (Figs. 16 and 17)

The rudimentary antennae elongate and the anlagen of the gnathal appendages appear. The protocorm thickens and becomes segmented. The opening of the developing proctodaeum forms at the extreme end of the neural groove.

Stage 5 (Figs. 18 and 19)

Three pairs of flat bulges (B_1, B_2 and B_3 in Figs. 18 and 19) form in the protocephalon. These structures correspond to the superficial structures of three pairs of protocerebral ganglia. The anlagen of the thoracic appendages also differentiate. A pair of bulges becomes visible between the bases of the appendages in each segment, indicating ganglion formation along the ventral nerve cord. The abdomen of the embryo begins to flex ventrally and its posterior end points anteriorly. The opening of proctodaeum assumes a T-shape.

Stage 6 (Figs. 20 – 23)

The three pairs of bulges in the protocephalon become distinct and the protocephalon begins to flex dorsally (Fig. 20). The maxillary and labial appendage anlagen elongate. At the same time, they divide into

two parts and the proximal parts of the rudimentary maxilla and labium split, forming the future lacinia and galea in the former, and the future glossa and paraglossa in the latter (Fig. 21). The distal parts of the appendage anlagen are the rudiments of palpi. The structures of the maxilla and labium are believed to be serially homologous; i.e., the lacinia, galea, and maxillary palp correspond to the glossa, paraglossa, and labial palp. The intercalary segment moves slightly anteromedially and soon disappears. The mandibular appendage anlagen do not undergo any morphological change.

Boundaries are observed between the rudimentary body wall and the bases of the maxillary, labial, and thoracic appendages, leading to the differentiation of the rudimentary tergum in each segment. The thoracic appendages divide transversely to form the coxopodites and telopodites.

The anlagen of the abdominal appendages first appear in this stage. Figure 22 shows the anlagen of the first abdominal appendages, formed as a pair of long bulges laterally. Late in this stage, the abdominal appendages of the anterior segments below the first one are likewise formed (Fig. 23), and the first abdominal appendage anlagen grow and become similar to those of the thoracic appendages. The proctodaeum, with its Y-shaped opening, becomes deeper. During this stage,

the anlage of the caudal filament forms as a small projection posterior to the anus.

Stage 7 (Figs. 24 and 25)

From Stage 6 on, the head lobes extend and curve antero- and dorsolaterally, so that the clypeolabrum and antennae begin to shift anterodorsally (Fig. 24). By a further flexing and spreading of the head lobes, their anterior and lateral edges fuse dorsally, forming the rudimentary head capsule (Stages 8 – 11). Formation of the rudimentary head capsule in Petrobius brevistylis (Larink, 1969) is the same as in Pedetontus unimaculatus. The two initial lobes of the labium, the primordia of the glossa and paraglossa, each divide into two (Fig. 25). Two morphological interpretations have been advanced with regard to the homologies of the four labial lobes in adult machilids: 1) the innermost pair corresponds to the glossae and the outer three pairs to the paraglossae (Börner, 1914; Snodgrass, 1935); or 2) the inner two pairs correspond to the glossae and the outer two pairs to the paraglossae (Verhoeff, 1904; Chaudonneret, 1948). At present, the latter interpretation is generally accepted, and this investigation supports it.

At this stage, a single bulge observed on the ventral surface between the mandibles is the anlage of the hypopharynx (Fig. 25). In the thoracic segments differentiation of terga proceeds.

Stage 8 (Figs. 26 – 28)

The head lobes spread further and flex upward (Fig. 26). The rudimentary hypopharynx grows and extends to the maxillary segment, and the prospective superlinguae form as a pair of small protuberances on the hypopharynx develops into the lingua (Fig. 27).

In the abdomen, differentiation of the terga proceeds, and as in thoracic segments the tergum rudiments come directly into contact with appendages in each segment. Figure 28 shows that a small protuberance forms laterally at the base of the right appendage anlage in the second abdominal segment; this manifests the differentiation of the inner ventral sac and the outer stylus. With subsequent development, anlagen of the abdominal appendages in the third to seventh abdominal segments likewise differentiate primordia of ventral sacs and styli.

Stage 9 (Figs. 29 and 30)

A pair of compound eye anlagen is formed on the posterolateral regions of the rudimentary head capsule, derived from the B_1 protocephalic bulges (Fig. 29). With morphogenesis of the head capsule, the B_1 bulges become dorsal to the maxillary and labial segments. The bases of labial appendages begin to spread and move mediad (Fig. 30).

The first abdominal appendages acquire the charac-

teristic form shown in Figure 29. At the same time, rudiments of the cerci form at the tip of the tenth abdominal segment.

Stage 10 (Figs. 31 – 36)

The head capsule is complete except for the posterior region, which has not yet undergone dorsal closure. The boundaries between the appendages and lateral body walls or tergum rudiments become distinct in the maxillary and labial segments. In the mandibular segment the boundary line also forms, but the anterior boundary of its tergum is not yet visible. The developing compound eyes are pigmented; Figure 31 shows that each eye consists of about ten rudimentary ommatidia in this stage. The median boundary of a pair of bulges (B_3) becomes faint, though prominent at Stage 9, and soon it becomes difficult to distinguish the three pairs of bulges, B_1, B_2, and B_3. The scapus develops in the rudimentary antenna. The maxillary palp elongates, and begins to divide into the trochanter and femur. A pair of labial anlagen moves further medially, and their bases spread over the labial sternum* (Fig. 32). They finally fuse over the sternum completely, forming the postmentum (Fig. 33). The labium acquires its definitive form, and then divides into a proximal and a distal part with the labial suture. At this time,

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* As for the nature of sternum, see Chapter G, I, 4 'Ventral epidermis'.

the mandible changes morphologically; a protuberance, the future molar forms medially from the mandibular base, and the tip of the mandibular rudiment becomes the future incisor (Fig. 36).

Segmentation of the three pairs of thoracic legs proceeds synchronously. By Stage 9, each leg has differentiated into two parts, the coxopodite and telopodite. At this stage, the coxopodite and telopodite are segmented. In the telopodite, the trochanter and pretarsus (whose tip is slightly split longitudinally) first become distinguishable, and then the coxopodite divides into two distal end of the telopodite begins to subdivide into the femur, tibia, and tarsus.

Now eleven abdominal segments are clearly observed, and the cerci are situated on the eleventh segment. The first abdominal appendages transform into sac-shaped pleuropodia. The pleuropodia maintain this configuration until eclosion. The second to seventh abdominal appendages have branched into the anlagen of ventral sacs and styli. They are better developed in the anterior segments than in the posterior ones. These segmental appendages become biramous. At this point in development, the eighth and ninth abdominal appendage anlagen are solid bulges (Fig. 34). Soon, protuberances arise from the outer side of each bulge in

the eighth and ninth abdominal segments, and elongate posteriorly (Fig. 35) to develop later into styli. The embryonic cuticle forms late in this stage.

Stage 11 (Figs. 37 – 39)

The compound eyes develop. A pair of posterior ocelli and a median ocellus are arranged in an inverted triangle. In the mandibular segment, the anterior boundary line of the tergum rudiment forms (Fig. 37), independently of the lateral or posterior boundary line of the bulge, B_1 (see Figs. 24, 26, 29, and 31). Dorsal closure of the head terminates, and the head capsule is now completed. The boundaries between the bulges B_1, B_2, and B_3 now disappear. The developing compound eyes begin to spread and fuse medially. The fusion line extends anteriorly from the eyes along the surface of the cranium, diverging above the median ocellus. This inverted Y-shaped line, the epicranial suture (Fig. 38), is independent of the median boundary line of the pair of bulges (B_3) observed in earlier stages; it includes the coronal suture of the vertex and the frontal suture of the facial region. In addition to the scapus, already developed, the pedicel and flagellum are visible in the developing antennae. The faint transverse line which marks off a small basal portion of the mandible (Fig. 37) can be seen up to Stage 13. The body of the maxilla differentiates into the cardo and stipes. A pit forms at the center of

the boundary line between the cardo and stipes. From the pit a shallow line runs at the surface of the stipes to form a T-shaped structure with the boundary line between the cardo and stipes. This structure persists until Stage 12. The palpifer forms on the basal part of the galea. The tibia and tarsus 1 become visible in the maxillary palp. The palpiger develops and the labial palp divides into three parts, as in an adult. The distal margin of the postmentum thickens (Fig. 39). Segmentation of the legs becomes obvious and the subcoxa enlarges.

The abdominal appendages are fundamentally complete and the coxites begin to differentiate from the basal parts. The caudal filament is clearly marked off from the abdomen (Fig. 37, cf. Fig. 56). In this stage, the dorsal closure is complete in the head, in the anterior half of the prothorax, and in the posterior abdominal segments. The tergum of each segment becomes thick. Figure 37 shows that the terga in the maxillary and labial segments thicken, as in the prothorax.

Stage 12 (Figs. 40 – 42)

During this stage, from late fall to late winter, the embryo of Pedetontus unimaculatus enters diapause.

The ocelli continue to develop. The posterior paired ocelli are less well developed than the median one (as in the first instar larva). Differentiation

of the facial region into the frons, clypeus, and labrum proceeds. The epicranial suture becomes faint, and only the coronal suture remains, later becoming unrecognizable. The inverted triangular area, including the three ocelli, protrudes on the facial region. The hypopharynx enlarges further, so that the lingua adjoins the labium (Fig. 40) and assumes the shape found in the early instar larvae. The flagellum of each antenna divides into about thirty annuli. The femur of the maxillary palp divides into two parts, and the terminal tarsal segment also divides into two parts, as found in the adult, so that the tarsus is composed of three annuli. The prelabium divides into two parts, the prementum and ligula. In the gnathal segments, the boundary lines of the terga appear to fuse with each other behind the compound eyes. A faint line occurs at the lower margins of the maxillary and labial terga, persisting until Stage 13.

A pit is visible on the boundary line between the coxa and subcoxa at the lateral side of each thoracic leg (Fig. 42). Each pretarsus splits longitudinally, later forming two claws each.

In each of the second to seventh abdominal segments, the ventral sac and stylus are basally separate (Fig. 41). Appendages are not visible in the tenth abdominal segment. In each of the first to ninth abdominal segment appendages, a pair of basal parts

spreads over each sternum, and approaches each other becomes fused. Simultaneously, the sternum becomes reduced to anteromedial and posteromedial triangular facets on the ventral surface of each segment (Fig. 41). The intersegmental lines are visible between the sterna of each segment, and the degenerate neural groove still exists. A small depression appears on the surface of each ventral sac; it is believed to be related to the attachment of the retractor muscle of the ventral sac. A ring-like thickening forms around the basal part of the cercus, dividing into five annuli. Three small swellings, which later become the three anal lobes, occur at the ventral surface of the eleventh abdominal segment.

The dorsal closure has been completed in the posterior half of the abdomen, in the first and second abdominal segments, and in the posterior half of the metathorax. The middle abdominal segments are not yet completely closed, so that yolk can still be seen. As mentioned above, the dorsal closure in Pedetontus unimaculatus does not proceed sequentially from the posterior to anterior segments, differing from that in Petrobius brevistylis (Larink, 1969).

Spiracles are first observed in the first to ninth abdominal segments. Pigmentation of the body wall begins to develop posteriorly from the head at this stage.

Stage 13 (Figs. 43, 44, 48, and 49)

With the termination of diapause, development of the embryo resumes. The mesothorax, the posterior half of the prothorax, and the middle abdominal segments finally close dorsally. The dorsal closure is complete in all segments. The larval cuticle then forms beneath the embryonic cuticle. Late in this stage, the setae also appear on the larval cuticle.

The boundary line between the maxillary and labial terga becomes faint (Fig. 43). The region behind the compound eyes (the occipital and postoccipital regions ?) becomes somewhat wider.

The pit on the boundary between the coxa and subcoxa becomes faint in the prothorax, but persists in the meso- and metathorax. The subcoxa is developing into the pleuron.

The coxite in the abdomen becomes thicker. The anterior (median plate) and posterior sternites of each segment also thicken (Fig. 44). The median line in the abdominal sterna finally disappears. Large apical setae form at the tip of each stylus. A pair of low swellings appears at the ventral surface of the tenth abdominal segment. The thickened area of the cercus base begins to spread over the eleventh sternum. Rudiments of the subanal plates become plate-like and extend posteromedially slightly. The rudiment of the supraanal plate becomes more extended.

At this stage, pigmentation develops in the appendages of the head and thorax. Swelling of the egg occurs (Figs. 48 and 49) and the embryo begins to move.

Stage 14 (Figs. 45 and 50)

The embryo grows, finally acquiring the same form as that of the first instar larva (Fig. 50). Soon thereafter, the larva hatches.

The developmental sequence of the pleuropodium and the ventral sac in the first abdominal segment is noteworthy. First, the stalk of the pleuropodium becomes slender and its distal sac diminishes in size. Later, a small section separates medially at the root of the stalk (Fig. 45). It is the anlage of the first ventral sac. Shortly thereafter, the pleuropodium collapses and degenerates. The ventral sac anlage persists and develops into the definitive ventral sac, as in other segments.

An egg tooth is not found in Pedetontus unimaculatus in any stage, as in Petrobius brevistylis (Larink, 1969). On the other hand, it is found in the Thysanura, such as Lepisma saccharina (Heymons, 1897a; Sharov, 1953; Larink, 1970), Ctenolepisma longicaudata (Lindsay, 1940), and Thermobia domestica (Sahrhage, 1953).

First instar larva (Figs. 46 and 47)

Although the boundary line between the maxillary and labial terga fades, the line between the mandibular and the maxillary terga remains, and a faint anterior

boundary of the mandibular segment can be observed (Fig. 46). The faint transverse line on the basal part of the mandible disappears. Just after hatching, the molar and incisor of the mandible are not as well developed as those of an adult. On the maxilla, the stipes elongates and the lacinia become denticulate apically. On the apex of the labial palp several sensory cones appear.

In the adult Pedetontus unimaculatus, the thoracic tarsus divides into three parts, but only one segment can be seen in the first instar larva. The thoracic styli of the meso- and metathorax, characteristic of the adult, have not appeared.

In the adult, a pair of ventral sacs exists in the first abdominal segment, two pairs in the second to fifth segments, and a pair each in the sixth and seventh abdominal segments. In the first instar larva, only one pair of ventral sacs is present throughout the first to seventh abdominal segments (Fig. 47), while during postembryonic development the ventral sacs of the second to fifth segments double. The cercus bases spread over the ventral surface, reaching the anterior margin of the eleventh abdominal segment, and medially, the subanal plates. In the eleventh segment, development of the tergum is incomplete. The subanal plates take their definitive form on the posterior midventral surface of the eleventh segment. The supraanal plates

are just posterior to the anus.

F. Formation of inner layer

The formation of inner layer begins in Stage 1. The germ disc is initially composed of only the ectoderm, of which cells are irregularly arranged (Fig. 4). Soon, the cell arrangement becomes vertical to the egg surface, and a group of cells irregularly arranged appears on the dorsal surface of the ectodermal region (Fig. 5). These newly differentiated cells are the inner layer or mesodermal cells. Although this cell group is bordered with the ectoderm by a basement membrane-like structure, they have a communication at the posterior end of germ disc, and for some time the communication is retained. Numerous mitotic figures are found in the ectodermal region, while in the inner layer rarely. The mesodermal cells probably migrate through this communication from the ectodermal region. The cell arrangement of ectodermal cells in the posterior end of germ disc suggests this idea (Fig. 5). The description mentioned above is very similar to that Larink (1969) did for Petrobius brevistylis.

In Stage 2, with the extension of the germ disc which now should be called the germ band or embryo, the inner layer also extends anteriorly on the dorsal surface of germ band (Fig. 80a). However, it does not reach the anterior extreme end and the lateral margins

of germ band. The inner layer, which is initially rather thick, is now thinned into an unicellular layer, although still more or less thick in the posterior region. A large number of mitotic figures are found in the ectodermal region, but the mesodermal cells do not undergo mitoses for a time, until it differentiates into mesodermal somites later. The anterior migration of mesodermal cells is, therefore, considered as the passive one that is responsible for the extension of the ectodermal part of germ band. It is possible that the additional inner layer cells should be further provided from the ectodermal region. In Stage 4, the bounding between the ectodermal region and inner layer at the posterior end of embryo is finally established, and this represents the completion of the differentiation of germ layers.

The proliferation zone of mesoderm in Pedetontus unimaculatus is confined to the posterior region of embryo, as in Petrobius brevistylis (Larink, 1969). In the Thysanura, the proliferation zone is also localized: upon the central region of embryo in Thermobia domestica and Ctenolepisma lineata (Woodland, 1957) and upon the anterior region in Lepisma saccharina (Sharov, 1953). In Pedetontus unimaculatus, the formation of inner layer does not involve the differentiation of primitive groove, as in Petrobius brevistylis and the Thysanura. The inner layer for-

mation in Ephemera strigata (Ando and Kawana, 1956) and the Odonata (Ando, 1962) is of so-called the proliferation type, and the primitive groove does not intervene the formation of inner layer. The proliferation zone, however, is not so localized, in contrast to the case in Pedetontus unimaculatus and so on. This type of the formation of inner layer, the proliferation type without the intervention of primitive groove, is also found in collembolans (cf. Jura, 1972) and myriapods (Heymons, 1901), but the proliferation zone is not localized in these animals. The inner layer formation has been one of the interesting subjects in the insect and arthropod comparative embryology. Detailed reviews on this subject has been made by Roonwal (1936, 1939a, b), Johannsen and Butt (1941), Siewing (1965) and Anderson (1972a, b, 1973).

G. Organogenesis

In this chapter the organogenesis of Pedetontus unimaculatus will be described under four sections: I. Ectodermal derivatives, II. Mesodermal derivatives, III. Endodermal derivatives, and IV. Other structures. The germ layer theory and the definition of germ layers are much controversial, but in this paper, each of germ layers will be dealt with as follows. The cells in the egg are at first differentiated into the yolk cells staying inside the yolk, and the

blastoderm and germ rudiment being on the surface of the egg. The former or yolk cells are the endoderm. The germ rudiment itself differentiates into two principal groups of cells in next development (see Chapter F). The organs derived from the outer (lower) of these groups of cells will be regarded as the ectodermal derivatives, and ones derived from the inner (upper) as the mesodermal derivatives.

I. Ectodermal derivatives

1. Nervous system

i) Central nervous system

a. Ventral nerve cord

The formation of ventral nerve cord is the most progressive in the gnathal segments, and towards the posterior segments its formation is more delayed. For example, in Stage 4 the differentiation of neuroblasts occurs in the thoracic segments, while in and after Stage 10 in the eleventh abdominal segment. The following descriptions are, so far as emphatically said, based on the observations on the thoracic segments. The manner of the formation of nervous system in the gnathal and abdominal regions is fundamentally the same as that in the thoracic segments.

Ganglion In Stage 3, a pair of swellings appear between the paired appendages on the ventral side of each segment of embryos. These represent the

differentiation of ganglion anlagen in each segment. The mid-ventral groove observed at this time is, therefore, the rudimentary neural groove (cf. Chapter E, Stage 3). The ectoderm between a pair of ganglion anlagen or lateral cords develops into the median cord (Fig. 51).

In Stage 4, the large cells whose nuclei are less stained with hematoxylin, i.e., neuroblasts, appear in the basal region of ganglion anlagen (Fig. 52). Each ganglion anlage has four to five neuroblasts in the transverse section and six to seven in the longitudinal. The cells ventral to the neuroblasts are thinned, to form the ventral epidermis. However, this epidermis is ephemeral, and called the 'provisional ventral epidermis' in this paper. In parallel with this, now the neuroblasts are situated at the venter-most region of the ganglion anlagen. In Pedetontus unimaculatus, when the differentiation of neuroblasts, the germ band is thick, and there are many cells dorsal to the neuroblasts (Fig. 52). These cells seem to develop into the ganglion cells, since no degeneration figure of cell is observed later.

The neuroblasts begin a series of divisions, the spindle axes of which are approximately at right angles to the surface of the embryo, to give rise to smaller and darker daughter cells or ganglion cells. With each subsequent division, the previously formed ganglion

cells are pushed farther away from the surface, forming a straight row above each neuroblast. The daughter cell just above the neuroblast is slightly larger than the other ganglion cells, and retains the neurogenic function. The spindle axis of its division is generally at right angles to the surface of the embryo. A few mitotic figures are also observed in the other regions of ganglion anlagen.

The ganglion cells thus increase in number, and gradually become concentrated into the ganglia which acquire a segmental nature corresponding to the external body segment. Then in Stage 10, the formation of ganglia at last finishes. A columnar arrangement of ganglion cells has not been recognized, and the neuroblasts become undistinguishable from their daughter cells. Since no degeneration figure is found where the neuroblasts were, it is considered that the neuroblasts probably change themselves into the ganglion cells proper, as suggested by Larink (1969) for Petrobius brevistylis and Roonwal (1937) for Locusta migratoria migratorioides.

Neuropile About in Stage 7, a pair of fibrous structures, i.e. neuropiles, begins to be produced at the dorsal side of the ganglion in each segment. A pair of neuropiles of each segment fuses medially with each other, with the extension of them. Two thick bundles are observed between a pair of neuropiles in

their communicating area. These bundles are the anterior and posterior commissures, and each is respectively composed of two subbundles. As the same time, the communication of neuropiles in each segment with the neuropiles in just anterior and posterior segments is established with the connectives. Coinciding with this, from the median outer side of each neuropiles, the paired nerve bundles extend out to innervate the corresponding segments. The ganglion cells between the paired connectives almost become degenerate to disappear.

The neuropiles of Pedetontus unimaculatus are not covered with any ganglion cells, as in the cases for Petrobius brevistylis (Larink, 1969), Lepisma saccharina (Heymons, 1897a) and Thermobia domestica (Woodland, 1957). This condition is one of the anatomical characteristics of the Microcoryphia and Thysanura.

Nerve cord In the gnathal and abdominal segments, the ganglia are formed in the same way as observed in the thoracic ones. In Stage 10, the eleventh abdominal ganglion differentiates finally. Now the seventeen ganglia, one for each segment from the mandibular to the eleventh abdominal, are observed, and they are connected with each other by the connectives, to form a ventral nerve cord. In lepismatids (Heymons, 1897a; Woodland, 1957), the connectives of abdominal segments are not formed until the postembryonic period, as in

a marked contrast to the cases in the machilidan Pedetontus unimaculatus and Petrobius brevistylis (Larink, 1969). The ganglia are extremely concentrated in the mandibular, maxillary and labial segments and the eighth to eleventh abdominal ones. The former ganglia form the suboesophageal ganglion, and the latter the eighth abdominal ganglion of the larval and imaginal insects.

•Suboesophageal ganglion Only one commissure is recognized in the mandibular ganglion (Fig. 53), while two in each of the maxillary and labial ganglia the same as previously described for the thoracic ganglia. This condition in the mandiublar ganglion is probably caused by the fusion of the anterior and posterior commissures, owing to the contraction of the mandibular segment associated with the progressing concentration of the head segments.

In Stage 10, the anterior and posterior commissures in each of the maxillary and labial segments fuse together respectively, and then the neuropiles of three gnathal segments begin to fuse with each other. Late in this stage, three ganglia fuse up together. With the progression of development, the solidness of gnathal ganglia is further promoted. The suboesophageal ganglion is definitively situated in the region surrounded anteroventrally with the hypopharynx and posteroventrally with the postmentum (Fig. 54).

•Eighth to eleventh abdominal ganglia The eleventh abdominal ganglion anlage differentiates in Stage 10 (Fig. 55). It is clearly marked off from the subanal plate anlagen. The two commissures are recognized in each of the eighth to eleventh abdominal segments as in the preceding segments, but in the eleventh abdominal segments only one, probably owing to the fusion of two commissures. Early in Stage 11, the ganglia of the tenth and eleventh segments begin to fuse together (Fig. 56), and the posterior commissure of the former fuses with the neuropile of the latter. This is followed by the fusions of the anterior and posterior commissures in each of the eighth to tenth abdominal segments. In Stage 12, the eighth to tenth with eleventh abdominal ganglia fuse together, to form the large but compact 'eighth abdominal ganglion', and the neuropiles of these ganglia are united with each other into solid. The newly formed eighth ganglion loses a communication with the ventral epidermis. With the extension and enlargement of each segment, the ganglion relatively shifts its position, and is definitively situated in the eighth and ninth abdominal segments in the embryo near the hatching (Fig. 76).

The eleventh abdominal ganglion has been reported in the most lower insects and some of the higher, such as the microcoryphian Petrobius brevistylis (Larink, 1969), the thysanuran Lepisma saccharina

(Heymons, 1897a) and Thermobia domestica (Woodland, 1957), the ephemeropterans (Heymons, 1896a), the dragonflies (Ando, 1962), the orthopteran Gryllotalpa vulgaris, Gryllus domestica, G. campestris (Heymons, 1895), and Locusta migratoria migratorioides (Roonwal, 1937), the blattarian Periplaneta orientalis (Heymons, 1895), the coleopteran Leptinotarsa decemlineata (Wheeler, 1889), Donacia crassipes (Hirschler, 1909), and Calandra oryzae (Tiegs and Murray, 1938), and the hymenopteran Apis mellifica (Nelson, 1915). The presence of the eleventh abdominal ganglion may be regarded as one of the fundamental characteristics of insect embryos.

Median cord The median cord is a part of the ventral plate which is not involved in the formation of ganglion anlagen or lateral cords and left between them (Fig. 51). Accordingly the enlargement of lateral cords, it is pushed away dorsally, to assume a wedge shape (Fig. 52). About in Stage 7, the boundary of the median cord and ganglion anlagen becomes obscure. Soon, the median cord is divided into right and left, and incorporated into the ganglion anlage in each side.

The median cord is wanting neuroblasts as in Petrobius brevistylis (Larink, 1969), in contrast to the case in the Odonata (Ando, 1962), Locusta migratoria migratorioides (Roonwal, 1937), Forficula auricularis (Heymons, 1895) and so on.

Various interpretations concerning the fate of

median cord has been made (cf. Johannsen and Butt, 1941; Okada, 1960; Ando, 1962). That is; differentiating into i) a part of the ganglion, ii) a part of the endoskeleton, iii) the neurilemma, iv) producing the fibers of commissures, or v) not developing into any tissues, i.e. degeneration. In Pedetontus unimaculatus, since the neuropile appears where the median cord was incorporated into ganglion cells, the median cord possibly contributes to the formation of the neuropile, mainly the commissures, as is coincident with Larink's (1969) and Woodland's (1957) views. In Lepisma saccharina, according to Heymons (1897a), a continuous median cord or "dunckler Streifen" is set free from the lateral cords, and presents in the freshly hatched insect, extending the entire length of the ventral nerve cord.

b. Tritocerebrum

The tritocerebrum is derived from the paired ganglia of the intercalary segment. The intercalary ganglion is formed in the same way as in the thoracic ganglia. The formation of intercalary ganglion is slightly progressive than those of the gnathal ones.

The paired intercalary ganglion anlagen are situated just posteriorly to the stomodaeum. They are apart from each other except for their posterior halves. The ectoderm between them which corresponds to median cords of the other segments is broad and

makes the posterolateral wall of the stomodaeum. The ganglion anlagen of the intercalary segment are in contact with anteriorly the antennal ganglion anlagen, and with posteriorly the mandibular ones. In Stage 7, the neuropile of the intercalary ganglion forms, and soon the communications with the antennal and mandibular ganglia are established by the connectives. In the intercalary ganglion, the anterior and posterior commissures are recognized as in the succeeding segments. When the progression of development, the intercalary ganglion becomes larger, and its neuropile also increases in size. Then, the intercalary ganglion or tritocerebrum fuses with the deutocerebrum.

In Stage 12, the tritocerebrum acquires the definitive structure and position. Its two commissures are the characteristic structures known as the suboesophageal commissures. Owing to the morphogenesis of the head, especially of the buccal cavity, the tritocerebrum comes to be apart from the suboesophageal ganglion, and the connectives between them, i.e. circumoesophageal connectives become longer. The ganglion cells between the tritocerebrum and suboesophageal ganglion are obliterated. There is no fundamentally difference between the manners of formation of the tritocerebrum in Pedetontus unimaculatus and in the other insects. The only one characteristic of the tritocerebrum of this species is concerning the

definitive position. That is, it conserves its original postoral position (Figs. 53, 54 and 70; cf. Figs. 57 and 58), while generally in insects the tritocerebrum shifts its position anteriorly from the original postoral. Therefore, the suboesophageal commissures are not so stretched, and each commissure is clearly recognized in Pedetontus unimaculatus. Furthermore, the circumoesophageal connectives remain rather posteriorly to the stomodaeum, in contrast to the case in the other insects. In the larvae and adults of Pedetontus unimaculatus, the tritocerebrum retains its original or embryonic postoral position as the definitive, as may be considered to reflect the primitive nature of this species.

The tritocerebrum innervates the clypeolabrum with a pair of thick nerve bundles, that is, labral nerves.

c. Deutocerebrum

The deutocerebrum is derived from the ganglia of antennal segment. It is formed, as well as the tritocerebrum, in the same way as the ganglia of the succeeding segments. Its formation is slightly more progressive.

The paired antennal ganglion anlagen are situated just anteriorly to the stomodaeum, and are in contact with the anlagen of the protocerebral ganglia lobi 3 anteirorly and with the intercalary ganglion anlagen

posteriorly. A pair of the antennal ganglion anlagen is apart from each other except for their anterior halves. The ectoderm between them which corresponds to median cords of the other segments is broad, and makes the anterolateral wall of stomodaeum and clypeolabral epidermis.

About in Stage 7, the neuropiles are formed. Soon, the neuropiles in both sides are connected with each other by a fibrous bundle, and fuse with neuropiles of protocerebral ganglia lobi 3. The antennal commissure is not doubled but single. Accompanied with the progression of development, the antennal ganglia become larger, and their neuropiles increase in size. Then the antennal ganglia (i.e. deutocerebrum) acquire its definitive form. The deutocerebrum fuses with the other parts of the brain. The definitive position of deutocerebrum is anterolateral to the stomodaeum, and it is the same as the original (cf. Figs. 54, 57, and 58). The deutocerebrum innervates the antennae with the thick antennal nerves. There is fundamentally no difference between the manner of deutocerebrum formation in Pedetontus unimaculatus and those in the other insects.

d. Protocerebrum

In Stage 3, the anterior broad region of the protocephalon differentiates into the ventral unicellular

structure and the dorsal multi-cellular one. The former is the future epidermis, and the latter whose cells are weakly stained with hematoxylin later develops into the protocerebral ganglia. The latter part is originally divided into two, right and left. In Stage 4, the each is transversely divided into three, from the most lateral to median, the lobus 1, lobus 2 and lobus 3 (cf. Fig. 57). These are the future three pairs of protocerebral ganglia (cf. Fig. 58). The lobus 1 is the "optic ganglion" and the lobus 3 is the ganglion of the so-called preantennal segment. The structures called the bulge 1, 2 and 3 in Chapter E respectively correspond to the superficial structures of lobus 1, 2 and 3. The neuroblasts, shortly, appear in the ventral region of each of the lobus 2 and 3. Each has four to five neuroblasts in the transverse section. These neuroblasts divide mitotically, and form a straight row of daughter cells above them, as observed in the ganglia of succeeding segments (Fig. 59). No special neurogenic cells are found in the lobus 1 as in Petrobius brevistylis (Larink, 1969), and so the columnar arrangements of ganglion cells are not observed. Many mitotic figures are distributed at random in the lobus 1. Such differences as observed in machilids between the lobus 1, 2, and 3 are general in insects (cf. Johannsen and Butt, 1941; Anderson, 1972a, b).

In Stage 7, the neuropiles are formed in the dorsal regions of each of the lobus 2 and 3. They, soon, extend, and the neuropiles of lobus 2 and 3 fuse with each other, and those of lobi 3 in each side are also fused together (Fig. 59). The rudimentary epidermis ventral to the lobus 1 becomes thick, and is the future optic plate. The lobus 1, in contrast to the lobus 2 and 3, loses the communication with its epidermis (Fig. 59). A continuous chain of neuropile of the lobus 2 and 3 is in contact with the lobi 1 in each side, but the neuropile formation in the lobus 1 is delayed. The mostmedian part of lobus 3 is marked off, to become a structure named lobus 3′, as Larink (1969) observed for Petrobius brevistylis.

With the advancement of development, each of the lobus 1, 2, 3, and 3′ increases in size, and their neuropiles also enlarge. These protocerebral ganglia begin to fuse with each other, to form the protocerebrum. Coinciding with fusion of protocerebral ganglia, the developing protocerebrum fuses with the deutocerebrum, and they form a solid brain with the tritocerebrum. With the morphogenesis of head (cf. Chatper E, Stages 7 – 11) and the enlargement of each cerebral ganglion, the relative positions of each ganglion in the brain are considerably changed (see e. 'Morphogenesis of brain'). For example, the lobus 3′ is originally a small section situated medially to the lobus 3, but

now it reaches the lobus 1, passing between the lobi 2 of each side (Fig. 63).

Some morphological differences are recognized among the nuclei of protocerebral ganglia about until Stage 12. The nuclei of the lobus 1 are apparently smaller and more darkly stained with hematoxylin than those of the lobus 2 and 3. The nuclei of the lobus 3′ are, not so as those of the lobus 1, smaller and darker. When the advance of development, these morphological differences become obscure. It is impossible to find any morphological differences between nuclei of the lobus 2 and 3.

Owing to the fusion of protocerebral ganglion, it becomes difficult to distinguish the lobus 1, 2, 3, and 3′ from each other. They are, however, sheathed with a fine membrane, i.e. neurilemma, so that they are barely distinguishable from each other. A pair of the anterior suspensions of anterior tentoria passes between the lobus 2 and 3′ in each side. The morphological differences of the nuclei of each ganglion, although not perpetual, also make the distinguishment of the protocerebral parts more or less easier.

In Stage 12, the protocerebrum or its three pairs of ganglia acquire the definitive forms. In the neuropiles of the lobus 3, a pair of centers, i.e. accessory lobes or Nebenlappen, differentiates, and the accessory lobes in both sides are connected by the accessory lobe

commissure (Fig. 61). The neuropiles of the lobi 2 make the principal parts of a pair of the large protocerebral lobes. The region surrounded by a pair of the protocerebral lobes, accessory lobes, and the accessory lobe commissure is the pars intercerebralis. It belongs to the lobus 3 and 3′ (Figs. 60 and 61). In general the pars intercerebralis of insects forms the upper protocerebral bridge and the lower central body (cf. Fig. 61). Three ocellar pedicels are formed on the frontal region of neuropile of the lobus 3′, be arranged in inverted triangle. These structures, however, are not clearly observed until the postembryonic period. The ocellus is, originally, the merely ectodermal thickening, and in Stage 11 it already differentiates into the outer corneagenous cell layer and the inner pigmented retinular cell layer. Later, the lobus 3′ innervates the retinular cells of ocelli with the ocellar nerve which are derived from the ocellar pedicels. The neuropile of lobus 1 is composed of the distal small and proximal large structures. The former is the lamina ganglionaris, and the latter is the composite of the distal medulla externa and proximal medulla interna (Fig. 62). The medullae interna and externa contact with the lobus 2 medially. A group of large cells appears medially to the medulla externa, to be situated at the region of lobus 2. These may be a kind of neurosecretory cells.

From the time of their differentiation, the optic plate and lobus 1 have been apart from each other. In Stage 8 or 9, the communication between them is re-established. That is, the posterolateral end of lobus 1 curves laterodorsally to contact with the optic plate (Fig. 53). This curving structure of lobus 1 develops into the postretinal fiber about in Stage 10. The cell arrangement in the optic plate in initially at right angle to its surface, but it is gradually converted into radial. In Stage 10, the optic plate except for its outer thin layer is pigmented. The pigmented region includes the retinular cells, and the cells of unpigmented outer layer develops into the corneagenous cells and Semper's nuclei. The postretinal fibers or optic nerves run from the lamina ganglionaris posterodorsally in the lobus 1, and curve anteriorly to reach the central region of radial cell arrangement of the optic plate or rudimentary compound eye, i.e. the lowest ends of retinular cells. In Stage 12, the postretinal fibers are partially pigmented.

e. Morphogenesis of brain

As a result of the curving and extending dorsally of the head lobe, the head capsule is formed (Stages 7 – 11). With these processes and the enlargement of cerebral ganglia themselves, the relative positions of each gagnlion of the brain, i.e. the protocerebral lobi 1, 2, 3, and 3′, the antennal (deutocerebrum) and

the intercalary (tritocerebrum) ganglia, are extremely converted. Figure 63 shows the processes of morphogenesis of the brain diagrammatically.

The deutocerebrum mounts the tritocerebrum, and the deutocerebrum itself is mounted by the protocerebral ganglia, lobi 3. The lobi 3′ extend posteriorly along the median line. The lobi 2 with contact with the lobi 3 shift their positions posteromedially, to acquire the communications with the lobi 3′ medially and with the deutocerebrum anteroventrally. The lobi 1 hanging over the lobi 2 move posteromedially in company with the lobi 2, to fuse with each other medially and to contact aneriorly with the lobi 3′. Thus, the solid brain is completed.

f. Neurilemma

In later stages, the ganglia are sheathed by a fine cellular membrane, that is, neurilemma. Although the neurilemma of the lobi 1, 2, 3, and 3′ of the protocerebrum proves to be derived from the preoral mesoderm (mentioned later), the author can not sufficiently refer to the origin of neurilemma in the other ganglia. The precise determination of its origin is rendered difficult by the presence of various loose cells of different origins, which lie in a more or less close association with the ganglia.

The neurilemma is generally originated from the outer layer of ganglia in insects (Heymons, 1895;

Strindberg, 1913; Eastham, 1930; Roonwal, 1937; Görg, 1959; Ando, 1962; Ashhurst, 1965). The different opinions regarding its origin are, however, reported in various insects (cf. Johannsen and Butt, 1941; Anderson, 1972a, b). Larink (1969) suggested the mesodermal origin of the neurilemma in Petrobius brevistylis. In Pedetontus unimaculatus, there are three possible interpretations concerning its origin: i) a part of secondary median mesoderm, ii) provisional ventral epidermis (see Chapter G, I, 4), and iii) outer layer of ganglionic cells. The possibility that it is formed with the median cord as in Xiphidium ensiferm (Wheeler, 1893) is precluded in Pedetontus unimaculatus.

ii) Stomatogastric nervous system

Hardly any available data on the development of stomatogastric nervous system in Pedetontus unimaculatus are obtained. Only the presence of the frontal ganglion and recurrent nerve are recognized. In Stage 12, these structures appear (Fig. 54). The frontal ganglion is situated on the anterior wall of the stomodaeum in the clypeus. The recurrent nerve starts from the frontal ganglion, to run backwards along the stomodaeum. The neuropile of these structures differentiates in their lower regions. A thin mesodermal layer is present between the stomodaeal wall and these structures.

Anatomical studies of the stomatogastric nervous

system in machilids were made by Bitsch (1963).

2. Invaginations (endoskeletons, glands and tracheae)

i) Tentoria

The tentoria are composed of the anterior and posterior tentoria. They are the endoskeletal braces of the cranium, giving attachments to the antennal and gnathal muscles.

The anterior tentorium is formed as the ectodermal invagination appearing medially to the mandibular bases in the intersegmental groove between the intercalary and mandibular segments in Stage 7 (Fig. 64). Since the ventral epidermis is derived from the appendages (see Chapter G, I, 4), the anterior tentorium is also appendicular in origin. The anterior tentorial anlagen gradually elongate. The pair is connected with a bundle of the mandibular mesoderm is Stage 10, which later develops into the tendon combining the paired anterior tentoria. In Stage 12, the blind ends of anterior tentorial anlagen enlarge and closely approach each other, and are bound by the tendon tightly. The blind ends assume triangular shape in the sagittal section, and now become situated just beneath the stomodaeum (Fig. 54), to make the bodies of anterior tentoria. In full-grown embryos, the lumen of the anterior tentorium which is initially more or less broad becomes narrow. The part near the aperture of

the invagination almost becomes very thin, but its communication with the epithelial ectoderm is retained. Accordingly the enlargement of the cranium, the anterior tentoria more elongate longitudinally.

The posterior tentorium is derived from the apodeme formed on the lateral wall of the head between the bases of anlagen of the maxillary and labial appendages (Fig. 62). Its invagination begins in Stage 11. The aperture of its invagination or the posterior tentorial pit is a longitudinally prolonged slit. The paired broad posterior tentorial anlagen extend, twisting themselves, along the suboesophageal ganglion to fuse together medially. The paired anlagen now make the broad plate or the posterior tentorium situated just above the suboesophageal ganglion (Fig. 65). The lumina in each plate are completely connected with each other, and are rather narrower than those in the anterior tentoria. As mentioned before, the posterior tentorium is originated from only the bases of the appendages, i.e. the maxillary and labial, and is appendicular in origin.

The anterior and posterior tentoria of Pedetontus unimaculatus approach each other, but they never contact or fuse together as in Petrobius brevistylis (Larink, 1969) and Lepisma saccharina (Larink, 1970), and there is a remarkable contrast to the cases in all pterygote insects: the anterior and posterior tentoria completely fuse together to form the central body. The unfused

tentoria are the considerable anatomical characteristics of the Microcoryphia and Thysanura. In general it is thought that this condition of the tentorium reflects the primitive nature of these insects. In full-grown embryos, on the outer or free surface of the walls of tentoria, cuticle is secreted, and is connected with the cuticle of body surface, assuming the same stainability as that of the latter: outer layer is darkly stained with the eosin or chromotrope 2R and inner one chromophobe.

In insects, the anterior tentorium generally originates in the ventrolateral ectoderm between the antennal and mandibular segments, and the posterior tentorium in that between the mandibular and labial segments (cf. Anderson, 1972a, b). The position of tentorial invagination is unsettled in insects, and there are wide variations. Further, although the anterior tentoria of the Odonata (Ando, 1962) and Locusta migratoria migratorioides (Roonwal, 1937) are originated from the bases of mandibles similarly to that in Pedetontus unimaculatus, but the relative position to the mandible is anterior in Locusta, and lateral in the Odonata, while medial in Pedetontus unimaculatus. Thus, the differences not to be ignored concerning the invaginating position of the anterior tentorium are found in insects. This is not only true of the anterior tentorium, but also holds good for the

posterior tentorium, and further the structures mentioned later, the corpus allatum, salivary gland, and so on. It remains to be proved how these differences should be dealt with in the view-point of the comparative embryology.

ii) Lacinial apodemes

The lacinial apodeme gives the attachments to the stipito-lacinial, tergo-lacinial and tentorio-lacinial muscles. In Stage 7, a pair of ectodermal invaginations appears near the middle of the medial side of each maxillary base, and they gradually proceed upwards. They are the developing lacinial apodemes and are appendicular in origin. In Stage 12, the mesoderm which is on the way of differentiation into the muscles attaches to the lacinial apodemes (Fig. 65). All or most of insects, of course, should possess the homologous structures with the lacinial apodemes of Pedetontus unimaculatus.

iii) Corpora allata

Yashika (1960) studied the development of corpus allatum of the thysanuran Ctenolepisma villosa in detail, and he, further, demonstrated its juvenile action in the experimental way. In Pedetontus unimaculatus, the organ whose manner of the development and morphological characteristics are very similar to those of the corpus allatum of Ctenolepisma villosa is observed. The author identifies this organ as the

corpus allatum, on the basis of these similarities between it and the corpus allatum of Ctenolepisma villosa.

The corpora allata of Pedetontus unimaculatus are formed as a pair of ectodermal invaginations which appears on the intersegmental groove between the mandibular and maxillary segments, just beneath their terga. The corpora allata are probably both tergal and appendicular in origin. Each proceeds ventromedially, and in Stage 12 it then slightly curves, to run dorsomedially. The lumen of the part in curving point is not small, but in the other parts it is hardly discernible (Fig. 65). In Stage 13, the parts both distal and proximal to the curving point become to degenerate, and only the part in the curving point remains to develop into the corpus allatum. In this stage, each of corpora allata is composed of 20 to 30 large cells whose cytoplasm is more or less darkly stained with hematoxylin, and is a little more than 20 μm in diameter (Fig. 66). The corpora allata generally originate in the blind ends of invaginations in insects, in a contrast to those of Pedetontus unimaculatus. The invaginating position of corpus allatum of Pedetontus unimaculatus is coincident with those of the phasmidan Carausius morosus (Leuzinger, Wiesmann and Lehmann, 1926), the orthopteran Locusta migratoria migratorioides (Roonwal, 1937) and the coleopteran

Silpha obscura (Smreczyński, 1932) and Corynodes pupis (Paterson, 1936). On the other hand, the corpora allata of the hymenopteran Myrmica rubra (Janet, 1899) and Apis mellifica (Nelson, 1915) originate in the mandibular segment, and those of the dermapteran Forficula auricularia (Heymons, 1895) originate in the maxillary segment, and those of the coleopteran Calandra oryzae (Tiegs and Murray, 1938) originate in the antennal segment. While the corpora allata are formed as the subdivisions of the anterior tentoria in the Odonata (Ando, 1962), the origin of the corpora allata is closely associated with the posterior tentorial arms generally in the hemimetabolous insects (cf. Anderson, 1972a).

iv) Salivary glands

In Stage 7, a pair of ectodermal invaginations arises close to the middle of the median side of each labial base (Fig. 67). They are the anlage of the salivary gland, and appendicular in origin. As they proceed dorsally, a pair of labial appendage anlagen gradually approachs each other (Stage 9), and they finally fuse together medially in Stage 10, to make the postmentum (see Chapter E). The labial apodemes situated at the inner base of each anlage of the appendages, therefore, also fuse with each other medially, to form a single tube. This single tube bifurcates right and left at the base of the

postmentum, and proceeds laterally (Fig. 68). Each tube becomes to be convoluted beneath the compound eyes, innerly to the gnathal terga, to form the salivary gland (Fig. 60). Its aperture is situated just behind the hypopharynx or lingua.

The salivary glands generally originate in the labial segment in insects (cf. Johannsen and Butt, 1941; Anderson, 1972a, b). The labial glands are generally the salivary ones, but in the Lepidoptera they are often the silk glands. In the Odonata (Ando, 1962) and the lepidopteran Pieris rapae (Eastham, 1930), the salivary glands originate in the mandibular segment, and in Locusta migratoria migratorioides (Roonwal, 1937) they are derived from the maxillary segment.

v) Tracheae

In the adults of Pedetontus unimaculatus, the spiracles are present in the meso- and metathorax, and the second to eighth abdominal segments. Each of them is situated at the anterolower region of the inner wall of the tergal extension in each segment. In the tracheal system of Pedetontus unimaculatus, the longitudinal tracheal trunks as found in the other insects are not formed.

In Stage 11, with the thickening of the terga, the ectodermal invaginations arise at the anterior regions between the each developing tergum and appendage in the meso- and metathorax (Fig. 69). These are

the tracheal anlagen.

The development of tracheae in the abdomen could not be followed in sectioned materials. In Stage 12, the small pits are formed at the anterolower region of each of the first to ninth abdominal terga (see Chapter E). They are probably the rudimentary spiracles, and the first and ninth pits are believed to be degenerate later. These pits are located in the outer surface of each tergum, while the spiracles are present at the inner walls of tergal extensions in adults. The spiracles of embryos of Lepisma saccharina (Heymons, 1897a), which arise in the first to ninth abdominal segments and rudimentarily in the tenth, occupy the similar positions on the terga to the pits of Pedetontus unimaculatus. The spiracles are, however, situated at the region between the terga and sterna (precoxosterna) in the adults (Sharov, 1953). In Lepisma saccharina, the migration of spiracles is, thus, recognized. Some kind of migration of spiracles, such as that in Lepisma saccharina, may also occur in Pedetontus unimaculatus.

vi) Suboesophageal process

A single ectodermal invagination formed between the circumoesophageal connectives is called the "suboesophageal process" here.

In Stage 9, the median part of the intersegmental groove between the intercalary and mandibular segments begins to invaginate (Fig. 53). It proceeds upwards

to enter the space between the paired circumoesophageal connectives (Fig. 70). This is the suboesophageal process. It is probably of the definitive ventral epidermis, or appendicular in origin (see Chapter G, I, 4).

It seems to serve as the endoskeletal brace for the hypopharynx and buccal region.

3. Alimentary canal

The alimentary canal is composed of three principal parts; the stomodaeum (foregut), the midgut and the proctodaeum (hindgut). The midgut epithelium is exclusively derived from the yolk cells or endoderm, and its developmental process will be later referred to in the other section (Chapter G, III, 1). Here, the ectodermal parts of alimentary canal, i.e. the stomodaeum and proctodaeum, and further the malpighian tubules which are accessories of the proctodaeum are dealt with.

i) Stomodaeum

In Stage 3, the shallow stomodaeal anlage appears at the extreme anterior end of the neural groove. Its position is between the antennal and intercalary segments. The stomodaeal invagination initially proceeds dorsally, and then gradually curves posteriorly. Shortly, the lumen of the stomodaeum becomes narrow, assuming cresent shape in the cross section. At this time,

the dorsal (anterior) wall of stomodaeum is, therefore, thicker than the ventral (posterior) (Figs. 53, 70, and 71). At about Stage 6, the blind end becomes thin, soon, to be unicellular. The stomodaeal invagination further proceeds backwards, and excludes the thick rudimentary midgut from the developing cranium, so that the large space appears beneath the developing protocerebrum. This additional space thus provided gives a room for further development to the rudimentary protocerebrum.

The tip of the stomodaeum begins to extend in Stage 12 (Fig. 73), to differentiate into the cardiac valve (cf. Fig. 72). In Stage 14, the septum between the developing stomodaeum and midgut breaks down, and the communication between them is established. The lumen of the posterior part of stomodaeum becomes round in the cross section. The inner walls of the stomodaeum and cardiac valve are covered with cuticle, as in other ectodermal epithelia.

ii) Proctodaeum

In Stage 4, the T-shaped shallow proctodaeal notch appears at the extreme posterior end of the neural groove. The proctodaeal invagination is initially covered with the mesodermal mass, but it soon penetrates the latter, to proceed dorsally (Fig. 74). The proctodaeal invagination arises in the abdominal region unsegmented yet. Only the observations on the

further development are able to provide sufficient answers for the question what segment the proctodaeum belongs to. This problem is equivalent to the one what segment the anal plates surrounding the proctodaeal aperture are derived from or they represent. As for this, it will be discussed in 'DISCUSSION, 8. Metamerism'.

The chitinous substance arises within the blind end of the developing proctodaeum late in Stage 4, as in Petrobius brevistylis (Abschlußmembran, Larink, 1969), and is named the 'proctodaeal plug' here. As the developing proctodaeum further proceeds, it inclines anteriorly, to become parallel to the body surface (Fig. 75). The developing proctodaeum further extends anteriorly (Figs. 55 and 56). Its lumen assumes Y-shape in the cross section. The three parts around the aperture of it, which is also Y-shaped, later develops into a supraanal plate and a pair of subanal plates.

Changes of the tip region of the proctodaeum with its development are diagrammatically summarized in Figure 73. The proctodaeal plug gradually becomes larger. In parallel with this, the anterior cell layer to the proctodaeal plug (ACL) becomes thinner (Figs. 74 and 75), and as the lumen of the developing proctodaeum widens, the posterior cell layer to the proctodaeal plug (PCL) also comes to be thinner. When the blind end of the developing stomodaeum breaks down in Stage

14, first the posterior cell layer (PCL) disappears (Fig. 76), and then the central part of the anterior cell layer (ACL) breaks down, and the communication between the developing proctodaeum and midgut is established. In the second instar larvae, the proctodaeal plug moves into the lumen of the midgut, and then is resolved. The midgut epithelium adjacent to the marginal part of the broken anterior cell layer thickens (Fig. 77), and differentiates into the pyloric valve. The pyloric valve of this species is not as developed as in the pterygote insects, and is partially heterogeneous in origin: the anterior part of midgut or yolk cell origin (see Chapter G, III, 1), the posterior part of anterior cell layer (ACL) or ectodermal origin.

The proctodaeum and the proctodaeal part of pyloric valve are covered with cuticle, as in other ectodermal epithelia.

iii) Malpighian tubules

In Stage 12, nine anlagen of malpighian tubules are evaginated at the anterior part of the developing proctodaeum which later develops into a part of the pyloric valve (Figs. 73 and 77). They windingly elongate in the body cavity.

4. Ventral epidermis

It is usually reported in insects that the ventral

epidermis is derived from the cells just ventral to neuroblasts (dermatoblasts), i.e. is ganglionic in origin (cf. Johannsen and Butt, 1941; Anderson, 1972a, b). Larink (1969) also made the similar observations for Petrobius brevistylis.

In Pedetontus unimaculatus, the cells just ventral to neuroblasts are flattened, and undergo mitoses of which axes are parallel with the body surface, to form the ventral epidermis indeed (Figs. 52 and 78). A small number of cells of the median cord probably also contributes to the formation of ventral epidermis. This kind of epidermis is, however, ephemeral generally in Pedetontus unimaculatus. About in Stage 7, in the thoracic segments, the bases of paired appendages begin to spread over the "provisional ventral epidermis", and in Stage 12 they fuse with each other along the median line, to form the definitive ventral epidermis. Therefore, the definitive ventral epidermis of thoracic segments is appendicular in origin.

The ventral epidermis in the first to eleventh abdominal segments is also derived from the bases of appendages or the homologues to them (see Chapter E; DISCUSSION, 6. 'Homologies of abdominal appendages'). The small sections or median plates between the coxites, however, are probably originated from the "provisional ventral epidermis".

The ventral epidermis of labial segment is also

appendicular in origin, to make the postmentum epidermis (cf. Chapter E; DISCUSSION, 4. 'Formation of postmentum'). The similar observations were made by Roonwal (1937) for Locusta migratoria migratorioides (see DISCUSSION, 4). The ventral epidermises of the maxillary, mandibular and intercalary segments fuse together and make the hypopharyngeal epidermis, which is also exclusively or mostly originated from the bases of appendages or the homologues of appendages of these segments.

As to the protocerebral region, in Stage 3, the ectoderm of the anterior broad region of protocephalon differentiates into the two groups, the ventral unicellular and the dorsal multicellular parts. The latter is the ganglion anlage, and the former makes the epidermis covering the protocerebrum. In the antennal segment, although data not sufficient, the ventral epidermis is formed probably with the extension of the bases of antennae and of the interganglionic ectoderm corresponding to the median cords in succeeding segments. The labral epidermis is originated from the interganglionic ectoderm of the antennal segment.

In Pedetontus unimaculatus, the definitive ventral epidermis, at least in the intercalary to the eleventh abdominal segments is, in all probability, appendicular in origin, and its formation is in a marked contrast to the previous reports for various insects. This conclusion probably valid for the antennal segment,

although partially. It has been reported generally in the other insects that the definitive ventral epidermis is derived from only the cells situated ventrally to the neuroblasts, but the reexaminations on this subject are desired. The manner of formation of the definitive ventral epidermis in Pedetontus unimaculatus is very similar to that observed in the chilopodan Scolopendra cingulata (Heymons, 1901).

The structure called the 'sternum' in chapter E and DISCUSSION correspond to the provisional ventral epidermis.

II. Mesodermal derivatives

All the organs mentioned in this section are exclusively derived from the inner layer or the mesoderm.

1. Segmentation of inner layer and formation of coelom

In Stage 2, the inner layer covering the germ band dorsally becomes thin except for in the posterior end. Soon, the cells at the mediolongitudinal region of inner layer, between the presumptive areas of the stomodaeum and proctodaeum, are obliterated, or diminish exceedingly in number (Fig. 80b). Consequently the paird continuous mesodermal bands are formed. These bands are then segmented first in the gnathal region into the somites (Fig. 80c), and subsequently the segmentation proceeds from there to the posterior and anterior regions. In parallel with it, the mesodermal

cells in each somite begin to divide mitotically, and the somite becomes thicker.

In the intercalary and the preoral segments, the separation of inner layer is incomplete, as in the case for Petrobius brevistylis (Larink, 1969), and a broad mesodermal plate spreads there (Fig. 57). In the region posterior to the intercalary segment, the mesodermal communication between the paired somites is generally abscent (Figs. 52 and 57). Whenever the communication or the so-called primary median mesoderm may be present, it is soon replaced with the secondary median mesoderm. Each of the segmented mesodermal somites shortly possesses a narrow lumen, namely coelomic cavity, within itself (Fig. 51). The coelomic cavity is formed by the delamination, i.e. a cleft that appears in the solid mesoderm, in a contrast with the general cases in insects such as in Thermobia domestica (Woodland, 1957) and Locusta migratoria migratorioides (Roonwal, 1937); the cavities are formed by the folding over the lateral margins of solid somites. In the Odonata (Ando, 1962), the coelomic cavities are produced through both the delamination and the folding-up. The coelomic sacs intrude into each appendage newly developed, and their cavities become somewhat larger (Fig. 52). However, these cavities do not develop into such large ones as generally observed in pterygote insects. The dorso-anterior part of each coelomic sac extends anteriorly,

to contact with the coelomic sac of just anterior segment (Fig. 79). This extending part corresponds to the rostral pouch in Locusta migratoria migratorioides (Roonwal, 1937).

The formation of coelomic cavities is most progressive in the gnathal segments, late in Stages 2 to 3. In the thoracic, antennal, intercalary and preantennal regions, the formation occurs in Stage 4. It is notable that the intercalary and preantennal somites possess the coelomic sacs, although small (Figs. 57 and 79). Late in Stage 5, the segmentation of mesoderm and the formation of coelomic cavities begin in the abdominal region. The paired mesodermal bands in the region connect posteriorly with the large mesodermal mass which surrounds the developing proctodaeum. The mesodermal bands are segmented anterior to posterior, in the same method as in the preceding segments, and the coelomic cavities appear in each somite. The formation of coelomic sacs proceeds in Stage 6 upto the fourth abdominal segment (Fig. 74), and in Stage 8 upto the seventh. Figure 74 indicates that the abdominal coelomic sacs also intrude into their appendages. Finally in Stage 10, the tenth abdominal coelomic sacs are formed (Fig. 81). In the eleventh abdominal segment, the mesodermal somites communicating with the tenth are also formed, but no coelomic sac appears as observed in Petrobius brevistylis (Larink, 1969), Lepisma saccharina (Heymons,

1897a) and Thermobia domestica (Woodland, 1957). The mesoderm intruding into the caudal filament is originally connected anteriorly with the unsegmented mesodermal mass (Fig. 75), but in Stage 10, the communication is lost (Fig. 55). At the same time, the mesoderm surrounding the proctodaeum becomes subsisting independently of the eleventh abdominal somites.

Thus, in Pedetontus unimaculatus, a total number of twenty pairs of mesodermal somites arises, one for each of the preantennal*, antennal*, intercalary, three gnathal, three thoracic and eleven abdominal segments**. The eleventh abdominal somites possess no cavity. The preantennal to intercalary somites and the tenth and eleventh abdominal somites are not separated from each other. The distribution of mesodermal somites and the relative positions of them to the ganglia in the cephalic region are diagrammatically shown in Figure 57.

The preantennal and intercalary somites differenti-

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* In this paper, a inclusive name 'preoral mesoderm' is often given to the preantennal and antennal mesoderms.

** All of these segments are regarded as the eusegments, as will be discussed later in the DISCUSSION, 8. 'Metamerism'. The segment just anterior to the antennal segment is called "preantennal segment" throughout this paper.

ate also in Petrobius brevistylis (Larink, 1969), Lepisma saccharina (Larink, 1970) and Thermobia domestica (Woodland, 1957), but no coelomic cavities appear, in a contrast to Pedetontus unimaculatus. The confirmation of the preantennal coelomic sacs in Pedetontus unimaculatus is the first report for the apterygote insects. In the collembolans, the coelomic cavities are totally lacking in Isotoma cinerea (Philiptschenko, 1912) and Tetrodontophora bielanensis (Jura, 1965, 1966, 1967a, b), although Hoffmann (1911) observed the coelomic cavities of intercalary somites in Tomocerus vulgaris, and Claypole (1898) postulated the presence of coelomic cavities in Anurida maritima. In the hemimetabolous insects, the coelomic cavities are formed in each of many segments as in Pedetontus unimaculatus. However, in general holometabolous insects, the coeloms do not well develop, in comparison with those in the hemimetabolous. The preantennal coeloms have been reported in the Odonata (Ando, 1962), Carausius morosus (Leuzinger, Wiesmann and Lehmann, 1926), Locusta migratoria migratorioides (Roonwal, 1937), Pteronarcys proteus (Miller, 1940), Pyrilla perpusilla (Sander, 1956), Forficula auricularia (Heymons, 1895), the lepidopteran Chilo suppressalis (Okada, 1960) and Pieris rapae (Eastham, 1930). The intercalary coeloms appear in the Odonata (Ando, 1962), Locusta (Roonwal, 1937), Pteronarcys (Miller, 1940), the hemipteran Rhodnius

prolixus (Mellanby, 1936), the coleopteran Donacia crassipes (Hirschler, 1909) and Euryope terminalis (Paterson, 1932). The coeloms of eleventh abdominal segment have been reported in the orthopteroid insects (Wheeler, 1889; Heymons, 1895; Roonwal, 1937).

2. Further development of mesodermal somites

In the gnathal segments, the further development of mesodermal somites is also most progressive, and slightly delayed in the thoracic. In the abdominal segments it is more delayed. The following descriptions in this and the succeeding sections are, so far as emphatically said, based on the observations on the thoracic segments. The developmental processes in the gnathal and abdominal segments are fundamentally the same as those in the thoracic. The coelomic sacs or somites differentiate in the posterior abdominal segments in and after Stage 9. In these segments the dorsal closure has already proceeded to a good extent or completed, as in a contrast to the preceding segments. This condition in the posterior abdominal segments, therefore, must cause some differences in the manner of further developmental processes of the mesodermal somites between the posterior abdominal segments and the preceding. No sufficient or available data are, however, obtained on the further developmental processes of the mesodermal somites in these posterior abdominal

segments.

As mentioned previously, the paired somites are not separated with each other in the preantennal, antennal and intercalary segments, but the primary median mesoderm is generally lacking in the gnathal, thoracic and abdominal segments. The coelomic sac intruding into the appendage, i.e. the so-called appendicular coelomic sac, begins to extend medially and dorsolaterally in Stage 5 (Fig. 82). The median extension of the coelomic sac fuses medially with the extension of another side, to make the secondary median mesoderm (Fig. 78). The secondary median mesoderm does not include the cavity within itself. The dorsolateral extension makes the dorsal coelomic sac. Although the dorsal coelom is usually flattened, a bilayered cell arrangement is clearly discernible. The coelomic sac remaining in the appendage is now the so-called ventral coelomic sac.

In Stage 7, the coelom begins to collapse (cf. Fig. 78). In parallel with this, the mesodermal cells of the ventral coelom begins to rearrange into the individual muscles. The lateral and median walls of the dorsal coelom are now connected with each other only at their dorsal apices. The collapsed coelom constitutes the mixocoel (=psudocoel, schizocoel), which is characteristic of the arthropods, with the epineural sinus. The coeloms of the other segments also break

down. The mesodermal cells of the collapsed coelomic sacs of each segment begin to differentiate into the individual organs.

3. Splanchnic mesoderm and somatic mesoderm

The cells of ventral coelomic sacs and the lateral wall of dorsal coelom are the somatic mesoderm, and those of the median wall of the dorsal coelom which contacts with the yolk becomes the splanchnic mesoderm.

The splanchnic mesoderm closely contacts with the ental membrane (see Chapter G, IV, 1) (Fig. 78). In Stages 11 to 12, the splanchnic mesoderm extends medially, substituting the ental membrane*, to fuse with the mesoderm of another side above the ganglion. In

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* In Locusta migratoria migratorioides (Roonwal, 1937), the splanchnic mesoderm extends on the ventral surface of the ental membrane. In Pedetontus unimaculatus, the nuclei of the splanchnic mesoderm closely resemble those of the ental membrane, and it is difficult to distinguish them. However, it is more natural to consider that the splanchnic mesoderm does not substitute the ental membrane, but the former practically only extends over the latter also in Pedetontus, as in Locusta. The author, however, will go a step forwards in the description, following the practically observed data that the splanchnic mesoderm appears to replace the ental membrane.

parallel with this process, the lateral and median wall of dorsal coelom also extend laterodorsally, with the progressing dorsal closure, to fuse with each other of the another side middorsally just above the developing midgut in Stages 12 to 13 (Figs. 83 and 84). The yolk is originally covered with the amnion dorsally, but is now with the splanchnic mesoderm derived from the median wall of the dorsal coelom instead of the amnion. A bilayered arrangement of splanchnic mesoderm is often observed (Fig. 84). It may represent the rudimentary condition of the bilayered enteric muscles.

The splanchnic mesoderm, thus, constitutes a thick and long sac filled up with the yolk, making the outline of developing midgut. Since the ental membrane intervenes between the tips of the stomodaeum and proctodaeum, the splanchnic mesoderm, which has replaced the ental membrane, now joins the ends of the stomodaeum and proctodaeum. It fuses with the stomodaeal and proctodaeal mesoderm layers, to develop into the musculature of the alimentary canal with the latters. On the inner surface of the splanchnic mesoderm, the definitive midgut epithelium is later formed with the yolk cells.

With the progression of dorsal closure, the lateral wall of the dorsal coelom extends dorsally in company with the median wall, and fuses with the one

of another side dorsomedially. The mesoderm of lateral wall or the somatic mesoderm differentiates into the heart, pericardial cells, fat bodies and musculatures. The mesoderm of the ventral coelom exclusively develops into the musculatures.

4. Heart, pericardial cells, diaphragm and fat bodies

All of the heart, pericardial cells, diaphragm and fat bodies are originated from the lateral wall of the dorsal coelom, i.e. the somatic mesoderm. The origins of these organs in Pedetontus unimaculatus are, on the whole, coincident with those in the other insects (cf. Roonwal, 1937; Johannsen and Butt, 1941; Ando, 1962; Anderson, 1972a, b). Other than the precursors of these organs, the lateral wall of the dorsal coelom includes a large number of myoblasts. The morphological differences between the cells, belonging to the lateral wall, different in their fates are not recognized until near to the completion of dorsal closure, although the differentiation of muscles is somewhat earlier.

i) Heart or dorsal blood vessel

A large cell taking its position at the innermost apex of the lateral wall of the dorsal coelom is the cardioblast (Fig. 83). It does not assume such characteristic crescent-shape or stainability as often observed in the other insects. The cardioblasts of each side dorsomedially fuse with each

other, above the developing midgut, to constitute a dorsal blood vessel or heart between themselves (Fig. 84). Blood cells are often observed in the vessel.

The formation of the heart or dorsal blood vessel occurs in the gnathal, thoracic and abdominal regions, and a continuous tube along the dorsomedian line is formed. Since the vessel lies throughout the whole length of body trunk, the last posterior abdominal segments probably also participate in the formation of the blood vessel.

ii) Pericardial cells

The pericardial cells are originated from the cells situated at the outermost apex of the lateral wall of the dorsal coelom. The pericardial cells are characterized by its large nucleus and a large amount of cytoplasm with the eosinophilic granules (Figs. 83 and 84). The pericardial cells definitively take their positions dorsally to the cardioblasts of each side. The pericardial cells are, usually in insects, located laterally or ventrolaterally to the heart.

With the progression of dorsal closure, the amnion is contracted dorsally, and it is gradually replaced with the tergum, to degenerate (Fig. 83). However, some amniotic cells are left just above the heart, and are taken into the body of the full-grown

embryo (Fig. 84) (see Chapter D). It is noteworthy that the pericardial cells connect with these amniotic cells. It indicates that the pericardial cells probably give the attachment of dorsal coelom to the amnion or the developing body wall.

Generally in insects, the functional property of the pericardial cells is regarded as their ability to absorb colloidal particles from the blood, i.e. the excretory function (Wigglesworth, 1950). The fact that the pericardial cells possess the eosinophilic granules of various sizes in Pedetontus unimaculatus may suggest this functional ability.

iii) Dorsal or pericardial diaphragm

The outermost cells of lateral wall of the dorsal coelom are arranged into a thin layer, to constitute the dorsal or pericardial diaphragm (Figs. 83 and 84). It links the body wall and the pericardial cells, and the space bounded by the diaphragm and the body wall is the "dorsal or pericardial sinus". The dorsal sinus is filled with the blood, and the blood cells are found there. The dorsal diaphragm of Pedetontus unimaculatus is not well developed, and its longitudinal running is often interrupted by the muscles such as the dorso-ventral. The dorsal diaphragm generally in insects lies just beneath the heart or is connected, with the inter-

vention of the pericardial cells, ventrolaterally to the heart, in a contrast to the case in Pedetontus unimaculatus. This difference is responsible for the unusual position of the pericardial cells in Pedetontus unimaculatus: they are situated dorsally to the heart.

Roonwal (1937) studied the development of the diaphragms and blood sinuses of Locusta migratoria migratorioides in detail. According to him, in the locust, the dorsal diaphragm is derived from the innermost cells of the lateral wall of the dorsal coelom, and the outermost cells differentiate into the suspensions of the heart. Contrary to the case in the locust, the dorsal diaphragm is originated from the outermost cells of the lateral wall, in Pedetontus unimaculatus, and the innermost cells does not develop into any particular organs. The ventral diaphragm, as develops in the Orthoptera, Odonata, Ephemeroptera, Hymenoptera and Lepidoptera, is lacking in Pedetontus unimaculatus.

iv) Fat bodies

The fat cells make the principal part of the lateral wall of dorsal coelom with the myoblasts. In Stage 12, the cytoplasm of the fat cells becomes reticulated, and it makes the clear distinguishment of the fat cells from the other cells. The fat bodies are formed in all of the gnathal, thoracic

and abdominal regions of the embryo.

5. Blood cells

The blood cells are produced mainly in the thoracic and gnathal regions in Pedetontus unimaculatus. The production of blood cells in the thoracic region seems to be biphasic. In Stages 9 to 10, the cells of lateral parts of the secondary median mesoderm are successively dissociated, to differentiate into the blood cells (Fig. 78). They suspend in the epineural sinus which has not been widened and is practically restricted only to the space above the appendages still now. In Stage 12, the blood cells are vigorously liberated from the median part of the secondary median mesoderm into the broadened epineural sinus (Fig. 69). Many blood cells are also liberated between the connectives. They are not originated from the cells of the ganglion or the median cord, but they are derived from the cells of the secondary median mesoderm fallen into the space between the connectives.

In Stage 12, a number of blood cells appears in the head, the broad epineural sinus above the suboesophageal ganglion (Fig. 54). They are probably derived from the secondary median mesoderm belonging to the labial segment. The secondary median mesoderm of the mandibular and maxillary segments mainly develops into the transverse muscles or tendons. The

possibility that the blood cells originate in the suboesophageal body as in Bombyx mori (Toyama, 1902; Wada, 1955a, b), is precluded in Pedetontus unimaculatus.

A small number of blood cells also appears in the abdominal region. They are derived from the lateral parts of the secondary median mesoderm.

Blood cells in insect embryos have been variously described as arising from yolk cells (Will, 1888); from the cells of the serosa (Ayers, 1884); from the walls of the heart (Wheeler, 1889); from undifferentiated mesoderm cells (Wheeler, 1892; Carrière and Bürger, 1897); from mesoderm cells at the junction of the somatic and splanchnic mesoderm (Patten, 1884); from the suboesophageal body (Toyama, 1902; Wada, 1955a, b) and from the median mesoderm or "Blutzellenlammele" (Heymons, 1895; Leuzinger, Wiesmann and Lehmann, 1926; Eastham, 1930; Roonwal, 1937; Bock, 1939; Okada, 1960; Ando, 1962; Mori, 1969). Contemporary authors, however, seem to agree in the view that the embryonic blood cells are median mesodermal in origin (cf. Mori, 1979).

6. Gonads

In adults of Pedetontus unimaculatus, three pairs of the testioles are present, and they occupy the laterodorsal portions of the metathorax. The ovary consists of seven pairs of the ovarioles, and they are situated at the laterodorsal portions of

the second to the sixth abdominal segments.

In pterygote insects, the germ cells are often recognizable by the time when the embryonic primodium has been established and has begun to elongate as a germ band. In apterygote insects, in Lepisma saccharina (Heymons, 1897a; Sharov, 1953) the germ cells also appear in early developmental stages. In collembolans, they become recognizable already during the cleavage (Philiptschenko, 1912; Jura, 1965), but the manner of formation of the germ cells exhibits a great contrast to that generally observed in the other insects. In Pedetontus unimaculatus, in Stage 2, a peculiar spherical body, ca 50 μm in diameter, which is composed of about fifteen to twenty of weakly stained large cells, is observed in the mesodermal mass at the posterior end of the germ band (Fig. 85). The further development and the fate of the body could not be followed. There may be, however, a high possibility that the body should be the germ cells.

The cells certainly identified as the germ cells first appear in Stage 5. In some thoracic and abdominal segments, several germ cells are observed in the dorsal wall of the appendicular coelom, which is the future median wall of the dorsal coelom, as in Thermobia domestica (Woodland, 1957) (Fig. 82). The nuclei of the germ cells are just spherical and slightly

larger than the nuclei adjacent to them, and they are characterized by their chromatines: the equal-sized compact chromatins are evenly distributed in the karyoplasm, so that the nuclei of the germ cells appear to be paler. The genital ridge, appearing in Lepisma saccharina (Heymons, 1897a; Sharov, 1953) and the most pterygote insects, is not formed in Pedetontus unimaculatus.

The germ cells increase in number, in Stage 9 upto about ten in each the group. In parallel with this, they slip out of the median wall of the dorsal coelom into the coelomic cavity which has been partially collapsed (Fig. 86). A clump of germ cells is enveloped with the thin mesodermal cells. Seven pairs of the clumps are present, one in each segment from the prothoracic to the fourth abdominal segments. For a time, each the clump of the germ cells is liberated from the other tissues, and takes its position ventrolaterally to the developing midgut, above the appendage of each segment (Fig. 78). With the progression of the dorsal closure, the clumps of the germ cells are carried dorsally, to be finally situated dorsolaterally to the developing midgut in the continuous chain of fat bodies of each side. In Stage 14, the paired clumps of the germ cells are segmentally arranged in the metathoracic to the sixth abdominal segments. One or two germ cells become larger than

the others in each clump, and possess a conspicuous nucleolus. The further development of the genital organs is not followed. Their completion occur in the postembryonic stages.

7. Suboesophageal bodies

A pair of the suboesophageal bodies develops from the intercalary mesoderm, as in Petrobius brevistylis (Larink, 1969) and Lepisma saccharina (Larink, 1970), in Stage 7. Each of the suboesophageal bodies is composed of about ten to fifteen vacuolated cells, and ca. 20 μm to 30 μm in diameter (Fig. 64). It is initially situated anterolaterally to each of the mandibular apodemes (anterior tentoria). The cells of the suboesophageal body are highly vacuolated.

The suboesophageal bodies move posteromedially, in company with the anterior tentorial anlagen. Their relative position to the latter changes into lateral and further into posterior. In Stage 12, the paired anterior tentorial anlagen fuse together medially, and the suboesophageal bodies of each side closely approach, or often they come to contact with each other (Fig. 62). The suboesophageal bodies definitively contact anteriorly with the anterior tentoria, and dorsally or dorsomedially with the stomodaeum. With their migration, the morphological characteristics of the suboesophageal bodies are altered: the vacuoles disappear, and the nuclei that are originally

flattened and pressed by the vacuoles become normal. In and after Stage 12, the cells of them are characterized by a large nucleus and a large amout of cytoplasm (Figs. 54 and 62). In Petrobius brevistylis, the suboesophageal bodies disappear just before hatching (Larink, 1969). In Pedetontus unimaculatus, however, they remain alive, and are found at least in the larvae of the early instars. In Gryllidae and Blattidae, they persist in the larvae (Heymons, 1895), and in the isopteran Eutermes chaquimayensis they are present even in the sexually matured individuals (Holmgren, 1909). The suboesophageal bodies are generally considered as one of the embryonic organs, but it cannot be absolutely said so.

The function of fate of the suboesophageal bodies are much controversial (cf. Roonwal, 1937; Johannsen and Butt, 1941; Anderson, 1972a). Concerning their function, however, the excretory is generally accepted, during the embryonic life (Wheeler, 1893; Hirschler, 1907; Roonwal, 1937; Kessel, 1961). Roonwal (1937) further suggested the homology between the suboesophageal bodies and pericardial cells.

The suboesophageal bodies show a uniform structure, and seem to be, in all probability, homologous in all insects. However, their origin is also remarkably varied (cf. Roonwal, 1937; Johannsen and Butt, 1941; Anderson, 1972a, b), although the mesodermal origin,

especially in the intercalary segment, is the most usual. Rempel and Church (1969) ascribed an ectodermal origin to it in the coleopteran Lytta viridana, but it is to be regarded as one of the extraordinary.

8. Mesoderm in head

The fate of the mesoderm in each segment of the head are summarized.

i) Preantennal and antennal mesoderms

The preantennal and the antennal mesoderms are connected with each other. Most of the preantennal mesoderm intrudes into the developing clypeolabrum, with the protrusion of the latter (Fig. 71), to differentiate into the labral and clypeal muscles. The stomodaeal musculature is derived from the preantennal mesoderm. It is possible that the antennal mesoderm also participates into its formation partially. The preantennal mesoderm also contributes to the formation of the stomodaeal suspensions connecting the stomodaeum with the clypeus (Fig. 87).

The antennal coelomic sacs intrude into the antennal anlagen, to develop into the antennal muscles. A part of the antennal muscles attaches the anterior tentoria (Fig. 87). A pair of the lateral suspensions of the anterior tentoria (Fig. 88), which runs in para-

llel with the antennal muscles from the posterior bases of the antennae to the anterior tentoria, is also derived from the antennal mesoderm. These suspensions pass between the deutocerebrum and the lobus 2 of the protocerebral ganglion.

The preantennal and the antennal mesoderms initially cover the head lobe dorsally (cf. Fig. 57). A part of them is involved between the protocerebral ganglia, with the progression of the cerebral morphogenesis to form the neurilemma of the protocerebral ganglia (Fig. 70). However, there are no defining the origins of the deuto- and tritocerebral neurilemma. In Stage 11, a pair of the anterior suspensions of anterior tentoria which connects the anterior tentoria with the body wall just anterior to the compound eyes, and which passes between the protocerebral ganglia lobus 2 and 3', are formed (Figs. 65 and 88). They originate in either the preantennal or the antennal mesoderm, but their origin can not be definitively attributed to the one for the present.

ii) Intercalary mesoderm

Most of the intercalary mesoderm develops into the suboesophageal bodies. Although the stomodaeal

musculature is mostly derived from the preoral mesoderm, the circular muscles at the base of the stomodaeum originate in the intercalary mesoderm, probably its primary median mesoderm (Fig. 71). The intercalary mesoderm forms also the paired suspensions of the stomodaeum (Fig. 87) which connect the latter with the anterior tentoria.

iii) Mandibular, maxillary and labial mesoderms

With the morphogenesis of the head capsule, three gnathal segments are extremely contracted, especially in their dorsal and lateral regions, so that the gnathal mesoderm is also concentrated in these regions. It is, therefore, difficult to judge which segment among the three the individual organs such as fat bodies, dorsal blood vessel, muscles and splanchnic mesoderm are originated from. As for the muscles, however, it is probably more natural to ascribe the origin of one muscle to one segment whose appendages are attached with the muscle. Figure 87 diagrammatically shows the distributions and the runnings of the principal muscles of the head. It is also difficult to determine the origin of the splanchnic mesoderm in the head, but it probably originates in every gnathal segments.

A pair of the posterior suspensions of anterior

tentoria is derived from the mandibular mesoderm (Fig. 88). It starts from the dorsoposterior angles of the anterior tentoria, passing laterally to the stomodaeum and between a pair of the lobi l of protocerebral ganglia, to the postocular epidermis, probably the mandibular tergum. The tendon binding the right and left anterior tentoria, and the mandibular transverse tendon is also originated from the mandibular mesoderm (Figs. 54, 70, and 87). Both of them are derived from the secondary median mesoderm. In Pedetontus unimaculatus, the mandibular transverse tendon and the fan-shaped muscles, namely the ventral adductor muscles, taking their origin on this tendon are well developed. It is one of the remarkable characteristics of most of the mandibulatan animals whose mandibles possess only a single articulation, i.e. the Apterygota except for the Thysanura, the Symphyla, Chilopoda, Diplopoda, Pauropoda, and Crustacea.

The blood cells appearing in the head probably originate only in the labial segment, i.e. its secondary median mesoderm, among the gnathal, as mentioned previously.

9. Musculature of alimentary canal

Initially, the stomodaeum is covered with the mesoderm mainly at its anterior (dorsal) and lateral sides (Fig. 71). Its posterior (ventral) surface of

it is also sheathed with the mesodermal layer, although thinly. It is probably responsible for the extension of the mesoderm present at the anterior (dorsal) and lateral sides. Thus, the outer surface of the stomodaeum is overlaid with a continuous mesodermal layer. The blind end, however, is always lacking the mesoderm. The midgut is also enveloped with a thin mesodermal layer, the splanchnic mesoderm, as previously mentioned (see Section 3. 'Splanchnic mesoderm and somatic mesoderm'). The proctodaeum is also covered with the mesoderm throughout all its surface, except for the blind end (Figs. 55 and 56).

The three principal parts of the alimentary canal are, thus, covered with the mesodermal envelopes. These envelopes fuse together, to develop into the musculature of the alimentary canal (Fig. 89). The stomodaeal muscular sheath consists of mainly circular fibers, and the longitudinal ones are present, innerly to the circular, only at the anterior base of the stomodaeum. The muscular sheath of the midgut, i.e. the enteric musculature, is principally made of the longitudinal muscles. The posterior part and the anterior one except for the anterior region of the gastric caeca are also sheathed with the circular muscles innerly to the longitudinal. The proctodaeal musculature is composed of an outer layer of longitudinal muscles and of an inner layer of the circular

ones.

The stomodaeal muscle is derived from the preantennal, antennal and intercalary mesoderms (see the preceding section). The enteric muscle is originated from the splanchnic mesoderm of the gnathal, thoracic and abdominal regions. The proctodaeal musculature originates in the mesodermal mass surrounding the proctodaeum anlage. Until long after the proctodaeal mesoderm differentiates, this mesodermal mass does not undergo the segmentation. It is, therefore, very difficult to determine what abdominal segment the proctodaeal mesoderm belongs to. For the solution of this problem, it is the most promising to ascertain the origin of the proctodaeum. Further, the dispute on the attribution of the proctodaeum will be provided with an answer by discussing what segment the anal plates constituting the aperture of proctodaeum or anus belong to or represent. It will be discussed in the DISCUSSION, 8. 'Metamerism'.

The proctodaeum is supported by the suspensions consisting of paired ventrolateral rows and a dorsal row (Fig. 76). Each row of suspensions attaches the tergum or the ventral plate of the eleventh abdominal segment. They are probably derived from the eleventh abdominal mesoderm.

III. Endodermal derivatives

1. Midgut epithelium

The formation of origin of the midgut epithelium are controversial subjects in the comparative embryology of insects. For the solution of this controversy, the investigations on the primitive groups, such as the Apterygota and the lower Pterygota, seem to be the most promising. The studies of the midgut epithelium formation of the Microcoryphia, which has not yet been reported, may provide some basis for discussing the formation and origin of the midgut epithelium in insects.

i) Contribution of the yolk cell* to midgut epithelium formation

In Pedetontus unimaculatus, the midgut epithelium develops entirely from the yolk cells, as shown diagrammatically in Figure 91. When the dorsal closure begins at the posterior abdominal segments, the amitoses of yolk cells are observed as in Lepisma saccharina (Sharov, 1953) and the yolk cells, with the spherical nucleus deeply stained with hematoxylin, differentiate (Fig. 91a). In Thermobia domestica (Woodland, 1957), however, yolk cells undergo both mitosis and amitosis.

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* In this paper, for convenience, the term 'yolk cell' has been adopted instead of 'yolk nucleus'.

With the progression of the dorsal closure, the yolk is covered up with the splanchnic mesoderm. The yolk cells mentioned above migrate to the yolk periphery and settle on the splanchnic mesoderm layer one by one in Stage 11, as in Lepisma saccharina (Sharov, 1953) and Thermobia domestica (Woodland, 1957) (Fig. 91b). They then undergo amitoses, as in Lepisma saccharina (Sharov, 1953) to form the cell groups, "crypts" (Fig. 69). The crypts of Pedetontus unimaculatus are closely similar to the "crypts" or the "regenerative nests" of Lepisma saccharina (Heymons, 1897a; Sharov, 1953), Thermobia domestica (Woodland, 1957), Tetrodontophora bielanensis (Jura, 1966), several species of the Odonata (Tschuproff, 1903; Ando, 1962) and the chilopodan Scutigera coleoptrata (Knoll, 1974).

In Stage 12, each crypt is composed of about ten cells as a result of amitoses. Then the crypt cells begin to undergo mitosis actively. At the same time the whole yolk commences to divide into blocks (yolk blocks), enveloped with fine membranes (Fig. 91c and d). The phenomenon is also reported in the animals mentioned above, but in Thermobia domestica (Woodland, 1957), the "yolk blocks" almost break down after blastokinesis. In Lepisma saccharina (Heymons, 1897a) and Thermobia domestica (Woodland, 1957), one yolk cell is found at the center of each yolk block, but in Pedetontus unimaculatus more yolk cells are present in each block. The nucleoli of the crypt and yolk cells are more con-

spicuously eosinophilic than those of the embryonic ones.

The yolk material incorporated into yolk blocks diminishes in quantity. With the further consumption of the material, the longitudinal lumen appears at the center of the yolk throughout the whole length of the developing midgut by shrinkage of the yolk blocks in Stage 14 (Figs. 90 and 91d). The crypt cells continue to divide mitotically and increase in number, so that they are compactly arranged there. A section of the crypt cells starts to slip away from the crypts along the periphery of the developing midgut (Figs. 90 and 91d). The nuclei of these cells (a in Figs. 90 and 91) morphologically differ from those of the original crypt cells: they are larger and more spherical with conspicuously eosinophilic nucleoli and less hematoxylinophilic karyoplasm. At about the same time, the yolk cells left behind in the yolk again actively undergo amitosis to increase in number two to three times. These yolk cells are frequently observed in groups of two or three, resulting from the amitotic divisions, and are sometimes situated at the fine boundary membrane of yolk blocks. Shortly they begin to migrate, settling at the periphery of the developing midgut (b in Figs. 90 and 91). These cells (b in Figs. 90 and 91) are similar to those slipping away from the crypts (a in Figs. 90 and 91). Morphological characters

of these two groups of cells (a and b) are like those of epithelial cells of the definitive midgut.

Both these cells (a and b) later develop into the midgut epithelial cells. They divide amitotically at the periphery of the developing midgut, so that they are often found in pairs. After hatching the cytoplasm starts to accumulate in the yolk blocks of the first instar larva, in which the digestion of yolk material is progressing. As development progresses, (due to further slipping of crypt cells, further migration of the newly proliferated yolk cells from the yolk and their amitosis), the cells increase in number at the periphery of the developing midgut (Fig. 91e). At the end of the second larval instar, as in Lepisma saccharina (Sharov, 1953), Thermobia domestica (Woodland, 1957) and the Odonata (Ando, 1962), the yolk material is at last consumed up and replaced by the accumulated cytoplasm. In the third instar larva, the midgut epithelium is essentially completed. These epithelial cells further undergo amitosis and the epithelium comes to be more densely cellular (Fig. 91f). The crypts are covered with the definitive epithelium and these cells preserve the ability for mitosis. The crypts possibly represent the regenerative nests of the midgut epithelium in older insects, as in Lepisma saccharina (Sharov, 1953) and Thermobia domestica (Woodland,

1957). The larvae of Pedetontus unimaculatus feed for the first time in the third instar.

Not all the yolk material is incorporated into the yolk blocks; a part of it is left behind in the lumen of the developing midgut. Shortly, the remainder of the yolk material is also digested with the proctodaeal plug mentioned previously in the lumen of the midgut. At the anterior and posterior ends and the ventral side of the developing midgut, the crypt cells are more densely distributed, and the yolk cells both proliferate and digest the yolk actively so that the midgut epithelium formation is more progressive in these regions. The regional differences in the epithelium formation are not due to the direct participation of any elements other than the yolk cells, such as components of the stomodaeum, proctodaeum or middle strand of the inner layer. In Lepisma saccharina (Sharov, 1953), the crypt cells begin to divide mitotically in the second larval instar, probably as "regenerative nests".

ii) Cardiac region and gastric caecum

As the blind end of the developing stomodaeum is thinned, its tip begins to extend in Stage 12 (Fig. 73b), as in Lepisma saccharina (Sharov, 1953). This extended part of stomodaeum is the developing cardiac valve (Fig. 73c and d). This part never

differentiates into the midgut epithelium and it preserves such histological characteristics as observed in the stomodaeum (Fig. 72), in contrast to that of Lepisma saccharina (Sharov, 1953).

The anterior region of the midgut epithelium in Pedetontus unimaculatus also originates exclusively from the yolk cells, as previously described, and develops into the gastric caeca (Fig. 73d). They consist of one pair of large and two pairs of small caeca in this species. Their formation begins with the cleaving of the anterior tip of the developing midgut into right and left. In the third instar larvae, each half again divides into three, and in the fourth instar six caeca are plainly visible.

iii) Pyloric region

The part of midgut epithelium develops into the anterior part of pyloric valve (Fig. 77): the pyloric valve is heterogeneous in origin in this species, and the posterior part is derived from the proctodaeum. As mentioned above, the blind end of proctodaeum is almost broken down in Stage 14, and only the marginal part of the anterior cell layer to the proctodaeal plug (ACL) persists, and differentiates into the posterior part of pyloric valve (Fig. 73). It preserves such histological characteristics as the proctodaeum assumes. Although the

anterior part of the proctodaeum in Lepisma saccharina differentiates into the midgut epithelium (Sharov, 1953), that in Pedetontus unimaculatus does not differentiate into it.

IV. Other structures

1. Ental membrane

About in Stage 9, the embryo is found to be covered dorsally with a fine membrane so sparsely cellulated. This is the so-called ental membrane.

The ental membrane contacts with the embryo at the point of the origin of the amnion where the dorsal coelom also attaches the embryo proper or ectoderm (Fig. 78). It covers the embryo throughout all its dorsal surface, and the anteriormost of the ental membrane attaches the margin of head lobe or the developing head capsule (Fig. 70), and the posteriormost attaches the developing terga of the posterior abdominal segments (Figs. 55 and 56). The blind ends of the stomodaeum and proctodaeum come to contact with the ental membrane (Figs. 53, 55, 56, and 70). The similar structures to the ental membrane of Pedetontus unimaculatus have been reported in the Odonata, Orthoptera, Plecoptera, Mallophage, Hemiptera, Neuroptera and so on (cf. Ando, 1962): for example, the ental membrane of some odonatans (Ando, 1962), the provisional dorsal closure of Locusta migratoria migratorioides (Roonwal, 1937) and the

ental anmion of Pteronarcys proteus (Miller, 1940). They are considered exactly homologous with the ental membrane of Pedetontus unimaculatus, on the basis of the close resembrances between them.

The origin and the exact time of the appearance of ental membrane could not be determined. It renders these determinations much difficult that the nuclei of ental membrane closely resemble those of splanchnic mesoderm. It was shown in Pyrilla perpsilla (Sander, 1956) and some odonatans (Ando, 1962) that the ental membrane is originated from the blind ends of the stomodaeum and proctodaeum. The ental membranes of the orthopteran Stenobothrus variabilis (Graber, 1888) and the locust (Roonwal, 1937) are, however, said to be derived from the lateral edges of the germ band. For the stonefly, Miller (1940) is not sure about its origin, but he suggested the probable origin of it from the lateral ectoderm or coelomic sac.

Roonwal reported the degeneration process of the provisional dorsal closure, but in Pedetontus unimaculatus, the further development and the fate of the ental membrane could not followed.

2. Epineural sinus

Generally in insects, the ental membrane is widely apart from the ventral nerve cord, and a broad space is formed between them throughout all

the length of the embryo. This is the "epineural sinus". In Pedetontus unimaculatus, the ental membrane initially stands close to the ventral nerve cord, and the epineural sinus is hardly discernible (Figs. 56, 70, and 75). In Stages 11 to 12, the ental membrane becomes apart from the latter, so that the epineural sinus enlarges. However, it is restricted only to the gnathal and the thoracic, mainly mesothoracic regions (Figs. 54 and 69). In the epineural sinus above the suboesophageal ganglion, the tentoria, suboesophageal bodies, gnathal transverse muscles and tendons, and so on take their positions. In the thoracic epineural sinus, the muscles run.

After the collapse of the coeloms, the epineural sinus is to be called the "mixocoel". The epineural sinus or the mixocoel extends, with the progression of the dorsal closure. The membrane bounding the epineural sinus dorsally is, originally, the ental membrane. The ental membrane is, however, replaced with the splanchnic mesoderm (see Chapter G, II, 3. 'Splanchnic mesoderm and somatic mesoderm'), so that the dorsal boundary of the epineural sinus is exclusively regarded as the splanchnic mesoderm, after the completion of the replacement, for example, in and after Stage 12 in the thorax.

DISCUSSION

The results of the present study have been discussed in each former section. Here, some subjects considered significant in the comparative embryology or morphology of insects will be further examined.

1. Embryonic membranes

Heymons and Heymons (1905) found that the amnion and serosa are formed without the intervention of the process of the anatrepsis-katatrepsis in the machilidan Machilis alternata (=Trigoniophthalmus alternatus), and they regarded the amnion and serosa of the species assuming one of the most primitive conditions among those of insects. Heymons and Heymons, further, believed that the embryonic membranes of the machilids are still more primitive than those of the lepismatids which are considered less developed than those of the pterygote insects. They also thought that the machilid embryonic membranes assume the intermediate developmental condition linking those of the lepismatids and pterygote insects, and those of the myriapods and other apterygote insects. These ideas formulated by Heymons and Heymons have afforded not a few significant bases for the phylogeny of the Insecta, and the systematical divisions of machilids and lepismatids in the suprafamily level until the present (cf. Sharov, 1966).

However, Larink (1969) contradicted Heymons and Heymons' ideas, from the basis of his investigations for the machilidan Petrobius brevistylis. In the species the fold of the embryonic membrane or blastoderm is formed over the embryo, as in Pedetontus unimaculatus (cf. Fig. 5). Larink (1969) regarded such a fold in the same light with the amnio-serosal fold of lepismatids and pterygote insects which is produced through the anatrepsis. He believed that the amnion and serosa of Petrobius brevistylis (and probably also of the other machilidans such as Machilis alternata) must be produced with the intervention of the process of the anatrepsis-katatrepsis in the same way as in the lepismatids and pterygote insects. From this, in the natural course of events, he reached the conclusion that there is no fundamental difference between the phylogenetical condition in embryonic membranes of the machilids and those of the lepismatids and pterygote insects. He appears to have supposed that Heymons and Heymons' conclusion had been inappropriately brought about by overlooking the folded condition of the embryonic membranes, although he did not directly say so.

However, the results of the present study of Pedetontus unimaculatus offer some new evidences against the Larink's conclusion. Larink (1969) supposed that the fold over the embryo is produced through

the process of the anatrepsis, but in Pedetontus unimaculatus such a process is not recognized at all. Instead, it is confirmed that the formation and structure of the fold is ascribed only to the cell arrangement of the marginal region of the germ rudiment in the most initial stages (see Chapter C. of OBSERVATIONS). It is not through the process of the anatrepsis that the fold should be constituted. Furthermore, on the basis of the morphological characteristics of the nuclei of the fold, it cannot be homologized with the "amnio-serosal fold" of the lepismatids and pterygote insects, but it should be identified as a kind of the blastodermal or serosal structure.

In the Thysanura and Pterygota, the amnio-serosal fold is well developed, and the amnion and serosa are formed through the process of the anatrepsis-katatrepsis. On the formation of their embryonic membranes and amnio-serosal fold, the developmental succession is recognized; that is, the thysanuran Lepisma saccharina and Thermobia domestica – the thysanuran Ctenolepisma lineata – the Pterygota (cf. Sharov, 1966; Jura, 1972). In a contrast with the cases in these insects, in the Myriapoda, Collembola and Diplura, the amnio-serosal fold or the cellular membrane such as the amnion that should envelope the venter of the embryo, are not, of course, differentiated. On the

other hand, in Pedetontus unimaculatus, although the amnion and serosa differentiate indeed, they are formed without the intervention of the process of the anatrepsis-katatrepsis. It is just coincident with Heymons and Heymons' conclusions. Now, it may be possible and reasonable to interpret the developmental condition of the embryonic membranes in Pedetontus unimaculatus as the intermediate or transient type between the Myriapoda, Collembola and Diplura on one hand, and the Thysanura – Pterygota on the other. That is to say, the author supports Heymons and Heymons' (1905) phylogenetical hypotheses referred to in the opening of this section. Reexaminations are desired on Larink's (1969) data.

There is little in doubt that the embryonic membranes of Pedetontus unimaculatus, Machilis alternata (Heymons and Heymons, 1905) and Petrobius brevistylis (Larink, 1969) assume the ancestral or primitive conditions of those of the pterygote insects, as well as those of the lepismatids* (Heymons, 1897a; Sharov, 1953; Woodland, 1957). Further, the differences on the embryonic membranes, have been mentioned

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* As for the comparative embryological discussions on the embryonic membranes laying stress on the lepismatids, see Heymons and Heymons (1905), Sharov (1966), Jura (1972) and Larink (in press).

previously, between the machilids and lepismatids deserves special emphasis, and they suffice to regard the embryonic membranes of the former as more primitive and ancestral than those of the latter.

2. Blastokinesis

In Pedetontus unimaculatus, the embryo deeply invaginates among the yolk folds, as in the cases for the other machilidan Machilis alternata (Heymons and Heymons, 1905) and Petrobius brevistylis (Larink, 1969). When discussing the phylogeny of insects, such an invagination of the embryo observed in the machilids is often compared with the immersion of the embryo into the yolk in the pterygote insects (cf. Sharov, 1966). However, they are not comparable to each other, as Jura (1972) pointed out, because the yolk folds are given rise to in the area consisting only of the amnion (see Chapter D. of OBSERVATIONS). They can be indeed homologized with each other in function, i.e. the protection of the venter of embryo, but there is, of course, no phylogenetical homology between them. Such an invagination of the embryo among the yolk folds as found in Pedetontus unimaculatus should be rather considered as a peculiar phenomenon to the Microcoryphia.

Since no process regarded as the anatrepsis and katatrepsis is, therefore, present in the machilids such as Pedetontus unimaculatus, it is difficult to

detect any fundamental differences in the blastokinesis between the machilids and the myriapods, collembolans and diplurans. It is in a marked contrast to the case in the lepismatids (Heymons, 1897a; Sharov, 1953; Woodland, 1957): both the remarkable anatrepsis and katatrepsis are performed as in the pterygote insects. However, when comparing the blastokinesis of the machilids with that of the myriapods, collembolans and diplurans, it is never to be forgotten that the former is accompanied with the differentiation of the amnion and serosa, as emphasized in the preceding section, in a marked contrast to the latter.

3. Terga of three gnathal segments

In Pedetontus unimaculatus, the embryonic terga of three gnathal segments, i.e., the mandibular, maxillary, and labial segments, form in the same manner as in the thoracic segments, and they are serially homologous with the thoracic terga. It is notable that the posterior part of the cranium derives from the terga of the gnathal segments. Bitsch (1963) determined the distribution of the head segments in Machilis burgundiae, based on details of musculature and innervation. The results of the present study agree with his work. According to Matsuda (1965), the boundary lines between the mandibular and maxillary terga, and between the maxillary

and labial terga, correspond to the occipital and postoccipital sutures in lower insects.

In the lower insects, cephalic segmental terga may be found. According to Sharov (1959), for instance, the fossil species Dasyleptus brongniarti of the Monura has mandibular, maxillary, and labial terga. The boundary lines between these terga, however, do not reach the vertex, and do come into contact with the lower edge of the compound eye, so that the compound eye seems to spread over these terga. Judging from the fact that in the embryo of Pedetontus unimaculatus the compound eye never spread over the terga of the gnathal segments, it is questionable whether these boundary lines of Dasyleptus are actually equivalent to the intersegmental sutures of the primary (or embryonic) segments, or are merely secondary structures. In the embryos and early instar larvae of Lepisma saccharina (Sharov, 1953) distinct terga of the maxillary and labial segments do occur, but Heymons (1897a) did not find these structures. It is noteworthy that the primitive thysanuran Tricholepidon gertschi, a living fossil, possesses a well developed occiput and postocciput (Wygodzinsky, 1961). In Epiophlebia superstes (Odonata), Ando (1962) has illustrated the structures thought to be the developing maxillary and labial terga.

4. Formation of the postmentum

Snodgrass (1935) illustrated the participation of the sternum in the postmentum formation of Machilis (p. 149, Fig. 83), while Chaudonneret (1948) concluded that no sternal element takes part in postmentum formation in Machilis annulicornis.

In Pedetontus unimaculatus, the bases of the labial appendage anlagen spread over the ventral surface of labial segment to form the postmentum. Although in Stages 10 and 11 the sternum* persists as small triangular part in the posterior margin of the labium (Figs. 33 and 39), this part gradually becomes unrecognizable due to further spreading of the bases of labial appendage anlagen. Thus, in Pedetontus unimaculatus, the postmentum derives from the bases of the labial appendages, and the sternum does not contribute to postmentum formation, as Chaudonneret (1948) suggested for Machilis annulicornis. The fact that the common duct of paired salivary glands runs down along the median line of postmentum throughout all the length of the latter indirectly supports this conclusion (see Chapter G, I, 2, 'Salivary gland' in the OBSERVATIONS).

In Eutermes chaquimayensis, the submentum — including the mentum — originates from the interseg-

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* As for the nature of sternum, see Chapter G, I, 4. 'Ventral epidermis' in the OBSERVATIONS.

mental membrane between the labial and prothoracic segments, and has no relation to the labial appendage (Holmgren, 1909). Crampton (1928) extended Holmgren's conclusions and said that the submentum is of sternal origin. In Locusta migratoria migratorioides, however, the submentum forms by the fusion of the labial appendage bases, and no sternal element participates (Roonwal, 1937). The development of the postmentum in Pedetontus unimaculatus is similar to that of the locust, but very different from that of Eutermes.

5. Coxopodites and telopodites of the gnathal appendages

As Figure 20 shows, the maxillary and labial appendage anlagen divide transversely into two parts in the same way as in the thoracic appendages. Accordingly, the distal parts of the maxillary and labial appendage anlagen are regarded as the telopodites, and the proximal parts as the coxopodites. In Pedetontus unimaculatus, only the palpi of the maxilla and labium originate in the distal parts (telopodites); the other structures originate from the proximal parts (coxopodites).

The lacinia and galea of the maxilla, and the glossa and paraglossa of the labium, come from the inner (medial) parts of their coxopodites. Since the inner part of the thoracic coxopodite, however,

forms no lobe during development, only the outer part of the maxilla and labium coxopodites corresponds to the thoracic coxopodite. The latter becomes subdivided into two parts, the coxa and subcoxa. Parts of the maxilla and labium corresponding to the thoracic coxopodite also divided into two parts: the stipes and cardo, and the prementum and postmentum, respectively.

No palp occurs in the mandible during development, so that in Pedetontus unimaculatus the entire mandible is the coxopodite, as with other insects. The mandible is temporarily (Stages 11 – 13) divided into two parts, however, as are the coxopodites of maxillary, labial and thoracic segments.

6. Homologies of abdominal appendages

During the embryonic development of Pedetontus unimaculatus, the appendage anlagen of the first to ninth abdominal segments form on the ventral surface of each segment. The coelomic sacs of each segment intrude into its appendage anlagen as those of gnathal and thoracic segments, and it is noteworthy that the appendage anlagen are arranged in a row with the head and thoracic appendage anlagen. Therefore, it is justifiable to believe that the abdominal appendage anlagen are true appendages. The bases of the anlagen gradually spread over the ventral surface of each segment, and become plate-like, differentiating into

the coxite. Thus, in the first to ninth abdominal segments, the appendage is fundamentally divided into two parts, a basal and a distal part, a coxopodite and a telopodite. Basal parts of abdominal appendage anlagen are the coxites of the first to ninth abdominal segments; the distal parts are discussed below.

The cercus is, as is generally accepted, an appendage of the eleventh abdominal segment. The eleventh abdominal appendage or cercus first differentiates into a basal part and a distal one, as in segments one to nine. In Stage 12, a ring-shaped part forms around the base of the cercus, and this basal ring is thought to be homologous with the coxite of the other abdominal segments. In the tenth abdominal segment, a pair of low swellings, which do not undergo further development, occur on the ventral plate during and after Stage 13 in Pedetontus unimaculatus and in Petrobius brevistylis (Larink, 1969). The observations on the sectioned materials show that the ventral epidermis of the tenth abdominal segment is probably derived from the homologous regions with the pleural ones or the appendicular bases of the other preceding segments. The pair of low swellings on the tenth abdominal segment possibly represents the rudimentary appendages of this segment.

A small protuberance appears distally at the lateral side of each anlage in the second to seventh

abdominal appendages, and each gradually elongates to form a rod. This later develops into the stylus, while the rest of the anlage also elongates and develops into the ventral sac*, as observed in Petrobius brevistylis (Larink, 1969). Thus these abdominal appendages become biramous. The eighth and ninth abdominal segments of Pedetontus unimaculatus lack ventral sacs and have only styli. The parts corresponding to the ventral sac anlagen of the second to seventh abdominal segments (Fig. 35, RVS) appear to remain undeveloped in the eighth and ninth abdominal segments; only the stylus anlagen develop.

The distal part of the first abdominal segment appendage is the pleuropodium in the embryo, but this degenerates as a ventral sac in larval and imaginal stages develops. The change occurs right before hatching (Stage 14: Fig. 45). The rudiment of the larval (or imaginal) ventral sac forms on the basal medial side of the degenerating pleuropodium, and thereby the pleuropodium and ventral sac become basally connected. Therefore, the first abdominal appendages as well as those of the second to the seventh abdominal segments are biramous. Pleuropodia

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* In the discussion, the term 'ventral sac' is applied only to the one formed during the embryonic stage; the one formed during the postembryonic stage is not taken into consideration.

and ventral sacs of the first abdominal segment are homologous with the styli and ventral sacs of the other abdominal segments.

In their embryological study of Machilis alternata, Heymons and Heymons (1905) thought that the pleuropodium ("Lateralorgan") was homologous with the ventral sac of subsequent abdominal segments, and regarded it as the "ventral sac" of the first abdominal segment. In support, they noted that the first abdominal appendage is only present in embryonic stages as the pleuropodium, while it is absent during larval and imaginal stages. However, a pair of ventral sacs is actually present on the first abdominal segment of the Machilidae, including Machilis (Trigoniophthalmus), and this contradicts the interpretations of Heymons and Heymons (1905). On the basis of their relative positions, it is more reasonable to regard the pleuropodia as homologues of the styli rather than of the ventral sacs. The author agrees with Heymons and Heymons (1905), however, in interpreting both the pleuropodia and ventral sacs as appendicular in origin.

As discussed above, each of the first to ninth abdominal segments of Pedetontus unimaculatus has a pair of biramous appendages, although they may be transitory or rudimentary in some cases. Heterochrony with regard to the formation of the outer

and inner parts is also observed. In the second to seventh abdominal segments the inner part (ventral sac) develops earlier; however, in the first, eighth, and ninth abdominal segments, the outer part (the pleuropodium or stylus) develops earlier. These differences in the first to ninth abdominal segments might result from secondary modifications in each segment. On the basis of Heymons' embryological study (1897a) of Lepisma saccharina, Snodgrass (1952) indicated that the styli do not represent abdominal appendages in the Thysanura, since in the embryo of Lepisma saccharina they unite entirely with the sternum and appear during postembryonic growth. However, in Pedetontus unimaculatus, the styli are derived directly from abdominal appendages, and are therefore clearly appendicular in origin, as Heymons (1897a) concluded. In the dipluran Campodea staphylinus (Uzel, 1898), the ventral sac and stylus form by the subdivision of the appendage anlage as in Pedetontus unimaculatus, and they seem to be homologous with the ventral sac and stylus of Pedetontus unimaculatus, respectively. In the Symphyla, the abdominal segment possesses a pair of legs, eversible sacs, and styli. In the symphylan Hanseniella agilis (Tiegs, 1940), the eversible sacs are formed independently of the appendages, whereas in Pedetontus unimaculatus, the ventral sacs are evidently appendicular in origin.

The different developmental processes through which the homologous structure, the ventral sac, is formed in Pedetontus unimaculatus and the Symphyla, illustrate a case of what Matsuda (1976) called "homology by substitution (in developmental process)". The developmental process through which the homologous structures – in the ventral sac and the stylus – are formed in Pedetontus unimaculatus and Campodea staphylinus represents a case of euhomology as proposed by Matsuda (1976). He regarded the substitution of homologous parts as the homeostasis of homology which has been maintained by natural selection. He also noted that the concept parallels Lerner's (1958) concept of genetic homeostasis.

7. Formation of midgut epithelium

i) Contribution of yolk cells to the midgut epithelium formation

In Tetrodontophora bielanensis (Jura, 1966; Jura and Krzysztofowicz, 1977), the midgut epithelium is formed by the only proliferation of the crypt cells. In the thysanuran Lepisma saccharina (Sharov, 1953) and Thermobia domestica (Woodland, 1957), the crypts are formed as in Tetrodontophora bielanensis, but they show no activity for the definitive midgut epithelium formation and become active only during the postembryonic period. In Lepisma saccharina (Sharov, 1953) and Thermobia domestica (Woodland,

1957), the definitive midgut epithelia are formed with the migration of the yolk cells, which are left behind in the yolk, to the periphery of the developing midgut. In Pedetontus unimaculatus (Microcoryphia), both the proliferation of crypt cells, as in Tetrodontophora bielanensis (Jura, 1966) and the migration of yolk cells to the periphery, as in Lepisma saccharina (Sharov, 1953) and Thermobia domestica (Woodland, 1957), contribute to the definitive midgut epithelium formation. Therefore, the manner of the contribution of yolk cell in Pedetontus unimaculatus is believed to be of the intermediate type between those in the collembolan, Tetrodontophora bielanensis and the Thysanura.

In Campodea staphylinus (Diplura) (Heymons, 1897b), the midgut epithelium is derived entirely from yolk cells, as in Pedetontus unimaculatus. However, it is formed by only the migration of yolk cells to the yolk periphery and no crypt is formed in this species.

According to Knoll (1974), it is considered that in Scutigera coleoptrata (Chilopoda) the midgut epithelium is of yolk cell origin throughout its length and is formed by the proliferation of the crypt cells. This process of the midgut epithelium formation in Scutigera coleoptrata, therefore, is similar to that in Tetrodontophora bielanensis (Jura, 1966). In the symphylan, Hanseniella agilis also (Tiegs, 1940), the

midgut epithelium develops entirely from the yolk cells. But crypts are not differentiated, and the midgut epithelium formation in Hanseniella agilis is similar to that in Campodea staphylinus (Heymons, 1897b). In Scolopendra cingulata (Chilopoda) (Heymons, 1901), the manner of midgut epithelium formation is very different from that in Scutigera coleoptrata (Knoll, 1974). Heymons' (1901) observation concerning the origin of endoderm is open to question, as Knoll (1974) pointed out.

ii) The phylogenetic consideration of the midgut epithelium formation in insects and myriapods

In Hanseniella agilis (Tiegs, 1940), Scutigera coleoptrata (Knoll, 1974), Tetrodontophora bielanensis (Jura, 1966), Campodea staphylinus (Heymons, 1897b) and Pedetontus unimaculatus, the midgut epithelium develops entirely out of yolk cells. On the other hand, in Lepisma saccharina (Sharov, 1953) the extended tips of the developing stomodaeum and proctodaeum differentiate into the midgut epithelium, so that the anterior and posterior regions of the epithelium are ectodermal and the middle region is of yolk cell origin. In Thermobia domestica, although Woodland (1957) did not clearly refer to the participation of the components of developing stomodaeum and proctodaeum in the midgut epithelium formation, Wellhouse (1954) reported that the components of the developing stomo-

daeum and proctodaeum participate in the midgut epithelium formation, as in Lepisma saccharina (Sharov, 1953). The extension of the tip of the developing stomodaeum of Pedetontus unimaculatus (Fig. 72) is very similar to that of Lepisma saccharina (cf. Sharov, 1953, Plate 5, Figs. 36 and 38). Their extended regions are considered homologous with each other, but the extended region of Pedetontus unimaculatus does not differentiate into the midgut epithelium, in contrast to that of Lepisma saccharina.

In the Odonata (Tschuproff, 1903; Ando, 1962), the middle region of the midgut epithelium is of yolk cell origin, and the anterior and posterior regions are derived from the stomodaeum and proctodaeum (that is ectodermal in origin), as in Lepisma saccharina (Sharov, 1953) and in Thermobia domestica (Wellhouse, 1954). These ectodermal regions are formed from the proliferation of midgut epithelium anlagen differentiated at the tips of the developing stomodaeum and proctodaeum (Ando, 1962). In most pterygote insects, the midgut epithelium is formed by a pair of midgut epithelium anlagen, derived from the developing stomodaeum and proctodaeum (the bipolar formation); these anlagen are more developed than those in the Odonata. However, it has been reported that in some of the hemimetabolous insects the yolk cells participate, although on a small scale, in the midgut epithelium formation,

as reviewed by Haget (1977). Further, in a water strider, Gerris paludum insularis (Mori, 1976), the yolk cells also participate in the midgut epithelium formation, and in the ephemeropteran, Ephemera strigata (Ando and Kawana, 1956), this event was also suggested as possible.

There are several reports on the midgut epithelium formation in the Collembola (cf. Jura, 1972). Philiptschenko (1912) made an embryological study on Isotoma cinerea and stated that the midgut epithelium is formed from the inner layer. Uljanin (1875) came to the conclusion similar to Philiptschenko's in other collembolan species, while other authors, such as Jura (1966) agreed that the midgut epithelium is of yolk cell origin. However, it is significant that in the symphylan, Hanseniella agilis and the chilopodan, Scutigera coleoptrata the midgut epithelium is entirely of yolk cell origin, and that in apterygote insects also it is generally derived from yolk cells. In the Pterygota, although it has been reported that in some species the midgut epithelium is derived from the inner layer, in most cases it is exclusively ectodermal in origin. The method of midgut epithelium formation in the Thysanura, Odonata and some other hemimetabolous insects is of the intermediate or transient type between the Apterygota and Myriapoda on one hand and most of the Pterygota on the other.

In the Symphyla, Chilopoda and Insecta (Trignatha), the developmental succession, as mentioned above, is recognized. In the Trignatha, therefore, the midgut epithelium is considered to be fundamentally of yolk cell origin, and the ectodermal bipolar nature found in most pterygote insects is regarded as the specialized type, with lesser participation of yolk cells in the midgut epithelium formation in higher insect orders. The midgut epithelium of Pedetontus unimaculatus develops entirely from yolk cells, and the formation is one of the representatives of the primitive type in the Insecta or the fundamental type in the Trignatha.

Although there are several reports on the midgut epithelium formation in the Diplopoda (Dignatha) (cf. Johannsen and Butt, 1941), the available information is more or less contradictory. However, the process of the midgut epithelium formation in the Diplopoda as well as in Pauropus silvaticus (Dignatha, Pauropoda) (Tiegs, 1947) is different from that in the Trignatha. For example, in the latter, the midgut is formed around the yolk, but not so in the Dignatha. This fact may suggest the validity of the division of the Antennata into the Dignatha and Trignatha, as proposed by Tiegs and Manton (1958) and others.

8. Metamerism

i) Criteria for metamerism

The following six criteria are usually employed

for the determination of metamerism: i.e., presence of 1) a pair of ganglia, 2) a pair of coelomic sacs, 3) a pair of appendages, 4) a pair of apodemes, and pattern of 5) innervation and 6) musculature. Matsuda (1965, 1970, 1976) and Rempel (1975) examined the validity of each criterion of these in detail. It is said that the last two of these criteria do not always indicate the primary or embryonic condition of the segment, because they tend to be considerably modified secondary with the functional requirement.

Now, the other four criteria will be reexamined and discussed. As for the appendages, they are directly associated with the function. It is indeed significant that a pair of appendages appears in a segment during the embryonic stage, even if they are absent in the segment during the larval or imaginal life (for example, the intercalary appendages of Pieris rapae, Eastham, 1930). However, whenever a pair of appendages may be absent during the embryonic life, it can not always offer any positive evidences for discussing the metamerism.

The apodemes are also directly associated with some function such as the endoskeletal brace, the attachment of muscles and so on. Therefore, as well as the appendages, the presence of apodemes is significant, but the absence of them can not always supply the positive grounds for the argument of metamerism.

The apodemes, in some cases (ex. posterior tentoria and corpora allata in most insects), can or should be qualitatively regarded as some kind of the intersegmental grooves. When employing this criterion in each segment, therefore, it may be justifiable to substitute the "intersegmental groove" for the "apodeme", although Rempel (1975) defined the apodemes as the well-developed ectodermal invaginations.

As for the coelomic sacs, even in the segment that should be regarded as the eusegment, the coelomic cavities in it are often less developed or lacking, such as in many collembolans (cf. Jura, 1972) and some groups of the dipterans (i.e. Nematocera and some Cyclorrhapha) (cf. Anderson, 1972b). Further, in the segments of the head and the posterior abdomen which must be rather modified or specialized, the mesodermal somites usually possess no coelomic cavity. They are often not completely separated with each other in some cases, and even their segmental condition is not recognizable at all in the other. Therefore, although the presence of coelomic sacs is fairly significant on the determination of the metamerism, it should be taken into consideration that there may be some cases where they do not develop well.

As for the ganglia, being a matter of course, the nervous system always goes straight backwards from the eye which is situated at the extreme anterior end of

it in all insects (and further the arthropods, onychophorans and annelids). All the segments are not lacking the nervous system, although there may be some exceptional cases such as the last abdominal region. In employing this criterion, it is not necessary to take account of the cases of "absent" at least in the anterior and intermediate regions of the embryo, in a contrast to the other criteria such as the appendage and apodeme. For this reason, this criterion is the most valid and promising among the four for both the morphological and phylogenetical considerations on the metamerism.

ii) Metemerism in the preoral region

On discussing the metamerism in insects, the most controversial is the problem concerning the preoral region. The detailed reviews on this subject have been given by Matsuda (1965) and Rempel (1975).

In Pedetontus unimaculatus, a pair of antennal ganglia is formed independently of the others, and the antennal segment possesses a pair of well-developed coelomic sacs and appendages. These represent this antennal segment to be one of the eusegments. This must be, in all possibility, true of all the other insects. The antennal segment of Pedetontus unimaculatus, however, possesses no apodeme, in a contrast to the cases in Carausius morosus (Leuzinger, Wiesmann and

Lehmann, 1926; Scholl, 1969) and Lytta viridana (Rempel and Church, 1971). The fact that the antennal ganglia are formed independently of the other ganglia in insects deserves special emphasis. The authors such as Holmgren (1916), Hanström (1927, 1928, 1930) and Snodgrass (1935, 1938, 1960) supposed that the antennal ganglion is not independently present and to be a part of the homologue of the annelid archicerebrum. That is, they did not regard the antennal ganglion or deutocerebrum as representing a neuromere of one complete segment, but as a part of the ganglion of the acron (=prostomium of annelids) or the archicerebrum. However, on the basis of the embryological data, it proves to be not necessary to connect the antennal ganglion with the archicerebrum of annelids.

In Pedetontus unimaculatus, as in the other insects, three pairs of ganglia are recognized anteriorly to the antennal segment. In this species, furthermore, a pair of coelomic sacs is formed anteriorly to the antennal coeloms. These are enough data to manifest the presence of one additional eusegment anterior to the antennal. The ganglion of this segment is regarded as the lobus 3 of protocerebral ganglion, which is situated just anteriorly to the antennal ganglion. This segment or the preantennal segment, however, possesses no appendage and apodeme. The preantennal or labral apodemes have been reported in Carausius

morosus (Leuzinger, Wiesmann and Lehmann, 1926; Scholl, 1969) and Lytta viridana (Rempel and Church, 1971).

The conclusion drawn in Pedetontus unimaculatus, as well as Larink's based on Petrobius brevistylis (1969) and Lepisma saccharina (1970), is coincident with those of Malzacher's (1968), Scholl's (1969) and Rempel and Church's (1971), which seem to be the most reliable at the present. According to Malzacher and others, the preoral region consists of the acron and the labral or preantennal and antennal segments. Now, there remain the difficult problems; whether the appendages are present in the preantennal segment, which can be regarded as the preantennal appendages, if present, or whether the labrum can be thought to be the preantennal appendage as maintained by Scholl (1969) and Rempel and Church (1971). The fact that the labral anlage assumes no paired condition in the apterygote insects (Collembola, Claypole, 1898, Folsom, 1900, Philiptschenko, 1912, Haget and Garaudy, 1964; Diplura, Uzel, 1898, Silvestri, 1933; Microcoryphia, Larink, 1969; Thysanura, Heymons, 1897a, Sharov, 1953, Larink, 1970), the symphylan Hanseniella agilis (Tiegs, 1940) and the chilopodan Scolopendra cingulata (Heymons, 1901) is said to constitute a barrier to regarding the labrum as the appendage. However, it is not so unreasonable to consider that a pair of the labral anlagen should fuse together prior to their enough protrusion and

development to be discerned in the apterygote insects and myriapods. Indeed in Pedetontus unimaculatus, as mentioned in chapter E of OBSERVATIONS, a pair of flat swellings has been observed where a single clypeolabrum anlage should be later given rise to, although only in several cases, but this fact is thought significant. Therefore, it may be considered that the unpaired labral anlage of the apterygote insects and myriapods does not always constitute an insuperable barrier to regarding the labrum in insects as an appendage of some segment. It is, however, confronted with a greater difficulty to regard the labrum as the appendage of the preantennal segment. That is, in Scolopendra cingulata (Heymons, 1901), one additional segment just anterior to the antennal, i.e. preantennal segment, is present other than the segment including the labral anlage. Further, Leuzinger, Wiesmann and Lehmann (1926) observed a pair of appendage-like structures between the anlagen of labral and antennal appendages in Carausius embryo. For the validity of the labral segment, Rempel (1975) offered some evidences, but they are not satisfactory. Further additional comparative embryological data are required on this subject. The present author takes a view that there is no necessity to connect the labrum with the preantennal segment.

The protocerebrum of Pedetontus unimaculatus possesses the other two pairs of ganglia, i.e. lobus l

and 2, than the lobus 3, the same as in most of the other insects. The remarkable structure, corpus pedunculatum, is not developed in the lobus 2 of Pedetontus unimaculatus, but the lobus 2 of this insects may well be homologized with that of the other insects, which usually contains the paired well-developed corpora pedunculata. It is often reported that the archicerebrum of the annelids possesses the corpora pedunculata, and so it is the most justifiable to consider that the lobus 2 of the insects corresponds to a part of archicerebrum of the annelids, and that the lobus 2 constitutes the neuromere belonging to the acron with the lobus 1 situated distally to the lobus 2. However, the ganglion cells of the lobus 2 are, in a marked contrast to the lobus 1, produced with the intervention of the neuroblasts, the same as in all the succeeding ganglia, including the lobus 3. This deserves special emphasis. Paying an attention to this characteristics of the lobus 2, it is not unnatural to consider that the lobi 2 may represent a pair of ganglia of one additional segment preceding the preantennal. This matter remains as a topic for further discussion.

iii) Metamerism in the intercalary, gnathal, thoracic, and abdominal regions

Each of the segments of the gnathal, thoracic, and the first to ninth abdominal segments fulfills

the criteria for metamerism aforesaid in this chapter, Section i). The tenth abdominal segment practically possesses no appendicular structure, but it may be considered that the structures regarded as homologous with segmental appendages, although they undergo no further development, may be present in this segment, as mentioned in DISCUSSION, 6. 'Homologies of abdominal appendages'. This is probably true in the intercalary segment, which also has no appendage. In the eleventh abdominal segment, a coelomic cavity is not produced, but this segment has a pair of the mesodermal somites, although connected with the tenth.

In Pedetontus unimaculatus, each segment of the intercalary to the eleventh abdominal may well be regarded as a eusegment, since each fundamentally fulfills the criteria for metamerism. Contemporarily, the same conclusion as this has been generally accepted in the other insects. The posterior segments of Pedetontus unimaculatus are more or less modified secondary as in the other insects. The degree of modification of these segments, however, is generally far lower in the machilids including Pedetontus unimaculatus and lepismatids (Heymons, 1897a; Sharov, 1953; Woodland, 1957; Larink, 1969) and the lower pterygote insects such as the Odonata (Ando, 1962) and Orthoptera

(Roonwal, 1937), comparing with the higher insects. In Pedetontus unimaculatus, some homological relationships among the segments of the mandibular to the eleventh abdominal are clearly recognized in the external features of embryos (see DISCUSSION, 3, 5, and 6), and it may represent that the segments of Pedetontus unimaculatus on the whole do not extremely undergo the modifications and they preserve the "primary" or "primitive" conditions.

iv) Metamerism in head

As have been discussed, the author, for the present, concludes as to the metamerism of the head in Pedetontus unimaculatus as follows. The head consists of an acron and six eusegments, i.e. the preantennal, antennal, intercalary, mandibular, maxillary, and labial. In the other apterygote insects, the similar interpretations have been made by many authors; in the Collembola by several authors such as Claypole (1898) and Philiptschenko (1912) (cf. Jura, 1972), in the Microcoryphia by Larink (1969) and in the Thysanura by Larink (1970). According to Uzel (1898) and Silvestri (1933), the head of the Diplura is also composed of six segments. However, it is highly doubtful whether their data possess the enough reliability for further comparisons, since these observations were mainly on the external features of embryos.

v) Interpretations on the metamerism in terminal region of the abdomen

The last problem remained is the metamerism concerning the terminal region of abdomen. Heymons, in his series of embryological works on insects (1895, 1896b, 1897a etc.), regarded the subanal and supraanal lobes as representing a segment (the twelfth abdominal), despite the lack of some attributes of a segment (segmental ganglia, coelomic sacs, appendages). However, Snodgrass (1935) said "In most insects no trace of a twelfth segment is to be found, and periproct must be supposed to be represented, if at all, by a circumanal membrane at the end of the eleventh segment". He regarded the supraanal lobe (Snodgrass' epiproct) and subanal lobes (paraprocts) as structures of the eleventh segment. Most recent workers apparently follow this interpretation of Snodgrass', and often the lobes in question are considered to be the structures of the eleventh or even of the tenth. Lately, however, Matsuda (1976), from the serious examinations on the data hitherto accumulated, came to the conclusion supportive for Heymons' interpretation on these lobes. In one view, Heymons' hypothesis, supported by Matsuda, may be accepted to be the denial to a popular idea that the anal lobes are the accessories of the eleventh abdominal segment.

In Pedetontus unimaculatus, the ectodermal part

of every segment consists of only the tergal, appendicular and ganglionic anlagen in the early stages of the differentiation, and no other element is recognized. Therefore, in the sagittal section of each segment, only the ganglionic anlage and, if already closed dorsally, the tergal one should represent the segment they belong to. Now, judging from the sagittal sections of terminal region of the abdomen newly segmented, it is found that the subanal and supraanal lobes differentiate, being clearly marked off from the anlagen of the eleventh abdominal ganglion and tergum (cf. Figs. 55 and 56). In these sections, the part to be regarded as representing the eleventh abdominal segment is occupied by only its ganglionic and tergal anlagen. Accordingly, it is confirmed that the anal lobes are formed independently of the eleventh abdominal segments, and they are the independent structures situated posteriorly to this segment. Although it remains as a unsettled problem whether the anal lobes represent the twelfth abdominal segment, they should be considered at least not to belong to the eleventh abdominal segment, and it supports Heymons' hypothesis.

Since the proctodaeum can be, in one view, regarded as the inner extension of anal lobes, its origin should be determined as the same as that of anal lobes. The proctodaeal musculature which differentiates and extends in company with the proctodaeum is probably inde-

pendent of the eleventh abdominal mesodermal somite, and it is justifiable to consider that the proctodaeal musculature originates from the twelfth abdominal mesoderm, if the anal lobes and proctodaeum can be representative of the twelfth abdominal segment.

Snodgrass (1935) supposed that the tergal region of the eleventh abdominal segment develops into the caudal filament in the machilids, and that in this group of the insects the generalized structure of this segment is most fully retained. In Pedetontus unimaculatus, shortly after the differentiation of the eleventh abdominal segment, the caudal filament anlage becomes clearly marked off from the eleventh segment and supraanal lobe (arrows in Figs. 55 and 56). It is significant that the true tergum of the eleventh abdominal segment is formed quite independently of the caudal filament (see Chapter E of the OBSERVATIONS). Therefore, it is the most reasonable to consider the caudal filament as a independent structure clearly separated from the body trunk, i.e. from the eleventh segment and even from the anal lobes (the twelfth segment ?), against Snodgrass' idea. The caudal filament of Pedetontus unimaculatus might have some relationship to the telson of the annelids.

vi) Conclusion

Thus, the body of Pedetontus unimaculatus is composed of an acron, six cephalic, three thoracic and

eleven abdominal, namely an acron and twenty segments, or an acron and twenty-one, if the anal lobes can be regarded as representing a segment (the twelfth abdominal).

9. Affinities of the Microcoryphia and their allies based on the embryological studies

Among the Apterygota, we have no available embryological knowledge for further comparisons on the Protura, although there is only a very brief report on their egg (Bernard, 1976). Here, the affinities of the Microcoryphia will be examined and discussed, by the aid of comparisons among the embryological data of Pedetontus unimaculatus, other apterygote insects except for the Protura and pterygote insects, and a few of myriapods.

The developmental processes of the Thysanura and Pterygota seem to resemble fundamentally each other, but there appear some differences not to be ignored on the formation of embryonic membranes and that of midgut epithelium. However, as for the formation of embryonic membranes the difference concerns only whethere the amniotic cavity remains open to the exterior at the amniotic pore or not*, and it is considered that the manner of the formation of midgut epithelium in the

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* For example, in Lepisma saccharina, Heymons (1897a) and Sharov (1953) reported that the amniotic pore is never closed, and it is said to be representative of

(→continued on the following page)

Thysanura sufficiently falls under the category of the lower pterygote type as previously-mentioned in the DISCUSSION, 7. 'Formation of midgut epithelium'. Therefore, these differences are regarded as simply representing the primitive nature of the Thysanura (see DISCUSSION, 1. 'Embryonic membranes' and 7), and the developmental process of the Thysanura can be fundamentally regarded in the same light with that of the Pterygota. This suffices to suggest the close affinity of the Thysanura to the Pterygota, and it should be believed that these groups of the insects together constitute a phylogenetically compact group (Thysanura-Pterygota group).

The developmental process of the Microcoryphia fundamentally resembles that of the Thysanura-Pterygota group, especially that of the Thysanura. Larink (in press) said that there is no essential difference between the developmental processes of the Microcoryphia and Thysanura. From the present embryological study of Pedetontus unimaculatus, however, some significant differences are found between them. First, the manner of the midgut epithelium formation in Pedetontus unimaculatus is closely similar to or fundamentally the same as

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(→) the condition of the embryonic membranes in the Thyeanura. However, Larink (in press), in the same species, observed that the amniotic pore is closed the same as in the Pterygota.

that in the Collembola, Diplura and trignathan Myriapoda, and it is practically different from that in the Thysanura-Pterygota group, although some resembrances are recognized (see DISCUSSION, 7. 'Formation of midgut epithelium'). Second, the developmental degree of the embryonic membranes of Pedetontus unimaculatus is thought as taking its position between the Myriapoda, Collembola and Diplura on one hand, and the Thysanura on the other. The developmental succession of the embryonic membranes of the Trignatha is considered as follows; Myriapoda, Collembola and Diplura — Microcoryphia — Thysanura — Pterygota (see DISCUSSION, 1. 'Embryonic membranes' and 2. 'Blastokinesis'). Therefore, the embryonic membranes of the present species seem to be more primitive, comparing that of the Thysanura-Pterygota, and this difference between Pedetontus unimaculatus and the Thysanura-Pterygota deserves special emphasis. Third, the ventral epidermis is, on the whole, regarded as appendicular in origin, in a remarkable contrast to the case in the Thysanura-Pterygota, i.e., the ventral epidermis is exclusively derived from the dermatoblasts situated ventrally to the neurogenic cells (see Chapter G, I, 4 of OBSERVATIONS). The manner of the formation of ventral epidermis in Pedetontus unimaculatus may closely resemble that of the trignathous myriapodan, Chilopoda (Heymons, 1901). These differences mentioned between Pedetontus unimaculatus of the Microcoryphia and the Thysa-

nura are considered to be far greater than those between the Thysanura and lower Pterygota, and it may be suggested that this group of the insects is much more primitive than the Thysanura. Consequently the Microcoryphia should be systematically regarded as apart from the Thysanura-Pterygota group. On the other hand, the close resemblance on the developmental process between the Microcoryphia and Thysanura-Pterygota should be fairly appreciated. That is, it may well be considered that the Microcoryphia should constitute a more extensive group with the Thysanura-Pterygota (the Microcoryphia-Thysanura-Pterygota group).

The developmental process of the other apterygote insects or the Collembola and Diplura is said to differ considerably from that of the Thysanura-Pterygota group. This is true of the relationship between the Microcoryphia, and the Collembola and Diplura. For example, first, in the Collembola and Diplura the primary dorsal organ, which is formed also in the Symphyla and some Diplopoda, appears during their embryogenesis, but all the insects of the Microcoryphia-Thysanura-Pterygota group are unexceptionally lacking this organ. Second, the general number of the abdominal segments is six in the Collembola, and ten in the Diplura, while it is fundamentally eleven exclusively in the Microcoryphia-Thysanura-Pterygota. Third, the cleavage in the Collembola is at first total (but later superficial),

while it is throughout superficial in the Microcoryphia-Thysanura-Pterygota (also in the Diplura superficial, Uzel, 1898; Asaba, unpublished). Thus, the developmental process in the Collembola and Diplura contrasts in s striking way with that in the Microcoryphia-Thysanura-Pterygota group. This difference is greater beyond comparison than that between the Microcoryphia and Thysanura-Pterygota and that between the Thysanura and Pterygota. The developmental processes of both the Collembola and Diplura are in some degree similar to those of the trignathan Myriapoda, especially the Symphyla, but they are considerably dissimilar to each other, mainly concerning their manner of cleavage and general number of abdominal segments. As the conclusion of these comparisons mentioned here, 1) the Microcoryphia and Thysanura or the Microcoryphia-Thysanura-Pterygota group should be regarded as phylogenetically apart from both the Collembola and Diplura, and 2) it is justifiable to consider that the Collembola and Diplura possess no close affinity with each other.

As previously mentioned, the Microcoryphia-Thysanura-Pterygota group can be subdivided into two major sections, the Microcoryphia and the Thysanura-Pterygota, and the difference of developmental process between the Microcoryphia and Thysanura is greater than that between each order of the Pterygota. Therefore, the conventional systematical treatment that the machilids

and lepismatids are collected under one order, the Thysanura (s. lat.), as suborders or families, seems not to be appropreate. It is, however, much difficult to determine what level in the systematical system of the insects these groups correspond to. But, here, the machilids and lepismatids are, for a convenience, treated as taxa in ordinal level. Some scientific names in ordinal level have been proposed for machilids and lepismatids; i.e. for machilids Microcoryphia Verhoeff, Trinemura Crampton, and Protothysanura Crampton, and for lepismatids Thysanura Verhoeff. The present author has employed 'Microcoryphia' and 'Thysanura s. str.' throughout the present paper, in the light of simply the priority.

The conclusion, brought about from the standpoint of the embryology, on the affinities of the Microcoryphia and their allies is summarized as follows.

1) Both the Microcoryphia and Thysanura are regarded as possessing close affinities to the Pterygota, and they are considered to constitute a single comprehensive group with the Pterygota, the Microcoryphia-Thysanura-Pterygota group. The compactness of this group may be suggested by the following section.

2) The Microcoryphia and Thysanura are considered to be much remote in affinity from the other apterygote

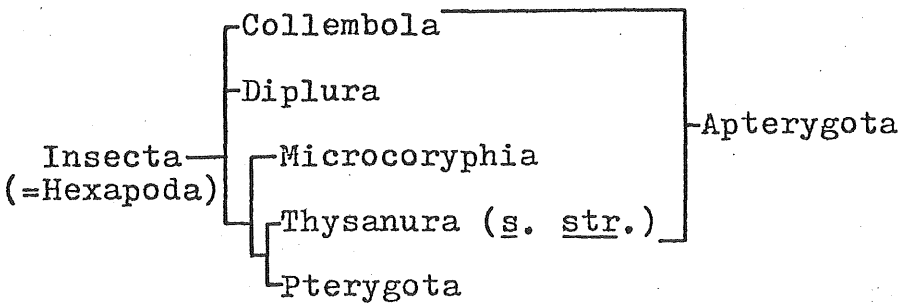
insects, the Collembola and Diplura. Nowadays, such interpretation is generally accepted from the standpoint of the phylogenetical considerations including the comparative embryology (cf. Johannsen and Butt, 1941; Manton, 1964, 1972; Jura, 1972; Anderson, 1973; Ando, 1981).

3) The Microcoryphia-Thysanura-Pterygota group can be phylogenetically subdivided into two major sections, the Microcoryphia group and the Thysanura-Pterygota one.

4) In the Microcoryphia-Thysanura-Pterygota group, the Microcoryphia are interpreted as the most primitive, and the Thysanura may follow in this respect, as is generally accepted.

5) It may be justifiable that the machilids and lepismatids should be systematically treated independently as taxa in ordinal or supra-ordinal level.

These foregoing conclusion is summed up in the following table.

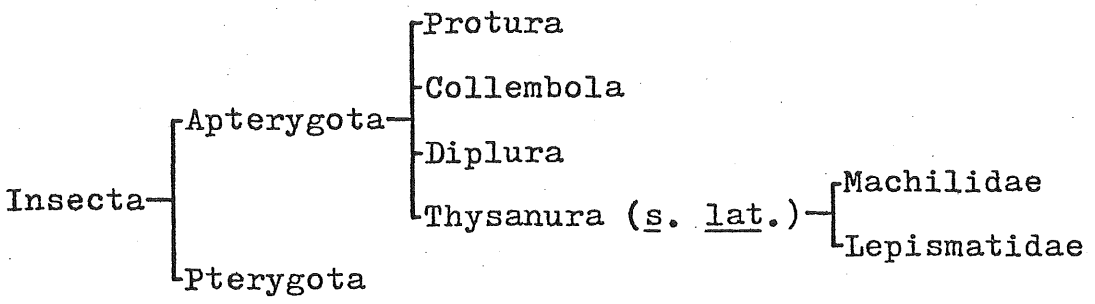


(The Protura are not taken into consideration.)

It is the third section that should deserve the most special emphasis among the five sections of the conclusion. It is on the whole coincident with Hennig's (1953,

1969) and Kristensen's (1975) ideas, which are mainly based on the comparative morphological data.

Lastly, one example of the conventional interpretations concerning the affinities within the Insecta in higher level is presented for the benefit of comparison.



(Compare this table with the one on the preceding page.)

SUMMARY

1. The development of a bristletail, Pedetontus unimaculatus is described, and the results obtained are discussed and compared with previous works.
2. The eggs display various shapes. The ellipsoidal eggs are about 1.3 mm long and 0.8 mm wide. The egg-period varies from 230 to 380 days at room temperature.
3. The cleavage is superficial.
4. A small germ rudiment is formed at the posterior pole of the egg.
5. Three-layered blastoderm cuticles are produced.
6. The serosa and amnion differentiate without the intervention of anatrepsis-katatrepsis process, and the "amnio-serosal fold" does not develop. The formation of embryonic membranes in insects is discussed.
7. The secondary dorsal organ is formed.
8. The blastokinesis is described.
9. The innerlayer formation is of the so-called proliferation type. The primitive groove does not develop.
10. The brain consists of three pairs protocerebral ganglia (lobus 1, 2, and 3+3′), the antennal ganglia (=deutocerebrum), and the intercalary ganglia (=tritocerebrum).
11. The development and fate of the protocerebral lobi are described. The lobus 3 represents the ganglion of preantennal segment.
12. The tritocerebrum (=intercalary ganglia) retains the original postoral position.

13. The ventral nerve cord consists of seventeen pairs of ganglia, one for each segment from the mandibular to the eleventh abdominal.
14. The median cord of the ganglia is lacking the neuroblasts, and is incorporated into each ganglion.
15. The anterior tentoria are formed as the paired ectodermal invaginations appearing medially to the mandibular bases in the intersegmental groove between the intercalary and mandibular segments, and do not fuse with each other.
16. The posterior tentorium is derived from the paired apodemes formed on the both lateral walls of the head between the bases of anlagen of the maxillary and labial appendages.
17. The anterior and posterior tentoria never fuse with each other.
18. The corpora allata are formed as a pair of ectodermal invaginations which appears on the intersegmental groove between the mandibular and maxillary segments.
19. The salivary glands are formed as the paired apodemes arising close to the middle of the median side of each labial base.
20. The spiracles arise in the meso- and metathoracic, and the first to the ninth abdominal segments.
21. The stomodaeum and proctodaeum are formed in the usual manner as ectodermal invaginations. The nine malpighian tubules arise from the proctodaeum.

22. The chitinal proctodaeal plug arises within the blind end of the proctodaeum.
23. The pyloric valve is heterogeneous in origin; anterior part of yolk cell origin, and posterior one ectodermal.
24. The ventral epidermis is appendicular in origin at least in the mandibular to eleventh abdominal segments, in a remarkable contrast to the cases in the other insects.
25. A total number of pairs of mesodermal somites is twenty, one for each of the preantennal, antennal, intercalary, three gnathal, three thoracic, and eleven abdominal segments. Each of the preantennal to tenth abdominal somites possesses a coelomic cavity.
26. The primary median mesoderm is generally lacking in the segments other than the preantennal, antennal, and intercalary.
27. The enteric muscle originates in the median walls of dorsal coeloms in the gnathal, thoracic and abdominal regions.
28. The heart, pericardial cells, dorsal diaphragm and fat bodies are derived from the lateral walls of dorsal coeloms in the gnathal, thoracic, and abdominal regions.
29. The blood cells arise from the secondary median mesoderm mainly of the gnathal and thoracic regions.
30. The peculiar clump of cells, which seem to be germ cells, are found in the mesodermal mass at the posterior end of the early germ band. The cells certainly identified as the germ cells first arise in the dorsal

walls of the appendicular coeloms.

31. The suboesophageal bodies are intercalary mesodermal in origin, and they persists at least in the early-instar larvae.

32. The development and fate of the mesodermal somites in the head are described and summarized.

33. The embryonic musculature of alimentary canal is described.

34. The external features of embryo and first instar larva are described in detail.

35. The homologies of segmental appendages are discussed.

36. The first abdominal appendages are well-developed pleuropodia. The preantennal, intercalary, and tenth abdominal segments practically possess no appendicular structure.

37. The terga of the mandibular, maxillary, and labial segments are obviously recognized, and they take part in the formation of the head capsule.

38. In the maxilla and labium, the palps are homologous with the telopodite of the legs; the other parts proximal to the palps are homologous with the coxopodites.

39. No sternal element contributes to the postmentum formation.

40. Both glossa and paraglossa consist of two lobes.

41. The pleuropodium of the first abdominal segment is homologous with the styli of the successive abdominal segments; the ventral sacs of succeeding segments are

serially homologous.

42. The basal parts of appendage anlagen cover each ventral surface in the first to ninth abdominal segments to form coxites, which are therefore appendicular in origin.

43. The basal part of the cercus also covers the ventral and lateral surfaces of the eleventh abdominal segment.

44. The midgut epithelium is entirely of yolk cell origin. The formation of midgut epithelium in the Trignatha is summarized and discussed.

45. The ental membrane is described. The epineural sinus is practically restricted only to the gnathal and mesothoracic regions.

46. The embryonic metamerism is discussed.

47. The body is composed of an acron and six cephalic (i.e., preantennal, antennal, intercalary, mandibular, maxillary, and labial), three thoracic, and eleven abdominal segments, namely an acron and twenty segments, or an acron and twenty-one segments, if the anal lobes may represent a segment (the twelfth abdominal).

48. The anal lobes and the caudal filament are the structures quite independent of the eleventh abdominal segment. The problems concerning these structures are discussed.

49. The affinities of the Microcoryphia and their allies are discussed, on the basis of the embryological data. The Microcoryphia are considered to constitute a compact

comprehensive group with the Thysanura and Pterygota (the Microcoryphia-Thysanura-Pterygota group), and this group may be phylogenetically subdivided into two major sections, the Microcoryphia and the Thysanura-Pterygota group.

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FIGURES

ABBREVIATIONS USED IN THE FIGURES

a, midgut epithelial cell derived from crypt
A, anus
AbT, abdominal tergum
ACL, anterior cell layer to proctodaeal plug
AcLo, accessory lobe
Am, amnion
AmC, amniotic cell
An, antenna
AnG, antennal ganglion
AnS, antennal segment
AnSo, antennal somite
App, appendage
App.I-XI, first to eleventh abdominal appendages
ASAT, anterior suspension of anterior tentorium
AT, anterior tentorium
b, midgut epithelial cell directly derived from yolk cells
B_{1-3}, protocephalic bulges 1, 2 and 3
BAT, binder of anterior tentoria
BC, blood cell
Bl, blastoderm
BlC 1-3, blastoderm cuticles 1, 2 and 3
Ca, cardo
Cb, cardioblast
CC, cleavage cell
CdV, cardiac valve
Ce, cercus
CE, compound eye or compound eye anlage
CeB, central body
CF, caudal filament or caudal filament anlage
Ch, chorion
CiCon, circumoesophageal connective
Cl, clypeus
Cllr, clypeolabrum
Cm, coelom
CmS, coelomic sac
Co, coxa
Cp, coxopodite
Cr, crypt
Cx, coxite
Dc, deutocerebrum
DCm, dorsal coelom
DDp, dorsal diaphragm
DSaGl, duct of salivary gland
DSn, dorsal sinus
DVE, definitive ventral epidermis
E, embryo
EM, embryonic membrane
Ench, endochorion
EnM, ental membrane
EnMu, enteric muscle
EpSn, epineural sinus
ESu, epicranial suture
Exch, exochorion
FB, fat body
FC, fat cell
Fe, femur
Fl, flagellum

FrG, frontal ganglion
G, ganglion
G.I-XI, first to eleventh abdominal ganglia
Ga, galea
GC, germ cell
GD, germ disc
Gl, glossa
GL, gelatinous layer
GnT, gnathal tergum
GnTMu, gnathal transverse muscle
GR, germ rudiment
GsCc, gastric caecum
H, heart
HC, heart cell
Hp, hypopharynx
IG, intercalary ganglion
IL, inner layer
IMe, intercalary mesoderm
In, incisor
IS, intercalary segment
ISo, intercalary somite
L1-3, 3', protocerebral lobi 1, 2, 3 and 3'
La, lacinia
LaAp, lacinial apodeme
Lb, labium
LbG, labial ganglion
LbP, labial palp
LbS, labial segment
LbSo, labial somite
LbSu, labial suture
LbT, labial tergum
LG, lamina ganglionaris
Li, lingua
LMg, lumen of midgut
Lr, labrum
LSAT, lateral suspension of anterior tentorium
LWDCm, lateral wall of dorsal coelom
M, mouth
MCd, median cord
Md, mandible
MdG, mandibular ganglion
MdS, mandibular segment
MdSo, mandibular somite
MdT, mandibular tergum
MdTTe, mandibular transverse tendon
Me, mesoderm
MEx, medulla externa
Mg, midgut
MgEp, midgut epithelium
MgEpC, midgut epithelial cell
MIn, medulla interna
Mo, molar
MP, median plate
MpTu, malpighian tubule
Mu, muscle
Mx, maxilla
MxAM, maxillary arthrodial membrane
MxG, maxillary ganglion
Mx-LbT, maxillolabial tergum
MxP, maxillary palp
MxS, maxillary segment
MxSo, maxillary somite
MxT, maxillary tergum
Nb, neuroblast
NG, neural groove

Nl, neurilemma
Np, neuropile
NsC, neurosecretory cell
O, ocellus
OPe, ocellar pedicel
OpP, optic plate
P, pleuron
PaIc, pars intercerebralis
Pc, protocerebrum
PcBr, protocerebral bridge
PCL, posterior cell layer to proctodaeal plug
PcLo, protocerebral lobe
Pd, proctodaeum
PdMu, proctodaeal muscle
PdP, proctodaeal plug
PdS, proctodaeal suspension
Pe, pedicel
PerC, pericardial cell
Pf, palpifer
Pg, palpiger
Pgl, paraglossa
Pl, pleuropodium
Pm, postmentum
Pp, periplasm
PPd, presumptive proctodaeum
PraSo, preantennal somite
PreoMe, preoral mesoderm
PrF, postretinal fiber or postretinal fiber anlage
PSAT, posterior suspension of anterior tentorium
PSd, presumptive stomodaeum
PT, posterior tentorium
Pta, pretarsus
PVE, provisional ventral epidermis
PyR, pyloric region
ReNv, recurrent nerve
RVS, rudimentary ventral sac
S, sternum or sternite
S.I-XI, first to eleventh abdominal sterna
SaGl, salivary gland
Sba, subanal lobe or plate
SbB, suboesophageal body
SbCom, suboesophageal commissure
SbG, suboesophageal ganglion
Sc, scapus
Sco, subcoxa
Sd, stomodaeum
SdMu, stomodaeal muscle
SDO, secondary dorsal organ
Se, serosa
SgNv, stomatogastric nerve
Sli, superlingua
SMMe, secondary median mesoderm
So, somite
So,I-XI, first to eleventh abdominal somites
SoMe, somatic mesoderm
Sp, spiracle
Spa, supraanal lobe or plate
SpMe, splanchnic mesoderm
Sti, stipes
Sty, stylus
T, tergum
T.I-XI, first to eleventh abdominal terga
Ta, tarsus
Tc, tritocerebrum
Th1-3, pro-, meso- and

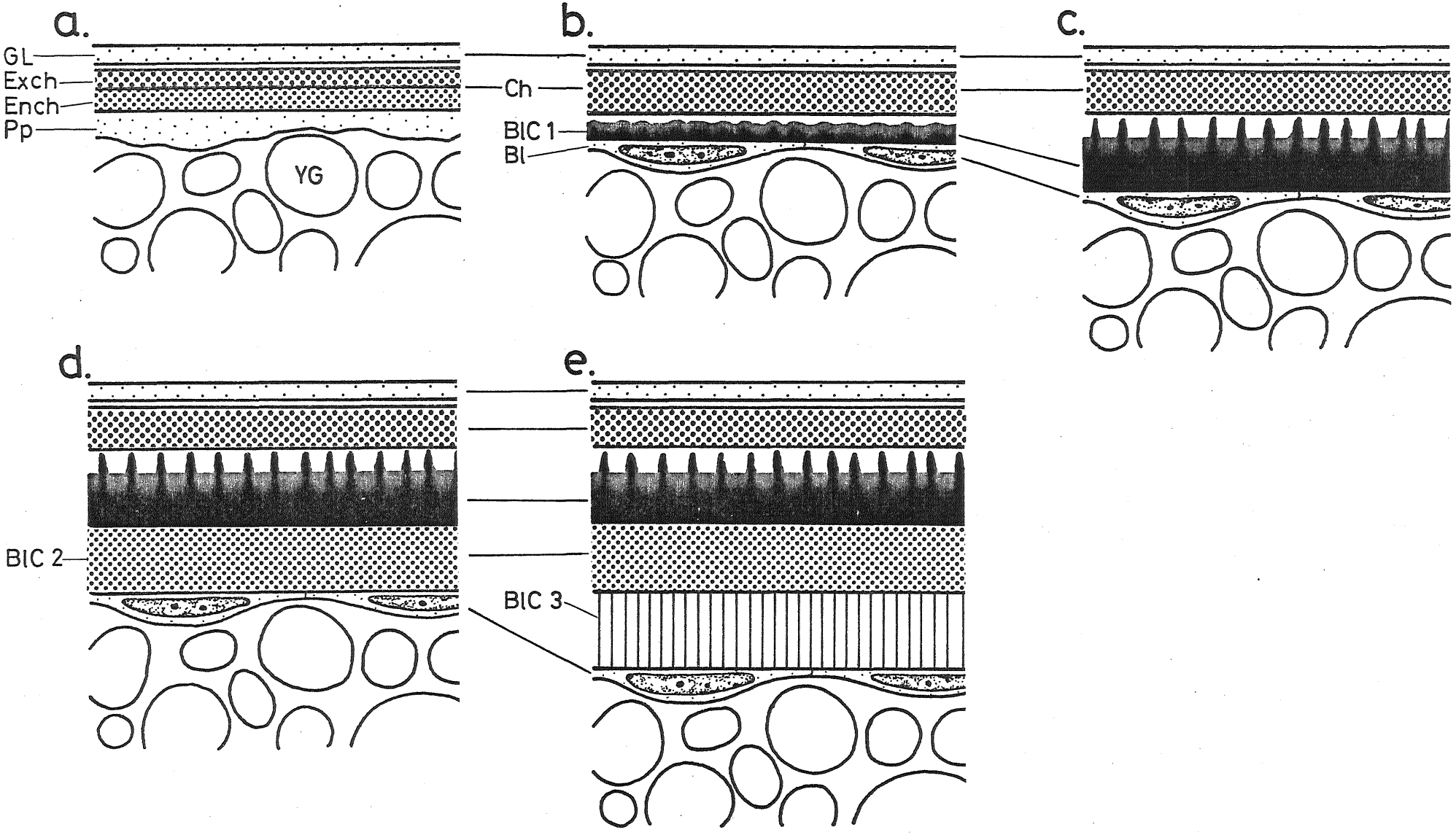
metathoracic segments
Th1-3So, pro-, meso- and
metathoracic somites
ThT, thoracic tergum
Ti, tibia
Tp, telopodite
Tr, trochanter
VCm, ventral coelom
VS, ventral sac
Y, yolk
YB, yolk bulge
YBl, yolk block
YC, yolk cell
YF, yolk fold
YG, yolk globule
I-XI, first to eleventh
abdominal segments

EXPLANATION OF FIGURE

1. Diagrams showing development of egg membranes (a–e).

Bl, blastoderm; BlC 1-3, blastoderm cuticles 1, 2 and 3; Ch, chorion; Ench, endochorion; Exch, exochorion; GL, gelatinous layer; Pp, periplasm; YG, yolk globule

1

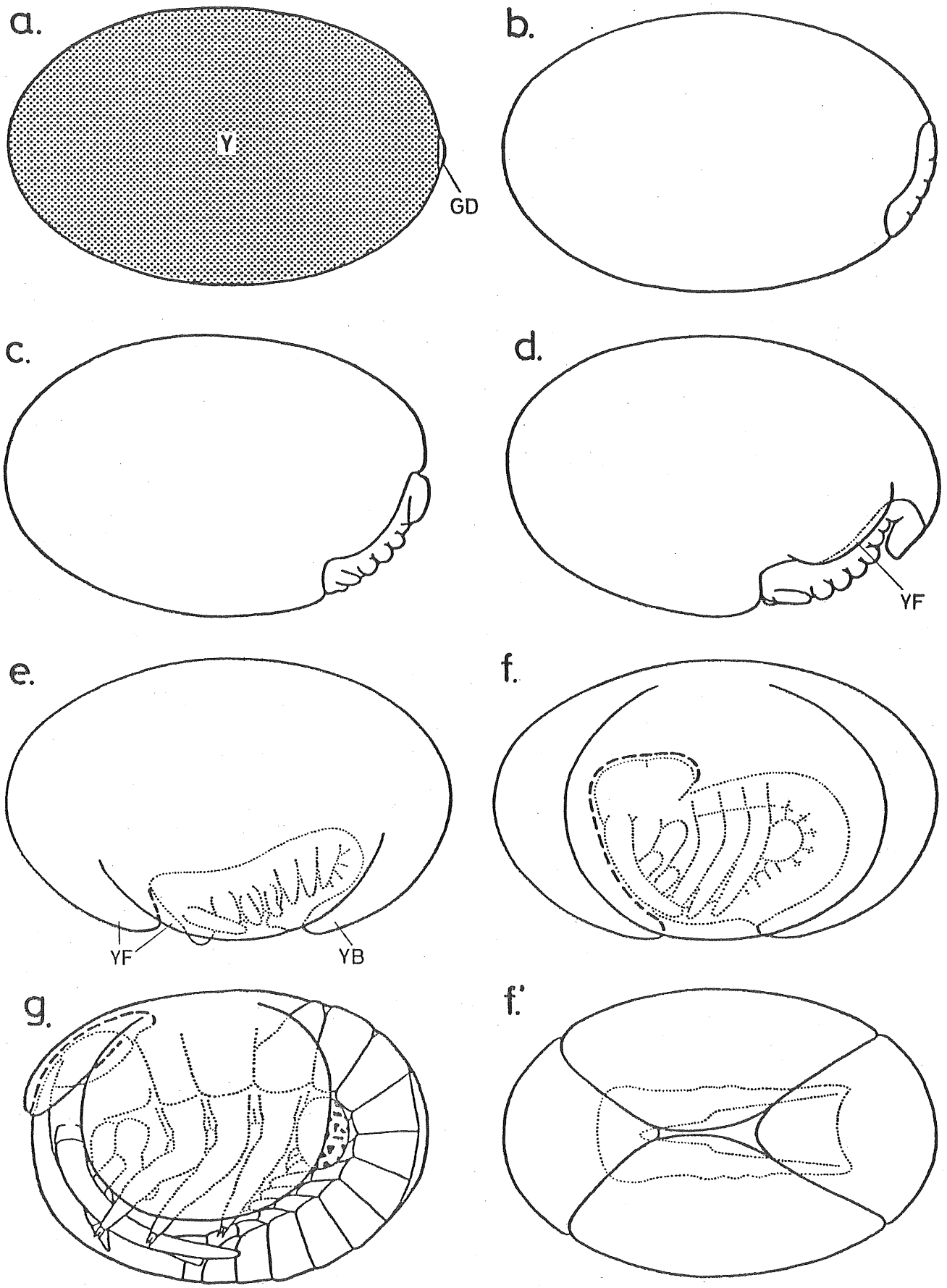


EXPLANATION OF FIGURE

2. Diagrams showing blastokinesis (a–g). Egg membranes omitted.

GD, germ disc; Y, yolk; YB, yolk bulge; YF, yolk fold

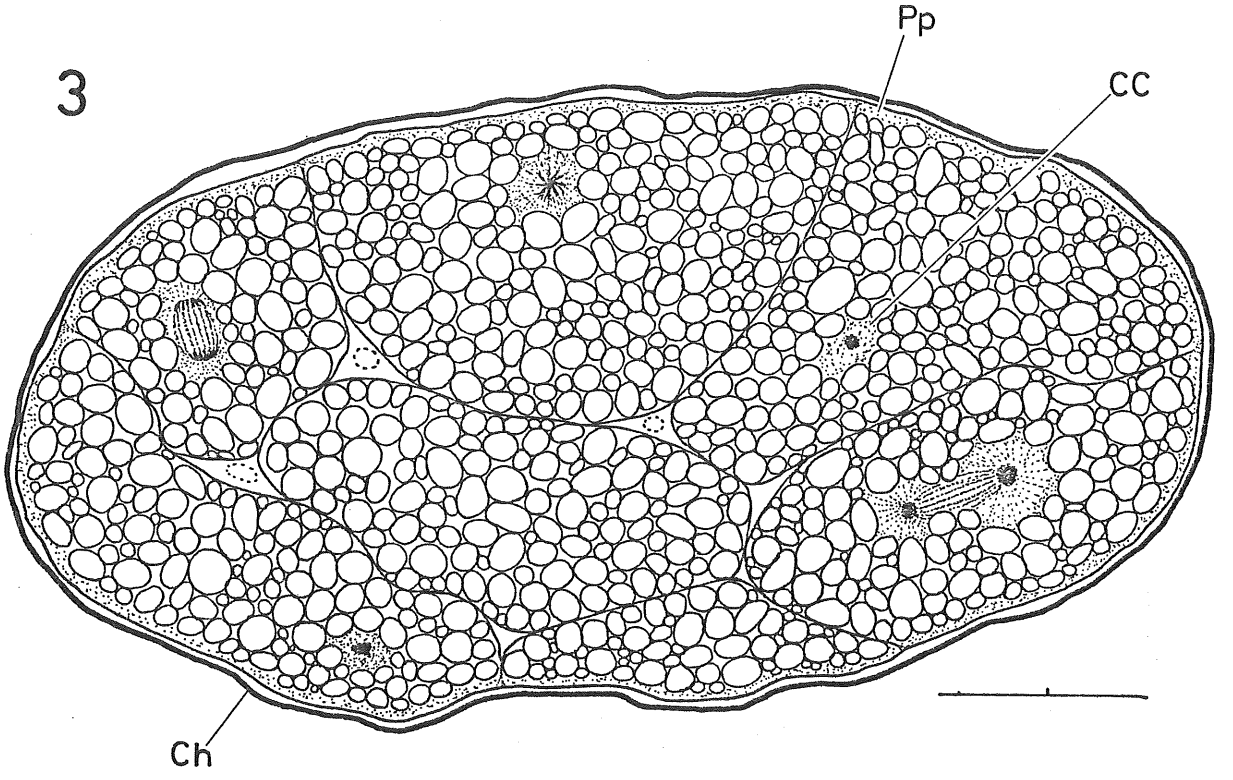
2

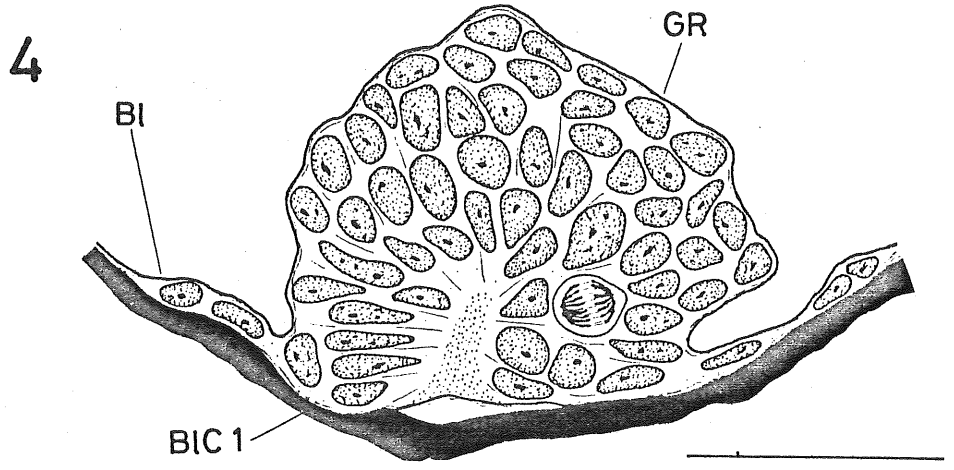


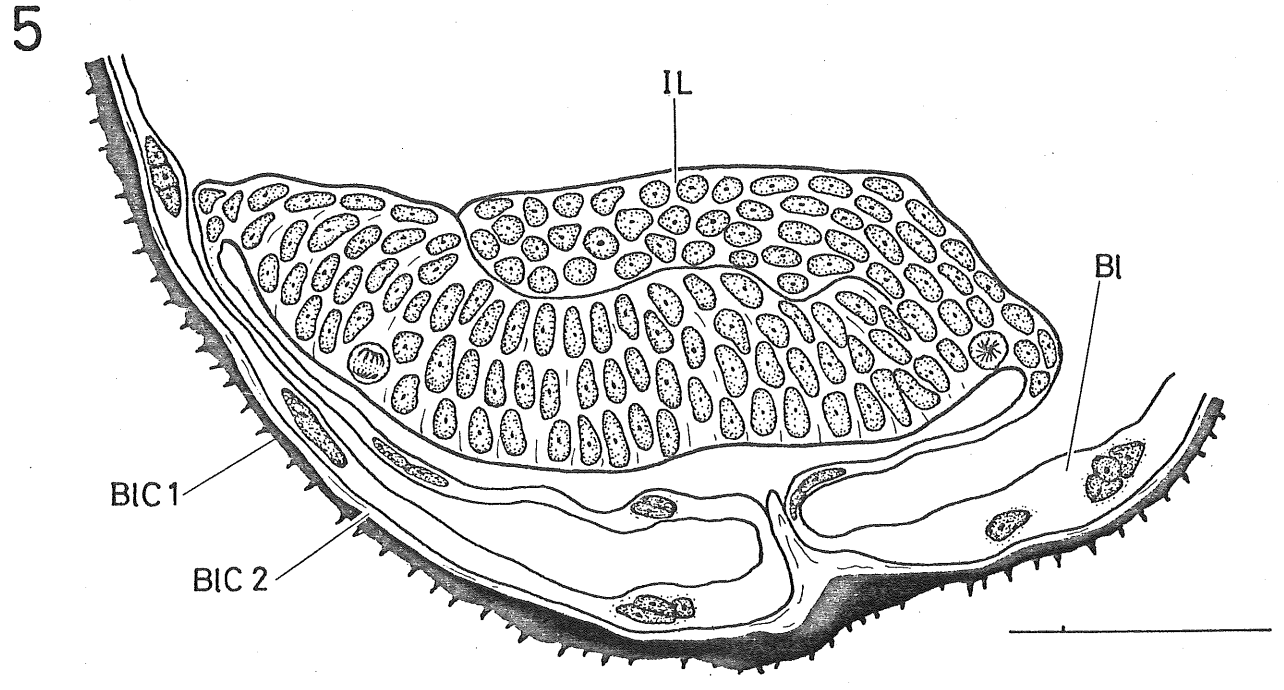
EXPLANATION OF FIGURES

3. Egg in cleavage. Scale = 100 μm.
4. Section of germ rudiment. Chorion omitted. Scale = 50 μm.
5. Sagittal section of germ disc with inner layer. Chorion omitted. Scale = 50 μm.

Bl, blastoderm; BlC 1, 2, blastoderm cuticles 1 and 2; CC, cleavage cell; Ch, chorion; GR, germ rudiment; IL, inner layer; Pp, periplasm


3
Pp
CC
Ch

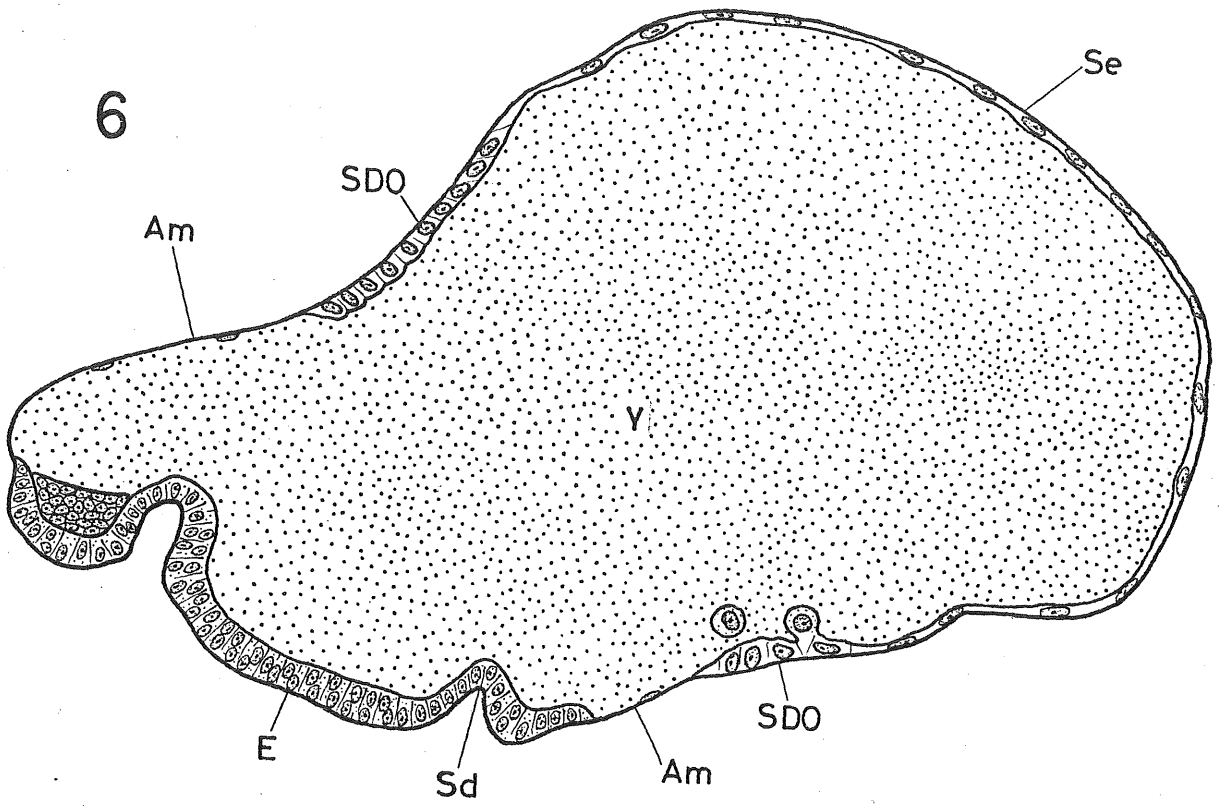

4
GR
Bl
BlC 1

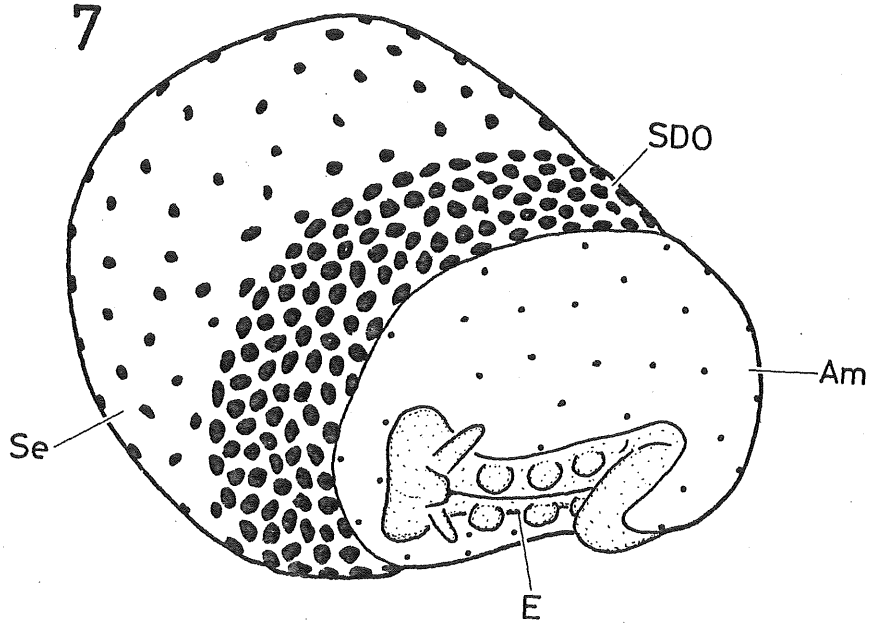

5
IL
Bl
BlC 1
BlC 2

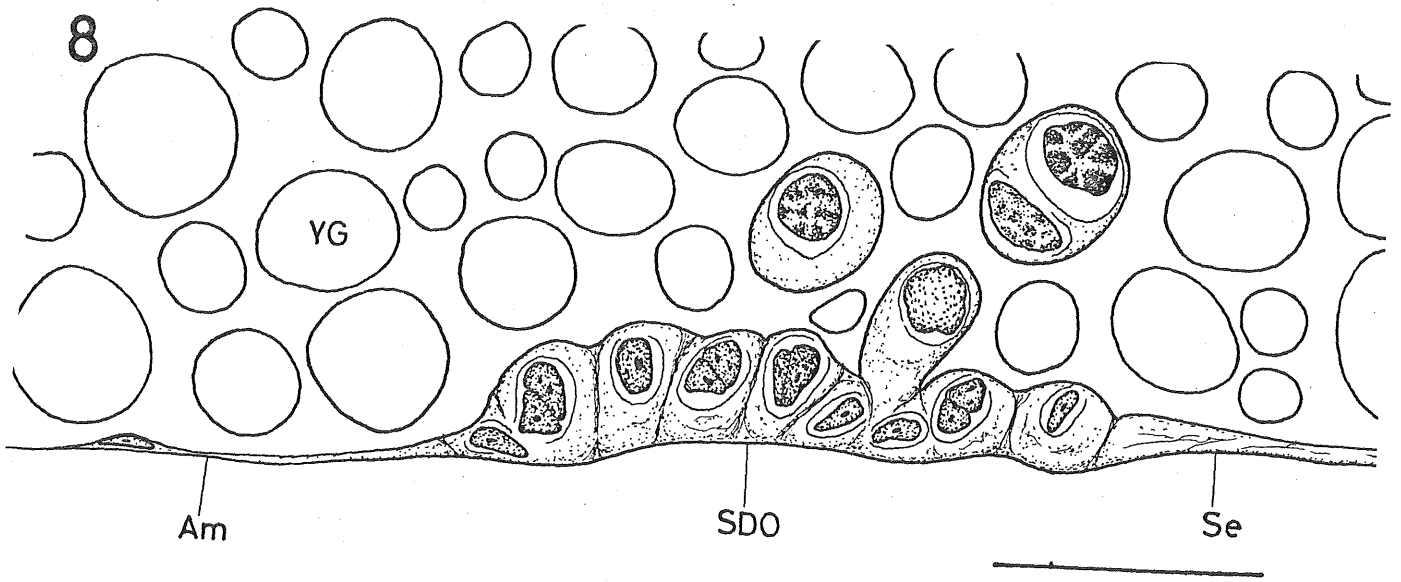
EXPLANATION OF FIGURES

6. Diagrammatic sagittal section of egg in Stages 4-5. Egg membranes omitted.
7. Same, in surface view.
8. Secondary dorsal organ and its cells separating into yolk (Stage 7). Scale = 50 μm.

Am, amnion; E, embryo; Sd, stomodaeum; SDO, secondary dorsal organ; Se, serosa; Y, yolk; YG, yolk globule


6
Se
SDO
Am
Y
E
Sd
Am
SDO


7
SDO
Am
Se
E

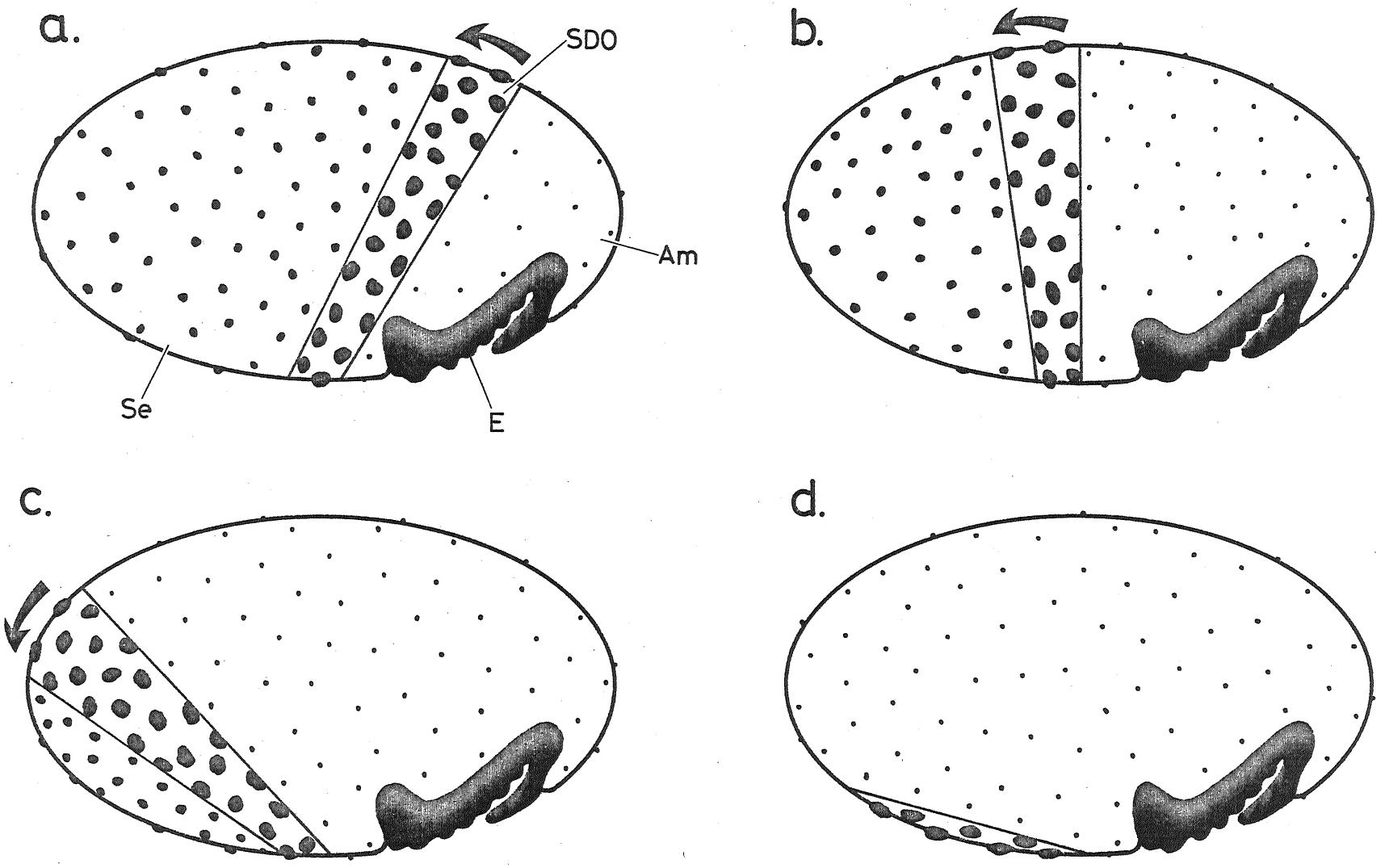

8
YG
Am
SDO
Se

EXPLANATION OF FIGURE

9. Diagrams showing the movement of secondary dorsal organ and the extension of amnion (a–d).

Am, amnion; E, embryo; SDO, secondary dorsal organ; Se, serosa

9

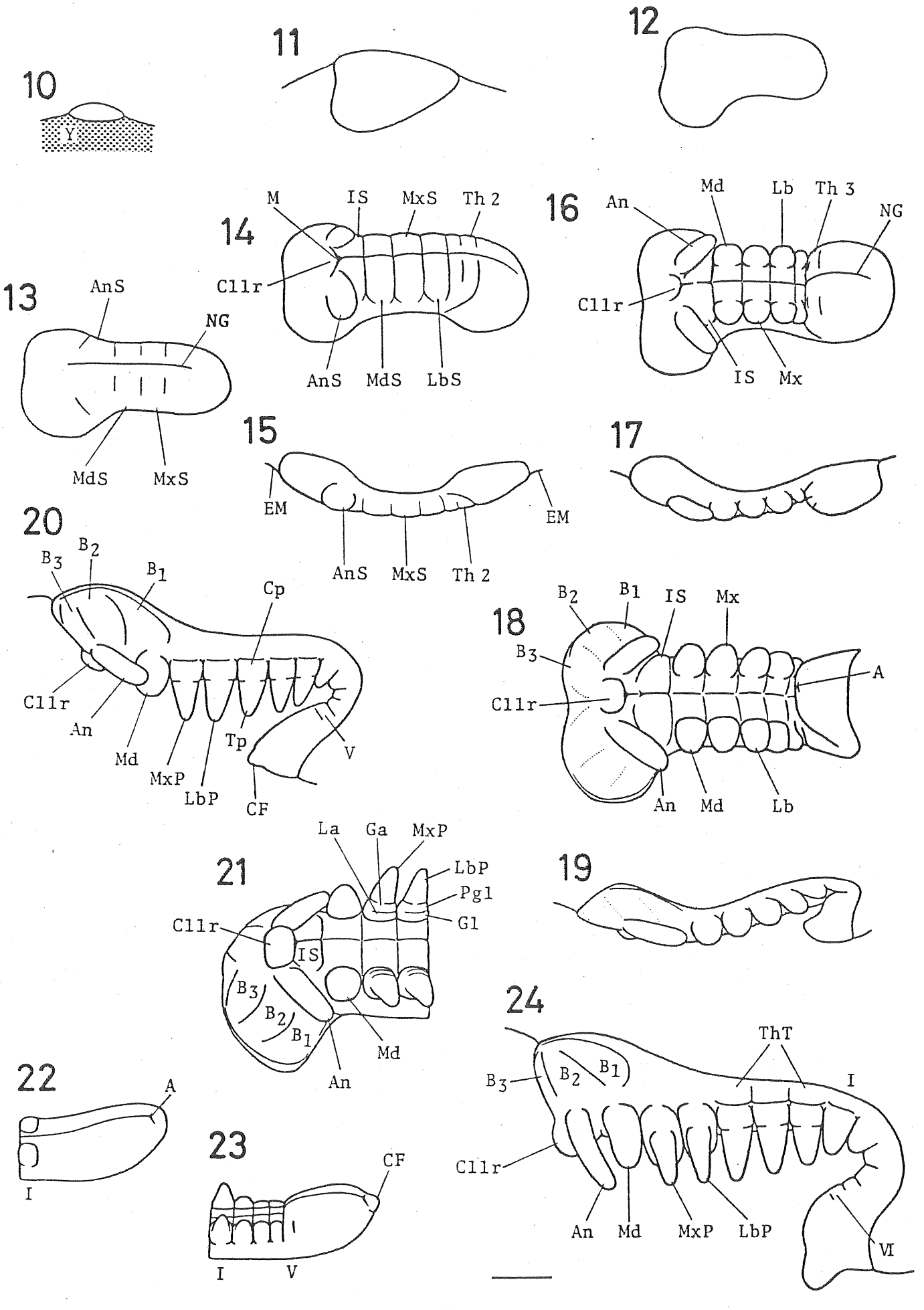


EXPLANATION OF FIGURES

Scale = 100 μm.

10. Ventrolateral view of early germ disc, Stage 1.
11. Ventrolateral view of developed germ disc, Stage 1.
12. Ventrolateral view of embryo in Stage 2.
13. Ventrolateral view of embryo in Stage 3.
14. Ventrolateral view of embryo late in Stage 3.
15. Lateral view of embryo in same stage as in Figure 14.
16. Ventrolateral view of embryo in Stage 4.
17. Lateral view of embryo in Stage 4.
18. Ventrolateral view of embryo in Stage 5.
19. Lateral view of embryo in Stage 5.
20. Lateral veiw of embryo in Stage 6.
21. Ventrolateral view of head of embryo in Stage 6.
22. Ventrolateral view of abdomen of embryo early in Stage 6.
23. Ventrolateral view of abdomen of embryo late in Stage 6.
24. Lateral veiw of embryo in Stage 7.

A, anus; An, antenna; AnS, antennal segment; B_{1-3}, protocephalic bulges 1, 2 and 3; CF, caudal filament; Cllr, clypeolabrum; Cp, coxopodite; EM, embryonic membrane; Ga, galea; Gl, glossa; IS, intercalary segment; La, lacinia; Lb, labium; LbP, labial palp; LbS, labial segment; M, mouth; Md, mandible; MdS, mandibular segment; Mx, maxilla; MxP, maxillary palp; MxS, maxillary segment; NG, neural groove; Pgl, paraglossa; Th2, 3, meso- and metathoracic segments; ThT, thoracic tergum; Tp, telopodite; Y, yolk; I, V, VI, first, fifth and sixth abdominal segments

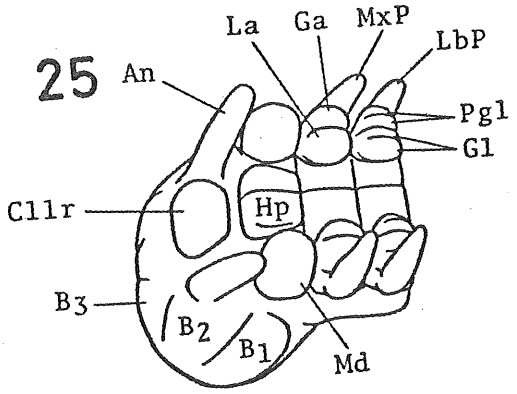

10
Y
11
12
13
AnS
NG
MdS
MxS
14
M
IS
MxS
Th 2
Cllr
AnS
MdS
LbS
15
EM
EM
AnS
MxS
Th 2
16
An
Md
Lb
Th 3
NG
Cllr
IS
Mx
17
18
B2
B1
IS
Mx
B3
A
Cllr
An
Md
Lb
19
20
B3
B2
B1
Cp
Cllr
An
Md
MxP
LbP
Tp
V
CF
21
La
Ga
MxP
LbP
Pgl
Gl
Cllr
IS
B3
B2
B1
Md
An
22
A
I
23
CF
I
V
24
ThT
I
B3
B2
B1
Cllr
An
Md
MxP
LbP
VI

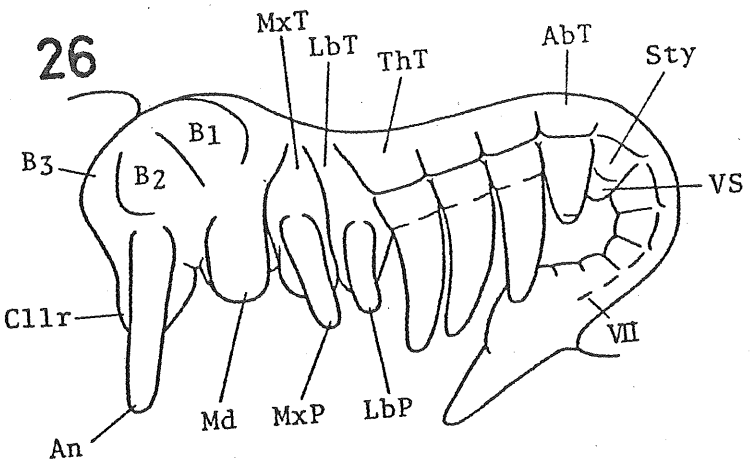
EXPLANATION OF FIGURES

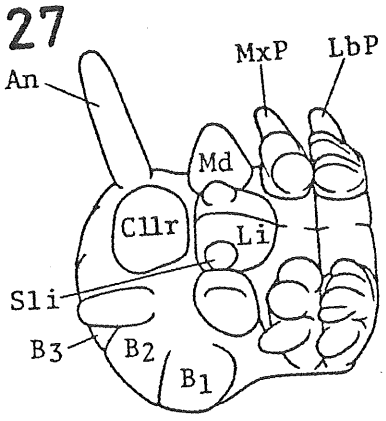
Scale = 100 μm.

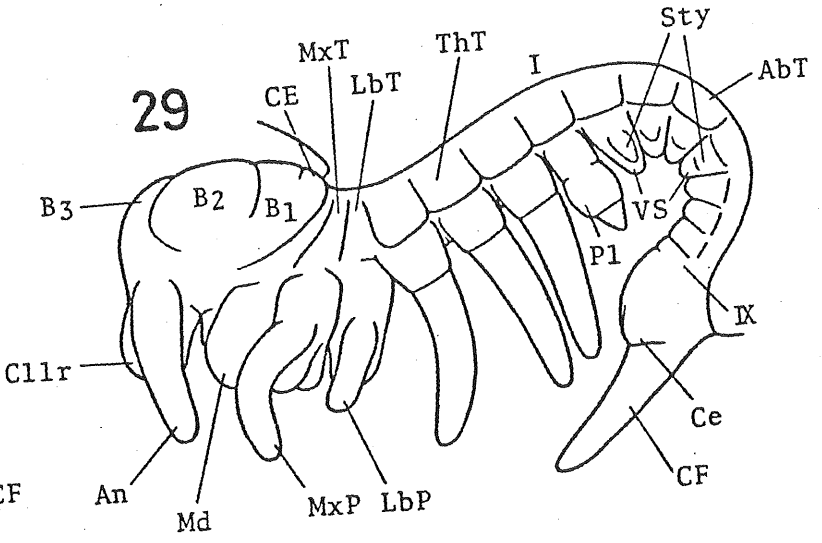
25. Ventrolateral view of head of embryo in Stage 7.
26. Lateral view of embryo in Stage 8.
27. Ventrolateral view of head of embryo in Stage 8.
28. Ventrolateral view of abdomen of embryo in Stage 8.
29. Lateral view of embryo in Stage 9.
30. Ventral view of head of embryo in Stage 9.
31. Lateral view of embryo in Stage 10.
32. Ventrolateral view of head of embryo in same stage as in Figure 31.

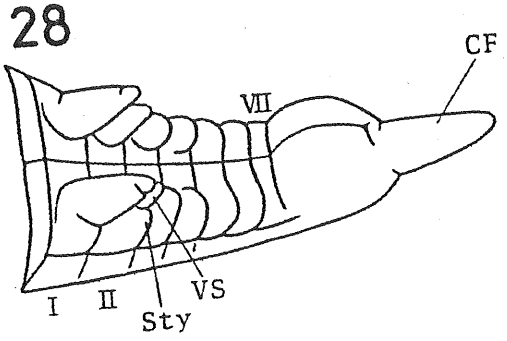
AbT, abdominal tergum; An, antenna; B_{1-3}, protocephalic bulges 1, 2 and 3; Ce, cercus; CE, compound eye anlage; CF, caudal filament; Cllr, clypeolabrum; Cp, coxopodite; Ga, galea; Gl, glossa; Hp, hypopharynx; La, lacinia, Lb, labium; LbP, labial palp; LbT, labial tergum; Li, lingua; Md, mandible; MxP, maxillary palp; MxT, maxillary tergum; Pgl, paraglossa; Pl, pleuropodium; S, sternum; Sc, scapus; Sli, superlingua; Sty, stylus; ThT, thoracic tergum; Tp, telopodite; VS, ventral sac; I-XI, first to eleventh abdominal segments

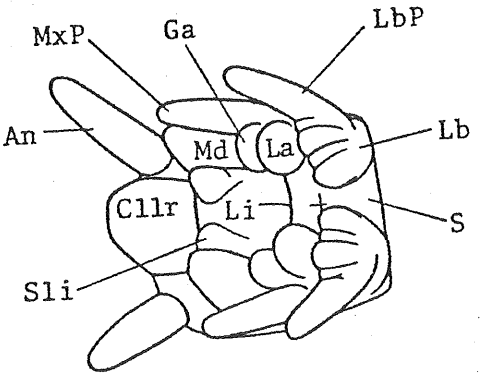

25
La
Ga
MxP
LbP
An
Pgl
Gl
Cllr
Hp
B3
B2
B1
Md

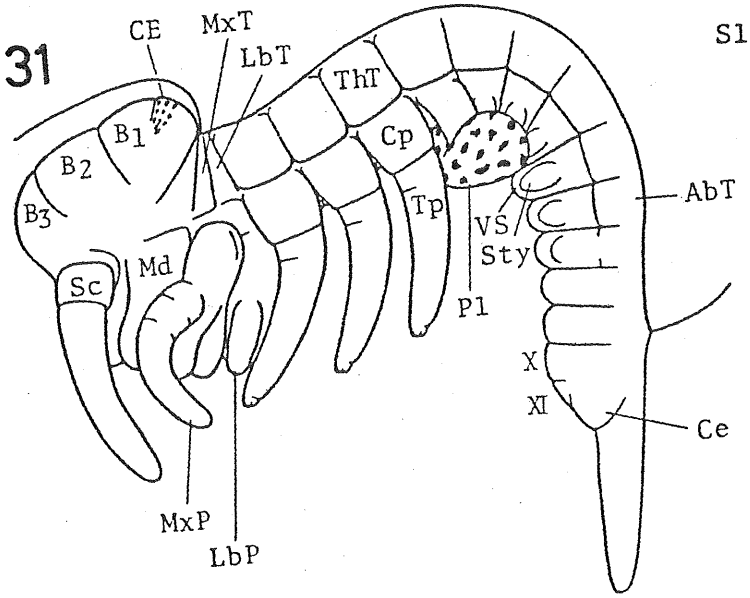

26
MxT
LbT
ThT
AbT
Sty
B1
B3
B2
VS
Cllr
VII
Md
MxP
LbP
An

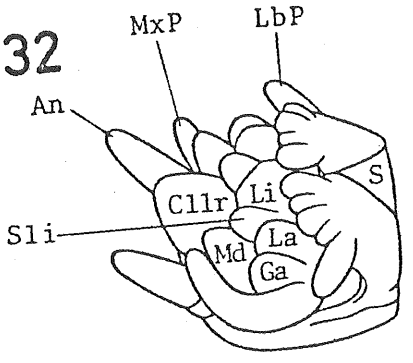

27
An
MxP
LbP
Md
Cllr
Li
Sli
B3
B2
B1


29
Sty
MxT
ThT
I
AbT
CE
LbT
B3
B2
B1
VS
P1
IX
Cllr
Ce
CF
An
Md
MxP
LbP


28
CF
VII
I
II
Sty
VS


30
MxP
Ga
LbP
An
Lb
Md
La
Cllr
Li
S
Sli


31
CE
MxT
LbT
ThT
B1
B2
Cp
B3
Tp
AbT
VS
Sty
Sc
Md
P1
X
XI
Ce
MxP
LbP

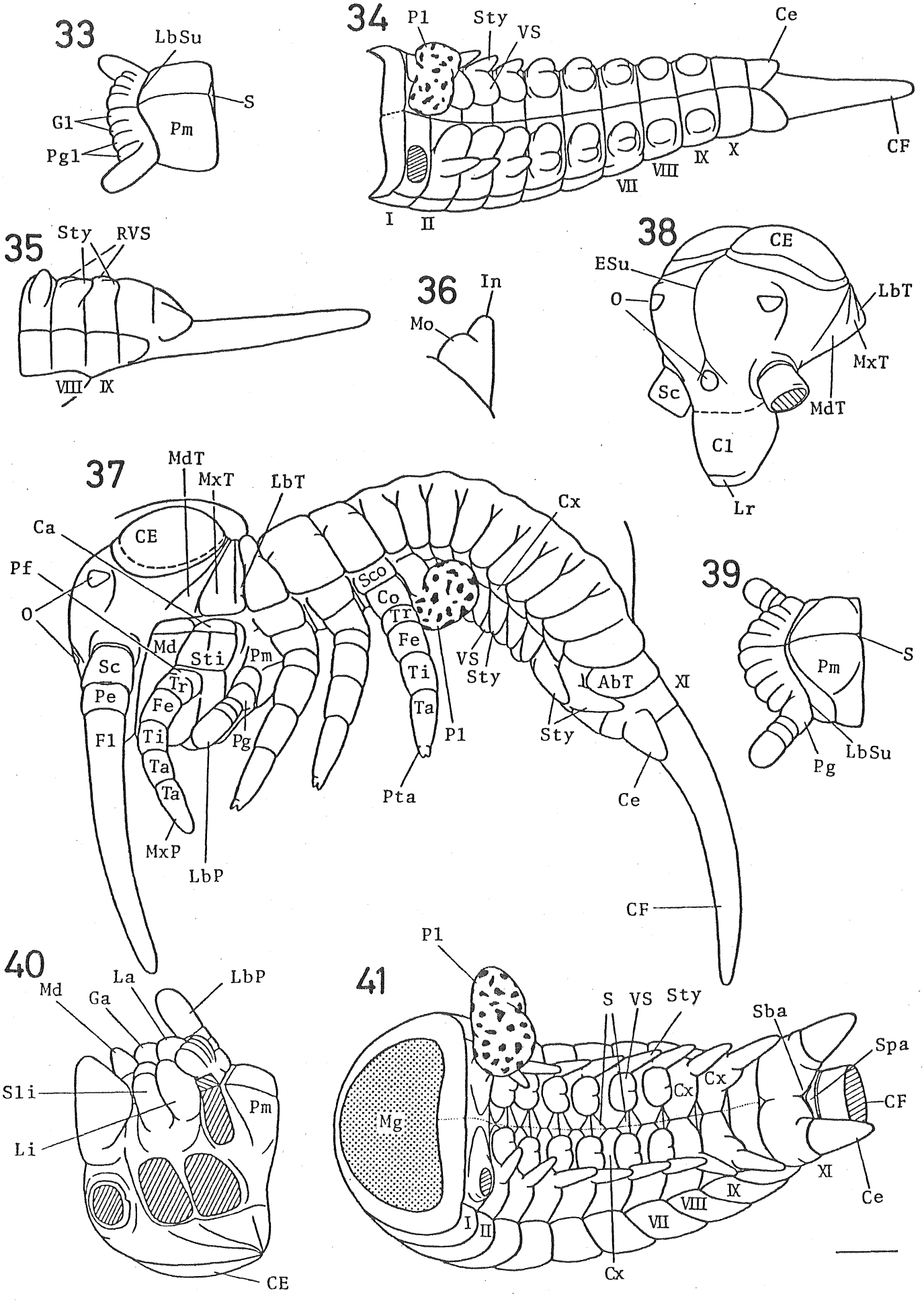

32
MxP
LbP
An
S
Cllr
Li
Sli
La
Md
Ga

EXPLANATION OF FIGURES

Scale = 100 μm.

33. Ventrolateral view of labium of embryo late in Stage 10.
34. Ventrolateral view of abdomen of embryo in same stage as in Figure 31. Right pleuropodium removed.
35. Lateral view of posterior abdominal segments of embryo late in Stage 10.
36. Posterior view of left mandible in Stage 10.
37. Lateral view of embryo in Stage 11.
38. Laterofrontal view of head of embryo in Stage 11.
39. Ventrolateral view of labium of embryo in Stage 11.
40. Ventrolateral view of head of embryo in Stage 12.
41. Ventrolateral view of abdomen of embryo in Stage 12. Caudal filament and right pleuropodium cut.

AbT, abdominal tergum; Ca, cardo; Ce, cercus; CE, compound eye; CF, caudal filament; Cl, clypeus; Co, coxa; Cx, coxite; ESu, epicranial suture; Fe, femur; Fl, flagellum; Ga, galea; Gl, glossa; In, incisor; La, lacinia; LbP, labial palp; LbSu, labial suture; LbT, labial tergum; Li, lingua; Lr, labrum; Md, mandible; MdT, mandibular tergum; Mg, midgut; Mo, molar; MxP, maxillary palp; MxT, maxillary tergum; O, ocellus; Pe, pedicel; Pf, palpifer; Pg, palpiger; Pgl, paraglossa; Pl, pleuropodium; Pm, postmentum; Pta, pretarsus; RVS, rudimentary ventral sac; S, sternite; Sba, subanal lobe; Sc, scapus; Sco, subcoxa; Sli, superlingua; Spa, supraanal lobe; Sti, stipes; Sty, stylus; Ta, tarsus; Ti, tibia; Tr, trochanter; VS, ventral sac; I-XI, first to eleventh abdominal segments


33
LbSu
S
Gl
Pm
Pgl
34
Pl
Sty
VS
Ce
CF
I
II
VII
VIII
IX
X
35
Sty
RVS
VIII
IX
36
In
Mo
38
CE
ESu
O
LbT
MxT
Sc
MdT
Cl
Lr
37
MdT
MxT
LbT
Ca
CE
Pf
O
Cx
Sco
Co
Tr
Fe
Ti
Ta
Pta
Md
Sti
Pm
Sc
Pe
Fl
Tr
Fe
Ti
Ta
Ta
Pg
MxP
LbP
VS
Sty
Pl
AbT
XI
Sty
Ce
CF
39
S
Pm
LbSu
Pg
40
Md
Ga
La
LbP
Sli
Li
Pm
CE
41
Pl
S
VS
Sty
Sba
Spa
Cx
Cx
CF
Mg
XI
IX
VIII
VII
I
II
Ce
Cx

EXPLANATION OF FIGURES

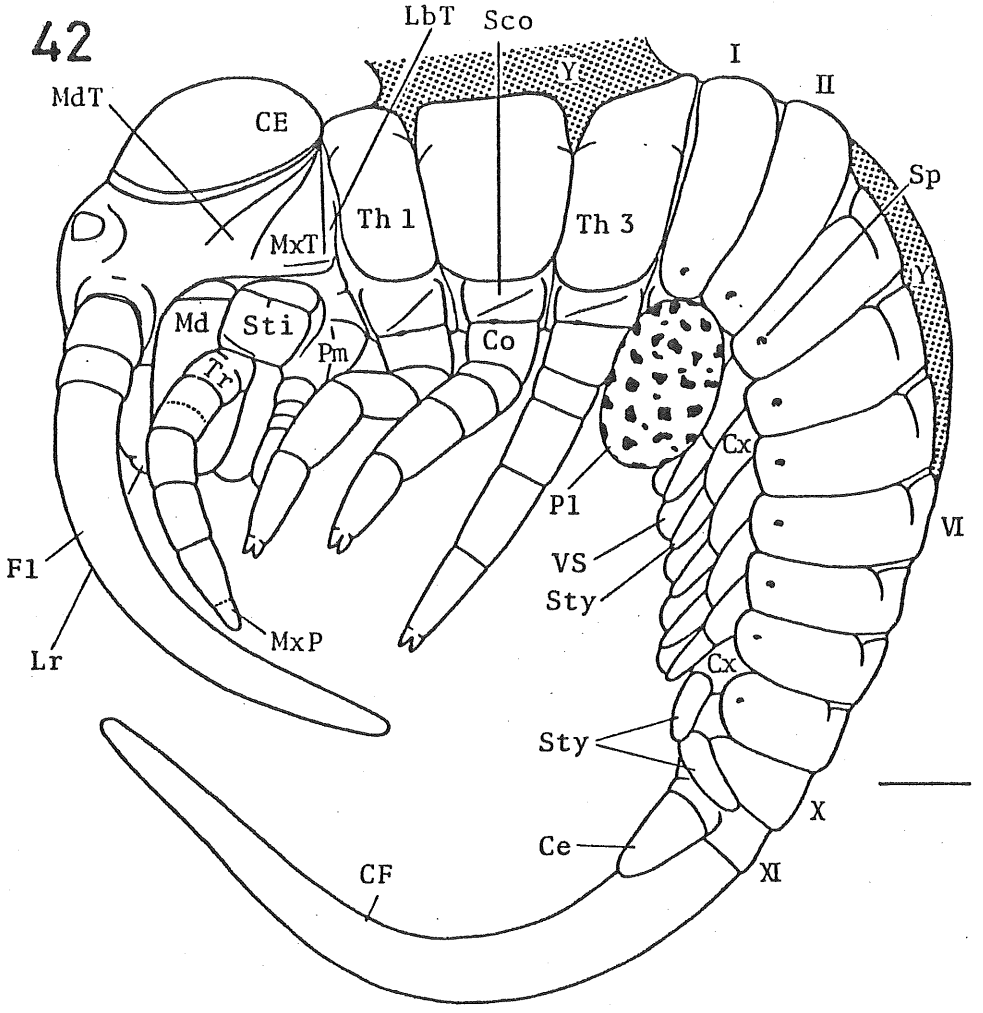
Scales = 100 μm.

42. Lateral view of embryo in Stage 12.

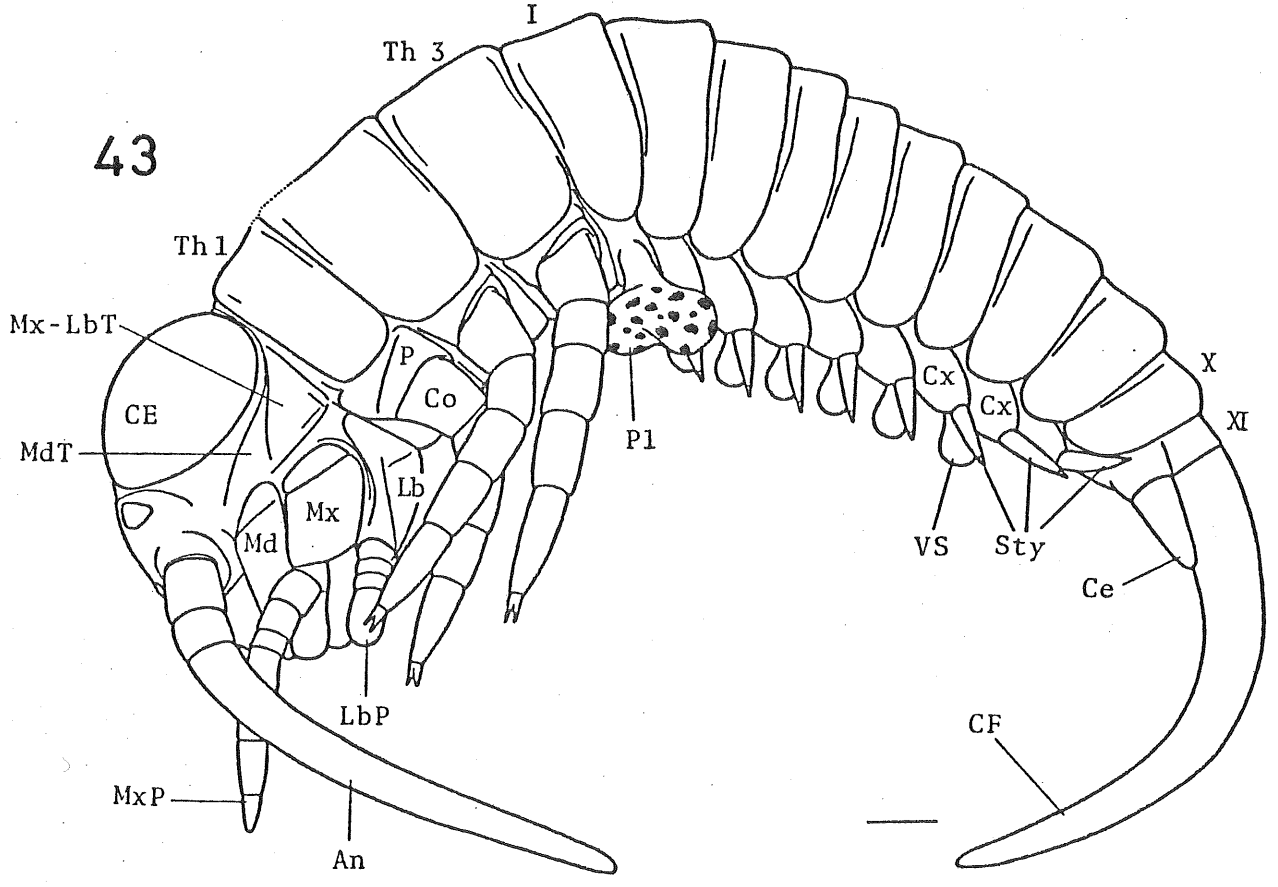
43. lateral view of embryo in Stage 13.

An, antenna; Ce, cercus; CE, compound eye; CF, caudal filament; Co, coxa; Cx, coxite; Fl, flagellum; Lb, labium; LbP, labial palp; LbT, labial tergum; Lr, labrum; Md, mandible; MdT, mandibular tergum; Mx, maxilla; MxP, maxillary palp; MxT, maxillary tergum; Mx-LbT, maxillo-labial tergum; P, pleuron; Pf, palpifer; Pg, palpiger; Pl, pleuropodium; Pm, postmentum; Sco, subcoxa; Sp, spiracle; Sti, stipes; Sty, stylus; Th1, 3, pro- and metathoracic segments; Tr, trochanter; VS, ventral sac; Y, yolk; I-XI, first to eleventh abdominal segments

42


LbT
Sco
MdT
CE
Y
I
II
Sp
Th 1
Th 3
MxT
Y
Md
Sti
Pm
Co
Tr
Cx
P1
VI
VS
Sty
F1
Lr
MxP
Cx
Sty
X
Ce
XI
CF

43

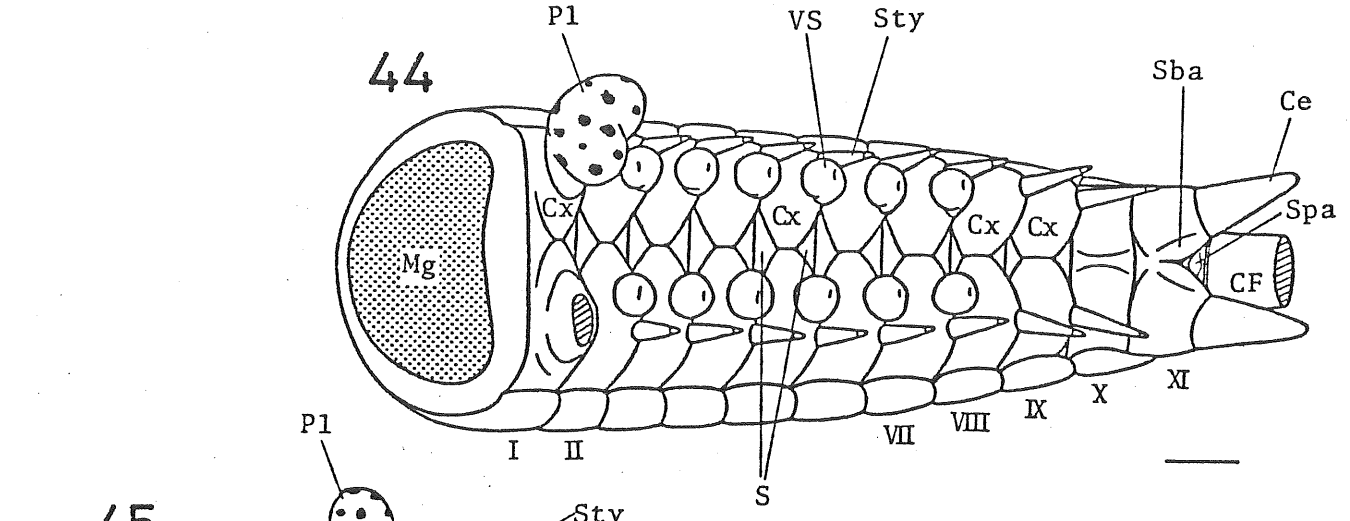

I
Th 3
Th 1
Mx-LbT
P
Co
CE
MdT
Lb
Mx
Md
P1
Cx
Cx
X
XI
VS
Sty
Ce
LbP
CF
MxP
An

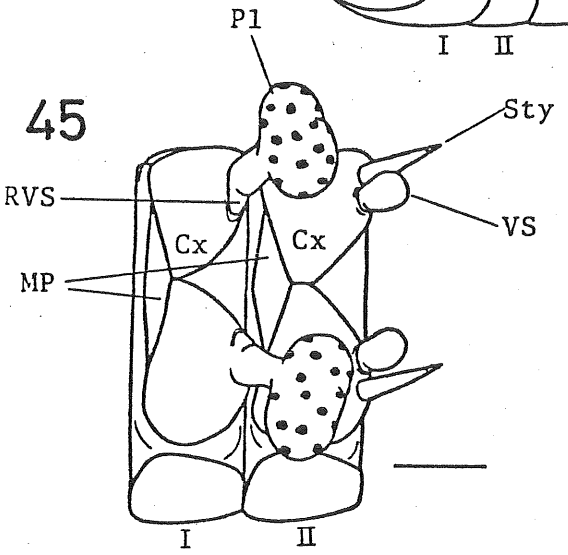
EXPLANATION OF FIGURES

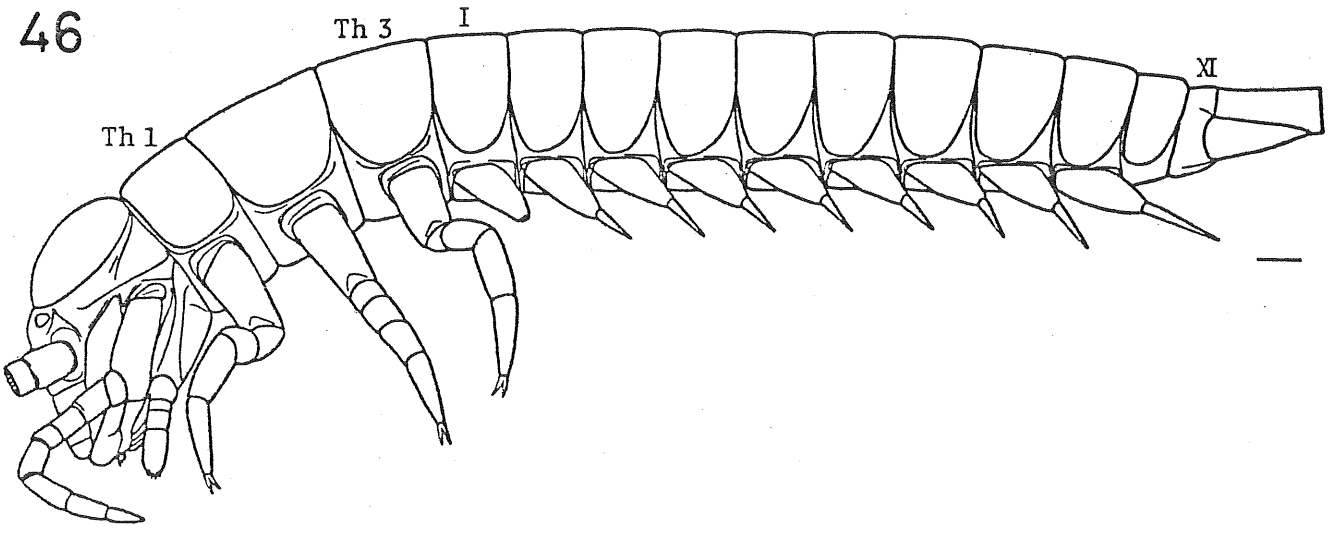
Scales = 100 μm.

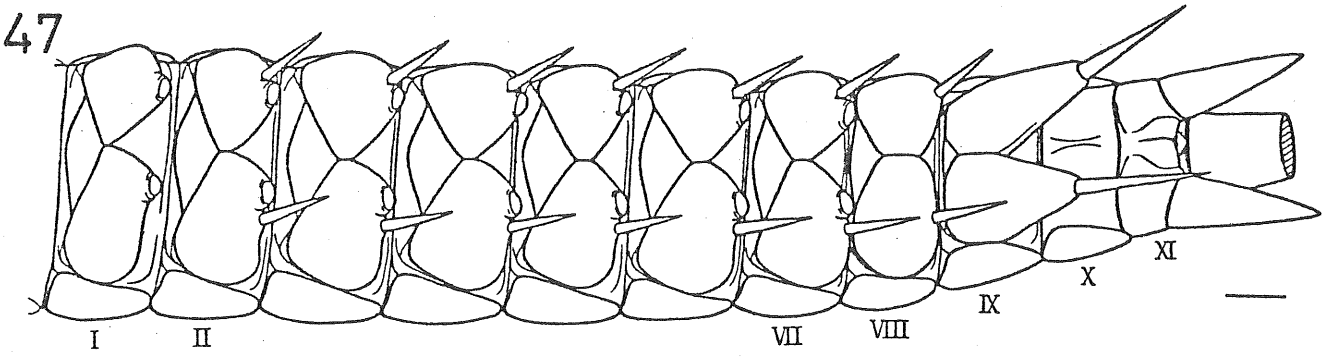
44. Ventrolateral view of abdomen of embryo in Stage 13. Caudal filament and right pleuropodium cut.
45. Ventrolateral view of first and second abdominal segments of embryo in Stage 14.
46. Lateral view of first instar larva. Flagellum and caudal filament cut.
47. Ventrolateral view of abdomen of first instar larva. Caudal filament cut.

Ce, cercus; CF, caudal filament; Cx, coxite; Mg, midgut; MP, median plate; Pl, pleuropodium; RVS, rudimentary ventral sac; S, sternite; Sba, subanal lobe or plate; Spa, supraanal lobe or plate; Sty, stylus; Thl, 3, pro- and metathoracic segments; VS, ventral sac; I-XI, first to eleventh abdominal segments


44
P1
VS
Sty
Sba
Ce
Spa
Cx
Cx
Cx
Cx
Mg
CF
I
II
VII
VIII
IX
X
XI
S


45
P1
Sty
RVS
VS
Cx
Cx
MP
I
II


46
Th 3
I
XI
Th 1


47
I
II
VII
VIII
IX
X
XI

EXPLANATION OF FIGURES

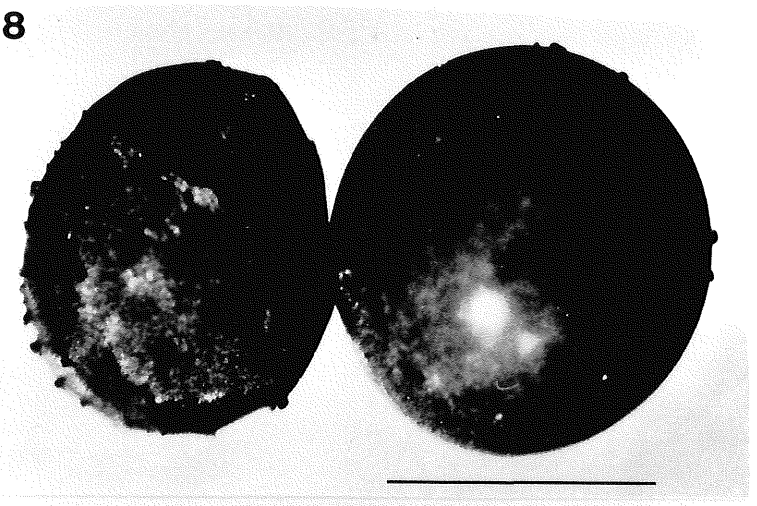
Scales = 1 mm.

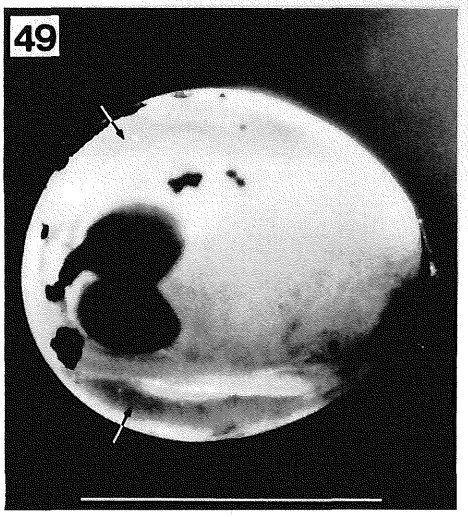
48. Photograph of eggs in Stage 13, before (left) and after (right) swelling. Chorion removed.

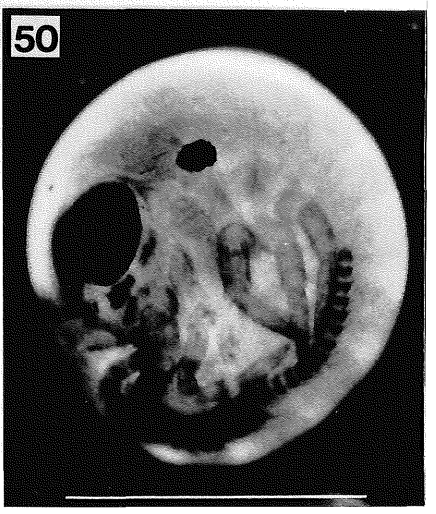
49. Photograph of swelling egg in Stage 13 (dorsal aspect). Arrows show the space produced with the swelling. Chorion removed. Outer dark blastoderm cuticle almost resolved by antiformin.

50. Photograph of egg in Stage 14 (lateral aspect), showing compactly packed embryo in egg membrane. Chorion removed. Outer dark blastoderm cuticle almost dissolved by antiformin.

48



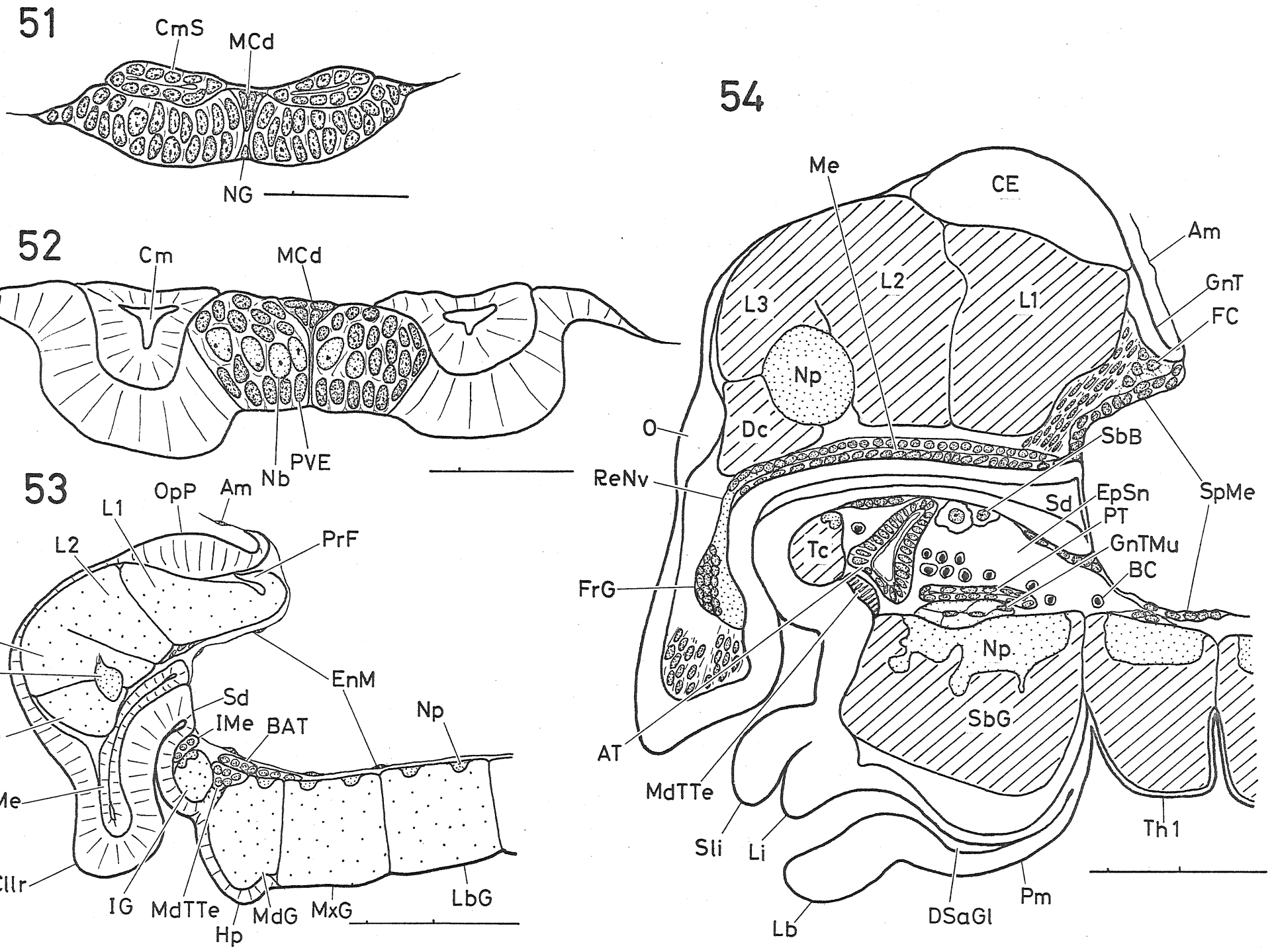




EXPLANATION OF FIGURES

51. Transverse section through thoracic region of embryo in Stage 3. Scale = 50 µm.
52. Transverse section through thoracic region of embryo in Stage 4. Scale = 50 µm.
53. Slightly oblique sagittal section through head of embryo in Stage 9. Scale = 100 µm.
54. Slightly oblique sagittal section through head of embryo in Stage 12. Scale = 100 µm.

Am, amnion; AnG, antennal ganglion; AT, anterior tentorium; BAT, binder of anterior tentoria; BC, blood cell; CE, compound eye; Cllr, clypeolabrum; Cm, coelom; CmS, coelomic sac; Dc, deutocerebrum; DSaGl, duct of salivary gland; EnM, ental membrane; EpSn, epineural sinus; FC, fat cell; FrG, frontal ganglion; GnT, gnathal tergum; GnTMu, gnathal transverse muscle; Hp, hypopharynx; IG, intercalary ganglion; IMe, intercalary mesoderm; Ll-3, protocerebral lobi 1, 2 and 3; Lb, labium; LbG, labial ganglion; Li, lingua; MCd, median cord; MdG, mandibular ganglion; MdTTe, mandibular transverse tendon; Me, mesoderm; MxG, maxillary ganglion; Nb, neuroblast; NG, neural groove; Np, neuropile; O, ocellus; OpP, optic plate; Pm, postmentum; PrF, postretinal fiber anlage; PT, posterior tentorium; PVE, provisional ventral epidermis; ReNv, recurrent nerve; SbB, suboesophageal body; SbG, suboesophageal ganglion; Sd, stomodaeum; Sli, superlingua; SpMe, splanchnic mesoderm; Tc, tritocerebrum; Thl, prothoracic segment


51
CmS
MCd
NG
52
Cm
MCd
Nb
PVE
53
OpP
Am
L1
L2
PrF
L3
Np
EnM
Sd
IMe
BAT
Np
AnG
Me
Cllr
IG
MdTTe
MdG
MxG
Hp
LbG
54
Me
CE
Am
L3
L2
L1
GnT
FC
Np
O
Dc
SbB
ReNv
Sd
EpSn
SpMe
PT
Tc
GnTMu
FrG
BC
Np
SbG
AT
MdTTe
Th1
Sli
Li
Pm
DSaGl
Lb

EXPLANATION OF FIGURES

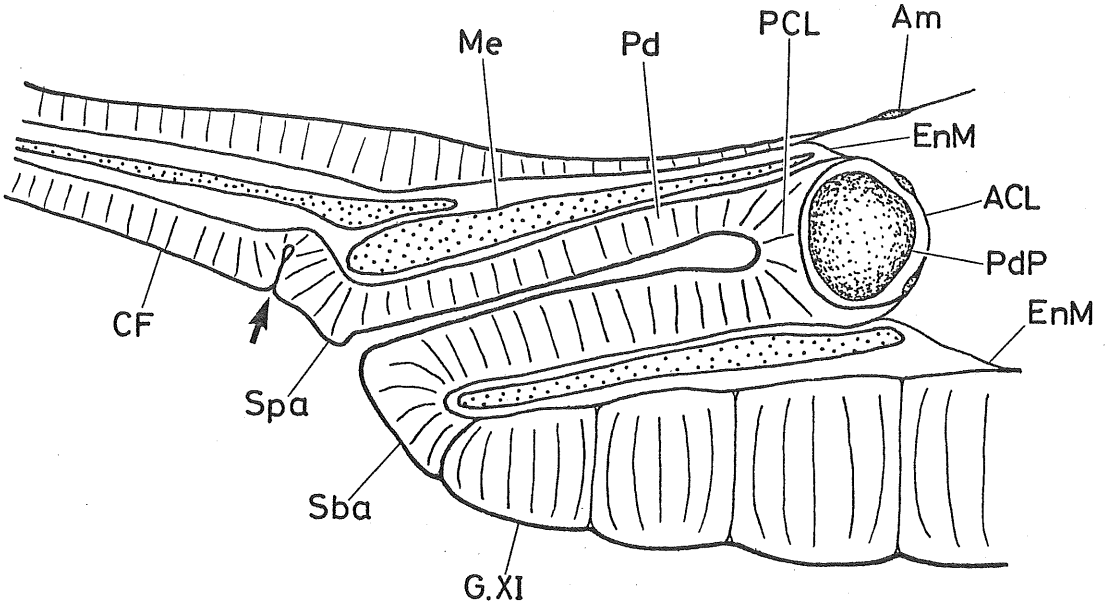
Scales = 100 μm. Arrows show the boundary of the body trunk and caudal filament.

55. Sagittal section through posterior abdominal region of embryo in Stage 10.

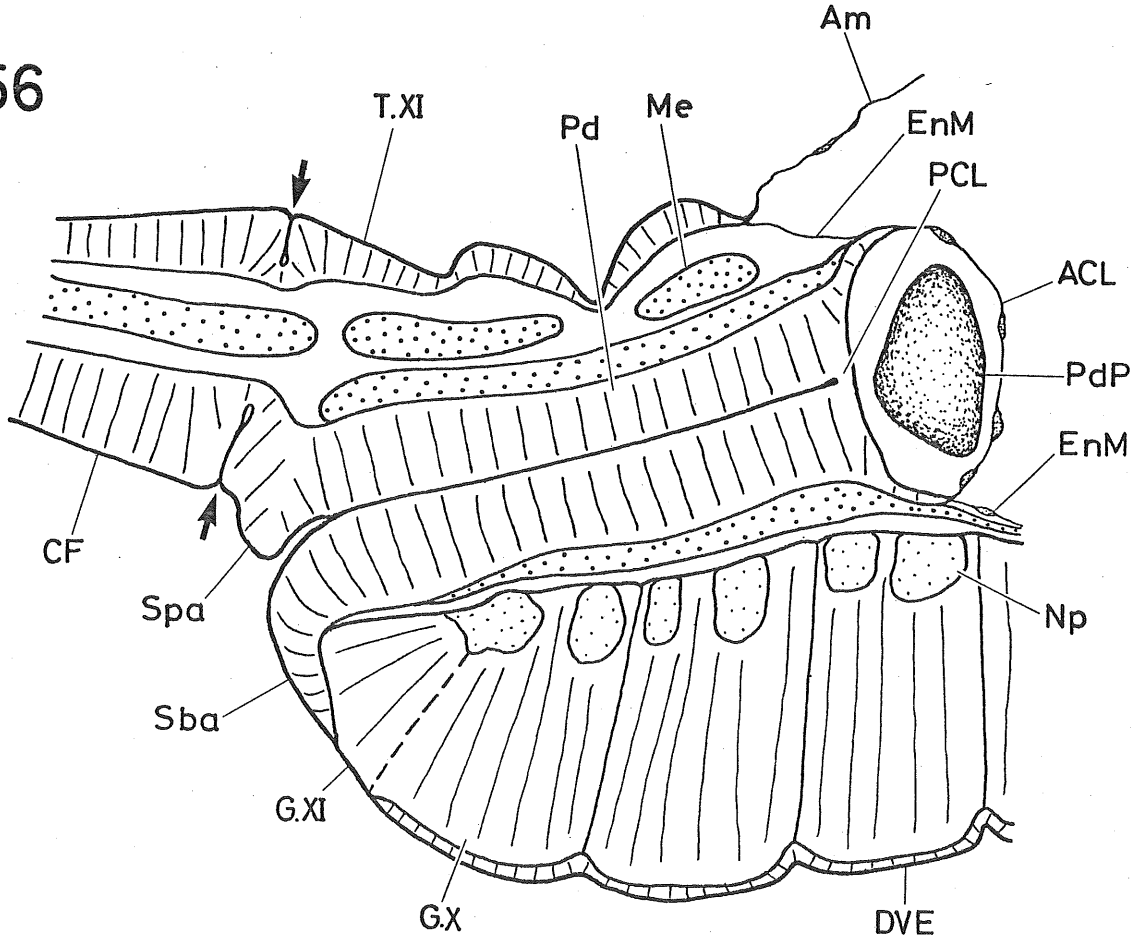
56. Same, in Stage 11.

ACL, anterior cell layer to proctodaeal plug; Am, amnion; CF, caudal filament; DVE, definitive ventral epidermis; EnM, ental membrane; G.X, XI, tenth and eleventh abdominal ganglia; Me, mesoderm; Np, neuropile; PCL, posterior cell layer to proctodaeal plug; Pd, proctodaeum; PdP, proctodaeal plug; Sba, subanal lobe; Spa, supraanal lobe; T.XI, eleventh abdominal tergum

55


Me
Pd
PCL
Am
EnM
ACL
PdP
EnM
CF
Spa
Sba
G.XI

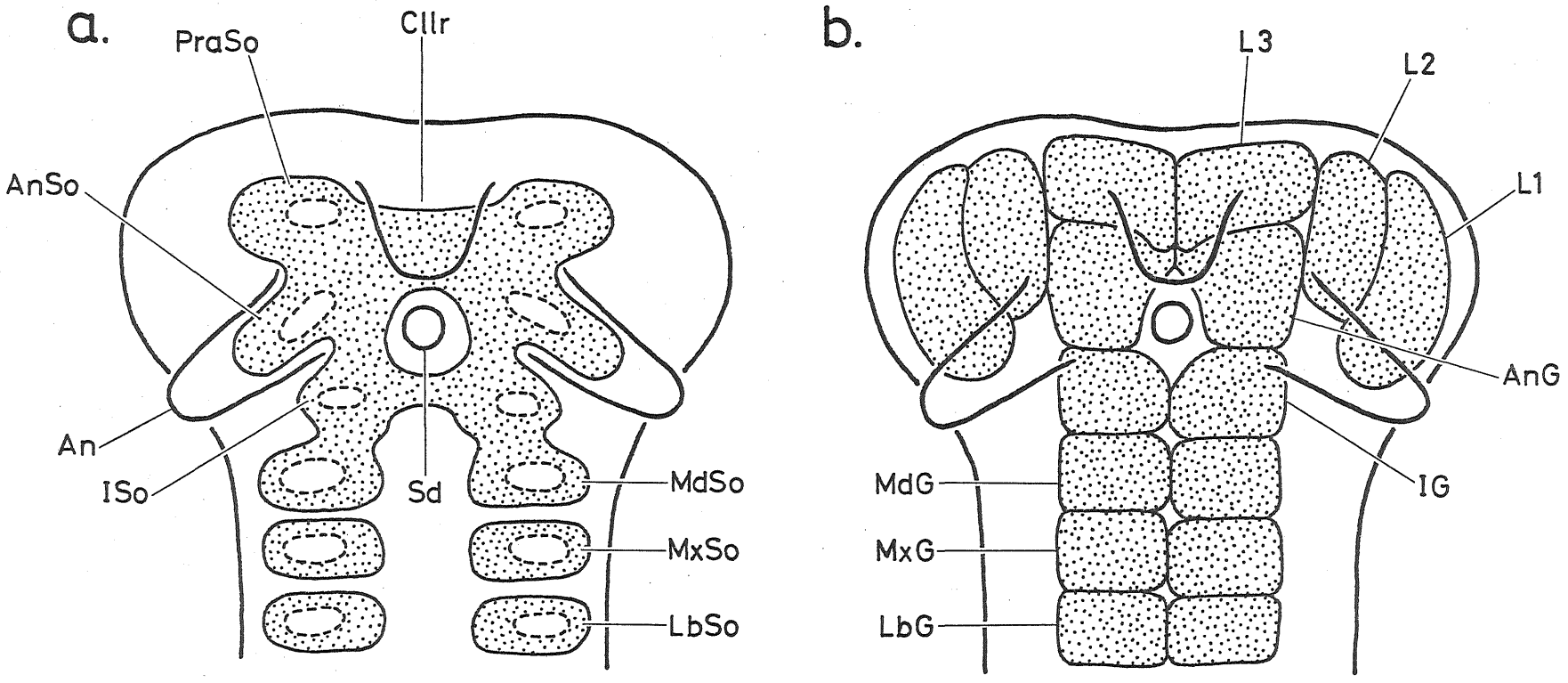
56


Am
T.XI
Pd
Me
EnM
PCL
ACL
PdP
EnM
CF
Spa
Np
Sba
G.XI
G.X
DVE

EXPLANATION OF FIGURE

57. Diagrams showing the distribution of mesoderm (a) and ganglia (b) in cephalic region of embryo in Stage 6.

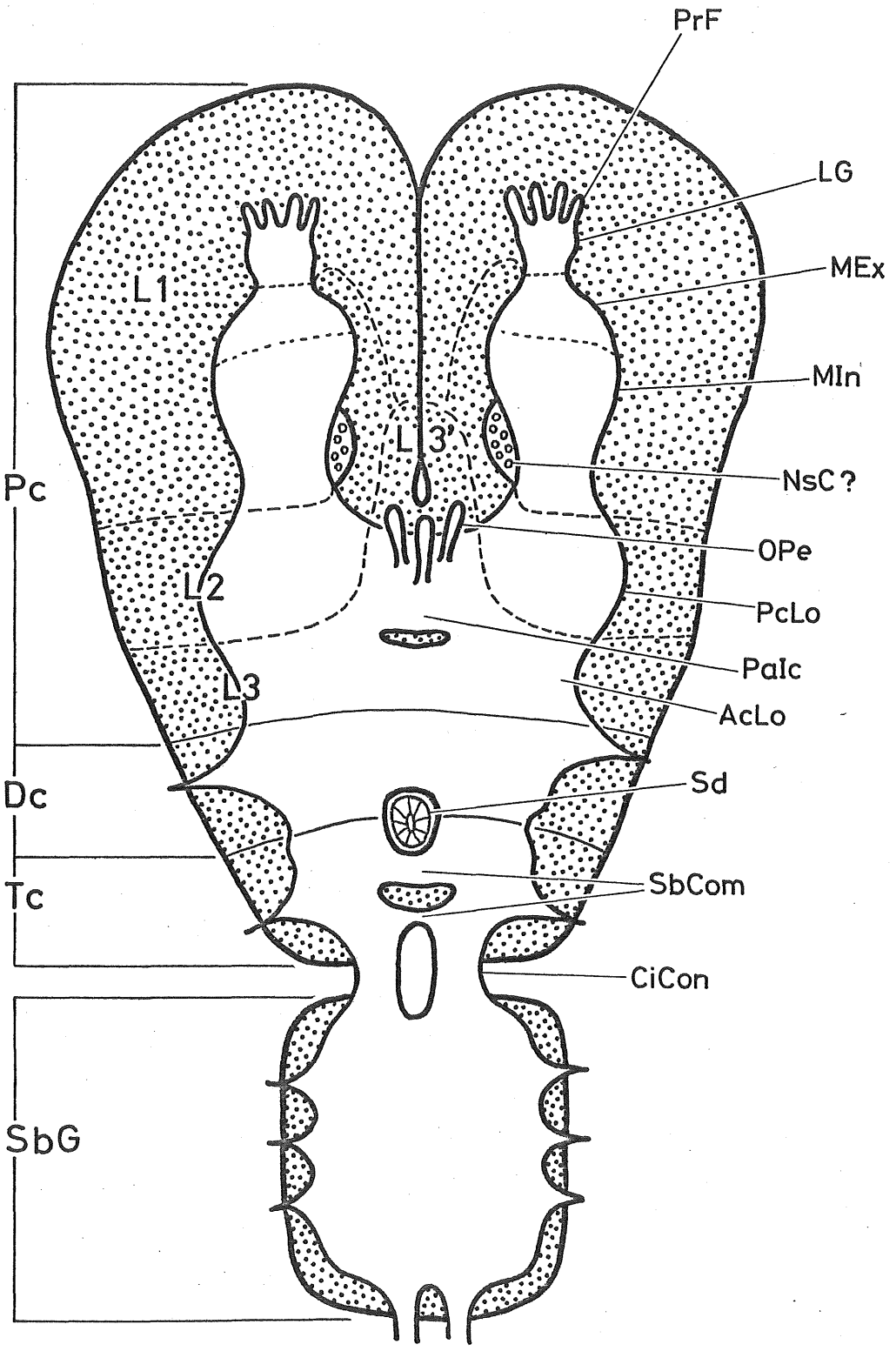
An, antenna; AnG, antennal ganglion; AnSo, antennal somite; Cllr, clypeolabrum; IG, intercalary ganglion; ISo, intercalary somite; Ll-3, protocerebral lobi 1, 2 and 3; LbG, labial ganglion; LbSo, labial somite; MdG, mandibular ganglion; MdSo, mandibular somite; MxG, maxillary ganglion; MxSo, maxillary somite; PraSo, preantennal somite; Sd, stomodaeum


a.
PraSo
Cllr
AnSo
An
ISo
Sd
MdSo
MxSo
LbSo
b.
L3
L2
L1
AnG
IG
MdG
MxG
LbG

EXPLANATION OF FIGURE

58. Diagrammatic representation of definitive construction of cephalic ganglia.

AcLo, accessory lobe; CiCon, circumoesophageal connective; Dc, deutocerebrum; Ll-3, 3′, protocerebral lobi 1, 2, 3 and 3′; LG, lamina ganglionaris; MEx, medulla externa; MIn, medulla interna; NsC, neurosecretory cell; OPe, ocellar pedicel; PaIc, pars intercerebralis; Pc, protocerebrum; PcLo, protocerebral lobe; PrF, postretinal fiber; SbCom, suboesophageal commissure; SbG, suboesophageal ganglion; Sd, stomodaeum; Tc, tritocerebrum


PrF
LG
MEx
MIn
NsC?
OPe
PcLo
PaIc
AcLo
Sd
SbCom
CiCon
L1
L2
L3
L3'
Pc
Dc
Tc
SbG

EXPLANATION OF FIGURES

Scales = 100 µm.

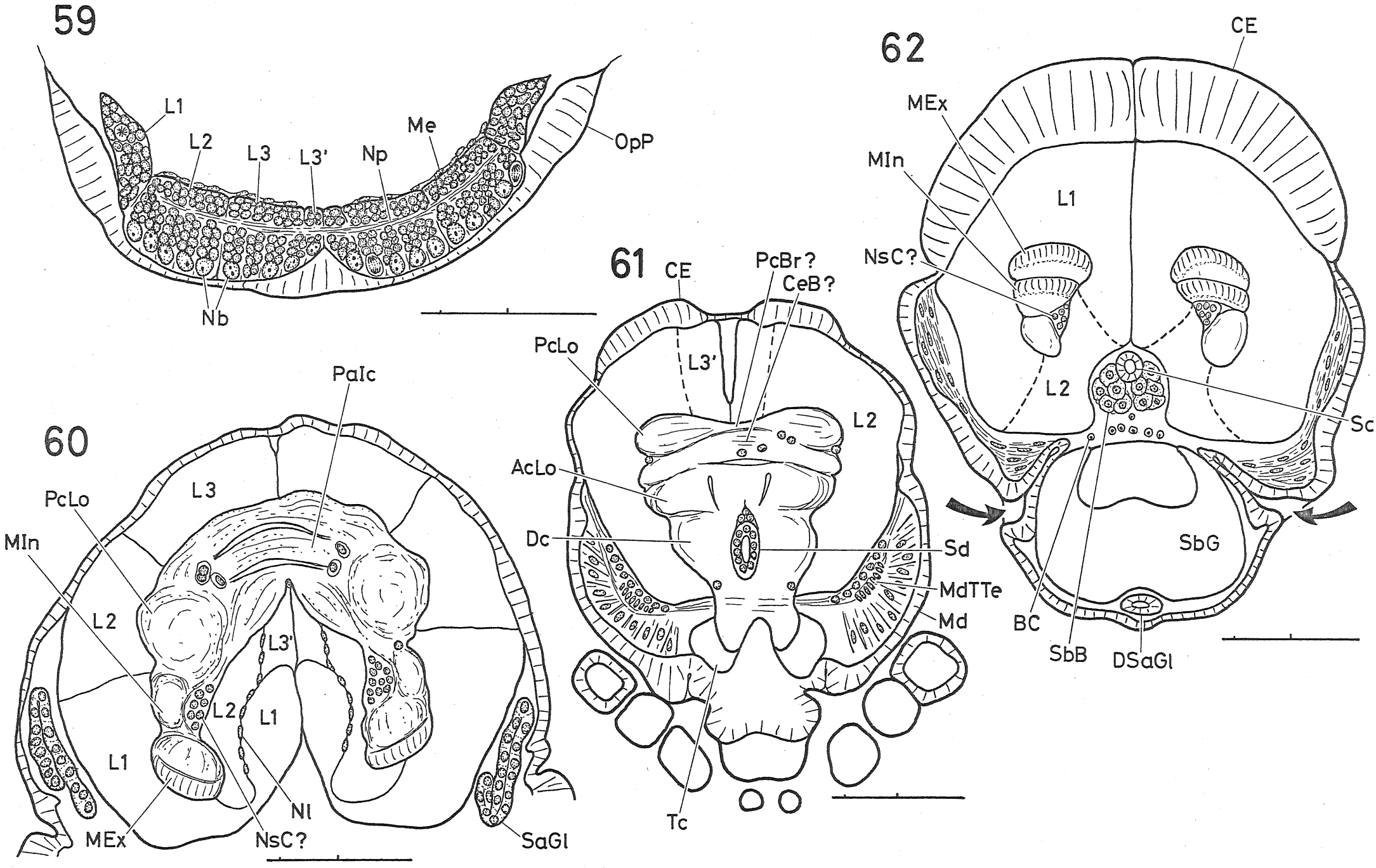
59. Transverse section of head lobe of embryo in Stage 7 through protocerebral ganglia.

60. Horizontal section of head of embryo in Stage 12 through pars intercerebralis.

61. Transverse section of head of embryo in Stage 12, through mandible.

62. Same, posterior by ca. 150 µm, through intersegmental region of maxillary and labial segments. Arrows show the invagination of posterior tentoria.

AcLo, accessory lobe; BC, blood cell; CE, compound eye; CeB, central body; Dc, deutocerebrum; DSaGl, duct of salivary gland; Ll-3, 3', protocerebral lobi 1, 2, 3 and 3; Md, mandible; MdTTe, mandibular transverse tendon; Me, mesoderm; MEx, medulla externa; MIn, medulla interna; Nb, neuroblast; Nl, neurilemma; Np, neuropile; NsC, neurosecretory cell; OpP, optic plate; PaIc, pars intercerebralis; PcBr, protocerebral bridge; PcLo, protocerebral lobe; SaGl, salivary gland; SbB, suboesophageal body; SbG, suboesophageal ganglion; Sd, stomodaeum; Tc, tritocerebrum

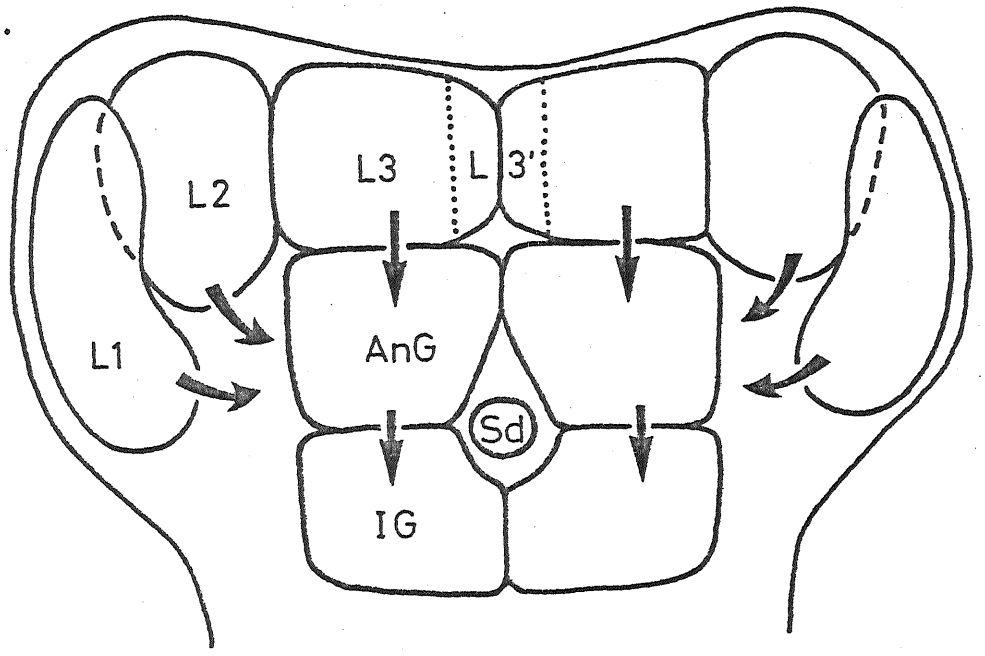

59
L1
L2
L3
L3'
Np
Me
OpP
Nb
60
PaIc
L3
PcLo
MIn
L2
L3'
L2
L1
L1
NI
MEx
NsC?
SaGl
61
CE
PcBr?
CeB?
PcLo
L3'
L2
AcLo
Dc
Sd
MdTTe
Md
Tc
62
CE
MEx
MIn
L1
NsC?
L2
Sc
SbG
BC
SbB
DSaGl

EXPLANATION OF FIGURE

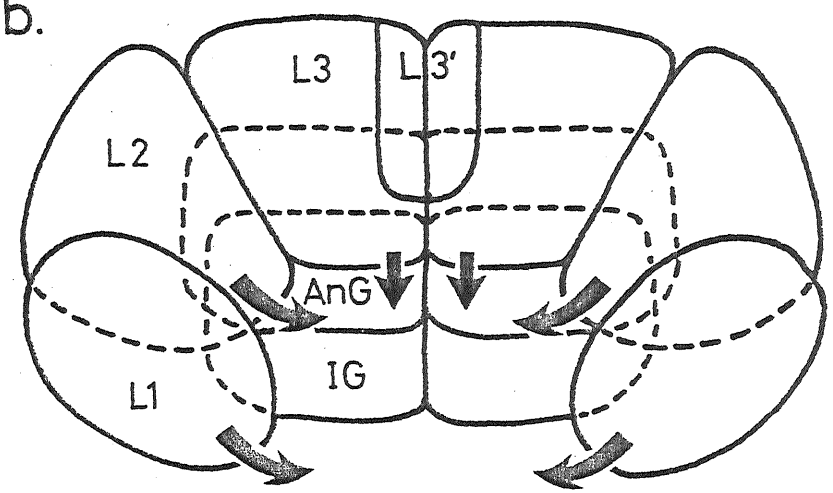
63. Diagrammatic representation of cerebral morphogenesis in dorsal view (a–c). Arrows show the directions of movement of each ganglion.

AnG, antennal ganglion; IG, intercalary ganglion; L1-3, 3′, protocerebral lobi 1, 2, 3 and 3′; Sd, stomodaeum

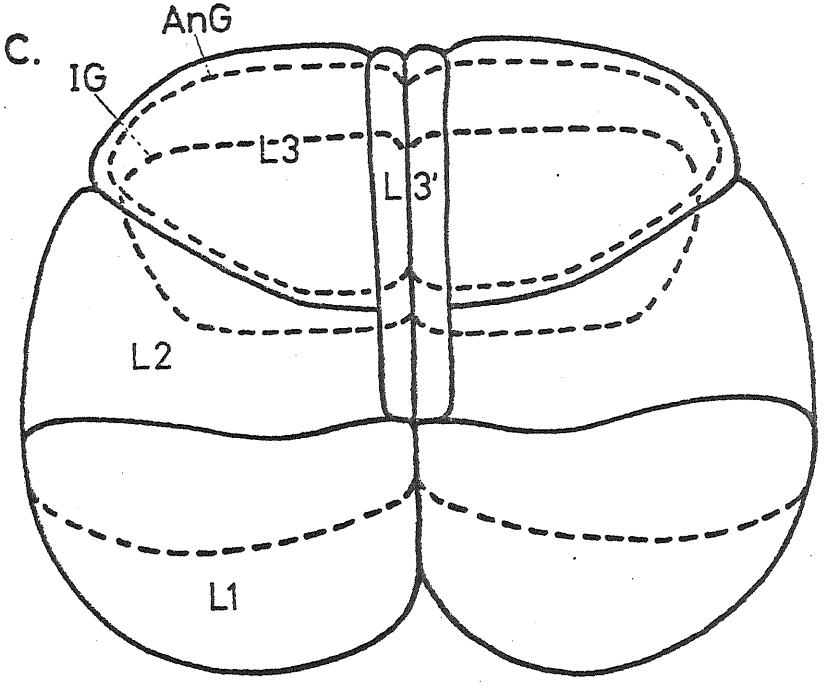
a.



b.



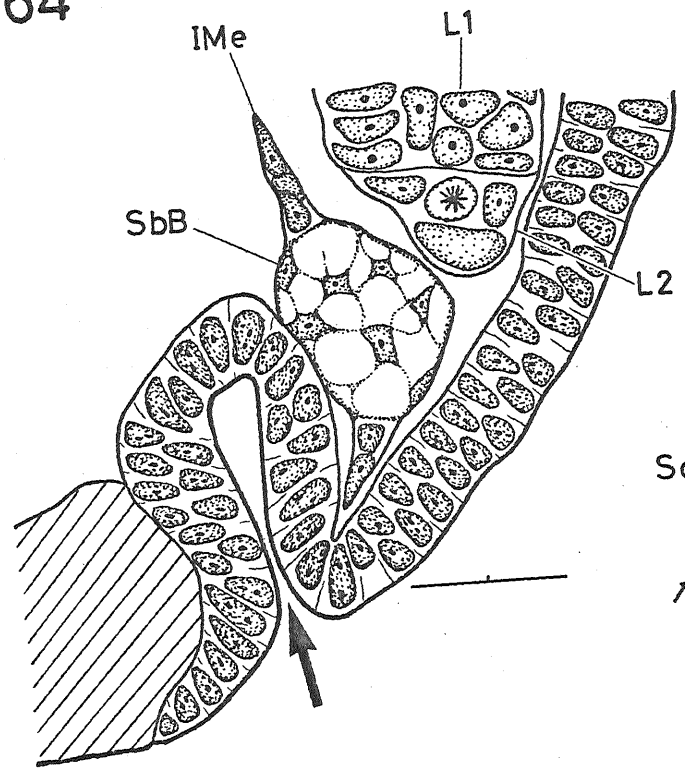
c.

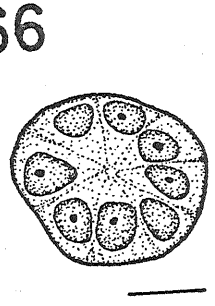


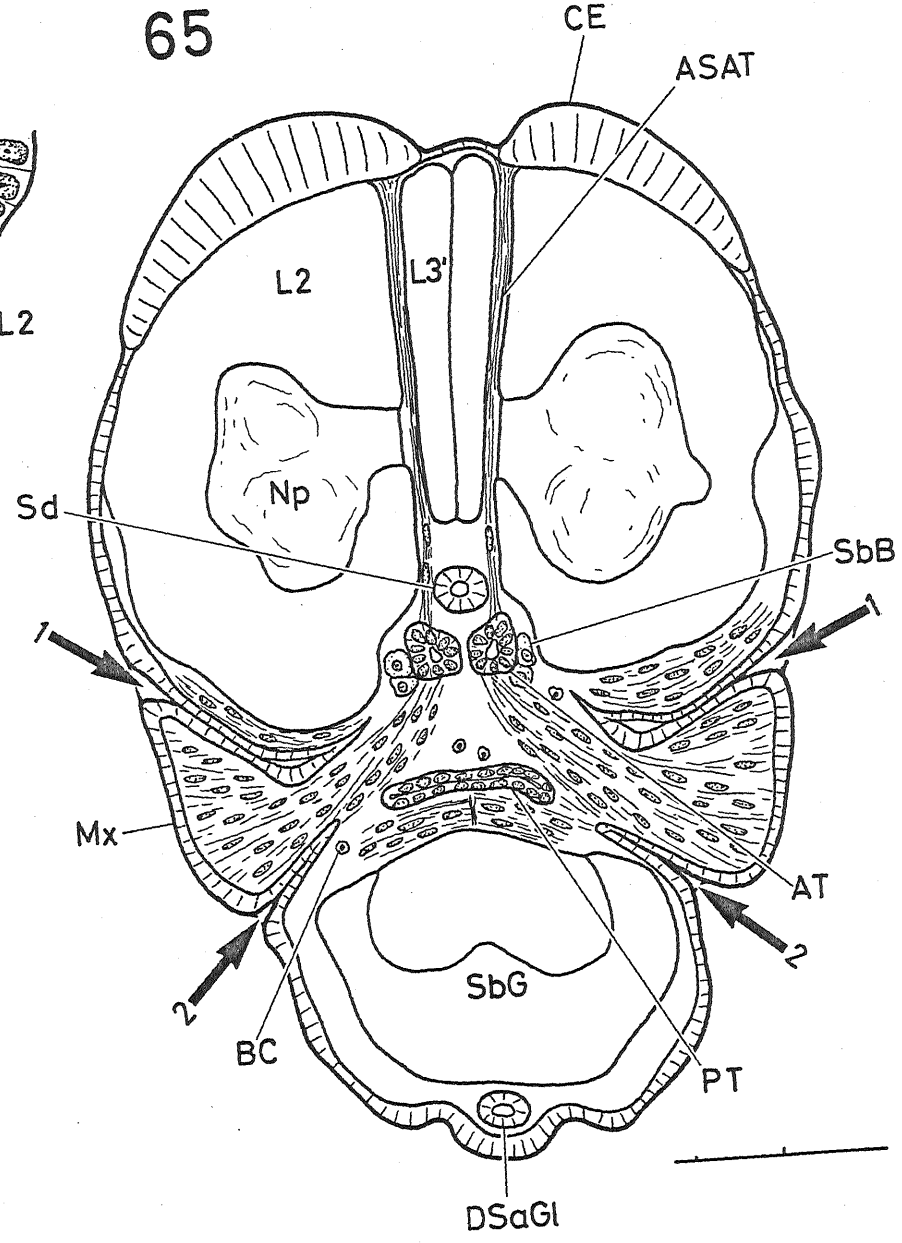
EXPLANATION OF FIGURES

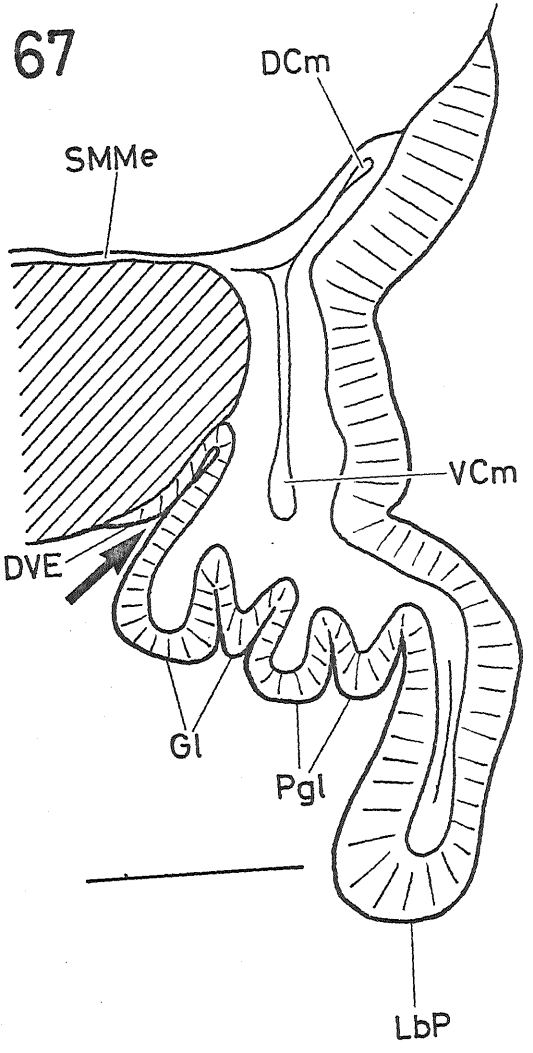
64. Part of transverse section through intersegmental region of intercalary and mandibular segments of embryo in Stage 7. Arrow shows the invagination of anterior tentorium. Scale = 20 μm.
65. Transverse section of head of embryo in Stage 12 through dorsal part of maxilla. Arrows 1 and 2 respectively show the invaginations of corpora allata and lacinial apodemes. Scale = 100 μm.
66. Corpus allatum in Stage 13. Scale = 10 μm.
67. Part of transverse section through labial segment of embryo in Stage 7. Arrow shows the invagination of salivary gland. Scale = 50 μm.

ASAT, anterior suspension of anterior tentorium; AT, anterior tentorium; BC, blood cell; CE, compound eye; DCm, dorsal coelom; DSaGl, duct of salivary gland; DVE, definitive ventral epidermis; Gl, glossa; IMe, intercalary mesoderm; Ll-3, 3′, protocerebral lobi 1, 2, 3 and 3′; LbP, labial palp; Mx, maxilla; Np, neuropile; Pgl, paraglossa; PT, posterior tentorium; SbB, suboesophageal body; SbG, suboesophageal ganglion; Sd, stomodaeum; SMMe, secondary median mesoderm; VCm, ventral coelom


64
IMe
L1
SbB
L2


66

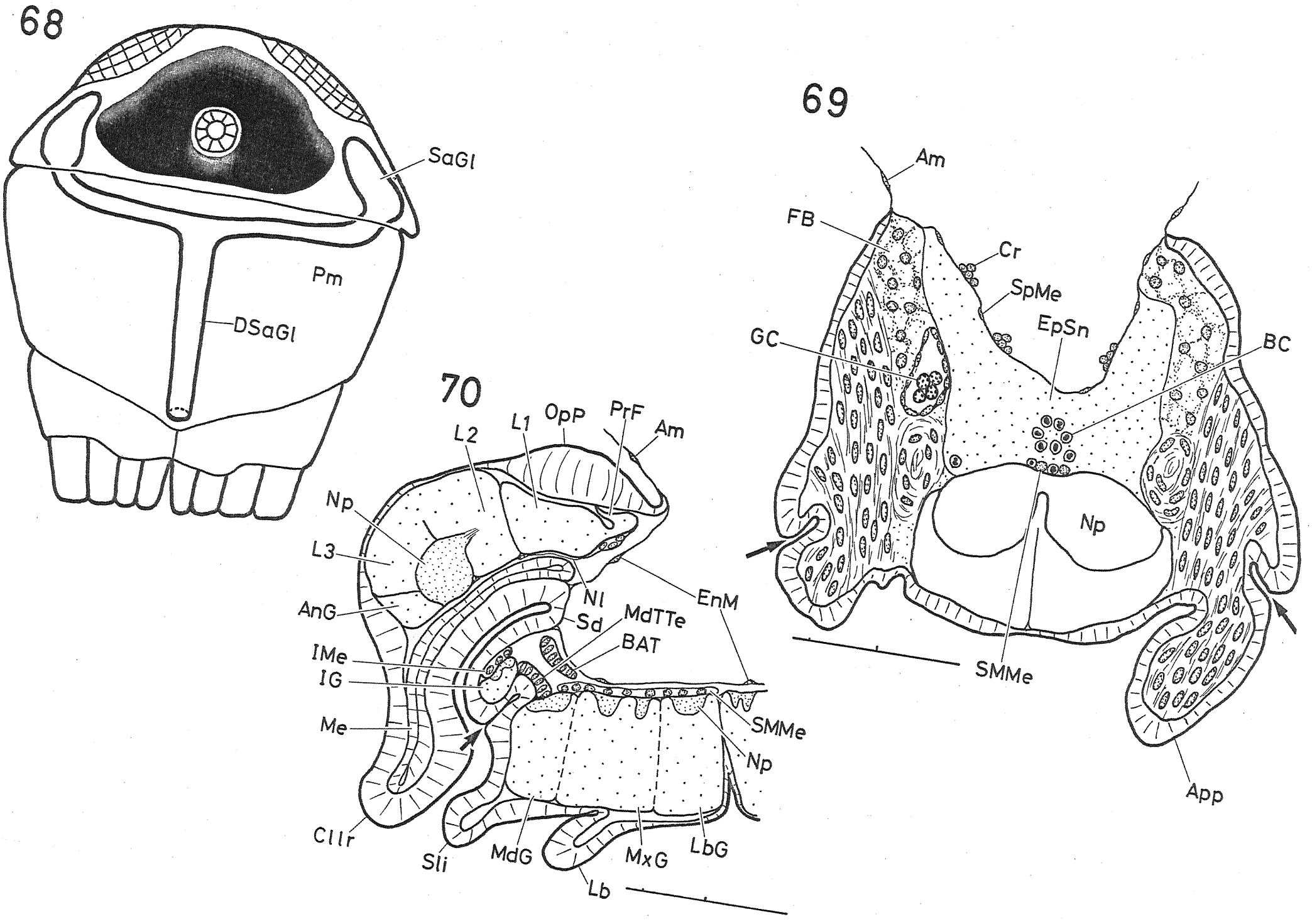

65
CE
ASAT
L2
L3'
Np
Sd
SbB
1
1
Mx
AT
2
2
SbG
BC
PT
DSaGl


67
DCm
SMMe
VCm
DVE
Gl
Pgl
LbP

EXPLANATION OF FIGURES

68. Diagram showing the definitive position of salivary glands and their duct in head (posterior view).
69. Transverse section through metathoracic segment of embryo in Stage 12. Arrows show the tracheal invaginations. Scale = 100 μm.
70. Slightly oblique sagittal section through head of embryo in Stage 10. Arrow shows the invagination of suboesophageal process. Scale = 100 μm.

Am, amnion; AnG, antennal ganglion; App, appendage; BAT, binder of anterior tentoria; BC, blood cell; Cllr, clypeolabrum; Cr, crypt; DSaGl, duct of salivary gland; EnM, ental membrane; EpSn, epineural sinus; FB, fat body; GC, germ cell; IG, intercalary ganglion; IMe, intercalary mesoderm; Ll-3, protocerebral lobi 1, 2 and 3; Lb, labium; LbG, labial ganglion; MdG, mandibular ganglion; MdTTe, mandibular transverse tendon; Me, mesoderm; MxG, maxillary ganglion; Nl, neurilemma; Np, neuropile; OpP, optic plate; Pm, postmentum; PrF, postretinal fiber anlage; SaGl, salivary gland; Sd, stomodaeum; Sli, superlingua; SMMe, secondary median mesoderm; SpMe, splanchnic mesoderm


68
SaGl
Pm
DSaGl
69
Am
FB
Cr
SpMe
EpSn
GC
BC
Np
SMMe
App
70
L2
L1
OpP
PrF
Am
Np
L3
AnG
Nl
Sd
MdTTe
EnM
BAT
IMe
IG
Me
SMMe
Np
Cllr
Sli
MdG
MxG
LbG
Lb

EXPLANATION OF FIGURES

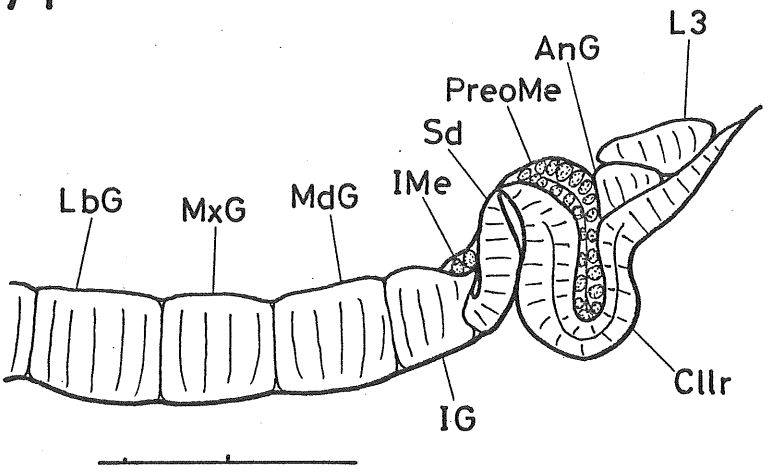
Scales = 100 μm.

71. Sagittal section through head of embryo in Stage 6.

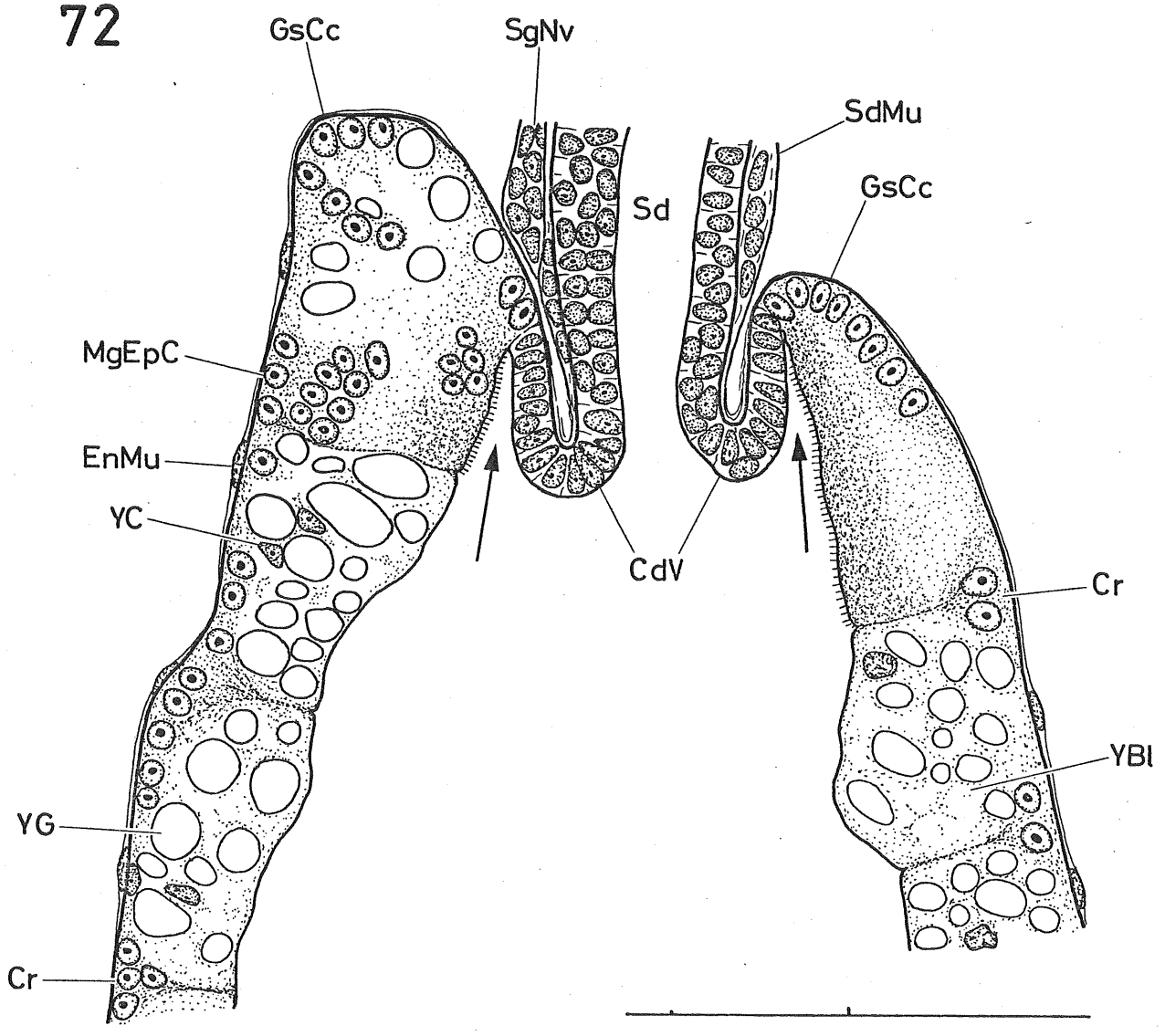
72. Part of sagittal section of stomodaeum and midgut in second instar larva. Midgut epithelium adjacent to stomodaeum is essentially completed. Arrows show boundary of stomodaeum and midgut.

AnG, antennal ganglion; CdV, cardiac valve; Cllr, clypeolabrum; Cr, crypt; EnMu, enteric muscle; GsCc, gastric caecum; IG, intercalary ganglion; IMe, intercalary mesoderm; L3, protocerebral lobus 3; LbG, labial ganglion; MdG, mandibular ganglion; MgEpC, midgut epithelial cell; MxG, maxillary ganglion; PreoMe, preoral mesoderm; Sd, stomodaeum; SdMu, stomodaeal muscle; SgNv, stomatogastric nerve; YBl, yolk block; YC, yolk cell; YG, yolk globule

71


L3
AnG
PreoMe
Sd
IMe
LbG
MxG
MdG
IG
CIIr

72

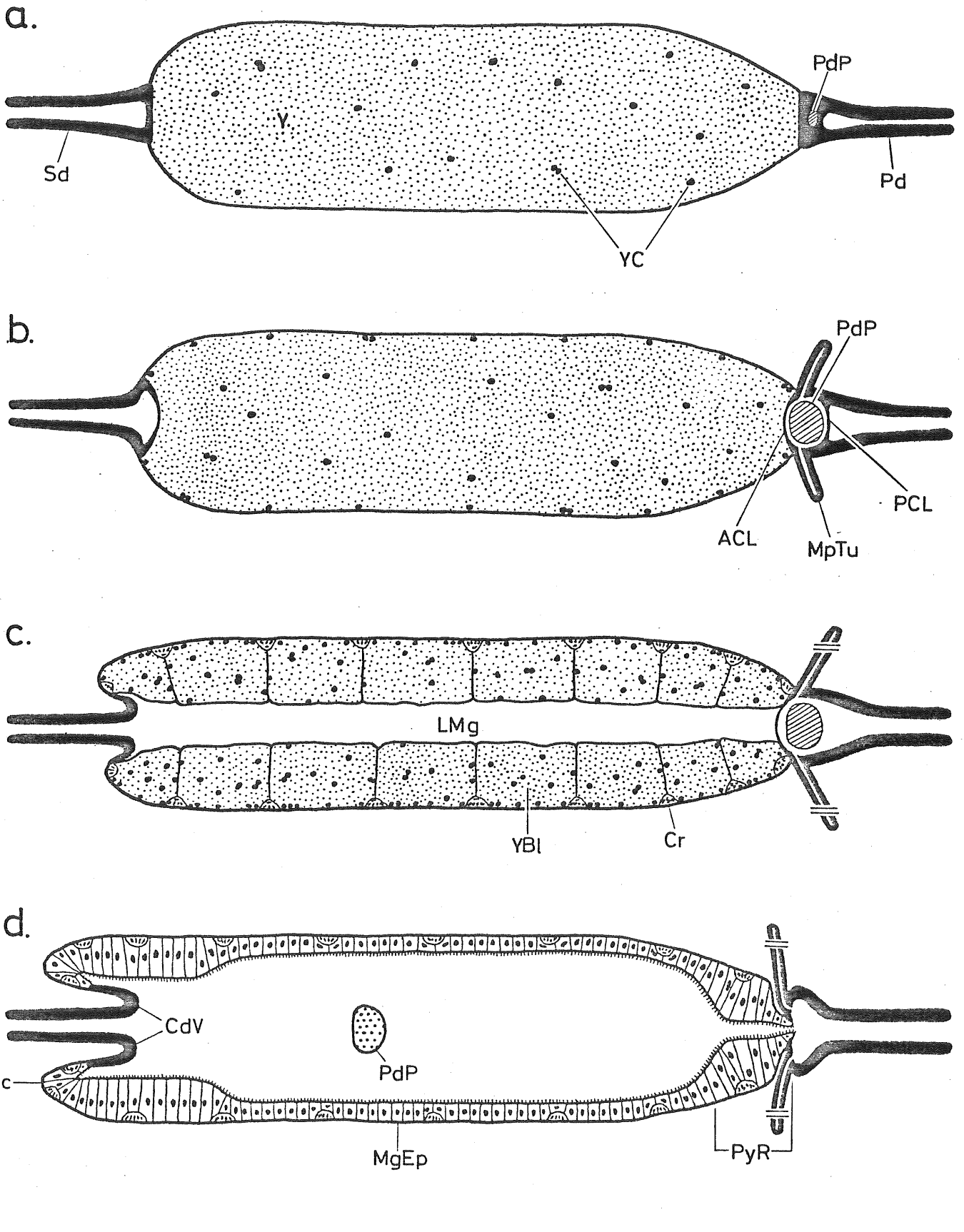

GsCc
SgNv
SdMu
GsCc
Sd
MgEpC
EnMu
YC
CdV
Cr
YBl
YG
Cr

EXPLANATION OF FIGURE

73. Diagrammatic sagittal section showing the development of alimentary canal (a–d).

ACL, anterior cell layer to proctodaeal plug; CdV, cardiac valve; Cr, crypt; GsCc, gastric caecum; LMg, lumen of midgut; MgEp, midgut epithelium; MpTu, malpighian tubule; PCL, posterior cell layer to proctodaeal plug; Pd, proctodaeum; PdP, proctodaeal plug; PyR, pyloric region; Sd, stomodaeum; YBl, yolk block; YC, yolk cell

73


a.
PdP
Y
Sd
Pd
YC
b.
PdP
PCL
ACL
MpTu
c.
LMg
YBl
Cr
d.
CdV
PdP
GsCc
MgEp
PyR

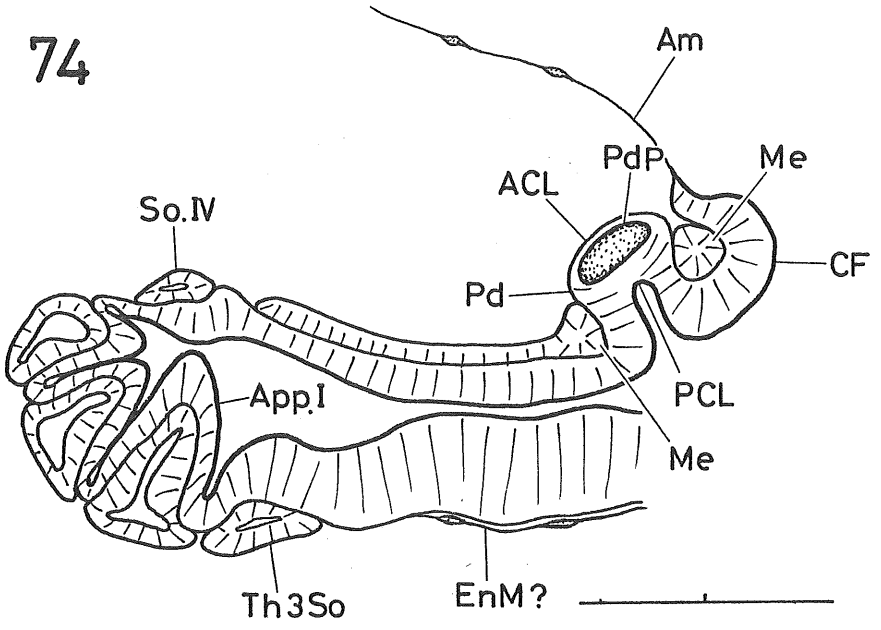
EXPLANATION OF FIGURES

Scales = 100 μm.

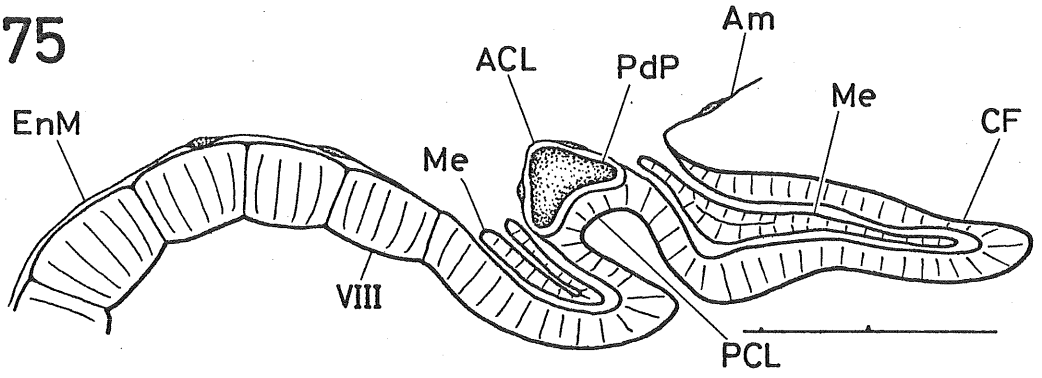
74. Part of a little oblique sagittal section through abdomen of embryo in Stage 6.
75. Part of sagittal section through abdomen of embryo in Stage 9.
76. Sagittal section through proctodaeum and part of rudimentary midgut of embryo in Stage 14.

ACL, anterior cell layer to proctodaeal plug; Am, amnion; App.I, first abdominal appendage; CF, caudal filament or caudal filament anlage; Cr, crypt; EnM, ental membrane; EnMu, enteric muscle; G.VIII, eighth abdominal ganglion; Me, mesoderm; MpTu, malpighian tubule; Nl, neurilemma; PCL, posterior cell layer to proctodaeal plug; Pd, proctodaeum; PdMu, proctodaeal muscle; PdP, proctodaeal plug; PdS, proctodaeal suspension; S.VIII, IX, XI, eighth, ninth and eleventh abdominal sterna; Sba, subanal lobe; So.IV, fourth abdominal somite; Spa, supraanal lobe; T.XI, eleventh abdominal tergum; Th3So, metathoracic somite; VIII, eighth abdominal segment

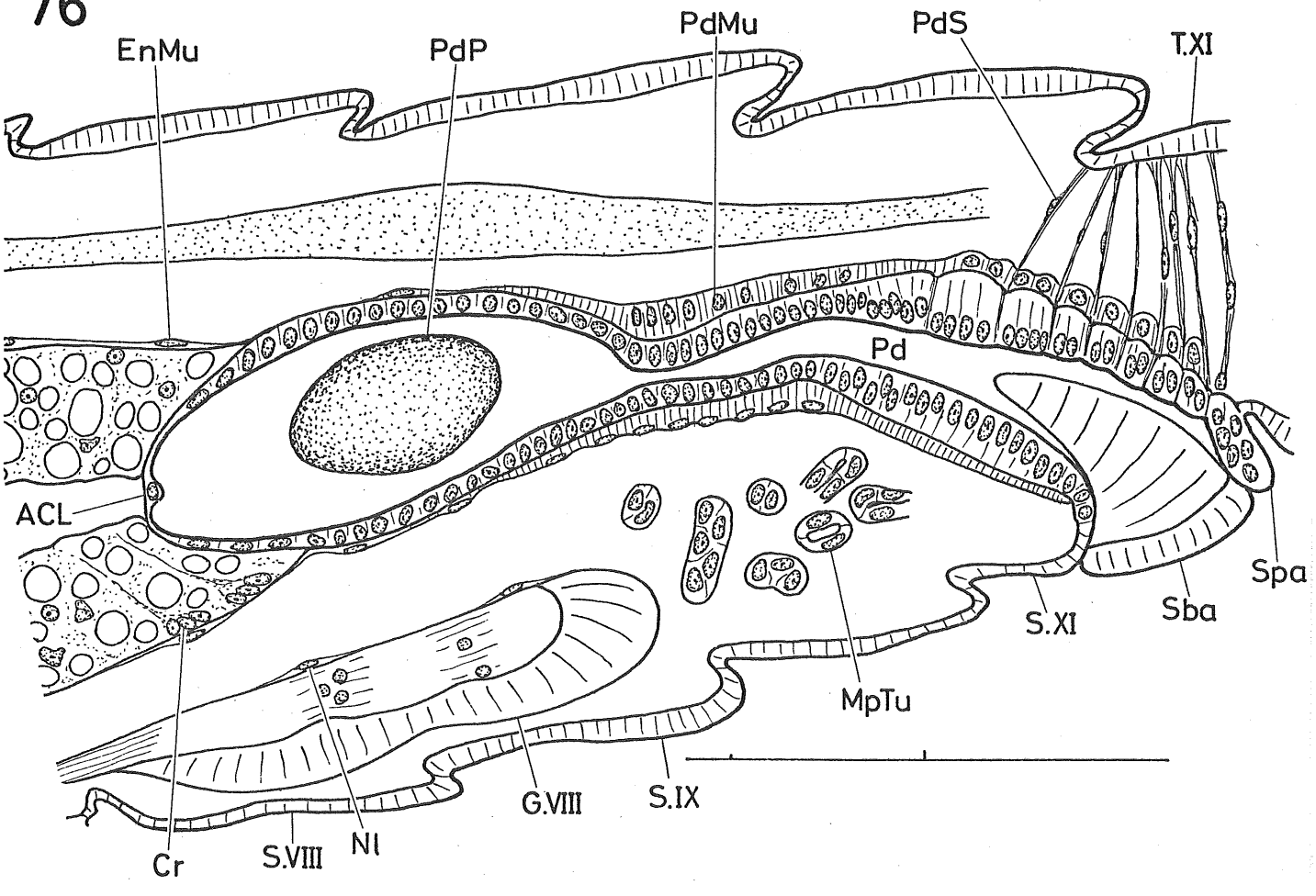
74


Am
PdP
Me
ACL
So.IV
CF
Pd
PCL
App.I
Me
Th3So
EnM?

75


Am
ACL
PdP
Me
EnM
CF
Me
VIII
PCL

76

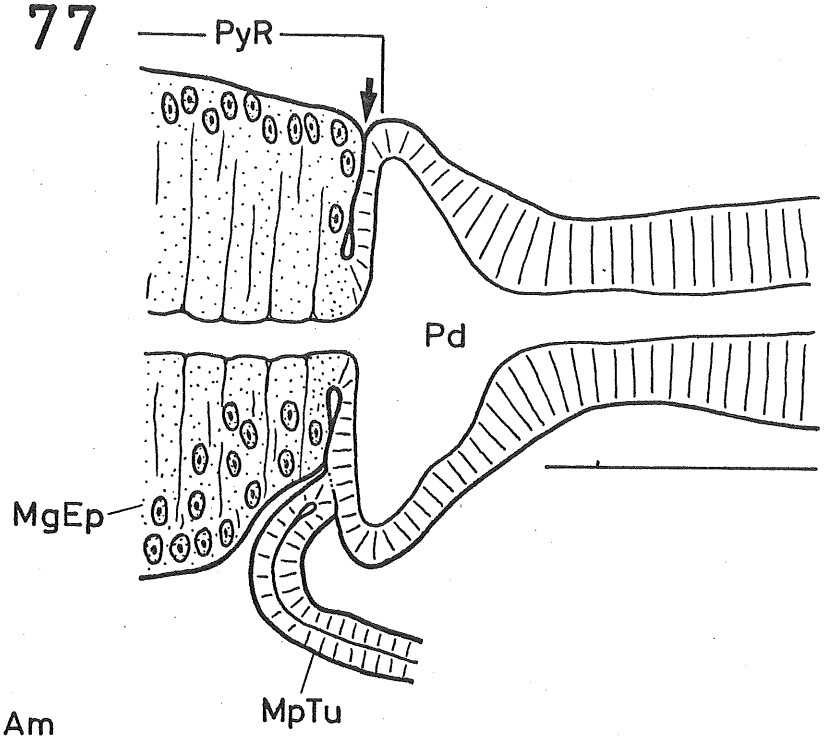

EnMu
PdP
PdMu
PdS
T.XI
Pd
ACL
Spa
Sba
S.XI
MpTu
G.VIII
S.IX
Cr
S.VIII
NI

EXPLANATION OF FIGURES

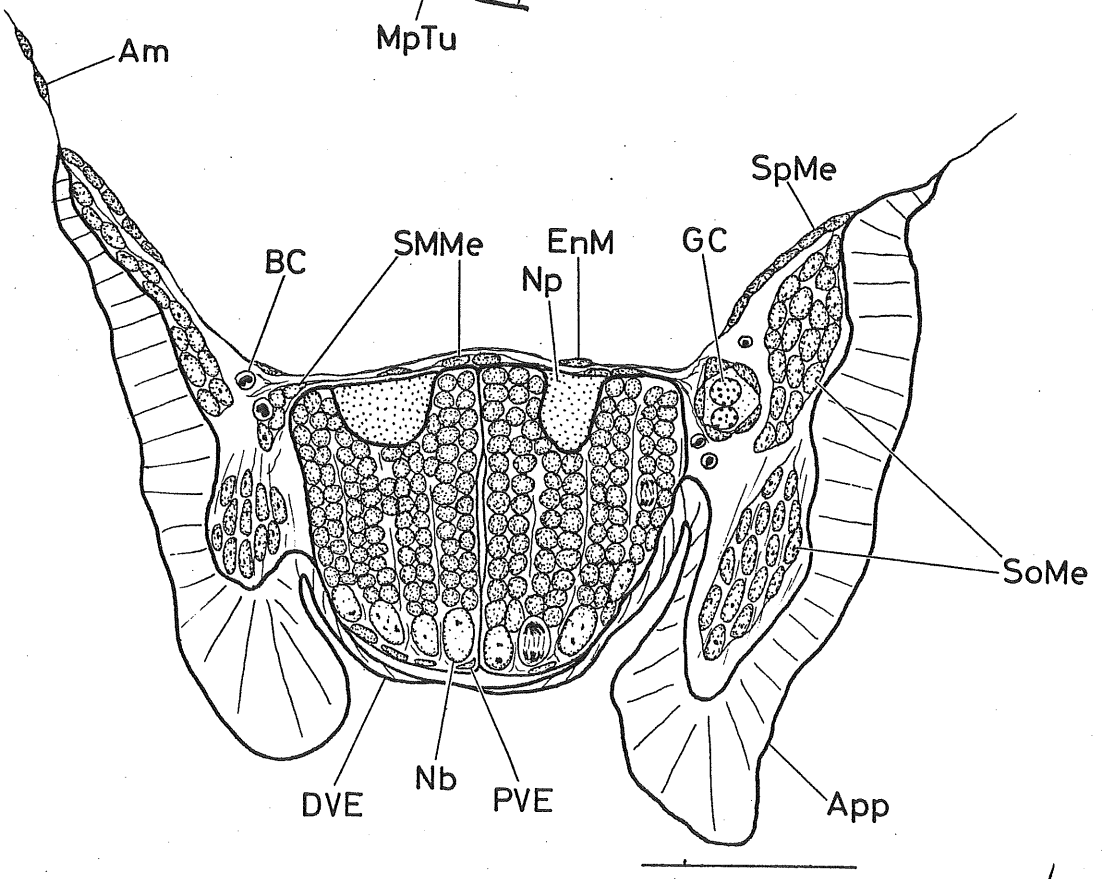
77. Part of sagittal section through midgut and proctodaeum in second instar larva. Arrow shows boundary of midgut and proctodaeum. Scale = 50 μm.
78. Transverse section through metathoracic segment of embryo in Stage 10. Scale = 50 μm.
79. Parasagittal section of embryo in Stage 4 through appendages. Scale = 100 μm.

Am, amnion; AnSo, antennal somite; App, appendage; BC, blood cell; DVE, definitive ventral epidermis; EnM, ental membrane; GC, germ cell; ISo, intercalary somite; LbSo, labial somite; MdSo, mandibular somite; MgEp, midgut epithelium; MpTu, malpighian tubule; MxSo, maxillary somite; Nb, neuroblast; Np, neuropile; Pd, proctodaeum; PraSo, preantennal somite; PVE, provisional ventral epidermis; PyR, pyloric region; SMMe, secondary median mesoderm; SoMe, somatic mesoderm; SpMe, splanchnic mesoderm; Th3So, metathoracic somite

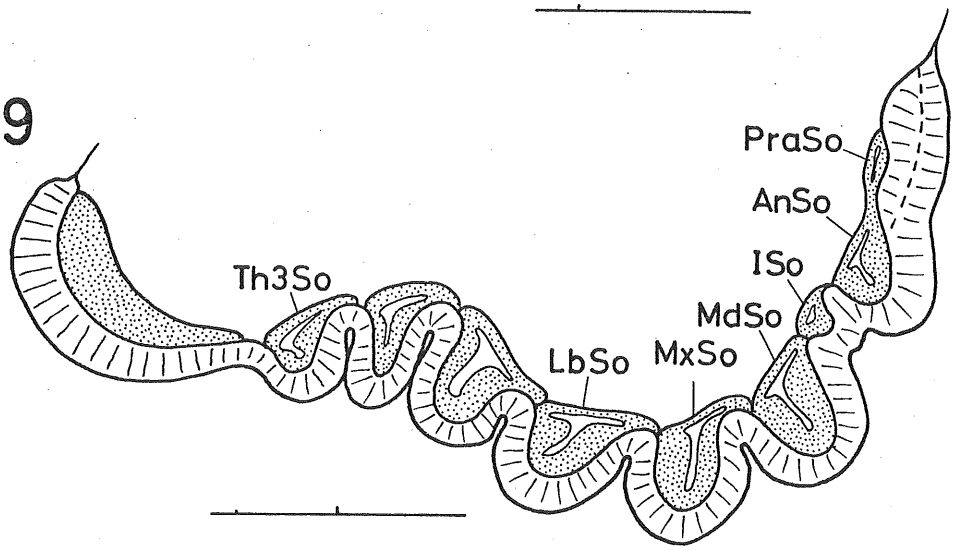
77


PyR
Pd
MgEp
MpTu

78


Am
SpMe
BC
SMMe
EnM
Np
GC
SoMe
DVE
Nb
PVE
App

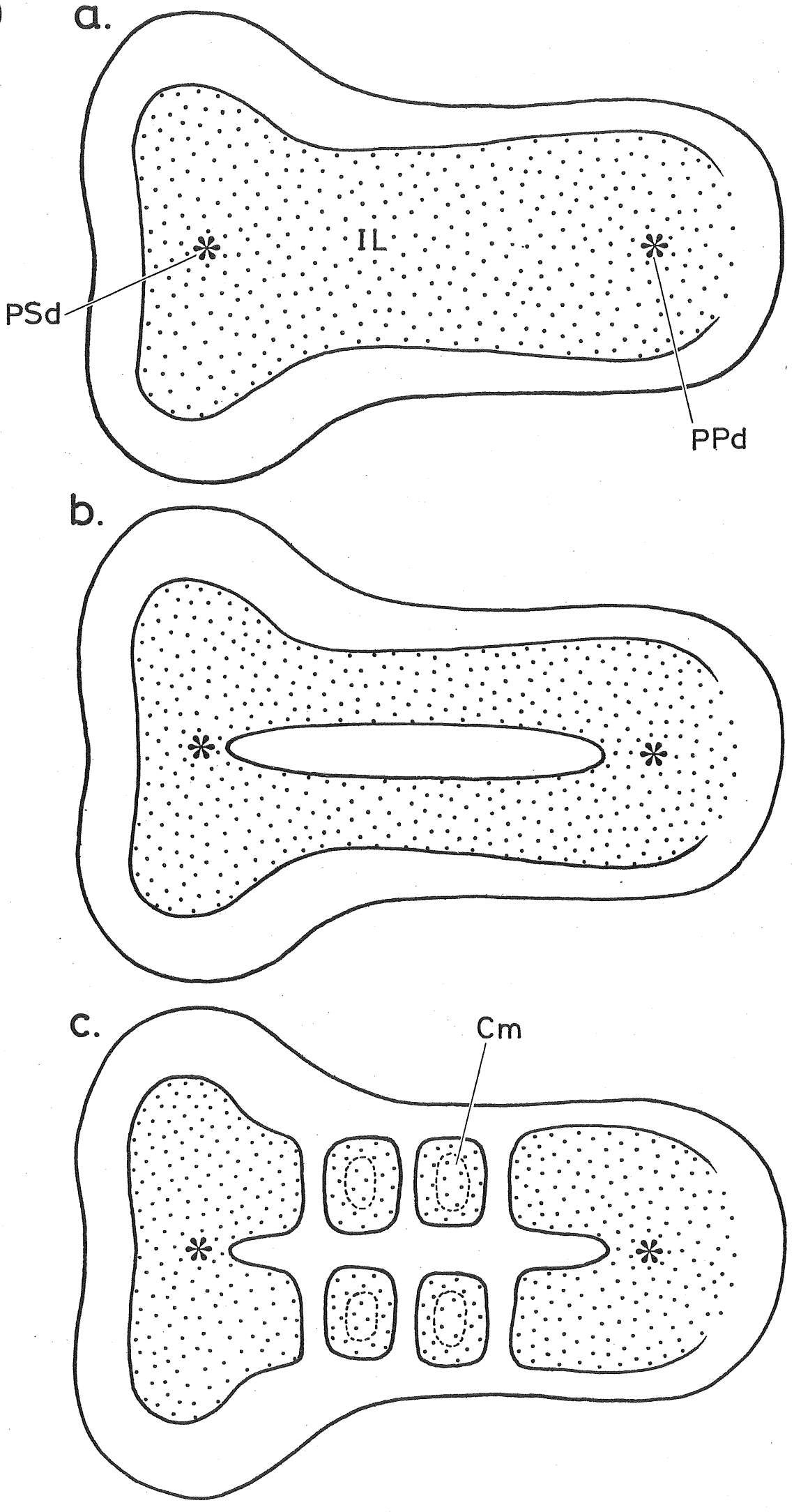
79


PraSo
AnSo
ISo
Th3So
MdSo
LbSo
MxSo

EXPLANATION OF FIGURE

80. Diagrammatic representation of early germ band (Stage 2), showing three successive stages in the development of inner layer (a–c).

Cm, coelom; IL, inner layer; PPd, presumptive proctodaeum; PSd, presumptive stomodaeum

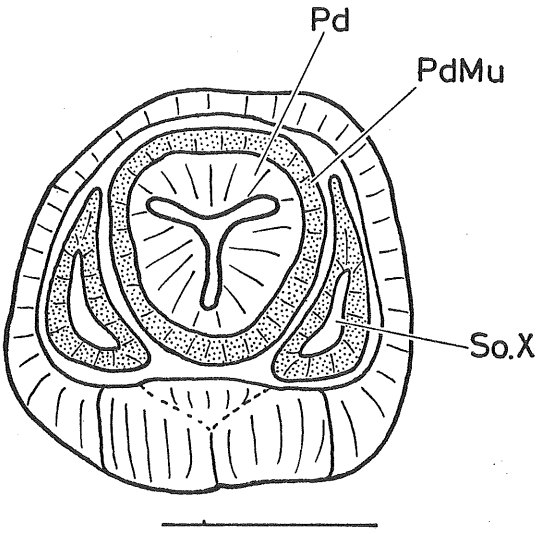

a.
IL
PSd
PPd
b.
c.
Cm

EXPLANATION OF FIGURES

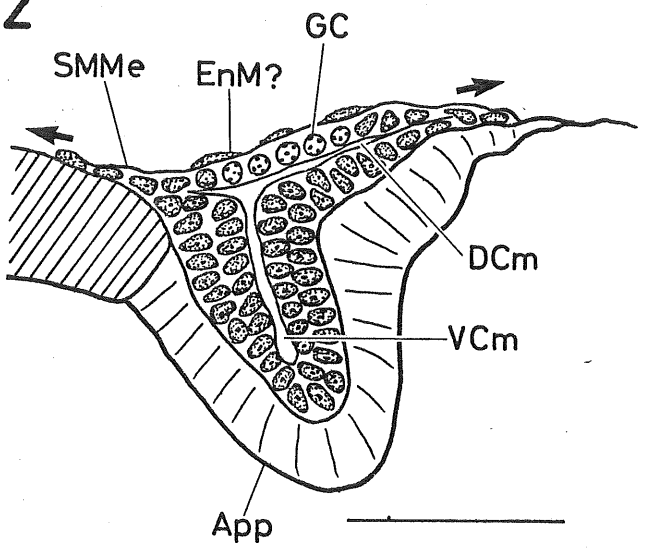
81. Transverse section through tenth abdominal segment of embryo in Stage 10.
82. Part of transverse section through mesothoracic segment of embryo in Stage 5. Arrows represent the extension of somite.
83. Part of transverse section through fifth abdominal segment of embryo in Stage 12.

AmC, amniotic cell; App, appendage; BC, blood cell; Cb, cardioblast; Cr, crypt; DCm, dorsal coelom; DDp, dorsal diaphragm; DSn, dorsal sinus; EnM, ental membrane; FB, fat body; GC, germ cell; Mu, muscle; Pd, proctodaeum; PdMu, proctodaeal muscle; PerC, pericardial cell; SMMe, secondary median mesoderm; So.X, tenth abdominal somite; SpMe, splanchnic mesoderm; T, tergum; VCm, ventral coelom

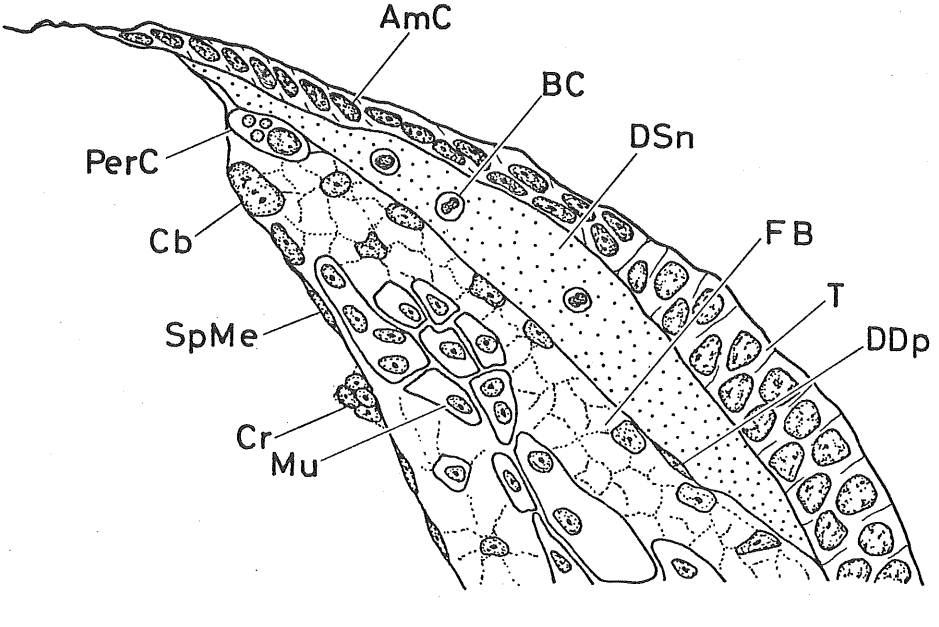
81


Pd
PdMu
So.X

82


SMMe
EnM?
GC
DCm
VCm
App

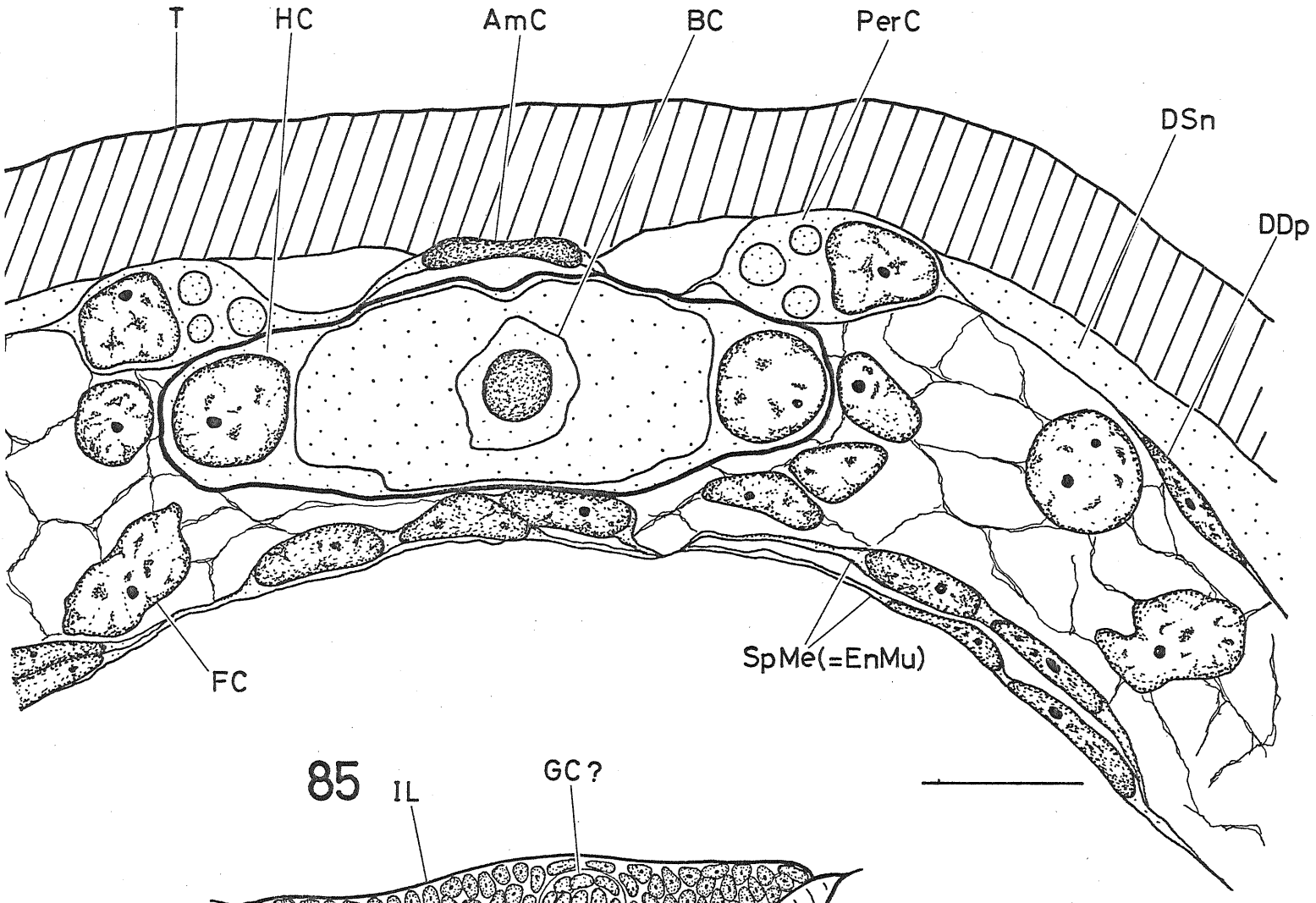
83

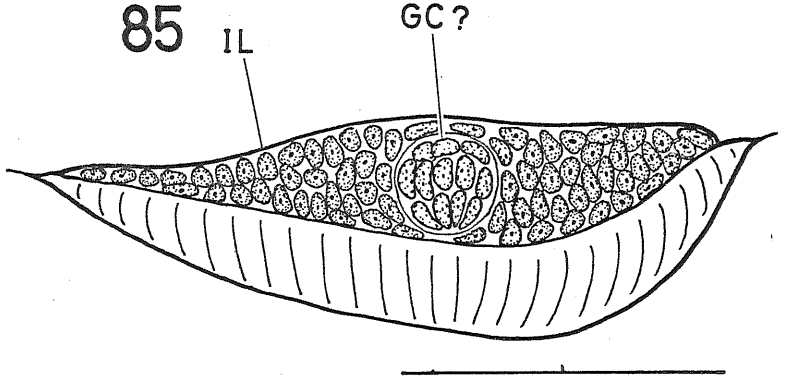

AmC
BC
DSn
PerC
Cb
FB
T
SpMe
DDp
Cr
Mu

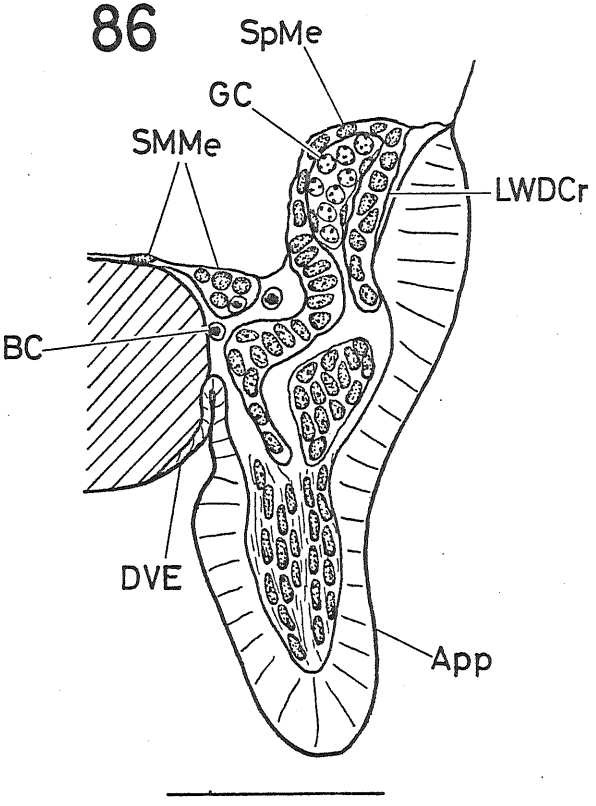
EXPLANATION OF FIGURES

84. Part of transverse section through sixth abdominal segment of embryo in Stage 12. Scale = 10 μm.
85. Transverse section through posterior region of germ band in Stage 2, showing peculiar cellular mass in inner layer. Scale = 100 μm.
86. Part of transverse section through metathoracic segment of embryo in Stage 9. Scale = 50 μm.

AmC, amniotic cell; App, appendage; BC, blood cell; DDp, dorsal diaphragm; DSn dorsal sinus; DVE, definitive ventral epidermis; EnMu, enteric muscle; FC, fat cell; GC, germ cell; HC, heart cell; IL, inner layer; LWDCm, lateral wall of dorsal coelom; PerC, pericardial cell; SMMe, secondary median mesoderm; SpMe, splanchnic mesoderm; T, tergum


84
T
HC
AmC
BC
PerC
DSn
DDp
FC
SpMe(=EnMu)

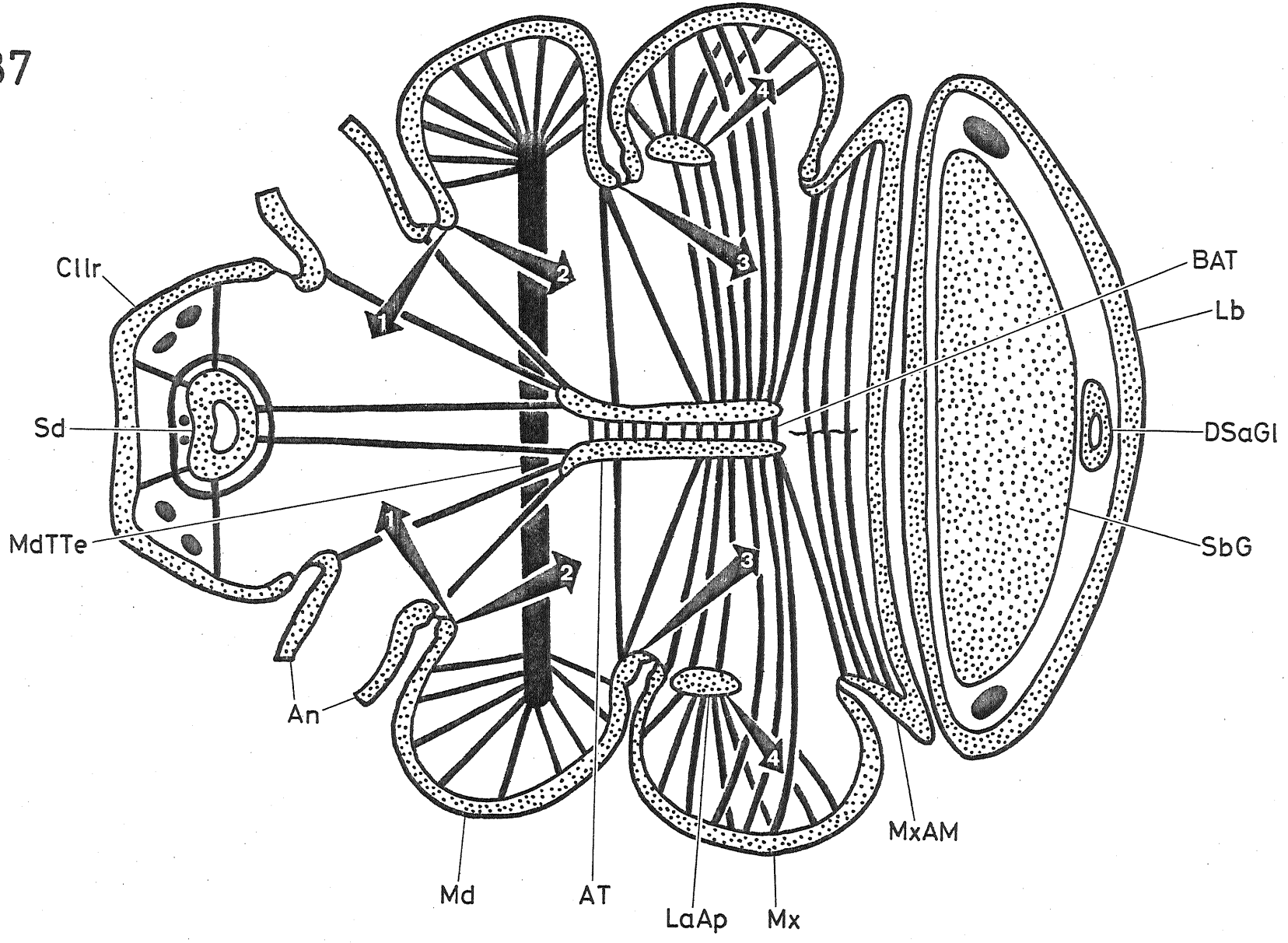

85
IL
GC?


86
SpMe
GC
SMMe
LWDCr
BC
DVE
App

EXPLANATION OF FIGURE

87. Diagrammatic horizontal section of head, showing the principal musculature. Arrows 1 to paired preocular apodemes, arrows 2 and 3 to postocular region or gnathal tergum, and arrows 4 to genal regions.

An, antenna; AT, anterior tentorium; BAT, binder of anterior tentoria; Cllr, clypeolabrum; DSaGl, duct of salivary gland; LaAp, lacinial apodeme; Lb, labium; Md, mandible; MdTTe, mandibular transverse tendon; Mx, maxilla; MxAM, maxillary arthrodial membrane; SbG, suboesophageal ganglion; Sd, stomodaeum

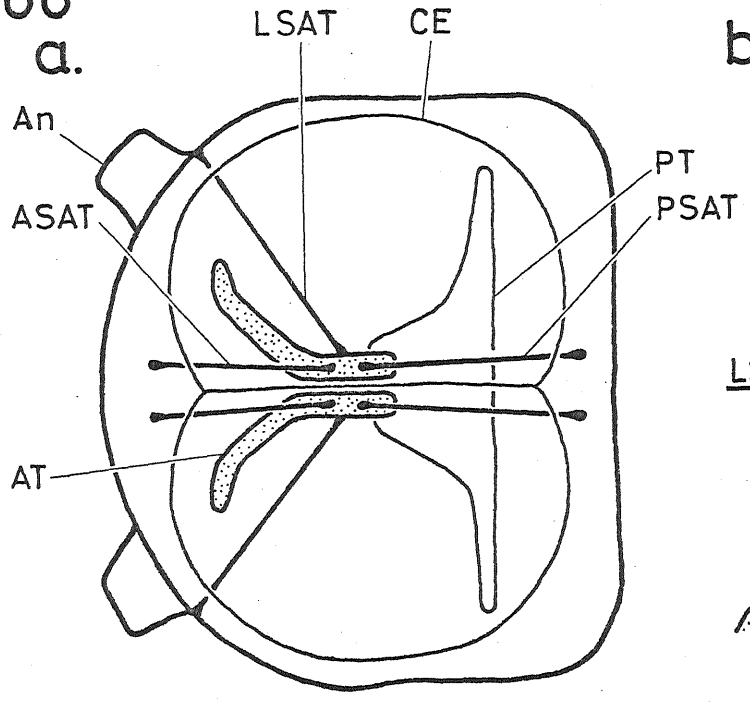

ClIr
Sd
MdTTe
An
Md
AT
LaAp
Mx
MxAM
BAT
Lb
DSaGl
SbG
1
2
3
4

EXPLANATION OF FIGURES

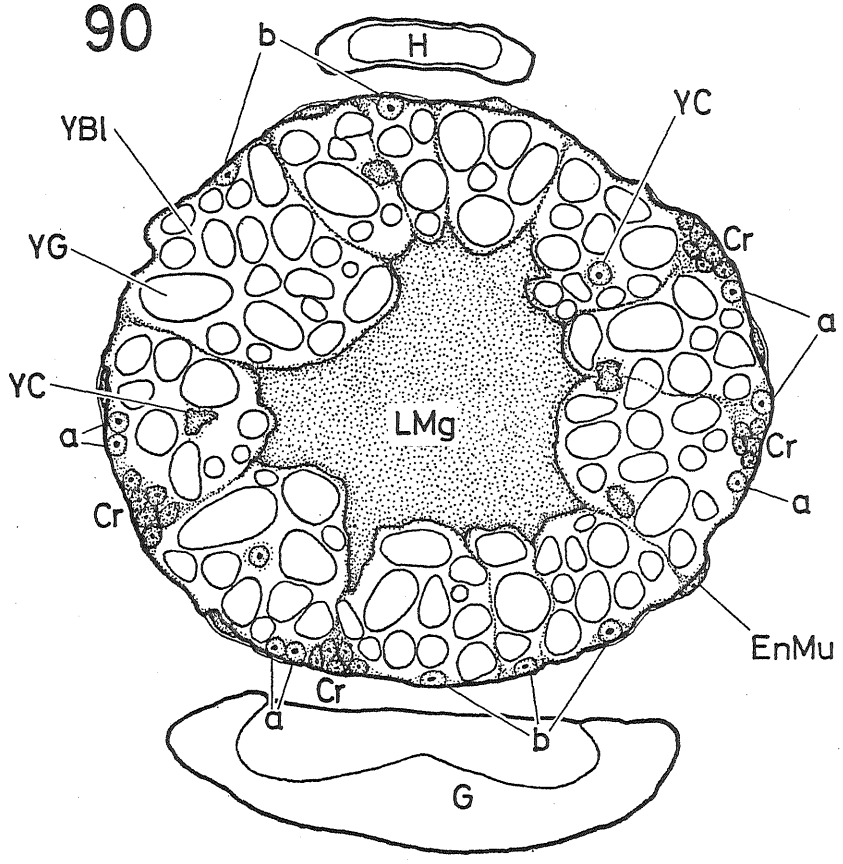
88. Diagrams showing the relative positions of tentorial suspensions to anterior tentoria (a, dorsal view; b, lateral view).
89. Diagrammatic sagittal section of alimentary canal, showing its musculature.
90. Transverse section through rudimentary midgut of embryo in Stage 14. The lumen filled with the liquefied yolk is formed at center of yolk blocks or developing midgut. Scale = 100 μm.

a, midgut epithelial cell derived from crypt; An, antenna; ASAT, anterior suspension of anterior tentorium; AT, anterior tentorium; b, midgut epithelial cell directly derived from yolk cells; CE, compound eye; Cr, crypt; EnMu, enteric muscle; G, ganglion; GsCc, gastric caecum; H, heart; LMg, lumen of midgut; LSAT, lateral suspension of anterior tentorium; Mg, midgut; Pd, proctodaeum; PSAT, posterior suspension of anterior tentorium; PT, posterior tentorium; Sd, stomodaeum; YBl, yolk block; YC, yolk cell; YG, yolk globule

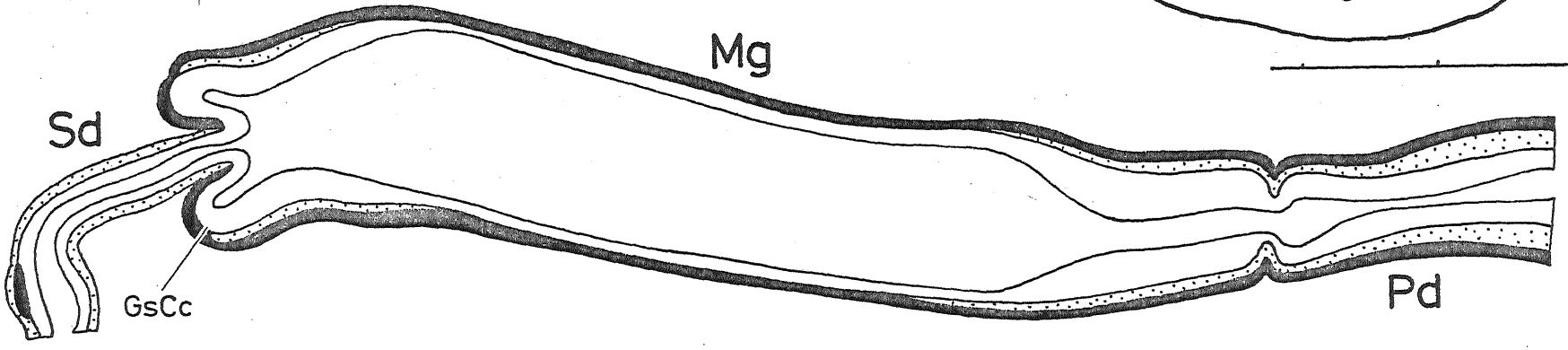
88



90



89



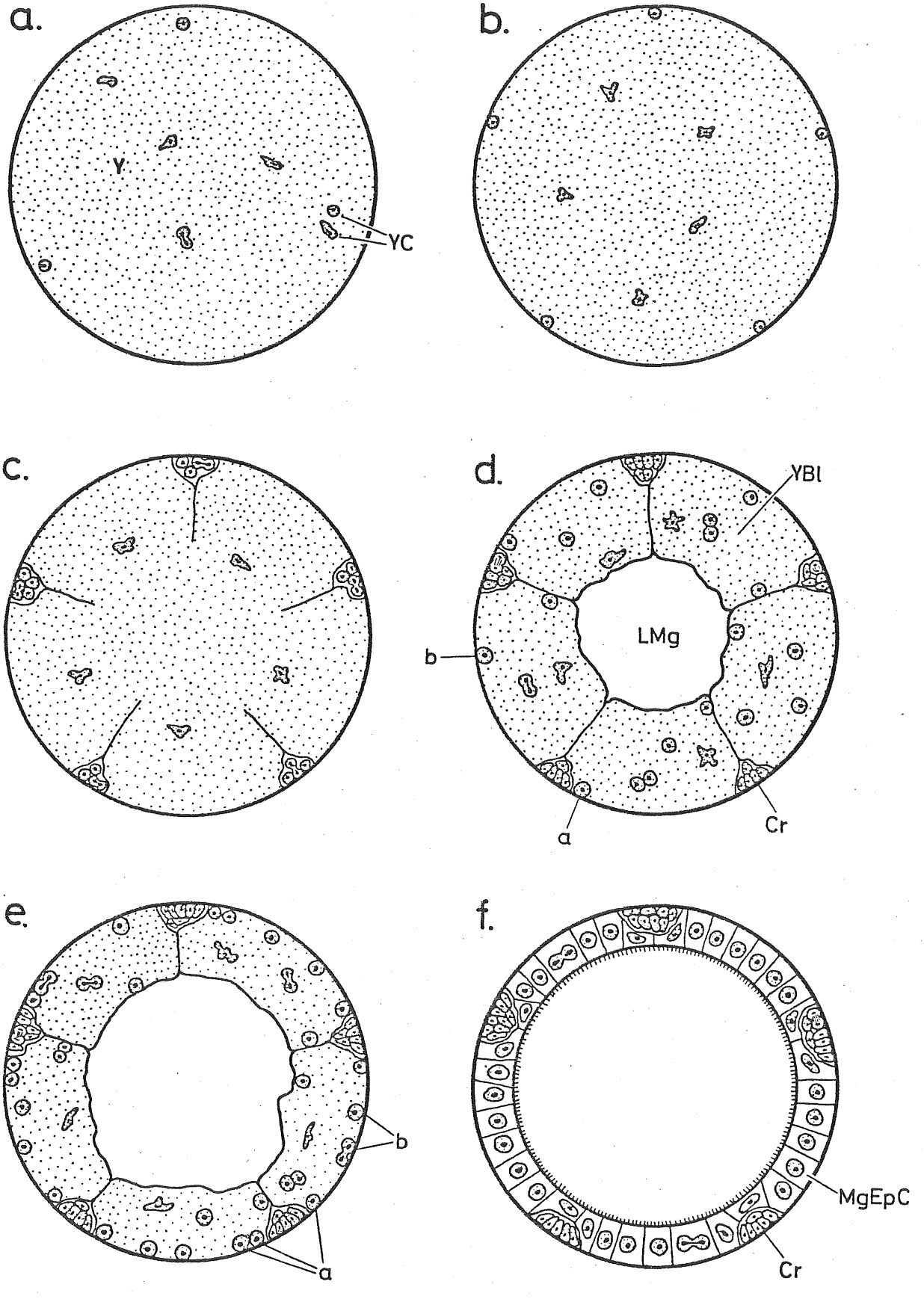
longitudinal muscle

circular muscle

EXPLANATION OF FIGURE

91. Diagrams showing development of midgut epithelium in transverse section (a–f).

a, midgut epithelial cell derived from crypt; b, midgut epithelial cell directly derived from yolk cells; Cr, crypt; LMg, lumen of midgut; MgEpC, midgut epithelial cell; Y, yolk; YBl, yolk block; YC, yolk cell


a.
Y
YC
b.
c.
d.
YBl
LMg
b
a
Cr
e.
b
a
f.
MgEpC
Cr