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The Embryology of the Caddisfly *Stenopsyche griseipennis* MacLachlan (Trichoptera, Stenopsychidae)

IV. Organogenesis: Mesodermal Derivatives

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Synopsis This paper describes the definitive coelomic sacs and the formation of the mesodermal organs of *Stenopsyche griseipennis* MacLachlan. The coelomic sacs are ill-developed and the appendicular coelomic sacs lack the dorsal wall. The lateral parts of the fat bodies arise from the lateral regions of the coelomic sacs. The formation of the other mesodermal organs is basically similar to those of other insect embryos.

Introduction

In previous papers (Miyakawa, 1973, 1974 a, b), the early developmental stages, changes in the external form of the embryo, the formation of germ layers and the organogenesis of ectodermal derivatives of *Stenopsyche griseipennis* MacLachlan were described.

This paper deals with the definitive coelomic sacs and the embryogenesis of the mesodermal organs: the muscular system, circulatory system, fat bodies, suboesophageal bodies and gonads.

Concerning the embryogenesis of the mesodermal derivatives for trichopteran insects, no paper has appeared, so far as the author is aware, except that by Patten (1884). Patten described the formation of the splanchnic mesoderm, heart, blood cells of *Neophalax*, and also described an endodermal cell-mass corresponding to the suboesophageal bodies. However, he gave no account of the formation of the muscular system and gonads of the species.

As the material and method used, and as the developmental stages are quite the same as those stated in the previous paper (Miyakawa, 1973), these details are omitted here.

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Observations

1. *Coelomic sacs* (Fig. 1)

By the end of stage 6, coelomic sacs and cavities make their appearance in the labral, the antennary, the three gnathal, the three thoracic and the first nine abdominal segments as previously described (MIYAKAWA, 1974 a). However, those of the intercalary and the tenth and eleventh abdominal segments are vestigial.

a) Coelomic sacs in protocephalic region

At the end of stage 5, the paired labral rudiments have a pair of mono-cellular inner layers at each side. These are the labral coelomic sacs, each containing a small lumen, the coelomic cavity. The coelomic sacs are open at the bases of the rudimental labra and continuous medially to the stomodaeal inner layer, latero-dorsally to those of the protocerebral lobe 3, and posteriorly to those of the antennal inner layer (MIYAKAWA, 1974 a, fig. 2–7 a). The cells of the labral coelomic sacs later differentiate into the clypeo-labral muscles.

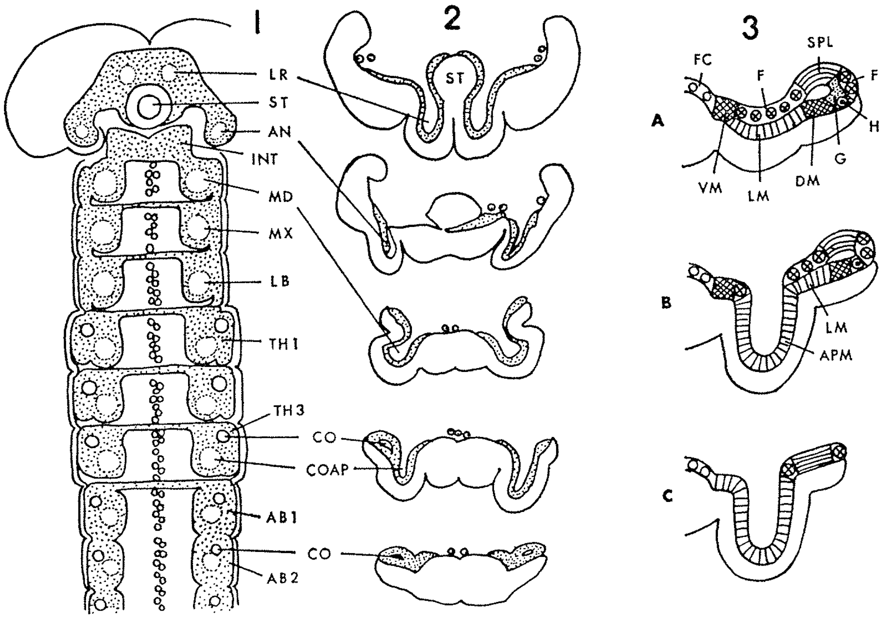


Fig. 1. Distribution of mesoderm (dotted part) at early pre-revolution stage and its fate, diagrammatic. —— 1. Dorsal view of mesoderm through anterior part of embryo. —— 2. Cross sections of embryo at each part shown by letterings. —— 3. Fate of parts of mesoderm in cross section of right side of embryo at abdomen (A), thorax (B) and gnathal region (C). AB 1 and 2, first and second abdominal segments; AN, antenna; APM, appendicular muscles; CO, coelom; COAP, appendicular coelom; DM, dorsal muscles; F, fat bodies; FC, paracytes and blood cells; G, gonad; H, heart; INT, intercalary segment; LB, labium; LM, lateral muscles; LR, labrum; MD, mandible; MX, maxilla; SPL, splanchnic mesoderm; ST, stomodaeum; TH 1 and 3, pro- and metathorax; VM, ventral muscles.

Antennary coelomic sacs localize in the antennary rudiments in the same way as the labral ones. They lack also the dorsal wall and extend medio-anteriorly to join labral coelomic sacs and the stomodaeal inner layer (MIYAKAWA, 1974 b, fig. 3–1 B). Consequently, the labral, the antennary coelomic sacs and the stomodaeal inner layer are continuous to each other and do not show any clear boundaries. In later stages, the cells of the sacs and the inner layer form the aorta and stomodaeal muscles. The antennary muscles are not recognized, since the antennae are quite ill-developed.

Along the distal borders of these protocephalic inner layers, the free cells are released, and they become the paracytes, blood cells and fat bodies.

b) Coelomic sacs in intercalary segment

As has already been described (MIYAKAWA, 1974 a, fig. 2–7 b), the coelomic sacs of the intercalary segment are vestigial and do not form the ordinary coelomic cavity. The intercalary inner layer is located along the ventral side of the stomodaeum near its base and later forms suboesophageal bodies.

c) Coelomic sacs in gnathal region

In each anlage of appendages, a large sac of the inner layer is formed. However, these sacs lack the dorsal walls as in the cephalic coelomic sacs. Laterally to these sacs, the inner layer extends to lateral margins of the embryo. These lateral ends of the inner layer correspond to the coelomic sacs of the thoracic and abdominal regions but lack the lumen or cavity. They are then cut off from the others and become the splanchnic mesoderm in the maxillary and labial segments, while in the mandibular segment they form the mandibular flexor and extensor muscles. The other parts of the inner layer form the muscles and the fat bodies.

d) Coelomic sacs in thoracic and abdominal regions

The coelomic sacs in the thoracic appendages are quite the same as in the gnathal ones. They are also continuous to the coelomic sacs at the lateral margins of the segments (MIYAKAWA, 1974 a, fig. 2–6 b).

At lateral margins of each thoracic and abdominal segment, the coelomic sacs are clearly formed (Fig. 1, CO). At first they consist of a single layer of cells, enclosing a small lumen, *i. e.*, the coelomic cavity (MIYAKAWA, 1974 a, fig. 2–6 a). The formation of the coelomic sacs is retarded in the posterior abdominal region, namely, the tenth and eleventh (?) abdominal segments. In these segments, the inner layer does not form the ordinary cavity at all, since the coelom formation of these segments is preceded by the morphogenetic movement during stage 6 through which the tenth and eleventh (?) abdominal segments are squeezed.

The fate of each part of the coelomic sacs is schematically shown in Fig. 1–3. The coelomic sacs are then dorso-ventrally divided into two solid cell-masses, *i. e.*, the splanchnic and somatic mesoderm. The splanchnic mesoderm later loses the segmental characteristics and becomes the enteric muscles. The somatic mesoderm forms the muscles, heart and fat bodies. The genital ridges are formed between the somatic and the splanchnic mesoderm. The coelomic sacs in the appendages or the appendicular coelomic sacs are regarded as a diverticulum of the somatic mesoderm.

2. *Musculature*

The muscles differentiate in the post-revolution period and they become striated and functional about the time of hatching. For the convenience of description the embryonic musculature is divided into three groups: the abdominal, the thoracic and the head muscles.

a) Abdominal muscles

In stage 7, the coelomic sacs rupture and the somatic mesoderm separates from the splanchinic mesoderm maintaining the connection with the ectoderm. The somatic mesoderm now consists of two or more layers of cells and occupies nearly one half of the inner surface of the ectoderm, just laterally to the ganglion (Fig. 2–1, SOM).

In stage 8, the somatic mesoderm begins to divide itself into several cell-masses to form the muscle rudiments. The middle part of the somatic mesoderm, at each side, gives rise to the lateral muscles, while the lateral and median parts of each somatic mesoderm form the dorsal and ventral longitudinal muscles, respectively (Fig. 2–2). As development proceeds the mesoderm extends dorsally with the ectoderm (Fig. 2–3).

In the latter half of stage 9, the musculature assumes a definitive state (Fig. 5–4). The ventral longitudinal muscles of a segment are well-developed, consisting of three pairs of antero-posterior bundles (VM 1–3) and two pairs of oblique bundles (VM 4, 5). The dorsal longitudinal muscles are weak, compared to the ventral ones, and they consist of three or four pairs of bundles (Fig. 2–4, DM). The lateral muscles are divided into two groups, the anterior and the posterior, corresponding to Musculi laterales externi and M. l. interni (SNODGRASS, 1935), respectively. The anterior lateral muscles connect the ventral body wall to the dorsal one in the anterior half of a segment. They comprise four or more separate muscle fibers (Fig. 5–4, ALM). The posterior lateral muscles obliquely connect the latero-ventral body wall of the posterior border of a segment to the dorso-lateral one (Fig. 5–4, PLM).

The musculature of the ninth abdominal segment differs from those of the anterior abdominal segments due to the occurrence of pygopods or anal appendages. A pair of the ventral longitudinal muscles of the ninth abdominal segment are directly inserted into the ventro-distal end of the basal segment of the pygopods (Fig. 5–5). In the ninth abdominal segment, the posterior lateral muscles are ill-developed.

The musculature of the pygopods, other than the above-mentioned muscles, seems to be of the vestigial tenth abdominal segment origin.

b) Thoracic muscles

The arrangement of the somatic mesoderm of the thorax is regarded as a modification of that of the abdomen due to the occurrence of legs. Its development is basically the same as the abdominal one, except the appendicular region (Fig. 3).

In stage 9, the ventral longitudinal muscles of thoracic segments appear in a quite similar way to those in abdominal segments (VM 1–3), but in the prothorax the muscles corresponding to VM 3 in other segments change direction, *viz.* passing obliquely outside the anterior lateral muscles. The dorsal longitudinal muscles of

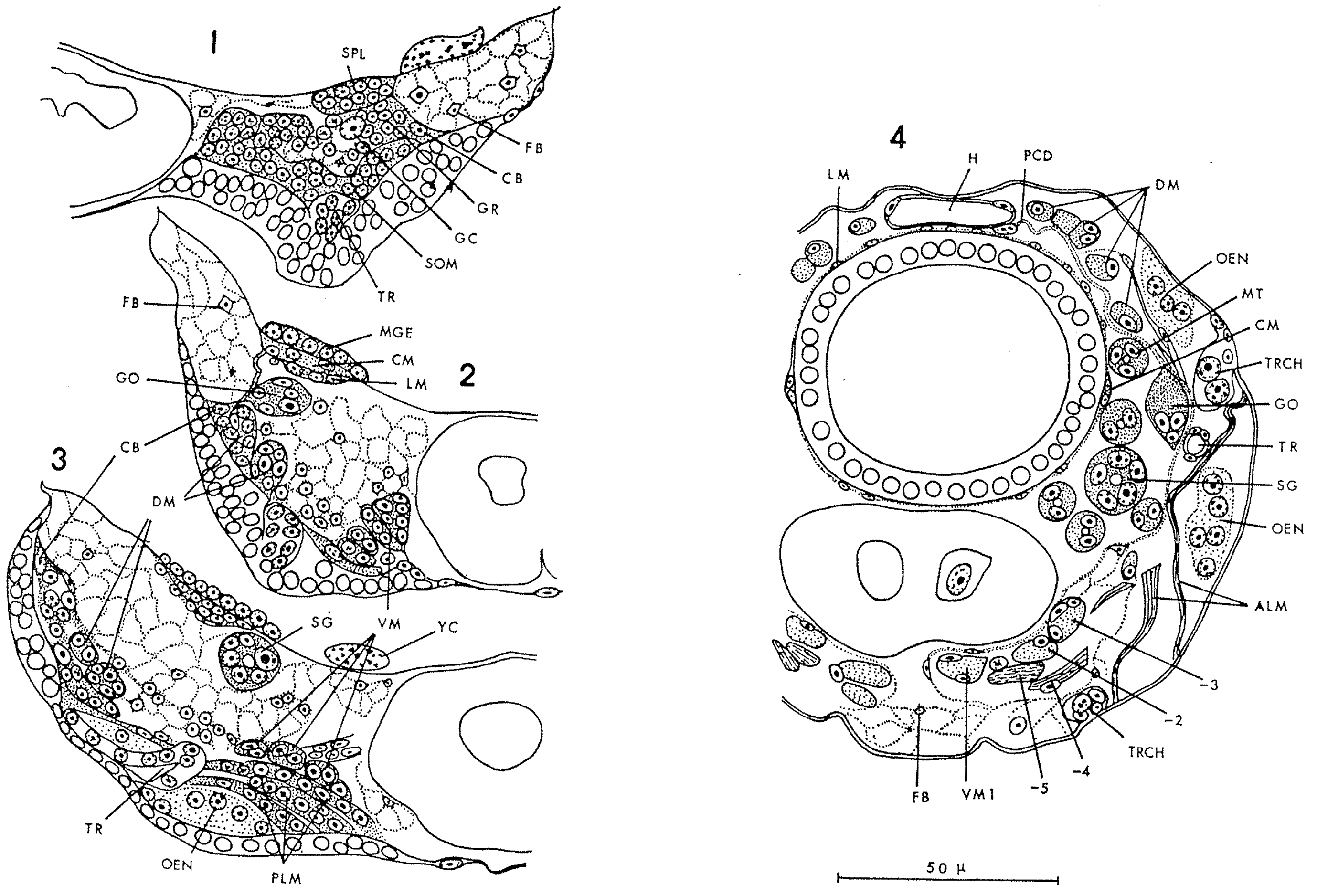


Fig. 2. Cross sections of abdomen through successive stages. —— 1–2. Posterior part of second abdominal segment at stages 7 and 8. —— 3. Posterior part of third abdominal segment at beginning of stage 9. —— 4. Middle part of fifth abdominal segment at end of stage 9. ALM, anterior lateral muscle; CB; cardioblast; CM, circular muscle (rudiment) of mid-gut; DM, dorsal muscle (rudiment); FB, fat body; GC, germ cell; GO, anlage of gonad; GR, genital ridge; H, heart; LM, longitudinal muscle (rudiment) of mid-gut; MT, Malpighian tubules; OEN, oenocyte; PCD, pericardial diaphragm; PLM, posterior lateral muscle (rudiment); SG, silk gland; SOM, somatic mesoderm; SPL, splanchnic mesoderm; TR, trachea (rudiment); TRCH, trichogen cell; VM, ventral muscle; YC, yolk cell.

the thorax are somewhat more complicated than those of the abdomen. There then appear additional muscle fibers which pass obliquely at the lateral side of the dorsal longitudinal muscles (Fig. 5–3).

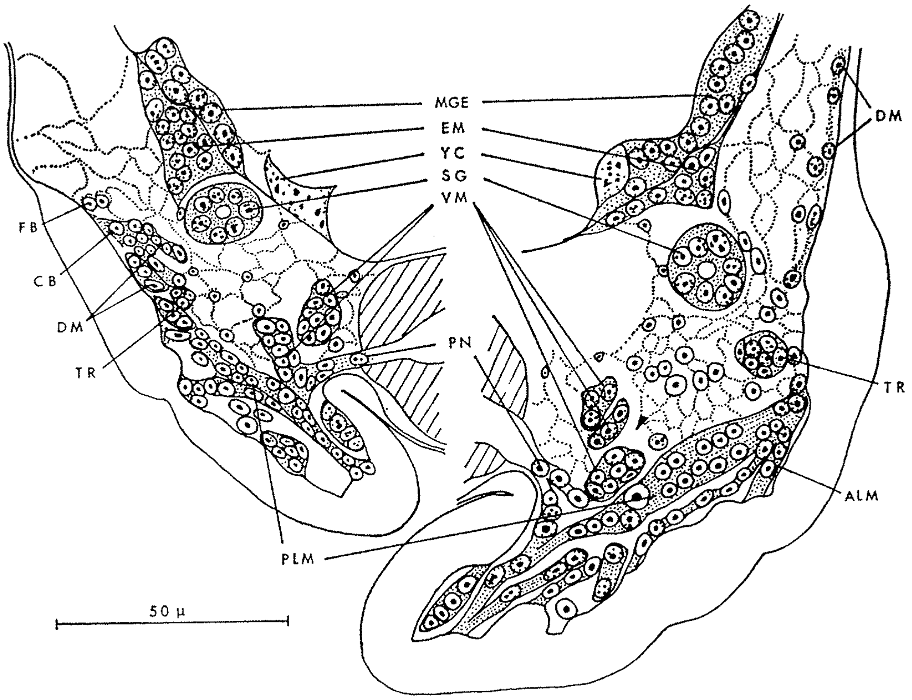


Fig. 3. Cross sections of embryo through mid-mesothorax at end of stage 7 (Left) and at beginning of stage 9 (right). ALM, anterior lateral muscle rudiment; CB, cardioblast; DM, dorsal muscle rudiment; EM, ental muscle rudiment; FB, fat body; MGE, anlage of mid-gut epithelium; PLM, posterior lateral muscle rudiment; PN, peripheral nerve rudiment; SG, silk gland; TR, tracheal anlage; VM, ventral muscle rudiment; YC, yolk cell.

The anterior lateral muscles are further divided into two groups: the anterior most and the middle. The latter group functions as the promotor of the coxa. The posterior lateral muscles become the remotor of the coxa in the prothorax, while in the meso- and metathoraces, the posterior lateral muscles, in large part, become the depressor of the trochanter, inserting into the base of the trochanter, and the rest becomes the remotor, inserting into the posterior part of the coxal base.

In the prothorax the dorsal muscles pass forward and enter the postoccipital region of the head capsule, playing part of the levator of the head (Fig. 5–3).

c) Head muscles

As a result of the morphogenetic movement of the cephalo-gnathal region during stages 7 and 8 (Fig. 4), the distal parts of the mandibular segment grow dorso-posteriorwards to occupy the region dorsal to the maxillary segment, whose lateral ends also shift medio-posteriorwards. Consequently, the mesoderm of each segment moves dorso-posteriorwards, the mandibular one to the position latero-dorsal of the maxillary rudiments and the maxillary one to the posterior of them. In the mean time, the labial anlagen shift medially to localize between the maxillary rudiments. During this morphogenetic movement the labral region remains near the original location.

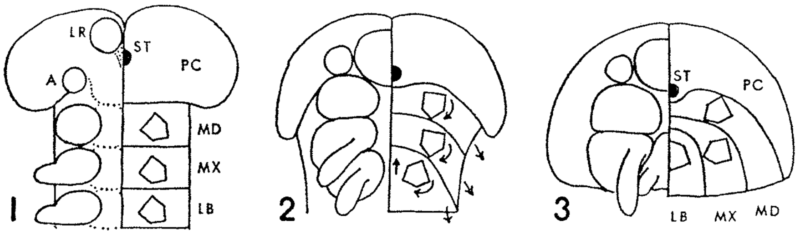


Fig. 4. Morphogenetic movement of cephalo-gnathal region, diagrammatic. —— 1.Stage 5. —— 2. Stage 7. —— 3. Stage 8. Pentagons show positions and directions of mandibular, maxillary and labial anlagen. Arrows indicate directions of growth or morphogenetic movement. A, antennal anlage; LB, labial segment; LR, labral anlage; MD, mandibular segment; MX, maxillary segment; PC, protocephalon; ST, stomodaeum.

In the meanwhile, the developing ectodermal invaginations connect with the corresponding mesoderms, *i. e.* the mandibular apodemes with the mandibular mesoderm and the anterior tentorial arms with the maxillary mesoderm. At stage 8, the mandibular mesoderm at lateral ends assumes conspicuous cell-masses along the lateral ectoderm near the brain and is divided into two groups, the anterior small ones and the posterior large ones. In all the gnathal appendages the mesodermal cells begin to arrange themselves into a pattern of definitive muscle fibers (Fig. 5–1).

In stage 9, the head musculature is completed. The labral mesoderm gives rise to the labral flexor and extensor muscles and also the dilator muscles of the stomodaeum, ranging from the labrum to the frons (Fig. 5–2, 1 to 11). The mandibular mesoderm gives rise to the strong flexor and weak extensor muscles of the mandibles. The flexor muscles pass from the mandibular apodemes to the lateroposterior end of the head capsule, and the extensor muscles pass outsides the former (Fig. 5–2, 12 and 13).

The maxillary and labial mesoderms give rise to the muscles which govern the movement of maxillo-labial parts. Most of them are connected to the maxillary base, passing inside the mandibular muscles, with the posterior end of the head (Fig. 5–2, 14, 16 and 17). In addition, a muscle bundle passes transversely from the medio-posterior base of the maxillae, crossing at the inside of the mandibular muscles, to the head capsule near frons. This muscle may be homologous to a maxillo-tentorial muscle of other insects (Fig. 5–2, 15). In the labium the mesoderm forms the three strong pairs of dilator and depressor muscles of the silk glands (Fig. 5–2, 18).

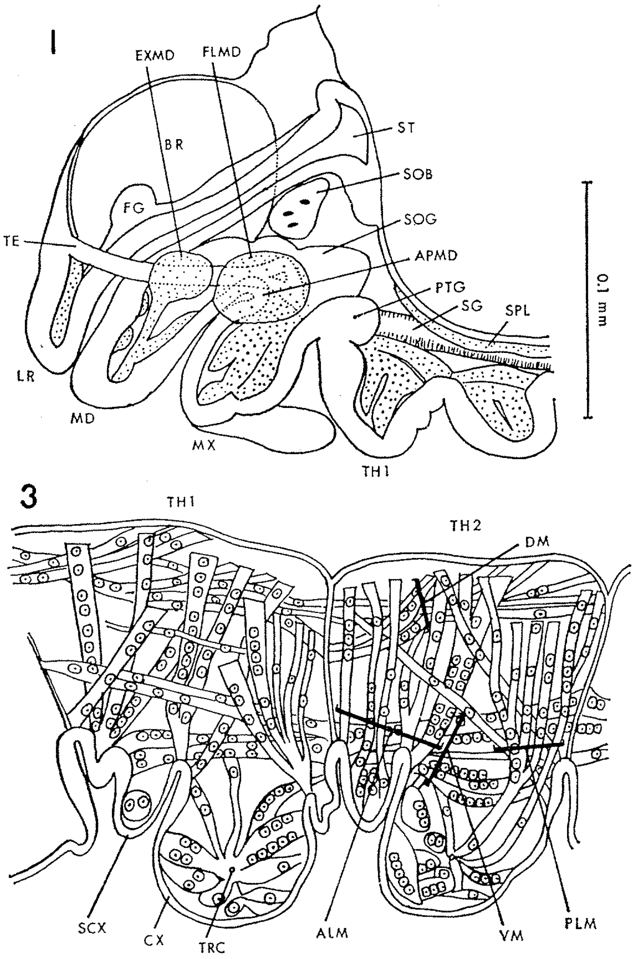
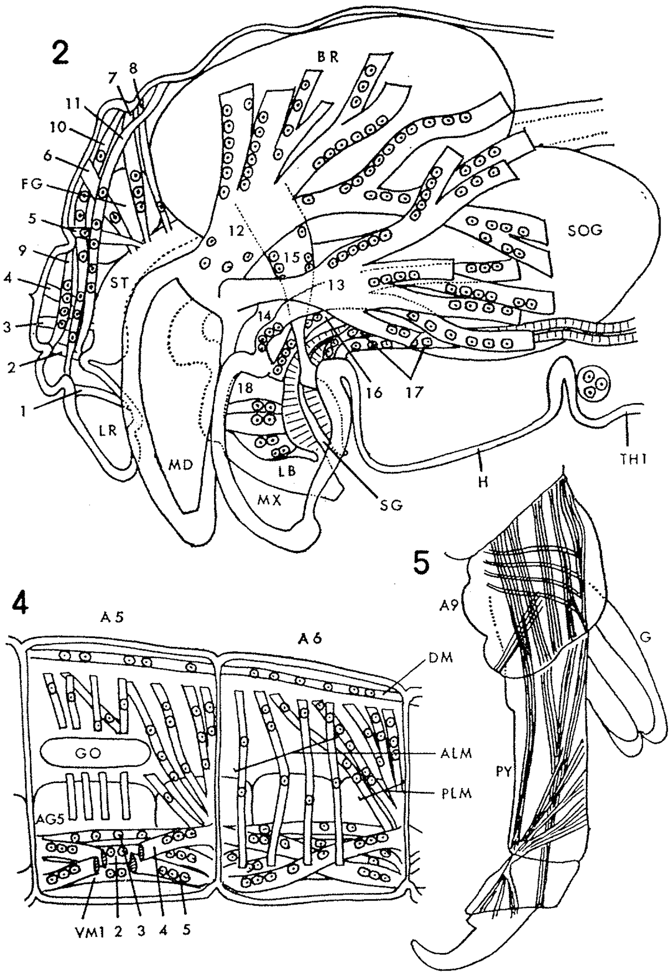


Fig. 5 (on pp. 458–459). Reconstruction of muscular system of embryo, lateral view from outer side, semidiagrammatic. —— 1. Head and anterior thorax at stage 8. —— 2. Head muscles at stage 9. —— 3. Pro- and mesothoracic muscles at stage 9. —— 4. Mid-abdominal muscles at stage 9. ——5. Muscles of posterior end of abdomen and pygopod of newly hatched larva. A 5 to 9, fifth to ninth abdominal segments; AG 5, fifth abdominal ganglion; ALM, anterior lateral muscles; APMD, mandibular apodeme; BR,

3. *Splanchnic mesoderm*

In stage 6, when the coelomic sacs are formed, the dorsal wall of the coelomic sacs comes in contact with the yolk sac. This occurs in the segments, from first maxillary to the ninth or tenth abdominal.

In stage 7, the coelomic sacs loosen and liberate the fat bodies from the median part and also from the lateralmost part of their dorsal wall. The solid parts of the dorsal walls of the coelomic sacs are the splanchnic mesoderm. It now assumes a pair of continuous longitudinal strands connected firmly to the yolk membrane and consists of two layers of cells in cross section (Fig. 2–1, SPL). In the second to the seventh abdominal segments, the splanchnic mesoderm is ventrally connected to the



brain; CX, coxa; DM, dorsal muscle; EXMD and FLMD, anlagen of mandibular extensor and flexor muscles; FG, frontal ganglion; G, rectal gills; GO, gonad; H, head capsule; LB, labium; LR, labrum; MD, mandible; MX, maxilla; PLM, posterior lateral muscles; PTG, prothoracic gland; PY, pygopod; SCX, subcoxa; SG, silk gland; SOB, suboesophageal body; SOG, suboesophageal ganglion; SPL, splanchnic mesoderm; ST, stomodaeum; TRC, trochanter; VM, ventral muscles of mesothorax; VM 1–5, ventral muscles of mid-abdomen; 1–17, head muscles.

genital ridge.

In stage 8, the splanchnic mesoderm abandons the connection with all the mesodermal components except the fat bodies, but maintains the initial appearance. Later it differentiates into the outer longitudinal and the inner circular muscles of the mid-gut, *viz.* the enteric muscles (Figs. 2 and 3, CM, LM and EM).

4. *Circulatory system*

a) Heart

At first the cardioblasts are discriminated from other mesodermal cells only in their position and their differentiation is retarded.

In stage 7, the cardioblasts are situated at lateral ends of the coelomic sacs throughout thorax and abdomen. In cross section, the cardioblasts appear as the outermost cells of the solid mesoderm connected with the ectoderm, while there appear several fat body cells lateral to them (Figs. 2–1 to 3, CB). There are about four cardioblasts in a longitudinal line at each side of a segment.

Early in stage 9, the cardioblasts maintain the connection with the ectoderm but are cut off from the splanchnic mesoderm (Fig. 2–3).

As development proceeds, both the outer sides of the ectoderm grow dorsalwards finally performing the dorsal closure. Consequently, the cardioblasts in both the sides approach and unite to each other (cf. Figs. 2–2 and 2–3). This morphogenetic movement begins first at the posterior abdomen and then proceeds forwards, finishing at the prothoracic segment. Thus the heart is formed (Fig. 2–4, H).

In cross section, the pericardial diaphragm is observed as a pair of thin membranes connected to the ventral or inner side of the heart and spread ventrally along the inner side of the other mesodermal tissues covering the definitive circumintestinal blood sinus. The pericardial diaphragm closely resembles the reticula produced by the fat body cells (Fig. 2–4, PCD).

b) Aorta

The aorta arises from the labro-antennal mesoderm on the dorsal side of the stomodaeum. The aorta makes its appearance at the beginning of stage 9 as a tubular structure along the mid-dorsal line of the stomodaeum, ranging from the anterior part of the intercerebral region to the posterior end of the stomodaeum (MIYAKAWA, 1974 b, fig. 3–3 A, ao). Near the junction of the stomodaeum to the mid-gut at the posterior end of the head, the aorta continues to the heart.

c) Blood cells

In stages 4 and 5, the free cells are liberated from the median mesoderm through the entire length of the embryo. A large number of them migrate into the yolk as the paracytes as described previously (MIYAKAWA, 1974 a), and the remainder stay as free cells in the epineural sinus. These cells are the precursors of blood cells.

In stage 9, when the heart is formed, the blood cells are found in it, assuming the definitive appearance quite similar to those of other insects, *i. e.* the nucleus with a large amount of chromatins and the cytoplasm with vacuoles.

5. *Fat bodies or fatty tissues* (Figs. 2 and 3, FB)

In stage 6, the fat bodies arise from the mesoderm throughout the entire length of the embryo, *i. e.* from the labral to the ninth abdominal segment. Its appearance in the posterior abdomen is retarded. Each fat body cell has a degenerating nucleus and a specialized cytoplasm involving large vacuoles. Consequently, during its development, the cell size increases to many times as large as the ordinary one.

In the labral, antennal and mandibular regions, the connection of cells comprising the dorsal wall of the coelomic sac loosens and the cells are converted into fat bodies. In the segments, from the maxillary to the posterior abdominal, the fat bodies appear first at lateral ends of the coelomic sacs and then at a median part of the dorsal wall of the coelomic sacs, just inside the splanchnic mesoderm.

As development proceeds, the fatty tissues fill up all the interspaces of the organs with the exception of the circumintestinal regions and the insides of appendages.

6. *Gonads*

The genital ridges or rudimental gonads appear, in stage 7, at each side of the second to the seventh abdominal segments as a bridge between the splanchnic and the somatic mesoderm. Inside the genital ridge, one or two germ cells are found at each side of a segment (Fig. 2–1). The germ cells have a large nucleus with a conspicuous large nucleolus and transparent nucleic fluid. The author failed to detect the germ cells until this stage.

As development proceeds, the genital ridges are cut off from the splanchnic mesoderm. They assume a somewhat depressed columnar shape and lie at each inside of the fatty tissue ventrally to the cardioblasts (Fig. 2–2, GO). In stage 8, the rudimental gonads range from the third to the seventh abdominal segment.

According to the revolution of the embryo, the anlagen of the gonads decrease in length and in stage 9 they come to range from the fourth to the fifth abdominal segment and finally condense within the fifth abdominal segment (Figs. 2–2, –4, and 5–4, GO). This state is maintained until an early stage of the pupa.

7. *Suboesophageal bodies*

The suboesophageal bodies arise from the mesoderm of the intercalary segment

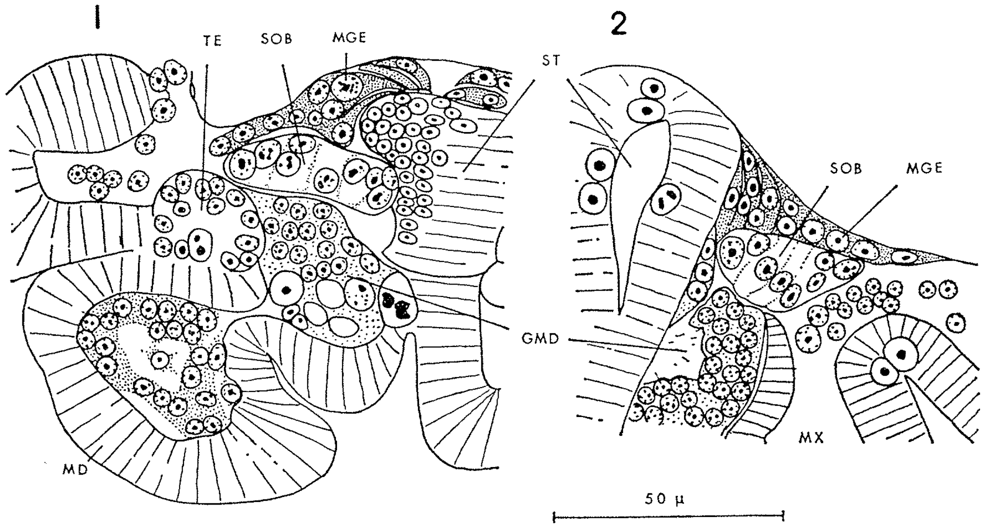


Fig. 6. Cross section (1) and parasagittal section (2) of embryo at stage 6 through anlage of suboesophageal body. GMD, mandibular ganglion; MD, mandible; MGE, anlage of mid-gut epithelium; MX, maxilla; SOB, suboesophageal body; ST, stomodaeum; TE, tentorial rudiment.

and maintain their existence throughout the embryonic period.

In stage 6, when the stomodaeal invagination deepens and the proliferation of cells of anterior mid-gut epithelium has begun, the mesoderm of the intercalary segment forms a laterally elongated cell-mass just behind the stomodaeum and just beneath the mid-gut epithelium. This cell-mass is the anlage of the suboesophageal bodies. The constituent cells increase in height and their cytoplasm becomes pale, assuming an appearance different from that of the surrounding cells (Fig. 6, SOB).

As development proceeds, the anlagen of the suboesophageal bodies detach from the ectoderm and attach to the ventral side of the posterior half of the stomodaeum. Consequently, the suboesophageal bodies move backwards with the development of the stomodaeum (Fig. 5–1, SOB) and in stage 9, they reach the posterior end of the head capsule. This position is maintained at least until the first instar larval stage.

Discussion

1. *Coelomic sacs and cavities*

JOHANNSEN and BUTT (1941) classified the types of formation of the coelomic cavities in insect embryos as follows: 1) by clefts appearing in the solid mesoderm, 2) by folding over of the lateral margin of the inner layer and 3) by diverticulation of the primitive groove, *i. e.* the archenteron.

According to EASTHAM (1930, in *Pieris,* Lepidoptera) the coelomic cavities of the thorax are formed by the folding over of the lateral margin of the inner layer, and those of the abdomen, except the first abdominal segment, are formed by clefts in the solid two-cell-layered inner layer. In the thorax of *Pieris* 'the subsomitic mesoderm' forms a cavity in the hollow of an appendage medially to the ordinary coelom of the latero-dorsal part of the germ band. Concerning this phenomenon JOHANNSEN and BUTT state that among more highly specialized insects the coelomic cavity does not extend to the appendages.

In *Stenopsyche,* the gnathal, thoracic coelomic cavities at the lateral ends of the segments are incompletely formed. However, the lateral margin of the inner layer tends to curl dorsally, representing a transitional phase to the second type, *i. e.* the folding over type. The appendicular coelomic cavities develop well and coincide with those of *Pieris* (EASTHAM, 1930). In the abdomen the coelomic cavities are formed at the lateral ends as clefts appearing in the inner layer, *i. e.* the first type, similar to other insects.

The antennal coelomic cavities in lower insect embryos are distinctly developed and are independent of the adjacent labral ones (*e. g.*, ANDO, 1962; MALZACHER, 1968; SCHOLL, 1969). In *Pieris* the antennal coelomic cavities also appear independent of other cephalic ones, though all of the preoral coelomic cavities are ill-developed.

In *Stenopyche* the antennal coelomic cavities are so incomplete that they are open at the dorsal side and, moreover, their sacs or walls are continuous to the labral coelomic sacs, lacking any clear boundary between them. Accordingly, it is difficult to decide accurately the segmental origin of the stomodaeal mesoderm and the aorta.

2. *Musculature*

Though the distribution of the muscles varies considerably according to the insect group, their embryonic origin is undoubtedly attributed to the somatic mesoderm. The general plan of the muscle distribution of the insects was described by SNODGRASS (1935) and that of the odonate embryos was illustrated by ANDO (1962). EASTHAM described the early development of muscles of *Pieris*. Recently SCHOLL (1969) gave a detailed account of the development of the head muscles in *Carausius* (Phasmida).

The rough feature of the development of the muscles of *Stenopsyche* coincides with that of other insects but it may be noted here that, first, in *Stenopsyche* the mandibular flexor and extensor muscles originate from the mandibular mesoderm, not from the maxillary mesoderm, supporting the view of SCHOLL (1969, in *Carausius*); second, in *Stenopsyche* there is a muscle connecting the median base of the maxilla with the dorsal head wall at each side, which is homologous to the muscle of other insects connecting the maxillary base with the tentorium; third, in *Stenopsyche* the ventral longitudinal muscles of the thorax and abdomen strongly develop in contrast to the dorsal ones; and fourth, the appendicular muscles seem to be only a variation of the lateral muscles of segments which lack appendages.

3. *Splanchnic mesoderm*

There are a few differences according to insects in the origin of the anterior and posterior ends of the splanchnic mesoderm. According to ROONWAL (1937, in *Locusta*) the splanchnic mesoderm arises in the segments posterior to the labial. ANDO (1962, in Odonata) says that it is formed in the segments, from the mandibular to the sixth (or seventh ?) abdominal.

In *Stenopsyche*, the splanchnic mesoderm originates in the segments, from the maxillary to the ninth abdominal.

4. *Circulatory system*

Concerning the heart formation for *Neophalax*, PATTEN (1884) describes that a solid cord of cells is formed in the median dorsal region by the fusion of the edges of the mesodermic folds and the cord becomes hollow and forms the heart.

In *Stenopsyche* the author failed to observe such a solid cord. The heart of *Stenopsyche* is formed in the usual way in the insect embryos. However, it must be noted that the cardioblasts of *Stenopsyche* differentiate much later than in other insects, and also they lie at first medial to the laterally distributed fat body cells, as described previously.

The blood cell formation of *Stenopsyche* is quite the same as in *Neophalax*

(PATTEN, 1884) and other insect orders (*e. g.*, TOYAMA, 1902; SAITO, 1937; OKADA, 1960; NELSON, 1915; HEYMONS, 1895; ANDO, 1962). EASTHAM (1930) says that the blood cells of *Pieris*, at first resembling normal insect blood cells, quickly take on a characteristic appearance. In *Stenopsyche* the blood cells at first do not show any definitive characteristics but assume an appearance quite similar to that of the paracytes.

5. *Fat bodies*

The fat bodies of *Stenopsyche* are well-developed. It is probably of interest to note that, in the trunk region, the fat bodies arise not only from the medio-dorsal part but also from the lateral side of the coelomic cavities. Consequently, there appears a considerable space occupied by the fat bodies lateral to the cardioblasts, genital ridges and splanchnic mesoderm until the dorsal closure occurs. So far as the author is aware there has been no description of such an occurrence of the fat bodies.

6. *Gonads*

The origin of the gonads varies according to the insects. The gonads arise in the abdominal segments, from the second to the seventh in *Apis* (Hymenoptera) and *Pyrrhocoris* (Hemiptera) (NELSON, 1915; SEIDEL, 1924), from the third to the fifth in *Chalicodoma* (Hymenoptera) (CARRIÈRE and BÜRGER, 1897), and from the fourth to the ninth in *Bombyx* (Lepidoptera) (MIYA, 1959).

The definitive location of the embryonic gonads is also variable. The gonads in the abdominal segments, from the fourth to the seventh in *Apis* (NELSON, 1915), from the second to the third in *Pyrrhocoris* (SEIDEL, 1924), and in the eighth in *Bombyx* (MIYA, 1959).

In *Stenopsyche*, the gonads originate in the second to the seventh abdominal segment, and by the end of the revolution of the embryo they come to lie in the fifth abdominal segment. This location of the gonads is maintained until the prepupal stage. The same observations have been made by several authors (MAKINO and KICHIJO, 1934, in *Stenopsyche* larvae; DODSON, 1935, in *Phryganea* larvae; GLASGOW, 1936, in *Hydropsyche* larvae; STITZ, 1904, in adult caddisflies).

7. *Suboesophageal bodies*

The suboesophageal bodies in *Neophalax* has been described by PATTEN (1884), though he did not use the term suboesophageal bodies. According to him it is endodermal in origin (*vide* his fig. 36, a)

The suboesophageal bodies occur in a large number of insect orders and they are regarded as the derivative of the mesoderm of the intercalary segment (*e. g.*, EASTHAM, 1930; JOHANNSEN and BUTT, 1941; OKADA, 1960). The same is true for *Stenopsyche*. Some authors describe that the suboesophageal bodies proliferate the blood cells (TOYAMA, 1902; WADA, 1955, in *Bombyx*), but in *Stenopsyche* the author failed to observe such a phenomenon.

Summary

1) The organogenesis of the mesodermal derivatives of *Stenopsyche griseipennis* MacLachlan was described.

2) The coelomic sacs in the cephalo-gnathal region are ill-developed; the labral and antennal coelomic sacs are continuous mutually and they lack dorsal walls, and the intercalary mesoderm does not form the coelomic cavities. The thoracic and the abdominal coelomic cavities are also ill-developed.

3) The splanchnic mesoderm arises in all the segments, from the maxillary to the ninth abdominal.

4) The fat bodies originate in all the body segments, from the labral backward, except the intercalary segment. They differentiate also from the lateral sides of the coelomic sacs.

5) The heart is formed from the cardioblasts in a way similar to other insects, but in a different manner from that in *Neophalax*.

6) The blood cells originate in the median mesoderm at an early stage. simultaneously with the paracytes.

7) The suboesophageal bodies are formed from the mesoderm of the intercalary segment. The proliferation of the blood cells from the suboesophageal bodies was not observed

8) The gonads arise as the genital ridges in the second to the seventh abdominal segment and finally come to lie in the fifth abdominal segment

9) The origin and formation of the muscles were described and discussed.

10) The mandibular flexor and extensor muscles arise from the mesoderm of mandibular segment, not from that of maxillary segment.

11) A longitudinal muscle of the ninth abdominal segment, at each side, inserts in the distal part of the basal segment of the pygopods.

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