Studies on the Pleuropodia of Embioptera, Thysanoptera and Mecoptera

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by
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PREFACE

Since the close of the last century, the pleuropodia of various insect orders have been studied by many investigators. At present, therefore, there is a considerable amount of knowledge concerning the pleuropodia of embryo insects. So far as the authors are aware, however, there are no papers regarding the pleuropodia of Mecoptera, and a few papers concerning those of Embioptera and Thysanoptera (MELANDER, 1903 ; STEFANI, 1961 ; BOURNIER, 1966).

This paper deals with the development of the pleuropodia of the abovementioned orders, but does not deal with the functions of the pleuropodia.

The senior author wishes to express his thanks to Dr. Akira NAGATOMI and Dr. Junichi YUKAWA of Kagoshima University and Mr. Akira MIYATA of Nagasaki University for their kind assistance in the present study.

MATERIALS AND METHODS

As materials the following species were used : *Oligotoma japonica* OKAJIMA as Embioptera, *Bactridothrips brevitubus* TAKAHASHI as Thysanoptera, *Panorpa pryeri* MACHLACHLAN and *Bittacus mastrillii* NAVAS as Mecoptera. *O. japonica* was collected in Kagoshima City, *B. brevitubus* was captured at Mino-o in Osaka Prefecture, and *P. pryeri* and *Bi. mastrillii* were caught at Sugadaira Plateau in Nagano Prefecture.

The eggs of these species were fixed in alcoholic Bouin's or Carnoy's fluid warmed to 60～70°C for 10～30 minutes and they were cut into 6～7 micra thicknesses and stained with Delafield's haematoxylin and eosin. All drawings were made with the Abbe camera lucida.

OBSERVATIONS

For the convenience of description, the development of the embryos of *O. japonica* and *B. brevitubus* is divided into the following stages, *viz.*, the early pre-revolution, the middle pre-revolution, the late pre-revolution, the post-revolution, the late embryonic, and the full grown embryonic.

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* Contributions from the Sugadaira Biological Laboratory of Tokyo Kyoiku University, No. 24

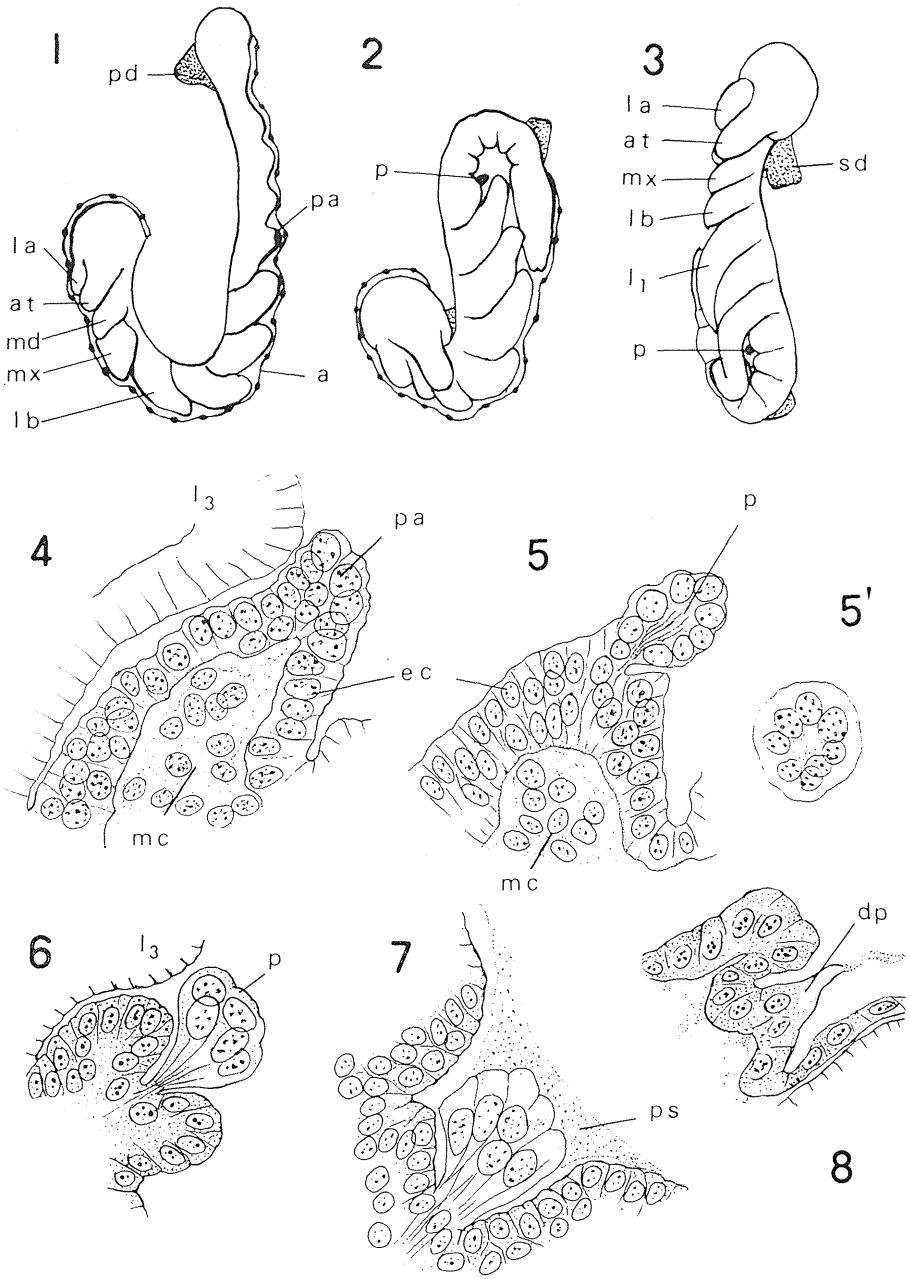

Fig. 1 Embryos and pleuropodia of *Oligotoma japonica*

1. Embryo of early pre-revolution stage, 2. Embryo of late pre-revolution stage, 3. Embryo of post-revolution stage, 4. Pleuropodial anlage of early pre-revolution stage (longitudinal section), 5. Pleuropodium of middle pre-revolution stage (long. sec., 5′. cross sec.), 6. Pleuropodium of late pre-revolution stage (long. sec.), 7. Pleuropodium of post-revolution stage (long. sec.), 8. Degenerated pleuropodium of late embryonic stage (long. sec.).

a : amnion, at : antennal rudiment, dp : degenerated pleuropodium, ec : ectodermal

(1) Embioptera : *Oligotoma japonica* OKAJIMA

1. Early pre-revolution stage : The paired appendages develop on the ventral side of the first to the fourth abdominal segments of the embryo. They are of the same shape and size as each other, but they are much smaller than the appendages or developing legs of the thoracic segments. The pleuropodial anlage is found only at the apical part of the first abdominal appendages. In longitudinal section it is seen that the anlage consists of several nuclei which are larger than those of the ectodermal cells forming the embryonic body wall. The size of the anlage is about 20×10 micra (Figs. 1-1,-4).

2. Middle pre-revolution stage : In this stage, a conspicuous constriction appears at the basal part of the pleuropodial anlage and consequently it is joined to the distal part of the rudimental appendage of the first abdominal segment through the neck region. The anlage differs from that of the preceding stage, that is, the nuclei in the anlage of this stage are arranged in a circle and the center of which is filled with cytoplasm. The anlage is about 20×15 micra in size (Figs. 1-2,-5).

3. Late pre-revolution stage : A notable change has occurred in the developing pleuropodium, namely, it has grown to a distinct bulbiformed organ projecting from the appendage which is now smaller in size. The pleuropodial cells themselves are especially rich in cytoplasm and their boundaries are not very distinct. They are greatly elongated and become two or three times as tall as the neighbouring ectodermal cells. The cytoplasmic basal part of the pleuropodium extends deeply into the body wall and makes a thick root-like region (about 10 micra long) in which may fine fibrilate threads run parallel to each other from the proximal to the distal part of the pleuropodium. A large nucleus containing remarkable chromatin granules is seen at the outer end of each pleuropodial cell. Its cytoplasm is slightly stained and contains few vacuoles. In the present stage, the secretion of the pleuropodium has already begun in some cases. The pleuropodium is about 25×18 micra in size (Fig. 1-6).

4. Post-revolution stage : The structure of the pleuropodium is much the same as that of the previous stage. When the secretion begins, numerous granulated coagulations of the secreted substance appear at the circumference of the pleuropodium. The four paired abdominal appendages quickly degenerate after the katatrepsis or revolution of the embryo. The pleuropodium attains about 35×20 micra in size (Figs. 1-3,-7).

5. Late embryonic stage : In this stage, the pleuropodium undergoes degeneration similar to that observed in many other insects. The abdominal appendages have already disappeared and the organ appears clearly atrophied. Cytolysis is progressing

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cells, 1_1, 1_3 : rudiments of 1st and 3rd thoracic legs, la : labral rudiment, lb : labial rud., mc : mesodermal cells, md : mandibular rudiment, mx : maxillary rud., p : pleuropodium, pa : pleuropodial anlage, pd : proctodaeum, ps : pleuropodial secretion, sd : stomodaeum

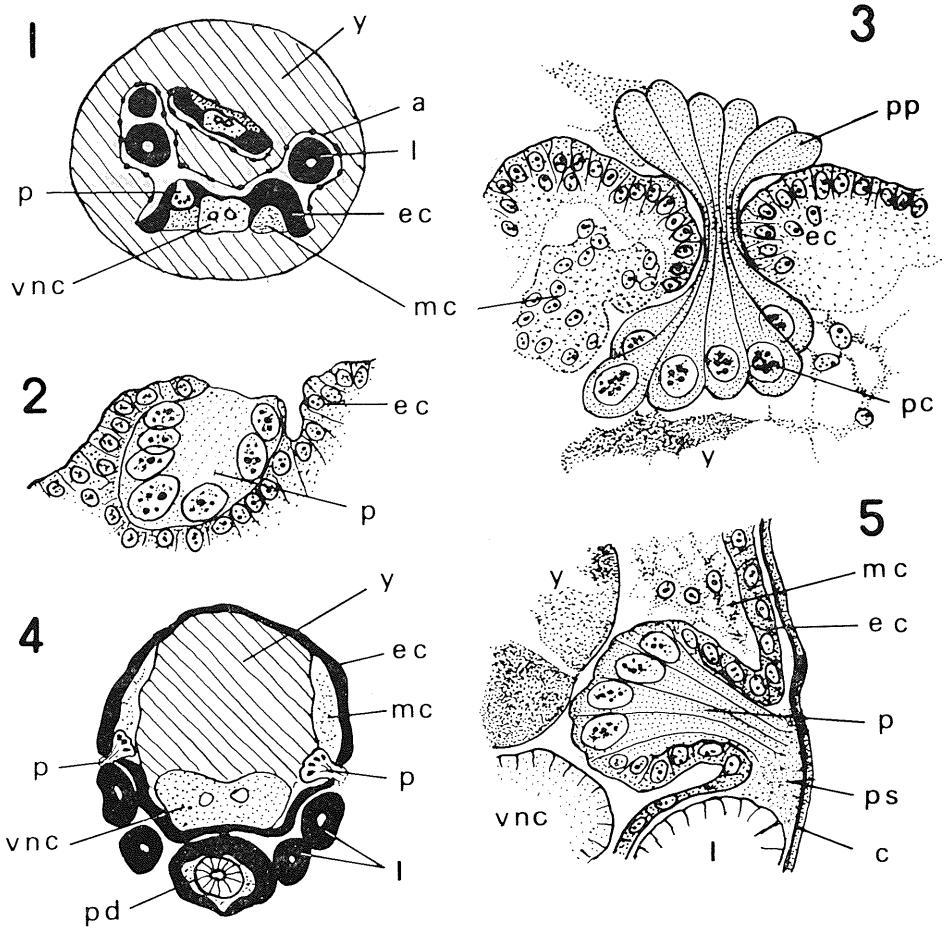

Fig. 2 Embryos and pleuropodia of *Bactridothrips brevitubus*
1. 1st abdominal segment of middle pre-revolution stage (cross section), 2. Pleuropodium of middle pre-revolution stage (longitudinal sec.), 3. Pleuropodium of late pre-revolution stage (long. sec.), 4. 1st abdominal segment of embryo of post-revolution stage (cross sec.), 5. Pleuropodium of post-revolution stage (long. sec.), a : amnion, c : chorion, ec : ectodermal cells, l : rudimental thoracic legs, mc : mesodermal cells, p : pleuropodium, pc : pleuropodial cell, pd : proctodaeum, pp : protrusion of pleuropodial cell, ps : pleuropodial secretion, vnc : ventral nerve cord, y : yolk

and rapidly advances towards dissolution, and at last no trace of the organ is to be found in the embryo just before hatching (Fig. 1–8).

(2) Thysanoptera : *Bactridothrips brevitubus* TAKAHASHI

1. Middle pre-revolution stage : In this stage the pleuropodium has grown to a distinct globular organ, perfectly embedded in the embryonic body wall as the pleuropodia of dragonflies (ANDO, 1953). One is located on each side of the ventral nerve

cord and opens into the amniotic cavity through an orifice (Figs. 2-1,-2). In longitudinal section, the pleuropodium is composed of several large nuclei containing remarkable chromatin granules, and it is filled with cytoplasm similar to that observed in *O. japonica*. As yet there is still no sign of the cytoplasmic protrusions seen in the next stage. The developing pleuropodium is about 20×15 micra in size.

2. Late pre-revolution stage : The pleuropodium attains full development in this stage. In longitudinal section, the pleuropodial cells are very clear and become greatly elongated and form the finger-like cytoplasmic protrusions projecting from the globular body of the pleuropodium. The boundaries of the cells are clearly seen in the present stage. The pleuropodium is about 40 micra long, about 30 micra wide, and the finger-like protrusion extending from the globular body of the pleuropodium is about 20~25 micra from the orifice and about 20~27 micra in width (Fig. 2-3).

3. Post-revolution stage : The embryo is undergoing dorsal closure. The secretion has occurred and the space between the ventral nerve cord and the inner margin of the pleuropodium has increased, showing that the pleuropodium has moved towards the pleural wall as the embryo increases in size. The size of the pleuropodium is about 25×30 micra (Figs. 2-4,-5).

4. Full grown embryonic stage : The pleuropodium has degenerated and disappeared

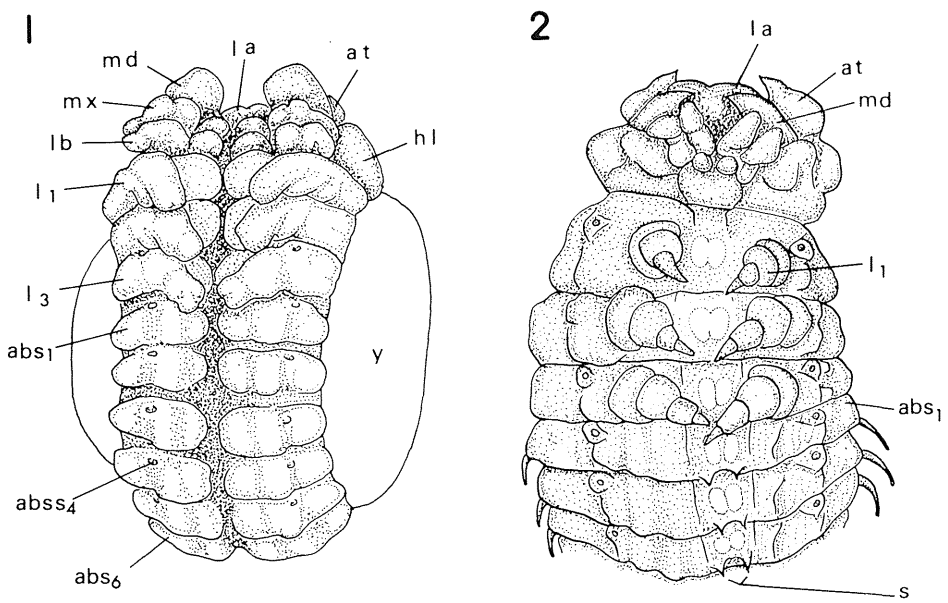

Fig. 3 Embryos of *Panorpa pryeri*
1. Embryo of 90 hrs. after oviposition, 2. Embryo of 127 hrs. after oviposition.
$abs_{1,6}$: 1st and 6th abdominal segments, $abss_4$: spiracle of 4th abdominal segment, at : antennal rudiment, hl : head lobe, $l_{1,3}$: rudiments of 1st & 3rd thoracic legs, la : labral rud., lb : labial rud., md : mandibular rud., mx : maxillary rud., s : styliform appendage, y : yolk

in the present stage.

(3) Mecoptera : *Panorpa pryeri* MACHLACHLAN and *Bittacus mastrillii* NAVAS

In the embryos of these species no pleuropodia develop in the embryonic life. However, a pair of styliform appendages are formed in the each of the first to the eighth abdominal segments along the median ventral line of grown embryos (Figs. 3-1,-2).

DISCUSSION

I. Embioptera.

MELANDER (1903) studied the structure and development of *Embia texana* (=*Oligotoma texana* (MELANDER)) and he briefly described the pleuropodia of this species as follows ; "The pleuropodia are large, the remaining abdominal appendages are uniformly smaller and disappear on the fifth segment. (p. 115, Fig. 6)." According to him, they disappear before the embryo hatches. This is the first record of the pleuropodia of Embioptera. In 1914, KERSHAW observed the embryonic development of *Embia uhrichi*, but he did not mention the pleuropodia. Recently STEFANI (1961) mentioned the pleuropodia of *Haploembia solieri* as follows ; "—— in questo precoce stadio embionale, degli abbozzi ben distinti di appendici (*pleuropodi* di Wheeler) di forma e costituzione simile a quelli toracici ma di mole ridotta. Nallo stadio rappresentato dalla fig. 9 sono gid comparse la primo quattro paia. (pp. 13~14)." The first and last statements seem to indicate the existence of the pleuropodia in the order Embioptera, but they contain no histological studies of the pleuropodia.

As a result of the present study, it is clear that the embryo of *O. japonica* has a pair of pleuropodia which are small bulbiformed organs projecting from the apical part of the first abdominal appendage. Consequently it is doubtful that the "large or distinct pleuropodia" observed by the two authors referred to the first abdominal appendage itself, and the present authors think that they may probably not be true pleuropodia, especially in the embryo of *O. texana*.

The pleuropodia of *O. japonica* seem to be evaginated pleuropodia, but they differ from the usual evaginated type, for instance those of *Opistoplatia orientalis* (ANDO, 1971).

The following are evident differences : 1. the pleuropodial anlage is formed by the constriction of the apical part of the first abdominal appendage instead of the evagination from the ectoderm of the first abdominal segment ; 2. no cavity is found in the basal part of the pleuropodia.

II. Thysanoptera

Since ULJANIN (1874) studied the embryonic development of *Thrips physapus*, but only by external observation, it is only natural that he did not notice the small pleuro-

podia of embryo thrips. Recently BOURNIER (1966) studied the embryogenesis of *Caudothrips buffai* and described the pleuropodia of this species.

As mentioned above, the embryo of *B. brevitubus* has a pair of well developed pleuropodia classified as the invaginated type. The development of pleuropodia of this species and *C. buffai* closely resembles those of heteropterous insects such as *Salda littoralis* (COBBEN, 1968) and others. They also resemble those of Odonata (ANDO, 1953), Lepidoptera and Coleoptera which have an invaginated type.

III. Mecoptera

In the middle stages of development, the embryos of *P. pryeri* and *Bi. mastrilli* have the rudimental appendages except the abdominal segments. In the latter stages of development, however, the embryos have the developed cephalo-gnathal and thoracic appendages and the paired styliform appendages in the first to the eighth abdominal segments occurred along the ventral median line. In these species belonging the families Panorpidae and Bittacidae, the pleuropodia, which are composed of glandular cells, are not formed in the embryonic life.

Therefore the authors believe that no pleuropodia are found in these families of the order Mecoptera.

IV. Examination of the term "pleuropodia"

In *O. texana*, *O. japonica* and *H. solieri*, the embryos in the pre-revolution stages of development have four paired abdominal appendages in the first to the fourth abdominal segments. MELANDER called the first appendages pleuropodia and also STEFANI called all four paired appendages pleuropodia. In 1890, WHEELER proposed the term "pleuropodia" for the appendages of the first abdominal segment of the insect embryo. He explained it as follows, "a name both suggestive of their origin from foot-like organs and their tendency, when fully developed, to take up a position on the pleural wall of the embryo. (p. 87)." In Embioptera, the pleuropodia and rudimental abdominal appendages run into each other as mentioned above. Accordingly it seems that the definition given by WHEELER is obscure in the case of Embioptera. The authors believe that one of the most important characteristics of pleuropodia is their glandular nature, so that, even though a pair of the rudimental appendages are formed in the first abdominal segment, if they have no glandular nature, it may safely be said that they are not true pleuropodia. Therefore it is desirable that the definition of pleuropodia must include the statement: "pleuropodia are glandular organs." Another problem occurs concerning the relationship between the pleuropodia and the prolegs or abdominal appendages which are thought to show the polypodism of the insect embryos. According to HINTON (1955) the prolegs are no true appendages in larval insects, but this problem will be discussed in future papers on the embryonic development of Mecoptera.

SUMMARY

1. In this paper, the pleurapodia of Embioptera, Thysanoptera are described.
2. *Oligotoma japonica* of Embioptera has pleuropodia of a new type, externally resembling the evaginated type, and *Bactridothrips brevitubus* of Thysanoptera has those of the invaginated type. *Panorpa pryeri* and *Bittacus mastrillii* of Mecoptera have no pleuropodia.
3. The secretion of the pleuropodia of *O. japonica* and *B. brevitubus* occurs during katatrepsis in most cases, and the pleuropodia begin to degenerate shortly after katatrepsis and disappear completely before hatching.
4. The pleuropodia of Thysanoptera most closely resemble those of the heteropterous insects.
5. Some problems related to the character of pleuropodia are examined, and the term pleuropodia is defined as the glandular appendages of the first abdominal segment of the insect embryos.

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