Studies on the pleuropodia of an ovoviviparous cockroach, *Opisthoplatia orientalis* BURMEISTER (Blattaria : Epilampridae)※

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安藤　裕：卵胎性サツマゴキブリ *Opisthoplatia orientalis* BURMEISTER (Blattaria : Epilampridae) の側脚の研究

Introduction

It has been known that on and after the middle stage of the embryonic development of cockroaches the pleuropodia are formed on the pleural walls of the first abdominal segment (PATTEN, 1884 ; CHOLODKOVSKY, 1889 ; WHEELER, 1890 ; HEYMONS, 1895 ; HAGAN, 1951, and ENGELMANN, 1957).

The cockroaches show oviparity, ovoviviparity or viviparity (ROTH, 1970) and the structures and probably also the functions of the pleuropodia may be altered in accordance with the above-mentioned three types.

For instance, in the oviparous cockroaches, *Blatta germanica* (PATTEN, 1884; CHOLODKOVSKY, 1889 ; WHEELER, 1890) and *Periplaneta orientalis* (WHEELER, 1890 ; HEYMONS, 1895), the pleuropodia are small in size and low in the degree of morphological differentiations. On the contrary, according to HAGAN (1951) and ENGELMANN (1957), the pleuropodia of the viviparous beetle roach, *Diploptera dytiscoides* and *Leucophaea maderae*※※ belonging family Blattidae, are highly developed in length and form, and they perform together with the adenopodia, situated in the ninth abdominal segment of the embryo, the function of a placenta. Therefore HAGAN called the pleuropodia of *Diploptera* embryo the "pseudoplacenta" which is analogous with the maternal and fetal pseudopracental organs of a dermapteran *Hemimerus talopoides* (HEYMONS, 1912).

Opisthoplatia orientalis BURMEISTER is one of the ovoviviparous cockroaches, in which the pleuropodia are expected to be more elongate and more modified than those of the oviparous cockroaches. The author has made some observations on the pleuropodia of this species to fill a few gaps in our knowledge.

This paper, does not however, aim at getting a final elucidation of the function of the pleuropodia of *Opisthoplatia*.

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※※ ENGELMANN considered *Leucophaea* as an 'ovoviviparous' cockroach.

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Materials and methods

The female adults of *Opisthoplatia* were collected in Udo of Miyazaki Prefecture and around the Unagi-Pond of Ibusuki of Kagoshima Prefecture. The cockroaches were kept at 24—28°C, and reared by a solid food for mice and 5 % solution of sugar which was soaked in the absorbent cotton. The eggs used were fixed by the aqueous or alcoholic BOUIN's fluid and CARNOY's fluid at room temperature. Of these the alcoholic BOUIN's fluid yielded most satisfactory results.

The oötheca was teared off the eggs and the chorion was also removed from the advanced embryos. The embryos were stained *in toto* with GRENACHER's borax-carmine and cut in sections at the thickness of 7μ. All drawings were made with ABBE's camera lucida.

Observations

(1) Some notes on the reproduction of *Opisthoplatia orientalis*

In laying eggs, the female begins to extrude a mass of mature eggs from vagina. The eggs are arrenged in two rows side by side with their micropylar ends towards the same direction and surrounded by the soft and thin oöthecal membrane that is pale yellowish brown and lustrous. Therefore the number of eggs contained is easily counted. At an early time the dorso-ventral axis of oötheca is held vertically to the horizontal plane of the body and is extruded from the abdominal end till four-fifths of the ootheca is exposed, then it begins very slowly to rotate during about fifteen minutes and is gradually and completely taken in the elastic brown uterus or brood sac lying under the alimentary cannal.

The time required from the bigining of extrusion of the deposited eggs to the enclosure in the uterus is about six hours. There they remain until the embryos mature, at which time the oötheca is reextruded and the hatching nymphs drop free from their chorion and oöthecal membrane.

The oötheca of *Opisthoplatia* is very long (About 3.2 cm. in the length). The cockroaches under culture conditions often lay eggs without oöthecal membrane and also often deposit the oötheca itself. In such cases, the eggs cannot develop and die through desication. The eggs are banana-shaped, white and opac, having sufficient yolk as those of oviparous cockroaches, *Blatta germanica* and *Periplaneta orientalis*. The size of eggs is 5.0—5.9×2.7 mm. at the deposition. The chorion is frail and thin (about 4μ in the thickness). The nymphs hatch out on 53—56 days after deposition under 24—28°C.

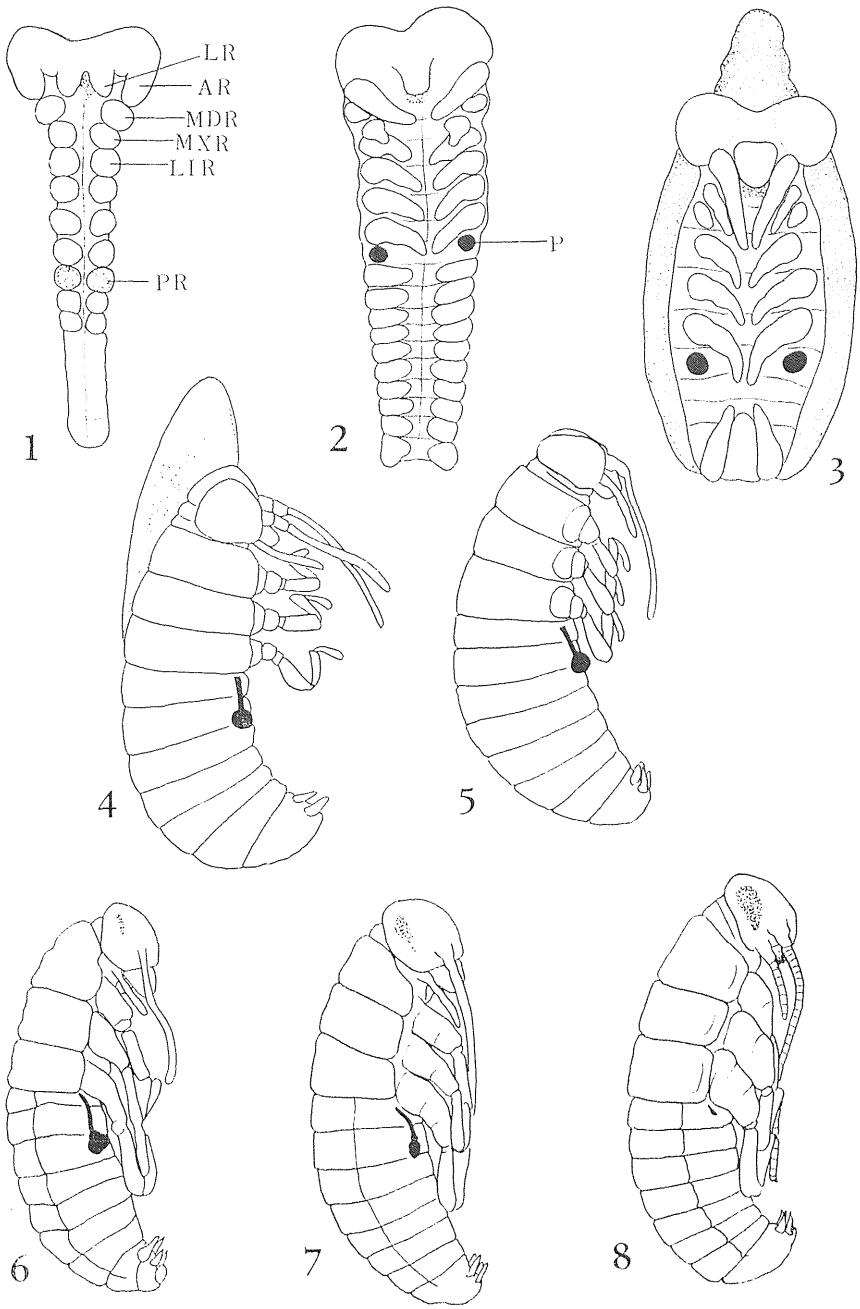

Fig. 1 Embryonic development of *Opisthoplatia orientalis* (diagrammatic)
1. Seven days after deposition, 2. Eleven days, 3. Sixteen days, 4. Twenty-one days, 5. Twenty-six days, 6. Thirty-seven days, 7. Fouty-two days, 8. Fifty-two days. ar : antennal rudiment; lr : labral r.; lir : labial r.; mdr : mandibular r.; mxr : maxillary r.; p : pleuropodium; pr : pleuropodial r.

(2) Development of pleuropodia of *Opisthoplatia orientalis*

For the convenience of description, the development of the embryos is divided into following several stages, *viz.*, the germ-band, the early embryo, the embryo with the bended abdomen, the embryos undergoing and completing the dorsal closure, the early full-grown embryo, and the later full-grown embryo.

a. Stage of the germ-band (Fig. 1-1)

The segmentation of the germ-band begins to appear a week after the deposition. The gnathal, thoracic, and anterior three segments are formed but the posterior part of the rudimental abdomen remains without metameres. In the protocephalic lobes the paired small rudiments of labrum and antenna are seen. The paired little elevations of rudimental appendages of the gnathal and thoracic segments also begin to differentiate.

The first abdominal segment has a pair of little elevations, namely, the anlagen of pleuropodia having the same form and size as those of the thoracic segments. In the pleuropodial rudiment the cells are of the same size, shape, and appearance as those of the ectodermal cells of the body wall. Accordingly, it shows no histological differentiation in this stage.

b. Stage of the early embryo (Fig. 1-2)

The embryo about eleven days old is located on the ventro-posterior half of the egg and is covered on its ventral surface by the amnion and serosa.

All the rudimental appendages of cephalic, gnathal, and thoracic segments are mere finger-shaped ectodermal outgrowths into each of which extends a similar evagination of the underlying mesodermal somite. At this time all of the abdominal segments are already visible. The first abdominal segment was of the same form and size as other segments of the abdomen until this stage. Now the rudimental pleuropodia which are paired ectodermal nipple-shaped evaginations of the body wall, resembling in shape the appendages of the gnathal segments in the early development, are located on the outer margins of the segment.

The histological differentiation of the rudimental pleuropodia is brought out in a manner by the modification of the individual ectodermal cells of which their outer layer consists.

c. Stage of the embryo with bended abdomen (Figs. 1-3, 2)

The embryo about sixteen days after the deposition is situated on the ventral side of the egg and covered by the embryonic membranes as in the previous stages.

At this time, the caudal end of the embryo is flexed ventrally. The developing pleuropodium (Fig. 2) is composed of two parts, *viz.*, a short and thick tubular stalk or peduncle (ca. 70—75μ in lenght and ca. 80μ in diameter), and a large solid hemispherical bulb (ca. 100μ in length and ca. 135—150μ in diameter). A broad lumen, which is freely communicated with the body cavity of the embryo, is found in the stalk. Inside its base there is a mass of the mesodermal cells continuous to the underlying somite. The wall of the stalk is formed of the ectodermal cells with small nuclei.

The cells differ in shape and size from those of the body wall in general. The bulb consists of the tapering cells quickly elongated by the rapid development of the pleuropodium. The nuclei of cells are arranged in two or three rows in the peripheral zone of the bulb. In contrast with the peripheral zone, the proximal one is free of the nuclei and contains radially arranged cytoplasm. No vacuoles and no granular plasmic secretions are found in the cytoplasm and the amniotic cavity, respectively.

d. Stage of the embryos undergoing and completing the dorsal closure (Figs. 1-4, 5)

In the embryo about twenty-one days old the embryonic membranes are ruptured and the dorsal closure is progressing. About twenty-six days after deposition the embryo completes the dorsal closuere, so that, it attains the final shape.

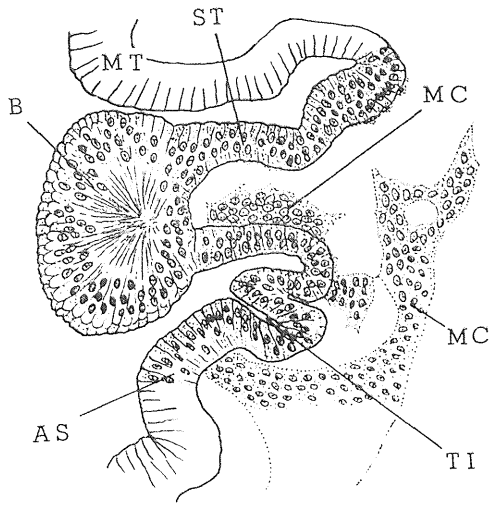

Fig. 2 Sagittal section of the pleuropodium (fifteen days old)
as, first abdominal segment ; b, bulb, mc, mesodermal cells ; mt, metathorax ; st, stalk ; ti, tracheal invagination

The yolk anterior to the head is now covered by a thick serosa. In this stage, all of the appendages of the embryo are better developed.

The pleuropodium, at this time, reaches the highest point of development. Consequently, the following considerable changes occur in the form and size of pleuropodium (Fig. 3). i) Its stalk becomes very long (ca. 400—450μ) and thick (150μ), that is, quintuple or sextuple as long as those in the previous stage. ii) A superficial constriction divides the bulbiform organ into two segments (Fig. 4-1). And the new solid calyciform part (ca. 350μ×ca. 150μ), constricted from the bulb itself, is added between the bulb and stalk. The outer zone of cytoplasm of the cells composing the new part has many colorless vacuoles, and small oval nuclei (ca. 8μ in long diameter) are seen in its peripheral zone. iii) The bulb becomes also very large (ca. 600μ in diameter and ca. 400μ in length), namely, quadruple of that in the previous stage. Its nuclei are large and two- or three-time sthose of the calyciform part (Figs. 4-2, 3).

The vacuoles are found also in the outer zone of the bulb cells. The central region of the bulb is composed of thread-like cytoplasm connecting with those of the calyciform part. The boundaries of cells are distinct in this stage. The remarkable granules, or the distinct pleuropodial secretions, which are heavily stained, are observed in the cavity between embryo and chorin. These granules are visible at

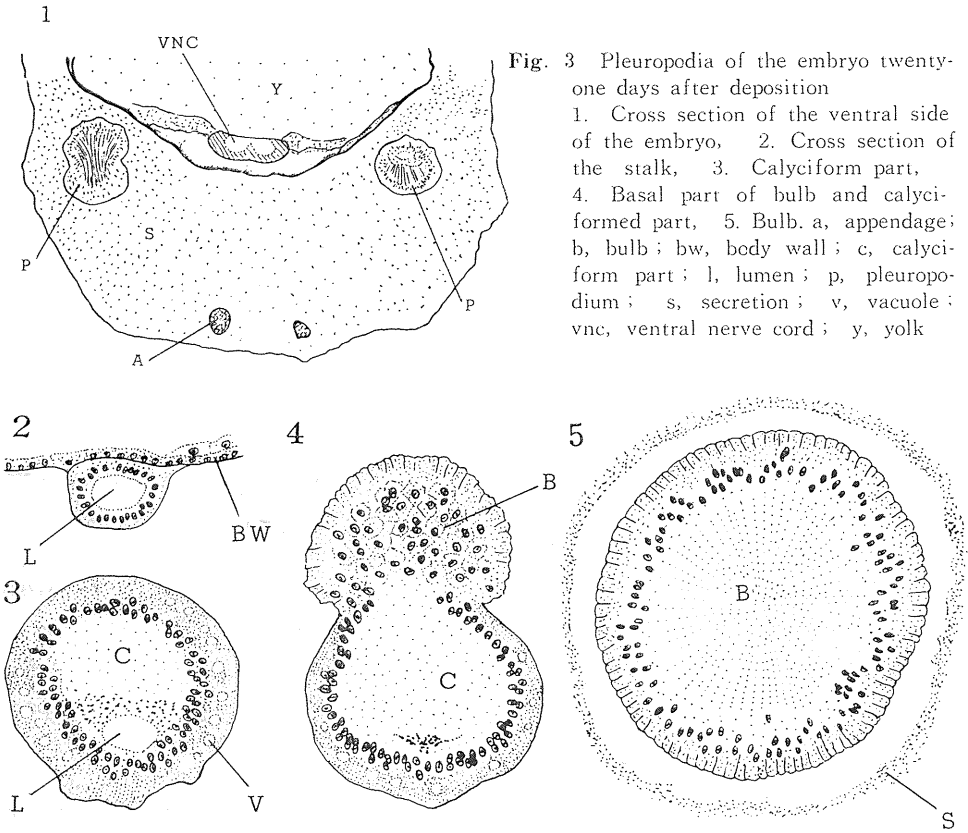

Fig. 3 Pleuropodia of the embryo twenty-one days after deposition
1. Cross section of the ventral side of the embryo, 2. Cross section of the stalk, 3. Calyciform part, 4. Basal part of bulb and calyciformed part, 5. Bulb. a, appendage; b, bulb; bw, body wall; c, calyciform part; l, lumen; p, pleuropodium; s, secretion; v, vacuole; vnc, ventral nerve cord; y, yolk

the surface of the stalk and on the body wall of the circumferential regions (Fig. 5).

In this stage the secretion of the pleuropodia is thought to be at the zenith, because of the following two points; numerous vacuoles are found in the cytoplasm of the cells consisting the bulb and remarkable granules appear in the neighboring cavity. These notable vacuoles are also observed in the secreting pleuropodia of *Blatta germanica*, *Periplaneta orientalis* (Wheeler, 1890), *Diploptera ditiscoides* (Hagan, 1951), *Belostoma flumineum*, *Ranatra fusca* (Hussey, 1926), some dragonflies (Ando, 1953), and others.

e. Stage of the early full-grown embryo (Fig. 1-6)

The embryo about thirty-seven days old is almost full-grown and the pleuropodium is the only part which is not covered by the chitinous cuticle secreted before the embryo hatches. The bulb of the pleuropodium is somewhat flattened (Fig. 6.) which may be an artefact. The bulb is composed of many tapering cells having large nuclei which lie in the peripheral ends of the cells. The broad ends of the tapering cells are directed toward the outer surface of the organ. Their narrow parallel arranged thread-like cytoplasmic ends meet in the central or basal part of the bulb organ. The most of their exceedingly delicate threads run parallel

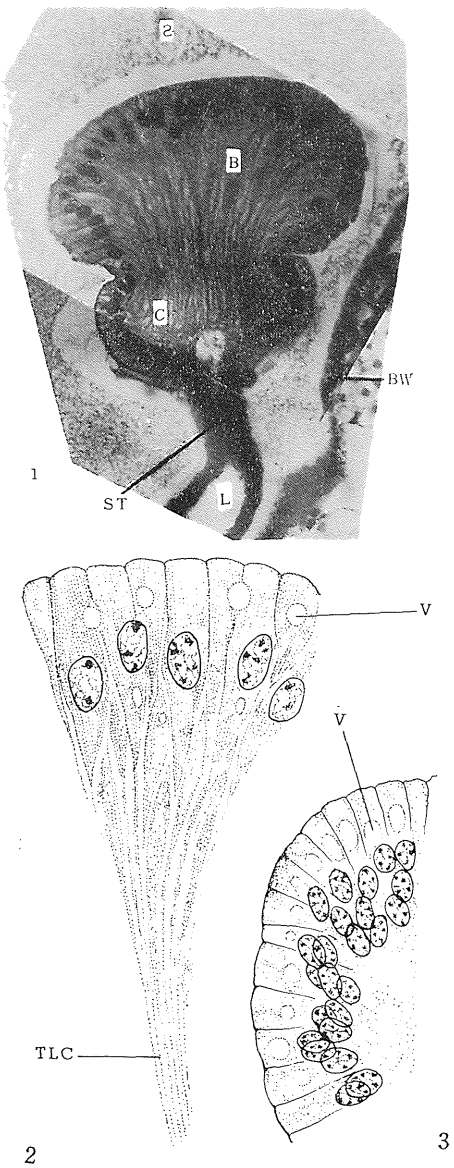

Fig. 4 Pleuropedium of the embryo twenty-one days after deposition
1. Photograph of the sagittal section of pleuropedium, 2. Cells of the bulb, 3. Cell of the calyciform part. b, bulb; bw, body wall; c, calyciform part; l, lumen; s, secretion; st, stalk; tlc, thread-like cytoplasm; v, vacuole

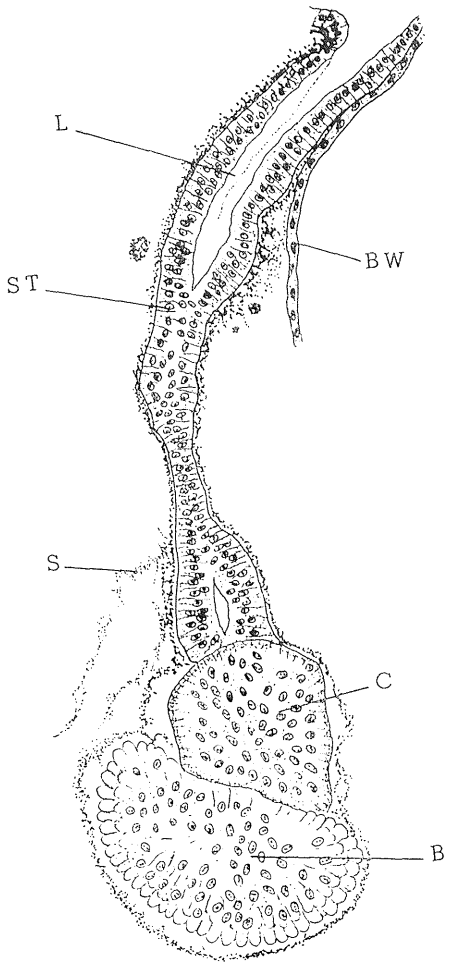

Fig. 5 Parasagittal section of the pleuropedium (twenty-six days) b, bulb; c, calyciformed part; bw, body wall; l, lumen; s, serection; st, stalk

with the long diameter of the cells and present the appearance of fine striation. The protoplasmic reticulum of the cytoplasm is indistinctly seen in these tapering cells.

Vacuoles observed in the previous stages almost disappear. The fine granules are also recognized in the lumen of the calyciform part and stalk.

The pleuropodia take almost the same feature as those of the previous stage, but they show sings of degeneration.

f. Stage of the later full-grown embryo (Figs. 1–7, 8)

About ten days before hatching the embryos (about fouty-two days old) the pleuropodia of *Opisthoplatia* undergo degeneration similar to that seen in *Blatta*, *Periplaneta*, and *Diploptera*.

The organ (Fig. 7) becomes very irrengular in outline and the old regular boundaries between the tapering cells disappear. Its apical or bulb part, still somewhat bulbous in shape, shows obvious atrophy, that is, there are seen several dissolving cells and many large spaces between them. The cytolysis is progressing and not a few cytoplasmic fragments, in the masses of irregular granules, leave the apical part of degenerating pleuropodium.

The calyciform part, however, shows some degree of atrophy in Fig. 7.

The pleuropodium, henceforth, rapidly advances towards dissolution, and at last no trace of the organ is to be found in an embryo just before hatching.

Discussion

As Hussey (1926) pointed out, the pleuropodia of insect embryos have been for years a subject of interest to embryologists. Many observations have been made as to their structure, and many speculations have appeared as to their function. Thereafter, Slifer (1937, 1938) elucidated the pleuropodial function of a grasshopper, *Melanoplus differentialis* by her clearcut experiment. According to her studies the pleuropodia of this insect secrete the hatching enzyme.

The papers which treat most extensively the pleuropodia of insects, in general, are Wheeler (1890) and Hussey (1926).

Studies of the pleuropodia of Order Blattaria are enumerated in the introduction, namely, there are six papers by Patten (1884), Cholodkovsky (1889), Wheeler (1890), Heymons (1895), Hagan (1951), and Engelmann (1957).

Patten (1884, pp. 596–597) briefly stated the development and structure of pleuropodia of *Blatta germanica*, and refered to their function as follows; ". . . . . yet its function is extremely problematical."

Cholodkovsky (1889) studied the embryonic development of *Blatta* (*Phyllodromia*) *germanica* by external observation and he observed the morphogenesis of the first abdominal appendages to some extent. According to him, the pleuropodia are composed of a "birnförmige Gestalt" and "dünner Stielchens" (pp. 93-94, Tafel VIII).

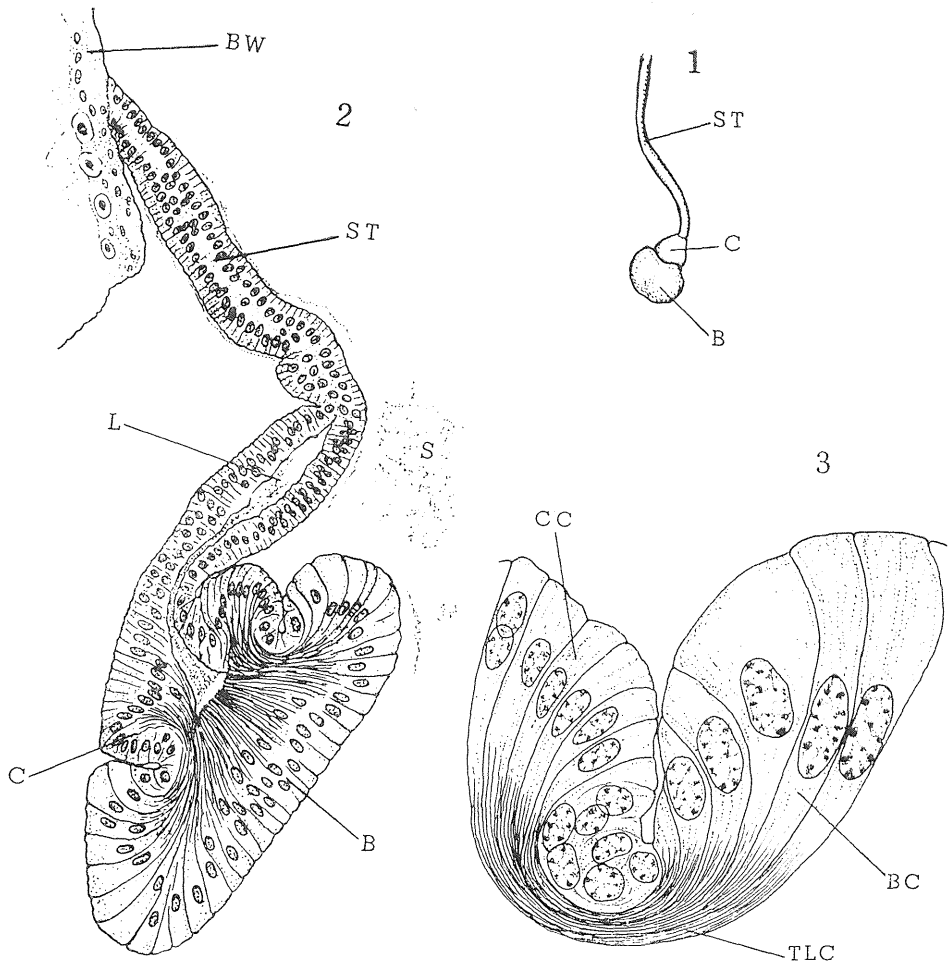

Fig. 6 Pleuropodium of the embryo thirty-seven days after deposition

1. Left pleuropodium, 2. Sagittal section, 3. Part of the calyciformed part and buld. b, bulb; bc, cell of bulb; bw, body wall; c, calyciform part; cc, cells of calyciform part; l, lumen; s, secretion; st, stalk; tlc, thread-like cytoplasm

WHEELER (1890, pp.88—93) described extensively the development of pleuropodia in *Blatta germanica* and *Periplaneta orientalis* with ten figures. These two examples belong to oviparous cockroaches.

HEYMONS (1895)* studied the embryonic development of *Periplaneta orientalis* and explained that the pleuropodia of this cockroach are almost similar with those of

* He made no mention of those of *Phyllodromia* and *Ectobia* (p. 24).

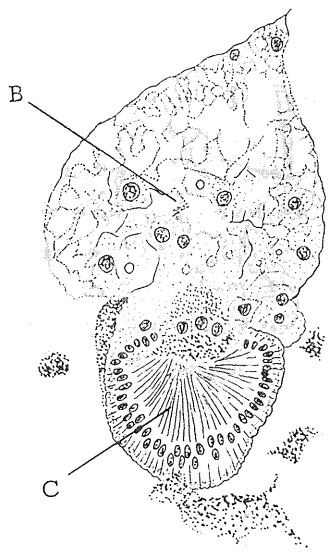

Fig. 7 Longitudinal section of the degenerating pleuropodium (fouty-two days) b. bulb; c. calyciform part

Phyllodromia (*Blatta*) described by PATTEN (1884), WHEELER (1890), and CHOLODKOVSKY (1889) (p. 23, Figs. VIII—IX).

HAGAN (1951, pp. 332—340 and 7 figures) described the development of pleuropodia of *Diploptera ditiscoides* in detail. This cockroach shows viviparity. In this species the pleuropodia are highly developed and differentiate into pleuropodial base, bulb, and extremely elongated extension.

Regarding the function of this curious pleuropodia and adenopodia, he stated as follows; ..... "They (adenopodium and pleuropodium) are tentatively offered in the present belief that nutritional or respiratory functions, or both, are the most plausible of the hypothesis offered to account for their development. The problem should be most alluring and profitable to anyone able to treat living speciemens with radioactive tracers." It is thought that the high specialization of the pleuropodia of *Diploptera* is caused by the viviparity.

ENGELMANN (1957) observed on the female genital apparatus of an ovoviviparous cockroach, *Leucophaea maderae*, and touched upon the structure and function of the pleuropodia (pp. 735—737, Figs. 21—24). According to his studies, the pleuropodia of *Leucophaea* are composed of three parts, namely, "kurzer Basalteil," "Bulbus" and "Langer fadenförmiger Distalteil" just like those of *Diploptera* described by HAGEN (1951). The pleuropodia of these two species show a close resemblance. He found that the thick end of "fadenförmiger Distalteil" comes in close contact with the serosal cuticle. By reson of this fact he believes that the hatching enzyme, for the solution of the chorion and serosal cuticle, is secreted by the pleuropodia as those of *Melanoplus* (SLIFER, 1937). His supposition on the function of pleuropodia differs from that by HAGAN.

In the present study the material is an ovoviviparous cockroach, but the development of pleuropodia shows some affinity with those of oviparous cockroaches, *Blatta* and *Periplaneta*.

The pleuropodia of *Blatta*, *Periplaneta* and *Opisthoplatia* consist of the stalk and bulb (or calyciform part and bulb). This is a fundamental structure of their pleuropodia. Moreover, the cytological characters of the pleuropodial bulb of *Opisthoplatia* too are somewhat similar to those of *Blatta* and *Periplaneta* (WHEELER, 1890). And the

secretion and the fate of pleuropodia are also the same as those of them.

From these points of view, the type of the pleuropodia of *Opisthoplata* falls under the category of the pleuropodia of the oviparous cockroaches, *Blatta* and *Periplaneta*.

On the other hand, the pleuropodia of *Opisthoplatia* are also thought to correspond with the pleuropodial base and bulb of those of *Diploptera* and *Leucophaea*. In this case the lack of the extremely elongated extension is a point distinguishing ovoviviparous from viviparous types. The extremely elongated extension is a feature quite characteristic of the viviparity.

These facts show that the pleuropodia of *Opisthoplatia* are only slightly modified in relation to the ovoviviparity. Consequently, the ovoviviparity of *Opisthoplatia* may have not been long since it was acquired.

Summary

1. In the present paper, the pleuropodia of an ovoviviparous cockroach, *Opisthoplatia orientalis*, are described.

2. The pleuropodia are composed of three parts, namely, stalk, calyciform part, and bulb.

3. The secretion of the pleuropodia occurs in most cases during the dorsal closure. The secreted substance accumulates in the circumference of the embryo.

4. The pleuropodia attain their maximum size in the late embryonic stage, begin to degenerate shortly after the completion of the dorsal closure, and entirely disappear before the hatching.

5. The development of the pleuropodia of this species is somewhat similar to those of *Blatta germanica* and *Periplaneta orientalis*, and differs from those of *Diploptera ditiscoides* and *Leucophaea maderae*.

6. From the standpoint of evolution of the pleuropodia in the order Blattaria, the low degree of the specialization of pleuropodia suggests that it was not long since this species acquired ovoviviparity, *viz.*, little modifications from the oviparity due to adaptation towards the ovoviviparity are seen in the development of the pleuropodia.

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摘　　要

卵生および胎生のゴキブリの胚子に側脚が形成されることが知られている。サツマゴキブリ *Opisthoplatia orientalis* Burmeister は卵胎生であるが，この胚子にも顕著な側脚が形成されることを観察した。

本種の側脚は若い胚子の腹部第1節の附属肢として発生を開始し，胚子の背部閉鎖の進行中に，側脚としての形態分化を終る。側脚は細長く，内腔を持つ柄部と，柄部に続くがく状部，および先端の球状部の3部より成る。いづれも外胚葉性であるが，柄部の基部内腔には，体腔嚢壁に続く中胚葉性の細胞群が見られる。この時期に側脚は最大に達し，分泌を終ると退化を始め，背部閉鎖が完成し，胚子の孵化が近づくと，崩潰し，遂には消失してしまう。

分泌が近づくと，球状部を構成する細胞の細胞質中に，vacuole が現われ，これと併行して，側側の分泌物が，無数の顆粒になって胚子の周囲に出現する。

サツマゴキブリの側脚の機能については不明である。

卵生の *Blatta germanica* や *Periplaneta orientalis* の胚子の側脚は，卵胎生のサツマゴキブリのそれに比し，形態的にも，大きさにおいても発達の度は低い。これに対して胎生の *Diploptera ditiscoides* の側脚は長大で，側脚自体の形態的分化も極めて高度であり，胎生に適応して機能的には「偽胎盤」である。サツマゴキブリはこの両者の中間的な側脚を持つが，卵生種のそれにむしろ類似することから，この種が卵胎生に移行してからの日が残いことを示すものであろう。

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