Oogenesis and Embryogenesis of the Idolothripine Thrips, *Bactrothrips brevitubus* (Thysanoptera, Phlaeothripidae)

Kazuo HAGA

Synopsis

The oogenesis and embryogenesis of *Bactrothrips brevitubus* are described and illustrated. The egg has a discoidal oosome near the posterior pole. Two mycetomes may always be found in each of the egg. The chorion is polygonally reticulated at the anterior third; neither the micropyle nor aeropyle are observed.

The cleavage center locates at the posterior third of the egg and the energids distribute more abundantly in the posterior half than in the anterior one. At the posterior pole of the egg the ventral plate invaginates and grows into the core of the egg, and within the yolk double-flexed S-shaped germ-band is consequently formed. The inner layer is formed by the cell proliferation. Katatrepsis of the embryo occurs at about the middle of embryonic development. The embryo rotates within the sagittal plane of the egg during this process.

The ventral nerve cord in the abdomen is seen to condense at the later phase of embryogenesis, and finally it becomes one big, spindle-shaped ganglion which situates in the thorax. Two pairs of salivary glands are invaginated from the labium. An unpaired mandibular gland is present, appearance of which is similar to the dorsal labial gland. A pair of invaginated type pleuropodia is formed on the first abdominal segment of the embryo. The germ cells are enclosed with the inner layers of the seventh and eighth abdominal segments, and later migrate to the fifth segment to form gonadal rudiments.

The midgut epithelium is derived from the rudiments occurred at the both ends of the embryo. The yolk cells form thin expanded membranes enveloping yolk globules during the process of mid-gut formation. Posterior portion of the midgut originally derived from the bipolar midgut rudiments is seen to form a chamber at the later phase of its development, into which liquefied yolk is subsequently incorporated.

The rudiment of malpighian tubules occurs in the telson as four glomerate cell masses as early as the proctodaeum develops.

Six paraneopteran orders are compared from a view point of the embryonic development. From the results of this comparison it is thought that the Thysanoptera possibly situates equidistant from the

Psocoptera, Homoptera and Heteroptera but far from the Mallophaga and Anoplura.

Thysanoptera must have derived from the ancestral group of Paraneoptera at the early phase of its ramification.

Introduction

The Thysanoptera is one of the insect orders that have scarcely been studied in the field of embryology, and only a few contributions of the embryogenesis are known up to this time.

The first description on the embryogenesis of the Thysanoptera appeared as early as 1874 by Uljanin who observed *Thrips physapus* (Terebrantia : Thripidae) embryos externally through the chorion. The embryonic development of the mouth-parts of *Heliothrips haemorrhoidalis* (Terebrantia : Thripidae) was partially studied by Reyne (1972). Bournier (1960, 1966) studied the embryogenesis of *Caudothrips* (=*Bactrothrips*) *buffai* (Tubulifera : Phlaeothripidae), and the gross embryology of Thysanoptera was revealed by him. Recently, Ando and Haga (1974) observed the pleuropodia of the present material, *Bactrothrips brevitubeus*. Most recently, Heming (1979, 1980) studied the embryos of *Haplothrips verbasci* (Tubulifera : Phlaeothripidae) with special reference to the origin and fate of the germ cells and development of the mouth-parts.

The knowledge on the embryology of thrips, however, is still very insufficient as contrasted with other insect orders, and detailed study on the embryogenesis of the order has never been accomplished.

Since *B. brevitubus* and allied species often retain eggs in the oviducts, and oviposit just fertilized, or embryologically developed eggs (Haga, 1975), oviposited eggs as well as those retained in the oviduct are employed for observation.

On the other hand, ovaries in the adults of various Thysanoptera are studied anatomically (Jordan, 1888; Uzel, 1895; Sharga, 1933; Melis, 1935; Bournier, 1956; Heming, 1968; Lewis, 1973; Haga, 1975). They show that each four panoistic ovarioles are found in a ovary without exception, but the type of ligation of the terminal filaments differ in a subfamilial level as discussed by Haga (1975). However, only a contribution on the development of the ovary was given by Heming (1970), who observed *Frankliniella fusca* (Terebrantia) and *Haplothrips verbasci* (Tubulifera), and no paper concerning the oogenesis of the order has appeared.

In this paper, the oogenesis and embryogenesis of *B. brevitubus,* together with some observations on the same topics of the allied species, are studied and described.

Materials and Methods

One of the largest thrips occurred in Japan, *Bactrothrips brevitubus* Takahashi (Thysanoptera, Phlaeothripidae, Idolothripinae) was used for the present studies. It lived on dead foliage of evergreen trees, mainly a kind of the chinquapin, *Castanopsis cuspidata* which distributes throughout the warm-temperate zone of Japan. In addition, a species of the same genus, *B. honoris* (Bagnall) was used for the material of the embryological studies. *B. brevitubus* and *B. honoris* were collected in Mino-o of Osaka, Kasuga-Yama of Nara, and

Mt. Tsukuba of Ibaraki. These two species are endemic in the warm temperate zone.

These thrips were cultured in petri-dishes each with a piece of the wet blotting paper to retain moisture. They were kept in the incubator kept at 25°C throughout or under room temperature between 20° - 25°C. As their food, the dead leaves infested by certain imperfect fungi were supplied. For the anatomical study, the thrips were anaesthetized by ethylalcohol, dissected in a physiological salt solution as used for *Drosophila* under a stereomicroscope. For the observation on living eggs, they were immersed in liquid paraffin or silicone oil KF-96. The chorion became semitranslucent in the liquids, and the embryo developed nearly alike as those in the air, but they hardly hatched.

For the observations of fixed eggs, they were stained by alcoholic thionine, cleared in terpineol after dehydration in ethylalcohol and ethylenglycol-monoethylether. For serial sections, eggs were fixed in the alcoholic Bouin's fluid warmed at about 60°C for half an hour or FAA fixative for 2 to 24 hours under room temperature. They were embedded in paraffin by Miyakawa's (1978) method, cut at 5-7 μm thickness, and stained with Delafield's haematoxylin and eosin.

16 mm time-lapse motion pictures were taken for analyzing the morphogenetic movement of developing embryos. The scanning electron microscope and differential interference microscope were used for the studies on the egg surface and living ovaries, respectively.

Figures were drawn using Abbe's camera lucida or with free hand retouching on the photomicrographs.

Observations

Ovarian Structure and Oogenesis

A pair of ovaries of *B. brevitubus* may be found along the both sides of the mid-gut (Fig. 1). The ovary consists of four ovarioles and their apices completely coalesce forming a common germarium in which any septa cannot be observed (Figs. 2, 3AB).

As no trophocytes or nurse cells are found in the germarium and vitellarium, the ovary of this insect belongs to the panoistic type as observed in other thrips.

In the distal part of the common germarium several depressed nuclei are piled with a membranous, triangular terminal filament upon them (Fig. 3). The thread-like apex of the terminal filament is suspended on the dorsal labial gland (= long salivary glnad) in the same side of the body (Fig. 1).

In the germarium three kinds of cells are recognized (Fig. 3B). The large globular cells of them are the primary oocytes, and have little cytoplasm and single nucleus, 5-6 μm in diameter, with a large nucleolus and numerous peripheral chromatins. The small globular cells are the oogonia lacking such large nucleoli, but have the reticular chromatins. The remainder cells have a flat or stick-like or irregular shaped nucleus (4. 6 -5 μm) with scattered chromatins. They are the rudimentary follicular cells and cytoplasmic projections of which are narrowly extended among the other cells. It seems that these cytoplasmic projections connect with each other and form a multinucleate tissue, but the boundary of the projection may only become observable by the electron microscope.

The oogonia are situated in the distal part of the germarium, while the remaining part of it is occupied with the primary oocytes and rudimentary follicular cells. The size of the
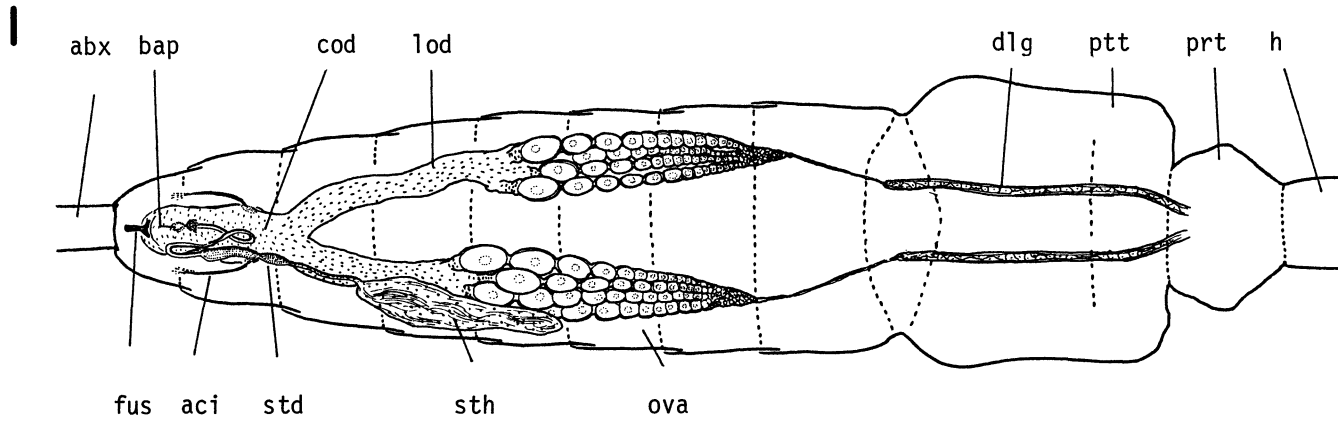
Fig. 1 Female reproductive system in *B. brevitubus,* dorsal view, diagrammatic.

abx 10th abdominal segment, aci acicula, bap Bournier apparetus, cod common oviduct, dlg dorsal labial gland, fus fustis, h head, lod lateral oviduct, ova ovary, prt prothorax, ptt pterothorax, std spermathecal duct, sth spermatheca.

(After Haga, 1975; modified)

nuclei of the primary oocytes is seen to increase gradually from distal to the proximal part of the germarium. No mitotic figures are observed in the germarium.

The germarium continues into four ovarioles. Each ovariole consists of 11-14 egg chambers each of which contains single oocyte, and rarely two oocytes may be found in the first and/or second egg chambers.

Oogenesis in *B. brevitubus* can be divided into five oogenetic stages .

Stage 1:   Previtellogenic stage (Fig. 3B).

In this stage, smaller oocytes are cuboid, their height is smaller than width; their nuclei are noticeably large, occupying about 4/5 of cell body. The follicular cells develop little and form a thin single sheet of cells. The clumps of two or three rudimentary follicular cells are found among the oocytes.

In the oocyte nucleus a basophilic nucleolus consisting of several droplet-like granules is observed, and the chromatins are seen at the subcortical layer of the nucleus. The cytoplasm lacks the vacuoles, bacilliform substances and endobodies described by Ando (1962) in *Epiophlebia superstes* of the Odonata. However, the clouded parts slightly stained by haematoxylin in the cytoplasm are present around the nucleus in the first stage oocyte.

Stage 2:   Early vitellogenic stage (Fig. 3C).

The oocytes become globular or ellipsoid, and are surrounded by the follicular epithelium made of coarsely arranged flat cells. The oocyte cytoplasm is poor in volume. Relative size of the nucleolus to the nucleus becomes smaller at this stage than that at the preceded one, but the size of the dropletlike granules mentioned before is larger.

The clouded parts in the cytoplasm mentioned earlier are also present, and in addition, unstained, vesicle-like parts are found in the subcortical layer of the oocyte.

The interfollicular tissues between the egg chambers begin to occur in this stage. The developed interfollicular tissue consists of more than ten spindle-like flat cells overlapping with each other, and the difference between 'follicular cells' and 'interfollicular cells' is only in shape and location.

Stage 3:   Middle vitellogenic stage (Fig. 3D).

The shape of the oocyte changes into long ellipsoid, and the oocytes have a few vacuoles around the germinal vesicle in which the nucleus is almost diffused, but reticulated chromatins are clearly appeared. The oocyte is covered by the follicular epithelium which is flattened in the middle portion, and thick at the both ends.

Two mycetomes become observable in this stage. They are found in the anterior and posterior parts in the oocyte. They are similar in size, about 10 μm in diameter, and have a hemispheroid structure. The concentric region of the non-vacuolated cytoplasm, about 15 μm in diameter, is found around each mycetomes.

Stage 4:   Late vitellogenic stage (Fig. 3E).

The height of the oocyte is about twice as long as wide; the germinal vesicle is a little
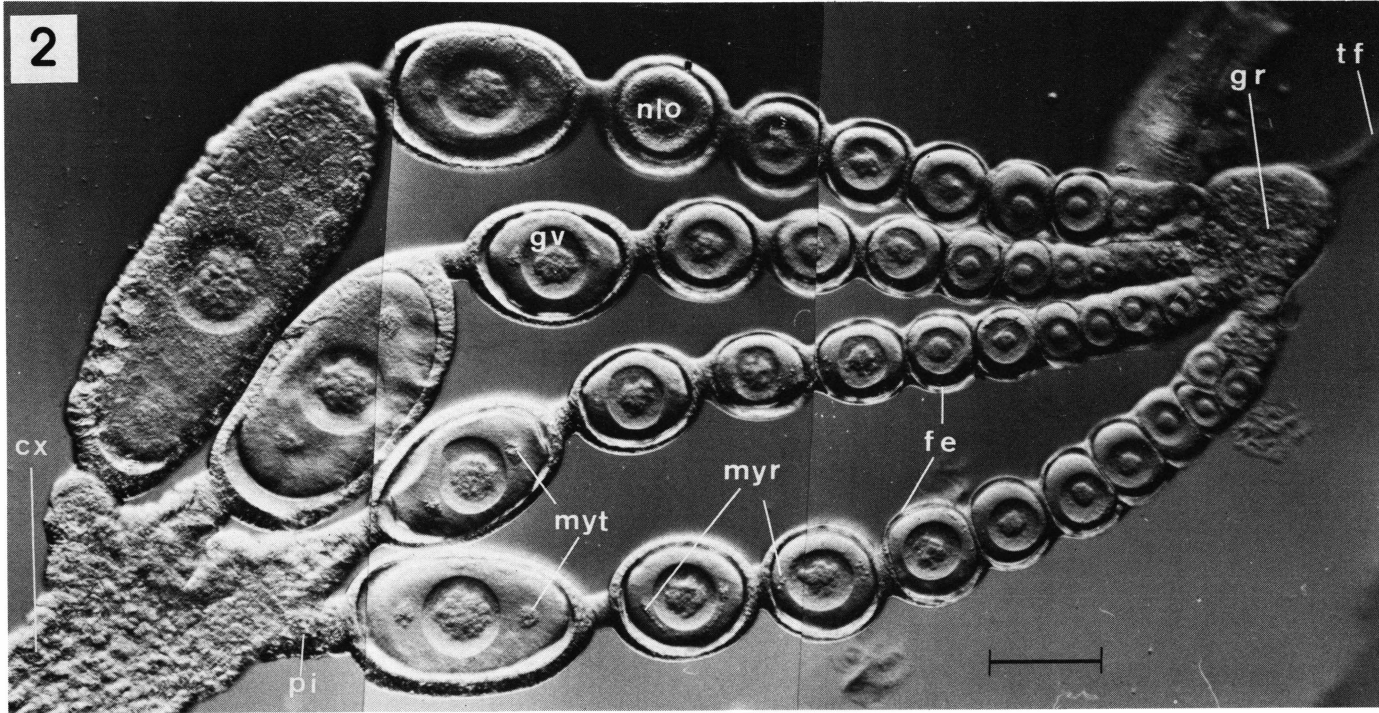
Fig. 2. Ovary of *B. brevitubus*. (Differential interference micrograph of a living ovary.)
Scale : 50 μm

cx calyx, fe follicular epithelium, gr germarium, gv germinal vesicle, myr mycetomic granule, myt mycetome, nlo nucleolus, pi pedicel, tf terminal filament.

enlarged, but its ratio to the oocyte is smaller than that in the former stage.

In this stage important and rapid changes take place concerning the germinal vesicle, oocyte cytoplasm, follicurar epithelium and mycetomes. The germinal vesicle is gradually transformed into an amoeboid shape while its reticular chromatins become paler and begin to diffuse. Fine yolk droplets, approximately 1 μm diameter, appear in the subcortical layer of the oocyte cytoplasm. They increase in number and the size, and subsequently they are observed among the cytoplasmic reticulum. These yolk droplets have an affinity to eosin and different kinds of yolk are not observable.

The mycetomes in the late stage 4 are doughnut-shaped, that is, the central globule of about 13 μm in diameter and the outer circle of about 17 μm; the former seems an accumulated body of many minute granules and the latter is a circular layer of cytoplasm without any vacuoles and yolk droplets.

Stage 5:   Chorion formation stage (Fig. 4A).

In this stage, the yolk is fully deposited, and consequently the ellipsoid oocyte is greatly enlarged.

As yolk deposition proceeds, the follicular epithelium becomes more thin and is more expanded. The oocyte of this stage has numerous yolk globules, and the scarce protoplasmic reticulum and periplasm.

The amoeboid germinal vesicle migrates from the center of the oocyte to the periphery in this stage. The volume of the oocyte decreases during its migration, and finally only a few nucleolar particles surrounded with nuclear substances are recognized at about the posterior third of the ventral side of the oocyte where the maturation division takes place.

The mycetomes transform their shape from hemispheroid to spheroid; they are no longer the aggregation of many granules at the earliest phase of its appearance but the solid ball which seems to be made of fibrous substances. Their surrounding cytoplasm is fused to the protoplasmic reticulum. The posterior mycetome migrates to the posterior pole of the oocyte and lies above the oosome, while the anterior mycetome is stationing near the anterior fourth of the oocyte. It is often observed that fragmental minute yolk droplets are present around these two mycetomes.

The terminal oocyte at the stage 5 is three times larger than those at the previous stage, and chorion is formed.

Three to several minute discs, about 4 by 2 μm and strongly stained by haematoxylin, appear near the posterior pole of the oocyte. Then they fuse with each other and form an ooplasm which is measured about 20 μm in diameter.

The follicular epithelium of the terminal oocyte is shrunken, condensed, and forms a corpus luteum in the pedicel after ovulation.

When the eggs are retained in the lateral oviducts and begin to develop, the terminal oocytes cease to develop further; the yolk deposition and chorion formation become abortive, and then are absorbed by the follicular cells which become again tall and columnar (Fig. 6A). At last the oocytes are almost resorbed and only mycetomes are remained, which may disappear later. These enlarged follicular cells contained transparent droplets form a large corpus luteum-like structure situating between the ovariole and the calyx which is fully expanded by the ovoviviparous eggs retaining in the lateral oviducts.
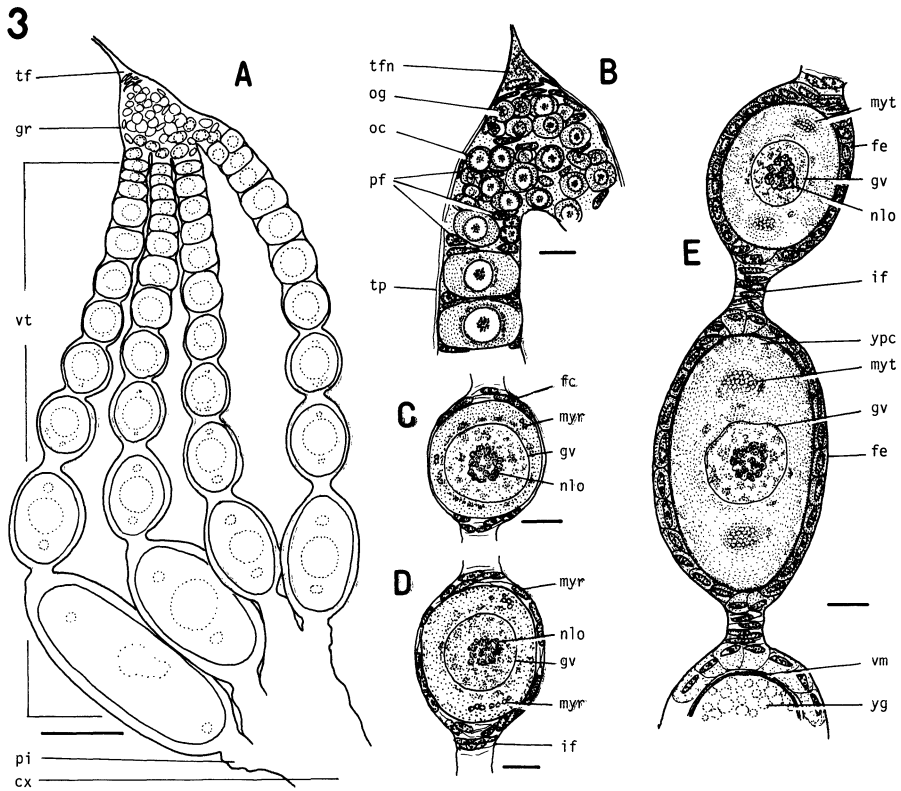
Fig. 3. Oogenesis of *B brevitubus*. A. Structure of ovary. Scale : 50 μm   B. Germarium and oogenetic Stage 1.   C. Oogenetic Stage 2.   D. Oogenetic Stage 3.   E. Oogenetic Stage 4. Scales for B-E : 10 μm

cx calyx,   fc follicular cell,   fe follicular epithelium,   gr germarium,   gv germinal vesicle,   if interfollicular tissue,   myr mycetomic granule,   myt mycetome, nlo nucleolus,   og oogonium,   oc primary oocyte,   pf prefollicular cell,   pi pedicel,   tf terminal filament,   tfn nucleus of terminal filament,   vm vitelline membrane,   vt vitellarium,   yg yolk globule,   ypc yolk particle.

This structure might have a function to retard the oogenesis until these ovoviviparous eggs are all oviposited or hatched out from their mother (Fig. 6B).

Eggs

The eggs of *B. brevitubus* are laid perpendicularly on the substratum by adhering substance secreted from the oviducts. Several to 125 eggs deposited are arranged tightly and adhered each other, and form a batch.

The egg is ovoid in shape. Its ventral side somewhat swells as shown in Figs. 4,5,and its size ranges between 0.58-0.61 mm by 0.26-0.28 mm. The eggs become 0.64-0.66 mm by 0.29-0.31 mm in size during their development.

The chorion is thin, pale yellowish orange and elastic just after oviposition, but it changes into brownish white and lacks elasticity about two hours later. Anterior third of the egg surface is reticulated pentagonally and hexagonally with ridges among these polygons which are made of minute digital processes and porous grooves (Figs. 5CD). These surface structures are well developed in the anterior fifth of the egg. The posterior two thirds lack the reticulation and are smooth (Fig. 5AE). When hatching a part of the polygonal grooves is cracked at about anterior fifth of the egg.

The author failed to observe any micropylar structures in the eggs of *B. brevitubus,* and *B. honoris* as like as *B. buffai* (Bournier, 1966), while there is a distinct micropyle on the posterior third ventral side of *H. verbasci* eggs (Heming, 1979). In *Bactrothrips,* the spermatozoa may probalby pass into the egg through porous ridges near the anterior pole where many pores penetrate the endochorion (Figs. 5CD).

The chorion consists of the exochorion and endochorion. The former is brownish white and 1-2 μm thick, and has a rough surface in the anterior third but it is more thin and smooth one in the posterior two-thirds. The latter is evenly about 2 μm thick and paler,with the smooth under surface without any pores.

Immediately below the endochorion there is a vitelline membrane (Fig. 4B) which is slightly stained blue by haematoxylin and has even thickness less than 1 μm. There are seen the thin periplasm of 1-5 μm in thickness, and the internal reticulum.

The female nucleus is found within the cytoplasmic island, about 30 by 14 μm, which is at the posterior third ventral side of the egg (Fig. 4B).

The egg has a discoid oosome about 23 by 2-3 μm, near the posterior pole (Fig. 7). It is clearly stained by haematoxylin and contains a few granules which are globular or ellipsoid, 1-2 μm, arranged in a row. They are homologous to those in *Drosophila* and holometabolous insects (Mahowald, 1972; etc.). Heming (1979) described the oosome of the eggs in *H. verbasci* for the first time.

As already mentioned, each of *Bactrothrips* eggs have always each two mycetomes (Figs. 7, 8). They are similar with each other in size and shape, globular, about 12-15 μm in diameter, and porous like as made of fibrous substance, with indistinct double layers. They are not well stained by eosin but slightly stained by haematoxylin. Bournier (1966) found the similar mycetomes in *B. buffai* eggs which are about 20 μm in diameter, and primarily only single mycetome is situated at the posterior pole, but later it divides into 2 or 3, and then they are enclosed into the newly formed mid-gut. His observation almost coincides with the present obsevation, however, the mycetomes of the *Bactrothrips* egg are found
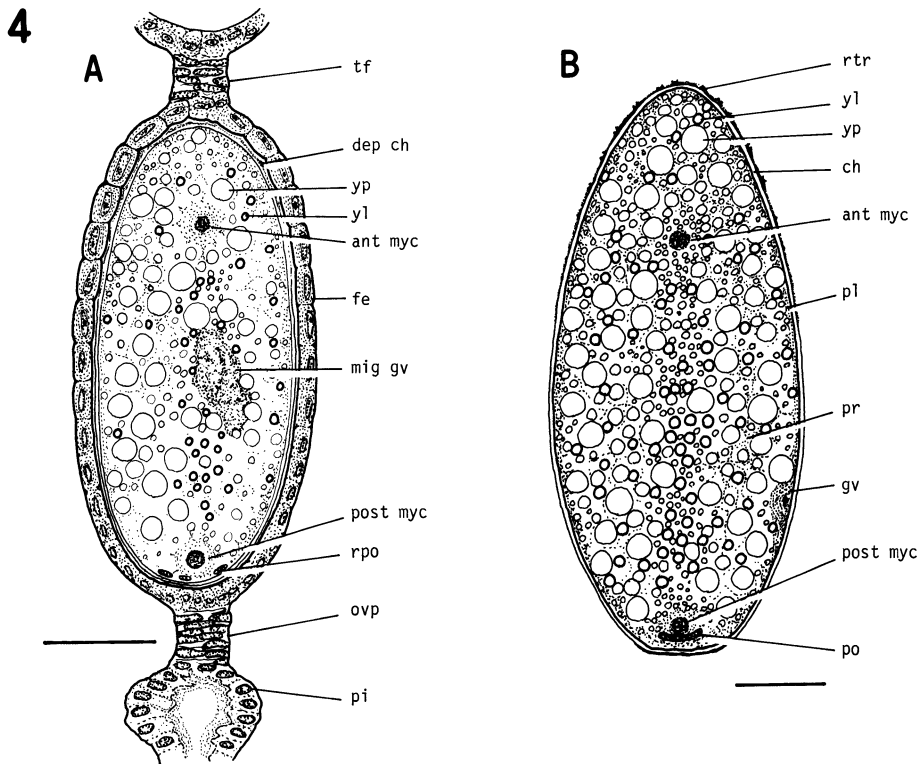
Fig. 4. Grown oocyte and newly ovulated egg in *B. brevitubus.*
    A.   Oocyte of the oogenetic stage 5.
    B.   Newly ovulated egg.   Scales : 50 μm

    ant myc anterior mycetome,   ch chorion,   dep ch depositing chorion,   fe follicular
    epithelium,   gv germinal vesicle,   if interfollicular tissue,   mig gv migrating germinal
    vesicle,   ovp plug of ovariole,   pi pedicel,   pl periplasm,   po oosome (pole plasm),
    post myc posterior mycetome,   pr protoplasm,   rpo rudimental granule of oosome,   rtr
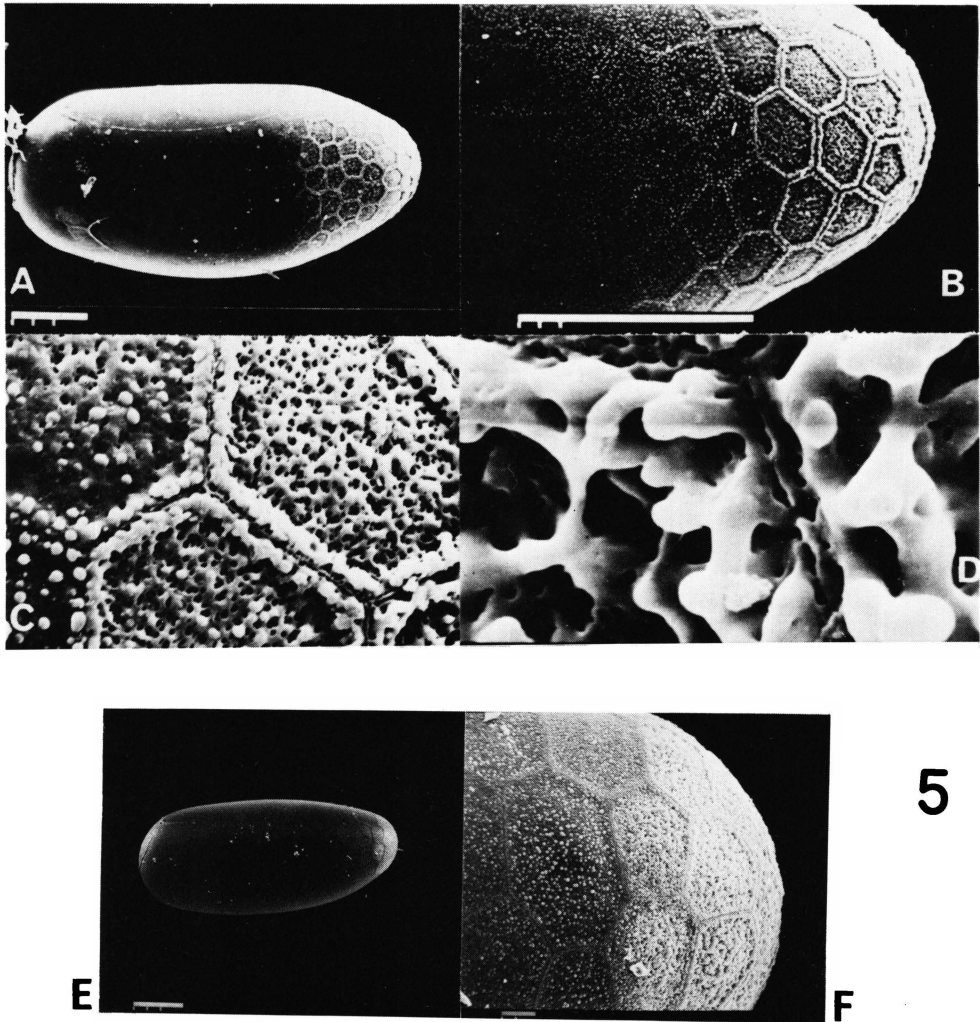   chorion reticulation,   yl lipid yolk,   yp proteid yolk.

Fig. 5. Scanning electron micrographs of egg surface.
        A — D. *B. brevitubus.*   A. Lateral view of egg, ventral side down. Scale : 50
        μm   B. Anterior half of egg, showing partial reticulation. Scale : 50 μm   C, D.
        Porous structure of reticulation. Scales : 5 μm
        E — F. *B. honoris.*   E. Lateral view of egg, ventral side down. Scale : 50 μm
        F. Anterior portion of egg, showing reticulation weaker than that of *B. brevi-*
        tubus. Scale : 5 μm

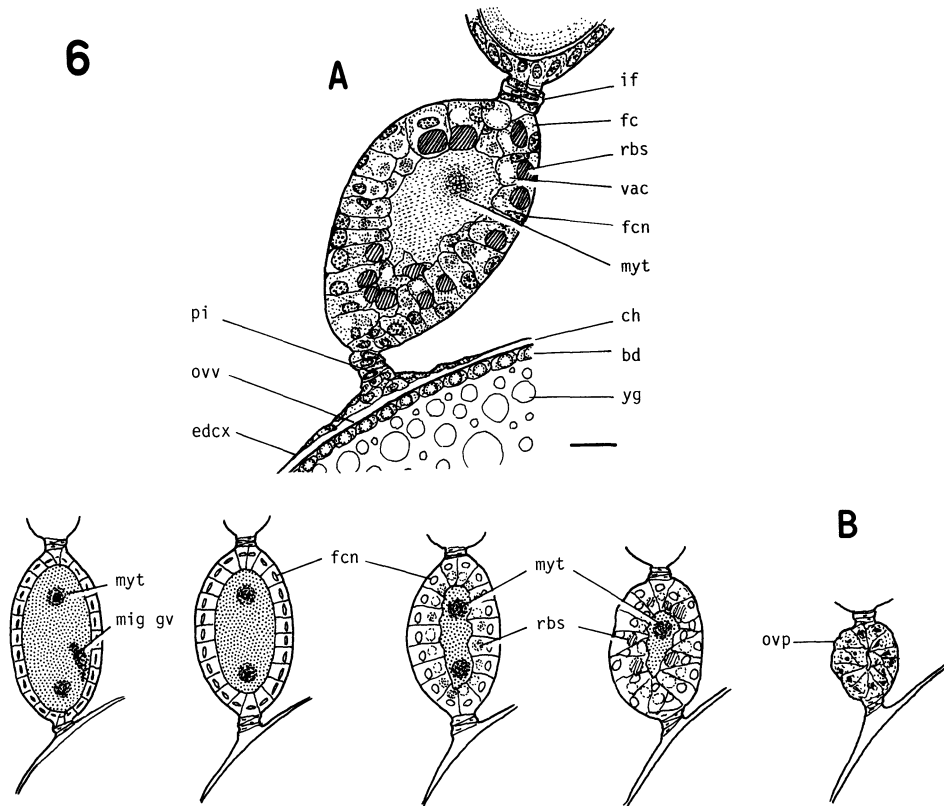Fig.   6.   Resorption of oocyte in ovoviviparity in *B. brevitubus*.
A.   Resorbing terminal oocyte.   Scale : 10 μm
B.   Process of resorption, diagrammatic.

bd blastoderm,   ch chorion,   edcx expanded calyx,   fc follicular cell,   fcn nucleus of
follicular cell,   if interfollicular tissue,   mig gv migrating germinal vesicle,   myt mycetome,
ovp plug of ovariole,   ovv ovoviviparous embryo,   pi pedicel,   rbs resorbed substance,
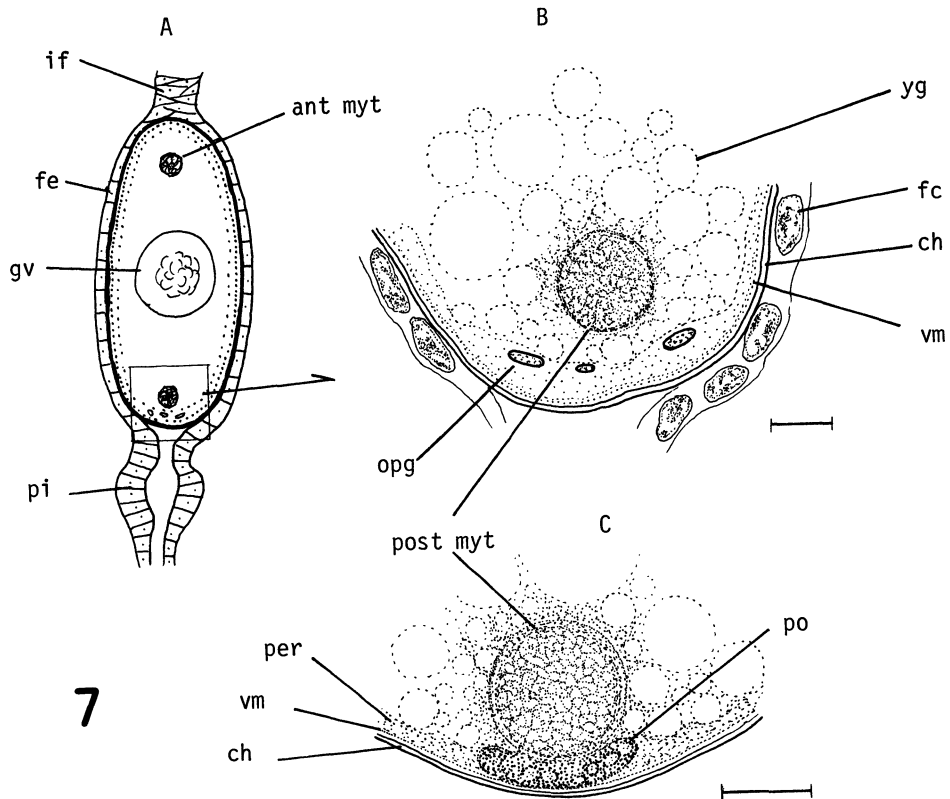vac vacuole,   yg yolk globule.

Fig. 7. Development of oosome in *B. brevitubus.*
A. Terminal oocyte, diagrammatic.
B. Posterior portion of the terminal oocyte, showing precursor granules of the oosome.   Scale : 10 μm
C.   Posterior portion of the ovulated egg, showing position of the oosome. Scale : 10 μm

ant myt anterior mycetome, ch chorion,   fc follicular cell,   fe follicular epithelium, gv germinal vesicle,   if interfollicular tissue,   opg precursor granule of oosome,   per periplasm,   pi pedicel,   po oosome (pole plasm). posy myt posterior mycetome, vm vitelline membrane,   yg yolk globule.

invariably two and never divide.

In the living egg, two kinds of yolk globules (Fig. 4B), *i. e.,* the lipid yolk and proteid yolk may be recognizable. The former is transparent, less than 5 μm in diameter, and the latter is about 1 to 16 μm. The lipid yolk, however, is almost all resolved during the treatment of the preparation.

Developmental Stages of Embryo

Based on the external observation and the examination of serial sections, the embryonic development from its commencement to the hatching of *B. brevitubus* is divided into the following 11 stages. Heming (1979) also divided the embryogenesis of *H. verbasci* into 11 stages similar to those of the psocopteran *Liposcelis divergens* (Goss, 1952), but he sets 7 stages before katatrepsis while the present author gives 6 pre-revolution stages.

It is unable to time complete developmental stages accurately. In the most embryological studies, the time of oviposition is arbitrarily set the beginning of the embryonic development, however, in *B. brevitubus* the developing eggs are often stored in the oviducts and oviposited at various stages as observed by Heming (1979) in *H. verbasci.* In the present study, the duration of each stages could be determined by an analysis of the movie films of the living eggs.

Stage I   (00:00 - 08:00 hr) (Cleavage)

The author could not observe the process of fertilization. The fertilized nucleus divides several times, synchronously at first but it becomes asynchronous. Cleavage nuclei arrive at the egg periphery at the end of this stage.

Stage II.   (08:00 - 18:00) (Ventral plate formation)

This stage is from the arrival of migrating nuclei at the periphery to the appearance of the ventral plate. The egg is covered by the blastodermal cells, but they are coarse and thin near the anterior pole of the egg. The boundary between the embryonic and the extraembryonic areas becomes somewhat clear. The ventral plate is formed in the former at the end of this stage.

Stage III.   (18:00 - 26:00) (Invagination of Germ-band)

In this stage the ventral plate invaginates into the yolk and the extraembryonic area differentiates into the serosa. The amnion is also formed. The germ-band grows along the longitudinal axis of the egg.

Stage IV.   (26:00 - 36:00) (Early Pre-revolution)

At the beginning of this stage the protocephalic lobes are formed. Rudiments of the antennae and gnathal appendages appear. The rudiment of labrum also appears between the antennae. In the elongating germ-band the first and second caudal fold may occur.

Stage V.   (36:00 - 52:00) (Middle Pre-revolution)

The germ-band elongates further and becomes longest in this stage. Thoracic appendages develop and the segmentation of the thorax and abdomen becomes distinct. Pleuropodia appear on the first abdominal segment.

Stage VI.   (52:00 - 64:00) (Late Pre-revolution)

The germ-band grows in width. The gnathal and thoracic appendages develop well. The position of the labrum moves posteriorly, and that of the antennae move anteriorly. The serosal cuticle is formed.

Stage VII.   (64:00 - 70:00) (Katatrepsis)

Embryonic envelopes break at the point of their fusion. Serosal cells begin to contact towards the anterior pole. The embryo is shortened with slight rotation, then it comes out from the yolk and moves along the ventral surface of the egg towards the anterior pole. At the end of this stage, the secondary dorsal organ is formed, and the provisional dorsal closure is completed.

Stage VIII.   (70:00 - 80:00) (Early Post-revolution)

The pleuropodia develop and their secretion is occurred. Anterior and posterior ribbons of the mid-gut epithelium elongate. Rectal papillae become distinct in the proctodaeum. The secondary dorsal organ disappears at the end of this stage.

Stage IX.   (80:00 - 94:00) (Middle Post-revolution)

The gnathal appendages of the embryo collectively form the mouth-cone, in which a pair of maxillary stylets is formed. The right mandible degenerates while the left one begins to form stout stylet. The dorsal closure is almost completed and the mid-gut is formed at the end of this stage. The embryo grows and its head reaches the anterior end of the egg.

Stage X.   (94:00 - 110:00) (Late Post-revolution)

The left mandibular stylet and a pair of the maxillary stylets are chitinized. The compound eyes are formed and the larval integument and major setae begin to appear. The yolk in the mid-gut is almost liquefied.

Stage XI.   (110:00 - 120:00) (Full-developed Embryo)

The head capsule is formed and hardened as well as pronotal plates, and the tube is sclerotized in this stage. The hypodermal pigmentation occurs under the tergites. The yolk is almost completely consumed. No egg-teeth is formed. Just before hatching the embryo begins expanding and retracting movement of its head and prothorax.
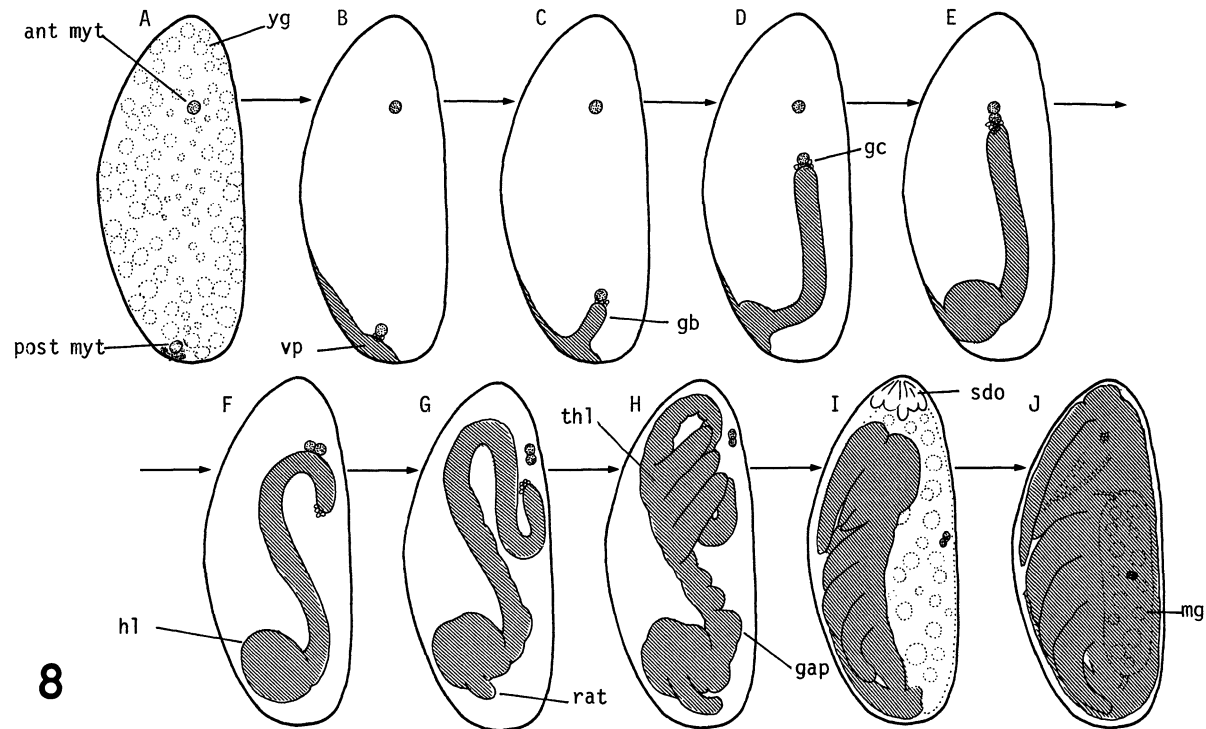
Fig. 8. Mycetomes behaviour during embryonic development in *B. brevitubus,* diagrammatic.
A. Position of two mycetomes. B. Ventral plate is formed. C. Invagination of the germ-band begins.   D. Germ-band grows along the median egg axis.
E. Two mycetomes anastomose each other. F. Germ-band flexes dorsally.
G. Germ-band flexes again, mycetomes are separated from it. H. Appendages grow before katatrepsis. I. After katatrepsis, mycetomes situate dorsally. J. Midgut is formed, mycetomes are enclosed in it.

ant myc anterior mycetome, gb germ-band, gc germ cell, hl head lobe, mg mid-gut, post myt posterior mycetome, rat rudimentary antenna, sdo secondary dorsal organ, thl thoracic appendage, vp ventral plate.
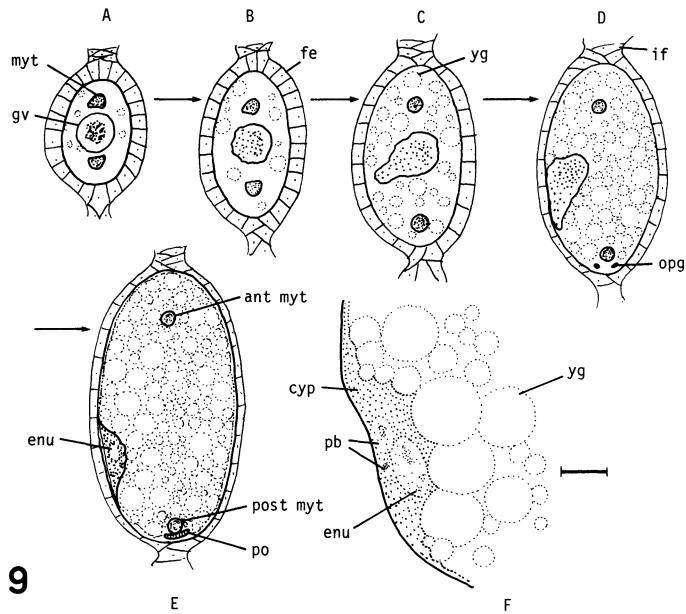
Fig. 9. Migration and transformation of germinal vesicle at the oogenetic Stage 5. in *B. brevitubus*.

A. — E. Successive changes and migration of the germinal vesicle, yolk globule deposition, transformation and migration of the mycetomes, formation of the oosome. (Chorion and vitelline membrane omitted). Diagrammatic.

F. Egg nucleus and polar bodies. Scale : 10 μm

ant myt anterior mycetome, cyp cytoplasmic area around the egg nucleus, enu egg nucleus, fe follicular epithelium, gv germinal vesicle, if interfollicular tissue, myt mycetome, pb polar body, po oosome, yg yolk globule.
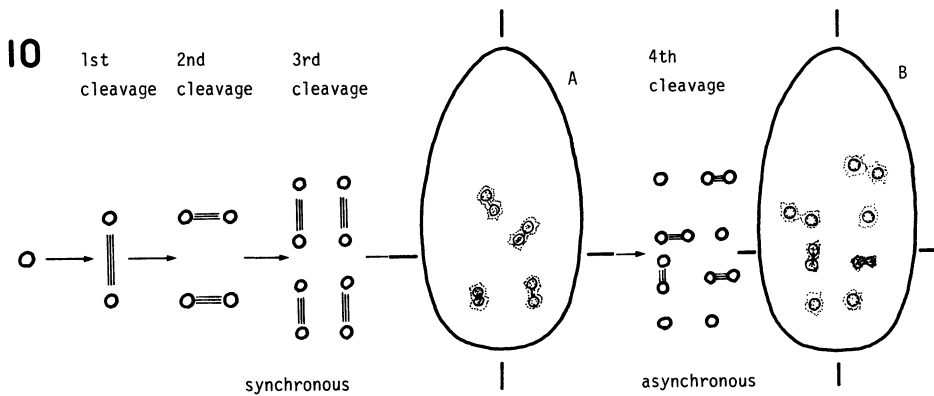

Fig. 10. Cleavage in *B. brevitubus*, reconstruction from serial sections and diagrams of cleavage directions. Bars show the location of cleavage center.

A. After 3rd cleavage (8-cell stage).

B. At 4th cleavage (11 energids).

Maturation and Cleavage

When the eggs are oviposited, the phase of the maturation is different according to the time that the eggs have spent in the oviduct. The youngest egg observed has two polar bodies situating close to each other. Depends upon the observations on the oogenesis and the above-mentioned results, it is assumed that the eggs at the ovulation (pushing out of the completed eggs from ovarioles to lateral oviducts) are at the metaphase of the first maturation division, and the second maturation division has already occurred while they were staying in the lateral or common oviduct.

The polar bodies are observed in the cytoplasmic island adjacent to the egg pronucleus, which are about 7 by 9 μm. The author could not observe the process of the fusion of nuclei, but studied the course of the first cleavage in two instances. In these cases the zygote locates at the posterior third of the egg longitudinal axis, and they are at the metaphase. The size of two nuclei with their surrounded cytoplasm are 26 by 20 μm, and 28 by 20 μm, respectively. In one case a nucleus has at least 12 chromosomes that are arranged on the equatorial plane; only previously known chromosomal number in Tubulifera is n=14 in *H. statices* (Risler and Kempter, 1961).

After the first cleavage, two energids are found at the posterior fifth and three-sevenths along the longitudinal egg axis (Fig. 10).

The second cleavage occurs synchronously but its divisional plane is vertical to the first cleavage. The distances between each pair of the daughter nuclei are shorter than that in the first cleavage. In one instance the size of these four energids is 14-18 by 16-22 μm.

The third cleavage occurs in the longitudinal direction of the egg, and nearly synchronous, but it is often observed that there are 6 or 7 energids in an egg. After the third cleavage, the energids are distributed randomly, and also the synchrony and orientation of the cleavages become irregular and the uniformities is gradually lost.

When the number of energids increases to about 100, their peripheral migration begins. In one instance (Table 1) in which containing about 97 energids (the intermediate stage between 6th and 7th cleavages), they are seen to distribute unevenly in the egg, and a few energids have a short cytoplasmic tail as if they are migrating towards the periphery (Fig. 11B).

Two or three energids are seen in contact with both the anterior and posterior mycetomes before the beginning of the energids migration. The cytoplasm of these energids fuses with the cytoplasm around the mycetoms.

At the end of Stage I, the energids are most abundant near the posterior third of the egg, and their number gradually decreases to the distal area where any energids cannot be found.

The energids reach the periphery of the egg probably at the 8th cleavage. The first arrival of the energid is observed at the posterior fifth of the ventral side of the egg, not far from the cleavage center. Prior to the first energid's arrival to the periphery, the energids contacting with the posterior mycetome begin to move posteriorwards, and finally penetrate into the oosome just below the mycetome, whereupon they will become the primordial germ cells (Fig. 11E).

The migrating energids have the cytoplasmic coating, about 5 μm thick, a part of which is often elongates as trail. When the energids attained to the periphery, they are measured 12-15 μm in diameter. The periplasm at this stage is only 5-10 μm thick, but later it slightly increases in thickness most probably due to the cytoplasm brought by arrived energids. At

this time, however, certain parts of the egg surface still lack the periplasm (Fig. 11).

As an example of the 8th cleavage, about 140 energids are counted, and 70% of which arrived at the egg periphery, but they are noticeably scanty near the anterior pole (Tables 2, 3).

The arrived cells repeatedly divide tangentially, and increase in number, whereas decrease in their nuclear size occurs. Some of them divide centripetally and their daughter cells may become the secondary yolk cells.

In the eggs of 5 hours after oviposition, either the 7th cleavage (no energids at the periphery) or 8th cleavage (several energids at the periphery) are observed.

Blastoderm Formation

The cells at the egg surface have a large nucleus with scarce cytoplasm just after arrival. According to the thin uncontinuing periplasm they are sparsely distributed until their number increases more than about 1000. Only a few cells can be found near the anterior egg pole in the 3059 cell-egg (Table 3). As the result of several mitoses, the size of the nuclei in these cells decreases from about 15 μm to less than 5 μm in diameter. These cells transform into flattened fusiform, and cover the surface of the egg. They are extended about 20 μm in diameter near the anterior egg pole, but those near the posterior pole are less than 10 μm. In succeeding stage the latter group of the cells increases in number, and the density becomes higher than in the previous stage. In this way the egg attains the blastodermal stage, but blastodermal cells is demarcated from each other in this stage. They arrange in a layer, but they are thick and cuboid in the posterior region of the egg while thin and flattened in the anterior region. The boundary of the thick blastoderm or embryonic area is distinct.

When the blastoderm is completed, an egg contains about 2987 cells, about 65 of which (primary yolk cell) still remain in the yolk (Table 3). As the development proceeds, the primary yolk cells increase in number, but the proportion of numbers of the blastoderm and primary yolk cells is nearly constant; in one instance about 100 primary yolk cells are recognized among about 5000 cells, which indicates that the proportion of primary yolk cell is approximately 2% of entire cell number. They (6-10 μm in size) are a little larger than the blastoderm cells (5-8 μm), and are globular or ovoid with a thin cytoplasm, and randomly distributed all over the yolk. Some primary yolk cells accompany with the mycetomes, and their cytoplasm is projected into the yolk.

As mentioned before, two or three cells penetrate into the oosome at the cell migration stage, and their number increases about 10 until the blastoderm is completed. They are the primordial germ cells, and repeatedly divide there. Then they aggregate at the site between the posterior pole and the posterior mycetome (Fig. 11).

As the cells in the embryonic area proliferate further, they increase in thickness. The embryonic area develops to the ventral plate or embryonic primordium. It is disc-like and occupies less than posterior one-third of the egg length (Fig. 12).

While the ventral plate formation, the number of the primordial germ cells increases, and reaches about 30 until the commencement of the invagination of the ventral plate. It takes about 10 hours from the first arrival of the energids at the egg periphery to the commencement of the anatrepsis; this is about 18 hours after the initiation of the embryonic development in *B. brevitubus*.

Haga, K.

Table 1. Distribution of energids of an about 97-cell egg (Stage I) in *B. brevitubus.*
(Anteroposterior locations).

SECTION NUMBER FROM ANTERIOR POLE	NUMBER OF NUCLEI IN CENTRAL YOLK	DISTRIBUTION OF NUCLEI
		0 *(Anterior pole)*
1 - 6	0	
7 - 12	0	
13 - 18	2	
19 - 24	8	
25 - 30	8	
31 - 36	10	
37 - 42	9	
43 - 48	10	
49 - 54	12	
55 - 60	14	
61 - 66	11	
67 - 72	5	
73 - 78	7	
79 - 84	1	
85 - 90	0	
		(Posterior pole)
	97	

Table 2. Distribution of energids of an about 140-cell egg (Stage II) in *B. brevitubus*.

O ... on periphery,   ● ... total.

SECTION NUM-BER FROM ANT-ERIOR POLE	NUMBER OF NUCLEI			DISTRIBUTION OF NUCLEI
	ON PERI-PHERY	IN CENT-RAL YOLK	TOTAL	0 (Anterior pole)
1 - 6	0	0	0	
7 - 12	0	1	1	
13 - 18	0	3	3	
19 - 24	0	3	3	
25 - 30	0	4	4	
31 - 36	1	5	6	
37 - 42	0	6	6	
43 - 48	5	2	7	
49 - 54	7	2	9	
55 - 60	8	0	8	
61 - 66	16	0	16	
67 - 72	11	2	13	
73 - 78	15	0	15	
79 - 84	18	0	18	
85 - 90	14	3	17	
91 - 96	1	7	8	
97 - 102	.2	4	6	(Posteaior pole)
	98	42	140	

Table 3. Distrubution of cells in a blastoderm (about 3059 cells of Stage II) in
        B. brevitubus.

○ . . . on periphery,   ● . . . total.
Numerals in parenthese mean number of germ cells.

| SECTION NUM-BER FROM ANT-ERIOR POLE	NUMBER OF NUCLEI			DISTRIBUTION OF NUCLEI (Anterior pole)
	ON PERI-PHERY	IN CENT-RAL YOLK	TOTAL	
1 - 5	30	0	30	
6 - 10	40	1	41	
11 - 15	67	0	67	
16 - 20	76	2	78	
21 - 25	110	2	112	
26 - 30	127	2	129	
31 - 35	173	4	177	
36 - 40	142	8	150	
41 - 45	178	5	183	
46 - 50	203	5	208	
51 - 55	189	10	199	
56 - 60	221	7	228	
61 - 65	233	7	240	
66 - 70	239	3	242	
71 - 75	242	5	247	
76 - 80	236	3	239	
81 - 85	209	0	209	
86 - 90	161 (3) + 1		165	
91 - 95	111 (4) + 0		115	
	2987 (7) + 65		3059	(Posterior pole)
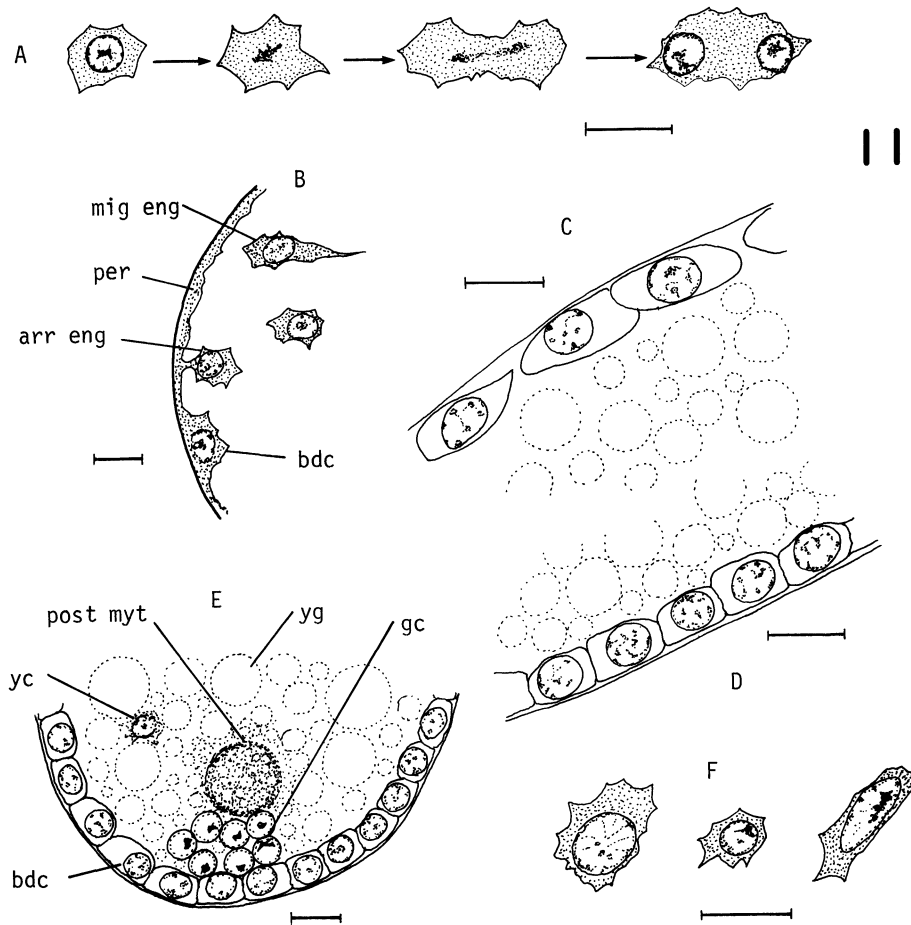
Fig. 11.   Blastoderm formation in *B. brevitubus*. Scales : 10 μm
A. Energid division.   B. Migration of energids.   C. Blastoderm near anterior
pole.   D. Blastoderm near posterior pole.   E. Posterior portion of an egg in
the blastoderm stage.   F. Yolk cells.

arr eng energid arrived to the periphery,   bdc blastodermal cell,   gc germ cell,   mig eng
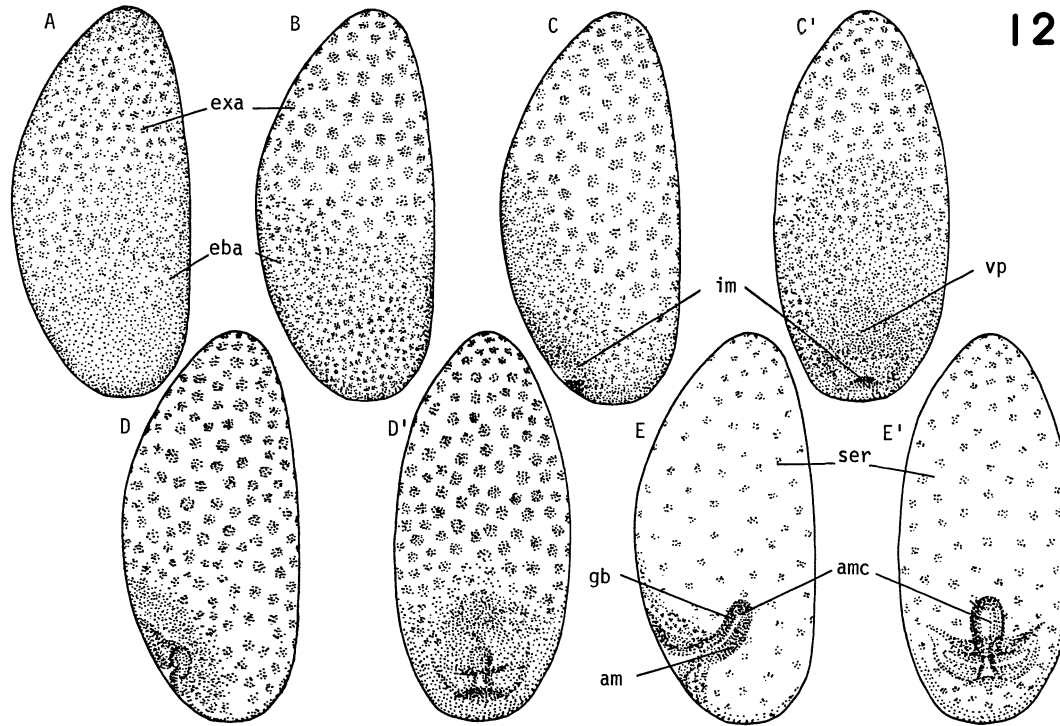migrating energid,   per periplasm,   post myt posterior mycetome,   yc yolk cell,   yg yolk
globule.

Fig. 12. Germ-band formation in *B. brevitubus*.
  A. Blastoderm, lateral view.   B. Ventral plate formation, ventral view.
  C. Beginning of invagination of ventral plate, lateral view and ventral view (C').
  D. Early stage of germ-band formation, lateral view and ventral view (D').
  E. Proceeded stage of germ-band formation, lateral view and ventral view (E').

am amnion,   amc amniotic cavity,   eba embryonic area,   exa extraembryonic area,   gb germ-band,   im mouth of invagination,   ser serosa,   vp ventral plate.

Germ-Band Formation

Before the biginning of the ventral plate invagination, the difference of the cell density between embryonic and extraembryonic areas becomes apparently distinguishable as mentioned above. The orifice of the invagination, at first, appears as a short transverse slit near the posterior end of the ventral plate, and the primordial germ cells with the posterior mycetome are situated inside near the mouth. Soon after this slit changes in shape to inverted letter "V".

It seems that the direction of the invagination is first horizontal, then changes perpendicularly and finally invaginating end of ventral plates points anteriorwards and it elongates along the longitudinal egg axis; this shift in the direction of invaginating ventral plate is due to the shifting of the orifice of the invagination to the posterior one-sixth of the egg (Fig. 12).

At this stage the germ-band is a flattened monocellular blind tube of the cells which has a narrow lumen, and its dorsal side is the embryonic primordium, and the ventral side is the rudimentary amnion, and the lumen later becomes the amniotic cavity (Figs. 12, 14). The cells of the caudal end of the germ-band increase in number by mitoses.

As above-mentioned, the posterior mycetome keeps in contact with the caudal end of the invaginating ventral plate, and when the mycetome reaches the anterior mycetome, the two mycetomes fuse each other (Fig. 8E). These mycetomes separate from the germ-band and are moved by yolk flows,and finally arrive at the anterior one-fourth of the egg on the dorsal side (Fig. 8G). In the course of the anatrepsis the primordial germ cells attach again to the caudal end of the germ-band. As the posterior end of the developing germ-band reaches at the position of the anterior mycetome, the germband flexes dorsally and curves again posteriorly, and once more flexes dorsad of the egg. Thus the germ-band is formed as double-flexed S-form as seen from the lateral view and keeps the form until the katatrepsis.

It is about 70 minutes from the beginning of the invagination of the ventral plate to the arrival of the caudal end of the germ-band to the anterior mycetome, and it needs further about 60 minutes for the double-flexed germ-band is formed.

At about 30 hours after the commencement of the embryonic development (about 20 hours after the beginning of the invagination of the germ-band), the germ-band of *B. brevitubus* is strikingly elongated. When the double-flexed germ-band becomes longest it is approximately 1.7 times as long as the egg length.

A flow of yolk globules may be observed at the time of germ-band formation using time-lapse microphotography. This yolk flow first occurs along the longitudinal egg axis, from posterior to anterior, and then the flow is recurrented along the egg periphery from anterior to posterior. Its velosity is higher along the axis than that along the periphery (Fig. 13B).

A pair of cephalic lobes develops during the invagination of the germ-band. At the outset, they are flattened cylindroid as like the rudimental gnathal, thoracic and abdominal regions. As the development proceeds, the germ-band transforms into V-shaped, then later U-shaped in cross view, and is extended, although its thickness decreased. As already mentioned, in the protocephalon and protocorm the rudimentary amnion is a thick cellular layer, but now it becomes very thin.

Haga, K.

A

110' 120' 130'
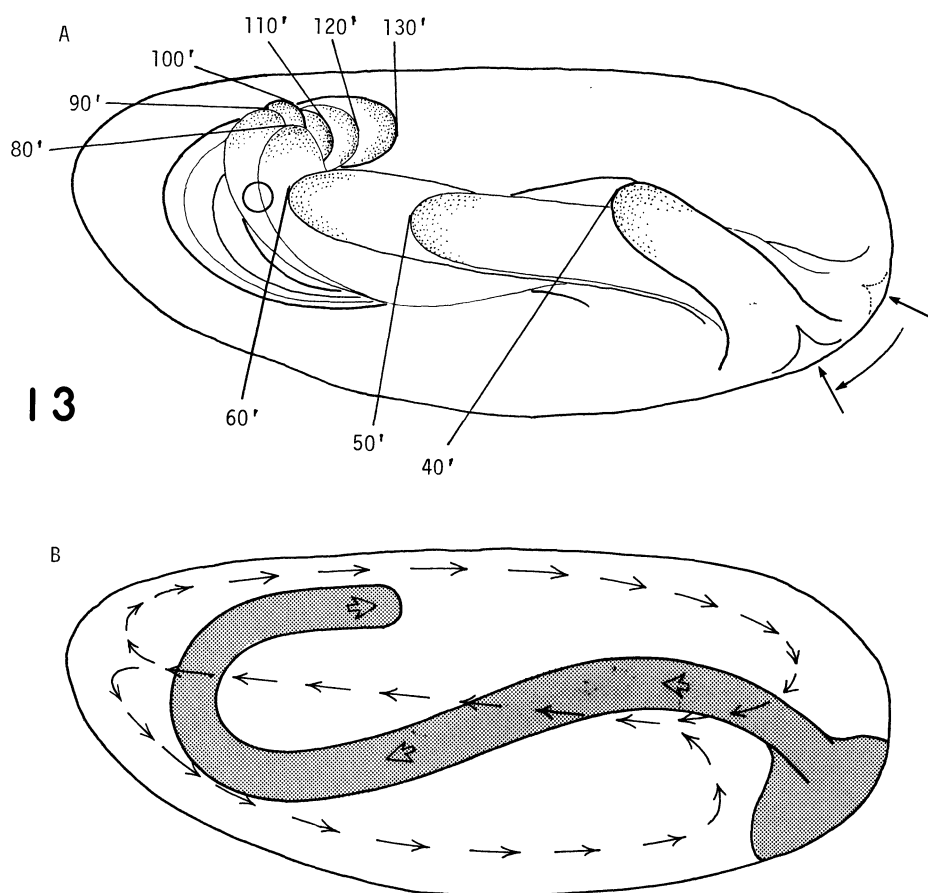
100'

90'

80'

| 3

60'

50'

40'

B

Fig. 13. Development of germ-band in *B. honoris*. (Reconstructed from 16 mm movie)
A.   Time lapse of the germ-band growth.   An arrow shows a migration of orifice
of the germ-band.   A circle indicates the position of the anterior mycetome.
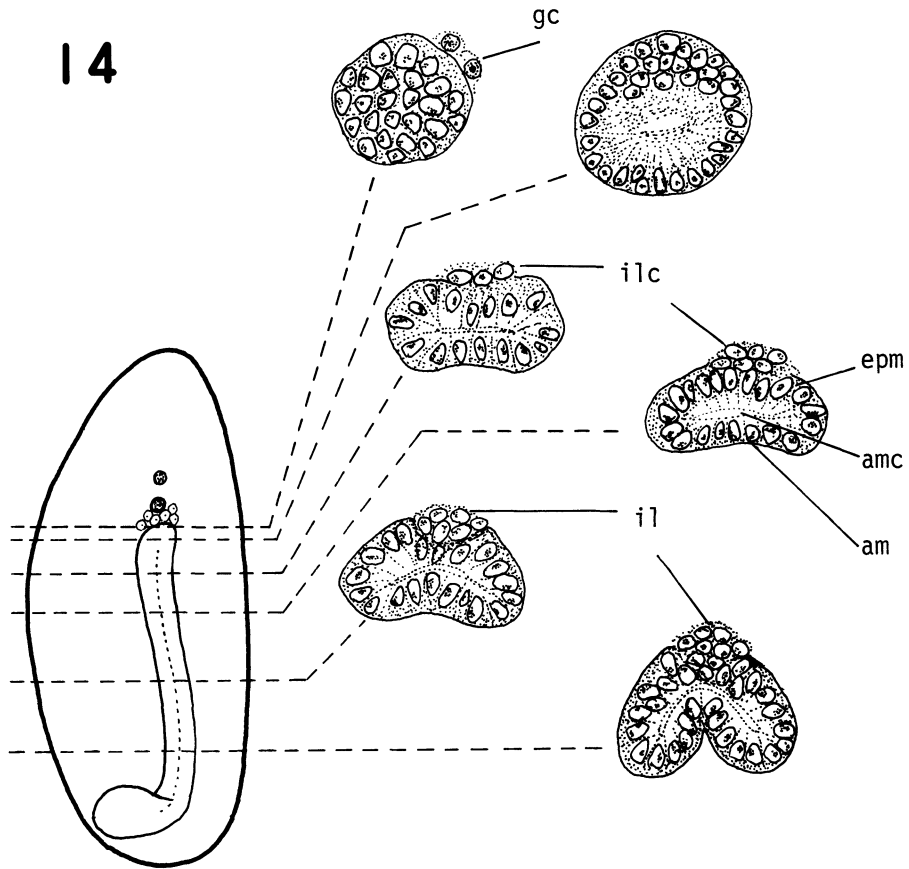B.   Yolk flow convection during the germ-band growth.

Fig. 14. Inner layer formation in *B. brevitubus*.
Serial cross sections of a Stage III embryo.

am amnion,   amc amniotic cavity,   epm embryonic primordium,   gc germ cell,   il
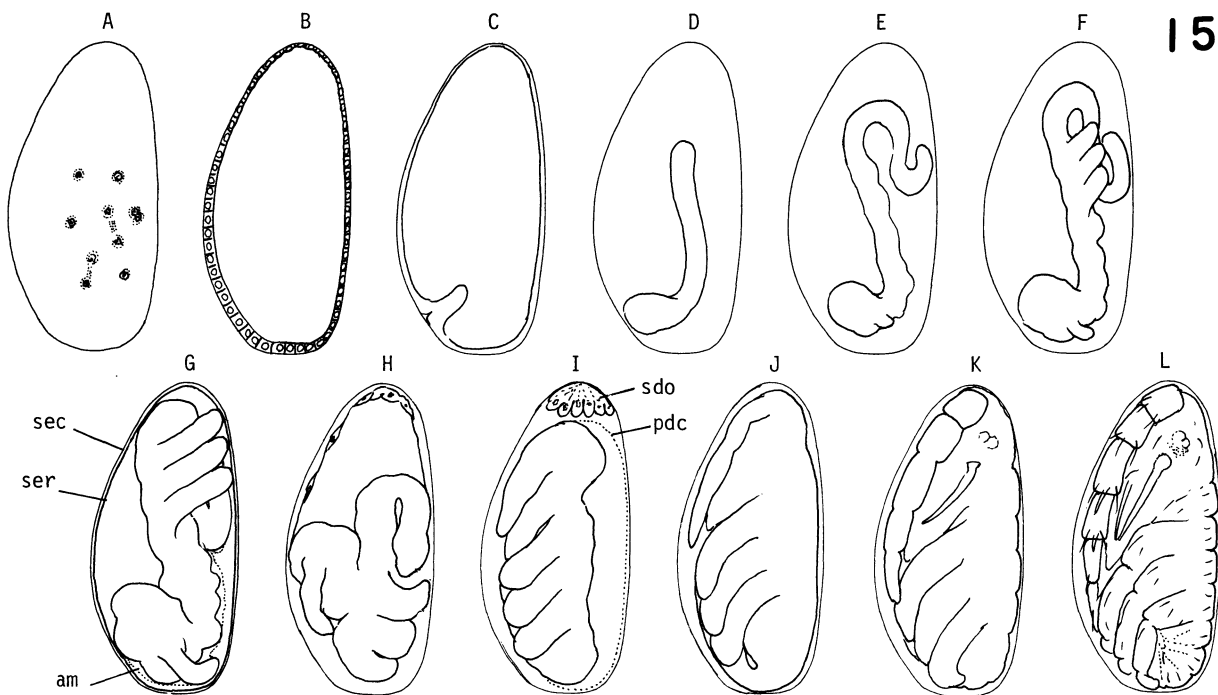inner layer,   ilc inner layer cell.

15

Fig. 15. Embryonic stages in *B. brevitubus*. (Chorion omitted, diagrammatic).
A. Stage I (cleavage), B. Stage II (blastoderm), C. Stage III, D. Stage III', E. Stage IV, F. Stage V, G. Stage VI, H. Stage VII (katatrepsis), I. Stage VIII, J. Stage IX, K. Stage X, L. Stage XI (prolarva).

am amnion, pdc provisional dorsal closure, sdo secondary dorsal organ, sec serosal cuticle, ser serosa.

Inner Layer Formation

The inner layer formation begins as early as the caudal end of the germ-band reaches near the egg center. At the gnathal region, the cells of the dorsomedian part proliferate and form a row of irregularly arranged cells which are very few at the initiation. Then the formation of the inner layer proceeds posterior- and anteriorwards from here. In cross section, the thoracic region represents a V-shape while it is oval in the abdominal region as mentioned above. In the former, the inner layer is formed on the dorsomedian part with a slight concave groove (Fig. 14), and it is also formed in the cephalic region.

In *B. brevitubus* the inner layer formation is of the proliferating type. It seems that this proliferating type is primitive among the method of the inner layer formation employed by the insects.

External Changes of Embryo

Pre-revolution Stage

In the middle Stage III when the caudal end of the germ-band attains near the anterior mycetome, the first sign of the metamerism can be seen in the gnathal region as slight swellings. Some other swellings appear followingly also in the thoracic region, but the segmentation is rather incomplete. In the same stage, the inner layer of the gnathal region is also obscurely segmented.

The mandibular, 1st maxillary and 2nd maxillary segments, three thoracic and 1st abdominal segments become distinct as early as at the 28-hour stage.

On the other hand, a pair of the labral rudiments or mere swellings contacting each other appears on the posterior cephalic region

At about 30 hours later (Stage IV), a part of the antennal rudiments adjacent to the labral rudiments begins to project and develops greatly. They gradually migrate anteriorwards, while the labral rudiments move posteriorwards and later fuse into an appendage.

In about 36-hour stage (late Stage IV), the rudimental gnathal and thoracic appendages appear simultaneously, but those of the intercalary segment are not recognizable.

In the middle Stage V, the appendages are more obvious; both the antennal and maxillary rudiments elongate and begin to metamerize near the base.

The proctodaeal invagnination is occurred on the ventral side of the enlarged distal segment of the germ-band, *i. e.*, the telson, in the late Stage V (about 44 hours). The stomodaeal invagination also occurs at this stage just behind the labrum.

The abdominal region has 11 segments, but the 11th segment may only be recognized by the constricted inner layer of the segment in this stage, henceforth it becomes indistinct, and fuses with the inner layer of the 10th segment.

The serosal cuticle appears outside of the serosa in the Stage V; it begins to form in the late Stage IV.

As the appendages develop, the germ-band gradually enlarged not only in length but also in width and consequently the spaces between the flexures of the germ-band become narrower. The telson containing the proctodaeal rudiment and the malpighian tubule rudiments is faced to the 6th to 9th abdominal segments with a narrow space between them
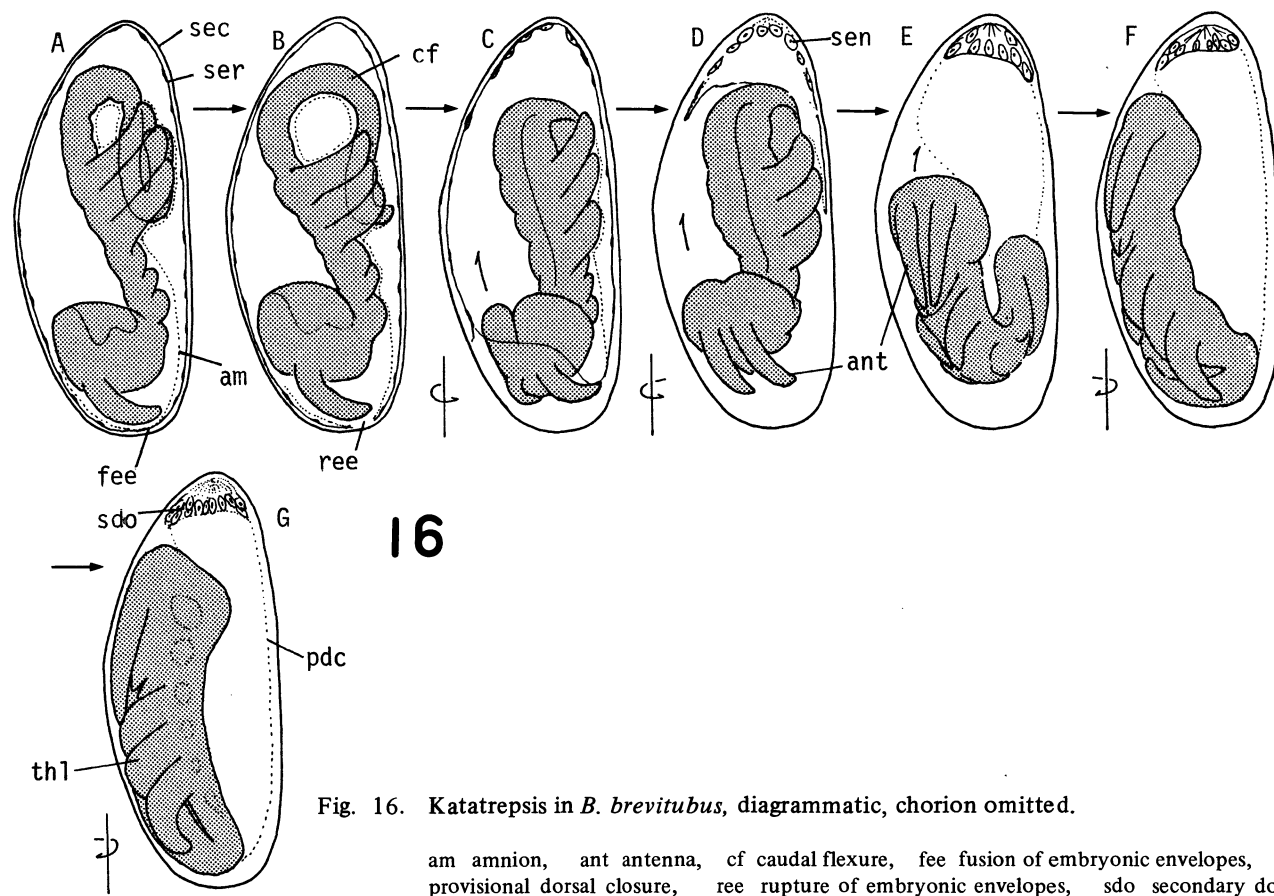
Fig. 16. Katatrepsis in *B. brevitubus,* diagrammatic, chorion omitted.

am amnion,　ant antenna,　cf caudal flexure,　fee fusion of embryonic envelopes,　pdc provisional dorsal closure,　ree rupture of embryonic envelopes,　sdo secondary dorsal organ,　sec serosal cuticle,　sen serosal nucleus,　ser serosa,　thl thoracic leg.

which is further completely closed (Fig. 28).

The primordial germ-cells that have been attached to the caudal end are moved anterior-wards by the colsing of the space of the flexed part. Thenceforth they are anastomosed with the inner layers of the 6th and 7th abdominal segments.

The cephalic lobes become a rugged shape until the initiation of the katatrepsis by the rapid growth of the developing optic lobes. In this period the antennal rudiments elongate almost reaching the mandibular ones.

In the Stage VI, just before katatrepsis, the antennal rudiments are metamerized into 3 segments as the thoracic appendages. The apices of the 2nd maxillary appendages are in-completely forked, while the 1st maxillary ones do not divide.

Katatrepsis

In Stage VII (64 hr after oviposition), the first indication of katatrepsis movement occurs in thoracic and abdominal regions of the embryo. This is contraction and relaxation of these regions which occur along the longitudinal axis of the embryo. This reciprocal movement of the embryonic regions extends to the cephalic region at about three hours later, and the interval of the movement becomes shorter and the amplitude of the movement becomes larger. At 67-hour stage, the embryonic envelopes are ruptured at the cephalic region of the embryo by a pulsative movement (Fig. 16B). The rupture immediately expands and the envelopes are rapidly hauled to the anterior pole (Fie. 16C).

Thus the embryonic head which occupies posterior half of the egg begins to move anteriorwards along the ventral side of the egg. Soon later, the embryo completes its revolu-tionary movement, and the dorsal side of the yolk is enveloped by the amnion (Fig. 16F).

The contracted serosal cells locating anterior to the embryonic head form a cap-like large, hemispherical secondary dorsal organ with diameter of about 150 μm. Formation of a strand from the serosal cells for pulling the embryo as described in *Tanypteryx* (Odonata; Ando, 1962) was not observed.

In the course of the katarepsis, the embryo moves not only anteriorly, but also rotates approximately 45 degrees around the longitudinal egg axis before it undergoes further rotation within the sagittal plane of the egg. This rotation is more apparent in the cephalic region than in the abdomen at early katatrepsis, then it rotates again the counter direction (Fig. 16FG). In one instance, this phase of katatrepsis took about 18 minutes.

Just after katatrepsis the embryo occupies three-fourths of the egg ventral side. It can be recognized at least three constricted parts on the antennal rudiments. The gnathal segments are remarkably transformed during the katatrepsis. Firstly, the position of labrum migrates posteriorly and labrum itself is seen to elongates, and the labium projects ventrally; these two gnathal appendages soon contact with each other to form a short rostrum. Secondly, a pair of maxillary rudiments and the left mandibular rudiment begin to form the long sclerotized stylets which are completed in the Stage X; the right mandibular rudiment, on the other hand, begins to degenerate.
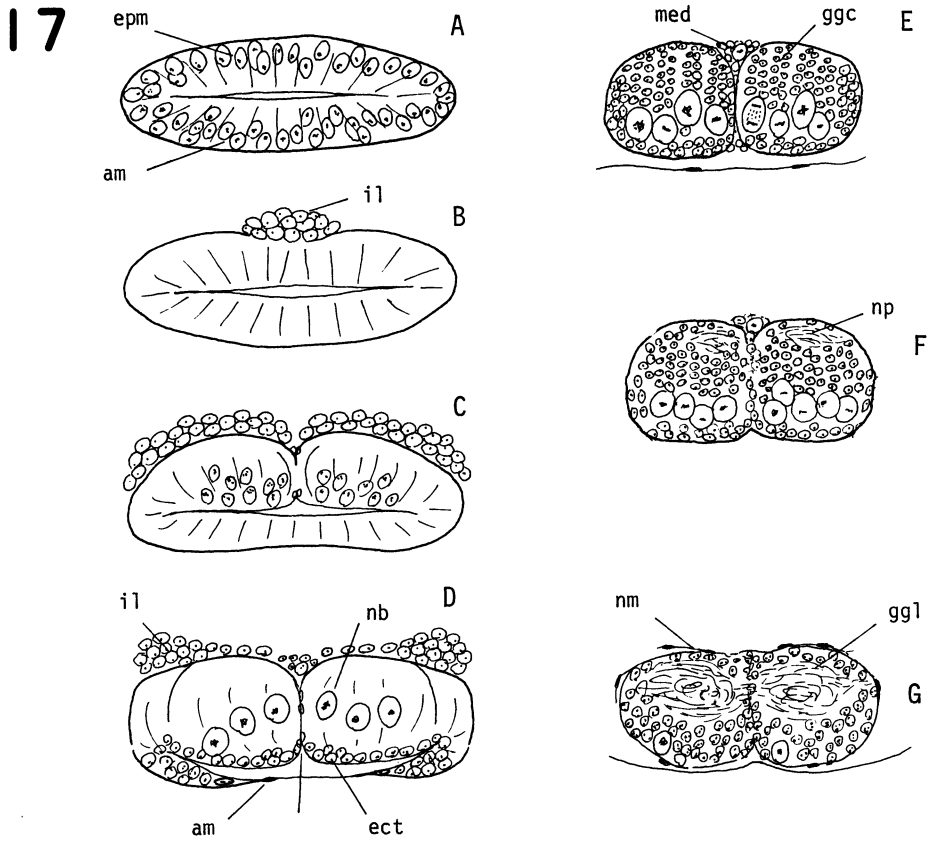
Fig. 17. Ventral nerve cord formation in *B. brevitubus,* cross view.
A — G. Successive development.

am amnion, ect ectoderm, epm embryonic primordium, ggc preganglionic cell, ggl ganglion, il inner layer, med median cord, np neurilemma.

Post-revolution Stage

Within 2 hours after katatrepsis (72 hours stage), the secondary dorsal organ becomes obscure during the definitive dorsal closure, and degenerates in the yolk by 80 hours (Stage VIII to IX). The dorsal closure completes about 10 hours after katatrepsis (Stage IX).

At the early Stage VIII, the anterior and posterior mid-gut epithelia from the stomodaeum and the proctodaeum envelop the yolk. Soon after, the developing embryo fills up the space in the egg.

In the Stage IX, paired maxillary stylets appear deep in the embryonic head, but they are not yet chitinized, and lie from near the compound eyes to the apex of the rostrum showing V-letter. A mandibular stylet is also formed at the left side of head, which is thicker but shorter than the maxillary ones in this stage.

The compound eyes, each consisted of only 2 ommatidia, have become visible because of dark red pigments deposited in Stage X. Ocelli are not differentiated in the embryonic stages.

In Stage X (about 100 hr after oviposition), the setae are formed and the peculiar structures of the pretarsus of the thoracic legs, *i. e.,* the unguis and sense hairs are differentiated. Integuments of the thorax and abdomen as well as the head capsule are rapidly formed, in which the maxillary and mandibular stylets are chitinized; the latter is stouter than the former.

In the Stage IX, three longitudinal rows of red hypodermal pigments appear in the dorsal parts of the thoracic and abdominal segments. In addition, the head, prothorax and 8th-10th abdominal segments are partly sclerotized and turn greyish. In this stage the full-grown embryo shows the pulsative movement. In the embryo of *B. brevitubus,* the eggtooth is not differentiated, but the chorion is cracked by the movement along the deep reticulations from where the first instar larva hatches out.

Organogenesis

Nervous system

A. Ventral Nerve Cord

Ventral nerve cord formation occurs in the Stage VI (28-hr). First the shallow neural groove is found in the gnathal region, and soon later, it extends into the thoracic region. In this stage, the germ-band is formed by evenly arranged columnar cells, but this sequence of the cells becomes lost near the groove (Fig. 17).

The first appearance of the neuroblasts can be seen at the Stage V (about 40 hr) in the gnathal region. The neuroblasts are 9-11 μm in long diameter, larger than the columnar epithelial cells which are 4-7 μm; size of the neuroblasts during mitosis exceeds more than 12 μm. Usually it can be observed up to 5 neuroblasts in each side of the germ-band in the cross section. They divide into two unequal-sized daughter cells, a preganglionic cell and a new neuroblast, respectively.

After the successive division of the neuroblasts the ganglionic cells are accumulated and form a cone-like pile.

In 50 hr embryo (Stage V-VI), the number of the preganglionic cells increases greatly,
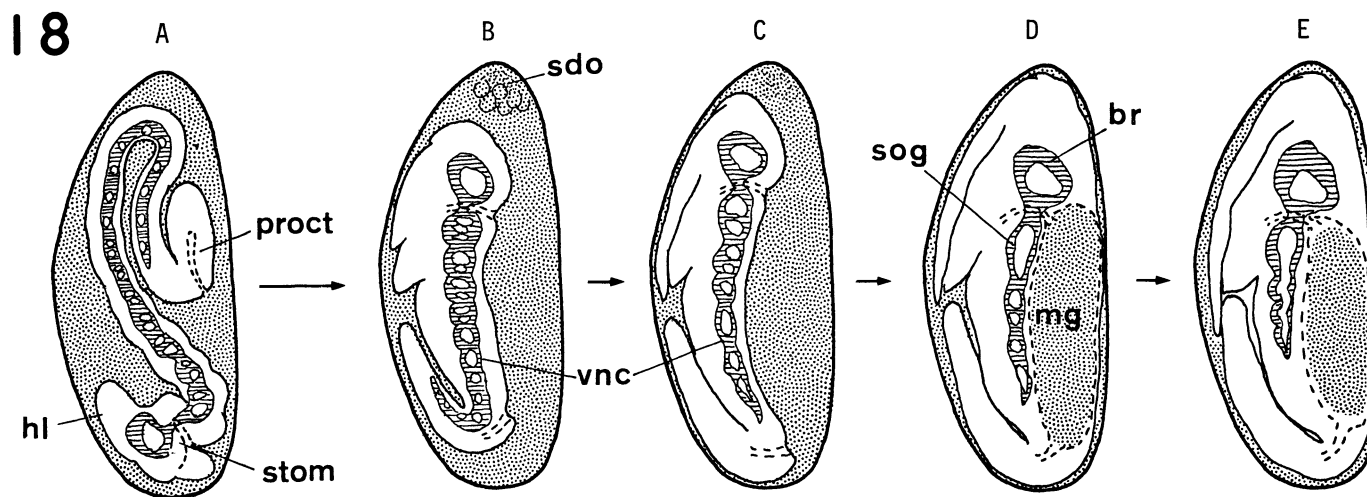
Fig. 18. Concentration of ventral nerve cord in *B. brevitubus,* diagrammatic.
A. Stage VI,   B. Stage VIII,   C. Stage IX,   D. Stage X,   E. Stage XI.

br brain,   hl head lobe,   mg mid-gut,   proct proctodaeum,   sdo secondary dorsal
organ,   sog suboesophageal ganglion,   stom stomodaeum,   vnc ventral nerve cord.
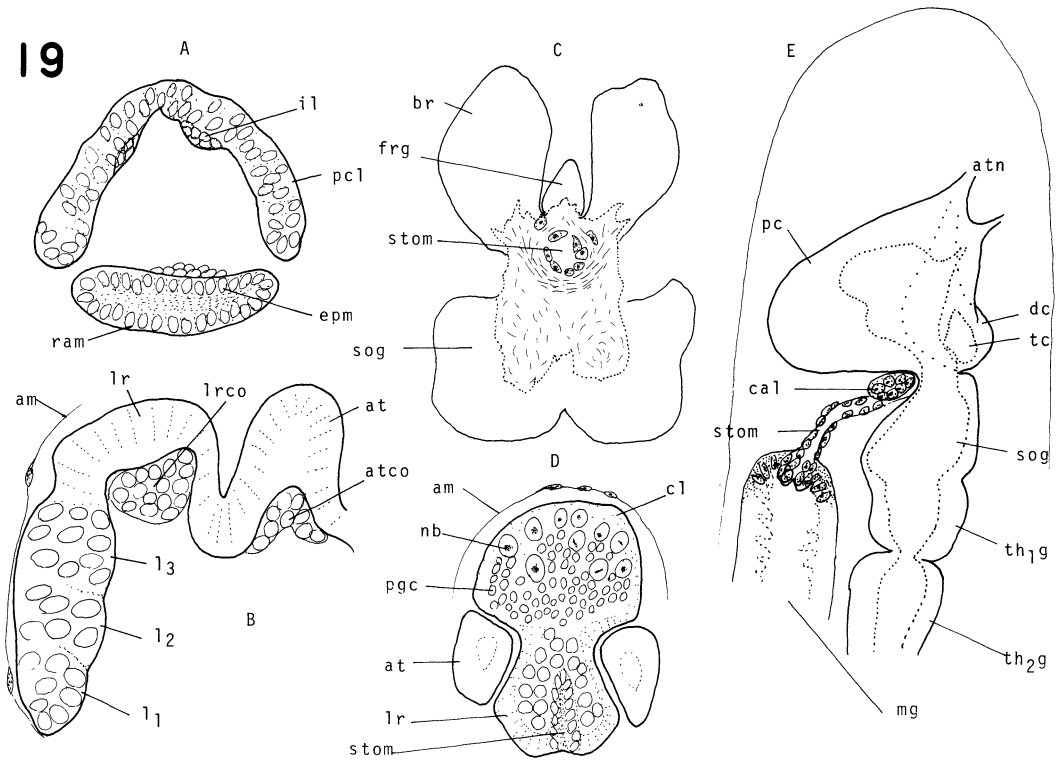
Fig. 19. Brain formation in *B. honoris*.
A. stage IV, cross section,   B. Stage V, sagittal section,   C. Stage VI, horizontal section,   D. Stage IX, horizontal section,   E, Stage XI, sagittal section.

am amnion,   at antenna,   atco antennal coelom,   atn antennal nerve,   br brain,   cl cephalic lobe,   dc deutocerebrum,   epm embryonic primordium,   frg frontal ganglion,   il inner layer, l_{1-3} lobus 1 — lobus 3 of protocerebrum,   lr labrum,   lrco labral coelom,   mg mid-gut,   nb neuroblast,   pcl protocephalic lobe,   pgc preganglionic cell,   pc protocerebrum,   ram rudimentary amnion,   stom stomodaeum,   sog suboesophageal ganglion,   tc tritocerebrum,   thg thoracic ganglion.
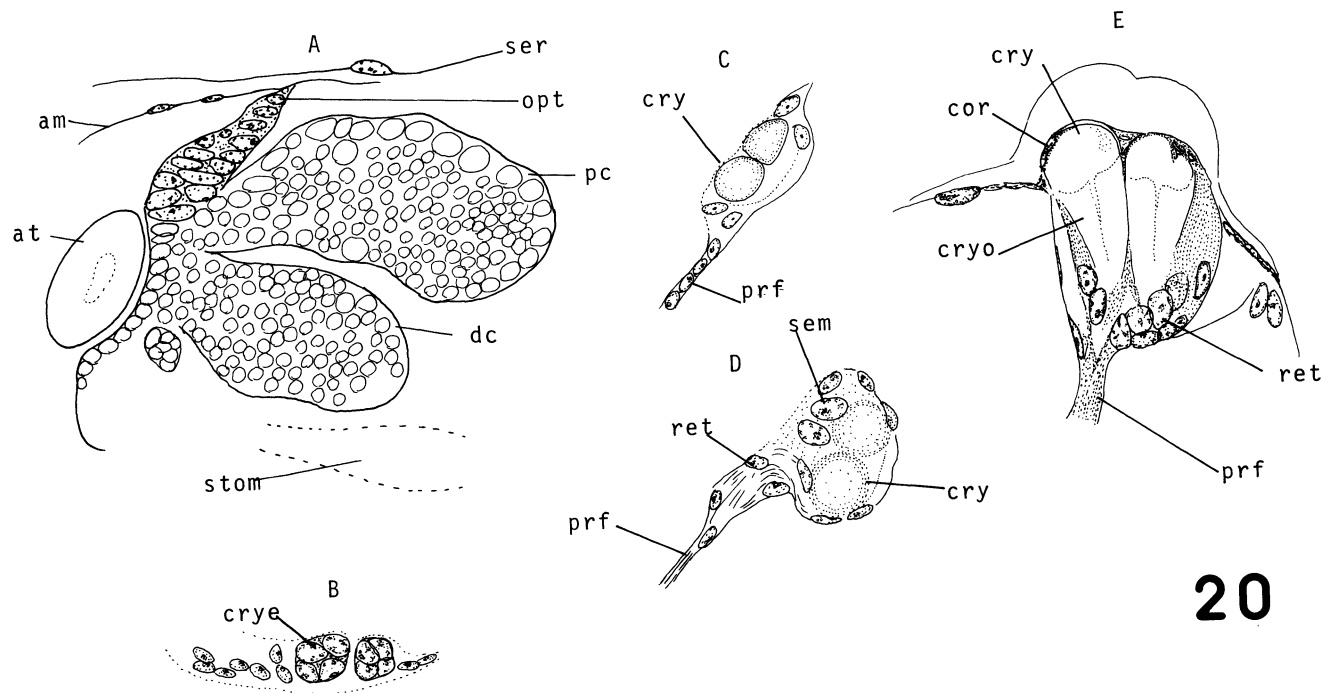
20

Fig. 20. Development of ommatidia in *B. honoris*.
  A. Stage VI, horizontal section.
  B. Stage VIII, horiz. s.
  C. Stage IX, horiz. s.
  D. Stage X, horiz. s.
  E. Stage XI, sagittal section.

am amnion,   at antenna,   cor cornegean cell,   cry crystalline,   cryo crystalline cone,
dc deutocerebrum,   opt optic plate,   pc protocerebrum   prf postretinal fiber,   ret
retinal cell,   sem Semper's cell,   ser serosa.

in one instance, their number counted in the gnathal segments was up to 14, that in the
thoracic segments was 16 and that in the 8th abdominal segment was 8, respectively. Then
fibrous substances appear in the apical region of the preganglionic cell cones. They join with
each other, thus forming a neuropile which is not stained by haematoxylin. The neuropile
is formed at the first in the gnathal region, then succeeded in the thorax and later in the
abdomen of the embryo.

The neuroblasts, preganglionic cells and neuropile are observed in each abdominal seg-
ment from the 1st to 10th. By Bournier's (1966) illustration, 9 abdominal ganglia can be
recognized in *C. buffai.*

In the early stage of Stage VI, a pair of ganglia is formed within each segment, and at the
same time, ganglionic commissures and connectives are formed. They are formed at first in
the gnathal region and later followed by the thoracic and abdominal regions.

At the bottom of the neural groove in the thoracic and abdominal segments there are
irregularly arranged cells including large ones that have the same affinity to haematoxylin as
neuroblasts. They often divide and form the cord thick in the interganglionic areas but
thinner in the ganglionic areas, but do not produce neuropile-like fibers.

It seems that the neurilemma is formed by a part of the ganglionic cells situated at the
dorsalmost of the ganglion which is extremely thinned and expanded into a membrane.

As a consequence each ganglion is completed and all connectives develop from the
premandibular segment to the 10th abdominal segment. Thus the ventral nerve cord formed
at 60 hr in the late pre-revolution stage (Stage VI) consists of 16 ganglia. However, the
number of the ganglia may not be correctly counted at later stages because the ventral nerve
cord begins to condense immediately after their completion.

The concentration of the ganglia commences in the gnathal segments. Their ganglia are
gathered through katatrepsis (Stage VII), and finally form the suboesophageal ganglion at
the late Stage VIII (80-hr). The condensation of the abdominal ganglia, on the other hand,
begins after katatrepsis. Condensation of the ventral nerve cord in the abdomen first occurs
at the extreme caudal end and then extends cephalad; ventral nerve cord becomes thick
while it shortens. It can be counted 10 abdominal ganglia in the Stage VI embryo, but in
the late Stage IX they consist of only 6 ganglia. Furthermore, this condensation becomes
more significant up to the late Stage X, by which time these abdominal ganglia lost all
connectives and transform into a short, thick, spindle-like synganglion. The ganglion locates
in the metathoracic segment, not in the abdomen.

Three thoracic ganglia also condense, and a pair of connectives between prothoracic and
mesothoracic ganglia is noticeably shortened. Another pair of connectives between meso-
thoracic and metathoracic ganglia is also shortened, but does not disappear. The anterior
half of these condensed ganglia contacts with the suboesophageal ganglion, and the rest
nearly fuses to form the spindle-shaped abdominal synganglion.

The suboesophageal, pro-, meso-, metathoracic and abdominal ganglia have two to several
number of neurosecretory cells. They are larger than the ganglionic cells with a few chro-
matins and relatively large nucleolus.

In the full grown embryo, the ventral nerve cord consists of two ganglionic blocks, that
is, the suboesophageal ganglion with the prothoracic and mesothoracic ganglia, and the
metathoracic ganglion and abdominal synganglion with thin nerve cord elongating into the
ventral part of the abdomen. These two blocks are contained in the thoracic region of the
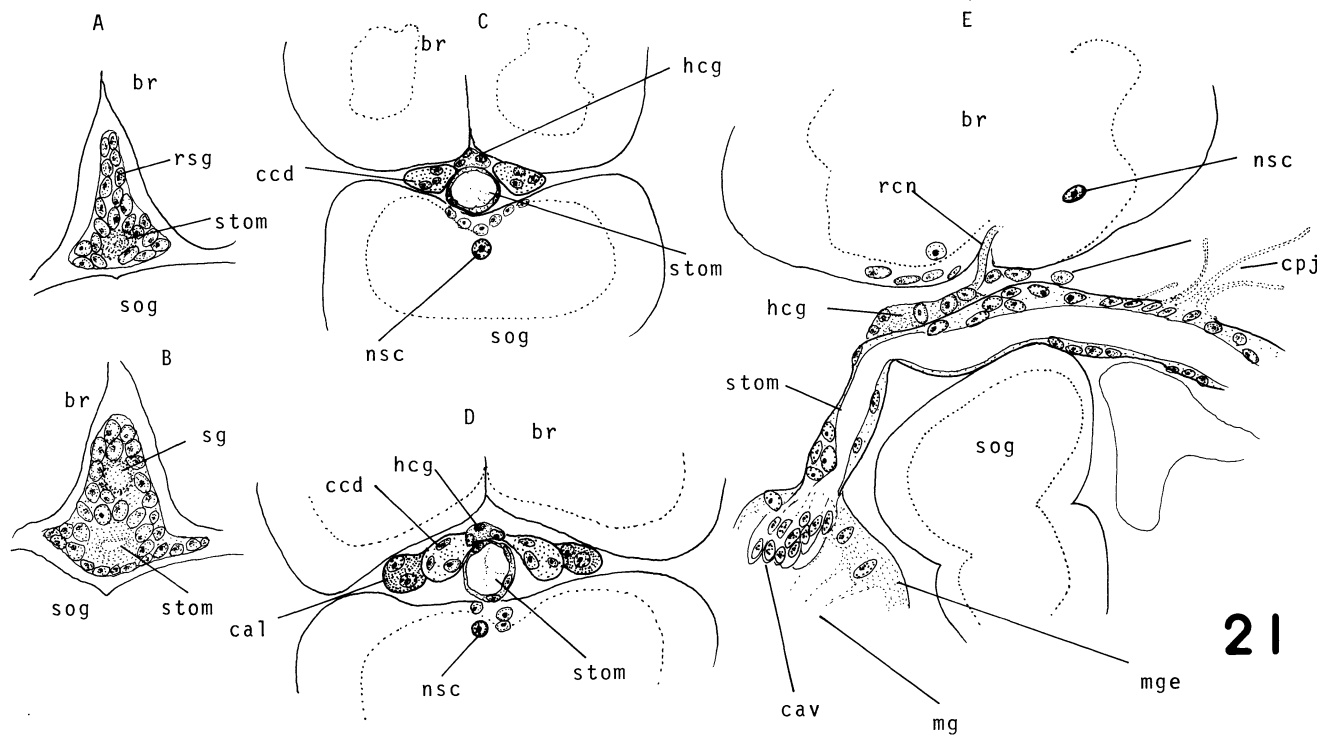embryo, as in the adult.

Fig. 21. Development of stomatogastric nervous system in *B. brevitubus*.
A. Stage VI, cross section. B. Stage VIII, cross s. C. Stage IX, cross s.
D. Stage X, cross s. E. Stage IX, sagittal s.

br brain, cal corpus allatum-like gland, cav cardiac valve, ccd corpus cardiacum-like gland, cpj cytoplasmic projection, hcg hypocerebral ganglion, mg mid-gut, mge mid-gut epithelium, nsc neurosecretory cell, rcn recurrent nerve, rsg rudiment of stomatogastric nerve, sg stomatogastric nerve, sog suboesophageal ganglion, stom stomodaeum.

B. Brain

As already explained, the protocephalic lobes are begun to form at the Stage III, and are similarly thick as the protocorm. However, no histological differentiation of the protocephalic lobes is observed in this stage.

In the following stage, the neuroblasts also occur in the protocephalic lobes which are single- or double-layered and accompanied with a small amount of the inner layer. The neuroblasts may be found in the region along margins of the lobes (Fig. 19D), and the preganglionic cells are arranged centripetally upon them.

In the Stage V, each protocephalic lobe is slightly constricted into 3 parts. The lateralmost of them somewhat thickens and forms an optic lobe in the middle Stage VI. The deutocerebral rudiment is formed posterior of the optic lobe rudiment. Neuroblasts of the rudimental protocerebrum and deutocerebrum actively divide and produce a lot of ganglionic cells. Their volumes rapidly increases after katatrepsis, and the neuropile develops in them.

In the late Stage VIII, thickened protocerebral lobes are in contact with each other, and paired intercalary ganglia migrate towards the head region. They finally situate both sides of the frontal ganglion and form a tritocerebrum in the Stage IX, which is much smaller than the protocerebrum and deutocerebrum.

Though the head region of the embryo elongates, the protocerebrum locates its dorsal and frontal sides while the deutocerebrum only can be seen near the stomodaeum.

In the grown embryo of *B. brevitubus,* the compound eyes develop at the both sides of the head capsule near its apex. The optic plate differentiates from the optic lobe in the Stage VI, just before katatrepsis. It is delaminated from the lobe and composed of single or partly double-layered columnar cells. After katatrepsis the optic plate joins the optic lobe with the postretinal fiber. Then Semper's cells and retinal cells differentiate in the optic plate. A crystalline cone is formed as a hyaline vacuole by 4 Semper's cells which are close together. A compound eye of *B. brevitubus* has only two ommatidia in the first larval stage. Two sets of the 4 Semper's cells can be observed on each side of the embryonic head (Fig. 20). In the Stage X, the crystalline cones are nearly completed and brownish dark red pigments are formed in each ommatidial rudiment. The corneageous cells are not distinct but the cornea is formed just before hatching.

C.   Stomatogastric Nervous System

In the Stage V and VI, as the developing stomodaeum is prolonged, few neuroblasts develop in its thickened dorsal wall, but it is difficult to recognize their daughter cells because size and form of these daughter cells are very similar to the stomodaeal wall cells.

The elongate cell mass forms a dorsal ridge on the stomodaeum, and the mass is occupied by a round portion made of neurofibrous substances surrounded by coarsely arranged cells which are not separated from the stomodaeal wall.

The stomatogastric nerve of *B. brevitubus* is derived from the dorsal wall of the stomodaeum in the Stage VIII.

In the next stage, its anterior portion largely develops to form the frontal ganglion while the posterior portion forms a hypocerebral ganglion, and the rest develops into the recurrent
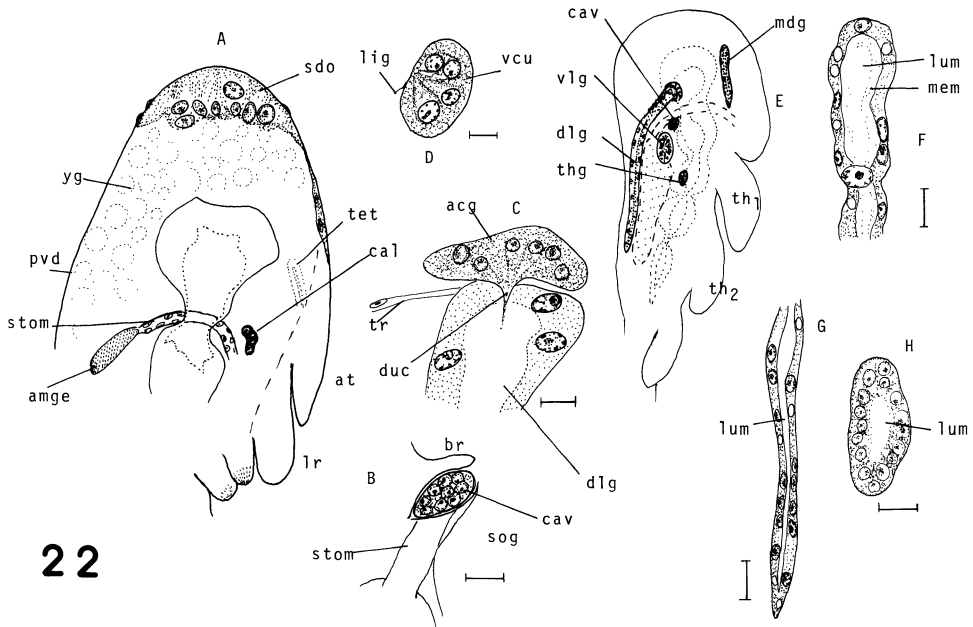
Fig. 22. Ectodermal invaginations in *B. brevitubus*.
A. Stage VIII, sagittal section.
B. Stage X, corpus allatum-like gland.
C. Stage X, terminal portion of dorsal labial gland and accessory organ.
D. Stage X, prothoracic gland-like structure.
E. Stage XI, showing position of glands.
F. Stage X, mandibular gland.
G. Stage IX, dorsal labial gland.
H. Stage IX, ventral labial gland.
Scales : for C, D 5 μm, for B, F, G, H, 10 μm

amge anterior mid-gut epithelium,   acg accessory organ of dorsal labial gland,   at antenna,
br brain,   cal corpus allatum-like gland,   duc duct of gland,   dlg dorsal labial gland,   lig
ligament,   lr labrum,   lum lumen,   mg mid-gut,   mdg mandibular gland,   mem mem-
branous structure,   pvd provisional dorsal closure,   sdo secondary dorsal organ,   sog
suboesophageal ganglion,   stom stomodaeum,   tet tentorium,   tgs prothoracic gland-like
structure,   th$_{1-2}$ thoracic leg,   tr trachea,   vcn vacuolar cytoplasm,   vlg ventral labial
gland,   yg yolk globule.

nerve.

At the lateral sides of the hypocerebral ganglion, a pair of tiny glandular cell groups is formed in the Stage X. These may be the rudiments of the corpus cardiacum and the corpus allatum which anastomose each other (Fig. 21).

Some fibrous cytoplasmic projections extending into the epipharynx from the anterior wall of the stomodaeum are observed after formation of the frontal ganglion.

Ectodermal Invagination

Several ectodermal invaginations in the gnathal and thoracic regions of the germ-band may be observed in the pre-revolution stage. They are the tentoria, mandibular and labial glands, corpora allata and a gland in mesothorax.

A pair of tentorial invaginations appears in the ventrolateral sides of labral rudiments at the late Stage IV, but it does not develop deeply. Although position of the labral rudiments moves posteriorly to form a mouth-cone, the invaginations of tentoria remain their original positions and their shallow appearance hardly changes. These tentorial invaginations make a pair of pits on the larval and adult head capsule, but these positions somewhat move asymmetrically according to the asymmetric development of the mouth-parts, as occurred in *H. verbasci* (Heming, 1980). In *B. brevitubus* only the anterior arms of the tentoria develop, while in the adult head of primitive thrips, *Aeolothrips fasciatus,* the posterior tentorial arms also develop (Mickoleit, 1963).

As already stated, a pair of mandibular rudiments is formed, and the size of right rudiment becomes gradually smaller than the left through katatrepsis. In the Stage VI, however, the invaginations appear in the ventrolateral sides of the mandibular segment, the left side of which forms a stylet-forming cell mass and the right one transforms into a tubular gland situated in the ventral right side of the head capsule in the Stage X. The tubular nature and cell size of the gland are similar to the dorsal labial gland, but the secreting duct cannot be observed.

Peterson (1915) observed the similar unpaired structure in *Heliothrips femoralis* (Terebrantia) adult head and called it the head gland. Later, Sharga (1933) also described an unpaired salivary gland near the mouthparts in *He. haemorrhoidalis.* Probably they are the same structure with the gland derived from the mandibular invagination in *B. brevitubus.*

In the labial segment, two pairs of glands invaginate in the late Stage IV. One of them elongates along the stomodaeum and finally locates dorsolaterally in the thoracic and abdominal segments. When the pair of glands completely develops, the glands reach the abdominal segment 4 or 5 at Stage XI. They are the dorsal labial gland (long salivary gland). Most part of the gland is a simple slender tube made of a single layer of the vacuolate cells surrounding a narrow lumen, however, the anterior end of the tube reaching the cephalic ganglion becomes enlarged considerably and irregularly deforms with a wider space of the lumen.

There is a proliferating cell mass covering the terminal part of the tube. It looks like as a glandular organ by having rich cytoplasm and a short duct opened into the swollen part of the dorsal labial gland. It is very likely that this cell mass is an accessory organ of the dorsal labial gland.

Another labial invagination is a pair of short and thick ventral labial glands. It is quite
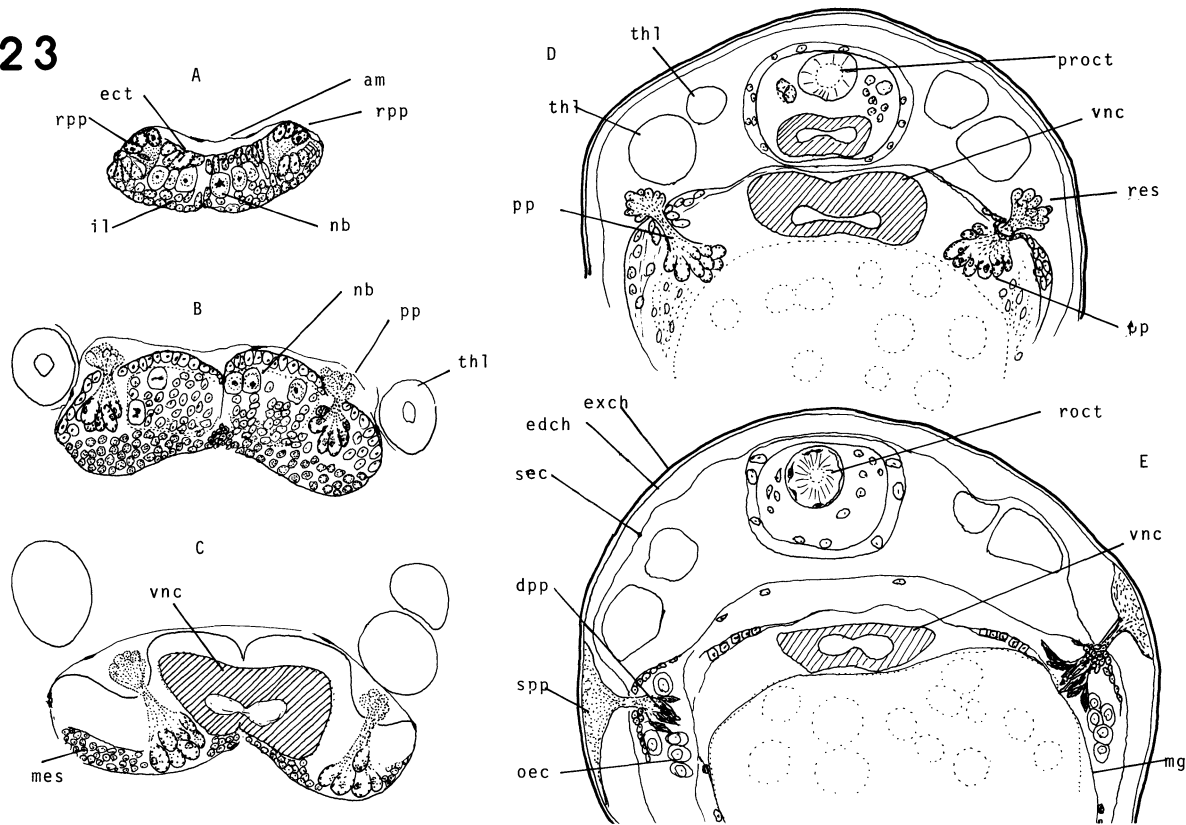
Fig. 23. Development of pleuropodia in *B. brevitubus*.
A. Stage IV, B. Stage V, C. Stage VI, D. Stage VIII, E. Stage IX.

am amnion, dpp degenerating pleuropodium, ect ectoderm, edch endochorion, exch exochorion, il inner layer, mes mesoderm, oec oenocyte, pp pleuropodium, proct proctodaeum, rpp rudimental pleuropodium, res reservoir of pleuropodium, sec serosal cuticle, spp secretion of pleuropodium, vnc ventral nerve cord.

different in structure to the dorsal labial glands. The ventral labial gland is only a cell mass made of 10-15 cells at the beginning, but it obviously develops in Stage IX. Its cells grow up to 15 μm in diameter in which vacuolate secreting substances are stored, and are arranged so as to form single cell layer around a narrow lumen. These vacuoles are basophil and well stained but young ones are not stained. The ventral labial glands gradually move towards in the mesothorax and the position of them is finally fixed on the ventral sides of the sub-oesophageal ganglion. A fine duct threads to the buccal cavity near the hypopharynx.

Another pair of glandular organs can be found in embryos of the post-revolution stage. It is a small oval body consisting of a few large cells and situates inside of the mesothoracic stigma near the base of coxa of the mesothoracic leg. Though it is not in the prothorax, it is very likely that this cell mass is the prothoracic gland rudiment. However, its origin and fate are still unknown.

Pleuropodium

The embryos of *B. brevitubus* have a pair of pleuropodia on their 1st abdominal segments. The first sign of the pleuropodium formation appears in the late Stage IV, which is a glomerate mass of a few cells separating from surrounding ectoderm in the ventrolateral sides of the segment. In the Stage V, the pleuropodial cells develop columnar and ventrally project their cytoplasm from the embryonic body wall.

In the Stage VI, the pleuropodia develop further, and their basal parts sink into the mesodermal layer, whereas the apical parts elongate and become tongue-shaped. This tongue-shaped apical part ruptures in the Stage IX.

The secretion from the pleuropadia is released into the space around the embryo. After the discharge of the secretion the pleuropodia become withered and degenerate. In the next stage, their vestiges are only observed among the oenocytes which are formed in the Stage VI and develop in Stage VIII and IX. The secreting substances are more thinly diffused, and the vestiges become unrecognizable.

The pleuropodia of *Bactrothrips*, therefore, are of an invaginated type as those of Odonata (Ando, 1953).

In general, the pleuropodia are so conspicuous as an embryonic organ that they are observed in many insect orders. The best known function of the pleuropodia is the secretion of the hatching enzyme in the American grasshopper, *Melanoplus differentialis* (Slifer, 1937). However, the pleuropodia in the embryos of Odonata and *B. brevitubus* are seen to degenerate by the time of hatching. Bournier (1966) observed that the pleuropodia of *C. buffai* begin to degenerate just after katatrepsis. He suggested that this organ secretes an enzyme which contributes rupture of the embryonic membranes and acts as the trigger inducing katatrepsis. In *B. brevitubus* and *B. honoris*, however, the secretion lasts through katatrepsis until the Stage IX.

Since the secreted substances from the pleuropodia are distributed along the inner surface of the chorion, it seems that the chorion is affected by them, but the timing of the secretion is too early to change the nature of the chorion and thus consequently conributes hatching of the larvae (Fig. 23).
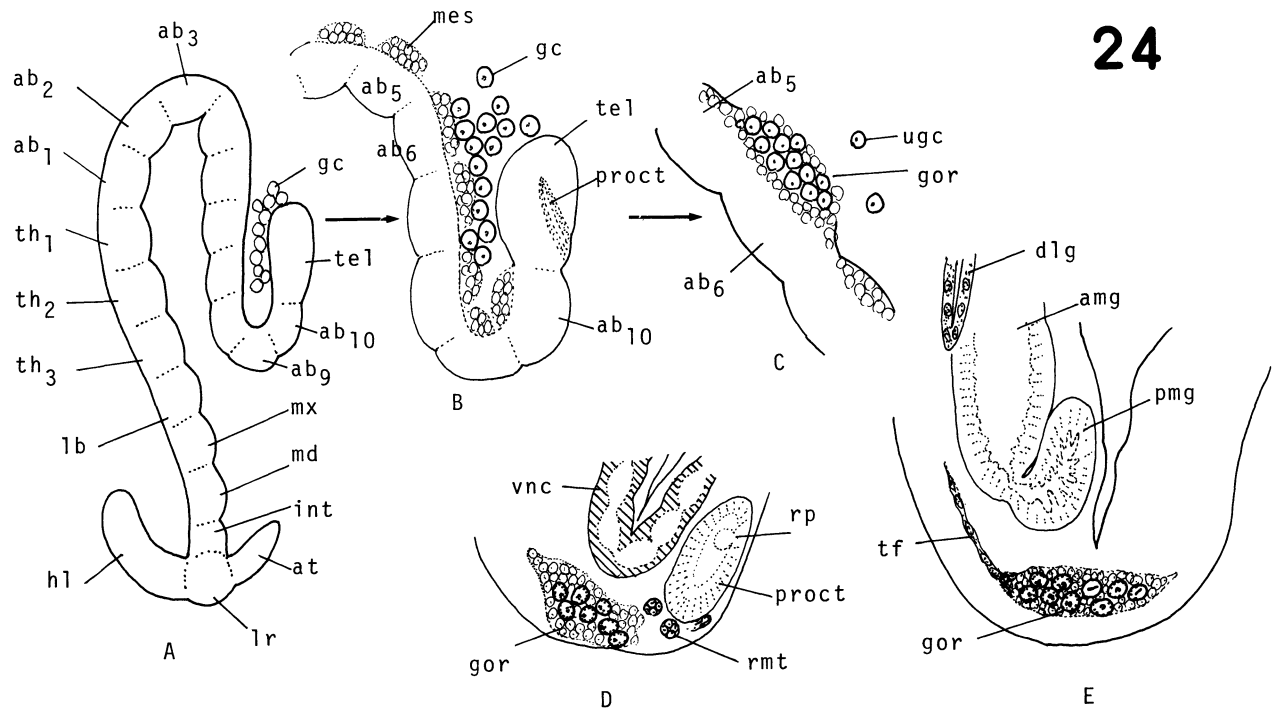
Fig. 24. Gonad formation in *B. brevitubus*.

A-B-C. Stage VI, appendages omitted, diagrammatic, showing enclosing of germ cells.

D. Stage VIII, sagittal section.

E. Stage X, sagittal section.

ab_{1-10} abdominal segment 1-10, amg anterior portion of mid-gut, gc germ cell, gor gonad rudiment, hl head lobe, int intercalary segment, lr labrum, lb labium, md mandible, mx maxilla, proct proctodaeum, pmg posterior portion of mid-gut, rmt rudiment of malpighian tubule, rp rectal papilla, th_{1-3} thoracic segment 1-3, tel telson, tf terminal filament, vnc ventral nerve cord.

Gonad

As mentioned in the previous chapter, the germ cells distribute on the caudal end of the germ-band. They are accompained with the mesodermal cells which are smaller and darker than the germ cells. While the thickening of the germ-band is occurring before katatrepsis, the most germ'cells are enclosed by the inner layer of the abdominal segment 6 or 7. They form a pair of gonad rudiments which move cephalad during katatrepsis and finally situate very close to the 5th abdominal segment. In the Stage VIII and IX, they locate on the fatty tissue of the 4th, 5th and 6th abdominal segments. They are spindle-like in shape and surrounded by thin epithelium derived from the mesodermal cells (Fig. 24).

At the anterior portion of the gonad rudiment the epithelium is seen to become a non-cellular thread which elongates towards the distal end of the dorsal labial gland of the same side. The posterior portion of the rudiment also elongates, but forms a cellular tubular structure which may transform thinner and becomes the genital duct in both sexes in the future.

In *B. brevitubus* and *B. honoris* the coelomic cavities of every abdominal segments do not develop well.

Some germ cells not enclosed in the abdominal segment are observable near the dorsal wall of the embryo in the Stage VIII. The non-enclosed germ cells of *H. verbasci* have been seen to become the yolk cells (Heming, 1979), but those of *B. brevitubus* seem to be gradually degenerate and absorbed in the yolk.

The mode of gonad formation in *B. brevitubus* is almost identical to that of *H. verbasci* reported by Heming (1979).

Alimentary Canal

As already mentioned the stomodaeum begins to invaginate at about 40 hours after the commencement of the embryonic development (Stage V). The stomodaeal invagination first appears just below the labrum; cells of this part become columnar gradually as the invagination deepens. The stomodaeal end is encircled by a thin membrane consisting of few cells that originated from the inner layer, and they form a muscle layer of the stomodaeum in future (Fig. 27).

Then the stomodaeum elongates into the space between the cephalic lobes and gnathal part of the germ-band. The end of stomodaeum is depressed and slightly expanded, and the cell masses of the mid-gut epithlium are recognized at the end. They grow laterally, forming a pair of ribbons, and the splanchnic mesodermal layer also grows with the ribbon, while the bottom of the stomodaeum is encircled only with a thin membrane.

The proctodaeum is formed in the swollen part of the caudal end of the germ-band, the telson (Fig. 28). In the Stage V, simultaneously with the stomodaeum formation, a pit appears in the ventral side of the telson. The invagination deepens in the Stage VI, just before katatrepsis. Its wall is thicker than that of the stomodaeum. A part of the inner layer of the 10th abdominal segment is crowded out in the space between the germ-band and the yolk, and covers the proctodaeal end. A pair of the posterior rudiments of the mid-gut epithelium is formed on the apical margin of the proctodaeum in the same manner as the anterior ones (Fig. 29).

In the Stage VI, 4 glomerate cell masses consisting of 4 or 5 cells are formed in the swollen caudal part of germ-band where occurrence of the proctodaeum is expected (Fig. 28), and the proctodaeum is seen to occur after they are formed. These cell masses are the rudiments of the malpighian tubules.

The rudiments of the malpighian tubules, in general, evaginate from the blind end of the proctodaeum in the stage of katatrepsis both in exopterygotes (Heymons, 1895; Roonwall, 1937; Butt, 1949; Goss, 1953; Ando, 1962) and endopterygotes (Henson, 1932; Butt, 1934; Okada, 1960; Miyakawa, 1975). In *B. brevitubus*, however, the rudiments are formed in the ectoderm of the telson as two pairs of glomerate cell masses before the invagination of the proctodaeum. This fact shows that the malpighian tubule is truly ectodermal in origin.

This also indicates that the method of malpighian tubule formation employed by *B. brevitubus* is thus entirely different from that by other insect embryos.

The number of the malpighian tubule rudiments has been considered phylogenetically significant, and varies one to three pairs depending on the insect groups. Johannsen and Butt (1941) stated that three pairs of the rudiments apparently being the primitive number. The embryos of *B. brevitubus* have two pairs of the rudiments, and the number may not change even in the adult.

In the lateral view the developing stomodaeum becomes arched posteriorly as a result of the condensation of the gnathal and thoracic segments, and the position of the oral opening also shifts posteriorly before katatrepsis. At the same stage some cell masses are formed inside the proctodaeal wall. They are the rudiments of rectal papillae, which are globular at first, but they are protruded into the lumen afterward. Five rudiments of the rectal papillae are observed in the embryos of *B. brevitubus*, whereas four of them may be found in the adults of other thrips (Jordan, 1888; Uzel, 1895; Sharga, 1933). The developing proctodaeum also contains granular substances which are stained weakly blue by haematoxylin and transform into a thin membranous structure in the Stage IX.

In the Stage VIII, the anterior rudiments of the mid-gut epithelium mentioned before develop as a pair of slender ribbons which direct towards the proctodaeal bottom at the position close to embryonic dorsum (Fig. 30A); the posterior rudiments elongate similarly towards the stomodaeal bottom. These ribbons meet with each other medially, forming a ring-like structure in cross sections, which is oblong anteroposteriorly as shown in Fig. 30. The ring is, then, seen to stretch dorsoventrally in the Stage X.

In this stage, the yolk ocuupies dorsal half of the egg, ranging from the secondary dorsal enlarges, the yolk is consumed and decreases in volume. The position of the secondary dorsal organ is seen to shift slightly posteriorly towards the posterior end of the egg, and finally degenerates within the yolk which is enclosed by the developing mid-gut epithelium. degenerates within the yolk which is enclosed by the developing mid-gut epithelium.

After katatrepsis, there can be observed many yolk cells (vitellophages) distributed all over the yolk, somewhat dense cortically (Fig. 25). They are almost the same in size and shapes, and sometimes two or three yolk cells are seen to aggregate. The yolk cells flatten and expand to form very thin interstitial membranes which envelop yolk globules. At the outermost part of the yolk, these membranes fuse with each other and form a thin, loose and porous membrane enveloping the entire yolk mass.

The enveloped yolk globules are gradually liquefied, a little part of which later flows out of the membrane. The formation of the membrane and the yolk-liquefying begin before the
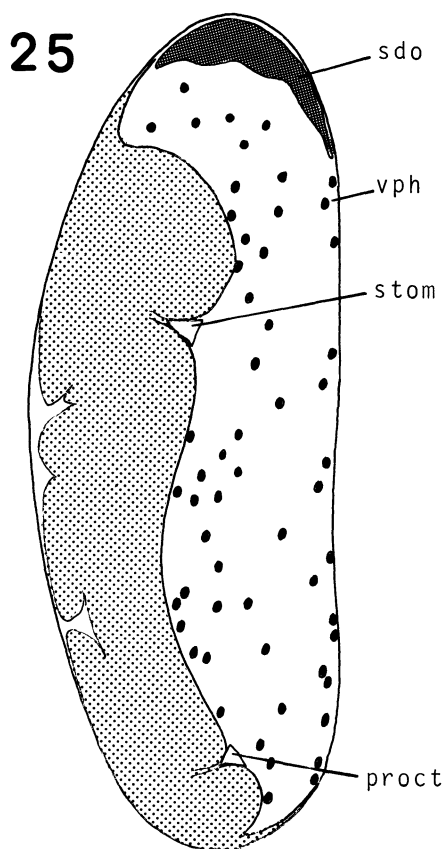
25

Fig. 25.　Distribution of yolk cells in Stage VIII embryo in *B. brevitubus*. (Reconstracted by serial 17 sagittal sections of a specimen)

proct proctodaeum,　sdo　secondary dorsal organ,　stom stomodaeum, vph vitellophage.

completion of the mid-gut.

Before the definitive dorsal closure the posterior mid-gut epithelium near the proctodaeal bottom evaginates to form a small chamber. The chamber (posterior portion of mid-gut; Sharga, 1933) does not contain any yolk fractions at first, but later, the liquefied yolk may often be found in the lumen of this chamber, most probably flowed in from the main part of the mid-gut. Since this portion so as to become more narrower and finally forms a loop in the Stage IX, the cross sections of the embryos at this part show three rings of the mid-gut.

The stomodaeal bottom partially forms the cardiac valve which consists of several thick cells arranged circularly. From the cardiac valve to the anterior third of the mid-gut, the epithelial cells transform into tongue-like villi. The distal part of these cells contains a large vacuole, which is often separated from the cells. These cells may be recognized as secretory, and it is likely that the cut-off parts are holocrine particles. The rest of the mid-gut epithelium (posterior two-thirds of the mid-gut) consists of flat and thin cells, each of which also contains a developing vacuole. In Fig. 31., these structures of the mid-gut epithelium are shown.

The spanchnic mesodermal layer which envelops the mid-gut epithelium develops in close association with the mid-gut ribbons. The single mesodermal layer is recognized in the Stage VIII and IX, but in early Stage X, thinly expanded cells appear upon the layer. They are
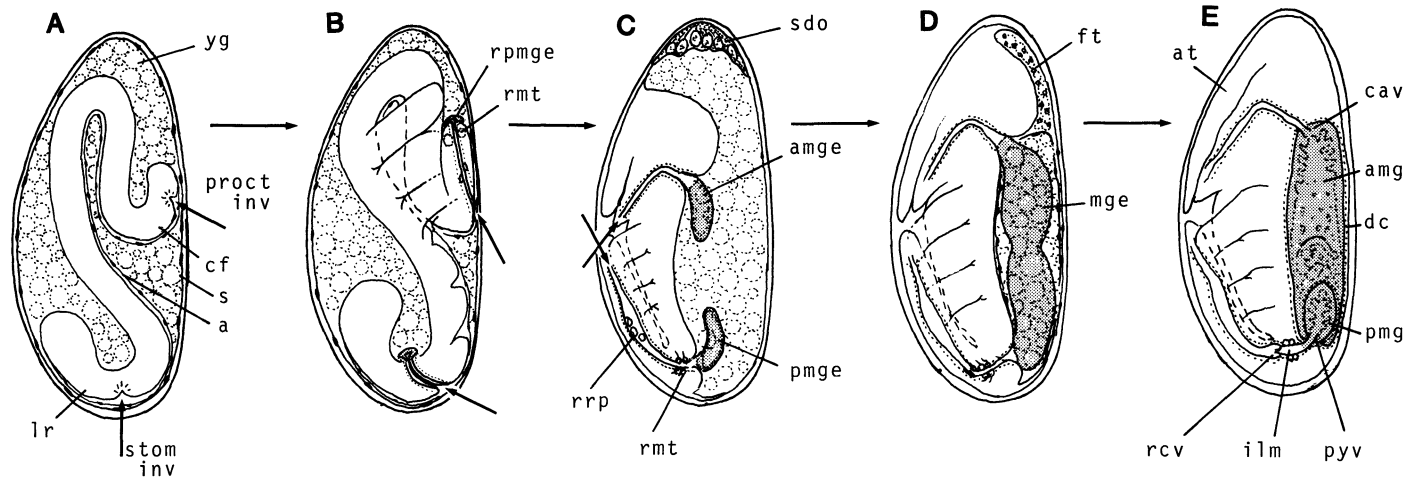
Fig. 26. Mid-gut formation in *B. brevitubus,* diagrammatic.
A. Stage IV,   B. Stage VI,   C. Stage VIII,   D. Stage IX,   E. Stage X.
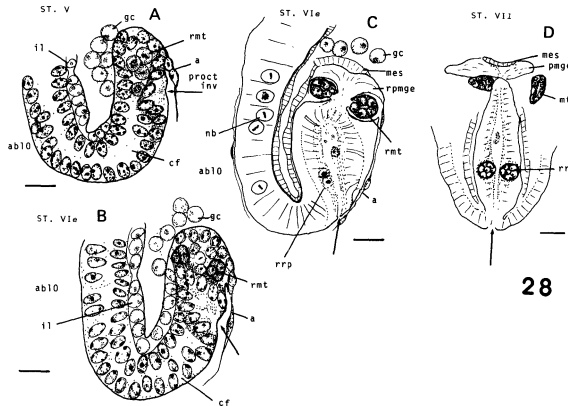
am amnion,   amge anterior mid-gut epithelial rudiment,   at antenna,   amg anterior portion of mid-gut,   cf caudal flexure,   cav cardiac valve,   dc dorsal closure,   ft fatty tissue,   ilm ileum,   lr labrum,   mge mid-gut epithelium,   pmg posterior portion of mid-gut,   pmge posterior mid-gut epithelium,   proct inv invagination of proctodaeum,   pyv pyrolic valve,   rcv rectal valve,   rmt malpighian tubule rudiment,   rrp rudiment of rectal papilla,   stom inv invagination of stomodaeum,   ser serosa,   sdo secondary dorsal organ,   yg yolk globule.
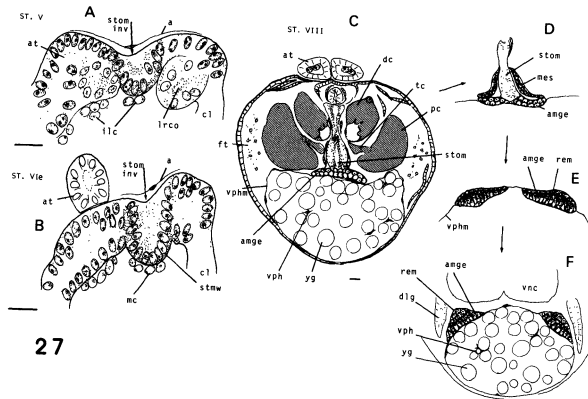
Fig. 27. Development of stomodaeum and anterior mid-gut epithelial rudiment in
B. honoris. Scale : 10 μm
A. Stage V, sagittal section, B. Early Stage VI, sagittal section, C-E. Stage
VIII, cross sections. (C. across brain, D, across thorax, E. across 4th ab-
dominal segment).

am amnion, amge anterior mid-gut epithelial rudiment, at antenna, cl cephalic lobe,
dce deutocerebrum, dlg dorsal labial gland, ft fatty tissue, ilc inner layer cell, mc
mesodermal cell, mes mesoderm, pc protocerebrum, rem rudiment of visceral muscle,
stom stomodaeum, stom inv invagination of stomodaeum, stw stomodaeal wall, vnc
ventral nerve cord, vph vitellophage, vphm membrane made by vitellophages, yg yolk
globule.

Fig. 28. Development of proctodaeum and posterior mid-gut epithelial rudiment in
B. honoris (Pre-revolution stage).
A. Stage V, sagittal section. B. Early Stage VI, sagittal section. C. Stage VI,
sagittal section. D. Late Stage VI, horizontal section.

ab_{10} 10th abdominal segment, am amnion, cf caudal flexure, gc germ cell, il inner
layer, mes mesoderm, mt malpighian tubule, nb neuroblast, proct inv invagination
of proctodaeum, pmge posterior mid-gut epithelial rudiment, rmt malpighian tubule
rudiment, rrp rudiment of rectal papilla.
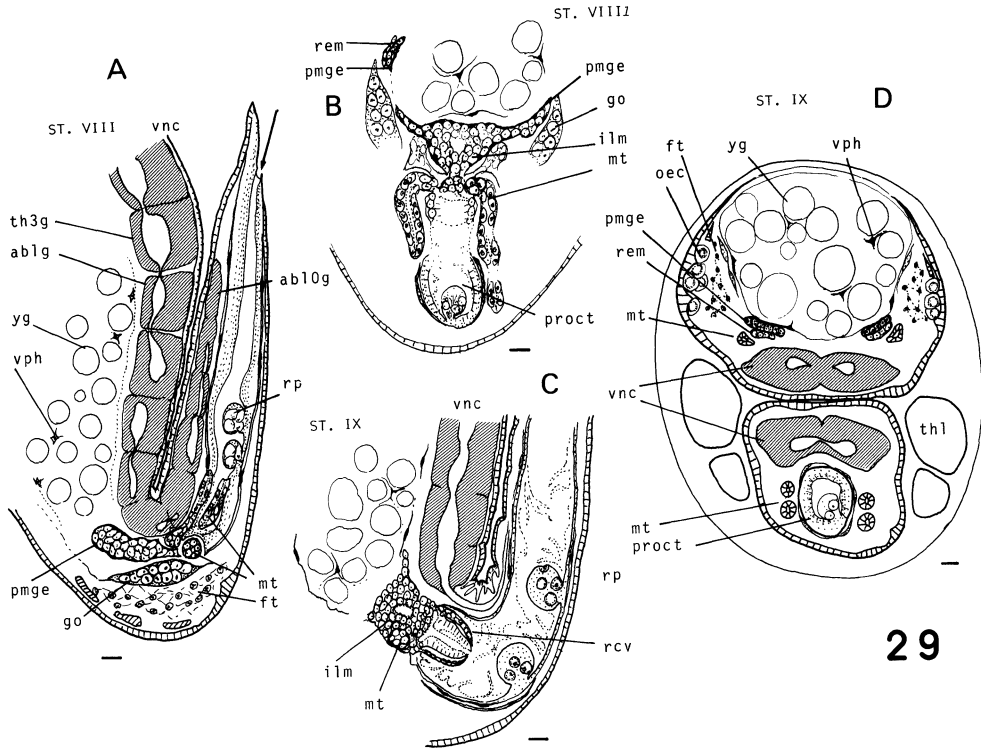
Fig. 29. Development of proctodaeum and posterior mid-gut epithelial rudiment in
B. honoris (post-revolution stage).
A. Stage VIII, sagittal section.   B. Late Stage VIII, horizontal section.
C. Stage IX, sagittal section. D. Stage X, cross section.

ab$_1$ g ganglion of 1st abdominal segment,   ft fatty tissue,   go gonad rudiment,   ilm ileum,
mt malpighian tubule,   oec oenocyte,   pmge posterior mid-gut epithelial rudiment,
proct proctodaeum,   rcv rectal valve,   rem rudiment of visceral muscle,   rp rectal
papilla,   th$_1$ 1st thoracic segment,   th$_3$ g ganglion of 3rd thoracic segment,   vnc ventral
nerve cord,   vph vitellophage,   yg yolk globule.

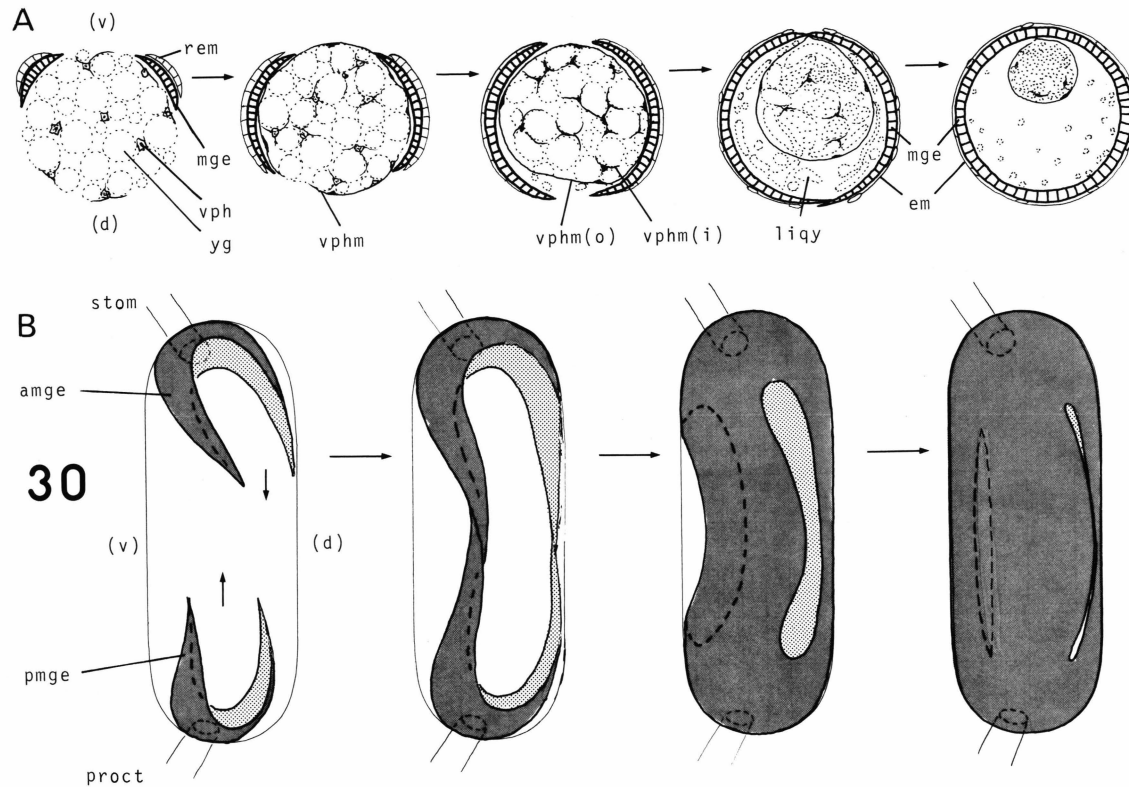Fig. 30. Mid-gut formation in *B. brevitubus* and *B. honoris*, diagrammatic.
A. Cross view.   B. Lateral view.

amge anterior mid-gut epithelial rudiment,   em visceral muscle,   liqy liquefied yolk,
mge mid-gut epithelium,   rem rudiment of visceral muscle,   stom stomodaeum,   vph
vitellophage,   vphm membrane made by vitellophages,   yg yolk globule.   (v) ventral,
(d) dorsal,   (o) outer,   (i) inner.
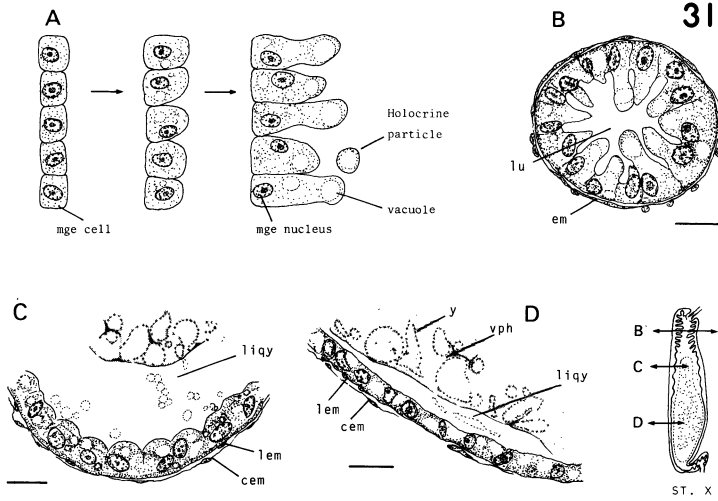
Fig. 31. Development of mid-gut epithelium.
A. Development of tongue-like holocrine tissue in *B. brevitubus* and *B. honoris*, diagrammatic.   B. Cross sections of embryonic mid-gut at Stage X in *B. honoris*, showing well or less developed villous tissues of three portions indicated by arrows. Scale : 10 μm.

cem circular visceral muscle,   em visceral muscle,   lem longitudinal visceral muscle,   liqy liquefied yolk,   lu lumen,   mge mid-gut epithelium,   vph vitellophage,   y yolk.

Fig. 32. Adult (A) and embryonic (B) alimentary canals in *B. brevitubus* compared with *Haplothrips distinguendus* (Sharga, 1933).

coarsely distributed, and later differentiate into longitudinal and circular muscles around the mid-gut at the end of the Stage X.

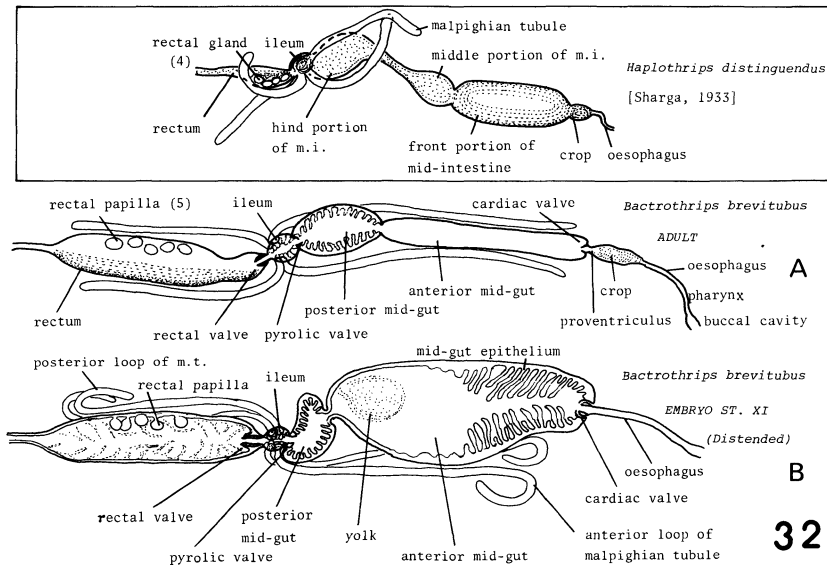The pyloric valve is formed between the posterior portion of the mid-gut and the proctodaeal bottom. It is more simple than the cardiac valve, and consists of flat cells which are arranged to form a ring.

Just posterior to the pyloric valve, a slightly swollen part of the mid-gut may be observed, into which the malpighian tubules open. Sharga (1933) called this portion the ileum in the adult thrips.

Additionally one more type of the valve is distinctly formed between the ileum and rectum which may be called the rectal valve. It is a nozzle-like valve being formed by the invagination of the proctodaeal wall. Heming (1979) has recognized this nozzle-like valve as the pyloric valve in *H. verbasci,* but it did not occur at the end of the mid-gut.

In the late Stage XI (Full-grown embryo), the yolk is completely liquefied and almost consumed in the mid-gut, then the membranes formed by vitellophages disappear. Most of the anterior portion of the mid-gut becomes empty, while a few yolk fractions are in the rest of the mid-gut.

Malpighian tubules develop both anteriorly and posteriorly, and a loop is formed at their distal portions. The anterior pair of malpighian tubules occur at the ventral side of the ileum and reaches the metathorax, while the posterior pair derives at the dorsal side of the ileum, and reaches the 9th abdominal segment.

The stomodaeum in the embryonic stage does not further differentiate to form into the crop and preventriculus.

The mid-gut formation in insect embryos is still controversial, but is summarized into three types (Roonwall, 1939; Johannsen and Butt, 1941; Ando, 1970): Type I. Mid-gut epithelium is formed mainly by yolk cells; Type II. Mid-gut rudiments are derived from the stomodaeum and/or the proctodaeum; Type III. Mid-gut epithelium is formed by the mid-gut rudiments, and a part of the inner layer. The first type is known in Collembola, Thysanura, Odonata. The last type is observed in *Phyllobius glaucus* (Coleoptera, Jura, 1956) and others. The most pterygote insects belong to the second type, and the present materials, *B. brevitubus* and *B. honoris* represent Type II, a typical bipolar formation of the mid-gut.

Discussion

By the present study and recent works mentioned at the beginning of this paper, the knowledge on the oogenesis and embryogenesis in the Thysanoptera has become increased. Though information on these subjects is still unsatisfactory, it may now be possible to compare the Thysanoptera with other insects of related orders.

The order Thysanoptera belongs to the Paraneoptera (= Acercarida of Boudreaux,1979). Usually the Paraneoptera consists of six orders/suborders, namely, Psocoptera, Mallophaga, Anoplura, Thysanoptera, Homoptera and Heteroptera. This group considered as the most evolved in the Exopterygota (= Hemimetabola).

As shown in Table 4, the embryogenesis of only a limited number of the insects belonging to those taxa have so far been studied. Further study of embryogenesis occurring in the insects which occupy phylogenetically important status in these insect orders seems to be very necessary.

Table 4. . List of insects embryologically studied in paraneopteran orders.

PSOCOPTERA

Archipsocus fernandi	Fernando, 1934
Liposcelis divergens	Goss, 1952, 53
Liposcelis bostrychophilus	Seeger, 1979
Lepinotus patruelis	Seeger, 1979
Psyllipsocus ramburi	Seeger, 1979
Prionoglaris stygia	Seeger, 1979
Ectopsocus meridionalis	Seeger, 1979

ANOPLURA

Pediculus humanus	Schölzel, 1937
Pediculus vestimenti	Piotrowski, 1953
Phthirus pubis	Schölzel, 1937
Pedicinus rhesi	Schölzel, 1937
Linognathus vituli	Schölzel, 1937
Haematopinus eurysternus	Schölzel, 1937
Haematopinus suisi	Young, 1953

MALLOPHAGA

Columibicola columbae	Schölzel, 1937
Gyropus ovalis	Schölzel, 1937
Trichodectes scalaris	Schölzel, 1937

HETEROPTERA

Rhodnius prolixus	Mellanby, 1935, 36
Oncopeltus fasciatus	Newcomer, 1948; Butt, 1949
Gerris paludum	Mori, 1969, 76

HOMOPTERA

Siphanta acuta	Muir and Kershaw, 1912
Icerya purchasi	Shinji, 1919, 24
Macrosiphum tanaceti	Uichanco, 1924
Lecaniodiaspis prumosa	Shinji, 1924
Pyrilla perpusilla	Sander, 1956

THYSANOPTERA

Thrips physapus	Uljanin, 1874
Heliothrips haemorrhoidalis	Reyne, 1927
Caudothrips buffai	Bournier, 1966
Haplothrips verbasci	Heming, 1979, 80
Bactridothrips brevitubus	Ando and Haga, 1974

Table 5. Comparison in ovary and egg among paraneopteran orders.

	PSOCOPTERA	MALLOPHAGA	ANOPLURA	THYSANOPTERA	HOMOPTERA	HETEROPTERA
Ovarian type	Polytrophic	Polytrophic	Polytrophic	Panoistic	Telotrophic	Telotrophic
Ovariole/ovary	3 - 5	3 - 5	5	4	2 - 25	2 - 8
Micropyle :	Absent	Present	Present	Absent or present	Present	Present
Symbiont	Absent	Present or absent	Present	Absent or present	Present	Absent or present
Oosome	Absent	Absent	Absent	Present	Absent	Absent

Table 6. Comparison in the early embryogenesis among paraneopteran orders.

	PSOCOPTERA	MALLOPHAGA	ANOPLURA	THYSANOPTERA	HOMOPTERA	HETEROPTERA
Cleavage center	Center	Center	Ant. 1/3	Post. 1/3	Ant. 1/3	Center
Synchrony	6th	8th	8th	3rd, 4th	7th	7th
Energid migration	After 7th	After 8th	After 8th	After 7th	After 9th	After 8th
Energid distribution	Uneven	Even	Even	Uneven	Even	Even
Primary yolk cell	−	+	+	+	+	+
Secondary yolk cell	+	−	−	+	+	+
Yolk cleavage	−	+	+	−	−	−
Inner layer formation	Proliferation	Invagination	Invagination	Proliferation	Invagination	Invagination

Table 7. Comparison in the organogenesis among paraneopteran orders.

	PSOCOPTERA	MALLOPHAGA	ANOPLURA	THYSANOPTERA	HOMOPTERA	HETEROPTERA
Coelomic Cavities	Developed	III developed	III developed	III developed	Developed	Developed
Mid-gut formation *	II	II + III	II + III	II	II	II or IP
Tentorium	Developed	III developed	III developed	III developed	Developed	Developed
Ganglia ** concentration	T1+2+3, Al	T1+2+3, AO	T1+2+3, AO	T1, T2+3, Al	T1+2+3, AO	T1+2+3, AO
Malpighian tubule rudiment	4	4	4	4	2 - 4	4
Rectal papilla	4 - 5	6	>4	4, 5	4 - 5	4 - 5

* Signs after Ando (1970).
** T thoracic ganglion, A abdominal ganglion, + fused, 1-3 segment (ganglion), without ganglion.
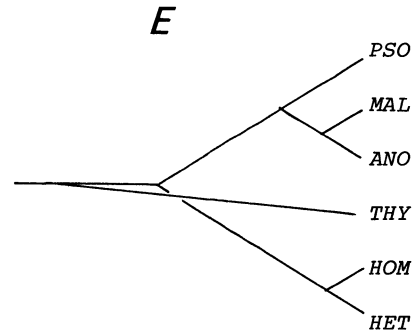
A

```
PARANEOPTERA ┬ PSOCOPTEROID ┬ PSOCOPTERA
              │               ├ MALLOPHAGA
              │               └ ANOPLURA
              ├ THYSANOPTEROID
              │               ─► THYSANOPTERA
              └ HEMIPTEROID ┬ HOMOPTERA
                            └ HETEROPTERA
```

B

```
ACERCARIDA ┬ PSOCODIDA ─── ┬ PSOCIDA         ─┬ CORRODENTIA
           │                └ PHTHRIAPTERIDA ┬ MALLOPHAGA
           │                                  └ ANOPLURA
           └ CONDYLO-    ┬ THYSANOPTERIDA ─┬ THYSANOPTERA
             GNATHIDA     └ HEMIPTERIDA ───┬ HOMOPTERA
                                            └ HETEROPTERA
```

C

```
                    PSO
                    MAL
                    ANO
                    THY
                    HOM
                    HET
```

D

```
                    PSO
                    MAL
                    ANO
                    THY
                    HOM
                    HET
```

E

```
                    PSO
                    MAL
                    ANO
                    THY
                    HOM
                    HET
```
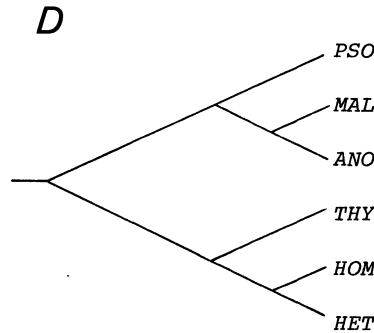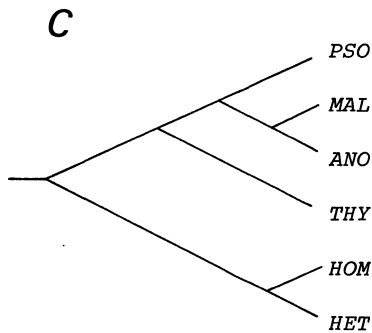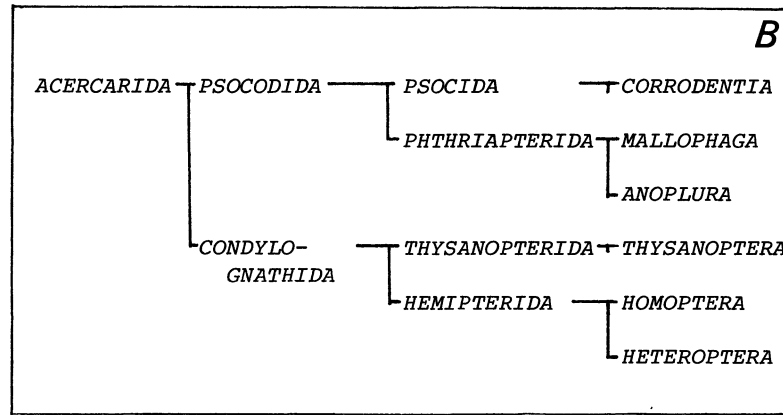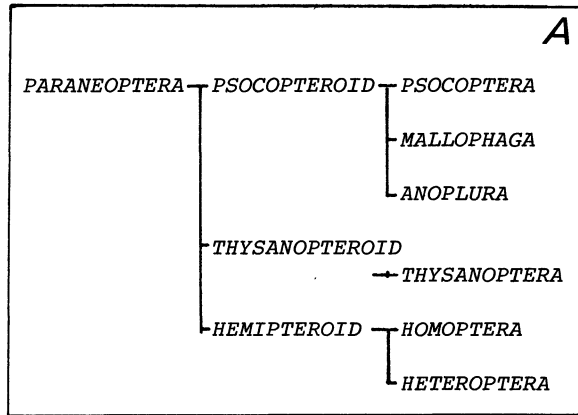
33

Fig. 33. Classification and phylogeny of the Paraneoptera, or Acercarida.
A. Pesson, 1951. B. Boudreaux, 1979.
C., D., E. Three types of the phylogeny of Paraneoptera.

The comparison of these orders was done on 19 characters which have a common or nearly common state in the ovarian and egg structures, early embryogenesis and organogenesis of each paraneopteran orders.

Comparison of Embryonic Development in the Paraneopteran Orders

A. Comparison of Ovary and Egg (Table 5)

Paraneopteran ovarian types can be classified into three categories, *i. e.,* the polytrophic type of the Psocoptera, Mallophaga and Anoplura, the telotrophic type of the Homoptera and Heteroptera, and the panoistic type of the Thysanoptera, respectively. The last type is considered as primitive plesiomorphic form.

On the other hand, Heming (1979) found out the oosome of *H. verbasci* egg, and the present author confirms it in the eggs of *B. brevitubus* and *B. honoris.* The oosome is often observed in the holometabolous insect eggs, but is scarsely known from the eggs of the other paraneopteran orders.

The mycetome exists in thrips eggs of the Idolothripinae, but does not exist in the Phlaeothripinae as like as those in the Psocoptera. On the contrary, the micropyle is only found in *H. verbasci* egg, and the author could not find it in *B. brevitubus* and *B. honoris.* The psocopteran *Liposcelis divergens* also lacks the micropyle in its eggs.

B. Comparison of the Early Embryogenesis (Table 6)

Generally the position of the cleavage center locates in the center or in the anterior half of the insect eggs, however, in the Thysanoptera *B. brevitubus, B. honoris* and *H. verbasci,* it locates in the posterior half of the egg. The cleavage synchrony observed in *B. brevitubus* lasts only until the 3rd cleavage, much shorter than that in the other orders.

Usually the energid density becomes even in the any part of the egg until just before blastoderm formation. However, in *B. brevitubus* it remains uneven distribution, dense in the posterior half and rare in the anterior half up to the period of the blastoderm formation.

The yolk cleavage is known in the Mallophaga and Anoplura, but it does not occur in the eggs of *B. brevitubus.*

It is said that the method of inner layer formation is phylogenetically significant even though there are exceptions. Three types of inner layer formation have been known, namely, invagination, overgrowth and proliferation, respectively. In the Paraneoptera the difference in the method may show certain relationships among them. In the Thysanoptera the inner layer is formed by the proliferation type like that in the Psocoptera, in contrast with the other four orders which have the invagination type.

C. Comparison in the Organogenesis (Table 7)

Concerning the formation of the coelomic cavity and tentorium, the Paraneoptera can be divided into two groups, *i. e.,* Psocoptera-Homoptera-Heteroptera group (developed) and

Mallophaga-Anoplura-Thysanoptera group (ill-developed). On the other hand, when ganglia of the ventral nerve cord concentrate anteriorwards and make synganglia, the abdominal ganglia still remain as a block in the Psocoptera and Thysanoptera, but they are completely contracted and coalesced with the thoracic ganglion in the other paraneopteran orders.

The Thysanoptera and most Hemiptera show the typical method in the mid-gut formation, the bipolar formation as described in the previous chapter.

Results of these comparisons may suggest following items:

1. The Mallophaga and Anoplura are close to each other.
2. The Homoptera and Hemiptera are also close to each other.
3. The Psocoptera resembles the all other members.
4. The Thysanoptera is segregated from the other members by having many proper character states.
5. The Thysanoptera positions nearly equidistant from the Psocoptera, Homoptera and Heteroptera, but far from the Mallophaga and Anoplura.

Above-mentioned affinity distances of the paraneopteran orders imply the oldest separation of the Thysanoptera from the other members, and the author agrees with Rodendorf *et al.* (1962) regarding the old ramification occurred before the branching of the psocoptera- and Hemiptera stems.

Pesson (1951) classified the Paraneoptera into 3 subgroups, *i. e.*, Psocopteroid (Psocoptera, Mallophaga and Anoplura), Thysanopteroid (Thysanoptera) and Hemipteroid (Homoptera and Heteroptera) (Fig. 32 A). Recently, Boudreaux (1979) proposed systematics of the supercohort Acercarida (Fig. 32 B). He arranged the Thysanopterida (Thysanoptera) as a subcohort at the same level to the Psocida (Psocoptera), Phthirapterida (Mallophaga and Anoplura) and Hemipterida (Homoptera and Heteroptera). The results of the present study support these classifications, and are more suitable for the former.

As shown in Fig. 32, it can be thought that there are three cladistic patterns concerning the phylogeny of the Paraneoptera (Asahina, 1970; Boudreaux, 1979; Heming, 1979, 1980; Kim and Ludwig, 1978; Mound and O'Neil, 1974; Mound *et al*, 1980; Pesson, 1951; Rodendorf *et al*, 1962; Schliephake, 1975; Schliephake and Klimt, 1979; Seeger, 1979; Sharov, 1972; Stannard, 1957; Wilson, 1971), and the results almost coincide the third type (32 E).

Acknowledgements

Dr. T. Yamasaki of Tokyo Metropolitan University, and to Dr. K. Miyakawa of Gakushuin High School for their helpful advices. His appreciations are extended to Prof. K. Miya of Iwate University and Dr. H. Mori of Tokyo Metropolitan University for their kind reading of the manuscript.

Most part of the present study was done at the Sugadaira Montane Research Center, University of Tsukuba, and the author is indebted to the staff and stayed students of the Center for their friendly supports in various ways.

References

Ando, H., 1953. Studies on the pleuropodium of Odonata. *Sci. Rep. Tokyo Bunrika Daigaku* B7: 167-181.

————, 1962. The comparative embryology of Odonata with special reference to a relic dragon fly *Epiophlebia superstes* Selys. *Jap. Soc. Promt. Sci.* Tokyo 1-225.

————, 1970. Embryonic development. *In* Systematic Zoology, IIIa Arthropoda,, Insecta I: 37-130. Nakayama-shoten, Tokyo. (Japanese)

Ando, H. and K. Haga, 1974. Studies on the pleuropodia of Embioptera, Thysanoptera and Mecoptera. *Bull. Sugadaira Biol. Lab.* 6: 1-8.

Asahina, S., 1970. Phylogeny and classification. *In* Systematic Zoology, IIIa Arthropoda, Insecta I: 203-343. Nakayama-shoten, Tokyo. (Japanese)

Boudreaux, H. B., 1979. Arthropod phylogeny with special reference to insects. John Wiley & Sons, Inc. 1-320.

Bournier, A., 1957. Un deuxiéme cas d'ovoviviparité chez les Thysanoptéres *Caudothrips buffai* Karny (Tubulifére). *Comp. rend. séan. Acad. Sci.* 244: 506-508.

————, 1960. Sur l'existence et l'évolution du corps dorsal secondaire dans l'ontogenése de *Caudothrips buffai* Karny (Thysanoptera, Tubulifera). *Ibid.* 278: 1347-1348.

————, 1962. L'appareil genital femelle de *Caudothrips buffai* Karny et sa pompe spermatique. *Bull. Soc. ent. Fr.* 67: 203-207.

————, 1966. L'embryogenese de *Caudothrips buffai* Karny (Thysanoptera: Tubulifera). *Ann. Soc. ent. Fr. (N. S.)* 11(2): 415-435.

Butt, F. H., 1934. Embryology of *Sciara*. *Ann. ent. Soc. Amer.* 27: 565-579.

————, 1949. Embryology of milkweed bug, *Oncopeltus fasciatus* (Hemiptera). *Cornell. Univ. Agr. Exp. St. Mem.* 283: 1-43.

Fernando, W., 1934. The early embryology of viviparous psocid. *Quart. J. micr. Sci.* 77: 99-119.

Goss, R. J., 1952. The early embryology of the book louse, *Liposcelis divergens* Badonnel (Psocoptera: Liposcelidae). *J. Morphol.* 91: 135-169.

————, 1953. The advanced embryology of the book louse, *Liposcelis divergens* Badonnel (Psocoptera, Liposcelidae). *Ibid.* 92: 158-205.

Haga, K., 1972. Thysanoptera occurring on dead leaves and dead branches. *Ann. Rep. Attached High School Osaka Kyoiku Univ.* 14: 99-112. (Japanese)

————, 1974. Postembryonic development of Megathripine species *Bactridothrips brevitubus* Takahashi (Thysanoptera). *Bull. Sugadaira Biol. Lab. Tokyo Kyoiku Univ.* 6: 11-32.

————, 1975. Female reproductive system of Megathripine species *Bactridothrips brevitubus* (Thysanoptera, Insecta). *Ibid.* 7: 13-24.

Heming, B. S., 1970a. Postembryonic development of the female reproductive system in *Frankliniella fusca* (Thripidae) and *Haplothrips verbasci* (Phlaeothripidae) (Thysanoptera). *Misc. Publ. Entomol. Soc. Amer.* 7(2): 199-234.

——————————, 1970b. Postembryonic development of the male reproductive system in *Frankliniella fusca* (Thripidae) and *Haplothrips verbasci* (Phlaeothripidae) (Thysanoptera). *Ibid.* 7(2): 235-272.

——————————, 1973. Metamorphosis of the pretarsus in *Frankliniella fusca* (Hinds) (Thripidae) and *Haplothrips verbasci* (Osborn) (Phlaeothripidae) (Thysanoptera). *Canad. J. Zool.* 51(12): 1211-1234.

——————————, 1975. Antennal structure and metamorphosis in *Frankliniella fusca* (Hinds) (Thripidae) and *Haplothrips verbasci* (Osborn) (Phlaeothripidae) (Thysanoptera). *Quest. Entomol.* 11: 25-68.

——————————, 1979. Origin and fate of germ cells in male and female embryos of *Haplothrips verbasci* (Osborn) (Insecta, Thysanoptera, Phlaeothripidae). *J. Morphol.* 160(3): 323-343.

——————————, 1980. Development of the mouthparts in embryos of *Haplothrips verbasci* (Osborn) (Insecta, Thysanoptera, Phlaeothripidae). *Ibid.* 164: 235-263.

Henson, H., 1932. The development of the alimentary canal in *Pieris brassicae* and the endodermal origin of the malpighian tubules of insects. *Quart. J. Micr. Sci.* 75: 283-309.

Heymons, R., 1895. Die Embryonalentwicklung von Dermapteren Berücksichtigung der Keimblätterbildung. Gustav Fischer, Jena 1-136.

Johannsen, O. A. & F. H. Butt, 1941. Embryology of insects and myriapods. McGraw-Hill, New York & Lond.: 1-462.

Jordan, K., 1888. Anatomie und Biologie der Physapoda. *Zeit. f. wiss. Zool.* 47: 541-620.

Jura, C., 1956. Embryogenesis of the alimentary system of the weevil, *Phyllobius glaucus* Scop. (Curculionidae, Coleoptera). *Zool. Poloniae.* 7: 155-176.

Kim, K. C. and H. W. Ludwig, 1978. Phylogenetic relationships of parasitic Psocodea and taxonomic position of the Anoplura. *Ann. ent. Soc. Amer.* 71(6): 910-922.

Lewis, T., 1973. Thrips, their biology, ecology and economic importance. *Academic Press,* Lond. & N. Y. 1-349.

Mahowald, A. P., 1972. Oogenesis. In Developmental Systems: Insects. 1: 1-47. Academic Press. London.

Mound, L. A. and K. O'Neill, 1974. Taxonomy of the Merothripidae, with ecological and phylogenetic considerations (Thysanoptera). *J. nat. Hist.* 8: 481-509.

——————————, B. S. Heming and J. M. Palmer, 1980. Phylogenetic relationship between the families of recent Thysanoptera (Insecta). *Zool. J. Linn. Soc.* 69(2): 111-141.

Mellanby, H., 1935. The early embryonic development of *Rhodnius prolixus. Quart. J. Micr. Sci.* 78: 71-90.

——————————, 1936. The later embryonic development of *Rhodnius prolixus. Ibid.* 79: 1-42.

Mickoleit, E., 1963. Untersuchungen zur Kopfmorphologie der Thysanoptera *Zool. Jb. Anat.* 81: 101-150.

Miyakawa, K., 1973. The embryology of the caddisfly *Stenopsyche griseipennis* MacLachlan (Trichoptera: Stenopsychidae) V. *Kontyu* 43: 55-74.

——————————, 1978. A paraffin technique for insect eggs. Gakushu'in Kotoka Kenkyu-Kiyo 9: 17-23. (Japanese)

Mori, H., 1969. Normal embryogenesis of the waterstrider, *Gerris paludum insularis* Motschulsky, with special reference to mid gut formation. *Jap. J. Zool.* 16: 53-67.

——————————, 1976. Formation of the visceral musculature and origin of the midgut epithelium in the embryo of *Gerris paludum insularis* Motschulsky (Hemiptera: Gerridae). *Int. J. Insect Morphol. Embryol.* 5: 117-125. 194-207.

Muir, F. and J. C. Kershaw, 1912. The development of the mouthparts in the Homoptera, with observations on the embryo of *Siphanta. Psyche* 19: 77-89.

Newcomer, W. S., 1948. Embryological development of the mouthparts and related structures of the milkweed bug, *Oncopeltus fasciatus* (Dallas). *J. Morphol.* 82: 365-411.

Okada, M., 1960. Embryonic development of the rice stem-borer, *Chilo suppressalis*. *Sci. Rep. Tokyo Kyoiku Univ.* Sec. B. 9: 243-296.

Pesson, P., 1951. Ordre des Thysanoptera. *In* Traité de Zoologie 10. Grassé ed. Masson, Paris. 1805-1869.

Peterson, A., 1915. Morphological studies on the head and mouthparts of the Thysanoptera. *Ann. Ent. Soc. Amer.* 8: 20-59.

Piotrowsky, F., 1953. The embryological development of the body louse *Pediculus vestimenti* Nitzsch. Part I. *Acta. parasitol. Pol.* 1(3): 61-84.

Reyne, A., 1927. Untersuchungen über die Mundteil der Thysanoptera. *Zool. Jb. Anat.* 49: 391-500.

*Rhodendorf, B. B., O. M. Martinov, E. Y. Bekker-Midgisova, & A. G. Sharov, 1962. Osynovy Palentologii. 1-560. Moscow.

Risler, H. and E. Kempter, 1961. Die Haploidie der Männchen und die Endopolyploidie in einigen gewehen von *Haplothrips* (Thysanoptera). *Chromosoma* 12: 351-361.

Roonwal, M. L., 1936. Studies on the embryology of the African migratory locusta, *Locusta migratoria migratorioides* R. and F. (I). *Trans. Roy, Soc. Lond.* b226: 391-421.

——————, 1937. Ditto (II). *Ibid.* B227: 175-244.

Sander, K., 1956. The early embryology of *Pyrilla perpusilla* Walker (Homoptera), including some observations on the later development. *Aligarh Muslim Univ. Publ. (Zool. Ser.)* 4: 1-61.

Schliephake, G., 1975. Beitrag zur phylogenetischen Systematik bei Thysanopteren. *Beitr. Ent.* 25: 5-13.

——————, and K. Klimt, 1979. Thysanoptera, Fransenflügler: *Die Tierwelt Deutschlands.* 66: 1-477.

Schölzel, G., 1937. Die Embryologie der Anopluren und Mallophagen. *Zeit. f. Parasitenkunde* 9: 730-770.

Seeger, W., 1979. Spezialmerkmale an Eihüllen und Embryonen von Psocoptera im Vergleich zu anderen Paraneoptera (Insecta); Psocoptera als monophyletische Gruppe. *Stuttgartner Beitr. Naturk. A* 329: 1-57.

Sharga, U. S., 1933. On the internal anatomy of some Thysanoptera. *Trans. Roy. ent. Soc. Lond.* 81(2): 185-202.

Sharov, A. G., 1972. On phylogenetic relations of the order of thripses (Thysanoptera). *Revue d'Ent. de l'URSS* 60(4): 854-858.

Shinji, O. G., 1919. Embryology of coccids, with special reference to the formation of the ovary, origin and differentiation of germ cells, germ layers, rudiments of the midgut, and the intracellular symbiotic organisms. *J. Morphol.* 33: 73-167.

——————, 1924. Embryology of coccids with special reference to the origin and differentiation of ovarian elements, germ layers, nervous and digestive systems. *Bull. Imp. Coll. Agr. Fores. Morioka* 6: 1-61.

Slifer, E. H., 1937. The origin and fate of the membranes surrounding the grasshopper egg; together with some experiments of the hatching enzyme. *Quart. J. Micr. Sci.* 79: 493-506.

Stannard, L. J., 1957. The phylogeny and classification of the North American genera of the suborder Tubulifera (Thysanoptera). *Ill. Biol. Monogr.* 25: 1-200.

Uichanco, L. B., 1924. Studies on the embryogeny and postnatal development of the Aphididae with special reference to the history of the "symbiotic organ" or "mycetom", *Philip. J. Sci.* 24: 143-247.

Uljanin, W. N., 1874. Observations on the development of thrips (Physopoda). *Izviastiia Imp. Ob. Luibit Estest. Anth. Ethnogr.* 10: 39-43.

Uzel, H., 1895. Monographie der Ordnung Thysanoptera. *Königgratz* 1-472.

Wilson, S. T., 1971. A revision of the subfamily Heliothripinae of the world. *Univ. Press Xerox Co.* 486 '71: 1-256.

Young, J. H., 1953. Embryology of the mouthparts of Anoplura. *Microentomol.* 18:
    85-133.

(* . . . After Asahina, 1970)

Author's address: Dr. K. Haga,
                                        Institute of Biological Sciences,
                                        University of Tsukuba, Sakura-mura,
                                        Ibaraki, 305 Japan