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Antennal formation of an idolothripine thrips, *Bactrothrips brevitubus* Takahashi (Insecta: Thysanoptera)

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Introduction

The pupa is a non-feeding, generally quiescent stage between the larva and the adult in holometabolous insects. Although this appears to be a resting stage, there are in fact numerous internal changes taking place. These involve the breaking down (histolysis), modification and reconstruction of larval organs and tissues and the differentiation and growth of adult organs.

Although Thysanoptera are classified among the Hemimetabola in which there is no pupal stage, they possess two or three quiescent stages called "pupa(e)" between the larva and the adult. In these "pupal" stages, they are non-feeding and inactive, and there are some histolysis and reconstruction of the cells of the gut, nervous system, body muscles, and especially of head muscles (Reed, 1970; Moritz, 1995). From this notable feature of metamorphosis in thrips, some workers describe this type of metamorphosis as intermediate between holometabolous and hemimetabolous (Miyazaki and Kudo, 1988; cf. Moritz, 1995).

Morphogenetical development in these quiescent stages in Thysanoptera has been reported in detail by Davies (1969) for the skeletal musculature in a thripine thrips, *Limothrips cerealium*; by Heming (1975) for antennal formation in a phlaeothripine thrips, *Haplothrips verbasci* and a thripine thrips, *Frankliniella fusca*; and by Moritz (1989, 1995) for the muscle and nervous systems in a panchaetothripine thrips, *Hercinothrips femoralis*. However, more detailed description, especially for thrips belonging to other subfamilies, is necessary to compare the developmental process in the "pupal" stages of thrips with that in the pupal stage of holometabolous insects. In the present study, we describe the antennal formation, especially morphogenesis of the antennal epidermis and cuticle, in an idolothripine thrips, *Bactrothrips brevitubus*.

Materials and Methods

Adults, pupae and larvae of *Bactrothrips brevitubus* Takahashi were collected at Mt. Tsukuba, Ibaraki Prefecture, Japan. They were anaesthetized by submerging in 70% ethanol for a short time (10–20 sec), and the heads and thoraces were removed from their bodies in fixative (2.5% glutaraldehyde). The heads and thoraces were then dehydrated in a graded ethanol–*n*–butanol series and embedded in paraffin. Serial sections of 5 or 7μm in thickness were stained with Mayer's acid haemalaum and eosin.

Results

Second instar larval stage (Fig. 3)

Each of the antennae consists of a scape (1st), a pedicel (2nd) and four flagellar segments (3rd–6th). The antennal epidermal cells in the early period of this stage line the whole antennal cuticle (Fig. 3a). The intrinsic antennal muscles are found only in the scape segment.

Shortly before the end of this stage, the second larva–first pupal apolysis occurs; that is, the antennal epidermis detaches from the cuticle and withdraws caudally down into the head capsule (Fig. 3b), and then the withdrawn epidermis begins to secrete a thin, folded cuticle of the first instar pupal antenna. The intrinsic antennal muscles in the scape segment completely disappear.

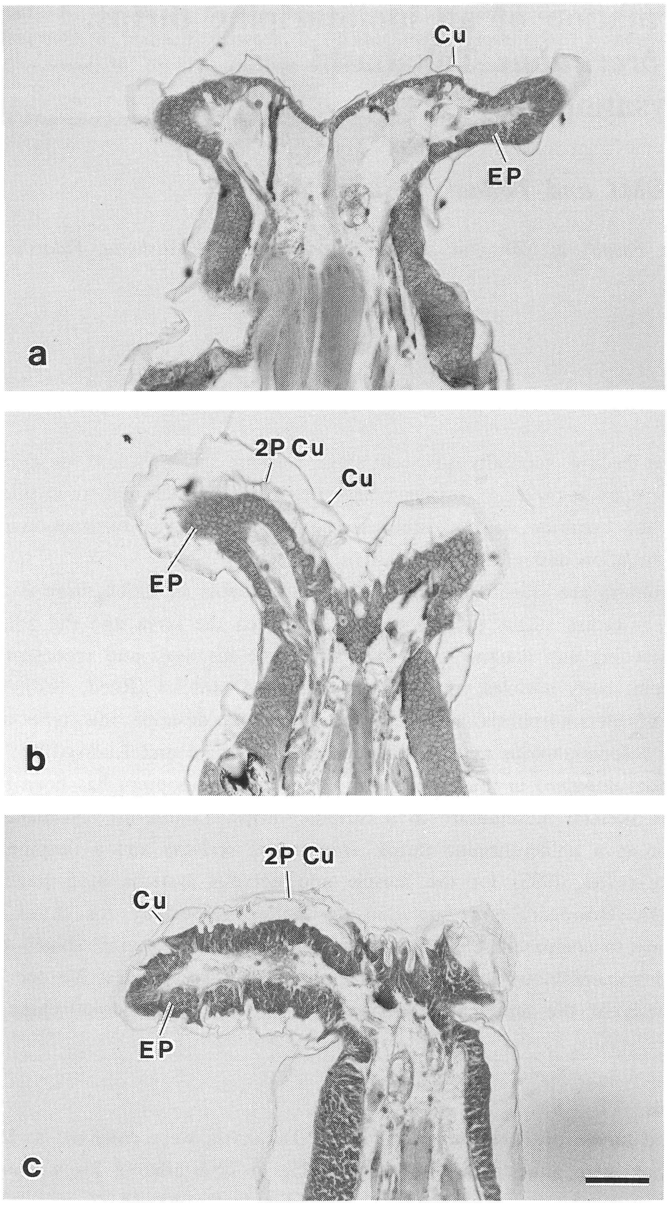


Fig. 1 Horizontal sections of antennal sheaths of *Bactrothrips brevitubus* in the early (a), middle (b) and late (c) first instar pupae. 2P Cu: cuticle of second instar pupa, Cu: cuticle of first instar pupa, EP: epidermis. Scale = 50 μm.

First instar pupal stage (Figs. 1, 4)

As soon as the first instar pupa emerges, the folded antennal cuticle stretches out. The pupal antennae (so-called antennal sheaths) completely lack segmentation (Figs. 1, 2, 4–6). The antennal cuticle is lined with a thin layer of epidermal cells, but as many mitotic divisions occur in these cells, the epidermis gradually thickens.

When the first–second pupal apolysis begins, the antennal epidermal cells separate away from the antennal cuticle (Figs. 1b, 4b) and then begin to secrete a thicker, folded cuticle of the second instar pupa

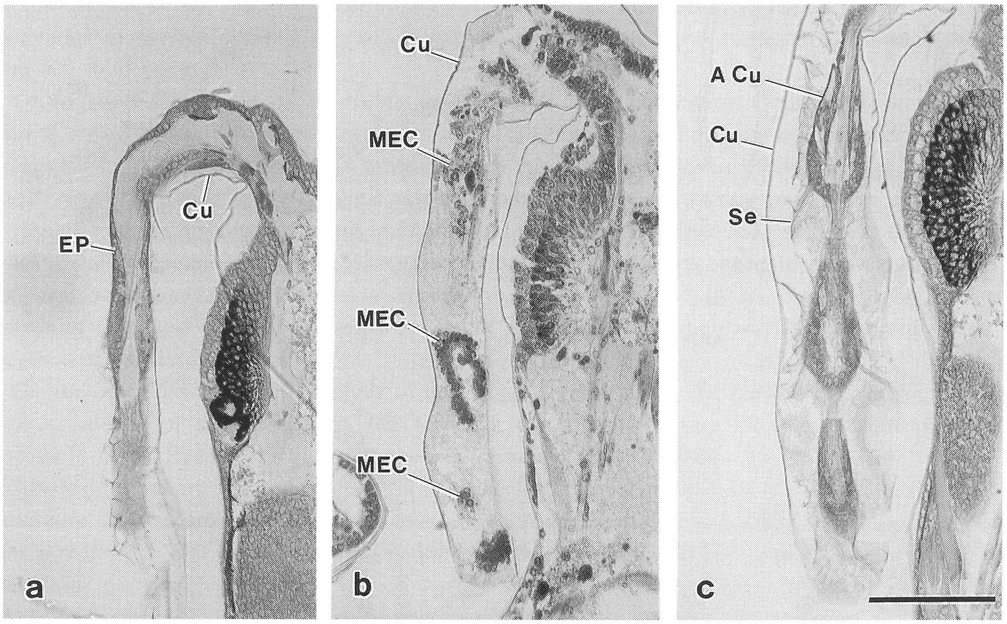


Fig. 2 Horizontal sections of antennal sheaths of *Bactrothrips brevitubus* in the early (a), middle (b) and late (c) third instar pupae. A Cu: adult cuticle, Cu: cuticle of third instar pupa, EP: epidermis, MEC: mass of epidermal cells, Se: seta. Scale = 100 μm.

(Figs. 1c, 4c). A part of these cells later degenerate with the result that the epidermis again becomes less thickened.

Second instar pupal stage (Fig. 5)

Transformation of antennal sheaths occurs in the same way as described for the previous stage.

Third instar pupal stage (Figs. 2, 6)

At the beginning of this stage, a thin layer of antennal epidermal cells lining the whole antennal cuticle is observed, as it is in the first and second pupal stages (Figs. 2a, 6a). These cells, however, immediately degenerate and become unrecognizable (Figs. 2b, 6b).

On the other hand, some cells observed inside the antennal sheath proliferate and aggregate to be spaced in such a way that they delimit eight masses (Figs. 2b, 6b, c). These masses of cells then begin to secrete an adult antennal cuticle of each segment (Figs. 2c, 6d).

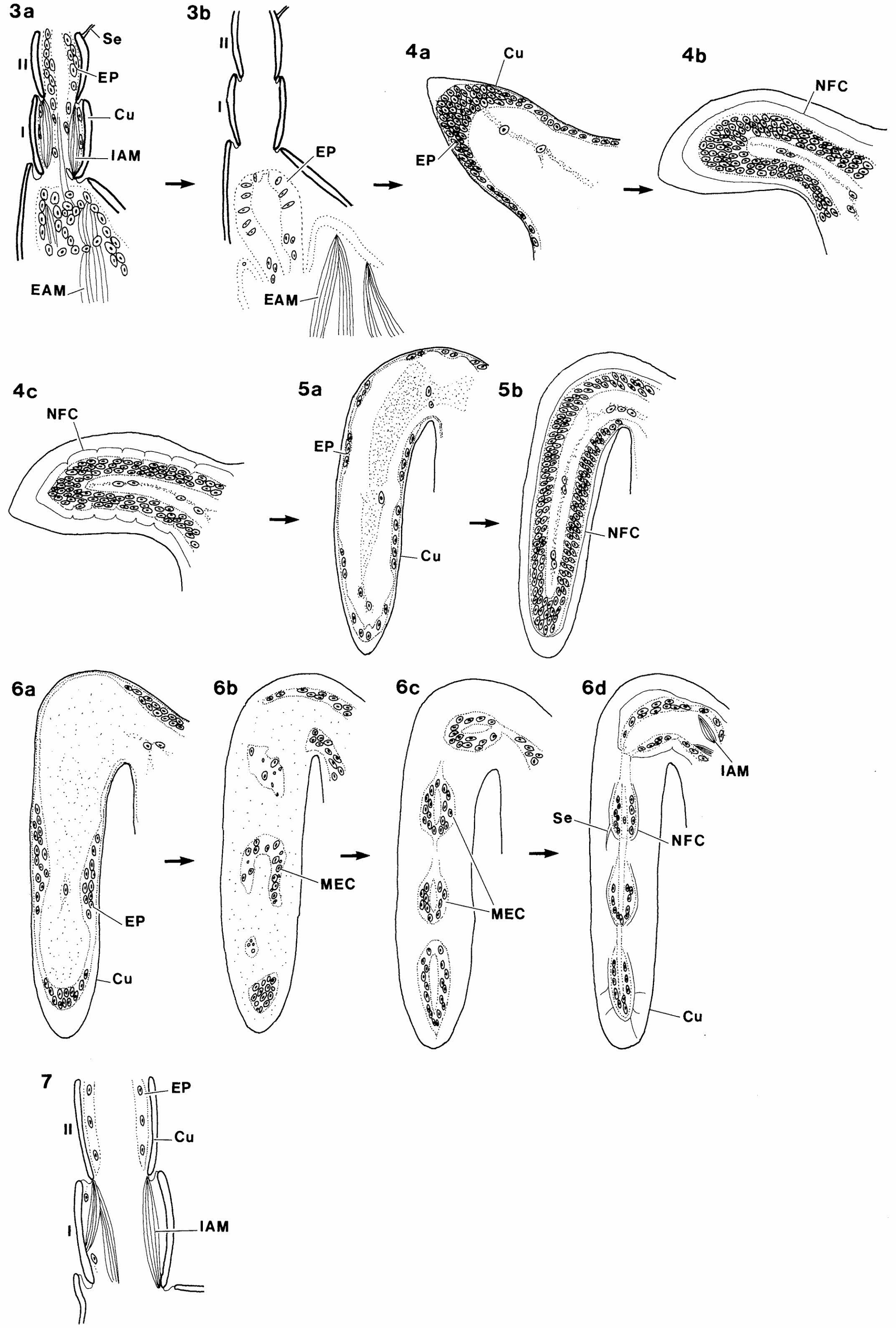
The intrinsic antennal muscles that disappeared completely in the late second instar larval stage reappear in the newly developed scape segment (Fig. 6d).

Imaginal stage (Fig. 7)

Each of the imaginal antennae consists of eight segments, and so it is morphologically different from the non-segmented antennal sheaths in pupal stages. The adult antennal cuticle is more thickened than in immature stages, because the endocuticle deposition in imaginal antennae continues until after the third pupal cuticle has been shed (Fig. 7).

Discussion

Findings concerning the morphogenetical development of antennae in a idolothripine thrips, *Bactrothrips brevitubus* in the present study are: 1) withdrawal of the antennal epidermis into the head capsule in the late second instar larval stage, 2) histolysis of the pupal epidermis of antennal sheaths and


3a
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II
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IAM
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5a
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5b
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6a
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new construction of the imaginal epidermis of antennae in the third instar pupal stage, and 3) complete degeneration of intrinsic antennal muscles in the late second instar larval stage and *de novo* regeneration in the late third instar pupal stage.

Of the above features, 1) and 3) are the same as those of the phlaeothripine thrips *Haplothrips verbasci* (Heming, 1975). In this species, however, no evidence of histolysis in the antennal tissue was found during any time of metamorphosis; instead, its antennal epidermis contracts away from the cuticle and immediately assumes the configuration of the imaginal antennal segments at the third instar pupa—adult apolysis.

Histolysis of the antennal epidermis in an idolothripine thrips, *B. brevitubus*, was briefly described from a whole mount preparation by Haga (1974). According to him, histolysis begins in the second instar pupal stage, and adult antennal segmentation appears in the same stage. In the present study, however, histolysis of the pupal antennal epidermis and adult antennal segmentation were not observed before the emergence of the third instar pupa.

On the other hand, neither histolysis of the antennal epidermis in the pupal stage nor its withdrawal in the second larval stage occurs in the following two thripine thrips belonging another subfamilies: *Frankliniella fusca* (Heming, 1975) and *Limothrips cerealium* (Davies, 1969).

Although there are some differences in the antennal formation among subfamilies, significant tissue degeneration and reconstruction have been found to occur during quiescent stages in all of the thrips species so far investigated. The similar morphogenetical changes between the larva and the adult have also been reported in the midgut epithelium, nervous system and body muscular system (Davies, 1969; Heming, 1973, 1975; Moritz, 1989, 1995). Thus, morphogenetical development in the "pupal" stages of thrips is very similar to that in the pupal stage of holometabolous insects.

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Figs. 3–7 Semidiagrammatic representation of the antennal morphogenesis in *Bactrothrips brevitubus*. 3. Antennal segments I and II of the early (a) and late (b) second instar larvae. 4. Antennal sheaths of the early (a), middle (b) and late (c) first instar pupae. 5. Antennal sheaths of the early (a) and middle (b) second instar pupae. 6. Antennal sheaths of the early (a), middle (b, c) and late (d) third instar pupae. 7. Adult antennal segments I and II. I, II: antennal segments I and II, Cu: cuticle, EAM: extrinsic antennal muscle, EP: epidermis, IAM: intrinsic antennal muscle, MEC: mass of epidermal cells, NFC: newly formed cuticle, Se: seta.