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ANTENNAL STRUCTURE AND METAMORPHOSIS IN
FRANKLINIELLA FUSCA (HINDS) (THRIPIDAE) AND
HAPLOTHRIPS VERBASCI (OSBORN) (PHLAEOTHRIPIDAE)
(THYSANOPTERA).

BRUCE S. HEMING

Department of Entomology
University of Alberta
Edmonton, Alberta T6G 2E3

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Larval and adult antennae, in both Frankliniella fusca and Haplothrips verbasci, consist of seven and eight segments respectively. In adults of both species and in larvae of F. fusca, the antennae are raised and lowered by levator and depressor muscles inserting into the bases of the scapi and originating on the anterior tentorial arms. Both these muscles, in larvae of H. verbasci, have additional branches originating on the vertex of the head.

Propupal antennae in F. fusca are short, weakly segmented and forward-directed; those of pupae unsegmented and flexed dorsally over the head and prothorax. During the quiescent stages, both the extrinsic and intrinsic antennal muscles maintain their myofibrils but cease to function because they are no longer attached to cuticle. They increase slightly in diameter and considerably in length, but are unchanged otherwise.

During the larva II-propupal apolysis of H. verbasci, all larval head muscles contract maximally; their myofibrils degenerating shortly thereafter. This contraction, plus changes in cell shape probably cause the complete withdrawal of epidermis from within the larva II antennae. At ecdysis, the propupal antennae are evaginated from epidermal pockets as short, unsegmented stubs. In the two pupal stages, they remain unsegmented but lengthen posteriorly along either side of the head. Imaginal segmentation and myofibrils begin to differentiate in the exuvial pharate adult stage.

Sense organs are similar in type, position, and number in larvae of both species but are very different in adults. No obvious sexual differences exist in the imaginal antennae of either species except for their smaller size in males.

The Johnston's Organ, in larvae of F. fusca, consists of three chordotonal organs having two scolopidia each; in H. verbasci of four having two or three each. In both species, the Johnston's Organ is carried through metamorphosis, two (H. verbasci) or three (F. fusca) chordotonal organs and additional scolopidia being added to each during the quiescent stages.

Antennal structure and development in thrips is compared with that occurring in other insects and an hypothesis is offered to explain the origin of the differences in antennal metamorphosis existing between the two species. It is concluded that the drastic events occurring in H. verbasci and other phlaeothripids have probably evolved in conjunction with the adoption, by this family, of a primarily cryptophilous existence.

Les antennes de Frankliniella fusca et de l'Haplothrips verbasci aux stades larvaires et adultes consistent respectivement de sept et huit articles. Chez les adultes de chaque espèce et la larve de F. fusca les antennes sont élevées et abaissées par les muscles levateurs et dépresseurs. Ces muscles sont attachés à la base des scapes antennaires et sur l'embranchement antérieur du tentorium. Ces deux muscles chez la larve de H. verbasci ont des embranchements additionnels allant sur le vertex de la tête.

Les antennes de la propupe de F. fusca sont courtes, faiblement articulées et dirigées antérieurement; celles de la pupa ne sont pas articulées et sont orientées dorsalement au-dessus de la tête et du prothorax. Lors des stades inactifs, les muscles intrinsèques et extrinsèques des antennes maintiennent leurs myofibrilles mais cessent toutes fonctions car ils ne sont plus

attachés à la cuticule. Elles ont un diamètre légèrement plus grand et sont très allongées, mais demeurent inchangées autrement.

Lors de l'apolyse de la seconde larve-propupale de l'H. verbasci tous les muscles larvaires de la tête se contractent au maximum; les myofibrilles dégénèrent peu après. Cette contraction avec un changement dans la forme des cellules épidermiques probablement provoque le détachement complet de l'épiderme à l'intérieur de l'antenne de la seconde larve. Lors de la métamorphose les antennes de la propupe apparaissent comme des petites projections de l'épiderme et n'est pas articulées. Durant les deux stades de la pupa les antennes demeurent inarticulées mais s'allongent postérieurement de chaque côté de la tête. Chez l'imago la segmentation et les myofibrilles commencent à se différencier lors de la formation de l'imago à l'intérieur de la pupa (Pharate stage).

Les organes des sens sont similaires au point de vue de la forme, de la position et du nombre chez les larves des deux espèces mais ils sont différents chez les adultes. Il n'y a aucune différence sexuelle évidente entre les antennes des adultes des deux espèces excepté qu'elles sont plus courtes chez les mâles.

L'organe de Johnston, chez les larves de F. fusca consiste de trois organes chordotonaux pourvus chacun de deux scolopidia; chez celles d'H. verbasci de quatre organes chordotonaux ayant chacun deux ou trois scolopidia. L'organe de Johnston est préservé durant les métamorphoses, mais deux (H. verbasci) ou trois (F. fusca) organes chordotonaux et des scolopidia additionnels sont ajoutés durant les stades inactifs.

La structure et le développement des antennes chez les thysanoptères sont comparés aux autres insectes et une hypothèse est offerte pour expliquer l'origine des différences observées entre les deux espèces lors de la métamorphose des antennes. Nous concluons que les événements importants se déroulant chez l'H. verbasci et les autres phlaeothripides ont probablement évolués conjointement avec l'adoption d'un mode de vie principalement cryptophile chez cette famille.

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INTRODUCTION

The antennae of adult Thysanoptera are their best known structures because of their importance in taxonomy. This is due to the diversity of shapes, lengths and numbers of their segments and to the numbers and kinds of sense organs present on these segments in different taxa (Doeksen, 1941; Priesner, 1960). The two larval stages have smaller antennae differing structurally from those of the adults (Priesner, 1960), while those of the quiescent instars (propupa and pupa in Terebrantia; propupa, pupa I and pupa II in Tubulifera) have reduced segmentation or lack it completely and are flexed dorsally over (Terebrantia) or laterally beside (Tubulifera) the head (Priesner, 1960; Lewis, 1973).

Melis (1934b), Risler (1957) and Mickoleit (1963) have described the structure and musculature of the adult antennae of several species of Aeolothripidae, Thripidae and Phlaeothripidae, while Melis (1934b), Davies (1969) and Haga (1974) have briefly discussed larval structure and metamorphosis of the antennae in representative species of Phlaeothripidae and Thripidae.

Abbreviations Used in Figs. 1-87

<i>a.</i>	anterior	<i>L. II. c. s.</i>	pedicellar campaniform sensillum of larva II
<i>a. c.</i>	adult cuticle		
<i>antf.</i>	antennifer(s)	<i>L. II. dep. ant.</i>	antennal depressor muscle of larva II
<i>ant. nv.</i>	antennal nerve		
<i>ant. s.</i>	antennal socket	<i>L. II. dep. ant. c.</i>	cranial branch of antennal depressor muscle of larva II
<i>ap. s. o.</i>	apical sense organ(s)		
<i>at.</i>	anterior tentorial arm(s)	<i>L. II. e.</i>	retracting epidermis of larva II antenna
<i>b. c.</i>	haemocyte		
<i>b. m.</i>	basement membrane	<i>L. II. lev. ant.</i>	antennal levator muscle of larva II
<i>c. a.</i>	cell in anaphase		
<i>c. m.</i>	cell in metaphase	<i>L. II. lev. ant. c.</i>	cranial branch of antennal levator muscle of larva II
<i>c. p.</i>	cell in prophase		
<i>c. pg.</i>	coeloconic peg(s)	<i>L. II. omtd.</i>	larva II ommatidia
<i>c. r.</i>	cuticular ring	<i>L. II. ped.</i>	larva II pedicel
<i>c. s.</i>	pedicellar campaniform sensillum	<i>L. II. scp.</i>	larva II scape
		<i>L. II. scp. m.</i>	scape muscles of larva II
<i>c. t.</i>	cell in telophase	<i>m.</i>	medial
<i>d.</i>	dorsal	<i>mb. c.</i>	membranous cuticle
<i>dep. ant.</i>	antennal depressor muscle	<i>md. s. o.</i>	mandibular stylet-secreting organ
<i>dep. ant. c.</i>	cranial branch of antennal depressor muscle	<i>m. t.</i>	microtrichea
<i>dil. cib.</i>	cibarial dilator muscles	<i>p. c.</i>	pupal cuticle
<i>d. seg.</i>	developing adult antennal segments	<i>p. c. s.</i>	pedicellar campaniform sensillum of pupa
		<i>ped.</i>	pedicel
<i>d. sh. s. o.</i>	dendritic sheath of sense organ	<i>p. n.</i>	degenerating (pycnotic) nucleus
<i>d. ter.</i>	dendritic terminals of Johnston's Organ	<i>pro. ant.</i>	propupal antenna
		<i>pro. c.</i>	propupal cuticle
<i>d. t.-w. chr.</i>	developing thin-walled chemoreceptors	<i>pro. c. s.</i>	pedicellar campaniform sensillum of propupa
<i>e.</i>	adult compound eye	<i>p. I. c.</i>	pupa I cuticle
<i>ext. ant.</i>	antennal extensor muscle	<i>p. I. c. s.</i>	pedicellar campaniform sensillum of pupa I
<i>fl.</i>	flagellum		
<i>flx. ant.</i>	antennal flexor muscle	<i>p. I. t. h.</i>	pupa I tactile hair
<i>img. e. dc.</i>	imaginal disc of compound eye	<i>p. II. c.</i>	pupa II cuticle
		<i>p. II. c. s.</i>	pedicellar campaniform sensillum of pupa II
<i>invg. pro. ant.</i>	invaginated pouch containing propupal antenna	<i>p. II. t. h.</i>	pupa II tactile hair
		<i>sarc.</i>	sarcolemma
<i>J. O.</i>	Johnston's Organ	<i>s. cl.</i>	group(s) of sensory neurons
<i>lev. ant.</i>	antennal levator muscle	<i>s. cl. J. O.</i>	sensory neurons of Johnston's Organ
<i>lev. ant. c.</i>	cranial branch of antennal levator muscle	<i>sco. J. O.</i>	scolopidia of Johnston's Organ
<i>L. I. at.</i>	anterior tentorial arm of larva I	<i>scp.</i>	scape
<i>L. I. c.</i>	larva I cuticle	<i>scp. m.</i>	scape (= intrinsic) muscles
<i>L. I. c. s.</i>	pedicellar campaniform sensillum of larva I	<i>t. cl.</i>	trichogen cell
		<i>t. h.</i>	tactile hair
<i>L. II. at.</i>	anterior tentorial arm of larva II	<i>tra.</i>	trachea
		<i>t.-w. chr.</i>	thin-walled chemoreceptor(s)
<i>L. II. ant. s.</i>	larva II antennal socket		
<i>L. II. c.</i>	larva II cuticle	<i>v.</i>	ventral
<i>L. II. cr.</i>	corneae of larva II eyes		

The ultrastructure of the imaginal, antennal sense organs of *Bagnalliella yuccae* (Hinds) (Phlaeothripidae) and *Frankliniella tritici* (Fitch) (Thripidae) has recently been described by Slifer and Sekhon (1974) (reprint was received after this study was completed).

As part of a continuing study of metamorphosis in thrips (see Heming (1973) for a summary of previous work), I here describe the structure and postembryogenesis of the antennae of two species, each representing one of the thysanopteran suborders. Development is compared with that occurring in other insects and an attempt is made to explain the origin of the differences between terebrantian and tubuliferan antennal metamorphosis.

METHODS

Cleared and uncleared whole mounts (Heming, 1969) and serial sections (Heming, 1970, 1971) were prepared of all stages of both sexes of *Frankliniella fusca* (Hinds) (Thripidae) and *Haplothrips verbasci* (Osborn) (Phlaeothripidae). Unmacerated whole mounts were studied under phase contrast and polarized light to show internal details, while sense organs were examined with phase contrast in cleared specimens mounted in Hoyer's medium (this medium has optical properties superior to those of Canada balsam). Illustrations were drawn with the aid of a drawing attachment through a Wild M20 microscope.

Specimens of all stages of *H. verbasci* were killed in hot water, washed in detergent, and prepared for scanning electron microscopy using the critical point drying technique (Hearle et al., 1972, pp. 197-198). Observations on living *H. verbasci* were made at low and high (x500) magnifications as previously described (Heming, 1971, 1972). Representatives of this species were reared on potted mullein (*Verbascum thapsus* L.) in the laboratory.

I also examined Canada balsam whole mounts of specimens of all stages of *Taeniothrips simplex* (Morison) (Thripidae), *Selenothrips rubrocinctus* (Girard) (Thripidae), *Parthenothrips dracaenae* (Heeger) (Thripidae), *Haplothrips graminis* Hood (Phlaeothripidae), *Gynaikothrips uzeli* Zimmermann (Phlaeothripidae), *Hoplothrips* sp. (Phlaeothripidae) and *Euoplothrips* sp. (Phlaeothripidae).

Illustrations in this paper are arranged by instar. Antennal postembryogenesis in *F. fusca* is illustrated in Figs. 1-33 and in *H. verbasci* in Figs. 34-87. Positions and angles of sections are indicated by numbered arrows on drawings of the entire antenna. Arrows having numbers in parentheses indicate that the sections in question were made from specimens at different stages in development than were the whole mounts used to make the drawings. Those with underlined numbers mark the positions of frontal sections.

OBSERVATIONS

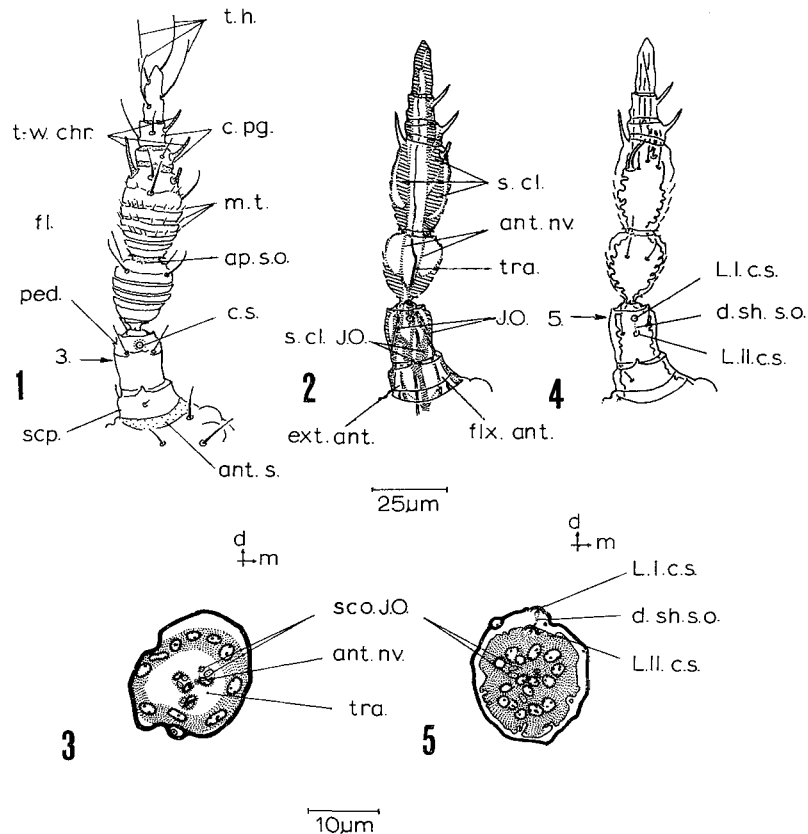
Frankliniella fusca

Under summer conditions in South Carolina, *F. fusca* has a generation time of about 16.7 days with 6.7, 2.8, 3.5, 1.1 and 2.6 days spent, respectively in the egg, first and second larval, prepupal and pupal stages (Watts, 1934). The species is polyphagous and specializes on seedlings. Larvae congregate at the growing points of plants, adults there or in flowers and prepupae and pupae within the leaf sheaths (Heming, 1970) or in the soil (Eddy and Livingstone, 1931; Newsom et al., 1953).

Larval Stages (Figs. 1-11).

Structure. — Antennae of the two larval stages are practically identical except for size (Figs. 1, 9). Each consists of a scape (scp.), a pedicel (ped.), and five flagellar segments (fl.) (usually called subsegments because they lack muscles). The scape of each antenna is inserted into a

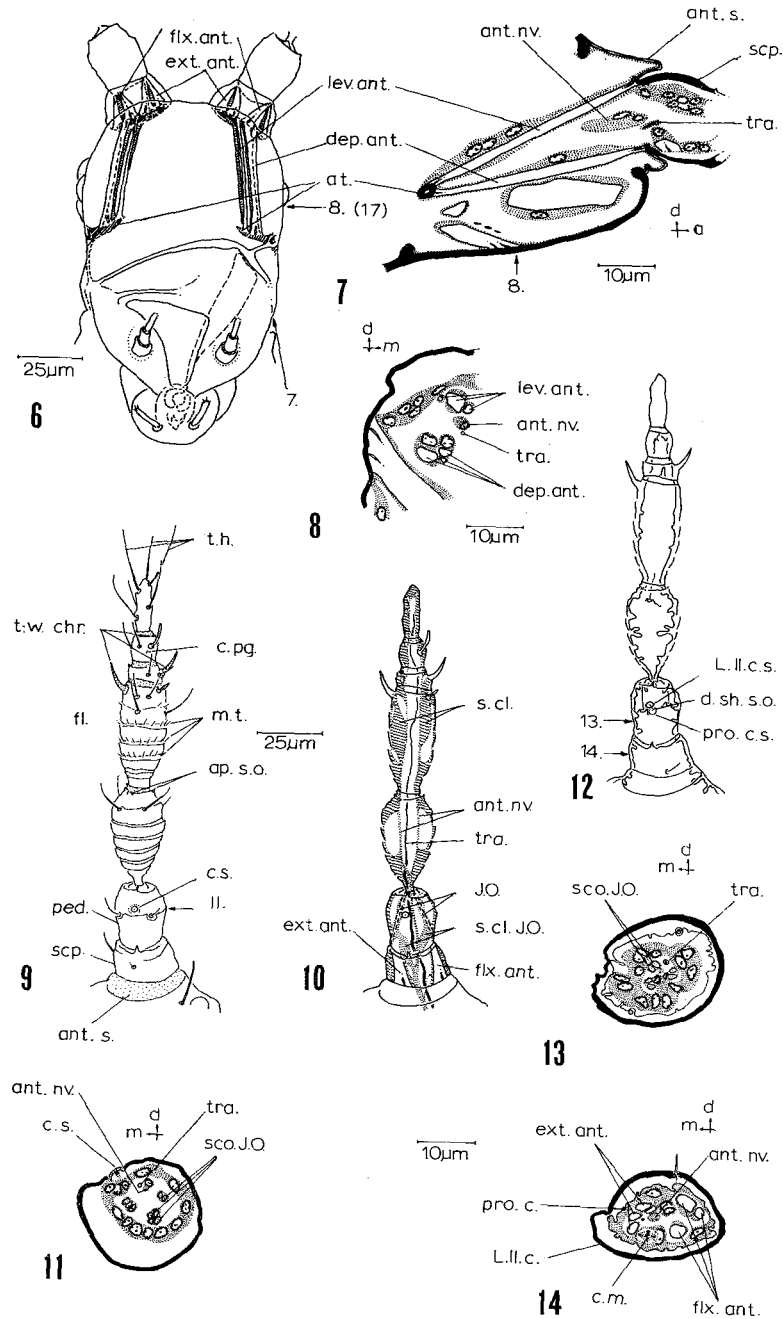
socket (ant. s.) in the head capsule and is articulated to it by means of weakly-developed lateral and median condyles (antennifers) extending inwards from the socket rim (not shown in figures because of their position). Large areas of membranous cuticle are present in each socket dorsal and ventral to the scape, allowing each antenna to be raised and lowered by levator (lev. ant.) and depressor (dep. ant.) muscles originating on the anterior tentorial arms (at.) of the head capsule and inserting, respectively, into the dorsal and ventral margins of the scape base (Figs. 6-8). Each of these muscles consists of three fibres (Fig. 8).



Figs. 1-5. *F. fusca*. Larva I: Fig. 1. Right antenna, dorsal aspect. Fig. 2. Same, optical section. In this and many other illustrations, the hatching represents epidermal and sensory cells. Fig. 3. Transverse section through pedicel and Johnston's Organ taken at point indicated by arrow in Fig. 1. Pharate larva II: Fig. 4. Right antenna, dorsal aspect, showing developing larva II antenna (Note that most larva I sensilla omitted from drawing). Fig. 5. Transverse section through pedicel and Johnston's Organ taken at point indicated by arrow in Fig. 4.

The pedicel (ped.) articulates with the scape (scp.) by means of a single dorsal condyle (Figs. 1, 9) in the apex of the latter and is flexed laterally and extended anteriorly by flexor (flx. ant.) and extensor (ext. ant.) muscles within the scape (Figs. 2, 6, 10). These muscles each consist of three fibres (Fig. 14), are inserted into the base of the pedicel on either side of the condyle, and arise proximally on the lateral and medial walls of the scape. The narrow

Heming



Figs. 6-14. *F. fusca*. Larva II: Fig. 6. Ventral aspect of head, showing origins and insertions of intrinsic (flx. ant.; ext. ant.) and extrinsic (lev. ant.; dep. ant.) antennal muscles (all setae have been omitted). Fig. 7. Oblique, parasagittal section taken at point indicated by arrow in Fig. 6., showing origins and insertions of antennal levator (lev. ant.) and depressor (dep. ant.) muscles. Fig. 8. Transverse section taken at point indicated by arrows in Figs. 6 and 7. Note the 3 fibres of each muscle. Fig. 9. Right antenna, dorsal aspect. Fig. 10. Same, optical section. Fig. 11. Transverse section through pedicel taken at point indicated by arrow in Fig. 9. Pharate Propupa: Fig. 12. Right antenna, dorsal aspect (Note: Most larva II sensilla omitted from drawing). Fig. 13. Transverse section through pedicel taken at point indicated by arrow in Fig. 12. Fig. 14. Same, through scape and antennal flexor (flx. ant.) and extensor (ext. ant.) muscles. Section taken at point indicated by arrow in Fig. 12.

base of the first flagellar segment (usually called the "pedicel" by thysanopterists) articulates with the pedicel via dorsal and ventral condyles in the latter's apex (Figs. 1, 9). Therefore, each antenna has two points of flexion and extension: the scape-pedicellar and the pedicel-flagellar joints.

Antennal segments three and four in both larval instars consist respectively of five and six lightly-sclerotized rings of cuticle (Figs. 1, 9). In segment four, rings two to five each subtend a whorl of delicate microtricheae (m. t.).

Sense Organs. — The antennal sense organs of larval *F. fusca* are illustrated in part in Figs. 1-3 and 9-11 and are listed in Table I for the second-stage larva. They are identical in larvae of both sexes and instars except where indicated. Not all sensilla listed are illustrated because they are either ventrally located or are too small to show up at the magnification of the drawings.

Table I. Sense organs on the antenna of the larva II of *F. fusca* (N = 8).

Segment	tactile hairs	campaniform sensilla	Johnston's Organ	thin-walled chemoreceptors	coeloconic pegs	apical sense organs
1	4 (2 in Larva I)					
2	5	1	1 (3 chordotonal organs)			
3	4			1 (ventral)	1	3
4	4 (3)			2		
5	3			1	1	
6	3			1	1	
7	6					
Totals	29	1	1	5	3	3
Grand Total	42					

The Johnston's Organ (J. O.) in larvae of *F. fusca* (Figs. 2, 3, 5, 10, 11) consists of three chordotonal organs each containing two scolopidia (sco. J. O.). Some of these appear to be innervated by one and others by two sensory neurons according to whether they contain one or two ciliary dilations (note dots inside each scolopale), but this requires verification by transmission electron microscopy. The cap cells of each organ insert into the articular membrane at the base of the first flagellar segment; the ligament of each arising basally on the walls of the pedicel (ped.) (Figs. 2, 10). The cell bodies of the sensory neurons innervating the organ (s. cl. J. O.) are situated basally within the pedicel with their axons joining the antennal nerve (ant. nv.) proximally (Figs. 2, 10). This nerve continues posteriorly through the small larval head and eventually enters the deutocerebrum of the brain, the latter being situated in the prothorax.

The three apical sense organs (ap. s. o.) of antennal segment three (Figs. 1, 9) appear to be universal in thrips as they are present in larvae and adults of both *F. fusca* and *H. verbasci*

(see below).

That portion of the antennal lumen occupied by epidermal and sensory cells (s. cl.) is shown in optical section (by hatching) in Figs. 2 and 10. Details are difficult to observe, even with phase contrast, because of the presence of obscuring yellow pigment granules within the epidermal cells. The antennal nerve bifurcates at the base of the first flagellar segment, each branch penetrating the basement membrane of the antennal epidermis laterally (Figs. 2, 10). Each branch then continues distally periodically receiving axons from the sensory neurones of the antennal sensilla.

Larva I-Larva II Moults. — Shortly before the end of the first instar, the mitotic rate increases in the epidermis of each antenna. Apolysis then occurs, including the origins and insertions of Johnston's Organ and the extrinsic and intrinsic antennal muscles. This is followed by secretion of a new, larger, second-instar cuticle inside the first (Figs. 4, 5). As soon as this secretion begins, the ends of Johnston's Organ and muscles attach to the new cuticle. All sense organs are duplicated exactly except that two additional tactile hairs (t. h.) develop on each scape. Each sensillum develops as a cytoplasmic extension of a trichogen cell around which cuticle is subsequently deposited. If a particular developing sensillum is unable to fit into the space available for it within the first stage cuticle, it is bent at the socket only. The cuticle of the second-instar antennal segments is deposited in a folded state (Fig. 4) and space is left apically in each first-stage antenna for the formation of the second-stage apical hairs. A dendritic sheath (d. sh. s. o.) is observed in some preparations extending through a central pore in the second-instar campaniform sensillum (L. II. c. s.) to the dome of that of the first (L. I. c. s.) (Figs. 4, 5), indicating that the first-instar sensilla function in the pharate second-instar. Such sheaths are probably associated with all sensilla but were not visible in either whole mount or sectioned preparations. The pharate larva II can move its antennae only slightly because their muscles detached from the first-instar cuticle at apolysis.

Shortly before ecdysis, the larva becomes quiescent. At ecdysis, the first-instar head capsule splits medially, with each new second-instar antenna being pulled out of the base of the first. This requires that the new flagellar segments of each antenna be pulled through the very narrow base of the first-instar flagellar segment (Fig. 4).

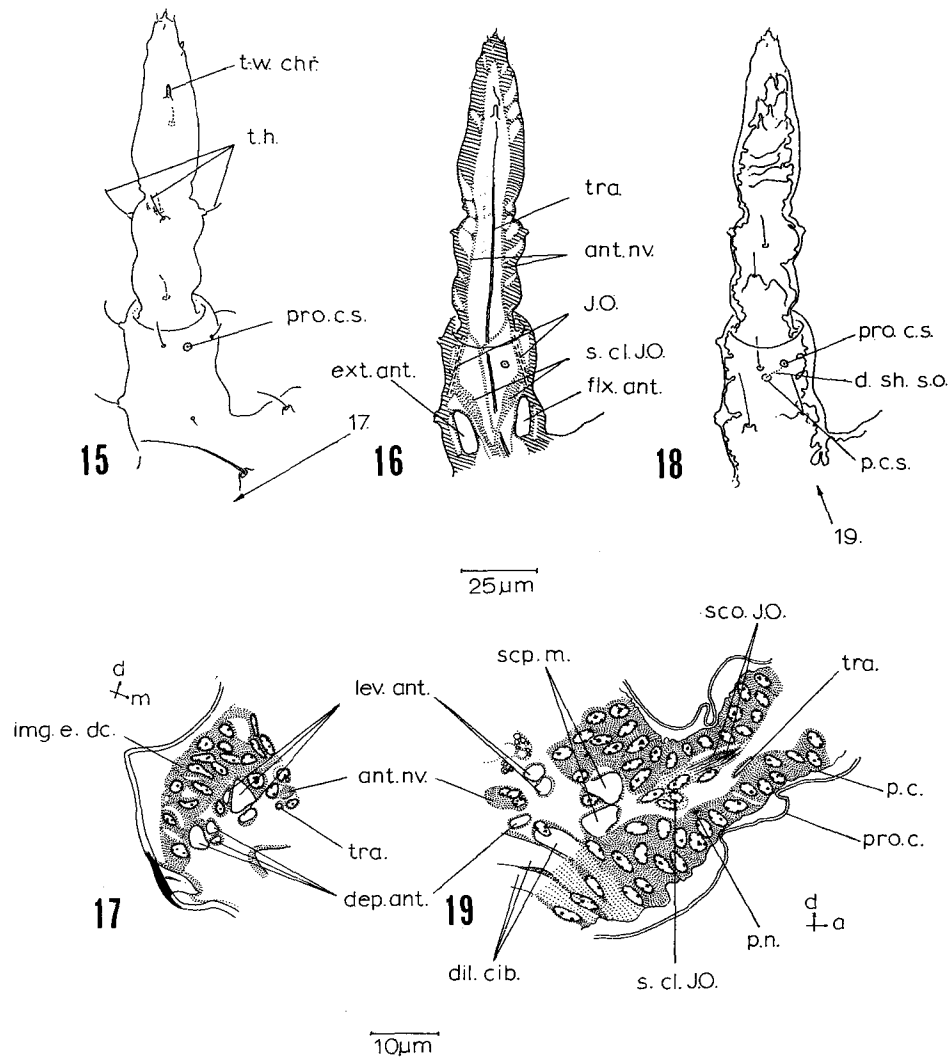
As soon as its old cuticle is shed, the larva swallows air, contracts its abdominal muscles, increases the blood pressure in its appendages, and stretches out the new second-instar cuticle. Sclerotization follows shortly thereafter.

Propupa (Figs. 12-17).

Larva II-Propupal Moults. — The details of apolysis and ecdysis at this moult are similar to those of the previous one just described, except that in the cuticular pharate phase, the extrinsic and intrinsic antennal muscles do not attach to the propupal cuticle as it is deposited (Figs. 12-14). In addition, whereas the larval moult always takes place on the host plant, this one usually occurs in the pupation site, either in a protected place on the host, or in the soil, both areas having been entered by the larva before moulting takes place.

Structure. — The propupal antennae of *F. fusca*, although directed anteriorly, are short, are of membranous cuticle, and lack well defined segmentation (Fig. 15). Just distal to the propupal campaniform sensillum (pro. c. s.), a deep, circular, annulus separates pedicellar and flagellar regions. Three additional, weakly-developed, annuli suggest additional segmentation. The homologies of these "segments" with their larval counterparts are best seen in pharate propupae (Fig. 12).

The extrinsic (lev. ant.; dep. ant.) and intrinsic (flx. ant.; ext. ant.; scp. m.) muscles of the larval antennae are unaltered in the propupal stage and maintain their birefringence (Figs. 14, 16, 17, 19). However, they do not function because they originate and insert in epidermis



Figs. 15-19. *F. fusca* Propupa: Fig. 15. Right antenna, dorsal aspect. Fig. 16. Same, optical section. Note presence of scape muscles (flx. ant.; ext. ant.). Fig. 17. Transverse section through head taken at point indicated by arrow in Fig. 6. Note presence of extrinsic antennal muscles (lev. ant.; dep. ant.). *Pharate Pupa*: Fig. 18. Right antenna, dorsal aspect (Note: Most propupal sensilla omitted from drawing). Fig. 19. Oblique sagittal section of base of antenna taken at point and angle indicated by arrow in Fig. 18. Note J.O. scolopidia (sco. J. O.) and intrinsic (scp. m.) and extrinsic (lev. ant.; dep. ant.) antennal muscles.

rather than on propupal cuticle (Figs. 16, 19). Propupae are probably unable to move their antennae because of this and because these appendages lack functional articulations.

Sense Organs. — Sensilla of the propupal scape and pedicellar regions are similar to those of larvae, although the tactile hairs are longer and more delicate, and arise from raised sockets (Fig. 15). Only two, well-developed thin-walled chemoreceptors (t-w. chr.) are visible on the flagellum, and many of its tactile hairs (t. h.) are either absent or much reduced (compare Fig. 9 and 15).

The larval Johnston's Organ (J. O.; sco. J. O.; s. cl. J. O.) is carried through unaltered into

the propupal stage (Figs. 13, 16, 19) but, like the musculature, has its origins and insertions in epidermis rather than in propupal cuticle. Thus, it probably ceases to function in this instar too.

Pupa (Figs. 18-21).

Propupal-Pupal Moults. — The details of apolysis, cuticle deposition and ecdysis in this moult are similar to those of the previous one (compare Figs. 12 and 18), and, again, take place in the hidden pupation site of the insect. The main events occurring in each antenna are (1) an increase in its length, (2) an increasing complexity in its Johnston's Organ, and (3) its dorsal flexion over the head and prothorax. Events (1) and (3) are both evident in the pharate pupal stage (Figs. 18 and 19). The larger pupal cuticle (p. c.), developing within the propupal cuticle (pro. c.), is deeply folded, particularly in the flagellar region and on the ventral side of the scape and pedicel. When the pupa emerges and expands its new cuticle, these folds straighten out. The expansion of the ventral folds causes each antenna to bend slowly back over the head, and of the flagellar ones to almost double the length of the flagellar region (compare Fig. 15 and 20).

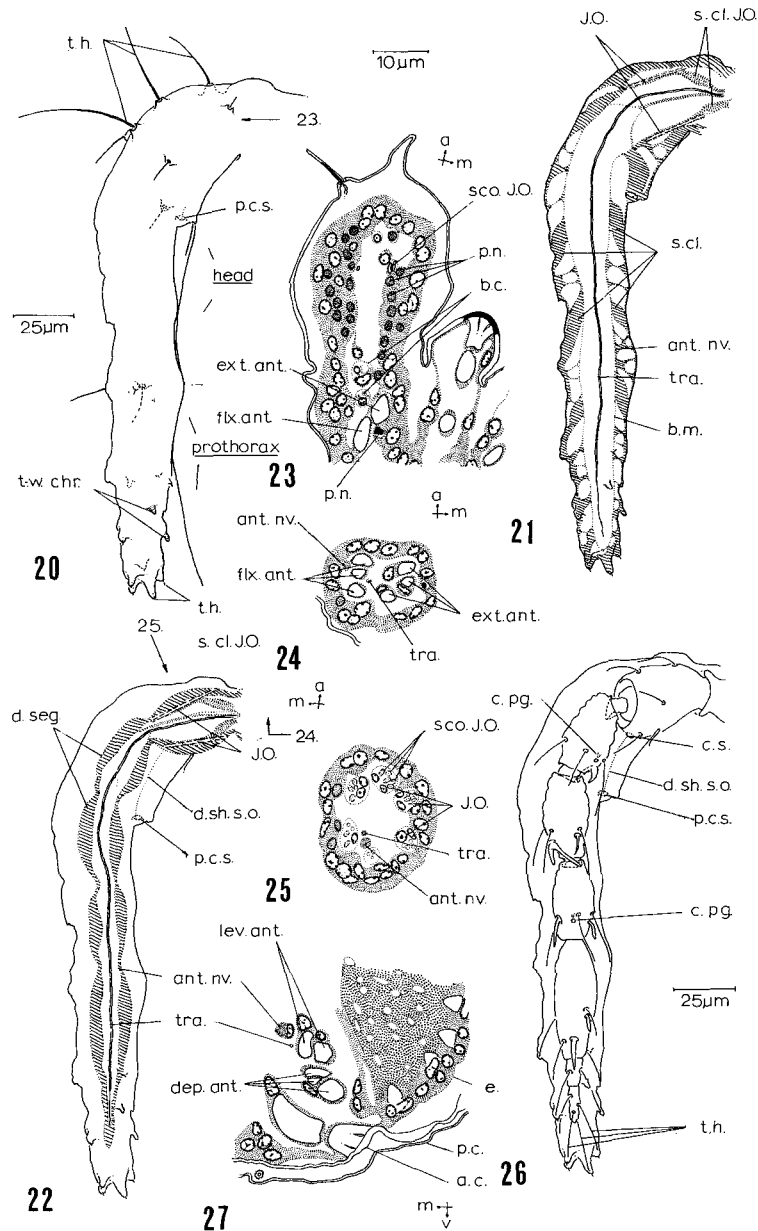
The Johnston's Organ (sco. J. O.; J. O.) in the propupa has its long axis slanted forward and upward at an angle of about 30° (Fig. 19). At pupal emergence it is flipped over vertically through an arc of about 90° with the result that its apex eventually points posteriorly at an elevation of about 60° (Figs. 21, 22). This movement is passive and is due completely to the expansion of pupal cuticle carrying along the underlying epidermis into which the apex of the organ is inserted.

During the pharate pupal and young pupal stages, three new chordotonal organs develop (for a total of six) and additional sensory elements are added to those already present (for a total of from three to five scolopidia per scoloparium) (compare Figs. 13 and 25). Since these have their imaginal form by the exuvial pharate adult stage (Fig. 25), the differentiative divisions responsible for their formation must occur earlier in the exuvial pharate pupal to newly-emerged pupal periods. Unfortunately, most preparations of animals at this stage in their development do not show the antennae to best advantage (frontal sections of the whole animal are the only ones of use) and those that do (e.g. Fig. 19 of a pharate pupa) show no evidence of increased mitotic activity. Therefore, more detailed study at this period of development, preferably with the transmission electron microscope, is required before positive conclusions can be drawn.

Structure. — The pupal antennae of *F. fusca* are of membranous cuticle, lack segmentation completely, and are bent back dorsally over the head and prothorax (Fig. 20 — a lateral view). As in the previous stage, both the extrinsic and intrinsic antennal muscles maintain their birefringence, and, presumably, their ability to function, even though they are unable to do so productively. As in the previous stage, they originate and insert in epidermis rather than in cuticle (Figs. 19, 23, 24).

Sense Organs. — It is difficult, except for those of the pedicellar region (pupal campaniform sensillum and Johnston's Organ), to homologize the sensilla of this stage with those of the propupa and adult. There are three, sub-apical, thin-walled chemoreceptors (t.-w. chr.). Most tactile hairs (t. h.) arise from sockets that are higher than those of the propupa (Fig. 20). The apex of each antenna bears six or seven protuberances, each topped by a tiny seta (t. h.). Some setae which were short in the propupa are long in the pupa and vice versa. Numerous additional small sense organs, just visible at the maximum resolving power of the light microscope, are scattered throughout the length of the flagellar region.

Although difficult to see because of its position, a pedicellar campaniform sensillum (p. c. s.) is situated at the base of each pupal antenna just behind its point of dorsal flexion (Figs. 20-



Figs. 20-27. *F. fusca*. Newly-emerged Pupa: Fig. 20. Right antenna, lateral aspect. Fig. 21. Same, optical section. Note groups of imaginal sensory neurons (s. cl.). Exuvial Pharate Adult: Fig. 22. Right antenna, optical section. Note developing adult antennal segments (d. seg.). Fig. 23. Oblique frontal section through developing scape and pedicel taken at point shown by arrow in Fig. 20. Note scape muscles (scp. m.), blood cells (b. c.), and degenerating epidermal nuclei (p. n.). Fig. 24. Transverse section through developing scape taken at point indicated by arrow in Fig. 22. Compare with Fig. 13 and note additional chordotonal organs (J. O.) and scolopidia (sco. J. O.). (Note that pupal cuticle omitted). Pharate Adult: Fig. 26. Right antenna, lateral aspect. Note that bases of antennal segments 3-5 are telescoped, into their respective segments and also the positions of the imaginal tactile hairs (t. h.). (Most sensilla are omitted from pupal cuticle in the drawing). Fig. 27. Transverse section through head taken at point indicated by arrow in Fig. 28. Compare with Figs. 8 and 17 and note similarity in extrinsic antennal muscles (lev. ant.; dep. ant.) in these stages.

22, 26). In the pharate pupa this sensillum is connected by a dendritic sheath (Fig. 18; d. sh. s. o.) to its propupal equivalent (pro. c. s.).

Adult (Figs. 22-33).

Pupal-Adult Moulting. — The actual pupal stage in *F. fusca* is very short, most time within the pupal cuticle being spent as a pharate adult. Shortly after pupal emergence (Fig. 21), apolysis occurs, the epidermal and sensory cells quickly assuming the configuration of the adult antenna (Fig. 22; hatching). Before imaginal cuticle deposition begins, a lengthened dendritic sheath (d. sh. s. o.) is associated with the pupal campaniform sensillum (p. c. s.) (Fig. 22). In whole mounts, many other pupal sensilla show similar, though finer sheaths. By this stage in development, most internal structures of the antenna have assumed their final position (Figs. 22-25), even though muscle fibres and scolopophorous organs have not yet connected to cuticle.

Adult tactile hairs (t. h.) and chemoreceptors (t.-w. chr.) develop and differentiate in the same way as those of the larva II. The apices of each of the long, apical, tactile hairs (t. h.) of the adult fit singly into apical protuberances available to them in the pupal antennal cuticle (Fig. 26), suggesting that the two are homologous.

The cuticle of antennal segments two, six, seven, and eight is deposited in its fully expanded configuration; whereas that of the scape (one) is thrown into folds, and that of the stalks of segments three to five laid down telescoped into the bases of their respective segments (Fig. 26). The fully-expanded parts start to harden before adult emergence, the process continuing in teneral individuals. When the adult emerges and expands its new cuticle, the folded and telescoped portions straighten out, remaining lighter in colour than the remainder of the antenna.

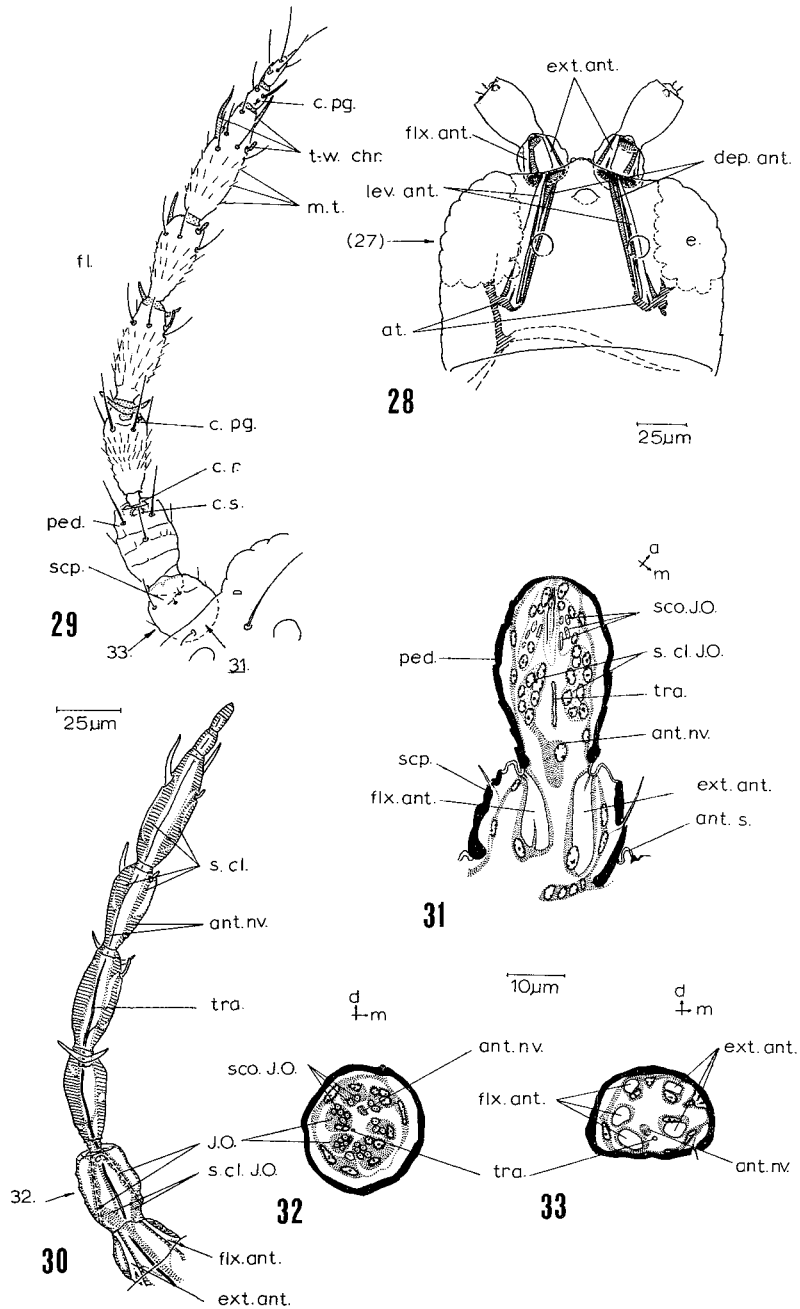
As imaginal cuticle deposition begins, the extrinsic and intrinsic antennal muscles, for the first time since the second larval instar, re-attach to the cuticle. At first, this attachment is by epidermal tendons; later, the myofibrils attach directly. Although they maintain their birefringence throughout metamorphosis, both groups of antennal muscles undergo some developmental changes in the pupa and pharate adult. The levator (lev. ant.) and depressor (dep. ant.) muscles increase in length from about 43 μm in the larva II to about 75 μm in the adult female and also in diameter (compare Figs. 27 and 28 with 6-8). Similar, though smaller changes occur in the scape muscles (flx. ant.; ext. ant.; scp. m.) (compare Figs. 31 and 33 with 14 and 24).

Shortly after adult emergence, most antennal epidermal cells (as is true of those elsewhere in the body) degenerate, leaving a thin epidermis with widely scattered nuclei in the mature adult (compare Fig. 25 with 32 and 24 with 33).

Structure. — The imaginal antennae of *F. fusca* are similar in the two sexes but are smaller in males. Each consists of a scape (scp.), a pedicel (ped.) and six flagellar segments (fl.) (Fig. 29). The scape of each is inserted into a socket (ant. s.) in the head capsule (Fig. 28) and is articulated to it by means of small median and lateral antennifers extending inwards from the socket rim (not shown because of their position). As in the larva, each antenna is raised and lowered by levator (lev. ant.) and depressor (dep. ant.) muscles originating ventrally on the anterior tentorial arms (at.) of the head capsule and inserting, respectively, into the dorsal and ventral margins of the scape base via short (9.0 μm) tendons (Figs. 27, 28). Each consists usually of three (rarely of two) fibres (Fig. 27).

The base of the pedicel articulates with the scape by means of a large dorsal and a very small ventral condyle borne at the apex of the latter. It is flexed laterally and extended anteriorly by the scape muscles (flx. ant.; ext. ant.) (Figs. 28, 30, 31, 33). These consist of three fibres each, as in the larva, and have the same origins and insertions.

Unlike that of larvae, the apex of the adult pedicel lacks dorsal and ventral condyles. Instead, a cuticular ring (c. r.) is present through which pass the cap cells of the Johnston's Organ



Figs. 28-33. *F. fusca*. Adult: Fig. 28. Dorsal aspect of head (♀), showing origins and insertions of intrinsic (flx. ant.; ext. ant.) and extrinsic (lev. ant.; dep. ant.) antennal muscles (All setae omitted). Fig. 29. Right antenna, dorsal aspect. Fig. 30. Same, optical section. Fig. 31. Frontal section through scape (scp.) and pedicel (ped.) of left antenna taken at point indicated by arrow in Fig. 29. Note position of Johnston's Organ sensory neurons (s. cl. J. O.). Fig. 32. Transverse section through pedicel taken at point shown in Fig. 30. Fig. 33. Same, through scape taken at point shown by arrow in Fig. 29. Compare with Fig. 14.

scolopidia (Figs. 29, 30).

Antennal segments two, three, four, five, and six bear, respectively, three, four, five, three, and three whorls of microtrichia (m. t.) (Fig. 29). In females, all antennal segments are dark brown, with segments three to five having yellowish stalks. Male antennae are yellow with some light brown color in segments one to five.

Sense Organs. — The sense organs of the antenna of an adult female are illustrated in Figs. 26, 29, 31 and 32 and are listed in Table II. As can be seen by comparing Tables I and II, there has been an increase in the number of tactile hairs (t. h.; from 29 to 53) and thin-walled chemoreceptors (t.-w. chr.; from five to nine), but an apparent replacement of the apical sense organs (ap. s. o.) of segment three of the larva by those of segment five of the adult. In addition, most adult chemoreceptors, including the coeloconic pegs (c. pg.), differ in size, shape and/or position from those of the larval stages (compare Fig. 29 with 1 and 9).

As already indicated, the imaginal Johnston's Organ of *F. fusca* consists of six chordotonal organs, each containing three to five scolopidia (Figs. 30-32). Since the latter are small and not in register, a single transverse section (Fig. 32) does not show them all so that counts are difficult to make. Since five were clearly visible in many of the sectioned organs, this is probably the number most characteristic.

As in larvae, some scolopidia appear to be innervated by one and others by two sensory neurones according to the number of ciliary dilations visible inside each scolopidium (note dots in Figs. 25 and 32). Insertions and origins of the chordotonal organs and the positions occupied by their sensory cells (s. cl. J. O.) are approximately the same as those of larvae (Figs. 30, 31). The antennal nerve (ant. nv.) of each antenna (Fig. 30, 31) proximally, enters the deutocerebrum of the brain; the latter now occupying the much larger adult head rather than the prothorax. As in larvae, the nerve of each antenna bifurcates within the base of the first flagellar segment (Fig. 30), the two branches coursing distally within the basement membrane of the antennal epidermis.

Table II. Sense organs on the antenna of the adult female of *F. fusca* (N = 15).

Segment	tactile hairs	campaniform sensilla	Johnston's Organ	thin-walled chemoreceptors	coeloconic pegs	apical sense organs
1	11					
2	7	1	1 (6 chordotonal organs)			
3	5			1	1	
4	5			2		
5	6			2	1	3
6	8			3	1	
7	3			1	1	
8	8(7)					
Totals	53	1	1	9	4	3
Grand Total	71					

Haplothrips verbasci

H. verbasci is confined to plants of the genus *Verbascum* (Scrophulariaceae) (Priesner, 1928; Bailey, 1939), the entire life cycle being spent on the host. The two larval stages congregate near the growing apex of the flower stalk or in the flowers, where they feed on the inner surfaces of the sepals. The quiescent propupae, pupae I and pupae II are usually hidden between the seed capsules and the sepals in the lower, older part of the inflorescence. Teneral adults stay in their pupation sites but mature ones are found wandering and feeding everywhere, particularly among the flowers.

Larval Stages (Figs. 34-43; 76-78).

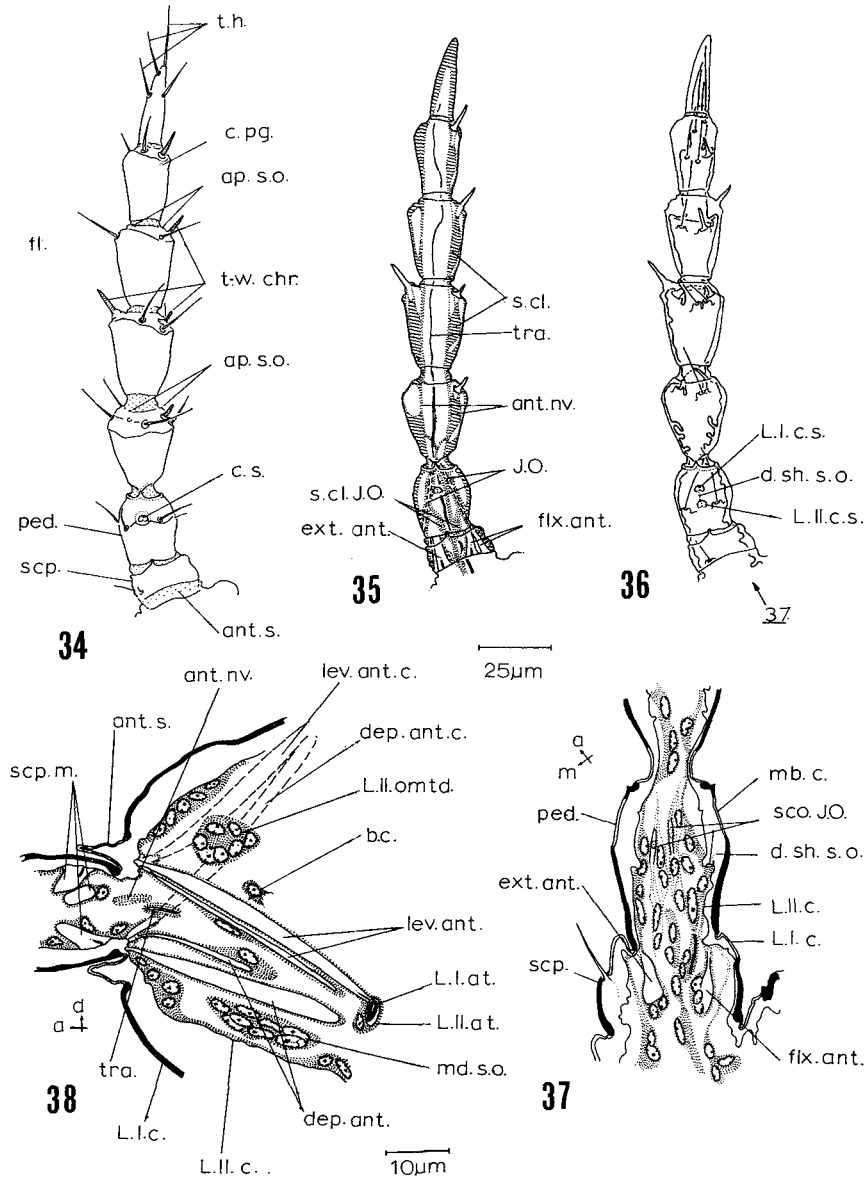
Structure. — Antennae of the two larval stages of *H. verbasci* (Figs. 34, 35, 40, 41) contain the same number of segments (seven) as those of *F. fusca*, but differ from them in shape. The scape (scp.) of each is inserted into a socket (ant. s.) in the head capsule (Fig. 39) but is articulated to it by a single median antennifer only. Each antenna is raised and lowered by two groups of extrinsic muscles. The first are identical to those of *F. fusca* and consist of levator (lev. ant.) and depressor (dep. ant.) fibres originating ventrally on the anterior tentorial arms (at.) and inserting respectively into the dorsal and ventral margins of the scape base (Figs. 38, 39). The second set (lev. ant. c.; dep. ant. c.) have the same insertions; but converge posterodorsally to a common origin mid-dorsally on the vertex of the cranium (Figs. 38, 39).

Proximally, the pedicel (ped.) articulates on dorsal and ventral condyles borne by the apex of the scape (scp.) (only the dorsal one is present in larvae of *F. fusca*). It is flexed and extended by 3-fibred scape muscles (flx. ant.; ext. ant.; scp. m.) with origins and insertions identical to those of *F. fusca* (Figs. 35, 37-39, 41, 42). As in *F. fusca*, the first flagellar segment articulates laterally and mesally on dorsal and ventral condyles borne by the apex of the pedicel (Figs. 34, 40).

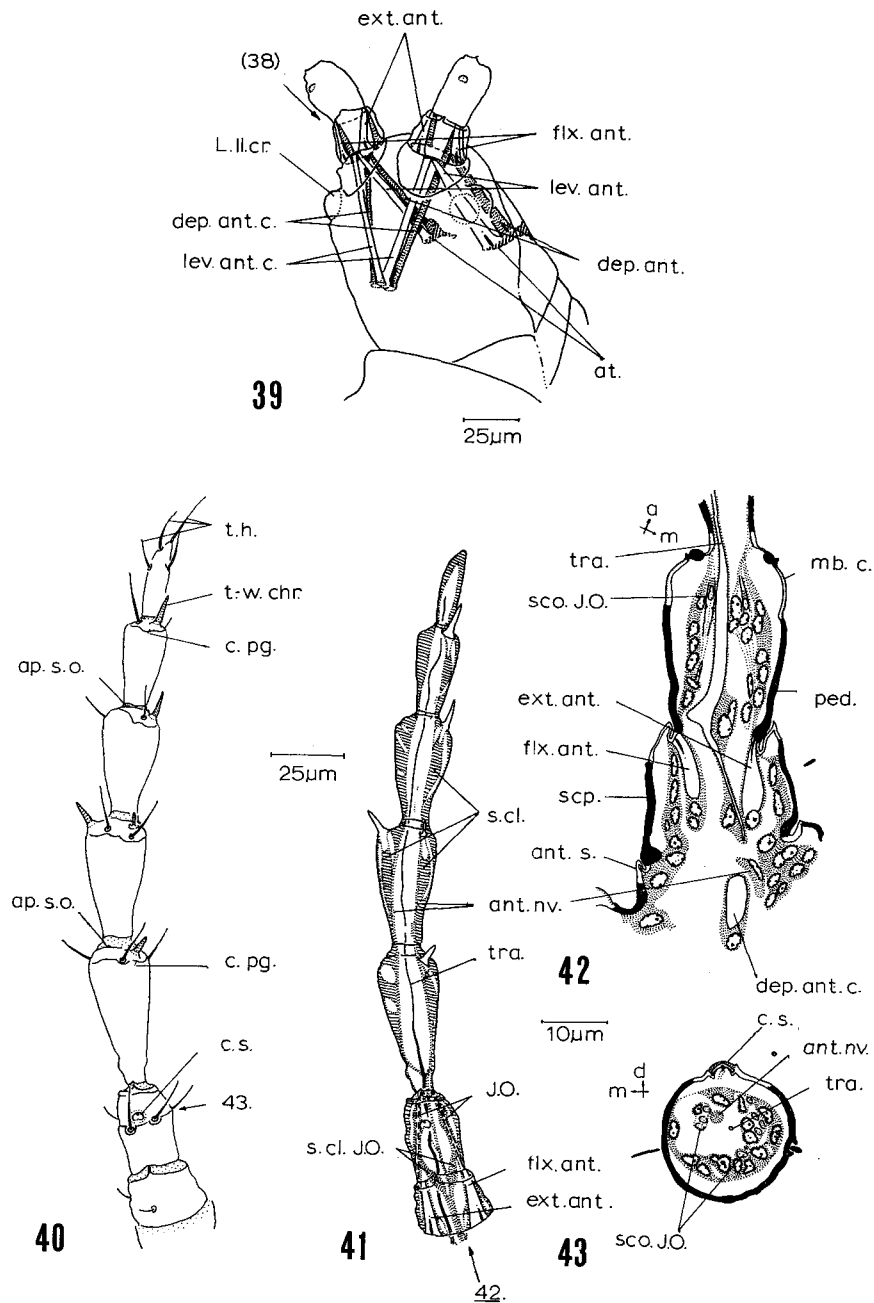
In living larvae of both sexes and stages, mounted in water under a coverslip (Heming, 1972) and viewed at X500, irregular pumping movements can be seen occurring just proximal to the base of each antenna. These movements vary in rate in fresh specimens observed at room temperature, from about 32 to 80 X per minute and are asynchronous in the two antennae. Usually, one contracts more rapidly than the other, with the pump of either antenna beating the faster. In specimens mounted venter uppermost, there appear to be two fibres to this pumping organ; one inserted dorsally, the other ventrally into the basal margins of the scape. I am unsure of their origins. In sections (Figs. 37, 38, 42), I have been unable to see muscular tissue in the site of the "pump" other than that of the extrinsic antennal muscles (lev. ant.; dep. ant.; lev. ant. c.; dep. ant. c.). Since they have approximately the same orientation as the antennal tentorial muscles, I, at first, thought them to be the same. However, the "pumps" continue to beat without interruption throughout the quiescent stages until the pharate adult, even during the pharate propupal period when massive changes occur in the structure of the antennae (see below). Since the contractile elements of the antennal muscles degenerate in the propupa, the antennal "pumps" cannot be these muscles. The "pumps" are not apparent in adults of either sex.

The cuticle of all seven larval segments is smooth and sclerotized and lacks the whorls of microtrichea present in those of *F. fusca* (Figs. 34, 40). The apical portions of segments two to six, bearing the sensilla, are of unpigmented, thinner cuticle (mb. c.) (Figs. 34, 37, 40, 42, 43).

Sense Organs. — The antennal sense organs of larval *H. verbasci* are identical in both instars and sexes. They are illustrated in part in Figs. 34, 35, 37, 40-43, 76-78 and are listed in Table III. Despite superficial differences in antennal structure existing between larvae of *H. verbasci* and *F. fusca* (compare Figs. 34 and 40 with 1 and 9), their sensilla are remarkably similar, both



Figs. 34-38. *H. verbasci*. Larva I: Fig. 34. Right antenna, dorsal aspect. Note the tiny coeloconic peg (c. pg.) on segment 6. Fig. 35. Same, optical section. Pharate Larva II: Fig. 36. Right antenna, dorsal aspect, showing developing larva II antenna (Note: Most larva I sensilla omitted). Fig. 37. Frontal section of scape (scp.) and pedicel (ped.) of right antenna taken at point indicated by arrow in Fig. 36. Note that the origins of the Johnston's Organ chordotonal organs (sco. J. O.) and the scape muscles (flx. ant.; ext. ant.) are detached from the larva I cuticle (L. I. c.). Fig. 38. Oblique parasagittal section of head taken at point indicated by arrow in Fig. 39. Note the common insertions of the dorsal (lev. ant. c.; dep. ant. c.) and ventral (lev. ant.; dep. ant.) branches of the extrinsic antennal muscles and that these are detached at both ends from the larva I cuticle (L. I. c.).



Figs. 39-43. *H. verbasci*. Larva II: Fig. 39. Dorsolateral aspect of head, showing origins and insertions of intrinsic (fix. ant.; ext. ant.) and extrinsic (lev. ant.; lev. ant. c.; dep. ant.; dep. ant. c.) antennal muscles. Compare with Fig. 6 of *F. fusca*, noting the additional, dorsal set of extrinsic antennal muscles (lev. ant. c.; dep. ant. c.) of this species. (All setae are omitted). Fig. 40. Right antenna, dorsal aspect. Fig. 41. Same, optical section. Fig. 42. Frontal section of scape (scp.) and pedicel (ped.) of left antenna, taken at point indicated by arrow in Fig. 41. (Note: The structure labelled trachea (tra.) may be a blood vessel). Fig. 43. Transverse section through pedicel taken at point indicated by arrow in Fig. 40. (Note: Johnston's Organ scolopidia (sco. J. O.) are not in register, so that not all are figured).

in number and in relative position in each segment (compare Tables I and III). The only differences are an apparent absence of three apical sense organs (ap. s. o.) from segment five of larval *F. fusca* (these are very small and may well be present in both species), and a shifting of the chemoreceptor (t.-w. chr.) of segment three to the dorsolateral side in *H. verbasci* (it is ventral in *F. fusca*; note absence in Figs 1 and 9).

Table III. Sense organs on the antenna of the larva II of *H. verbasci* (N = 5).

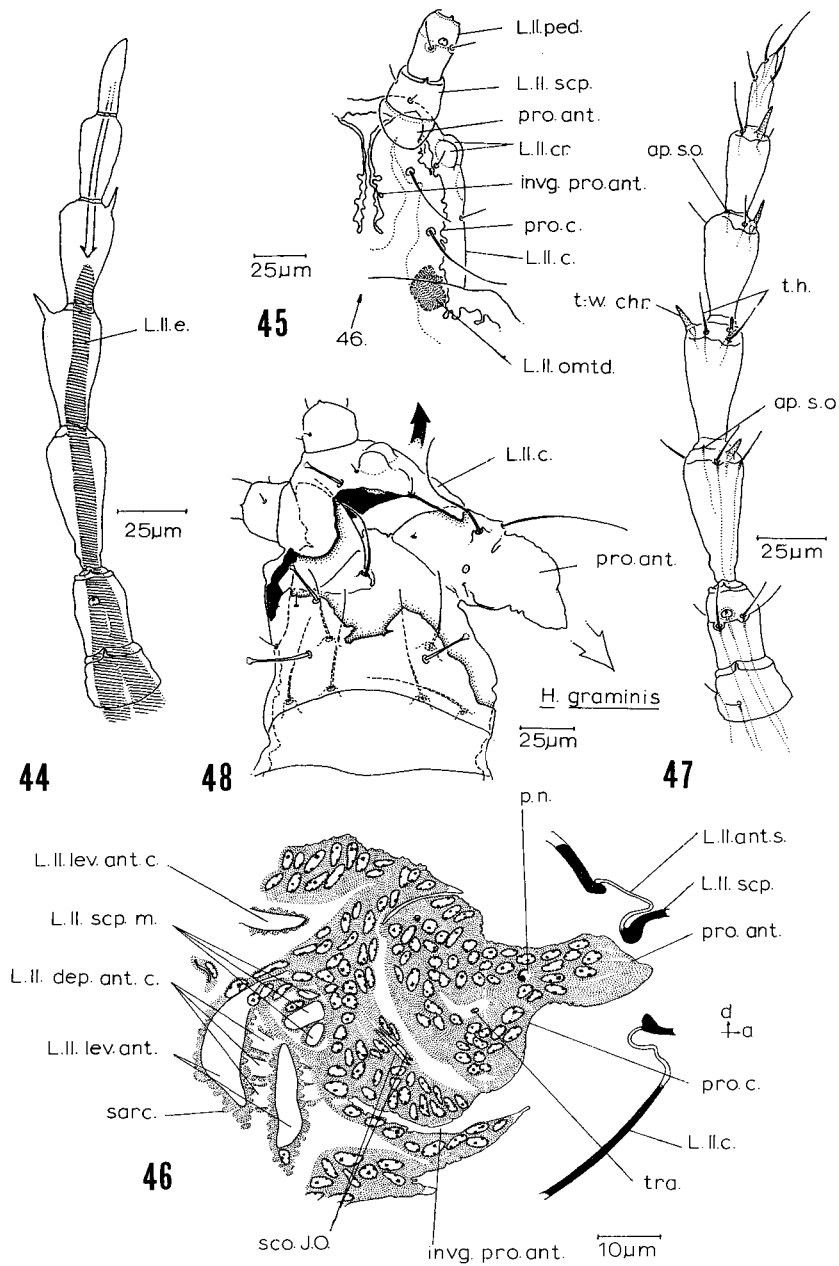
Segment	tactile hairs	campaniform sensilla	Johnston's Organ	thin-walled chemoreceptors	coeloconic pegs	apical sense organs
1	4					
2	5	1	1 (4 chordotonal organs)			
3	4			1	1	3
4	3			2		
5	3			1	1	3
6	3			1	1	
7	6					
Totals	28	1	1	5	3	6
Grand Total	44					

The Johnston's Organ (J. O.) in larvae of *H. verbasci* consists of four chordotonal organs each containing two or three scolopidia (sco. J. O.) (Figs. 35, 37, 41-43 – contrasting with three containing two in larvae of *F. fusca*). Scolopidial counts are difficult to make in larvae of this species because they are not in register as they are in *F. fusca*. All scolopidia are probably associated with two sensory neurons as most contain two ciliary dilations (Fig. 43 – note dots). The origins and insertions of the Johnston's Organ and the disposition of its sensory neurons are similar to those of *F. fusca* (Figs. 35 and 41). As in that species, the larval head is relatively small so that the brain is situated in the prothorax. The nerve of each antenna likewise bifurcates within the base of the first flagellar segment (Figs. 35, 41).

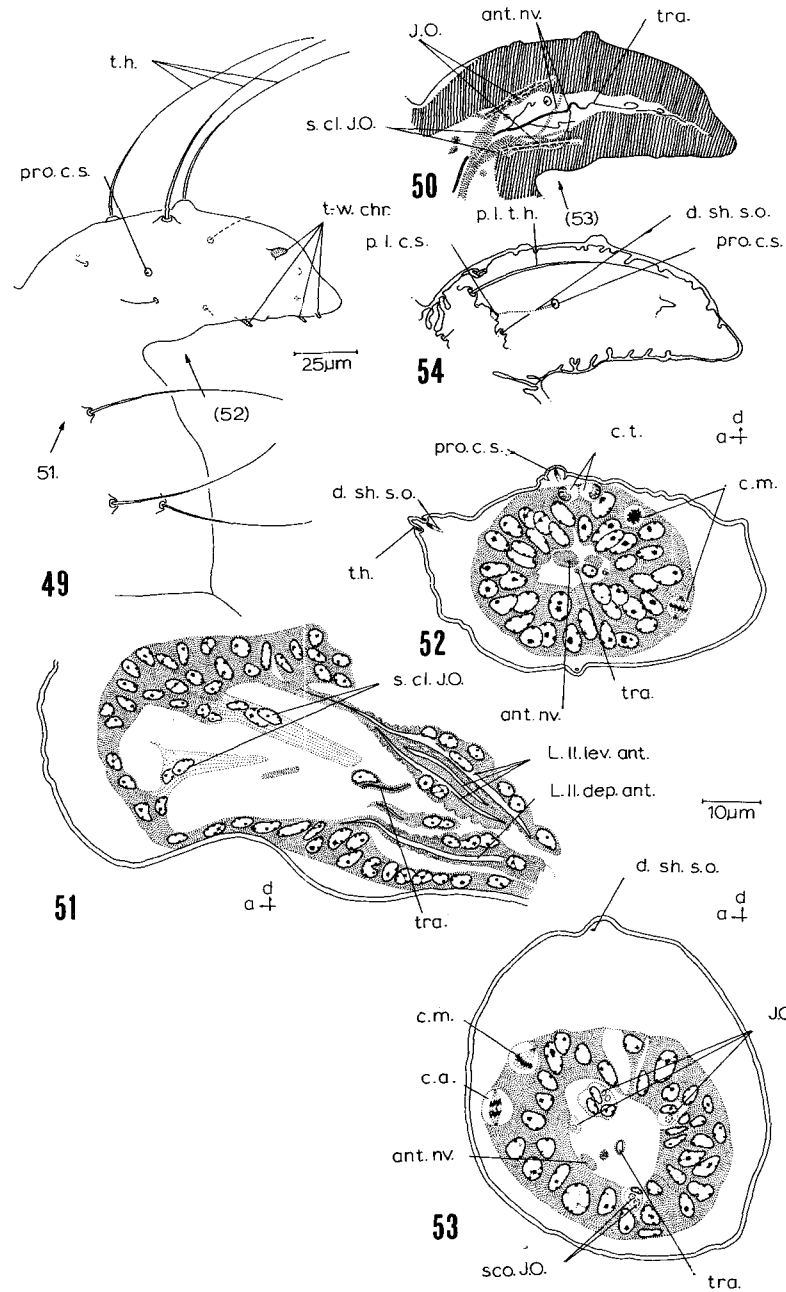
Larva I-Larva II Moults. – Replacement of the first by the second-instar antennae in *H. verbasci* transpires in the same way as described for *F. fusca* (Figs. 36-38). In the pharate larva II (Fig. 36) the old (L. I. c. s.) and new (L. II. c. s.) pedicellar campaniform sensilla are likewise connected by a dendritic sheath (d. sh. s. o.). During apolysis and ecdysis, the antennal “pumps” continue to beat.

Propupa (Figs. 44-53; 79, 80).

Larva II-Propupal Moults. – The events occurring during replacement of the second larval by the propupal antennae in *H. verbasci* are far more complex than those taking place in *F. fusca*. At the larva II-propupal apolysis, all cells within each larval antenna detach from the cuticle and withdraw caudally down the length of the antenna into the head capsule (Fig. 44).



Figs. 44-48. *H. verbasci*. *Exuvial Pharate Propupa*: Fig. 44. Right antenna, optical section, showing larval antennal epidermis (L. II. e.) being withdrawn proximally. *Pharate Propupa*: Fig. 45. Dorsal aspect of head, showing propupal antenna (pro. ant.) invaginated into a pouch (invg. pro. ant.) in the head epidermis. Note that the larval eye (L. II. omtd.) is situated in the prothorax far caudad of the larva II cornea (L. II. cr.). (Note: Propupal sensilla and dendritic sheaths of larva II sensilla (Fig. 47) are omitted from the drawing). Fig. 46. Sagittal section through antenna taken at point indicated by arrow in Fig. 45. Note that the sarcolemma (sarc.) of the contracted, larval muscles is thrown into folds and also the posterior position of the Johnston's Organ scolopidia (sco. J. O.). Fig. 47. Larva II right antenna, dorsal aspect. Notice the long dendritic sheath of each sensillum and also that those of the scape and pedicel run proximally to the propupal antenna (Fig. 45). *Emerging Propupa*: Fig. 48. Dorsal aspect of head, showing right propupal antenna (pro. ant.) evaginating from its pouch (Note that this drawing is of a specimen of *Haplothrips graminis* Hood not *H. verbasci*).



Figs. 49-54. *H. verbasci*. Newly-emerged Propupa: Fig. 49. Right antenna, dorsal aspect. Fig. 50. Same, optical section. Note the thick epidermis. Fig. 51. Oblique sagittal section of antennal base taken at point indicated by arrow in Fig. 49. Note that the extrinsic antennal muscles (L. II. lev. ant.; L. II. dep. ant.) of the larva have lost most of their myofibrils (white). Exuvial Pharate Pupa I: Fig. 52. Transverse section through antenna taken at point indicated by arrow in Fig. 49. Note shape of propupal campaniform sensillum (pro. c. s.), the large size of epidermal nuclei (compare with Fig. 46), and the dividing cells (c. m.; c. t.). Fig. 53. Same, taken at point indicated by arrow in Fig. 50. Note that the Johnston's Organ (J. O.) still consists of 4 chordotonal organs. Pharate Pupa I: Fig. 54. Right antenna, dorsal aspect, showing developing pupa I antenna (Note: Propupal sensilla omitted from drawing).

This withdrawal appears to have two causes. First, all extrinsic and intrinsic antennal muscles contract maximally, the sarcolemma (sarc.) of each fibre being thrown into folds (Fig. 46) (this contraction involves all head muscles (Heming, in prep)). Since all head muscles have separated from the larval cuticle, this contraction serves to bunch epidermal and sensory cells together in the centre of the head capsule (compare Fig. 46 with 38). In addition, there must also be some change in shape in individual antennal epidermal cells, since muscle contraction alone cannot account for complete withdrawal of all cells from within each antenna, and because these cells are bunched, when completely retracted, even distal to the intrinsic muscles (L. II. scp. m.) (Fig. 46). At the completion of withdrawal, the ommatidia of the larval eyes (L. II. omt.) are situated anteriorly in either side of the prothorax (Fig. 45) and the Johnston's Organ (sco. J. O.) and scape muscles (L. II. scp. m.) far caudad of the base of each larval antenna (Fig. 46).

Although I have not watched epidermal withdrawal in living specimens in its entirety (all larvae drowned before completion), I know that it takes place rather slowly. Posterior movement of the cells is imperceptible in live specimens and there is sufficient time for the tormogen cell of each sense organ to produce a long dendritic sheath (Fig. 47). In spite of these, at the completion of withdrawal, only the sensilla of the larval scape and pedicel appear to maintain contact with the prepupa within (Fig. 47).

A small number of degenerating cells (p. n.), as is usual for a moult (Heming, 1973), are visible (Fig. 46) in each antenna during and after withdrawal, but cell death does not play a major role in metamorphosis. However, individual cell nuclei are smaller (Fig. 46) than they are later (Figs. 51-53).

As soon as antennal withdrawal is complete, the epidermis begins to deposit propupal cuticle (Figs. 45, 46). At this stage, one can see that each antenna (pro. ant.) is sunk to its tip in a pocket (inv. pro. ant.) in the head epidermis (Figs. 45, 46). As the long, propupal tactile hairs (t. h.) (Fig. 49) develop, they poke apically out of these pockets where they are easily confused with the elongated dendritic sheaths of the larval scape and pedicellar sensilla (Fig. 47).

All head muscles, except for two delicate fibres inserting into the anterior wall of the cibarium, begin to regress shortly after propupal cuticle deposition begins. Loss of birefringence in their myofibrils is much more rapid than that occurring in the pretarsal depressor muscles of this species (Heming, 1973), and is complete by the middle of the propupal stage. The tentorial extrinsic antennal muscles (L. II. lev. ant.; L. II. dep. ant.) are the last to lose it (Fig. 51). As occurs in the pretarsal depressor muscles, regression in the head muscles involves only their contractile elements, their sheaths remaining recognizable throughout metamorphosis. However, both the scape muscles and the dorsal contingent of antennal extrinsic muscles disappear completely.

A pharate prepupa is easy to recognize under the stereoscopic microscope because it is sluggish, is very fat, cannot move its larval antennae, and has its larval maxillary stylets extruded (Heming, in prep.). At ecdysis, the larval head capsule (L. II. c.) fractures behind the eyes (L. II. cr.) and the propupal antennae are everted out of their pouches by pressure of haemolymph (Fig. 48). The antennal "accessory hearts" maintain their beating throughout the period described above.

Structure. – The propupal antennae of *H. verbasci* and other phlaeothripids are short, thick, unsegmented, membranous stubs (Figs. 49, 50, 79). In newly-emerged individuals, the antennal epidermis is very thick and consists of numerous closely-packed nuclei having large nucleoli (Figs. 50, 51-53). Many cells are in various stages of mitosis (c. a.; c. m.; c. t.). These divisions are probably both multiplicative and differentiative, presumably giving rise to the numerous sensory, trichogen and tormogen cells of the imaginal array of sensilla as well as to additional

epidermal cells contributing to the longer antennae of subsequent instars. Some birefringence is still evident in the larval antennal levator (L. II. lev. ant.) and depressor (L. II. dep. ant.) muscles until the propupal-pupa I apolysis (Fig. 51).

Sense Organs. — Each propupal antenna bears three large, two medium, and three small tactile hairs (t. h.), at least four thin-walled chemoreceptors (t.-w. chr.), and a pedicellar campaniform sensillum (pro. c. s.) (Figs. 49, 52, 79, 80). There are also a few, very fine sensilla at the antennal apex just visible at the maximum resolving power of the light microscope. The propupal campaniform sensillum (pro. c. s.) is smaller than that of the larva II and is more convex (Figs. 52, 80).

The Johnston's Organ in propupae still contains four chordotonal organs and is embedded in thickened epidermis (Figs. 50, 53) proximal to the campaniform sensillum. I was unable to determine the number of scolopidia (sco. J. O.) contained in each chordotonal organ, but the larval number (three) is probably still present.

Antennal nerve (ant. nv.) and trachea (tra.) persist, with the latter thrown into loops (Fig. 50).

Pupa I (Figs. 54-58; 81, 82).

Propupal-Pupa I Molt. — During the propupal-pupa I apolysis, the epidermis separates from the cuticle and begins to secrete a larger, folded, pupa I cuticle within (Fig. 54). The pupa I campaniform sensillum (p. I. c. s.) develops some distance proximal to the propupal one (pro. c. s.), so that the dendritic sheath (d. sh. s. o.) connecting the two is quite long. The new, long tactile hairs (p. I. t. h.) develop with their long axes parallel to that of the propupal antenna (Fig. 54). The increase in antennal length arises in the apical half of the propupal antenna between the bases of the long tactile hairs (t. h.) proximally, and the apical chemoreceptors (t.-w. chr.) (Figs. 49, 54, 55, 79, 81).

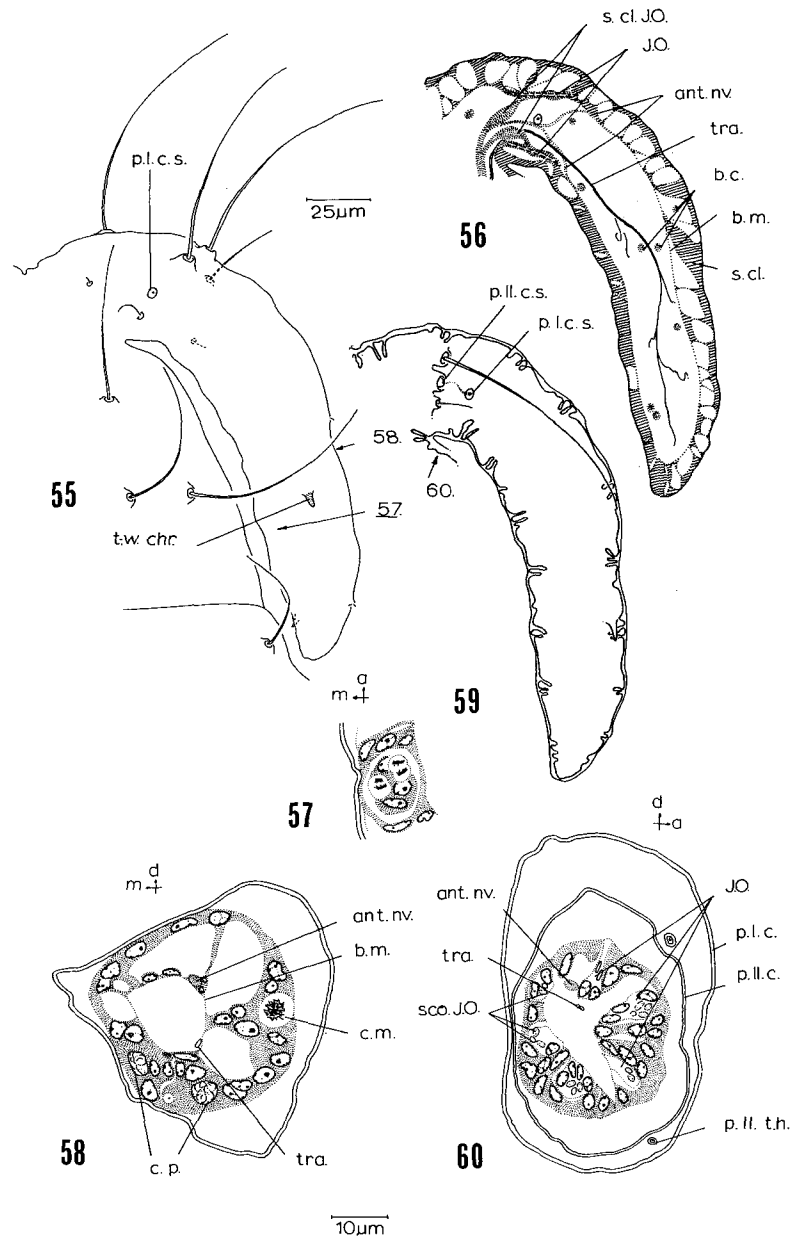
That the pupa I antenna is bent back posteriorly alongside the head (Figs. 55, 81) is due to the way that its cuticle is deposited in the pharate pupa I (Fig. 54). More cuticle is produced anteriorly than posteriorly and more folds develop here. At ecdysis, the fragile, propupal cuticle remaining splits between the antennae and the new antennae are pulled out of the bases of the old. On expansion of the new cuticle, these folds stretch out and the antennae slowly assume their characteristic flexed position. Although not as drastic, the process is very similar to that occurring after the propupal-pupal ecdysis of *F. fusca*.

Structure. — Pupa I antennae (Figs. 55, 81) are very similar to propupal ones (Figs. 49, 79) except for their greater length, reflexed orientation and thin, attenuated epidermis (Fig. 56).

Sense Organs. — Antennal sensilla of this instar are practically identical to those of the previous one, including their relative positions (compare Figs. 55, and 56 with 49 and 50). The pupa I antenna lacks two chemoreceptors apically, and there are additional small setae (not illustrated because of their size) scattered throughout. Sense organ positions indicate that most of the increase in antennal length is interposed in its middle.

The high mitotic rate (c. p.; c. m.) characteristic of the antennal epidermis of the propupal stage, continues during this instar (Figs. 57, 58). When the epidermis is attenuated in newly-emerged individuals (Fig. 56), sensory cells (s. cl.) are easy to recognize because they adhere together in groups (Figs. 56, 57). The mitoses taking place within these bunches are undoubtedly differentiative (Fig. 57).

In the pharate pupa II (Fig. 60), each Johnston's Organ comprises six chordotonal organs containing three (sometimes four) scolopidia each. These, again, are difficult to see because they are embedded in epidermis and are not in register. As only four chordotonal organs are present in the young propupa (Fig. 53), the additional ones must have been added sometime between the pharate pupa I and the exuvial pharate pupa II stages. The many mitotic divisions



Figs. 55-60. *H. verbasci*. Newly-emerged Pupa I: Fig. 55. Right antenna, dorsal aspect. Fig. 56. Same, optical section. Note attenuated epidermis and haemocytes (b. c.). Fig. 57. Frontal section, through antenna, taken at point indicated by arrow in Fig. 55, showing differentiative mitotic divisions in a developing sensory cell group. Fig. 58. Transverse section, through antenna taken at point indicated by arrow in Fig. 55. Note cells (c. p.; c. m.) in various stages of mitosis. Pupa II: Fig. 59. Right antenna, dorsal aspect, showing developing pupa II antenna. (Note: Most pupa I sensilla omitted from drawing). Notice that the folds in the pupa II cuticle delimit 8 "segments". Fig. 60. Transverse section through pedicellar region taken at point indicated by arrow in Fig. 59. Compare with Fig. 53 and note the additional 2 chordotonal organs comprising the Johnston's Organ (J. O.).

occurring in this area during this period probably contribute to the development of these new structures. Details of their development are difficult to follow because only perfect sagittal sections of the animal can be used.

Pupa II (Figs. 59-63; 83-86).

Pupa I-Pupa II Moul. – The first clear indication of adult segmentation appears in the pharate pupa II (Fig. 59) where, new cuticle, as it is deposited, is thrown into folds. These are not dispersed evenly throughout each antenna but, instead, are spaced in such a way that they delimit eight segments. When the pupa II emerges, these folds stretch out with the result that segmentation again becomes less distinct (Figs. 61; 83, 85). In other respects, events are the same as those occurring in the previous moult.

Structure. – Except for their increased length, pupa II antennae (Figs. 61; 83-86) are similar to those of propupa (Figs. 49, 79) and pupa I (Figs. 55, 81). They are about 1.5 fold longer than those of the pupa I, are more tightly fitted to the sides of the head (which now has the shape and size of the adult head) and are arched dorsally at their bases and bent ventrally and medially at their apices under the prothorax (Figs. 83-85).

Sense Organs. – Sensilla in pupae II are similar in number and placement to those of pupae I (compare Figs. 61 and 62, with 55 and 56), but only one large chemoreceptor (t.-w. chr.) is present on each antenna. There are also many small sensilla scattered throughout that I have not illustrated. Most increase in antennal length again has arisen distal to the pedicellar campaniform sensillum (p. II. c. s.).

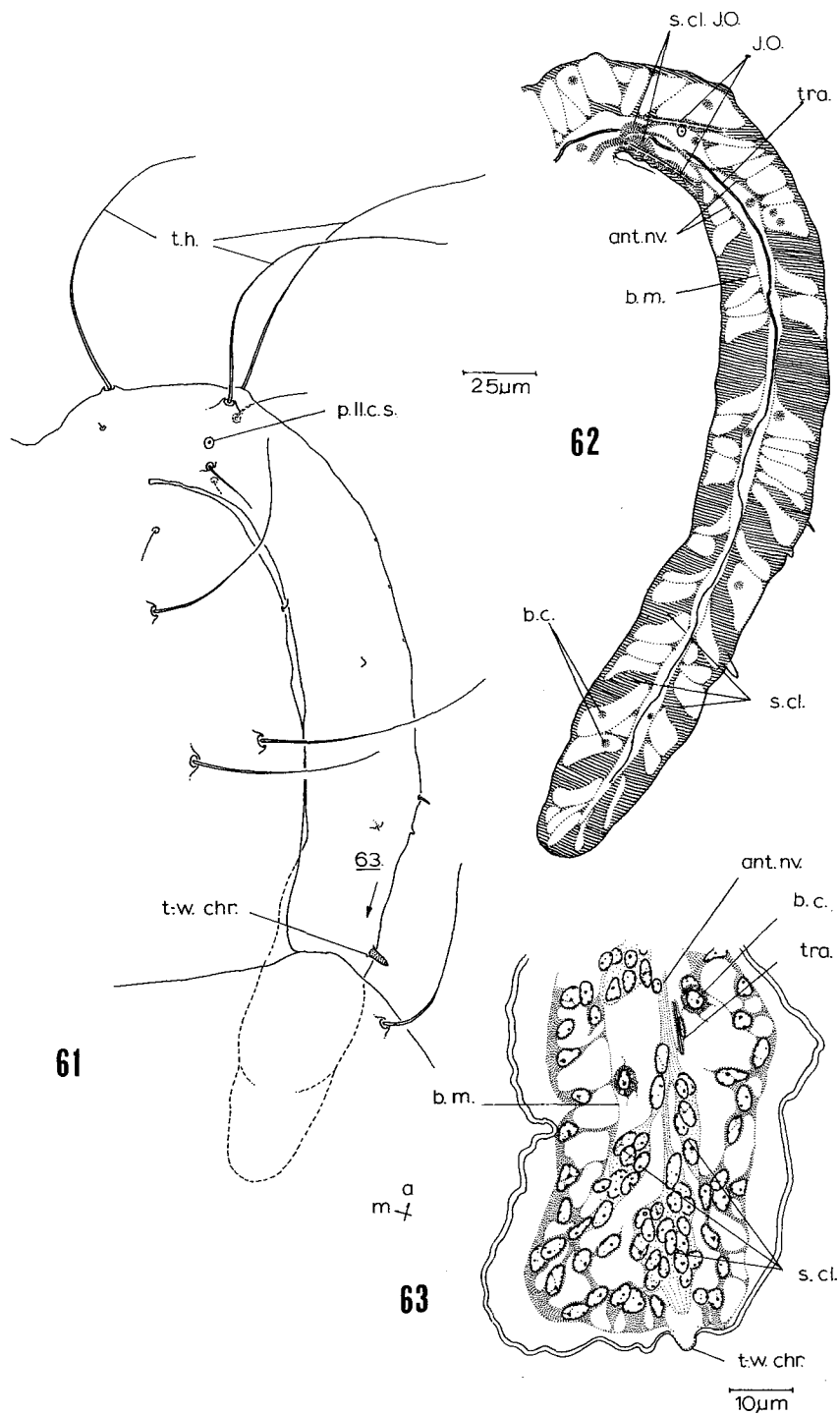
Mitosis in epidermis and in sensory cell groups practically ceases in this instar and most subsequent development involves the movement and differentiation of already-present cells. The epidermis is, again, greatly attenuated in teneral forms (Figs. 62, 63), with groups of sensory cells clearly defined.

Adult (Figs. 64-75; 87).

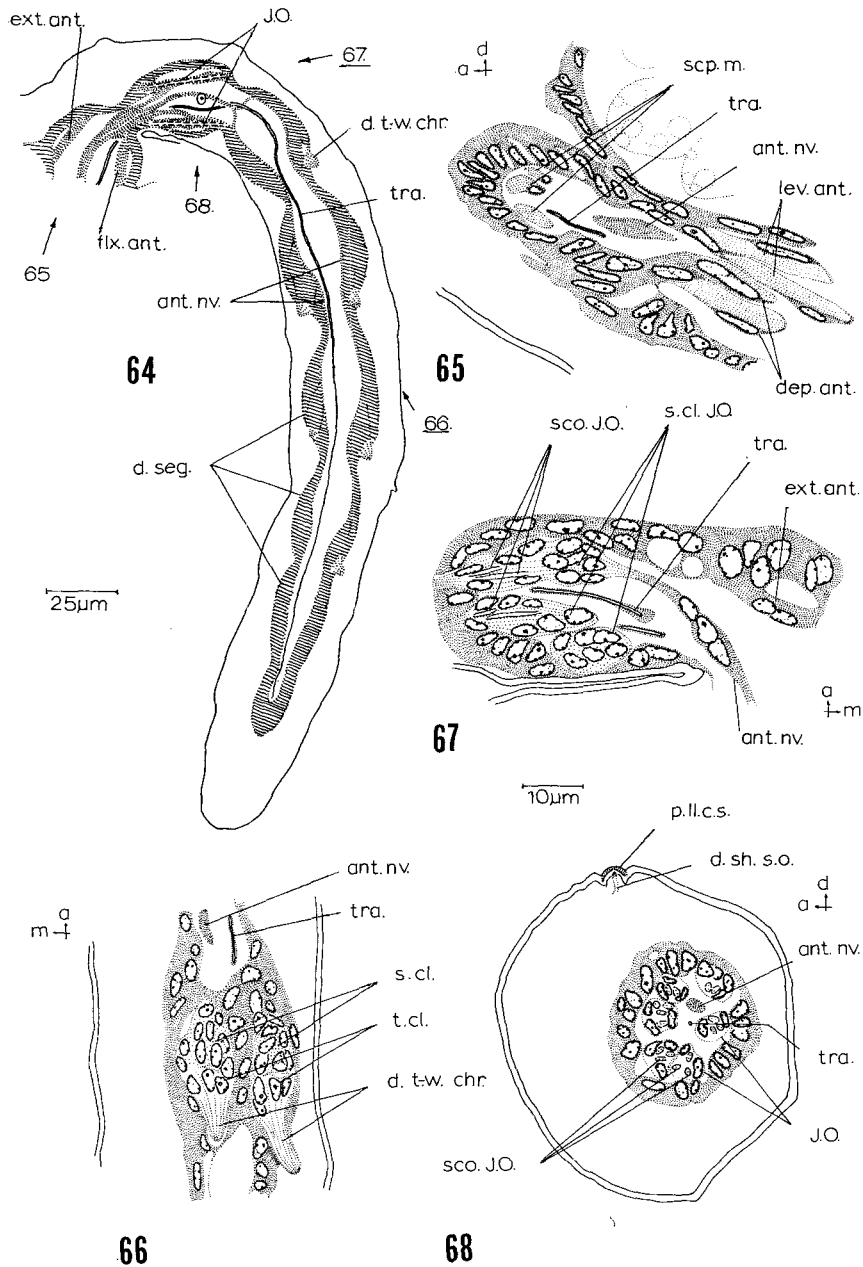
Pupa II-Adult Moul. – Most time within the pupa II cuticle is spent as a pharate adult, (Figs. 64-69). At the pupa II-adult apolysis (Fig. 64), the epidermis contracts away from the cuticle and almost immediately assumes the configuration of the imaginal antennal segments. Trichogen cells (t. cl.) begin to send out protoplasmic extensions around which cuticle is deposited in the cuticular phase to form the external parts of adult sense organs. (Figs. 64, 66). All tactile hairs are at first protoplasmic too, but I have not drawn them in. Their disposition from the beginning, is as is shown in Fig. 69. By the exuvial pharate adult stage, most internal structures have their imaginal positions (Figs. 64-68).

Figure 69 shows the position of adult antennal segments shortly before adult eclosion. This drawing is fore-shortened proximally and apically because of the arched condition of the pupa II antennal sheath (foreshortening is also present in Figs. 61, 62, and 64). Notice that the cuticle of antennal segments two, seven and eight is deposited fully-expanded, whereas that of segment one is folded, and that of the stalks of segments three to six is telescoped into the bases of their respective segments. As in *F. fusca*, the fully expanded parts start to preharden before adult emergence. After the pupa II cuticle is shed, the scape and the reflexed portions expand and straighten, the antenna assuming its mature length (Fig. 71 – drawn at same magnification as Fig. 69). Most epidermal cells degenerate soon thereafter.

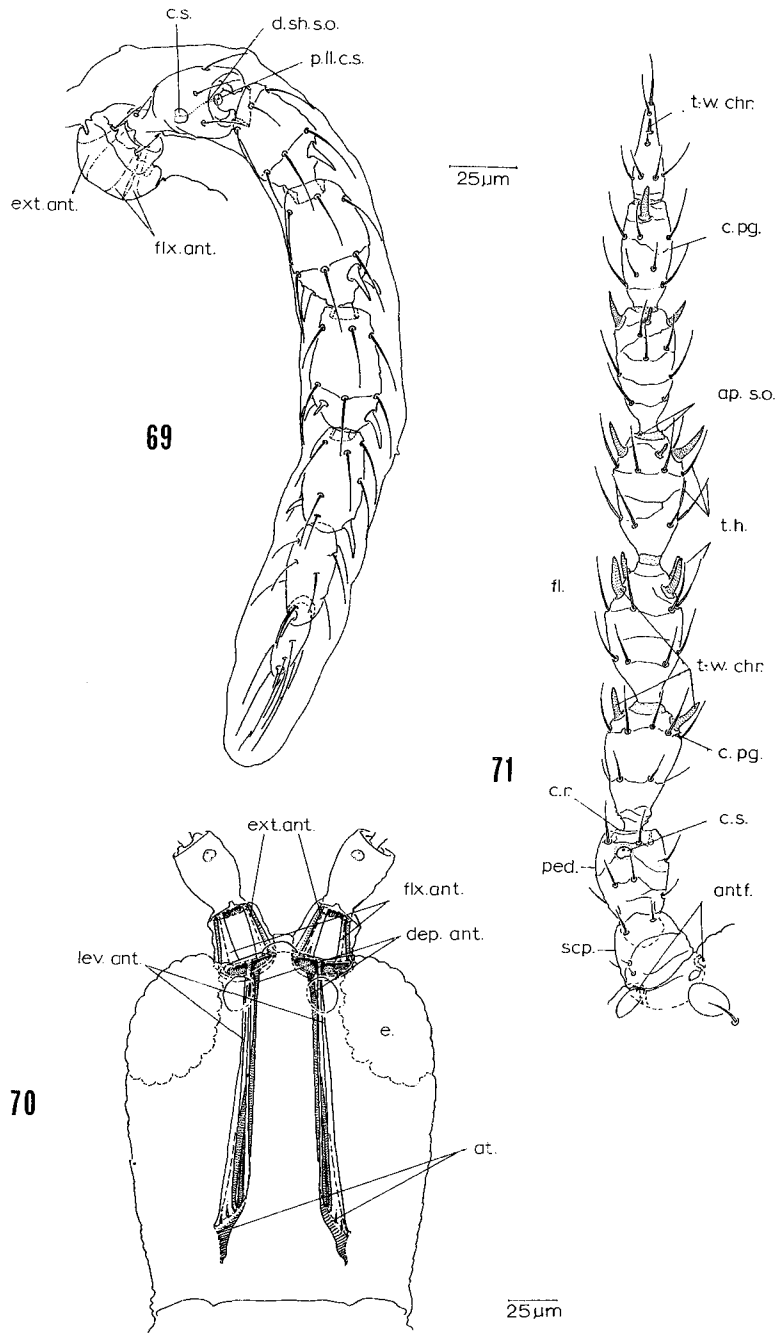
In the exuvial pharate adult stage, the cells of the remnants of the extrinsic antennal muscles (lev. ant.; dep. ant.) begin to show signs of renewed physiological activity. Their nuclei and nucleoli enlarge and their cytoplasm increases in volume and in susceptibility to basic dyes (Fig. 65). The cells begin to synthesize new myofibrillar material at about the same time as adult cuticle deposition begins and birefringence begins to become apparent in these muscles



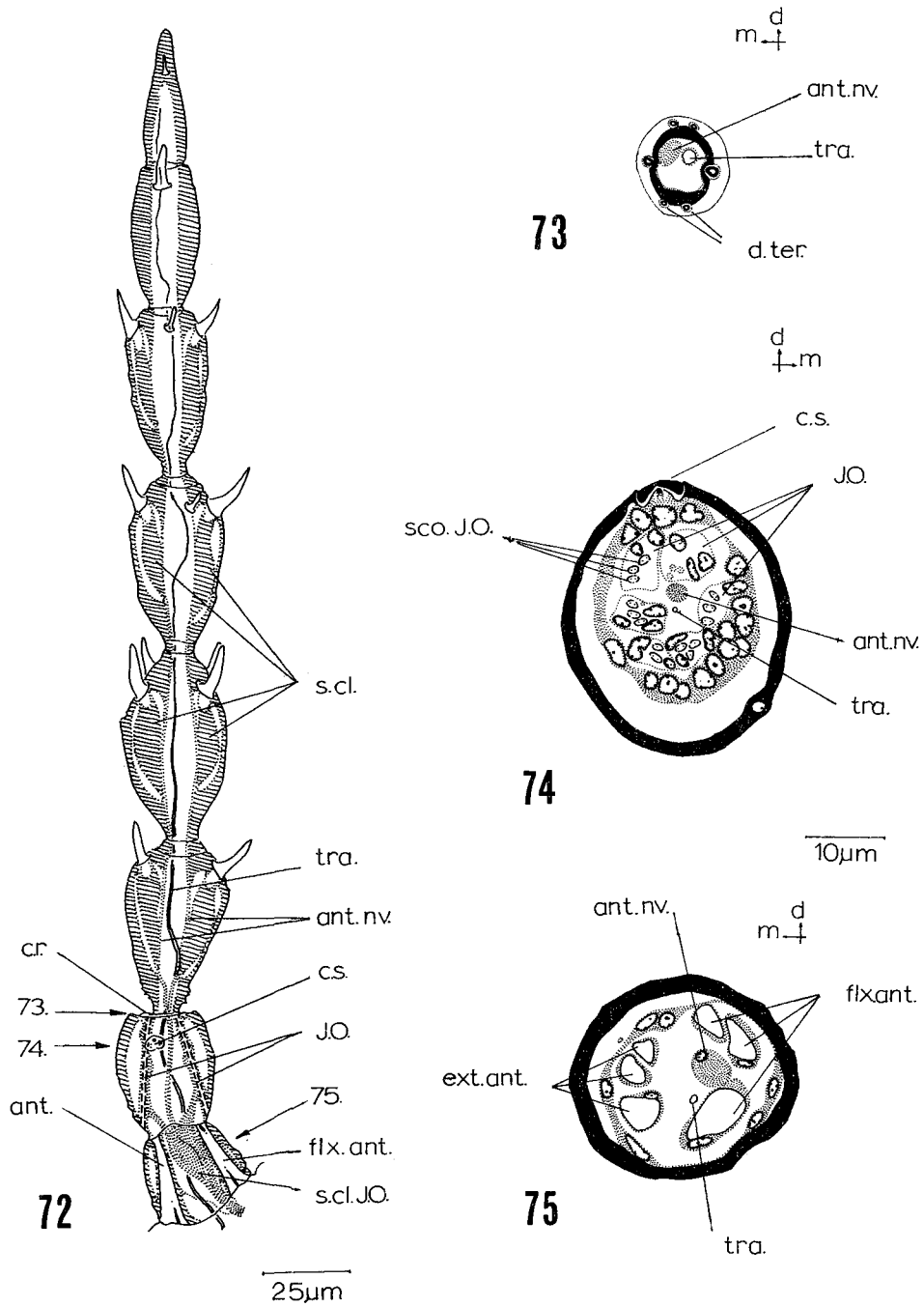
Figs. 61-63. *H. verbasci*. Newly-emerged Pupa II: Fig. 61. Right antenna, dorsal aspect. Compare with Figs. 49 and 55 and note the common chaetotaxy of the antenna in all 3 quiescent stages. Fig. 62. Same, optical section. Notice attenuated epidermis and groups of sensory cells (s. cl.). Fig. 63. Frontal section through antenna taken at point indicated by arrow in Fig. 61. Notice the haemocytes (b. c.) and the groups of sensory neurons (s. cl.) and their support cells.



Figs. 64-68. *H. verbasci*. Exuvial Pharate Adult: Fig. 64. Right antenna, optical section. Notice developing segments (d. seg.) and thin-walled chemoreceptors (d. t-w. chr.). Fig. 65. Oblique sagittal section of antennal base taken at point indicated by arrow in Fig. 64. Notice the developing, imaginal intrinsic (scp. m.) and extrinsic (lev. ant.; dep. ant.) antennal muscles. Fig. 66. Frontal section of antennal segment 4, taken at point indicated by arrow in Fig. 64. Trichogen cells (t. cl.) have sent out protoplasmic extensions around which cuticle will subsequently be deposited. Compare with Fig. 63 and notice the re-arrangement of the epidermal cells. Fig. 67. Frontal section of scape and pedicel taken at point indicated by arrow in Fig. 64. Notice the developing extensor muscle (ext. ant.), and the position of the sensory cells of the Johnston's Organ (s. cl. J. O.). Fig. 68. Transverse section through pedicel taken at point indicated by arrow in Fig. 64.



Figs. 69-71. *H. verbasci*. *Pharate Adult*: Fig. 69. Right antenna, dorsal aspect. The adult cuticle of the scape is folded, while that of the bases of segments 3-6 is telescoped into their respective segments. Notice that the pedicellar campaniform sensilla of the adult (c. s.) is larger than that of the pupa II (p. II. c. s.). (Note: Other pupa II sensilla omitted from drawing). *Adult*: Fig. 70. Dorsal aspect of head (♂), showing origins and insertions of the intrinsic (flx. ant.; ext. ant.) and extrinsic (lev. ant.; dep. ant.) antennal muscles. Compare with Fig. 39 (of the larva) and notice the absence of the dorsal contingent of extrinsic muscles (All setae are omitted). Fig. 71. Right antenna, dorsal aspect.



Figs. 72-75. *H. verbasci*. Adult: Fig. 72. Right antenna, optical section. (Note: The sensory cells of the Johnston's Organ (s. cl. J. O.) are actually situated in the base of the pedicel). Figs. 73-75. Transverse sections through antenna taken at points indicated by arrows in Fig. 72. Fig. 73. Through junction of pedicel and stalk of first flagellar segment, showing dendritic terminals (d. ter.) of Johnston's Organ. Fig. 74. Through pedicel, Johnston's Organ (J. O.), and pedicellar campaniform sensillum (c. s.). Fig. 75. Through scape and intrinsic antennal muscles (flx. ant.; ext. ant.).

in specimens examined under polarized light. Birefringence increases throughout the remainder of the pharate adult stage with banding appearing shortly before adult emergence. In the exuvial period (Fig. 65), the rejuvenating fibres are attached to the epidermis. When cuticle begins to appear, they attach to it, first by epidermal tendons; later directly.

The description above holds true also for most other head muscles (Heming, in prep.) and for the pretarsal depressor muscles of the legs (Heming, 1973). No myoblasts have been observed to take part in their development.

The scape muscles of the larva, unlike the tentorial complement of extrinsic muscles, appeared to disappear completely during the propupal stage. In the exuvial pharate adult, these muscles reappear as short strings of cells arising and inserting in the developing scape epidermis (Figs. 64, 65, 67; scp. m.; ext. ant.; flx. ant.). I have not observed myoblasts in this region of the head (although haemocytes (b. c.) are present in large numbers shortly after pupa II emergence (Fig. 62)), although these cells do take part in the *de novo* formation of other, solely imaginal, muscles (Heming, 1973). Their subsequent development is identical to that described above for the extrinsic muscles.

Structure. — Except for their slightly smaller size in males, antennae of the two sexes are very similar. Each consists of a scape (scp.), a pedicel (ped.) and six flagellar segments (Fig. 71). The scape of each is inserted into a socket in the head capsule between the eyes (e) and is articulated to it by well-developed median and lateral antennifers (antf.) extending inwards from the socket rim (Fig. 71). As in adults of *F. fusca*, each antenna is raised and lowered by levator (lev. ant.) and depressor (dep. ant.) muscles inserting respectively, by tendons into the dorsal and ventral margins of the scape base and originating ventrally on the anterior tentorial arms (at.) (Fig. 70). The cranial branches of these muscles, present in larvae (Fig. 39), are absent in adults.

Each pedicel (ped.) articulates with the apex of the scape (scp.) by means of dorsal and ventral condyles borne by the latter, and is flexed and extended by muscles situated, respectively, laterally (flx. ant.) and medially (ext. ant.) within the scape (Figs. 69, 70, 72, 75). As in *F. fusca*, these consist of three fibres each (Fig. 75).

The imaginal pedicel lacks the dorsal and ventral condyles of the larval one and has, instead, a cuticular ring (c. r.) through which pass the cap cells (d. ter.) of the Johnston's Organ chordotonal organs (Figs. 69, 71-73).

In adults of both sexes, segments one and two are dark brown, three to six yellow and seven and eight light brown. Adults have no antennal "pumps".

Sense Organs. — The sense organs on the antenna of a female of *H. verbasci* are shown in Figs. 71, 72, 74 and 87 and are listed in Table IV. As can be seen by comparing Tables III (larva) and IV, there has been an increase in the number of tactile hairs (t. h.; from 28 to 97), thin-walled chemoreceptors (t.-w. chr.; from five to 14), and coeloconic pegs (c. pg.; from three to four), but the three apical sense organs (ap. s. o.) of segment three of the larva are absent in adults. In addition, all adult chemoreceptors differ in size, shape and position from those of the larval stages.

The imaginal Johnston's Organ of *H. verbasci* comprises six chordotonal organs each containing three (sometimes four) scolopidia (Figs. 72, 74) (compared with four chordotonal organs of three scolopidia in the larva). Each scolopale is probably innervated by two sensory neurons since most contain two ciliary dilations (indicated by dots in Fig. 74). The position of the Johnston's Organ and its sensory cells (s. cl.) in the adult antenna, is similar to that of the larva (Fig. 72; sense cells in base of pedicel not in scape as shown). The dendritic terminals (d. ter.) of the Johnston's Organ fit into grooves in the stalk of the first flagellar segment (Fig. 73).

The pedicellar campaniform sensillum (c. s.) of the adult is much larger than that of the

three quiescent stages, is not as convex, and differs in structure (compare Figs. 69, 71, 72 and 87 with 49, 52, 55, 61, 68, 80, 82, 86).

Proximally, the nerve from each antenna (ant. nv.) enters the deutocerebrum of the brain. This is now, as in adults of *F. fusca*, situated mostly in the much larger adult head. As in larvae, the nerve of each antenna (ant. nv.) bifurcates within the base of the first flagellar segment (Fig. 72).

Table IV. Sense organs on the antenna of the adult female of *H. verbasci* (N = 11).

Segment	tactile hairs	campaniform sensilla	Johnston's Organ	thin-walled chemoreceptors	coeloconic pegs	apical sense organs
1	11					
2	12	1	1 (6 chordotonal organs)			
3	13			2	1	
4	11			4		
5	13			3	1	3
6	12(10-12)			3		
7	12			1	1	
8	13(12)			1	1	
Total	97	1	1	14	4	3
Grand Total	120					

DISCUSSION

Larval Stages

Thysanoptera

Structure and variation in the antennae of larval aelothripids, thripids and phlaeothripids are briefly discussed by Priesner (1960). They are usually seven-segmented, as in the two species of this paper, but those of *Merothrips morgani* Hood (Merothripidae) are six-segmented, and there is a greater (in urothripines) or lesser (eg. *Liothrips* spp.) amount of fusion in the distal segments of some phlaeothripids (Priesner, 1960; Heming, in prep.). Microtrichia are usually present on the antennal segments of larval aelothripids and most thripids, but are absent from those of merothripids and phlaeothripids (the antennae of larval Heterothripidae remain undescribed).

The numbers, kinds and positions of sense organs on the larval antennae of *F. fusca* and *H. verbasci* are very similar (compare Tables I and III), even though these two species are not closely related (see Fig. 50 in Heming, 1973). When larvae of Aeolothripidae, Heterothripidae and Merothripidae are similarly investigated, their sensillar arrays will therefore, probably be

shown to have this common pattern too. Because of this similarity, larval antennae will probably be shown not to have the usefulness in taxonomic studies that imaginal antennae have had – at least not at the generic and specific level.

Other Insects

With the exception of some sternorrhynchous Homoptera (see below), the antennae of immature exopterygotes usually resemble those of their adults except for their reduced number of segments. In young endopterygotes, larval antennae are usually greatly simplified and in some taxa (e.g. Diptera - Cyclorrhapha) are practically absent (Grassé, 1951; Snodgrass, 1954; Imms, 1957; Peterson, 1960, 1965; Mackerras, 1970).

Metamorphosis

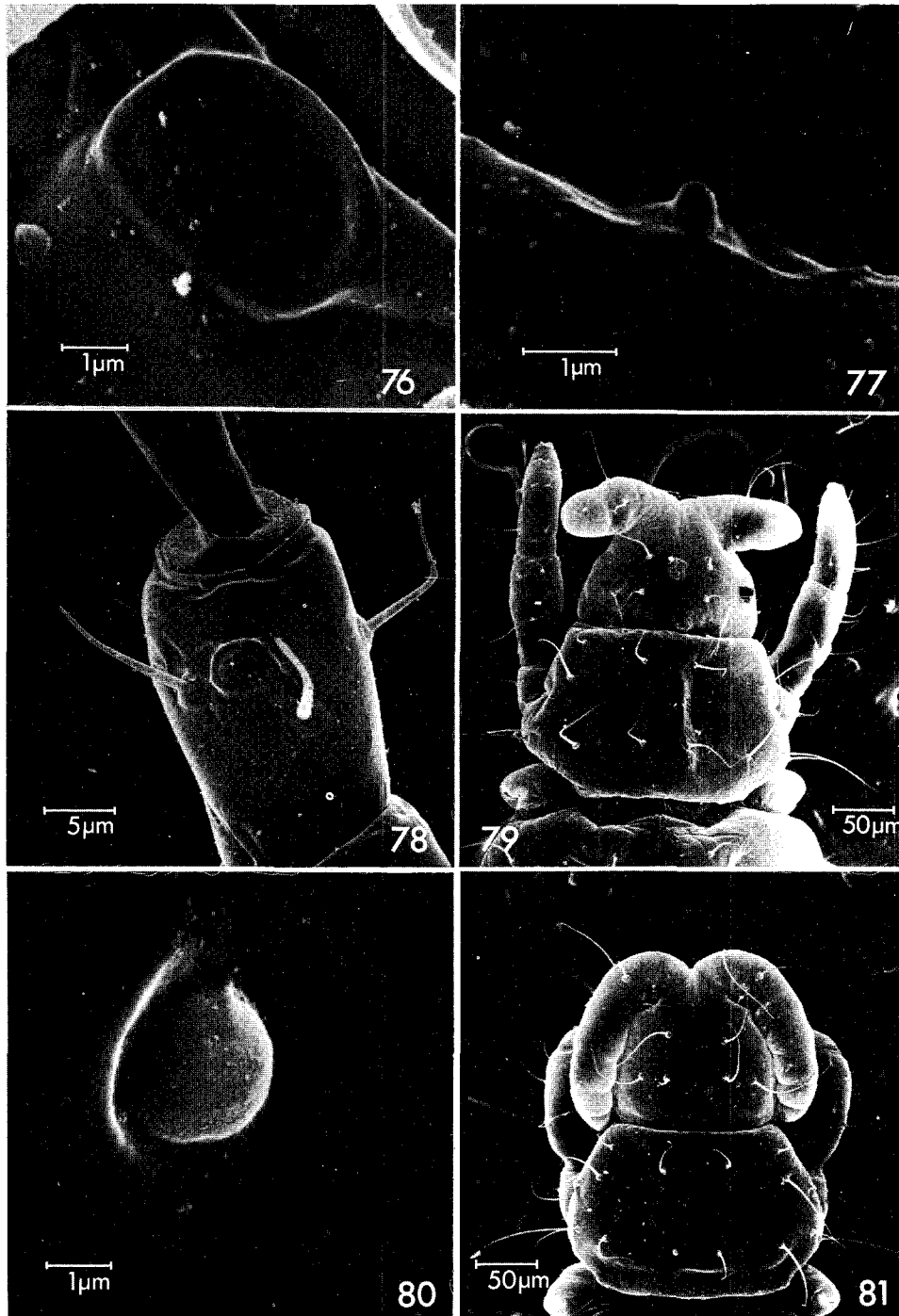
Thysanoptera

The propupal and pupal antennae of thrips are briefly described by Priesner (1960) and have been illustrated for some species that have been the subject of detailed life history studies (eg. Lange and Razvyazkina, 1953; Loan and Holdaway, 1955; Derbeneva, 1962, 1967; Lewis, 1973 (refs.) and Haga, 1974). In most aeolothripids, *both* propupal and pupal antennae are unsegmented and are flexed dorsally over the head and prothorax (Priesner, 1960; Derbeneva, 1967). Members of the genus *Franklinothrips* Back, however, apparently lack a propupal stage (Reyne, 1920). In the pupa, the antennae are very long and reach posteriorly to the second abdominal segment. This suggests, that in the species of this genus, there is no telescoping of the adult antennal segments as they are forming. In thripids and phlaeothripids the antennae are, respectively, as described here for *F. fusca* and *H. verbasci*. The quiescent stages of Heterothripidae and Merothripidae, so far as I know, remain undescribed. Since the Heterothripidae is probably a sister group of the Thripidae (see Fig. 50 in Heming, 1973), the antennae of the quiescent stages of species in this family will probably be shown to be similar to those of *F. fusca* and other thripids. Similarly, evidence from many sources (Heming, in prep.), suggests that the Merothripidae and Phlaeothripidae are sister groups (see Fig. 50 in Heming, 1973). Therefore, the quiescent stages of merothripids, when discovered, may well prove to have some antennal characteristics in common with those of Phlaeothripidae. It will be particularly interesting to learn whether species of this family have one or two pupal stages.

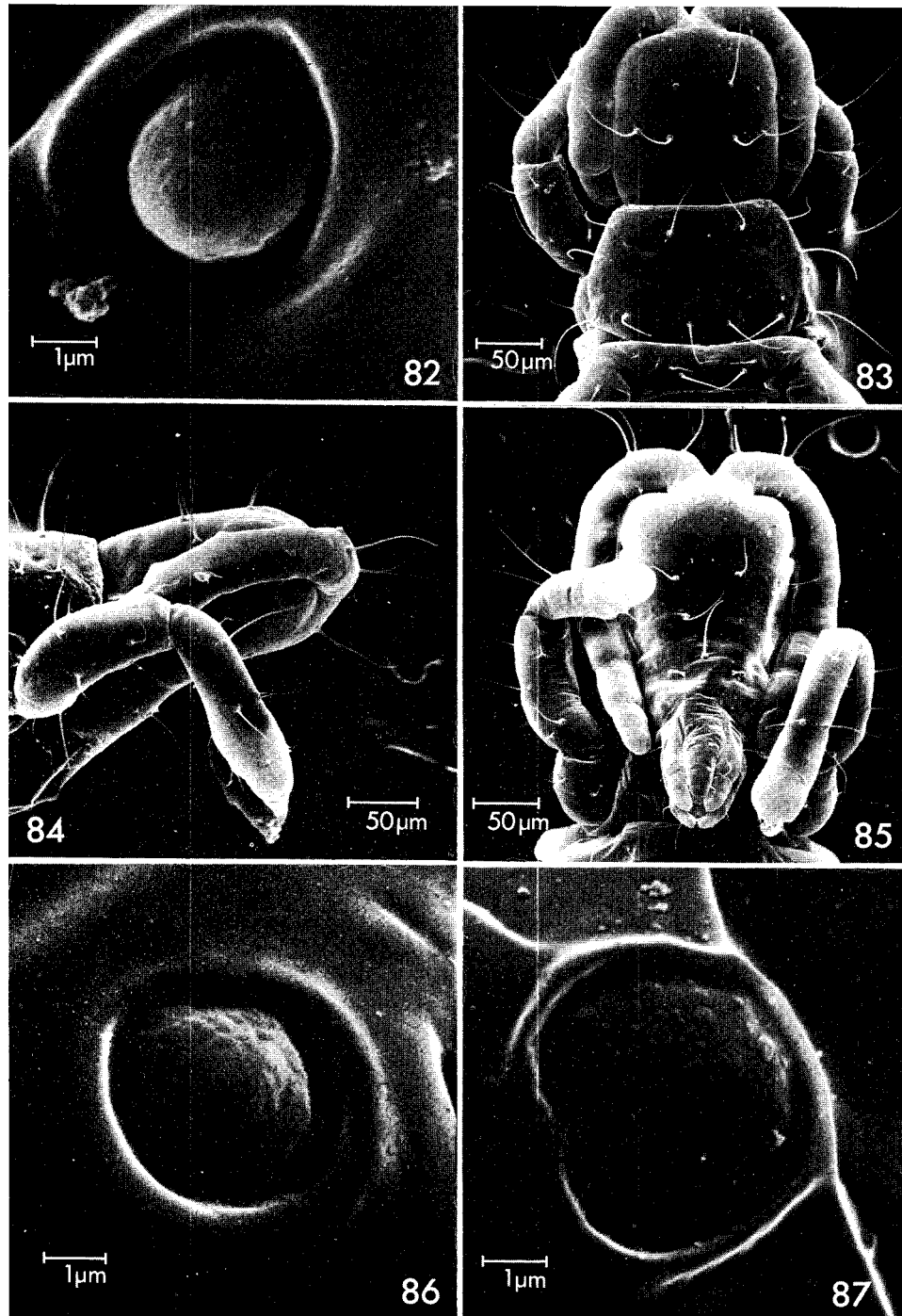
Events occurring during antennal metamorphosis have been briefly described in *Limothrips cerealium* Haliday (Thripidae) by Davies (1969), in *Liothrips oleae* (Costa) (Phlaeothripidae) by Melis (1934) and in *Bactridothrips brevitubus* Takahashi (Phlaeothripidae) by Haga (1974).

In *L. cerealium*, the head musculature, as in *F. fusca*, is carried through practically unaltered from larva to adult (Davies, 1969), although “one or two additional fibres” (p. 213) are present in the extrinsic antennal muscles of the adult that are absent in larvae. During the propupal and early pupal periods in this species, “. . . a hollow tube of densely packed nuclei” develops on each side of the head, having an orientation parallel to that of the larval antennal levator and depressor muscles. These nuclear aggregates are temporary however, and have disappeared by the middle of the pupal stage without appearing to have contributed to the imaginal musculature (p. 220). I have observed nothing in *F. fusca* resembling these aggregations except for the antennal nerves which are shorter and thicker in the quiescent stages, and the antennal tracheae which have a thicker epidermis when they are secreting a new intima during the pharate portion of each instar. Davies (1969) may have interpreted these structures as myoblast aggregations.

Davies (1969) also mentioned that the larval extrinsic muscles of the antennae seem to undergo “some kind of reconstruction” during the quiescent stages, even though they main-



Figs. 76-81. *H. verbasci*. Stereoscan micrographs. *Larva I*: Fig. 76. Pedicellar campaniform sensillum. Fig. 77. Apical sense organ of antennal segment 3. *Larva II*: Fig. 78. Pedicellar campaniform sensillum. *Propupa*: Fig. 79. Head and prothorax, dorsal aspect. Fig. 80. Pedicellar campaniform sensillum. *Pupa I*: Fig. 81. Head and prothorax, dorsal aspect. Notice the slight indication of segmentation in the antennae.



Figs. 82-87. *H. verbasci*. Stereoscan micrographs. *Pupa I*: Fig. 82. Pedicellar campaniform sensillum. *Pupa II*: Fig. 83. Head and prothorax, dorsal aspect. Fig. 84. Same, lateral aspect. Fig. 85. Same, ventral aspect. In these three figures, notice the slight segmentation evident in the antennae. Fig. 86. Pedicellar campaniform sensillum. *Adult*: Fig. 87. Pedicellar campaniform sensillum. Compare with Figs. 76, 78, 80, 82, and 86 and notice the large size of the imaginal organ.

tain their susceptibility to eosin. This also occurs in these muscles in *F. fusca*, giving rise to the longer and more robust fibres of the adult.

Early in the propupal stage of *L. oleae*, there occurs, just as in *H. verbasci*, “*una dissoluzione completa dei muscoli intrinseci*” (p. 288-289) of the head, including those of the antennae (Melis, 1934b). From the dense masses of nuclei and cytoplasm remaining, the imaginal muscles are reconstructed by secretion of new fibrillar material during the second pupal stage. These events are described in detail in Melis’ text, but are illustrated inadequately in his photomicrographs (Fig. 3, plate 16; Fig. 6, plate 17 and Fig. 2, plate 19). His discussion is weakened further by his failure to discriminate between the events occurring during the two pupal stages. Nevertheless, the events taking place in *H. verbasci* and *L. oleae* appear to be very similar.

Haga figures accurately the heads of the pharate propupa (Fig. 11), pharate pupa I (Fig. 12), pharate pupa II (Fig. 13) and pharate adult (Figs. 14-16) of *B. brevitubus*. As in *H. verbasci*, imaginal segments three to six in this species form in a telescoped manner (Haga was the first to describe this). Because the adult antennal segments of this megathripine are, relatively, very much longer than those of *H. verbasci*, the degree of telescoping is very much greater (compare his Figs. 15 and 16 with Fig. 69). However, his interpretation of what goes on during metamorphosis is inaccurate because of his apparent complete reliance on whole mount preparations (in spite of a statement to the contrary in his “Method” section). According to Haga (1974), “The histolysis of the antennal tissue begins after the fourth ecdysis, and two days later the segmented blocks of the tissue appear again. These blocks are transformed into each of the antennal segments of the adult.” (p. 22). I have found no evidence of histolysis occurring at any time during metamorphosis of *H. verbasci* other than the usual isolated cellular degenerations accompanying and following moults (Heming, 1973). His interpretation of events occurring in the pharate propupa is similarly “off base” (p. 21).

Many of the discrepancies in musculature and metamorphosis that exist between *L. cerealium* and *L. oleae* are not due to the inadequacies of Melis’ (1934b) investigation, as Davies (1969) sometimes implied, but, instead are related to fundamental differences between the two insects: the head muscles of thripids (*F. fusca* and *L. cerealium*) are carried through practically unaltered, whereas those of phlaeothripids (*H. verbasci* and *L. oleae*) degenerate almost completely and are rebuilt.

The presence of a dorsal group of antennal extrinsic muscles (lev. ant. c.; dep. ant. c.) in larvae of *L. oleae*, *H. verbasci* (Figs. 38, 39) and other phlaeothripids, may be required for successful retraction, into the head, of the larval antennal epidermis at the end of the second instar. This withdrawal does not occur in larvae of *F. fusca* and *L. cerealium*, and these muscles are correspondingly absent. They are absent also from adults of species in both families (Risler, 1957; Mickoleit, 1963; Davies, 1969; here).

The Phlaeothripidae is probably the most recently derived (Stannard, 1957) and the most apomorphic of the five thysanopterous families (Stannard, 1957; Heming, 1970, 1973; see Fig. 50). Therefore, the additional extrinsic antennal muscles of the larva must be derived secondarily along with the type of head metamorphosis undergone by insects of this family.

Metamorphosis of the Musculature and Epidermis

Remarks made previously (Heming, 1973; pp. 1227-1229) concerning the metamorphosis of musculature and epidermis in thysanopteran legs, are equally pertinent to the antennae. The antennal muscles of *F. fusca* are midway between Snodgrass’ (1954) types (1) and (2) in terms of their metamorphosis. Although larval fibres are reconstructed into adult ones, they maintain their contractile elements throughout the process.

In *H. verbasci*, the dorsal extrinsic antennal muscles of the larva degenerate completely and, therefore, belong in Snodgrass’ (1954) category (3) (larval muscles destroyed and not

replaced). The tentorial extrinsic antennal muscles undergo a reconstruction similar to that followed by the pretarsal depressor muscles (Heming, 1973), differing only in that they lose their contractile elements more quickly (completed by the mid-propupal stage instead of the early pupa I stage). These muscles likewise are assigned to Snodgrass' (1954) category (2) (larval muscles reconstructed into adult muscles).

The developmental history of the intrinsic antennal muscles in this species differs from that of the extrinsic muscles in that they apparently degenerate completely and then regenerate *de novo*. They thus fit in Snodgrass' (1954) category (4) (larval muscles that degenerate completely and are replaced by equivalent adult muscles).

Withdrawal of epidermis from within the larval antennae of *H. verbasci* at the end of the second-instar, appears to involve both muscular contraction and changes in cell shape. Before withdrawal, the epidermal cells are attenuated; after withdrawal, columnar or cuboidal. Similar changes in shape, in a reverse sequence, occur during appendage eversion in the exuvial pharate pupa of *Drosophila melanogaster* Meigen (Diptera-Cyclorrhapha) (Poodry and Schneiderman, 1971 — and refs.). These authors have experimental evidence that this change in shape is caused by a change in intercellular adhesivity between cells of the imaginal discs.

Other Insects

The amount of reorganization occurring in the antennae of insects during metamorphosis varies, depending on how far the young stages have diverged in form and habit from the adults (Snodgrass, 1954). In the "segmented" antennae (ie. those having muscles in the flagellar segments) of entognathous ametabolous apterygotes, additional segments are added throughout postembryogenesis by continuous subdivision of the apical segment (Imms, 1940). In Thysanura and the orthopteromorph insects, new segments are added by division of the first flagellar segment (meriston) and sometimes also by those situated immediately distal to it (Imms, 1940; Schafer, 1973 — and refs.).

In certain sternorrhynchous Homoptera, there is a tendency for the juveniles to develop special characters of their own that are absent from their adults (Snodgrass, 1954). Such differences often show up on their antennae. *Psylla buxi* L. (Psyllidae) has five nymphal stages (Wilcke, 1941). Antennae of the first stage are 1-segmented; of the second and third, 3-segmented (but quite different); of the fourth, 5-segmented; of the fifth, 9-segmented and of the adult, 10-segmented. As additional segments are added, the shapes of other segments change and new kinds of sensilla appear (his Figs. 26-30). Similar changes occur also in the antennae of adelgids and some aphids (Weber, 1930; Pesson, 1951a; Woodward et al., 1970).

In *Trialeurodes vaporariorum* (Westwood) (Aleyrodidae), there are four nymphal stages (Weber, 1934). First-stage nymphs are free-living "crawlers" with long, 3-segmented antennae. The sessile second-, third-, and fourth-stage nymphs all have greatly reduced antennae which are, respectively, annulated, unsegmented but with curled apices, and 2-segmented (his Fig. 1). In the pharate adult, the long, 6-segmented adult antennae develop beneath their stubby, fourth-stage counterparts in a looped configuration (his Fig. 9). Thus, whiteflies resemble *F. fusca*, and *H. verbasci* in having a simplification of antennal structure in their intermediate instars but, in the former insects, this reduction is correlated with the sessile habits of these instars.

Depending on the family to which they belong, male Coccoidea undergo a variable amount of antennal metamorphosis. (see table p. 569 in Weber (1933) for a comparison of life histories). In *Mytilaspis fulva* Targioni (= *Lepidosaphes beckii* Newman) (Diaspididae), the first-instar "crawlers" have well developed, 5-segmented antennae (Fig. 1456 in Pesson, 1951a). In the second-instar, these are atrophied; whereas in male propupae and pupae they reappear as successively longer but unsegmented appendages bent back laterally on either side of the head

(Fig. 1456). Imaginal antennae are moniliform and 10-segmented.

Similar changes occur in the antennae of male Pseudococcidae, except that those of the intermediate stages also are well developed (Mäkel, 1942). In these mealy bugs, the four extrinsic antennal muscles are carried through the quiescent stages (Mäkel's table p. 506) just as they are in *F. fusca*, even though the propupal and pupal antennae are unsegmented, inflexible and flexed posteriorly on either side of the head. Although she did not discuss them in the text, Mäkel illustrated also the scape muscles for second-stage nymphs (Fig. 4) and adults (Figs. 14 and 15), but not for propupae (Figs. 6-8) or pupae (Figs. 10-12). Perhaps they degenerate and then regenerate as do those of *H. verbasci*.

A detailed study of antennal metamorphosis in scale insects is lacking, so far as I know, but events resolved up to now seem to be similar to those described here for *F. fusca* and to a lesser extent, for *H. verbasci*. Although Thysanoptera and Coccinea are quite closely related (see Fig. 64 in Hennig, 1969), the similarities in antennal metamorphosis summarized above have probably arisen through convergent evolution.

In the less derived endopterygote insects (ie. Hymenoptera-Symphyta, most Coleoptera, Raphidioidea, Megaloptera, Neuroptera, Mecoptera, Trichoptera, and Lepidoptera), each adult antenna arises through a proliferation and reorganization of epidermal cells at the base of the larval antenna (Eassa, 1953, Snodgrass, 1954). This new appendage then everts onto the surface of the developing head at the larval-pupal apolysis and in the pupa is unsegmented, is flexed ventrally or laterally, and is either free (exarate pupae) or fused to the body (obtect pupae).

The antennae of those holometabolous insects (Hymenoptera-Apocrita, some Coleoptera, Siphonaptera, Diptera-Cyclorrhapha) having apodous larvae, usually differentiate from antennal disc cells that are invaginated into the larval head shortly before or after the insect hatches from the egg (Murray and Tiegs, 1935; Bodenstern, 1950; Snodgrass, 1954; Anderson, 1963; Postlethwait and Schneiderman, 1971). Their subsequent eversion at the larval-pupal apolysis is similar to that mentioned in the previous paragraph as is their later development.

Adult

Structure

Thysanoptera. — The imaginal structure of thysanopterous antennae has been described in greater or lesser detail; for representatives of all five families of the order (Buffa, 1898; Peterson, 1915; Reyne, 1927; Priesner, 1928, 1960; Melis, 1934a, b; Doeksen, 1941; Pesson, 1951b; Risler, 1957; Mickoleit, 1963; and Davies, 1969). The most detailed studies are those of Risler (1957) on *Thrips physapus* L. (Thripidae) and of Mickoleit (1963) on *Aeolothrips fasciatus* (L.) (Aeolothripidae), *Haplothrips sticticus* Haliday (Phlaeothripidae) and *Phlaeothrips coriaceus* Haliday (Phlaeothripidae). Both gave details of antennal structure, musculature and innervation that are supported completely by my own observations. In addition, Risler (1957) described the origin of each antennal nerve in the deutocerebrum of the brain (Figs. 41-43), and the innervation of the extrinsic and intrinsic antennal muscles by branches of this nerve (Fig. 9).

The anterior tentorial arms, upon which the extrinsic antennal muscles originate, are more or less developed according to whether the tentorium is complete (Aeolothripidae, some Heterothripidae) somewhat reduced (Merothripidae), or greatly reduced (most Heterothripidae, all Thripidae and Phlaeothripidae). (Doeksen, 1941; Risler, 1957; Mickoleit, 1963; Heming, in prep.).

Other Insects. — The structure of insect antennae is reviewed by Imms (1939), Schneider (1964), Matsuda (1965) and Gouin (1968), is summarized in Weber (1933), Snodgrass (1935)

and Chapman (1969) and is described for insects in all orders by Imms (1957), and by the various authorities in Grassé (1951) and Mackerras (1970).

All thrips have the "annulated" antennae characteristic of Thysanura and the pterygote insects, in which intrinsic muscles are limited to the scape. Their antennae are unusual in that each scape has a dicondylar articulation with the head capsule. Usually, only a single, ventral antennifer is present (Snodgrass, 1935; Chapman, 1969). Although the dicondylar articulation is considered by some (eg. Matsuda, 1965) to be primitive, this condition in Thysanoptera is probably secondarily derived since the closely related Psocoptera have a single ventral condyle (Heming, per. obser.).

Matsuda (1965) has proposed that primitively, the extrinsic antennal muscles of insects consisted of two dorsal levator and two ventral depressor muscles, all originating on the dorsal or anterior tentorial arms. In psocids, one of the ventral muscles has been lost and in thrips only single levator and depressor muscles remain.

The primitive number of intrinsic muscles in insects is also considered to be four, comprising single depressor, flexor, extensor and levator muscles (Matsuda, 1965). All investigated thrips have the usual derived condition of two scape muscles functioning in flexion and extension (although, in many insects, these are levators and depressors instead). Each consists of three fibres, a characteristic shared with those of Psocoptera (Badonnel, 1951, his Fig. 1159).

In Thysanura and the orthopteromorph insects, the antennae are usually many-segmented and filiform (Imms, 1957). In hemipteroids (= Acercaria of Hennig, 1969), there is a strong tendency towards reduction, the Psocoptera having 13 to 50, the Phthiraptera three to five, the Thysanoptera six to ten, the Homoptera three to 20 and the Heteroptera four or five. The Thysanoptera are considered to have arisen from a psocopteroidean ancestor and are usually placed after the Psocodea (Psocoptera + Phthiraptera) and before the Homoptera-Sternorrhyncha in phylogenies of the Paraneoptera (see Fig. 64, Hennig, 1969). The number of antennal segments in adult Thysanoptera supports this placement.

All insects that have been thoroughly studied, including the Psocoptera (Badonnel, 1951; his Fig. 1153), have been shown to have a blood vessel in each antenna, often associated with a more or less well-developed, basal, "accessory heart" (Schneider, 1964). Slifer and Sekhon (1974) have described such a vessel in antennae of *Bagnalliella yuccae* (Hinds) (Phlaeothripidae) and *Frankliniella tritici* (Fitch) (Thripidae) three to four μm in diameter, this being "best seen in electron micrographs of the entire cross section of the antenna" (p. 446). Neither I (Figs. 32, 33, 73-75), nor Risler (1957; Figs. 7, 8), nor Mickoleit (1963; Fig. 12) have found such a vessel in our sections through scape and pedicel, but all of us have described an antennal trachea that we may have confused with the blood vessel since "The trachea is small and difficult to identify in sections with the light microscope." (Slifer and Sekhon, 1974; p. 447). Although my transverse sections of antennal flagella are rather poor, the only structure possibly a blood vessel appears to me to be the basement membrane of the antennal epidermal cells. I have already mentioned that immature *H. verbasici* have a "pumping organ" at the base of each antenna.

Sense Organs

Thysanoptera. — Sense organs on the antennae of adult Thysanoptera, particularly those of segments three and four are important key characters because of their diversity in different taxa (Doeksen, 1941; Priesner, 1960). Thin-walled chemoreceptors (called "sensory areas" or "sense cones" by thysanopterists) are used most frequently with the result that their variation within the order is well known.

Slifer and Sekhon (1974) have recently described the ultrastructure of the adult sense organs of antennae of *B. yuccae* and *F. tritici*, using, for the first time, a terminology conforming

with that developed for other insects. My observations on antennal sensilla agree with theirs with the following exceptions:

(1) Using crystal violet stain and electron microscopy, Slifer and Sekhon (1974) have shown that six of the 13 "tactile hairs" of segment eight (= subsegment six) in *B. yuccae* and four of six in *F. tritici* are, in fact, thick-walled chemoreceptors. Such hairs are round-tipped, double-walled, and curved or wavy. A similar number of terminal setae in larvae and adults of *F. fusca* and *H. verbasci* are probably also of this kind.

(2) I have observed a single, small coeloconic peg (c. pg.) in each of antennal segments three, five, six and seven in *F. fusca* (Fig. 29; Table II) and in segments three, five, seven and eight in *H. verbasci* (Fig. 71; Table IV) that are not mentioned by these authors. I have since seen them in antennae of *F. tritici*, and they are undoubtedly present in *B. yuccae* as well. They are rather small ($1-4 \times 0.5-1.0 \mu\text{m}$) and are easily overlooked, even in macerated specimens mounted in Hoyer's medium and examined with phase contrast. Similar structures have recently been described by Koteja (1974) from the antennae of certain scale insects (Fig. 1B).

(3) Slifer and Sekhon (1974) also failed to notice the three "apical sense organs" of antennal segment five, that I have found in adults of both *F. fusca* (Table II) and *H. verbasci* (Fig. 71; Table IV). I have since located them on this same segment in *F. tritici* and they are probably present also in *B. yuccae*. Slifer (*in litt.*), after reading my description of them, suggests that these organs may be campaniform sensilla as the latter are found in the antennal intersegmental membrane of insects of several orders. They need additional study by transmission electron microscopy. Figure 77 is a scanning electron microscope photo of one of these structures from segment three of a larva I of *H. verbasci*.

(4) The single, large sensillum on the dorsal apex of the pedicel that I have called the "pedicellar campaniform sensillum" (see Figs. 29, 69, 71, 74, 86) was shown by Slifer and Sekhon (1974) in *B. yuccae* (but not in *F. tritici*) to be "a typical coeloconic chemoreceptor". They based their conclusion on the uptake, by the "peg" of this structure, of crystal violet stain. These sensilla are present in all species of thrips in all life stages (Priesner (1960) termed each an "areola") and are presumably homologous. Their failure to stain this organ in *F. tritici* is probably due to its small size in this species. It is unfortunate that these authors provided no electron micrographs of the organ, since, in immature stages (Figs. 5, 11, 43, 47, 52, 68, 76, 78, 80, 82, and 85), it has more resemblance to a campaniform sensillum.

(5) In *F. tritici* and *B. yuccae* "The axons from the sensory neurons of the flagellum join to form two nerves that pass proximally and unite in subsegment 1 (= antennal segment three) to form the antennal nerve." (p. 446; Slifer and Sekhon, 1974). These nerves "are embedded in the epidermis one opposite the other, and are separated from the lumen by the basement membrane that lines the cavity". This aspect was overlooked by me until I read Slifer and Sekhon's paper and also by Risler (1957) and Mickoleit (1963). Such details are difficult to see in sections because they are at the maximum resolving power of the light microscope. I have since re-examined sections of both larvae and adults of *F. fusca* and *H. verbasci* and found a similar disposition of the antennal nerve in both species (see Figs. 2, 10, 30, 35, 41, 72).

The Johnston's Organ of thrips has been previously described in the imaginal pedicel of *T. physapus* by Risler (1957; Fig. 8a, b) and in those of *A. fasciatus*, *H. statives* and *P. coriaceus* by Mickoleit (1963). In all these species it consists "aus 5-6 Gruppen von je 3 Scolopidien" (p. 113 in Mickoleit). That of *H. verbasci* is the same, but the Johnston's Organ of *F. fusca* contains up to five scolopidia per chordotonal organ.

Other Insects. — The sense organs of insects are presently being studied intensively by electron microscopists and electrophysiologists (see reviews of Schneider, 1964; Bullock and Horridge, 1965; Howse, 1968; Chapman, 1969; Slifer, 1970; Masson and Gabouriaux, 1973;

and numerous others). Those of Thysanoptera are similar to those of other insects with the exception of the pedicellar coeloconic chemoreceptor (= pedicellar campaniform sensillum of this paper). According to Slifer and Sekhon (1974), "This is the only instance known to us of the presence, on the pedicel, of this type of chemoreceptor." (p. 450). Similar organs on the pedicels of psocids (Badonnel, 1951) and ants (Masson and Gabouriaux, 1973; Fig. 3) may also prove to be chemoreceptors.

The scolopidia of the Johnston's Organ of insects can each be innervated by one, two or three sensory neurons (Howse, 1968; Masson and Gabouriaux, 1973), with two probably being the characteristic number for Thysanoptera. Ultrastructural details are now known of the Johnston's Organ of several species in several different orders (Masson and Gabouriaux, 1973; and references).

Most male insects have more complex sensilla arrays on their antennae than do females (Schneider, 1964). This complexity is usually correlated with the ability of their females to release sex attractants. Such differences are usually absent or are small in insects which live gregariously or use auditory or visual organs for sexual orientation (Schneider, 1964). Since most Thysanoptera are gregarious (Lewis, 1973), it is not surprising that the sensilla of the adults of both sexes are similar. There is no evidence that thrips produce pheromones nor that "the sexes find each other by means of sense cones on the antennae" (p. 13, Lewis, 1973).

Sense Organ Development. — Most sense organs in insects develop from solitary, epidermal "mother cells" (*Stammzellen*) after a characteristic number of mitotic "differentiative" divisions (see Fig. 28 in Weber, 1954). Much of the mitotic activity observed in propupal (*F. fusca*, *H. verbasci*) and pupa I (*H. verbasci*) antennal epidermis is probably of this kind. The number of divisions giving rise to each antennal sensillum of *F. fusca* and *H. verbasci* is unknown as it is for those of most insects. The ultrastructural details of sensillum differentiation have been followed in the tactile hairs, thick-walled chemoreceptors and campaniform sensilla of the cerci of *Gryllus bimaculatus* Degeer (Orthoptera, Gryllidae) (Schmidt and Gnatzy, 1971; Gnatzy and Schmidt, 1972a, b) and in a thin-walled chemoreceptor of the antennae of *Necrophorus vespilloides* Herbst (Coleoptera, Silphidae) (Ernst, 1972). Details described in these papers are probably similar to those occurring during sense organ development in *F. fusca*, *H. verbasci* and other insects since the fully-developed structure of insect sensilla is basically the same in all groups (Slifer, 1970).

Evolutionary Considerations

Three closely related evolutionary questions are raised by this study: (1) Why is a more (*H. verbasci*) or less (*F. fusca*) drastic metamorphosis required of the antennae of thrips, when the larval and imaginal structure of these appendages is no more divergent than that of insects in which less drastic changes occur (eg. Psyllidae)? (2) How can one account for the origin of the very different antennal metamorphosis of thripids (*F. fusca*, *L. cerealium*) and phlaeothripids (*H. verbasci*, *L. oleae*)? (3) Why are antennae of the quiescent stages of thripids and aeolothripids flexed dorsally over the head while those of phlaeothripids are flexed laterally?

My answers to these questions are best understood in the context of some of my previous conclusions. In two papers on the thysanopteran pretarsus (Heming, 1972, 1973), I suggested that some structural differences between larvae and adults can be accounted for by the usually more cryptophilous habits of larvae. I hypothesized also that the quiescent stages of thrips arose as a consequence of structural divergence between the young and adults of some ancestral form (Heming, 1973). Finally, I proposed that many of the structural differences existing between adults of Terebrantia and Tubulifera, had arisen as a result of the adoption, by the latter insects, of a mostly cryptophilous existence (Heming, 1970, 1972, 1973).

Many of the changes occurring during metamorphosis in thrips do not seem to be necessary. A particularly good example of this is provided by the mouthparts. These are very similar in larvae and adults (Peterson, 1915; Heming, in prep.) but are greatly reduced and lack functional stylets in the quiescent stages (Reyne, 1920, 1927; Heming, in prep.). In Homoptera (except for male Coccoidea whose adults lack mouthparts) and Heteroptera, functional mouthparts are usually present in all stages (Weber, 1930; Pesson, 1951a; Poisson, 1951; Woodward et al., 1970), even in those taxa (eg. Aleyrodidae) having widely divergent juveniles and adults (Weber, 1934). I suggest here that the metamorphosis of the antennae may be another example of this. Therefore, one answer to question (1) is that the quiescent stages of thrips are relicts of an ancestral situation in which differences between larvae and adults were greater and pupal stages more necessary, than is true of present forms. An indication of this is that species in the more primitive families (Aeolothripidae, Heterothripidae and possibly Merothripidae), still pupate within a cocoon spun by the second-stage larvae (see Heming, 1973 for a fuller discussion). Also, members of the primitive, aeolothripid genus *Franklinothrips* have only a single pupal stage (Reyne, 1920), just like holometabolous insects. Finally, the quiescent stages of at least some aeolothripids, unlike those of thripids and phlaeothripids, are unable to move when disturbed (Derbeneva, 1967), suggesting that greater structural changes occur during metamorphosis of these insects. Another possibility, of course, is that there are reasons for holometabolism in present-day thrips that we have not yet discovered.

The answers to questions (2) and (3) may be related to the more cryptophilous life habits of both larvae and adults of Phlaeothripidae. Aeolothripids, heterothripids and Thripinae usually pupate in soil (Priesner, 1960; Lewis, 1973) or in cocoons on the leaves (some aeolothripids). Heliiothripinae, which are mostly leaf feeders, pupate on the underside of leaves (Lewis, 1973). In these pupation sites, dorsally flexed antennae are no problem to the bearer. Phlaeothripids, however, usually pupate in crevices, either on their host plants (gall formers and other phytophagous species) or under bark and litter (mycophagous forms) (Lewis, 1973). Because their antennae are either short (propupae) or flexed back tightly against their heads (pupae I and II), they would offer little hindrance to the movement of the animal if it were disturbed. The prothorax is usually as wide or wider than the reflexed antennae (Figs. 79, 81, 83-85), and, together, they form a wedge, enabling these stages to further push themselves into crevices. Their antennae would also not keep them from backing out, whereas the dorsally-flexed ones of aeolothripids and thripids would.

The Aeolothripidae is probably the most primitive family of the Thysanoptera (Stannard, 1957; Mickoleit, 1963; Heming, 1973, in prep.). Therefore, the dorsally flexed position of the antennae in both propupae and pupae is probably primitive in this order. That they are oriented thus rather than laterally or ventrally as they are in most insect pupae (Peterson, 1960, 1965), is further evidence that the pupal stages of Thysanoptera are independently derived.

The reason that the antennal (and most other head) muscles of Phlaeothripidae undergo almost complete dissolution followed by regeneration during metamorphosis, whereas those of thripids do not, is probably associated with mouthparts and feeding and I prefer to leave speculation on this topic to a future contribution on the metamorphosis of the mouthparts.

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Note added in proof: "A recent paper by Mound and O'Neill (1974) (Mound, L. A., and K. O'Neill. 1974. Taxonomy of the Merothripidae, with ecological and phylogenetic considerations. (Thysanoptera). Journal of Natural History 8: 481-509.) received after this manuscript was submitted, contains a convincing discussion of the phylogeny of the Thysanoptera that differs somewhat from that illustrated in my 1973 paper (Fig. 50, Heming, 1973). These authors show a fully-developed tentorium to be present in the heads of adult *Damerothrips* Hood and *Erotidothrips* Hood (Merothripidae) and also illustrate representative antennae for most species in the Merothripidae. They conclude that the Merothripidae, not the Aeolothripidae, is the most plesiomorphous of the thysanopteran families."

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