

VOLUME TWO
ILLUSTRATIONS AND MICROGRAPHS

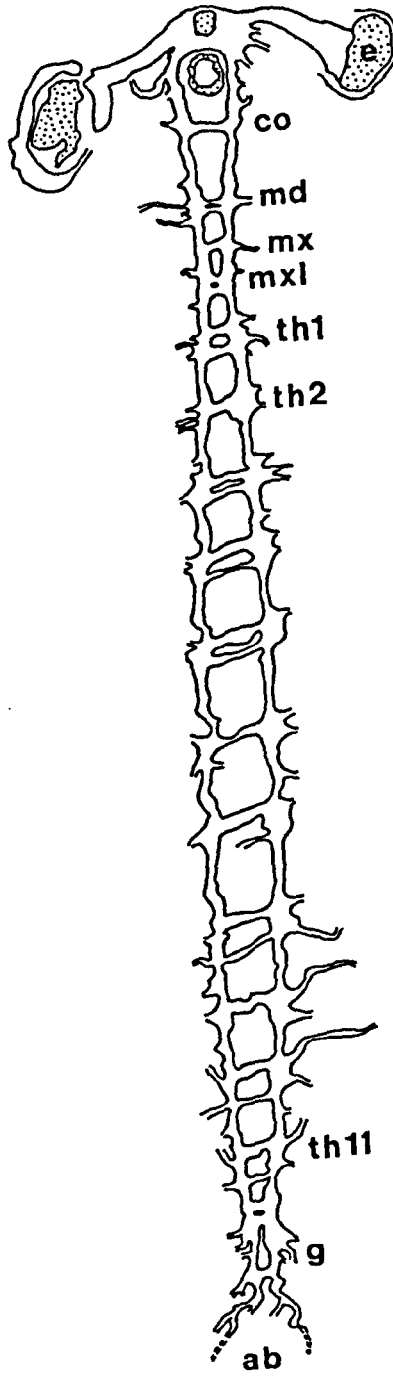
FIGURE 1.1

Diagrammatic reconstruction of the central nervous system of an adult male Artemia, from Warren (1930). A dorsal projection is illustrated, derived from serial wax sectioning. The circumoesophageal ganglia (co) are indicated and anterior (A) to them are the cerebral ganglia and the eyes (e). The other ganglia lead in a chain posteriorly as follows: mandibular, md; maxillar, mx; maxillular, mxl; thoracic, th (1-11); genital, g; abdominal nerves, ab.

Scale bar

500 μ m

A



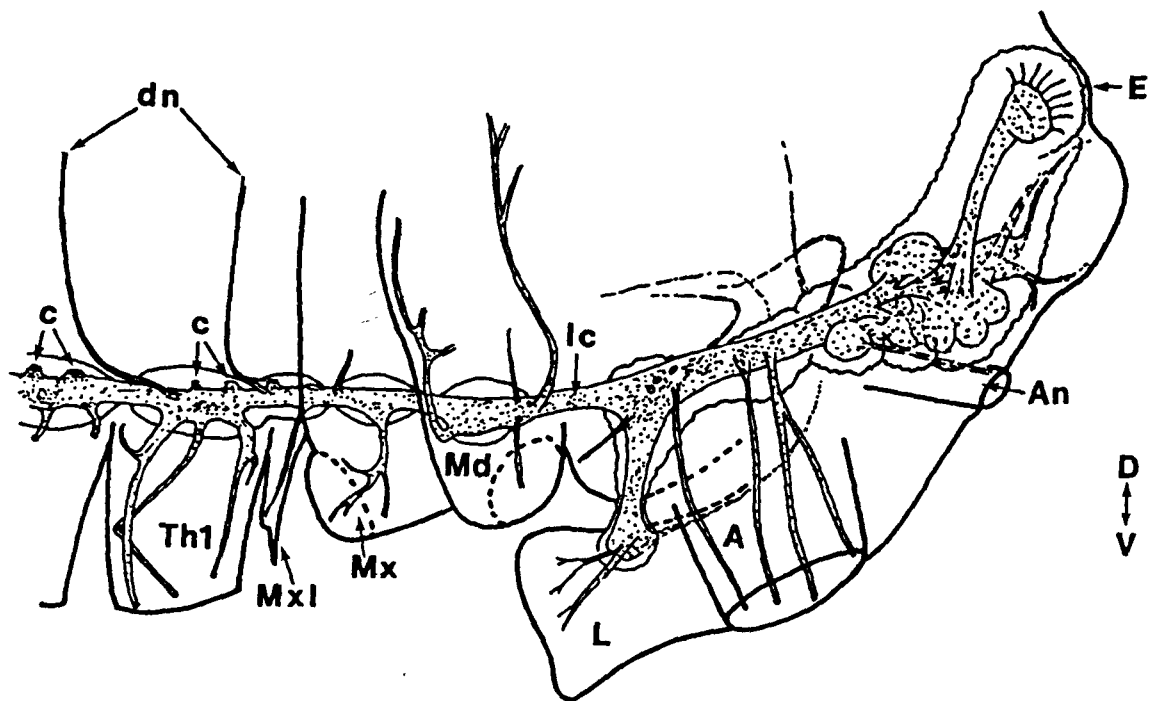
P

FIGURE 1.2

Diagrammatic reconstruction of the nervous system of the head and first thoracic segment of a larva near metamorphosis, adapted from Benesch (1969). The central fibre tracts (e.g. neuropile of ganglia, connectives) and peripheral nerves are shaded, the cell bodies forming the cortex of the ganglia are indicated by lines around these shaded regions. Only one side of the ladder-like nerve cord is shown. Commissures (c), longitudinal connectives (lc) and dorsal nerves (dn) are indicated. The position of the eye (E) is marked, also the antennule (An), antenna (A), labrum (L), mandible (Md), maxilla (Mx), maxillule (Mxl) and first thoracic segment (Th1).

D, dorsal; V, ventral.

No scale was indicated on original.



1.2

FIGURE 2.1

Diagrammatic representation of the ventral view of a first instar larva of Artemia. The larva bears two antennules (An), two antennae (A) and two mandibles (M). Each antenna is composed of a protopod (pr), endopod (en) and exopod (ex). The oral region is covered by the flap-like labrum (L). The post mandibular region is unsegmented.

Scale bar

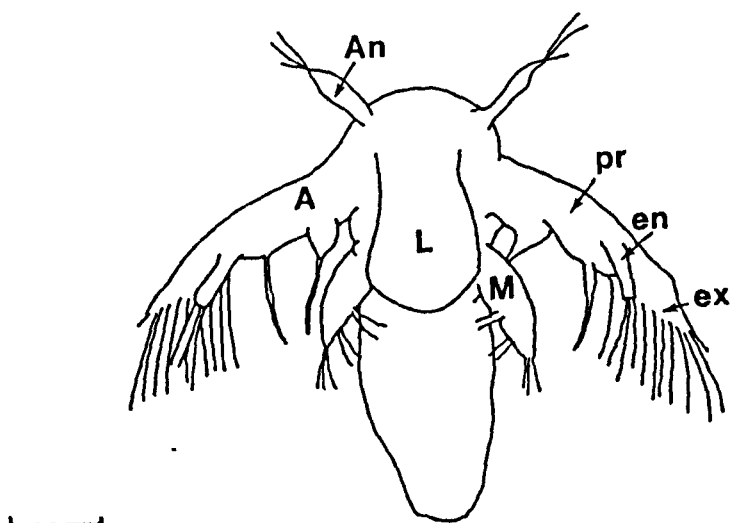
100 μ m

FIGURE 2.2

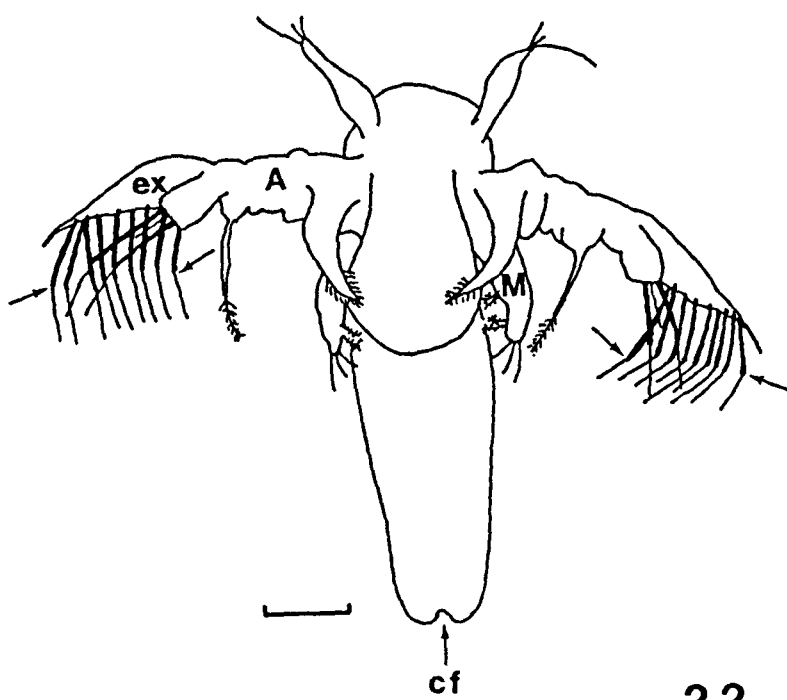
Diagrammatic representation of the ventral view of a second instar larva of Artemia. The proximal setae of the mandibles (M), and antennae (A), are all setulated. The distal swimming setae of the exopod (ex) have grown longer and are hinged (arrows). The caudal furca (cf) is indicated.

Scale bar

100 μ m



2.1



2.2

FIGURE 2.3

Diagrammatic representation of the ventral view of a third instar larva of Artemia. There are more setules on the proximal setae of the antennae (A) and the basal enditic process of the protopod (pr) has bifurcated (starred).

NE, nauplius eye; M, mandible.

Scale bar

100 μ m

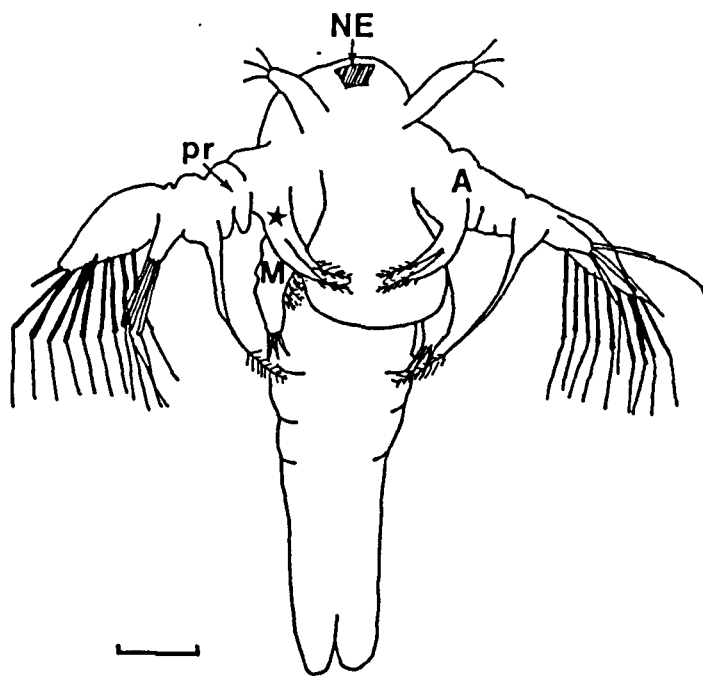
FIGURE 2.4

Diagrammatic representation of the ventral view of a fourth instar larva of Artemia. The maxillules (mx) are visible as paired swellings, the maxillae are covered by the labrum (L). Evaginating phyllopods (curly arrows) can be seen on the first three trunk segments.

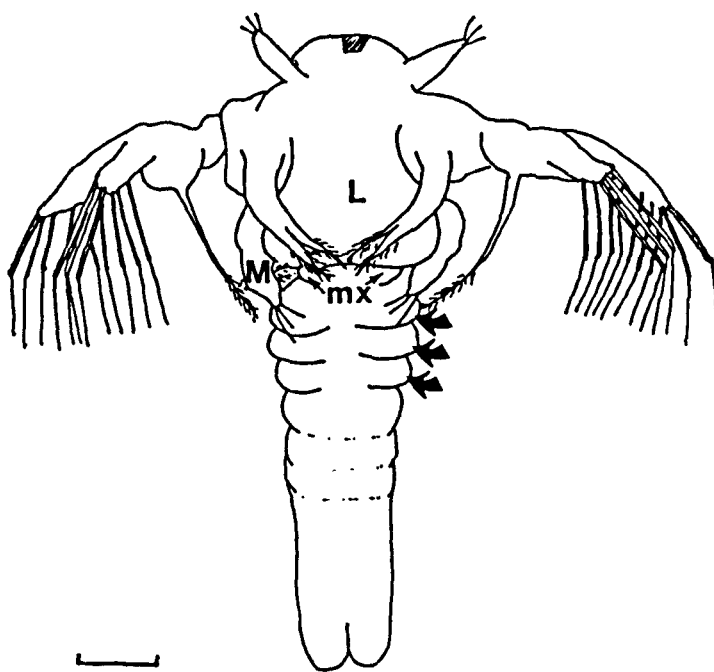
M, mandible.

Scale bar

100 μ m



2.3



2.4

FIGURE 2.5

Diagrammatic summary of development of the first 10 instars of Artemia development, adapted from Anderson (1967). The meaning of the symbols is as follows:

- mesoderm band segregated
- band externally delineated
- ★ appendage bud subdividing
- ⊙ rudimentary lobation and setation of appendage
- ✱ functional appendage

		I N S T A R									
		1	2	3	4	5	6	7	8	9	10
S E G M E N T	a1	*	*	*	*	*	*	*	*	*	*
	a2	*	*	*	*	*	*	*	*	*	*
	mb	*	*	*	* _g	* _g	* _g	* _g	* _g	* _g	* _g
	mx	•	•	•	★	★	★	★	★	★	★
	mxl	•	•	•	★	★	★	★	★	★	★
	T1	•	•	○	★	★	⊗	⊗	⊗	*	*
	T2	•	•	○	★	★	⊗	⊗	⊗	*	*
	T3	•	•	○	★	★	⊗	⊗	⊗	*	*
	T4			•	○	★	★	⊗	⊗	*	*
	T5			•	○	★	★	⊗	⊗	*	*
	T6			•	○	★	★	⊗	⊗	*	*
	T7				•	○	★	★	⊗	*	*
	T8					○	★	★	⊗	⊗	*
	T9						○	★	★	⊗	*
	T10						○	★	★	⊗	*
	T11						○	○	★	⊗	⊗
	G1						○	○	○	★	★
	G2							○	○	○	○
	A1							○	○	○	○
	A2							○	○	○	○
	A3							○	○	○	○
	A4								○	○	○
	A5								○	○	○
	A6									○	○

FIGURE 2.6

Diagrammatic representations of the head of a male Artemia at five instars (a-e) after metamorphosis.

(a) Tenth instar larva, immediately post-metamorphosis. The antennae (A) have rotated to lie in the sagittal plane. The basal enditic process, distal curved seta and endopod have virtually disappeared. The mandibles have decreased in size and are covered by the labrum (L).

Mx, maxillule; p, phyllopod.

Body length of specimen; 2.4 mm.

(b) Eleventh instar larva. The antennae have increased in size, and the exopod (ex) and protopod (pr) form an obtuse angle.

Body length of specimen; 3.4 mm.

(c) Twelfth instar larva. The tips of the antennae can cross at the midline and there is a 'frontal knob' (fk) on the anteromedial edge of the protopod (pr).

Body length of specimen; 4.7 mm.

FIGURE 2.6 (contd.)

(d) Thirteenth instar larva. The large antenna bears a flattened exopod (ex) at right angles to the protopod (pr). The outer margin of the exopod is curved (arrow).

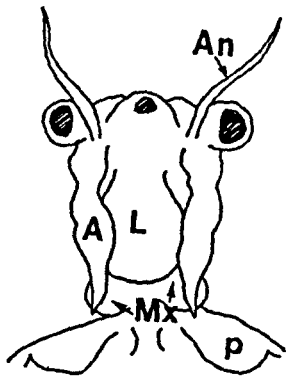
Body length of specimen; 5.2 mm.

(e) Fourteenth instar larva. The antenna is larger and the angle between the protopod (pr) and exopod (ex) has decreased.

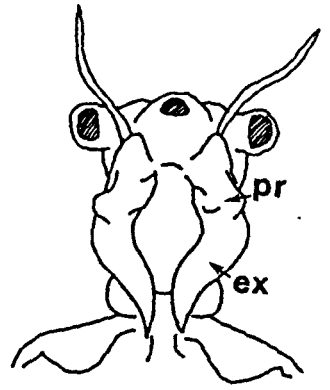
Body length of specimen; 6.4 mm.

An, antennule.

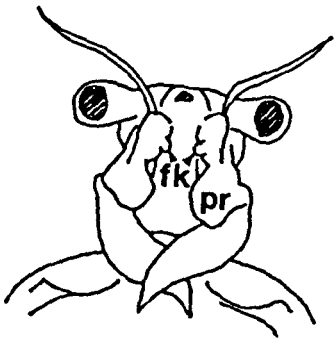
(adapted from Heath (1924).



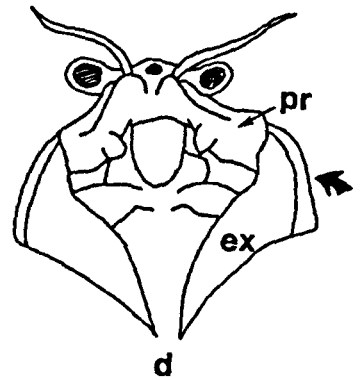
a



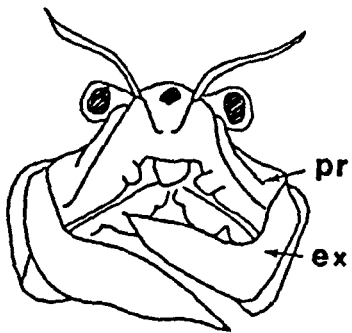
b



c



d



e

FIGURE 3.1

Diagrammatic representation of the method of Sjöstrand (1967) for making collodion films and their subsequent use with slot grids. Steps a-f are described in full in the text.

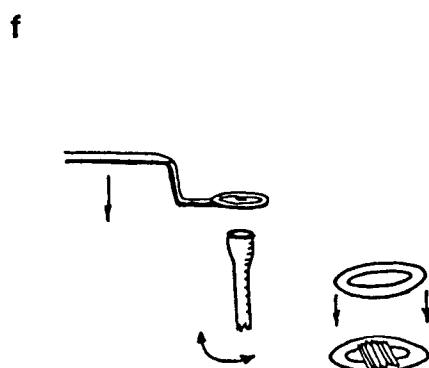
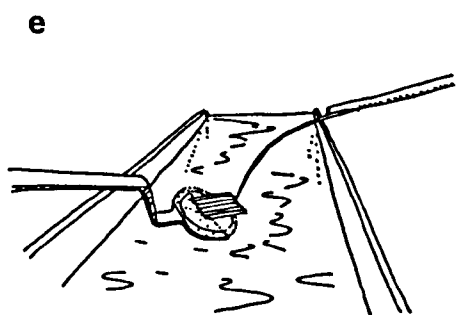
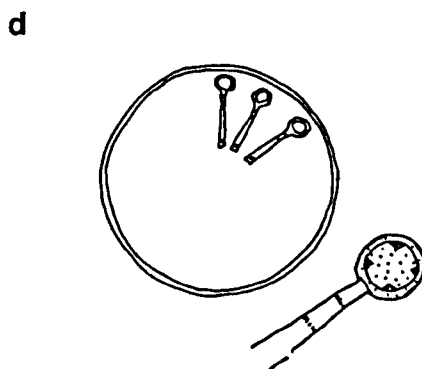
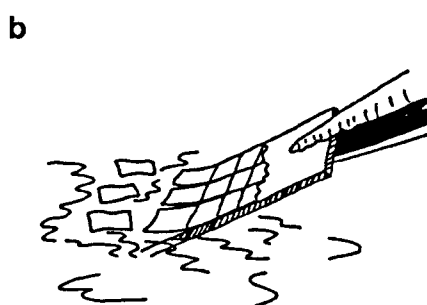
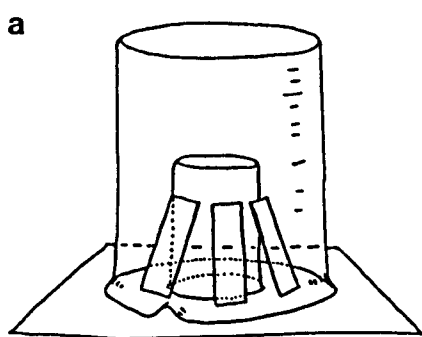


FIGURE 4.1

Scanning electron micrograph of the inside of the ventral surface of part of a second instar larva. The mesoderm cells (M) lying on the epidermis (E) can be seen clearly as a loosely organised sheet in the growth zone, and as pairs of bands either side of the ventral midline (black arrows) in the pre-stage 1 segments. The stage 1 segment has a few strands of dorsoventral muscle (arrowheads) posteriorly. In the stage 2 segment the dorsoventral muscles are more clearly defined (arrowheads), and the hollow region (*) of the evaginating phyllopod bud is visible. The lining of mesoderm cells within the phyllopod bud is clear.

The labels A to I indicate the levels which are illustrated by sections in subsequent figures within this chapter. (The stage 3 segment is not illustrated in this micrograph.) Approximate location of segment borders is indicated by dotted lines.

Scale bar

20 μ m

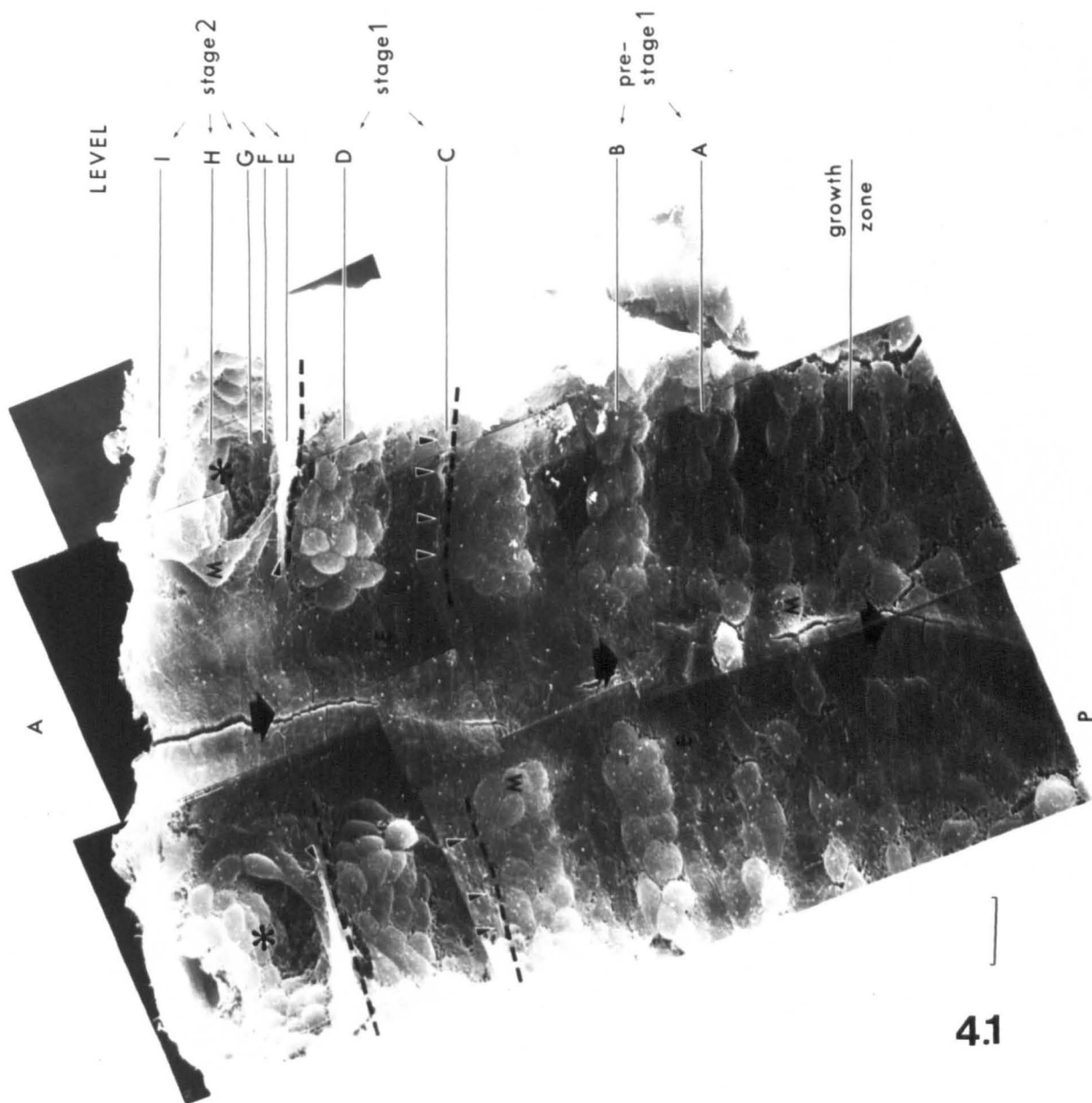


FIGURE 4.2

Drawings derived from the ventral parts of transverse sections through a fourth instar larva in the regions of pre-stage 1 segmentation, showing the organisation of the mesoderm bands.

- (a) At a level equivalent to A on figure 4.1, the mesoderm cells (M) in the newly-segregated band are spindle-shaped and loosely packed. They lie on a thin layer of epidermis (E).

G, gut; *, haemocoel.

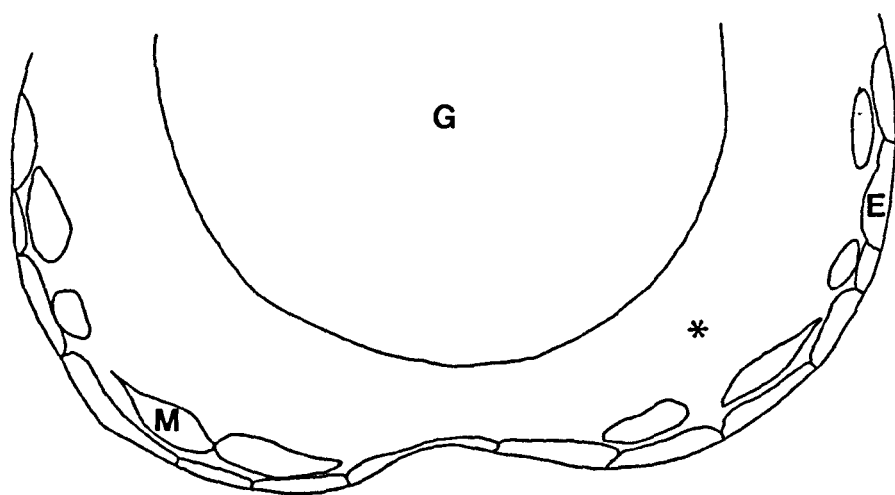
- (b) Just before stage 1, at a level equivalent to B on figure 4.1, the mesoderm cells (M) are more closely packed and more cuboidal in shape.

Abbreviations as for fig. 4.2.a.

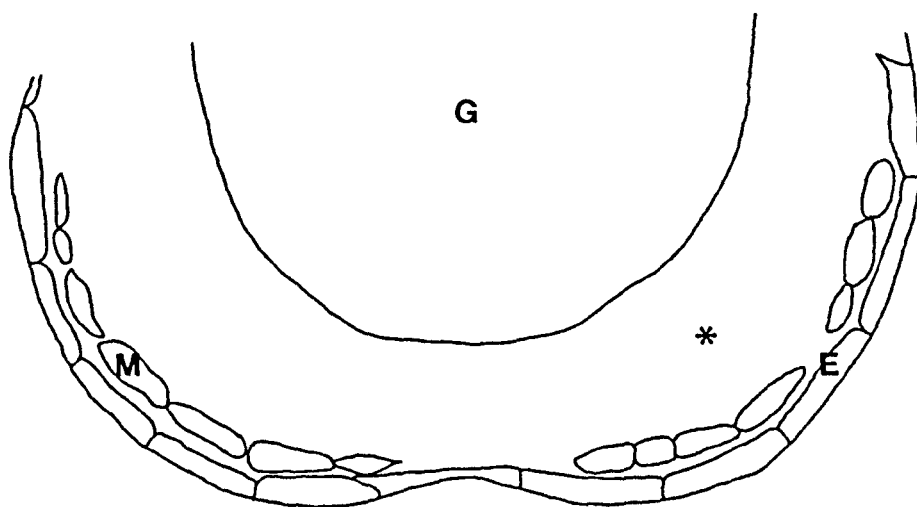
Scale bar

10 μ m

pre-stage 1



(a)



4.2

(b)

FIGURE 4.3

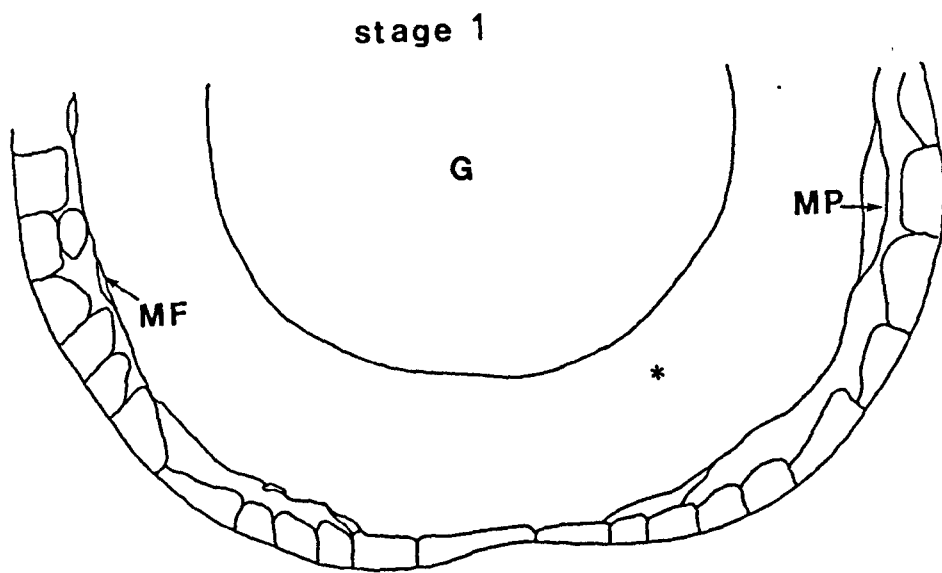
Drawings derived from the ventral parts of transverse sections through a fourth instar larva in the region of a stage 1 segment.

- (a) At the posterior of the segment at a level equivalent to C on figure 4.1, one of the four muscle pioneer cells (MP) is visible and muscle pioneer fibres derived from such cells (MF) can be seen to stretch from the ventral epidermis towards the dorsal part of the larva.
- (b) At the anterior of the segment at a level equivalent to D on figure 4.1, there are two bands of ectoderm either side of the ventral midline which have expanded to form neural ectoderm (NE). These cells are actively dividing, a mitotic figure (MIF) is visible.

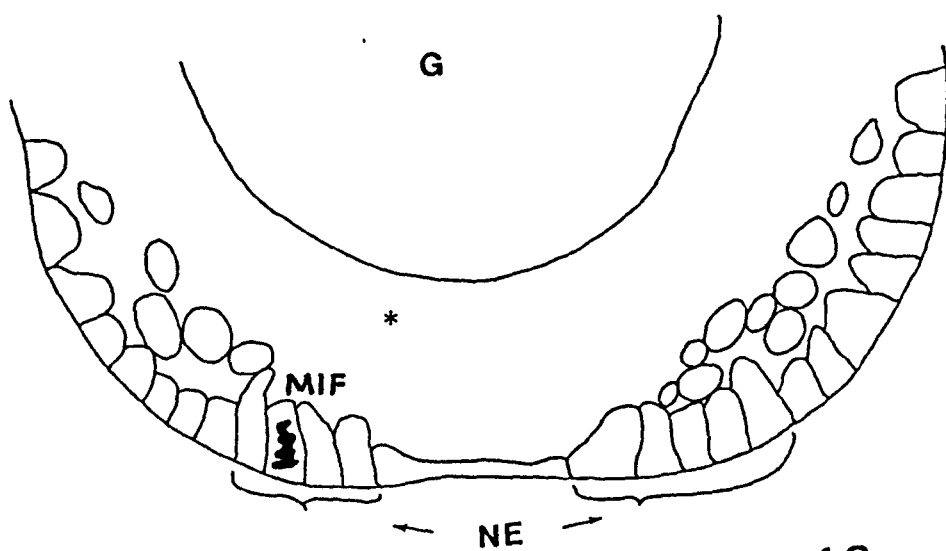
G, gut; *, haemocoel.

Scale bar

10 μ m



(a)



(b)

FIGURE 4.4

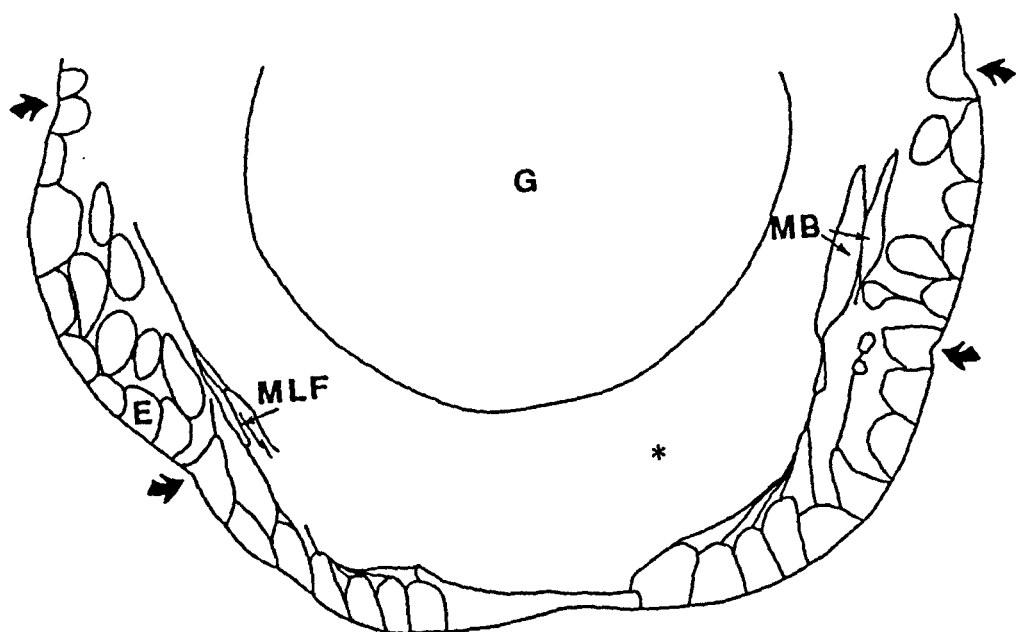
Drawings derived from the ventral parts of transverse sections through a fourth instar larva in the region of a stage 2 segment. The evagination of the ectoderm beginning the formation of the phyllopod can be seen (curly arrows).

- (a) At the posterior of the segment at a level equivalent to E on figure 4.1, the dorsoventral muscle fibres (MLF) and cell bodies (MB) are visible stretching from the ventral epidermis towards the dorsal surface of the larva. The epidermis (E) at this level is loosely packed with rounded cells.
- (b) At the posterior/middle of the segment at a level equivalent to F on figure 4.1, the ectoderm cells of the evaginating phyllopod are tightly packed and columnar and a few strands of the dorsoventral muscle (ML) are visible.

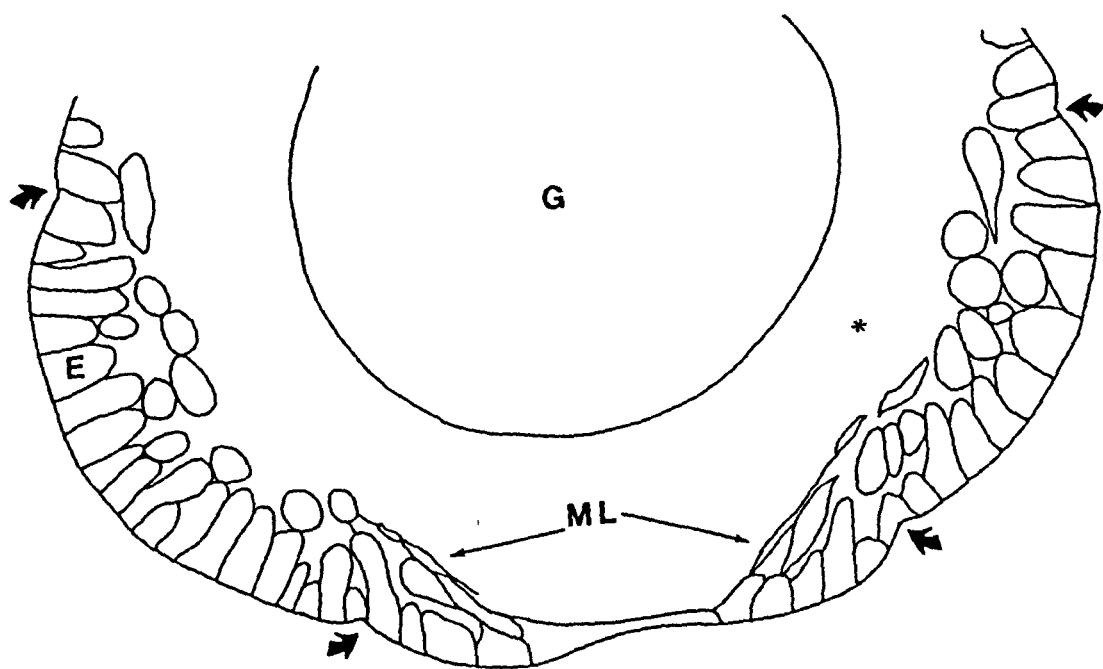
Scale bar

10 μ m

stage 2



(a)



(b)

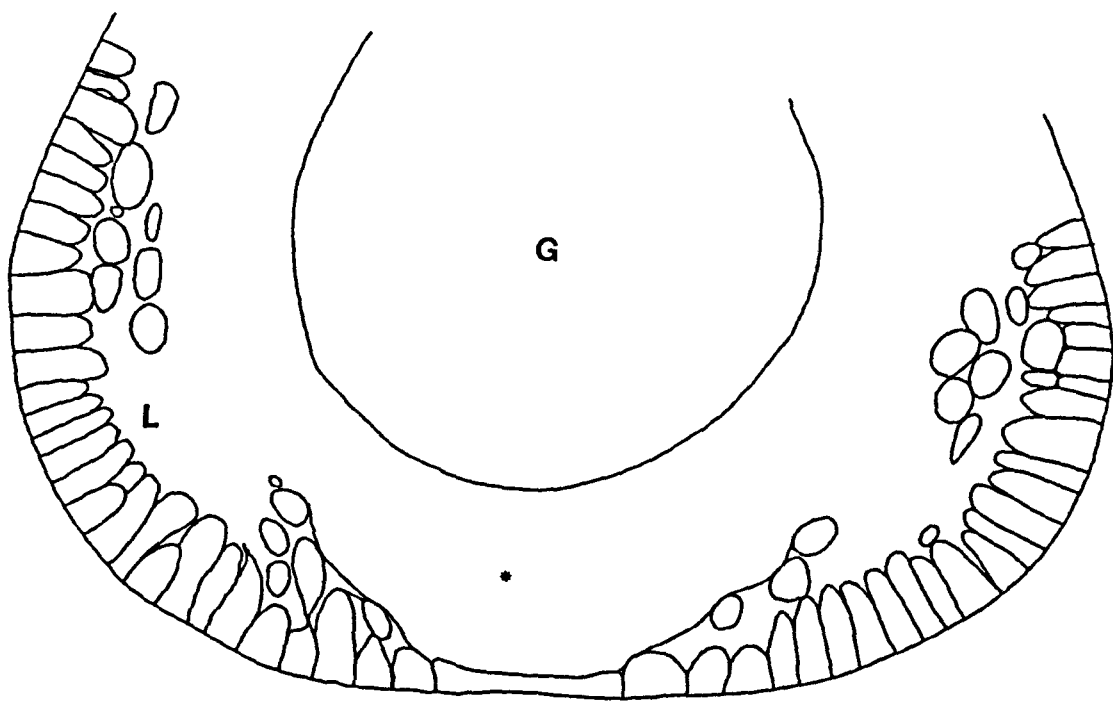
FIGURE 4.4 continued (Stage 2)

- (c) At the middle of the segment at a level equivalent to G on figure 4.1. A slight lumen (L) has been formed within the evaginating phyllopod bud.

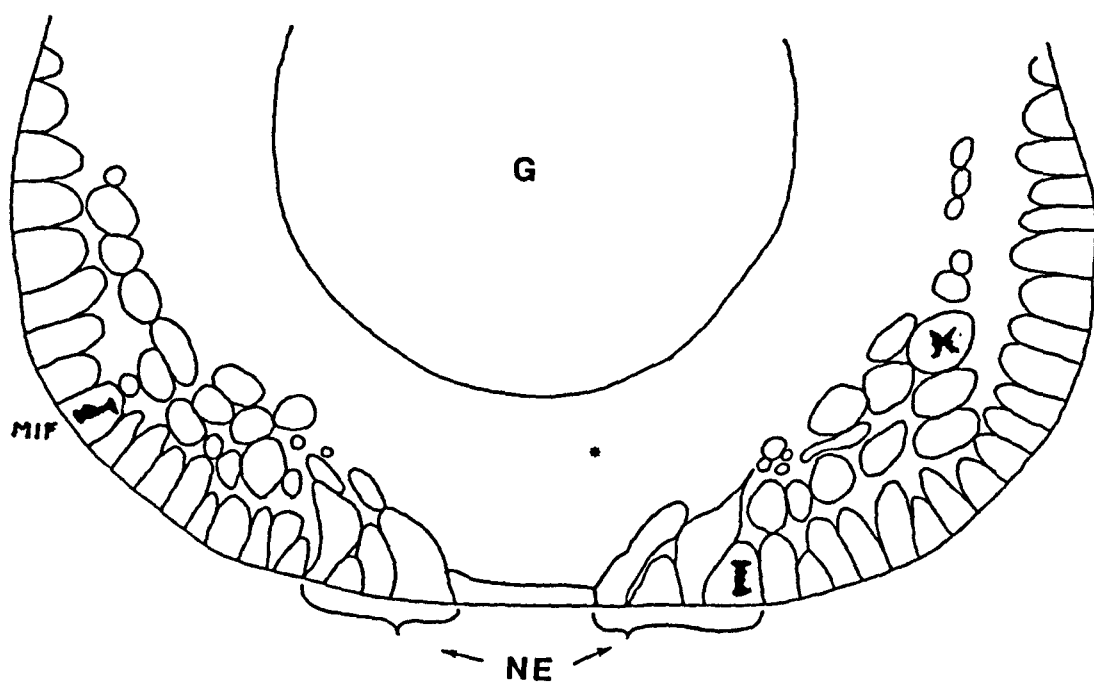
- (d) At the middle/anterior of the segment at a level equivalent to H on figure 4.1, the enlarged cells of the neural ectoderm (NE) can be seen, they are dividing to form ganglion mother cells. Ganglion, ganglion mother, and the mesoderm cells which are destined to form the phyllopod musculature are not easily distinguishable at this level and stage and are not labelled.

Scale bar

10 μ m



(c)



(d)

FIGURE 4.4 continued (Stage 2)

- (e) At a level equivalent to I on figure 4.1, there is very little mesoderm and the neural ectoderm (NE) is active and dividing to form ganglion mother cells (GMC). The non-neural epidermis is composed of loosely packed, rounded cells (E).

G, gut; *, haemocoel.

Scale bar

10 μm

P

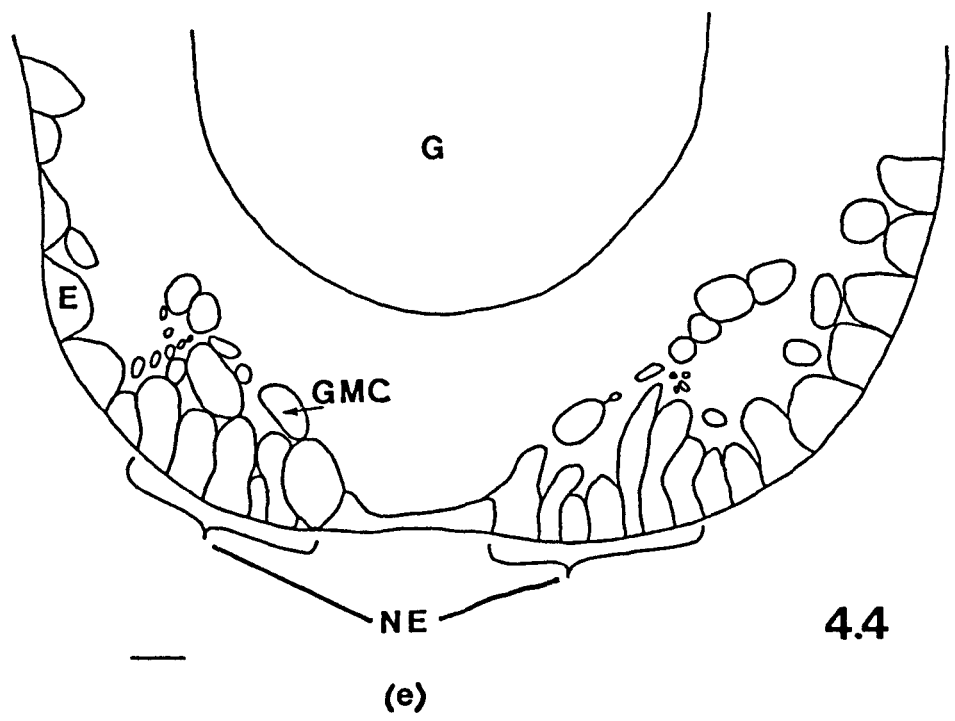


FIGURE 4.5

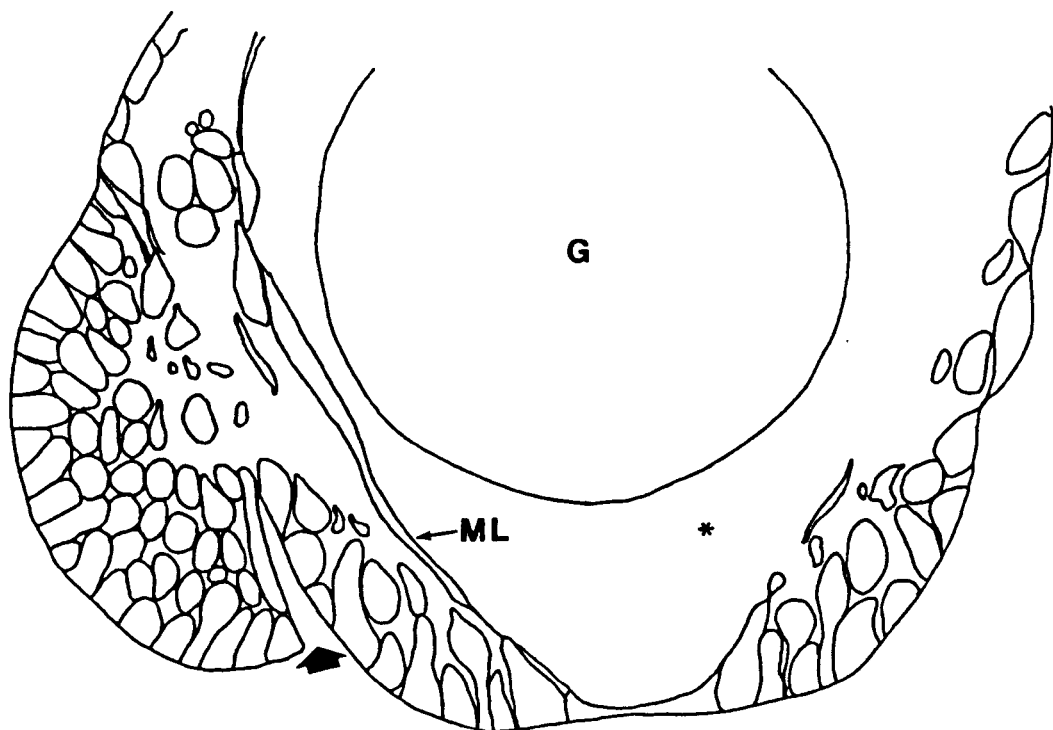
Drawings derived from the ventral parts of transverse sections through a fourth instar larva in the region of the stage 3 segment.

- (a) This section is through the posterior of the segment, it is slightly oblique so that the left is slightly anterior to the right hand side of the diagram. A distinct phyllopod bud separated from the ventral surface of the segment by a deep crease (arrowed) can be seen on the left. The dorsoventral muscle (ML) is distinct, stretching from the ventral epidermis dorsally.
- (b) At the middle of the segment the first lobe of the developing phyllopod to become distinct, the exopodite (EX) is beginning to be delineated by folds in the epidermis.

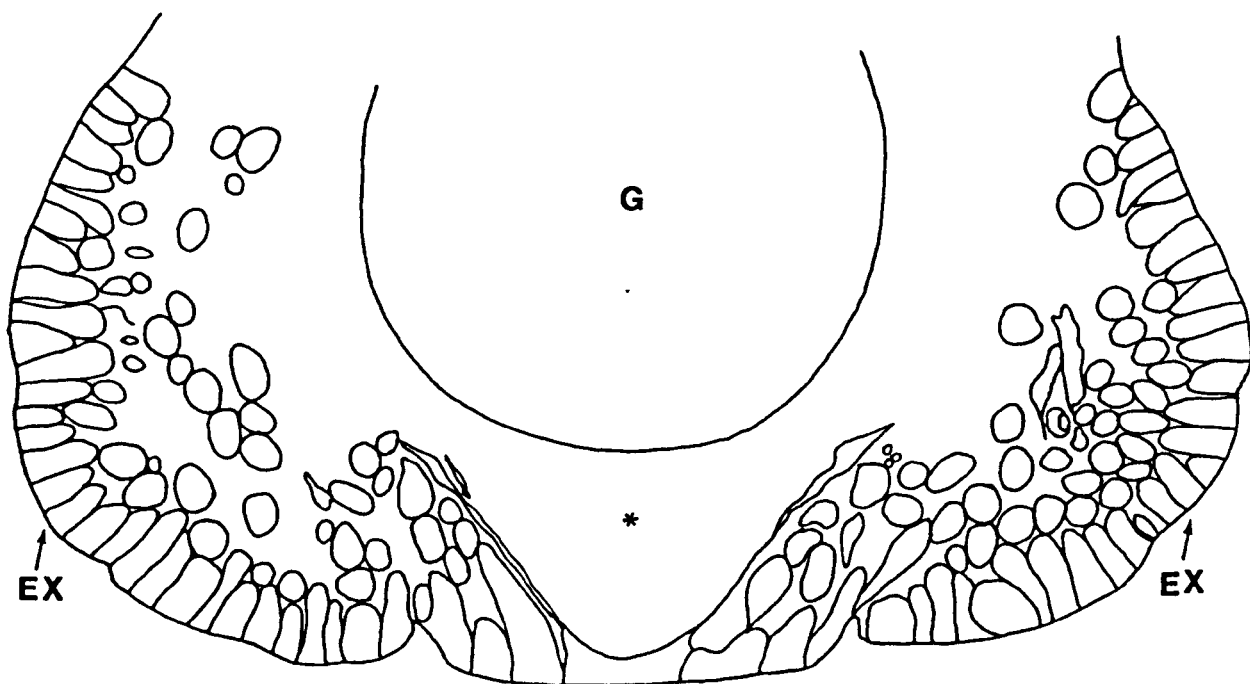
G, gut; *, haemocoel.

Scale bar

10 μ m



(a)



(b)

FIGURE 4.6

A summary table showing the major features of early thoracic segment formation, from the growth zone to stage 3 of development.

	Ventral mesoderm	Ventral ectoderm	dorsoventral muscle	Heart
growth zone	undifferentiated sheet	epidermal	-	basic framework formed
Pre-stage 1	pairs of bands 1-3 cells wide	epidermal	-	basic framework maturing
Stage 1	bands grow and differentiate	neural and epidermal ectoderm	pioneer cells span future muscle site	basic framework maturing
Stage 2	lumen forms as phyllopod evaginates	neural and epidermal ectoderm	muscle forms around pioneer fibres	basic framework maturing
Stage 3	phyllopod bud distinct	neural and epidermal ectoderm	muscle forms around pioneer fibres	basic framework maturing

FIGURE 4.7

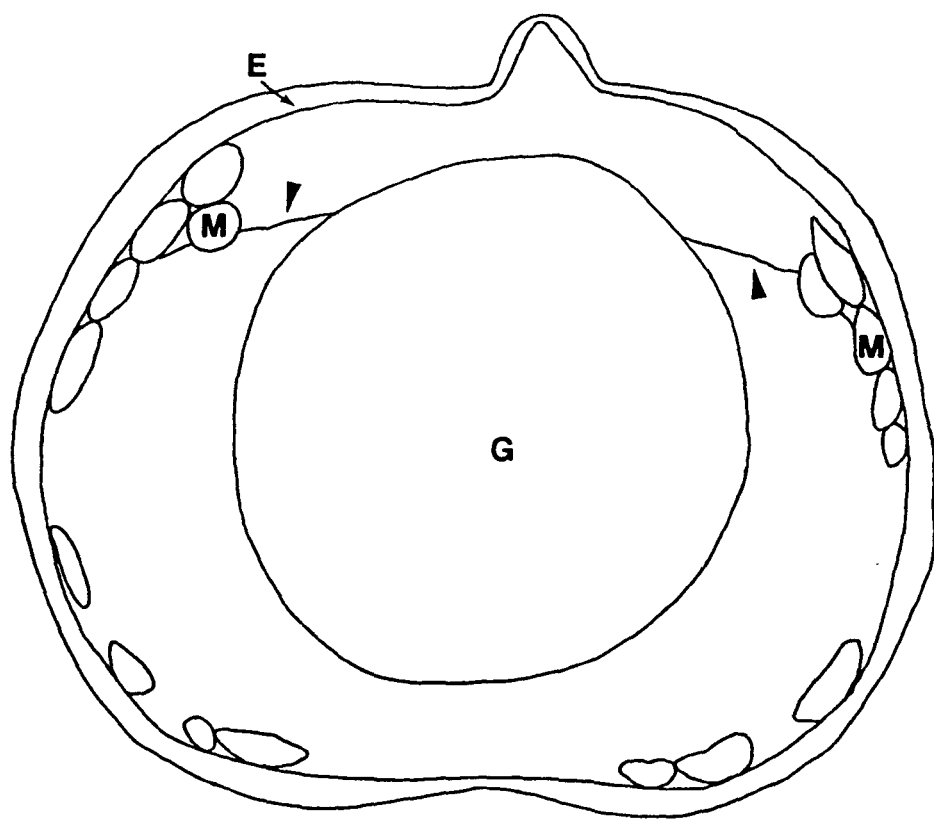
Drawings derived from transverse sections through the growth zone stage of a fourth instar larva at a level equivalent to A on fig. 4.1, showing the early development of the heart.

- (a) The first indication of heart formation is the grouping of five mesoderm cells (M) on the dorsolateral epidermis either side of the dorsal midline. One of these cells lies on the inner surfaces of the most dorsal cells of the group and sends a process (arrowheads) medially to contact the gut (G).
- (b) Slightly anterior to (a), there are no groupings of cell bodies dorsally but there are still muscle cell processes (arrowheads) joining the dorsolateral epidermis and the gut.

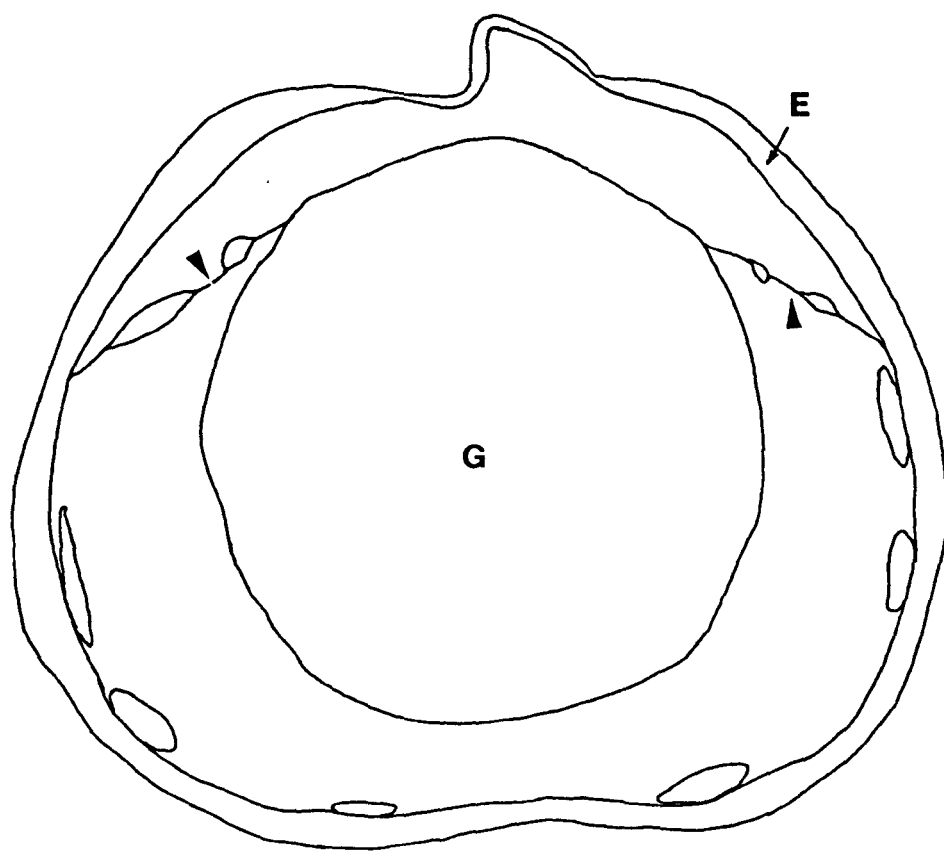
E, epidermis.

Scale bar

10 μ m



(a)



(b)

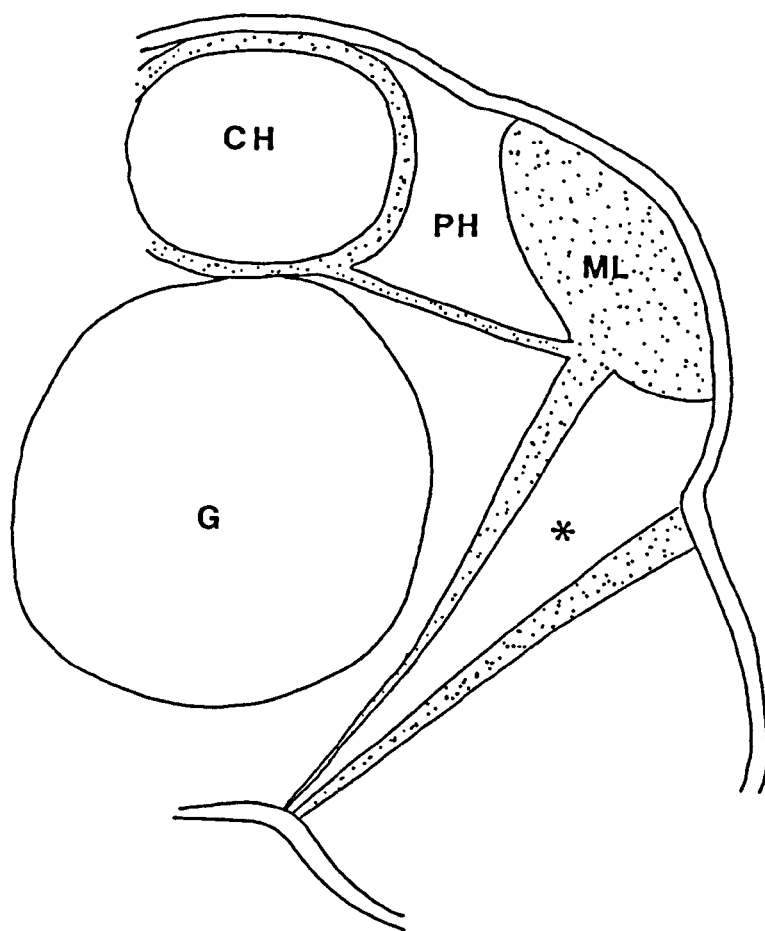
FIGURE 4.8

Drawing derived from the dorsal part of a transverse section through a stage 2 segment of a fourth instar larva showing the maturing structure of the heart. The most dorsal cavity is formed above the gut: the cardiac haemocoel (CH). Two lateral cavities, the pericardial haemocoels (PH) are positioned ventro-laterally with respect to the cardiac haemocoel. On either side of the larva within these two cavities runs the dorsal longitudinal muscle (ML).

G, gut; *, perivisceral haemocoel.

Scale bar

10 μ m



—

FIGURE 4.9

Micrographs of the ventral parts of four semithin (1 μ m) transverse sections through the anterior of a stage 2 segment in a fourth instar larva at a level equivalent to H in figure 4.1, showing the cells of the neural epidermis and the formation of ganglion and ganglion mother cells.

- (a) The enlarged cells of the neural epidermis (NE) occupy two bands 3-5 cells wide, either side of the ventral midline. These have cytoplasm and nuclei that are less dense than those of the adjoining cells, and immediately above them are the daughter cells called ganglion mother cells (GMC), that have been budded off.
- (b&c) The nuclei of these ganglion mother cells have condensed chromatin and in some cases are in division (DI).

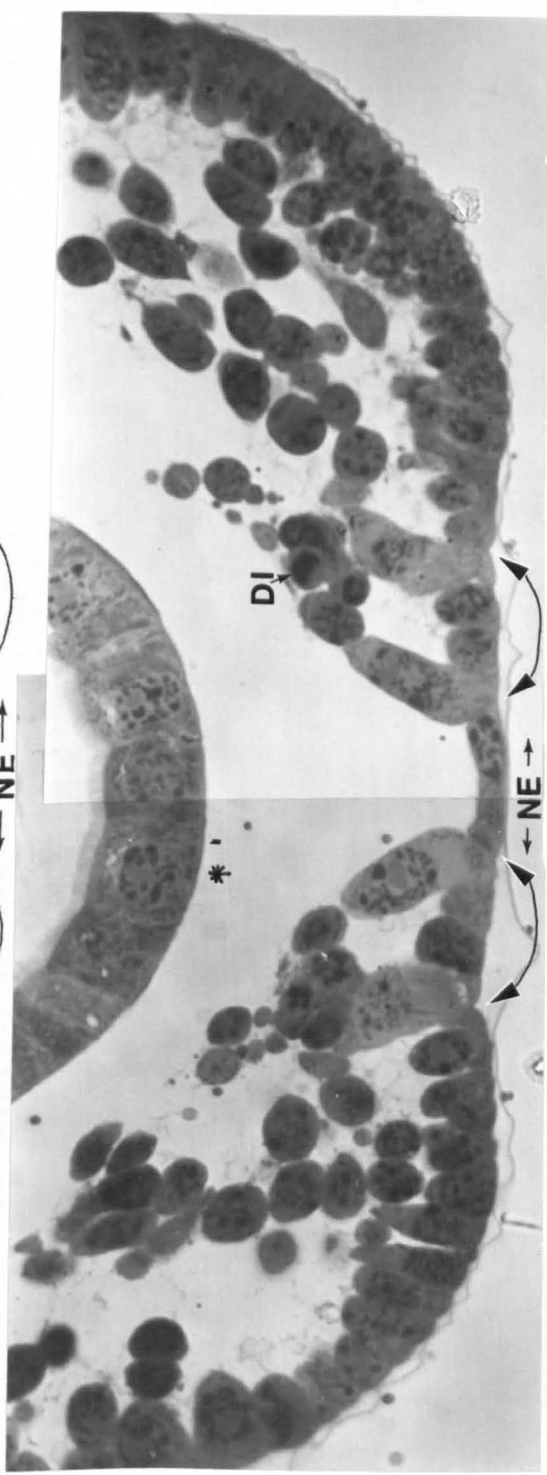
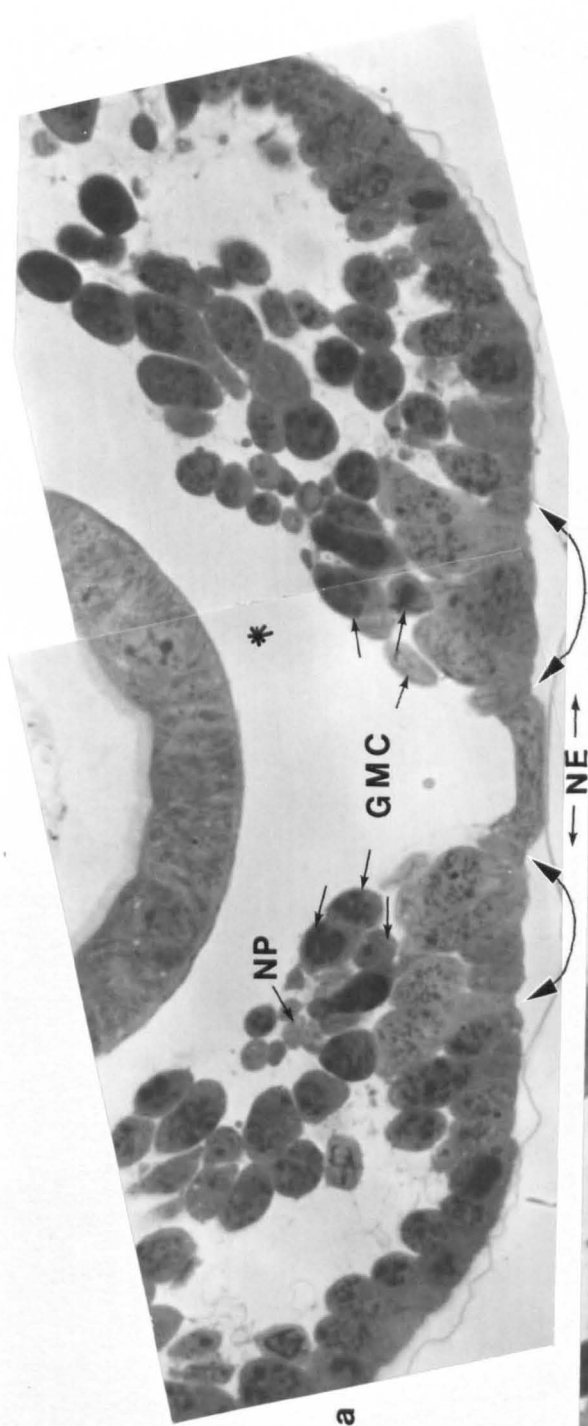
FIGURE 4.9 (contd.)

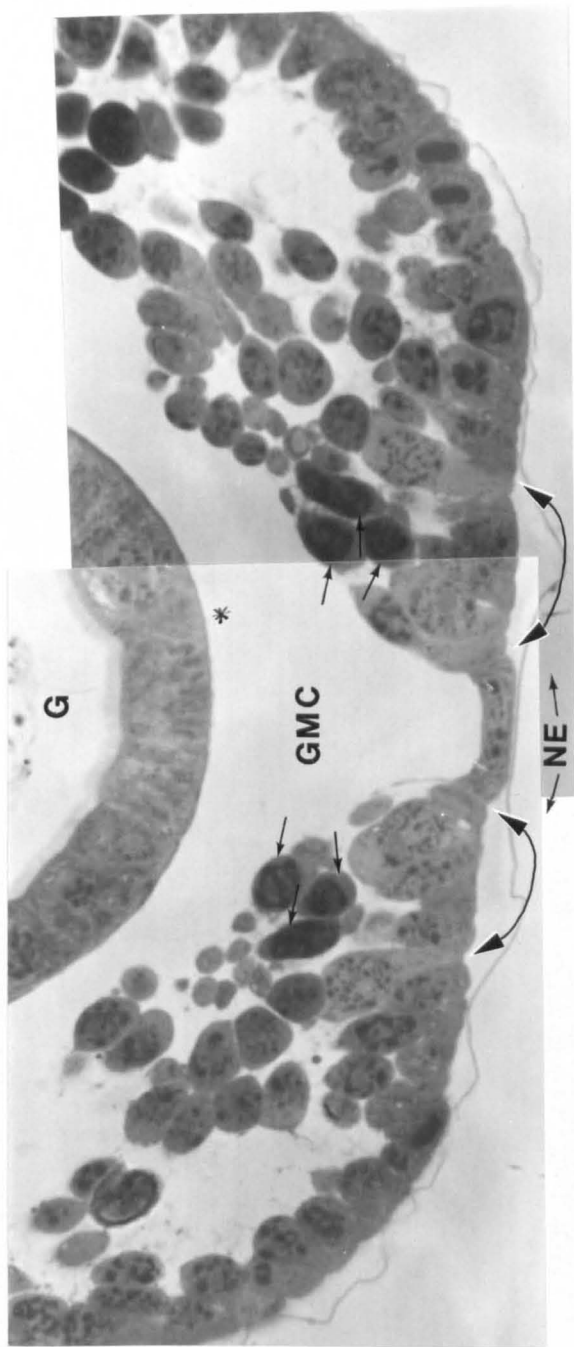
- (d) Each ganglion mother cell divides to produce a pair of cells, ganglion cells (GA), which can be seen, in pairs, slightly lateral to the neural epidermis.

G, gut; *, haemocoel; NP, neuropile.

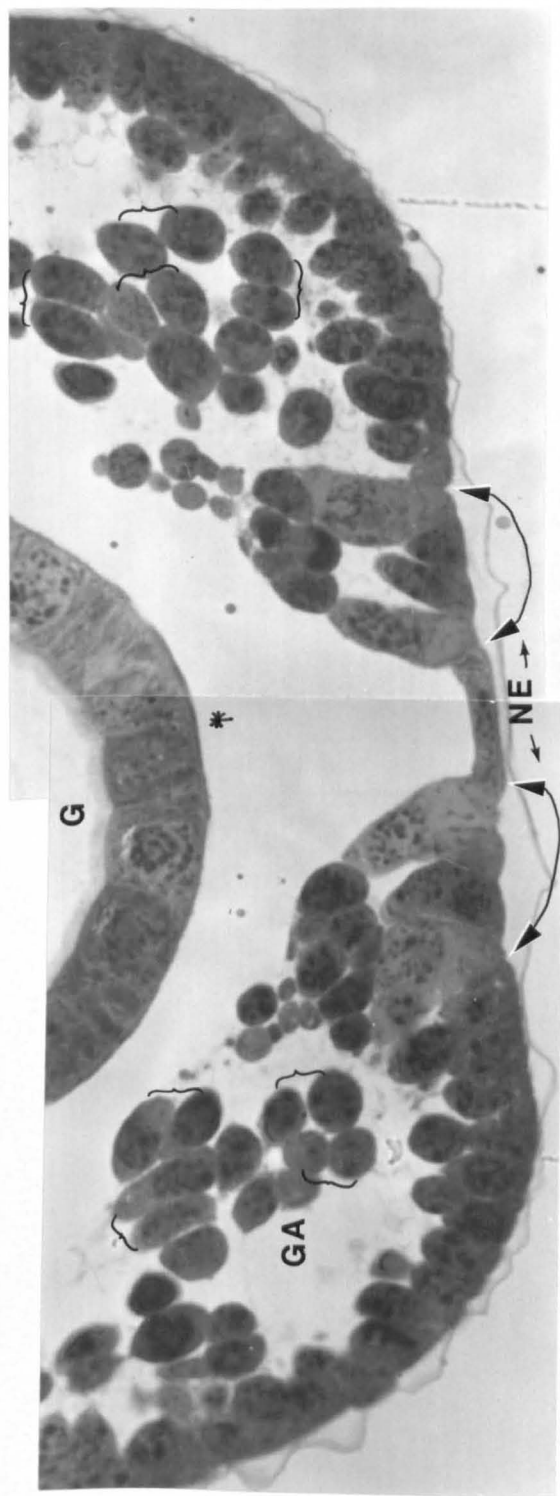
Scale bar

10 μm





c



d

FIGURE 5.1

Posterior end of a 2nd instar Artemia larva viewed with Nomarski optics. The cell bodies of the two pairs of terminal pioneer neurons (TP1 and 2) are visible on the ventral epidermis posterior to the mesodermal teloblasts. Single, unbranched axons (arrowheads) lead anteriorly and branched dendrites (DT, black arrowheads) extend posteriorly from these cell bodies. One posterior dendrite from TP1 L leads to the cell body of a terminal seta neuron (*).

G, gut; A, anterior; P, posterior, TS, terminal seta.

Scale bar

10 μ m

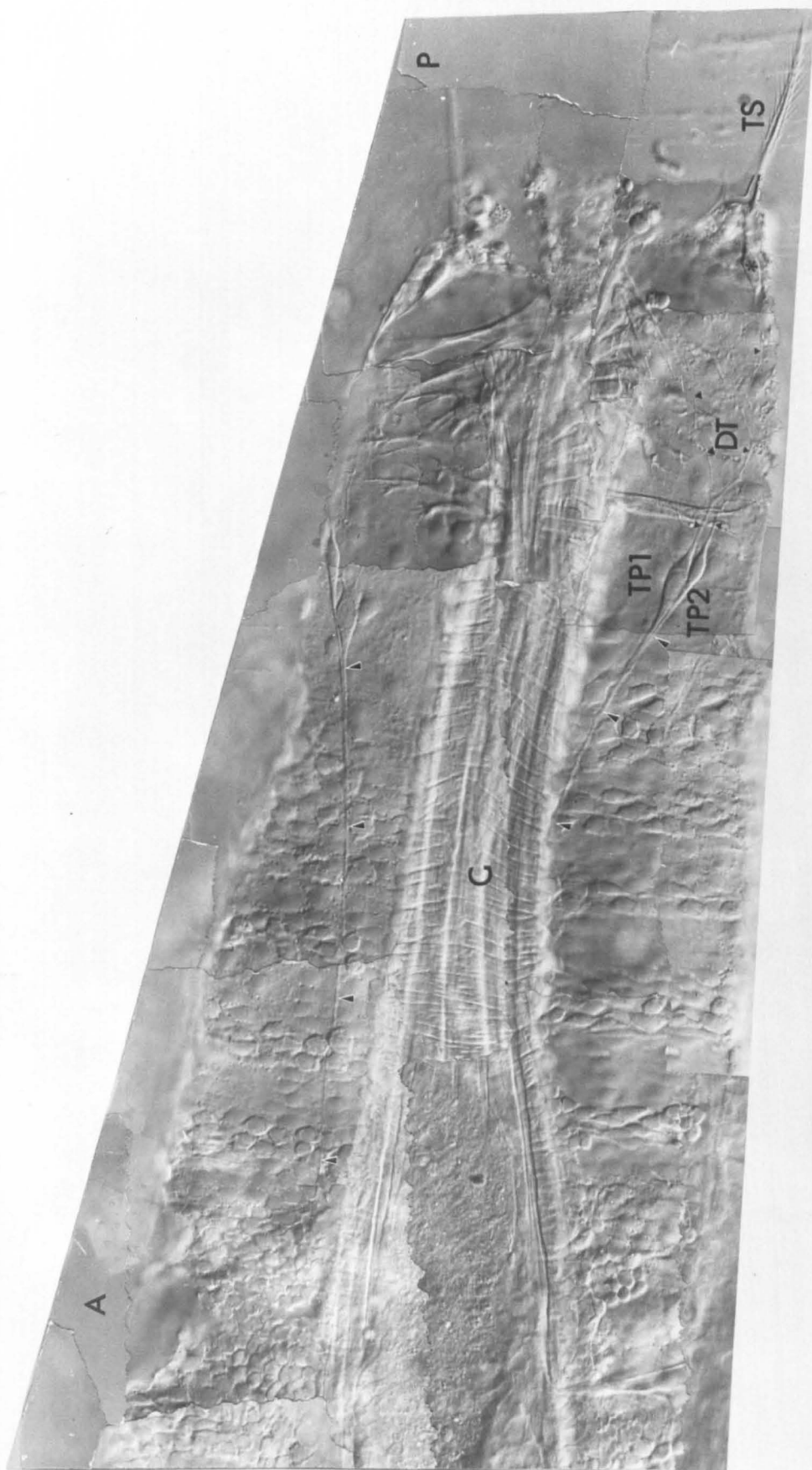


FIGURE 5.2

Micrograph of a transverse section through the cell body of TP1 from a 2nd instar Artemia larva. The cell body lies on the inner surface of the ventral ectoderm (E).

The characteristic large vesicles (LV) and small vesicles (SV) that are found in the TP neuron cell bodies can be seen, they are associated with extensive endoplasmic reticulum (ER).

*, haemocoel.

Scale bar

1 μ m



FIGURE 5.3

Micrograph showing the cell body of TP1 and next to it a dendrite (DT) from TP2 in the region just anterior to the TP2 cell body. Both cells contain the membrane-bound electron-dense vesicles (V) characteristic of the terminal pioneer neurons.

*, haemocoel; E, epidermal cell.

Scale bar

1 μm

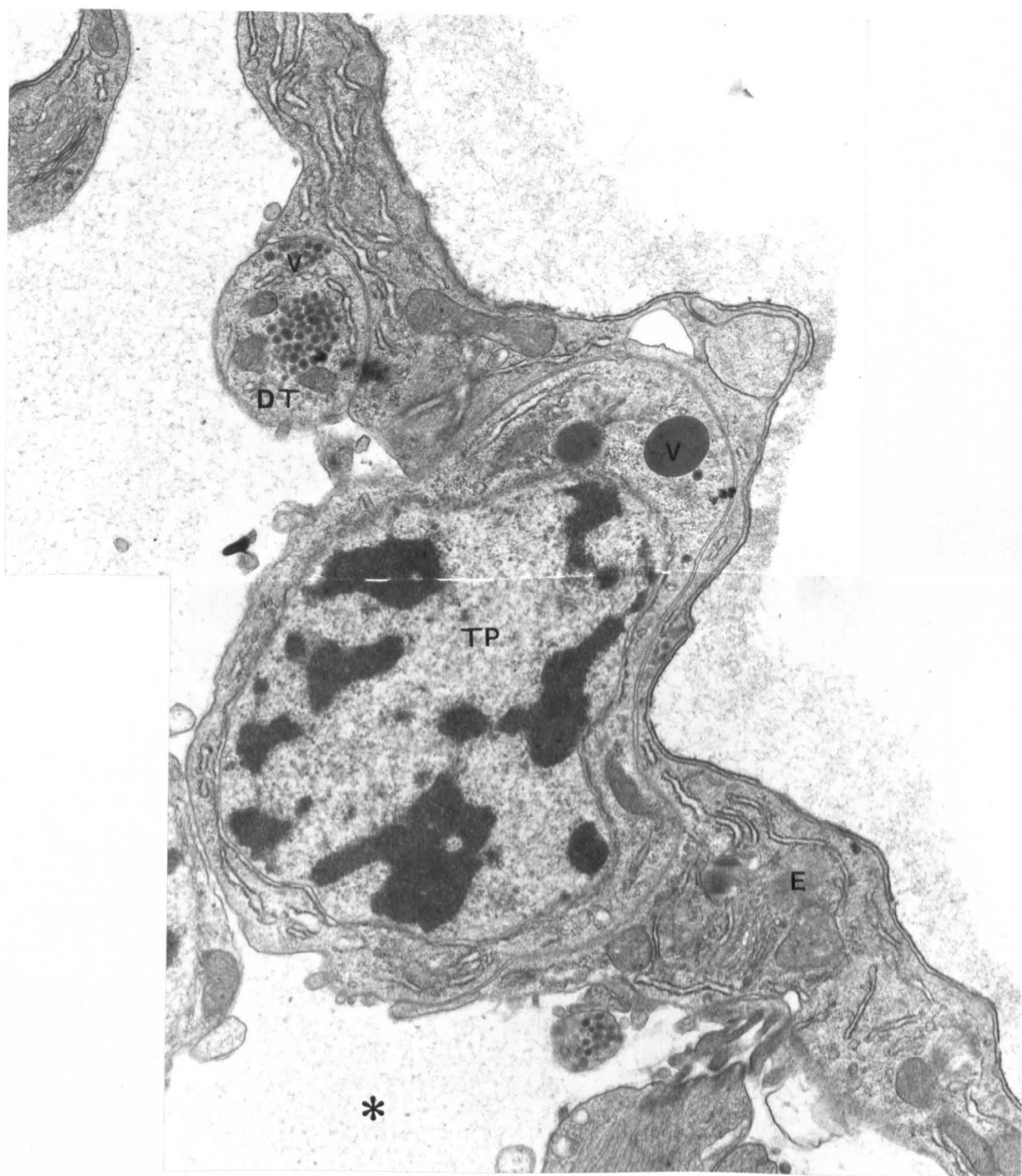


FIGURE 5.4

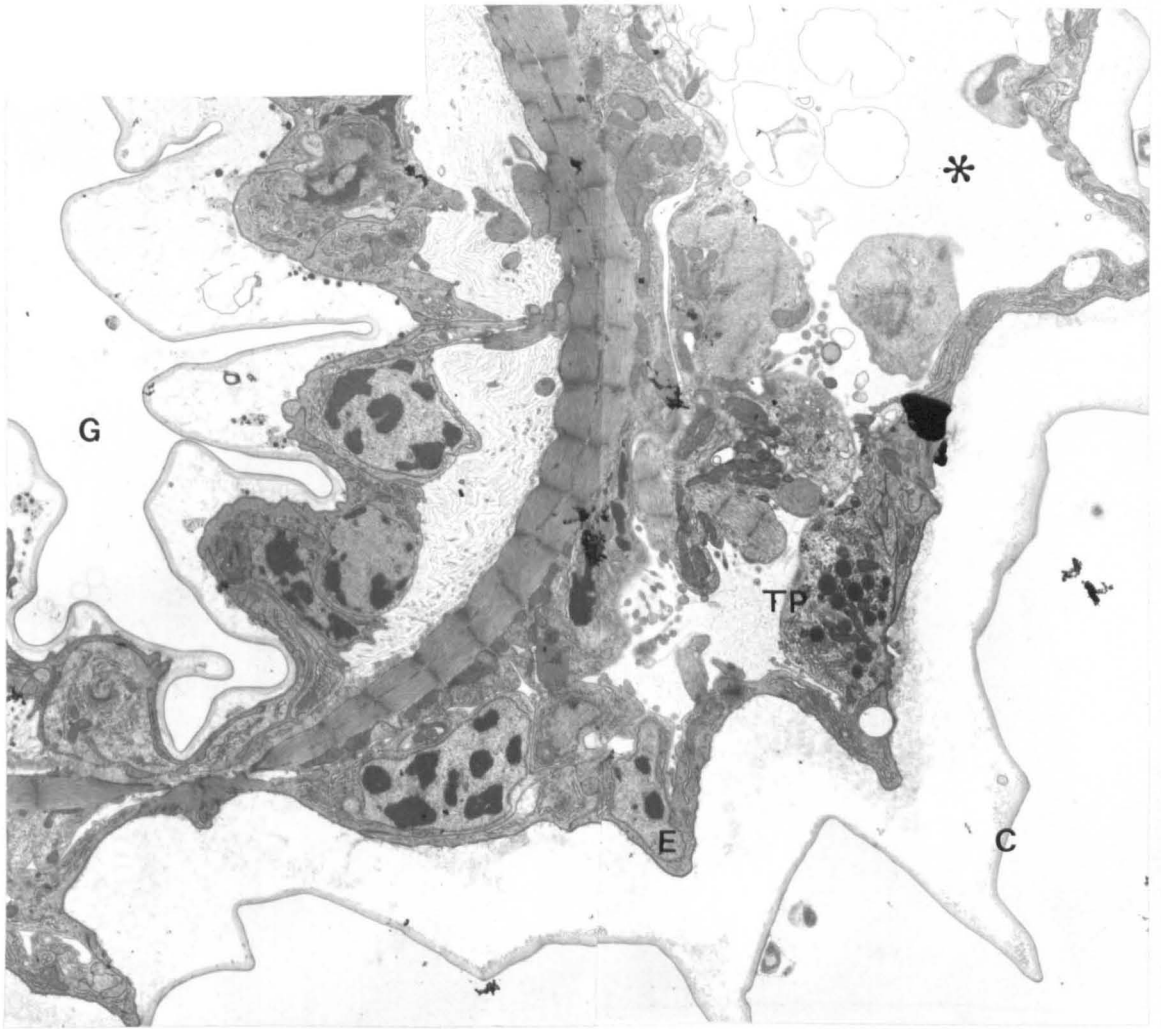
- (a) Micrograph of the ventral part of a 2nd instar Artemia larva at the level of the TP2 cell body where it lies within the epidermis.
- (b) Detail from (a) showing the point where TP2 is inserted into the epidermis. The cell membrane is ruffled at the point of insertion (arrowed).

G, gut; *, haemocoel; E, epidermal cell; C, cuticle.

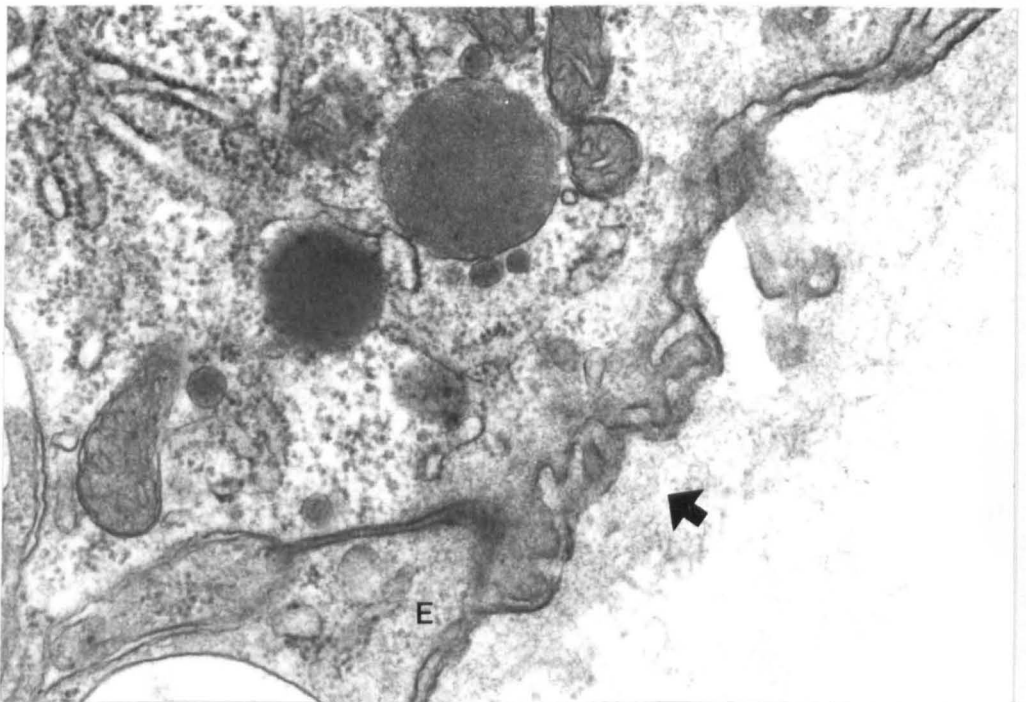
Scale bar

5 μm (a)

0.5 μm (b)



a



b

FIGURE 5.5

(a&b) Micrographs of the TP2 cell body showing the fine hair-like structure (H) containing many microtubules (arrowed) which projects to the exterior.

(c) Micrograph of a section slightly anterior to that from which (a) and (b) were derived. A basal-body like structure (BB) can be seen at the apical surface of TP2, in the region where the hair emerges.

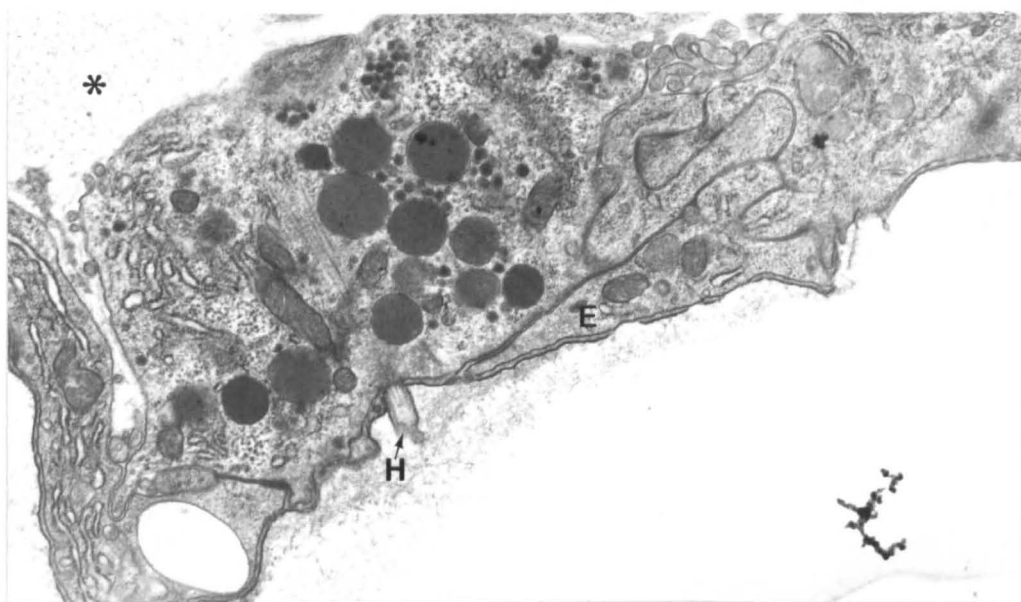
E, epidermal cell; *, haemocoel; ML, muscle.

Scale bar

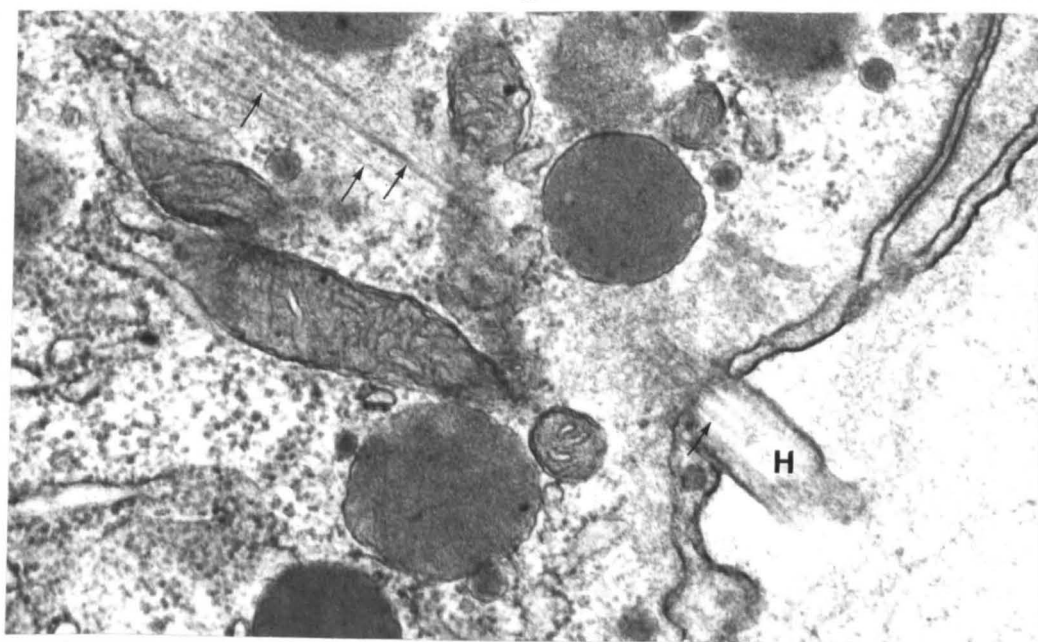
1 μm (a)

0.5 μm (b)

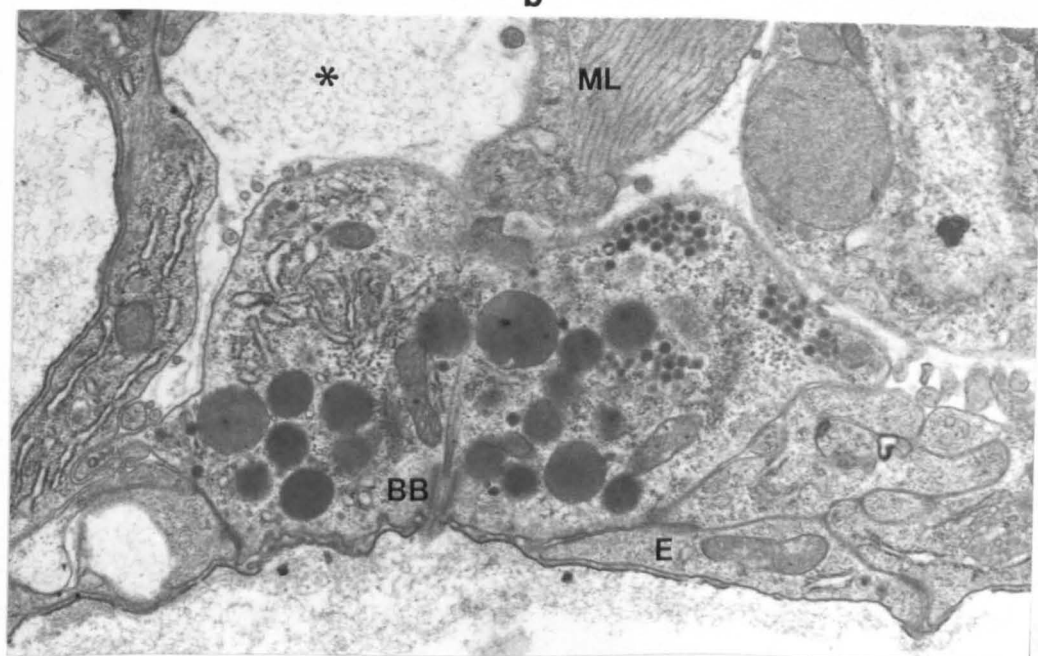
1 μm (c)



a



b



c

FIGURE 5.6

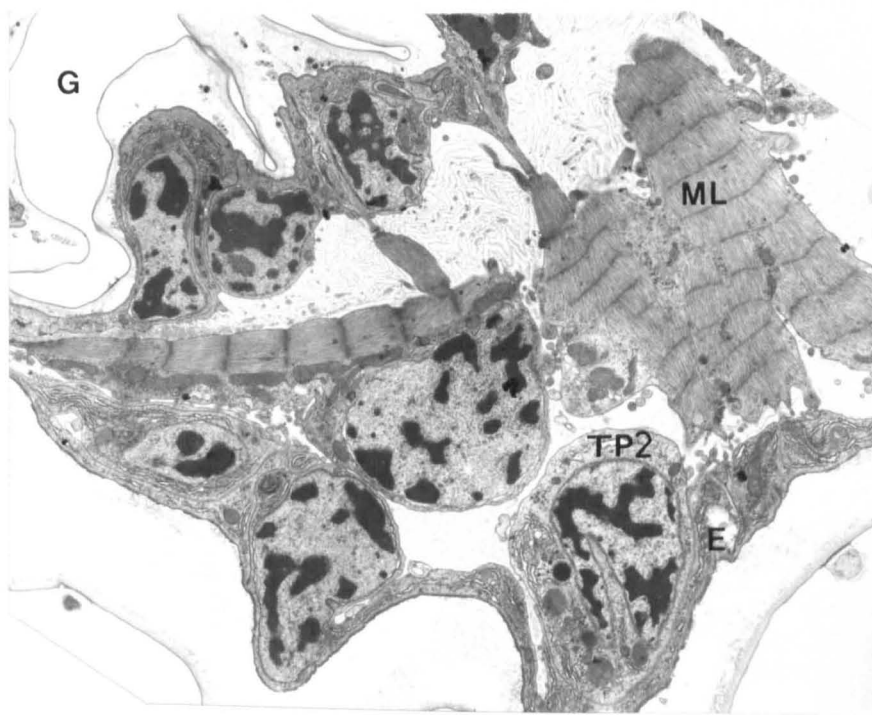
- (a) Transmission electron micrograph of a section through TP2 in the posterior region of the cell body where the nucleus is located. At this point TP2 is not inserted into the epidermis but lies on a thin part of an epidermal cell (E).
- (b) Detail from (a) showing a deep cleft (Cl) in the nucleus of TP2 in this region.

G, gut; *, haemocoel; ML, muscle; C, cuticle.

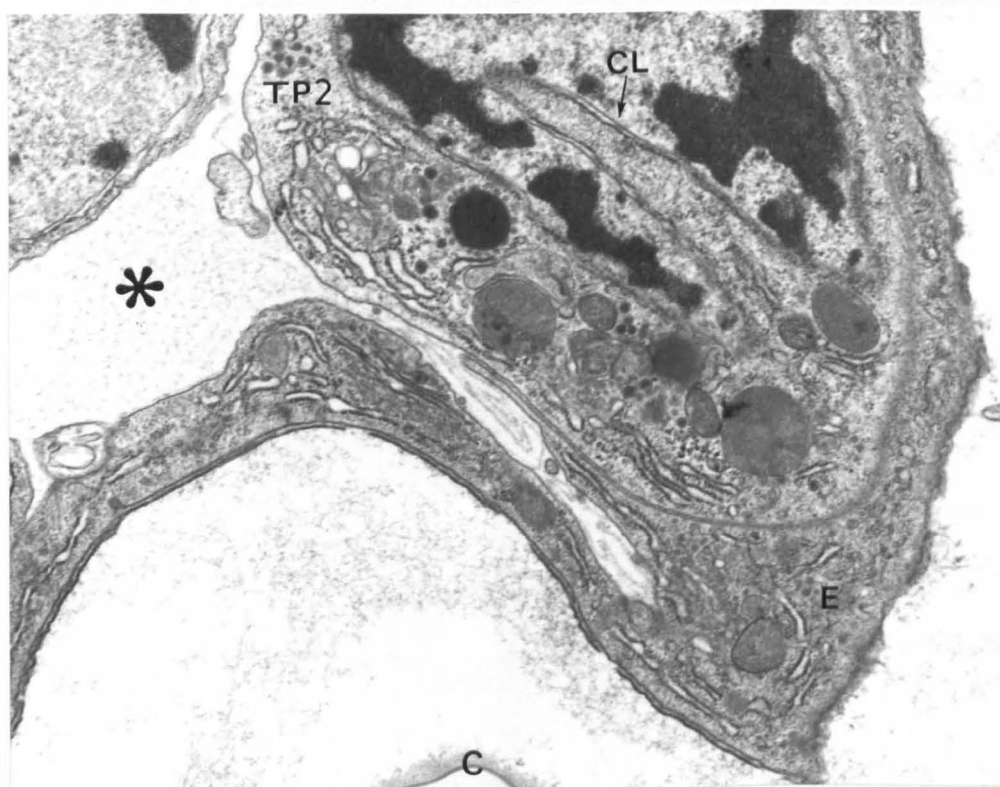
Scale bar

5 μm (a)

1 μm (b)



a



b

5.6

FIGURE 6.1

Transverse sections through the TP axons (arrowheads) at the growth zone level. (a) to (f) are sections taken from progressively more anterior regions of the growth zone. The axons lie beneath the epidermal basal lamina (BL) among many processes from epidermal (E) and mesodermal (M) cells.

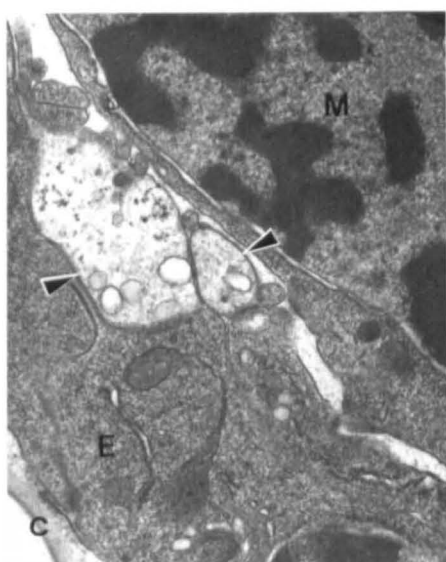
(b), (d) and (f) show the usual appearance of the axons.

(a), (c) and (e) show the appearance of the axons in the periodic regions where one is swollen.

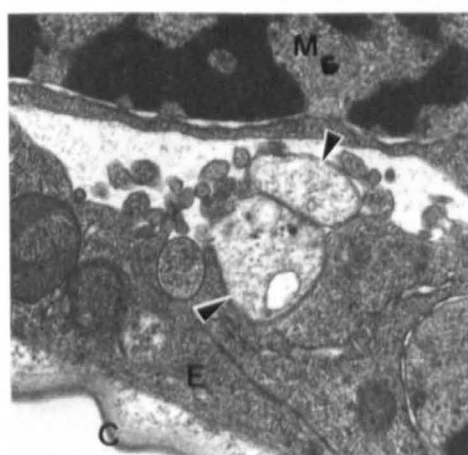
C, cuticle; star, mitochondrion.

Scale bar

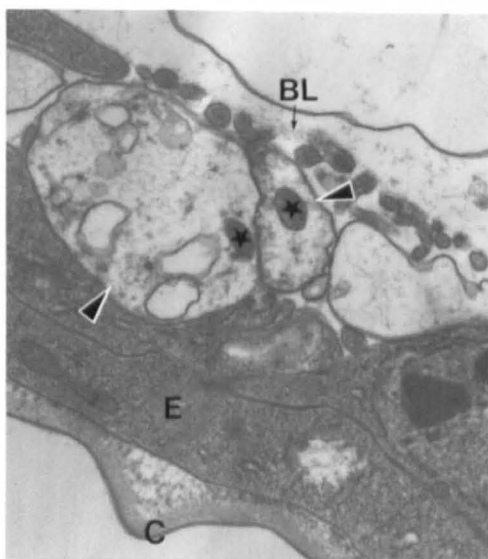
1 μm



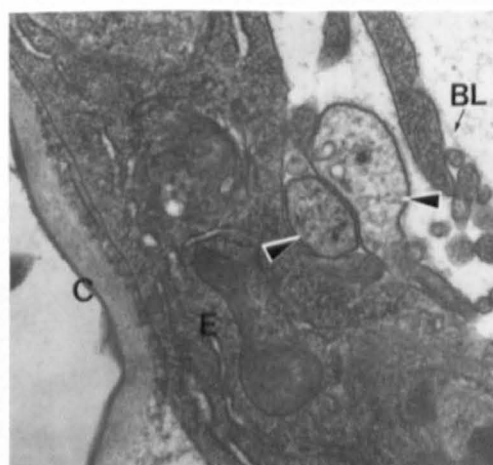
a



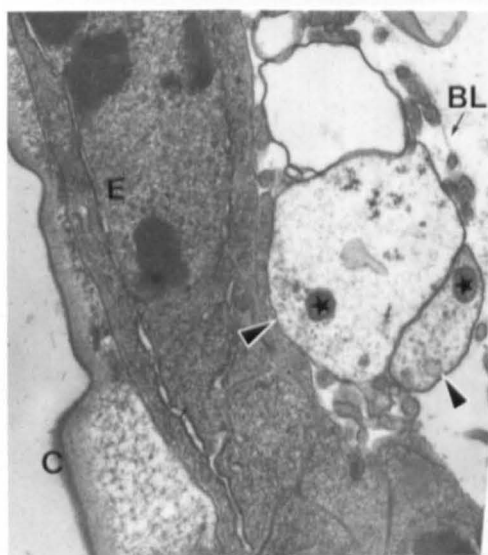
b



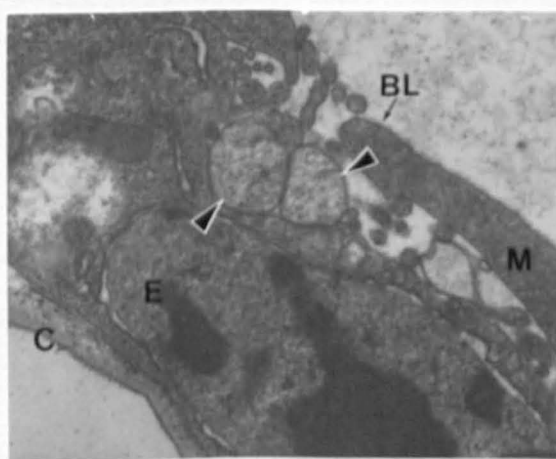
c



d



e



f

FIGURE 6.2

Transverse sections through the TP axons (arrowheads) at the growth zone level.

(a) shows the axons lying on a thin monolayer of epidermal cells.

(b) shows the microtubules (small arrows) that are characteristic of the axons, and the occasional mitochondria (stars) that are seen orientated longitudinally along the axon at the non-swollen levels.

C, cuticle; *, haemocoel.

Scale bar

1 μm (a)

0.1 μm (b)

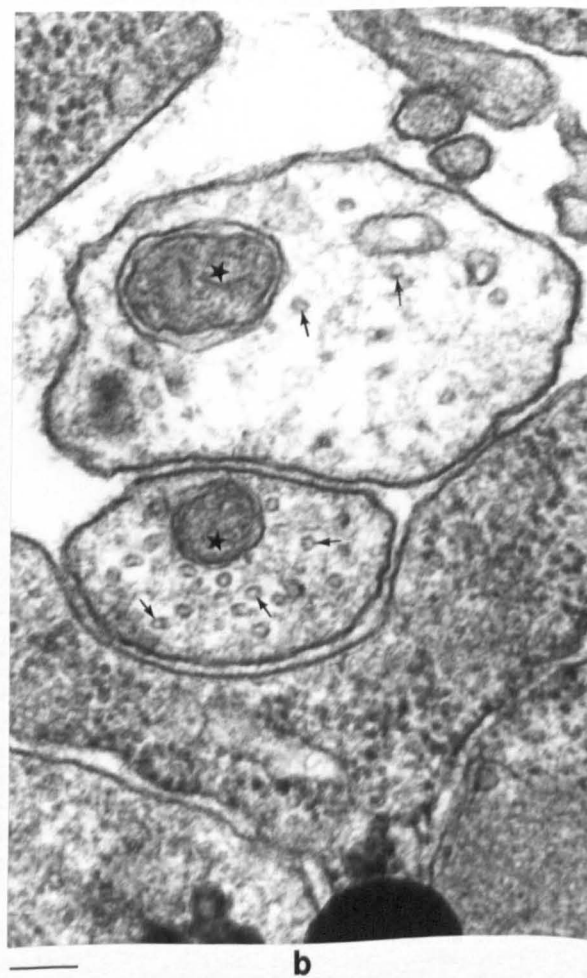
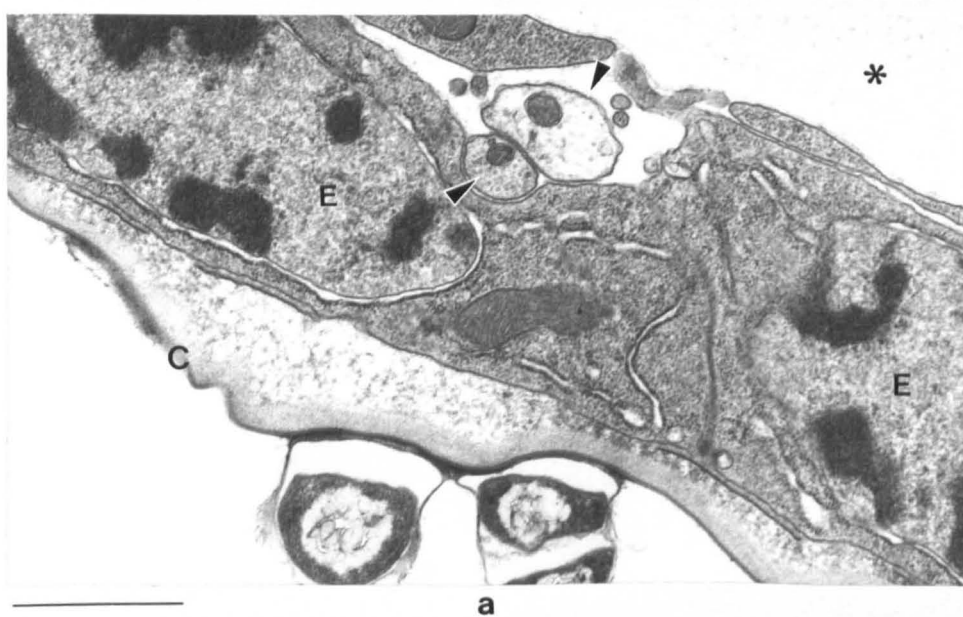


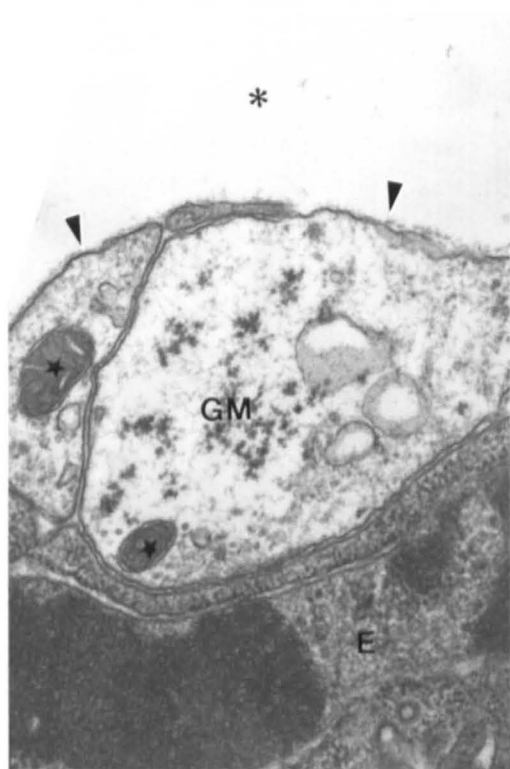
FIGURE 6.3

Transverse sections through the TP axons (arrowheads) at the level between the growth zone and the first mesoderm band on the left (a-d) and right (e-g) sides of one specimen. The appearance of both axons in the particular region where one is swollen can be seen in detail. All axons contain mitochondria (black stars) (a-g), there are vesicular extensions of outer mitochondrial membranes (OMM) clearly associated with some mitochondria (c & d, e, f, & g). Granular material (GM) can sometimes be seen in one axon of the pair (a, b and e). The axons are closely associated such that one is occasionally almost surrounded by the other (c, f). Smooth endoplasmic reticulum (ER) can sometimes be observed (g), perhaps associated with OMM.

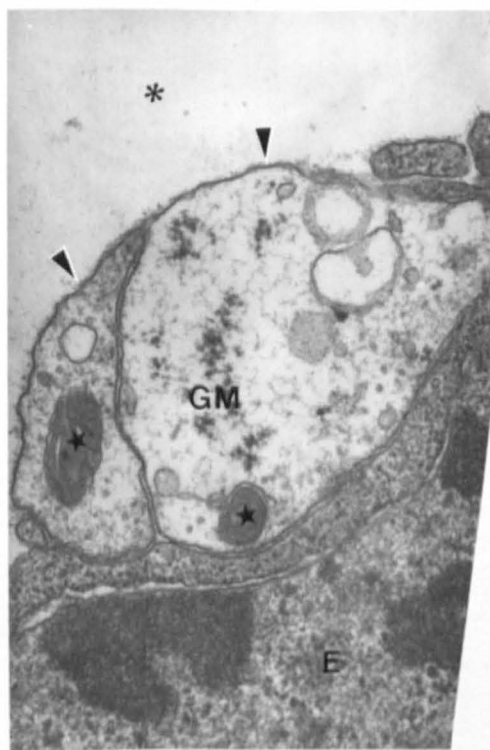
E, epidermal cell; *, haemocoel.

Scale bar

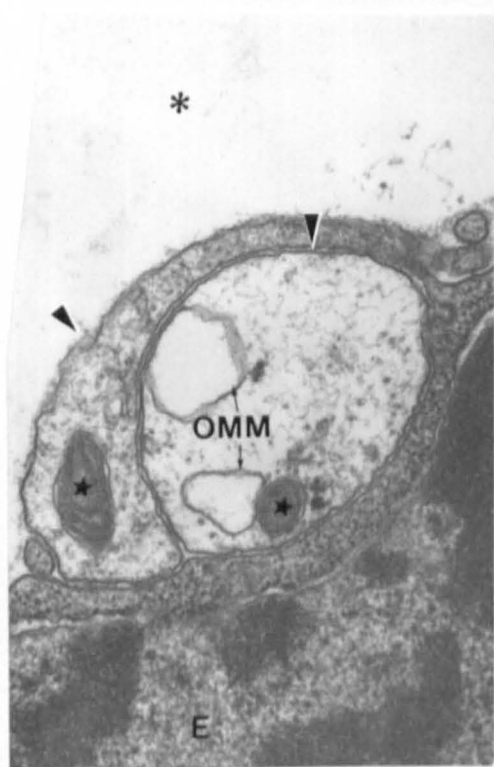
0.5 μm



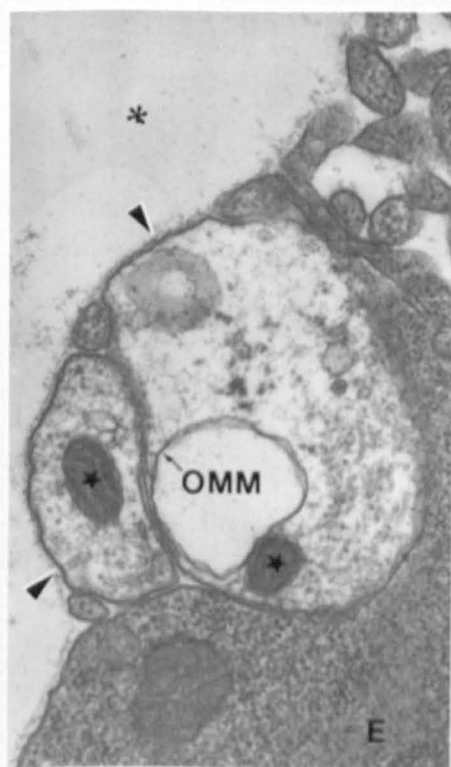
a



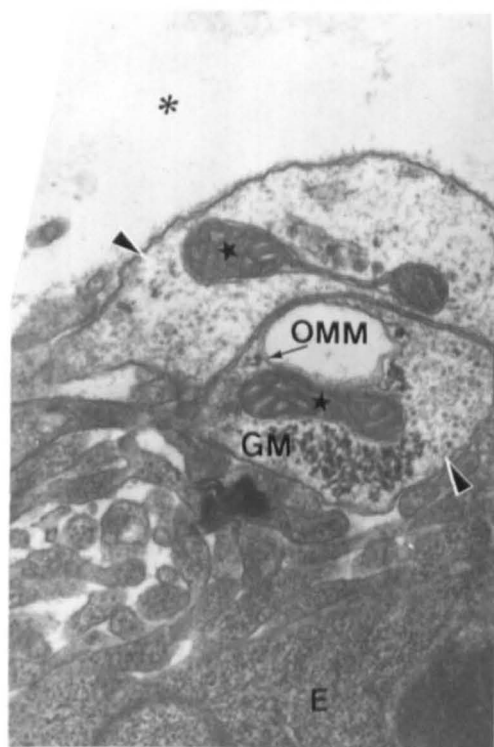
b



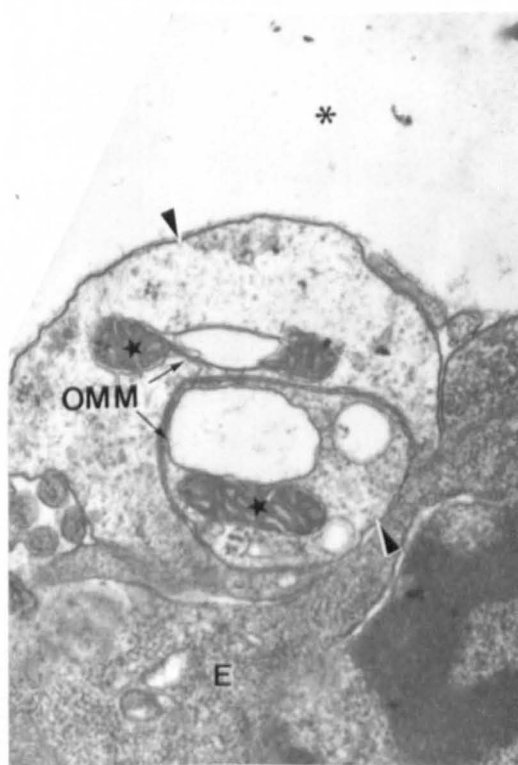
c



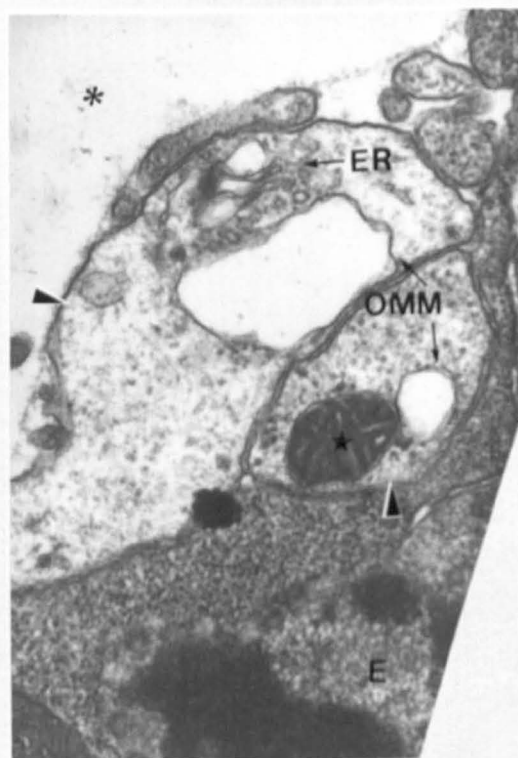
d



e



f



g

6.3

FIGURE 6.4

Diagrammatic representation of the arrangement of the axons on the inner ventral surface of a thoracic segment at stages 1 and 2.

In stage 1 the two pairs of TP axons (TPA) lie longitudinally along the length of the segment. Growing out at right angles to their paths, along the posterior edge of the dorsoventral muscle (ML), are the pairs of axons from the dorsal setae (DSA).

In stage 2 the pairs of axons from the dorsal setae have reached the TP axons and fasciculated with them. One dorsal seta axon (DS1) has bifurcated and sent a branch anteriorly (A) and posteriorly (P). The other dorsal seta axon (DS2) has turned to grow anteriorly only. Also in stage 2, the posterior commissure axons (PCA) begin to grow out as branches from the longitudinal TP axons. They grow medially along the anterior edge of the dorsoventral muscle insertion.

FIGURE 6.4 (contd.)

A series of progressively anterior transverse levels through the segment are indicated by letters A to D, these levels are referred to in the text.

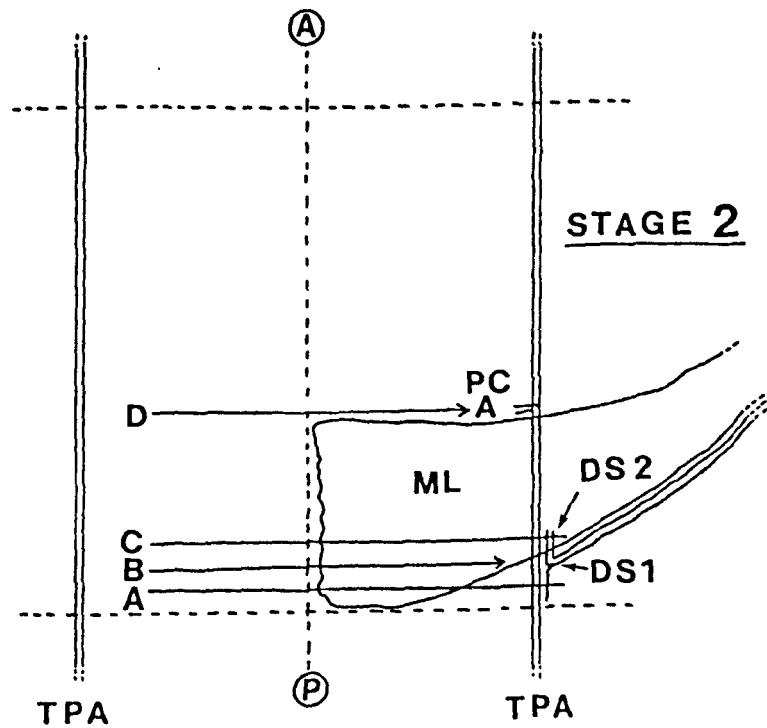
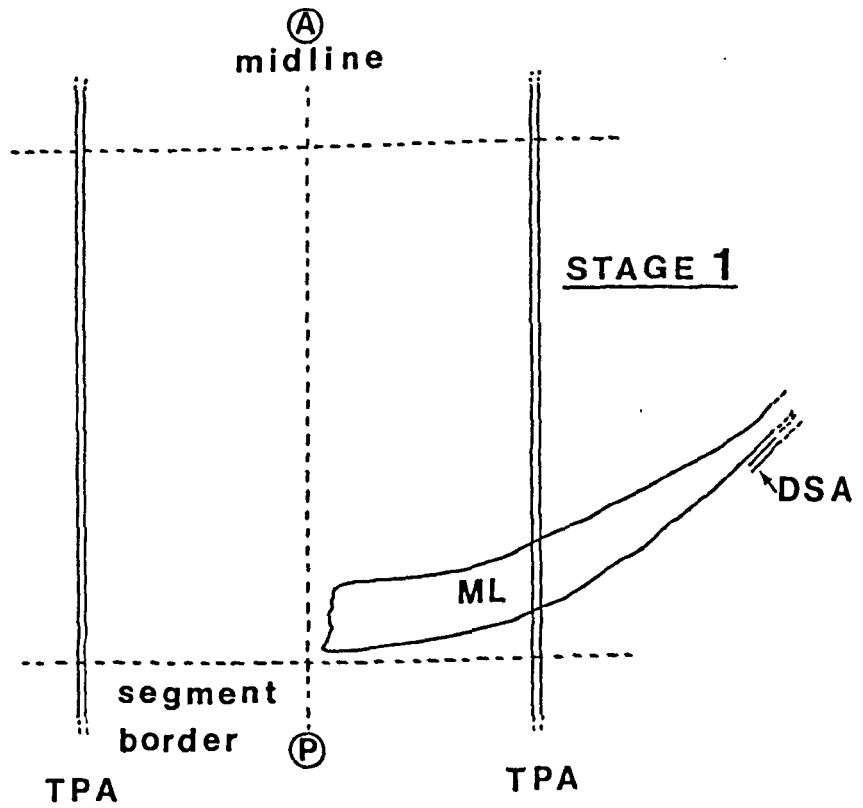


FIGURE 6.5

A selection of transverse sections through the TP axons (arrowheads) in the region of the newly-formed, undifferentiated mesoderm bands. The axons are all approximately equally sized and circular in profile. They do not lie on any distinctive feature of the epidermis (E), they always lie beneath the epidermal basal lamina (BL) and are associated with other cell processes (stars).

M, mesoderm cell; *, haemocoel.

Scale bar

0.5 μm

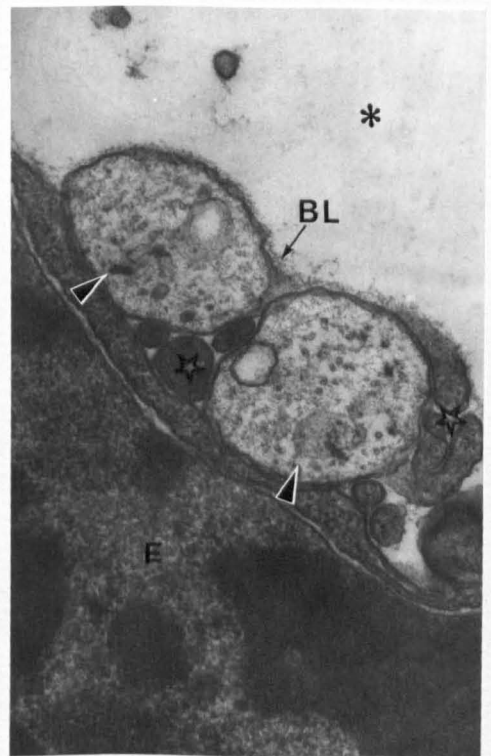
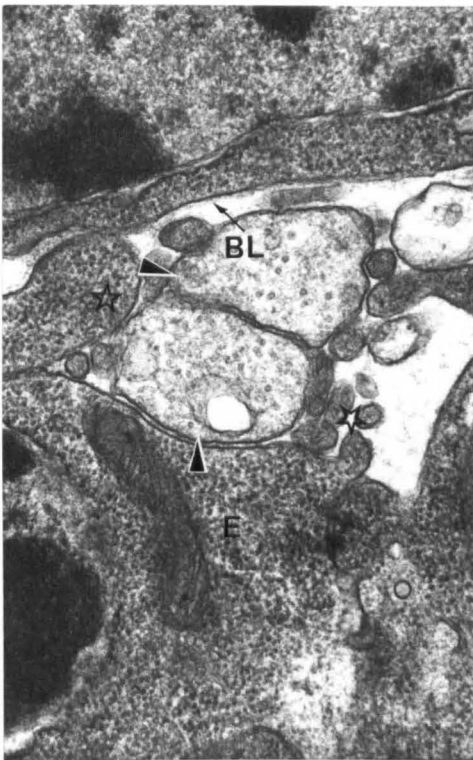
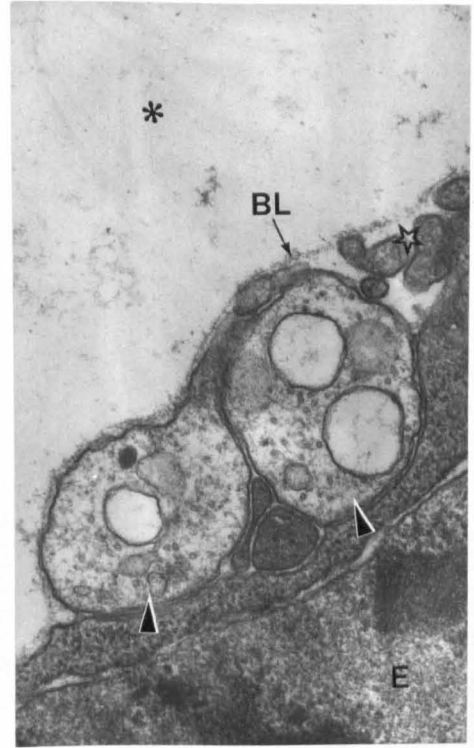
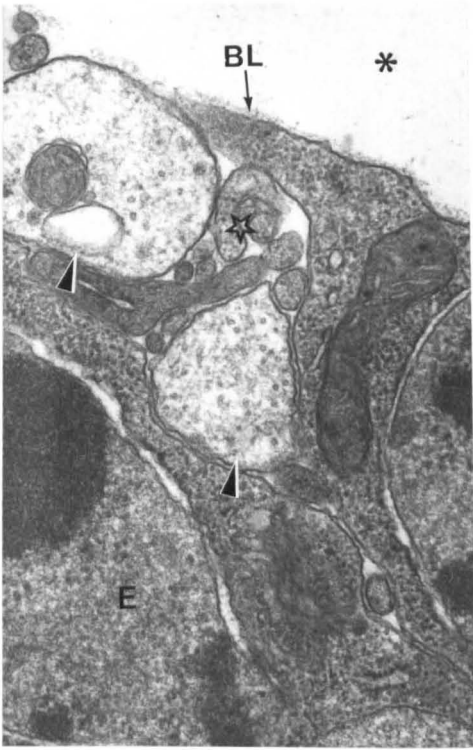


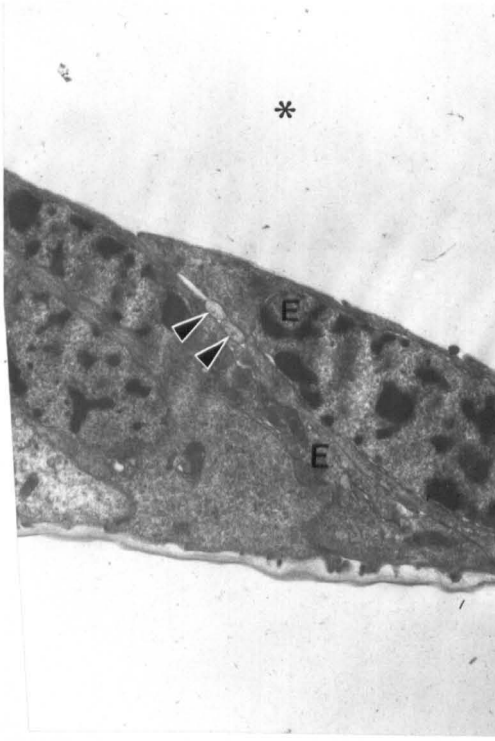
FIGURE 6.6

Two pairs of micrographs of transverse sections through the TP axons (arrowheads) in a stage 1 segment. The cellular environment of the axons can be seen in the micrographs on the left and details of the axons themselves in the micrographs on the right. The axons lie between (a) or on (b) epidermal cells (E) and no other axons have fasciculated with them at this stage.

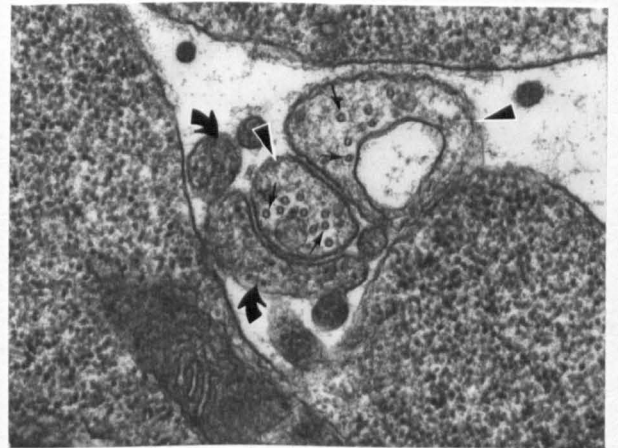
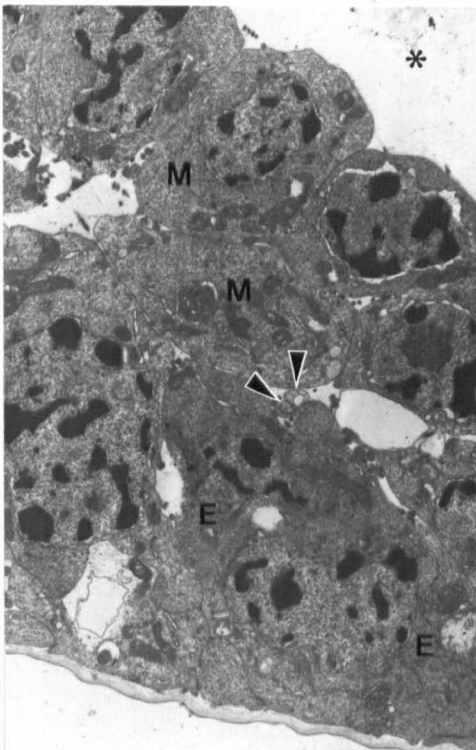
*, haemocoel; M, mesoderm cell; small arrows, microtubules; curly arrows, cell processes.

Scale bar

0.5, 1 μ m



a



b

FIGURE 6.7

A pair of micrographs of a transverse section through a stage 2 thoracic segment from the level designated A in fig. 6.4.

(a) Shows the cellular environment of the axons.

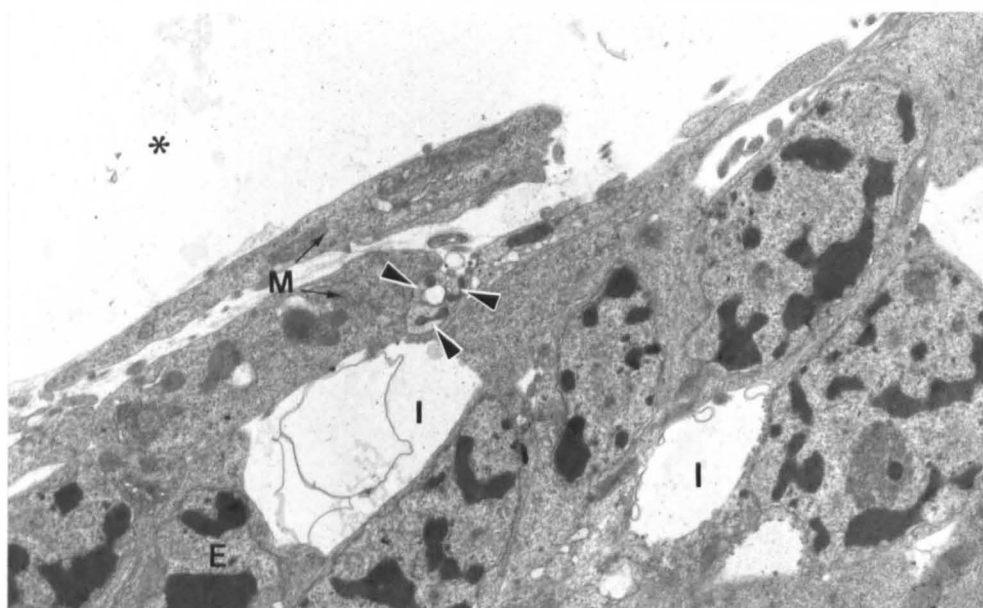
(b) Shows shows the axons in detail. A third axon has fasciculated with the pair of TP axons, it is the posterior branch of the axon DS1 (referred to in fig. 6.4.), which has joined the TP axons more anteriorly in the segment.

arrowheads, axons; *, haemocoel; E, epidermal cell; M, mesoderm cell; I, intercellular space.

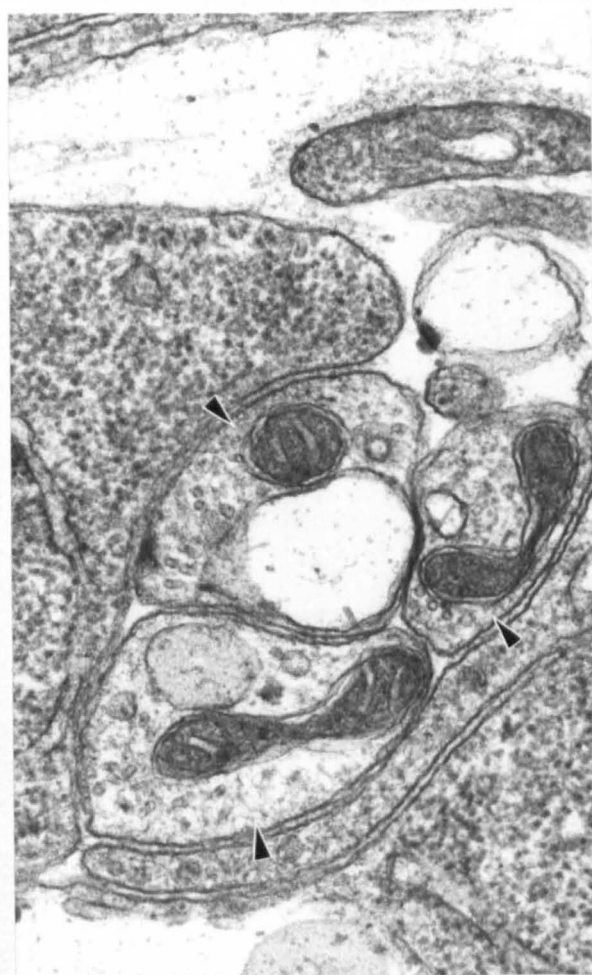
Scale bar

1 μm (a)

0.5 μm (b)



a



b

FIGURE 6.8

Two transverse sections through a stage 2 thoracic segment from the level designated C in fig. 6.4. Two axons have fasciculated with the pair of TP axons, one is the anterior branch of the axon DS1 referred to in fig. 6.7., and one is DS2.

arrowheads, axons; E, epidermal cell; star, cell process.

Scale bar

0.5 μm

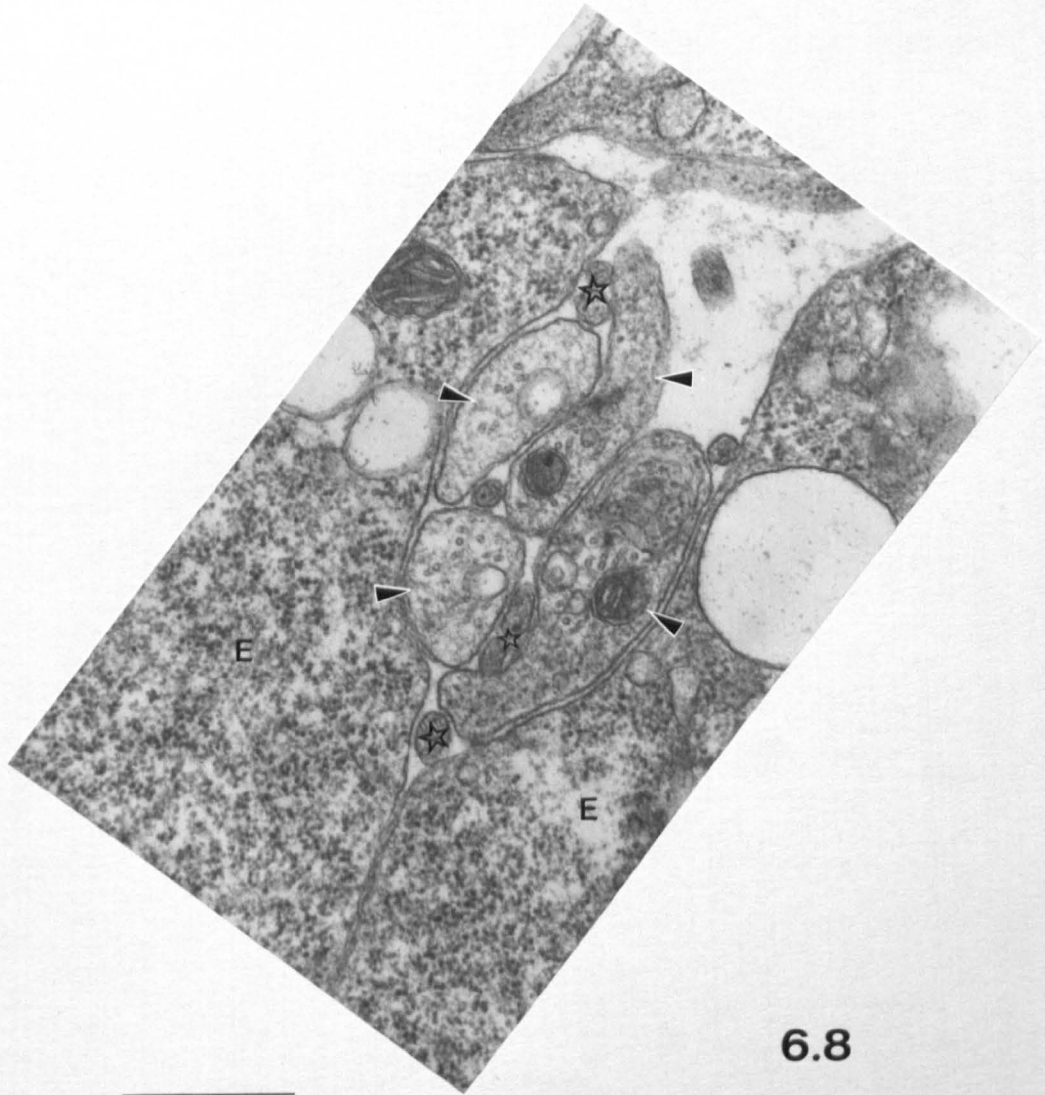
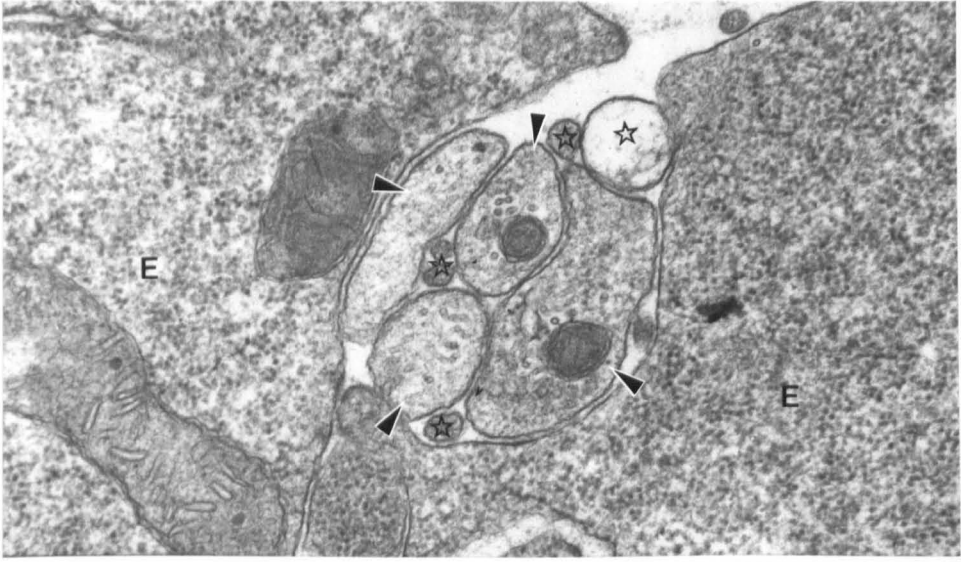


FIGURE 6.9

Two representative series of micrographs derived from serial (posterior to anterior) transverse sections through two stage 2 thoracic segments at the level designated B in fig. 6.4. There is an explanatory diagram of the traced outlines of the axons to the right of each micrograph. The fasciculation of the two dorsal seta axons (arrowheads) with the TP axons (arrows) is shown.

- (a) The transverse, approximately circular profiles of the two TP axons are clear in all micrographs.
- (i) The arrival of dorsal seta axon 2 (DS2) at the TP axons is shown, and the posterior branch of dorsal seta axon 1 (DS1) can be seen.
- (ii)&(iii) DS2 has turned anteriorly and fasciculated with the TP axons. DS1 is shown at its branch point where it is arriving from the dorsolateral direction, and is branching anteriorly and posteriorly.

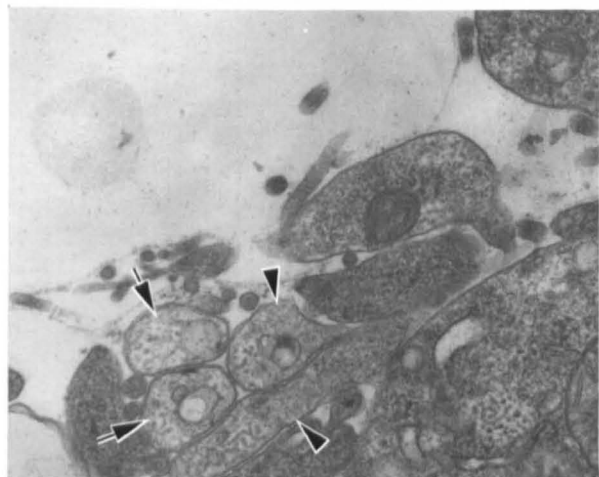
FIGURE 6.9 (continued)

- (iv) The anterior branches of the two DS axons have formed a longitudinal axon bundle with the TP axons.

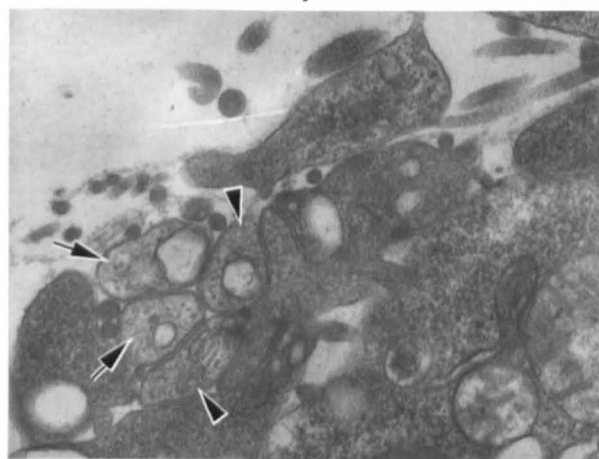
E, epidermal cell; M, mesoderm cell;
*, haemocoel.

Scale bar

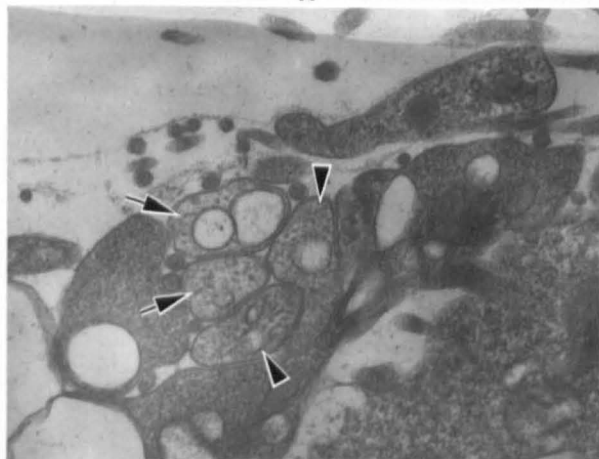
1 μm



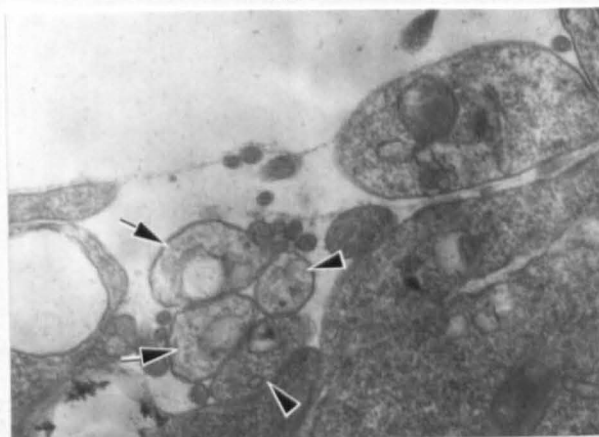
i



ii



iii



iv



6.9a



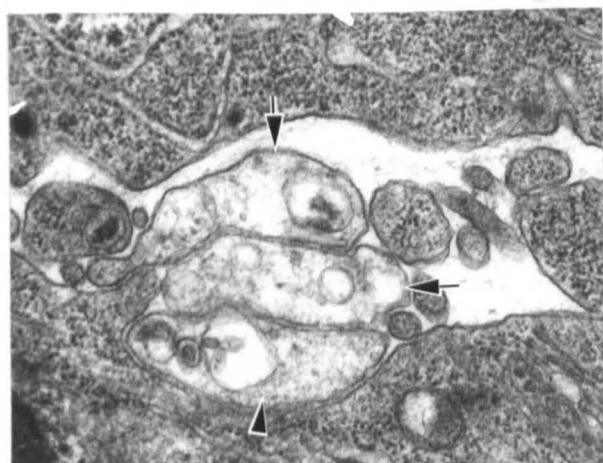
FIGURE 6.9 (b)

The transverse profiles of the two TP axons are seen in each micrograph.

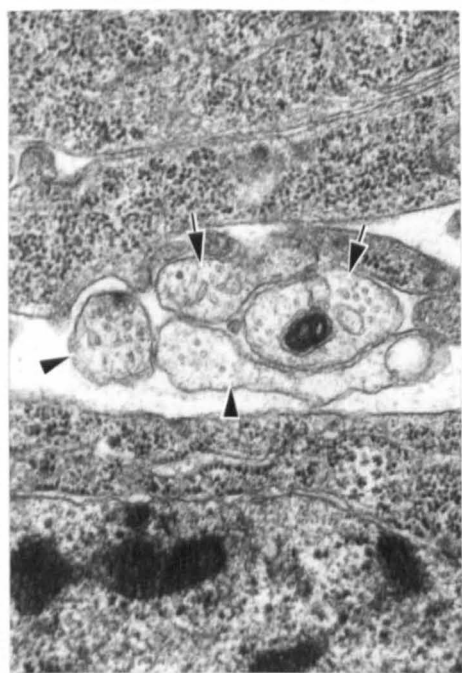
- (i) The posterior branch of DS1 is shown.
- (ii) The two TP axons and DS1 are joined by the arriving DS2 axon.
- (iii)-(v) The irregular profiles of the two DS axons at their points of branching and of arrival from the dorsolateral region is shown.
- (vi) The anterior branches of the two DS axons have formed a longitudinal bundle with the TS axons.

Scale bar

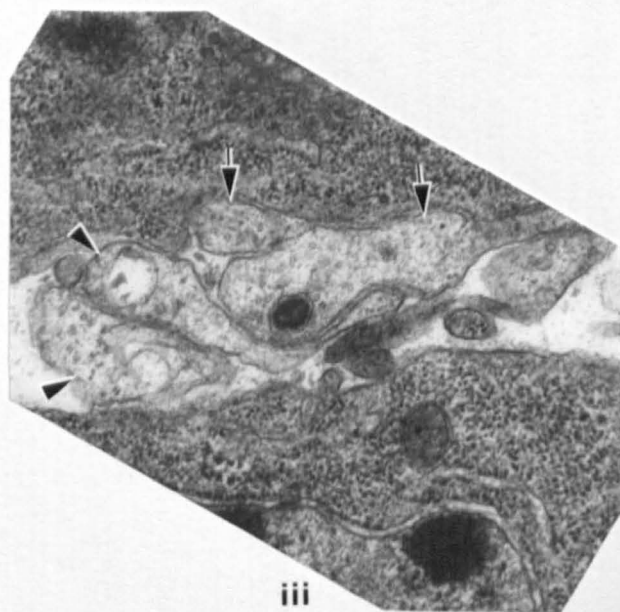
0.5 μm



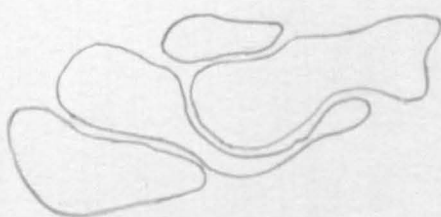
i



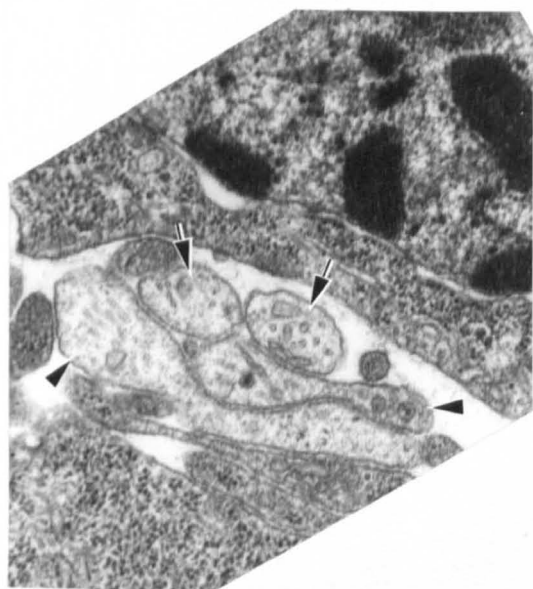
ii



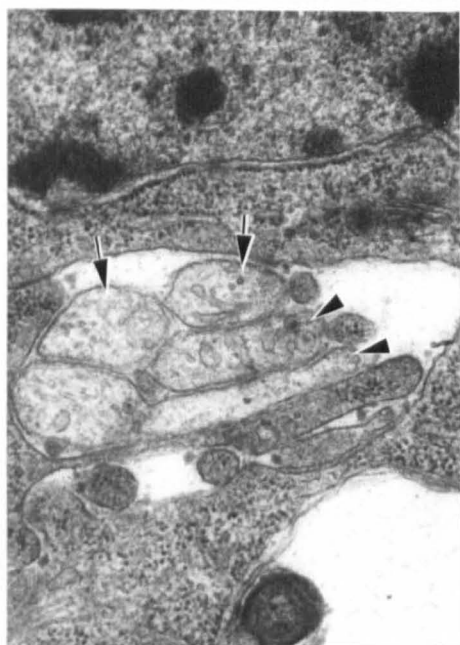
iii



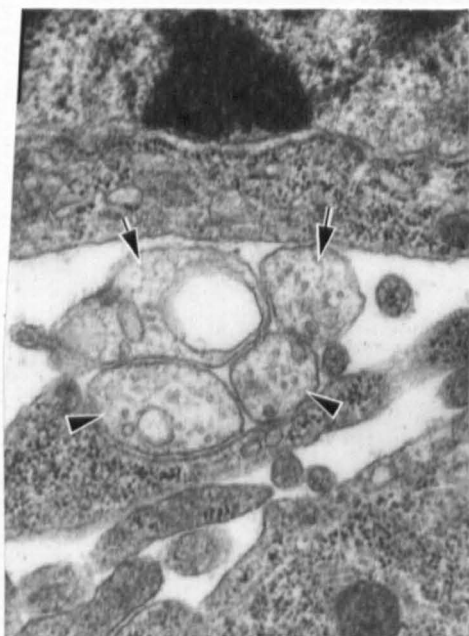
6.9b



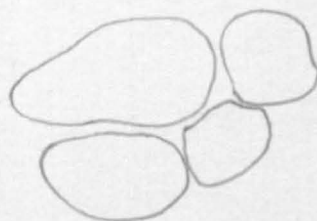
iv



v



vi



6.9b

FIGURE 6.10

Longitudinal section through a stage 2 thoracic segment in the region of the posterior commissure, at the level designated D in fig. 6.4. Two medially-directed branches of the TP axons which pioneer the posterior commissure (arrowheads) are visible. These axons grow out at a level in the segment which is at the anterior edge of the dorsoventral muscle (ML) and at the posterior edge of the ganglion cells (G).

NE, neural ectoderm; *, haemocoel; A, anterior; P, posterior.

Scale bar

5 μ m

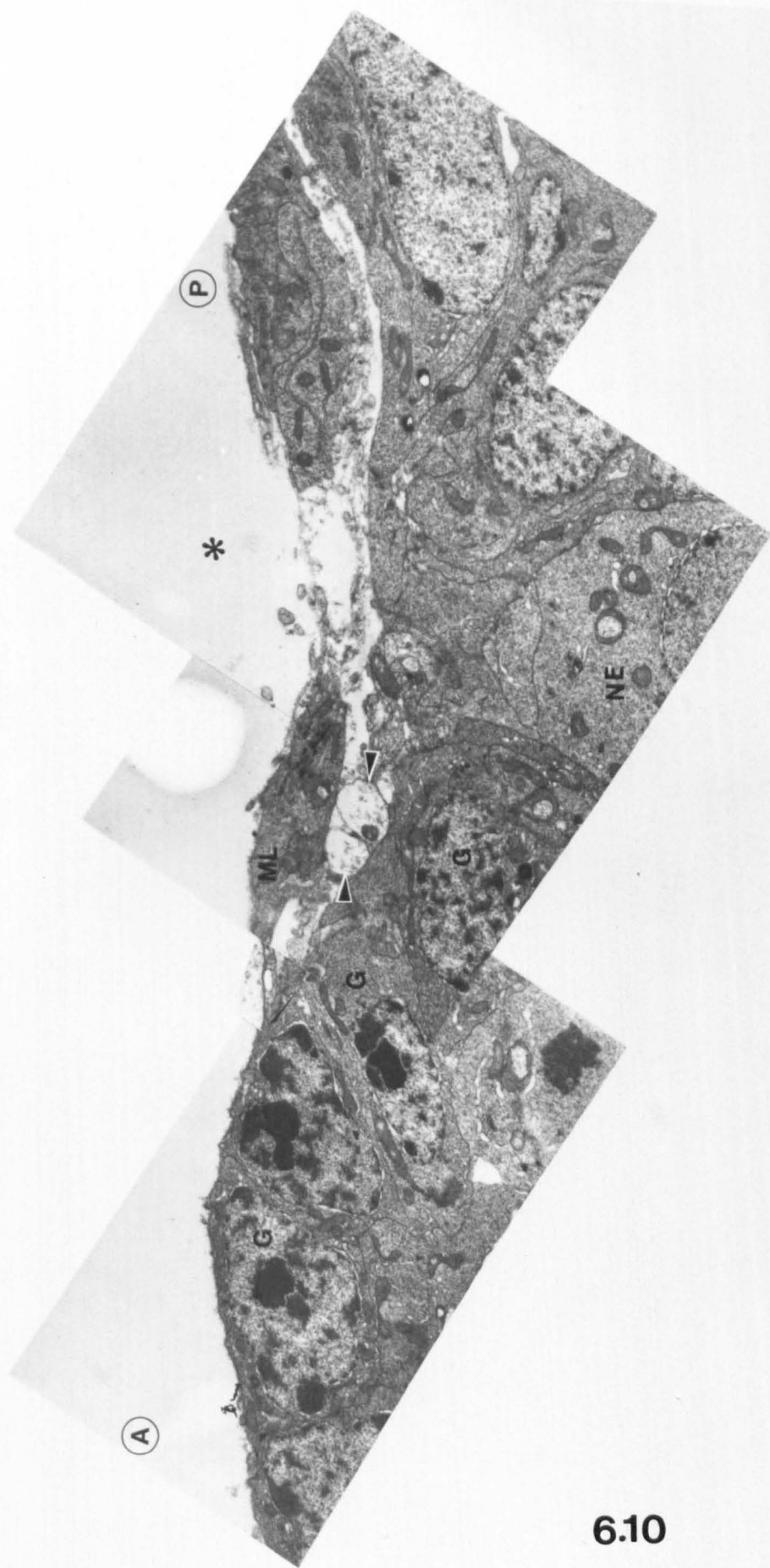


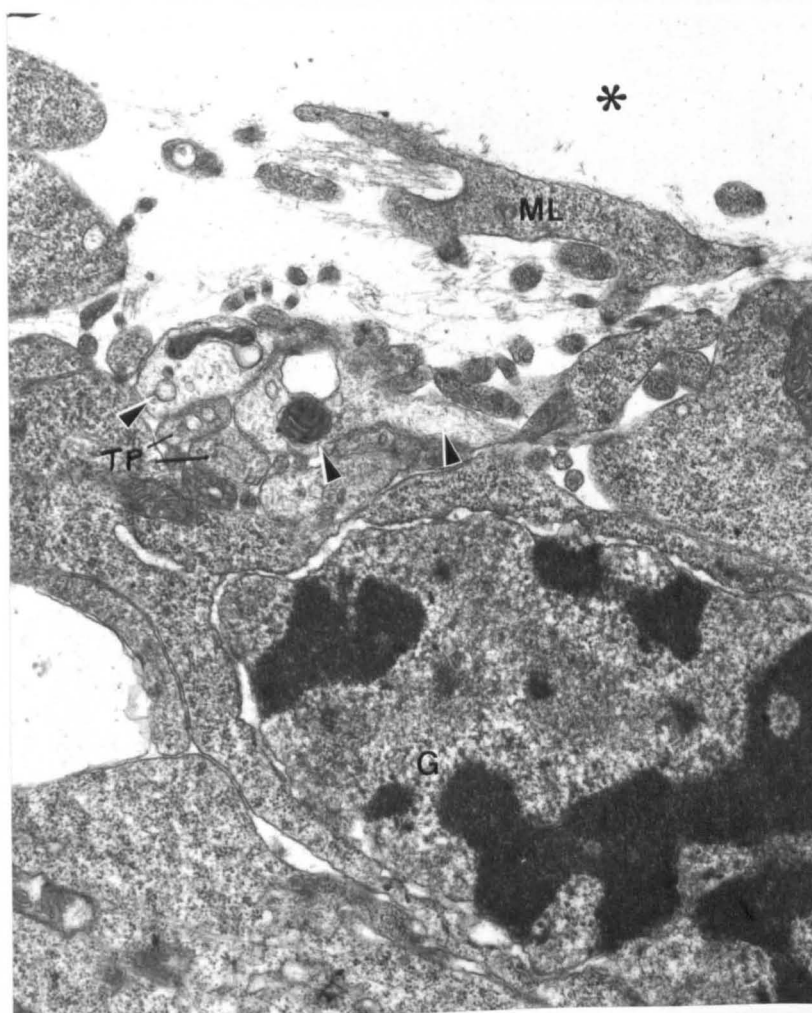
FIGURE 6.11

Serial transverse sections through a stage 2 thoracic segment in the region of the posterior commissure at the level designated D in fig. 6.4. Two medially-directed branches (arrowheads) of the TP axons (TP) grow out only a short distance during this stage to begin to pioneer the posterior commissure pathway.

E, epidermal cell; C, cuticle; *, haemocoel; ML, posterior edge of the dorsoventral muscle; G, ganglion cell; L, lateral; M, medial.

Scale bar

1 μ m



L ← → M

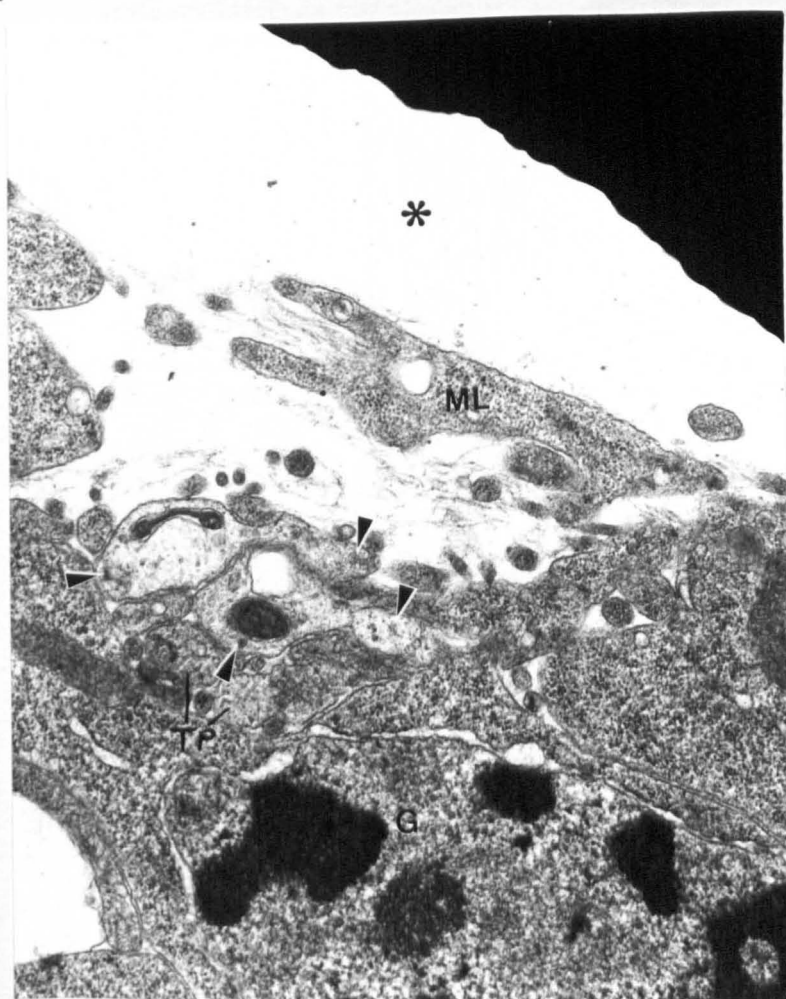


FIGURE 6.12

Diagrammatic representation of the arrangement of the axons on the inner ventral surface of a thoracic segment at stages 3 and 4.

In stage 3 the posterior commissure axons (PCA) from the left and right sides meet and overlap at the midline to complete the commissure pathway. During this stage the anterior commissure axons (ACA) branch medially from the TP axons in the anterior of the segment. They grow along an edge of a dorsoventral muscle (ML) insertion and closely approach the midline, but they do not overlap in this stage. The two anterior commissure axons are followed medially by a pair of axons (L1 and L2) from unknown neurons lateral to the TP axons (TPA).

In stage 4 the two commissure pathways are complete and each contains many axons.

A series of progressively more medial levels through the stage 3 segment is indicated by letters E to H; these levels are referred to in the text.

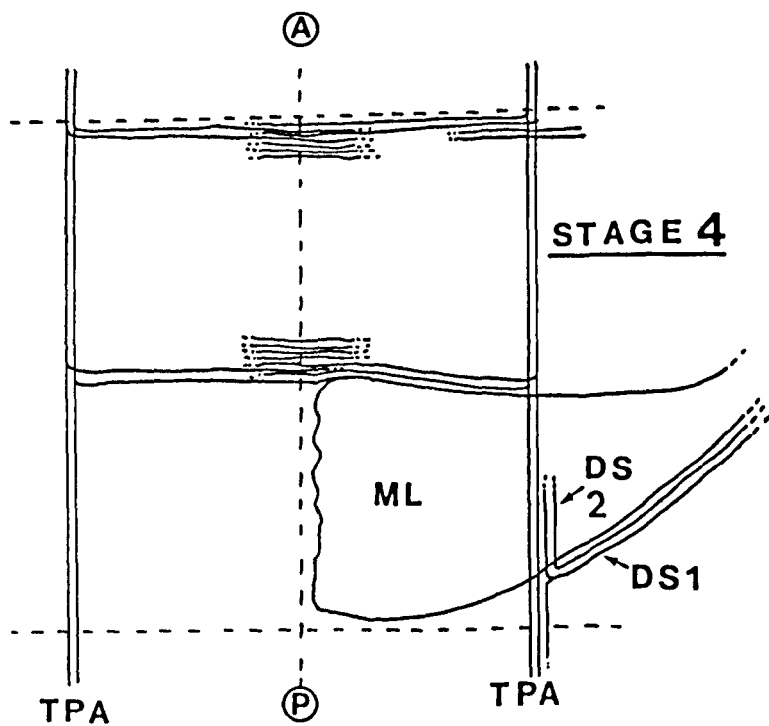
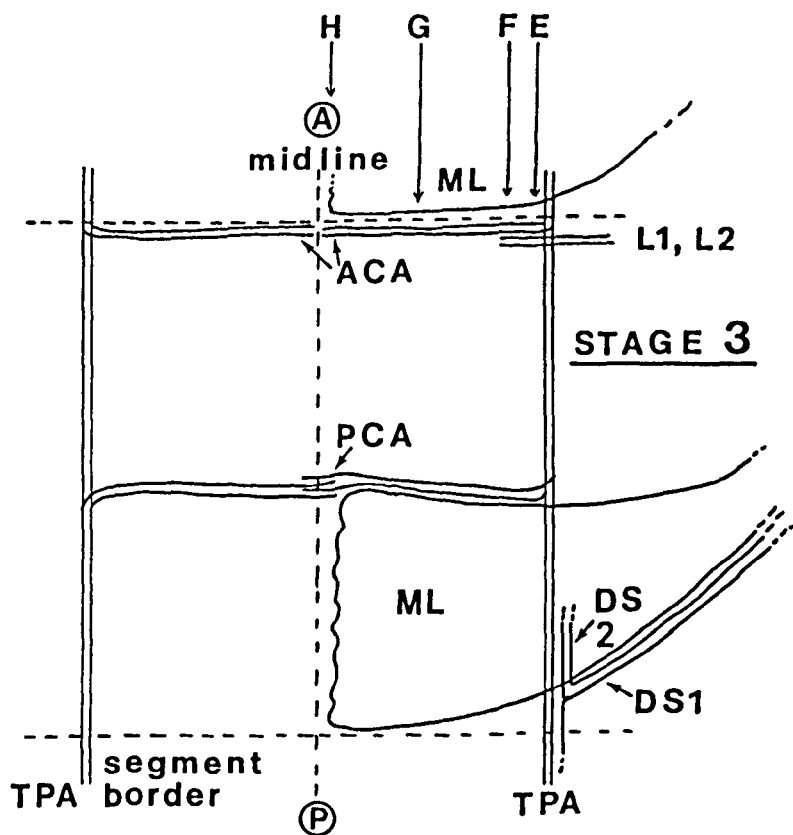


FIGURE 6.13

Longitudinal sections through a stage 3 segment from a level just medial to the TP axons (a level equivalent to E on fig. 6.12).

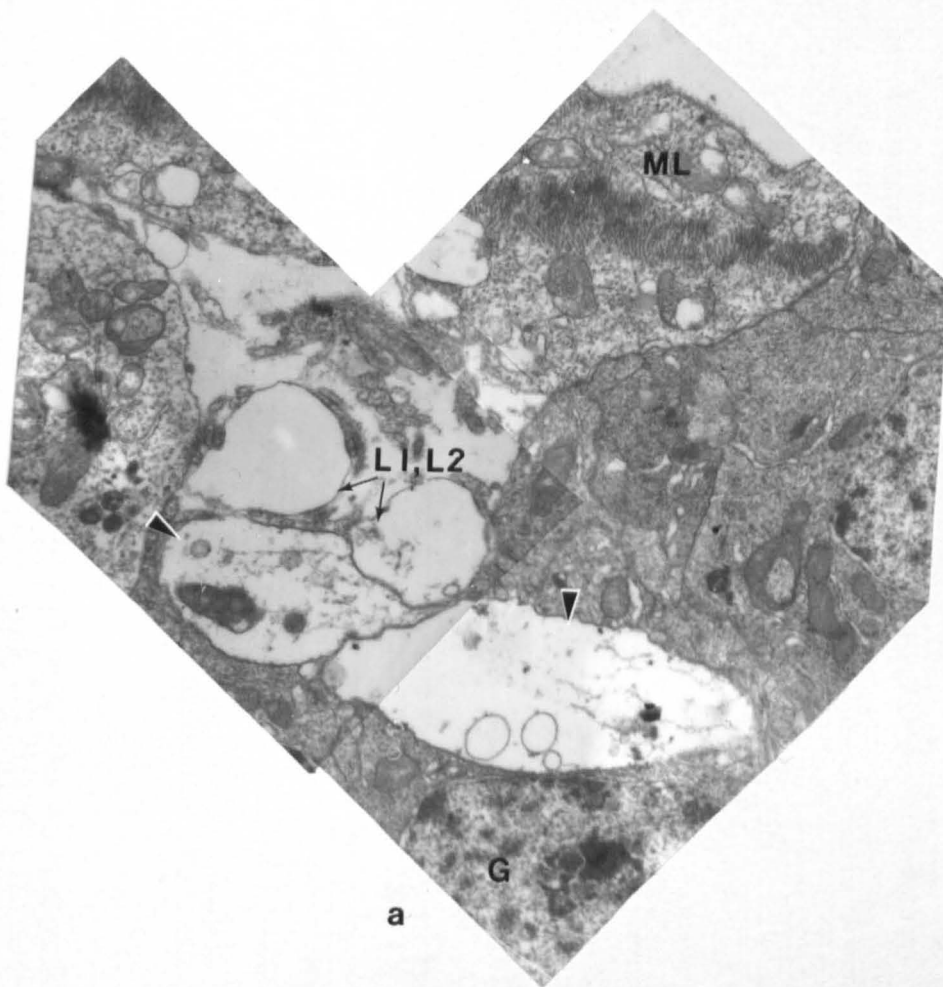
- (a) The branches of the TP axons (arrowheads) which pioneer the anterior commissure can be seen growing out at a level in the segment where there is an edge of a dorsoventral muscle insertion. These axons are being followed by two axons (L1, L2) derived from unidentified, laterally positioned neurons.
- (b) The branches of the TP axons (arrowheads) which pioneer the posterior commissure can be seen, they also grow out at a level in the segment where there is an edge of a dorsoventral muscle insertion.

ML, muscle; E, epidermal cell; G, ganglion cell/
ganglion mother cell.

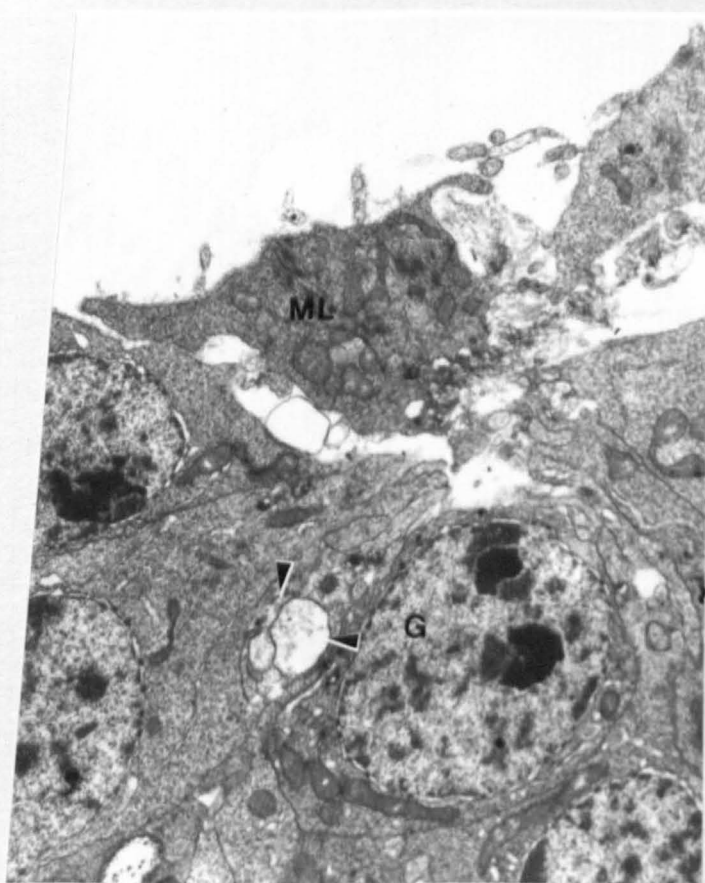
Scale bar

1 μ m (a)

1 μ m (b)



a



b

FIGURE 6.14

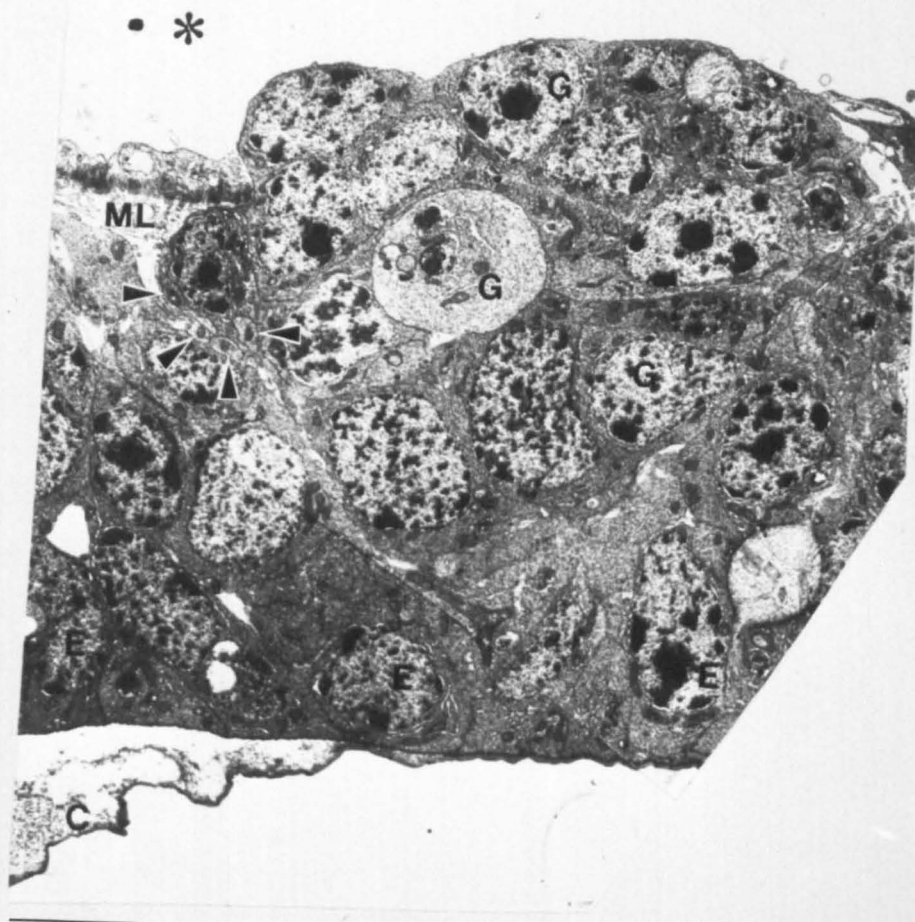
- (a) Longitudinal section through the anterior of a stage 3 segment from a level just medial to the point at which the axon branches of the TP axons grow out to pioneer the anterior and posterior commissures (equivalent to level F on fig. 6.12). The four axons (arrowheads) in the anterior commissure are shown, they are smaller and are filled with dense axoplasm and mitochondria, (seen in more detail in (b)), in contrast to their appearance at the point of branching (fig. 6.13).

ML, muscle; E, epidermal cell; G, ganglion/ganglion mother cell; C, cuticle; *, haemocoel.

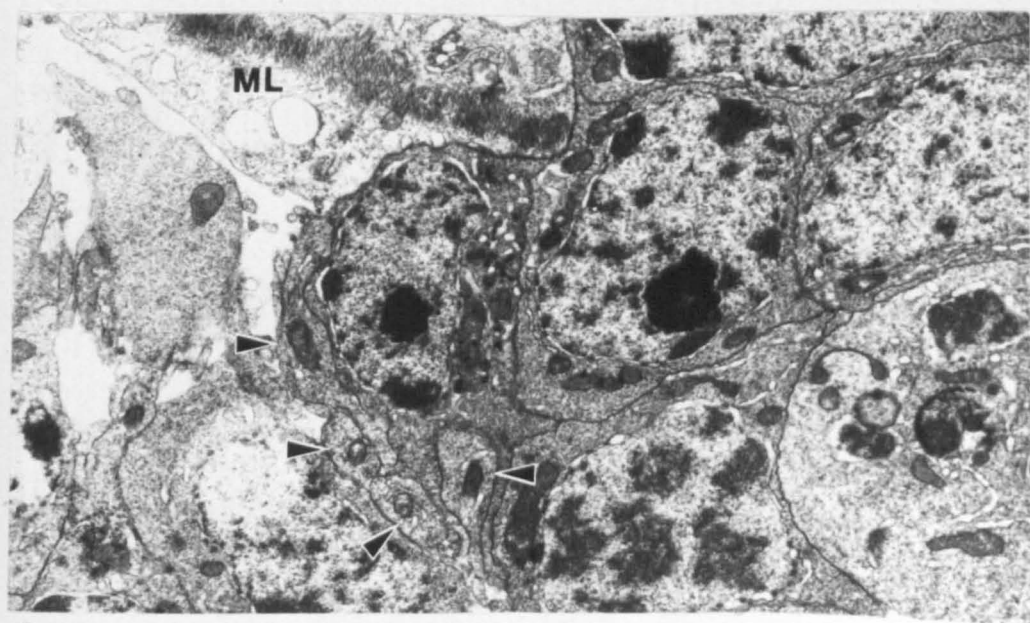
Scale bar

5 μm (a)

1 μm (b)



a



b

FIGURE 6.15

Longitudinal section through a stage 3 thoracic segment from a level equivalent to G in fig. 6.12. There are two axons (arrowheads) in the anterior (ACA) and the posterior (PCA) commissure pathways. There are intercellular spaces and vesicles (V) in the regions where the dorsoventral muscle (ML) is inserted. The axons are always adjacent to or immediately below the edge of a muscle insertion.

ML, muscle; E, epidermal cell; G, ganglion/ganglion mother cell; *, haemocoel; C, cuticle.

Scale bar

5 μ m

ACA

PCA

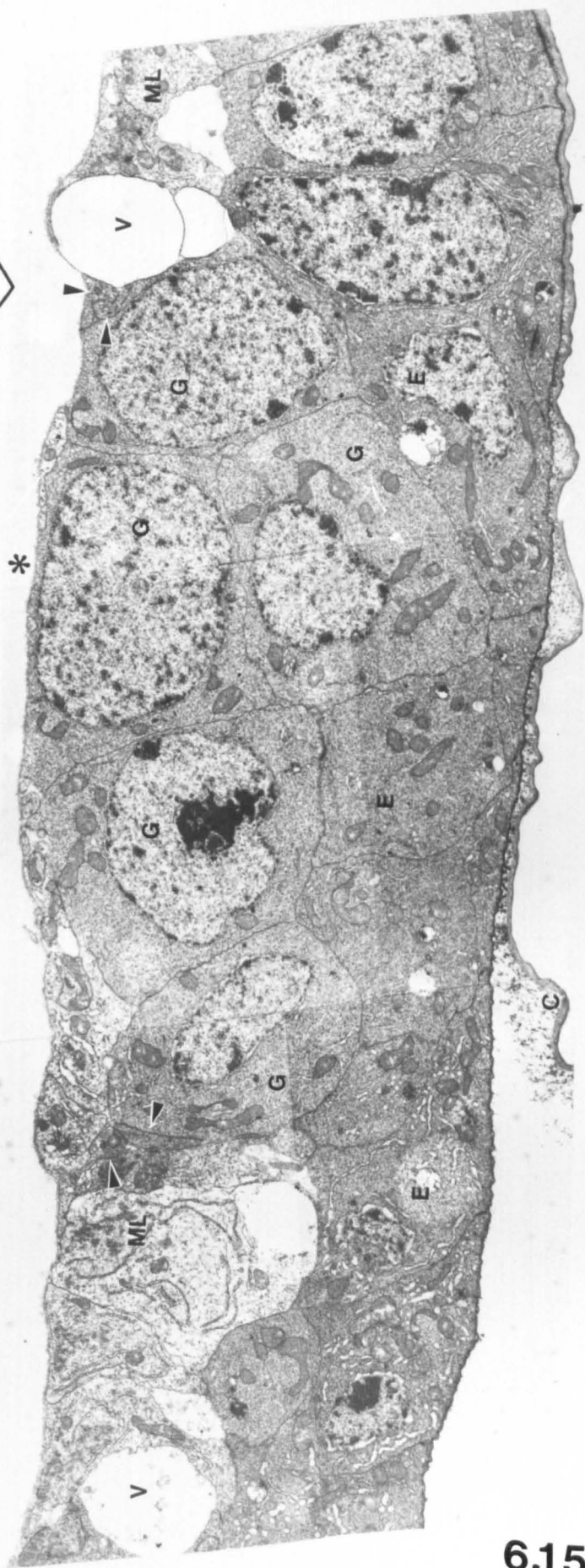


FIGURE 6.16

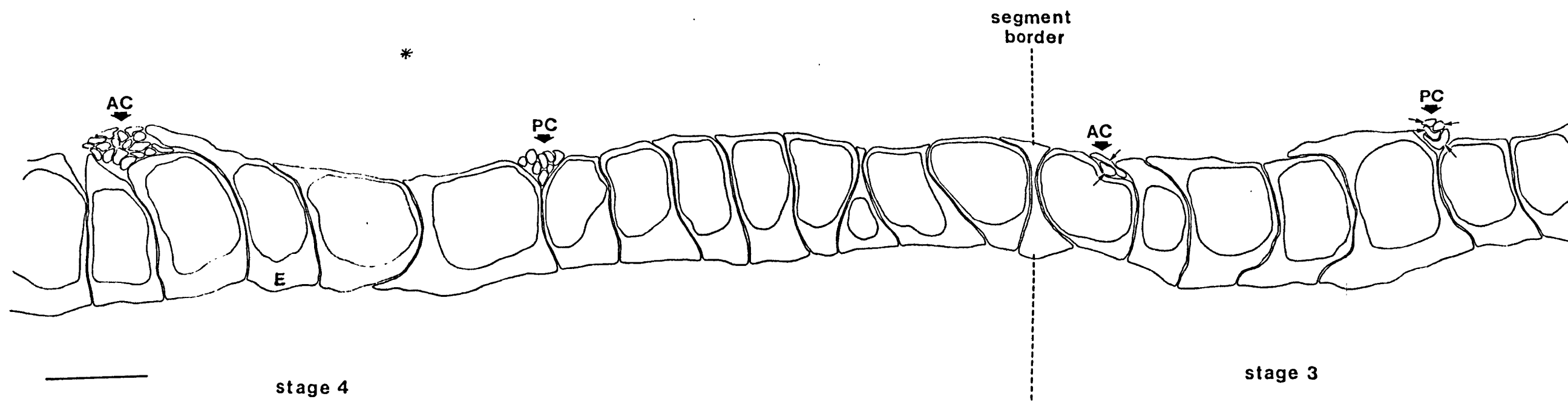
Drawing of a longitudinal section through a stage 3 and an adjoining stage 4 thoracic segment near the midline, at a level equivalent to H on fig. 6.12. There are four axons (PC) in the stage 3 posterior commissure where the two from either side have overlapped. There are two axons (AC) in the anterior commissure. In the stage 4 segment there are many axons in each commissure pathway.

E, epidermal cell;

*, haemocoel.

Scale bar

5 μ m



6.16

FIGURE 6.17

Diagrams of the profiles of the axons (solid shading) in the anterior and posterior commissure positions, derived from longitudinal sections through a stage 3 thoracic segment close to the midline (a) and progressively more laterally (b-e) between levels equivalent to G and H on fig. 6.12. There are four axons in the posterior commissure in (a) to (d), where the two axons from either side have overlapped. There are two axons in the anterior commissure at these same levels, which have a relatively flattened appearance indicative of growth cones. At level (e) both commissure pathways contain only two axons.

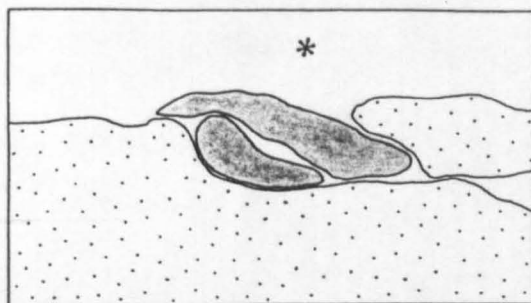
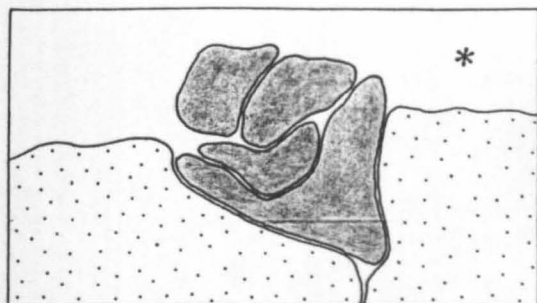
stippled area, epidermal cell; *, haemocoel; banded area, Vacuolated cell process; unshaded regions, cell processes.

Scale bar

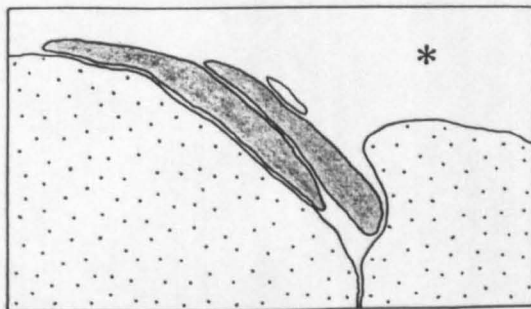
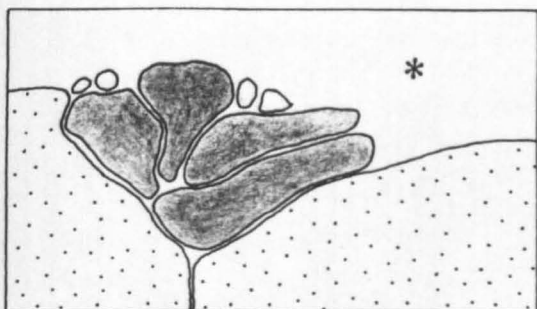
1 μm

posterior commissure

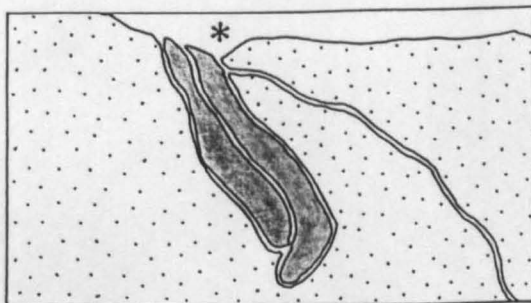
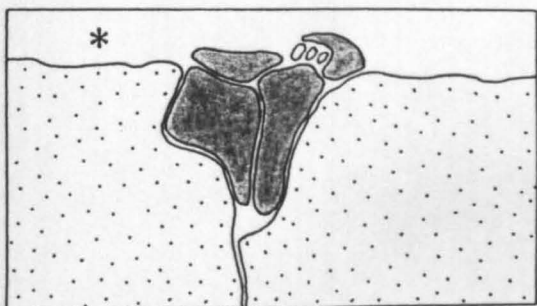
anterior commissure



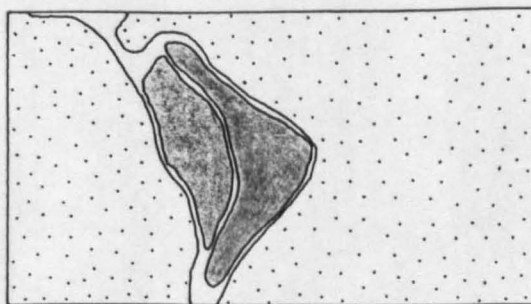
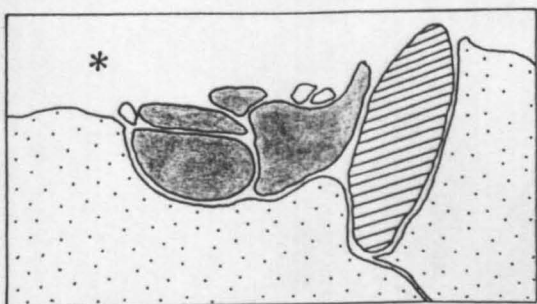
a



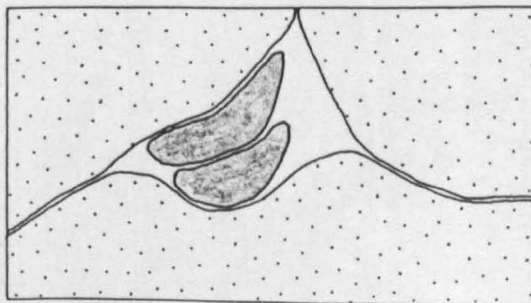
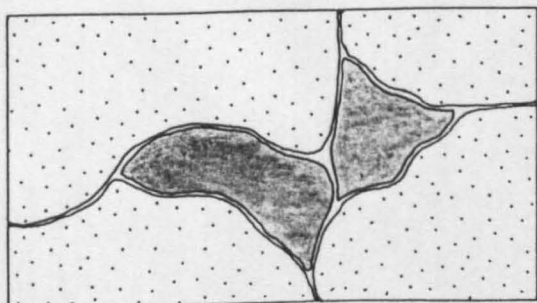
b



c



d

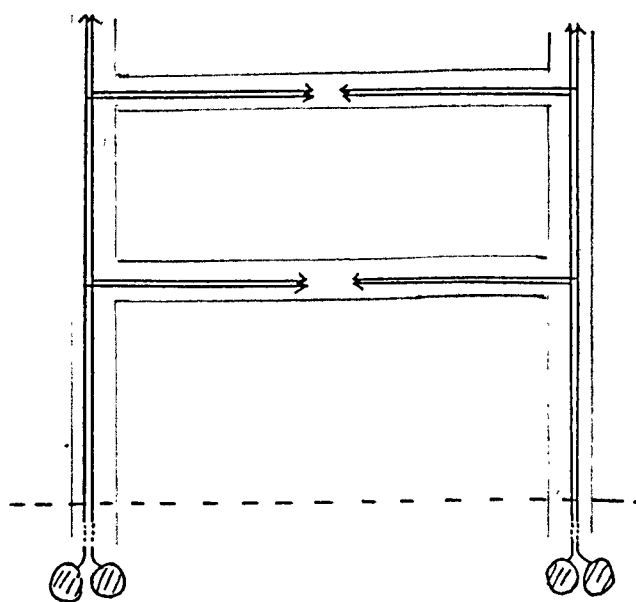
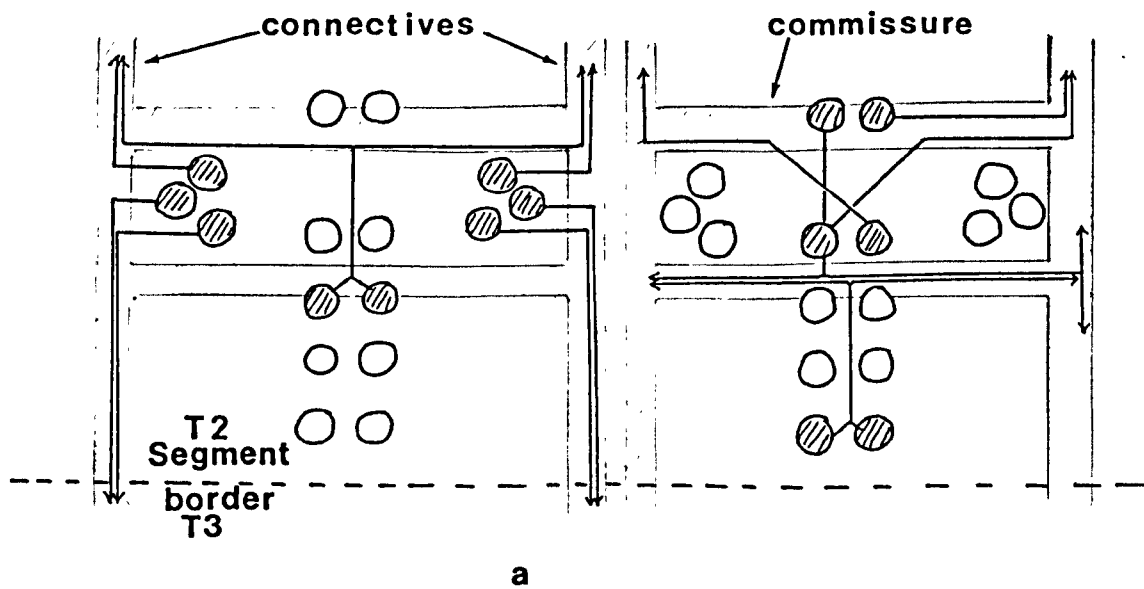


e

FIGURE 6.18

Diagrammatic representations of the early formation of the first C.N.S. pathways in the thorax of (a) the grasshopper and (b) Artemia.

There are many more neurons involved in the formation of the basic framework of pathways in the grasshopper thoracic segment than Artemia.



6.18

b

FIGURE 7.1

Scanning electron micrograph of the dorsal surface of a 3rd instar larva showing the appearance and early development of the dorsal setae (arrowed). They are the first external segmental structures to develop on the thoracic segment. The early development of the exites can be seen, a crease (arrowhead) between the proximal exite (PE) and the bract (BR) first appears in stage 4.

Scale bar

100 μm

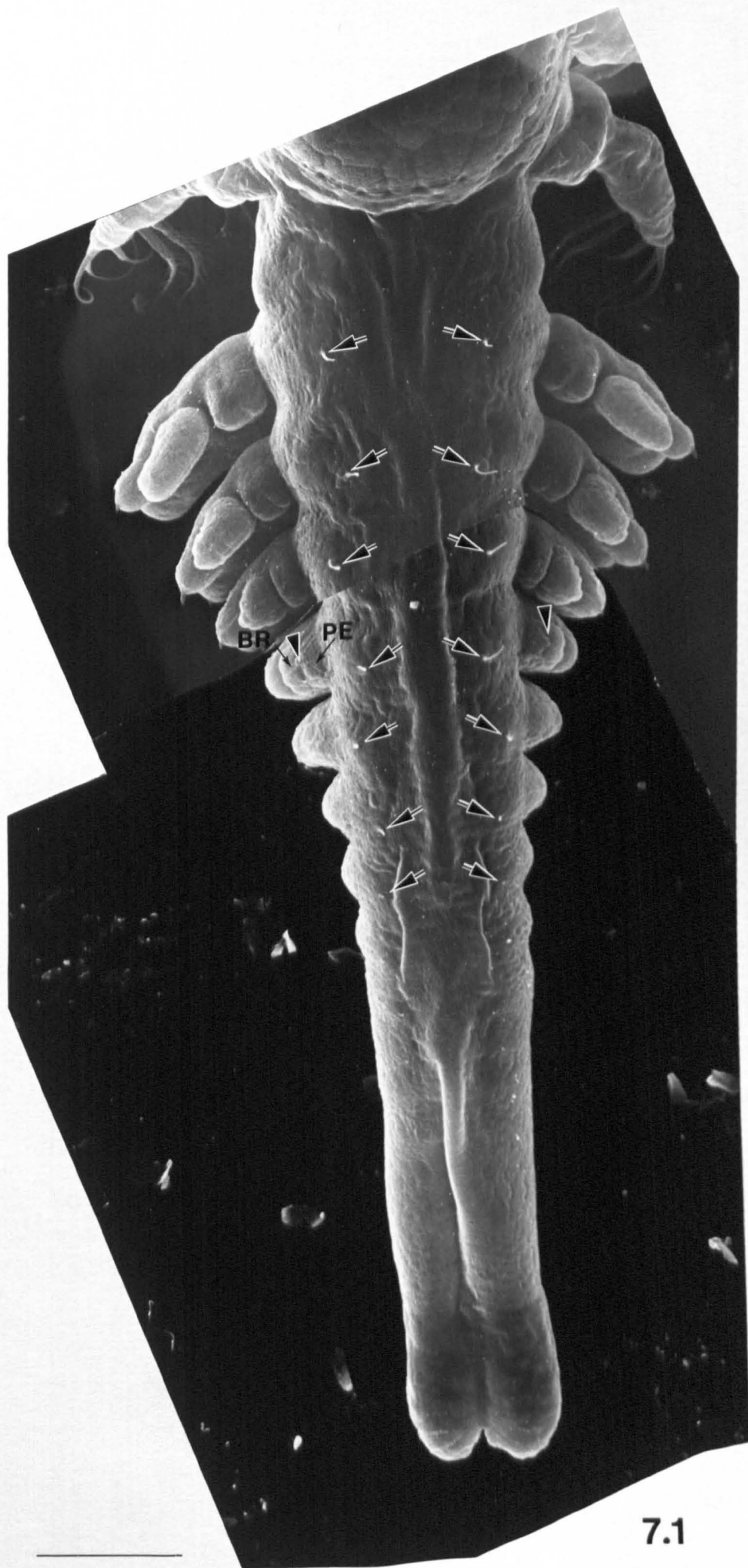


FIGURE 7.2

Scanning electron micrograph of a 7th instar larva showing the outer lateral surfaces of the thoracic segments from stage 1 to stage 7 of development. At stage 1, the segment is delineated by a circumferential groove in the epidermis and cuticle (arrowheads). The development of the first crease in the phyllopod bud during stage 3 is visible (black arrow). The first lobe of the phyllopod: the exopodite (EO) is visible in stage 4. In stage 5 the bract (BR) and proximal exite (PE) are distinct, rounded lobes, in stage 6 the bract begins to expand distally while the proximal exite remains shorter.

Scale bar

50 μm

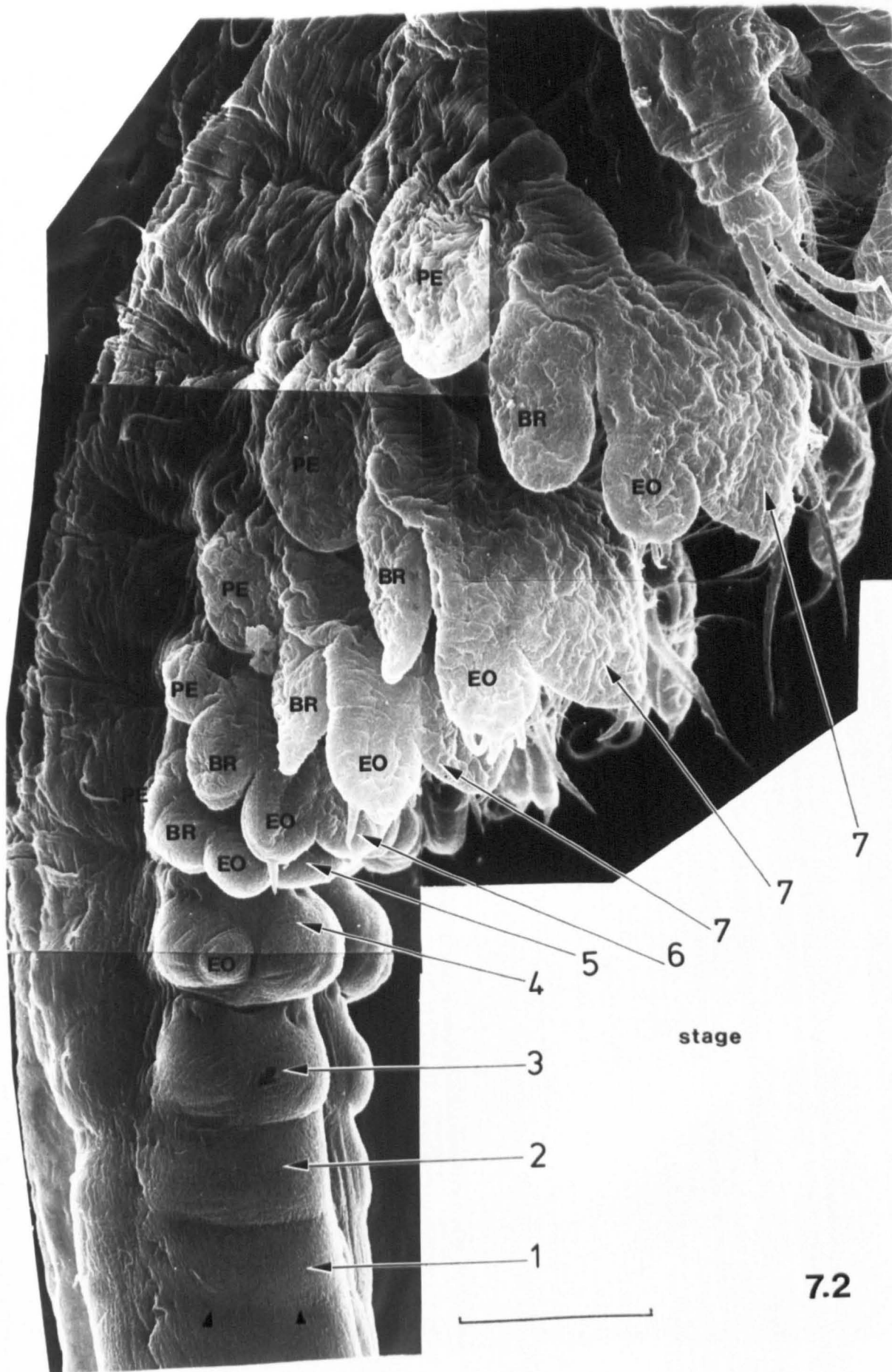


FIGURE 7.3

Diagrammatic representations of posterior views of the development of the phyllopods of Artemia in stages 1 to 7 (illustrated with micrographs in later figures). The phyllopod develops from a slight bulge (p) in stages 1 and 2, into a flattened, leaf-like appendage composed of lobes in stages 3-7, some of which bear setae. Setae are labelled by numbers only.

During stage 3 the first crease appears in the surface of the phyllopod bud, between the regions that will become the exopodite (EO) and endopodite (EDP). In stage 4 the exopodite emerges as the first discrete phyllopod lobe and bears the first seta (1). In stage 4 the delineation of the endites: endite 1 (E1), endite 2 (E2), endite 3 (E3) and the proximal endite (PEN) begins. In stage 5 all the lobes of the phyllopod are clear and distinct and the endites begin to show a division into an anterior and posterior edge (indicated by dashed line).

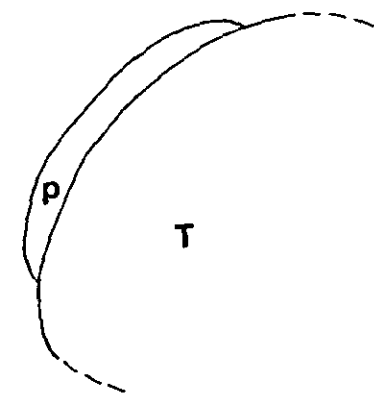
FIGURE 7.3 (contd.)

During this stage there is a gradual increase in the number of setae on both edges of the endites. Both early and late stage 5 phyllopods are shown. During stage 6 each lobe begins to acquire its particular shape. New setae appear on the exopodite, endopodite and endites. The numbers of anterior edge setae do not change after stage 6. The overall shape of the phyllopod in stage 7 is shown but the many setae are not indicated. Section C of the ^{lobes (A,B+C)}3endopodite becomes the widest of the phyllopod lobes.

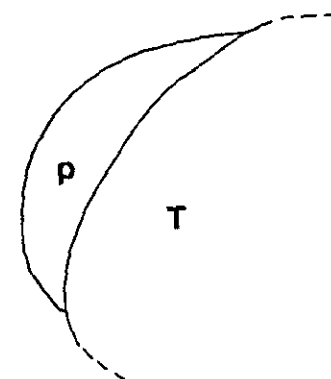
BR, bract; PE, proximal exite.

Scale bar

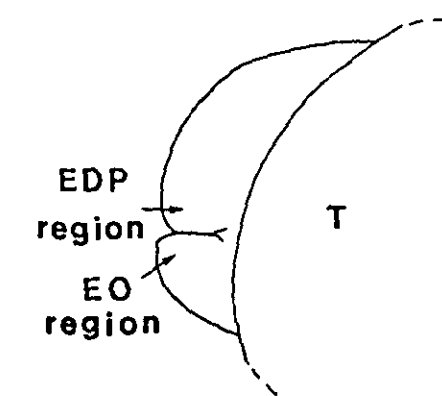
50 μ m



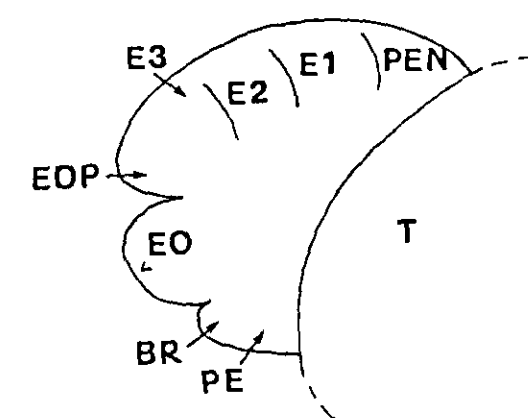
stage 1



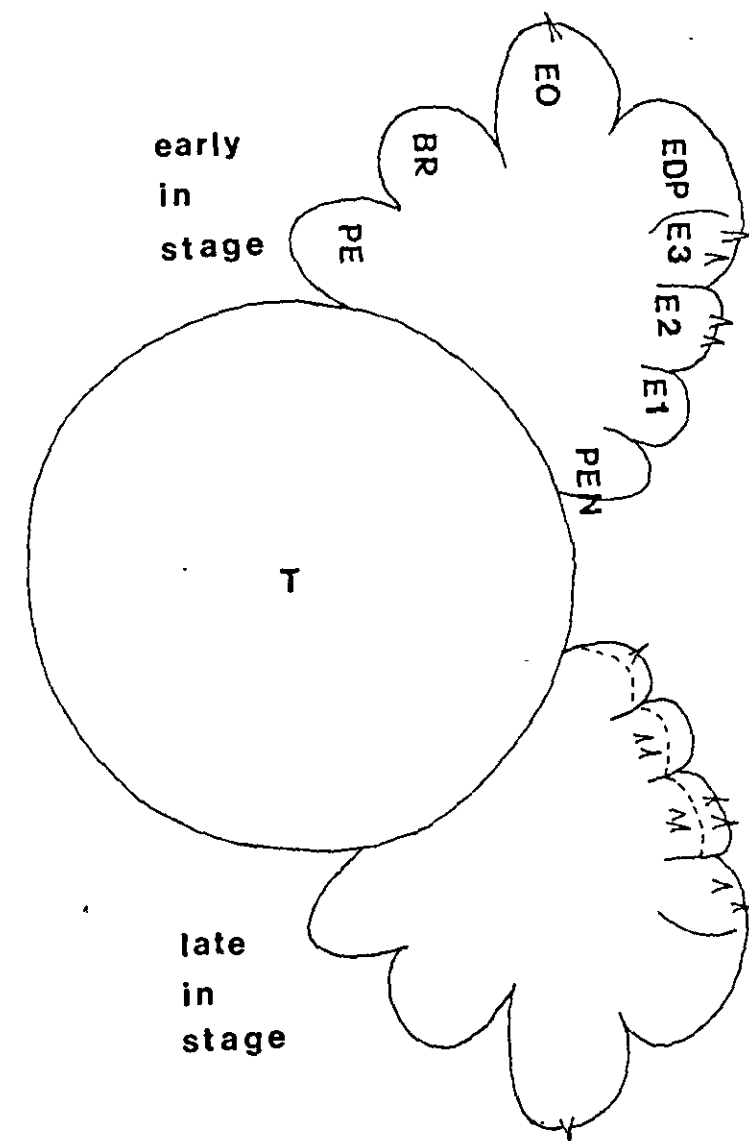
stage 2



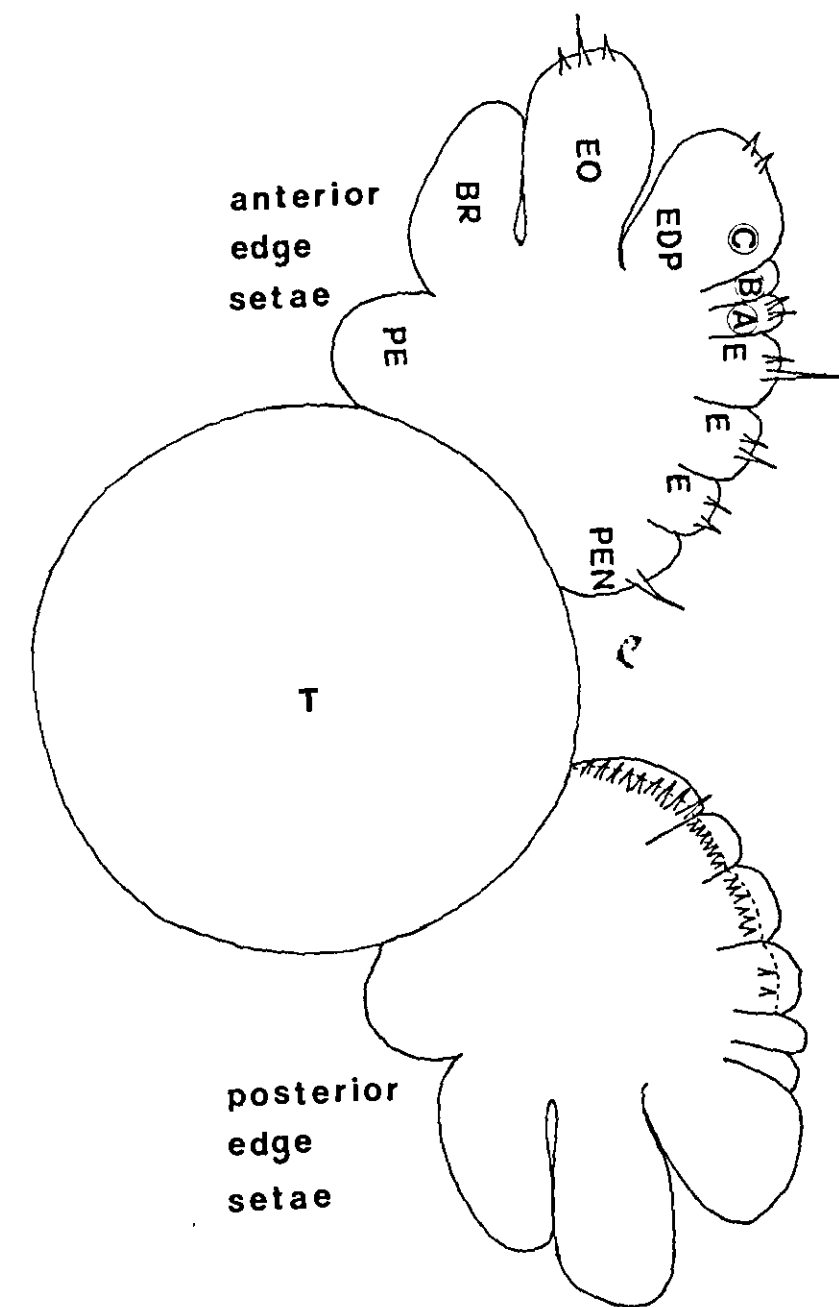
stage 3



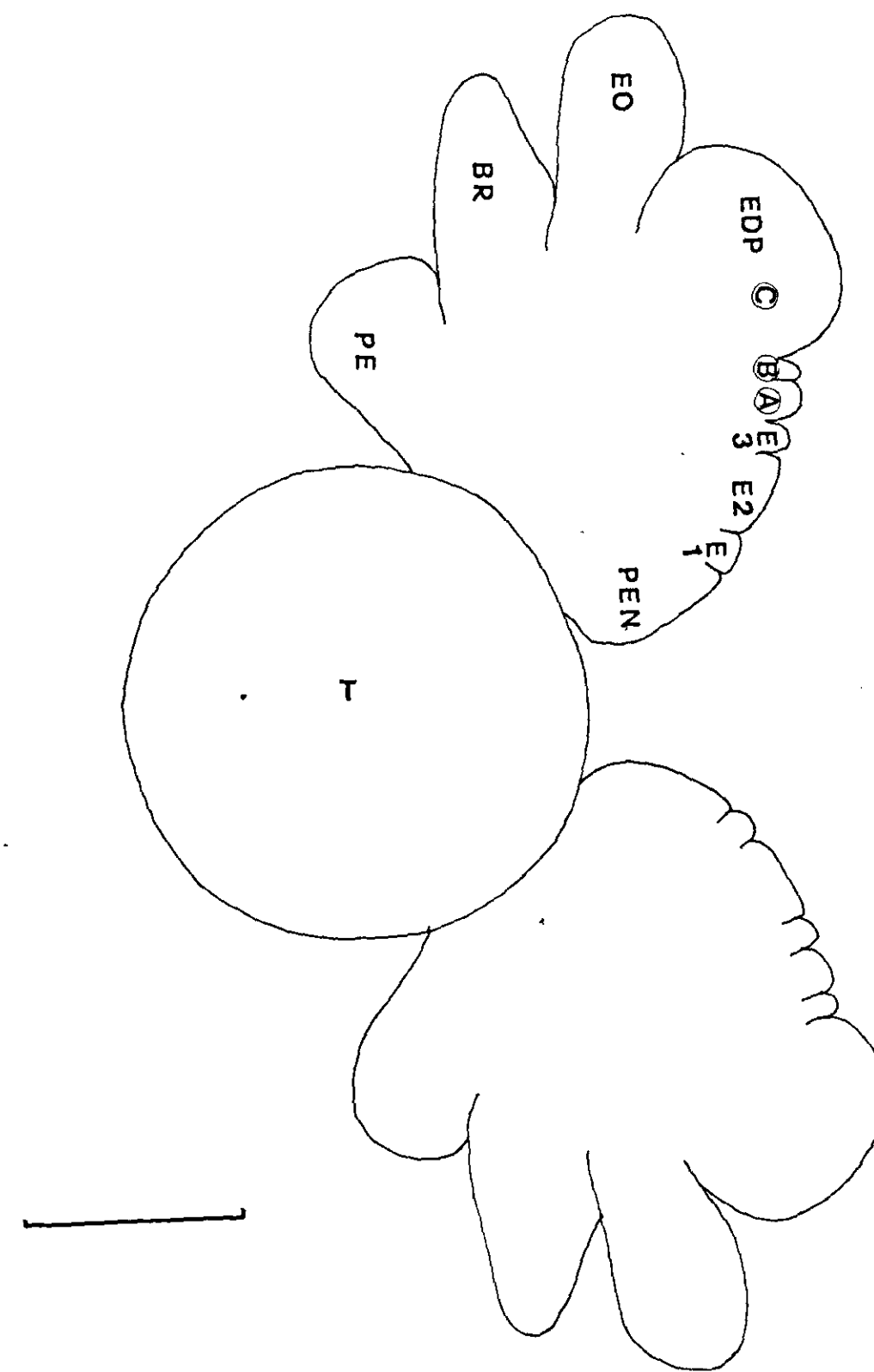
stage 4



stage 5



stage 6



stage 7

FIGURE 7.4

Scanning electron micrograph of the ventral surface of a 7th instar larva showing the developing first seta (arrowed) of the phyllopod on the exopodite (EO) at stage 4 (stage numbers circled) when it first appears. It is also shown at stages 5 and 6. The folded surface (arrowhead) of the bract (BR) on the stage 5 phyllopod is shown. The development of seta 9 on the medial side of the exopodite next to seta 1 in stage 6 is shown. *EDP, endopodite.*

Scale bar

10 μm

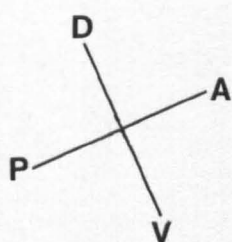
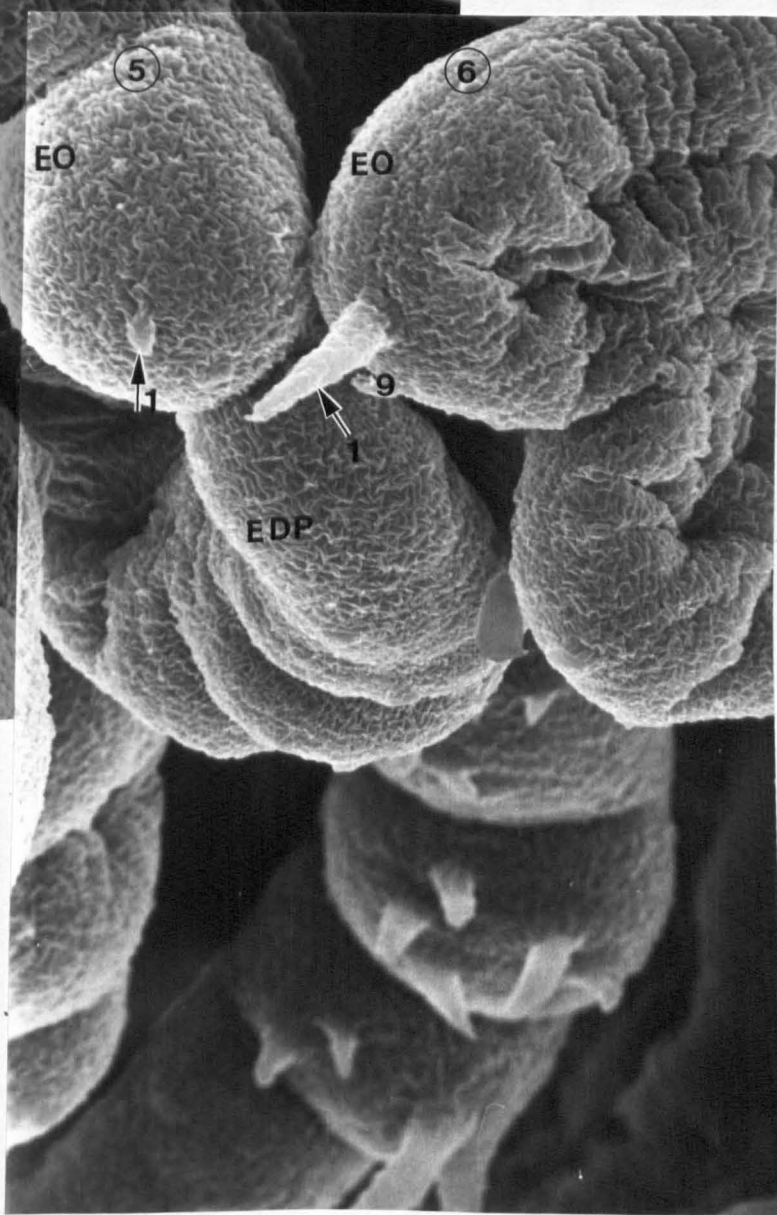
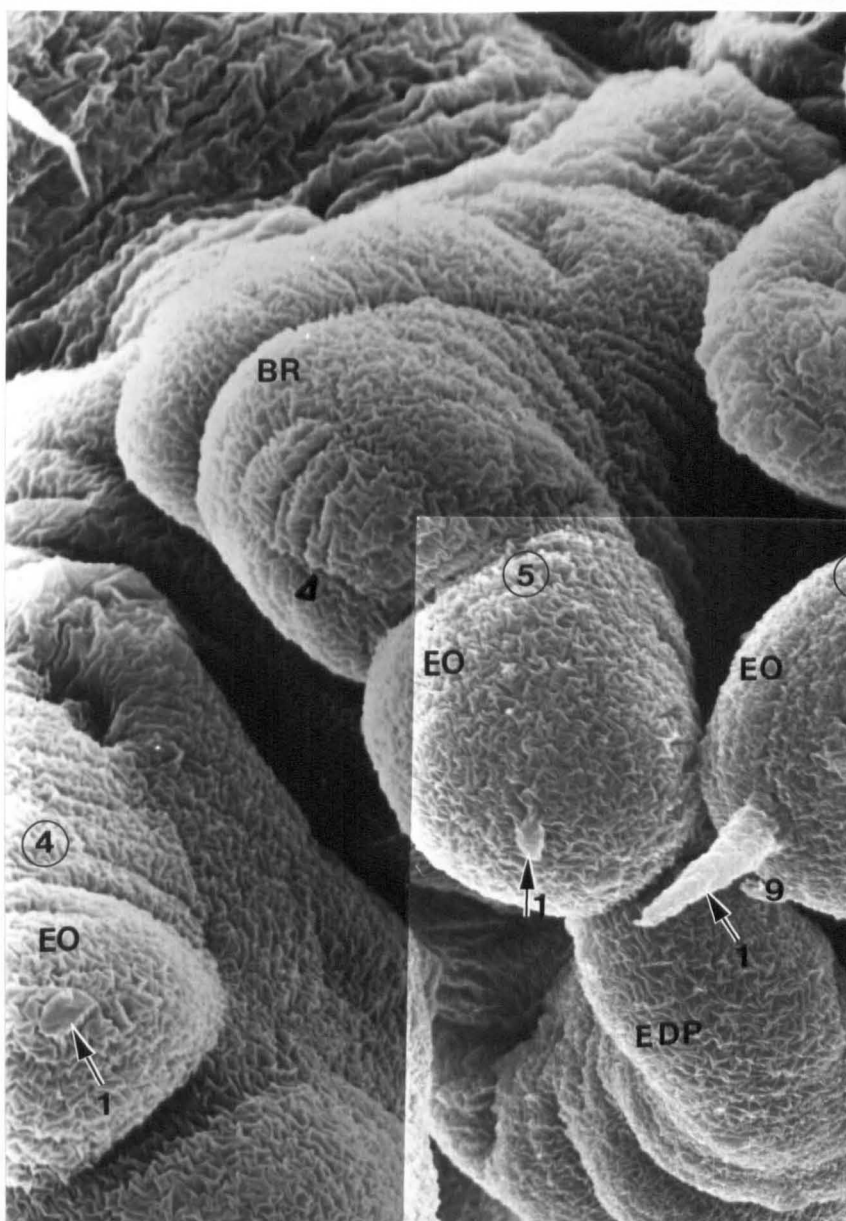


FIGURE 7.5

Scanning electron micrograph of a medial view of the ventral surface of a 7th instar larva showing thoracic segments up to stage 6 on the left hand side of the animal. The gradual subdivision of the endite surface of the phyllopod bud into the different endites (endite 1 (E1), endite 2 (E2), endite 3 (E3), proximal endite (PEN)) during stages 4.5+6 is shown. The last major subdivision to develop is the crease (arrowheads) between endite 3 and the endopodite (EDP), which occurs in stage 5. The ventral midline is indicated by a line, it points posteriorly (P).

EO, exopodite; A, B, C, endopodite regions.

Scale bar

20 μm

stage

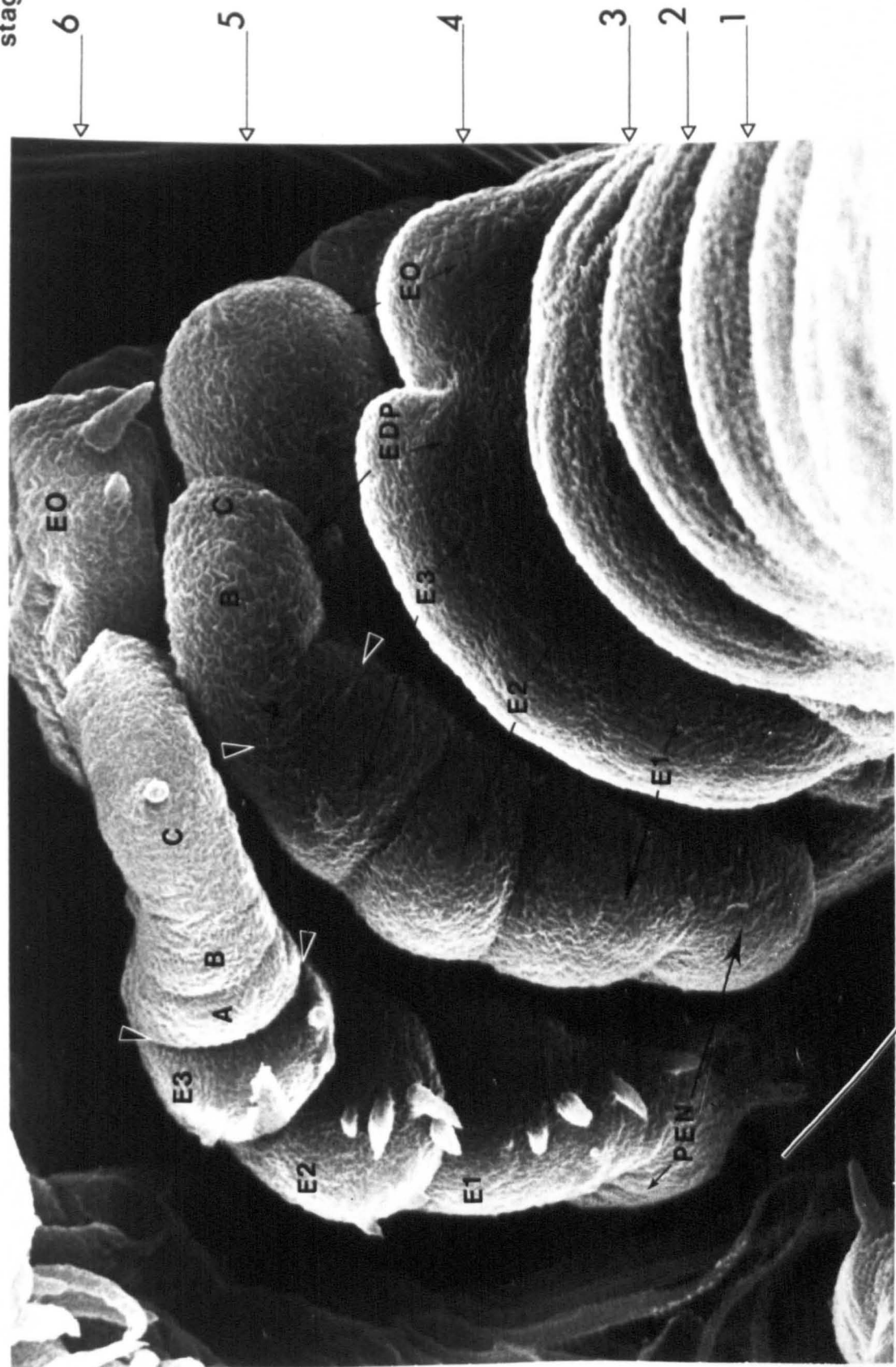


FIGURE 7.6

Scanning electron micrograph of the ventral surface of an early 6th instar larva, showing the development of the endite surface of phyllopods during stages 5 and 6. The dashed line differentiates between the regions designated as the anterior or posterior edges of the endites. Only anterior edge setae are labelled by numbers. The early appearance of setae 2-5 on endites 2 and 3 (E2 and E3) during stage 5 can be seen. The subdivision of the endopodite (EDP) into sections A, B and C during stage 6 is seen, and seta 11 appears on section C at this stage. Also during stage 6, seta 2 on E3 grows relatively much longer than the other anterior edge endite setae. Some posterior edge endite setae develop during stage 6. The ventral midline is indicated by a line, it points posteriorly.

E1, endite 1; EO, exopodite; PEN, proximal endite.

Scale bar

20 μm

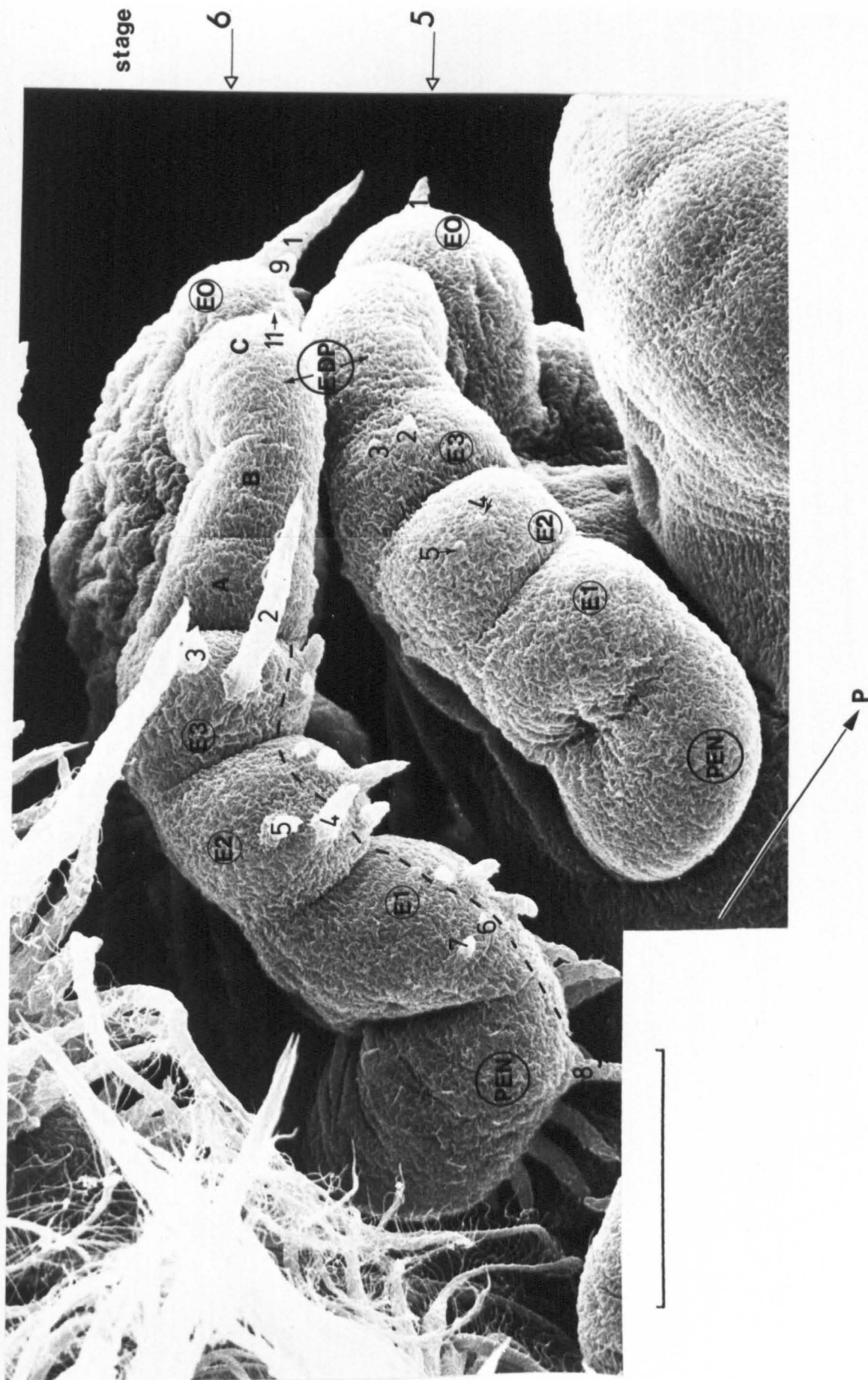


FIGURE 7.7

Scanning electron micrograph of the ventral surface of a 7th instar larva where the left and right halves of the animal bear developing phyllopods which are out of synchrony with the contralateral homologues by nearly a complete stage (the right half shows later stages than the left).

During stage 5 the endites (endite 1 (E1), endite 2 (E2), endite 3 (E3), proximal endite (PEN)) begin to show the organisation of their setae into two rows (indicated by dashed lines where possible): the anterior and posterior edge rows. Only anterior edge setae have been numbered, approximately in order of appearance ie. seta 1 was the first seta to appear, and setae 2-5 all appear in stage 5 but in an unknown order. Posterior edge setae begin to appear on the endites in late stage 5 (right hand side) and are well-developed in stage 6.

FIGURE 7.7 (continued)

During stage 6, two new setae appear either side of S1 on the exopodite (EO), these are S9 and S10. Three further setae (11, 12 and 13) also develop during stage 6 on sections C (11) and A (12 and 13) of the maturing endopodite (EDP) (left side of micrograph).

In stage 7, section C of the endopodite expands relative to sections B and A. Further setae are added to the exopodite and endopodite during this stage. The ventral midline is indicated by a line which points anteriorly (A).

Scale bar

20 μm

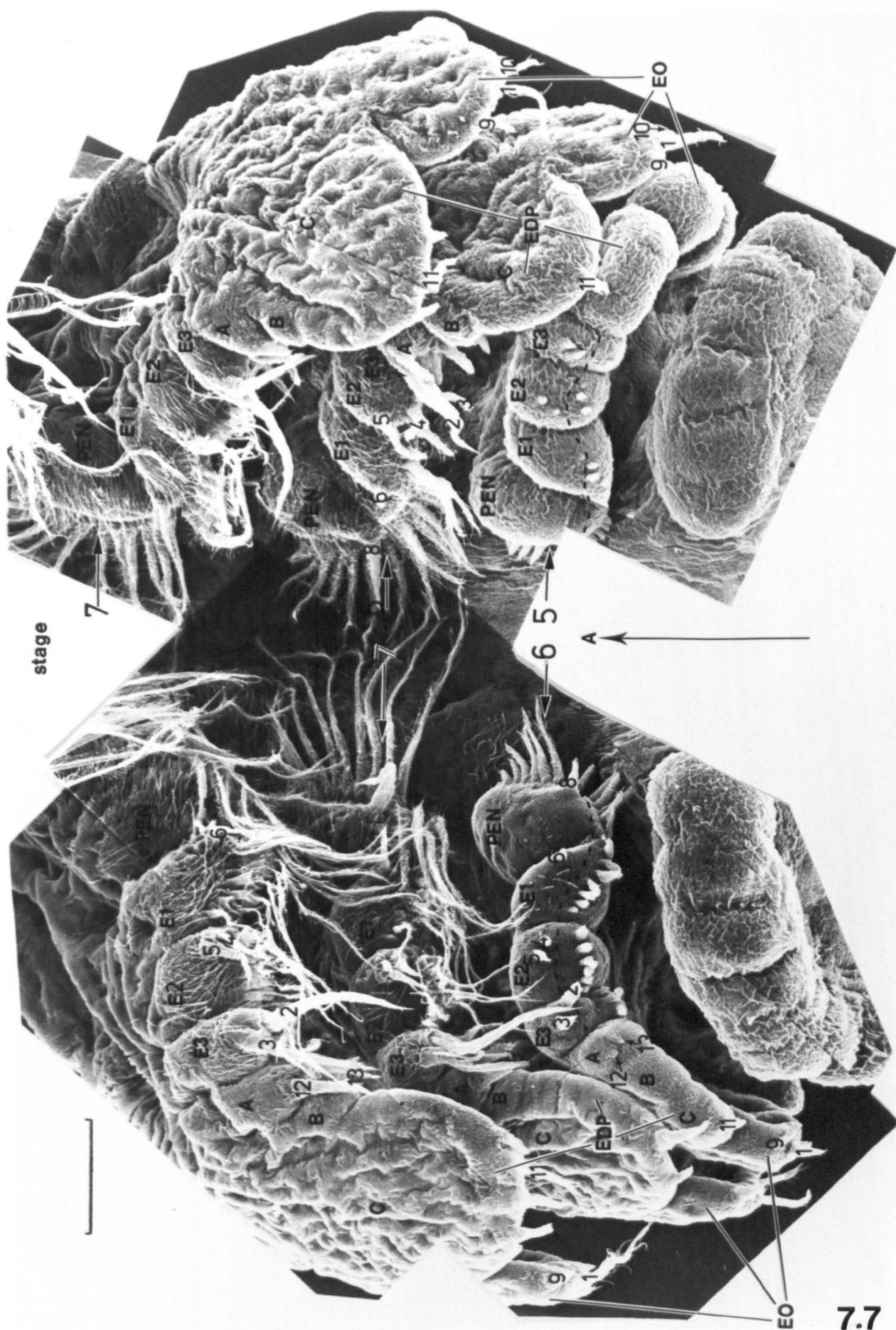


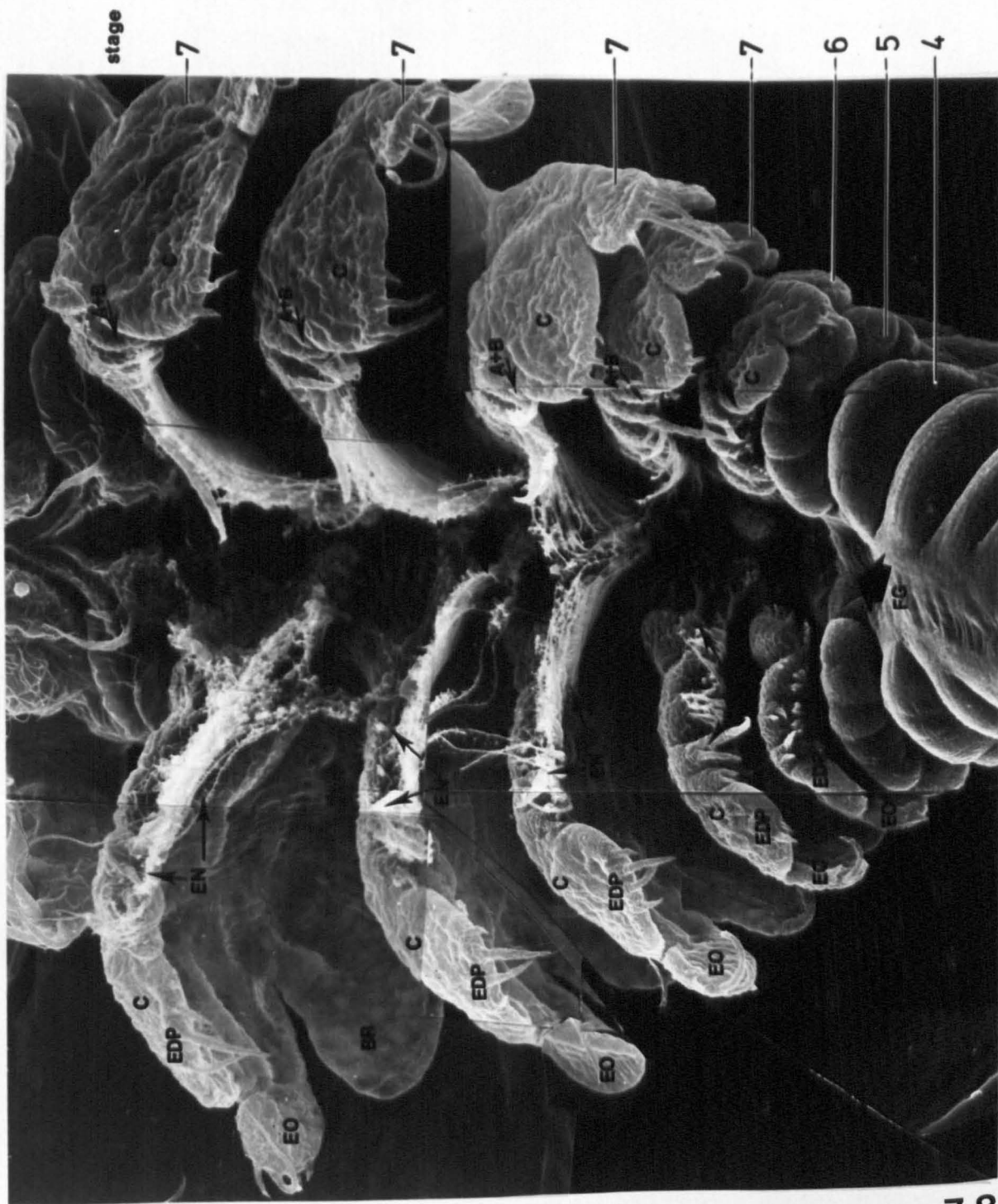
FIGURE 7.8

Scanning electron micrograph of the ventral surface of a 7th instar larva. There are pairs of phyllopods at stages 4, 5 and 6, and four pairs of phyllopods at stage 7. At stage 7 there are four setae on section C of the endopodite (EDP), and this section expands greatly relative to sections A and B. The endite (EN) setae become long enough to meet those of the opposing limb along the ventral midline. A food groove (FG) is formed between the left and right rows of endite setae. Food particles can be seen caught on these setae.

EO, exopodite; A, anterior; P, posterior.

Scale bar

50 μm



A ← → P

FIGURE 7.9

Scanning electron micrograph of the ventral surface of a 9th instar larva about to undergo metamorphosis. There are seven pairs of phyllopods at stage 7 of development (arrowheads). The unusually long S2 on endite 1 is noticeable on the phyllopods (black arrows). The antennae of the larva point laterally at this stage.

Scale bar

250 μm



FIGURE 7.10

- (a) Scanning electron micrograph of the ventral surface of an 8th instar larva showing the development of the endite setae in stage 6 and progressively more mature stage 7 phyllopods.
- (b) A detail from (a). The setae on the posterior edges of the endites merge together to form a continuous row for filter-feeding (curly black arrows). The proximal endite becomes the widest of the endites. The stage number of the phyllopod is circled.
- PE, proximal endite, E1,2,3, endites.*

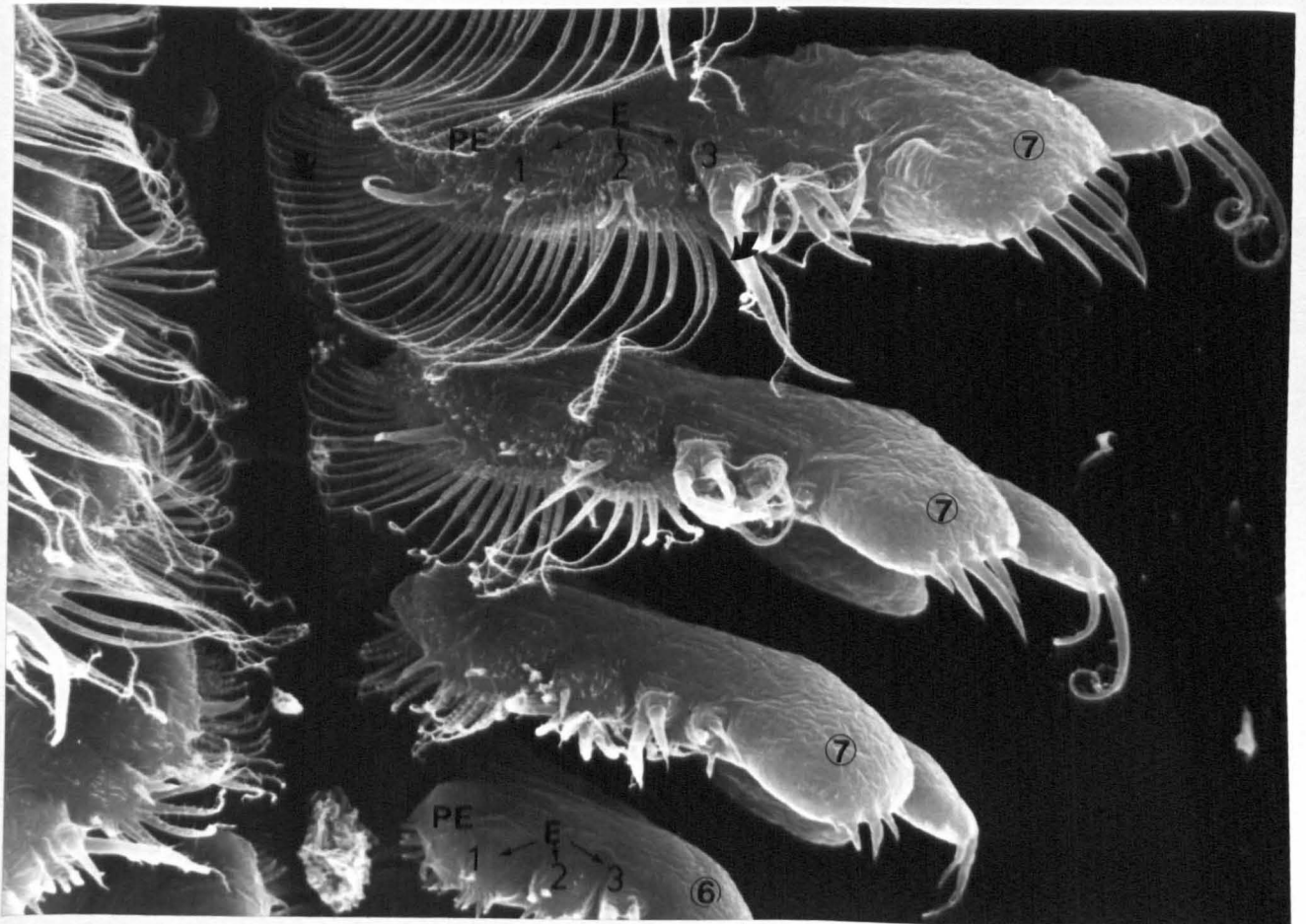
Scale bar

250 μm (a)

50 μm (b)



a



b

FIGURE 7.11

Scanning electron micrograph of the ventral surface of a post-metamorphosis, 10th instar larva. The endite surfaces of the phyllopods lie almost in the dorso-ventral plane and face their contralateral homologues across the ventral midline. A food groove (FG) is created along the ventral midline by this orientation of the phyllopods.

Scale bar

250 μm

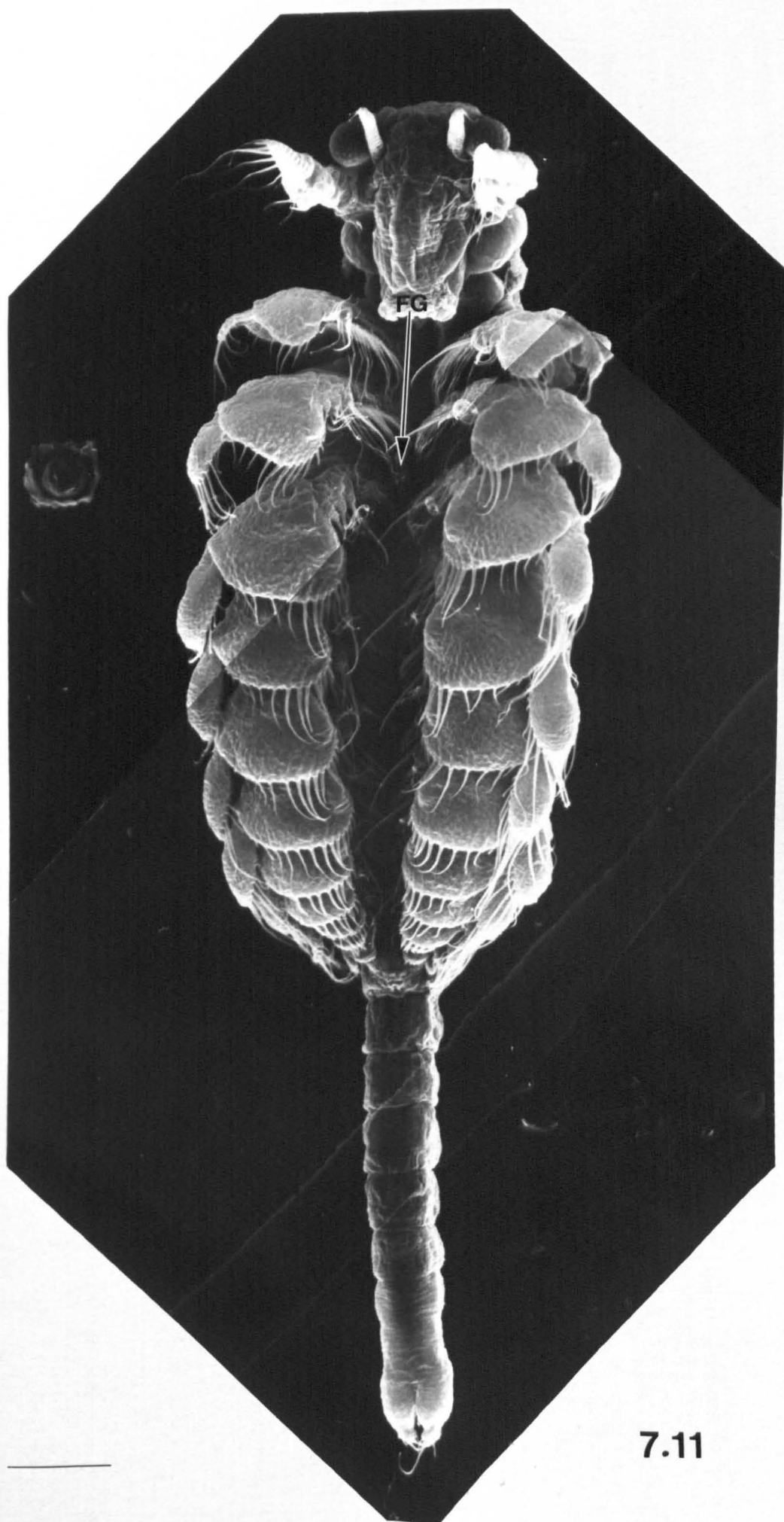
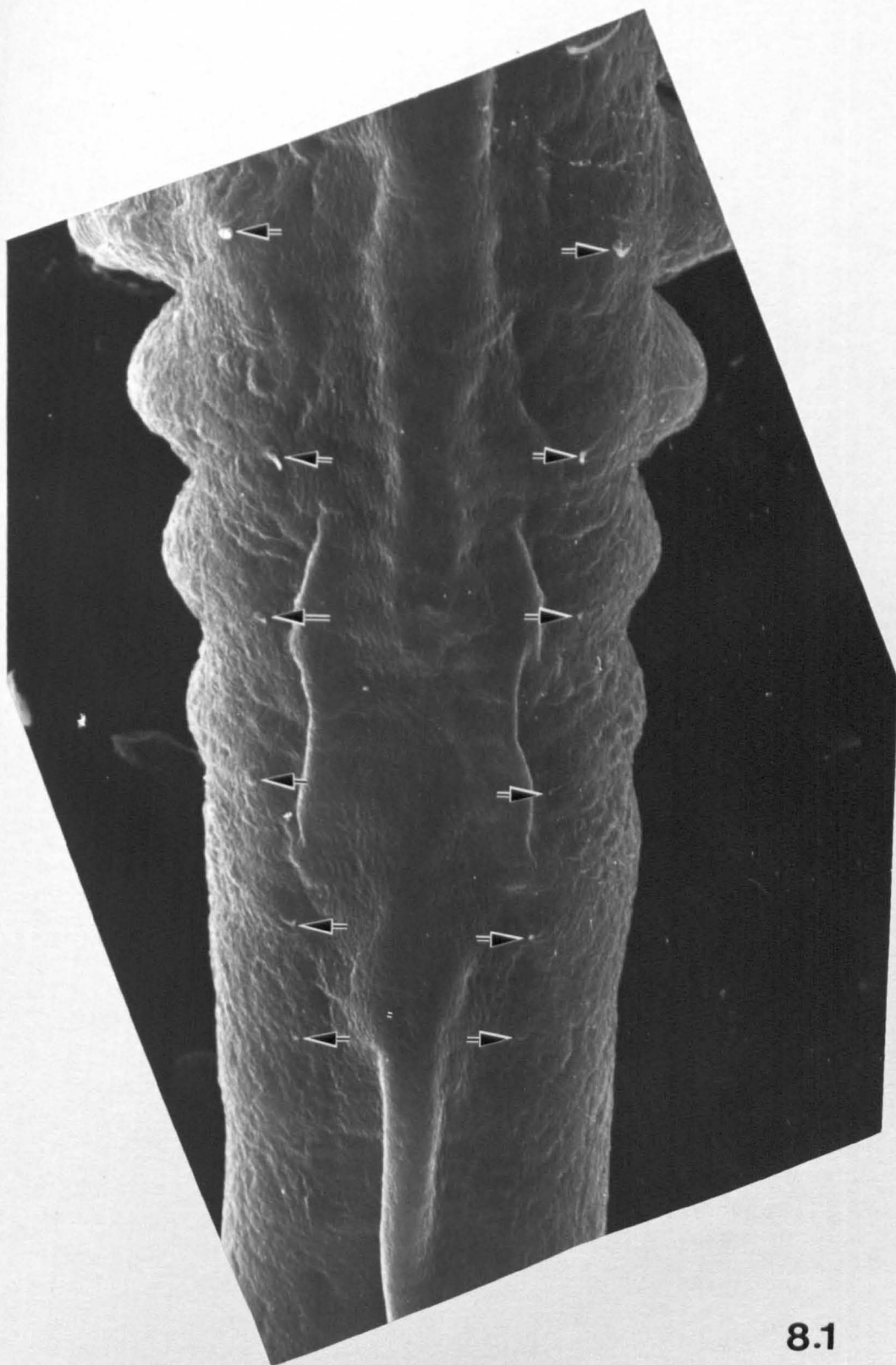


FIGURE 8.1

Scanning electron micrograph of the dorsal surface of the thorax of a 3rd instar Artemia larva. The early development of the dorsal setae can be seen (arrowed). They first appear (as slight cuticular protrusions) during pre-stage 1 of segment development. They grow in size as the thoracic segment progressively develops through the subsequent stages.

Scale bar

50 μm



8.1

FIGURE 8.2

Scanning electron micrograph of the dorsal surface of the thorax of a 3rd instar Artemia larva. The development of the dorsal seta during stages 1 to 6 is shown. Setae (arrowheads) are located towards the posterior of the segment and point posteriorly, except for the stage 5 seta which has been bent anteriorly during specimen preparation. The setae gradually increase in length between stages 1 and 6.

Scale bar

20 μm

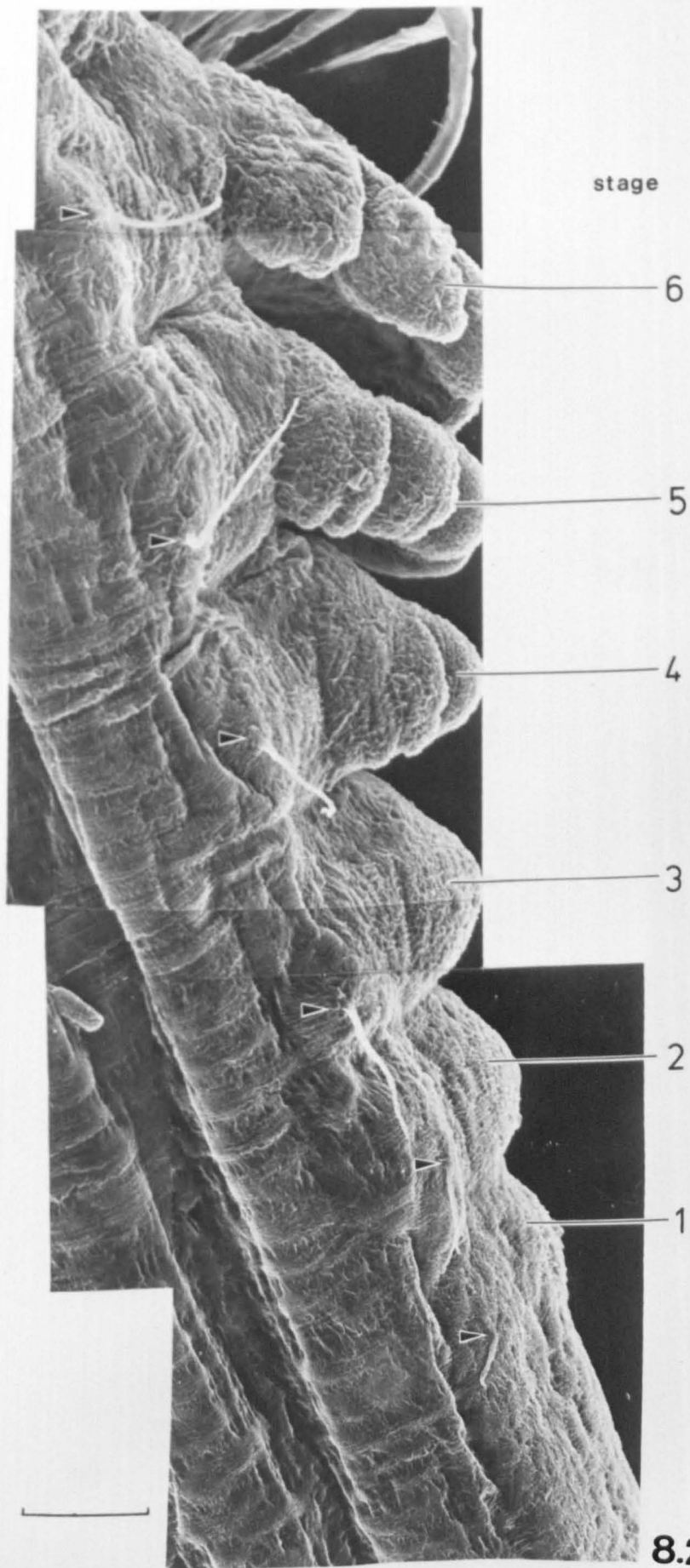


FIGURE 8.3

Diagrammatic representation of neurons N1 and N2 and the associated cells that form the dorsal seta. The socket cells (SK 1 and SK 2), the companion cells (CO 1 and CO 2), the shaft cell (SF) and some epidermal cells (E) are shown partially cut away to reveal the positions of the axons (A) and the neurites (NT) and dendrites (D) of the neurons. The turn of the axons towards the epidermal surface while within socket cell 1, and the emergence of cilium-like dendrites from the axons at this point is shown. The socket and companion cells lie within the epidermis, the shaft cell is situated beneath the socket cells and encloses the neurites from N1 and N2 that emerge from their dorsal sides. The cell bodies of N1 and N2 lie on the inner surface of the epidermis in a more ventral position than the previously mentioned cells. They are located at a level in the antero-posterior axis of the segment which is three epidermal cells width further posterior than the spine. There is a cuticular covering over all epidermal cells and the seta, but this is only

FIGURE 8.3 (continued)

illustrated in part of the diagram.

ML., dorsal longitudinal muscle; C, cuticle; *,
haemocoel.

Scale bar

5 μm

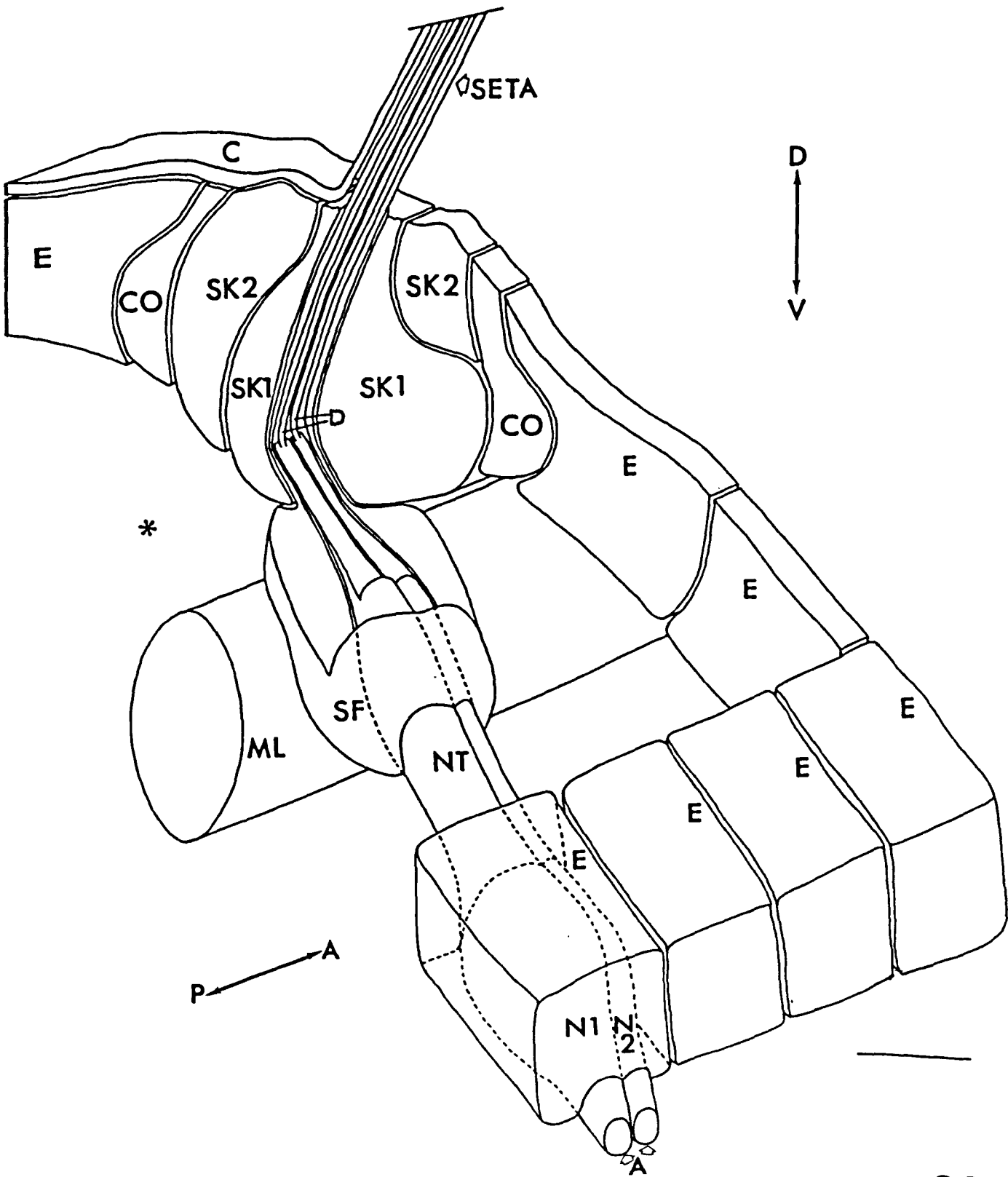


FIGURE 8.4

Diagrammatic representation of a transverse section through the dorsal region of a stage 2 segment showing the locations of the cells that form the seta and associated structures, relative to the rest of the segment. The section is slightly oblique to show the cell bodies of the neurons (which are actually more posterior than the seta). The socket of the seta is formed by specialised epidermal cells of the pericardial haemocoel. The shaft cell body lies within the pericardial haemocoel and the somata of the neurons N1 and N2 lie outside the heart on the epidermis of the perivisceral haemocoel.

SK 1, socket cell 1; SK 2, socket cell 2; CO, companion cell; SF, shaft cell; ML, dorsal longitudinal muscle; E, epidermal cell.

Scale bar

10 μm

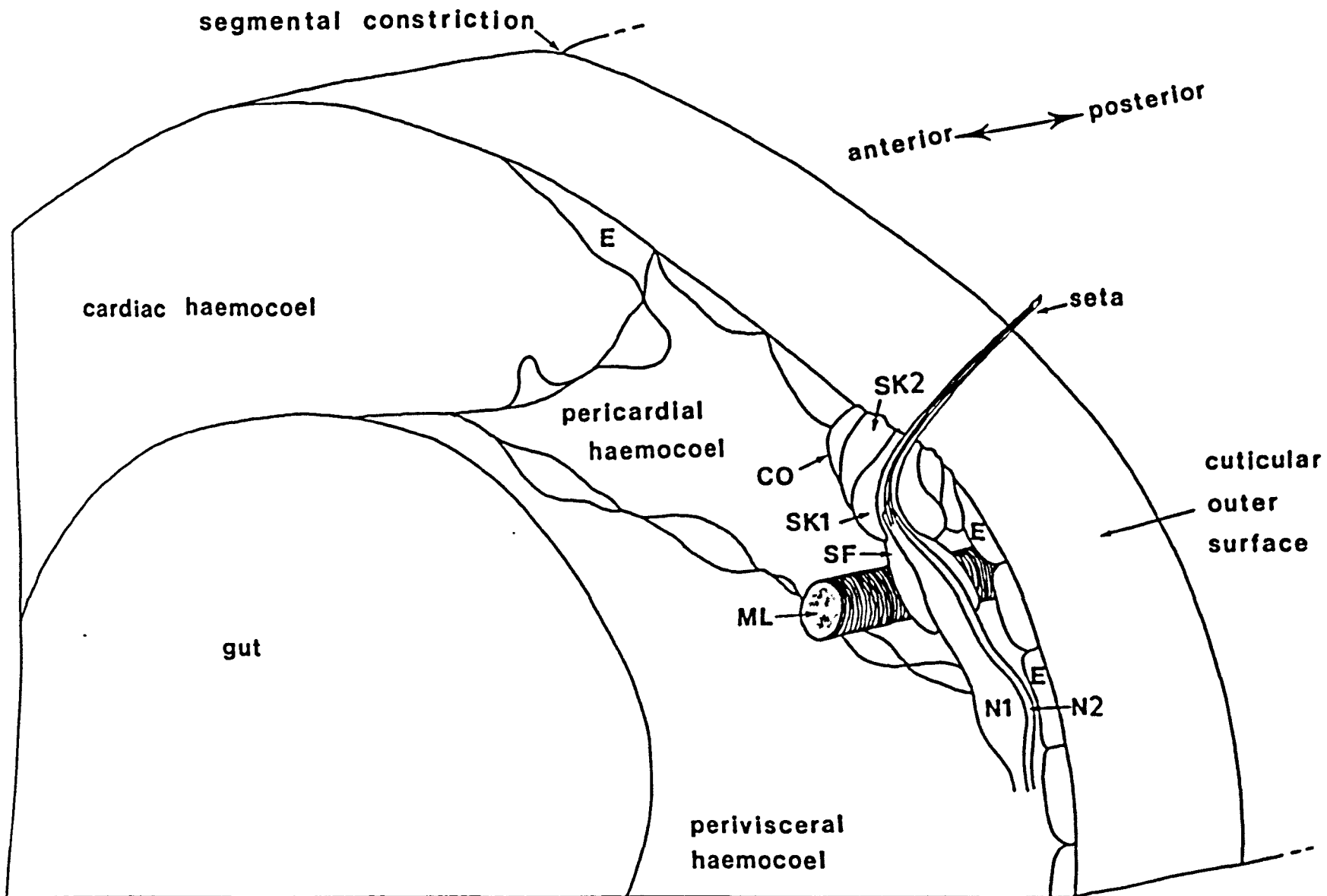


FIGURE 8.5

Transmission electron micrograph of a section through a dorsal seta and associated cells in a plane perpendicular to the axis of the spine. The two equally sized socket cells (SK 1 and 2) are flattened together to enclose the shaft cell process (SF) and cilium-like dendrites (D) of the neurons. The neurites (NT) of N1 and N2 contain many mitochondria (curly black arrows). The extension of the shaft cell which encloses the dendrites contains dark, fibrous material (F). The cell body of the shaft cell cannot be seen in this section.

E, epidermal cell; CO, companion cell; *, haemocoel; C, cuticle.

Scale bar

5 μ m

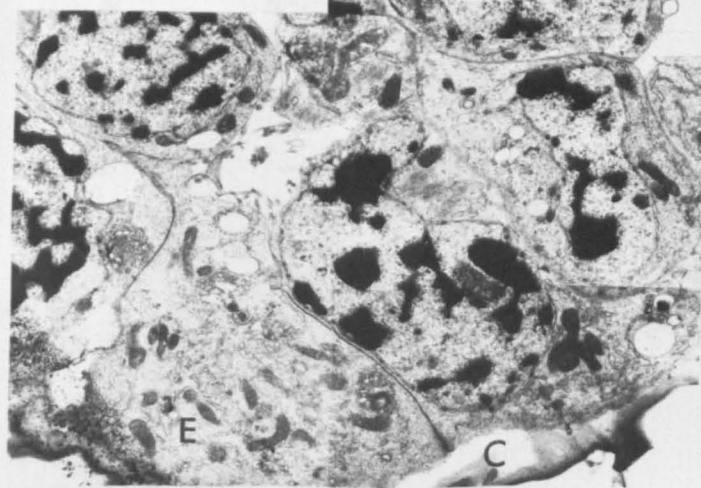
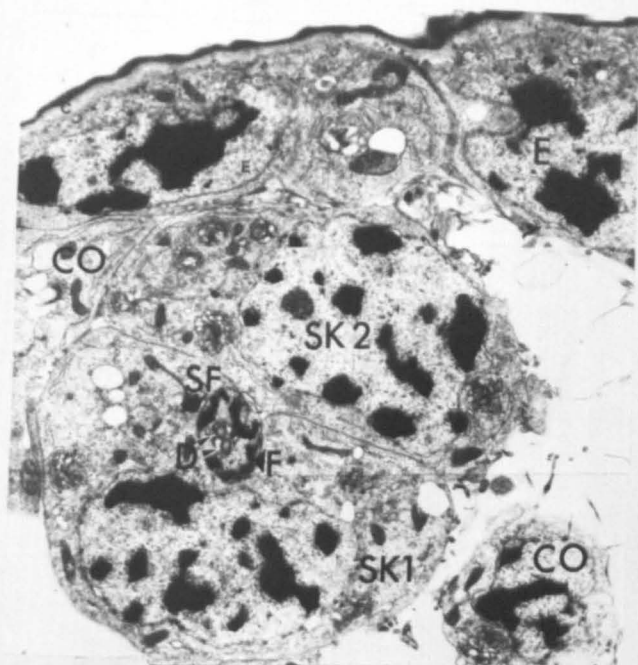


FIGURE 8.6

Diagrammatic representation of a section through a dorsal seta and associated cells. The interrelationship of the socket cells at the epidermal surface is shown, demonstrating the short shaft formed by socket cell 1 (SK 1) on its apical side, and the way this is encircled by part of socket cell 2 (SK 2). Two companion cells (CO) can be seen, these encircle the socket cells at the epidermal surface. The cell body of the shaft cell (SF) can be seen.

E, epidermal cell; C, cuticle; *, haemocoel; N1, N2, seta neurons 1+2; DT, dendrite.

Scale bar

5 μ m

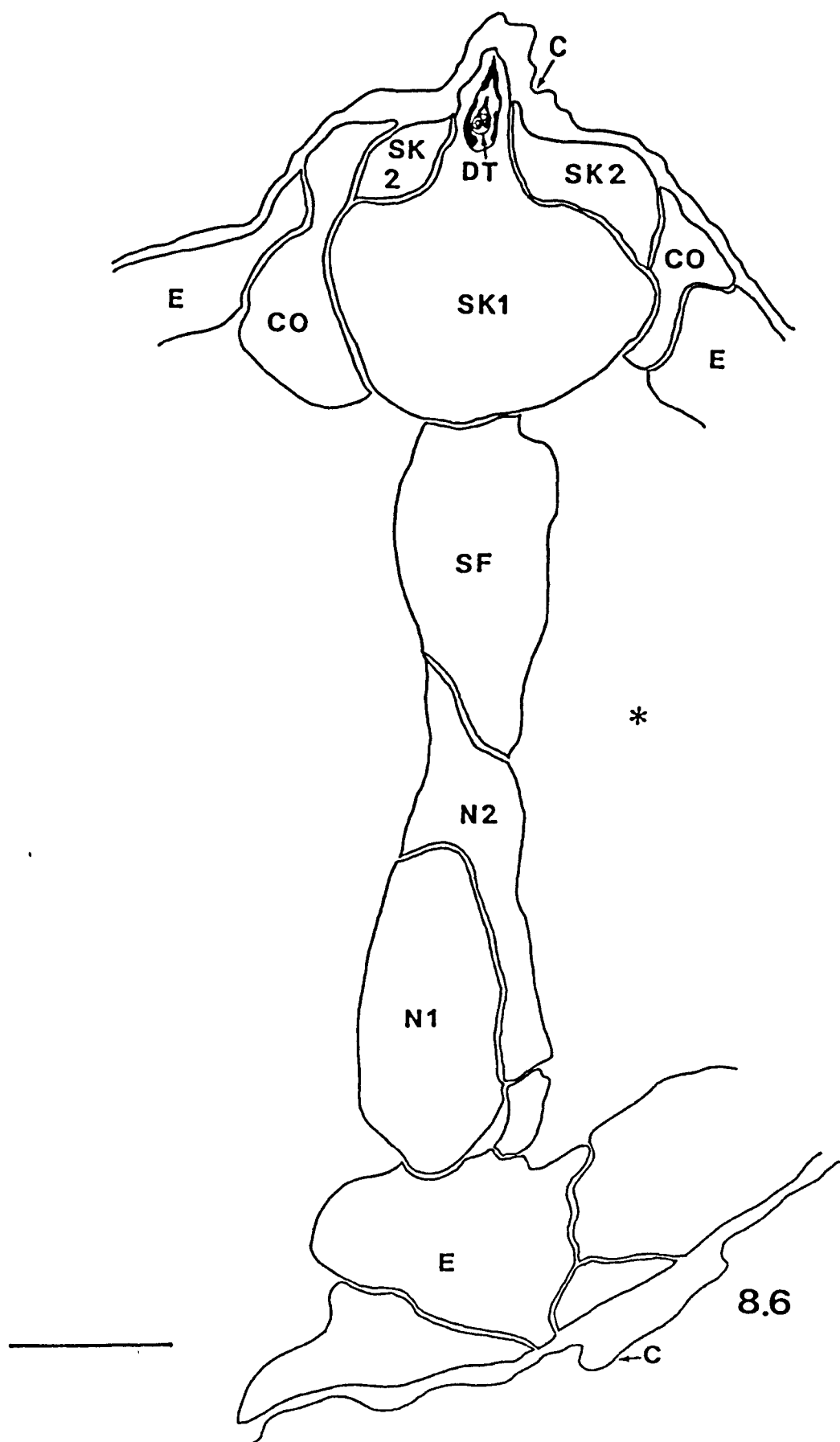


FIGURE 8.7

Transmission electron micrograph of a section through the two socket cells (SK 1 and 2) of the dorsal seta in a plane parallel to the epidermal surface and \perp perpendicular to the long axis of the seta. It is from a level near the base of the cells, where the neurites (NT), surrounded by the shaft cell process (SF) enter between two cells. There is an accumulation of bundles of electron-dense fibrous material (F) known as scolopale material in the cytoplasm of the shaft cell process at this level. Some of this material is closely associated with the membranes of the neurites.

E, epidermal cell; *, haemocoel; ML, dorsal longitudinal muscle.

Scale bar

1 μm

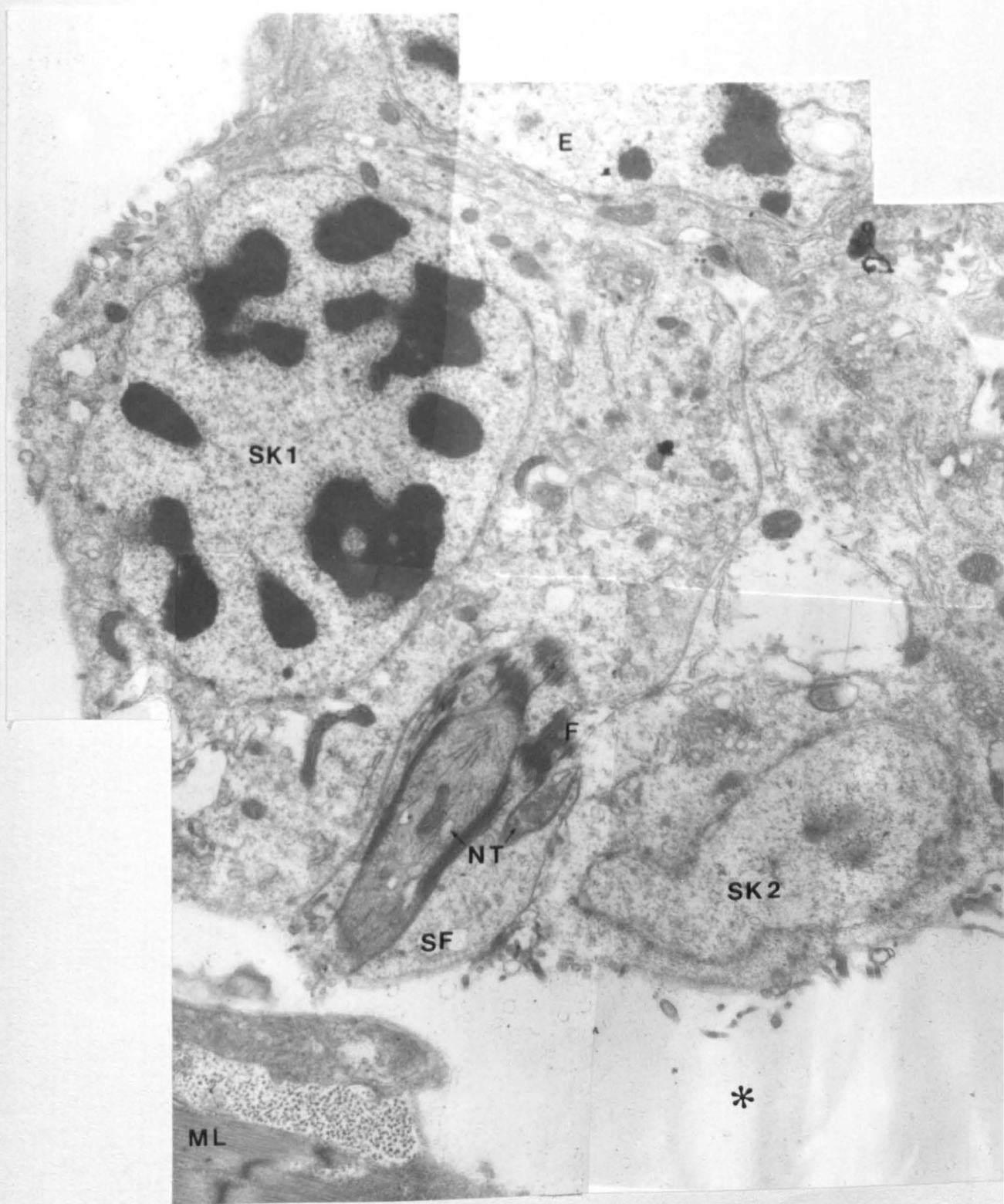


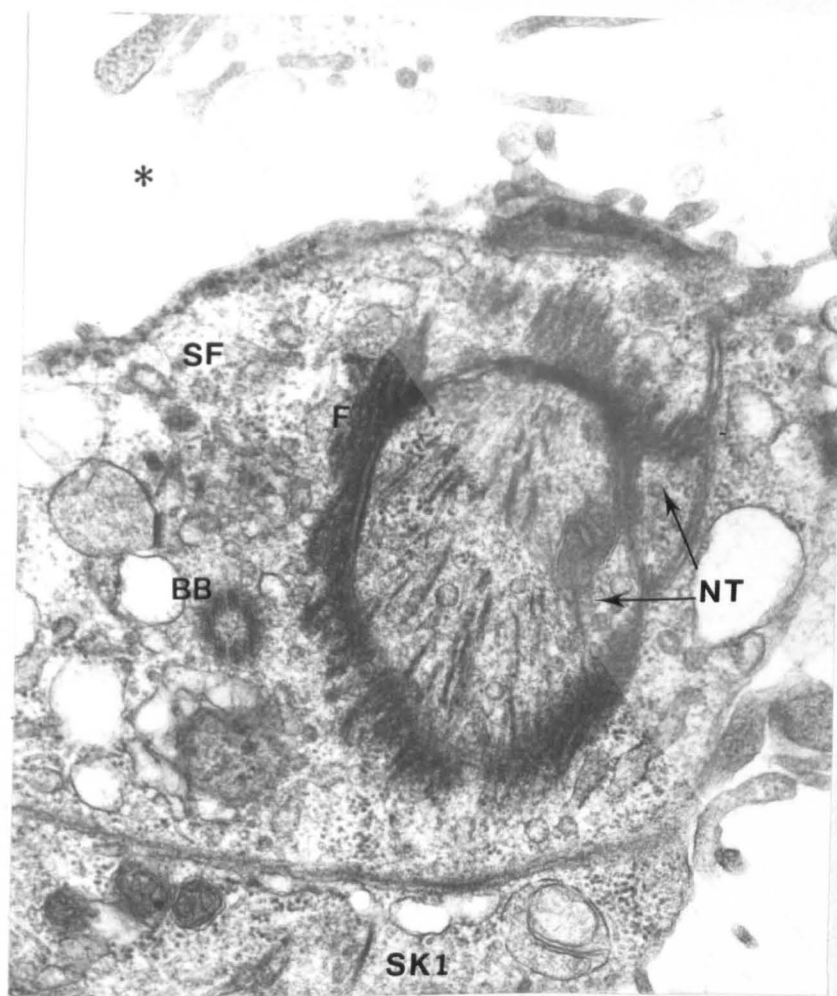
FIGURE 8.8

Transmission electron micrographs of sections through the shaft cell (SF) and the two terminal neurites (NT) of neurons N1 and N2 as they enter the basal surface of socket cell 1 (SK 1). The section is \pm transverse to the neurites. (a) is from a section at a level further into the socket cell than (b). The shaft cell cytoplasm contains bundles of electron-dense fibres (F) of scolopale material. There is also a basal body (BB) in the shaft cell cytoplasm in (a).

*, haemocoel.

Scale bar

0.5 μm



a



b

FIGURE 8.9

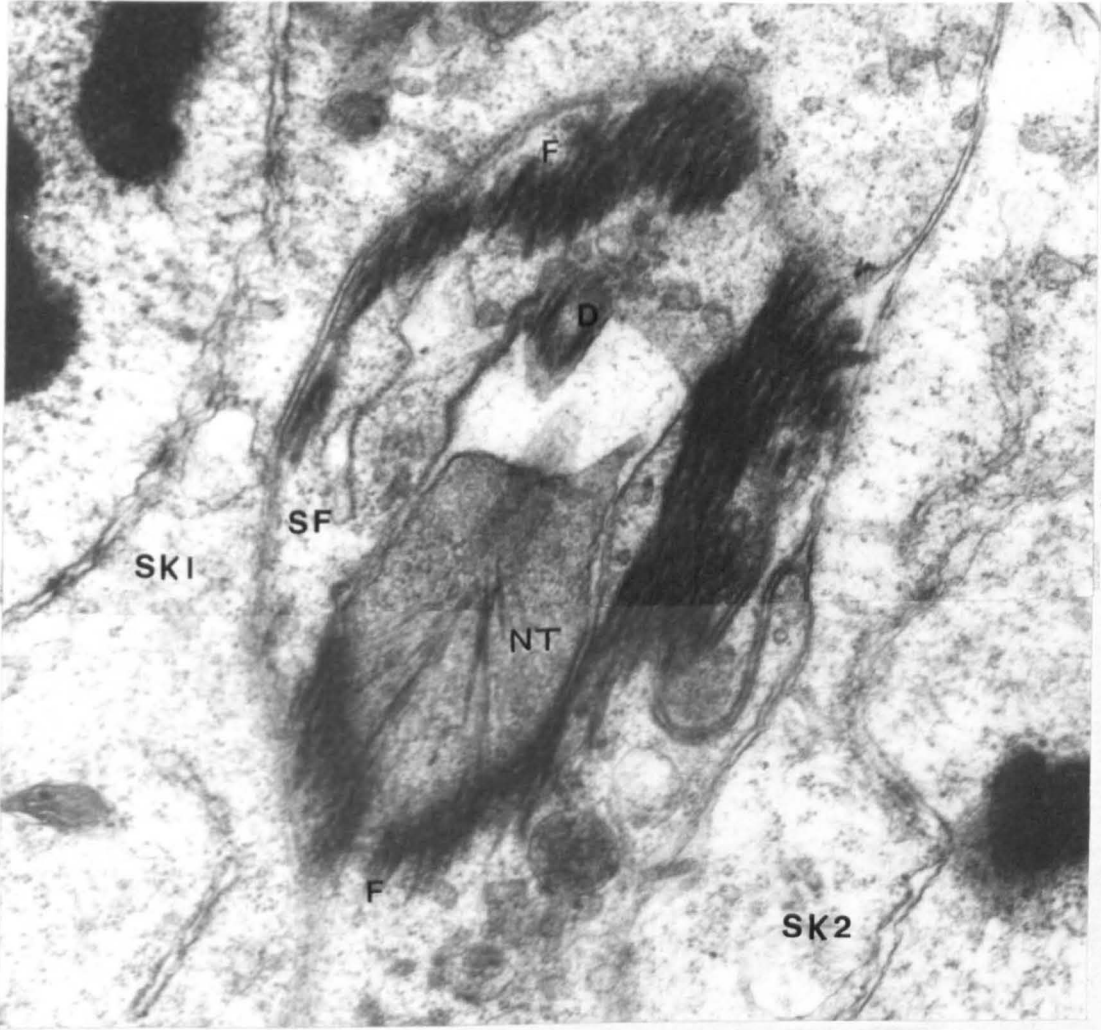
Transmission electron micrographs of \pm transverse sections through the shaft of a dorsal seta within socket cell 1 (SK 1).

- (a) One neurite (NT) and one cilium-like dendrite (D) is shown. The electron-dense fibres (F) of the shaft cell (SF) scolopale material are closely associated with the membrane around the neurite but not with the cilium-like dendrite.
- (b) At the slightly more distal level in the same specimen, a cilium-like dendrite can be seen emerging from the second neurite.

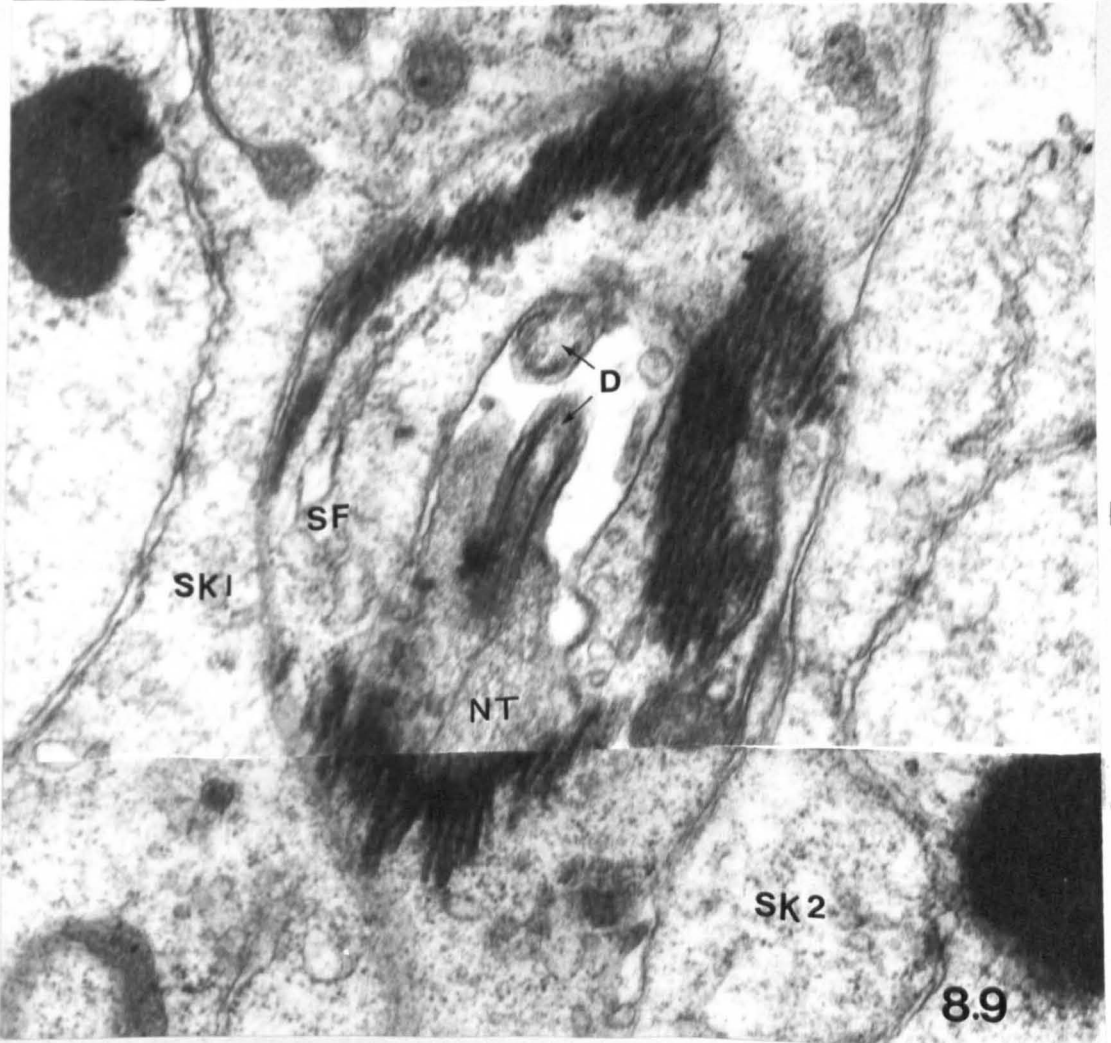
SK 2, socket cell 2.

Scale bar

0.5 μm



a



b

FIGURE 8.10

Transmission electron micrograph of a longitudinal section through the shaft cell process and the dendrites within socket cells 1 and 2 (SK 1 and SK 2). There is basal body 2 (arrowed), visible within the cytoplasm of the shaft cell (SF), near the epidermal surface. There is a finger-like protruberance (P) formed by SK 1 near the base of the seta.

C, cuticle.

Scale bar

1 μm

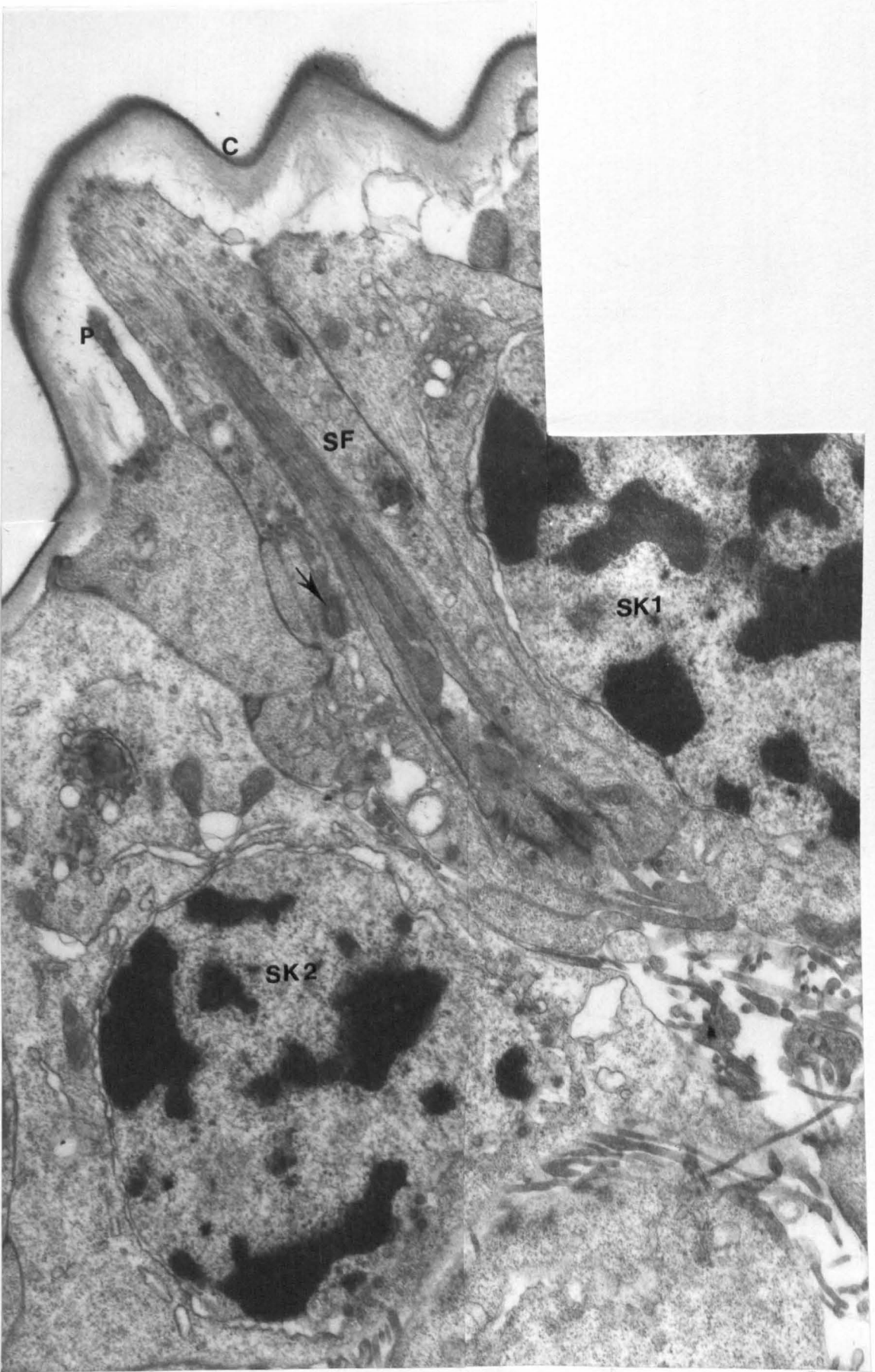


FIGURE 8.11

Tracing of a transmission electron micrograph of half a transverse section through a stage 2 segment, just posterior to the plane of the dorsal seta, at the level where the cell bodies and axons of neurons N1 and N2 are located (shaded). The position of the neuronal cell bodies on the dorsolateral epidermis is shown and also the path followed by their axons along the epidermal cells E1 and E2, onto the dorsoventral muscle (ML) towards the ventral surface of the segment. These axons ultimately reach the position of the terminal pioneer axons (arrowheads).

DML, dorsal longitudinal muscle.

Scale bar

10 μ m

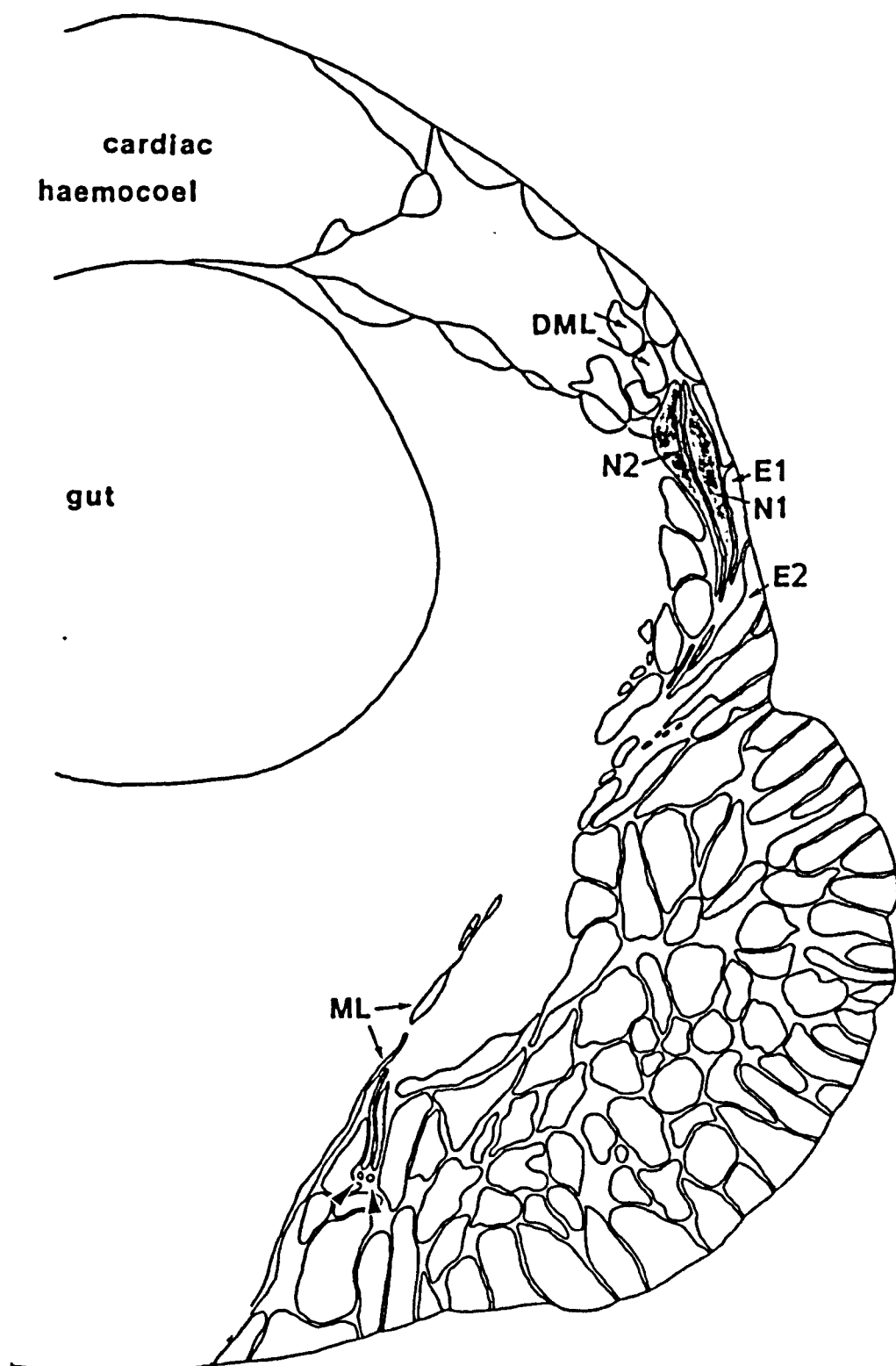


FIGURE 8.12

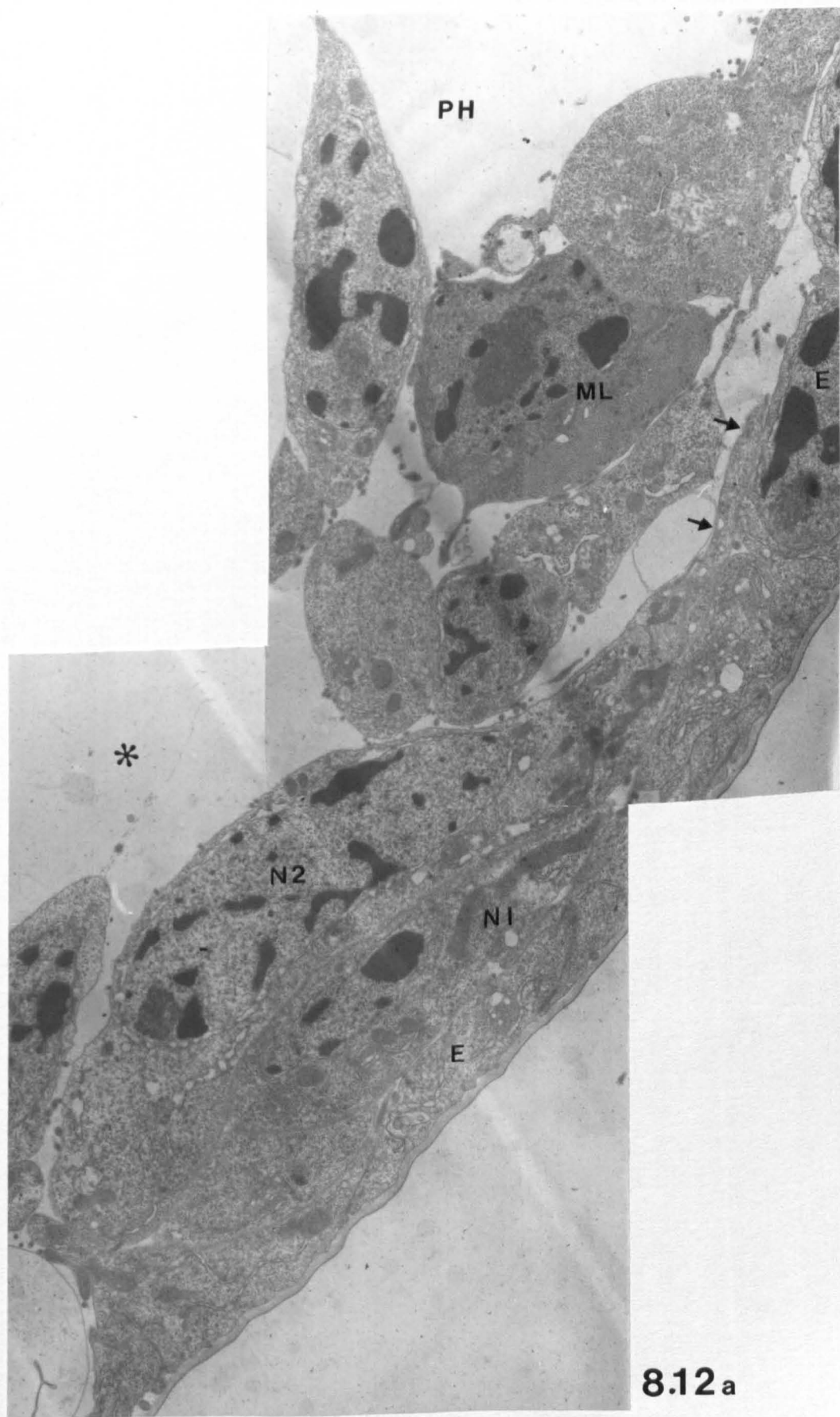
Transmission electron micrograph of transverse sections through the animal, showing neurons N1 and N2. They are elongated bipolar neurons, N1 lying on the epidermis with N2 lying over N1 and flattened against it.

- (a) The neurons lie just ventral to the pericardial haemocoel (PH). Their distal neurites (black arrows) grow between epidermal cells (E) and the dorsal longitudinal muscle (ML).
- (b) The two axons (arrowheads) are intimately associated and are closely apposed to the epidermis. They grow a short distance ventrally over the epidermis and then turn medially to follow an epidermal cell (E1) which is attached to the dorsoventral muscle (not shown).

M, mesoderm cell; *, haemocoel.

Scale bar

1 μ m





8.12b

FIGURE 8.13

Transmission electron micrograph of a transverse section through the animal, showing the axons (arrowheads) of neurons N1 and N2. They are in contact with two successive epidermal cells (E1 and E2), that have medially elongated processes to which the dorsoventral muscle (not shown) is attached.

*, haemocoel; M, mesoderm cell.

Scale bar

1 μm

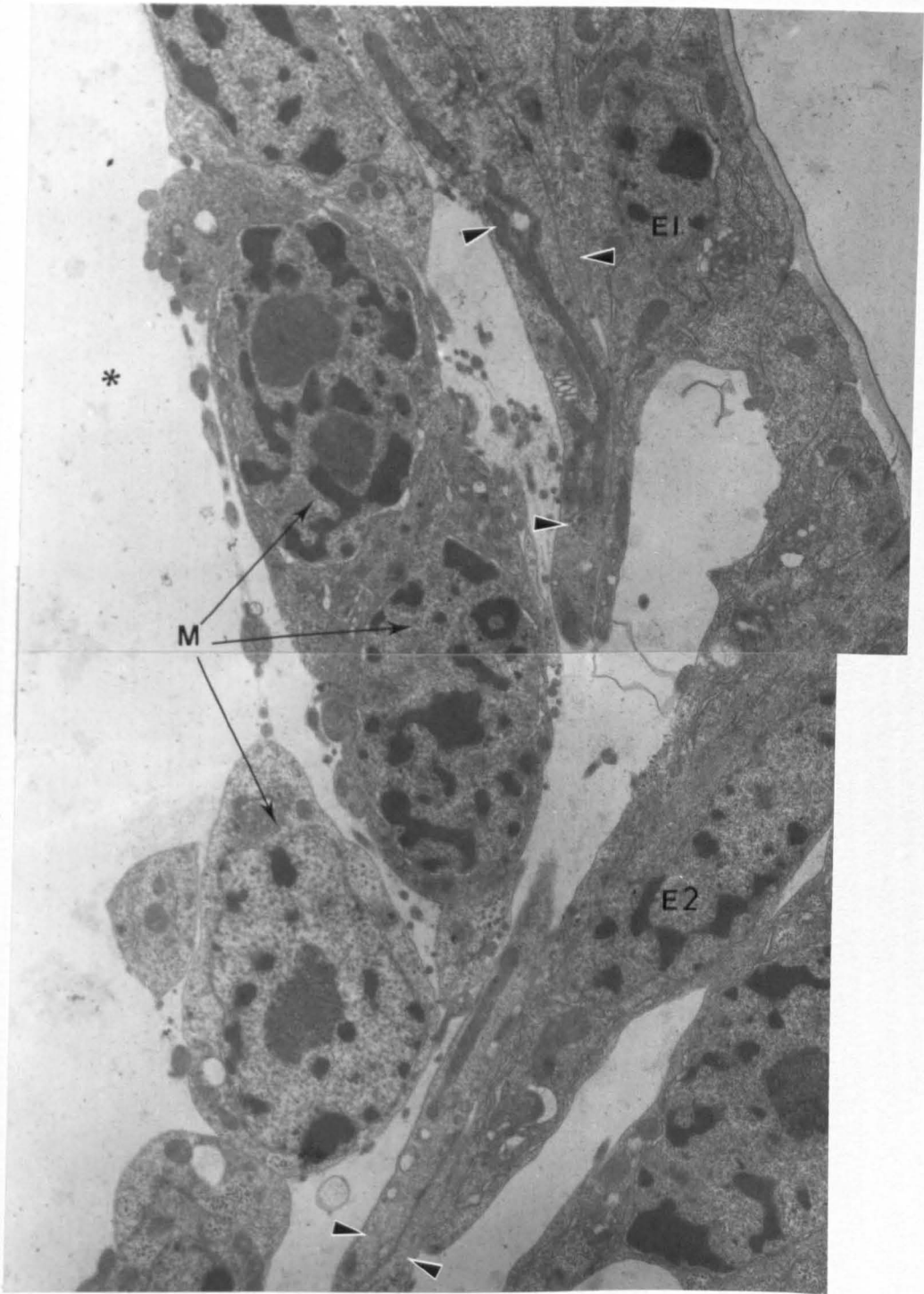


FIGURE 8.14

Transmission electron micrographs of transverse sections through the ventral region of a stage 2 segment where the axons (arrowheads) of N1 and N2 turn towards the terminal pioneer axons (TP) and fasciculate with them.

(a) A low power micrograph showing the muscle (ML), C1 and C2 and the position of the terminal pioneer (TP) axons. The N1 and N2 axons (arrowheads) leave the muscle and enter a groove in C2 before passing between cells C1 and C2.

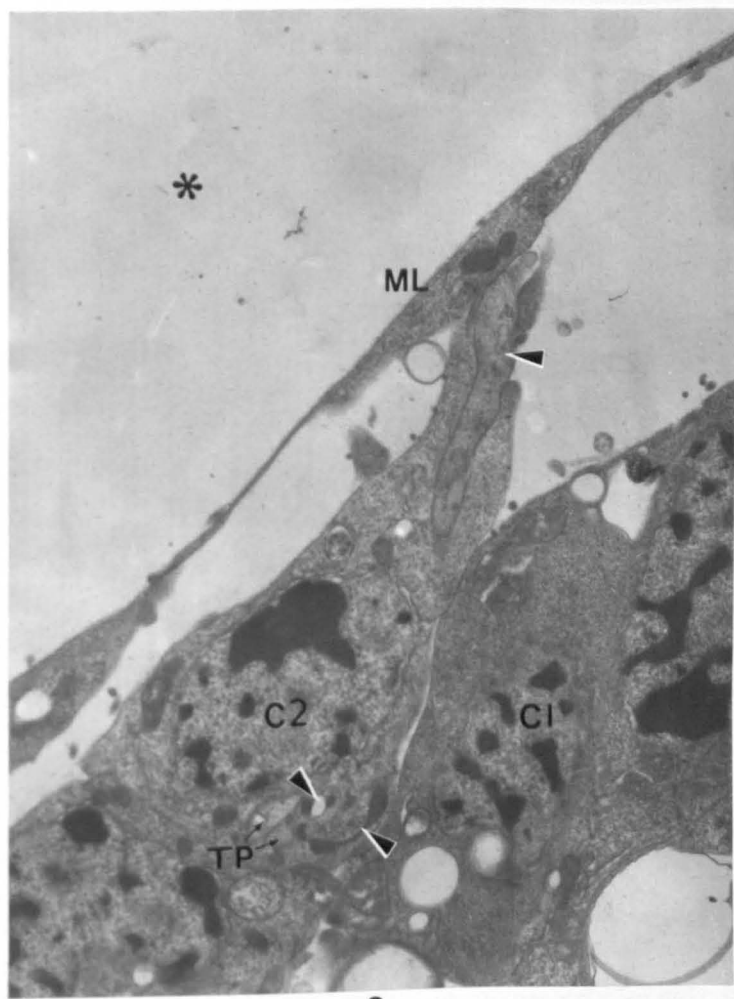
(b) This is a higher power ^{a section near} detail from (a), showing the axons of N1 and N2 closely apposed to each other and the groove formed by C2.

(c)&(d) Show each of the axons of N1 and N2 in the groove formed by C2, as they reach the TP axons.

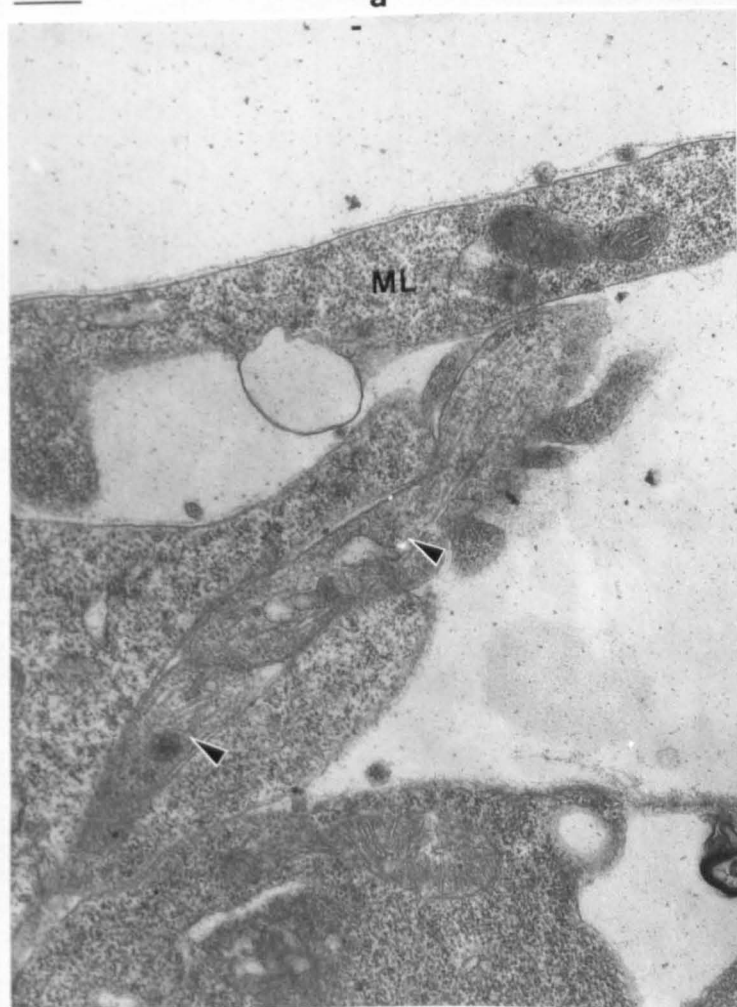
*, haemocoel.

Scale bar

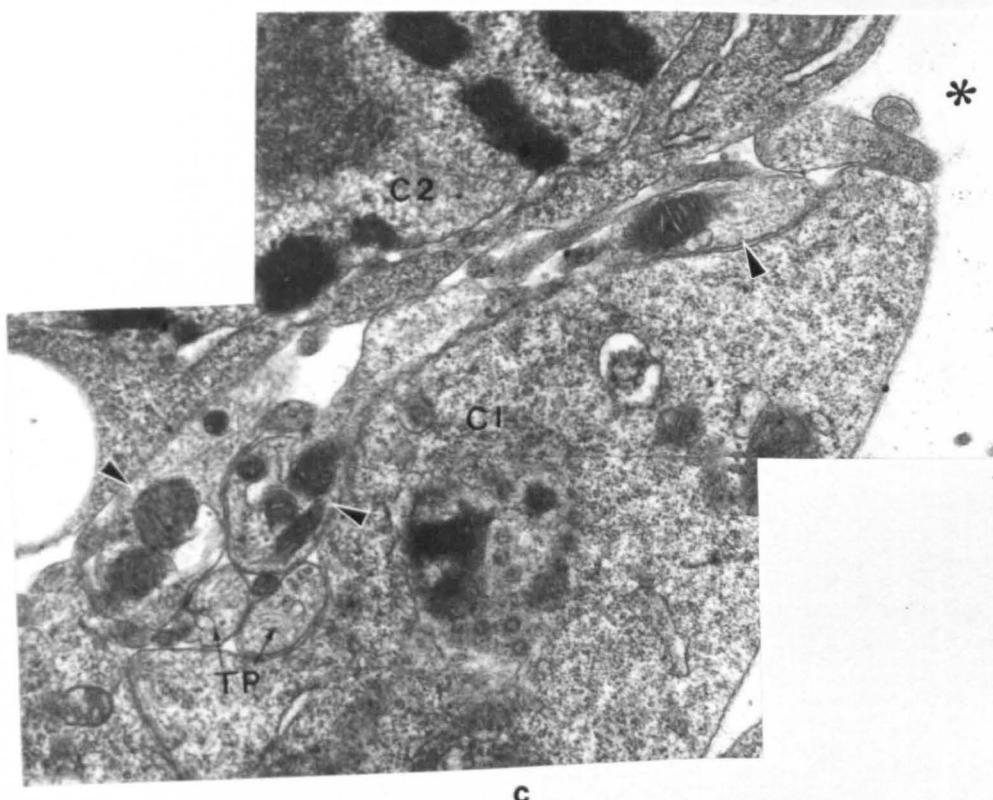
1 μm



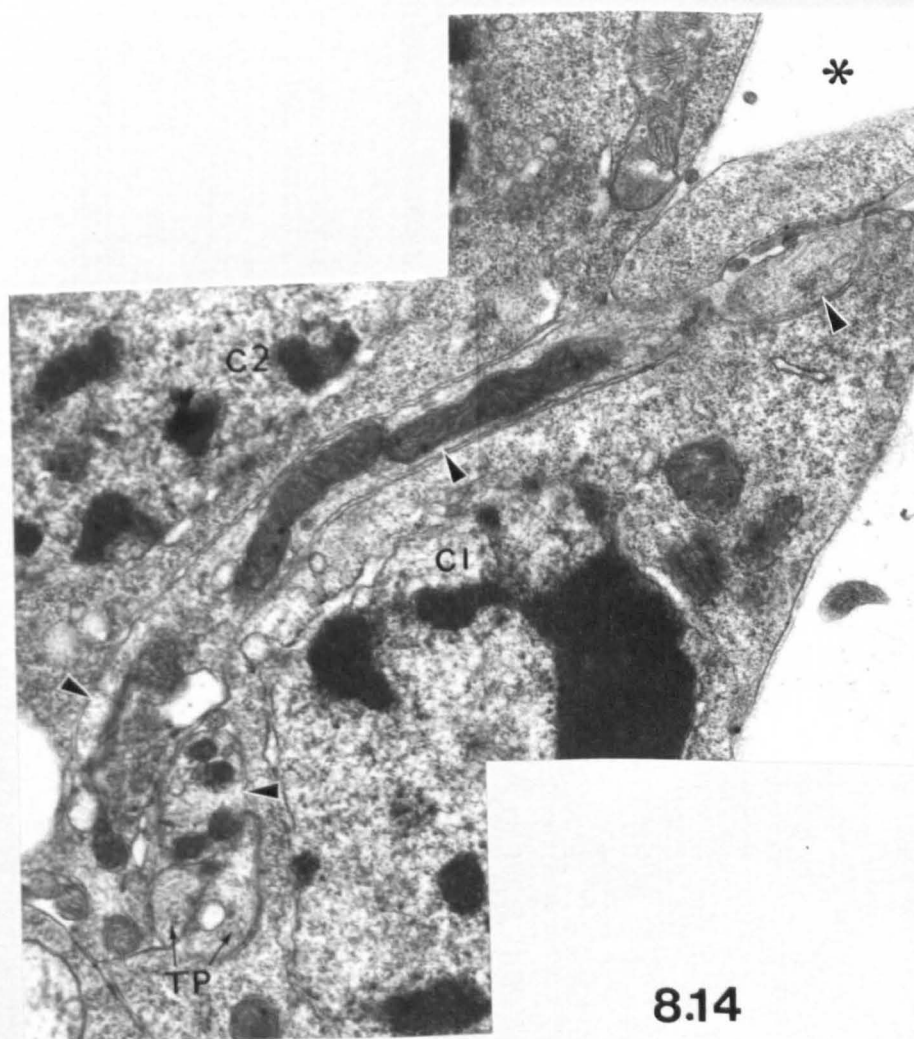
a



b



c



d

8.14

FIGURE 8.15

Transmission electron micrographs of three sections from a stage 3 segment showing a third axon has fasciculated with the two axons of neurons N1 and N2. The three axons are loosely associated with the dorsoventral muscle (ML).

arrowheads, axons.

Scale bar

0.5 μm

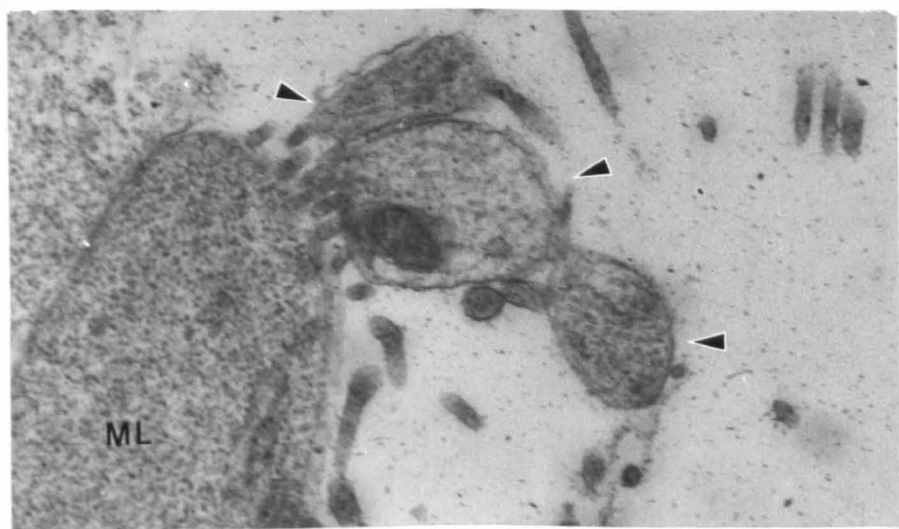
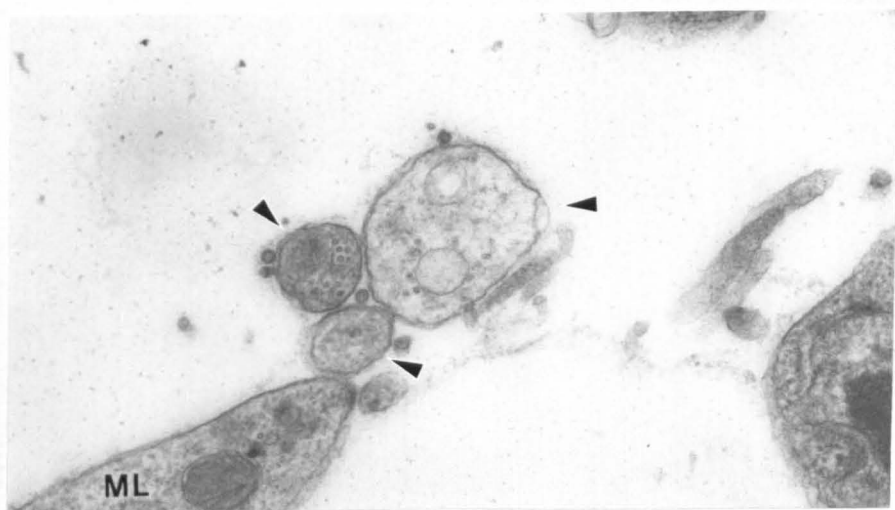
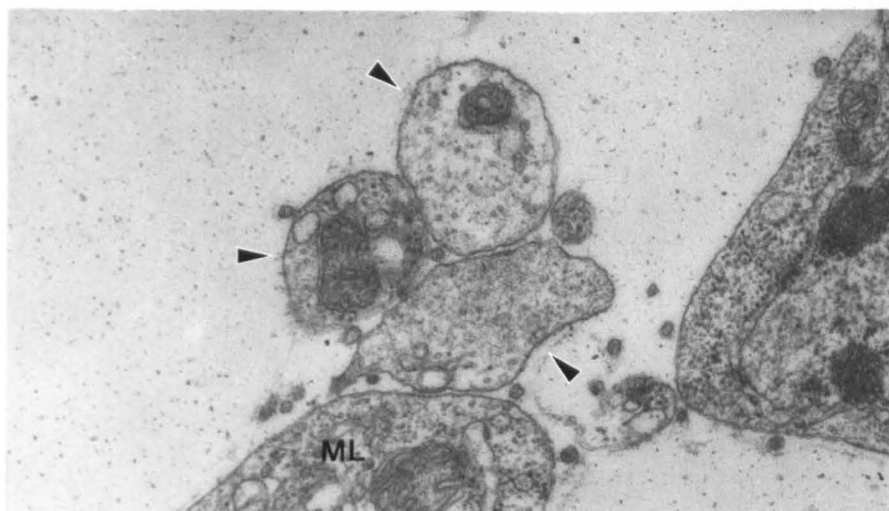


FIGURE 9.1

Diagrammatic representations of longitudinal sections through four different types of arthropod mechanoreceptor. These show how modifications of the basic structure of a mechanoreceptor similar to the Artemia dorsal seta could have occurred to secondarily derive complex, subcuticular chordotonal receptors from simple cuticular hairs.

- (a) The dorsal seta of Artemia. This receptor shows the simplest arrangement of the scolopale material (S) around a pair of ciliary dendrites (D) within a cuticular hair (H).
- (b) A seta of the first antenna of Cyclops (adapted from Strickler and Bal, 1973). This cuticular hair (H) contains a bundle of 100-200 microtubules, whereas below the cuticular surface (within the antenna), these microtubule bundles are connected to two ciliary dendrites (D), surrounded by scolopale material (S).

Scale bar

10 μ m
285

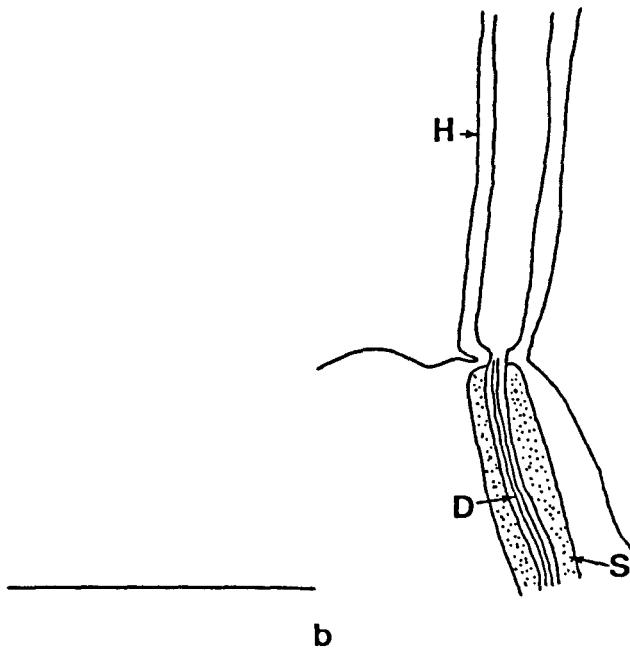
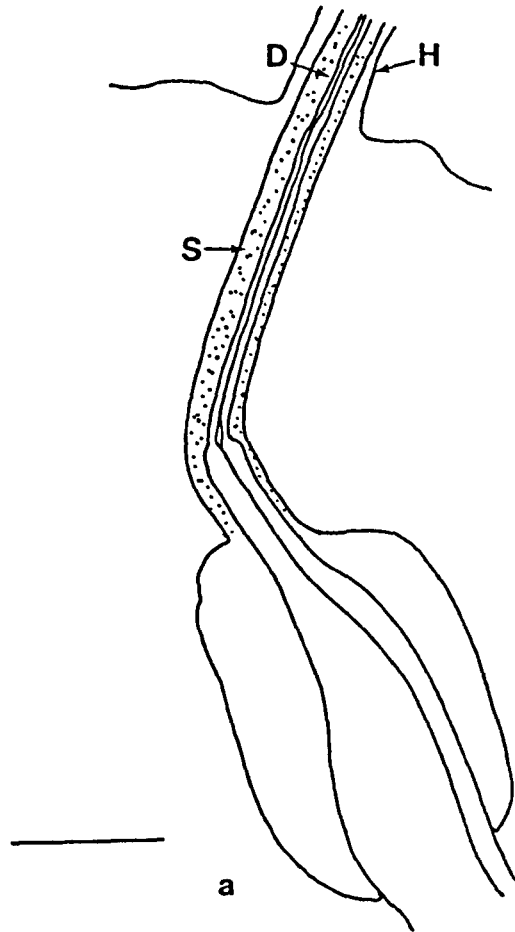
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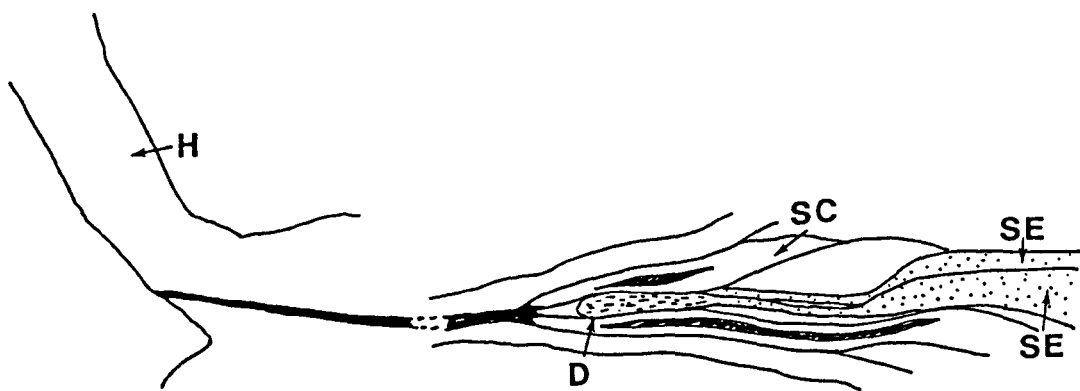
FIGURE 9.1 (continued)

- (c) A seta of the second antenna of Procambarus (adapted from Kouyama and Shimozawa, 1981, 1982). This hair contains no sensory cell processes and is connected to a scolopidium (sensory cells (SE) surrounded by a scolopale cell (SC)) containing three sensory cells. There are microtubule-filled terminal dilations of the sensory dendrites (D), which are otherwise cilium-like proximally.
- (d) A stretch-receptive crab chordotonal organ (adapted from Mill and Lowe, 1973). There is no external cuticular specialisation e.g. hair. There is an extracellular tube (T) and elastic strand (ES) connecting the exoskeleton to a scolopidium (SC) containing two sensory cells.

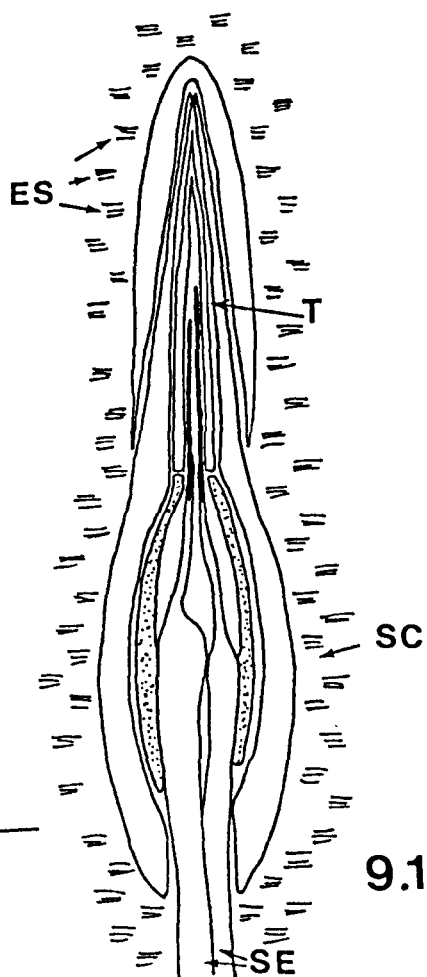
Scale bar

10 μm





c



d

9.1