Atlas of Drosophila Development

by Volker Hartenstein

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Information (from Atlas back cover)

This Atlas features several groups of color illustrations that follow the main events of embryogenesis and post-embryonic development of Drosophila. The following organs systems are considered:

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Gut and Annexes
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Fat Body
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The atlas was created by Volker Hartenstein to assist students of Drosophila biology in comprehending how the intricate body pattern of the fly gradually evolves during development. This web-based version is presented in the Interactive Fly by permission of Volker Hartenstein and Cold Spring Harbor Laboratory Press.
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The precursors of the CNS derive from specialized parts of the ectoderm, the neurogenic regions, which are shown here projected on a stage 5 embryo. The ventral neurogenic region gives rise to the neuroblasts of the ventral nerve cord, the part of the CNS belonging to the segmented germ band. The precursors of the CNS (neuroblasts) derive from specialized parts of the ectoderm, the neurogenic regions, which are shown here projected on a stage 5 embryo (see Campos-Ortega; Goodman and Doe; both this volume). The ventral neurogenic region (VNE) gives rise to the neuroblasts of the ventral nerve cord, the part of the CNS belonging to the segmented germ band (Hartenstein and Campos-Ortega 1984). Separating the ventral neurogenic region from the mesoderm (ms) is the mesectoderm (mec), a single row of cells on either side of the embryo that, among other cell types, gives rise to a number of neuronal precursors. The pro-cephalic neurogenic region (PNE) generates the brain. Adjacent to the procephalic neurogenic region is the anlage of the optic lobe (ol), which develops differently from the rest of the brain (see below). It should be emphasized that the neurogenic regions contain not only neuroblasts, but also epidermal precursors that give rise to the ventral epidermis and the head epidermis.

Shortly after gastrulation [stage 8], the cells of the ventral neurogenic region swell. Whereas the primordium of the dorsal epidermis (DEA) undergoes its first postblastoderm division, mitosis is delayed in the neurogenic regions.

Starting at stage 9, neuroblasts delaminate from the ectoderm. For the ventral neurogenic region, delamination occurs in three waves (Hartenstein and Campus-Ortega 1984; see Campus-Ortega, this volume). The first wave (beginning of stage 9) yields two rows of neuroblasts (SI) on either side. The neuroblasts delaminating during the second wave (SII) fill the gap between the two rows of SI neuroblasts. The figure of a stage 9 embryo depicts the pattern of SI and SII neuroblasts. SIII neuroblasts segregate from predominantly medial positions throughout stage 10 and the beginning of stage 11. The full complement of neuroblasts of a stage-11 embryo is illustrated to the left. The pattern of neuroblast segregation in the procephalic neurogenic region is insufficiently known; the drawings of the stage 9 embryo and stage 11 embryo (left) give a rough approximate of the population of procephalic neuroblasts (pnb) present at these stages.
 Shortly after their segregation, neuroblasts start dividing with a perpendicularly oriented spindle. During stages 9-13, neuroblasts (nb) undergo eight waves of mitosis (Hartenstein et al. 1987). Their progeny, called ganglion mother cells (gmc), are placed between the neuroblasts and the mesoderm (ms).

Each ganglion mother cell performs one equal division yielding two neurons. Ganglion mother cells and neurons form an irregular layer of increasing thickness on top of the neuroblasts. With the onset of overt segmentation during stage 12, deep indentations appear in the flanks of the developing CNS. Throughout stages 9 and 10, the mesectoderm (mec) formed a double row of cells between the neuroblast layers of either side. During stage 11, the mesectoderm loses contact with the outer surface. Segmentally repeated
swellings mark the appearance of neuronal precursors (the so-called midline neuronal precursors, median neuroblasts, and midline glial cells, mp) that originate from the mesectoderm.

In a stage 11 embryo, the cells that will form the optic lobe are still in the head ectoderm where they occupy a dorsal-lateral position behind the developing brain (optic lobe placode, op). During stage 12, these cells invaginate. Unlike all other neuroblasts, the optic lobe precursors maintain their epithelial characteristics. From stage 13 onward, they form a vesicle (ol) that is attached to the basal surface of the brain hemispheres.

Neuronal differentiation begins at stage 13 (see Goodman and Doe, this volume). A population of identifiable neurons lays down a scaffold of fibers on the dorsal surface of the CNS. Later-appearing axons fasciculate along the pioneer tracts. Longitudinal fibers form the connectives (cn); transversal fibers form two commissures (co) in each segment that cross the midline while in contact with the midline glial cells, descendants of the mesectoderm. Axons that leave the CNS form an anterior fascicle (af; also called intersegmental nerve) and a posterior fascicle (pf; segmental nerve). Ingrowing sensory axons (pn) fasciculate with both of these tracts.
Starting at **stage 14**, the ventral nerve cord condenses. At **stage 17**, the deep indentations in the lateral margins of the ventral nerve cord (vg) that had separated individual neuromeres have disappeared. The CNS becomes invested with a sheet of perineurial cells.

(br) Brain;
(mg) midgut;
(mu) somatic musculature;
(myo) myoblasts;
(pn) peripheral nerve;
(tp) tracheal pit
Unlike most other larval organs, the CNS persists into the adult stage. Recent evidence (for review, see Truman 1990; Truman et al., this volume) suggests that most motor neurons and large interneurons of the insect adult nervous system are of embryonic origin. To this set of embryonically born neurons, a large number of neurons are added during larval and early pupal stages. The neuroblasts that generate these postembryonic neurons seem to be the same as those that had produced the larval CNS in the embryo (Prokop and Technau 1991).

In the first larval instar, these neuroblasts reappear at the outer surface of the CNS (see enlarged view of L3). In some parts of the CNS (e.g., thoracic segments), they closely match the number of neuroblasts present in the embryo (Truman and Bate 1988). In other regions (e.g., posterior abdominal segments), the number of postembryonic neuroblasts is very small. Each neuroblast resumes its proliferatory activity. As before in the embryo, neuroblasts divide in a stem cell mode with a perpendicularly oriented spindle. Their progeny, the presumptive adult neurons, remain undifferentiated until pupal stages. The optic lobe (ol), which started out as a small vesicle attached to the basal surface of the early larval brain, proliferates and gives rise to the outer and inner optic anlagen (outer optic anlage, ooa on drawing of pupa). These structures are curved epithelial sheets that cap the lateral aspect of the brain hemispheres throughout larval life. The outer optic anlage forms the lamina and part of the medulla; the inner optic anlage gives rise to the remaining part of the medulla, the lobula, and the lobula plate (Hertweck 1931; Hofbauer and Campos-Ortega 1990; see Meinertzhagen and Hanson in Bate and Arias, 1993).
The gross anatomy of the CNS changes markedly during late postembryonic development (Hertweck 1931). The larval brain hemispheres (br) to which the massive optic lobes and several central brain structures are added, become the supraesophageal ganglion (seg) of the adult brain. Another part of the adult brain is the subesophageal ganglion (sub). This structure develops from the neuromeres of the three gnathal segments that, in the larva, had formed part of the ventral ganglion (vg).

The three thoracic neuromeres of the larval ventral nerve cord, which had grown massively by postembryonic neuroblast proliferation, form the major part of the adult thoracico-abdominal ganglion (tha). The fused abdominal neuromeres remain small; they form an unpaired 'cone' attached to the third thoracic neuromere. (cn) Cervical connective.