APPENDIX 3
Cell Lineage

Compiled by John Sulston,* H. Robert Horvitz,† and Judith Kimble‡

*MRC Laboratory of Molecular Biology, Cambridge, England
†Massachusetts Institute of Technology, Cambridge, Massachusetts
‡University of Wisconsin, Madison, Wisconsin

Part A: Lineage Charts

Part B: Positions of Nuclei

  0-87969-307-X/88 $1 + .00.

Part A: Lineage Charts

Figure 1 Embryonic cell lineage of *C. elegans*. All interconnecting lines between the separate panels have been drawn, so that the pages can be copied, trimmed, and pasted together to give a complete chart. Vertical axis represents time at 20°C, from 0 min at first cleavage to 800 min at hatching. Many of the observations were made on eggs that were developing at slightly different rates (due to temperature variation and the effect of prolonged illumination); these primary results were normalized, by means of certain prominent cell divisions, to the course of events in eggs kept at 20°C and viewed infrequently. Precise times of individual events should not be taken too seriously; likely error varies from ±10% at the beginning of the lineage to ±2% at 400 min. Horizontal axis represents the direction of cell division. The majority of divisions have a marked anterior-posterior bias and are shown with anterior to the left and posterior to the right, without any label. Only when this would lead to ambiguity in naming the daughters is an alternative direction indicated (l = left; r = right; d = dorsal; v = ventral); thus, the system is taxonomic, rather than fully descriptive. The natural variation seen suggests that the precise direction of cell divisions is unimportant, at least in later development. Note that the daughters of a left-right division are not necessarily bilaterally symmetrical: For example, all of the cells derived from ABalaaapa lie on the left of the animal and the right-hand daughters lie nearer the midline. Each terminal branch of the embryonic lineage is labeled either with X (indicating cell death; the position of the X on the time axis indicates the time of maximum refractility) or with a lineage name followed by a functional name. Large arrowheads denote cells that divide postembryonically, and small arrowheads denote nuclei that divide postembryonically. O and --- link precursors that give rise to bilaterally symmetrical groups of cells, the symbol ~ being included for cases of imperfect symmetry. (cord) Ventral cord; (gang) ganglion; (lumb) lumbar; (d-r) dorsorectal; (p-a) preanal; (r-v) retrovesicular; (lat neur) isolated neuron lying laterally. (Reprinted, with permission, from Sulston et al. 1983.)

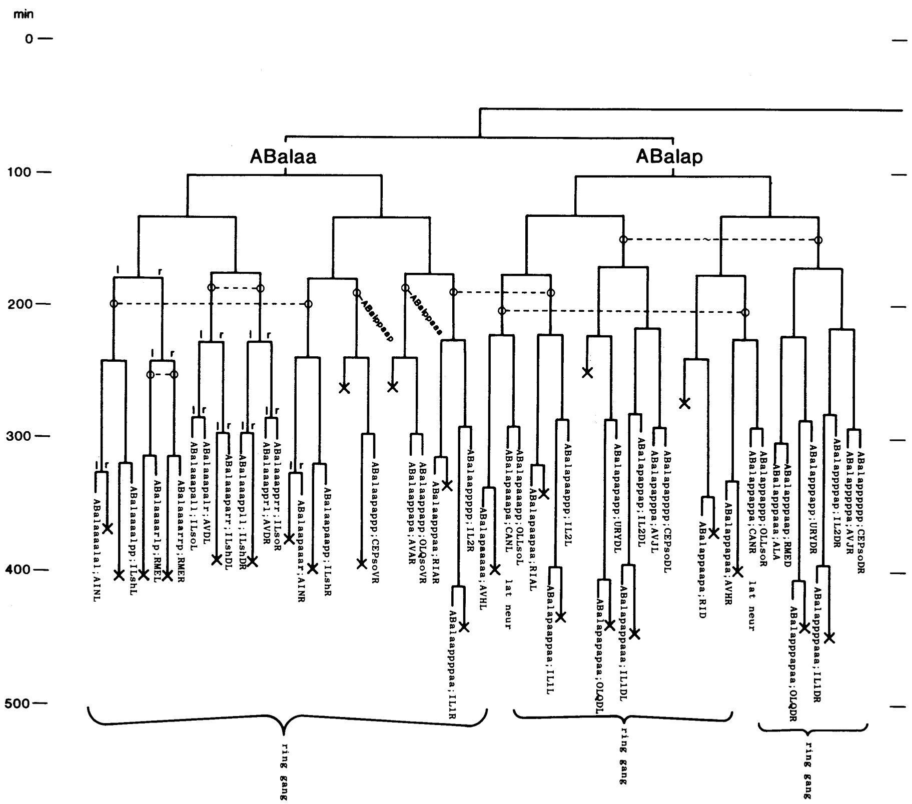

Figure 1 (*Continued on following pages.*)

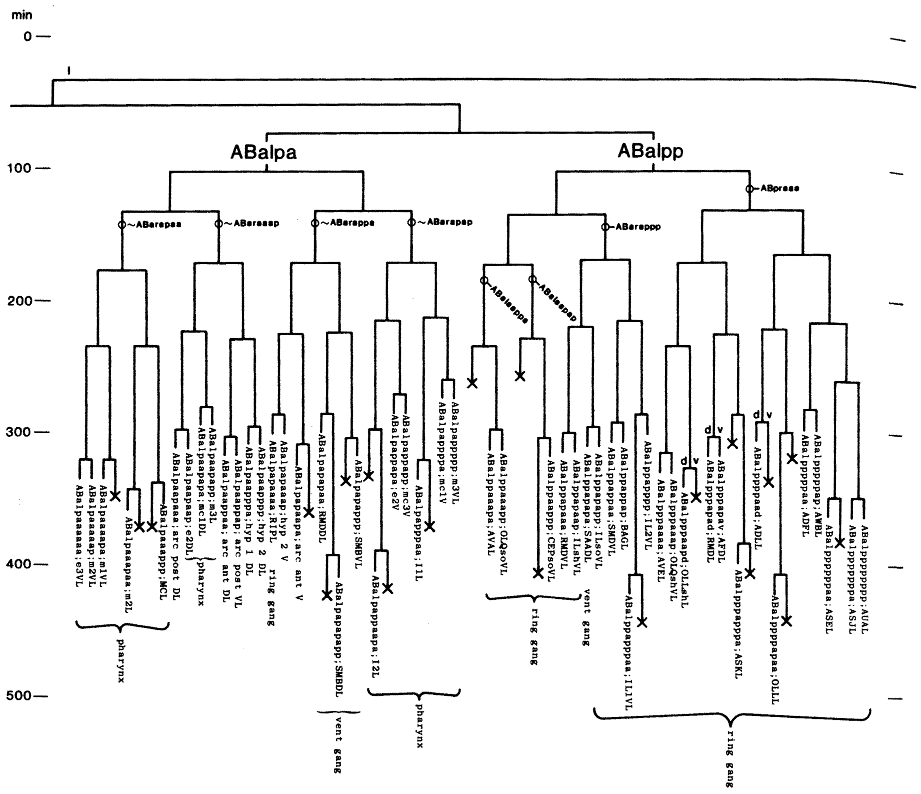

Figure 1 (*Continued.*)

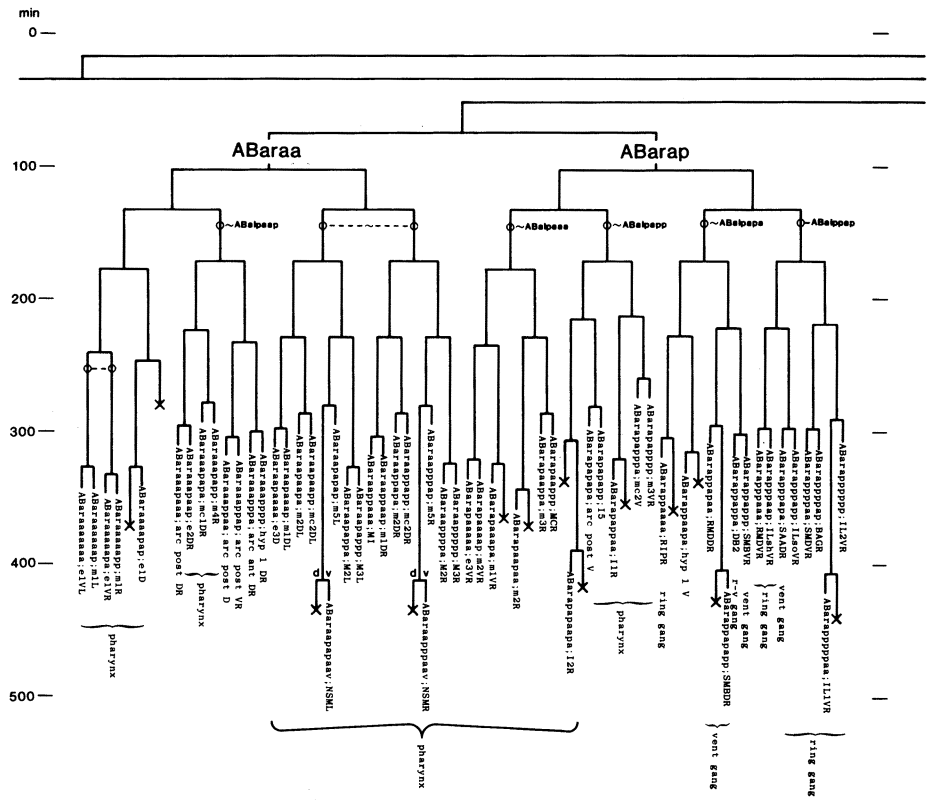

Figure 1 (*Continued.*)

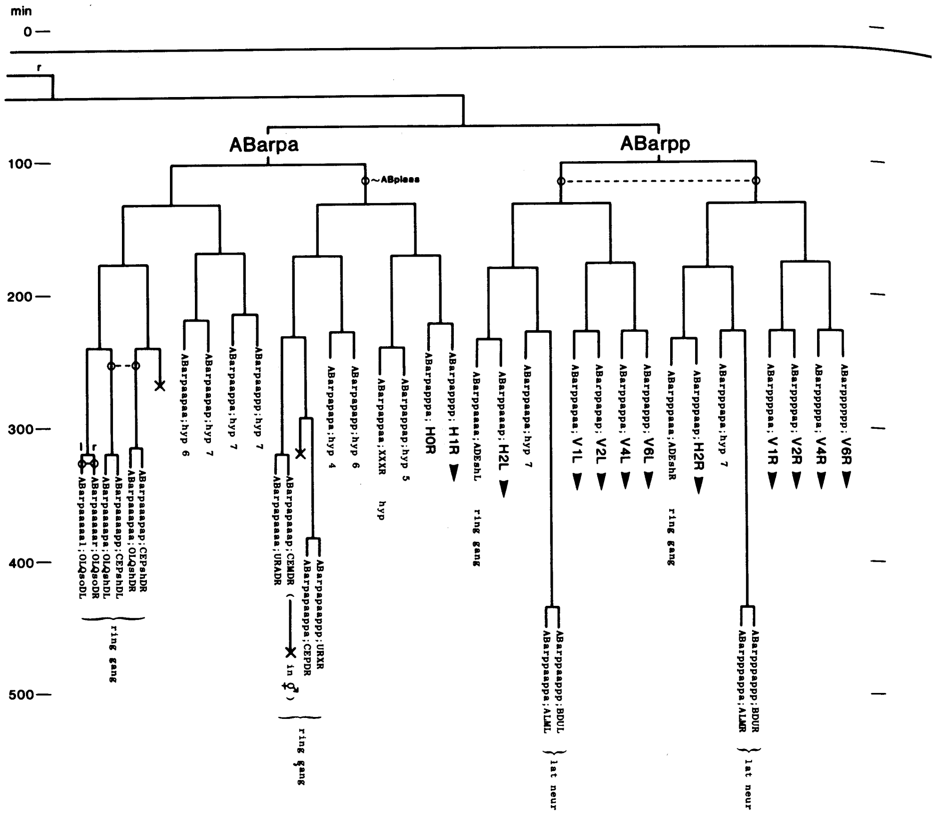

Figure 1 (Continued.)

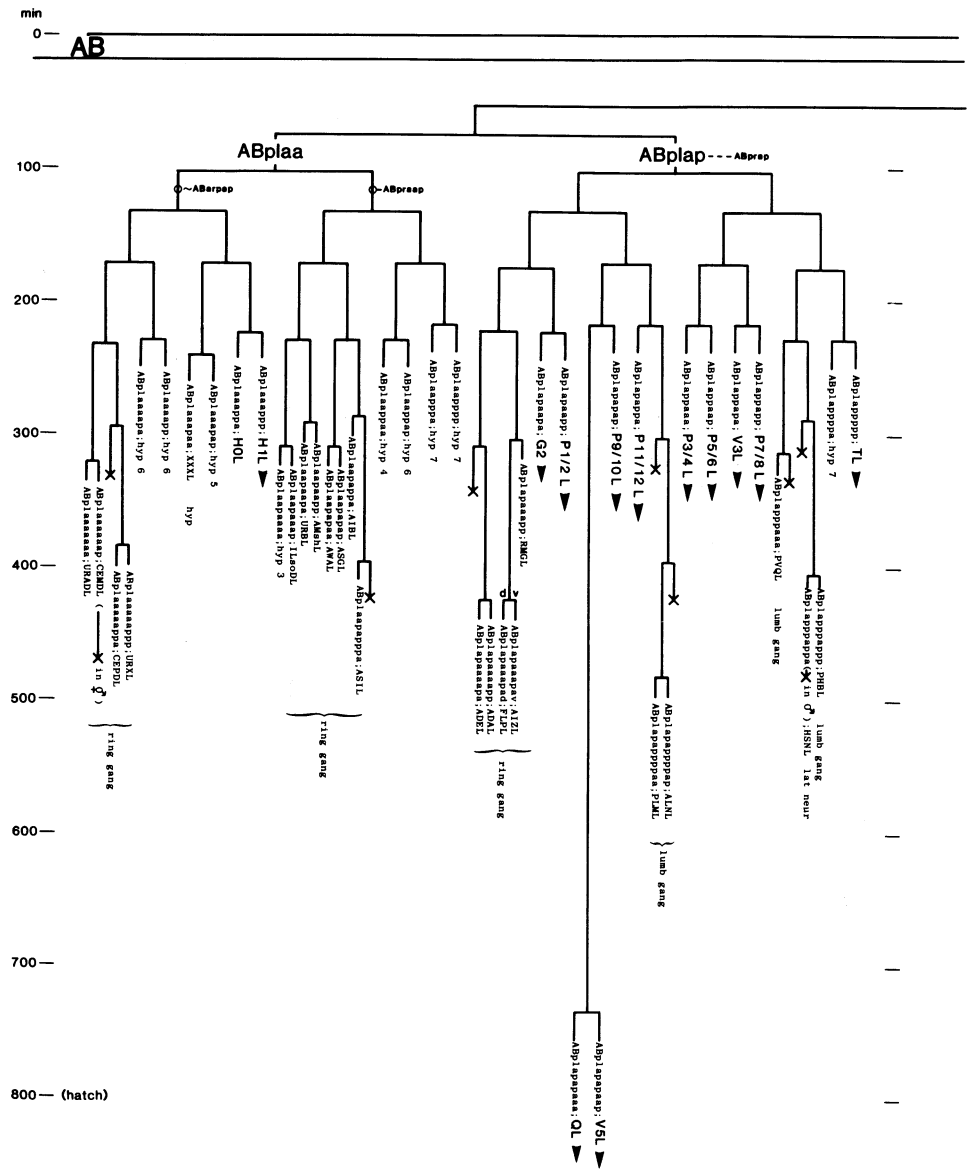

Figure 1 (Continued.)

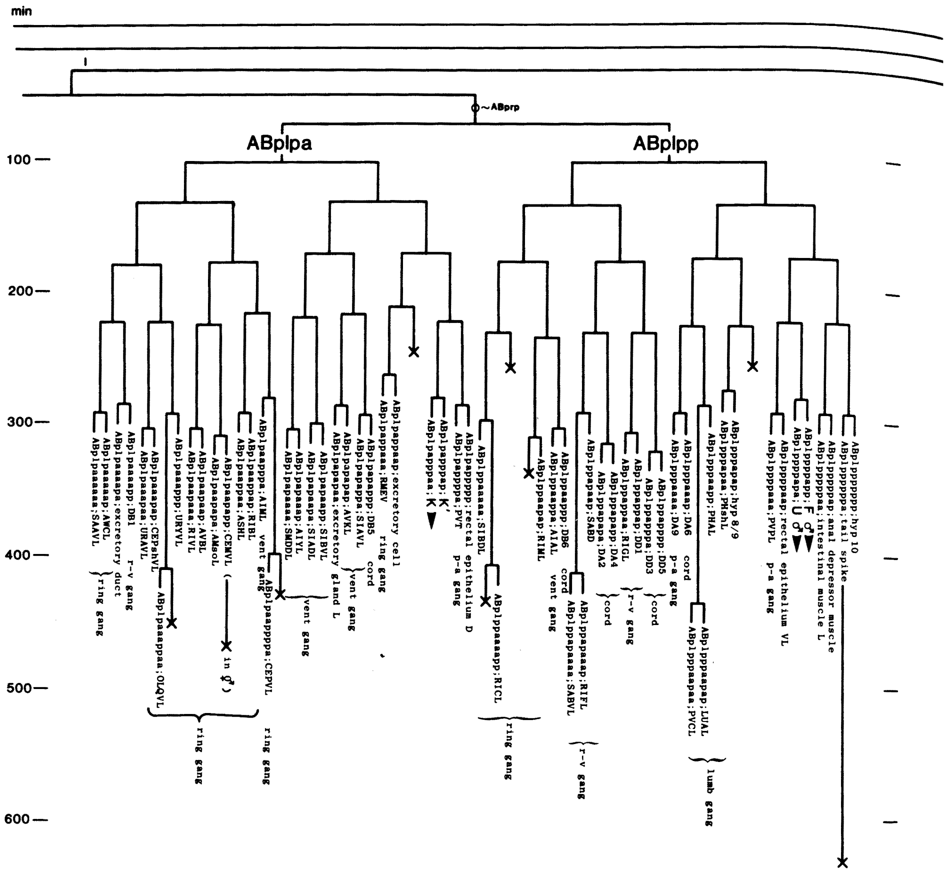

Figure 1 (*Continued.*)

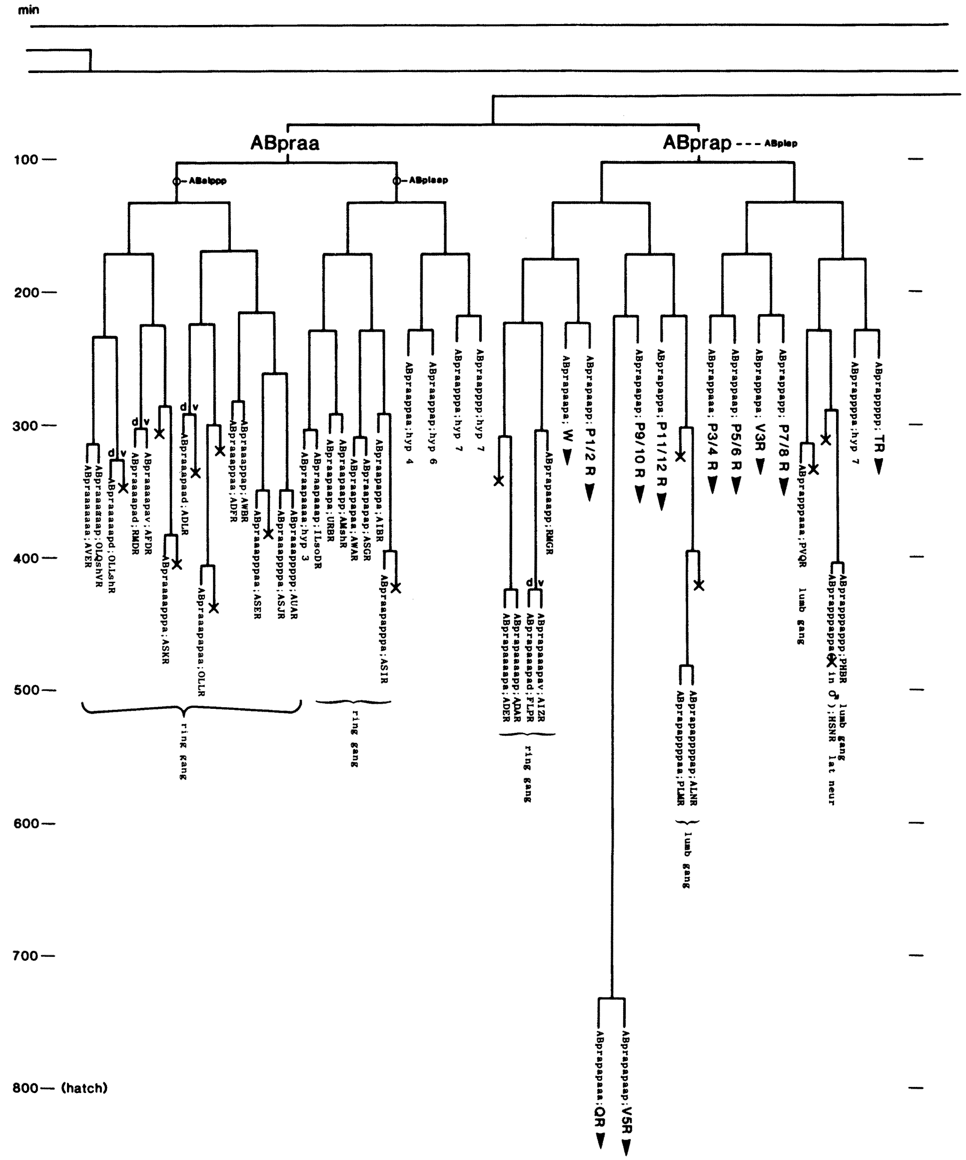

Figure 1 (*Continued.*)

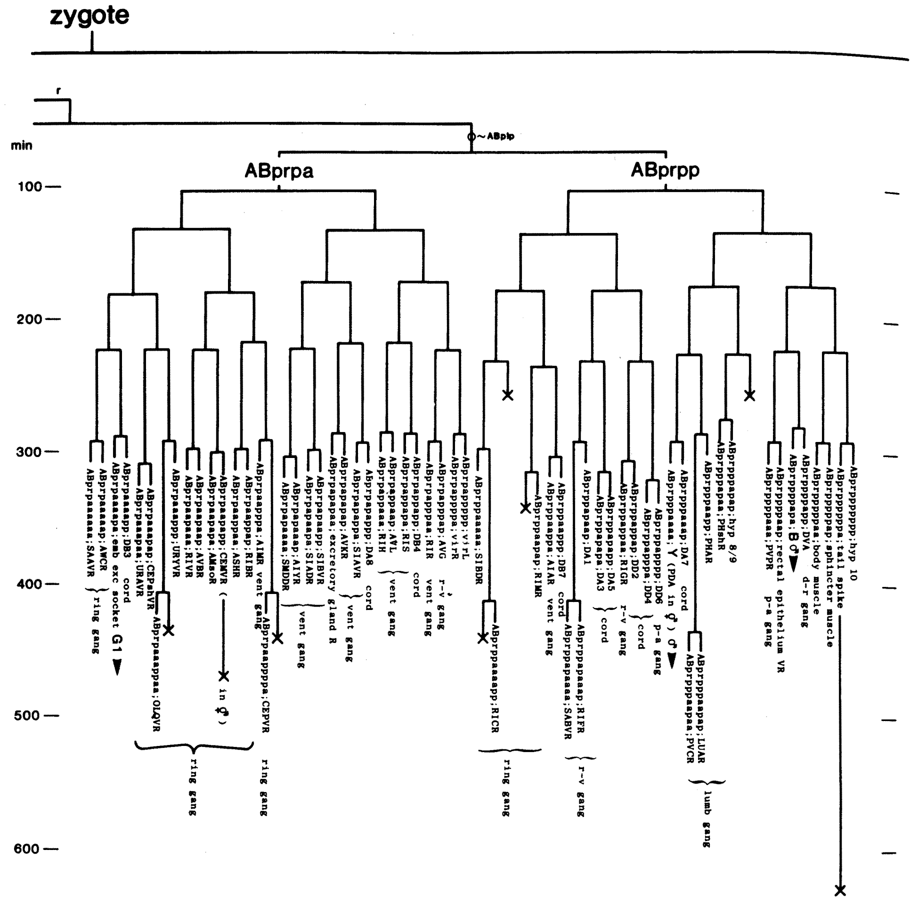

Figure 1 (*Continued.*)

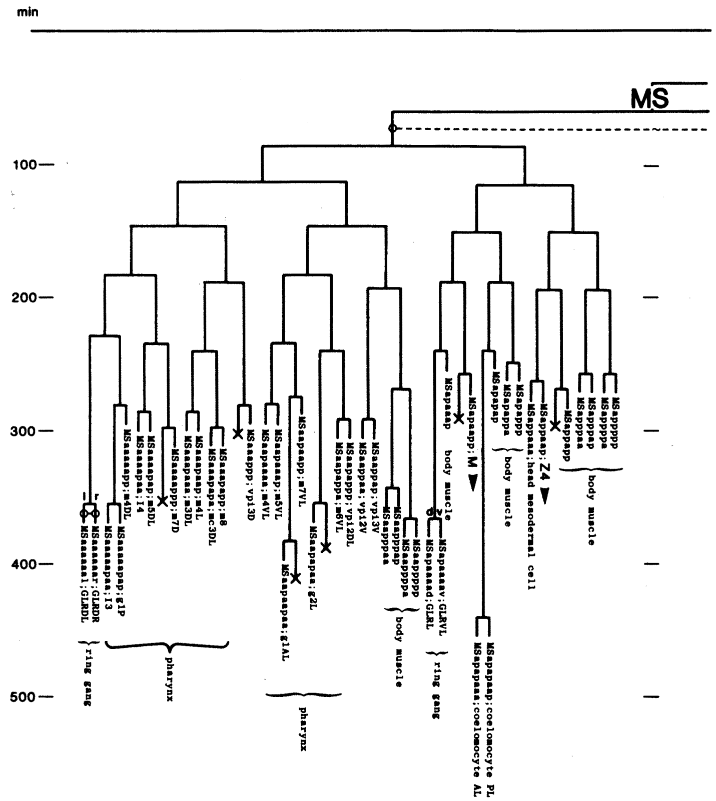

Figure 1 (*Continued.*)

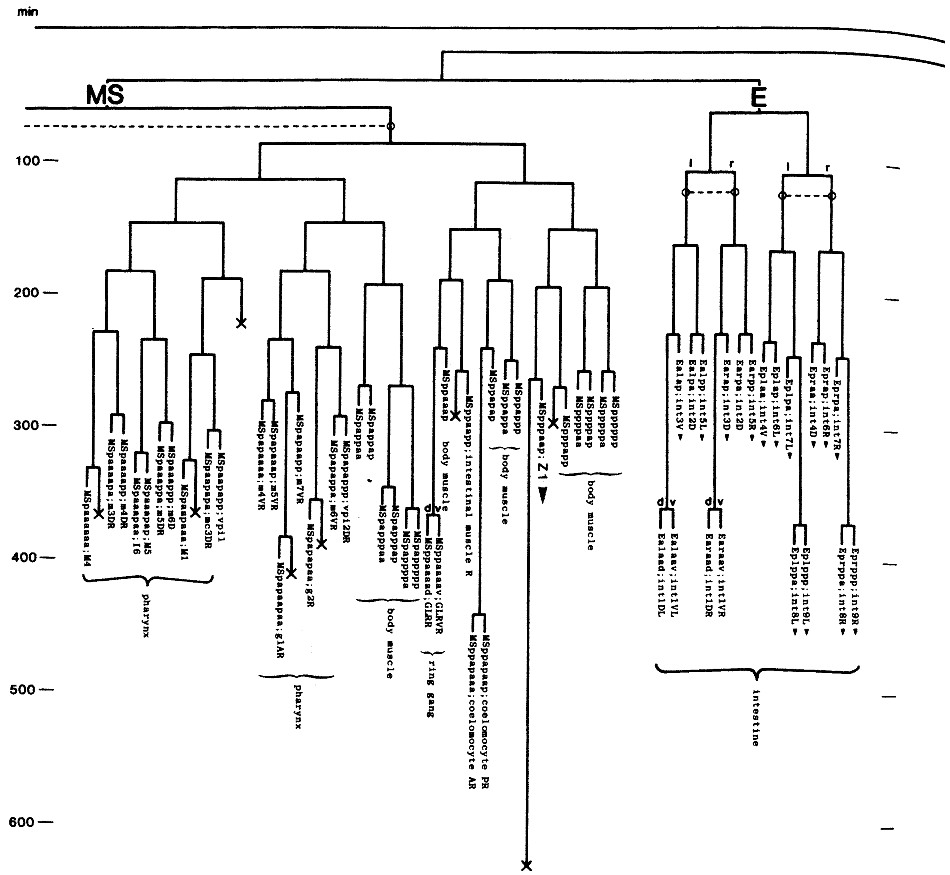

Figure 1 (Continued.)

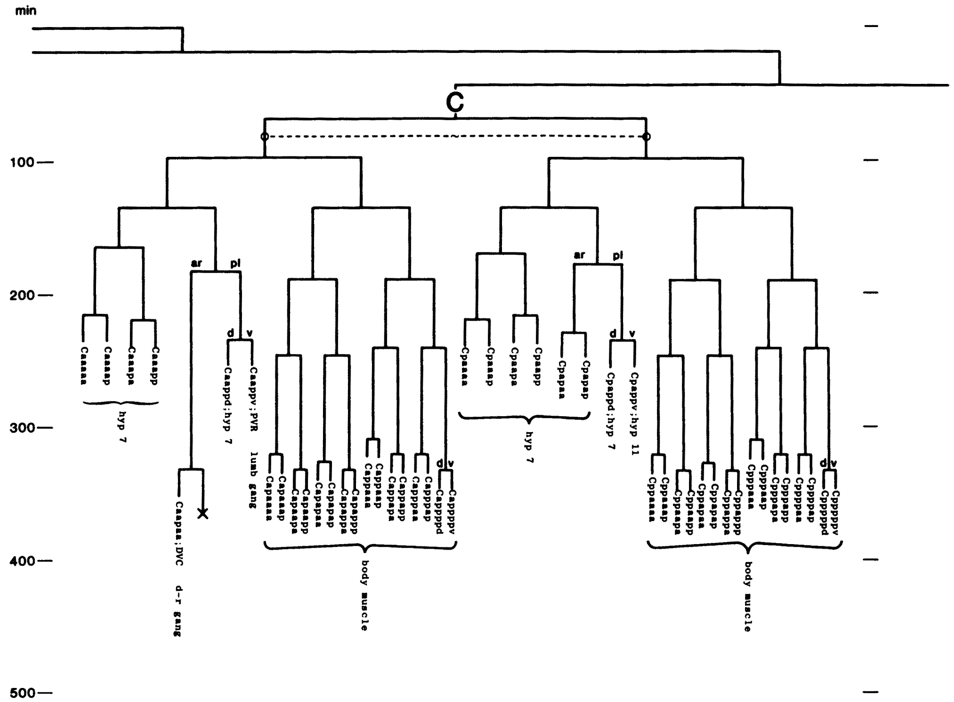

Figure 1 (Continued.)

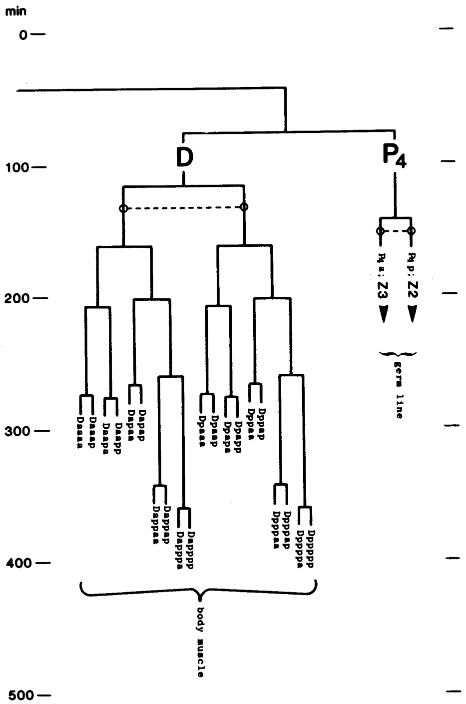

Figure 1 (*Continued.*)

Figures 2–8 Postembryonic cell lineages of *C. elegans.* All divisions are anterior-posterior unless otherwise indicated. Molts are indicated by solid lines on the time axis, the adjacent stippling indicating the period of lethargus. (Reprinted, with permission: Figs. 2–6 are from Sulston and Horvitz [1977]; Figs. 7–8 are from Kimble and Hirsh [1979].)

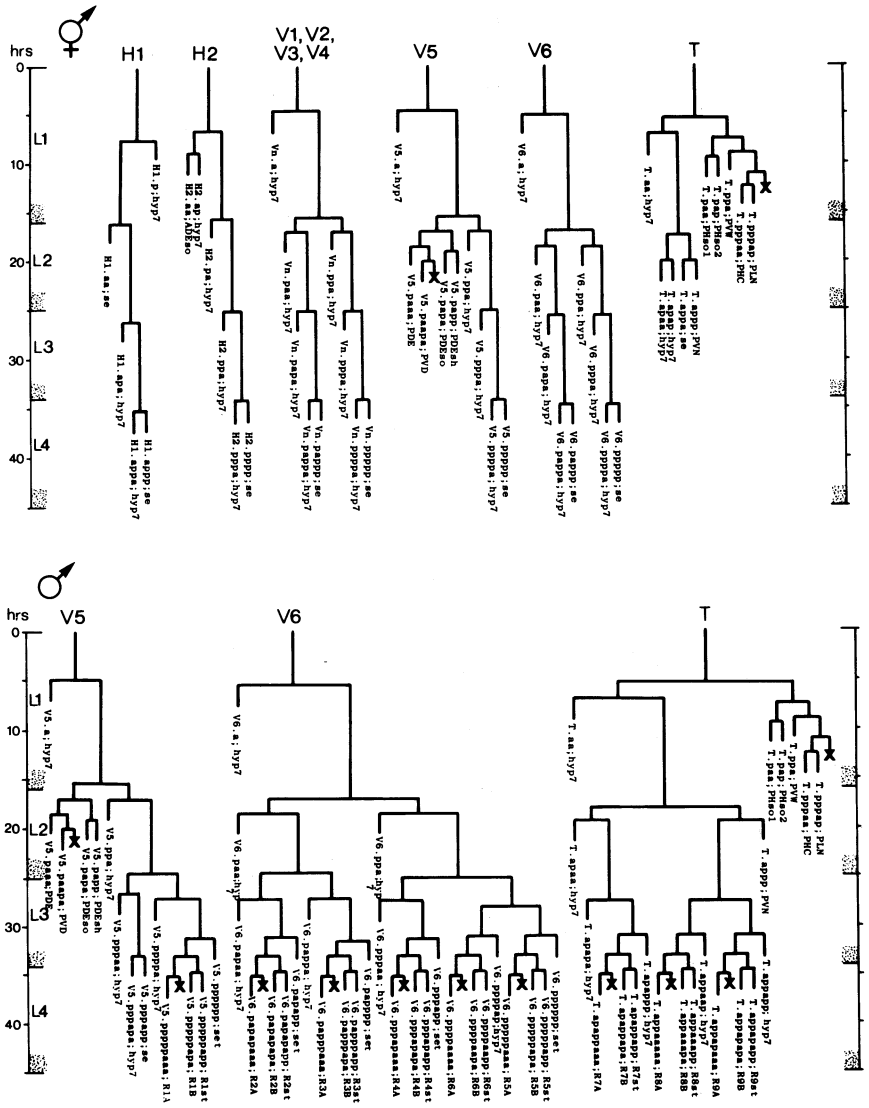

Figure 2 H, V, and T lineages: development of the lateral hypodermis. (se) Seam; (set) tail seam.

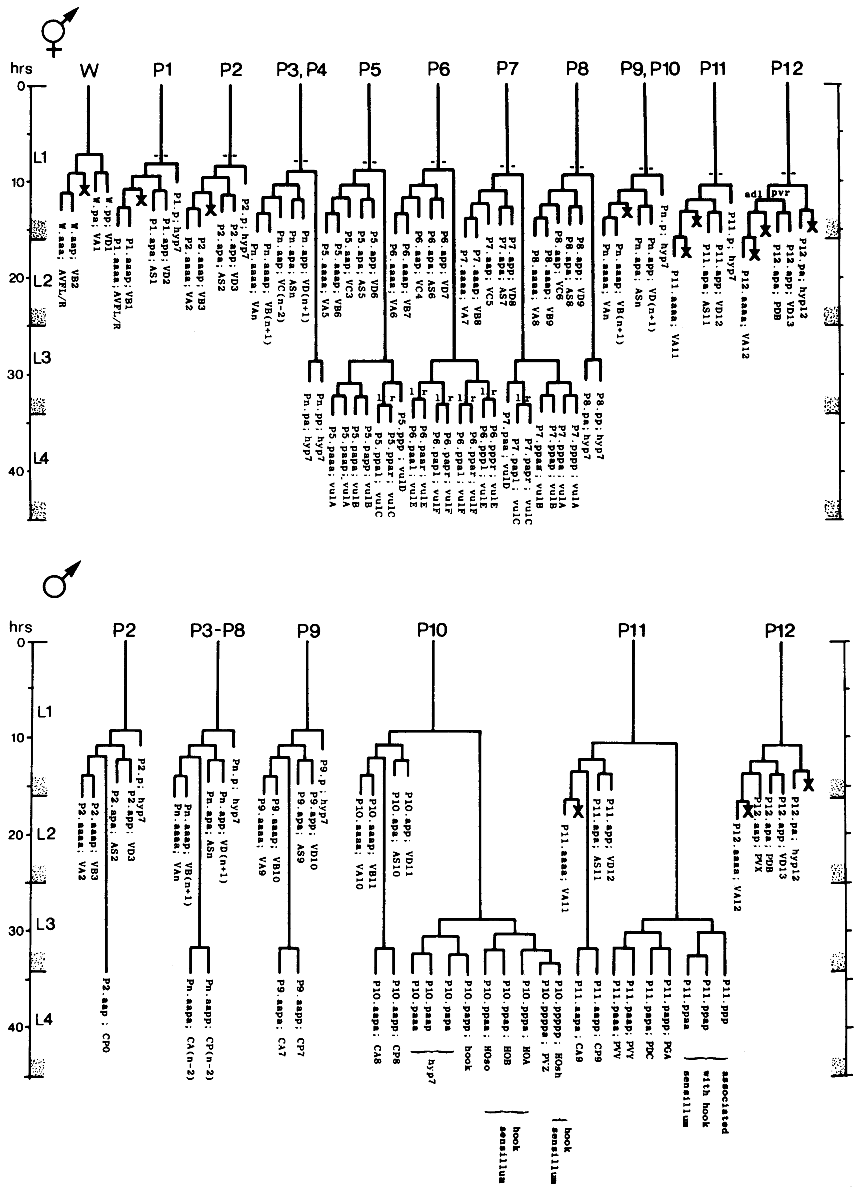

Figure 3 P lineages: development of the ventral nervous system. Dotted lines indicate the times at which nuclei migrate into the ventral cord.

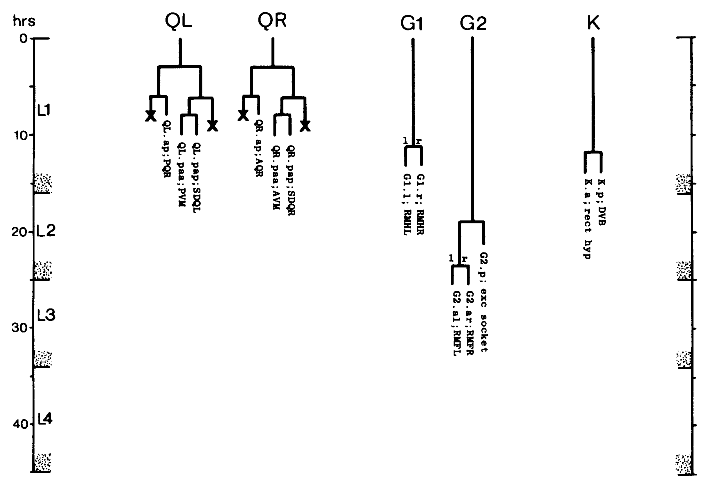

Figure 4 Q, G, and K lineages: other neuroblasts.

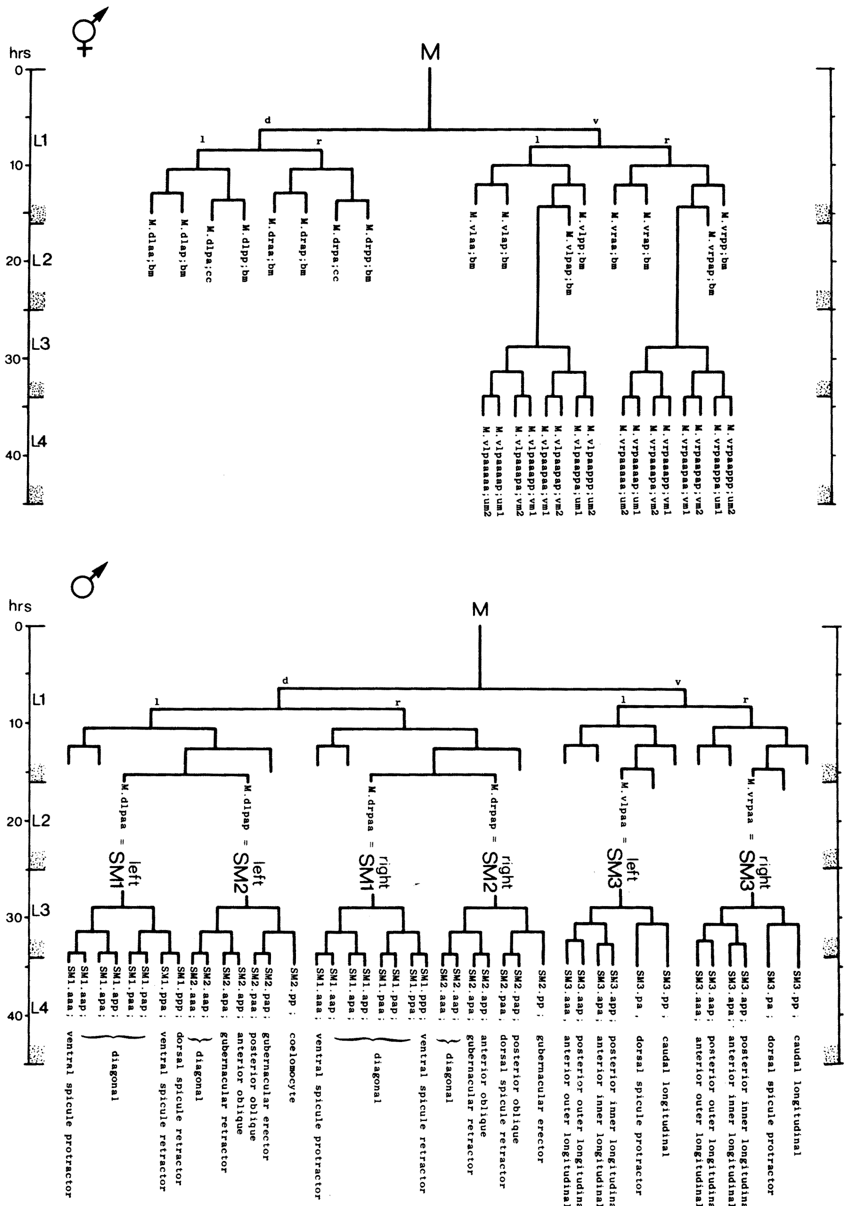

Figure 5 M lineage: mesodermal development. (bm) Body muscle; (cc) coelomocyte.

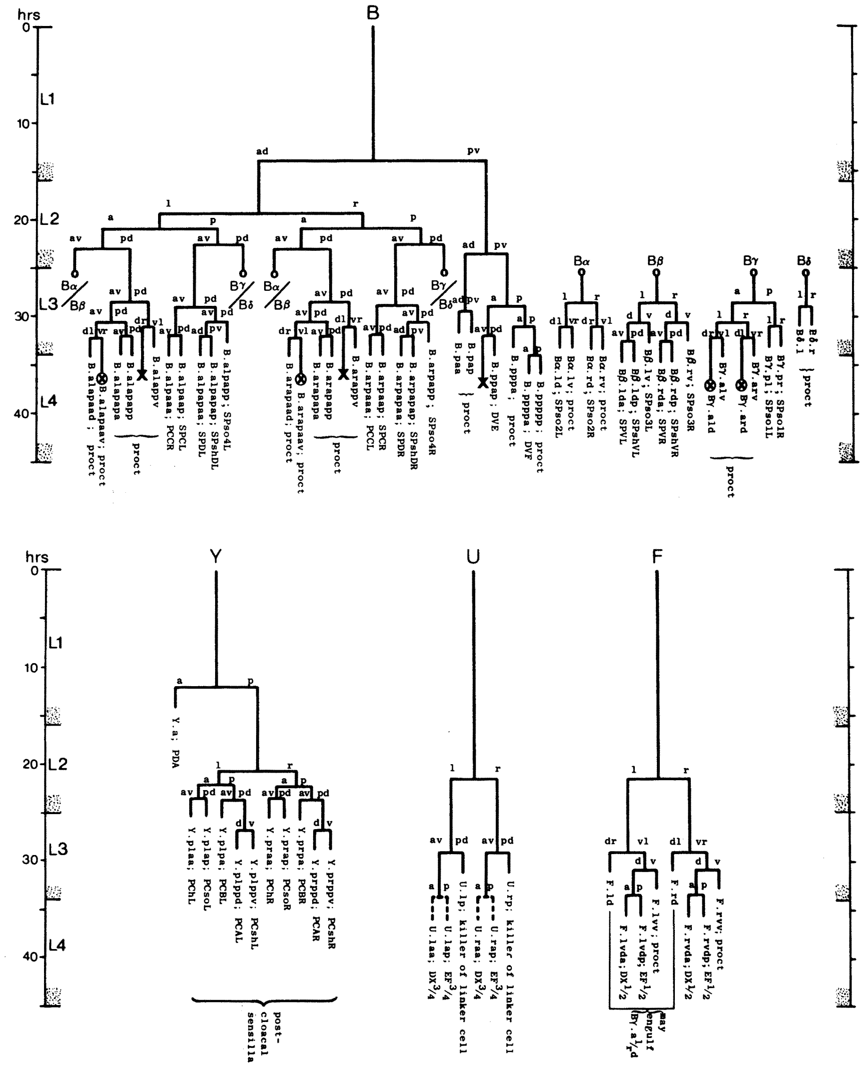

Figure 6 B, Y, U, and F lineages: ectodermal development in the male tail. Y, U were formerly C, E, respectively.

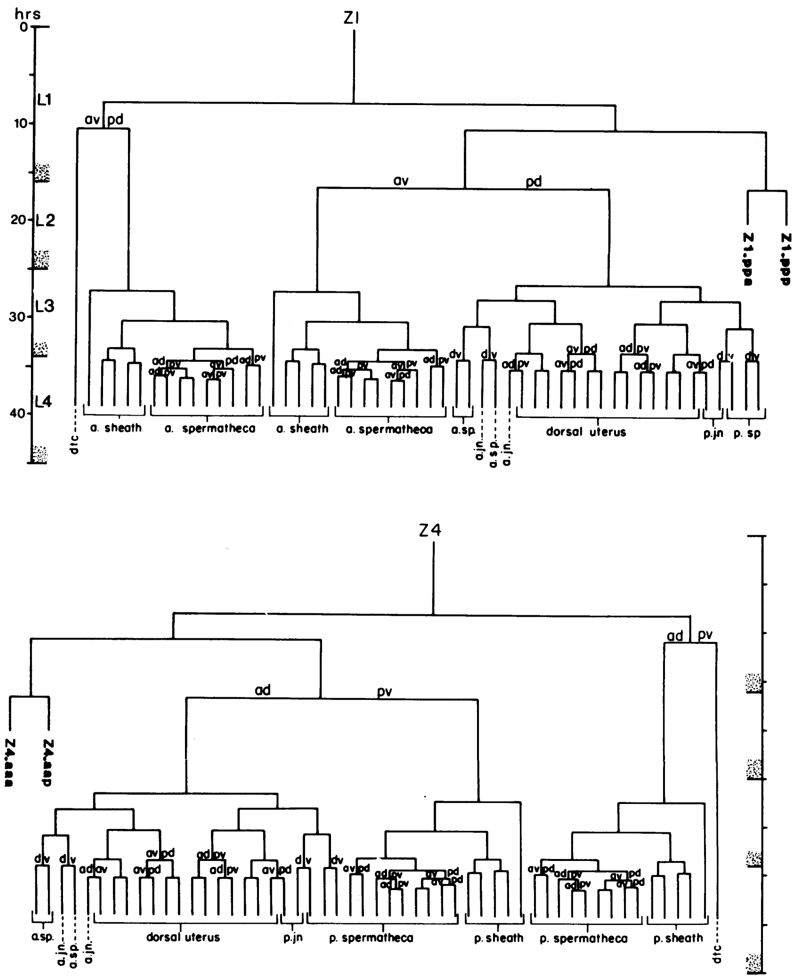

Figure 7 (*Continued on facing page.*)

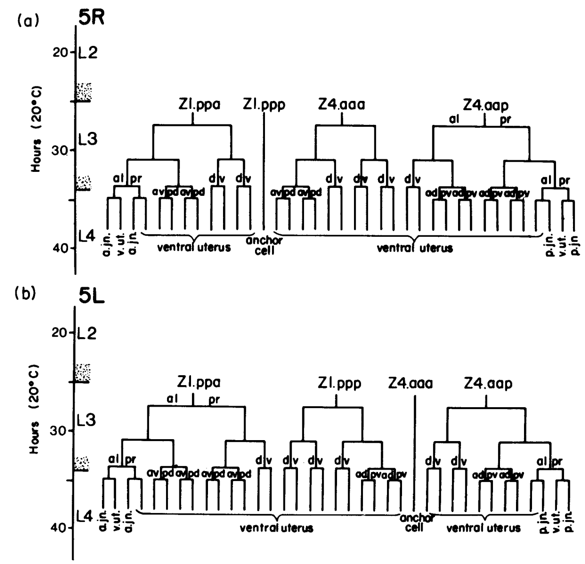

Figure 7 Z1 and Z4 lineages: development of the somatic gonad in the hermaphrodite. (*Left-hand page*) Invariant lineages; (*above*) the two alternative lineages followed by Z1.ppa, Z1.ppp, Z4.aaa, and Z4.aap. (a) Anterior; (p) posterior; (dtc) distal tip cell; (sp) spermatheca; (jn) spermathecal-uterine junction; (v.ut.) ventral uterus.

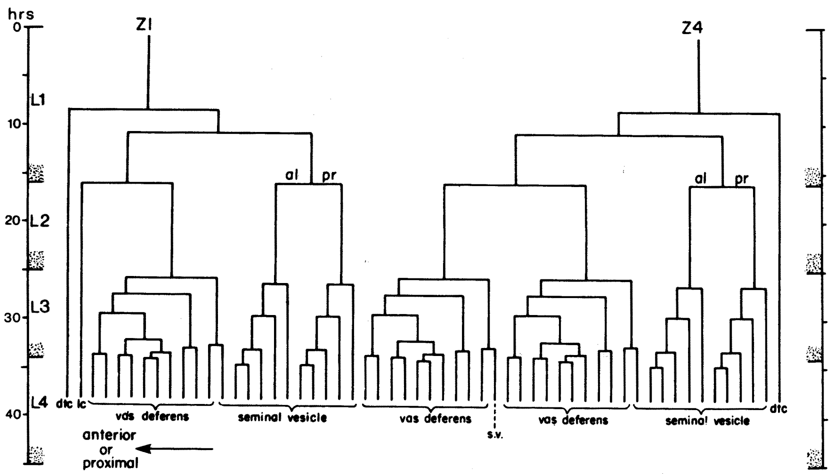

Figure 8 Z1 and Z4 lineages: development of the somatic gonad in the male. One of the two alternative lineages is shown here; in the other, the fates of Z1.paa and Z4.aaa are exchanged. (dtc) Distal tip cell; (lc) linker cell; (s.v.) seminal vesicle.

Part B: Positions of Nuclei

Figures 9–11 Drawings of embryos. Circles and ovals represent nuclei, traced by means of a camera lucida, the thickness of the lines being inversely related to depth; outlines of the egg, embryo, and internal structures are traced with thin lines (regardless of depth). Anterior is toward the top of the page. Dying nuclei are stippled. (Reprinted, with permission, from Sulston et al. 1983.)

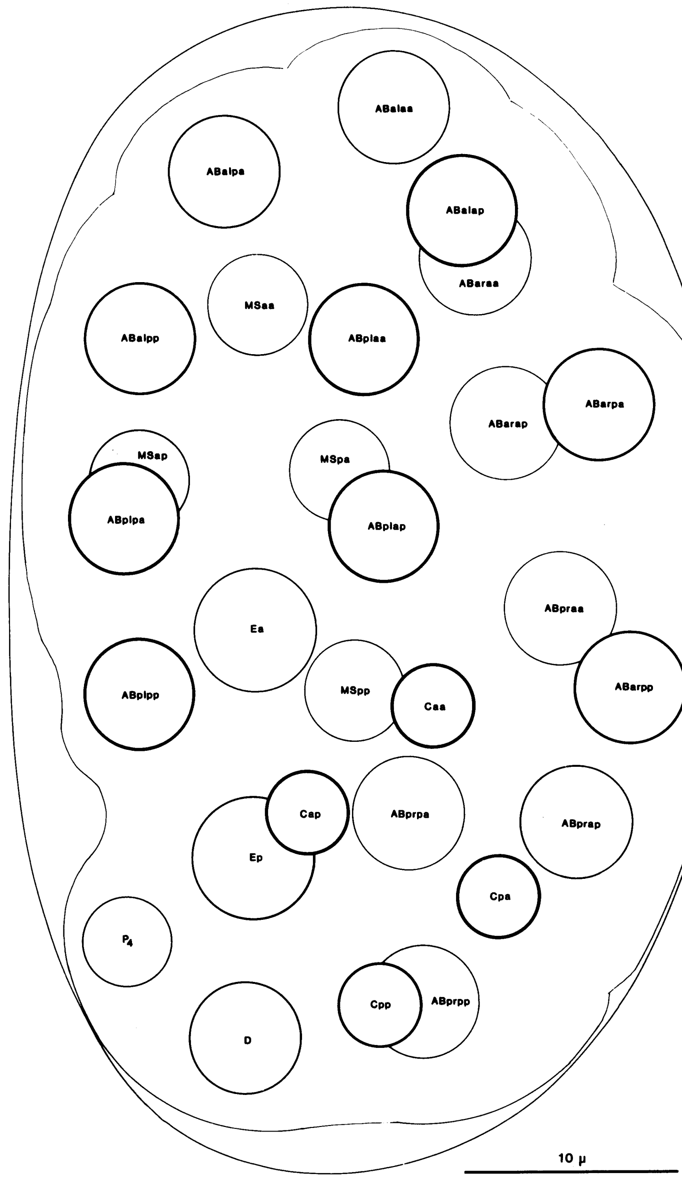

Figure 9 Embryo, 100 min, left dorsal aspect; all nuclei included. This stage has been well characterized, and the observer quickly learns to recognize all the nuclei; it is a useful starting point both for lineages and for ablation experiments. An embryo in the orientation shown will present a dorsal aspect until it turns at 350 min; an embryo with the MS cells uppermost will present a ventral aspect. The intestinal precursors are entering the interior, leaving a characteristic depression on the ventral side.

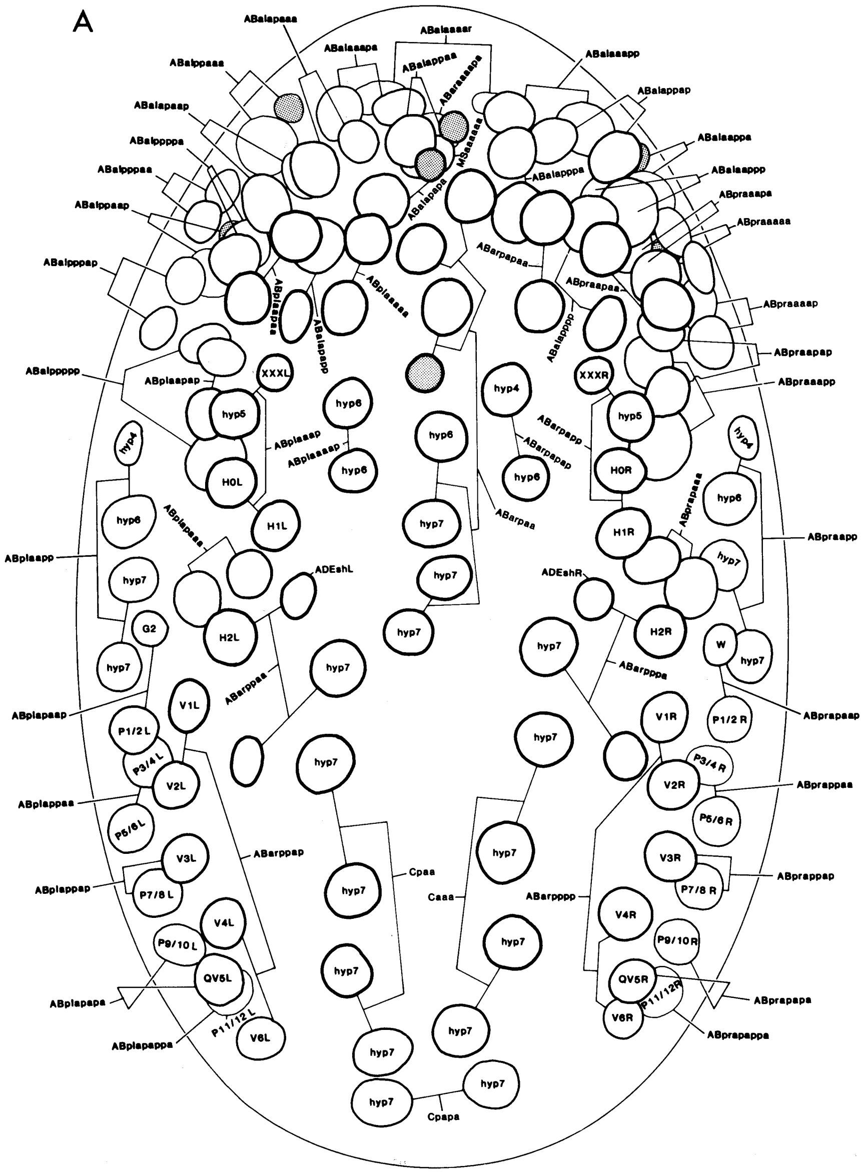

Figure 10 (*A*) Embryo, 260 min, dorsal aspect, superficial nuclei. Landmarks: nuclei of hyp4-hyp7, cell deaths; time points: division of various neuroblasts. Dorsal hypodermal cells have very granular cytoplasm and form prominent transverse ridges. Here and in Figure 10B some licence has been allowed in depicting cell deaths, because of their importance in pattern recognition; in fact, they do not all become refractile simultaneously.

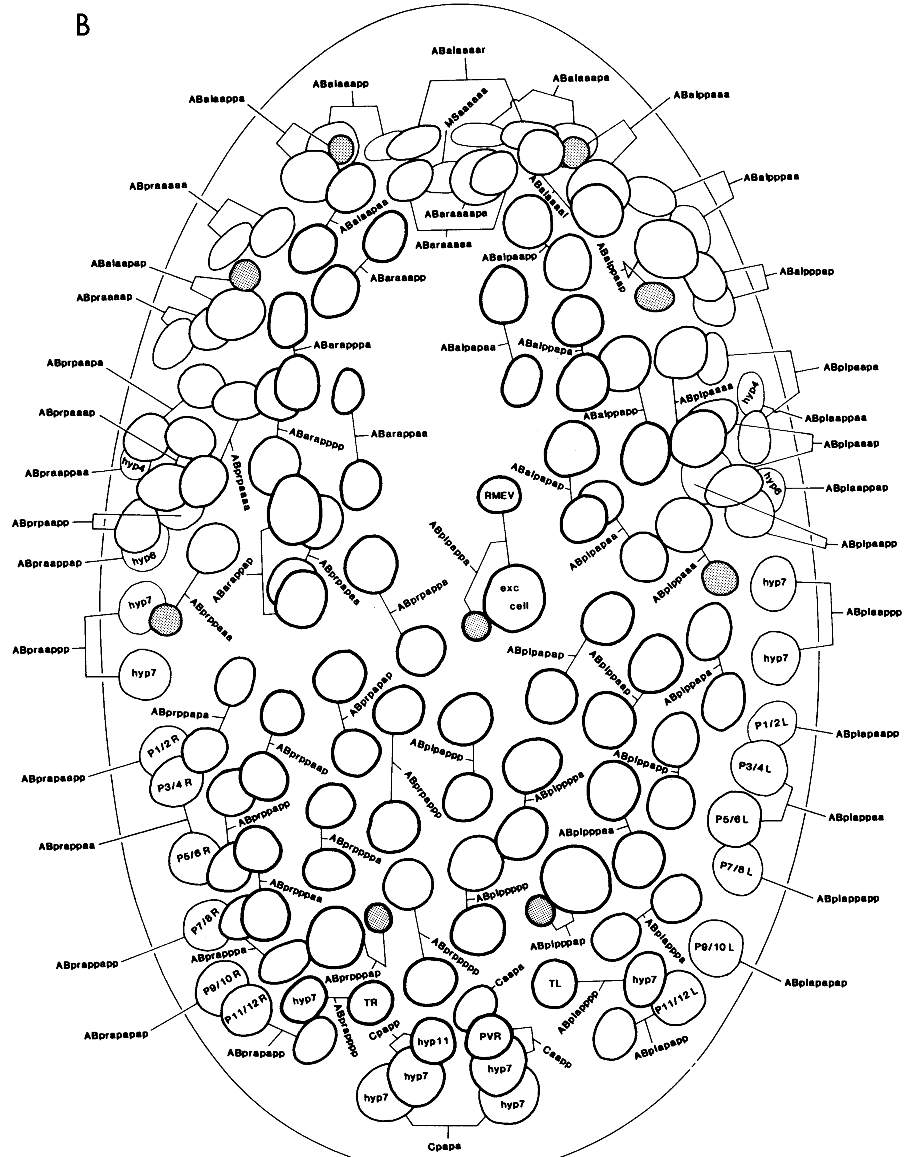

Figure 10 (*Continued.*)
(*B*) Embryo, 270 min, ventral aspect, superficial nuclei. Landmarks: excretory cell, cell deaths; time point: division of mother of excretory cell. The gap anterior to the excretory cell contains pharyngeal and buccal precursors which are entering the interior.

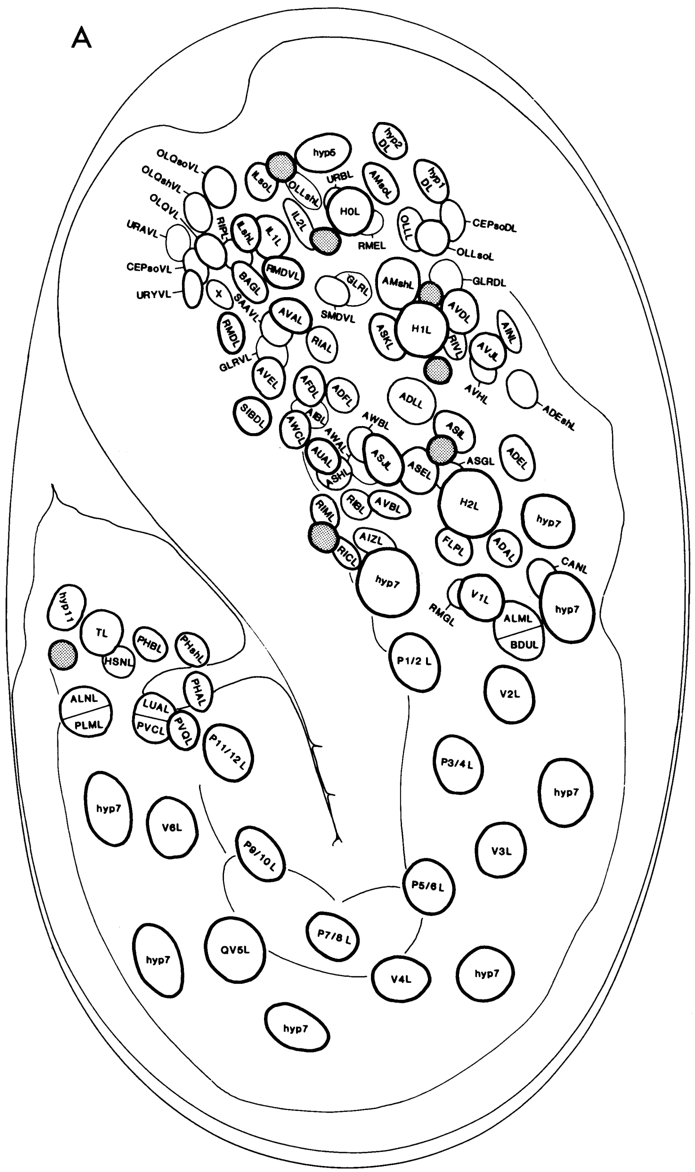

Figure 11A (See facing page for part B.)

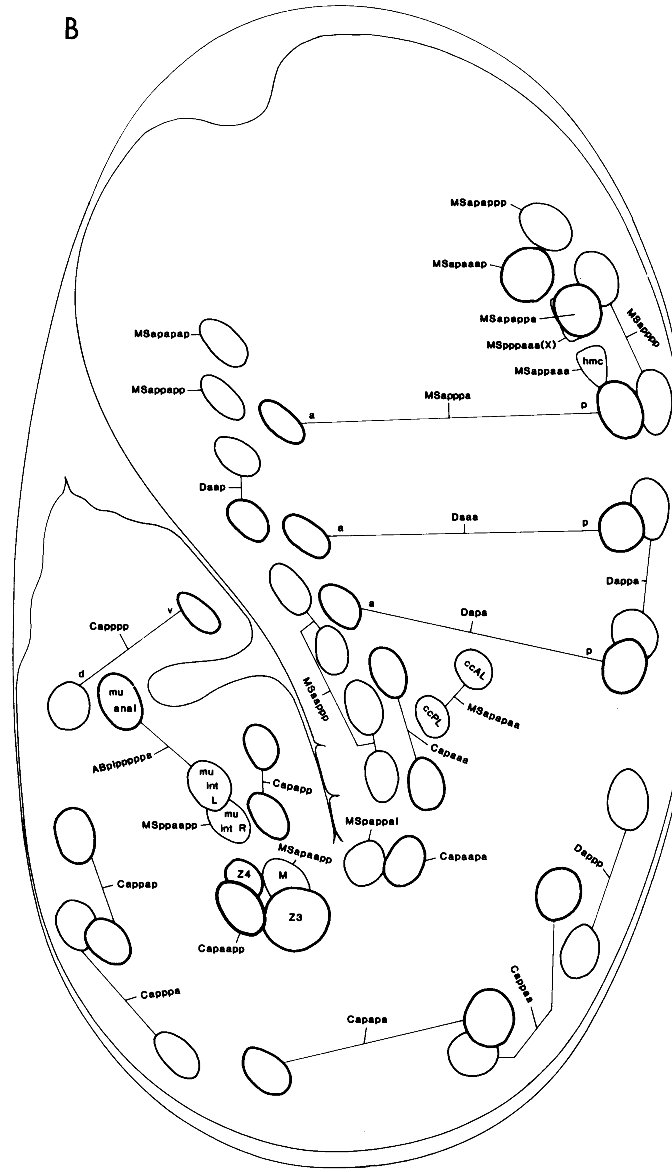

Figure 11B (See following pages for part C and legend.)

C

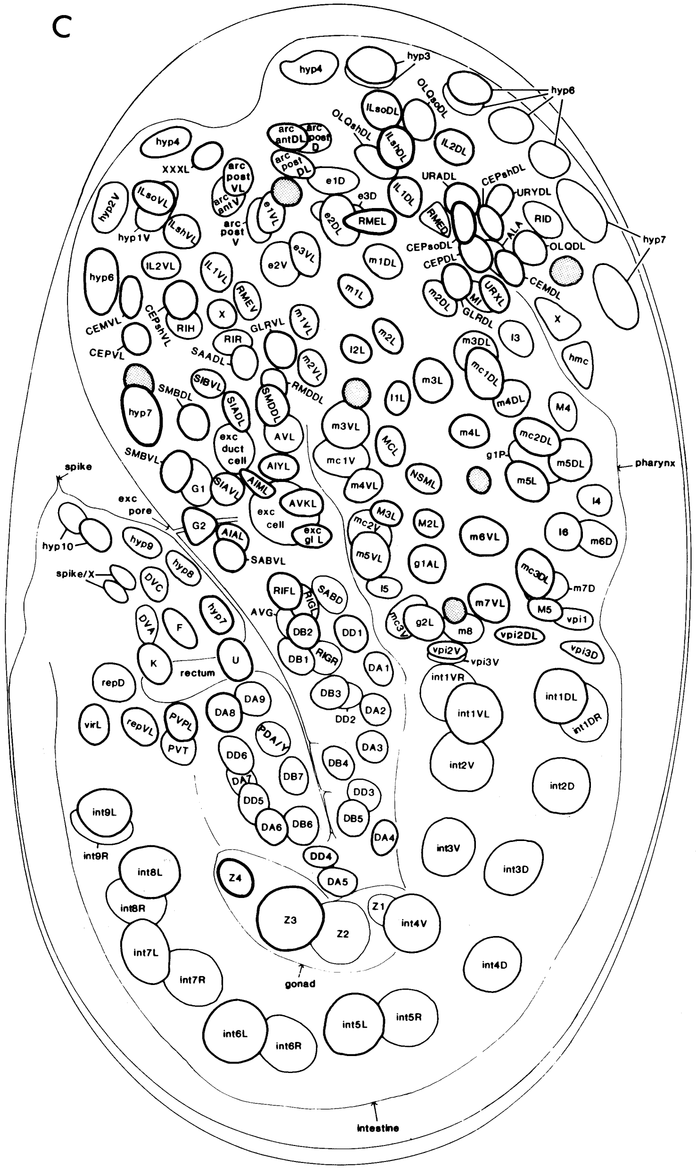

Figure 11C (*See facing page for legend.*)

Figure 11 This figure illustrates the arrangement of all left and central nuclei at 430 min after first cleavage; the right-hand side is a mirror image of the left, except where otherwise indicated. The three parts roughly represent three planes of focus (from superficial to central), but there is considerable overlap between them. The anterior sensory depression (not a mouth opening) is at the top and the lengthening tail, terminating in the spike, curves round to the left. On the ventral side of the tail, the rectal opening has appeared, and on the ventral side of the head the excretory duct leads to the excretory pore. (*A*) Left lateral ectoderm. No mid-plane nuclei are included, but the outlines of the pharynx, intestine, and gonad are shown for reference. Nuclei that will soon divide are labeled with the names of both presumptive daughters. The parent of QL and V5L is named QV5L. The pattern on the right is identical, except that: the homolog of hyp11 is PVR; an extra hyp7 nucleus (ABarpaappp) lies dorsal to H2R; there is no hyp2 DR. (*B*) Left and central mesoderm (excluding pharynx). M, mu int R, hmc, and MSpppaaa lie in the mid-plane. Unlabeled nuclei are in body muscles. The pattern on the right is identical, except that ABprpppppaa and ABprpppppap become a body muscle and the sphincter muscle, respectively, and lie slightly more anteriorly than their left-hand homologs. (*C*) Intestine, gonad, left central pharynx, and ectoderm. The pattern on the right is identical, except that: the homolog of G2 is W, of I6 is M1, of U is B, and of K is K′; an asymmetric neuron RIS (ABprpappapa) lies anterior to AVKR.

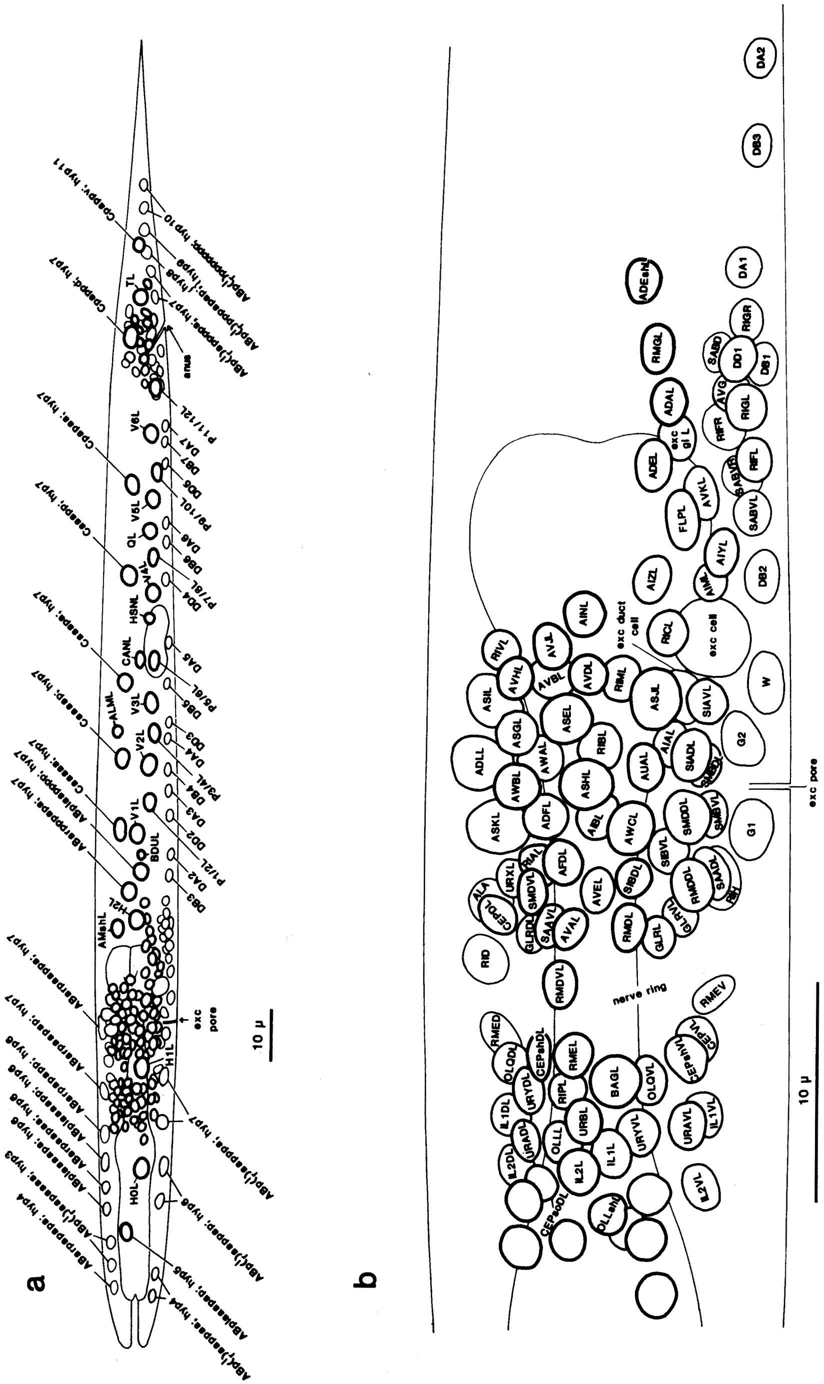

Figure 12 (See facing page for legend and parts c and d)

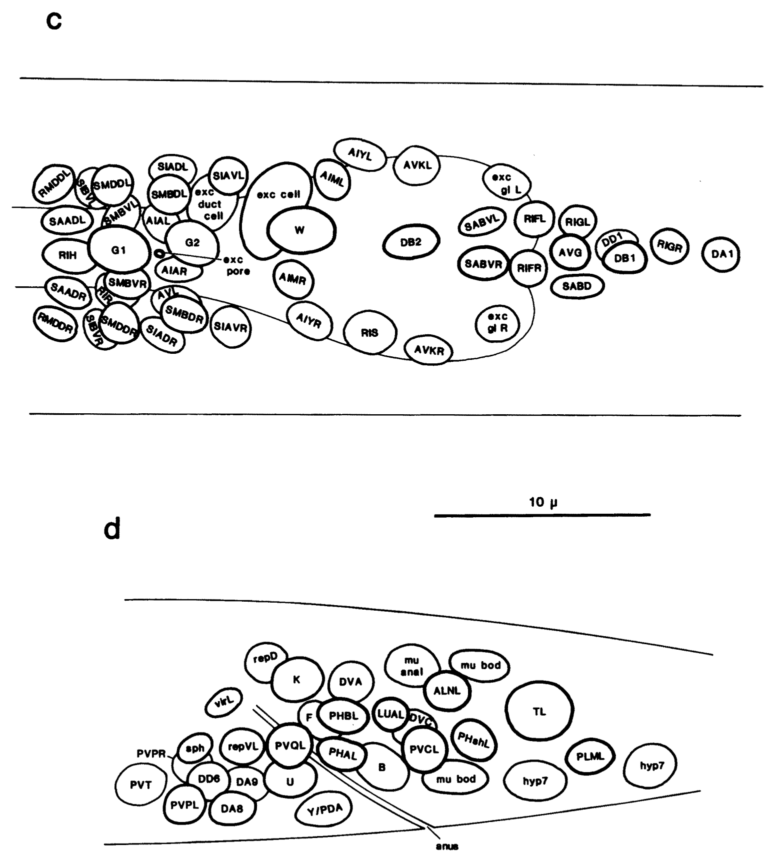

Figure 12 Arrangement of neuronal and larger hypodermal nuclei in newly hatched L1; based on camera lucida drawings. (*a*) Entire animal; left lateral aspect. Pattern on the right is identical, except that: an additional hyp7 nucleus (ABarpaappp) lies dorsal to H2R; homolog of QL is QR, of hyp11 is PVR. (*b*) Ring, ventral, and retrovesicular ganglia; left lateral aspect. Note that arrangement of ring ganglion cells around posterior bulb of pharynx is very variable at this stage. Anatomy anterior to the ring is not wholly known, since cells in this region were mostly identified by their processes in the embryo. (*c*) Ventral and retrovesicular ganglia; ventral aspect. (*d*) Preanal and left lumbar ganglia, rectal cells; left lateral aspect. (Corrected, with permission, from Sulston et al. 1983.)