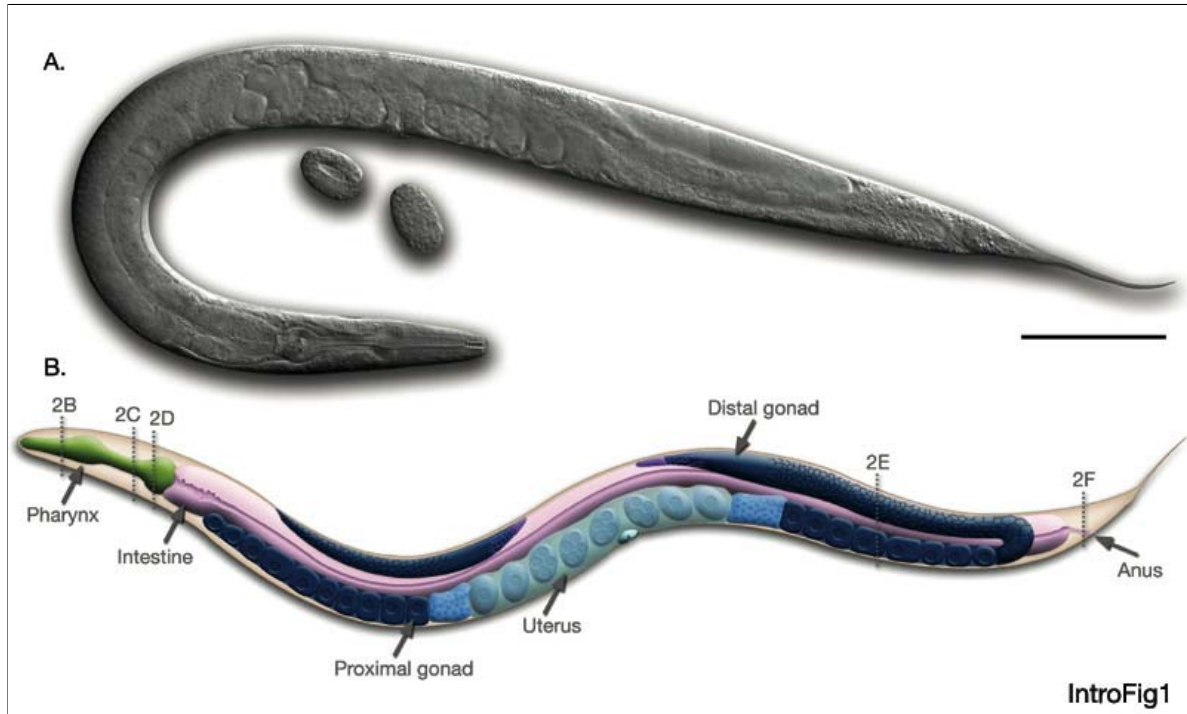


## INTRODUCTION TO *C. elegans* ANATOMY

[Ceasgeneticorganism](#) - [Adult anatomy](#) - [Life cycle](#) - [Back to Contents](#)

### CAENORHABDITIS *elegans* AS A GENETIC ORGANISM

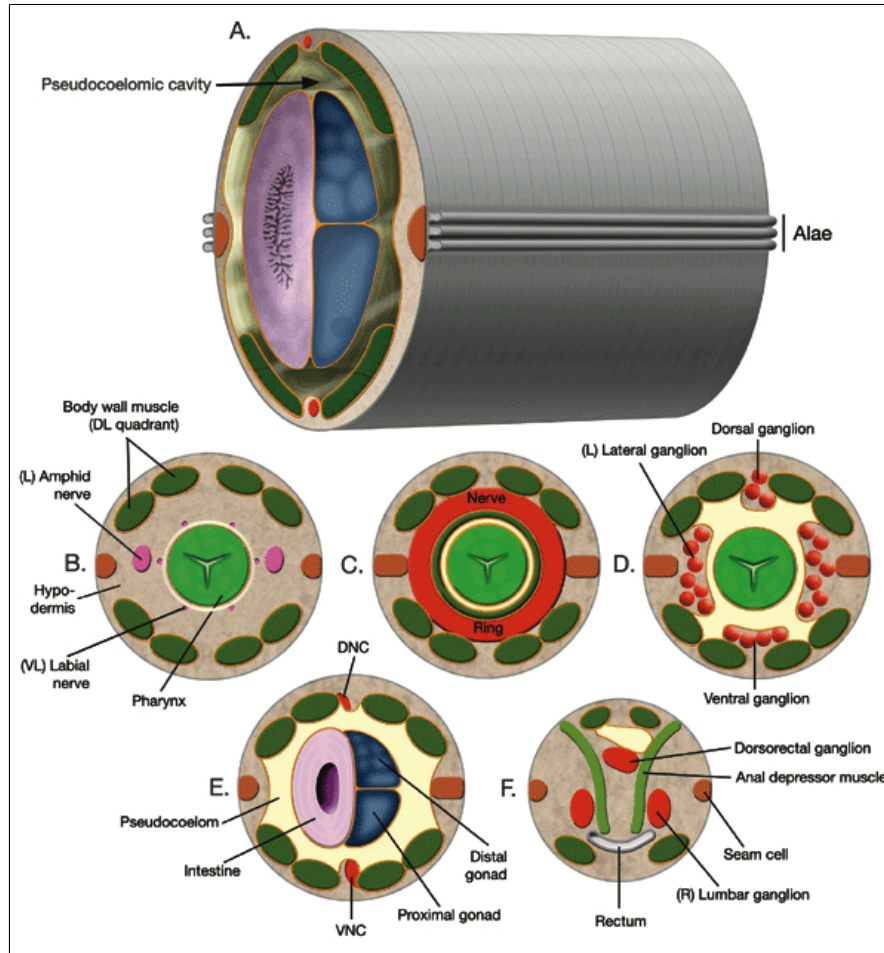
*Caenorhabditis elegans* is a small, free-living soil nematode (roundworm) that lives in many parts of the world and survives by feeding on microbes, primarily bacteria (**IntroFig1A&B**). It is an important model system for biological research in many fields including genomics, cell biology, neuroscience and aging (<http://www.wormbook.org/>). Among its many advantages for study are its short life cycle, compact genome, stereotypical development, ease of propagation and small size. The adult bodyplan is anatomically simple with about 1000 somatic cells. *C. elegans* is amenable to genetic crosses and produces a large number of progeny per adult. It reproduces with a life cycle of about 3 days under optimal conditions. The animal can be maintained in the laboratory where it is grown on agar plates or liquid cultures with *E. coli* as the food source. It can be examined at the cellular level in living preparations by differential interference contrast (DIC) microscopy, since it is transparent throughout its life cycle. The anatomical description of the whole animal has been completed at the electron microscopy level and its complete **cell lineage**, which is invariant between animals, has been established (**Brenner, 1973; Byerly et al., 1976; Sulston et al., 1983; Wood, 1988a; Lewis and Fleming, 1995**). There are two *C. elegans* sexes, a self-fertilizing hermaphrodite (XX) and a male (XO). Males arise infrequently (0.1%) by spontaneous non-dysjunction in the hermaphrodite germ line and at higher frequency (up to 50%) through mating (hermaphrodites can also be induced to generate male progeny spontaneously at a higher rate by treatment at high temperature). Self-fertilization of the hermaphrodite allows for homozygous worms to generate genetically identical progeny and male mating facilitates the isolation and maintenance of mutant strains as well as moving mutations between strains. Mutant animals are readily obtained by chemical mutagenesis or exposure to ionizing radiation (**Anderson, 1995; Jorgensen and Mango, 2002**). The strains can be kept as frozen stocks for long periods of time. *C. elegans* can also endure harsh environmental conditions by switching to a facultative diapause stage called dauer larva that can survive 4 to 8 times the normal 3-week life span (**Cassada and Russell, 1975**). Despite its simple anatomy, the animal displays a large repertoire of behavior including locomotion, foraging, feeding, defecation, egg laying, dauer larva formation, sensory responses to touch, smell, taste and temperature as well as some complex behaviors like male mating, social behavior and learning and memory (**Rankin, 2002; de Bono, 2003**).



**IntroFIG1.** Anatomy of an adult hermaphrodite. **A.** DIC image of an adult hermaphrodite, left lateral side. Scale bar 0.1 mm. **B.** Schematic drawing of anatomical structures, left lateral side. Dotted lines and numbers mark the level of each section in IntroFIG2.

## ADULT ANATOMY

**I. BODY SHAPE.** Similar to other nematodes, *C. elegans* has an unsegmented, cylindrical body shape that is tapered at the ends (**IntroFIG1A&B**). It shows the typical nematode body plan with an outer tube and an inner tube separated from each other by the pseudocoelomic space (**IntroFIG2**). The outer tube (body wall) consists of cuticle, hypodermis, excretory system, neurons and muscles, and the inner tube, the pharynx, intestine and, in the adult, gonad. All of these tissues are under an internal hydrostatic pressure, regulated by an osmoregulatory system (see [Excretory System](#) Chapter).



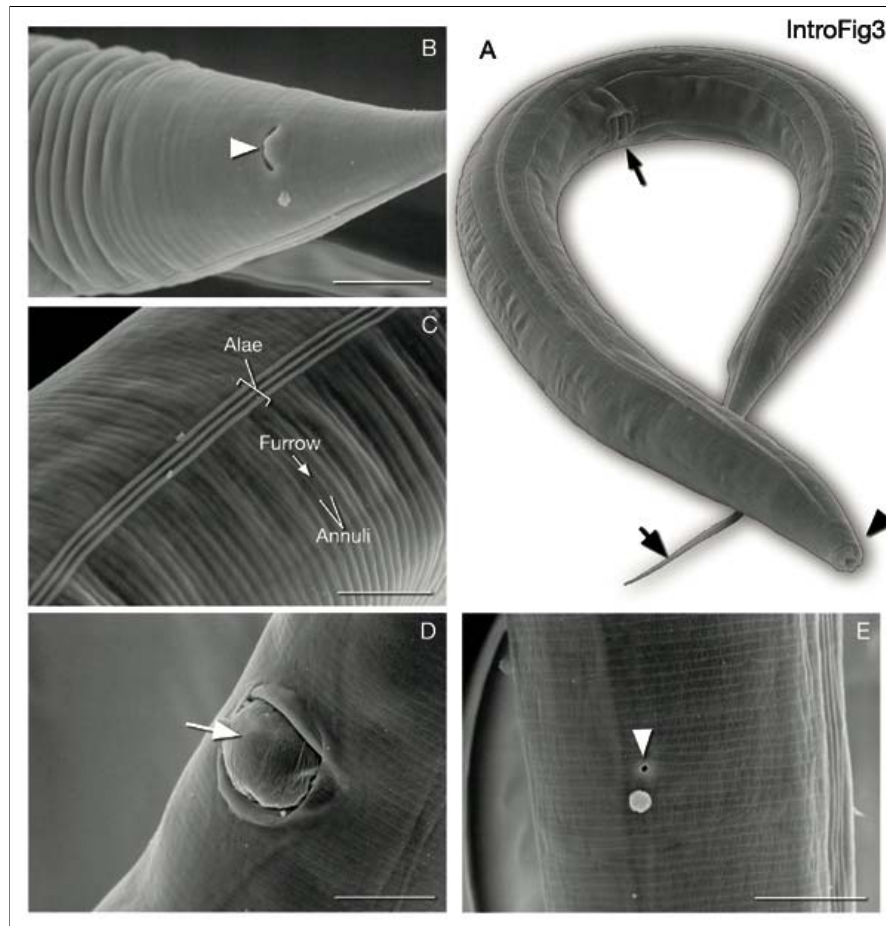
**IntroFIG2.** Nematode body plan with cross sections from head to tail. Approximate level of each cross section is labeled in IntroFIG1B. **A.** Posterior body region. Body wall (outer tube) is separated from the inner tube (alimentary system, gonad) by a pseudocoelom. Orange lines indicate basal laminae. **B.** Section through anterior head. The narrow space between the pharynx and the surrounding tissues anterior to the NR can be considered an accessory pseudocoelom since the main pseudocoelom is sealed off by the GLRs at the NR level. **C.** Section through the middle of head. **D.** Section through posterior head. **E.** Section through posterior body. **F.** Section through tail, rectum area. DNC: Dorsal nerve cord; VNC: Ventral nerve cord.

## II. ADULT HERMAPHRODITE ORGANS AND TISSUES

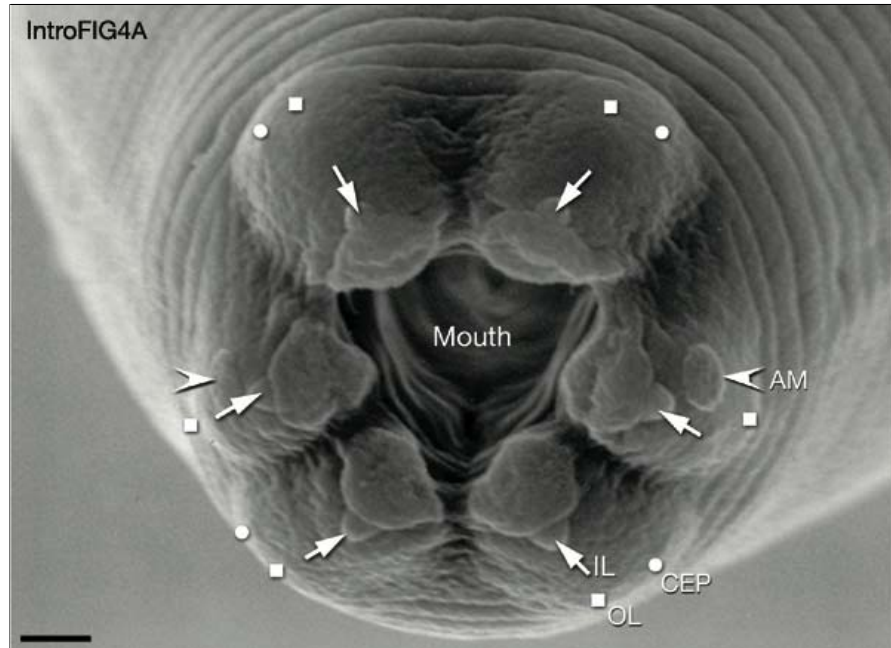
### A- BODY WALL

**Cuticle:** A collagenous cuticle, secreted by the underlying epithelium, surrounds the worm on the outside and also lines the pharynx and rectum (See [Cuticle](#) Chapter). Various tissues open to the outside through this cuticle (**IntroFIG3**). On the ventral side of the head, the excretory pore is located at midline (**IntroFIG3E**). Another larger opening on the ventral side at the midbody is the vulva (**IntroFIG3D**). The anus forms another ventral opening, just before the tail whip (**IntroFIG3B**). There are two cuticular inpockets forming narrow openings at the lateral lips for the amphid sensilla (**IntroFIG4A** and **IntroTABLE 1**). The lips also contain papillae for 6 inner labial (IL) sensilla, and small bumps for 6 outer labial (OL) sensilla, and 4 cephalic (CEP)

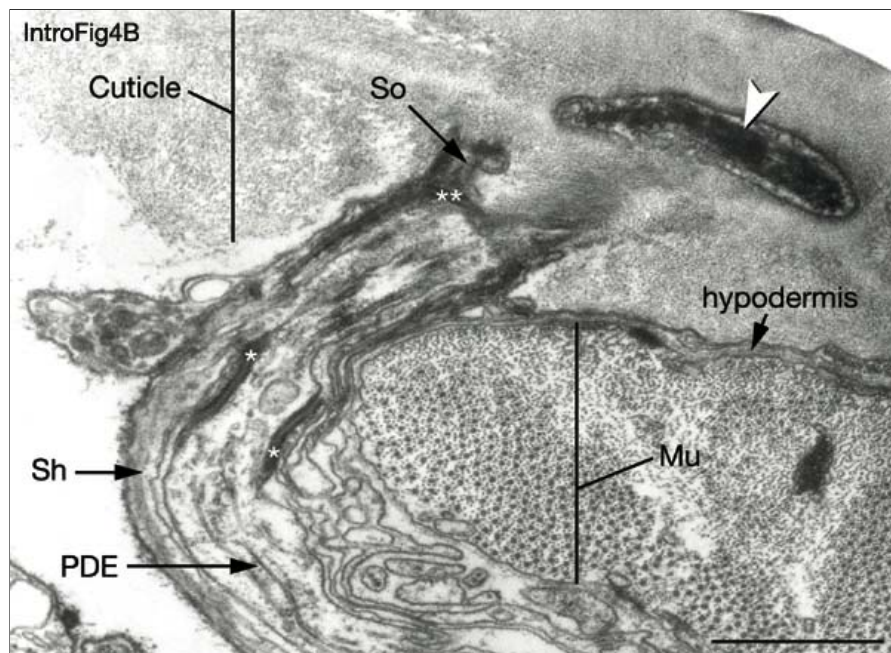
sensilla (**IntroFIG4A** and **IntroTABLE 1**). There are two papillae for anterior deirids at the posterior of the head. These are situated within the lateral alae at the level of the excretory pore (**IntroFIG4C** and **ExcFIG2B**). The two posterior deirids are situated dorsal to the cuticular alae (**IntroFIG4B,C**). Two much narrower openings on the lateral sides of the tail whip exist for the phasmid sensilla at the junction of the seam cells and the tail hypodermis (**IntroFIG4C**).



**IntroFIG3.** SEMs of adult *C. elegans* and various body regions. **A.** Adult hermaphrodite lying on its right lateral side. Arrowhead shows the lip, arrow, the tail, and thin arrow, the vulva at midbody. Image source: Juergen Berger. **B.** Alimentary canal opens to outside through anus at ventral midline (arrowhead). Magnification: 2,300x. Scale bar: 10 micrometers. Image source: SEM (Hall) 4605. **C.** Outside surface of cuticle on the lateral side bearing circumferential ridges (annuli) and furrows. Alae form over the seam cells. Magnification: 2,200x. Scale bar: 10 micrometers. Image source: SEM (Hall) 4603. **D.** An egg (arrow) being expelled from vulva. Magnification: 2,300. Scale bar: 10 micrometers. Image source: SEM (Hall) 4610. **E.** Excretory pore (arrowhead) located at the ventral midline of head. Magnification: 2,700. Scale bar: 10 micrometers. Image source: SEM (Hall) 4609.



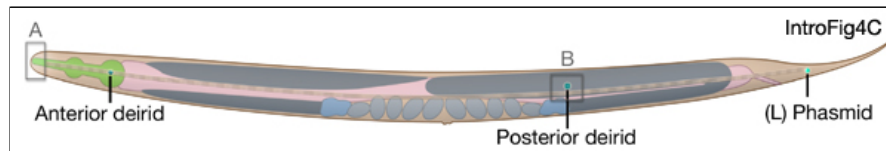
**IntroFIG4A.** (*C. elegans* sensilla) SEM of adult *C. elegans* showing the six symmetrical lips surrounding the opening of the mouth and the sensilla of the lip region. OL, Outer Labial; CEP, Cephalic; AM, Amphid; IL, Inner Labial. Magnification: 9,000x. Scale bar: 1 micrometer. Image source: SEM (Hall) 3918.



**IntroFIG4B.** (*C. elegans* sensilla) TEM, transverse section of the ending of a posterior deirid sensillum. Arrowhead points to cytoplasmic material within PDE neuron ending in the cuticle. The neuron is concentrically surrounded by the sheath (Sh) and socket (So) cells which connect to each other by adherens



junctions (asterisks). Socket cells, in turn are connected to the hypodermis by adherens junctions (double asterisk). Bar: 1 micrometer. Image source: (MRC) N2Y 2761-15.



**IntroFIG4C.** (*C. elegans* sensilla) Paired sensilla of the anterior deirid, posterior deirid, and phasmid as seen from the left lateral side. The rectangle labeled A points to the section shown in IntroFIG4A.

Sensilla	Open to outside	Papilla	Nubbin
Amphid <sup>1</sup>	+	-	-
Phasmid	+	-	-
Inner Labial <sup>3</sup>	+	+	-
Outer Labial <sup>2</sup>	-	-	+
Cephalic <sup>2,4</sup>	-	-	+
Anterior Deirid <sup>2</sup>	-	-	+
Posterior Deirid <sup>2</sup>	-	-	+

**IntroTable I**

**IntroTable.** Structure of the sensilla. (1) The two amphids open to outside through little pockets on the cuticle. (2) Nubbins are located at the distal regions of the cilia. (3) The six IL1 and six IL2 endings share the same inner labial sensilla, but IL2 dendrites protrude to the outside while IL1 endings do not. (4) In males the four CEM neurons open to outside through cephalic sensilla ([Ward et al., 1975](#)).

**The Epithelial System:** The hypodermis, which secretes cuticle, is made up of the main body syncytium (hyp 7), a series of concentric rings of five smaller syncytial cells in the head, and three mononucleate and one syncytial cell in the tail (See Epithelial System Chapter-[Hypodermis](#)). On the lateral sides, hypodermis is interrupted by the syncytial row of seam cells which form alae on the cuticle surface during certain developmental stages ([IntroFIG3C](#)) (See Epithelial System Chapter-[Seam Cells](#)). Hypodermis and the inner tissues that open to the outside are connected to each other by specialized interfacial cells (See Epithelial System Chapter- [Glia](#) and [Other Support](#) cells).

**The Nervous System:** The cells of the nervous system are organized into ganglia in the head and tail. The majority of *C. elegans* neurons are located in the head around the pharynx. In the body, a continuous row of neuron cell bodies lies at the midline, adjacent to ventral hypodermis. In addition, there are two small posterior

lateral ganglia on the sides as well as some scattered neurons along the lateral body. The processes from most neurons travel in either the ventral or dorsal nerve cord and project to the nerve ring in the head which constitutes the major neuropil in the animal (**IntroFIG2C**).

*The Muscle System:* Neurons and hypodermis are separated from the musculature by a thin basal lamina. The muscles receive input from the neurons by sending muscle arms to motor neuron processes that run along the nerve cords or reside in the nerve ring. The obliquely striated body wall muscles are arranged into strips in four quadrants, two dorsal and two ventral, along the whole length of the animal (**IntroFIG2A-F**) (See Muscular System Chapter-**Somatic muscle**). Smaller, nonstriated muscles are found in the pharynx and around the vulva, intestine and rectum (See Muscular System Chapter-**Nonstriated muscle**).

*The Excretory System:* Four cells situated on the ventral side of the posterior head make up the excretory system which functions in osmoregulation and waste disposal. It opens to the outside through the excretory pore (**IntroFIG3E**) (see **Excretory System** Chapter).

#### B- PSEUDOCOELOMIC CAVITY ORGANS

*The Coelomocyte system:* Three pairs of coelomocytes located in the pseudocoelomic cavity function as scavenger cells that endocytose fluid from the pseudocoelom and are suggested to comprise a primitive immune system in *C. elegans* (See **Coelomocyte System** chapter).

#### C- INTERNAL ORGANS

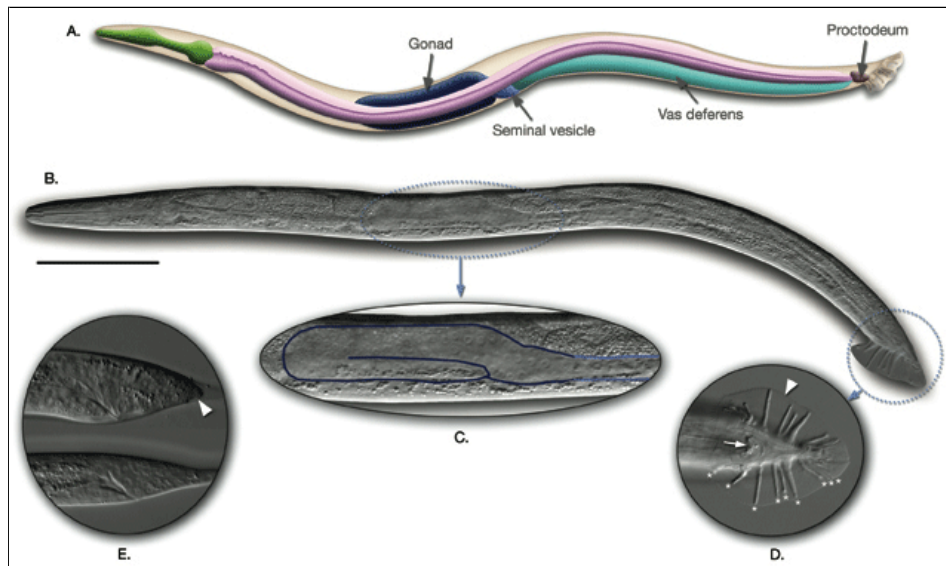
*The Alimentary System:* *C. elegans* feeds through a two-lobed pharynx which is nearly an autonomous organ with its own neuronal system, muscles, and epithelium (**IntroFIG1**). Pharynx is separated from the outer tube of tissues and pseudocoelom by its own basal lamina (**IntroFIG2B-D**) (See Alimentary System chapter-**Pharynx**). The lumen of the pharynx is continuous with the lumen of the intestine and the pharynx passes ingested and ground food into the intestine via the intestinal pharyngeal valve. The intestine which is the only somatic tissue derived from a single (E blast cell) lineage, is made of 20 cells arranged to form a tube with a central lumen (See Alimentary System chapter- **Intestine**). The apical surfaces of the intestinal cells carry numerous microvilli. The intestinal contents are excreted to the outside via a rectal valve that connects the gut to the rectum and anus. The four enteric muscles that contribute to defecation are located around the rectum and posterior intestine (See Alimentary System chapter-**Rectum and Anus**).

*The Reproductive System:* This system consists of somatic gonad, the germ line and the egg-laying apparatus. There are two bilaterally symmetric, U-shaped gonad arms that are connected to a central uterus through spermatheca (**IntroFIG1**). The germ line within the distal gonad arms (ovaries) is syncytial with germline nuclei surrounding a central cytoplasmic core. More proximally germ cells go sequentially through the mitotic, meiotic prophase and diakinesis stages. As they pass through the bend of the gonad arm (oviduct), the nuclei acquire plasma membrane to form oocytes which enlarge and mature as they move more proximally. They fertilize with the sperm in spermatheca and the zygotes are stored in the uterus and laid outside thorough the vulva which protrudes at the ventral midline (see **Reproductive System** chapter).

### III. ADULT MALE ANATOMY

The male anatomy is the subject of a separate section in this atlas (See Introduction to Male Anatomy-**Part I** and **Part II**), but in this chapter we will provide an overview of major differences between this and the hermaphrodite sex. Male *C. elegans* larvae initially display the same simple cylindrical body plan as hermaphrodites, but from L2 stage onwards, the shape of their posterior half changes as their sexual organs begin to develop (**IntroFIG5**) (**Sulston and Horvitz, 1977**; **Sulston et al., 1980**; **Nguyen et al., 1999**). With

the exception of perhaps the pharynx and the excretory system virtually all tissue systems exhibit some degree of sexual dimorphism. The most profound differences are seen in tissues of the posterior, which bears the male copulatory apparatus. The muscle system of the male contains additional 41 sex-specific muscles. The reproductive system consists of a single armed gonad (**IntroFIG5C**) that opens to the exterior at the cloaca (anus) via a modified rectal epithelial chamber called the proctodeum (**IntroFIG5D**). The proctodeum includes two sclerotic sensory spicules used by the male during mating to locate the hermaphrodite vulval slit and to hold the vulva open during sperm transfer (**Liu and Sternberg, 1995; Garcia et al., 2001**). The nervous system has 89 additional neurons that include several classes of tail sensilla: the rays which extend from the tail and lie in a cuticular fan, the hook and the post-cloacal sensilla which are located on the ventral exterior of the tail.



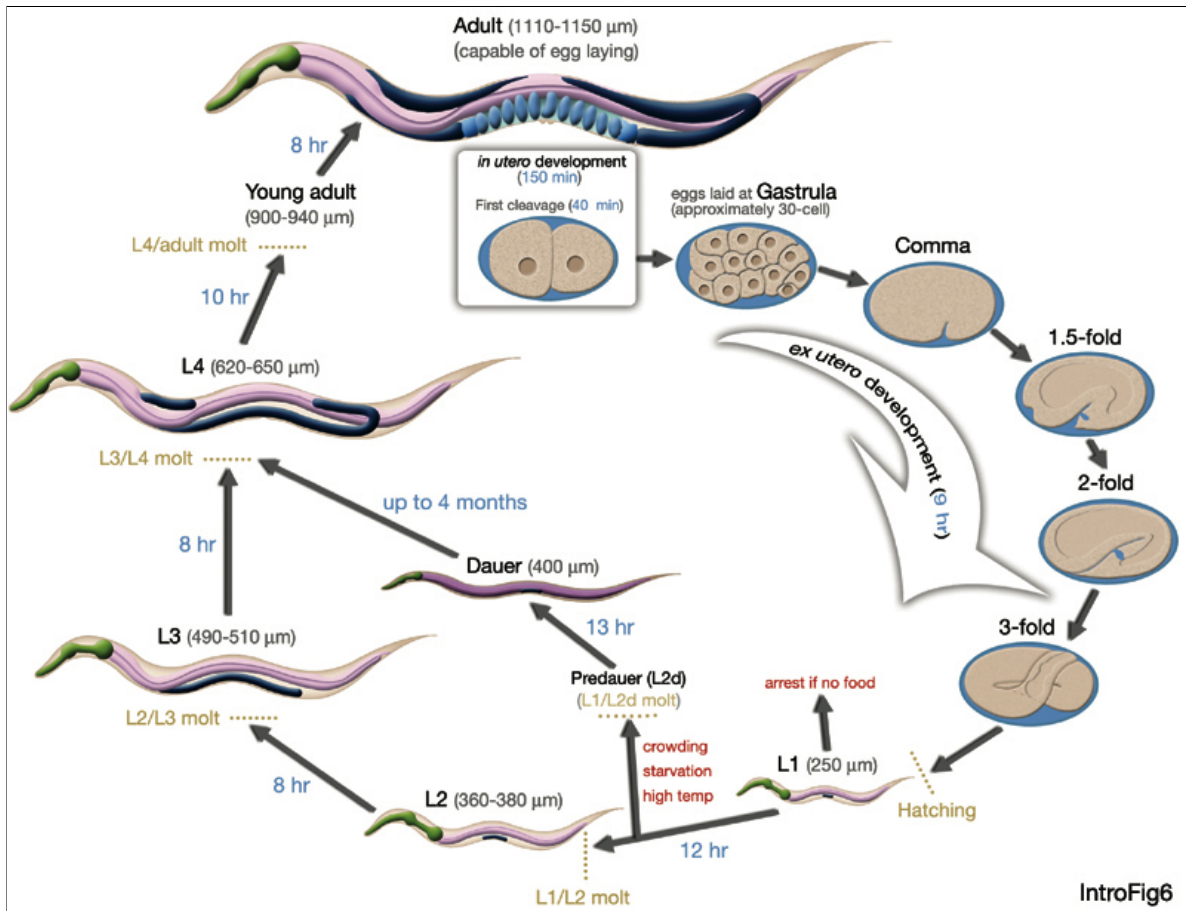
**IntroFIG5.** *C. elegans* male. **A.** Schematic drawing of anatomical structures, left lateral side. **B.** DIC image of an adult male, left lateral side. Scale bar 0.1 mm. **C.** The unilobed distal gonad of the animal in B is shown as enlarged. **D.** The adult male tail, ventral view. Arrow points to cloaca, arrowhead marks the fan. Rays 1-9 are labeled with asterisks on the left side. **E.** L3 tail, bottom, is starting to bulge (compare with **IntroFIG8** panel I). Tail hypodermis has retracted in L4 tail (arrowhead), top.

## LIFE CYCLE

Similar to other nematodes, the life cycle of *C. elegans* is comprised of the embryonic stage, four larval stages (L1-L4) and adulthood (**IntroFIG6**). The end of each larval stage is marked with a **molt** where a new, stage-specific cuticle is synthesized and the old one is shed (**Cassada and Russell, 1975**). Molting is accomplished in three steps; Step 1- the separation of old cuticle from the hypodermis (**apolysis**), Step 2- the formation of new cuticle arising from the hypodermis, and Step 3- the shedding of the old cuticle (**ecdysis**). Cuticle protein synthesis has been found to be high during molting and is very much reduced during intermolt periods. Furthermore, the cuticle ultrastructure and protein composition differ at each molt (**White, 1988**). Just before apolysis, pharyngeal pumping ceases and the animal enters a brief lethargus. Lethargus is divided into two phases; in the first phase locomotion stops and the cuticle becomes loosened from the lips, the buccal cavity and around the tail. This is followed by the second phase of lethargus when the larva starts to flip around its longitudinal axis, loosening the old cuticle further (**Bird and Bird, 1991**). About 30 min before ecdysis the



terminal bulb of the pharynx begins to twitch spasmodically, large refractile granules accumulate in the pharyngeal glands and the body starts to move. Subsequently the cuticular lining of the pharynx breaks down into the intestine at the posterior and through the mouth at the anterior. The larva further pushes against the old cuticle, and makes a hole at the head region through which it emerges. The larva then starts to feed immediately.

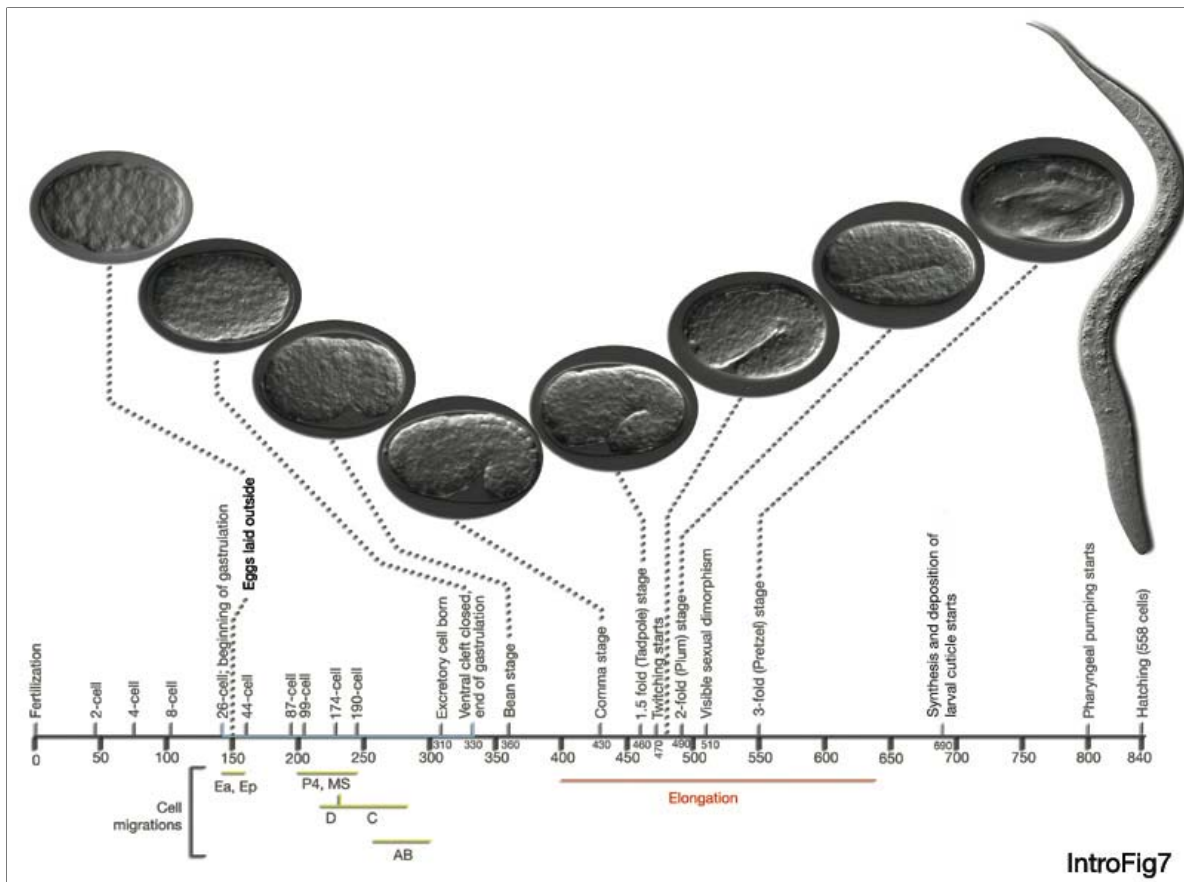


**IntroFIG6.** Life cycle of *C. elegans* at 22°C. 0 min is fertilization. Numbers in blue along the arrows indicate the length of time the animal spends at a certain stage. First cleavage occurs at about 40 min. postfertilization. Eggs are laid outside at about 150 min. postfertilization and during the gastrula stage. The length of the animal at each stage is marked next to the stage name in micrometers.

#### i- Embryo.

Embryogenesis in *C. elegans* is roughly divided into two stages: (i) **proliferation** and (ii) **organogenesis/morphogenesis** (Sulston et al., 1983) (IntroFIG7). (i) **Proliferation** (0 to 330-350 min post-fertilization at 22°C): This stage involves cell divisions from a single cell to 558 essentially undifferentiated cells by the end of "16 E stage" (von Ehrenstein and Schierenberg, 1980; Wood, 1988b). This stage is further subdivided into two phases: The first phase (0 to 150 min) spans the time between zygote formation to generation of embryonic founder cells, and the second phase (150 to 350 min) covers the bulk of cell divisions and gastrulation until the beginning of organogenesis (Bucher and Seydoux, 1994). The initial 150 min of

proliferation takes place within the mother's uterus, and the embryo is laid outside when it reaches approximately 30-cell stage (at gastrulation). There is considerable rearrangement of cells in the proliferation stage due to short range shuffling, and once gastrulation begins, due to specific cell migrations. From this time onward, the embryonic substages are defined by specific cell migrations, the gain in cell number, and periods of synchronous stem cell divisions. At the end of proliferation, the embryo is a spheroid of cells organized into three germ layers; ectoderm that gives rise to hypodermis and neurons, mesoderm that generates pharynx and muscle, and endoderm that gives rise to germline and intestine. (ii) Organogenesis/morphogenesis (5.5-6 hr to 12-14 hr): During this stage terminal differentiation of cells occurs without additional cell divisions, the embryo elongates threefold and takes form as an animal with fully differentiated tissues and organs. Morphogenesis starts with the "lima bean" stage, and the first muscle twitches are observed at 430 min after first cell cleavage (between 1 1/2 and 2-fold stages) (**IntroFIG7**). In the late three-fold stage, the worm can move inside the egg in coordinated fashion (rolling around its longitudinal axis) indicating advanced motor system development. The embryo starts pharyngeal pumping at 760 min after first cell cleavage and hatches at 800 min (**von Ehrenstein and Schierenberg, 1980; Sulston et al., 1983; Bird and Bird, 1991**). In *C. elegans*, at the end of the embryogenesis, the main body plan of the animal is already established. This general body plan does not change during postembryonic development.



**IntroFIG7.** Embryonic stages of development. The numbers below the horizontal axis show approximate time in minutes after fertilization at 22°C. First cleavage occurs at approximately 40 min. after fertilization. The yellow bars indicate the period of time during which cells from a certain lineage migrate towards inside of the embryo through the entry zone (aka gastrulation cleft or ventral cleft) during gastrulation (blue bar). During

gastrulation, precursors to the intestine, the germline, the pharynx and the body wall muscles move into the interior of the embryo from the ventral surface, leaving hypodermal cells covering the dorsal and lateral surfaces and neuroblasts exposed on the ventral surface. The first cells that move inwards from the ventral surface are gut precursors (E), followed by germline (P4) and mesoderm (MS) precursors. Gastrulation cleft is closed by short range movement of ectodermal (neuroblasts, postmitotic neurons, glia and glia precursors) cells between 270-330 min ([Chin-Sang and Chisholm, 2000](#)). After the end of gastrulation, as the neuroblasts complete their divisions, the hypodermal cells spread over the ventral surface from both sides and meet each other along the ventral midline to cover the surface of the embryo and complete the epithelium formation. Red bar indicates elongation of the embryo that takes place between 400- 640 min. due to circumferential contraction within the hypodermis. During elongation, the embryo becomes threefold thinner and its length increases about fourfold. The stages, number of nuclei, marker events and DIC images of the embryos and a newly hatched larva is shown above the horizontal axis. Sexual dimorphism becomes visible for the first time at 510 min when the cephalic companion neurons (CEM) die through programmed cell death in the hermaphrodite, whereas the hermaphrodite-specific neurons (HSN) die in the male. Based on [Bucher and Seydoux, 1994](#); [von Ehrenstein and Schierenberg, 1980](#); [Wood, 1988b](#), and [Sulston et al., 1983](#).

#### ii- Postembryonic development.

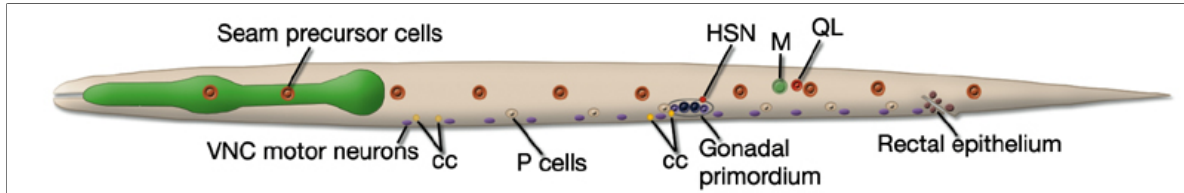
Postembryonic development is triggered by feeding of the larva after hatching. In the presence of food, cell divisions resume and postembryonic developmental program begins 3 hours after hatching ([Ambros, 2000](#)). The animal normally passes through four larval stages to reach adulthood ([IntroFIG8B](#)). Numerous blast cells set aside at the end of embryogenesis divide in nearly invariant temporal and spatial patterns through the four larval stages and give rise to a fixed number of cells with determined fates ([Sulston and Horvitz, 1977](#); [Wood, 1988b](#)). Of the 671 nuclei generated in the embryo, 113 undergo programmed death in the course of development ([Sulston et al., 1983](#); [Bird and Bird, 1991](#)). About 10% of the remaining 558 cells in a newly hatched larva (51 in hermaphrodites, 55 in the male), are blast cells that divide further ([von Ehrenstein and Schierenberg, 1980](#); [Sulston and Horvitz, 1977](#)). If the embryos hatch in the absence of food, however, they arrest development until food becomes available, and survive up to 6-10 days without feeding ([Johnson et al., 1984](#)) ([IntroFIG6](#)). After food becomes available, these arrested L1s progress through normal molting and development ([Slack, and Ruvkun 1997](#)).

#### L1 Larva

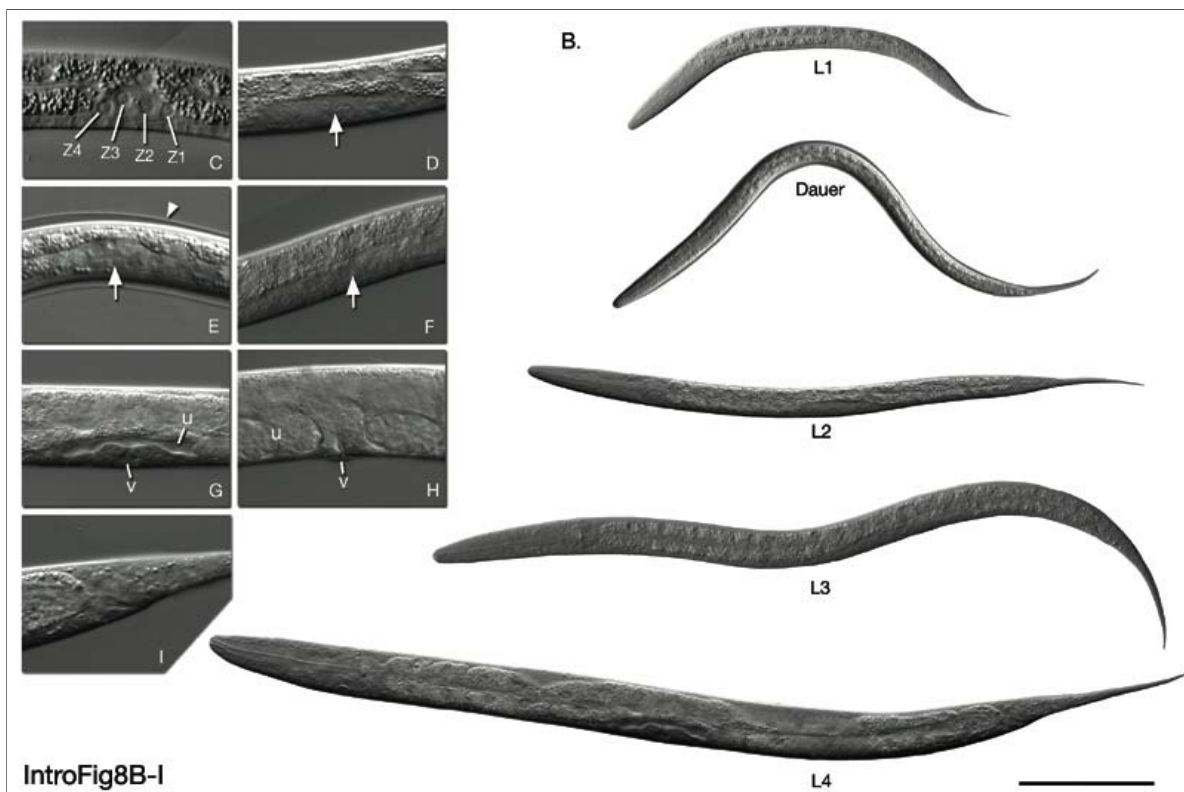
*Nervous System:* Of the eight classes of motor neurons (DAn, DBn, VAn, VBn, VCn, ASn, VDn, and DDn) in the adult hermaphrodite ventral cord, five (VAn, VBn, VCn, ASn, VDn) are generated at the end of L1 stage from 13 precursors (W, P1-P12) ([IntroFIG8A](#)) ([Chalfie and White, 1988](#); [Sulston J.E., 1976](#); [Sulston and Horvitz, 1977](#)). A few other neurons are generated from Q, G1, H2 and T blast cells. Also, during L1 stage one class of ventral cord motor neurons (DDn) go through complete synaptic reorganization without any cell shape change. The initial pattern of synapses made by DD neurons are presynaptic and inhibitory to ventral body wall muscles while being postsynaptic to neurons that activate dorsal body wall muscles. During late L1, after the birth of VD motor neurons, DD neurons change their synaptic pattern such that their dorsal branches become presynaptic and inhibitory to dorsal body wall muscles while their ventral branches become postsynaptic to excitatory neurons that synapse on ventral body wall muscles ([White et al., 1978](#); [Walthall et al., 1993](#)).

*Reproductive System:* During the second half of L1, somatic gonad precursors Z1 and Z4 produce 12 cells in the hermaphrodite ([IntroFIG8C](#)). The germ line precursors Z2 and Z3 also start to divide. These Z2-Z3 divisions occur continuously from L1 through adulthood ([Kimble and Hirsh, 1979](#)). Ventral Pn.p cells are born. A central subset will give rise to the vulva in L3 and L4.

**Coelomocyte system:** By the end of L1 stage, the M mesoblast gives rise to two additional (dorsal) coelomocytes in the hermaphrodite (**IntroFIG8A**). **Male:** At hatching, males are already distinguishable from hermaphrodites due to the more posterior location of one ventral coelomocyte, the larger size of the nuclei of two rectal cells (B and Y), the absence of hermaphrodite specific neurons (HSN) that undergo programmed cell death during embryogenesis, and the presence of CEM neurons. As in the hermaphrodite, Z1 and Z4 divide producing 10 somatic gonad precursor cells. Rectal blast cells B and Y, which will ultimately generate the proctodeum and posterior sensory structures, begin to divide towards the end of L1.



**IntroFIG8A.** L1 larva at 2 hr after hatching. The anterior ventral pair of coelomocytes (cc) and the M cell are located on the right. Rectal epithelial cells are in the middle plane, and VNC motor neurons are located at the ventral midline. The remaining cells are as seen from the left lateral side. VNC motor neurons are more numerous than shown. HSN: Hermaphrodite-specific neuron. Seam precursor cells are H1 (anteriormost), H2, V1-6 and T (posteriormost) cells. P cells are P1/2 at the anterior to P11/12 at the posterior. Based on [Sulston and Horvitz, 1977](#).



IntroFig8B-I

**IntroFIG8B-I.** Larval stages of development. **B.** DIC images of each stage larva. Bar 0.1 mm. **C.- H.** Enlarged DIC images of gonads of L1-adult stage animals respectively. Sizes are not to scale. Arrows point to gonads in D-F, v: vulva, u: uterus. (C) Four primordial gonad cells are labeled in L1. (D) Germ cells increase in number in L2. (E) The gonad is similar to an early L2 stage gonad in dauer. Arrowhead points to dauer specific cuticle. (F) Gonad has extended along the ventral body in L3. (G) hermaphrodite somatic structures have formed by mid-L4 stage. (H) Vulva is open to outside and uterus is full of fertilized eggs in adult. **I.** The thin, tapered tail of an L4 hermaphrodite (compare with IntroFig5 panel E).

### L2 Larva

There are few cell divisions during L2 stage.

*Nervous system:* V5.pa generates the postdeirid sensilla and G2 produces two ventral ganglion neurons.

*Reproductive System:* In this stage, the germ cell (Z2, Z3 daughters) divisions continue, approximately quadrupling in number (**IntroFIG8D**). However, no divisions occur in Z1 and Z4 (somatic primordial gonad) lineages. Somatic and germ cells are intermingled until the L2/L3 molt where upon they rearrange establishing the general organization of the future gonad; distal tip cells (DTC) positioned at the anterior and posterior ends, a somatic gonadal primordium at the center and anterior and posterior arm germ line populations (**Kimble and Hirsh, 1979**). The gonad begins to elongate, lead by the DTC cells. Male: At around L1/L2 molt, the gonad extends, but only at the anterior end, and is lead by the linker cell (**Antebi et al., 1997**). Around mid L2 linker cell halts and reorients to move dorsally. Cells of the male gonad also rearrange in late L2 to resemble the adult form with somatic gonad cells towards the posterior and germ cells displaced to the anterior.

### Dauer Larva

At the end of L2 stage, the animal may enter an arrested state called the dauer larva if the environmental conditions are not favorable for further growth. Environmental factors, including the presence of a pheromone (an indicator of population density), absence of food, and high temperature act as signals that can trigger formation of a morphologically distinct L2 stage larva designated L2d. The critical period for this dauer signal begins after the middle of the first larval stage. The L2d larva retains the potential to form either a dauer larva or an L3 larva depending on the persistence of the dauer inducing environmental parameters (**Riddle, 1988**). If the environment continues to be disadvantageous, L2d molts into a dauer (**IntroFIG6**). The dauer state is a non-aging state since its duration does not affect postdauer life span. During the dauer state, feeding is arrested indefinitely and locomotion is markedly reduced. The dauer state ends when the animal experiences favorable conditions. Within 1 hr of accessing food, the animal exits dauer, starts to feed after 2-3 hours, and after about 10 hrs molts to the L4 stage. Morphologically, dauer larvae are very thin (with a length-width ratio of about 30:1) and have a thick, altered cuticle (**IntroFIG8E** and **IntroFIG8B**) (see **Cuticle** chapter). The buccal cavity is sealed by a cuticular block, the gut cells have a dark appearance and the pharyngeal and intestinal lumens are shrunken, with small and indistinct microvilli in the intestine. The excretory gland lacks secretory granules, although the excretory pore remains open. The gonad of dauer is arrested at the L2 stage (**IntroFIG8E**) (**Riddle, 1988**; **Cassada and Russell, 1975**; **Sulston, 1988**).

### L3 Larva

*Reproductive System:* During L3, as well as first part of L4, somatic gonad precursors yield a total of 143 cells that form the anterior and posterior gonadal sheaths, the spermathecae and the uterus (**Kimble and Hirsh,**



1979). The extension of gonad arms continues in opposite directions until mid L3 when distal tip cells halt and then slowly start to reorient themselves in dorsal directions (Antebi et al., 1997) (IntroFIG8F, also see Reproductive system chapter-The Somatic Gonad). Vulval precursor fates are specified, and committed cells divide to generate vulval terminal cells by early L4. The two sex myoblasts, formed in L3, divide to generate 16 sex muscle cells. Male: Somatic gonad blast cells divide to generate 53 somatic gonad cells that will form the vas deferens and the seminal vesicle. The male linker cell of the somatic gonad reorients and migrates posteriorly until mid L3 extending the proximal gonad. After mid L3, it migrates obliquely towards ventral (Antebi et al., 1997). Six male sex myoblasts are generated. As posterior blast cells divide the tail become visibly swollen under the dissecting scope (IntroFIG5E). Posterior Pn.p cells divide to add 16 cells to the preanal ganglion. More anterior Pn.p lineages contribute cells to the ventral nerve cord. Rectal lineages produce proctodeal and sensilla cells (Sulston et al., 1980; Sulston, 1988). In the male germline, which produces only sperm, meiosis begins during L3 stage.

#### L4 Larva

*Reproductive System*: Gonadogenesis, which starts at approximately 7 hr after hatching is completed in the L4 stage. The distal gonad arms continue their migration centripetally along the dorsal body wall muscles and by the L4/adult molt they complete their trajectory close to midline (Antebi et al., 1997). Meiosis in the germ line begins at L3/L4 molt in the proximal arms of the gonad and the germ cells differentiate into mature sperm. At the L4/adult molt, sperm production stops and the remaining germline cells continue to undergo meiosis and differentiation to generate exclusively oocytes instead. Vulval and uterine terminal cell generation is followed by tissue morphogenesis (IntroFIG8G). Egg-laying neurons (VCs and HSNs), and sex muscles, generated from sex myoblasts, associate with these structures to form the egg-laying apparatus. (Greenwald, 1997, see Reproductive system chapter-Egg-laying apparatus). Male: 41 male sex muscles and a coelomocyte are formed from the M mesoblast lineage during the L4 stage in males (Sulston et al., 1980). The cells around the rectum form the proctodeum which contains the spicules. The gonad continues to grow posteriorly along the ventral midline and the vas deferens and the seminal vesicle differentiate. The linker cell reaches the developing cloaca by mid L4 where it dies and is then engulfed by two cells of the proctodeum, thereby opening the vas deferens to the outside (Antebi et al., 1997; Sulston, 1988). Tail tip hypodermal cells remodel, generating the rounded tail of the adult (IntroFIG5E) (Nguyen et al., 1999). Tail seam (set) is formed. Eventually, a general forward movement of posterior tissues and collapse of the cuticle reshapes the male tail and generates the copulatory bursa with rays and fan as well as the ventral hook and post-cloacal sensilla. (Emmons and Sternberg, 1997, also see Male anatomy-Neuronal Support Cells and Sensilla and Reproductive Systems).

#### Adult

Approximately at 45-50 hrs posthatch at 22-25°C, a newly matured hermaphrodite lays its first cells, hence completing its 3-day reproductive life cycle (Lewis and Fleming, 1995; Byerly et al., 1976). The adult hermaphrodite produces oocytes for about 4 days and after this fertile period of 3-4 days, the mature adult lives for an additional 10-15 days. A hermaphrodite that self-fertilizes will produce about 300 progeny because of the limited number of sperm, whereas if mating with a male occurs, the progeny number can increase to 1200-1400. Males can successfully mate with a hermaphrodite for 6 days after their last larval molt and can father approximately 3000 progeny (Hodgkin, 1988). Out of 1090 somatic cells generated during hermaphrodite development, 131 undergo programmed cell death at characteristic times (Driscoll, 1995). Hence, the adult hermaphrodite has 959 somatic nuclei, 302 of which are neurons and 95 are body wall muscle cells (White, 1988). The adult male, on the other hand, has 1031 somatic nuclei and 381 of these are neurons (extra neurons are mostly dedicated to male mating behavior) (White, 1988). Although it has more cells, the adult *C. elegans* male is more slender than the hermaphrodite and slightly shorter (approx. 0.8 mm)

(IntroFIG5).

---

---

[Home](#) [User Guide](#) [Handbook](#) [Slidable worm](#) [Comments](#)

All contents are copyright ©2002-2006 WORMATLAS unless otherwise noted. See [copyright and use policy](#).