

Early Development of Other Insects

Drosophila is a highly derived insect. Many other insects have evolved patterns of development that are very different from that of *Drosophila*.

Short and Intermediate Germ Band Insects

Drosophila is an example of a long germ band insect. That is to say, the embryonic primordium of the embryo, the germ band (*keimanlage*) extends through the entirety of the egg. Indeed, in *Drosophila*, the germ band has to wrap itself around the egg. This long germ band contains the primordia of all the segments that will form in the embryo (and adult). Long germ band insects include the *Diptera* (flies), *Lepidoptera* (butterflies and moths), *Hymenoptera* (bees, wasps, ants), and some *Coleoptera* (beetles).

In addition, there are those insects with short or intermediate germ bands. In species with short germ bands (such as the short-horned *Orthopterans*--the grasshoppers), the germ band is a relatively short anterior structure that will eventually form the anterior parts of the head. However, in the caudal portion of that short germ band is a posterior proliferation zone that will bud off new cells to form the additional segments. This posterior proliferation zone remains in the posterior portion of the insect, continually producing cells immediately anterior to it (Anderson, 1973). This type of segmentation can be seen in *Tribolium*, a short germ band beetle. In situ hybridization in *Drosophila* shows that the *engrailed* mRNA is localized in the posterior cells of each segment. The expression of *engrailed* mRNA in *Drosophila* is seen to occur in each segment at the same time. In *Tribolium*, there is still one stripe of *engrailed* mRNA per segment, but each segment is added sequentially (Sulston and Anderson, 1996).

In intermediate germ band insects such as damsel flies (*Odonata*) and long-horned *Orthoptera* (i.e., crickets), germ bands form from two ventrolateral aggregations that cover about 50% of the surface of the egg. After these two rudiments have fused ventrally, they become the primordia of the head and thoracic segments, while a posterior proliferation zone buds off the abdominal segments (Schwalm, 1988; 1997).

In intermediate and short germ band insects, the mesoderm forms by cell invagination and the delamination of newly divided cells along a primitive groove that begins centrally behind the presumptive head. The posterior proliferative zone forms the precursors of ectoderm and mesoderm simultaneously. These embryos develop much more like the other arthropods (spiders, crustaceans) than *Drosophila* does, and like these other arthropods, the embryo immerses itself into the yolk and then resumes its place on the surface (Figure 1A).

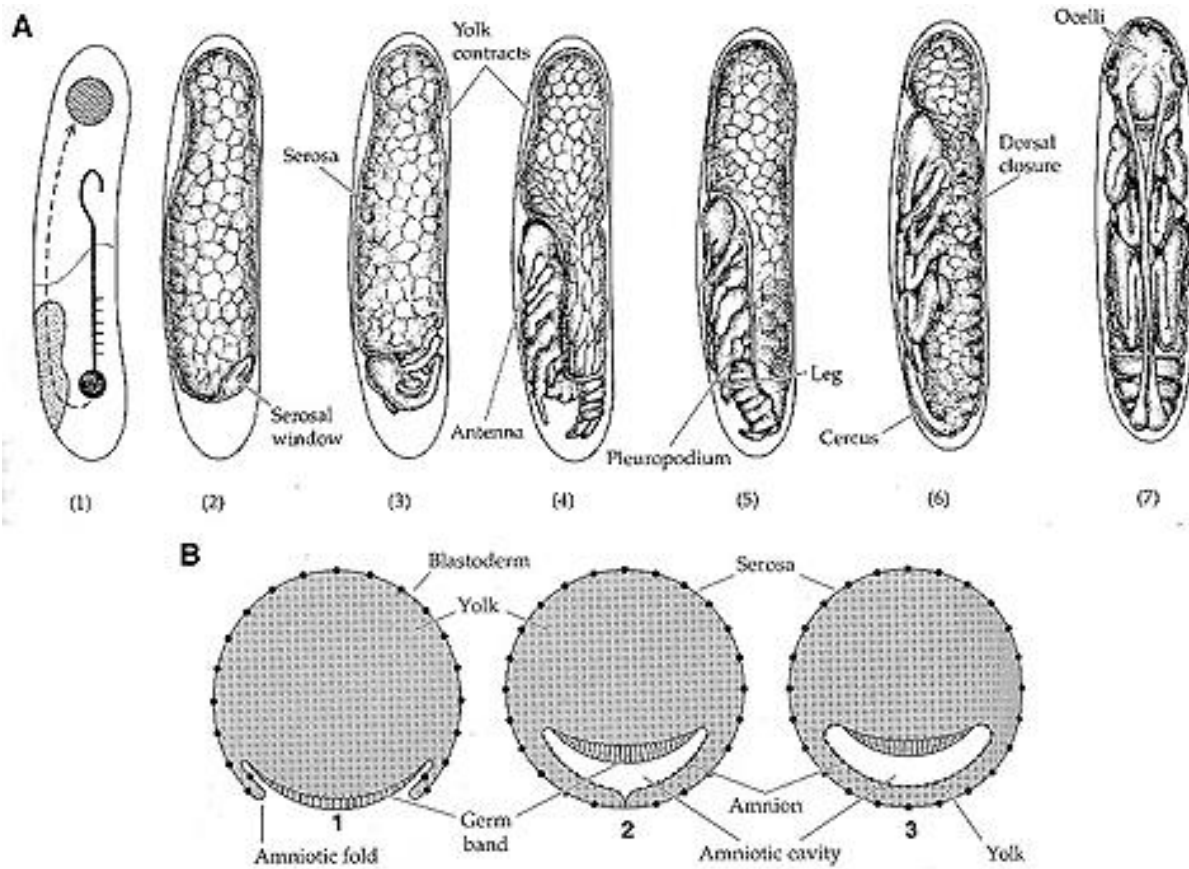


Figure 1 Development of the cricket *Acheta domestica*, an intermediate germ band insect. (A) Major features of development. (1) The ventral germ band becomes immersed inside the yolk and migrates posteriorly. After establishing segmentation, the embryo revolves around the posterior end of the egg and assumes its final position. (2-4) The head emerges from the yolk and moves anteriorly. The embryo begins to progressively cover the yolk sac as tissues differentiate. (5, 6) The embryo closes its dorsal flanks. The leading edge contains the mesodermal cardioblasts. (7) Frontal view of the cricket embryo during the completion of organogenesis. (B) Schematic diagram of the development of the amniotic cavity in intermediate germ band insects. (1) Lateral folds starting at the edges of the germ band grow over the germ band. (2) The lateral folds meet ventrally beneath the germ band. (3) The membranes fuse, causing the separation of the amnion and serosa, thereby surrounding the embryo with yolk. (After Schwalm, 1997).

As the embryos thicken, they produce amniotic folds from the surface, extending toward the center of the embryo. This results in a cellular covering over the ventral portion of the embryo (Figure 1B). These folds will pull the serosa downward so that the embryo will eventually be covered by two layers of cells. The head, which was originally formed over the ventral surface, moves around the posterior end of the egg such that it is now in the anterior. The dorsal part is last to differentiate, and eventually the flanks of the folds extend dorsally and fuse. From then on development appears similar to that of a long germ band embryo.

Polyembryony: The Parasitic Wasps

What we consider "normal" and what we marginalize as "exceptions" often reflect which animals are most readily accessible to study and most easily domesticated for laboratories. Needless to say, this does not necessarily reflect the condition of the natural world. Rather, our discussions of animal development are often bottlenecked through particular organisms. The development of amphibians is generally represented by *Xenopus laevis*, and the mouse and human are the only mammals

whose development is usually studied. Similarly, although there are over 800,000 known species of insects, most developmental biologists know only the development of one species: *Drosophila melanogaster*. *Drosophila* gained preeminence only after it was thought necessary to relate embryological phenomena to particular genes. In 1941, the major compendium of insect development (Johannsen and Butt's *Embryology of Insects and Myriapods*) didn't even mention this species in its index.

Insects are an exceptionally successful and widespread subphylum, however, so it is not surprising to find an enormous amount of variability in their development. The development of the parasitic wasp *Copidosomopsis tanytmemus* differs remarkably from that of the canonical *Drosophila*. Like several other parasitic species, the female *C. tanytmemus* deposits her egg inside the egg of another species. As the host egg (usually that of a moth) is developing, so is the parasite's egg. However, while the host egg begins development in the usual superficial pattern, the wasp egg divides holoblastically. Moreover, instead of differentiating a body axis, the cells of the parasitic embryo divide repeatedly to become a mass of undifferentiated cells called a polygerm. By two weeks, the growing polygerm is suspended in the host, remaining loosely attached to the larval brain and trachea (Figure 2A; Cruz, 1986a).

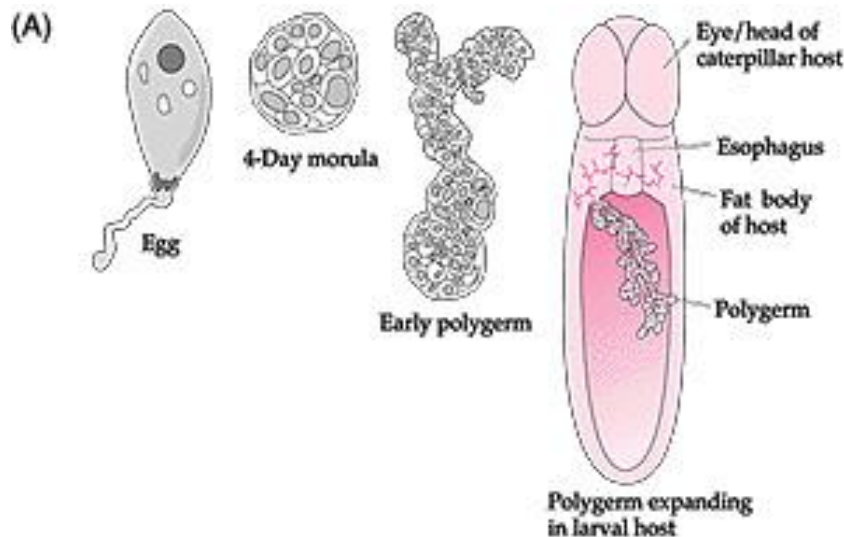


Figure 2 Development of parasitic wasps (Encyrtidae). (A) Holoblastic cleavage of the *Copidosomopsis tanytmemus* egg produces a polygerm of undifferentiated cells. (B) Precocious larvae of a related genus, *Pentalitomastix*, attacks a larva of *Trathala* inside the same host. The photograph is of a freshly opened host. (A after Cruz, 1986a; B from Cruz, 1981, courtesy of Y. Cruz.)

As the polygerm grows, it splits into dozens (sometimes thousands, depending on the species) of discrete groups of cells. Each of these groups of cells becomes an embryo! The polyembryonic wasp *Copidosoma floridanum* produces up to 2000 individuals from a single fertilized egg (Grbic et al., 1996; 1998). This ability of an egg to develop into a mass of cells that routinely forms numerous embryos is called polyembryony. (Polyembryony is characteristic of certain insect groups and certain mammalian species, such as the nine-banded armadillo, whose eggs routinely form identical quadruplets.) Remarkably, even in the absence of a syncytium, the segmentation genes and homeotic genes are appropriately activated (Grbic et al., 1996).

Most of these parasitic wasp embryos develop into normal wasp larvae that take about 30 days to develop. A smaller group, about 10 percent of the total number of embryos, become precocious larvae (Figure 2B), which develop within a week. Not only are they formed earlier, but precocious larvae have very little structure and do not undergo metamorphosis. They are essentially a mobile set of jaws. These larvae do not reproduce, and they die by the time the normal larvae are formed. While they live, however, they go through the host embryo killing the parasitic larvae of other individuals (of different species and of other clones of the same species). In other words, the precocious larvae are predatory forms that kill possible competitors (Cruz, 1981, 1986b; Grbic and Strand, 1992).

C. floridanum can produce about 2,000 embryos from a single egg, and only about 4% of the total number of larvae produced per host are soldiers. The difference between the reproductive caste and the soldier caste appears to involve the protein Vasa, a protein that is widely used to specify germ cells. In *C. floridanum* the Vasa-containing germplasm is prepackaged into eggs and is inherited specifically by a small blastomere that forms after second cleavage. This cell divides to form a germline lineage. Those embryos with such a Vasa-containing lineage become the reproductive caste. During morphogenesis, these Vasa-expressing cells localize to the posterior of the embryo and generate the gonads and the germ cells. In contrast, embryos without the Vasa-lineage undergo morphogenesis into soldiers. If the Vasa-expressing blastomere is removed at the four-cell stage of embryogenesis, the resulting embryo will form a soldier larvae. Thus, in addition to specifying the germ line, the germ cell lineage in *C. floridanum* also regulates caste specification (Donnell et al. 2004; Zhurov et al. 2004).

As the precocious larvae (and their prey) die, the normal larvae emerge from their first molt, and they begin feeding voraciously on the host's larval organs. By 40 days, the parasitic brood has finished eating its host's muscles, fat bodies, gonads, silk glands, gut, nerve cord, and hemolymph, and the host is little more than a sac of skin holding about 70 pupating wasp larvae. After another 5 or 6 days, the new adults gnaw holes in the host's integument, and in a scene repeated in the movie *Alien*, chew their way out of the host's body. These adults then copulate (often on the body of their dead host), find another host in which to deposit an egg, and die shortly thereafter. (The wasps even are more nefarious than you would think. When the female lays her eggs in the host, she injects a virus that incapacitates the host's immune system [Beckage, 1997]).

Such a life cycle discomfited Charles Darwin and made him question the concept of a benign and all-knowing deity. In 1860, he wrote to the American biologist Asa Gray, "I cannot persuade myself that a benevolent and omnipotent God would have designedly created the Ichneumonidae with the express intention of their feeding within the living bodies of Caterpillars." However, in addition to their usefulness in provoking disquieting notions concerning natural order and the nature of "individuality," parasitic wasps may have important economic consequences. *Macrocentrus grandii* is a polyembryonic wasp that parasitizes the European corn borer. The ability of an insect to form from a holoblastically cleaving embryo should also encourage us to appreciate some of the plasticity of nature and discourage us from making sweeping generalizations about an entire subphylum of organisms (Strand and Grbic, 1997; Grbic and Strand, 1998).

Literature Cited

- Anderson, D. T. 1973. *Embryology and Phylogeny in Annelids and Arthropods*. Pergamon Press, NY.
- Beckage, N. E. 1997. The parasitic wasp's secret weapon. *Sci. Amer.* (Nov.) 82-87
- Cruz, Y. P. 1981. A sterile defender morph in a polyembryonic hymenopteran parasite. *Nature* 294: 446-447.
- Cruz, Y. P. 1986a. Development of the polyembryonic parasite *Copidosomopsis tanytmemus* (Hymenoptera: Encyrtidae). *Ann. Entomol. Soc. Am.* 79: 121-127.
- Cruz, Y. P. 1986b. The defender role of the precocious larvae of *Copidosomopsis tanytmemus* Caltagirone (Encyrtidae, Hymenoptera). *J. Exp. Zool.* 237: 309-318.
- Darwin, C. 1860. Letter to Asa Gray, May 22, 1860. In F. Darwin (ed.), *The Life and Letters of Charles Darwin*, Vol. 2. Appleton, New York. [p.105].
- Donnell, D. M. , Corley, L. S., Chen, G. and Strand, M. R. 2004. Caste determination in a polyembryonic wasp involves inheritance of germ cells. *Proc Natl Acad Sci USA.* 101: 10095–10100.
- Gerhart, J. and Kirschner, M. 1997. *Cells, Embryos, and Evolution*. Blackwell Science, Malden, MA.
- Grbic, M. and Strand, M. R. 1992. Sibling rivalry and brood sex ratios in polyembryonic wasps. *Nature* 360: 254-256.
- Grbic, M. and Strand, M. R. 1998. Shifts in the life history of parasitic wasps correlate with pronounced alterations in early development. *Proc. Natl. Acad. Sci. USA* 95: 1097-1101.
- Grbic, M., Nagy, L. M., Carroll, S. B. and Strand, M. 1996. Polyembryonic development: insect pattern formation in a cellularized environment. *Development* 122: 795-804.
- Grbic, M., Nagy, L. M., and Strand, M. R. 1998. Development of polyembryonic insects: a major departure from typical insect embryogenesis. *Dev. Genes Evol.* 208: 69-81.
- Johannsen, O.A. and Butt, F.H. 1941. *Embryology of Insects and Myriapods*. McGraw-Hill, NY.
- Strand, M. R. and Grbic, M. 1997. The development and evolution of polyembryonic insects. *Current Top. Dev. Biol.* 35: 121-159.
- Sulston, I.A. and Anderson, K. V. 1996. Embryonic patterning mutants in *Tribolium castaneum*. *Development* 122: 805-814.
- Schwalm, F. E. 1988. *Insect Morphogenesis. Monographs in Developmental Biology*. Vol. 20. H. W. Sauer, Basel.
- Schwalm, F. E. 1997. Arthropods: The Insects. In *Embryology: Constructing the Organism*. (S. F. Gilbert and A. M. Raunio, eds.) Sinauer Associates, Inc., Sunderland, MA p. 259-278.
- Zhurov, V, Terzin, T. and Grbić, M. 2004. Early blastomere determines embryo proliferation and caste fate in a polyembryonic wasp. *Nature* 43: 764–769.

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