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Parasitoid Wasp Development

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.

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 1B), 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 2000 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 hostis larval organs. By 40 days, the parasitic brood has finished eating its hostis 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 hostis integument, and in a scene repeated in the movie *Alien*, chew their way out of the hostis 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 discomforted 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).

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