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Aphids

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What is an aphid?

Aphids are small, soft-bodied insects that feed by inserting their slender mouthparts into phloem cells, the food conduits of plants. Most aphid species feed on only one species of plant and closely related aphid species tend to feed on closely related species of plants. Once an aphid finds the correct plant species, it simultaneously feeds and reproduces. Offspring settle close to their mothers, spawning large colonies. Newborn nymphs molt four times, each time growing larger but otherwise looking similar to their previous incarnation.

Though small in size and simple in appearance (Figure 1), aphids have played an outsized role in the history of biology. Aphid embryos were first studied by Anton van Leeuwenhoek, who essentially discovered that aphids were parthenogenetic, although he thought they were hermaphroditic. Thomas Henry Huxley, Darwin's 'Bulldog', calculated that in ten generations a single aphid might produce the biomass equivalent to 500,000,000 stout men. Thomas Hunt Morgan, while founding *Drosophila* genetics, studied aphid cytogenetics to bolster the chromosome theory of sex determination. Aphids attack both common garden plants and several major crops, and are vectors for many plant viruses that cause more damage than the aphids themselves. *Phylloxera vitifoliae* decimated French grape vines in the late 19th century, until the vines were rescued by *Phylloxera*-resistant root-stocks from North America. Now, because of an aphid, all French wine is grown on American roots.

An affair of the gut

Aphids feed on phloem, which poses two problems. First, phloem contains high concentrations of sugars. To avoid being — literally — sucked dry by the high osmotic potential of phloem fluid, aphid guts convert the abundant simple sugars into long-chain oligosaccharides. Aphids then excrete the excess sugar-rich honeydew, which often attracts ants. The ants protect aphids from predators.

Second, phloem fluid contains an unbalanced spectrum of essential amino acids. Thus, aphids harbor endosymbiotic bacteria, *Buchnera aphidicola*, which provide aphids with many essential amino acids. The *Buchnera* genome underwent a dramatic reduction in gene content — to about 500 genes — soon after the origin of the symbiosis, about 200 million years ago. *Buchnera* have dispensed with most of the genes that would allow them to live in the wild and they must import many essential proteins and biosynthetic products from the aphid cell. Thus, while aphids cannot live long without *Buchnera*, *Buchnera* also depends on aphids. This obligate mutualism between eukaryote and prokaryote might resemble early stages of organelle evolution. Aphids also possess facultative symbionts that confer other benefits, such as resistance to heat and to parasitoid attack.

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Sex and the single aphid

Most aphids are born pregnant and beget females without wastrel males. These parthenogenetic oocytes result from a modified meiosis that skips the reduction division, maintaining diploidy and heterozygosity. Embryos complete development within the mother's ovary one after another, in assembly line fashion. These developing embryos contain developing embryos of the third generation within *them*, like Russian dolls.

Once a year, most aphids quit this hectic lifestyle and have sex. In temperate regions, autumnal conditions induce sexual forms. Sexual females look superficially like asexual females, but their ovaries produce eggs, rather than embryos. Males are produced by another trick of asexual meiosis leading to loss of one X chromosome.

Masters of polyphenism

The switch between sexual and asexual reproduction is one example of a polyphenism: alternative phenotypic forms that carry out specialized tasks. Some species can produce up to eight different alternative morphs, all genetically identical, during their life-cycle. Polyphenisms result from alternative modes of development induced in response to specific environmental cues. For example, most aphids develop without wings, investing the extra resources in more offspring. But as colonies grow and attract the attention of predators, they produce winged morphs that fly to new plants.

While most aphids run from predators, some choose to fight. About one percent of the 4,000 species of aphids produce a specialized soldier caste. Most aphid soldiers inject predators with a protein-digesting cocktail. Some jab predators with their sharp horns. And some squeeze their enemies into submission — just imagine — with their fat hind legs.

Masters of plant engineering

Some aphids instruct plants to produce a gall, a novel plant structure that insulates aphids from the elements and predators (Figure 1). Aphids induce orderly and patterned plant growth, not cancerous growths, by injecting unknown signals into plant cells. Furthermore, they can repair damaged galls caused by predators or meddlesome scientists. Again, aphids inject unknown signals into plant cells surrounding the wound, causing plant growth that mends the breach.

Genomic prospects

This précis includes only a few of the many novel biological phenomena that can be studied with aphids. The genome of the pea aphid, the primary aphid model system, is being sequenced by the Baylor Human Genome Sequencing Center (http://www.hgsc.bcm.tmc.edu/projects/aphid/) with funding from NHGRI. The pea aphid genome will represent the most basal insect genome sequenced to date and the first genome of a hemimetabolous insect. In contrast to the holometabolous flies, beetles and butterflies, aphids do not undergo a complete metamorphosis. The pea aphid genome therefore provides an outgroup to study the origin of holometabolous insects. Most importantly, the pea aphid genome provides a springboard for functional genomic studies of biological problems unique to aphids, such as those discussed above.

Where can I find out more?

1. Information about aphid genomics and additional web resources. www.aphidbase.com
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Figure 1.
Aphids and their galls.
Top: Mating pea aphids, *Acyrthosiphon pisum*. The diminutive male on the right, sexual female below. Middle: Gall of the soldier-producing aphid *Ceratovacuna japonica* formed on the tree *Styrax japonica*. Bottom: Gall of the soldier-producing aphid *Tuberaphis taiwana* formed on the tree *Styrax formosana*. All photos by David Stern.