GENOMICS

A Genome for the Environment

Gene duplication might explain the phenotypic adaptability of water fleas.

Dieter Ebert

Water fleas of the genus *Daphnia* are among the oldest model systems in biological research. Today, we know more about their natural history and ecology than of any other taxon. The *Daphnia* model also has left a notable mark on other fields. Élie Metchnikoff (*1*) used *Daphnia* to test his 1908 Nobel prize–winning idea that macrophages attack invading parasites as part of cellular immunity. August Weismann's studies of water fleas were instrumental in developing his theory that only germ cells transmit heritable information in animals (*2*). Richard Woltereck (*3*) used *Daphnia* to develop the notion of phenotypic plasticity—that an organism can change its characteristics in response to the environment—an idea that still guides experiments with many organisms that distinguish genetic from environmental effects. With all of these historical achievements, why did the National Institutes of Health (NIH) only recently add *Daphnia* to its list of model organisms (*4*) for biomedical research? Moreover, why has *Daphnia*, at this point in time, become NIH's 13th model system?

The answer to both questions lies, at least partly, in the very late start of genetic research on *Daphnia*. Until about 10 years ago, hardly

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any genetic experiments had been conducted on *Daphnia*. Even today, although researchers routinely cross clones, they have not yet developed methods for reverse genetics, including RNA interference. On page 555 of this issue, however, Colbourne *et al.* (*5*) take a substantial step forward in genetic research on the *Daphnia* system. They report on the genome of *D. pulex*—the world's first crustacean genome—and point to 37 companion papers (*6*). Their research demonstrates the powerful combination of genomic resources and ecological knowledge provided by the *Daphnia* system and opens the door to further exploration of the links between genomics and environmental adaptation.

Daphnia are small planktonic crustaceans ranging in length from less than 1 to about 5 mm. Found all over the world in standing bodies of water, from small ephemeral pools to large lakes, *Daphnia* are keystone species in aquatic food chains. Their biology superbly suits them for scientific experimentation: They are transparent, have a short life cycle, and are easy and cost-effective to maintain through clonal reproduction. *Daphnia* clones can be crossed, which is important for genetic research. Lake sediments harbor layered archives of resting *Daphnia* eggs and sometimes even the transmission stages of the symbionts that have coevolved with water fleas. Indeed, *Daphnia* and symbionts can be brought back to life and used to trace genetic adaptation

over periods of environmental change (*7*).

Of the many intriguing features of *Daphnia* biology, the hallmark is their amazing phenotypic plasticity. Water fleas react to chemicals (kairomones) released by different predators by expressing highly specific characteristics, such as protective tail spines, helmets, and neck teeth (see the figure) (*8*). They are also able to adapt physiologically to wide ranges of pH, toxins, oxygen concentrations, food, and temperature regimes (*9*). Moreover, maternal effects allow them to prepare their offspring for environmental challenges, including infectious disease (*10*), and the offspring's sex depends on the mother's environmental conditions. Colbourne *et al.* suggest that the secret of this success lies in the genome, with its unusually large repertoire of tandemly duplicated genes and a high proportion of genes specific to the *Daphnia* lineage.

Although the *D. pulex* genome is comparatively modest in size, measuring about 200 megabases, with more than 30,000 genes it exceeds the number found in many other genomes, including the human genome. It also shares more genes with the human genome than any other arthropod model. However, 36% of *D. pulex* genes have no detectable homologs; many of them are part of lineage-specific gene families. About 13,000 *Daphnia* genes—an unusually high number—have been identified as paralogs, that is, genes within the same genome that are related by duplication. It appears that

Daphnia longicephala
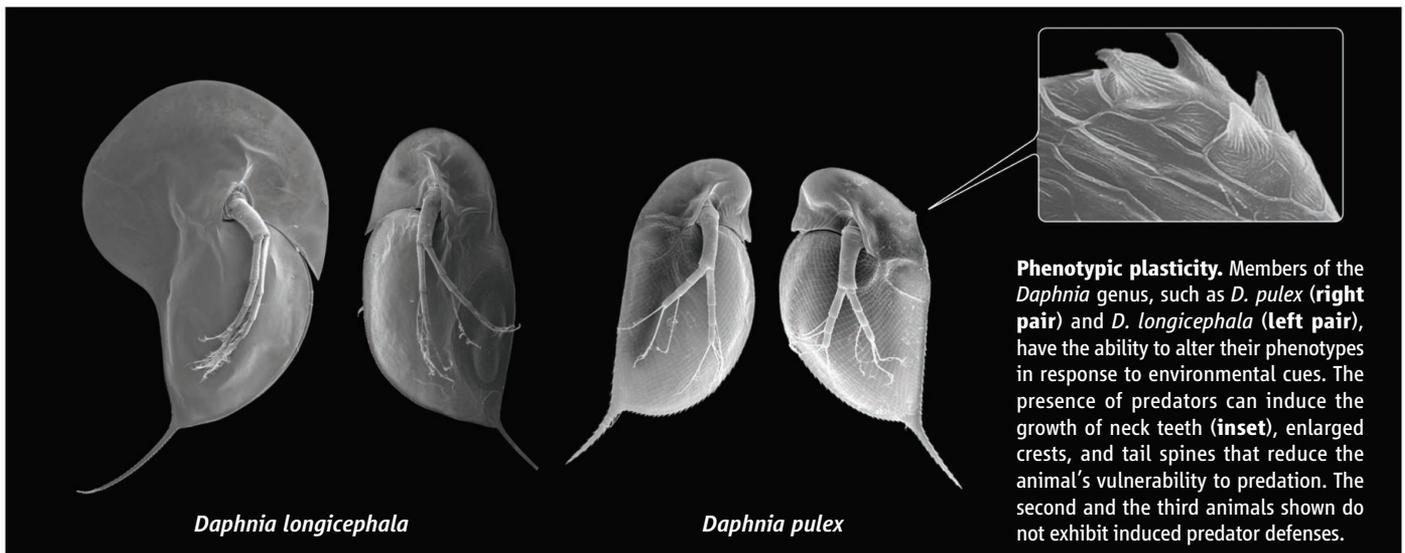
Daphnia pulex

Phenotypic plasticity. Members of the *Daphnia* genus, such as *D. pulex* (**right pair**) and *D. longicephala* (**left pair**), have the ability to alter their phenotypes in response to environmental cues. The presence of predators can induce the growth of neck teeth (**inset**), enlarged crests, and tail spines that reduce the animal's vulnerability to predation. The second and the third animals shown do not exhibit induced predator defenses.

these genes arose not by whole genome duplications, as is the case for many human paralogs, but through an accumulative process by which the *Daphnia* genome gained more genes by tandem duplication and lost fewer genes than other lineages.

Gene duplication is an important evolutionary force (*11*, *12*). The conventional view of the fate of duplicated genes is that genetic redundancy reduces constraints on their evolution, allowing for the accumulation of mutations. If these genes escape silencing, they may evolve altered functions. As a consequence, three variables—time since duplication, sequence divergence, and the degree of functional change—should correlate positively with each other, a pattern present in the *Daphnia* genome. In addition, Colbourne *et al.* support an entirely different model for the evolution of novel functions in duplicated genes. In this model, benefits arise from novel gene-gene interactions. The expression pattern of the duplicated gene changes as the result of interactions with a different interacting gene at, or soon after, the time of its duplication. Novel combinations of interacting genes may be expressed in a different tissue, phase of development, or under different environmental conditions. Novel expression patterns may arise by integrating the copied gene into a new genomic location or dissociating the gene from its previous regulatory framework. To support this claim, the authors provide evidence that paralogs, with no or little sequence differences, have in many cases diverged in their expression patterns.

But where is the link to the environment? A strength of the *Daphnia* system, as the present study beautifully demonstrates, is the way it allows investigators to conduct gene expression experiments under diverse ecological conditions. Using expressed sequence tag libraries and genome-wide tiling microarray experiments, the authors demonstrate that genes responsive to specific ecological conditions are overrepresented in duplicated genes, in genes without known homologs, and in genomic regions without gene models (intergenic regions). Thus, *D. pulex* is equipped with a large array of genes with environment-specific functions, allowing these critters to call into play an extraordinary degree of phenotypic plasticity. The same seems to be true for *D. magna*, whose draft genome has been used in some of the comparative work conducted by Colbourne *et al.*

The *Daphnia* model is currently being used in such fields as ecotoxicology, population genetics, the evolution of sex, phenotypic plasticity, ecophysiology (including global change biology), and *Daphnia*-par-

asite interactions. The publication of the *D. pulex* genome will allow this list to expand to embrace the emerging field of environmental genomics. Scientists in this field have already begun exploring how organisms adapt genetically to environmental stressors like heavy metals, rising temperatures, emerging diseases, and bioreactive organic compounds. By focusing on how organisms like *Daphnia* have evolved to cope with such stressors, this new approach goes well beyond questions of what these stressors are, and boldly takes on uncovering the kinds of solutions that evolution can bring about (*13*, *14*). The signatures of these evolutionary answers, of course, are archived in the genomes of populations with different histories and ecologies. As global and local environmental change dominates world news today, understanding links between genes and environments becomes more and more vital. With the *D. pulex* genome, environmental health has found its genomic model.

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ANTHROPOLOGY

Climate and Human Evolution

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Climate change and its effects on African ecosystems may have played a key role in human evolution.

Did climate change shape human evolution? This question has old, deep roots (*1*, *2*), but in recent decades, the fossil record of hominin evolution and behavior has improved, although it remains incomplete, and great progress has been made in the quality and number of African paleoclimate records from land and ocean sediments (*3*). A recent National Research Council (NRC) report (*4*) examines emerging faunal and paleoclimate evidence underlying the hypothesis that past climate changes may have influenced our evolution.

The basic premise is that large-scale shifts in climate alter the ecological structure and resource availability of a given setting, which leads to selection pressures (*3*, *5*). Indeed, some of the larger climate shifts in Earth history were accompanied by unusually high rates of faunal turnover—bursts of biotic extinction, speciation, and innovation (*6*–*8*). For example, a large turnover event occurred near 34 million years ago (Ma) when Earth cooled abruptly and large glaciers first expanded upon Antarc-

tica (*8*, *9*). Many of the taxa that appeared after 34 Ma were better adapted to the new environments that emerged, which included cooler polar regions, greater seasonality, and arid grasslands.

Notable hominin extinction, speciation, and behavioral events appear to be associated with changes in African climate in the past 5 million years. First appearance and extinction events, as well as key behavioral milestones, cluster between 2.9 and 2.6 Ma and again between 1.9 and 1.6 Ma (see the figure, panel A). In the earlier group, these events include the extinction of *Australopithecus afarensis* ("Lucy") near 2.9 Ma; the emergence of the robust australopiths (*Paranthropus* spp.), with large jaws and grinding teeth, near 2.7 Ma; and the emergence of the larger-brained *Homo* lineage sometime after 2.6 Ma, near the time when the first evidence for Oldowan stone tool manufacture, use, and transport appears (*10*).

Important evolutionary developments between 1.9 and 1.6 Ma (*4*) included the first appearance of *Homo erectus*—the first hominin species to resemble modern humans, with large brains, similar dentition, and a lithe frame—near 1.9 Ma. By 1.6 Ma, the

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