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that synthesize prophenoloxidase.

Plasmatocytes and granular hemocytes are usually the two most abundant hemocyte types, although their proportions can vary between species and within a species at different developmental stages. These two hemocyte types participate in immune responses, including: (1) phagocytosis of small organisms such as bacteria; (2) nodule formation, in which multiple hemocytes aggregate to trap microorganisms; and (3) encapsulation, in which hemocytes attach to the surface of a larger parasite and form a multilayered hemocyte capsule, in which the parasite is killed. Nodules and capsules often become melanized through the action of phenoloxidase. Hemocytes, especially plasmatocytes, also aggregate in a type of coagulation response, sealing wounds to prevent hemolymph loss. Another function of hemocytes is in synthesis of the extracellular matrix that covers tissues exposed to the hemolymph. Granular hemocytes appear to be the primary cell type involved in this aspect of hemocyte function.

#### See Also the Following Articles

*Circulatory System • Fat Body • Immunology • Vitellogenesis • Water and Ion Balance, Hormonal Control of*

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## Hibernation

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Hibernation refers to the state in which animals pass the winter. In discussion of insects overwintering is often used as a synonym for hibernation; usually hibernation is associated with entry into a dormant state. Estivation is a term used for animals that become dormant in the summer. Some insects enter an extended period of dormancy, referred to as estivohibernation, which begins in summer and continues through the winter. This term also is used commonly in connection with those mammals that lower their body temperature slightly (e.g., carnivorean lethargy in bears and skunks) or extensively (e.g., hibernation *sensu stricto* in ground squirrels) during the winter.

It is critical for insects to synchronize their periods of feeding, growth, and reproductive activities with those times of the year when food is available and environmental conditions are suitable. Hibernation generally includes entry into diapause, a dormant state that promotes survival by depressing metabolism and energy utilization when host plants and other food sources are unavailable. Typically, this also includes reduced morphogenesis in immature stages; hibernating adults typically hibernate before reproducing.

Specific behavioral changes are often associated with movement to overwintering sites, termed hibernacula. One of the most extreme examples is the monarch butterfly (*Danaus plexippus*), which may migrate more than 5000 km from southern Canada and New England to mountain sites in central Mexico. Other insects migrate locally as they move to hibernacula within the soil where they may burrow to avoid exposure to winter cold. Still others seek sites beneath rocks, logs, bark, and leaf litter.

In temperate regions, insects typically hibernate in a specific life stage. The egg, larva, and pupa are more common stages for overwintering than is the adult. However, alpine and polar insects or others living in extreme environments, in which growing seasons are short or unpredictable, and having life cycles that may be extended over several years may hibernate multiple times in one or more life stages.

In temperate regions, most hibernating insects enhance their resistance to environmental extremes, particularly cold and desiccation. During autumn, many species markedly enhance their tolerance to low temperature, termed cold-hardening. Most insects are freezing intolerant and are unable to survive freezing within their body fluids. These species typically enhance their capacity to supercool (i.e., remain unfrozen at temperatures below the melting point of their hemolymph) by synthesizing glycerol, sorbitol, trehalose, or other cryoprotective compounds, often at high concentrations of 1 M or more. Production of antifreeze proteins, avoidance

## Heteroptera

see *Prosorrhyncha*

of inoculative freezing by external ice, and ridding the body of ice nucleators that may catalyze ice formation are other mechanisms used to avoid lethal freezing.

In contrast, a few insects are freeze tolerant and can survive the freezing of 70% or more of their body water. Cryoprotectants are also commonly synthesized by freeze-tolerant species, as are ice-nucleating proteins that induce ice formation at high subzero temperatures. Overwintering insects also may acquire exceptionally high levels of desiccation resistance, comparable to those of desert species.

Behavioral and physiological changes associated with hibernation, diapause, and cold-hardening are commonly triggered by environmental cues, including photoperiod, temperature, moisture conditions, and changes in host plant quality. These cues ensure that adaptive responses occur before severe winter conditions arrive.

#### See Also the Following Articles

*Aestivation • Cold/Heat Protection • Diapause • Dormancy • Monarchs*

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# History of Entomology

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This brief history traces the interactions of humans and insects dating from the adoption of agriculture and its inherent ecological disruptions. Humankind's early preoccupation with survival focused on insects as relentless pests, competitors for food and fiber, threats to health and comfort. The high hopes following World War II for relief from the bondage of insects through the use of chemical insecticides such as DDT proved unrealistic. The reassessment that followed

led to a concept based on ecological principles which is referred to as integrated pest management (IPM). In this system, multiple control technologies are used, with the additive effect being to hold insect injury at acceptable levels while avoiding excessive environmental insult. The age-old struggle continues; entomologists are now armed with the lessons of the past; advances in insecticidal chemistry, biological control, and cultural methods; and visionary new technologies based on genetic modification of plants and animals. Simultaneously, the rise of the environmental movement and ecological awareness has placed insects in a new context, highlighting their essential role in biodiversity on which the viability of the Earth depends. The vision for the 21st century calls for compatibility between insect control and conservation; both are prerequisites to human well-being. Stewardship of the Earth is the greatest challenge ahead and one that places awesome responsibility on the shoulders of entomologists.

## IN THE BEGINNING

The history of life on earth reaches back some 4 billion years. From this beginning the long evolutionary trail unwound. Along the way, 99% of the forms that appeared met with extinction.

The great exterminations that have occurred since the appearance of insects in the Devonian period, 400 mya, revealed insects' remarkable survival qualities. Insects witnessed the last of the trilobites that preceded them by 175 million years. By the time the dinosaurs appeared in the Triassic period, 210 mya, the major orders of insects existing today were already well established. Dinosaurs became extinct 66 mya, leaving a niche occupied in time by mammals. The mammals, in turn, provided a niche for insects, offering furry cover and warm meals. The disappearance of the dinosaurs coincided with a great radiation of insects based on insects' symbiosis with flowering plants. For the past 150 million years, the flowering plants and insects have honed their intricate coevolution, which accounts for their immense biodiversity on which human habitability of the earth depends.

Insects have withstood trial by ice and fire, meteorite strikes, volcanic eruptions, global dust veils, acid rain, and continental upheavals. This evolutionary experience is encoded in their DNA and attests to the advantage of their small size, external skeleton, flight, metamorphosis, and specialized systems of reproduction. These are significant credentials in insects' rivalry with *Homo sapiens*, a species that draws on an evolutionary history of a scant 7 million years.

## COEXISTENCE, HUMANS AND INSECTS

Class Insecta has plagued and fascinated humans for all of their history. The most striking features of the Insecta are diversity and numerical superiority. Of the 5 to 30 million