8956

### Relationships between ants and insectivorous plants

Carnivorous plants of diverse forms occur on infertile soils in various locations throughout the world, and are united by their use of trapped insects as a nitrogen source. Pitcher plants are a particularly fascinating life form, which lure insects to the slippery edges of steep-walled pitchers, into which fluids with digestive enzymes are secreted and protected from dilution by rainfall by a sort of "roof." Ants are among the most abundant prey of pitcher plants, being attracted to the pitcher edges by a form of extrafloral nectar. However, C.M. Clarke and R.L. Kitching show that one *Camponotus* species has evolved a more complicated relationship, perhaps a mutualism, with a carnivorous pitcher plant in Borneo. Thus, the hollow tendrils of *Nepenthes bicalcarata* house ants that feed on both large insects trapped by its pitchers as well as on mosquito larvae living there. Unlike smaller prey, large insects apparently overwhelm the plant's digestive capacity and lead to the accumulation of ammonia in the pitcher fluids. The removal of excess prey by the *Camponotus* prevents the putrefaction of the fluids. Thus, although the ants do rob some prey from their host plants, the net effect of their presence may be positive.

Diane W. Davidson
University of Utah,
Salt Lake City, Utah, USA

### References

Davidson, D. W. 1997. The role of resource imbalances in the evolutionary ecology of tropical arboreal ants. *Biological Journal of the Linnean Society* 61: 153–181.

Davidson, D. W., and W. W. Epstein. 1989. Epiphytic associations with ants. Pp. 200–233 in U. Lüttge (ed.), *Vascular plants as epiphytes*. Springer-Verlag, New York, New York.

Davidson, D. W., R. S. Inouye, and J. H. Brown. 1984. Granivory in a desert ecosystem: experimental evidence for indirect facilitation of ants by rodents. *Ecology* 65: 1780–1786.

Davidson, D. W., and D. McKey. 1993. Ant-plant symbioses: stalking the Chuyachaqui. *Trends in Ecology and Evolution* 8: 326–332.

Ghazoul, J. 2001. Can floral repellents pre-empt potential ant-plant conflicts? *Ecology Letters* 4: 1–5.

Hickman, J. C. 1974. Pollination by ants: a low-energy system. *Science* 184: 1290–1292.

Hölldobler, B., and E. O. Wilson. 1990. The ants. Belknap Press of Harvard University, Cambridge, Massachusetts.

Izzo, T. J., and H. L. Vasconcelos. Cheating the cheater: stability of a mutualism between an ant-plant and its associated ants. *Oecologia* (in press).

Mueller, U. G., T. R. Schultz, C. R. Currie, R. M. Adams, and D. Malloch. 2001. The origin of the attine ant-fungus mutualism. *Quarterly Review of Biology* 76: 169–197.

**ANTS.** Certain members of an order of insects (order Hymenoptera). See also, ANTS (HYMENOPTERA: FORMICIDAE), and WASPS, ANTS, BEES, AND SAWFLIES.

**ANTS (HYMENOPTERA: FORMICIDAE).** Ants are one of the most highly evolved and dominant insect groups. They are the largest family of insects in terms of the diversity of species and certainly sheer numbers of individuals. Currently there are well over 9,500 described species of ants, and some suggest that a similar number is yet to be discovered. Individual colonies of some species can contain over 20 million members. Ants belong to the family Formicidae, which according to Bolton (1994), consists of 16 subfamilies and 296 genera.

Order Hymenoptera
  Suborder Apocrita
    Superfamily Vespoidea
      Family Formicidae

They are found in all terrestrial regions of the world, including the cold subarctic tundra and dry deserts. Following is a list of the 16 subfamiles with their zoogeographical distribution. Almost all of the precinctive genera are from the Neotropics (51%) and the Afrotropical [sub-Saharan Africa] (33%) regions. Five of the 16 subfamilies are very small, with each containing less than 10 described living species (Aenictogitoninae, Aneuretinae, Apomyrminae, Leptanilloidinae, Nothomyrmeciinae). The subfamily with the greatest number of species is the Myrmicinae, and is followed by the Formicinae.

Ants are true social (eusocial) insects, which is defined by the following characteristics: 1) cooperative brood care, where immature ants are tended by groups of adults that are not their parents; 2) overlapping generations, where at least two different generations of adults occur simultaneously in the same colony; and 3) reproductive and non-reproductive castes, where only the reproductives are capable of



Oi, D.H. 2004. Ants. Capinera, J.L., editor. Kluwer Academic Publishers, Norwell, MA. Encyclopedia of Entomology. v. 1. p. 120-126.

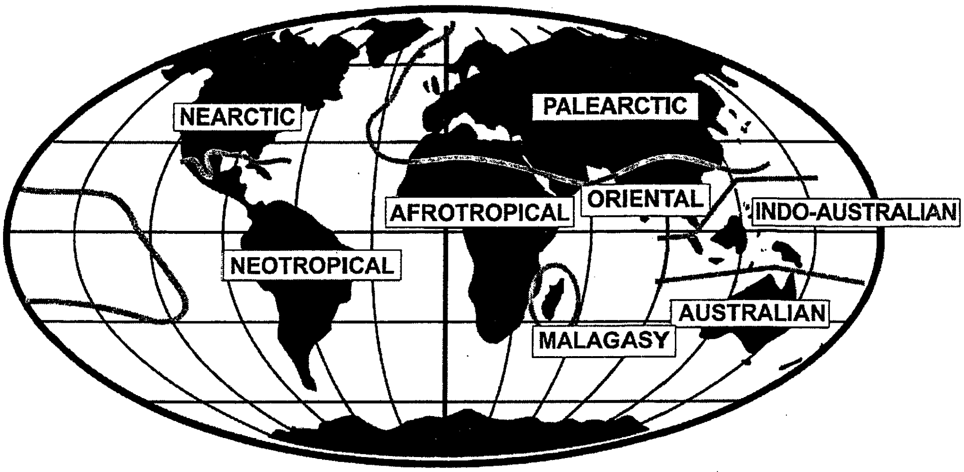


**Fig. 48** Zoogeographical regions as defined by Bolton (1994). Note that Afrotropical region is sub-Saharan Africa or the traditional Ethiopian region, but excludes Madagascar and nearby islands, which comprise the Malagasy region. The traditional Oriental region has been divided into the 1) Indo-Australian region, which includes the Malay peninsula, Philippines, East Malaysia, Indonesia including New Guinea and islands in the Pacific, and 2) Oriental region which encompasses the remaining areas of the traditional Oriental region.

producing fertile offspring. The non-reproductives, or workers, perform tasks necessary for colony survival, such as foraging for food, caring for immature ants and reproductives, and nest building. Eusocial insects have a competitive advantage over nonsocial insects because there is a better probability that groups of

List of subfamilies in the family Formicidae with zoogeographical distribution (adapted from Bolton 1994).

| | Zoogeographical region | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Subfamily | Palaearctic | Afrotropical[1] | Malagasy[2] | Oriental[4] | Indo-Australian[3] | Australasian | Nearctic | Neotropical |
| Aenictinae | x | x | | x | x | x | | |
| Aenictogitoninae | | x | | | | | | |
| Aneuretinae | | | | x | | | | |
| Apomyrminae | | x | | | | | | |
| Cerapachyinae | x | x | x | x | x | x | x | x |
| Dolichoderinae | x | x | x | x | x | x | x | x |
| Dorylinae | x | x | | x | x | | | |
| Ecitoninae | | | | | | | x | x |
| Formicinae | x | x | x | x | x | x | x | x |
| Leptanillinae | x | x | | x | x | x | | |
| Leptanilloidinae | | | | | | | | x |
| Myrmeciinae | | | | | | x | | |
| Myrmicinae | x | x | x | x | x | x | x | x |
| Nothomyrmeciinae | | | | | | x | | |
| Ponerinae | x | x | x | x | x | x | x | x |
| Pseudomyrmecinae | x | x | x | x | x | x | x | x |

1 Afrotropical = Ethiopian region, but excludes Madagascar and nearby islands.
2 Malagasy = Madagascar and nearby islands.
3 Indo-Australian = Melesian which includes Malay peninsula, Philippines, East Malaysia, Indonesia including New Guinea and islands in the Pacific. This was formerly part of the traditional Oriental region.
4 Oriental = traditional Oriental region excluding Indo-Australian region.

sterile workers will be able to complete a task necessary for the survival of the reproductive queen, and also complete a series of tasks simultaneously. If a task is not completed by one worker, another worker can finish the job. This is opposed to a solitary insect where the entire burden of completing tasks from start to finish rests with the individual.

Communication needed to coordinate the activities within a colony is mediated by chemical signals called pheromones. Some of the pheromones that have been isolated include a queen pheromone that allows worker ants to recognize a queen, trail-following pheromone which workers use to mark paths between the nest and food, and alarm pheromones which cause ants to disperse and/or attack. Chemical cues also are used in the recognition of colony nestmates, and play a role in aggression and establishing territorial boundaries between colonies.

Ants are omnivorous and mobile, allowing them to exploit a wide range of habitats. This is in contrast to termites, another abundant eusocial insect, which are restricted to feeding on wood or other vegetation. Moist environments are conducive to microbial contamination. Secretions from the ant's metapleural gland contain antibiotics that disinfect moist environs. Having a portable means of sanitation allows ants to exploit areas that other organisms may not be able to live in. These attributes permitted ants to become a dominant terrestrial organism, especially in the tropics. With their large populations and adaptation to a plethora of ecological niches, ants play an important role in natural ecosystems. They are tremendous earth-movers because of their underground nest building, and thus contribute greatly to the cycling of nutrients. They disperse seeds, scavenge dead organisms, and are a major predator of other arthropods and small invertebrates. In some instances they are directly beneficial to man by being major predators of pests such as crop feeding caterpillars, and ticks of livestock.

**Morphology**

Ants are easy to distinguish from other insects mainly because of the combination of a thin waist and the presence of elbowed antennae. The waist refers to a segmented constriction called the petiole, located between the thorax and the gaster. The gaster is composed of the broad 4 or 5 posterior segments of the abdomen. Morphologically ants are distinguishable by having a one or two-segmented waist; always consisting of a petiole if one-segmented, and both a petiole and a postpetiole if two-segmented. The petiole and postpetiole are actually the second and third segments of the abdomen that are reduced or constricted in size. They often have a distinctive node-like form, however in some species it is scale-like or just a small cylindrical segment. Following is a list of four terms that describe sections of the ant abdomen and the corresponding abdominal segments for ants with one- and two-segmented waists.

The adult workers and queens have antennae that are geniculate, meaning bent or elbowed. The elbowed appearance arises from having a long first, or basal, antennal segment called the scape, followed by 3 to 11 short segments (collectively called the funiculus). The basal segments in male antennae are usually not long, and thus, the antennae will not appear to be elbowed. Another unique feature of ants is the small opening or orifice of the metapleural gland. This is located just above the basal segment of the third leg, but often requires magnification to be visible.

**Life/colony cycle**

Ants are holometabolous, having a complete life cycle consisting of eggs, larvae, pupae, and adults. Thus, little adult ants do not grow into big adult ants. The eggs, larvae, and pupae are collectively called brood. In general, colony development is as follows:

Abdominal segments that compose sections of the abdomen for ants with one- and two-segmented waists.

| Abdominal sections | One-segmented waist | Two-segmented waist |
|---|---|---|
| propodeum | abdominal segment 1 fused to posterior of thorax | |
| petiole | abdominal segment 2 | abdominal segment 2 |
| postpetiole | none | abdominal segment 3 |
| gaster | abdominal segments 3–7 | abdominal segments 4–7 |

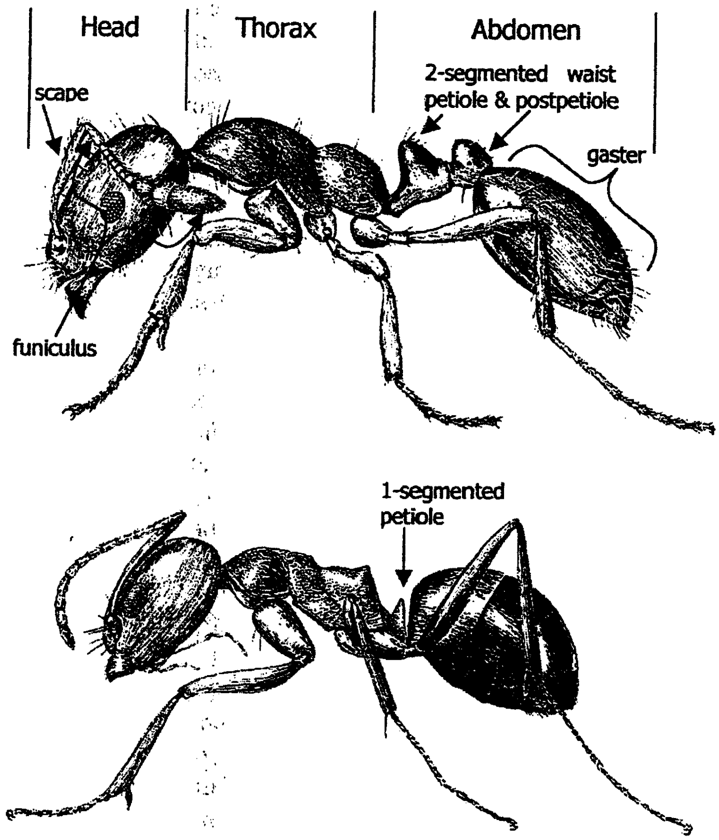


**Fig. 49** Distinguishing morphological structures of ants: above) two-segmented petiole or below) one-segmented petiole. Elbowed antenna consisting of a long basal segment (scape) and 3–11 short segments (funiculus); posterior portion of abdomen beyond petiole (gaster) [drawings modified from M.R. Smith 1965, above) *Monomorium minimum*, below) *Dorymyrmex pyramicus*].

ant colonies originate after a mating flight when winged virgin queens mate with winged males. After mating, the males die, while the newly mated queen sheds her wings and finds a protected location or excavates a chamber in soil. Within this chamber she will lay a batch of eggs and care for the subsequent larvae and pupae until they become adults. These adults are usually sterile females, which are the worker caste, and they will assist the queen by caring for additional brood, foraging for food, and expanding the nest. An important aspect to the survivorship and growth of ant colonies is trophallaxis, or the exchange of regurgitated food among nestmates. Trophallaxis ensures that food is distributed to all members of the colony including the queen and brood. Once the colony is well established, winged virgin females and males (reproductives) will be produced and will proceed to have a mating flight when environmental conditions are suitable. The original colony will continue to be maintained and produce new reproductives as long as the queen is able to produce viable eggs. Depending on the species, queens have been reported to live from less than a year to as long as 29 years. A major variation to this cycle is the absence of a mating flight by the virgin queens in some species. Mating takes place within the nest with either their brothers or males that fly in from other colonies. New colonies are formed by budding, where a portion of the colony, containing adults, brood, and either or both mated or virgin queen(s), separate from the original colony and move to a new location.

In addition to the tremendous number of ant species, there is a broad range of interesting behaviors or life styles among species. Many species have mutualistic relationships with honeydew-producing insects such as aphids and mealybugs (hemipterans). Ants will transport and protect these insects in order to harvest the honeydew they produce. In essence, these ants tend and herd the honeydew producers as if they were cows. Some hemipterans carry plant pathogens, and disease spread is facilitated by ants moving the infected hemipterans to other plants.

Another agrarian life-style is that of the leaf-cutting ants that raise their food in fungal gardens within their nest. These ants use leaves and other fresh vegetation to provide a substrate on which to grow the fungus, and these ants can defoliate trees overnight. Leaf-cutting ants cut pieces of leaves or flowers with their jaws and then carry them back to their nest. Once in their nest, they further chew the vegetation and add feces to form a suitable medium for fungal growth. Finally, they plant and maintain a specific fungus species on the substrate. In Central and South America, leaf-cutting species in the genus *Atta* and *Acromyrmex* (subfamily Myrmicinae) can have colonies with an estimated 1 to 8 million individuals. They build nests consisting of an extensive network of subterranean galleries, and are the most significant pests of agriculture in South America, feeding on of citrus, forage grasses, and other crops.

Symbiotic relationships with plants have been reported for several ant species. One well-studied mutualistic relationship is that between *Acacia cornigera* trees and the ant *Pseudomyrmex ferruginea* (subfamily Pseudomyrmecinae). The acacia tree produces thorns, which serve as nesting sites for the ants and it produces structures, called Beltian bodies, that are eaten by the ants. The ants protect the plant from herbivorous arthropods and vertebrates, and destroy competing plants that sprout nearby.

Besides their symbiotic interactions with plants and other insects, ant species also have parasitic relationships among each other of which slavery, or dulosis, is one of the more interesting forms. The genus *Polyergus* (subfamily Formicinae) consists entirely of slave-making species. Workers of *Polyergus* colonies dash into the nests of ants in the genus *Formica* (subfamily Formicinae) and steal their larvae and pupae. The stolen immatures are allowed to develop into adult workers and carry out colony maintenance tasks for their abductors. In fact, the *Polyergus* workers are so specialized for raiding and killing other ants that their jaws are like sharp curved sabers, morphologically ill-suited for nest building, tending immatures, and food gathering.

More extreme extensions of this parasitism are species without a worker caste. These species contain only males and queens that are cared for by the workers of a host colony, which they have infiltrated. They are either fed by the workers or steal food from the host queen, which they often mount and hold onto. The eggs of the parasite are reared to adulthood by the host workers. Parasitized host colonies can be smaller in size, presumably because of the partial diversion of resources to the parasites. Examples of these parasitic ants include *Solenopsis daguerrei*, a parasite of imported fire ants (*Solenopsis invicta*, *S. richteri*), and *Teleutomyrmex schneideri*, a parasite of *Tetramorium caespitum* and *T. impurum* (all in the subfamily Myrmicinae).

In contrast to the symbiotic life-styles, many species of ants are extremely predatory and have gained the reputation of being an unrelenting scourge of the jungle. The subfamily Dorylinae consists of a single genus, *Dorylus*, which contains the African driver ants, also referred to as army ants or legionary ants. Most species are found in the Afrotropical region (sub-Saharan Africa), but a few species are also found in the southern Palearctic, Oriental, and Indo-Australian regions. The various species of African driver ants have colonies with millions of individuals, which regularly move nesting sites and forage for food in large swarming columns or groups. The columns can fan out to produce a large moving front that preys on anything that remains in its path, especially arthropods. At night the colony forms a bivouac, protecting their queens and brood within a mass of worker ants. Thus, there is no permanent nest structure for these nomadic ants. Besides the army ants in the Dorylinae, the subfamily Ecitoninae contain many species of army ants found in the Neotropics, and a few species in the Nearctic. These armies are smaller than the African species, with colonies of hundreds of thousands rather than millions.

The pillaging, nomadic life of the army ants requires a high level of organization and cooperation. Extraordinary cooperative behavior is further exhibited during nest construction by the weaver ants in the genus *Oecophylla* (subfamily Formicinae). These ants are dominant arboreal ants of the Afrotropical region. They link their bodies together to form chains by grasping the petiole of an adjacent worker with their jaws. The living chains are used to pull the edges of leaves together. Once leaves are held in a desired positioned, other workers bring forth silk-producing larvae and individually press larval heads to one leaf surface then another, resulting in thousands of sticky silk threads being drawn between the leaves to hold them together. Eventually leaves and stems are bound together to form a tent within which a nest of silken galleries is constructed. This communal nest construction is unique in that it involves the use of immature stages that secrete silk on command. It has allowed these ants to build expansive networks of nests across several trees, which can house a colony of over 500,000 individuals.

The adaptability and high reproductive output of many species of ants allow them to thrive in many environments, including that of humans. As such, ants that live in buildings or have high populations in areas used by man are often considered pests. Many pest ants have characteristics that typify the 'tramp species'. These ants generally have 1) spread around the world via human commerce; 2) can thrive in man-made environments; 3) have colonies that are not territorial and thus can result in interconnected nest sites; 4) have many queens per colony; and 5) have limited or no mating flights resulting in colony reproduction by budding. Ants that sting, such as red imported fire ants (*Solenopsis invicta*, subfamily: Myrmicinae), are of veterinary and medical importance. Newborn livestock can be blinded or killed by stings at birth. The red imported fire ant now occupies about 150 million hectares in the U.S., and people in urban and rural areas who are stung can have hypersensitive reactions, resulting in anaphylaxis and even death in rare instances. Non-stinging ants, such as the Pharaoh ant (*Monomorium pharaonis*, subfamily: Myrmicinae) may be a nuisance to building occupants and are also known to contaminate sterile surgical units, supplies, and food items in hospitals. Invasive ant species, such as the red imported fire ants and the Argentine ant (*Linepithema humile* subfamily: Dolichoderinae), establish and thrive in non-native locations, invade surrounding areas, and eventually become the dominant faunal species. Invasive ants are a major concern in many areas, ranging from nature preserves to suburbia, because they displace native ants as well as other native organisms.

## Control

Controlling pest ants can be a difficult task given their broad habitat range, large populations, and a social organization that protects the queen(s) from external influences such as insecticides. Because traditional control approaches of excluding ants from buildings by sealing cracks and crevices or applying insecticides directly to ants or nests generally do not target the queen, significant population reductions, if any, are temporary. Ant baits, however, were developed to use the foraging and nest mate feeding behaviors of ants to distribute a toxicant throughout a colony, including the queen(s). Ant baits typically contain a toxicant dissolved into a liquid food preferred by the pest ant species. This poisoned food can be mixed with an absorbent carrier such as corn grit or formulated into a gel to facilitate handling and application. Some baits are left in liquid form and must be dispensed in a container that serves as a feeding station.

Key to effective ant bait is a toxicant with the following three characteristics. First, the concentration of toxicant used should not deter feeding on the bait, because ideally enough bait should be readily foraged upon to be shared with adults and immature stages of all castes within a colony. Second, the toxicant should not immediately kill the ants foraging upon the bait. In general, a delay in death or sickness of a minimum of 24 hours from the time of ingestion is required to allow sufficient toxicant to be collected and fed to a significant portion of the colony. If the toxicant causes sickness or death too quickly, distribution of the bait to the rest of the colony stops before enough of the colony is affected, and control will not be obtained. Third, the toxicant must not deter feeding on the bait and provide a delay in mortality over a wide range of concentrations (typically at least a 10 fold range) because the toxicant is diluted as it is shared among nestmates. Depending on the type of toxicant and colony size, ant baits may take from 2 weeks to several months to eliminate a colony. Some bait toxicants do not kill adults but instead disrupt reproduction by the queen, whereby worker caste ants are no longer produced. As the original adult worker population dies naturally, the lack of replacement workers dooms the colony to a slow death as functions that sustain a colony such as food gathering, defense, nest repair, and queen care cannot be carried out.

While ant bait development has been a major focus for ant control, other strategies have been developed for specific species. For example, planting forage grasses that are a non-conducive substrate for the growth of fungus needed by leaf-cutting ants can significantly reduce their populations. Natural enemies of ants are also used to suppress ant populations. In particular, tiny parasitic flies, in the genus *Pseudacteon*, that develop in the heads of ants, and a pathogen, *Thelohania solenopsae*, that debilitates queens are being used to suppress populations of imported fire ants. These natural enemies require development within fire ants and unlike chemical control measures, are self-sustaining and can spread naturally among fire ant populations. Effective control of pest ants, as with most insect pests, generally requires the use of several control tactics adapted for a particular species and circumstance.

See also MYRMECOPHILES, MYRMECOMORPHY, ANT-PLANT INTERACTIONS.

David H. Oi
U.S. Department of Agriculture,
Agricultural Research Service,
Gainesville, Florida, USA

**References**

Bolton, B. 1994. *Identification guide to the ant genera of the world.* Harvard University Press, Cambridge, Massachusetts. 222 pp.

Bolton, B. 1995. *A new general catalogue of the ants of the world.* Harvard University Press, Cambridge, Massachusetts. 504 pp.

Hölldobler, B., and E. O. Wilson. 1990. *The ants.* Harvard University Press, Cambridge, Massachusetts. 732 pp.

Smith, M. R. 1965. *House-infesting ants of the eastern United States: their recognition, biology and economic importance.* United States Department of Agriculture, Agricultural Research Service Technical Bulletin No. 1326. 105 pp.

Williams, D. F. (ed.). 1994. *Exotic ants: biology, impact, and control of introduced species.* Westview Press, Boulder, Colorado. 332 pp.

**ANUS.** The external opening of the digestive tract, through which the food remnants and metabolic waste products are passed. See also, ALIMENTARY CANAL AND DIGESTION, INTERNAL ANATOMY OF INSECTS.

**AORTA.** A tube located dorsally in the insect's body that conducts blood from the heart forward to the head region.

**APATELODIDAE.** A family of moths (order Lepidoptera). They commonly are known as American silkworm moths. See also, AMERICAN SILKWORM MOTHS, BUTTERFLIES AND MOTHS.

**APHELINIDAE.** A family of wasps (order Hymenoptera). See also, WASPS, ANTS, BEES, AND SAWFLIES.

**APHELOCHEIRIDAE.** A family of bugs (order Hemiptera). See also, BUGS.

**APHICIDE.** An insecticide that is especially effective against aphids.

**APHID FLIES.** Members of the family Chamaemyiidae (order Diptera). See also, FLIES.

**APHIDIDAE.** A family of insects in the order Hemiptera. They sometimes are called aphids, green flies, and plant lice. See also, APHIDS, BUGS.

**APHIDS.** Aphids are among the most interesting, unusual, and thoroughly studied of all insect groups. They are worldwide in distribution, and are also called plant lice, antcows, green flies, die Blattläuse, les aphides, los áfidos, etc. They have economic importance because many aphid species are pests of agricultural crops, forest and shade trees. Although small in size (1–10mm) compared to many other insects, professional as well as amateur entomologists have always been intrigued by their specialized life cycles that are influenced by their host plant relationships. This results in both sexual and asexual reproduction, with a highly dependent, almost parasitic mode of sessile existence that can be parthenogenetic during lengthy periods with a telescoping of generations. Yet, when the photoperiod shortens and the temperature cools, offspring are produced that reproduce sexually. In addition, aphids have life cycles with a polymorphism in adults that have wingless (apterous) and winged (alate) forms or morphs, as well as polyphenism or different morphs even within clones. As alates, migration is enhanced, and this can be involved with overwintering behaviors because of host plant