References

Barlow HS (1982) An introduction to the moths of South East Asia. Malayan Naturalist Society, Kuala Lumpur, Malaysia, 305 pp, 50 pl

Common IFB (1990) Moths of Australia. Melbourne University Press, Carlton, Australia, 535 pp, 32 pl

Covell CV Jr, (1984) A field guide to the moths of eastern North America. Houghton Mifflin, Boston, MA, 496 pp, 64 pl

Dominick RB, Hodges RW, Dominick T, Edwards CR, Hodges ER (eds) (1971) – The moths of America north of Mexico, including Greenland. Wedge Entomological Foundation, Washington, DC, 27 fasc

Hering EM (1951) Biology of the leaf miners. W. Junk, The Hague, The Netherlands, 420 pp, 2 pl

Holloway JD, Kibby G, Peggie D (2001) The families of Malesian moths and butterflies. E. J. Brill, Leiden, The Netherlands, 455 pp, 8 pl

Inoue H, Sugi S, Kuroko H, Moriuti S, Kawabe A (1982) Moths of Japan. Kodansha, Tokyo, Japan, 2 vol, 392 pl

Krenek V (2000) Small moths of Europe. Cesky Tesín, Czech Rep, 174 pp

Pinhey EGC (1975) Moths of Southern Africa. Tafelberg, Capetown, South Africa, 273 pp, 63 pl

Robinson GS, Tuck KR, Shaffer M (1994) A field guide to the smaller moths of south-east Asia. Malaysian Naturalist Society, Kuala Lumpur, Malaysia, 309 pp, 32 pl

Watson A, Whalley PES (1975) The dictionary of butterflies and moths in color. McGraw Hill, New York, NY, 296 pp, 144 pl

Young M (1997) The natural history of moths. T. & A.D. Poyser, London, United Kingdom, 271 pp, 16 pl

Motile

Active. Able to move freely.

Motor Neurons

Neurons associated with the central nervous system that transmit information to muscles and glands.

Motschulsky, Victor Ivanovich

Victor Motschulsky was born in 1810 in Russia, and became one of the most famous Russian entomologists and greatest coleopterists of his time. He collected extensively from Russia, including Siberia and Russia's (at the time) possessions of Alaska and California. As a colonel in the military, he had unusual access to travel, and took full advantage of his journeys, collecting and studying Coleoptera in Europe, North Africa, and much of North America in addition to the locations previously mentioned. Indeed, it is sometimes stated that his collecting trips were a cover for military intelligence. He also processed enormous amounts of material collected by others. Motschulsky was a strong-illed, independent, and controversial individual. He was possessive, superficial with his descriptions, rough on specimens, and unconventional with his mounting techniques. This led him to clash with other coleopterists of the time, particularly Kraatz. He died June 5, 1871, at Simferopol, Crimea, Russia.

References

Essig EO (1931) A history of entomology. The Macmillan Company, New York, 1029 pp

Herman LH (2001) Motschulsky, Victor Ivanovich. Bull Am Mus Nat Hist 265:110–112

Mountain Midges

Members of the family Deuterophlebiidae (order Diptera).

► Flies

Mountain Pine Beetle, Dendroctonus ponderosae (Coleoptera: Curculionidae, Scolytinae)

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The mountain pine beetle, *Dendroctonus ponderosae* Hopkins, is considered one of the most economically important insect species in coniferous forests of western North America. Adult beetles are capable of successfully reproducing in at least 12 North American species of *Pinus* (Pineacea) from southern British Columbia to northern Baja Mexico. Mountain pine beetle adults attack live trees, and typically must kill the host for successful reproduction. Population outbreaks are most common in a few selected host species, such as lodgepole pine (*P. contorta*), ponderosa pine (*P. ponderosa*), western white pine (*P. monticola*), whitebark pine (*P. albicaulis*), and sugar pine (*P. lambertiana*), which often grow in relatively homogeneous groups over large acreages. Mountain pine beetles typically attack older lodgepole and whitebark pine (e.g., greater than 80 years), while younger ponderosa, western white, and sugar pine can also be attacked. Trees that are stressed by factors such as overcrowding, water, and pathogens are especially vulnerable.

The lifecycle of the mountain pine beetle is highly dependent upon temperature. Commonly, populations are univoltine, although at higher elevations where average temperatures are colder, 2 and sometimes 3 years are required to complete a generation. Adult beetles emerge from host trees and disperse to new hosts in the warm summer months when temperatures are above 15.5°C. Although timing of emergence will vary from year to year depending on beetle development and temperature, peak adult emergence typically occurs within a 2–3 week time span. Rapid and synchronous emergence of the population is essential for mountain pine beetle success in overcoming the resinous defenses of healthy host trees. Adult dispersal involves movement within an infested patch of trees, movement between infested patches of trees, and movement out of the immediate area for initiation of new patches. Long range dispersal to new areas is often aided by wind currents, whereas local dispersal is directed by aggregation pheromones, compounds released when adult beetles attack and feed on new host trees. Monoterpenes, which are major constituents of pine resin, are converted by adult beetles to compounds which, when released, act to aggregate other mountain pine beetles on the tree. Aggregation pheromones enable mountain pine beetles to overcome the defenses of large, vigorous host trees by rapid and highly concentrated attacks. In this manner, mountain pine beetles are functionally able to expand their own food supply. Larger trees require more adults to overcome the tree resin defensives, but also produce a larger number of brood the following generation for continued tree attack. Because a single tree is a finite resource, pheromones are also produced which interrupt the aggregation of adults on a tree. The interruptive aggregation pheromones direct incoming adults to unoccupied portions of the tree under attack, and also to nearby host trees, thereby reducing competition for resources within a single tree. In this manner, during an outbreak, thousands of trees can be attacked and killed in a single year.

Once inside a new host tree, adults mate and eggs are laid individually on each side of galleries excavated vertically in the phloem. Phloem is the inner tissue layer just below the outer bark which translocates carbohydrates up and down the tree. Mountain pine beetle larvae feed horizontally in the phloem, cutting off nutrient translocation, thereby killing the host tree. Larval development rate, which is highly dependent on temperature, dictates the life stages present during the winter. Available evidence indicates that the mountain pine beetle does not diapause, and all larval life stages may be found overwintering under the bark of host trees. The larvae, which are intolerant of freezing temperatures, survive low temperatures by supercooling. Populations in Idaho have been found to survive temperatures as low as −35°C. Mortality due to cold temperatures is usually greatest during the spring and fall months when larvae may not be appropriately acclimated to dramatic swings in temperature. Woodpeckers, clerid beetles (*Enoclerus* spp., *Thanasimus* spp.), and parasitic wasps are also the cause of a small amount of mountain pine beetle mortality, mostly at endemic population levels.

Pupation occurs in the early summer followed by a teneral adult stage during which the new adults feed on a diverse flora of microbial symbionts including fungi (*Ophiostoma* spp.) and yeasts found within the pupal chamber. During this feeding period, the microorganisms are acquired in the mycangia, a specialized structure of the integument. When the adult beetle emerges from the host tree for dispersal to a new tree, the fungi and yeasts are carried inside the mycangia and inoculated into the phloem of the new host. Although the role of *Ophiostoma* spp. in mountain pine beetle population dynamics are not fully understood, at least one species appears to be beneficial to population success, while detrimental effects are attributed to another species. Following maturation feeding in the teneral adult stage, new adults emerge from the dead trees to disperse, attack new live host trees, and begin the cycle again.

Given appropriate weather and stand conditions, populations of mountain pine beetles are capable of attacking and killing hundreds of thousands of trees in a few years. This magnitude of mortality can disrupt forest management plans, recreation, watershed, wildlife, and timber production. In areas of high value, such as forest campgrounds and ski areas, direct control tactics such as insecticides are often used to temporarily reduce mountain pine beetle caused mortality. Synthetic forms of the aggregation pheromone may also be used to concentrate adults in traps or trees which are then removed from the area. Ongoing research is aimed at understanding the role of interruptive aggregation pheromones in mountain pine beetle population dynamics, in the hope that synthetic forms of these compounds may also provide a tool for direct population control. While direct control tactics are useful in small, high value areas, they are not effective or feasible over large areas, and do not alter the habitat and stand conditions that are favorable to mountain pine beetle populations. The optimum approach in areas which have been targeted for management is prevention. Silvicultural practices such as thinning, which decrease the density of host trees, help to maintain vigorous trees and create a less favorable habitat for mountain pine beetle population growth. A mosaic of vegetation types across a landscape, partitioned by age and host and non-host species, may also help to reduce large scale, widespread mortality.

Options for management of mountain pine beetle populations depend on the specific land use objectives. Forested areas targeted for timber production can be silviculturally treated to facilitate reduced susceptibility to mountain pine beetle outbreaks. Many areas designated as wilderness, however, are managed as natural areas and timber harvest is not a major objective. Within these areas the historical role of the mountain pine beetle in forest ecosystems may be emphasized. Mountain pine beetle populations, which are native to western North America, have evolved with their pine hosts and are significant components of healthy, functioning ecosystems. In particular, the mountain pine beetle and fire are considered important disturbance agents favoring the regeneration of lodgepole pine. While tree death is a difficult concept for humans, it is a normal step in the rejuvenation and succession of forest ecosystems, and the mountain pine beetle is an important part of this process.

► Bark Beetles in the Genus *Dendroctonus*

References

Amman GD, Cole WE (1983) Mountain pine beetle dynamics in lodgepole pine forests Part II: Population Dynamics. USDA Forest Service, Intermountain Forest and Range Experiment Station, General Technical Report INT-145

Borden JH, Chong LJ, Lindgren BS (1990) Redundancy in the semiochemical message required to induce attack on lodgepole pines by the mountain pine beetle *Dendroctonus ponderosae* Hopkins (Coleoptera: Scolytidae). Can Entom 122:769–777

Logan JA, Bentz BJ (1999) Model analysis of mountain pine beetle (Coleoptera: Scolytidae) seasonality. Environ Entomol 28:924–934

McGregor MD, Amman GD, Schmitz RF, Oakes RD (1987) Partial cutting lodgepole pine stands to reduce losses to the mountain pine beetle. Can J For Resour 17:1234–1239

Raffa KF (1988) The mountain pine beetle in western North America. In: Berryman AA (ed) Dynamics of forest insect populations, patterns, causes and implications. Plenum Press, New York, NY, pp 506–531

Shore TL, Safranyik L (1992) Susceptibility and risk rating systems for the mountain pine beetle in lodgepole pine stands. Forestry Canada, Pacific Forestry Centre, Victoria, Canada

Mouth Beard

In robber flies (Asilidae), the prominent tuft of hairs at the front of the head. This is also called the mystax.

Mouth Cone

A term used to describe the mouthparts arrangement of thrips (Thysanoptera).

► Mouthparts of Hexapods

Mouth Hooks

In larvae of the higher Diptera, the mandible-like feeding structures located at the oral cavity.

Mouthparts of Hexapods

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The hexapods are trignathan, that is to say they present three pairs of buccal appendages, each one of them situated in the corresponding cephalic segment: a pair of mandibles (mandibular segment), a first pair of maxillae (maxillary segment), and a second pair of maxillae that fused, form the labium (labial segment).

Recently, certain authors affirm that the classic point of view, according to which the true capacity of "biting" by the Dicondylia [Thysanura (Zygentoma) plus Pterygota] is functionally correlated to the acquisition of dicondylic mandibles, cannot be maintained, taking into account that the capacity of "biting" transversely is a trait characteristic of the hexapods. Therefore, the division of the mandibles into mono- and dicondylic is not fitting (Koch 2001); because of this, and owing to the great variability existing in the hexapods, this author prefers to treat separately the mandibles of each one of the large groups: Collembola, Protura, Diplura, Archaeognatha, Thysanura and Pterygota.

Despite the opinion of Koch, many authors consider, at least from a practical point of view, the type and number of articulations within the head capsule to separate two fundamental types of mandibles: monocondylic (one articulation) and dicondylic (two articulations). The monocondylic type is characteristic of the majority of Apterygota, although in Collembola, Protura and Diplura an authentic mandibular condyle does not exist as in the case of Archaeognatha. This monocondylic type appears secondarily in entognathous Pterygota, with mouthparts transformed into stylets.

The dicondylic type is typical of the Pterygota, where two mandibular articulations are differentiated, one in the anterior position and another posterior. An intermediate condition exists between the mono- and dicondylic types. In it the mandibles, in addition to the principal articulation (corresponding to the only condyle of Archaeognatha), present a secondary articulation known as the epicondyle. It is situated in the anterior third of the mandibular body and therefore differs from the second articulation of Pterygota, which has a clearly posterior position. This intermediate model is displayed in Thysanura and nymphs of Ephemeroptera.

The morphology of the mandible varies according to the diet and is usually characteristic in each of the hexapod orders. Nevertheless, it basically consists of an incisor zone in the distal or subdistal position and another molar zone situated on the internal mandibular face. The greater or lesser development of these two zones is found in the function of the alimentary behavior. Thus, in predatory species the incisory zone is usually well developed, since it serves to cut and tear the prey. On the contrary, in phytophagous species