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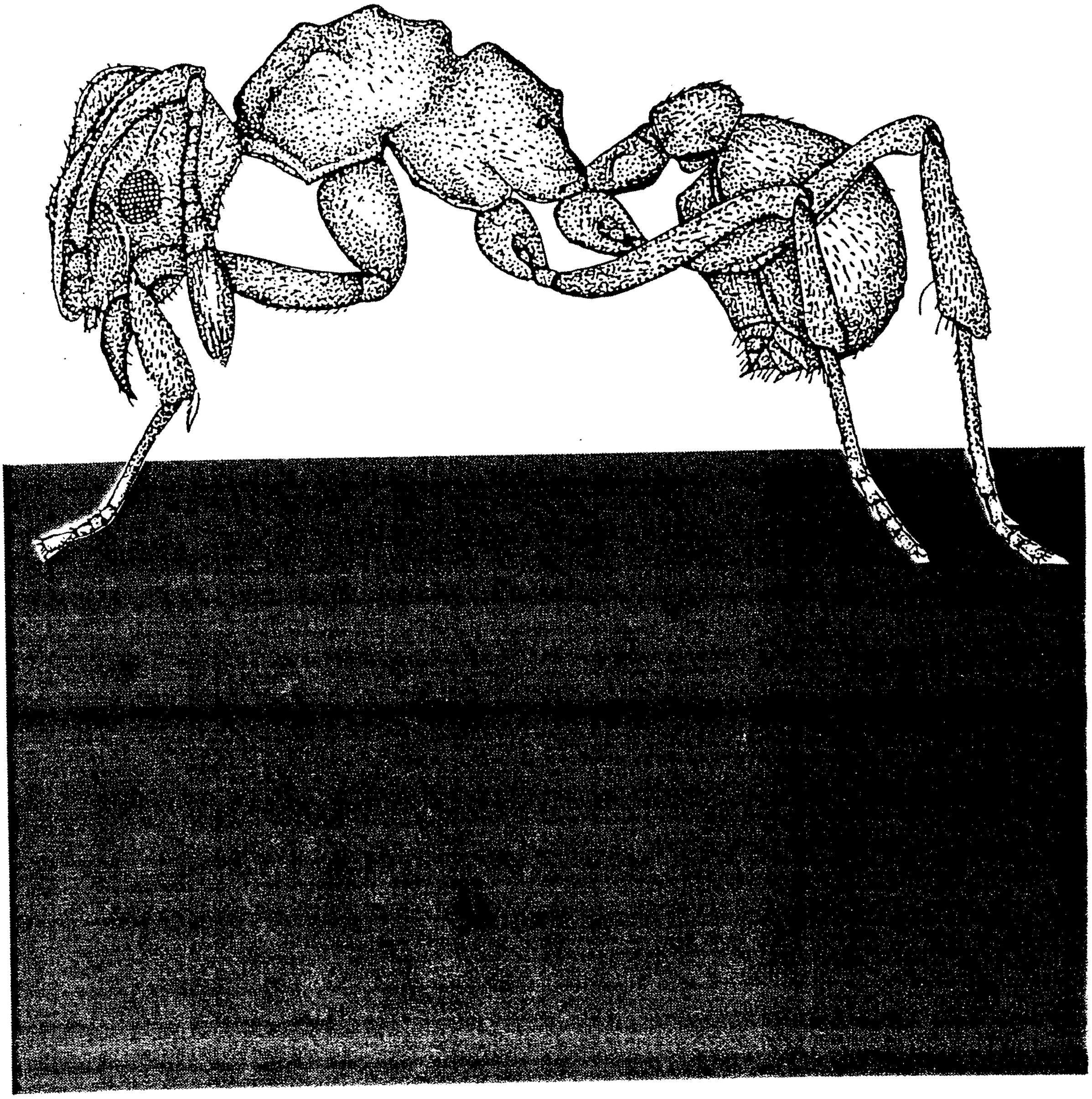
Insects of the Luquillo Mountains, Puerto Rico

Juan A. Torres



SUMMARY

In this review of the literature on forest entomology in Puerto Rico, emphasis is given to research conducted in the Luquillo Experimental Forest (LEF). This review should serve as an introduction to the insects inhabiting the LEF for researchers and as a guide for the identification of possible insect pests. There are three sections to this review. The first deals with basic insect ecology; the second, forest insect pests; and the third, insect attacks on dry wood and during wood seasoning. The reference section and appendixes contain information on the systematics and taxonomy of different insect orders found in Puerto Rico.

ACKNOWLEDGMENTS

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INTRODUCTION

There is a generalized belief that Puerto Rico lacks problems with forest insects. The reason for this belief may be that, unless forests are profoundly disturbed through silvicultural practices or natural disasters, indigenous insect pests normally do not cause catastrophic or appreciable damage to stands. The initial success of exotic tree species does not guarantee that they will not eventually face insect or disease problems. Time is required for populations of insect pests and pathogens to build up and for local pests to adapt to a new host (Bakshi 1976). In addition, increases in the area of forest cultivation will lead to an increase in insect pests associated with the host (El Servicio de Extensión Agrícola 1948, Strong 1979). The cultivation of small areas to examine the adaptability of a plant species to a new environment cannot test this phenomenom. The rapid growth rates of some tropical tree species, as well as the fact that the growth is continuous over much of the year, allow trees to outgrow the attacks from most leaf-feeding insects (Hodges and McFadden 1987). However, some tropical insects may be more difficult to control because they thrive throughout the whole year. In tropical areas with a prolonged dry season, the weather can keep insect populations at relatively low levels (Janzen 1973a).

The problems created by insects in forests often require different control approaches than those used in agriculture. The use of insecticides can be economically prohibitive even when it is a reasonable alternative for forest insect pest control. Thus, it is important to include entomologists as part of forest management teams for evaluating the effects of management practices and natural disturbances on insects and vice versa. Management practices developed for agricultural systems are labor intensive and incorporate vast quantities of fertilizers and other inputs, which are often not economically feasible for use in forest systems. For these reasons, many of the inputs that keep a forest in a healthy condition must be provided by the organisms that comprise the community.

Insects have several beneficial roles in a forest. Many plants require insects for pollination and seed dispersal (Beattie 1985). Many vertebrate species that humans consider esthetic elements of the biota are completely or partially dependent on the presence of insects for their nutrition (García 1938, Janzen 1973b, Ross and others 1982). In bodies of water in the forest, many fish rely on insects for much of their food, and aquatic insects recycle nutrients in their habitats before the nutrients are carried downstream into the ocean (Ross and others 1982). Insects are also important in nutrient recycling in terrestrial systems. Many species of birds and other terrestrial predators feed on aquatic insects, returning nutrients back to the terrestrial environment. The burrowing activities of invertebrates, including several insect species, help reduce soil erosion by facilitating the penetration of water and reducing overland runoff (Anderson 1988).

In this paper, the literature on forest entomology in Puerto Rico is reviewed, giving emphasis to the work done in the Luquillo Mountains. The Luquillo Mountains are located in the northeast corner of Puerto Rico and mainly include four subtropical life zones: wet forest, rain forest, lower montane wet forest, and lower montane rain forest. There are four predominant plant associations in the mountains: tabonuco, colorado, palm, and dwarf forests. These four plant associations are roughly stratified by altitude. The tabonuco forest is found below 600 m and occupies nearly 70 percent of the Luquillo Mountains. The colorado forest, which covers about 17 percent of the mountains, is found above 600 m. On peaks and ridges above 750 m (2 percent of the Luquillo Mountains) the dwarf forest is found. The palm forest is interspersed within the colorado and dwarf forests and covers 11 percent of the Luquillo Mountains (Brown and others 1983).

This review is divided in three sections: (1) insect ecology, (2) insect pests of forest trees and shrubs, and (3) insect pests of forest products. The first section covers the research on insects that are not generally considered economically important but perform many important ecological functions. The section on insect

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Juan A. Torres is an associate professor, Department of Biology, University of Puerto Rico, Bayamón, PR 00959-1919. Research and data compilation for this publication were done by the author while he was conducting postdoctoral research at the Institute of Tropical Forestry, U.S. Department of Agriculture, Forest Service, Southern Forest Experiment Station, Río Piedras, PR 00928-2500.

pests of forest trees and shrubs deals with insects that have created problems in important (or potentially important) timber species that grow in the Luquillo Mountains. Forest insect pests appear to have been more common in the first half of this century than at present in Puerto Rico. This may be related to the widespread use of modern insecticides and the introduction of the frog *Bufo marinus* to Puerto Rico in the 1920's (Wolcott 1948b). In the last section, insects that attack wood during the drying process and insects that consume dry wood are discussed. The section contains a thorough discussion of termites, which is necessary due to the importance of this group of insects and the extensive misconceptions about feeding preferences of termites. Appendix A lists forest and plantation trees and their associated potential insect pests. Appendix B provides a list of contributions that provide a quick introduction to the ecology and pest insects in the Luquillo Mountains. Appendix C is an annotated bibliography of additional references that deal with the systematics of some insect groups. Wolcott (1948a, 1948b, 1948c, 1948d) and Maldonado and Navarro (1967) can be consulted for additional references on systematics.

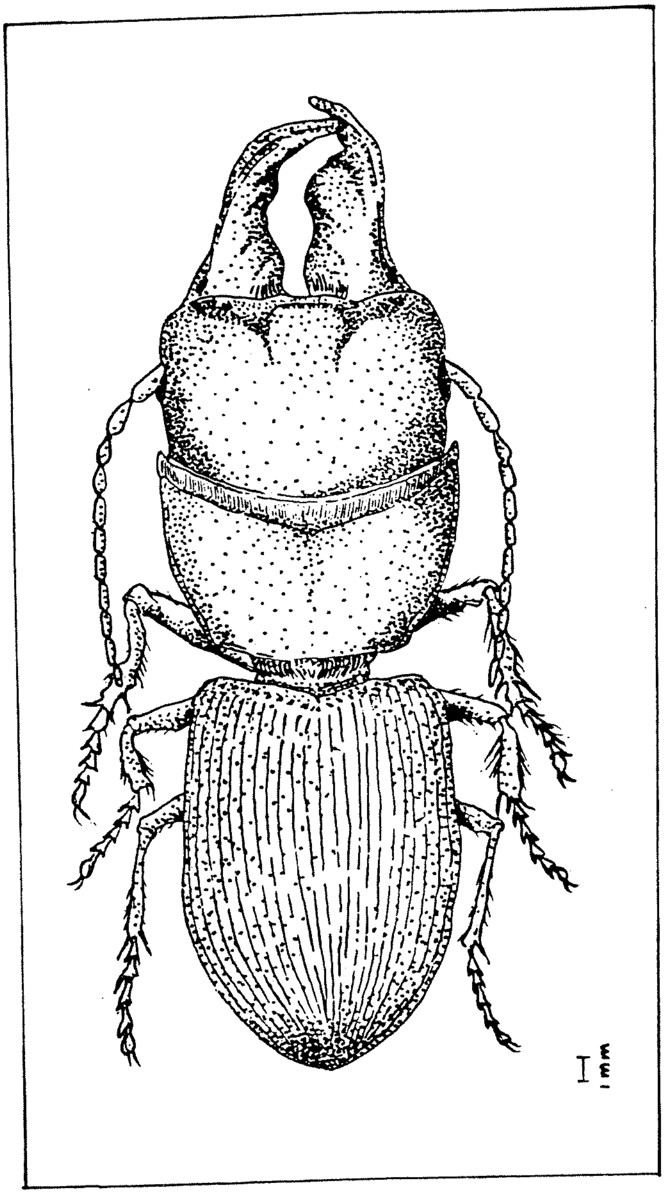

Figure 1.—*A ground beetle* Antilliscaris megacephalus; *actual length of the beetle is approximately 35 mm (adapted from Darlington 1970 with permission of "Biotrópica").*

The radiation experiment referred to in this review involved the exposure of a section of the tabonuco forest near El Verde Field Station to a 10,000 curie cesium source for 92.8 days (Jan. 19 to Apr. 27, 1965). Comparisons with a mechanically pruned area known as the north cut center and a little-disturbed south control center were made to determine the effects of radiation. This radiation study was conducted under the sponsorship of the U.S. Atomic Energy Commission and the results are summarized in the book "A tropical rain forest: a study of irradiation and ecology at El Verde, Puerto Rico" (U.S. Atomic Energy Commission 1970).

INSECT ECOLOGY

Order Coleoptera (beetles)

Carabidae (ground beetles).—Most species of ground beetles (the Carabidae family) hide during the day and feed at night. Nearly all are predaceous on other insects. Darlington (1970) studied the ground beetles, finding a reduction in the number of species at high elevations in Puerto Rico and a tendency for wing atrophy. Lowland species are usually small and have well-developed wings. Darlington reported *Antilliscaris megacephalus* (recorded as *Scarites megacephalus)* from the Luquillo Mountains as the largest Carabidae (30 to 35 mm) found in the Antilles (fig. 1). Hlavac (1969) presented taxonomic keys for the genus *Antilliscaris* and compared the Puerto Rican species with the ones from Jamaica. There are 8 known montane species of carabids in Puerto Rico (3 in the genus *Antilliscaris)* and 17 in Jamaica, an island of similar size. In Jamaica, nine of the carabid species belong to the genus *Colpodes,* and there are no *Antilliscaris.* The montane biota of Puerto Rico is unique in not having members of the ecologically variable carabid genus *Colpodes.*

Hlavac (1969) suggested the occurrence of a shift from burrowing to crawling on the ground surface in the *Antilliscaris* of Puerto Rico. Short antennae are characteristic of diverse burrowing Coleoptera that have evolved a pedunculate body form. In *A. megacephalus,* 50 percent of the antennae extend beyond the mandible. If *A. megacephalus* burrows, the antennae would have to be doubled over during this activity. The long antennae of this species strongly suggest that it is not a burrowing one. *Antilliscaris megacephalus* is doubtless one of the top predators among ground invertebrates (Hlavac 1969).

Based on larval characters, *Antilliscaris* is closely aligned with genera of the Afrotropical region, especially with *Prodyscherus,* which is endemic to Madagascar (Nichols 1986). The abundance of *Antilliscaris* may have been severely affected by the introduction of predators and omnivores, such as mongooses *(Herpestes auropunctatus),* feral cats *(Felis catus),* toads *(Bufo marinus),* the wharf rat *(Rattus norvegicus),* and the black roof rat *(R. rattus)* to Puerto Rico (Nichols 1988).

The presence of three species of *Antilliscaris* and the relatively high percentage of endemism (38 percent) in the Puerto Rican Scaritinae fauna suggest that Puerto Rico is the oldest emergent land mass in the Greater Antilles (Nichols 1988).

The carabid genus *Platynus* is composed of at least 66 species in the West Indies. Most of these species are restricted to single islands, some to only one mountain on an island (Liebherr 1988). There are 25 endemic species of *Platynus* in Hispaniola and 12 in the Lesser Antilles. Although Puerto Rico has suitable mountain and forest habitats for beetles of the genus, no *Platynus* beetles have been found. The small size of Puerto Rico and its geographical location at the eastern end of the Greater Antilles make the island a comparatively poor candidate for receiving water-transported immigrants (Liebherr 1988).

Leiodidae (round fungus beetles). – Round fungus beetles (the Leiodidae family) occur in fungi, under bark, in decaying wood, in carrion and in other similar habitats (Borror and others 1981). Peck (1970, 1972) studied the subfamilies Catopinae and Leiodinae in Puerto Rico and Jamaica. Most of the Catopinae beetles occur in carrion. Peck found that members of the Catopinae were rare in the Luquillo Forest and suggested that high humidity may be the reason for the low numbers of these insects. In addition, the zoogeography of the family is delineated.

Scarabaeidae (scarab beetles). – The scarab beetles (the Scarabaeidae family) vary greatly in feeding habits. Many feed on dung, decaying plant material, carrion, etc.; others feed on live plants. Matthews (1965), in his detailed study of the dung beetles of the Luquillo Mountains, showed that the species were separated according to altitudinal belts, behavior, and diel cycle (figs. 2, 3). He compared the Puerto Rican species with the ones from Mauritius (in the Indian Ocean). Several patterns were found to be in common, including the distributions of species highly influenced by altitude and bird and mollusk excrement as the main sources of food for these beetles before humans came. Food is now provided by the excrement of an introduced monkey, *Macaca,* in Mauritius, and the roof rat, *Rattus rattus,* in Puerto Rico. The parallelisms are the result of adaptations by beetles of the same tribe to similar tropical oceanic islands of mountainous topography. Matthews also delineated possible historical diet changes for these beetles in Puerto Rico, and, for the scarab *Canthochilum histeroides,* he reported altitudinal variation in morphology. The scarab beetles are important in nutrient cycling. In Puerto Rico, the absence of large dung beetles capable of exploiting large masses of excrement in open areas such as cow pastures, results in areas that are temporarily unavailable for grazing and provides breeding media for horn flies.

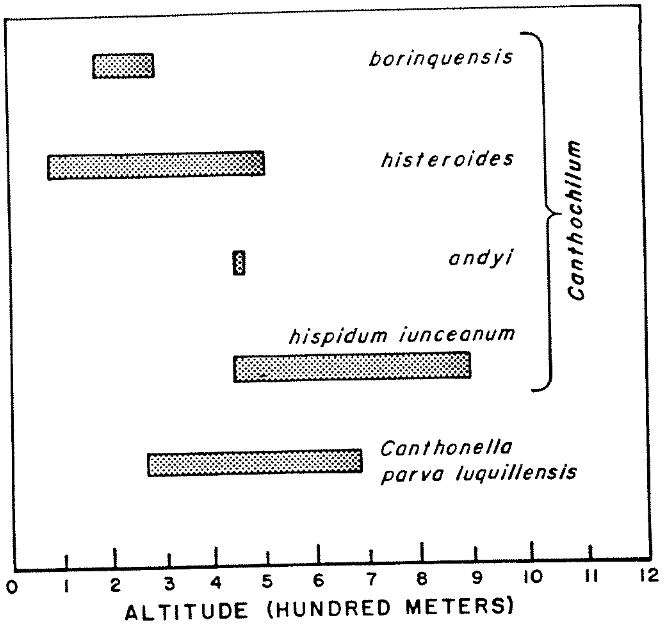

Figure 2. – *Altitude distribution of the dung beetles found in the Luquillo Mountains of Puerto Rico (adapted from Matthews 1965 with permission of "Transactions of the American Entomological Society").*

Matthews (1966) also wrote a treatise on the taxonomy, zoogeography, ecology, and evolution of the subfamily Scarabaeinae in the Antilles. The ecogeographic, adaptive radiation in the genus *Canthochilum,* in Puerto Rico and Cuba, and other patterns of endemism were discussed. Matthews found that the neotropical species of the Antillean scarabaeine fauna comprise a minority; the majority of the species are possibly of Old World origin. The high endemicity of the Greater Antilles Scarabaeinae fauna is a reflection, not of insular evolution, but of the survival of an ancient fauna for which these islands have become a refuge. The restriction of the beetle *Oniticellus cubensis* to open terrain points to the presence of natural savannas before the advent of humans to the region. Matthews invoked interspecific competition to explain the patterns of distribution on many islands. The highland, humid forest belt is not invaded by dung beetles except under the pressure of interspecific competition result-

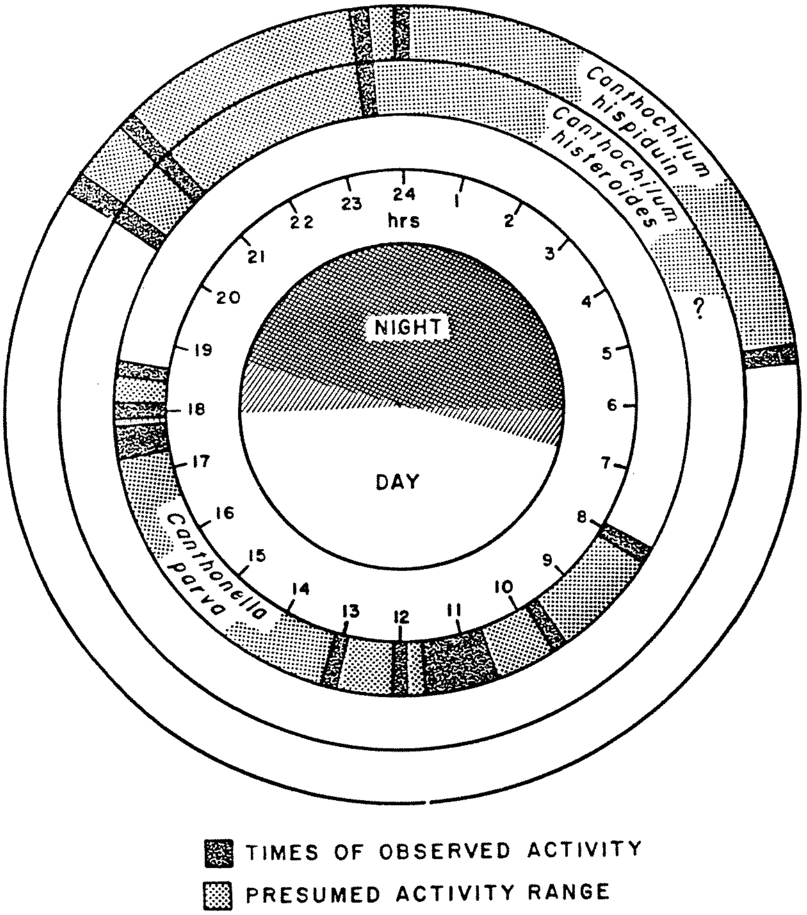

Figure 3.—*Diel activity cycles of the three most abundant species of dung beetles in the Luquillo Mountains of Puerto Rico (adapted from Matthews 1965 with permission of "Transactions of the American Entomological Society").*

ing from the invasion of a second species of the same genus. One of the species may be displaced into the montane zone, while the other remains in the lowland belt.

Scolytidae (bark beetles) and Platypodidae (pin-hole borers).—The Scolytidae family contains two main groups: the bark beetles, which feed on the phloem tissue, and the ambrosia beetles, which bore into the wood and cultivate a fungus upon which they feed. Some scolytids feed on seeds. Janzen (1972) described the interaction between the scolytid beetle *Coccotrypes carpophagus* and the palm *Prestoea montana.* Janzen hypothesized that seed predation by the beetle is the selective force producing fruiting synchrony in the palm. Nonetheless, Wood (an authority on this family of beetles, Janzen 1972) thinks that *C. carpophagus* was introduced to Puerto Rico from the Old World around 1900. This implies that the interaction between the beetle and the palm is recent and does not represent an example of coevolution. Bannister (1970) found that *P. montana* germination percentages in plots where *C. carpophagus* was abundant did not differ from plots where the beetles were scarce.

It appears that tropical cyclones can affect the abundance of these organisms because plant phenology changes after tropical storms (Bates 1929). When this happens, pollinators and seed eaters are stressed. Nonetheless, organisms that feed on dead or damaged wood like scolytids, platypodids, cerambycids, and termites increase in abundance after storms (Bates 1929, Wolcott 1932).

Schedl (1961), in his treatise of the Scolytidae and Platypodidae families, gave information about distribution and hosts for some Puerto Rican members of the two families. Bright (1985) compiled a checklist of the West Indies Scolytidae.

Order Diptera (flies)

Culicidae (mosquitoes).—Mosquitoes (the Culicidae family) are important because the females are blood feeders; many species bite humans, and they serve as vectors in the transmission of diseases. In a study of the effects of cesium gamma radiation on the mosquito populations at El Verde, Weinbren and Weinbren (1970) argued that the mosquito *Aedes*

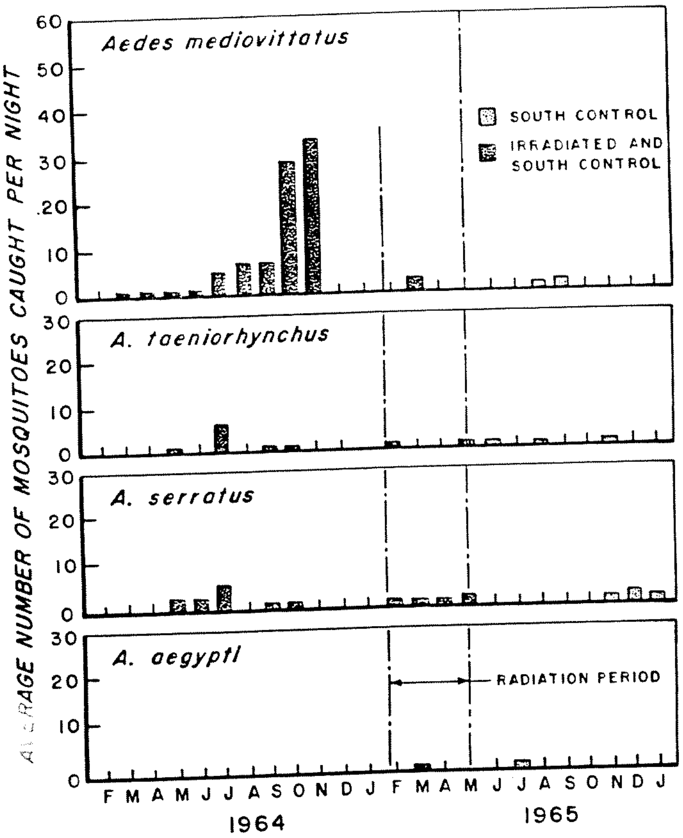

Figure 4. – *Monthly capture record of four mosquito species of* Aedes *in El Verde, Puerto Rico, before and after radiation (adapted from Weinbren and Weinbren 1970).*

aegypti seemed more prevalent after radiation, although the number captured was small (fig. 4). The mosquitoes appeared to belong to a wild strain of this species that is generally found in the Old World. Breeding inside dense forests is not documented in the New World *A. aegypti* and is only rarely encountered in the wild strains of this species in Africa (Haber and Moore 1973).

Weinbren and Weinbren (1970) furnished a list of the members of the family Culicidae found in Puerto Rico and information on the temporal abundance of other mosquito species in the Luquillo Mountains. Because there were no replications in the experiment and no appropriate statistical analyses, the changes in abundance of these mosquito species could not be directly related to the effects of radiation or the opening of the canopy. Five years after the study by Weinbren and Weinbren, Haber and Moore (1973) conducted a survey of the same area and did not find *A. aegypti* in the dense forest. It appears that the increase in numbers of *A. aegypti* at El Verde was not due to the effects of radiation, but to the result of the intense human activity inside the forest during and after the radiation experiment. The traffic of equipment and materials to the experimental area increased the breeding area. After much of the research activities ceased, both habitats and hosts may have diminished below the level needed to support a breeding population.

Tulloch (1938) made notes on the mosquitoes associated with bromeliads in the Luquillo Mountains and the Maricao State Forest. Information on the temperature and pH of the water where the mosquitoes bred is provided. These pH readings, along with those presented in Paz (1974), could serve as a baseline to study possible changes in water pH due to atmospheric pollution.

Muscidae (muscid flies). – Many muscid flies are important pests, among them the house fly, *Musca domestica,* and horn flies, *Haematobia irritans,* which are pests of cattle. The larvae of the flies *Philornis* spp. parasitize several bird species in Puerto Rico, including the Puerto Rican parrot *Amazona vittata* (Arendt 1985a, 1985b, Pérez and Collazo 1976, Snyder and others 1987). The incidence of parasitism varies geographically and among bird species. Thrasher nestlings, *Margarops fuscatus,* have been found infested a few hours after hatching. Seasonal and annual variations occur in the level of parasitism of thrashers. Arendt found that 97 percent of nestling mortality in the pearly-eyed thrasher was due to parasitism by larval *Philornis* spp. Ninety-six percent of 448 nestlings examined from 1979 to 1982, harbored *Philornis* larvae (table 1), whereas 31 percent of adult birds harbored the larvae. Infested thrasher nestlings were underweight and showed retarded tarsus growth as well as delayed emergence of the ninth primary pinfeather. The survival of post-fledge juveniles was influenced by parasitism while in the nest (Arendt 1985a, 1985b; Uhazy and Arendt 1986).

Phoridae (humpbacked flies). – Phorid adults are abundant in decomposing vegetation. Larvae occur in decaying animal or plant matter, in fungi, as internal parasites of other insects, and as parasites or commensals in the nests of ants or termites (Borror and others 1981). Villa and Townsend (1983) found the larvae of the phorid fly, *Megaselia scalaris,* eating viable eggs of the frog *Eleutherodactylus coqui.* In 1982, the flies infested approximately 3 percent of the frog egg clutches. The fly's larval stage lasts between 34 and 46 hours, and the pupal stage lasts a minimum of 242 hours (10 days).

Syrphidae (flower flies). – Adult syrphid flies are common near flowers and often do a great deal of hovering. Many are brightly colored and resemble wasps or bees. Syrphid larvae are predaceous on aphids. They live in the nests of social insects, decaying wood, or polluted aquatic habitats (Borror and others 1981). In Puerto Rico, most of the members of this family (fig. 5) feed on aphids and are beneficial in suppressing aphid outbreaks. Life history studies on the subfamily Syrphinae have been undertaken on few species. Telford (1973) suggested that some Syrphinae species

Table 1.—*Prevalence and mean intensity of* Philornis *spp. larvae on 448 nestling pearly-eyed thrashers, 1979-1982 (adapted from Arendt 1985a with permission of The Auk)*

Month	Nestlings sampled	Prevalence	Total number of parasites	Intensity (range)
		Percent		*Parasites per bird*
January	3	100	69	23.0 (19–26)
February	25	80	432	20.6 (0–49)
March	43	81	1,086	25.3 (0–73)
April	97	96	4,215	40.9 (0–220)
May	115	100	4,720	45.4 (6–131)
June	95	100	6,294	61.7 (3–169)
July	70	100	2,946	42.1 (5–135)

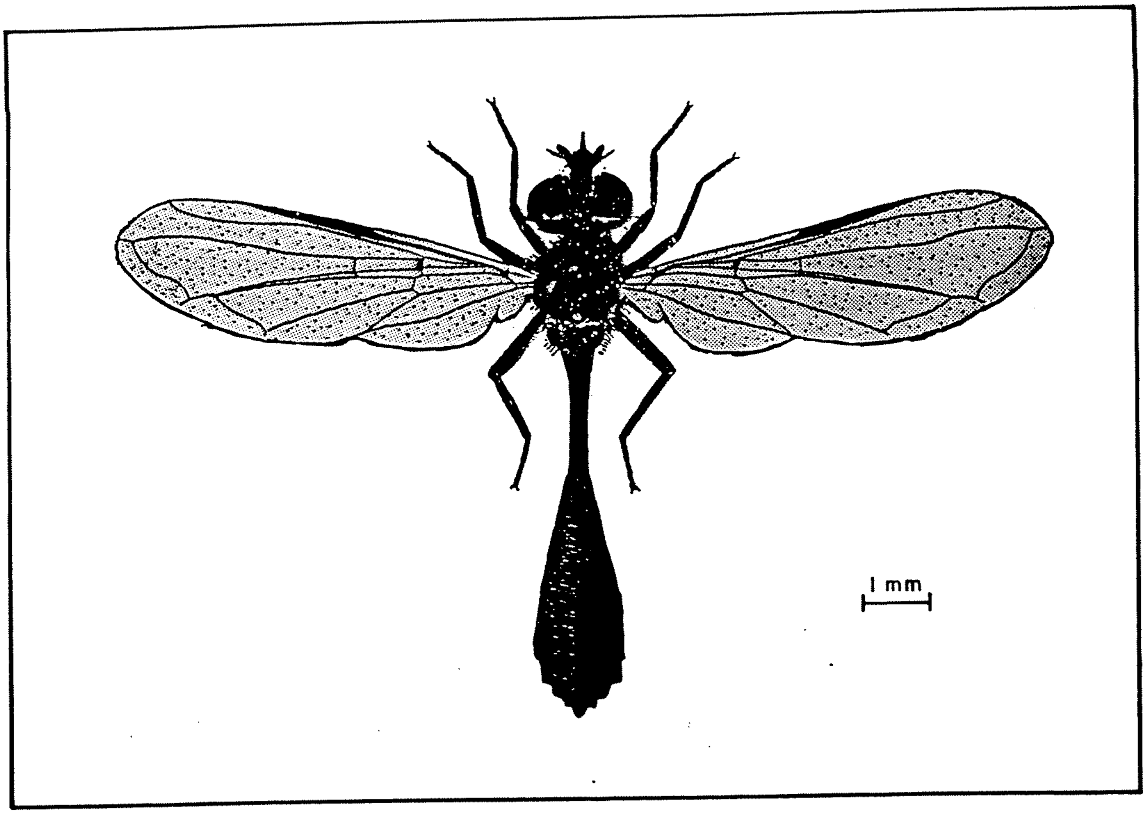

Figure 5.—*A flower fly,* Baccha clavata *(adapted from Wolcott 1948c).*

can be facultative predators or some subsist solely on plant food. It is possible that some species feed on decomposing plant material as well as on insect prey.

Tipulidae (crane flies).—Most of the adult tipulids resemble overgrown mosquitoes with extremely long legs, which are easily broken off (Borror and others 1981). The larval food of most species consists of decayed vegetation. The larvae of some species feed on algae and the roots of plants; others are carnivorous (Peterson 1982). In Puerto Rico, the various Tipulidae species tend to exhibit different patterns of distribution (Alexander 1932). Some tend to be isolated at higher elevations in the mountains of Puerto Rico, others tend to be widespread. The Luquillo Mountains are of unusual interest because several crane fly species are apparently restricted to this area. The ecology of this group is quite variable. Some crane fly larvae are found on the wet faces of cliffs at the margins of streams; others are aquatic and carnivorous. The latter group pupates on land, and the adults occur in swarms close to rivers. Larvae of Tipulidae have been found feeding on tabonuco fruits, *Dacryodes excelsa,* and in fallen decomposing wood.[1] Some crane flies suck the nectar of various flowers (Alexander 1932).

Order Hymenoptera (ants, bees, and wasps)

Anthophoridae (carpenter bees, cuckoo bees and digger bees). – The family Anthophoridae is large, diverse, and widely distributed. Nesting females may be solitary, but in many genera, they form large aggregations (Snelling 1981).

Bees of the genus *Xylocopa* include some of the largest bees. They construct nests in dead wood. Jackson and Woodbury (1976) published a list of the plants used by the carpenter bee, *Xylocopa mordax* (recorded as *X. brasilianorum)* (fig. 6), for nesting and sources of food. In Puerto Rico, this species of bee uses 285 plant species for food and is responsible for the pollination of 25 fruit and seed crop species used by humans.

Apidae (honey bees). – Eusociality (truly social behavior) attains its highest development among the bees in the family Apidae. Not all Apidae are social; the Euglossinae subfamily includes only solitary or communal species. The Apinae subfamily includes only the genus *Apis* and is best known by the common honey bee, *Apis mellifera.* This is one of the most important animals domesticated by humans; it is valued for pollination and for the production of honey and wax (Snelling 1981).

The number of tree cavities occupied by the honey bee *A. mellifera* is 0.29 colonies per hectare in the upper Luquillo Mountains, representing a threat to the Puerto Rican parrot, *Amazona vittata,* by occupying potential parrot nest sites. Cavities in palo colorado, *Cyrilla racemiflora,* are the nesting sites most used by the Puerto Rican parrot. Apparently, palo colorado nectar and pollen are responsible for poisoning the brood of *Apis mellifera* in Florida, U.S.A. (Sanford 1987). Most swarms of *A. mellifera* take place from June to September, coinciding with the peak flowering of the sierra palm *(Prestoea montana)* on which *A. mellifera* feeds heavily (Snyder and others 1987).

Formicidae (ants). – Ants (the Formicidae family) are numerically the most abundant of the social insects. They occur nearly everywhere except on Antarctica, in the extreme north, and on a few oceanic islands (Snelling 1981). Janzen (1973a) analyzed the interaction between ants and yagrumo hembra, *Cecropia peltata,* in the Caribbean. He postulated that a reduction in herbivores and interspecific competition from trees and vines, in insular habitats, allows the

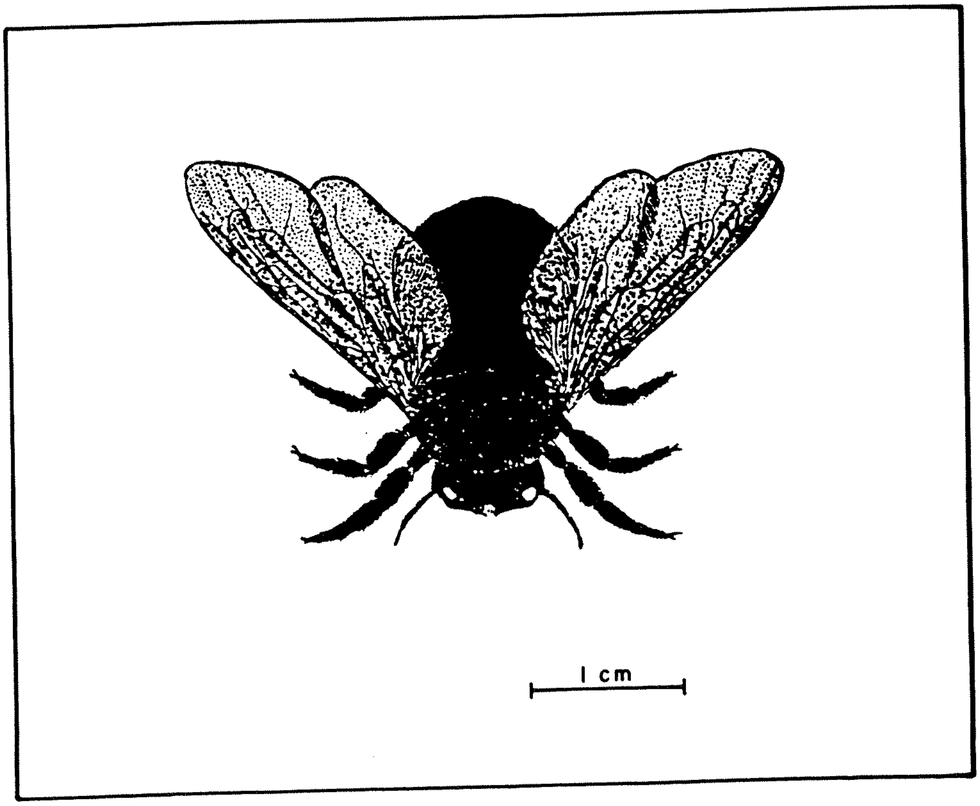

Figure 6. – *The carpenter bee* Xylocopa mordax *(adapted from Wolcott 1948d).*

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[1] Personal observation by the author.

plant to survive without *Azteca* ants. Nonetheless, *Cecropia* leaves are not defenseless without ants; they are physically tough, have dense trichomes, and contain alkaloids and phenolic compounds (Putz and Holbrook 1988). Schupp (1986) found that ant-free trees suffered more destruction by herbivores in Ecuador, but the leaves were not completely destroyed and the saplings continued their growth. In Malaysia, *Cecropia* trees without ants suffered less from vines than did other pioneer species (Putz and Holbrook 1988). De Andrade and Carauta (1982) cast further doubts on the importance of *Azteca* ants for the survival of *Cecropia*. De Andrade and Carauta found severe damage caused by insects on these plants. Ants attacked only the insects that competed with them for the plant resources while ignoring the insects that fed in the adaxial surface of the leaves (de Andrade 1984, de Andrade and Carauta 1982).

The level of protection that *Cecropia* trees receive from *Azteca* ants depends on the ant species that inhabit the tree. Members of the *Azteca alfari* group usually do not provide good protection. Also, aggressiveness varies through the ranges of the *Azteca* species (Longino 1991).

Lavigne (1970a, 1977) presented information on nesting sites, colony size, diel activity, feeding relations, and predators on ants at the Luquillo Mountains. On a numerical basis, ants may constitute more than a third of the diet of many species of frogs and lizards inhabiting the Luquillo Mountains. Lavigne (1970a) developed a taxonomic key to identify ants, placing emphasis on the antennae and mandibular dentition to aid in the identification of isolated heads as typically found in the stomachs of predators. Torres and Canals (1983) reported on the nesting sites of ants in the different forest associations and found a reduction in species diversity along an altitudinal gradient at the Luquillo Mountains. Hernández (1986), working in the dwarf forest, reported four ant species and other insects that participated in the robbing of nectar from roble de sierra, *Tabebuia rigida*.

Vespidae (wasps).—The family Vespidae is virtually cosmopolitan, present on all continental land masses, except Antarctica, and is found on distant oceanic islands. The genus *Polistes* is worldwide in distribution (Snelling 1981). Nevling (1971) found that the most conspicuous insect in the dwarf forest was the paper wasp *P. crinitus*. Many wasps hovering above the canopy were observed after the forest became illuminated, but they were not involved in the pollination of vegetation. Nests of this wasp are located in open areas, not usually found under the closed canopy of the forest.

Polistes crinitus has been observed in enormous numbers on El Yunque Rock (Wolcott 1948d). The wasps were so active and abundant that one could not safely approach them. Nothing was observed in the surrounding vegetation on which they might have been feeding. One suggested reason was that air currents had carried the wasps up the mountain and concentrated them, despite their efforts to fly away (Wolcott 1948d). Another reason could be that these wasps were part of a mating swarm. In Florida (U.S.A.), thousands of paper wasps are attracted to tall structures such as the space shuttle launch pads, where they have been observed mating (Landolt and Reed 1990).

Order Isoptera (termites)

Termites (the order Isoptera) play a major part in decomposing dead trees in the Tropics. To help digestion, termites have micro-organisms in the hind gut. In the more primitive families, obligate flagellate protozoa digest intracellularly, but in the Termitidae, bacteria help in the digestion of cellulose. Some members of the Termitidae produce their own enzymes to digest cellulose. Most wood eaters leave living wood alone, and many make a distinction between dry wood and wet wood (Brian 1983, Wilson 1971).

Martorell (1941) and Martorell and García (1971) published a list of the trees infested by the termite *Nasutitermes costalis* (fig.7). This species is common at low altitudes; it has not been observed above 933 m. *Nasutitermes costalis* does not feed on live trees and is highly abundant at Guánica State Forest and in mangrove areas. Martorell (1941, 1945a, 1976) reported food habits and altitudinal distribution of other termite species. Martorell (1976) reported the termite *Glyptotermes pubescens* on the high altitudes of the island attacking palo colorado, *Cyrilla racemiflora,* and nuez moscada, *Ocotea moschata*.

The first record of the termite *G. liberatus* for the island was made by Martorell (1973) in the Luquillo Mountains and Maricao. Snyder (1956) developed keys for termite workers and alates from the West Indies. He suggested that many termite species in the West Indies have a limited distribution. The tropicosmopolitan drywood termite *(Cryptotermes brevis)* and *N. costalis* readily become established on any island in which environmental conditions are suitable (Snyder 1956).

McMahan (1968b, 1970c) studied the effects of cesium 137 gamma radiation on termites and found a decrease in both nests and tunnel occupancy in the irradiated area (fig. 8). In 1968, 3 years after the removal of the gamma source from the radiation center, twice as many nests were abandoned by *N. costalis* in the radiation center as compared to the south control center, and *N. costalis* had established a new nest in the irradiated area (McMahan 1969). Four years after the radiation exposure, tunnel occupancy in the radiation center was comparable to that in the control centers (table 2). In the radiation center, there was a marked increase in tunnels occupied by *N. costalis* and only a slight increase in tunnel occupancy by the termite *Parvitermes discolor*. In the south control center,

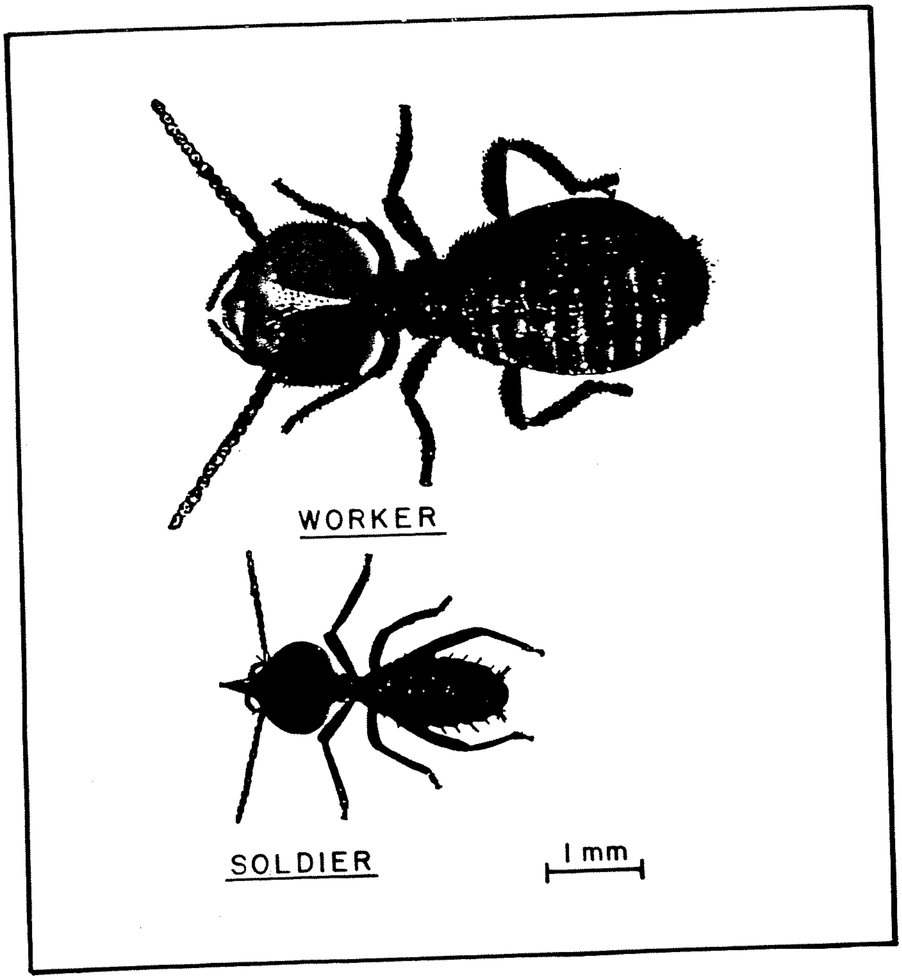


Figure 7.—*Worker and soldier of the termite* Nasutitermes costalis *(adapted from Wolcott 1948a).*

there was an increase in tunnel occupancy by *N. costalis* but a decrease by *P. discolor*. This was correlated with the establishment of two new *N. costalis* nests in this area.

McMahan (1970a, 1970b) also found behavioral differences (polyethism) in expansion and repairs of nests within the worker caste of *N. costalis* in the irradiated and control nests. Nonetheless, the average number of termites were slightly lower at disturbed surfaces in the irradiated area compared to the control.

Termites exposed to a cobalt 60 source in the laboratory were more sensitive to radiation than expected when compared to other insects of their size (McMahan 1968a). McMahan discovered significant differences in radiation sensitivity between *N. costalis* and *P. discolor*, but not between *N. costalis* and *N. nigriceps*. In addition, workers of all species were more radiosensitive than soldiers (fig. 9).

Weigert (1970a) conducted a study on the energetics of *N. costalis*, finding that the role of this termite was relatively minor in the total decomposer energy budget in an El Verde tabonuco forest. The food supply of this species is restricted to dead wood not yet in an advanced state of decay. Although thoroughly rotted wood is attractive to some termite species, it is avoided by others, possibly because of its low carbohydrate content (La Fage and Nutting 1978). Weigert concluded that the number of termites in an *N. costalis* colony was correlated with the surface area of the arboreal nest, possibly due to the necessity for gas exchange to occur throughout the nest surface. Although Weigert was impressed by the small amount of dead wood consumed by *N. costalis*, it should be recognized that *P. discolor* is quite abundant in the forest and may be more important than *N. costalis* in the consumption of dead wood. *Parvitermes discolor* can be found in logs and branches in advanced stages of decay and has a greater altitudinal distribution than *N. costalis*, which is found mostly in the foothills of the forest. Since *P. discolor* does not build arboreal nests, its presence is more difficult to detect. In addition, coleopterans (e.g., cerambycids) are very important in dead wood consumption in the Luquillo Mountains.[1]

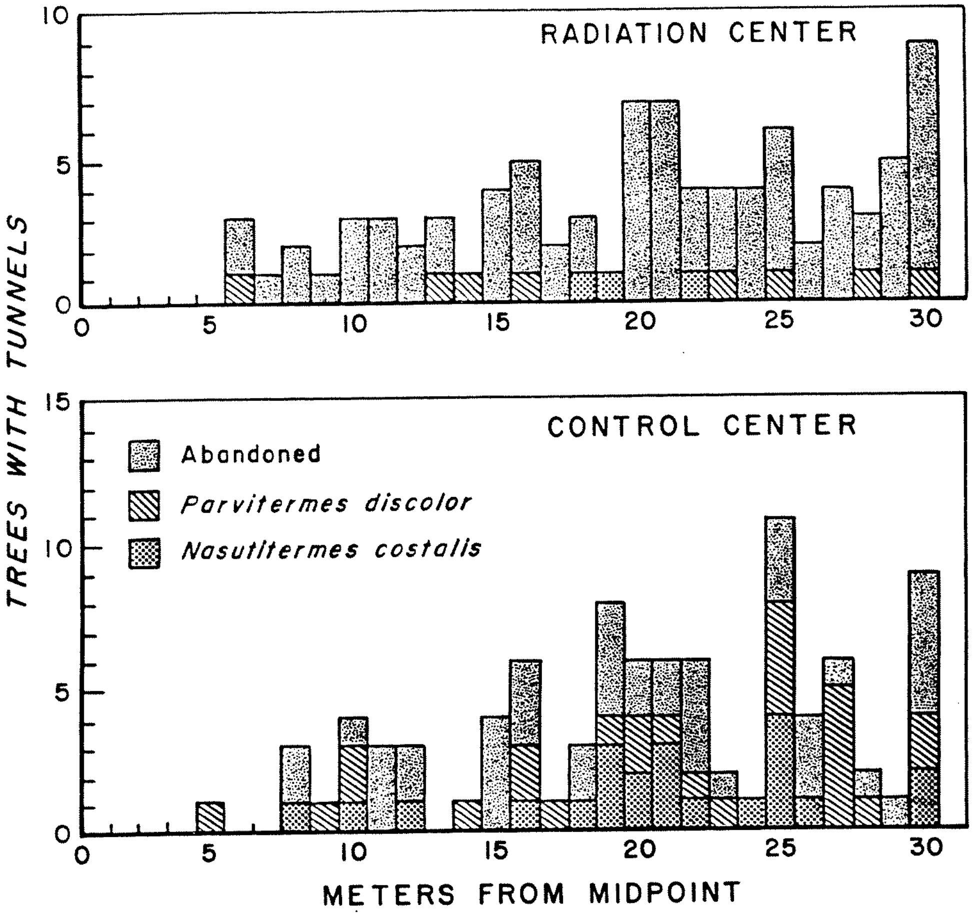


Figure 8.—*Histograms of tunnel-bearing trees at increasing distances from midpoints of radiation and control centers 18 months after radiation (adapted from McMahan 1970c).*

Table 2.—*Tunnel survey data from* Nasutitermes costalis *in the three centers (adapted from McMahan 1970a)*

	Irradiated area		South control		North cut center	
Year	Trees with tunnels	Tunnels occupied	Trees with tunnels	Tunnels occupied	Trees with tunnels	Tunnels occupied
	--------- *Number* ---------		--------- *Number* ---------		--------- *Number* ---------	
1966	90	3	92	22	29*	0
1967	102	1	108	21	78	7
1968	93	15	136	23	82	9
1969	89	39	120	44	82	10

*Survey to 20-m radius only.

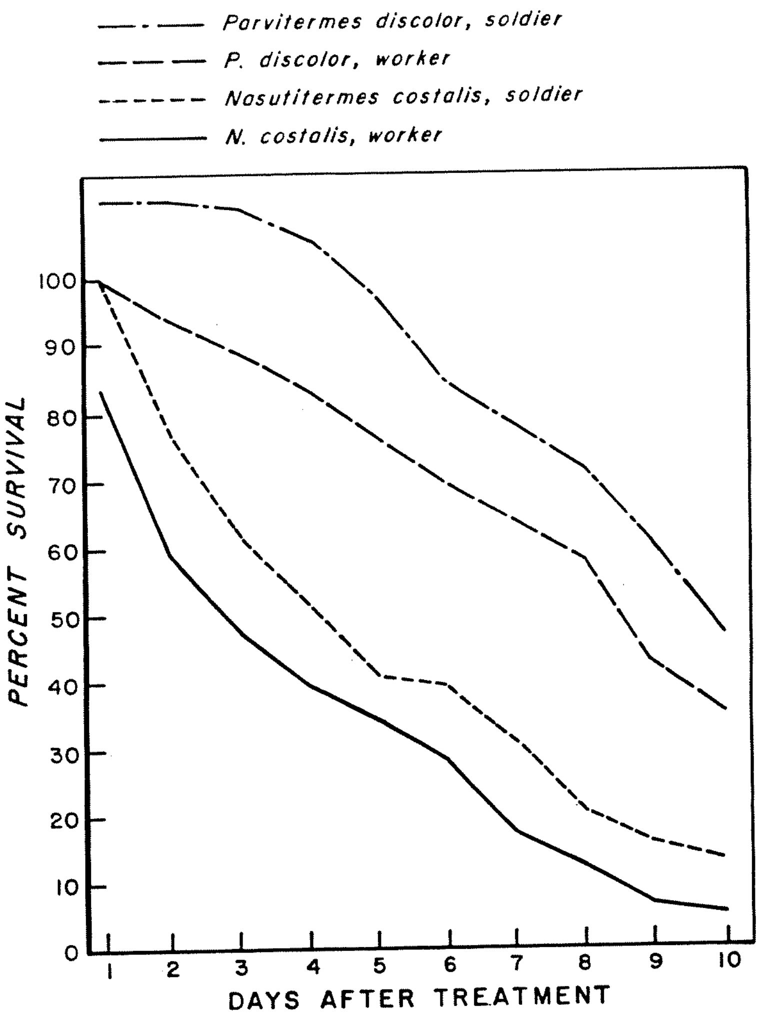
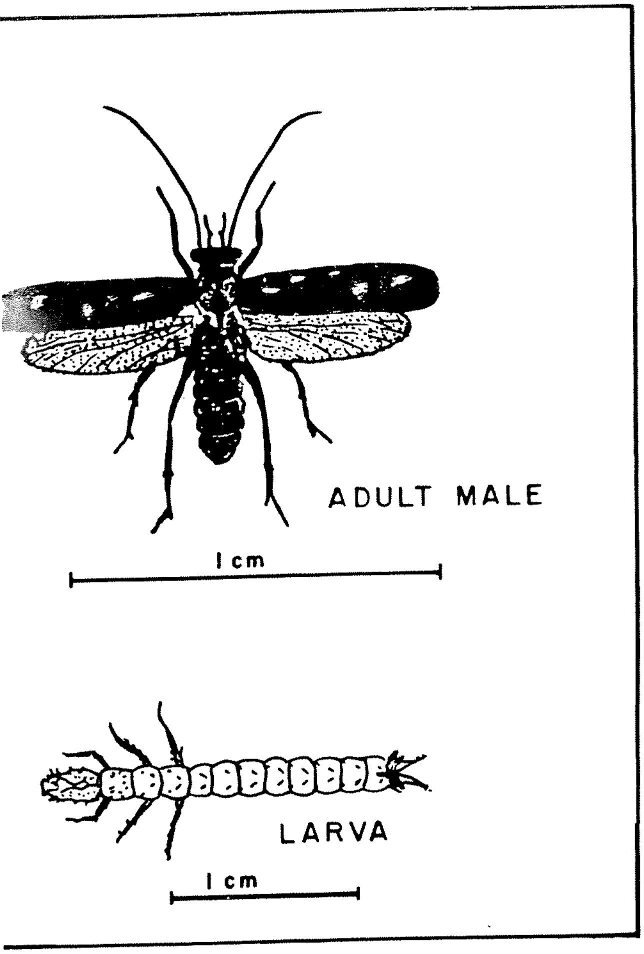


Figure 9. – *Soldier and worker survival rates for the termites,* Parvitermes discolor *and* Nasutitermes costalis, *after radiation treatments. Percentages exceed 100 because all data were corrected for control mortality (adapted from McMahan 1968b).*

Order Odonata (dragonflies and damselflies)

Members of the order Odonata are relatively large insects that spend a large part of their time in flight. The nymphs are aquatic, and the adults are generally found near water (Borror and others). García (1938), in the appendix to his ecological survey of the freshwater insects of Puerto Rico, listed the aquatic species by order, with the exception of the Odonata, which he covered extensively. The work of García is rich in information about the Odonata in Puerto Rico. García found that species are distributed according to altitude (table 3), and he summarized the information on the rate of predation by insectivorous birds on insects of the Odonata. In some insectivorous bird species, as much as 84 percent of their stomach contents consisted of nymphs and adults of the Odonata. Fish are also heavy predators of the Odonata, but data do not exist for fish predation on the Odonata in Puerto Rico. There is interspecific predation among odonate species (among adults and nymphs). Cannibalism is practiced by several species, which could explain the fact that few nymphs reach the adult stage.

Odonates in their adult stage are beneficial because they destroy many harmful insects such as mosquitoes. Nymphs could also be beneficial, but their contribution is reduced by the fact that they may destroy young fish. Dragonfly nymphs, together with the predaceous water beetle *Megadytes gigantea* (Dytiscidae) (fig. 10), were found to be the worst enemies of tadpoles of the introduced toad, *Bufo marinus* (Wolcott 1948b). Adult bullfrogs, *Rana catesbiana,* feed on ants, cockroaches, spiders, millipides, snails, and aquatic insects, such as dragonfly nymphs, the electric light bug, *Belostoma boscii,* and the dytiscid beetle, *Megadytes gigantea.* These aquatic insects are in turn predaceous



gure 11.—*Larvae and adult of the common caddisfly* Chimarrha albomaculata *(adapted from Wolcott 1948a).*

rious groups. He postulated that the negative asso-ations between mosquitoes and ostracods, copepods, d nauplii were the result of competition (fig. 12). aguire used glass jars to simulate microhabitats for uatic organisms and found that cesium gamma radi-ion had no appreciable effects on these communities. out a year after termination of irradiation, auto-aved glass bottles filled with water from the nearby nadora River were left in the field to determine the te of invertebrate colonization. The rate of coloniza-n was remarkably rapid. Populations were estab-hed within 2 weeks in these autoclaved glass bottles.

Seed and Fruit Consumers.—Lavigne (1970b) blished a list of insect species that use fruit and eds as food or breeding grounds (table 4). The princi-l users of these resources were members of the ders Diptera, Coleoptera, and Hymenoptera (For-icidae). The study was preliminary in design, and avigne indicated that the data were insufficient to termine if there was resource specialization. Nieves 979) found heavy attack by insects on the fruits and eds of yagrumo macho, *Didymopanax morototoni,* but did not identify the insect species. Silander (1979) found beetle larvae (Coleoptera: Nitidulidae) feeding on the seeds of yagrumo hembra, *Cecropia peltata.* Beetles (Nitidulidae) and Lepidoptera larvae eat the mesocarp of granadillo, *Buchenavia capitata,* fruits at El Verde (Sastre 1979).

Insect Diversity and Abundance.—Drewry (1970) furnished a list of 1,200 insect species collected at El Verde, many of which are deposited in the collection at El Verde Field Station. This information, along with the findings of Allan and others (1973) on foliage arthropods in second-growth vegetation, shows the depauperate nature of the Puerto Rican insect fauna. Mosquitoes and other blood-sucking Diptera are scarce in the Luquillo Mountains despite the prevalence of water (Snyder and others 1987). Martorell (1945a) presented several reasons that explain the depauperate Puerto Rican insect fauna: (1) Puerto Rico's position in relation to the other islands of the Greater and Lesser Antilles restricts the arrival of colonizers (Puerto Rico is farthest east of the large islands in the Greater Antilles and farthest north of the islands of the Lesser Antilles), (2) the Antillean trade winds coming from the east or northeast, where land masses are almost nonexistent, do not help in the distribution of insects in a west to east direction, and (3) the destruction of lowland forests and the partial deforestation in the mountains might have contributed to the local extinction of some insect species. Estrada and others (1982) contributed a list of the flora and fauna near El Verde Field Station. For the invertebrates, information is presented on the strata where they occur (e.g., soil, litter, understory, and canopy). The list has information on major components of food webs based on abundance or size of the organisms.

Snyder and others (1987) used sticky-paper strips to monitor the abundance of insects in the Luquillo Mountains. Insect abundance in disturbed forests was double that of virgin forests; and abundance was lowest in the palo colorado and dwarf forests. More insects were trapped in the sierra palm forest than in the tabonuco, although this could be an artifact due to the deficient understory growth in the sierra palm forest. Diptera comprised 63 percent, Homoptera, 9 percent, Coleoptera, 9 percent, Lepidoptera, 5 percent, and other insect orders, 16 percent of the insects captured in all forest types. Because a relative method of abundance estimation was used (Southwood 1971), results cannot be used to estimate the absolute density of insects in the different forest types. Snyder and others (1987) found seasonal changes in insect abundance. Numbers began to increase in February (during the dry season), they peaked in May, at the start of the rainy season, and decreased thereafter. The insect abundance peak in late spring and summer was correlated with the period of reproduction of many insectivorous birds. The pattern of bird abundance and

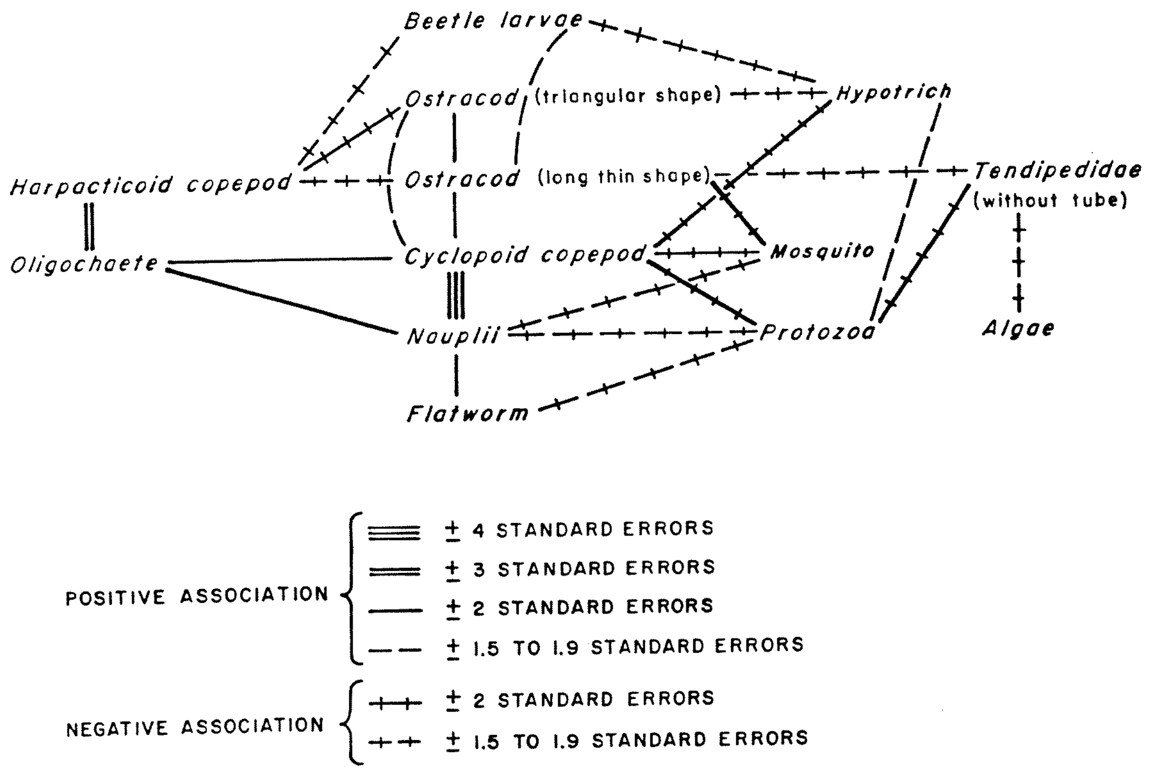


Figure 12.—*Patterns of faunal associations in aquatic biotas of bromeliads (adapted from Maguire 1970).*

diversity parallels the trends exhibited by the flora and insects. The major factor in the reduction of bird species with increasing altitude may be the reduction in insect prey. Though the data on insect abundance in this study cannot be considered definitive due to the limitations in the sampling methods, the study suggests interesting patterns that deserve to be studied with more precise sampling techniques.

McMahan and Sollins (1970) found no cesium radiation effects on microarthropods at El Verde, 2 years after the irradiation experiment. However, the study lacks replication of the experimental units, and the species were not identified. The study does not present evidence of the adequacy of the sampling scheme, in order to compare the different sites, and lacks the necessary statistical analyses. Although the results indicate that some groups differed in abundance among the sites, the above limitations cast doubts on the results of the study. Weigert (1970b) found neither radiation effects on soil and litter microarthropods 1 year after the irradiation, nor a relation between litter standing crop and microarthropod abundance. This study also lacks experimental replications.

Drewry (1969) discussed the pitfalls of measuring and comparing insect diversity among sites. Linear methods, such as William's log series or an incorrect assumed constancy of Brillouin's H with increasing sample size, can be misleading. Plotting a diversity index curve can reveal nonlinearities, and the composite ratio provides a view of total sample composition, giving a foundation to whichever diversity index is chosen.

Herbivores.—Odum and Ruíz (1970) did not find significant changes in the level of herbivory in an irradiated area at El Verde. This was contrary to the findings at Brookhaven, where an epidemic of aphids occurred after exposure to radiation. One of the drawbacks of the El Verde study is that the authors did not distinguish between insect herbivory and herbivory caused by other herbivores, such as snails.

Fifteen species of Lepidoptera occurred in large numbers 7 months after the passage of Hurricane Hugo over the Luquillo Mountains. *Spodoptera eridania* (Lepidoptera: Noctuidae) was the most common of the larvae and fed on 56 plant species belonging to 31 families. All the Lepidoptera fed on early successional vegetation. The outbreaks appeared to be based on the flush of new foliage that developed in the Luquillo Mountains after the passage of the hurricane. The end of the *S. eridania* outbreak was concurrent with the consumption of its preferred host plants and to an apparent increment in parasitism by ichneumonids (Torres 1992).

A factor that reduces the metabolic production of plants in the dwarf forest is damage to the foliage (Howard 1969). Howard found that many plants pre-

Table 4.—*Insects reared from or associated with the tree fruits found in the forest litter, El Verde Field Station, Puerto Rico (Lavigne 1970b)*

	Insects		
Tree species	Diptera	Coleoptera	Other orders
Andira inermis	Tipulidae *Limonia willistoniana** *Limonia domestica** Ceratopogonidae *Forcipomyia genualis** Sciaridae Sciarid B* Sciarid E* Stratiomyidae *Nothomyia nigra** Chironomidae Chironomid DD Chironomid OO Psychodidae (undet.) Phoridae (undet.)	Scarabaeidae *Canthochilum histeroides* Endomychidae Endomychid B† Staphylinidae Staphylinid C Curculionidae Curculionid C	
Sloanea berteriana	Chironomidae Chironomid KK* Psychodidae (undet.)	Nitidulidae Nitidulid A	Hymenoptera Formicidae *Paratrechina* sp. (EE) Formicid Z
Byrsonima coriacea	Drosophilidae (undet.)		Hymenoptera Formicidae *Cyphomyrmex minutus*
Paullinia pinnata			Hymenoptera Formicidae *Mycocepurus smithi*
Buchenavia capitata		Nitidulidae Nitulid A	
Manilkara bidentata	Drosophilidae (undet.)*	Nitidulidae Nitulid A	Hymenoptera Formicidae *Pheidole moerens* *Solenopsis* sp. (JJ) Formicid Z
Genipa americana		Nitidulidae Nitulid A Staphylinidae Staphylinid G Staphylinid N	
Prestoea montana		Scolytidae Scolytid F*	
Dacryodes excelsa	Drosophilidae (undet.)* Psychodidae (undet.)* Chironomidae Chironomid KK*	Nitidulidae Nitulid A Endomychidae Endomychid B	Hymenoptera Formicidae *Solenopsis* sp. (JJ) *Pheidole moerens*
Eugenia stahlii			Orthoptera (undet.)*
Inga fagifolia	Tipulidae *Limonia willistoniana** Chironomidae (undet.)*		Hymenoptera Formicidae *Pheidole moerens* *Solenopsis* sp. (JJ) Formicid Z
Inga vera	Phoridae Phorid Q*	Nitidulidae Nitidulid B	Lepidoptera Microlepidoptera (undet.)*

Table 4.—*Insects reared from or associated with the tree fruits found in the forest litter, El Verde Field Station, Puerto Rico (Lavigne 1970b)—(Continued)*

Tree species	Insects		
	Diptera	Coleoptera	Other orders
	Cecidomyiidae Cecidomyiid F* Lonchaeidae *Lonchaea* sp. (B)* Drosophilidae (undet.)* Ceratopogonidae (undet.)* Mycetophilidae *Boletina* sp. (B)*		Hymenoptera Formicidae Formicid Z *Myrmelachista ramulorum* *Pheidole* sp. (HH)
Guarea guidonia	Sciaridae (undet)* Drosophilidae (undet.)	Staphylinidae Staphylinid C Staphylinid G Staphylinid K Staphylinid L Staphylinid M Endomychidae Endomychid B Scarabaeidae *Canthochilum borinquensis* Nitidulidae Nitidulid A	Hymenoptera Formicidae Formicid Z *Solenopsis* sp. (GG) *Solenopsis* sp. (JJ) *Solenopsis corticalis* *Pheidole moerens*

*Reared from fruit.

†Letters represent different species and relate the species to previous diversity studies conducted at El Verde Field Station.

sent in the dwarf forest were consumed by insects. In six species, the leaf area was reduced by over 16 percent (table 5). Succulent young leaves were preferentially consumed by insects. Howard (1969) provided common names of insects that consumed the plants during the study, as well as information about their appearance. The author could not correlate leaf texture, liquid content, aromatic constituents, or pH with the degree of consumption by insects.

Assuming that the only herbivores present were insects, Benedict (1976) studied herbivory rates in four forests, including the dwarf forest at the Luquillo Mountains, and correlated herbivory rates with some physical and chemical properties of the leaves. She found that plant species with leaves that were tough, thick, dry, or highly pubescent were avoided (table 6). Many species that had leaves with palatable textures were not consumed. These species were either pubescent or members of families that produce aromatic oils or calcium carbonate concretions. Most dwarf forest leaves do not possess any apparent defenses, although many are thick, which may reduce palatability. Several dwarf forest plant species belonging to aromatic-oil producing families were among the species with high herbivory rates. Probably, volatile oils do not reduce herbivory in the dwarf forest due to the high moisture content of the leaves and the constant washing by rainfall. Contrary to the findings of Howard, Benedict considered that the herbivory rate was relatively low in the dwarf forest, and she attributed this to unfavorable weather conditions for insects, rather than to the lack of palatable food. The low herbivore pressure, due to environmental limits on insect populations, may explain the apparent palatability of leaves in the dwarf forest. Vines (e.g., *Marcgravia sintenisii*) in the dwarf forest had some of the highest herbivory rates of the species studied and tended to be low to intermediate in toughness, thickness, and dryness (Benedict 1976).

Insect Biomass.—Odum and others (1970) presented estimates of biomass from different anima groups in a tabonuco, *Dacryodes excelsa,* forest in Puerto Rico. Although organisms were not sampled with accuracy, the animal (including the insect) consumer biomass was small, relative to the great mass o live plant material.

Pollinators.—In a study of the flowering cycle in the dwarf forest, Nevling (1971) found an apparent lack of insect pollinators. Only one definite pollinator, a species of bee fly (Bombyliidae), was observed pollinating the sierra palm, *Prestoea montana*. The lack o pollinators could be one of the reasons for the low percentage of fruit set in the dwarf forest. This lack o pollinators may be due to the high frequency of rainfal and high humidity, which dilutes nectar concentration and decreases flower attractiveness. Also, where fruit set occurred, the fruits were subject to insect and bird predation to the extent that few plant species brough fruit to maturation (Nevling 1971).

Lizard and Frog Predation on Insects.—Liste (1981) showed that arthropod densities within th Luquillo Mountains remained stable between the summer and winter, in the lower strata of the forest, bu

Table 5.—*Plants most susceptible to insect damage in the dwarf forest (adapted from Howard 1969 with permission of the "Journal of the Arnold Arboretum," copyright President and Fellows of Harvard College)*

Tree species	Damage	Reduction in surface area	pH[*]	Leaf water content
	Percent			*Percent*
Clusia clusioides	98	24	3.9–4.3	66
Haenianthus salicifolius	86	19	5.1–5.2	62
Wallenia yunquensis	84	16	3.5–4.2	75
Eugenia borinquensis	81	25	4.8	30
Miconia foveolata	81	35	3.9–4.0	71
Miconia pachyphylla	79	21	3.7–4.3	60
Cybianthus sintenisii	77	...[†]	4.1–4.5	84
Hornemannia racemosa	73	...	3.9–5.3	67
Rajania cordata	70	...	4.9	...
Peperomia hernandiifolia	70	...	4.6–5.1	...

[*] The pH of liquid in leaves.

[†] Blank fields indicate no data available.

decreased during the winter, at the higher strata. The taxonomic composition of samples did not differ between the seasons. Lister displayed the taxonomic distribution of insect prey biomass for three lizard species. Members of the Orthoptera, Coleoptera, and Hymenoptera (Formicidae) were the most important prey items for these lizards. Rivero and others (1963), in a preliminary study of the food habits of the frog *Eleutherodactylus karlschmidti* (the most aquatic of the *Eleutherodactylus*) in the Luquillo Mountains, found that most of the food eaten by these frogs was terrestrial. About 90 percent of the food was composed of insects. Dipterans (many aquatic larvae) comprised 44 percent of the insects. Trichopterans and hymenopterans each comprised about 15 percent of the insects consumed. Most of the hymenopterans were ants. Lavigne and Drewry (1970) studied the feeding habits of frogs and lizards at El Verde, listing the prey items consumed by order or class (tables 7, 8). Members of the Hymenoptera and Diptera were among the dominant food items. Lavigne and Drewry (1970) also developed a classification of prey types to be used as indicators of habitat type. Cintrón (1970) found a high consumption of coleopterans and hymenopterans (mainly ants) by tree frogs of the genus *Eleutherodactylus* in palm *(Prestoea montana)* forests (fig. 13).

Bird Predation on Insects.—Wetmore (1916) studied bird predation on insects throughout Puerto Rico. The following are highlights of his observations by bird species:

- Puerto Rican woodpecker, *Melanerpes portoricensis.* Larvae and adults of wood borers (mainly cerambycids) form 24 percent of this bird's diet. The woodpecker uncovers and drags these larvae from beneath the bark, where they are protected from other birds. Ants form 10 percent of the diet. La hormiguilla, *Myrmelachista ramulorum,* is one of the preferred ants.
- Puerto Rican tody, *Todus mexicanus.* Diptera formed 30 percent, coleopterans, 23 percent, and homopterans, 9 percent of the animal food items consumed by this species. Many insects eaten by this bird are injurious in coffee plantations.
- Puerto Rican screech-owl, *Otus nudipes.* This owl feeds largely on May beetles *(Phyllophaga)* and weevils (e.g., *Diaprepes*) that damage crops and forest trees. The owl, a night feeder, is highly adapted to eat the nocturnal May beetles.
- Puerto Rican flycatcher, *Myiarchus antillarum.* Caterpillars and fragments of adult lepidopterans comprise 25 percent, and hymenopterans, 11 percent of the animal food eaten by this species.
- Adelaide's warbler, *Dendroica adelaidae.* This warbler feeds mostly on animal matter and consumes enormous numbers of small homopterans. Lantern flies (Fulgoridae) appear to be a favorite food item of all warblers in Puerto Rico.
- Black and white warbler, *Mniotilta varia.* Coleopterans constitute the highest percentage of this bird's diet. Engraver beetles (*Platypus* sp.) were also taken by this species and by other warblers.
- Bananaquit, *Coereba flaveola.* This bird feeds mostly on small caterpillars and lantern flies (Fulgoridae).
- Greater Antillean grackle, *Quiscalus niger.* Lepidopterans and coleopterans (may beetles and weevils) are important items in the diet of this species.
- Puerto Rican tanager, *Nesospingus speculiferus.* Caterpillars constituted the large bulk of the animal food consumed by this bird.

Table 6.—*Leaf area indices, leaf characteristics, and herbivory rates for the trees in the dwarf forest (adapted from Benedict 1976)*

Tree species	Leaf area index	Toughness	Thickness	Moisture percent of wet weight	Toughness-thickness-dryness index	Weight/area ratio	Herbivory rate	Browning rate
		$kg \cdot cm^{-2}$	*mm*			*$mg \cdot cm^{-2}$*	*cm^2 holes·m^{-2} leaf·day^{-1}*	*cm^2 brown spots·m^{-2} leaf·day^{-1}*
Alsophila bryophila (Cyatheaceae)	0.42	. . .[*]	0.32	78	n.d.	10	0.57	0.14
Calycogonium squamulosum (Melastomataceae)	0.60	4.47	0.33	79	25	9	0.42	0.47
Calyptranthes krugii (Myrtaceae[†])	0.05	9.91	0.44	64	125	20	0.00	7.89
Eugenia borinquensis (Myrtaceae[†])	0.25	9.70	0.91	67	235	18	1.04	0.69
Guarea glabra (Meliaceae)	0.05	5.38	0.25	72	30	6	0.05	0.24
Guzmania berteroniana (Bromeliaceae)	0.13	12.77	0.27	86	39	7	0.02	0.54
Marcgravia sintenisii (Marcgraviaceae[†])	0.33	5.92	0.56	78	57	17	1.55	0.59
Miconia pachyphylla (Melastomataceae)	0.12	. . .	0.42	66	n.d.	11	0.35	1.34
Micropholis garcinifolia (Sapotaceae)	0.04	13.61	0.49	65	187	17	0.06	0.42
Ocotea spathulata (Lauraceae[†])	0.15	7.86	0.44	67	91	13	0.22	2.35
Tabebuia rigida (Bignoniaceae)	0.48	7.17	0.54	80	62	11	0.09	1.89
Total	2.60							
Weighted average		7.02	0.40	76	75	12	0.53	1.00

[*] Blank field indicates no data available.
[†] Family that characteristically produces aromatic oils or cystoliths.

INSECTS THAT ATTACK FOREST TREES AND SHRUBS

In this section, insects that attack vines, weeds, and grasses are excluded; those insects are reviewed by Martorell (1976). Some insects presented in Martorell's work (e.g., many homopterans) are not included here if there is no indication of the damage these insects can cause to trees. Several of Martorell's records pertain to insects that have been collected only from the Luquillo Mountains. Insects that attacked plants or shrubs in other areas of Puerto Rico are included here because those plants can also occur in the Luquillo Mountains.

Order Coleoptera (beetles)

Bostrichidae (branch and twig borers).—Most of the species of the Bostrichidae family attack wood, either living trees or seasoned lumber. These beetles, in rare instances, can cause damage to older dwellings and furniture (Dillon and Dillon 1972). Sein (1931) reported an outbreak of the bostrychid beetle, *Apate monacha* (fig. 14) in coffee, *Coffea arabica,* plantations and pigeon peas, *Cajanus cajan.* This wood borer attacked live trees of several important timber species like cedar. Sein suggested ideas for controlling the insect. The bostrychid beetle also attacked many agri-

Table 7.—*Feeding habits of adult frogs by sex, based on stomach content, in the Luquillo Mountains (Lavigne and Drewry 1970)*

	Eleutherodactylus															*Leptodactylus*
	coqui		*portoricensis*		*richmondi*		*wightmanae*		*eneidae*	*antillensis*		*brittoni*		*locustus*		*albilabris*
	♂	♀	♂	♀	♂	♀	♂	♀	♂	♂	♀	♂	♀	♂	♀	♀
	Number of frogs examined															
Taxon	17	12	6	8	8	5	11	2	5	13	7	6	3	3	1	3
	Number of organisms/frog															
Araneida	0.4	0.6	0.3	0.5	0.6	0.4	0.2	0.5	0.2	0.6	0.3	0.5	0.6	1.3	1.0	0.3
Acarina	0.6	0.3	...*	3.1	0.4	0.4	2.0	...	0.2	0.5	0.4	1.6	...	3.6	5.0	...
Chilopoda	0.05	...	...	...	...	0.2	...	...	...	...	...	...	...	...	...	...
Diplopoda	0.1	0.15	...	0.1	0.3	...	0.4	0.5	...	...	...	...	...	...	...	0.3
Chelonethida	0.05	...	...	...	...	...	0.2	1.0	...	...	...	...	...	...	...	...
Isopoda	...	...	...	0.1	0.1	0.2	...	...	...	...	0.1	0.15	...	...	...	...
Mollusca	...	...	...	0.1	0.1	0.2	0.1	...	...	0.07	...	0.25	...	...	...	...
Collembola	...	...	...	...	...	...	...	...	0.4	...	...	0.15	0.3	1.3	3.0	...
Orthoptera	0.5	0.9	...	0.4	0.4	...	0.1	...	0.2	0.2	0.1	...	...	0.3	...	...
Psocoptera	0.05	0.25	...	0.1	...	...	0.1	...	0.2	0.07	...	...	...	...	1.0	...
Coleoptera	0.2	0.25	0.5	0.5	0.7	1.8	0.9	...	...	0.15	0.3	...	...	0.3	...	...
Homoptera	0.6	0.5	0.3	0.4	0.1	...	0.6	1.5	0.4	0.6	0.4	0.8	...	...	...	...
Hemiptera	0.05	0.15	...	0.2	...	...	0.2	...	...	0.15	0.3	0.25	0.3	...	...	0.3
Diptera	0.7	4.1	1.3	1.1	1.0	0.4	0.6	...	1.8	1.8	3.0	1.15	4.6	3.3	3.0	...
Hymenoptera	7.6	6.8	3.5	5.1	1.0	1.0	10.0	11.0	3.0	1.8	6.7	1.8	2.0	3.3	4.0	3.0
Lepidoptera	0.5	0.5	0.5	0.6	...	...	0.2	...	...	1.5	4.6	0.7	1.3	0.3	...	...
Isoptera	...	...	...	...	...	...	1.3	0.5	...	...	...	...	...	...	...	...
Thysanoptera	...	...	...	...	...	...	...	...	...	...	...	...	0.3	...	...	...

*Blank fields indicate no data available.

Table 8.—*Feeding habits of lizards, based on organisms collected from lizard stomachs in the Luquillo Mountains (adapted from Lavigne and Drewry 1970)*

	Anolis						
	gundlachi		*stratulus*		*evermanni*	*gundlachi*	*evermanni*
	♂	♀	♂	♀	♂	juvenile	juvenile
	Number of lizards examined						
Taxon	3	3	1	3	3	2	1
	Number of organisms/lizard						
Araneida	0.3	2.0	1.0	1.0	0.6	...	1.0
Acarina	...*	...	...	4.5	0.3	0.5	...
Chilopoda	...	...	...	...	...	...	...
Diplopoda	...	0.3	...	...	...	1.0	...
Chelonethida	...	...	...	...	...	...	...
Isopoda	...	0.3	...	...	...	...	...
Mollusca	...	...	...	...	...	...	...
Collembola	...	0.3	...	...	...	...	...
Orthoptera	1.0	1.0	...	...	0.3	...	1.0
Psocoptera	...	...	...	0.5	1.3	...	...
Coleoptera	0.3	8.6	...	0.5	...	2.0	6.0
Homoptera	0.6	1.6	1.0	2.0	1.6	1.0	5.0
Hemiptera	0.6	2.3	3.0	...	...	...	1.0
Diptera	1.3	1.0	...	1.5	1.3	1.0	2.0
Hymenoptera	4.6	28.0	29.0	27.0	12.0	4.5	43.0
Lepidoptera	0.3	1.0	1.0	1.0	0.3	2.0	...
Isoptera	...	1.0	...	...	...	0.5	...
Thysanoptera	...	...	...	...	...	...	...
Trichoptera	0.6	...	...	...	...	...	...

*Blank fields indicate no data available.

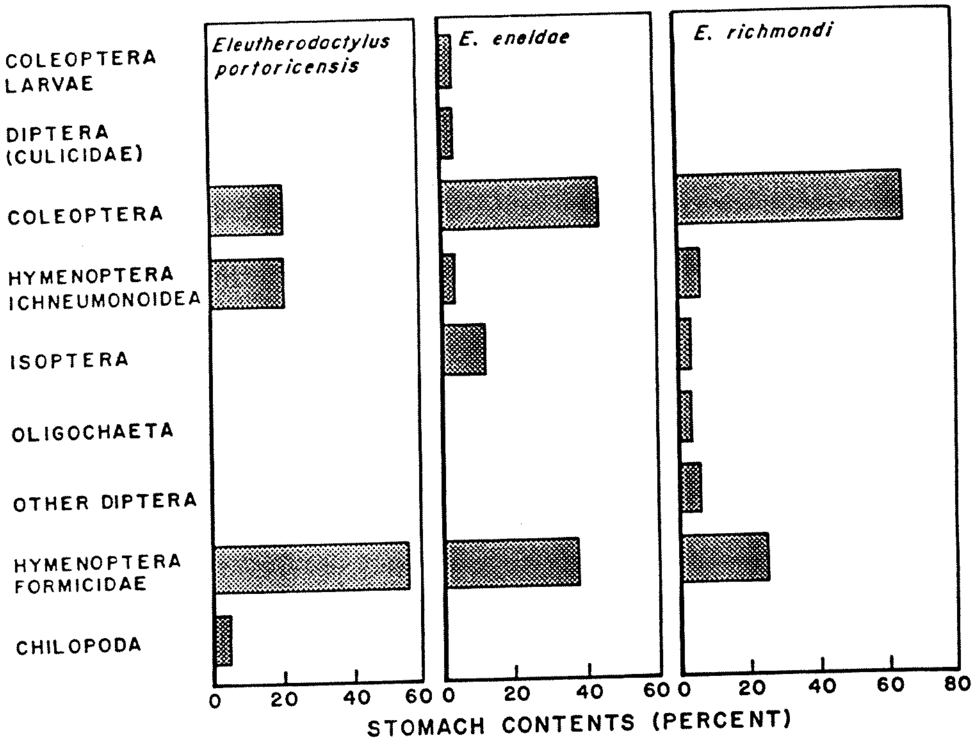


Figure 13.—*Stomach contents of three* Eleutherodactylus *species of tree frogs trapped in the Luquillo Mountains of Puerto Rico (adapted from Cintrón 1970).*

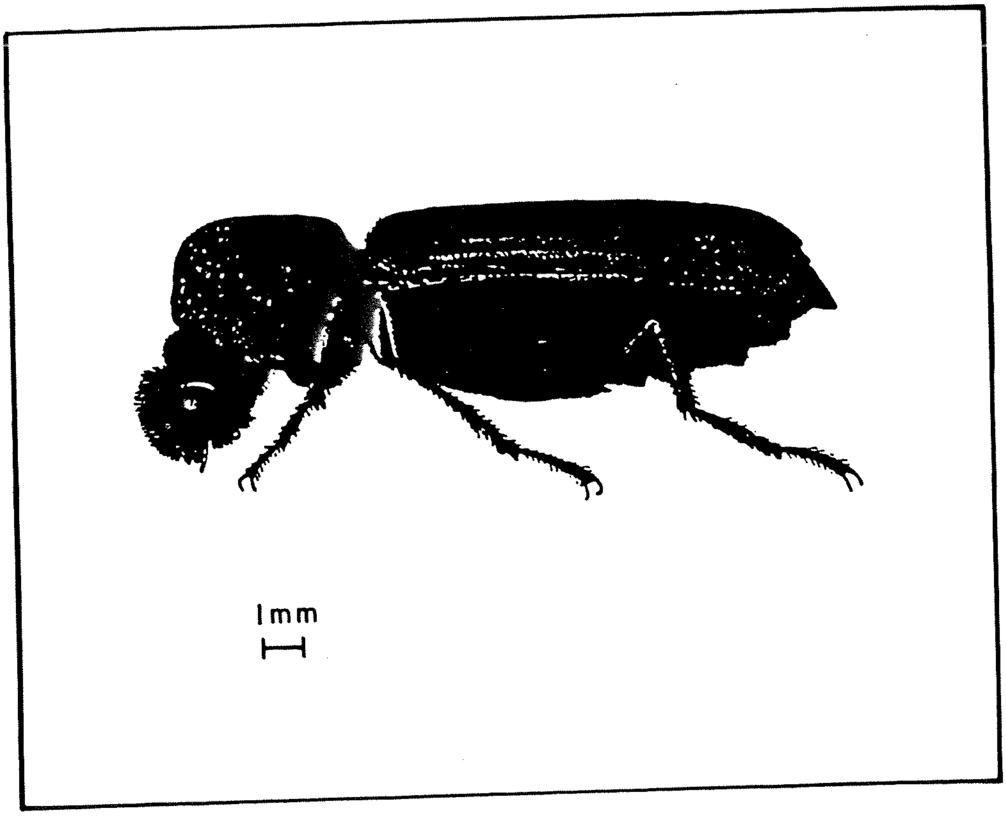


Figure 14.—*A wood/twig boring beetle,* Apate monacha *(adapted from Wolcott 1948b).*

cultural trees including grapefruit, *Citrus paradisi;* orange, *Citrus sinensis;* avocado, *Persea americana;* and others. *Apate monacha* attacked Dominican mahogany, *Swietenia mahogani,* near Guayanilla in 1937. The outbreak was related to the presence of dead wood remaining after the cutting of inferior species in the mahogany plantation. Dead wood served as breeding grounds for the borer. Some trees were so damaged that they died a few months after infestation (Martorell 1939). During this outbreak, the infestation spread to adjacent 4-year-old Australian pines, *Casuarina equisetifolia,* and to úcar trees, *Bucida buceras. Apate monacha* breeds in dead wood and, when abundant, can attack every tree in the vicinity, whether alive or dead. Attacks by *A. monacha* have been reported on the following trees; achiote, *Bixa orellana;* flamboyán, *Delonix regia,* guaba, *Inga vera;* palo de hueso, *Chionanthus domingensis; alilaila, Melia azedarach;* dry post of hueso, *Picramnia pentandra;* tamarindo, *Tamarindus indica;* pomarrosa, *Syzygium jambos;* granada, *Punica granatum;* and algodón, *Gossypium barbadense* (Martorell 1945a, Wolcott 1948b).

Buprestidae (metallic wood-boring beetles).—Many adult buprestids are attracted to dead or dying trees, logs, or slash. Most buprestid larvae bore under bark or in wood (Borror and others 1981). In Puerto Rico, buprestids seem to be more abundant in lowland habitats, such as dry forests and mangrove areas. Wolcott (1948b) reported the introduction of the buprestid *Polycesta depressa* to Puerto Rico as a result of the unrestricted lumber traffic from Hispaniola. The larvae attack West Indian mahogany *(Swietenia mahogani)* and other trees of lesser economic value, feeding on the cambium, when trees are young, and on the heartwood, when they approach maturity.

Cerambycidae (long-horned beetles) and Elateridae (click beetles).—The brightly colored adult cerambycids generally feed on flowers. Many are nocturnal (Borror and others 1981). Most cerambycid larvae are wood borers. Wolcott and Martorell (1942) reported the presence of the cerambycid *Lagochirus araneiformis* and the elaterid *Chalcolepidius silbermanni* (fig. 15) in Puerto Rico. The larvae of elaterids are mostly predaceous on other insect larvae, and *C. silbermanni* appears to be a predator of the cerambycid. Wolcott and Martorell (1942) hypothesized that these beetles arrived in wood shipped from Santo Domingo to Puerto Rico. Mahogany planks and unbarked railroad ties were observed to be heavily infested with cerambycid larvae upon arrival to Puerto Rico. It is possible that the wood and sugarcane trades were primary routes for the introduction of many insect species to Puerto Rico.

Cerambycids, along with buprestids and scolytids, were attracted to guanacaste trees, *Enterolobium cyclocarpum,* after the trees were infested by a fungus that caused an unidentified disease. Weakened limbs may fall suddenly in the absence of wind or external force, due to their own weight (Francis 1988b).

Curculionidae (snout beetles).—Beetles that have a well-defined beak compose this large family. Most snout beetles are plant feeders (Dillon and Dillon 1972). They may be found on flowers, leaves, fruits, or roots. Two species of vaquitas, *Diaprepes abbreviatus* (fig. 16) and *Compsus maricao,* attacked the seedlings of almendrón, *Prunus occidentalis,* in nurseries, often defoliating the young plants (Wolcott 1956).

The weevil *D. abbreviatus* is one of the major causes of defoliation in Puerto Rico. Martorell (1945b) listed 44 plant species attacked by this insect. Among the trees attacked by this weevil are the following: acacia amarilla, *Albizia lebbeck;* gongolí, *Ilex sideroxyloides;* moca, *Andira inermis;* and cedro, *Cedrela odorata. Diaprepes abbreviatus* partially defoliated mahogany seedlings and fed on their roots at the Catalina Nursery (USDA FS 1981). The larvae caused about 25 percent

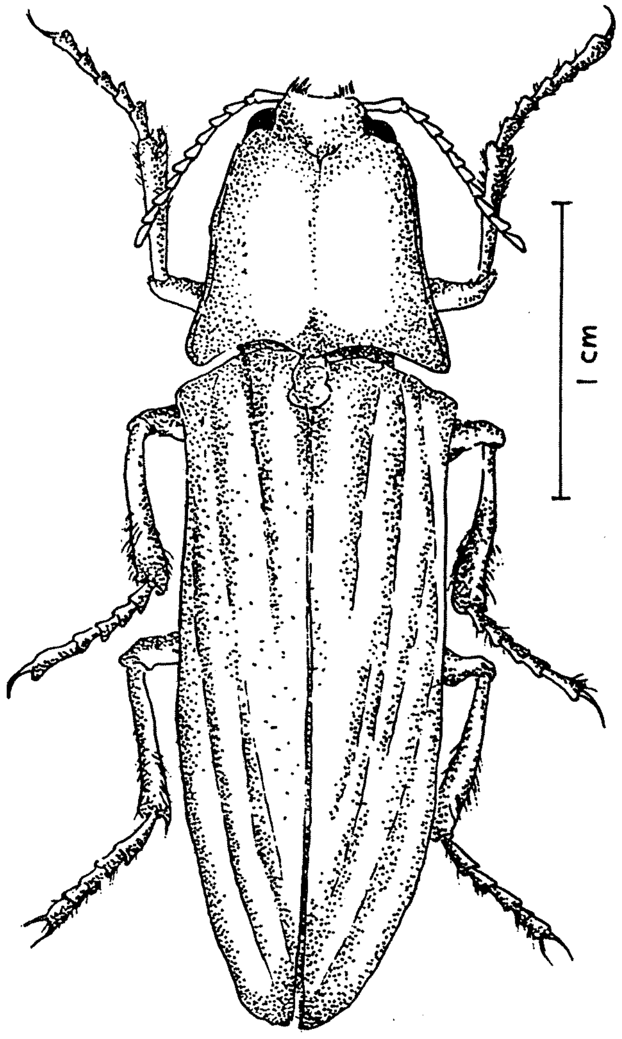


Figure 15.—*An elaterid beetle,* Chalcolepidius silbermanni.

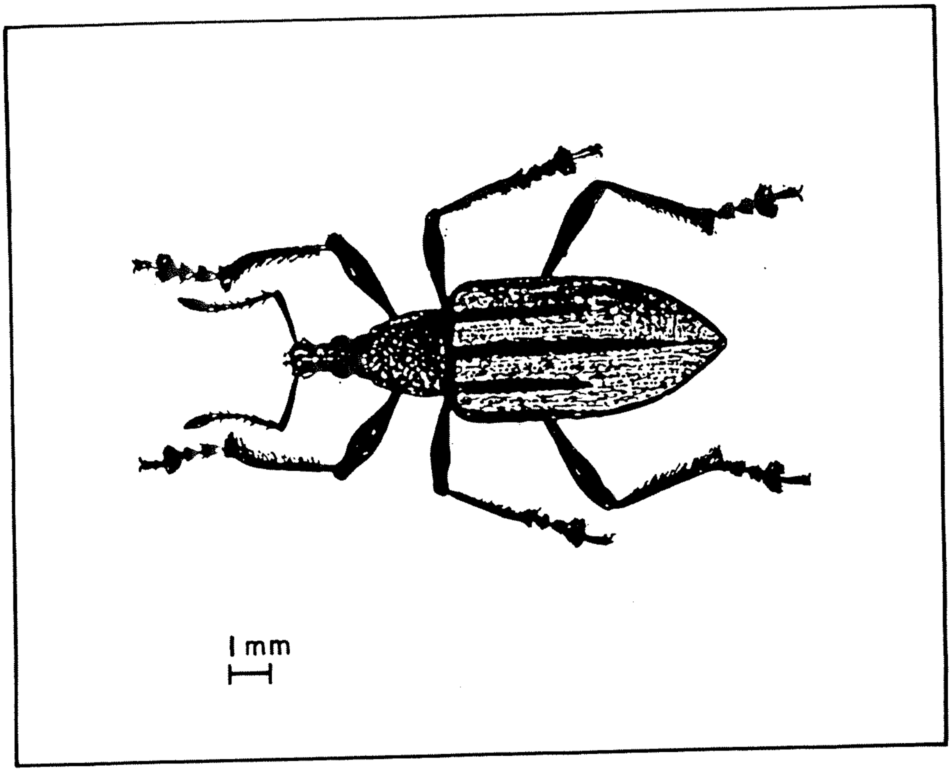


Figure 16.—*A snout beetle,* Diaprepes abbreviatus *(adapted from Wolcott 1948b).*

mortality in transplanted stocks from nurseries at Dorado and Monterrey (USDA FS 1976). Outbreaks of this weevil resulted in intensive defoliation of ceiba, *Ceiba pentandra,* at different localities in Puerto Rico. *Diaprepes abbreviatus* is one of the favorite foods of insectivorous birds in Puerto Rico (Martorell 1945b).

A weevil larva (subfamily Cryptorhynchinae) was reported to attack the bark of eucalyptus trees *(Eucalyptus deglupta* and *E. decaisneana)* in a trial experimental planting on the Río Abajo Forest. Larval girdling and mining often result in windthrow at the point of attack (USDA FS 1976). Larvae of the weevil, *Pseudomopsis cucubano,* were reported to feed on the seeds of ortegón, *Coccoloba swartzii,* but the extent of seed damage is not known (Wolcott 1948b).

Platypodidae (pin-hole borers).—The platypodids (fig. 17) are wood-borers. Their larvae feed on fungi cultivated in their galleries. *Platypus punctulatus* appears to be the most abundant member of the Platypodidae in Puerto Rico. It was found boring into broken limbs of moca, *Andira inermis;* diseased coconut palms, *Cocos nucifera;* logs of tabonuco, *Dacryodes excelsa;* and almácigo, *Bursera simaruba. Platypus compositus* was collected in a tabonuco log at Toro Negro. The platypodid *Platypus ratzeburgi* was found under the bark of guamá, *Inga fagifolia,* and in logs of guaba, *Inga vera,* in Lares and Ciales (Martorell 1976). *Platypus ratzeburgi* was also found recently attacking coffee, *Coffea excelsa,* at Castañer (Gallardo 1987). Another platypodid, *Platypus excisus,* has been reported in logs of *Inga vera* at Aibonito (Martorell 1976).

Scarabaeidae (scarab beetles).—Individual feeding habits indicate that there are two distinct groups in the Scarabaeidae family. In one group, both larvae and adults feed on dung, carrion, and skin feathers. The second group feeds on roots, plant juices, and decaying wood, as larvae, and on leaves, flowers, and pollen, as adults. The latter group includes insects of great economic importance (Dillon and Dillon 1972). Larvae of the coconut rhinocerus beetle (fig. 18), *Strategus oblongus,* feed in rotting wood of coconut palms, *Cocos nucifera;* guaba, *Inga vera;* guamá, *Inga fagifolia;* chinas, *Citrus sinensis;* tulipán africano, *Spathodea campanulata;* jobo, *Spondias dulcis;* and palma de sombrero, *Sabal causiarum.* In coconut palms, the result of larval infestation is nearly complete pulverization of the interior of the wood (Plank 1948b). *Strategus oblongus* is one of the largest beetles found in Puerto Rico. The adult beetle feeds mostly on the germinal tissue and meristem of young coconut palms. Adults also feed on young palma real, *Roystonea borinquena,* and on some palms of the genera *Phoenix* and *Pritchardia.*

Approximately 2 years after a major hurricane, reports of extensive damage to replanted and naturally

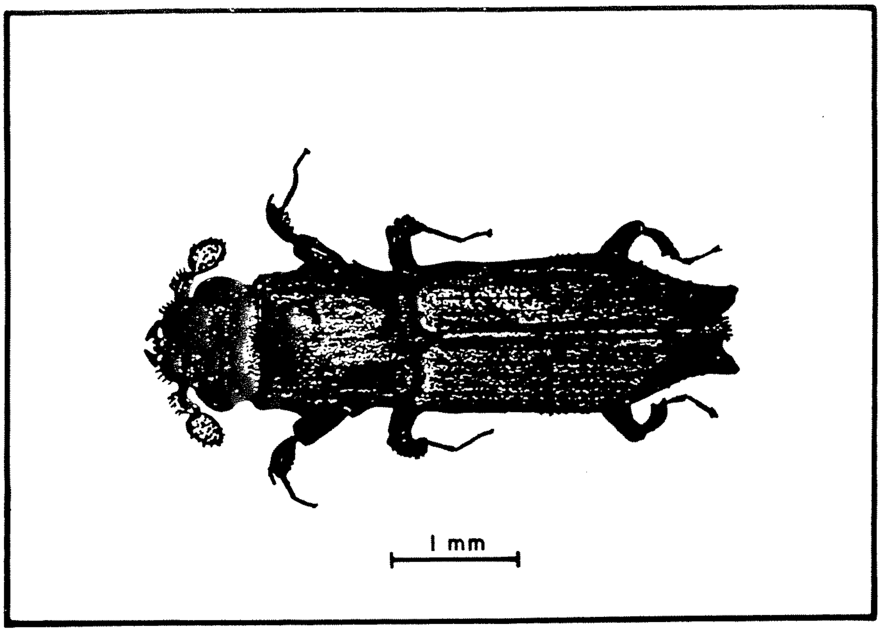


Figure 17.—*A pin-hole borer,* Platypus parallelus *(adapted from Equihua and Atkinson 1987 with permission of "Folia Entomológica Mexicana").*

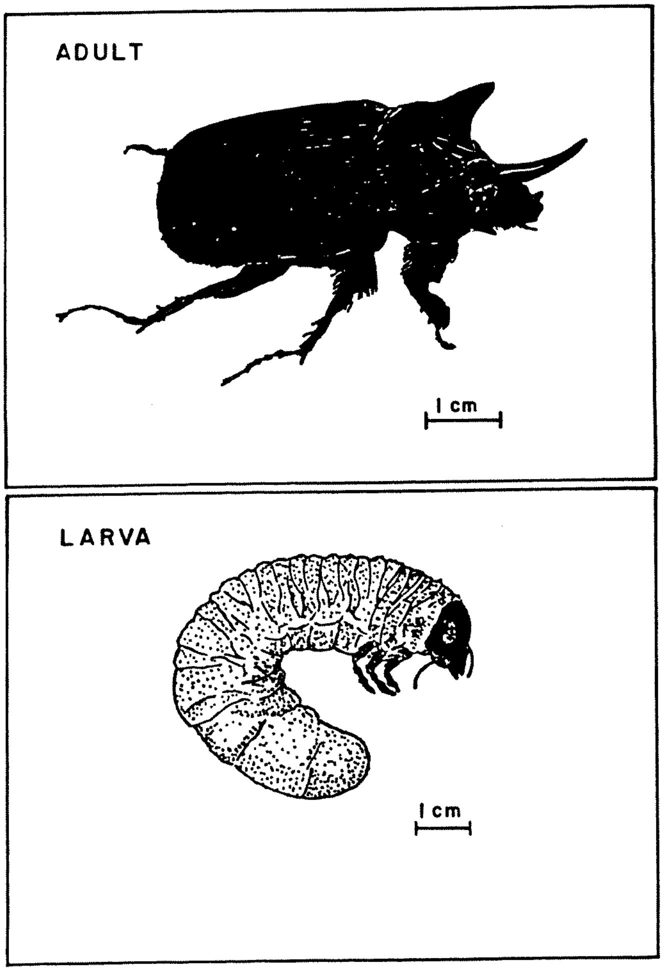


Figure 18.—*Adult and larva of the coconut rhinocerus beetle* Strategus oblongus *(adapted from Plank 1948b, Wolcott 1948b).*

regenerated palms appeared (Plank 1948b). Hurricanes uprooted or broke off many coconut palms. In subsequent years, the decay of this wood increased the food supply for the larvae and ultimately resulted in a population explosion of the adult beetles. The damage to coconut plantations caused by this beetle was so large that in 1935, as part of a clean-up campaign, a bounty of one cent was paid for each beetle, and one-half cent was paid for each larva, by the superintendent of the Puerto Rico Emergency Relief Administration. After 3 days of this campaign, 2,405 beetles were collected in 1 large grove near the town of Río Grande, where some 22,000 palms had been blown down by hurricanes (Plank 1948b).

Adults of the May beetle, *Phyllophaga portoricensis* (fig. 19), defoliated large trees of yagrumo macho, *Didymopanax morototoni,* at Río Blanco, Naguabo, from 1940 to 1941 (Martorell 1945a). The adults of the May beetle *P. vandinei* fed on the foliage of palma real, *Roystonea borinquena,* causing considerable damage at Isabela in 1941. These beetles feed voraciously in caoba hondureña, *Swietenia macrophylla* (Martorell 1945a).

Scolytidae (bark and ambrosia beetles). Adults and larvae of the Scolytidae family live in timber and beneath the bark of trees. Usually, dead or dying trees are attacked, but some species live in apparently healthy trees (Dillon and Dillon 1972). Boring holes caused by the scolytid beetle, *Xylosandrus compactus,* appear to provide infection courts for a fungus that causes dieback in mahogany *(Swietenia macrophylla).* Generally, beetle incidence at Catalina, Río Grande, was less than 5 percent, but areas with a beetle incidence of 50 percent have been reported (USDA FS 1982). The susceptibility of mahogany to these beetles was not related to the tree vigor (USDA FS 1984). *Xylosandrus compactus* was also reported attacking orchid pseudobulbs, *Cattleya* spp., in a greenhouse at Barranquitas (Martorell and Medina 1974).

Guaba, *Inga vera,* and guamá, *I. fagifolia,* are two of the most important shade trees in coffee groves. The scolytid *Xyleborus affinis* was reported to attack live *I. vera* and *I. fagifolia* trees, killing many. Infested trees recovered only occasionally and, then, only from very light attacks (Porto Rico Agricultural Experiment Station 1915, Wolcott 1948b). Martorell (1945a) found *X. affinis* attacking *I. fagifolia,* the dry fruits of guava, *Psidium guajava,* and the stalks of sugarcane, *Saccharum officinarum* (Wolcott 1948b).

The scolytids *Xyleborus affinis* and *X. volvulus* killed apparently healthy trees of acacia amarilla, *Albizia lebbeck,* in Río Piedras in 1945. *Xyleborus affinis* was collected in decaying coconut palms, *Cocos nucifera;* and *X. volvulus* was collected from under the dead bark of granadillo, *Buchenavia capitata,* and in logs of almácigo, *Bursera simaruba,* (Wolcott 1948b). Another scolytid, *X. ferrugineus,* was collected from coconut

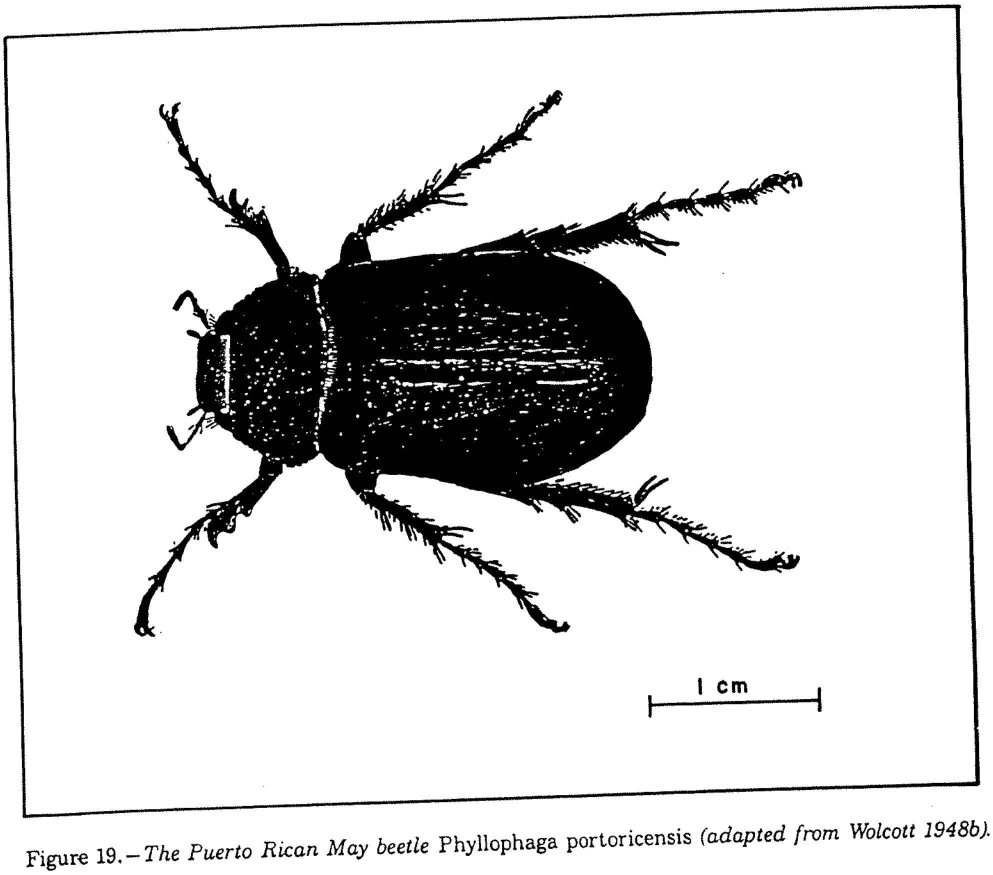


Figure 19.—*The Puerto Rican May beetle* Phyllophaga portoricensis *(adapted from Wolcott 1948b).*

palms; the bark of moca, *Andira inermis;* dead almácigo trees; and dead bucayo trees, *Erythrina poeppigiana* (Martorell 1976). The beetle *X. xylographus* was seen on mango, *Mangifera indica* (Bright 1985, Martorell 1945a).

Members of the scolytid genus *Hypothenemus* have been collected from several hosts. *Hypothenemus obscurus* was reared from a dead branch of flamboyán, *Delonix regia,* and from fruits of almendra, *Terminalia catappa. Hypothenemus obscurus* was apparently common in pods of algarroba, *Hymenaea courbaril,* and tamarindo, *Tamarindus indica,* in several localities in Puerto Rico. *Hypothenemus trinitatis* was collected in dead branches of guaraguao, *Guarea guidonia* (Martorell 1945a). *Hypothenemus* sp. (near *eruditus*) was collected in seed pods of maga, *Thespesia grandiflora; H. crudiae, H. obscurus,* and *H. seriatus* were collected in the dry fruits of guava, *Psidium guajava. Hypothenemus eruditus* was collected in pods of emajagüilla, *Thespesia populnea;* in a dead pole of maricao, *Byrsonima coriacea;* and in dry twigs of masa, *Tetragastris balsamifera* (Bright 1985; Martorell 1945a, 1976). *Hypothenemus brunneus* was recorded in the seed balls of the mangrove, *Conocarpus erectus,* and *Hypothenemus sp.* (near *hampei*) was found in mummied or culled berries of Liberian coffee, *Coffea dewevrei,* in 1941 (Wolcott 1948b).

The scolytid *Ambrosiodmus lecontei* was abundant in dead branches of Spanish cedar, *Cedrela odorata,* at El Verde in 1940 (Martorell 1945a); it was also found attacking logs of tabonuco, *Dacryodes excelsa,* and dead twigs of aceitillo, *Zanthoxylum flavum.* Another scolytid, *Monarthrum sp.,* was collected in tabonuco logs (Martorell 1976). Plank (1950a) reported that the scolytid *Poecilips* sp. attacked the seeds of mamey, *Mammea americana.*

Smith (1966) reported that after the termination of cesium irradiation at El Verde, bark beetles were very active in severely damaged trees, but not in moderately damaged ones. He found that bark beetle activity was delayed in sabinón, *Croton poecilanthus;* ausubo, *Manilkara bidentata;* and palo colorado, *Cyrilla racemiflora;* a fact suggesting that tree species of more hydric climatic preference were slower to react to radiation. One problem with Smith's analysis is that he did not present information on bark beetle attacks outside the irradiated area for control purposes. The tree species early attacked by bark beetles *(Inga* spp., *Didymopanax morototoni, Buchenavia capitata,* and *Dacryodes excelsa)* at El Verde are highly susceptible to bark beetles. Smith did not take into account tree susceptibility when assessing radiation effects.

Order Diptera (flies)

Tephritidae (fruit flies). – The larvae of many tephritids feed on plants, and some are serious pests. The adults are found on flowers or vegetation (Borror and others 1981). An outbreak of the fruitfly *Anastrepha suspensa* (fig. 20) occurred on the fruits of pomarrosa, *Syzygium jambos,* at Maricao in 1917 (Martorell 1945a). *Anastrepha suspensa* also causes considerable damage to guava fruits, *Psidium guajava,* and jobo, *Spondias dulcis.* The fruits of almendrón, *Prunus occidentalis,* are edible but are heavily infested by *A. suspensa* (Wolcott 1956). Another fruitfly, *Anastrepha obliqua,* is an important fruit pest of mango, *Mangifera indica,* in Puerto Rico (Martorell 1976).

Order Hemiptera (bugs)

Pyrrhocoridae (red bugs or stainers). – Members of the Pyrrhocoridae family are elongate-oval bugs that are usually brightly marked with red or brown and black (Borror and others 1981). The cotton-stainers *Dysdercus andreae* and *D. neglectus* were abundant on maga, *Thespesia grandiflora,* where they were found feeding on its seeds (Martorell 1976). *Dysdercus andreae* also feeds on the seeds of ceiba, *Ceiba pentandra,* and cotton, *Gossypium* spp. (Wolcott 1948b).

Tingididae (lace bugs). – The lacelike appearance of lace bugs (the Tingididae family) is found only in the adults; nymphs are usually spiny. Lace bugs are plant feeders; their feeding causes a yellow spotting of the leaves, with continued feeding, the leaves become entirely brown and fall off (Borror and others 1981). A heavy infestation of capá prieto, *Cordia alliodora,* by the tingid *Dictyla monotropidia* occurred in several parts of Puerto Rico in 1940. The attack caused a chlorotic condition on the leaves and subsequent defoliation. Many trees were completely defoliated due to the intense attack and the high abundance of nymphs and adults on the leaves (Martorell 1940b). Another lace bug, *Dictyla monotropidia,* fed on mago, *Hernandia sonora,* along Highway 191 near Mameyes in 1940. Chlorosis of the trees was reported there (Martorell 1945a).

Order Homoptera (aphids, scale insects, leafhoppers, and mealybugs)

Aphididae (aphids). – Aphids are found in large numbers sucking sap from the stems or leaves of plants. They excrete honeydew, which may be produced in sufficient quantities to cause the surface of objects beneath them to become sticky (Borror and others 1981). The honeydew is a favorite food of many ant species. Smith and others (1963, 1971) discussed the Puerto Rican Aphididae, providing information on the Luquillo Mountains, but did not provide sufficient quantitative data on damage to trees. The foliage of madre de cacao *(Gliricidia sepium),* a popular ornamental or hedge plant that was naturalized in Puerto Rico and is common in dry regions and lower mountain

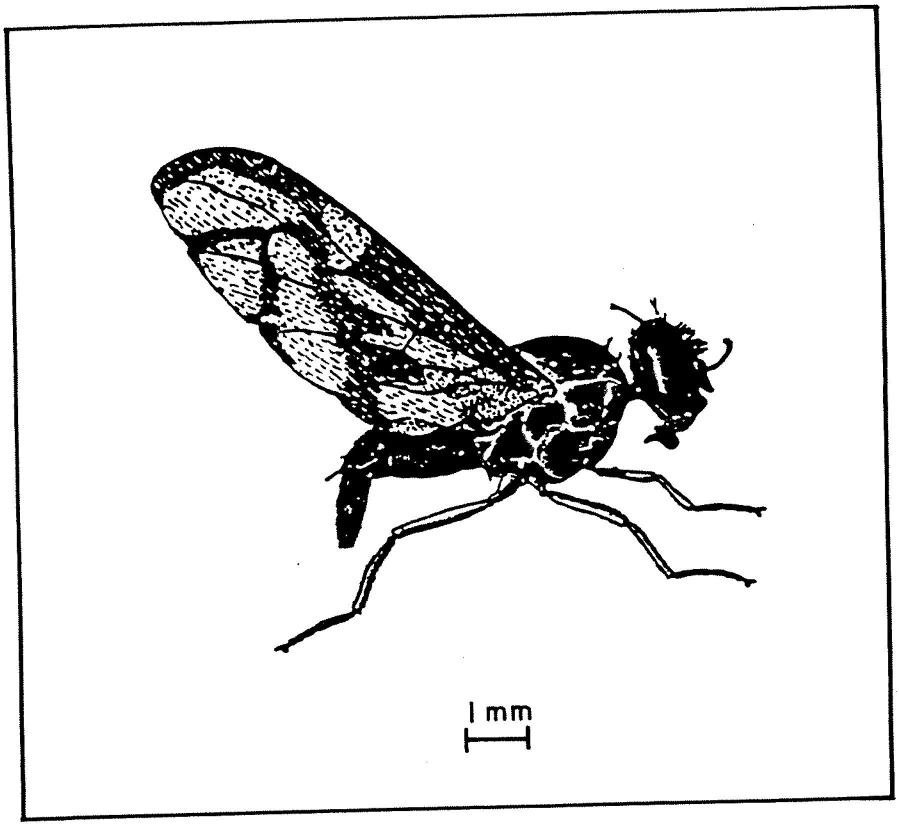


Figure 20.—*A fruit fly,* Anastrepha suspensa *(adapted from Wolcott 1948c).*

regions, is often attacked by the aphid *Aphis craccivora.* The aphid's honeydew attracts ants and promotes the growth of fungus over the leaves (Little and Wadsworth 1964).

Asterolecaniidae (pit scales).—Members of the Asterolecaniidae family are called pit scales because many of them produce gall-like pits in the bark of trees (Borror and others 1981). The pustule scale, *Asterolecanium pustulans,* was responsible for the near eradication of the silver oak, *Grevillea robusta,* in Puerto Rico (Martorell 1943). The scale also killed many trees of guara, *Cupania americana,* and yellow cassia, *Cassia siamea,* which is a good species for firewood. Wolcott (1940c) found the scale attacking maga, *Thespesia grandiflora;* its infested leaves and branches turned brown and died. Sometimes as many as half of the lateral branches were infested and killed. Wolcott suggested the eradication of the introduced tree, *C. siamea,* to reduce the infestation on maga. The pustule scale was very common on several exotic trees. *Asterolecanium pustulans* is susceptible to attack by three species of parasitic wasps that could control the scale in maga if some of the alternative host trees were eliminated (Wolcott 1940c). Wolcott's suggestion was not taken into consideration since the introduction of the ladybird beetle, *Chilocorus cacti,* for the control of the bamboo scale resulted in the control of the pustule scale (Wolcott 1953). The ladybird beetle preferred *A. pustulans* over the bamboo scales *A. bambusae* and *A. miliaris.* That is an example of fortuitous biological control of a pest.

The scales *Asterolecanium bambusae* and *A. miliaris* feed on bamboo. In many countries, these species are confined to the common bamboo, *Bambusa vulgaris.* In Puerto Rico, these scales also attack most of the introduced species of bamboo. These scales attack *B. vulgaris* from the lowlands to altitudes up to 600 m in the Luquillo Mountains (Martorell 1976). Several species of predatory beetle were introduced from the Guianas and Trinidad in an attempt to control the scale (Bartlett 1938). White (1948) reported that the beetles achieved good control of the scales. The control of *A. bambusae* by the ladybird beetle, *Cladis nitidula,* is another example of effective biological control.

Cicadellidae (leafhoppers).—The Cicadellidae family is the largest in the order Hemiptera. Leafhoppers are often destructive to certain plants, not only by damage caused by their feeding, but also because they transmit plant diseases (Ross and others 1982).

Wood of the roble blanco, *Tabebuia heterophylla,* has many uses, and the tree is also planted as an ornamental. During long dry periods, the leafhopper *Rabela tabebuiae* feeds on roble blanco, defoliating it or causing its leaves to turn yellow (Little and Wadsworth 1964, Martorell 1976). Another leafhopper, *Dikrella cedrelae,* became so abundant on the cedar (*Cedrela* spp.) leaves that premature yellowing and shedding occurred (DeLeon 1941, Wolcott 1948a). The damage can affect the annual growth rate of cedar trees. These leafhoppers, together with the mahogany shoot borer, *Hypsipyla grandella* (Lepidoptera-Pyralidae), which causes low branching, prevented the cedars from rapidly developing marketable lumber in Puerto Rico (Wolcott 1948a). The leafhopper *Omegalebra cordiae* caused yellowing of foliage and subsequent defoliation on capá prieto, *Cordia alliodora,* in Cayey and San Lorenzo between 1940 and 1947 (Martorell 1976).

Coccidae (soft, wax, and tortoise scales). – The females in the Coccidae family are elongate-oval, usually convex, but sometimes flattened, with a hard smooth exoskeleton or covered with wax. The males may be winged or wingless (Borror and others 1981). Soft scales are pests of ornamentals throughout most of the world, although they are more abundant in tropical and subtropical areas.

A heavy infestation of the black scale *Saissetia oleae* on twigs and smaller branches resulted in terminal death in moca, *Andira inermis,* in Patillas in 1940 (Martorell 1976). Heavy infestations of the greenish-brown scale, *Pulvinaria psiddii,* on trunks and branches of 4 to 5-year-old Spanish cedar, *Cedrela odorata,* were observed along the Cayey-Salinas road in 1941 (Martorell 1976). The present scarcity of the greenish-brown scale on cedar is due to the introduction of the ladybeetle, *Cryptolaemus montrouzieri,* into Puerto Rico for the control of mealybugs on sugarcane (Wolcott 1948a).

The coccoid, *Octaspidiotus araucariae,* attacked an *Araucaria cunninghamii* plantation in Carite (Francis 1988a). The twigs soon blackened and fell off, leaving the plantation nearly defoliated. If *A. cunninghamii* is attacked by *O. araucariae* in all parts of Puerto Rico, it will be impractical to grow *A. cunninghamii* on the island.

Diaspididae (armored scales). Diaspididae is the largest family of scale insects. The actual insect has a delicate oval body hidden beneath a scale. The appendages are reduced, the body, at maturity, is a little more than an egg sac (Ross and others 1982). An intense attack of the white peach scale, *Pseudaulacaspis pentagona,* occurred on ash, *Fraxinus uhdei,* resulting in the destruction of 44 percent of the introduced trees at Toro Negro plantations (Martorell 1940a, 1943, 1976). Quina, *Cinchona* spp., (which is used in the preparation of quinine) plantings near Maricao also suffered heavy losses (Martorell 1943, Plank and Winters 1949). Several trees of almendrón, *Prunus occidentalis,* were attacked by *P. pentagona* in a nursery in the Doña Juana Forest (Wolcott 1956), and a heavy scale infestation was observed on a cabrilla tree, *Trema lamarckianum,* in the Luquillo Mountains in 1940 (Martorell 1976). *Pseudaulacaspis pentagona* deformed and killed many mahoe trees, *Hibiscus elatus,* in the Toro Negro Forest (Tropical Forest Experiment Station 1954).

The white peach scale attacked toon, *Toona ciliata,* seedlings in Corozal and Vega Alta in 1972 (Whitmore and Medina 1974). The scale affects tree vigor and form. There are several parasitic wasps (Eulophidae) that attack this scale in Puerto Rico (Wolcott 1948d). Toon is a promising tree for replacement of cedar, *Cedrela odorata,* one of the most important timber trees native to the neotropics. Cedar encountered problems in Puerto Rico related to site requirements and attacks by the shoot borer, *Hypsipyla grandella* (Lepidoptera: Pyralidae).

The black thread scale, *Ischnaspis longirostris,* attacked guaraguao, *Guarea guidonia,* quite severely at El Verde. It also caused chlorosis followed by defoliation on caoba hondureña, *Swietenia macrophylla,* in 1940 and 1942 (Martorell 1940b, 1976).

Margarodidae (giant coccids and ground pearls). – The Margarodidae family includes some of the largest species in the superfamily Coccoidea. Some species may reach a length of about 25 mm. The name ground pearls was given because of the pearllike appearance of the cysts of females in the genus *Margarodes;* those insects live in the roots of plants (Borror and others 1981). The cottony cushion scale *Icerya purchasi* (fig. 21) attacks the needles of the Australian pine, *Casuarina equisetifolia,* and is also a pest of citrus in Puerto Rico. The scale is controlled by the

Figure 21. – *The cottony cushion scale* Icerya purchasii.

imported ladybird beetle, *Vedalia cardinalis* (Wolcott 1943b, 1960). In some humid citrus groves, the fungus *Spicaria javanica,* caused complete eradication of the scale (Wolcott 1951); that was an excellent example of biological control of an insect pest in Puerto Rico.

Pseudococcidae (mealybugs). – The Pseudococcidae family is cosmopolitan in distribution. The mealybugs make no scale but secrete waxy filaments that are especially noticeable about the body margin (Ross and others 1982). The mealybug, *Nipaecoccus nipae,* is the most common member of the genus found in Puerto Rico. It caused damage to 32 species of trees and shrubs, many found in the Luquillo Mountains (Martorell 1945b). It is found from the lowest elevations in Puerto Rico up to around 830 m, but rarely at higher elevations. The insect is controlled in Puerto Rico by a group of parasites and predators, among them, ladybird beetles and entomogenous fungi (Martorell 1945b, 1976).

Order Hymenoptera (ants, bees, sawflies, and wasps)

Argidae (sawflies). – Most of the argids are black or a dark color. The larvae feed mainly on trees. The sawfly, *Schizocerina krugii* (fig. 22), is the only species of this family found in Puerto Rico. The larvae of *S. krugii* cause intensive defoliation on seagrape, *Coccoloba uvifera,* which has been introduced to the Luquillo Mountains (Little and Woodbury 1976). *Schizocerina krugii* is also considered a pest of moralón, *C. pubescens,* and other *Coccoloba* species (Martorell 1976).

Formicidae (ants). – The use of seeds to supplement a diet based on insect prey is common in ants of the subfamily Myrmicinae. Many of the seeds that the ants transport are not eaten; thus the ants contribute to the dispersal of plants (Brian 1983). Natural regeneration of the Australian pine *Casuarina equi-*

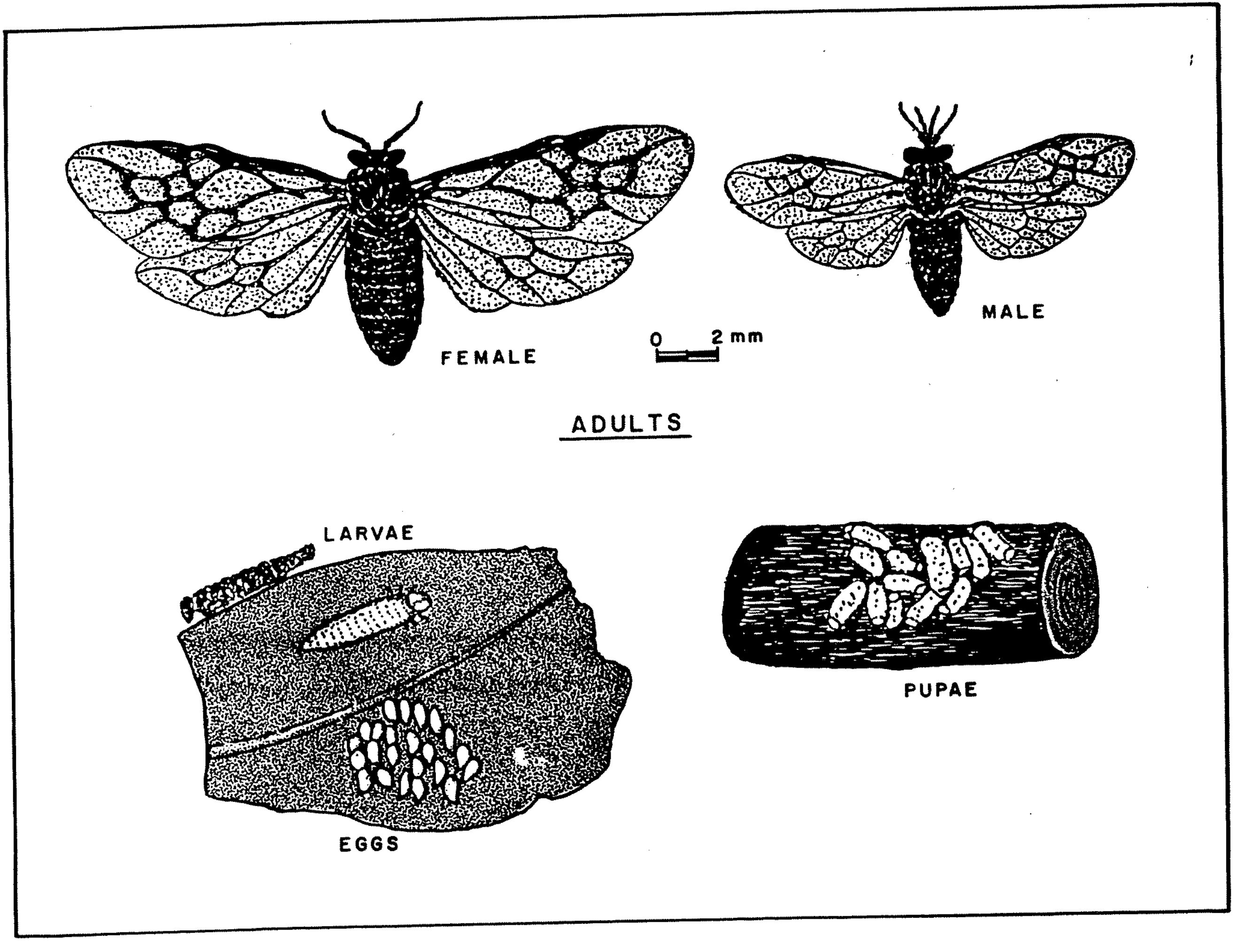


Figure 22. – *Adults, larvae, cocoons, and eggs of the tenthredinid wasp* Schizocerina krugii *(adapted from Martorell 1945b).*

setifolia is rare in Puerto Rico due to seed consumption by ants (Little and Wadsworth 1964). The introduction of guamá venezolano, *Inga quaternata,* for use as shade in coffee plantations, failed because the tree is susceptible to the ant *Myrmelachista ramulorum,* a pest of coffee. Nonetheless, the tree survives well in several areas in Puerto Rico (Little and Wadsworth 1964).

Myrmelachista ramulorum forms irregular tunnels in coffee trees. In some parts of the tunnels, the ants tend mealybugs or scale insects, which suck sap from the trees and reduce the production of coffee berries (Wolcott 1933, 1951). Tunneled coffee trees are easily broken by wind and storms. This ant is highly abundant in the canopy of Puerto Rican forests and can be responsible for the death of small branches. *Myrmelachista ramulorum* infestations on pomarrosa, *Syzygium jambos,* caused the death of more than 50 percent of the tree terminals at Lares in 1940 (Martorell 1976).

Order Lepidoptera (butterflies and moths)

Cosmopterygidae (cosmopterigid moths).– Most of the members of the Cosmopterygidae family are leaf miners in their larval stage. Severe infestations of the palmetto leaf-miner, *Homaledra sabalella,* occurred in palma de sierra, *Prestoea montana,* in the Luquillo Mountains, Toro Negro, and Cayey in 1940 (Martorell 1945a). The caterpillars of *H. sabalella* are gregarious and feed on the underside of palm leaves. This moth also feeds on coconut palms and ornamental palms. The moth occurs in all parts of the island (Wolcott 1948c). Parasitic wasps (Chalcididae) are responsible for the control of the caterpillars of *H. sabalella* in the field (Martorell 1945b).

Gelechiidae (gelechiid moths).– Members of the Gelechiidae family may mine, roll, or web together leaves of several plants. Some species produce galls, others are pests in stored seeds, cereals, and tubers (Peterson 1984).

Maga, *Thespesia grandiflora,* was formerly planted for timber throughout Puerto Rico and for esthetics along roadsides. Its wood is superior to mahogany in many aspects (Wolcott 1940a). Since maga was an alternative host to the pink bollworm, *Pectinophora gossypiella,* its planting was discontinued in the cotton regions (Little and Wadsworth 1964). *Pectinophora gossypiella* feeds on the pods or seeds of maga and emajagüilla, *T. populnea.*

Geometridae (measuring worms).– The larvae of geometers have two or three pairs of prolegs at the posterior end of the body and none in the middle. The locomotion is accomplished by placing the posterior end of the body close to the thoracic legs and then moving the anterior end, thus progressing in a looping fashion (Borror and others 1981). The larvae feed chiefly on foliage (Peterson 1984). Larvae of the moth *Semiothisa diffusata* (recorded as *Macaria diffusata)* defoliated flamboyán, *Delonix regia,* trees in Guánica in 1916 (Martorell 1976).

Hyblaeidae (hyblaeid moths).– The Hyblaeidae is an Old World tropical family. The leafroller, *Hyblaea puera,* is an introduced species in Puerto Rico. The caterpillars of *H. puera* do considerable damage to teak, *Tectona grandis,* in the Orient (Forbes 1930). *Hyblaea puera* heavily infested capá blanco, *Petitia domingensis,* in a USDA Forest Service nursery at Cayey in 1937. Subsequently, only small outbreaks have occurred (Martorell 1939).

Megalopygidae (flannel moths).– Moths of the Megalopygidae family have a coat of scales mixed with fine curly hairs, which give the moth a somewhat woolly appearance (Borror and others 1981). The larvae have stinging spines under the hairs and can cause severe irritation to humans. The family is mainly found in the New World, in the Tropics and warm temperate regions (Forbes 1930).

The larvae of la plumilla, *Megalopyge krugii* (fig. 23), caused considerable damage and defoliated several maricao trees, *Byrsonima coriacea,* at Aguas Buenas in 1940. An outbreak of caterpillars occurred on moca, *Andira inermis,* causing complete defoliation at Ponce (Martorell 1945a). Guamá, *Inga fagifolia,* one of the most important shade trees in coffee groves, was attacked by the larvae of *M. krugii.* Caterpillars were very abundant, causing considerable damage to leaves (Porto Rico Agricultural Experiment Station 1915). *Megalopyge krugii* defoliated flamboyán trees, *Delonix regia,* at Ponce in 1940 (Martorell 1945a).

Noctuidae (noctuid moths).– Noctuidae is the largest family in the order Lepidoptera. The larvae are usually leaf feeders. Some are stem or root borers, and others gnaw in fruits (Ross and others 1982).

The flamboyan, *Delonix regia,* widely planted as an ornamental and found in some island forests, is attacked occasionally by the caterpillars of the moth *Melipotis acontioides* (recorded as *Lyncestis acontioides).* Trees can be completely defoliated (Little and Wadsworth 1964) and damage can be extensive (Wolcott 1945b). This moth is usually a lowland insect and has not been observed at middle elevations. Caterpillars of another moth, *Spodoptera frugiperda,* attacked small seedlings of *Eucalyptus robusta* in USDA Forest Service nurseries at Río Piedras (Martorell 1976). The caterpillars were kept under control by parasitic larvaevorid flies, parasitic wasps, and entomogenous fungi. Caterpillars were also attacked by a carabid beetle and an assassin bug. Insectivorous birds and some lizards preyed on the caterpillars or the moths. Caterpillars of the moth *Diphthera festiva* (recorded as *Noropsis hieroglyphica)* bored in the trunks of *Casuarina equisetifolia* causing severe damage to young trees at Guánica in 1923 (Martorell 1976).

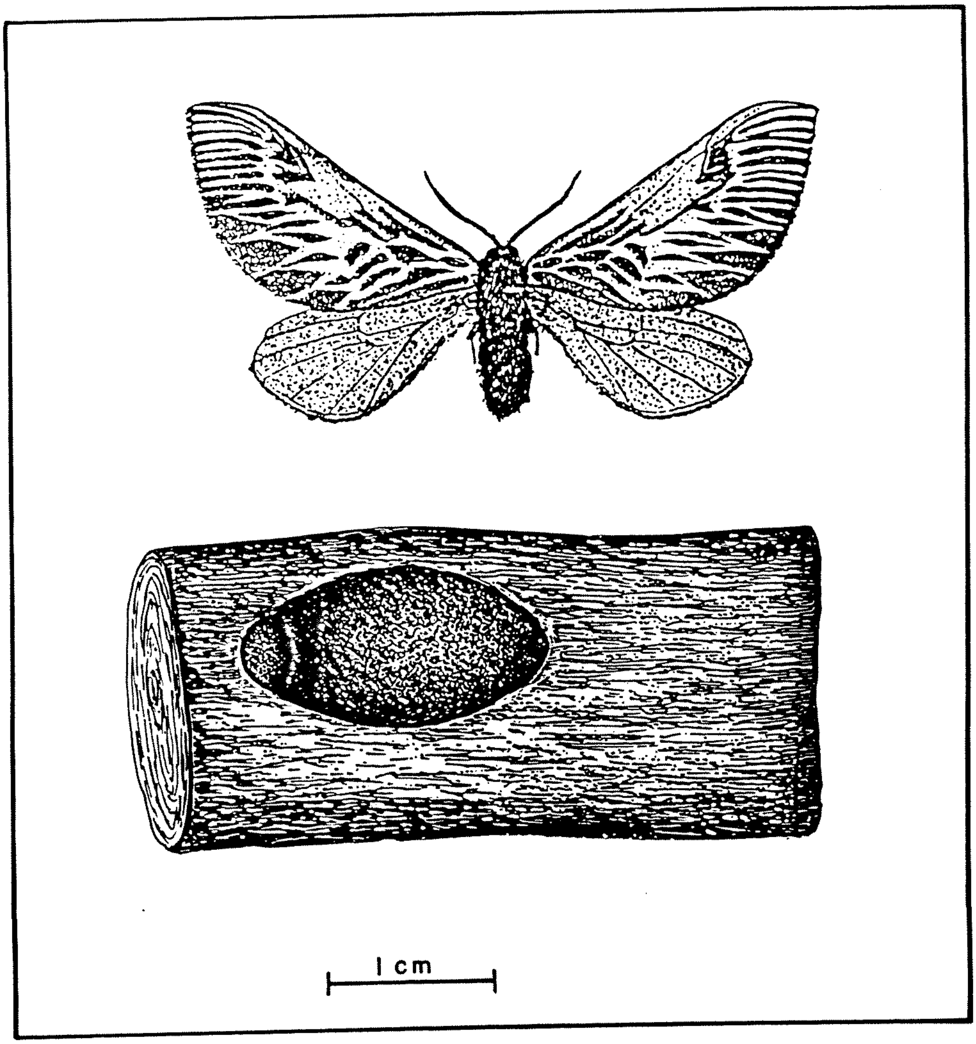


Figure 23.—*Adults and cocoons of la plumilla* Megalopyge krugii *(adapted from Wolcott 1948c).*

Psychidae (bagworms).—The adult males of the Psychidae moths have wings, but the females are wingless, legless, and usually never leave the bag in which they pupated. The caterpillars of *Oiketicus kirbyi* almost defoliated trees of guano, *Ochroma lagopus,* at Catalina in the Luquillo Mountains in 1940. Also, caterpillars of *O. kirbyi* caused defoliation of several almendra, *Terminalia catappa,* trees at La Muda in 1938 (Martorell 1945a).

Pyralidae (snout and grass moths).—The Pyralidae is one of the most economically important families in the order Lepidoptera. The larvae, some being saprophagous and a few, predaceous, exhibit a broad range of habits such as feeding on leaves, fruits, flowers, and boring in stems (Ross and others 1982).

The shoot borer, *Hypsipyla grandella,* does only minor damage in native forests, but causes severe damage in mahogany plantations (Hodges and McFadden 1987). *Hypsipyla grandella* larvae bore into stem tissues and hollow out the shoots. This results in retardation of stem growth, profuse branching, and possible shoot deformities. After continual attack, the trees either die or become so deformed that the possibility of reaching merchantability is minimal (Gara and others 1973). The ichneumonid wasp, *Calliephialtes ferrugineus,* attacks the shoot borer (Martorell 1945a, 1945b; Wolcott 1948d).

In Puerto Rico, Dominican mahogany *(Swietenia mahogani)* is seldom attacked, but Honduras mahogany, *S. macrophylla,* is highly susceptible to *H. grandella.* Weaver and Bauer (1986) reported infestation rates as high as 57 percent (table 9) in areas using line plantings, a silvicultural technique in which most of the native forest is left intact. Mahogany trees in plantations or dense line plantings present ideal conditions for maintaining large borer populations. Planting mahogany alternately with other species in line plantings in Africa has provided some control of the shoot borer (Roberts 1968). Attacks are either reduced or nonexistent in shaded plantations in some instances, often due to factors such as low seedling density (Whitmore 1978b). Weaver and Bauer (1986) suggested that

Table 9.—*Percent of shoot borer damage to surviving trees in line plantings established in 1974 and 1980 in Puerto Rico (adapted from Weaver and Bauer 1986 with permission of Turrialba)*

Year	Trees damaged	Trees measured
	Percent	*Number*
1974	57	214
1979	11	672
1980	17	643

the presence of surrounding shade helps in the control of weeds and probably assists the mahogany tree in the development of a single shoot, even if infested by the moth. Weaver and Bauer (1986) also suggested that chemical control of the borer is most easily accomplished when seedlings are kept in the nursery until they reach at least 1 meter in height. This will reduce weeding costs and the time available for infestation to take place. Mahogany grown on open sites that were extensively site prepared suffered severe attacks by the borer (USDA FS 1976). Gara and others (1973) found that the attacked mahogany trees had new flushes of growth. The most serious attack occurred on trees with a high new leaf to total leaf ratio. This indicates that faster growing trees that produce abundant new leaves are more subject to attack than moderate- to slow-growing trees. The fact that shaded trees are slower growing than open grown trees may explain the conclusions of silvicultural studies that recommend growing mahogany under shade to prevent attacks by *H. grandella.*

Toon, *Toona ciliata,* (an Australian Meliaceae) is not attacked by *H. grandella* in Latin America, but it is heavily attacked in its native habitat by the moth *H. robusta.* It appears that the family Meliaceae has evolved the capacity to produce poisonous substances to deter *Hypsipyla.* The shoot borers have coevolved with each particular tree species, adapting to the secondary substances to the point that the toxins have become an attractant to the insect. Due to chemical differences between the compounds produced by different Meliaceae species, trees introduced into new geographical areas will be immune to the native shoot borer for an unknown period (Gara and others 1973). Contrary to the situation in Puerto Rico, in Haiti the shoot borer prefers *S. mahogani,* which is native, and refuses *S. macrophylla.* This suggests that the borer and *S. mahogani* coevolved in Haiti and supports the conclusion that *S. mahogani* is not native to Puerto Rico. Apparently, the shoot borer has not evolved a taste for *S. mahogani* in some 200 years since the tree was introduced to Puerto Rico (Whitmore and Hinojosa 1977). Recently *S. macrophylla* has been attacked by *H. robusta* in Timur (Ngatiman 1989).

Spanish cedar, *Cedrela odorata,* a member of the mahogany family, is also attacked by *H. grandella* in Puerto Rico. Trees growing in the open were attacked more often than trees growing under shade. Whitmore (1978a) found a weak relationship between vertical growth and borer attack (the borer tends to attack trees that grow fast and have fresh, green growth). Lamb (1968) found that heavy resin flow in vigorous trees discourages the insect.

The roble leaf-webber, *Eulepte concordalis,* is considered a destructive foliage pest of roble rosado, *Tabebuia heterophylla,* and roble de sierra, *T. rigida.* This moth occurs from the lowlands to elevations of 800 m. About 50 percent of the trees in a large group were attacked by the larvae of this species along the Mount Britton trail in the Luquillo Mountains in 1940. The larva of *E. concordalis* is a leaf-webber that eats the leaf epidermis of *Tabebuia* and higüera, *Crescentia cujete.* After attack, trees exhibit skeletonized, brownish leaves that are webbed together in bunches. *Eulepte concordalis* is parasitized by the tachinid *Sturmia albincisa,* the chalcid *Brachymeria incerta,* and the braconid *Bracon cushmani* (Martorell 1940c). The caterpillars of the moth *Epicorsia oedipodalis* (recorded as *Pyrausta cerata*) fed on péndula de sierra, *Citharexylum caudatum,* in the Luquillo Mountains, but there was no indication of the damage caused by this species. *Epicorsia oedipodalis* caterpillars caused heavy defoliation on péndula colorada, *Citharexylum fruticosum,* particularly in the middle elevations of Puerto Rico. The caterpillars are parasitized by the ichneumonid wasp, *Eiphosoma insularis.* Another moth, *Pachymorphus subductellus,* is a common twig borer of *Tabebuia heterophylla.* It also attacked *Tabebuia rigida.* The caterpillars of *Tetralopha scabridella* caused heavy defoliation to guaba, *Inga vera,* during the insect's peak of abundance (Martorell 1945a, 1945b, 1976).

The caterpillars of *Agathodes designalis* (fig. 24) are leafrollers and twig borers in bucayo, *Erythrina* spp. This moth is a voracious pest that causes heavy defoliation and destruction of new shoots, year after year. The caterpillars also bore into guaba, *Inga vera.* The caterpillars of *Terastia meticulosalis* (fig. 25) are twig and pod borers of *Erythrina fusca.* They infested 90 percent of the trees in an experimental planting at Río Piedras in 1921. *Terastia meticulosalis* attacked other *Erythrina* species and capá blanco, *Petitia domingensis* (Martorell 1945b, 1976).

The moth *Phostria originalis* attacked moca, *Andira inermis,* in several towns in February and March of 1940 (Martorell 1976). This insect is a webworm and is found in clusters of 80 to 100 larvae at the end of branches. Its larvae can completely defoliate trees (Martorell 1939). Another moth, *Blepharomastix ebulealis,* has small, but very voracious, caterpillars that feed on camasey peludo, *Heterotrichum cymosum.*

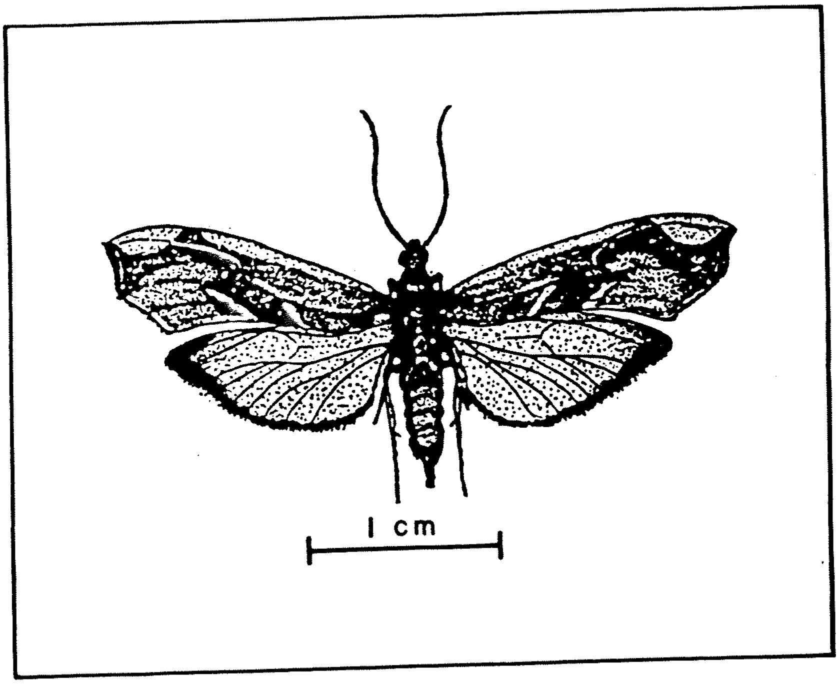


Figure 24.—*A pyralid moth,* Agathodes designalis *(adapted from Wolcott 1948c).*

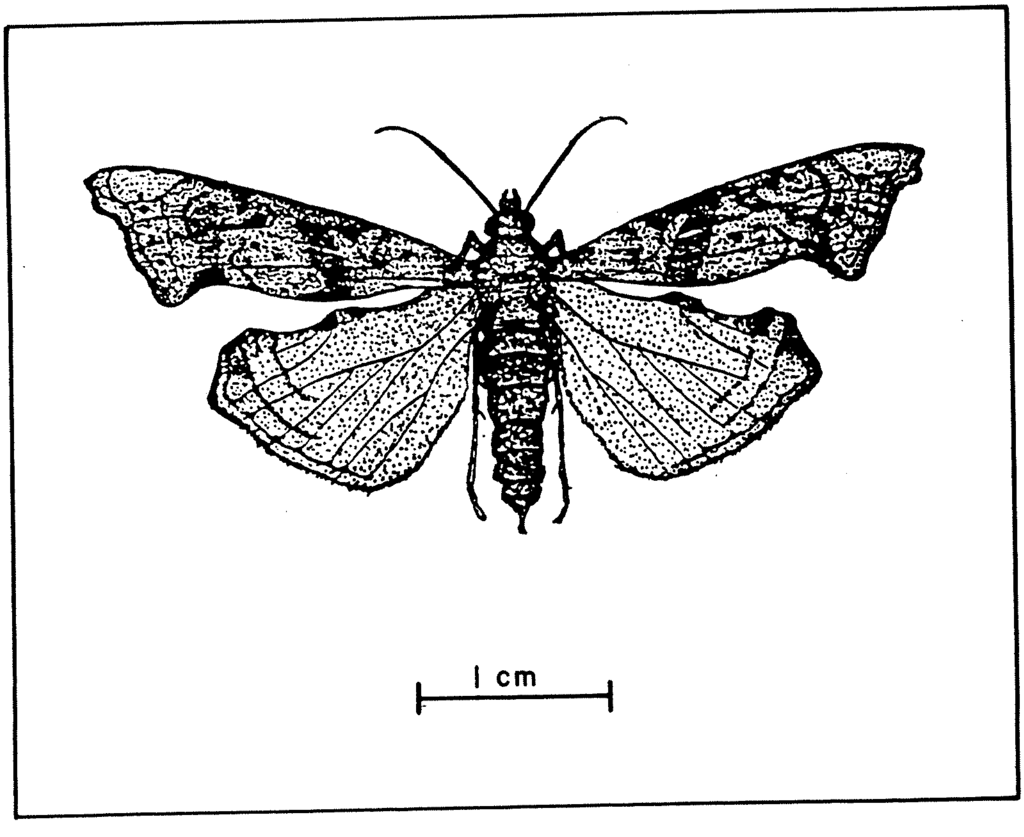


Figure 25.—*A pyralid moth,* Terastia meticulosalis *(adapted from Wolcott 1948c).*

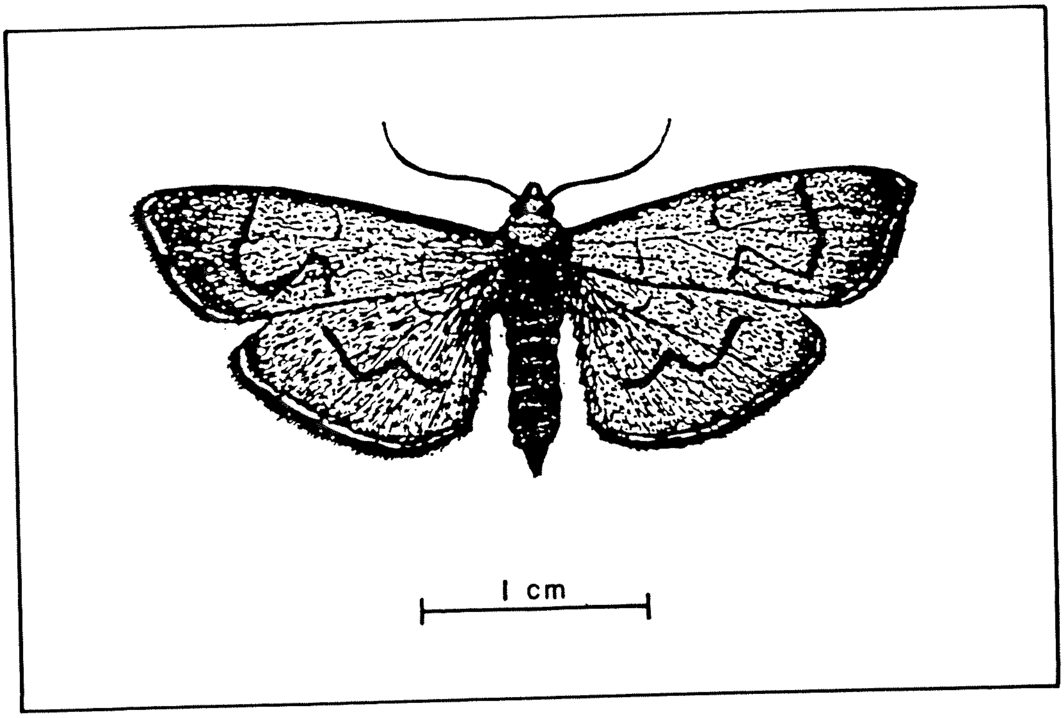


Figure 26.—*Adult of the Cecropia leaf-roller* Syllepte silicalis *(adapted from Wolcott 1948c).*

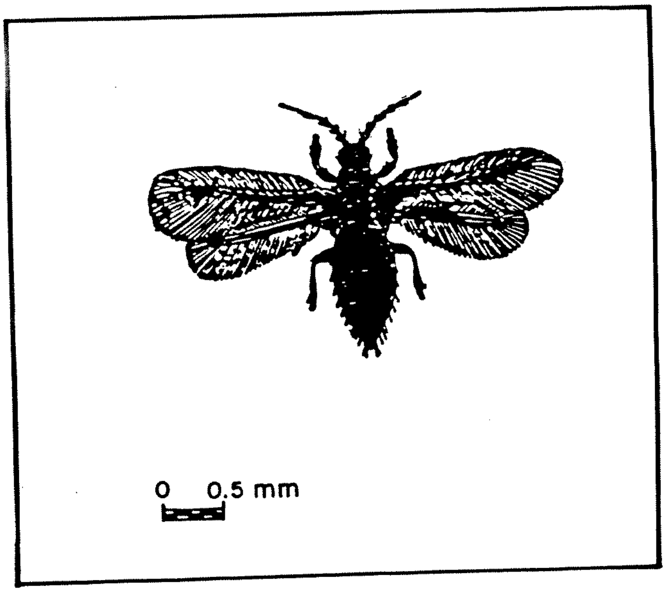


Figure 27.—*Adult of the thrip* Selenothrips rubrocinctus.

Blepharomastix ebulealis infested many trees but most of the caterpillars were parasitized by larvaevorid flies (Martorell 1945b).

The caterpillars of the yagrumo leafroller, *Syllepte silicalis* (fig. 26), fed on the buds of terminal branches of *Cecropia peltata*, along the Mount Britton trail in the Luquillo Mountains, causing considerable damage. There are four additional species of Lepidoptera that feed on *C. peltata* in Puerto Rico (Martorell 1976).

Order Thysanoptera (thrips)

Most thysanopterans are between 2 and 3 mm long. Thrips occur commonly in flowers. Many species are destructive to plants and are found in the leaves of the infested hosts (Ross and others 1982). The thrips, *Selenothrips rubrocinctus* (fig. 27), attack kadam trees, *Anthocephalus chinensis*, reducing their leaf area, but do not kill them (Lugo and Figueroa 1984). Thrips attack old leaves, but damage does not appear visible until the leaves are nearly ready to drop (USDA FS 1976). Heavy feeding on leaves caused premature leaf drop and, ultimately, complete defoliation and death of trees (USDA FS 1972). A growth study is needed to measure any effects of infestations by thrips on tree height and diameter over time. If damage is significant, possible solutions may include growing kadam in mixed stands or selection of resistant clones. Clone selection in cocoa, *Theobroma cacao*, was successful in reducing damage by the same species of thrips in Trinidad (USDA FS 1976). This thrip also attacks almendra, *Terminalia catappa*, causing a silvery appearance in the leaves (Martorell 1976).

Other Insect Groups

El Servicio de Extensión Agrícola (1948) listed the common names of insects that attack laurel sabino, *Magnolia splendens;* guaba, *Inga vera;* pines; eucalyptus; etc. Several suggestions for dealing with these insect pests are available.

Plank (1950a) studied the insecticidal properties of 48 species of plants in 23 families. Thirteen local, economically important species of insects belonging to four orders were tested. Mamey, *Mammea americana,* exhibited the greatest insecticidal potential of the plants examined. The half-ripe fruits, seeds, and leaves showed insecticidal value, either as an internal poison, as a contact poison, or both. The active chemical in the mature seeds (the most toxic part of the plants) was mameyin, a substance that is similar in composition and has similar effects to those of pyrethrins. One of the earliest uses of mamey in the Caribbean was in the control of fleas that attack humans and domestic animals. Mamey leaves were used successfully for many years in Puerto Rico to wrap the trunks of newly set garden plants for the prevention of insect attack (Plank 1950a).

INSECTS THAT ATTACK FOREST PRODUCTS

Order Coleoptera (beetles)

Bostrichidae (branch and twig borers).—In Puerto Rico, harvested bamboo (one of the most commonly used plants in the Tropics) is attacked by the escarabajo del bambú seco, *Dinoderus minutus,* a member of the Bostrichidae. Few beetles are found in the field, but high populations may be found under storage conditions (White 1948). Dead or dying culms left in the field are rarely attacked (Plank 1948a). Severe infestations weaken and mar the stored culms to the extent that they are worthless. Bamboo culms that do not become infested within 1 or 2 months are usually not attacked later.

The adults of *D. minutus* appear to be crepuscular, and they attack dry vegetable products like corn, *Zea mays.* A braconid parasite, *Doryctes jarvus;* a pteromalid parasitic wasp, *Proamotura aguila;* and a reduviid predator, *Peregrinator biannulipes,* proved to be ineffective in reducing the beetle populations before considerable damage had occurred (Plank 1939, 1948a). Plank (1950b) found that infestations were correlated more with starch concentration (table 10) than moisture content or specific gravity of the wood (table 11). Susceptibility to the beetles varies along the length of the culm. The distal ends of culms are more resistant than basal parts. The susceptibility to the attack by the beetle differed among species and varieties of bamboo. In addition, susceptibility was correlated with the age of the bamboo at harvest. Plank (1950b) proposed ways to protect the wood from the beetle. White and others (1946) studied the relation between curing and durability in bamboo, *Bambusa tuldoides,* finding that even the best curing treatment resulted in 66 percent of infestation by the beetle.

Boone and others (1969) discussed chemical control of the bostrichid *Tetrapriocera longicornis* during air-drying of fenceposts. Fenceposts require drying to reach a moisture content compatible with a preservation treatment. During the drying interval, posts are attacked by the bostrichid *T. longicornis.* This bostrichid can also attack freshly felled wood.

Table 10.—*Susceptibility of 1-year-old culms of various species and varieties of bamboo to attack by the bamboo powderpost beetle compared with* Bambusa vulgaris *and the corresponding iodine-starch score at time of exposure to infestation (adapted from Plank 1950b)*

Bamboo species	Susceptibility	Average iodine-starch score
	Percent	*Number*
Bambusa vulgaris	100.0	78.7
B. vulgaris vittata	44.2	74.0
B. polymorpha	16.8	64.0
Dendrocalamus strictus (large-leafed var.)	9.6	18.0
B. tuldoides	9.0	37.0
D. membranaceous	9.0	32.0
D. giganteus	6.7	35.0
B. longispiculata	6.2	26.0
B. tulda	4.9	26.5
*B. tulda**	2.4	35.0
Sinocalamus oldhami	1.5	18.0
B. textilis	0.3	12.0

*Variety P.I. No. 74413.

Table 11.—*Moisture content and specific gravity of wood in 1-year-old culms of various species and varieties of bamboo at the time of exposure to infestation, with corresponding number of powderpost beetle attacks (adapted from Plank 1950b)*

Bamboo species	Average* moisture content	Average specific gravity	Average attacks per 60 test pieces
	Percent	*g/cm³*	*Number*
Bambusa textilis	53.6	0.727	2.5
B. longispiculata	68.4	0.675	57.5
Dendrocalamus membranaceous	76.4	0.634	83.0
B. vulgaris vittata	77.8	0.626	408.0
B. vulgaris	79.5	0.615	1,174.8
B. tulda	80.4	0.634	76.3
D. strictus (large-leafed var.)	83.1	0.608	75.0
B. tuldoides	85.7	0.586	123.3
B. polymorpha	88.3	0.588	300.0
B. tulda†	95.1	0.557	42.0
Sinocalamus oldhami	102.9	0.528	12.0
D. giganteus	123.2	0.463	119.5

*Because moisture content is expressed as a percentage of the weight of the ovendry wood, it is possible for this percentage to be 100 or greater.

†Variety P.I. 74413.

Lyctidae (powderpost beetles). – Beetles of the Lyctidae family attack seasoned timber (preferring a moisture content of 10 to 18 percent), the pith of vines, and the dried roots of herbaceous plants (Dillon and Dillon 1972). The lyctid, *Trogoxylum aequale,* was reported to attack the sapwood but to spare the heartwood of furniture made of West Indies mahogany, *Swietenia mahogani* (Wolcott 1948b).

Two species of the Lyctidae family were reported to infest cut culms of bamboo, but the damage done was relatively minor (Plank 1948a).

Order Hymenoptera (ants, bees, wasps, and allies)

Eumenidae (mason and potter wasps). – Wasps of the genus *Zethus* are frequently attracted to flowers. They use old insect burrows in twigs or wood for nesting (Bohart and Stange 1965). Larvae of the wasps feed on caterpillars deposited in the nest by the reproductive female. These wasps do not use mud to line the nest tunnels (Bohart and Stange 1965, Wolcott 1948d). In Puerto Rico, the eumenid wasp, *Zethus rufinodis,* apparently causes damage by burrowing in fenceposts made of different kinds of woods (Martorell 1941).

Order Isoptera (termites)

There are 17 termite species in Puerto Rico, and 4 are economically important. These are *Nasutitermes costalis,* the dry-wood termite, *Cryptotermes brevis,* and the subterranean termites, *Heterotermes tenuis* and *H. convexinotatus* (Wolcott 1921, 1939, 1946c). *Nasutitermes costalis* builds arboreal nests that are easily seen and destroyed, either mechanically or chemically. *Nasutitermes costalis* requires subterranean sources of water in addition to water obtained from dead branches. The termite will perish if the ground water supply fails (Wolcott 1954). It is mainly a rural dweller that can destroy fenceposts and other wooden structures.

The subterranean termites (*Heterotermes* spp.) may occur anywhere in Puerto Rico, and the geographical area of infestation appears to be increasing. The historical concentration of subterranean termites was in the cities. These species do not build visible nests, and for that reason they are difficult to control. Species of *Heterotermes* feed on both topwood and roots and can penetrate concrete houses through cracks in the floor or through pieces of wood that contact the soil (Wolcott 1939, 1954). *Heterotermes tenuis* was considered the most destructive of the subterranean termites in much of the New World Tropics. In Trinidad, *H. tenuis* was reported to attack all dead wood in contact with the soil within a few months (Brooks and others 1941).

The dry-wood termite, *C. brevis,* is able to obtain all required moisture from dry wood. *Cryptotermes brevis* does not appear to live in the ground at any point of its existence, and it usually does not live outside buildings. Only the heartwood of West Indies mahogany, *Swietenia mahogani, is* resistant to *C. brevis;* but even this wood may be eaten to a slight extent (Wolcott 1940b). Philippine mahogany, *Shorea negrosensis;* African mahogany, *Khaya ivorensis;* and even Honduras mahogany, *Swietenia macrophylla,* are damaged by *C. brevis* (Wolcott 1954). Termite resistance of *S. macropylla* heartwood is comparable to the resistance of *S. mahogani* sapwood, which is relatively low (Wolcott 1948e, 1950).

The defenses of wood against termites involve toxic or repellent chemicals, adverse physical characteristics, moisture content, nutrient imbalance or lack of specific growth factors needed by the insects, and microbial associations present in the wood (La Fage and Nutting 1978, Waller 1988). These factors vary inter- and intraspecifically (e.g., a log may contain palatable wood near unacceptable wood). In addition, the termites may respond to these defenses in a hierarchical fashion such that wood may be accepted or rejected depending on other available food. Woods detrimental to protozoans living in the hind gut of termites can be eaten if beneficial woods are also available. Workers that have lost their protozoans can be reinoculated by their nestmates (Waller 1988). Age, degree of seasoning, fungal damage, weathering, and even peculiarities of individual trees also affect termite attack (Brooks and others 1941).

The extractable organic compounds deposited in the heartwood during its transformation from the sapwood generally are more important contributors to the natural resistance of wood than are inorganic constituents or physical factors, such as wood density and degree of cellulose crystallinity. Due to the mechanical nature of termite attack on wood, density probably plays some initial protecting role, since harder woods are more difficult to fragment by termite mandibles. For woods with low density, antitermitic substances must constitute the major line of defense (Bultman and Southwell 1976). The natural resistance of wood to termites tends to decrease with time. The following mechanisms have been proposed to explain this tendency: oxidative enzymes of host origin detoxify the protectant, auto-oxidation of the protectant, microbial or fungal degradation, or leaching of the protectant over the years (Bultman and Southwell 1976).

Wolcott's work (1921, 1924, 1939, 1940c, 1943a, 1945a, 1946a, 1946b, 1946c, 1947, 1948e, 1950) is often cited in publications dealing with wood resistance to termites (e.g., Little and Wasdworth 1964, Longwood 1971, Weaver 1988). Nonetheless, his work deals mostly with the dry-wood termite, *C. brevis.* There is some discussion by Wolcott on the habits of *N. costalis* and *Heterotermes* spp., but his research on wood resistance to termite attack applies only to *C. brevis.*

Wolcott's (1943a, 1945a, 1946c, 1947) experiments on termite repellents have several drawbacks. Among them: lack of replications (sample size is one), use of several treatments in the same experimental petri dishes, and use of the same termites in subsequent experiments. The use of several experimental treatments in the same petri dish could create interactions that could affect the results of the experiments. In the case of use of termites from previous tests, the results could be affected by previous exposure of the termites to chemical substances. McMahan (1966) found that conditioning in *C. brevis* affects food selection. Termites preferred poplar, on which they had been previously fed, instead of maple, to which they were unaccustomed, though maple was preferred over poplar when the termites had not been conditioned.

Wolcott (1924, 1940b, 1946b, 1948e, 1950) elaborated lists of the comparative resistance of several woods to the attack of the dry-wood termite, *C. brevis*. The information on these lists can only be used in a qualitative manner. Because of sample size, none of Wolcott's papers presented estimates of mean resistance and variance to termite attack. In many of his experiments, the results on wood preference by *C. brevis* were contradictory (see Wolcott 1924). Wolcott (1940b) tried to explain the inconsistency of his experimental results and recognized that "the positions assigned in the list for each wood are relative only to some of the other woods, and not absolute for each of the other woods." The contradictions were often easily dismissed as can be seen in the following explanation: "While one cannot be sure that all of the samples used in either of these series of tests were typical of the species, the error due to this factor is naturally less in woods of most uniform composition." Also, wood samples used in his experiments were of straight grain, without knotholes or other imperfections, to avoid usual or exceptional points of attack by the termites (Wolcott 1940b). The presence of these factors could facilitate termite attack under normal circumstances, affecting the ranking of woods in terms of resistance to the dry-wood termite. These factors have to be taken into account in practical situations to assess the resistance of different woods to termite attack.

In order to evaluate Wolcott's experiments and others dealing with wood preferences of termites, it is important to recognize other factors that could affect their food selection. Fungi may attract termites and stimulate wood consumption. Decay caused by some fungi can improve the nutritional conditions of wood for the termites. Also, some fungi can break down inhibitory compounds in the wood, rendering it suitable as food for termites (Becker 1975, Carter 1975, Wood 1978). For example, the termite *Coptotermes niger* lives in the heartwood of standing pino hondureño, *Pinus caribaea*, only if the heartwood has been attacked by the fungus *Lentinus pallidus*. The resins and turpentine, repellent and toxic to *C. niger*, are broken down by *L. pallidus* (Williams 1965). The improvement in nutritional value of the wood after fungal attack is probably based on the increase in protein, vitamins, and other substances. Some termite species survive better in wood decayed by fungi than in undecayed wood (Becker 1975, Breznak 1982, Carter 1975). Nonetheless, some fungi have harmful effects (repellent or toxic) on termites (Becker 1975). Sands (1969) found that adaptation of the termites to special fungi in their diet can influence their response in comparative nutrition tests. The importance of choice tests in termite wood preference studies is demonstrated by Waller (1988). Waller found that less-preferred woods were eaten in large amounts in nonchoice tests, and the woods appeared favorable for the termites and their protozoans symbionts. Food selection is affected by the availability of the various food sources, so that in the absence of the preferred food alternatives, other sources may be exploited (Lepage 1974, Wood 1978). Lastly, it is important to have appropriate controls in feeding preference studies. Usually, samples from the colonized wood are used as a control (Carter 1975).

Brooks and others (1941) studied the resistance of untreated wood to termites in Trinidad. *Heterotermes tenuis* and *N. costalis*, two of the most damaging termites according to their experiments, are present in Puerto Rico. Ten-year old teak, *Tectona grandis*, which is supposedly very resistant to termite attack, was easily attacked. Under their experimental conditions (favorable to fungi that attack wet wood), fungi attack was responsible for more damage than termite attack, although very large populations of *Heterotermes* spp. developed during the first 6 months of the experiments. They did not find that termite attack was favored by fungal attack or that penetration of fungi was greatly accelerated by the inroads of termites.

Marchan (1946) gave information on the concentration of lignin in wood from different species and the degree of susceptibility to the attack by the dry-wood termite, *C. brevis*. Although Marchan did not conduct any statistical analyses on the data, it appears that the species most resistant to the dry-wood termite tend to exhibit high lignin content. However, Wolcott (1940b) did not think that lignin is a predictor of wood resistance to *C. brevis* attack.

The preservative treatments and service life of fenceposts of several species are discussed in the publications of Angleró (1963), Chudnoff and Goytía (1971, 1972), Englerth (1960), Maldonado (1962), Ortíz (1963), and Tropical Forest Experiment Station (1952, 1953, 1958). Density was not a predictor of fencepost service life (Englerth 1960). Average service life of untreated fenceposts is about 1.5 years. The longer life for some species can be attributed to the presence of a large volume of heartwood (Chudnoff and Goytía 1972). Additional information on timber durabilities can be found in Longwood (1971).

Fungi and termites are the principal damaging agents of fenceposts. Decay fungi were responsible for most of the deterioration of posts (Englerth 1960). There is a tendency for termites to be more important as fencepost-damaging agents in the dry forests and for fungi to be more important in highland wet forests (Chudnoff and Goytía 1972). Bultman and Southwell (1976) also found that in Panamanian humid forests, fungi were more important agents of decay than termites. Nonetheless, Bultman and Southwell found that wood attacked by termites decomposed faster than wood attacked by fungi.

Termites of the genus *Nasutitermes,* such as *N. corniger,* fix nitrogen at a rate that, in theory, could provide all the nitrogen for one to two doublings of the colony per year. This could explain the ability of some termite species to live in wood with low amounts of nitrogen. Termites are also very efficient at recycling nutrients, which can also explain these responses. They eat dead and unhealthy nestmates and, with the help of symbiotic bacteria, can recycle uric acid to obtain nitrogen (Breznak 1982). Termites are so efficient at recycling that some species do not even discard their feces; they use them for the construction of nests and tunnels (Wood 1976). The ecological implications of these findings are yet to be explored in the Luquillo Mountains.

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Appendixes

Appendix A.—Forest and Plantation Trees and Their Associated or Potential Insect Pests[*]

Tree species	Insect pest	Order[†]	Parts attacked
Andira inermis	*Diaprepes abbreviatus*	Col.	Leaves
	Megalopyge krugii	Lep.	Leaves
	Phostria originalis	Lep.	Leaves
	Platypus rugulosus	Col.	Limbs (borer)
	Saissetia oleae	Hom.	Twigs, branches
	Xyleborus ferrugineus	Col.	Bark
Anthocephalus chinensis	*Selenothrips rubrocinctus*	Thy.	Leaves
Araucaria cunninghamii	*Octaspidiotus araucariae*	Hom.	Twigs
Bambusa spp.	*Asterolecanium bambusae*	Hom.	Culms
	Asterolecanium miliaris	Hom.	Leaves
	Dinoderus minutus	Col.	Culms (borer)
Bixa orellana	*Apate monacha*	Col.	Wood (borer)
Buchenavia capitata	Lepidoptera	Lep.	Mesocarp
	Nitidulidae	Col.	Mesocarp
	Xyleborus volvulus	Col.	Bark
Byrsonima coriacea	*Hypothenemus eruditus*	Col.	Dead pole
	Megalopyge krugii	Lep.	Leaves
Casuarina equisetifolia	*Apate monacha*	Col.	Wood (borer)
	Diphthera festiva	Lep.	Trunk (borer)
	Formicidae	Hym.	Seeds
	Icerya purchasii	Hom.	Leaves
Cecropia peltata	Nitidulidae	Col.	Seeds
	Syllepte silicalis	Lep.	Leaves
Cedrela odorata	*Ambrosiodmus lecontei*	Col.	Dead branches
	Apate monacha	Col.	Wood (borer)
	Diaprepes abbreviatus	Col.	Leaves
	Dikrella cedrelae	Hom.	Leaves
	Pulvinaria psiddii	Hom.	Branches, trunks
Ceiba pentandra	*Diaprepes abbreviatus*	Col.	Leaves
	Dysdercus andreae	Hem.	Seeds
Cinchona spp.	*Pseudaulacaspis pentagona*	Hom.	. . . .[‡]
Citharexylum fruticosum	*Epicoris oedipodalis*	Lep.	Leaves
Coccoloba pubescens	*Schizocerina krugii*	Hym.	Leaves
Cordia alliodora	*Dictyla monotropidia*	Hem.	Leaves
	Omalegra cordiae	Hom.	Leaves
Cupania americana	*Asterolecanium pustulans*	Hom.	Leaves
Dacryodes excelsa	*Ambrosiodmus lecontei*	Col.	Logs
	Monarthrum sp.	Col.	Logs
	Platypus compositus	Col.	Logs (borer)
	Platypus rugulosus	Col.	Logs (borer)
Delonix regia	*Apate monacha*	Col.	Wood (borer)
	Hypothenemus obscurus	Col.	Dead branch
	Melipotis acantioides	Lep.	Leaves
	Megalopyge kruggii	Lep.	Leaves
	Semiothis diffusata	Lep.	Leaves
Didymopanax morototoni	*Phyllophaga portoricensis*	Col.	Leaves
Erythrina fusca	*Terastia meticulosalis*	Lep.	Twigs, pods
Erythrina poeppigiana	*Xyleborus ferrugineus*	Col.	Dead wood
Erythrina spp.	*Agathodes designalis*	Lep.	Leaves, twigs
	Terastia meticulosalis	Lep.	Twigs, pods
Eucalyptus robusta	*Spodoptera frugiperda*	Lep.	Leaves

Appendix A.—Forest and Plantation Trees and Their Associated or Potential Insect Pests* —Continued

Tree species	Insect pest	Order†	Parts attacked
Syzygium jambos	*Anastrepha suspensa*	Dip.	Fruits
	Apate monacha	Col.	Wood (borer)
	Myrmelachista ramulorum	Hym.	Twigs
Fraxinus uhdei	*Pseudaulacaspis pentagona*	Hom.	Trunk
Grevillea robusta	*Asterolecanium pustulans*	Hom.	Leaves
Guarea guidonia	*Hypothenemus trinitatis*	Col.	Dead branches
	Ischnaspis longirostris	Hom.	Leaves
Hernandia sonora	*Dictyla monotropidia*	Hem.	Leaves
Heterotrichum cymosum	*Blepharomastix ebulealis*	Lep.	Leaves
Hibiscus elatus	*Pseudaulacaspis pentagona*	Hom.	....
Hymenaea courbaril	*Hypothenemus obscurus*	Col.	Seed pods
Inga fagifolia	*Megalopyge kruggii*	Lep.	Leaves
	Myrmelachista ramulorum	Hym.	Twigs
	Platypus ratzeburgi	Col.	Bark
	Xyleborus affinis	Col.	Wood (borer)
Inga quaternata	*Myrmelachista ramulorum*	Hym.	Twigs
Inga vera	*Agathodes designalis*	Lep.	Twigs (borer)
	Apate monacha	Col.	Wood (borer)
	Myrmelachista ramulorum	Hym.	Twigs
	Platypus excisus	Col.	Logs
	Platypus ratzeburgi	Col.	Logs, trunk
	Tetralopha scabridella	Lep.	Leaves
	Xyleborus affinis	Col.	Wood (borer)
Chionanthus domingensis	*Apate monacha*	Col.	Wood (borer)
Mammea americana	*Poecilips sp.*	Col.	Seeds
Mangifera indica	*Anastrepha obliqua*	Dip.	Fruits
	Xyleborus xylographus	Col.	Wood (borer)
Ochroma lagopus	*Oiketicus kirbyi*	Lep.	Leaves
Petitia domingensis	*Hyblaea puera*	Lep.	Leaves
	Pilocrosis secernalis	Lep.	Leaves
Picramnia pentandra	*Apate monacha*	Col.	Wood (borer)
Prestoea montana	*Cocotrypes carpophagus*	Col.	Seeds
	Homaledra sabalella	Lep.	Leaves
Prunus occidentalis	*Anastrepha suspensa*	Dip.	Fruits
	Diaprepes abbreviatus	Col.	Seedling leaves
	Pseudaulacaspis pentagona	Hom.	....
Psidium guajava	*Anastrepha suspensa*	Dip.	Fruits
	Hypothenemus crudiae	Col.	Dry fruits
	Hypothenemus obscurus	Col.	Dry fruits
	Hypothenenus seriatus	Col.	Dry fruits
	Xyleborus affinis	Col.	Fruits
Roystonea borinquena	*Phyllophaga vandinei*	Col.	Leaves
Spondias dulcis	*Anastrepha suspensa*	Dip.	Fruits
Swietenia macrophylla	*Diaprepres abbreviatus*	Col.	Leaves, roots
	Hypsipyla grandella	Lep.	Stems (borer)
	Ischnaspis longirostris	Hom.	Leaves
	Phyllophaga vandinei	Col.	Leaves
	Xylosandrus compactus	Col.	Wood (borer)
Swietenia mahogani	*Apate monacha*	Col.	Wood (borer)
	Polycesta porcata	Col.	Cambium, Heartwood
Swietenia spp.	*Trogoxylon aequale*	Col.	Sapwood

Appendix A.—Forest and Plantation Trees and Their Associated or Potential Insect Pests*—Continued

Tree species	Insect pest	Order†	Parts attacked
Tabebuia heterophylla	*Eulepte concordalis*	Lep.	Leaves
	Pachymorphus subductellus	Lep.	Twigs (borer)
	Rabela tabebuiae	Hom.	Leaves
Tabebuia rigida	*Eulepte concordalis*	Lep.	Leaves
	Pachymorphus subductellus	Lep.	Twigs (borer)
Tamarindus indica	*Apate monacha*	Col.	Wood (borer)
	Hypothenemus obscurus	Col.	Seed pods
Terminalia catappa	*Hypothenemus obscurus*	Col.	Fruits
	Oiketicus kirbyi	Lep.	Leaves
	Selenothrips rubrocinctus	Thy.	Leaves
Tetragastris balsamifera	*Hypothenemus eruditus*	Col.	Dry twigs
Thespesia grandiflora	*Asterolecanium pustulans*	Hom.	Leaves
	Dysdercus andreae	Hem.	Seeds
	Dysdercus sanguinarius	Hem.	Seeds
	Hypothenemus sp.	Col.	Seed pods
	Pectinophora gossypiella	Lep.	Seed pods
Thespesia populnea	*Hypothenemus eruditus*	Col.	Seed pods
	Pectinophora gossypiella	Lep.	Seed pods
Toona ciliata	*Pseudaulacaspis pentagona*	Hom.	Trunk
Trema lamarckianum	*Pseudaulacaspis pentagona*	Hom.	Trunk, branches

*See Martorell (1976) for a more complete list.

†Col. = Coleoptera; Dip. = Diptera; Hem. = Hemiptera; Hom. = Homoptera; Lep. = Lepidoptera; Hym. = Hymenoptera; Thy. = Thysanoptera.

‡Unrecorded.

Appendix B.—List of Important Entomological Studies in the Luquillo Mountains, Puerto Rico (complete citations are given in the literature cited section)

Author	Year of publication	Topic
Arendt, W. J.	1985a, 1985b	Bird parasitism
Benedict, F. F.	1976	Insect herbivory
Chudnoff, M; Goytía, E.	1972	Service life of fenceposts
Drewry, G. E.	1970	List of insects from El Verde
García, J.	1938	Fresh water insects
Hlavac, T. F.	1969	Carabidae morphology and evolution
Janzen, D. H.	1973a	General information on tropical insects
Lavigne, R. J.	1977	Ants of Luquillo Forest
Lavigne, R. J; Drewry, G.	1970	Feeding habits of frogs and lizards
Lister, B. C.	1981	Lizard insect food
Martorell, L. F.	1976	Food catalog of the insects of Puerto Rico
Matthews, E. G.	1965, 1966	Scarab beetles of the Luquillo Mountains
Nevling, L. I.	1971	Insect pollination
Nichols, S. W.	1988	Carabidae biogeography
Plank, H. K.	1948b	Rhinocerus beetles
Plank, H. K.	1950a	Insecticidal properties of plants
Weaver, P. L; Bauer, G. P.	1986	Shoot borer in mahogany
Wetmore, A.	1916	Insect bird predation
Wolcott, G. N.	1940c, 1946a	Wood termite resistance
Wolcott, G. N.	1948a, 1948b 1948c, 1948d	Insects of Puerto Rico

Appendix C.—Additional References

Alexander, C.P. 1932. The crane-flies of Puerto Rico (Diptera). Journal of the Department of Agriculture of Puerto Rico. 16(4): 347–387.

Describes several endemic crane-fly species of the Luquillo Mountains and suggests that there may be additional new species of Tipulidae confined to the Luquillo Mountains. Discussion of the possible origin of the Puerto Rican crane-flies and descriptions that aid in the species identification are also included.

Barber, H.G. 1939. Insects of Porto Rico and the Virgin Islands—Hemiptera-Heteroptera (excepting the Miridae and Corixidae). New York Academy of Sciences Scientific Survey of Puerto Rico and the Virgin Islands. 14(3): 263–441.

Information about families, subfamilies, and keys to the genera and species of Hemiptera.

Bell, R.T. 1970. The Rhysodini of North America, Central America, and the West Indies (Coleoptera: Carabidae or Rhysodidae). Miscellaneous Publications of the Entomological Society of America. 6: 289–324.

Descriptions of the two Rhysodini from Puerto Rico. Some notes on behavior and ecology are provided.

Bell, R.T.; Bell, J.R. 1985. Rhysodini of the world, part 4. Quaestiones Entomologicae. 21: 1–172.

Descriptions of the two Rhysodini from Puerto Rico.

Blake, D.H. 1941. New species of *Chaetocnema* and other chrysomelids (Coleoptera) from the West Indies. Proceedings of the Entomological Society of Washington. 43(8): 171–180.

This and the following publications by Blake cover the taxonomy of the chrysomelids.

Blake, D.H. 1943. New species of the genus *Hadropoda* Suffrian from the West Indies. Bulletin of the Museum Comparative Zoology. 92(8): 413–441.

Blake, D.H. 1948. Six new species of West Indian Chrysomelidae. Proceedings of the Entomological Society of Washington. 50(5): 121–127.

Blake, D.H. 1950. A new genus of flea-beetles from the West Indies. Psyche. 57(1): 10–25.

Blake, D.H. 1951. A revision of the beetles of the genus *Chalcosicya* Blake (Chrysomelidae) from the West Indies. Bulletin of the Museum Comparative Zoology. 106(7): 287–312.

Blake, D.H. 1952. Six new species of *Megistops* with keys to the known species (Coleoptera). Psyche. 59(1): 1–12.

Blake, D.H. 1953. The chrysomelid beetles of the genus *Strabala* Chevrolat. Proceedings of the United States Natural Museum. 103(3319): 121–134.

Blake, D.H. 1964. Notes on new and old species of *Alticinae* (Coleoptera) from the West Indies. Proceedings of the United States Natural Museum. 115(3477): 8–29.

Blake, D.H. 1970. A review of the beetles of the genus *Metachroma* Chevrolat (Coleoptera-Chrysomelidae). Smithsonian Contributions to Zoology. 57: 1–109.

Bohart, R.M.; Stange, L.A. 1965. A revision of the genus *Zethus Fabricius* in the Western Hemisphere. University of California Publications in Entomology. Berkeley, CA: University of California Press: 12–147.

Subspecies of *Zethus rufinodis* found in the Caribbean are discussed.

Bright, D.E. 1985. Studies on West Indian Scolytidae (Coleoptera). Entomologische Arboretum Museum George Frey. 34: 169–187.

A checklist of the West Indian scolytids.

Caldwell, J.S.; Martorell, L.F. 1950a. Review of the Auchenorhynchous Homoptera of Puerto Rico. 1: Cicadellidae. Journal of Agriculture of the University of Puerto Rico. 34(1): 1–132.

A review of the Auchenorhynchous Homoptera of Puerto Rico.

Caldwell, J.S.; Martorell, L.F. 1950b. Review of the Auchenorhynchous Homoptera of Puerto Rico. 2: The Fulgoridae except the Kinnaridae. Journal of Agriculture of the University of Puerto Rico. 34(2): 133–269.

A review of the Auchenorhynchous Homoptera of Puerto Rico.

Caldwell, J.S.; Martorell, L.F. 1951a. A brief review of the Psyllidae of Puerto Rico (Homoptera). Annals Entomological Society of America. 44(4): 603–613.

A review of the Psyllidae of Puerto Rico.

Caldwell, J.S.; Martorell, L.F. 1951b. New leafhoppers from Puerto Rico (Cicadellidae: Homoptera). Journal of Agriculture of the University of Puerto Rico. 35(2): 88–89.

A review of the new leafhoppers from Puerto Rico.

Colón, M. 1981. Contribution to the systematics of the diaspidids (Homoptera: Diaspididae). Mayagüez, PR: University of Puerto Rico. 199 p. M.S. thesis.

The taxonomy, host plants, predators, and parasites of 77 homopteran species are discussed.

Comstock, W.P. 1944. Insects of Porto Rico and the Virgin Islands—Lepidoptera (suborder) Rhopalocera (superfamily) Papilionoidea (true butterflies) (superfamily) Hesperioidea (skippers). New York Academy of Sciences Scientific Survey of Puerto Rico and the Virgin Islands. 12(4): 421–622.

Descriptions and notes on the natural history of the Puerto Rican Lepidoptera (suborder Rhopalocera).

Curran, C.H. 1928. Insects of Porto Rico and the Virgin Islands: Diptera or two-winged flies. New York

Academy of Sciences Scientific Survey of Puerto Rico and the Virgin Islands. 11(1): 3–118.

Taxonomic keys and description of species of the order Diptera including species found in the Luquillo Mountains.

Curran, C.H. 1931. First supplement to the Diptera of Puerto Rico and the Virgin Islands. American Museum Novitates. 456: 1–23.

Taxonomic keys and description of species of the order Diptera including species found in the Luquillo Mountains.

Davis, W.T. 1928. The cicadas of Puerto Rico with a description of a new genus and species. Journal of the New York Entomological Society. 36: 29–34.

A review of the cicadas of Puerto Rico.

Drake, C.J.; Maldonado, J. 1954. Puerto Rican waterstriders (Hemiptera). Proceedings of the Biological Society of Washington. 67: 219–222.

Checklist of the Puerto Rican water striders (Hebridae, Hydrometridae, Gerridae, and Veliidae). It also includes information on collecting sites. A new species of water strider on the Island is described, and it is suggested that many species remain undiscovered.

Drewry, G.E. 1969. Animal diversity. In: Jordan, C.F.; Drewry, G.E., eds. The rain forest project. Annual Rep. 129. Río Piedras, PR: Puerto Rico Nuclear Center: 107–121.

Key to the Muscidae family at El Verde (Anthomyiidae and Muscidae).

Equihua, A.; Atkinson, T.H. 1987. Catálogo de Platypodidae (Coleoptera) de Norte y Centroamérica. Folia Entomológica Méxicana. 72: 5–31.

A checklist of the Central American pin-hole borers (Platypodidae).

Fisher, W.S. 1935. New cerambycid beetles from Puerto Rico. Journal of Agriculture of the University of Puerto Rico. 19(2): 51–63.

Twelve new species of Cerambycidae from Puerto Rico are described. Additional references to Puerto Rican Cerambycidae and Buprestidae families can be found in "An annotated bibliography of Puerto Rican entomology" (Leonard 1933) and in Wolcott (1948b).

Flint, O.S. 1964. The caddisflies (Trichoptera) of Puerto Rico. Tech. Pap. 40. Río Piedras, PR: University of Puerto Rico, Agricultural Experiment Station: 5–80.

A taxonomical account of the caddisflies of Puerto Rico and information on the natural history of some species.

Forbes, W.T.M. 1930. Insects of Porto Rico and the Virgin Islands – Heterocera or moths (excepting the Noctuidae, Geometridae, and Pyralidae). New York Academy of Sciences Scientific Survey of Puerto Rico and the Virgin Islands. 12(1): 4–171.

A review of the taxonomy and natural history of moths (suborder Heterocera).

Forbes, W.T.M. 1931. Supplementary report on the Heterocera or moths of Porto Rico. Journal of the Department of Agriculture of Puerto Rico. 15(4): 339–394.

A review of the taxonomy and natural history of moths (suborder Heterocera).

Fox, I. 1946. A review of the species of biting midges or culicoides from the Caribbean region. Annals of the Entomological Society of America. 39(2): 248–258.

Taxonomic keys to the females and geographical distributions of species of biting midges or culicoides.

Fox, I. 1957. The insect family Japygidae (Order Thysanura) in Puerto Rico. Journal of Agriculture of the University of Puerto Rico. 41(1): 35–37.

Discussion on the Japygidae family in Puerto Rico.

García, J. 1938. An ecological survey of the fresh water insects of Puerto Rico. Journal of Agriculture of the University of Puerto Rico. 22(1): 43–97.

Mayflies (order Ephemeroptera) are reported as uncommon in the lowlands, but numerous along the creeks in the higher areas.

Garrison, R.W. 1986. *Diceratobasis melanogaster* Spec. Nov., a new damsel-fly from the Dominican Republic (Zygoptera: Coenagrionidae) with taxonomic and distributional notes on the Odonata of Hispaniola and Puerto Rico. Odonatologica. 15(1): 61–67.

Seven new records from Puerto Rico are reported, increasing the number of known Odonata species to 49. A key for most neotropical coenagrionids lacking postocular spots is included.

Grimaldi, D.A. 1988. Relicts in the Drosophilidae (Diptera). In: Liebherr, J.K., ed. Zoogeography of Caribbean insects. Ithaca, NY: Cornell University Press: 183–213.

A list of the endemic species of Antillean Drosophilidae. Many records from the Luquillo Mountains are included. *Drosophila carcinophila* larvae feed on the exudate in nephric grooves of the black land crab, *Gecarcinus ruricula,* at El Yunque.

Klots, E.B. 1932. Insects of Puerto Rico and the Virgin Islands: Odonata or dragon flies. New York Academy of Sciences Scientific Survey of Puerto Rico and the Virgin Islands. 14(1): 3–107.

Descriptions of and keys to the species of dragonflies of Puerto Rico.

Leonard, M.D. 1933. An annotated bibliography of Puerto Rican entomology. Journal of the Department of Agriculture of Puerto Rico. 17(1): 5–96.

References to former taxonomic works for Puerto Rican entomology.

Liebherr, J.K. 1986. *Barylaus,* new genus (Coleoptera: Carabidae) endemic to the West Indies with Old World affinities. Journal New York Entomological Society. 94(1): 83–97.

The new genus was erected based on two species:

Colpodes estriatus from Puerto Rico and *C. puncticeps* from the Dominican Republic.

Liebherr, J.K., ed. 1988. Zoogeography of Caribbean insects. Ithaca, NY: Cornell University Press. 285 p.

Publications on the zoogeography of the following groups: Lygaeidae (Hemiptera), Auchenorrhynchous Homoptera, Carabidae (Coleoptera), Polycentropodidae (Trichoptera), Drosophilidae (Diptera), Formicidae (Hymenoptera), and Halictidae (Hymenoptera).

Maldonado, J. 1969. The Miridae of Puerto Rico (Insecta, Hemiptera). Tech. Pap. 45. Río Piedras, PR: University of Puerto Rico, Agricultural Experiment Station. 133 p.

The first systematic study of the Puerto Rican Miridae, which includes discussion on the species from the Luquillo Mountains. Description of each genus is given. Keys to the neotropical species (if the number of species is not large) are provided. Otherwise, a key to the Puerto Rican species is included.

Maldonado, J. 1980. The genus *Jorbetus* Distant, 1884 (Hemiptera: Miridae: Orthotylinae). Journal of Agriculture of the University of Puerto Rico. 64(3): 304–309.

Revision of the genus *Jobertus,* including *J. gracilentus,* collected in the Luquillo Mountains.

Maldonado, J.; Navarro, C.A. 1967. Additions and corrections to Wolcott's "Insects of Puerto Rico." Caribbean Journal of Science. 7: 45–64.

The approximate number of insects found in Puerto Rico is indicated and the presence of the order Zoraptera on the island is reported. The zorapterans were collected in a rotting log in the Luquillo Mountains. The order Zoraptera is mostly found in tropical regions and contains approximately 25 described species.

Mari, J.A. 1976. The genera of Collembola (Insecta) in Puerto Rico: keys, diagnosis, and general comments. Journal of Agriculture of the University of Puerto Rico. 60(1): 113–128.

Keys for the Collembola families and genera of Puerto Rico. The keys and diagnostic criteria are elaborated for the nonspecialist.

Mari, J.A. 1987. Puerto Rican species of Paronellidae (Insecta: Collembola). Caribbean Journal of Science. 23: 400–416.

A discussion of the members of the Paronellidae. Additional species of the genera *Dicranocentruga* may be discovered by additional collecting in the Luquillo Mountains.

Medina, S. 1961. The Thysanoptera of Puerto Rico. Tech. Pap. 32. Río Piedras, PR: University of Puerto Rico, Agricultural Experiment Station. 159 p.

Keys to families, genera, and species for the Thysanoptera of Puerto Rico.

Medina, S. 1978. The Muscidae (Diptera) of Puerto Rico. Iowa State University. 308 p. Ph.D. thesis.

Keys to subfamilies, genera, and species of Muscidae (sensu lato) of Puerto Rico, describing several species from the Luquillo Mountains.

Medina, S.; Martorell, L.F. 1973. New insect records for Puerto Rico. Journal of Agriculture of the University of Puerto Rico. 57 (3): 247–254.

This paper complements Maldonado and Navarro (1967).

Miller, L.D.; Miller, J.Y. 1989. The biogeography of West Indian butterflies (Lepidoptera: Papilionoidea, Hesperioidea): a vicariance model. In: Woods, C.A., ed. Biogeography of the West Indies: past, present and future. Gainesville, FL: Sandhill Crane Press: 229–262.

A combination of vicariance/dispersal model for the evolution of the Antillean butterfly fauna is presented.

Moxey, C.F. 1972. The stick-insects (Phasmatodea) of the West Indies – their systematics and biology. Cambridge, MA: Harvard University. 211 p. Ph.D. thesis.

The most recent publication dealing with Puerto Rican walking stick taxonomy.

Needham, J.G. 1941. Life history notes on some West Indian coenagrionine dragonflies (Odonata). Journal of Agriculture of the University of Puerto Rico. 25 (3): 1–19.

Information on the life history of four genera of damselflies in the West Indies. Also contains keys to the adults and nymphs, but without reference to collection localities from the Luquillo Mountains.

Nosek, J. 1978. Protura: a new insect order record for Puerto Rico with description of new species. Journal of Agriculture of the University of Puerto Rico. 62(2): 133–138.

A new insect order for Puerto Rico.

Osborn, H. 1935. Insects of Porto Rico and the Virgin Islands: Homoptera (excepting the Sternorhynchi). New York Academy of Sciences Scientific Survey of Puerto Rico and the Virgin Islands. 14(2): 111–260.

Information on host plants, economic importance, and the effects of tropical storms on Homoptera abundance. Also contains taxonomic keys and information on natural history for some species.

Ramos, J.A. 1957. A review of the Auchenorhynchous Homoptera of Puerto Rico. Journal of Agriculture of the University of Puerto Rico. 41(1): 38–117.

Review of the families Kinnaridae, Cercopidae, Membracidae, and Cicadidae. Taxonomic keys for the identification of species, notes on the distribution, abundance, and host plants are provided. This work complements the works on the Cicadellidae, Psyllidae, and Fulgoroidea conducted by Caldwell and Martorell (1950a, 1950b, 1951a, 1951b).

Ramos, S.J. 1982. Checklist of the butterflies of Puerto

Rico (Lepidoptera, Rhopalocera, West Indies). Caribbean Journal of Science. 17: 59–68.

A checklist of the butterflies of Puerto Rico.

Riley, N.D. 1975. A field guide to the butterflies of the West Indies. New York: Demeter Press. 224 p.

Information on the life history and distribution of Puerto Rican butterflies.

Ruíz, M.J. 1989. Revisión del género *Penichrophorus* Richter (Homoptera: Membracidae, Cerescini). Mayagüez, PR: University of Puerto Rico. 104 p. M.S. thesis.

A review of the genus *Penichrophorus* (Homoptera: Membracidae).

Schauss, W. 1940. Insects of Porto Rico and the Virgin Islands. Moths of the family Noctuidae. New York Academy of Sciences Scientific Survey of Puerto Rico and the Virgin Islands. 12(2-3): 177–417.

Description of the moths of the family Noctuidae.

Selander, R.B.; Bouseman, J.K. 1960. Meloid beetles (Coleoptera) of the West Indies. Proceedings of the United States Natural Museum. 111(3428): 197–226.

Comments on the scarcity of this family in the West Indies and the origin of the Caribbean meloids. Meloidae larvae are parasitic on grasshopper egg pods and the contents of nesting cells of wild bees. They are generally phytophagous as adults. Because of the complexity of their ecology, the Meloidae face problems of dispersal, and it is expected that they will be poorly represented in areas having a prolonged history of isolation. Selander and Bouseman postulated that phoresy (especially on bees) was a prerequisite to successful colonization of meloid beetles on the Caribbean islands.

Selander, R.B.; Bouseman, J.K. 1961. Supplementary records of meloid beetles (Coleoptera) of the West Indies. Entomological News. 72(7): 190–191.

Records of meloid beetles in the West Indies.

Smith, C.F. 1970. Notes on the genus *Picturaphis* and related genera with a new species of *Picturaphis* from Puerto Rico (Aphididae: Homoptera). Journal of Agriculture of the University of Puerto Rico. 54(4): 683–688.

Description of a new species of *Picturaphis* from the Luquillo Mountains.

Smith, D.R.; Lavigne, R.J. 1973. Two new species of ants of the genera *Tapinoma* Forester and *Paratrechina* Motschoulsky from Puerto Rico (Hymenoptera: Formicidae). Proceedings of the Entomological Society of Washington. 75(2): 181–187.

Description of *Paratrechina cisipa* as a new species based on material collected near El Verde.

Smith, M.R. 1936. The ants of Puerto Rico. Journal of Agriculture of the University of Puerto Rico. 20(4): 819–875.

Keys to the Puerto Rican ants and notes on the natural history of the species.

Snelling, Roy R. 1986. New synonymy in Caribbean ants of the genus *Leptothorax* (Hymenoptera: Formicidae). Proceedings of the Entomological Society of Washington. 88(1): 154–156.

Review of the genus *Lepthotorax* found in the Luquillo Mountains.

Snyder, F.M. 1957. Puerto Rican *Neodexiopsis* (Diptera: Muscidae: Coenosiinae). Journal of Agriculture of the University of Puerto Rico. 41(3): 207–229.

Description of flies of the genus *Neodexiopsis,* which are limited to the higher elevations of the island of Puerto Rico. The majority of the holotypes for the descriptions of 10 new species came from the Luquillo Mountains.

Soto, F.N. 1988. Nuevos dicirtumídos de Puerto Rico (Insecta: Collembola: Dicyrtomidae): New Dicyrtomidae species from Puerto Rico (Insecta: Collembola: Dicyrtomidae). Caribbean Journal of Science. 24: 60–70.

Four additional Collembola species for Puerto Rico are reported.

Steyskal, G.C. 1973. The Clusiidae of Puerto Rico and the Virgin Islands (Diptera). Studia Entomologica. 16(1–4): 439–444.

Description of and general information on the family Clusiidae in Puerto Rico.

Telford, H.S. 1973. The Syrphidae of Puerto Rico. Journal of Agriculture of the University of Puerto Rico. 57(3): 217–246.

A taxonomic review of the Syrphidae. Also includes keys, illustrations of some species, and notes on the natural history of the group.

Travers, J.R. 1938. Mayflies of Puerto Rico. Journal of Agriculture of the University of Puerto Rico. 22(1): 5–42.

Keys to the mayflies of Puerto Rico (for both adults and nymphs) and descriptions of new Puerto Rican species. Many of the specimens collected by Travers were from the Luquillo Mountains.

Tulloch, G.S. 1937. The mosquitoes of Puerto Rico. Journal of Agriculture of the University of Puerto Rico. 21(4): 137–167.

Information on the natural history and economic importance of Puerto Rican mosquitoes (Culicidae). Health problems caused by mosquitoes are discussed. Taxonomic keys are presented.

Wheeler, M.R.; Takada, H. 1963. A revision of the American species of *Mycodrosophila* (Diptera: Drosophilidae). Annals of the Entomological Society of America. 56(3): 392–399.

Revision of the genus *Mycodrosophila* describing new species. Includes records from the Luquillo Mountains.

*U.S.GPO:1994-565-016/00012

Torres, Juan A. 1994. Insects of the Luquillo Mountains, Puerto Rico. Gen. Tech. Rep. SO-105. New Orleans, LA: U.S. Department of Agriculture, Forest Service, Southern Forest Experiment Station. 53 p.

The literature on forest entomology in the Luquillo Mountains is reviewed, and information on basic insect ecology, insect pests, and systematics is provided.

Keywords: Bark beetles, herbivorous, termites, tropical forests, wood.