HILGARDIA

A Journal of Agricultural Science Published by the California Agricultural Experiment Station

VOLUME 16 JULY, 1944 NUMBER 4

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UNIVERSITY OF CALIFORNIA · BERKELEY, CALIFORNIA

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NATURAL SOURCES, HABITATS, AND RESERVOIRS OF INSECTS ASSOCIATED WITH STORED FOOD PRODUCTS[1]

E. GORTON LINSLEY[2, 3]

INSECTS have long infested man's household and his stored food products, as is evidenced by their presence in Egyptian tombs (Alfieri, 1931)[4] and by references in the Bible (Marlatt, 1896). Yet their place and mode of origin are not well known—an unfortunate fact, since the natural habitats may provide a clue to sources of infestations and other matters of economic import. Apparently no serious attempts have been made to account on this basis for more than a few of the numerous species that infest stored products. (See Marlatt, 1896; Good, 1933; Linsley, 1942*a*; Hatch, 1942; Hinton, 1943*b*.) Hatch, in a discussion of the habitat and distribution of some of the more important stored-grain pests, emphasizes the ecological aspects of the problem:

> The entomologist .... sees in these creatures not pests that are competing with humans for the product of their agricultural labors. Rather he finds in them a group of beetles and moths and other insects that at the time when man began the cultivation of wheat had evolved in such a fashion that they fit in with the sort of conditions furnished by the storage and processing of grain. The grain elevator, the flour mill, the grocery store, the housewife's kitchen are simply an enormous insect habitat extending its tentacles into all portions of the wheat-consuming world. The factors governing the occurrence of insects in this vast complex constitute an ecological problem of considerable magnitude.

Entomological literature seldom records the occurrence of stored-products insects in nature. The better the species is known to the economic entomologist, the more is this likely to be true. Since the important stored-products insects are mostly cosmopolitan in distribution, the average collector ignores them and fails to record their capture. Field entomologists have likewise generally ignored them, often assuming that their presence was accidental or resulted from contamination. The present paper will bring together the records[5] available to the writer, together with personal observations, in the hope of clarifying certain problems and of stimulating further research.

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[3] The writer wishes to express his appreciation to Professor O. W. Richards of the Imperial College of Science and Technology, London, and to Dr. H. E. Hinton of the British Museum of Natural History, London, as well as to his colleagues in the Division of Entomology and Parasitology, University of California, for critically reading the manuscript, offering helpful suggestions, and supplying pertinent references.

[4] See "Literature Cited" for complete data on citations mentioned in the text by author and date of publication.

[5] Admittedly some (perhaps many) records derived from the literature may be based on misidentifications. Although this fact may sometimes affect interpretation, it will probably not materially change the conclusions: the latter are based largely on ecological considerations that apply at the generic or group level rather than at the species level. Error might also arise from inaccuracies in the current phylogenetic interpretation of the groups involved. In a few cases, conclusions based on the relatives or congeners of a particular species would perhaps be invalidated by further taxonomic study; some of the supposedly phylogenetic groupings that we now accept may yet prove to have been based on superficial characters.

Stored-products insects undoubtedly share a number of biological characteristics which have combined to bring about their wide distribution and to make them pests of mankind.

One of the most important of these characteristics appears to be a relatively wide range of tolerance for physical factors of the environment, especially moisture. Since in any given environment the extremes may be more significant than the means, these insects can probably tolerate more extreme conditions of temperature and humidity (especially moisture content of food materials) than many less widely distributed forms. Most of the important species can survive, for example, in foodstuffs with a moisture content far below the optimum for their development. Further, although these insects apparently have a broad tolerance for extremes of humidity (and frequently temperature), man maintains optimum conditions for most of the species in buildings, warehouses, and food-storage units.

Second, most stored-products insects have a wide range of food habits, and many include in their diet the majority of dry food and drug products of plant and animal origin. This food range is greater than that generally attributed to most other insects.

Third, nearly all the species involved reproduce more or less continuously under favorable environmental conditions and, with only a few notable exceptions, require no winter diapause. In addition, many of the species are long-lived in the adult stage and may live and reproduce over a period of two or three years.

Fourth, some of the most important species can survive in the adult stage for relatively long periods without food. This fact favors their accidental transportation from one part of the world to another even in the absence of suitable food materials.

Finally, the small size of most of the species may cause them to be overlooked. Frequently their presence remains undetected until a large population has been built up.

HABITS OF SPECIES IN RELATION TO POSSIBLE SOURCES AND RESERVOIRS

ACARINA

Acaridae.—With the exception of the predaceous and parasitic families (Cheyletidae, Parasitidae, Tarsonemidae, Pediculoididae), most mites associated with stored products are phytophagous. Probably some of these are to be classed as plant scavengers, since they are related to forms which live on corms, roots, and bulbs of living plants. Most of the species, however, are more abundant on stored products when these materials are damp and moldy. This suggests that they feed wholly or partly on molds and other fungi. Several species of *Tyrophagus,* including the sugar mite, *T. longior* (Gerv.), the cereal mite, *T. americanum* (Banks), and a related but unidentified British species (Ewing and Nesbitt, 1942) are recorded as pests of commercial mushroom plantings, a fact which bears out this conclusion. Where direct injury to stored food products has been observed, it has involved mainly the germ area of wheat and other grain.

THYSANURA

Lepismatidae.—The common silverfish, *Lepisma saccharina* Linn., the firebrat, *Thermobia domestica* Pack., and a few other thysanuran species are known to infest stored products. As food they much prefer starchy materials and cellulose, and their infestation of stored products is largely casual. Both species seek warm locations and are thus rarely found outdoors in the temperate regions, though they have been reported occasionally from under bark, in bird, mammal, and insect nests, in debris, and so forth.

COLLEMBOLA

Entomobryidae.—Two springtails, *Sira buski* Lubb. and *S. platani* Nic., have been reported in meal in houses (Mills, 1930), as well as outdoors under bark and in garbage. Apparently they subsist largely on molds and fungi.

BLATTARIA

Blattidae.—Several common roaches, including the oriental cockroach, *Blatta orientalis* Linn., the Australian cockroach, *Periplaneta australasiae* (Fab.), and the American cockroach, *Periplaneta americana* (Linn.), are contaminants or casual pests of stored products. Most of them are omnivorous, feeding on materials of both plant and animal origin. Although they prefer warm habitats, especially heated buildings, they are occasionally found outdoors, even in temperate regions, occurring under bark, in refuse dumps, and the like. Most of the native roaches of the temperate regions are bark inhabitants, but none of these appear to have been recorded from stored food materials.

Phyllodromiidae.—Some phyllodromiids, including the German cockroach, *Blattella germanica* (Linn.), and the Surinam roach, *Leucophaea surinamensis* (Linn.), are also casual pests of stored products. In their habits they resemble the true blattids.

CORRODENTIA

Caeciliidae.—*Lachesilla pedicularia* (Linn.) occasionally infests stored food products in Europe and North America. In nature it is found about old wood, straw, ground litter, and plant materials, both living and dead, as well as in birds' nests. It has generally been regarded as a scavenger on plant materials, but may prove to be a fungus feeder.

Liposcelidae.—The best-known member of the Liposcelidae is the book louse, or cereal psocid, *Liposcelis divinatorius* (Müll.). It is credited with omnivorous food habits because of the wide variety of plant and animal materials which it infests. Hinton (*in litt.*), however, suggests that this species, as well as most psocids, is probably a fungus feeder. In nature the various species occur under bark, in the nests of birds, mammals, and insects, on fungi, lichens, and algae, as well as in ground debris, straw, and decomposing plant materials—facts which bear out this suggestion.

Atropidae.—*Atropos pulsatorium* (Linn.), a common European and North American species infesting furniture, carpets, stored grain, and farinaceous foods, has been found in nature in nests of *Polistes* wasps as well as deserted beehives. Its true food habits are not well known.

LEPIDOPTERA

Pyralididae.—*Pyralis farinalis* (Linn.), the meal snout moth, is a typical feeder on dead and decomposing vegetable materials. It is more common and widely distributed in nature, where it breeds in damp, moldy straw and other plant materials, than it is in stored products. The fact that this species much prefers moldy plant materials and has even been reared from mushroom beds in Virginia (Davis, 1935) suggests that in part, at least, it is a fungus feeder.

Galleriidae.—The rice moth, *Corcyra cephalonica* Staint., and a number of its relatives that are found in stored food products are general plant scavengers. It has been found under bark in Australia. But the wax moth, *Galleria mellonella* (Linn.), and the lesser wax moth, *Achroia grisella* (Fab.), are well-known occupants of the hive, where they feed as scavengers on brood combs, frass, pollen, and the like. The lesser wax moth is also said to eat dried apples, raisins, crude sugar, many kinds of seeds, and dried insects. The bumblebee moth, *Aphomia sociella* (Linn.), a common pest of bumblebees' nests in Europe, has occasionally been reported from combs of the honeybee. A related species, *Aphomia gularis* Zell., feeds on many stored products.

Phycitidae.—Most of the phycitids are plant scavengers. In this category belong the Indian-meal moth, *Plodia interpunctella* (Hbn.), the Mediterranean flour moth, *Ephestia kühniella* Zell., and other species of *Ephestia,* all of which breed in nature in a wide variety of plant materials (Richards and Thomson, 1932). The tobacco moth, *E. elutella* (Hbn.), the raisin moth, *E. figulilella* Gregs., and the almond moth, *E. cautella* (Walk.), infest dried fruits on the ground in the field as well as in storage.

Since the pests in this family are mostly scavengers, it is not surprising that they can be found breeding in nature under bark or in old wood. *Ephestia elutella* has been found in rotten wood in New York state; *E. cautella* and *E. kühniella* in wood or bark in Europe and North America.

In addition, several species are associated in nature with bees and wasps. *Plodia interpunctella* is a common occupant of bees' nests. Long known as a pest of hives and stored frames (Dunham, 1929), it has also been reported from nests of *Bombus, Anthophora,* and *Osmia. Ephestia kühniella* is not uncommon in the combs of honeybees and bumblebees as well as social wasps (*Vespa* and *Vespula*). *E. cautella* and *E. elutella* have also been reported from combs of the honeybee. Moths of the genus *Vitula* appear to be definitely associated with social bees (bumblebees and honeybees) and carpenter bees. One of these, the dried-fruit moth, *Vitula serratilineella* Rag., occurs in weak colonies of honeybees and has recently been found breeding in nests of carpenter bees (Linsley, 1943). The closely related *V. edmandsii* (Pack.) often inhabits nests of bumblebees in the eastern United States and has been reported from combs of honeybees in Colorado and Nebraska. It is not yet known to be a pest of stored products.

Gelechiidae.—The angoumois grain moth, *Sitotroga cerealella* (Oliv.), is a primary grain pest and infests grain in the field as well as in storage. Since many other species in the same family infest seeds, its food habits are not aberrant. Two related species, *Aristotelia austeropa* Meyr. and *Epithectis studiosa* Meyr., infest stored rice in India (Fletcher, 1916).

Oecophoridae.—At least three of the oecophorids occur in stored food products: the seed moth, or brown house moth, *Hofmannophila pseudospretella* (Staint.), and the white-shouldered house moth, *Endrosis lactella* (D. and S.) *Anchonoma xeraula* Meyr. The first two are more or less cosmopolitan; the last is known from India and Japan. They infest dried plant materials, seeds, carpets, clothing, hides, bookbindings, and similar products. In nature they are found in fungi, animal detritus, ground litter, and the like (Morley, 1935, and others). Hinton (1943*a*) has called attention to larvae of *H. pseudospretella* feeding on dead honeybees near a bees' nest in an old house. He also notes the breeding of this species and one or two of *Endrosis* on dead insects in spider webs under conditions similar to those noted below for certain Dermestidae. The writer has found both *H. pseudospretella* and *E. lactella* breeding in black-widow-spider webs and in house-finch nests.

Tineidae.—The members of this family which infest stored products are mostly clothes moths. Concerning the origin of clothes moths, Marlatt (1896) has commented as follows:

> The common species of clothes moths have been associated with man from the earliest times and are thoroughly cosmopolitan. They are all probably of Old World origin, none of them being indigenous to the United States. That they were well known to the ancients is shown by Job's reference to "a garment that is moth eaten," and Pliny has given such an accurate description of one of them as to lead to the easy identification of the species. That they were early introduced into the United States is shown by Pehr Kalm, the Swedish scientist .... who seemed to take a keen interest in house pests. He reported Tineids to be abundant in 1748 in Philadelphia, then a straggling village, and says that clothes, worsted gloves, and other woolen stuffs hung up all summer were often eaten through and through by the worms, and furs were so ruined that the hair would come in handfuls.
>
> What led to the first association of these and other household pests with man is an interesting problem. In the case of clothes moths, the larvae of all of which can, in case of necessity, still subsist on almost any dry animal matter, their early association with man was probably in the role of scavengers, and in prehistoric times they probably fed on waste animal material about human habitations and on fur garments. The fondness they exhibit nowadays for tailor-made suits and expensive products of the loom is simply an illustration of their ability to keep pace with man in his development in the matter of clothing from the skin garments of savagery to the artistic products of the modern tailor or dressmaker.

In the field the clothes moths breed in animal hair, feathers, insect remains, and other dry animal products. Thus Baer (1924) has reported the carpet moth, *Trichophaga tapetzella* (Linn.), from casts (mainly mouse hair, ejected by birds of prey, especially owls); and Laing (1932) from rabbit skins outdoors. One species, the webbing clothes moth, *Tineola bisselliella* (Hüm.), frequents stored food products of animal origin and occasionally plant products that are infested with other insects. The writer has found it breeding in nests of the English sparrow as well as in cells of the bee *Anthophora* in California. Since this species feeds almost exclusively on animal products it probably lives in bees' nests as a scavenger both on insect remains and on stored pollen (which is high in nitrogenous materials).

Several species of *Tinea* also breed under bark, especially when fungus is present (Escherich, 1931). The European grain moth, *Tinea granella* (Linn.), and species of *Setomorpha* have been recorded from this habitat. The writer has found *Tineola bisselliella* breeding under loose bark in southern California. The larvae were apparently feeding on insect remains and detritus.

The so-called cork moth, *Tinea cloacella* Haw., breeds in grain and certain other dried plant products, especially in damp cellars. Since it seeks food of a high moisture content, and occurs in mushrooms (Krause, 1916) and in the fungus *Polyporus* (Morley, 1935), it may be primarily a fungus feeder. Its association with corks of wine flasks is probably due to the presence of molds.

COLEOPTERA

Histeridae.—At least six species of histerids occur in stored food products although but three of these, *Carcinops 14-striata* Steph., *Dendrophilus punctatus* Hbst., and *Saprinus semistriatus* Scriba, are widespread and common. *C. 14-striata* is a cosmopolitan species found about stored grain and flour, where it is predaceous on grain insects. This species, as well as others in the genus, occurs frequently in rotten wood and under bark. *D. punctatus* is also found in grain, flour, and various stored food products (Cotton and Good, 1937; Ross, 1940). It occurs occasionally under bark in Europe, North America, and probably elsewhere, but most often in nests of ants and of birds (owls, various woodpeckers, crows, the hoopoe, the jackdaw, the starling, screech owls, hawks); also in pigeon and other birdhouses. A related species, *D. opacus* Ross, occurs in nests of woodrats, and *D. tularensis* Ross in those of the ground squirrel. *C. 14-striata* has also been recorded from nests of owls and storks and from birdhouses occupied by starlings and purple martins. *S. semistriatus* Scriba occurs in burrows of the prairie dog.

Corynetidae.—The species of *Necrobia* are mainly found associated with decomposing animal matter and oleaginous vegetable materials. Thus the red-legged ham beetle (copra beetle), *Necrobia rufipes* (DeG.), and the red-shouldered ham beetle, *N. ruficollis* (Fab.), often occur in association with *Dermestes*. In the bone rooms of the Museum of Vertebrate Zoölogy of the University of California, where *Dermestes* are used for cleaning skulls, it has not proved practicable to eliminate *Necrobia* completely from the cultures. Both *N. rufipes* and *N. ruficollis,* however, as well as the cosmopolitan *N. violacea* (Linn.), are predaceous or semipredaceous, feeding on other insects (skin beetles, cheese skipper, mites) in the same habitat. This is also true of *Corynetes coeruleus* Dej., a species found about bones, meat, flour, grain, and other products infested with larvae of Dermestidae, Anobiidae, and Ptinidae (Zacher, 1927).

Dermestidae.—Characteristic of this group are the skin beetles, *Dermestes* spp., which attack hams and other cured meats, dried fish products, and similar foods of animal origin, and are serious pests in silkworm culture because they injure silk of cocoons. Under natural conditions they breed in dry carcasses of dead animals or in the nests of birds and mammals. Thus *Dermestes bicolor* Fab. occurs in pigeon lofts; *D. elongatus* Lec. in nests of the black-crowned night heron; *D. talpinus* Mann. and *D. signatus* Lec. in those of the magpie, the latter also in crows' nests. In fact, dermestids are among the commonest inhabitants of nests of birds and mammals. In California the writer has frequently encountered the black carpet beetle, *Attagenus piceus* (Oliv.), and the related *Attagenus schäfferi* Hbst. in chipmunk nests; infestations from this source have annoyed many persons in mountain summer cabins. Back and Cotton (1938) have recorded *Attagenus piceus* from birds'

nests; and McAtee (1929) from birdhouses occupied by starlings, English sparrows, purple martins, house wrens, and bluebirds. The related *Attagenus pellio* (Linn.) has also been found in birds' nests. Davis (1934) records *Attagenus elongatulus* Csy. as a regular inhabitant of woodrats' nests in California. *Trogoderma ornatum* (Say) and *T. versicolor* Creutz. have been found in numbers in nests of English sparrows and house wrens; and *Anthrenus occidens* Csy. in magpie nests. Yokoyama (1929) records adults and larvae of *Anthrenus pimpinellae* (Fab.) in sparrows' nests; and in California *Anthrenus lepidus* and *Attagenus nigripes* Csy. are both common in the nests of the English sparrow, house finch, black phoebe, barn swallow, and cliff swallow.

With few exceptions, the dermestid beetles feed only on products of animal origin. Chittenden (1895*a*, 1897) and various other authors have called attention, however, to the granivorous habits of a few species, primarily *Trogoderma versicolor* Creutz. and *T. granarium* Everts, but also *Attagenus piceus* and *Anthrenus verbasci* (Linn.).

As might be expected, dermestids inhabit nests of both bees and wasps as well as other insects. Unfortunately the species involved have seldom been carefully identified. Hinton (1934*b*) has stated that "in practice the nests of Aculeate Hymenoptera are rarely of even slight importance as reservoirs of injurious Dermestidae, and in this respect cannot be compared with either bird (chiefly sparrow) or spider nests which, because of their greater abundance and proximity to houses and warehouses where stored products are kept, are a factor to be reckoned with in the control of these beetles." Possibly Hinton's statement is true for England, but it certainly does not apply to California. In this state, by far the most injurious dermestid to fabrics is *Anthrenus verbasci;* to foodstuffs, *Trogoderma sternale.* In a recent survey the former species was encountered in birds' nests only once and in this case the nest was surrounded by those of *Sceliphron servillei* Sauss. On the other hand, both *Anthrenus verbasci* and *Trogoderma sternale* are common in the nests of *Sceliphron, Polistes, Odynerus,* and *Osmia,* which regularly nest about buildings as well as in old nests of *Dolichovespula* and *Apis.* In many parts of California where carpet beetles are a serious problem, nests of *Sceliphron* and *Polistes* are far more numerous about buildings than are birds' nests.

According to Hinton (*in litt.*), *Attagenus pantherinus* Ahrens, *Globicornis corticalis* (Eich.), and *Phradonoma villosulum* (Dufts.) all occur in bee or wasps' nests in Europe. Hicks (1926), Mickel (1928), and numerous other authors mention the abundance of *Anthrenus* spp. in nests of *Anthophora, Osmia,* and certain other bees. The varied carpet beetle, *Anthrenus verbasci,* is common in wasps' and bees' nests in California; *Anthrenus museorum* (Linn.) and *Anthrenus* (*Helocerus*) *fuscus* (Latr.) breed in the nests of *Osmia* or other bees in Europe; and Hinton (1943*a*) has recorded *Attagenus pellio* from the vicinity of honeybees' nests in England. In California *Attagenus ?piceus, Trogoderma ajax* Csy., and *T. sternale* Jayne occur in the nests of *Anthophora* and *Osmia. Trogoderma glabrum* Hbst. breeds in the nests of *Osmia* and *Odynerus* in Europe; the larger cabinet beetle, *T. versicolor,* in bees' and wasps' nests in North America; and the common *T. ornatum* has been recorded from honeycomb and from the nests of spiders. Another species, *T. socium* Lea, was originally described from ants' nests in Sydney. *Megatoma*

undata (Linn.) also lives with bees in Europe, and *Perimegatoma vespulae* Milliron was bred originally from the nests of *Dolichovespula arenaria* (Fab.) in Minnesota. Riley (1870), Lintner (1890), and others have noted the feeding of the larder beetle, *Dermestes lardarius* Linn., in combs of the honeybee; and Milum (1940*b*) discusses Dermestidae feeding on brood combs containing pollen, dead larvae, or bees but does not specify the species involved.

It may be significant that at least four species of *Trogoderma* live in nests of bees or wasps. In California, *T. ajax* can be reared entirely upon a diet of pollen, but will also consume animal products (insect parts) and grain. The larvae of both *Attagenus piceus* and *Anthrenus verbasci* also feed on cereal products (Griswold, 1941). Both these species occur in bees' nests and in the larval stage may be reared on pollen. Most of the species of *Attagenus* and *Anthrenus* feed as adults upon pollen and nectar, which they obtain directly from flowers. Possibly, therefore, pollen may have influenced the evolution of food habits of certain small dermestids associated with stored food products.

Dermestids are also commonly associated with nests and webbing of various caterpillars. In Japan and elsewhere they are among the most important pests of the silk industry. The breeding of *Dermestes* in nests of processionary and tent caterpillars has been noted by several writers (Perris, 1853; Bristowe, 1928, and others). Hinton (1943*b*) summarizes these as follows:

> In Europe a few Dermestidae are known to breed in the nests of certain gregarious caterpillars of the families Thaumetopoeidae and Lymantriidae. *Dermestes mustelinus* Er., *D. aurichalceus* Kuster, *D. lardarius* L., and *Anthrenus vorax* Waterh. are found in the nests of *Thaumetopoea pityocampa* Schiff. *D. aurichalceus* has also been recorded in the nests of *T. processionea* L. *D. erichsoni* Ganglb. and *D. tessellatus* F. have been found in the nests of the brown-tail moth, *Euproctis chrysorrhoea* L. and the former also in the nests of *Euproctis similis* Fuess. The larvae and adults of the species of *Dermestes* feed on the dead or injured moth larvae. *Dermestes mustelinus* is said to be of some value in controlling *T. pityocampa* in Catalonia.

Strickland (1929) has recorded larder-beetle infestations in Canada arising from nests of tent caterpillars. Donohoe (1939) has also called attention to the abundance of dermestids in webbing of *Ephestia* in raisin storage. He found thousands of larvae of *Trogoderma versicolor* Cz. breeding in webbing under stacks of the dried fruit. *Trogoderma sternale* Jayne and *Perimegatoma variegatum* Horn were also found in the same habitat.

A related habitat which may provide sources of household and warehouse infestation in spiders' sheet-webbing, which provides sources of dead insects (Auten, 1925; Hinton, 1943*b*, and others). In California both *Anthrenus verbasci* and *Trogoderma sternale* breed in this habitat. Hinton has summarized the published records as follows:

> Seven species of Dermestidae have been recorded in or near spider webs, *Attagenus pellio* L., *Ctesias serra* Steph., *Megatoma undata* L., *Globicornis marginata* Payk., *Trogoderma ornata* Say, *Anthrenus museorum* L., and *Trinodes hirtus* F. A further species *Anthrenus fuscus* Oliv., has recently (vi-xi. 1942) been found by me to be very common in Linton and Little Abington, Cambs. about stone walls, sheds, barns, and houses in or about the webs of *Tegenaria domestica* L. and other spiders. *A. museorum* frequently occurred in the same webs. The larvae of both species of *Anthrenus* are also very common in spider webs about sheds and outhouses in Reading (*A. S. Corbet*) and Slough (*O. W. Richards*). A few

larvae of both species were found by me during the summer of 1942 under bark in Linton with the spiders *Clubiona corticalis* Walck., *Ciniflio ferox* Walck., *Harpactea hombergii* Scopoli and *Segestria senoculata* L. The breeding habits out of doors in Britain of these two species of *Anthrenus* [do] not appear to have been previously known.

Many of the household and food-infesting dermestids are also common under bark, where they feed on debris of animal origin. This is especially true of the smaller species (*Trogoderma, Anthrenus, Attagenus*). Many authors have recorded instances of *Dermestes* attacking wood; but Walker (1884), Richards (1931), and others have pointed out that attacks of dermestids on certain plant materials (wood, cork, tobacco, bales of cotton, and books, as well as such inorganic materials as salt, plaster, asbestos, and lead) are due to larvae seeking a place for pupation. Patton (1931) illustrates injury to wood by pupating larvae of the hide beetle, *D. vulpinus* Fab.

Among the dermestids common under bark and in old burrows of wood borers are species of *Trogoderma. T. ornatum* breeds in this habitat in many localities in eastern North America and perhaps also in California. (Records from this state are possibly the result of misidentification.) Auten (1925) records it as feeding on spiders' eggs under bark in Ohio. *T. sternale* occurs under bark in San Diego County, California; and another species (identity uncertain) is not uncommon in the same habitat in the Sierra Nevada and northern California. The same species or a closely related one has also been found in Colorado under bark of ponderosa and limber pine (De Leon, *in litt.*). *T. versicolor* has been reared from dead hickory in New York, as well as from woolens and stored grain. Exact records of the occurrence of *Anthrenus* and *Attagenus* are rare because of uncertainties of identification. Both genera breed, however, in the bark habitat; and at least two species of the former and one of the latter occur under bark of various trees in California. The skin beetles, *Dermestes* spp., have also been found under bark from time to time, but probably mainly during hibernation (Blatchley, 1910).

Ostomatidae.—Nearly all ostomatids are predators living under bark or in the galleries of wood-boring insects. The species of *Temnochila* are characteristic of the group, spending both the adult and the larval stages as predators on wood-boring insects. One species, however, *T. coerulea* (Oliv.), occurs also in granaries (Zacher, 1927; Cotton and Good, 1937), where it is presumably predaceous on grain-feeding insects.

The species of *Tenebroides* are also typical inhabitants of bark and wood. Both as larvae and as adults, they live under bark as semipredators. When ready to hibernate or pupate, the larvae bore into the bark and construct a resting cell. At least three species of *Tenebroides,* however, are found in stored food products. The best-known is the cadelle, *T. mauritanicus* (Linn.). This pest probably does as much harm by boring into wood and other food containers for hibernation and pupation as by injuring or contaminating food. The adults are predaceous on their own larvae as well as on those of *Plodia interpunctella, Oryzaephilus surinamensis* (Linn.), and other food-inhabiting insects. The larvae feed on broken grain and certain other plant products, but are also semipredaceous and on some materials cannot complete development without supplementing their diet with dead or living insects. The cadelle has been found living under bark in both Europe and North America. The nor-

mally bark-inhabiting species *T. nanus* (Melsh.) and *T. corticalis* (Melsh.) both also infest stored grain in North America (Cotton and Good, 1937). The latter is also a predator of codling-moth larvae (Woodside, 1942). A related species, *T. maroccanus* Reitt., is predaceous on gypsy-moth eggs (de Lepiney, 1933).

The Siamese grain beetle, *Lophocateres pusillus* (Klug), infests a wide variety of stored foodstuffs in tropical and subtropical regions. It has occasionally been found under bark in nature.

Nitidulidae.—The most important members of this family, the dried-fruit beetles, *Carpophilus* spp., have come directly from forms that naturally feed either on dry or rotting fruit or upon oozing sap, pollen, fungi, or other plant materials. *Haptoncus luteolus* (Er.) lives in the field on similar materials and has been reported from mealybug-infested sugar cane (Swezey, 1942). It infests granaries and dried-fruit warehouses in California and elsewhere. *Nitidula ziczac* Say has sometimes infested hides in California. In nature it is found on dead birds and reptiles (Blatchley, 1910). A few species also occur in nests of bees. In Australia, *Carpophilus planatus* Mur., *Brachypeplus auritus* Mur., and *B. basalis* Er. occur in nests of *Trigona; B. inquilinus* Lea and *B. blandus* Mur. in wild nests of the honeybee.

Silvanidae.—The silvanids are common in nature beneath bark. Various species of *Silvanus* have been noted in this habitat by many authors. The saw-toothed grain beetle, *Oryzaephilus surinamensis,* and the merchant grain beetle, *O. mercator* (Fauv.), both may occasionally breed under bark, especially in tropical and subtropical regions. The same is true of the square-necked grain beetle, *Cathartus quadricollis* (Guer.), and the foreign grain beetle, *Ahasverus advena* (Watl.). Lucas (1849) found the latter species under cork-oak bark in North Africa; and Fall (1901) found it, possibly hibernating, under eucalyptus bark in southern California in December. *C. quadricollis* feeds on grain and farinaceous materials, and infests wheat and corn in the field as well as in storage. *Ahasverus advena* is commonly found on grain in the field and on stored grain and milled products which are slightly out of condition (Cotton and Winburn, 1941). It probably feeds on molds and fungi. The food habits of *Monanus concinnulus* Walk. and *Nausibius clavicornis* Kug. are not well understood. The former has been recorded in bran and flour in Mauritius; the latter is common among ships' stores and tropical cargoes, especially sugar. It may feed largely on molds and fungi.

Cucujidae.—Most of the cucujids live in nature under bark of trees. This is true of the flat grain beetles (*Laemophloeus* spp.); and, in fact, the generic name *Laemophloeus* means "bark eater." Wheeler (1921) summarizes the habits of twenty species, most of which live under bark in association with bark beetles (Scolytidae). The rust-red grain beetle, *L. ferrugineus* (Steph.), has often been recorded from under bark as well as in the nests of *Vespa.* Sheppard (1936) observed that it is at least to some extent predaceous on other insects. He found the oviposition rate highest when females were fed only on eggs of the Angoumois grain moth, and larval development most rapid when insects were available as food. Several other bark- and wood-inhabiting species are recorded as contaminants of stored food products: *L. ater* (Oliv.) and *L. emgei* Reitt. in Europe; *L. janeti* Grouv. in England, Africa, and the Orient;

and *L. turcicus* Grouv. in many parts of the world. Glover (1869) has recorded *L. modestus* Say from stored hempseed in the United States.

One additional bark-inhabiting cucujid is a stored-products pest. *Laemotmetus rhizophagoides* (Walk.) is found in stored rice in Africa, the Indo-Malay and other Asiatic regions, and certain parts of Europe.

Cryptophagidae.—Approximately nineteen species of *Cryptophagus* and a half-dozen other members of this family—such as *Henoticus californicus* Mann. and *Pharaxonotha kirschi* Reitt.—have been recorded from houses, warehouses, mills, and granaries. *Cryptophagus distinguendus* Sturm has been recorded from an edible fungus (*Psalliota*) by Ripper (1930); and Hinton and Stephens (1941) have reared *C. acutangulus* Gyll. on a wide variety of fungi, finding that the species would thrive on a diet of *Penicillium* conidia. *C. acutangulus* also proved to be capable of mechanical, internal, and external transportation of fungi. Other cryptophagids probably have habits similar to these and feed almost entirely on fungi and molds rather than the stored food products in which they are found. In nature they occur under bark; in nests of birds, mammals, and insects; and in fungi, ground debris, straw, and decomposing plant materials.

At least three genera of cryptophagids have been found in nests of bees or wasps. Many of the species of *Cryptophagus* recorded from buildings have sometimes been found living with social bees and wasps in Britain. *C. badius* Sturm occurs with the giant hornet, *Vespa crabro* Linn.; *C. pubescens* Sturm, *C. pilosus* Gyll., and *C. distinguendus* with one or more species of *Vespula;* and *C. punctipennis* Bris., *C. umbratus* Er., and *C. saginatus* Sturm with *Bombus. C. distinguendus* has also been found in bumblebee nests, as has *C. croceus* Zimm. Falcoz (1929–1931) has recorded the well-known *C. cellaris* (Scop.) from beehives in Europe.

Atomaria ruficornis Marsh. and *Atomaria peltata* Kraatz have occurred in nests of *Vespa. Antherophagus pallens* (Fab.) and *Antherophagus nigricornis* (Fab.) are common in bumblebees' nests in Europe; and *Antherophagus ochraceus* Melsh. in similar situations in the eastern United States. Cryptophagids have also been found in nests of processionary caterpillars (Bristowe, 1928, and others).

Mycetophagidae.—Several mycetophagids may also be found in stored products. The hairy fungus beetle, *Typhaea stercorea* (Linn.), is the best known of these. *Mycetophagus quadriguttatus* Müll., *M. bipustulatus* Melsh., and *Litargus balteatus* Lec. are less common. All have been recorded from fungi in nature, and their food habits probably resemble those of the preceding family

Lathridiidae.—Thirty or more species of lathridiids have been recorded from stored food products, warehouses, granaries, or mills. *Corticaria serrata* Payk. has also been found in mushroom beds (Davis, 1935); and Hinton (1941*b*) has shown that both larvae and adults of the species studied by him feed on mycetozoa and fungi, particularly molds.

Thus it is not surprising that various species occur under bark, where many kinds of fungi are available. Of the lathridiids recorded from stored food products, *Holoparamecus caularum* (Aubé), *H. depressus* Curtis, *H. singularis* (Beck), *Coninomus constrictus* (Gyll.), *Coninomus nodifer* (Westw.),

Enicmus minutus (Linn.), and *Corticaria fenestralis* (Linn.) have all been found commonly under bark.

Many lathridiids also regularly live with bees, wasps, and ants. Among the stored-products species recorded from this habitat are *Coninomus constrictus* from ants' nests (*Lasius* spp.); and *C. nodifer* and *Enicmus minutus* from nests of bumblebees (*Bombus* spp.) and wasps. (*Vespa* spp.).

Lathridiids also often inhabit the nests of birds and mammals. *Enicmus crenatus* Lec., *E. suspectus* Fall, *Metophthalmus trux* Fall, all occur in nests of wood rats (*Neotoma*) at Berkeley, California. *E. minutus* and *Cartodere ruficollis* (Marsh.) have been recorded from storks' nests in Europe, and *Corticaria pubescens* (Gyll.) from birds' nests in England. But since lathridiids are primarily fungus feeders, their occurrence in animal nests indicates little more than the presence of suitable molds.

Mycetaeidae.—The hairy cellar beetle, *Mycetaea hirta* Marsh., is found in Europe and North America. It has been recorded from fungi, stored grain, wine cellars, and corks. According to Hinton (*in litt.*) fungus is its primary, if not exclusive, food. Its presence on corks is undoubtedly due to fungi or molds.

Tenebrionidae.—The stored-products pests of the family Tenebrionidae belong, with few exceptions, to the Ulominae. Most members of this subfamily live under bark or in rotting wood as semipredators and scavengers. In the United States, native species of *Uloma* are common in this habitat. In Europe, *Uloma culinaris* (Linn.) is said to be injurious in granaries and other places of food storage (Zacher, 1927; Cotton and Good, 1937). In nature it lives under bark and in burrows of bark beetles and wood borers.

The broad-horned flour beetle, *Gnathocerus cornutus* (Fab.), occurs under bark in California (Chittenden, 1895*b*; Essig, 1926) and North Africa (Lucas, 1849). The slender-horned flour beetle, *Gnathocerus maxillosus* (Fab.), is not uncommon under bark in tropical and subtropical regions. Wollaston (1860) noted it from under bark of plane trees in Madeira, and it has also been recorded from under bark of poplar in Europe. De Leon (*in litt.*) found it abundant under bark of *Pistacio simarubra* in Puerto Rico; and the writer took it under bark in Java.

Cynaeus angustus (Lec.) has been recorded from flour mills in Washington state (Hatch, 1940), and shelled corn in Minnesota. Both this species and the related *C. depressus* Horn are native to western North America. In nature they breed under bark, or about the base of yucca plants in Arizona and southern California.

The long-headed flour beetle, *Latheticus oryzae* Waterh., also lives in rotten wood and under bark. Blair (1930) records it in India as having been bred from wood, where it may have fed on remains of wood borers. A closely related native American species, *L. prosopis* Chitt., breeds regularly under bark of dead mesquite in the southwestern United States.

The various species of *Tribolium* are also to be found under bark (Good, 1936). The rust-red flour beetle, *T. castaneum* (Hbst.), is occasionally found in this habitat in Britain and the United States; more frequently in the Dutch East Indies, the Malay region, and India. According to Stebbing (1914) it preys upon the small bamboo shot borer, *Dinoderus minutus* (Fab.). The confused flour beetle, *T. confusum* duV., occurs under bark in California and

parts of southern and southwestern United States. Stebbing recorded it from India as a semipredator on the bamboo shot borer, *Dinoderus pilifrons* Lesne. Many have noted its semipredaceous behavior in stored food products. In Europe and North America the black flour beetle, *T. madens* Charp., lives regularly under bark. De Leon (*in litt.*) records it from ponderosa and limber pine in Colorado, and it has been found breeding in similar habitats elsewhere. Leech (1943) found it in beehives in British Columbia as well as under boards and stones. Adults were observed to kill larval Bibionidae in leaf mold under a log. *T. indicum* Blair, which lives under bark in India (Blair, 1930), has not yet been recorded from stored food products.

The small-eyed flour beetle, *Palorus ratzeburgi* Wissm., and the depressed flour beetle, *P. subdepressus* Woll., have both been found under bark in Europe; the former also in Guam. *P. depressus* (Fab.) apparently breeds regularly in dead wood and under bark. In grain and flour it appears to be less common than the two other species. Blair (1930) has recorded nine additional species of *Palorus* from on or under the bark of trees infested with borers in India, presumably the original home of the group.

The false flour beetles (*Aphanotus* spp.) are common bark inhabitants in western North America. *A. parallelus* Csy. breeds under bark in Arizona and southern California and has also been found in various stored food products. The increasingly injurious *A. destructor* (Uytt.) occurs under bark in central California, and *A. brevicornis* (Lec.) in many parts of the Pacific Coast. The latter, however, is primarily associated with wood-nesting bees (*Xylocopa*).

The lesser mealworm, *Alphitobius diaperinus* (Panz.), was once found by the writer in large numbers under bark of a dead oak tree near Crockett, California. It occurs most commonly in moldy flour. According to Tischler (1937), the adults also feed on dead insects; but they are perhaps not predaceous. The grain mold beetle, *A. piceus* (Oliv.), has also been found under bark in southern California and in India. Both species probably subsist largely on molds and fungi.

Sitophagus hololeptoides (Cast.) breeds under bark in Central America. It has also been recorded from cereals and other stored products (Chittenden, 1911*a;* Cotton and Good, 1937).

The species of *Doliema* and *Platydema* also regularly live under bark. Thus Blatchley (1910) records *D. pallida* (Say) from this habitat in Indiana, and Fall (1901) states that *D. plana* (Fab.) is common in southern California under bark of sycamores. P. C. Ting reports that the latter is commonly intercepted in quarantine from under bark of lignum vitae logs from Mexico, Nicaragua, Guatemala, and Costa Rica. *P. ruficorne* Sturm, a common native bark inhabitant, has attacked shelled corn and shorts in Kansas (Cotton and Good, 1937).

The species of *Tenebrio* may also be found in old wood and under bark. The commonest species in this habitat is *T. picipes* Hbst., which occurs under bark of various trees from coast to coast. The related *Idiobates castaneus* (Knoch) occupies the same habitat.

Many bark-inhabiting tenebrionids are fungus feeders. Most of the species found in stored food products will probably feed on any fungi available. Several, including the two-banded fungus beetle, *Alphitophagus bifasciatus*

(Say), *Alphitobius piceus* (Oliv.), and *Alphitobius diaperinus,* appear to be primarily fungus feeders and are found in food products only when these materials are in a somewhat deteriorated condition.

Several tenebrionids inhabit bees' nests. The false black flour beetle, *Aphanotus destructor,* occurs in the nests of *Osmia* and *Anthophora;* and the closely related *Aphanotus brevicornis* breeds regularly in cells of *Xylocopa* and has also been recorded from those of *Anthidium.* Another flour beetle, *Cynaeus angustus,* has been found in *Osmia* nests in southern California. *Tribolium castaneum* has also been reported from nests of *Megachile* in Hawaii; *Tribolium confusum,* from cells of *Anthophora, Osmia,* and *Clisodon* in California. Frison (1926) has recorded two species of mealworms, *Tenebrio obscurus* Fab. and *Tenebrio tenebroides* Beauv., from *Bombus* nests in Illinois. In Australia, Lea (1905) has described *Tribolium myrmecophilum* Lea from the nests of ants, and *Palorus eutermiphilus* Lea from those of termites.

Ptinidae.—The ecology and habits of ptinids in nature are not well understood. A few species, however, occur under bark or in rotten wood. Among the economic species, Fowler (1890) has noted in old wood the white-marked spider beetle, *Ptinus fur* (Linn.), the brown spider beetle, *P. hirtellus* Sturm, and *P. subpilosus* Sturm. The white-marked spider beetle has also been found under bark in Ohio (Auten, 1925). Hinton (1941*a*) records *P. rufipes* Oliv. from dead branches and *P. palliatus* Perris from old posts and similar places. According to Picard (1919), the larvae of *P. lichenum* Marsh. live in the dry wood and bark of fig trees. Blair (1930) records *P. pusillus* Sturm from a rotten staircase, and De Leon (*in litt.*) has reported *Ptinus* sp. from under bark of limber pine. A native bark- and wood-inhabiting species, *P. gandolphei* Pic, has been reported from raisins in California (Donohoe, 1939). Finally, Stebbing (1914) has noted *Gibbium* sp. living under the bark of teakwood.

More important, however, is the fact that several ptinids are found in nests of birds and rodents. *Tipnus unicolor* Pill. and Mitt. occurs in nests of the house martin and other birds; *Ptinus sexpunctatus* Panz. in those of the house martin; *P. hirtellus* Sturm in those of the English sparrow; *P. fur* in robins' nests and in birdhouses occupied by house wrens and bluebirds; and *P. agnatus* Fall in nests of a woodrat (*Neotoma*). The writer has found *P. gandolphei* breeding in nests of the barn owl, and on several occasions *Mezium affine* Boield has been found in nests of Norway rats in San Francisco. Hinton (*in litt.*) notes that many species feed on rodent dung, a fact which may account for their occurrence in nests of birds and mammals. Such nests, however, frequently contain other plant and animal products acceptable to ptinids.

Ptinids also occur in nature in nests of other insects. *Ptinus sexpunctatus* was apparently the first ptinid species taken in association with bees. In 1872, Bebel reported its capture at the nest entrances of *Megachile muraria* (Retz.). It has since been recorded from nests of the following bees: *M. muraria, M. willughbiella* (Kirby), *Osmia rufa* (Linn.), *O. cornuta* (Latr.), *O. emarginata* Lep., *O. villosa* (Schenck), *O. mitis* Nyl., *Hoplitus adunca* (Panz.), *Chelostoma nigricorne* (Nyl.), and possibly also *Bombus* sp. The well-known white-marked spider beetle, *Ptinus fur,* also feeds on pollen in bees' nests. It has been recorded from *O. tridentata* Duf. and Per., *O. rufa,* and *C. maxillosa* (Linn.), as well as from the combs of the honeybee, *Apis mellifera* Linn., and

the giant hornet, *Vespa crabro*. Cros (1932) describes *P. vaulogeri* Pic living in the nests of *O. longispina* Perez; and Linsley and MacSwain (1942*a*) have discussed the California spider beetle, *P. californicus* Pic, as a depredator in nests of *O. lignaria* (Say) and *Anthophora linsleyi* Timb. Arnhart (1929) and Brassler (1929) have also called attention to depredations of *P. raptor* (Linn.) on pollen stores of honeybees in Europe; and Lea (1905) records *P. exulans* Er. from deserted hives in Australia. The latter author has also reported a long series of ptinids (*Polyplocotes, Diplocotes, Diphobia, Paussoptinus, Hexaplocotes, Ectrephes*) that appear to live regularly in nests of ants of the genus *Iridomyrmex*. In Europe the golden spider beetle, *Niptus hololeucus* (Fald.), has been reported from nests of the wasp *Dolichovespula*, and in California *P. hirtellus* breeds in nests of *Sceliphron servillei*.

Anobiidae.—The drugstore beetle, *Stegobium paniceum* (Linn.), and the tobacco beetle, *Lasioderma serricorne* (Fab.), are principally scavengers on dead plant products, but were doubtless derived originally from wood-boring ancestors, for other anobiids are notorious wood borers. The literature often reports the tobacco beetle as occurring under bark or boring in woods; but there is some question about the identification of the species. The writer has found the drugstore beetle boring in bamboo mah-jongg playing pieces, where the larvae fed also on the glue supporting the ivory face; and in thin wood forms of food containers. Linsley and MacSwain (1942*b*) have noted the drugstore beetle feeding on pollen in the nests of *Anthophora linsleyi* in southern California. Rayment (1935) states that the tobacco beetle lives in the cells of *Anthophora* in Australia; but his figures (pl. 45, figs. 19, 21) are of the drugstore beetle, a much more likely nest inhabitant.

Bostrichidae.—This family is composed of true wood borers. A few species have, however, transferred from a wood-boring to grain-boring habit. The best known is the lesser grain borer, *Rhyzopertha dominica* (Fab.). It must also be classed as a seed-infesting species that has been carried over from field to stored products. Gurney (1918) actually records it from wheat ears in the field. Nevertheless, the species must have been derived originally from a wood-boring type. Potter (1935) writes as follows:

> There seems little doubt that *R. dominica* originally fed solely on wood, probably living wood. Lesne .... records having seen a pair working at a communal gallery on a tree, probably *Quassia* spp., in French Guinea, and Lucas .... has recorded it under the bark of *Quercus suber* and *Cytisus spinosus*. More recently Gardner .... records a long series bred from wood of *Artocarpus hirsutus*. The species of tree or shrub that was the original host of *R. dominica* cannot definitely be ascertained, since, in addition to the above records, it is reported as attacking various unidentified woods.

Experimentally, Potter induced the species to attack young maize plants in confinement; also the soft inner cane and pith of bamboo. It has attacked cork in insect boxes (Riley, 1882, and others), wood of sugar casks (Gorham, 1883), wooden bins and containers for wheat and other grains (Mackie and Carter, 1937), and wooden packing cases (Froggatt, 1918). As a grain feeder it retains the boring habit, the young larva tunneling into the grain, the larva feeding and pupating within the kernel, and the adult boring its way out upon maturity. A related species, *R. hordeum* Mats., has been recorded from stored grain and plant products in Formosa (Clausen, 1931).

The genus *Dinoderus* contains several species that bore in bamboo. Two of these are known to infest grain, spices, and drugs. The small bamboo shot borer, *D. minutus,* a well-known bamboo pest, has been recorded from spices, cacao, and the like by Richards and Herford (1930); and from stored grains, flour, tobacco, and nuts by other authors. *D. bifoveolatus* Woll. has been found in similar products in England (Laing, 1929).

The larger grain borer, *Protostephanus truncatus* (Horn), a species related to *Dinoderus,* also infests stored grains and tubers (Chittenden, 1911*b*).

Bruchidae.—Practically all bruchids are seed-infesting species in nature, and most of them are restricted to seeds of legumes. Of these, a great many infest stored seeds, including the bean weevil, *Acanthoscelides obtectus* (Say), the spotted bean weevil, *Callosobruchus maculatus* (Fab.), the Mexican bean weevil, *Zabrotes pectoralis* Sharp, and several other species which attack beans and peas both in the field and in storage. Certain others, including the pea weevil, *Bruchus pisorum* (Linn.), cannot reproduce in stored beans and peas and are classed as pests of stored food products only because they emerge from material previously infested in the field.

Curculionidae and Platystomidae.—The weevils, particularly the granary weevil, *Sitophilus granarius* (Linn.), and the rice weevil, *S. oryza* (Linn.), were obviously derived from types infesting grain in the field. Although both appear to be natives of the Old World, their geographical or topographical origins may not have been identical, since the former prefers the more temperate regions north of 40 degrees latitude, the latter the regions southward. Other true weevils, including the broad-nosed grain weevil, *Caulophilus latinasus* (Say), and platystomids such as the coffee-bean weevil, *Araecerus fasciculatus* (DeG.), must have had a similar origin, since nearly all of them infest seeds in the field as well as in storage.

Scolytidae.—The scolytids are mainly bark beetles, only a few species being classed as true wood borers. Three species, all belonging to the genus *Pagiocerus,* have been recorded as damaging corn in Central and South America (Cotton and Good, 1937). They are obviously derived from wood-boring types.

DIPTERA

Piophilidae.—Few Diptera other than fruit flies and muscoid scavengers are true pests of stored products. The best-known species, the cheese skipper, *Piophila casei* (Linn.), feeds on moist animal products, especially those that are high in fat content (such as cheese, bacon, ham). In nature it breeds in excrement, dead animals, and similar materials.

DISCUSSION

NATURAL SOURCES OF STORED-PRODUCTS INSECTS

As we have seen, insects associated with stored food products have come from a variety of habitats. They may be classified according to their sources as follows: (1) seed-infesting species; (2) fungus-feeding-species; (3) scavengers on dead plant materials; (4) scavengers on dead animal materials; (5) scavengers or semipredators living under bark; (6) wood borers and wood scavengers; (7) scavengers or depredators in the nests of other insects and

spiders; (8) parasites and predators. Naturally, there is a considerable overlap; some species belong in two or more categories.

Seed-infesting Species.—Of the many insects that infest seeds under natural conditions, a number will attack seeds stored by man. Such behavior involves little change in food habits and probably little adjustment to a new environment, although some change in tolerance of relative humidity and moisture content of food was probably required in many cases. The surprising thing, perhaps, is that so few species of stored-food insects, except the coleopterous family Bruchidae, are of this sort. Among the few involved, however, are some serious pests. Certain of these are still to be found infesting the flower head or the seed pod; others the seeds that have been shed on the ground. A few species avail themselves of the seed storages of birds and mammals and have had to make only a small transition to the storehouses of man. The following list includes the better-known seed-infesting species:

Lepidoptera
- Gelechiidae
  - *Sitotroga cerealella* (Oliv.)

Coleoptera
- Bruchidae
  - *Acanthoscelides obtectus* (Say)
  - *Callosobruchus maculatus* (Fab.)
  - *Zabrotes pectoralis* Sharp
  - Etc.

Coleoptera, *continued*
- Platystomidae
  - *Araecerus fasciculatus* (DeG.)
  - *Brachytarsus alternatus* (Say)
  - *Brachytarsus sticticus* (Boh.)
- Curculionidae
  - *Sitophilus granarius* (Linn.)
  - *Sitophilus oryza* (Linn.)
  - *Caulophilus latinasus* (Say)

Fungus-feeding Species.—Numerous species of insects which occur in stored food products are primarily fungus feeders. They are most commonly found in old, damp products and probably confine their feeding to the fungi and molds present. Included are beetles of the families Cryptophagidae, Mycetophagidae, and Lathridiidae, of which many species have been found in grain and grain products. Some of the Tenebrionidae, and some moths and mites also belong wholly or partly in this category.

Acarina
- Acaridae
  - *Acarus siro* Linn.
  - *Carpoglyphus passularum* Her.
  - *Tyrophagus americanum* (Banks)
  - *Tyrophagus putrescentiae* (Schr.)
  - Etc.

Collembola
- Entomobryidae
  - *Sira buski* Lubb.
  - *Sira platani* Nic.

Lepidoptera
- Tineidae
  - *Tinea cloacella* Haw.
- Pyralididae
  - *Pyralis farinalis* (Linn.)
  - *Pyralis lienigalis* Zell.
  - *Hypsopygia costalis* (Fab.)

Coleoptera
- Cryptophagidae
  - *Henoticus californicus* Mann.
  - *Cryptophagus acutangulus* Gyll.
  - *Cryptophagus* spp.

Coleoptera, *continued*
- Lathridiidae
  - *Holoparamecus depressus* Curtis
  - *Metophthalmus serripennis* (Broun)
  - *Coninomus nodifer* (Westw.)
  - *Enicmus minutus* (Linn.)
  - *Adistemia watsoni* (Woll.)
  - *Cartodere filum* (Aubé)
  - *Cartodere filicornis* (Gyll.)
  - *Cartodere ruficollis* (Marsh.)
  - *Corticaria fulva* (Com.)
  - Etc.
- Mycetophagidae
  - *Mycetophagus bipustulatus* Melsh
  - *Mycetophagus quadriguttatus* Müll.
  - *Typhaea stercorea* (Linn.)
  - *Litargus balteatus* Lec.
- Mycetaeidae
  - *Mycetaea hirta* Marsh.
- Tenebrionidae
  - *Alphitophagus bifasciatus* (Say)
  - *Alphitobius piceus* (Oliv.)
  - *Alphitobius diaperinus* (Panz.)

Scavengers on Dead Plant Materials.—Insect scavengers of plant materials provide an obvious source for stored-food-products pests. A few of the many species involved are listed below.

Thysanura
- Lepismatidae
  - *Lepisma saccharina* Linn.
  - *Thermobia domestica* Pack.

Blattaria
- Blattidae
  - *Blattella germanica* (Linn.)
  - *Blatta orientalis* Linn.
  - *Periplaneta americana* (Linn.)
  - *Periplaneta australasiae* (Fab.)
  - *Leucophaea surinamensis* (Linn.)

Corrodentia
- Caeciliidae
  - *Lachesilla pedicularia* (Linn.)
- Liposcelidae
  - *Liposcelis divinatorius* (Müll.)
- Atropidae
  - *Atropos pulsatorium* (Linn.)

Lepidoptera
- Galleriidae
  - *Corcyra cephalonica* Staint.
- Phycitidae
  - *Ephestia cautella* (Walk.)
  - *Ephestia elutella* (Hbn.)
  - *Ephestia figulilella* Gregs.
  - *Ephestia kühniella* Zell.
  - *Plodia interpunctella* (Hbn.)

Coleoptera
- Nitidulidae
  - *Carpophilus dimidiatus* (Fab.)
  - *Carpophilus hemipterus* (Linn.)
  - *Carpophilus decipiens* Horn
  - *Carpophilus ligneus* Mur.
  - *Carpophilus pallipennis* Say
  - *Carpophilus* spp.
  - *Urophorus humeralis* (Fab.)

Scavengers on Dead Animal Materials.—Here again we find many insects that have carried over their preference for dead animal materials in the field to products of a similar origin stored by man.

Coleoptera
- Dermestidae
  - *Dermestes* spp.
  - *Attagenus* spp.
  - *Anthrenus* spp.
  - *Perimegatoma* spp.
  - *Trogoderma* spp.
- Nitidulidae
  - *Nitidula ziczac* Say

Lepidoptera
- Tineidae
  - *Trichophaga tapetzella* (Linn.)
  - *Tineola bisselliella* (Hüm.)
  - *Tinea* spp.
  - *Setomorpha insectella* (Fab.)
  - *Setomorpha margaloestriata* Keuch.

Diptera
- Piophilidae
  - *Piophila casei* (Linn.)

Scavengers or Semipredators Living under Bark.—Many pests of stored food products appear to have been derived from forms that live under bark, the majority coming originally from tropical and subtropical regions. The bark habitat, aside from offering protection and favorable physical conditions, provides varied foods of both plant and animal origin. Decomposing plant materials, fungi, other insects, both living and dead, all abound. Of the insects occupying this habitat, the majority are scavengers; many are fungus feeders; some are semipredators, feeding on both dead and living materials; a few are strictly predators as larvae or adults or both. Associated with stored food products are species from each of these sources. The species listed below, with the exception of the Tenebrionidae, fall largely in the last category.

Coleoptera
- Corynetidae
  - *Corynetes coeruleus* Dej.
- Ostomatidae
  - *Temnochila coerulea* (Oliv.)
  - *Tenebroides mauritanicus* (Linn.)
  - *Tenebroides manus* (Melsh.)
  - *Tenebroides corticalis* (Melsh.)

Coleoptera—*Continued*
- Cucujidae
  - *Laemophloeus ferrugineus* (Steph.)
  - *Laemophloeus minutus* (Oliv.)
  - *Laemophloeus ater* (Oliv.)
  - *Laemophloeus janeti* Grouv.
  - *Laemophloeus turcicus* Grouv.
  - *Laemotmetus rhizophagoides* (Walk.)

Coleoptera—*Continued*
Tenebrionidae
Uloma culinaris (Linn.)
Gnathocerus cornutus (Fab.)
Gnathocerus maxillosus (Fab.)
Cynaeus angustus (Lec.)
Latheticus oryzae Waterh.
Tribolium castaneum (Hbst.)
Tenebrionidae—*Continued*
Tribolium confusum duV.
Tribolium madens Charp.
Palorus ratzeburgi Wissm.
Palorus subdepressus Woll.
Aphanotus destructor (Uytt.)
Sitophagus hololeptoides (Cast.)
Platydema ruficorne Sturm

Wood Borers and Wood Scavengers.—A very few of the insects that attack stored food products were derived from wood-boring types. Most of these retain boring characteristics and attack either whole grains and seeds or processed foods of a compact nature. The ptinids and anobiids also infest loosely packed and ground products.

Coleoptera
Ptinidae
?Ptinus spp.
Anobiidae
Lasioderma serricorne (Fab.)
Stegobium paniceum (Linn.)
Catorama mexicana Chev.
Catorama punctulata Lec.
Bostrichidae
Rhyzopertha dominica (Fab.)
Dinoderus bifoveolatus Woll.
Dinoderus minutus (Fab.)
Protostephanus truncatus (Horn)
Scolytidae
Pagiocerus frontalis (Fab.)
Pagiocerus rimosus Eich.
Pagiocerus zeae Eggers

Scavengers or Depredators in the Nests of Other Insects.—The nests of bees, wasps, ants, and certain other insects present an advantageous environment for many insects. This habitat offers protection, favorable temperatures and humidities (sometimes actually kept under some degree of control), and usually stored food materials (pollen, seeds, dead insects). Several stored-products pests may have come originally from this environment; others (dermestids, cucujids, silvanids, tenebrionids, anobiids) find it favorable.

Pollen stored in bees' nests may have greatly affected the evolution of insect food habits by bridging the gap between plant and animal foods. Pollen has a high protein content and in many of its chemical properties resembles animal materials on the one hand, and grains, seeds, and certain other concentrated plant products on the other. Many predaceous or parasitic insects can subsist wholly or partially on pollen—for example the ichneumonid genus *Grotea,* members of which are bee-egg predators in the primary larval stage, pollen feeders in later instars. The clerids as a group must be classed as predators; and the genus *Trichodes* contains many species predaceous on larvae of bees and wasps, or on eggs of grasshoppers. Yet *Trichodes* larvae, apparently unable to subsist on other plant materials, can be reared on pollen alone, though this diet greatly retards their development rate. Meloid beetles also live either as predators on grasshopper eggs or in bees' nests. As with *Grotea,* the primary larvae are egg predators, and subsequent instars are pollen feeders. Other groups of insects exhibit similar habits, a fact indicating the dietary relation between pollen and animal food (especially insect eggs). At least two groups of stored-products pests—the ptinids and the dermestids—bridge the gap between plant and animal foods; both these groups are found commonly in bees' nests, subsisting wholly or partially on pollen.

Apparently, gregarious bees (especially anthophorids), associates of gregarious bees (especially *Osmia*), social bees (*Apis, Bombus*), and social wasps

(*Vespa, Vespula, Dolichovespula*) provide more favorable conditions for stored-food-inhabiting insects than do other groups of bees and wasps. The explanation, undoubtedly, is that such species use their nesting sites for longer periods, develop larger and more concentrated populations, and store more food than do the more solitary forms. The following groups appear to be referable to this habitat.

Lepidoptera
- Galleriidae
  - *Achroia grisella* (Fab.)
  - *Galleria mellonella* (Linn.)
- Phycitidae
  - *Vitula serratilineella* Rag.
  - *Vitula edmandsii* (Pack.)

Coleoptera
- Dermestidae
  - *Trogoderma* spp.
  - *Anthrenus* spp.
  - *Attagenus* spp.
- Ptinidae
  - *Ptinus* spp.

Parasites and Predators.—Among the hundreds of parasites and predators associated with stored food products (Cotton and Good, 1937; Clausen, 1940), it is not known which species are attracted to their hosts by the food materials and which by the environment in which these are stored. The primary attraction seems clear, however, in some of the coleopterous predators (especially Histeridae, Ostomatidae, Cleridae, Corynetidae). The ostomatids and clerids are primarily bark and wood inhabitants; the histerids live in nests of birds, mammals, aculeate Hymenoptera, and so forth; and the corynetids in both types of habitat. The anthocorid bugs exhibit a similar pattern: *Lyctocoris campestris* (Fab.) occurs under bark, in birds' nests, and in nests of wasps and bumblebees.

Corbett, Yusope, and Hassan (1937) found that *Necrobia rufipes* prefers decomposed, moldy copra. Apparently, however, it is attracted not by the molds, coconut oil, or fatty acids, but by the decomposition products of the molds. Conceivably, the beetles associate these products with the presence of *Carpophilus* and other larvae upon which they are predaceous. This species and other cosmopolitan, semipredaceous *Necrobia* are probably attracted by the habitat (animal and oleaginous plant products) rather than by the insects (*Dermestes, Piophila, Carpophilus*) which constitute much of their diet. The same is probably true of the window fly, *Scenopinus fenestralis* Linn., the larvae of which feed on mites and other small insects in various animal and plant products (hair, feathers, grain, farinaceous foodstuffs, and the like).

NATURAL RESERVOIRS FOR STORED-PRODUCTS INSECTS

Closely tied up with the origin and evolution of stored-food-products insects is the problem of natural reservoirs. Insufficient attention has been given to the occurrence of these insects in nature and to the role of their habitats as reservoirs that may maintain foci for future infestations. Balzer (1942) remarks: "Stored grain insects can and do enter warehouses and mills by flight. In an experiment conducted during the summer of 1937, nine species of stored grain insects, including the worst enemies of milled and rough rice, were collected in insect flight traps at two rice mills." Since these insects do migrate into storage units, natural reservoirs may perhaps be important in maintaining pest populations.

Bark and Decomposing Wood Habitat.—The pests of stored food products

have an important natural habitat beneath the bark of trees—a protected environment with favorable temperatures and humidities approaching those of many food-storage units. Unfortunately, records of their occurrence under bark or in wood are scanty and widely scattered; yet in the writer's experience they are not at all uncommon in this environment. Among the species recorded from under bark and for which this habitat may possibly act as a reservoir are the following:

Thysanura
  Lepismatidae
Blattaria
  Blattidae
Corrodentia
  Caeciliidae
  Liposcelidae
  Atropidae
Lepidoptera
  Galleriidae
    Aphomia sociella (Linn.) (Forbes, 1920)
  Phycitidae
    Ephestia elutella (Hbn.) (Forbes, 1920)
  Tineidae
    Tinea cloacella Haw. (Escherich, 1931)
    Tinea parasitella Hbn. (Escherich, 1931)
    Tinea corticella Curt. (Escherich, 1931)
    Tinea quercella H. S. (Escherich, 1931)
    Tineola bisselliella (Hüm.) (Linsley ms.)
Coleoptera
  Histeridae
    Dendrophilus punctatus Hbst. (Stephens, 1839; Fowler, 1889; Blatchley, 1910)
    Carcinops sp. (Stebbing, 1914)
    Carcinops 14-striata Steph. (Linsley ms.)
  Corynetidae
    Corynetes coeruleus Dej. (*auct.*)
  Dermestidae
    Trogoderma versicolor Creutz. (Blackman and Stage, 1924, as *tarsalis*)
    Trogoderma ornatum (Say) (Auten, 1925)
    Trogoderma sternale Jayne (Linsley ms.)
    Trogoderma spp. (De Leon, 1939; Linsley ms.)
    Attagenus pellio (Linn.) (Linsley ms.)
    Attagenus piceus (Oliv.) (Linsley ms.)
    Anthrenus verbasci (Linn.) (Linsley ms.)
    Dermestes lardarius Linn. (Day, 1922; Walsh, 1931; Richards, 1931*a*)
  Ostomatidae
    Temnochila caerulea (Oliv.) (Clausen, 1931)
    Tenebroides corticalis (Melsh.) (Blackman and Stage, 1924; Cotton and Good, 1937)
    Tenebroides mauritanicus (Linn.) (Stephens, 1839; Fowler, 1891; Fall, 1901)
    Tenebroides nanus (Melsh.) (Cotton and Good, 1937)
    Lophocateres pusillus (Klug) (Linsley ms.)
  Nitidulidae
    Carpophilus hemipterus (Linn.) (Stebbing, 1914)
    Carpophilus spp. (Stebbing, 1914)
  Silvanidae
    Oryzaephilus mercator (Fauv.) (Guillebeau, 1890)
    Oryzaephilus surinamensis (Linn.) (Fowler, 1891; Champion, 1896)
    Cathartus quadricollis (Guer.) (Linsley ms.)
    Ahasverus advena (Watl.) (Lucas, 1849; Fall, 1901)
    Nausibius clavicornis Kug. (*auct.*)

Cucujidae
Laemophloeus ferrugineus (Steph.) (Fowler and Donisthorpe, 1913; Picard, 1919; Beare and Donisthorpe, 1922; Cotton and Good, 1937)
Laemophloeus ater (Oliv.) (Perris, 1853; Fowler, 1889; Picard, 1919)
Cryptophagidae
Cryptophagus spp. (*auct.*)
Mycetophagidae
Typhaea stercorea (Linn.) (Beare and Donisthorpe, 1922)
Litargus balteatus Lec. (Linsley ms.)
Lathridiidae
Holoparamecus caularum (Aubé) (Fall, 1899)
Holoparamecus depressus Curtis (Hinton, 1941*b*)
Coninomus constrictus (Gyll.) (Fowler, 1889)
Coninomus nodifer (Westw.) (Reitter, 1911)
Enicmus minutus (Linn.) (Beare and Donisthorpe, 1922)
Corticaria fenestralis (Linn.) (Donisthorpe, 1939)
Tenebrionidae
Alphitophagus bifasciatus (Say) (Mulsant, 1854, *et auct.*)
Platydema ruficorne Sturm (Blatchley, 1910)
Doliema pallida (Say) (Blatchley, 1910)
Doliema plana (Fab.) (Fall, 1901; Ting, *in litt.*)
Gnathocerus cornutus (Fab.) (Lucas, 1849; Chittenden, 1895*b*; Essig, 1926)
Gnathocerus maxillosus (Fab.) (Wollaston, 1860; De Leon, *in litt.*)
Latheticus oryzae Waterh. (Blair, 1930)
Latheticus prosopis Chitt. (Chittenden, 1904)
Tribolium castaneum (Hbst.) (Stephens, 1830; Lucas, 1849; Fowler, 1891; Fall, 1901; Stebbing, 1914; Blair, 1930)
Tribolium confusum duV. (Stebbing, 1914; Van Dyke, *in litt.*; Linsley ms.)
Tribolium madens Charp. (Redtenbacher, 1858; Good, 1933; De Leon, 1939)
Tribolium indicum Blair (Blair, 1930)
Aphanotus parallelus Csy. (Linsley ms.)
Aphanotus brevicornis (Lec.) (De Leon, *in litt.*; Van Dyke, *in litt*; Blaisdell, *in litt.*; Linsley ms.)
Aphanotus destructor (Uytt.) (Linsley ms.)
Cynaeus angustus (Lec.) (Van Dyke, *in litt.*; Blaisdell, *in litt.*; Linsley ms.)
Cynaeus depressus Horn (Van Dyke, *in litt.*)
Palorus ratzeburgi Wissm. (Stephens, 1832; Wissmann, 1848; Champion, 1896; Fowler and Donisthorpe, 1913; Swezey, 1942)
Palorus depressus (Fab.) (Fowler, 1891; Champion, 1896; Blair, 1930)
Palorus subdepressus Woll. (Champion, 1896)
Palorus spp. (Blair, 1930)
Uloma culinaris (Linn.) (Zacher, 1927)
Alphitobius diaperinus (Panz.) (Fall, 1901; Linsley ms.)
Alphitobius piceus (Oliv.) (Stebbing, 1914)
Sitophagus hololeptoides (Cast.) (Linsley ms.)
Tenebrio picipes Hbst. (Fall, 1901; Blatchley, 1910; Blackman and Stage, 1924)
Ptinidae
Gibbium sp. (Stebbing, 1914)
Ptinus fur (Linn.) (Fowler, 1890)
Ptinus palliatus Perris (Hinton, 1941*a*)
Ptinus rufipes Oliv. (Hinton, 1941*a*)
Ptinus lichenum Marsh. (Picard, 1919)
Ptinus hirtellus Sturm (Fowler, 1890)
Ptinus pusillus Sturm (Blair, 1930)
Ptinus subpilosus Sturm (Fowler, 1890)
Ptinus sp. (De Leon, *in litt.*)
Tipnus unicolor Pill. and Mitt. (Fowler, 1890)
Anobiidae
Stegobium paniceum (Linn.) (Stebbing, 1914; Linsley, 1942*c*, 1942*d*)

Bostrichidae
Rhyzopertha dominica (Fab.) (Gorham, 1883; Lesne, 1924; Froggatt, 1918)
Dinoderus spp. (*auct.*)
Protostephanus truncatus (Horn) (*auct.*)

Insect Nests and Food Caches.—Bee, wasp, and ant nests provide a favorable environment for other insects. Moderate temperatures, favorable humidities, and stores of food materials (pollen, seeds, dead insects) offer conditions not unlike those encountered in warehouses and human habitations. As a result, stored-products pests (and certain other household insects) are not uncommon in such nests. Unfortunately, most observers either have failed to record their occurrence or have noted them only in passing, except in the hive of the honeybee, where the presence of pests has some economic significance. Even in apicultural literature published data are inadequate, the more typical pests of stored products having been commonly confused with certain other inhabitants of the hive, especially wax moths.

In the spring of 1941, in connection with another study, eight nesting sites of *Anthophora* (five species) in seven localities in central and southern California were examined. Dermestids of several types abounded in all the sites; the California spider beetle, *Ptinus californicus,* and the confused flour beetle, *Tribolium confusum,* were present in three; the Indian-meal moth, *Plodia interpunctella,* the drugstore beetle, *Stegobium paniceum,* and the false black flour beetle, *Aphanotus destructor* in two; and the saw-toothed grain beetle, *Oryzaephilus surinamensis,* and the webbing clothes moth, *Tineola bisselliella,* each in one site. In a single colony on the edge of the Mojave Desert about 10 miles from the nearest human habitation were *S. paniceum, O. surinamensis,* and one of the dermestid beetles, *Trogoderma ajax;* and in a second area, only slightly less isolated, *Plodia interpunctella* and *Tineola bisselliella.*

Of these insects, *Ptinus californicus* is a native species which seems to be definitely associated with bees, never having been recorded as breeding outside of bees' nests. It is most common as a pollen feeder in cells of *Osmia,* especially where nesting sites are used repeatedly year after year. In the laboratory, however, it can be readily reared on cornmeal, whole wheat flour, and other cereal products. *Trogoderma ajax* is also a native species. It is the commonest dermestid associated with anthophorid bees in California and has been found infesting grain. *Aphanotus destructor* is a common pest of many stored products, especially dog biscuits, rabbit food, and various cereal products. Of the remaining species, *Plodia interpunctella, Stegobium paniceum,* and *Oryzaephilus surinamensis* live on a wide variety of plant products, apparently finding the pollen stored by bees one of many suitable foods. *Tineola bisselliella* lives as a scavenger on products of animal origin. Probably no one of these last species is native to California; yet their presence even in isolated habitats suggests that they find the environment of bees' nests satisfactory and may possibly have occupied it for a long period of time.

Among the stored-products insects and their relatives that breed or occur in nests of ants, bees, and wasps, the following may be noted:

Acarina
Acaridae
Tyrophagus sp. (bees, Linsley ms.)

Thysanura
  Lepismatidae
    Lepisma saccharina Linn. (*Vespa,* Tuck, 1896; *Anthophora, Osmia,* Linsley ms.)
    Ctenolepisma urbani Slaugh. (*Anthophora,* Linsley ms.)
Corrodentia
  Atropidae
    Atropos pulsatorium (Linn.) (*Apis, Polistes,* Essig, 1942)
  Liposcelidae
    Liposcelis divinatorius (Müll.) (bees, Linsley, 1942*a*)
    Liposcelis formicarius (Hagen) (ants, Essig, 1942)
Lepidoptera
  Phycitidae
    Plodia interpunctella (Hbn.) (*Bombus,* Frison, 1926; *Apis, auct.; Anthophora* and *Osmia,* Linsley and MacSwain, 1942*b*)
    Ephestia kühniella Zell. (*Bombus,* Davidson, 1894; *Apis, auct.; Vespa* and *Vespula, auct.*)
    Ephestia cautella (Walk.) (*Apis,* Milum, 1940*a*)
    Ephestia elutella (Hbn.) (*Apis,* Laboulbene, 1864)
    Vitula serratilineella Rag. (*Apis,* Cockle, 1920; *Xylocopa,* Linsley, 1943)
    Vitula edmandsii (Pack.) (*Bombus,* Packard, 1865, *et auct.; Apis,* Milum, 1940*b*)
  Galleriidae
    Achroia grisella (Fab.) (*Apis, auct.*)
    Aphomia sociella (Linn.) (*Bombus, Apis, Vespa, auct.*)
  Pyraustidae
    Chalcoela iphitalis (Walk.) (bees, Linsley, 1942*a*)
    Dicymolomia pegasalis (Walk.) (bees, Linsley, 1942*a*)
  Oecophoridae
    Hofmannophila pseudospretella (Staint.) (*Apis,* Hinton, 1943*a*)
    Endrosis lacteella (D. and S.) (*Acanthomyops,* Donisthorpe, 1927*b; Sceliphron,* Linsley ms.)
  Tineidae
    Tineola bisselliella (Hüm.) (*Formica,* Donisthorpe, 1927*b; Anthophora,* Linsley and MacSwain, 1942*b*)
    Trichophaga tapetzella (Linn.) (*Sceliphron,* Linsley ms.)
Coleoptera
  Histeridae
    Dendrophilus punctatus Hbst. (*Formica,* Fowler, 1889; *Lasius,* Donisthorpe, 1927*b*)
    Dendrophilus pygmaeus (Linn.) (*Formica,* Fowler, 1889; Donisthorpe, 1927*b*)
  Corynetidae
    Corynetes coeruleus (Dej.) (*Vespa,* Butler, 1896)
  Dermestidae
    Attagenus pellio (Linn.) (*Apis,* Hinton, 1943*a*)
    Attagenus pantherinus Ahrens (bees, wasps, Hinton, *in litt.*)
    Attagenus piceus (Oliv.) (*Anthophora, Osmia,* Linsley and MacSwain, 1942*b*)
    Megatoma undata (Linn.) (*Andrena,* Fowler and Donisthorpe, 1913)
    Perimegatoma vespulae Milliron (*Dolichovespula,* Milliron, 1939)
    Perimegatoma variegatum Horn (*Sceliphron,* Linsley ms.)
    Perimegatoma jaynei Csy. (*Sceliphron,* Linsley ms.)
    Trogoderma glabrum Hbst. (*Osmia, Odynerus,* Maréchal, 1932)
    Trogoderma ornatum (Say) (*Apis,* Chittenden, 1897; Patton, 1931)
    Trogoderma versicolor Creutz. (*Pelopoeus, Odynerus, Anthophora,* etc., Riley, 1883; *Sceliphron,* Linsley ms.)
    Trogoderma ajax Csy. (*Anthophora,* Linsley and MacSwain, 1942*b*)
    Trogoderma sternale Jayne (*Dolichovespula, Sceliphron, Osmia,* Linsley ms.)
    Trogoderma socium Lea (*Iridomyrmex,* Lea, 1905, 1911)
    Anthrenus museorum (Linn.) (bees, wasps, Hinton, *in litt.*)
    Anthrenus fuscus (Latr.) (*Osmia,* Maréchal, 1932)
    Anthrenus verbasci (Linn.) (*Osmia,* Linsley and MacSwain, 1942*a; Polistes, Dolichovespula, Sceliphron,* Linsley ms.)

Anthrenus spp. (*Anthophora,* Hicks, 1926; Mickel, 1928)
Dermestes lardarius Linn. (*Apis,* Riley, 1870; Lintner, 1890; Hinton, 1943*a*)
Dermestes murinus Linn. (*Philanthus,* Latreille, 1802)
Globicornis corticalis (Eich.) (bees, wasps, Hinton, *in litt.*)

Nitidulidae
Brachypeplus inquilinus Lea (*Apis,* Lea, 1912)
Brachypeplus auritus Mur. (*Trigona,* Lea, 1911)
Brachypeplus basalis Er. (*Trigona,* Lea, 1911)
Brachypeplus blandus Mur. (*Apis,* Lea, 1912)
Aethina tumida Mur. (*Apis,* Lundie, 1940)
Carpophilus planatus Mur. (*Trigona,* Lea, 1912)

Silvanidae
Oryzaephilus surinamensis (Linn.) (*Anthophora,* Linsley and MacSwain, 1942*b*)

Cucujidae
Laemophloeus ferrugineus (Steph.) (*Vespula,* Tuck, 1896)
Cryptamorpha delicata Blackb. (*Ectatomma,* Lea, 1912)

Cryptophagidae
Cryptophagus setulosus Sturm (*Vespula,* Tuck, 1896; *Bombus,* Tuck, 1896; Sladen, 1912)
Cryptophagus populi Payk. (*Colletes* and *Dasypoda,* Champion, 1918)
Cryptophagus lœvendali Ganglb. (*Vespa,* Donisthorpe, 1927*a*)
Cryptophagus pubescens Sturm (*Vespula,* Tuck, 1896; Britten, 1911; Donisthorpe, 1927*a*)
Cryptophagus umbratus Er. (*Bombus,* Tuck, 1896)
Cryptophagus punctipennis Bris. (*Bombus,* Tuck, 1896)
Cryptophagus pilosus Gyll. (*Vespula,* Tuck, 1896)
Cryptophagus scanicus (Linn.) (*Vespula, Bombus,* Tuck, 1896; *Acanthomyops,* Walker, 1920)
Cryptophagus saginatus Sturm (*Bombus,* Tuck, 1896)
Cryptophagus distinguendus Sturm (*Vespula,* Tuck, 1897; *Bombus,* Fowler and Donisthorpe, 1913)
Cryptophagus badius Sturm (*Vespa,* Tuck, 1897)
Cryptophagus dentatus Hbst. (*Acanthomyops,* Walker, 1920*b*)
Cryptophagus affinis Sturm (*Acanthomyops,* Walker, 1920*b*)
Cryptophagus fumatus Sturm (*Acanthomyops,* Walker, 1920*b*)
Cryptophagus croceus Zimm (*Bombus,* Frison, 1926)
Cryptophagus cellaris (Scop.) (*Apis,* Falcoz, 1929–1931)
Atomaria ruficornis (Marsh.) (*Vespula,* Tuck, 1896)
Atomaria peltata Kraatz (*Vespula,* Tuck, 1896)
Antherophagus pallens (Fab.) (*Bombus,* Tuck, 1896; Sladen, 1912 [as *silaceus*])
Antherophagus nigricornis (Fab.) (*Bombus,* Tuck, 1896; Sladen, 1912)
Antherophagus ochraceus Melsh. (*Bombus,* Packard, 1865; Frison, 1926; Plath, 1934)

Mycetophagidae
Mycetophagus quadriguttatus Müll. (*Vespa,* Tuck, 1896; *Acanthomyops,* Walker, 1920*b*)

Lathridiidae
Coninomus constrictus (Gyll.) (*Acanthomyops,* Walker, 1920*b*)
Coninomus nodifer (Westw.) (*Bombus,* Frison, 1926)
Enicmus minutus (Linn.) (*Bombus, Vespa,* Morley, 1899; *Acanthomyops,* Walker, 1920*b*)
Enicmus transversus Oliv. (*Acanthomyops,* Walker, 1920*b*)
Enicmus histrio Joy (*Acanthomyops,* Walker, 1920*b*)

Tenebrionidae
Tenebrio molitor Linn. (*Apis,* Hinton, 1943*a*)
Tenebrio obscurus Fab. (*Bombus,* Frison, 1926)
Tenebrio tenebroides Beauv. (*Bombus,* St. George, 1925; Frison, 1926)
Tribolium castaneum (Hbst.) (*Megachile,* Kotinsky, 1907)
Tribolium confusum duV. (*Clisodon, Anthophora, Osmia,* Linsley and MacSwain, 1942*a*)

Tribolium madens Charp. (*Apis*, Leech, 1943)
Tribolium myrmecophilum Lea (*Iridomyrmex*, Lea, 1905)
Aphanotus brevicornis (Lec.) (*Xylocopa*, Davidson, 1893; Nininger, 1916; Linsley, 1943; *Anthidium*, Hicks, 1929)
Aphanotus destructor (Uytt.) (*Osmia, Anthophora*, Linsley, 1942*a*)
Cynaeus augustus (Lec.) (*Osmia*, Linsley, 1942*a*)

Ptinidae
Ptinus fur (Linn.) (*Osmia*, Enslin, 1925; Schmitt, 1929; *Chelostoma*, Maréchal, 1932; *Vespula*, Tuck, 1896; *Vespa*, Tuck, 1896; Butler, 1896; and Husing, 1935; *Apis*, Hinton, 1943*a*)
Ptinus sexpunctatus Panz. (*Megachile*, Bedel, 1872; Redtenbacher, 1874; Maneval, 1929; *Osmia*, Hamm, 1924; Maneval, 1929; Maréchal, 1932; *Hoplitis*, Maneval, 1929; *Chelostoma*, Maneval, 1929; *Bombus*, Fowler, 1889; *Lasius*, Walker, 1920*b*)
Ptinus subpilosus Sturm (*Acanthomyops*, Fowler, 1890; Walker, 1920*b*; Donisthorpe, 1927*b*)
Ptinus hirtellus Sturm (*Sceliphron*, Linsley ms.)
Ptinus vaulogeri Pic (*Osmia*, Cros, 1932)
Ptinus californicus Pic (*Osmia, Anthophora*, Linsley and MacSwain, 1942*a*)
Ptinus raptor (Linn.) (*Apis*, Arnhart, 1929; Brassler, 1929)
Ptinus exulans Er. (*Apis*, Rayment, 1935)
Niptus hololeucus (Fald.) (*Dolichovespula*, Tuck, 1897)
Diphobia familiaris Oll. (ants, Lea, 1905)
Paussoptinus laticornis Lea (*Iridomyrmex, Cremastogaster*, Lea, 1905)
Polyplocotes longicollis Westw. (ants, Lea, 1911)
Polyplocotes nitidus Westw. (ants, Lea, 1911)
Diplocotes howittanus Westw. (ants, Lea, 1911)
Diplocotes foveicollis Oll. (ants, Lea, 1911)
Diplocotes armicollis Lea (ants, Lea, 1911)
Ectrephes formicarium Pasc. (ants, Lea, 1911)
Ectrephes kingii Westw. (ants, Lea, 1911)
Hexaplocotes sulcifrons Lea (ants, Lea, 1911)

Anobiidae
Stegobium paniceum (Linn.) (*Anthophora, Osmia*, Linsley and MacSwain, 1942*b*)

Nests and Food Caches of Birds and Mammals.—Undoubtedly a great many household pests live in the nests of birds and mammals. Included are many insect inhabitants of stored food products. A few are listed below.

Thysanura
Lepismatidae
Sp. indet. (woodrat, Davis, 1934)

Corrodentia
Liposcelidae
Sp. indet. (woodrat, Davis, 1934)
Liposcelis divinatorius (Müll.) (purple martin, bluebird, house wren, crested flycatcher, McAtee, 1927; starling, English sparrow, McAtee, 1929)

Coleoptera
Histeridae
Dendrophilus punctatus Hbst. (owl, Walker, 1896, 1904; Bickhardt, 1907; woodpecker, Auzat, 1925; Ross, 1940; jackdaw, hawk, screech owl, pigeon, Auzat, 1925; crow, hoopoe, Bickhardt, 1916; starling, Joy, 1905; Auzat, 1925; McAtee, 1929; squirrel, Donisthorpe, 1927*b*)
Dendrophilus opacus Ross (woodrat, Ross, 1940)
Dendrophilus tularensis Ross (ground squirrel, Wenzel, *in litt.*)
Saprinus semistriatus Scriba (prairie dog, Brown, 1928)
Carcinops 14-striata Steph. (owl, Walker, 1896, Bickhardt, 1907; starling, purple martin, McAtee, 1929)

Dermestidae
Trogoderma ornatum (Say) (English sparrow, house wren, McAtee, 1929)

Trogoderma versicolor Creutz. (English sparrow, house wren, McAtee, 1929)
Trogoderma sternale Jayne (Cliff swallow, Linsley ms.)
Trogoderma sp. (purple martin, McAtee, 1929)
Anthrenus verbasci (Linn.) (sparrow, Yokoyama, 1929; Herfs, 1936)
Anthrenus fuscus (Latr.) (sparrow, Yokoyama, 1929; Herfs, 1936)
Anthrenus scrophulariae (Linn.) (sparrow, Herfs, 1936)
Anthrenus pimpinellae (Fab.) (sparrow, Yokoyama, 1929; Herfs, 1936)
Anthrenus occidens Csy. (magpie, Jellison and Philip, 1933; English sparrow, house finch, black phoebe, barn swallow, Linsley ms.)
Attagenus piceus (Oliv.) (chipmunk, Linsley, 1942*b*; birds, Back and Cotton, 1938; starling, English sparrow, purple martin, house wren, bluebird, McAtee, 1929)
Attagenus schäfferi Hbst. (chipmunk, English sparrow, house finch, Linsley ms.)
Attagenus pellio (Linn.) (birds, Zacher, 1939)
Attagenus elongatulus Csy. (woodrat, Davis, 1934)
Attagenus nigripes Casey (English sparrow, house finch, black phoebe, cliff swallow, Linsley ms.)
Attagenus japonicus Reitt. (sparrow, Yokoyama, 1929; Herfs, 1936)
Dermestes elongatus Lec. (black-crowned night heron, Barber, 1914)
Dermestes signatus Lec. (crow and magpie, Jellison and Philip, 1933; house finch, Linsley ms.)
Dermestes talpinus Mann. (magpie, Jellison and Philip, 1933)
Dermestes bicolor Fab. (pigeon loft, Bickhardt, 1907)

Lathridiidae
Metophthalmus rudis Fall (woodrat, Davis, 1934)
Metophthalmus trux Fall (woodrat, Davis, 1934)
Coninomus nodifer Westw. (mole, Bickhardt, 1907; woodrat, Davis, 1934)
Melanophthalma villosa Zimm. (woodrat, Davis, 1934)
Melanophthalma americana Mann. (woodrat, Davis, 1934)
Melanophthalma distinguenda Com. (woodrat, Davis, 1934; Linsley ms.)
Melanophthalma similata Gyll. (woodrat, Davis, 1934; Linsley ms.)
Melanophthalma sp. (robin, Dobroscky, 1925)
Enicmus minutus (Linn.) (stork, Schaufuss, 1916)
Enicmus crenatus Lec. (woodrat, Davis, 1934)
Enicmus suspectus Fall (woodrat, Davis, 1934)
Cartodere ruficollis (Marsh.) (stork, Reitter, 1911)
Corticaria pubescens (Gyll.) (birds, Donisthorpe, 1939)
Fuchsina occulta Fall (woodrat, Linsley ms.)

Tenebrionidae
Tenebrio molitor Linn. (pigeon loft, *auct.*)

Mycetaeidae
Mycetaea hirta Marsh. (owls, Walker, 1896)

Cryptophagidae
Atomaria apicalis Er. (field mouse, Beare, 1921)
Atomaria fuscata Sch. (field mouse, Beare, 1921)
Atomaria sp. (woodrat, Davis, 1934)
Atomaria melas Csy. (woodrat, Linsley ms.)
Atomaria subdentata Csy. (woodrat, Linsley ms.)
Atomaria dispersa Csy. (woodrat, Linsley ms.)
Anchicera fallax Csy. (woodrat, Linsley ms.)
Anchicera nanula Csy. (woodrat, Davis, 1934)
Cryptophagus lyraticollis Csy. (woodrat, Linsley ms.)
Cryptophagus badius Sturm (owl, Fowler and Donisthorpe, 1913)
Cryptophagus umbratus Er. (rabbit, Bickhardt, 1907)
Cryptophagus schmidti Sturm (marmot, Bickhardt, 1907)
Cryptophagus sp. (woodrat, Davis, 1934)
Cryptophagus setulosus Sturm (field mouse, Beare, 1921)
Cryptophagus pubescens Sturm (field mouse, Beare, 1921)

Ptinidae
Ptinus agnatus Fall (woodrat, Davis, 1934)

Ptinus hirtellus Sturm (rats, Pilate, 1905; English sparrow, McAtee, 1929)
Ptinus fur (Linn.) (rats, Pilate, 1905; robin, Dobroscky, 1925; house wren, bluebird, McAtee, 1929)
Ptinus gandolphei Pic (barn owl, Linsley ms.)
Ptinus sexpunctatus Panz. (house martin, Blair, 1924)
Tipnus unicolor Pill and Mitt. (birds, Fowler, 1890; house martin, Hinton, 1941*a*)
Mezium americanum Lap. (sparrow, Zimmerman, 1940)
Mezium affine Boield (rats, Linsley ms.)
Curculionidae
Sitophilus granarius (Linn.) (ground squirrel, Davis and Sloop, 1934)
Lepidoptera
Tineidae
Tinea fuscipunctella Haw. (starling, English sparrow, purple martin, house wren, bluebird, crested flycatcher, McAtee, 1929)
Tineola bisselliella (Hüm.) (kangaroo rat, Hubbard, 1899)

SUMMARY

Stored-food-products insects are widely distributed in nature as well as in the warehouses, granaries, and households of mankind. This fact is probably due to a broad range of tolerance for physical factors of the environment, a wide range of food habits, and the optimum conditions for existence frequently provided by these man-made structures.

Several of the species involved (Bruchidae, *Sitophilus,* spp., *Sitotroga,* spp., and so forth) infest seeds in nature. These insects have become stored-seed pests without having to undergo further evolution of food habits.

Many insects (Cryptophagidae, Mycetophagidae, Lathridiidae, Acaridae) associated with stored products are actually fungus feeders and seek out the molds and fungi existing in the foodstuffs. In nature these species are found under bark; in nests of birds, mammals, and insects; in decomposing plant material; or in any other places where molds and fungi are present.

Many food-products pests are general scavengers on dead plant materials, principally moths (phycitids, pyralids), but also a few other groups (anobiids, nitidulids).

Scavengers on dead animal materials provide a similar source of pests. Included are *Dermestes, Piophila, Tineola,* and others.

An important natural source of stored-products pests lies among the scavengers or semipredators living under bark. To this source we must credit almost all the Tenebrionidae (flour beetles, mealworms), Cucujidae, and Ostomatidae.

The Ptinidae, Anobiidae, Bostrichidae, and Scolytidae probably had a wood-boring origin.

Insect nests also contribute a number of pests—in particular, several of the Galleriidae, Phycitidae, Ptinidae, and Dermestidae. The pollen stored by bees may sometimes have influenced the evolution of food habits by serving as a bridge between zoophagy and phytophagy.

Many insects in stored food products are predators and parasites of other insects present. A few of these, especially Histeridae, Corynetidae, Anthocoridae, are probably attracted to the products and habitat directly rather than by any specific insects present.

Primary natural reservoirs are to be found in the following habitats: (1) bark and decomposing wood; (2) nests and food caches of other insects, especially bees, wasps, and ants; and (3) nests of birds and rodents.

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