



Ecological Relations of Certain Animals in Dead Pine and Oak Logs

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ECOLOGICAL RELATIONS OF CERTAIN ANIMALS IN DEAD PINE AND OAK LOGS

By

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A thesis submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy in the Graduate School of Arts and Sciences of Duke University, Durham, North Carolina.

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INTRODUCTION

Many animals are known to live in dead tree trunks, and much is known of the habits of some of the species. Entomologists interested in economic species, taxonomists, and naturalists in general have long been interested in various groups. The purpose of this study was to make a general survey of animals in dead pine and oak tree trunks that had been cut for various lengths of time and to study the relations of certain species to their environment. A fallen tree trunk, which will be referred to as a log, is recognized as harboring a small, separate society that normally constitutes a unit (stratum) in a forest association. A log also has a microclimate that is different in many respects from climatic conditions in other parts of a forest (Graham, 1925). The knowledge of this led to the study of the factors involved in the microclimate of logs and this in turn to the effects of high temperatures and various humidities on representative species. In a study of a community of animals the subject of food is of great importance. It has been possible to deal with only a very few of the problems involved in food relations of animals in logs and their many individual physiological adaptations to their food supply.

The Duke Forest, in the midst of which Duke University is located, afforded an abundance of logs in all stages of decay, particularly of pines and oaks. For this reason, these two types of trees were selected for study. Collections were made in the Duke Forest wherever logs were found over a period of eighteen months, from September 1936, through February, 1938. All animals except nematodes and protozoans were collected. It is believed that most of the common species in the Duke Forest were thus obtained, but the number of species found is far short of all those that probably occur in the logs studied.

I wish to express my gratitude to Dr. A. S. Pearse, who suggested this problem and has given many helpful suggestions and criticisms. I am indebted to the following people for the indicated identifications: Dr. H. B. Mills, *Collembola*; Dr. A. B. Gurney, *Orthoptera* and *Zoraptera*; Dr. H. G. Barber, *Heteroptera*; Dr. Z. P. Metcalf, *Homoptera*; Dr. L. L. Buchanan, Dr. W. S. Fisher, Dr. E. A. Chapin, Dr. H. S. Barber, Dr. M. W. Blackman, and Dr. C. S. Brimley, *Coleoptera*; Dr. R. A. St. George, *Tenebrionidae* (larvae); Dr. Carl Heinrich, *Lepidoptera*; Dr. David G. Hall, Dr. Alan Stone, and Dr. C. T. Greene, *Diptera*; Dr. Grace Sandhouse, Dr. C. F. W. Muesebeck, and Dr. R. A. Cushman, *Hymenoptera*; Dr. M. R. Smith and

Miss Carolina Powell, Formicidae; Dr. R. V. Chamberlain, Myriapoda; Dr. H. E. Ewing and Mr. G. W. Wharton, Acarina; Dr. Henry van der Schalie, Mollusca. I am especially grateful to Dr. Adam G. Boving for the identification of coleopterous larvae and for his kindness in permitting me to use the collection of coleopterous larvae in the National Museum. Thanks are due to Dr. F. G. Hall and Dr. George S. Eadie for the use of their laboratory equipment. Thanks are also due to Dr. C. F. Korstian for his helpful suggestions and his kindness in furnishing logs for experimental work, to Dr. E. S. Harrar for identification of wood and advice on wood structure, and to Mr. M. R. Blackman for furnishing cutting dates of trees in the Duke Forest.

LITERATURE

SUCCESSION

The change in the fauna of logs from the time they are dead until they are completely decayed is obvious to anyone who has had much experience collecting from them, and is common knowledge to those who are familiar with forest insects. Systematic studies of logs with the view of obtaining more exact information about these changes have, however, been undertaken in only a few cases. Probably the development of the field of ecology is responsible for directing attention to logs as the habitat of a characteristic group of animals, where previously only individual species or a small number of species had been studied. Many of the early accounts of insects in rotting logs have been incidentally included in works dealing with economically important species, which are present only in weakened or recently dead trees (Packard 1890, Townsend 1886, Felt 1906). Most of the insects first attacking a tree after it dies are fairly well known since they are of economic importance.

Shelford (1913) recognized fallen tree trunks as constituting an ecological unit (stratum) in forest associations and pointed out that there is a succession of animals in a log as it decays. Stages in the succession in beech logs were outlined, and some of the characteristic animals named. Adams (1915) gave a more detailed account of the succession of species in decaying tree trunks. He pointed out that the first animals to enter a log feed in the phloem layer in which starches and sugars are stored. These species aid the entrance of wood-destroying and other fungi and after the phloem has been destroyed and the wood has begun to decay, species of animals that prefer rotten wood make their entrance. As a log sinks lower and lower into the soil and becomes covered with leaves, it blends with the humus of the forest floor. Thus, Adams says, is completed one of the most important cycles of transformation to be found in the forest habitat. Blackman and Stage (1918) bred insects from larch and list those associated with that tree the first year

after it dies. Graham (1925) studied the early invaders of coniferous logs in relation to the temperature and moisture content of the wood and discussed the factors influencing ecological succession in logs.

The work of Blackman and Stage (1924) demonstrated the succession of insects in dead hickory. Their results were obtained by caging samples of wood over a period of five years and taking the insects that emerged. Their views of succession were in accord with those of Shelford (1913) and Adams (1915). Species of animals occurring in pine stumps on a burned English heath were recorded by Richards (1926). He indicated their general food habits and the stage of decay in which they occurred (whether early or late).

MICROCLIMATE

During the past few years the term "microclimate" has come into general use in ecological literature. Uvarov (1931) points out that in ecological studies climate of the actual habitat in which an animal lives must be considered, because the standard climatic data often do not accurately represent the conditions to which an animal may be subjected. He proposes to call the climatic factors that obtain in a given medium, such as a tree trunk, a microclimate. A study of the microclimate of the actual medium where an animal lives becomes, therefore, inevitable if all the conditions to which it is subjected are to be understood.

The temperature in logs exposed to the sun has been found to vary widely from that in air. Craighead (1920) found that when logs were exposed to the sun in summer that temperatures under the bark might reach 60°C., resulting in the death of certain wood borers. This discovery led to further experiments on the application of this method for the control of injurious bark beetles (Patterson, 1930; Miller, 1931). Graham (1921, 1922, 1924, 1925) has found that the temperature under the bark of logs does not depend entirely on the air temperature but on several other factors, chief of which are: intensity of solar radiation; angle of incidence of the sun rays; color, thickness and structure of the bark; evaporation from the bark surface; air movement; and the relative humidity and temperature of surrounding air. Graham showed further that the larvae of wood borers differed in their distribution in a log according to the temperature gradient. Conspicuous for their toleration to high temperatures were species of Buprestidae and Scolytidae. The moisture gradient in a log was also shown to be correlated with the distribution of wood borers.

Harvey (1923a, 1923b) found that in winter the subcortical temperatures of plum trees with dark colored bark might be 4.5°C. warmer than similar trees with light colored bark. Gottlieb (1929) reports that pine logs about six inches in diameter have the highest subcortical temperature when exposed to the sun, other factors being equal. It has been shown that when rotten oak logs are covered with snow, temperatures in the logs did not go

below — 1.5°C. even when air temperature reached — 16°C. (Holmquist, 1931).

No references to the composition of the air under the bark of logs or in cavities made by insects have been found in the literature.

TOLERATION OF HIGH TEMPERATURES

The toleration by insects of high temperatures has been investigated by many authors. The literature on the subject has been reviewed by Uvarov (1931) who finds that, in general, insects can survive temperatures up to 50°C. He points out, however, that most of the data are not comparable since hardly any two investigators used the same experimental conditions.

The work of Mellanby (1932) has recently added much to the knowledge of the relation of insects to temperature and relative humidity. He has shown that the upper limit of toleration to temperature for small insects (larvae of *Tenebrio molitor* and flea larvae weighing less than 100 mg.) is independent of relative humidity or evaporation deficit when they are exposed for short times (one to two hours). Such insects are said to die as a result of heat rather than desiccation. Longer exposure of the same insects (twenty-four hours) results in the death of those in low humidities at lower temperatures than those in high humidities, showing that over longer periods of time death may result from desiccation or a combination of heat and desiccation. When larger larvae (*Tenebrio molitor*, weighing more than 100 mg.) were subjected to similar conditions it was found that they survived a higher temperature in dry air than in moist air. Mellanby explains that this results from the cooling effect of the evaporation of water from the bodies of larvae in dry air, enabling them to maintain a body temperature lower than that of their surroundings. That certain insects can maintain a lower body temperature than that of their surroundings by the evaporation of water from their bodies has been shown by various authors (Necheles 1924, Buxton 1924). Mellanby (1935), in a review of literature on evaporation of water from insects, concludes that in general large insects may be capable of surviving higher temperature in dry air than in moist as a result of the cooling effect produced by evaporating water.

FOOD RELATIONS

Exact knowledge of the food eaten by many common insects found in logs is very meager. Uvarov (1928) pointed out that this was true of insects in general, and that before insects could be accurately classified as to their food habits, more exact information must be obtained for a large number of species. A summary of the food habits of North American families of Coleoptera was given by Weiss (1922). In other papers, Weiss (1923, 1924) and Weiss and West (1920) have shown a large number of insects associated with various fungi. Many of these insects occur under the bark of logs. The food habits of certain predacious Staphylinidae were studied by Mank

(1923). Baumberger (1919) showed that certain dipterous larvae and mites living under bark feed on the hyphae and spores of fungi. Dipterous larvae of the genus *Miastor* also feed on fungi (Harris, 1923). The predacious habits of certain histerid beetles which as a family are considered to be saprophagous, were demonstrated by Selous (1911) and Steele (1927). The family Elateridae, whose members are largely plant feeders also include several predacious species (Fisher 1907, Thomas 1931). By examining the gut contents of carabid beetles Forbes (1883) found that many of them were not wholly predacious, and warned against suppositions as to an insect's food from its structural adaptations.

It has long been an unsettled question as to how certain insects can live on wood, since it is composed largely of cellulose and is poor in nitrogen. Cleveland (1925) at first thought termites could live without nitrogen, but it is now known that they are similar to other animals in requiring this element (Cook and Scott, 1933). The way in which insects utilize cellulose has had various explanations. Certain coleopterous larvae have been shown to secrete enzymes that break down cellulose (Cambell 1929, Ripper 1930, Falck 1930, Mansour and Mansour-Bek, 1934a). Microorganisms living in the gut of certain insects have been generally thought to enable their host to live on cellulose (Uvarov, 1928). Some evidence shows that the hosts digest part of the microorganisms (Wideman 1930, Hungate 1938). The general occurrence of mycetones in wood-eating insects had led to the assumption that they are in some way connected with cellulose digestion. Mansour and Mansour-Bek (1934b), however, are strongly opposed to such an assumption.

Another group of insects apparently do not depend at all on cellulose in wood for their carbohydrates, but subsist on stored starches and sugars in wood. This is particularly true of certain cerambycids living in the phloem of freshly cut trees (Mansour and Mansour-Bek, 1934a) and of *Lyctus* power-post beetles living in the xylem (Wilson 1933, Parkins 1936).

METHODS

SUCCESSION

Collections were made from logs and from slash of trees that had been cut for logs. Animals were found by peeling off the bark or by cutting into the wood with a hand ax. Some were preserved in alcohol and others were brought to the laboratory alive in one-ounce, metal, ointment boxes. Attempts were made to rear all larvae found. The larvae were put in individual ointment boxes with some of the wood from which they had been taken. These boxes were kept in a closed wooden cabinet at room temperature, a few drops of water being added from time to time. Wood-eating larvae were successfully reared when the moisture conditions were properly maintained and when they were not attacked by fungi.

All pine logs from which collections were made were probably either short leaf pine (*Pinus echinata* Mill) or loblolly pine (*Pinus taeda* L.), since these are the common species of pines in the Duke Forest. The common oaks in the Duke Forest are white oak (*Quercus alba* L.), southern red oak (*Quercus borealis* Michx., *rubra* L.), northern red oak (*Quercus borealis* Michx., *maxima* (Marsh) Ashe), black oak (*Quercus velutina* Lam.), and post oak (*Quercus stellata* Wang). No attempt was made to separate species of animals according to the species of oak or pine in which they were found. Logs were considered as either pines or oaks. No difficulty was found in distinguishing very rotten pines and oaks.

The cutting dates of many logs were obtained from the foreman of the Duke Forest. Though this paper, the "age of logs," refers to the length of time since the tree was felled and not the age of the tree. Where cutting dates were not available the age of a log was estimated by comparison with logs of known age. Since cutting dates were not available for many logs over three years old they were all classed as later stages.

MICROCLIMATE

Temperature in logs. Records of the temperature under the bark and in the wood of logs were obtained with a three pen, Friez thermograph, of the vapor pressure type, taking a weekly record sheet. Three thermograph bulbs made it possible to obtain simultaneous records at three separate points. The thermograph bulbs were 18 cm. long and 0.6 cm. in diameter, and were attached to the recorder by a 3.0 meter flexible cable. A hole of the proper diameter to take a bulb was bored in the end of a log to a depth great enough for the sensitive part of the bulb to be at least 12 cm. from the outside. After the bulb was inserted, the space around the cable was packed with sawdust or asbestos paper. The recording part of the instrument was housed in a standard Weather Bureau shelter. In the same shelter a combined hydrograph and air temperature recorder, making weekly records, was kept. The accuracy of both instruments was checked frequently with a thermometer. Temperatures as recorded by the instruments never differed more than $\pm 0.3^{\circ}\text{C}$. from the reading of the thermometer. Part of this inaccuracy results from the coarseness of the line traced on the record sheet by the recording pen.

These instruments were put into operation in February, 1937. Pine and oak logs that had been freshly cut, and one-, two-, and three-year-old logs were hauled to one place. They were from 30 cm. to 60 cm. in diameter and about two meters long. They were arranged parallel to each other in two rows and the weather shelter containing the instruments was placed between the rows. In this way, any log could be reached by the cable of the temperature recorder. The situation chosen was on level ground on top of a hill, in shade, in a stand of oaks. Records were obtained of the temperature at different depths in the series of logs.

The instruments were moved in June, 1937, to an open situation where temperature records were obtained from logs in full sun. During the winter of 1937-1938, temperature was recorded in logs in full sun and in logs in an advanced stage of decay.

Moisture of Wood. Samples of wood were collected in the field and placed in soil sample cans with tight covers. The samples were weighed and dried to constant weight at 105°C. Moisture was calculated as percentage of the dry weight of the wood.

Air in Logs. A survey was made of some logs that had been dead from 2 to 4 years to see if unusual amounts of CO₂ could be found in the air under the bark. Some preliminary trials during November and December were made, but the methods of sampling permitted a certain amount of contamination of the air sample. A mercury reservoir was attached by a convenient length of rubber tubing to a glass tube 8 cm. in diameter and about 25 cm. in length. Constrictions were placed in the glass tube near the ends to facilitate sealing with a blow torch. A needle was attached to the sample tube. A small hole was drilled through the bark and the needle was inserted quickly and packed with plasticene. The mercury had previously been brought up to the end of the needle. Thus, when the reservoir was lowered, a sample of gas was drawn into the sampling tube. The air sample obtained was approximately 10 cc. in volume.

During June and July the possibility of contamination of the sample was greatly lessened by rigid emplacements of copper tubing under the bark of several selected logs. These tubes were packed with putty and painted with shellac until there were no leaks around them. They were kept closed by a section of thick rubber tubing closed with a pinch clamp. A "T" of glass tubing placed between the sample tube and the copper tubing made it possible to expel all air from the sampling apparatus before a sample was drawn in.

The samples were analyzed in a Henderson modification of the Haldane apparatus.

TOLERATION OF HIGH TEMPERATURES

To test the toleration of some coleopterous larvae to high temperatures of two hours duration, two methods were used. By the first, a Warburg apparatus with Barcroft manometers was used. In the second, an apparatus similar to that used by Mellanby (1932) was used. In both methods relative humidity was controlled by the use of proper concentrations of an aqueous solution of potassium hydroxide following the tables given by Buxton and Mellanby (1934) for the relation between the specific gravity of the hydroxide solution and the humidity of the air over it. The water bath was heated electrically and the temperature controlled to within $\pm 0.25^{\circ}\text{C}$.

In testing the toleration of coleopterous larvae by the first method the following procedure was carried out. Solutions of potassium hydroxide were

made up to the required specific gravity for each degree of relative humidity used. One cc. of potassium hydroxide solution was placed in each manometer cup—0.5 cc. in side arm and 0.5 cc. in the central cup. The cups were then attached to the manometers and placed in the water bath and left for 10 to 15 minutes to allow them to reach the temperature of the water bath. The manometers were then removed. A larva that had been weighed was placed in each cup, and returned as quickly as possible to the bath to prevent too much cooling. After two hours, the larvae were removed from the bath, weighed and placed in petri dishes with moistened paper. It was not always possible to tell immediately if the larvae were alive after subjection to high temperatures, since they were limp and immobile. After two to three hours, however, a larva that had not been killed would usually move when it was disturbed. The procedure was repeated using fresh larvae and different temperatures until the limit of toleration was reached.

The apparatus for the second method consisted principally of a one-pint glass Mason fruit jar with a screw cap. A wide-mouthed bottle, small enough to go in the mouth of the Mason jar, was cemented bottom side down on the inside of the screw cap. A larva to be tested was placed in the small jar, over the mouth of which a piece of cheese cloth was secured with a rubber band. When the jar cap was screwed on, the small bottle cemented to it was suspended upside down over the potassium hydroxide solution with the larva resting on the cheese cloth. The jars were placed in a water bath for temperature regulation.

FOOD RELATIONS

In order to gain a knowledge of the materials eaten by certain insects, microscopic examinations were made of the gut contents and feces by spreading them out on a slide in glycerine. Fungus hyphae and spores could be identified as such, but the species of fungi to which they belonged were not determined. Predaceous species were found to contain mostly liquid and semi-solid material in their gut. Interspersed in this material were many oily droplets. When such material was found in insects of unknown feeding habits it was assumed that it was of animal origin. This criterion was used by Forbes (1883) in similar studies on predaceous Carabidae, and seems to be valid. In some cases fragments of exoskeletons could be identified, but species of animals that served as food could not be determined.

The habits of a cerambycid (*Callidium antennatum* Newn.) and a buprestid (*Chrysobothria* sp.) living under the bark of pine logs made it possible to determine the approximate amount of wood they consumed as larvae. A larva of *Callidium antennatum* Newn. begins its burrow entirely within the inner layer of phloem, which is from 0.5 to 1.5 millimeters thick, but as it grows it makes its burrow deeper by gnawing into the sapwood. An examination of the frass in the burrows showed that the fecal pellets contain only phloem, the greater portion of the frass being sapwood that

had never been eaten. When the larva is mature (in the prepupal instar) it makes a burrow 3 to 9 cm. into the sapwood toward the heartwood, and somewhat concentric with the annual rings. It then turns sharply and bores 5 to 10 cm. lengthwise of the grain. The frass accumulated from this boring is cast out of the burrow and some is pushed out through holes that are bored in the bark. The larva then seals itself into the end of its burrow with a tightly packed wad of fine frass.

When the bark was carefully removed from logs containing larvae, it was possible, in some cases, to expose the tortuous burrow of one larva that was separate from any other burrow. The fine, tightly packed frass in all of the burrow except in the area around the hole into the sapwood was removed. A piece of paper was then placed over the burrow and pressed with the fingers so that an impression was formed in the paper by the rim of the burrow. This impression was then outlined with a pencil and its area determined in the laboratory with a planimeter. Such data were obtained from October to December, 1937, at which time most of the larvae were in the sapwood in their cells. In each case the larvae were dug out, weighed, and placed in an oven at 60°C. to determine the amount of water they contained.

Ten samples of living phloem from five freshly cut loblolly pines from 20 to 30 cm. in diameter were collected in November, 1937. The bark was carefully removed so as to get all the living phloem off with the cork layer. Measured areas of the living phloem were then removed and placed in separate containers. The dry weight of these samples was then used to arrive at the average dry weight of the phloem covering one square centimeter of surface. The area of a burrow was multiplied by the average dry weight of the phloem covering one square centimeter of surface to obtain the approximate amount of wood that a larva had consumed.

Since *Chrysobothris* sp. had habits similar to *Callidium antennatum*, the same procedure was carried out for it. During the time when collections were made some were still feeding, while others were in cells in the sapwood.

Some qualitative tests for an enzyme attacking cellulose were carried out following a method similar to that described by Mansour and Mansour-Bek (1934a). The gut of the larva to be tested was dissected out and the juice it contained drained into a depression slide. A series of these slides were prepared using the juice from one larva, or from two larvae in the case of smaller individuals, for each slide. The materials tested were sections of lettuce midrib, slices of white pine wood, and filter paper. To each slide were added a few drops of toluol to prevent bacterial action. The slides were covered and left at room temperature. Control slides were prepared with water and boiled juice, to which were added the materials to be tested. They were examined after 6, 12, and 24 hours for evidence of breakdown of the fibers in the case of filter paper, or the cell walls in the case of wood

and lettuce, by removing the section from the slide, washing with water, and staining with zinc-chlor-iodide solution. Evidence of breakdown of the cell walls was taken as a positive test.

Portions of the gut contents of each larva were studied microscopically to see if bacteria or protozoa could be found that might possibly be considered as symbiotic.

Samples of living phloem were obtained from three freshly fallen shortleaf pines (*Pinus echinata*) in November, 1937. The samples were from trees about 30 cm. in diameter and were taken about 1.3 meters from the base of the tree. The living phloem was obtained by scraping it from the bark and sapwood after the bark was peeled off. The samples were dried at 105°C. and ground in a ball mill. The part passing through a 100 mesh screen was taken for analysis.

The method described by Sullivan (1935) was used for the determination of the amount of starch in two-gram portions of the ground wood samples. In this method, starch is extracted from the wood by boiling the sample in a concentrated calcium chloride solution. The starch is precipitated with alcohol and caught on a filter, redissolved in water, precipitated with iodide and ammonium sulphate and caught again on a filter. The starch is hydrolyzed with hydrochloric acid, and glucose determined by the Hagerdorn-Jenson method. The amount of starch is calculated by multiplying the glucose by the conversion factor, 0.9. For qualitative tests for starch, a potassium iodide-iodine solution was used.

RESULTS

SUCCESSION

A complete list of the animals collected from pines and from oaks is given in the appendix. The age of the log, where each species was found, the stage in its life cycle occurring in logs, the relative frequency of its occurrence, and its food habits are given. Estimates of the frequency of occurrence of the various species is based on the number of logs from which they were collected and their relative abundance in a log. The estimates are, therefore, not very accurate, but, in the writer's opinion, are better than no estimate at all. If an animal was found in over 50 per cent of the logs examined, it is considered to be "common." The occurrence of an animal in small numbers and in less than half the logs is called "occasional" in the table. Animals found only once or a few times are considered to be "rare." Those animals that are considered to be "common" undoubtedly include most of those important in the ecology of logs in the Duke Forest. Many species are known to breed in logs, and the number of species reported in this paper might easily be doubled by long and careful collecting. All the logs examined were in upland forest. Logs in swamps and river bottoms might contain additional species.

The small number of parasitic Hymenoptera and Diptera shown is due to the fact that no special effort was made to rear parasites from various hosts and therefore does not indicate their relative importance. Caged samples of wood containing larvae would undoubtedly have yielded many more parasitic Hymenoptera and Diptera. A total of about 155 pine logs were examined over a period of 18 months from September, 1936, to February, 1938. Over 135 species of animals were found. During the same period about 125 oak logs were examined and a total of over 165 species of animals were collected.

SUCCESSION IN PINES

First-Year Pine

About fifty logs of various sizes and in various situations (both in shade and exposed to sun) were examined. Collections were made in all seasons of the year from logs less than one year old. About 95 species of animals were found. Since a few species in several groups, particularly Diptera and Acarina, were not determined, a more exact number cannot be given. According to their known or probable feeding habits, the animals collected may be grouped as follows: phloem-feeders, 22; sapwood feeders, 4; saprophytic or myctetophagous, 37; predacious, 29; parasitic, 9. The number of species was distributed in various groups as follows: Insecta, 76; Myriapoda, 4; Chelonethida, 3; Acarina, 8. The Insecta were represented by the following orders: Collembola, 6; Thysanura, 1; Orthoptera, 1; Heteroptera, 1; Homoptera, 1; Coleoptera, 55; Hymenoptera, 7; Diptera, 9.

The first animals found in logs after they were cut were beetles feeding in the phloem. In this group of animals there were eight cerambycids, four buprestids, three curculionids, and seven scolytid. As a result of the activity of these insects the bark becomes loosened from the sapwood. From an ecological viewpoint, the cerambycids and scolytids are very important, since they are responsible for most of the destruction of the phloem.

Monochamus titillator and *Acanthocinus obsoletus* were the most common cerambycids found, but under certain conditions other species were predominant. For example, in pine logs up to 30 cm. in diameter that were in contact with the ground and were in dense shade, the cerambycid *Rhagium lineatum* was commonly found, and in some cases, to the exclusion of other phloem feeders. *Rhagium lineatum* was also associated with *Monochamus titillator* and *Acanthocinus nodosus* in logs exposed to sunlight, but in such cases they confined their activities to the lower parts of a log, away from regions of bark that might be exposed to direct sun rays. *Acanthocinus nodosus* was rarely found in logs, but was a characteristic species in stumps. *Asemum moestum* was found only rarely in logs, but was common in stumps and the lower parts of standing dead trees.

In some pine poles, up to 20 cm. in diameter, that had been split from large logs and piled in open racks exposed to partial sunlight, a cerambycid,

Callidium antennatum, and a buprestid, *Chrysobothris* sp., were the only phloem feeders found. In certain racks a difference in the fauna of poles at different heights from the ground could be seen. In poles next to the ground, away from direct sunlight, *Rhagium lineatum* was the characteristic phloem feeder. In some cases *Asemum moestum* was also present. In certain poles, which were partially or totally shaded and about 0.6 meters above the ground. *Monochammus titillator*, *Acanthocinus obsoletus*, and *Ips calligraphus* were characteristic. Poles on top of racks about one to two meters high had become quite dry from exposure to the sun and contained only larvae of *Callidium antennatum* and *Chrysobothris* sp.

In general, species of scolytids and curculionids were more abundant in logs during the spring and early summer. Most of the pine logs examined had been cut in winter. Therefore the beetles probably oviposited in the spring when the phloem was still fresh. The fact that they complete their life cycle within three to four months would thus partially explain their greater abundance during the spring and early summer. Logs that had been cut in July contained many scolytids, principally *Ips calligraphus* and *Dendroctonus valens*, as late as the following November.

From the viewpoint of the amount of phloem they destroy, the most important scolytids in logs in the Duke Forest appear to be *Ips calligraphus* and *Ips grandicollis*; the most important curculionids, *Pissodes memorensis* and *Hylobius pales*. *Pachylobius picivorus* was found only once.

Following the loosening of the bark by the activity of various beetles feeding in the phloem, another group of animals, having quite different habits from the phloem-feeders, begin to appear under the bark. In such situations about 60 species of animals were collected, most of which were insects. The orders of insects represented were: Collembola, 6; Orthoptera, 1; Heteroptera, 1; Homoptera, 1; Coleoptera, 29; and Diptera, 3. Classed according to their known or probable food habits, there were 37 species found feeding on fungi or decaying animal and vegetable matter and 23 species with predatory habits. Collembolans, mites and Diptera were by far the most numerous from the standpoint of number of individuals. From the standpoint of number of species, the Coleoptera were most numerous, being represented by 29 species.

Predacious species associated with the subcortical fauna were of two types; those that lived entirely under the bark in the larval or adult stage, or both, and species such as centipedes and ants that were found running over the outside of logs as well as under the bark. The latter do not confine their activities to logs, but may also be found in the litter of the forest floor. Certain beetles were found that are predacious in both the larval and adult stage, such as ostomids, clerids, histerids, and staphylinids. Other species, such as *Alaus myops*, are predacious in logs only in the larval stage. Predacious insects associated with the phloem feeders were *Alaus myops*, *Tem-*

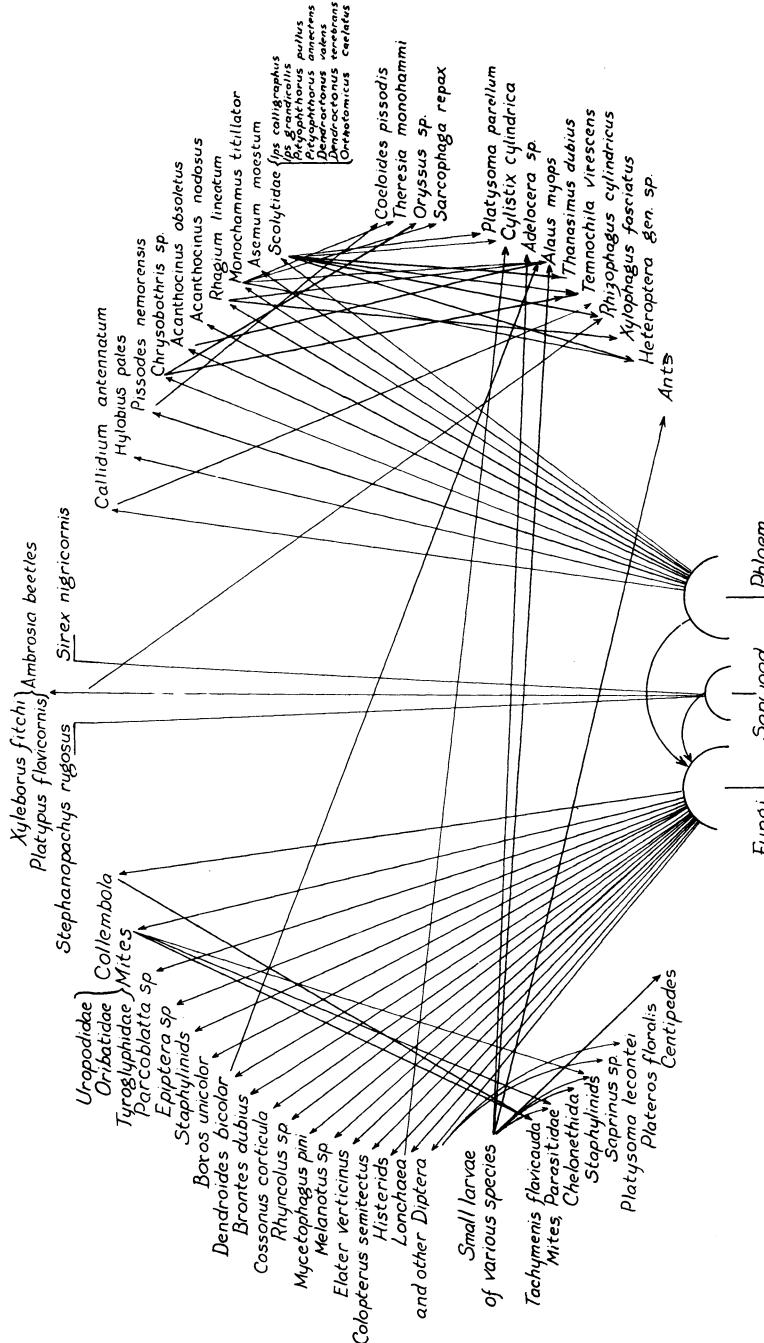


FIG. 1. The food relations of animals in a pine log the first summer after it is cut. The arrows point from the source of food to the animal consuming it. The figure is based on observations of logs in various situations and is not entirely applicable to any particular log.

nochila virescens, *Thansimus dubius*, and an unidentified heteropteran. The clerid, *Thanasimus dubius*, confines its attacks almost exclusively to scolytids. Adults prey on adult scolytids; larvae feed on the larval scolytids in their galleries under the bark. The unidentified heteropteran also feeds largely on scolytids both as a nymph and as an adult, but it was also seen to pierce the bodies of *Monochamus titillator* and *Acanthocinus nodosus*. *Temnochila virescens* and *Alaus myops* feed on various phloem feeders.

The parasitic Hymenoptera and Diptera collected were all from phloem-feeding larvae. Those obtained were usually reared from cocoons found in burrows.

Sapwood contained very few species of animals. A siricid, *Sirex nigricollis*, was the only species found that probably feeds for most of its life in the sapwood. Species of cerambycids and buprestids that form pupal chambers in the sapwood probably do not feed to any great extent on the wood removed from their burrows. Sapwood removed by *Monochamus titillator* in forming its pupal chamber is usually in long shreds which obviously have not been eaten. A platypodid, *Platypus flavigornis*, found in the sapwood, is known to be one of the ambrosia beetles that feed on fungi growing in its burrow. A scolytid, *Xyleborus fitchi*, also has similar habits. Species such as cerambycid, *Asemum moestum*, and the buprestids, *Buprestis* sp. and *Chalcophra* sp., apparently feed in the sapwood after they have first bored through the phloem, and continue to feed in it the second year after a tree is dead.

Second-Year Pine

About 50 logs, up to about 0.6 meters in diameter, exposed to various amounts of sunlight were examined. About 67 species of animals were found. Classed according to their known or probable food habits there were: phloem-feeders, none; sapwood-feeders, 11; saprophytic or mycetophagous, 28; predacious, 27; parasitic, none; nesting in log, 1. The number of species in each group of animals was as follows: Insecta, 54; Myriapods, 4; Cheloneethida, 3; Acarina, 3; Mollusca, 2. The class Insecta was represented by six orders: Collembola, 6; Thysanura, 1; Orthoptera, 1; Isoptera, 1; Coleoptera, 36; Diptera, 4.

During the second year after a pine log is cut, the activity of wood-rotting fungi, which began during the first year, becomes more apparent. The two most common wood-rotting fungi in pine logs in the Duke Forest are *Polyporus abietinus* (Dicks) Fries and *Peniophora gigantea* (Fries) Massee. The bark is usually very loose and, after the emergence of the various phloem feeders, is punctured by many holes. This permits more water to get under the bark during rains, and at the same time probably permits more rapid evaporation of water from under the bark. In most of the logs investigated the phloem had been entirely eaten away during the first year. Small logs exposed to the sunlight or not in contact with the ground

were exceptions. They were probably much drier than larger logs which were either partially shaded or in contact with the ground.

The characteristic phloem-feeding insects of the first year logs are not present during the second year, except such species as *Asemum moestum*, *Buprestis* sp. and *Chalcophoro* sp. all of which were found in rotting sapwood. Eleven species of insects were found feeding in the sapwood. The most characteristic of these was the termite, *Reticulitermes flavipes*. It was rarely found in logs less than one year old, but during the second year, large colonies were frequent in logs in contact with the ground. Species of elaterids that entered logs the first year and fed on frass were also present, but in many cases they were feeding in sapwood that had become soft from wood-rotting fungi. Larvae of the tenebrionid, *Xylopinus rufipes*, and the melandryid, *Hypulus concolor*, were found feeding in soft rotting sapwood. A species of Bostrichidae, commonly called "powder-post beetles," was found in pine holes that had been piled in open racks exposed to sunlight.

The subcortical fauna of animals that followed the phloem-feeders into logs the first year was present during the second year. Larvae of *Dendroides bicolor* and *Boros unicolor*, both typical subcortical larvae, were more abundant. Nests of the ants, *Camponotus herculeanus pennsylvanicus* and *Lepitinothrox curvispinosus* were common. In some logs two or more large colonies were found.

Species of predators, such as *Thanasimus dubius*, *Temnochilla virescens*, and an unidentified heteropteran, that was associated with phloem-feeders in the first year were not found. *Alaus myops*, however, was present. Larvae of this species found in one-year-old logs had never been longer than 10 to 15 mm., but in two-year-old logs larvae up to 30 mm. in length were found. It seems probable that they require at least two years for their development. A pupa and an adult were found in October, 1937, in a large pine stump that was about two years old. Small larvae (up to 10 mm. long) of *Alaus myops* were also found, which indicates that the females do not restrict their oviposition to first-year logs. Predators, such as species of histerids and staphylinids, that probably feed on mycetophagous species were still present. Nests of a solitary wasp *Trypoxylon clavatum* were found in the emergence holes of *Monochamus titillator* and *Acanthocinus nodosus*.

Third-Year Pine

About 30 logs that were between two and three years old were examined. Logs of this age usually had little bark left on them, especially if it had been thin. Bark as thick as 3 cm. and over was usually still on a log during the third year, but such bark was found only on logs as much as 40 to 50 cm. in diameter. The extent to which logs had rotted varied. Logs in the forest, where they were partially shaded were attacked by fungi to a greater extent than logs exposed to more sunlight. In some places on a log fungi

often had reduced the sapwood to a punky condition, while on the same logs areas that had not been attacked to such an extent could be found. When bark had fallen away, the sapwood was relatively solid for a depth of 2 to 5 cm., forming a rather solid shell of wood around the log. Beneath this shell the sapwood was usually rotted to a much greater extent, and contained more moisture.

About 50 species of animals were collected. According to their known or probable food habits, they may be grouped as follows: feeding on rotting sapwood, 15; saprophytic or mycetophagous, 25; predaceous, 12; nesting in logs, 1. Most of the insects found in two-year-old logs were also found in three-year-old logs, along with several additional species. Termites were still present with the addition of another large elaterid larvae, *Orthostethus infuscatus*. Two tenebrionids not previously found were *Uloma punctulata* and *Scotobates calcaratus*. Both species were characteristic of soft punky wood. Larvae and adults of *Uloma punctulata*, both of which feed on rotting wood, were present. *Xylopinus rufipes* larvae had been found in two-year-old logs and were still quite common in soft wood. Another species found for the first time was an Oedemerid, *Copidita thoracica*. A cerambycid larva belonging to the genus *Leptura* was also found in three-year-old logs, and is probably the same species found in two-year-old logs. *Passalus cornutus* were present in only one log.

The presence of a subcortical fauna was, of course, dependent on the presence of bark. The number of species was not as great as in the first- and second-year logs. Collembola were common and always associated with them was a carabid *Tachymenis flavicauda*. Larvae and adults of a cucujid, *Brontes dubius*, were found in some logs. Under fragments of bark remaining on logs next to the ground, the larvae of *Dendroides bicolor* occurred. The adult of the weevils, *Cossinus corticola* and *Rhyncolus* sp. were present, but never in the large number found in first- and second-year logs. The snails *Euconulus cherisinus* and *Zonitoides arboreus* were found under logs and under bark. A slug, *Philomycus carolinensis* was present under the bark of some logs that were very moist.

Fewer species of predaceous insects were collected than in one- and two-year-old logs, chiefly because fewer predaceous staphylinids and histerids were taken. *Alaus myops* was still present under bark and in the burrows of *Leptura* sp. and *Xylopinus rufipes*. Centipedes were common under bark, and in some cases small spiders were present, but the latter were not identified.

Logs Over Three Years Old

Since cutting dates for logs over three years old were not available, the latter stages of succession in pines could not be followed in logs of known age. In order to learn what animals might be present in the latter stages of decay, logs that were entirely softened or punky were selected for examination. Probably the age of logs over three or four years old is not very

significant because the amount of decay seems to vary considerably in logs of different sizes and under different conditions of moisture. The fungi that cause sapwood rot in pines in the Duke Forest usually leave the wood in a soft and somewhat stringy condition. Since the summer wood is attacked more slowly, the wood may be pulled apart with the hands into strips held together by summer wood. The bark had fallen off of most logs. Those exposed to partial sunlight usually had a dry shell of relatively sound wood from 3 to 6 cm. thick around them. Beneath this shell the wood had the typical punky texture.

Twenty-five logs were examined and over 35 species of animals were collected. The following groups of animals were represented by the number of species indicated: Insecta, 26; Acarina, 3 +; Myriapoda, 2; Mollusca, 2; Vertebrata, 1. The insects were represented by the following orders: Collembola, 4; Orthoptera, 1; Coleoptera, 14; Diptera, 3 ±; Hymenoptera, 3 ±. On the basis of their food habits, the animals collected may be classified as follows: feeding on rotting wood, 9; probably saprophytic or mycetophagous, 20; predaceous, 7. A solitary bee, *Halictus* sp., was found in its nest in three logs. Larvae, pupae, and adults were collected in August, 1937. Species that were found for the first time were *Derobrachus brunneus*, *Halictus* sp., *Polygyra thyroidus*, *Polydesmus serratus*, and a salamander, *Plethodon glutinosus*.

The most common wood-feeders were elaterid larvae. Large larvae of *Orthostethus infuscata*, and smaller larvae of the genera *Melanotus* and *Elater* were common. *Derobrachus brunneus* was found in very rotten pine but there were never more than two or three individuals in a log. *Leptura* sp. was also present in moist wood. Probably the most characteristic insect of this stage of wood decay was a tenebrionid, *Uloma punctulata*, which feeds in both larval and adult stages on decayed wood. It was found in every log examined. *Reticulitermes flavipes* was present in a few rotten logs of this stage, but large colonies were never found. When present, it was attacking portions of log that were not punky. In a very moist wood, fly larvae belonging to the families Chironomidae, Cecidomyidae, and Dolicopodidae were found. Representatives of other families of flies probably occur in such wood. A snail, *Polygyra thyroidus* was present in three logs. *Philomyicus carolinensis* was common in and under moist logs. Beneath logs the larvae of a lucanid, *Pseudolucanus capreolus*, were regularly found along with larvae of an unidentified scarabid.

A predaceous carabid, *Tachmenis flavicauda*, was still present in moist wood where there were many collembolans. The larvae of *Alaus myops*, a predaceous species, were collected in logs containing larvae of *Leptura* sp. and *Derobrachus brunneus*. A carabid, *Clitina* sp., was present in one log. This species is possibly not predaceous, since other species of the genus are known to feed on sprouting corn (Blatchley, 1910). Adults of *Platysoma*

lecontei that were found were probably feeding on dipterous larvae with which they were associated. Only two species of centipedes were found, but it is likely that others occur since they migrate into logs from the soil.

None of the species found were very numerous in any log. In the logs examined there was a striking scarcity of animals in comparison to earlier stages of decay in pines, or in comparable stages of decay in oaks.

SUCCESSION IN OAKS

First-Year Oak

About 40 logs of various sizes and in various situations (both in shade and exposed to sun) were examined for animals. Collections were made in all seasons of the year from logs less than one year old, and about 50 species of animals were found. Unidentified species of Diptera and Acarina make it impossible to give a more exact number. The following groups were represented by the numbers of species indicated: Insecta, 37; Chilopoda, 2; Chelonethida, 2; Acarina, 9. Insects were represented by the following orders: Collembola, 4; Orthoptera, 1; Coleoptera, 2; Hymenoptera, 9; and Diptera, 3. All these animals may be classified according to their known or probable feeding habits as follows: feeding on phloem, 7; feeding in the sapwood, 1; saphrophytic, mycetophagous, or scavengers, 20; predacious, 17; parasitic, 5.

The common cerambycids found boring in phloem were *Xylotrechus colonus*, *Graphisurus fasciatus*, and *Romaleum atomarium*. *Neoclytus scutellaris* was found only once. Many other species are known to feed in the phloem of oak and doubtless occur in the Duke Forest, but are probably not of general occurrence.

Only one species of scolytid, *Orthotomicus collatus*, was collected. Most of the logs examined had been cut longer than six months, thus many scolytids had probably left the logs. The burrows of several species of scolytids could be seen in logs, but specimens were not obtained. Only one species was found feeding in the sapwood of oak logs less than a year old; this was a wood-boring hymenopteran, *Tremex columba*. In logs exposed to the sun only species of buprestids were found boring in the phloem on the top side of the logs. The most common species was *Chrysobothris femorata*. Larvae of a species of *Dicerca* were also present. Larvae of a species of *Agrilus* were very common in oak stumps, but only rarely present in oak logs. In the same logs in which buprestids were boring on the top side, larvae of *Romaleum atomarium* and *Graphisurus fasciatus* were consistently found boring in the phloem on the lower parts which were partially shaded, or did not receive the direct rays of the sun during the middle of the day.

The activity of phloem-feeding larvae had the effect of loosening the bark, but it also was found that the bark might become loosened by drying of the sapwood and bark. A subcortical fauna, not feeding on phloem, was

found where the bark had become loosened either by the action of phloem-feeding larvae or by drying of the sapwood. Some of the most characteristic species under such bark were Diptera. Larvae of a phorid, *Megaselia* sp. and a sapromyzid, *Lonchaea* sp., were bred. The larvae of *Lonchaea* sp. were often present in great numbers where the bark was moist. As many as 30 larvae were found in an area of about 25 cm.² The phorids are probably predacious on other fly larvae. The cucujids, *Silvanus imbellis*, *S. planatus*, and *Brontes dubius* were in nearly every log that contained a subcortical fauna. Both adults and larvae were present. The adults, and probably the larvae, feed on fungi. Mites of several species were present in great numbers. Some, such as the Parasitidae, are doubtless predacious, while other species, such as the Uropodidae, probably feed on fungi, or are scavengers. Several species of Collembola were present. Other species feeding on fungi were staphylinids and a histerid, *Acritus exiguus*. The small histerids, *Bacanius punctiformis*, *Epierus* sp., and *Epierus regularis* also probably feed on fungi. The larvae of *Melanotus* sp. were common in frass left by wood-borers.

Probably the most characteristic predator in oak logs is a carabid, *Tachyta nana*. It feeds on mites and collembolans, and was present in every log examined that was sufficiently moist to be tolerable to its prey. The histerids, *Platysoma lecontei* and *P. carolinum*, were common under bark and were usually associated with fly larvae on which they feed. *Chariessa pilosa marginata* was common. It is predacious (Felt, 1906) and was associated with podurans, fly larvae, and cucujid larvae. All the parasite species were associated with wood-borers, and were usually reared from cocoons found in burrows. In some cases the remains of a cerambycid host made its identification possible. An unidentified tachinid was reared from *Romaleum atomarium* and larvae parasitized with as many as nine fly larvae (probably of the same species) were found.

Second-Year Oak

About 40 logs less than two years old were examined. A total of about 88 species of animals were collected, which belonged to the following groups: Insects, 68; Chilopoda, 6; Chelomethida, 2; Acarina, 9 +; Mollusca, 3. Insects were represented by the following orders: Collembola, 6; Thysanura, 1; Zoraptera, 1; Isoptera, 1; Orthoptera, 1; Coleoptera, 42; Hymenoptera, 9; Diptera, 4 ±. Classed according to their probable food habits, the animals may be divided thus: feeding in rotten sapwood, 19; feeding in phloem, 4; saprophytic and mycetophagous, 40 +; predacious, 30; parasitic, 4.

During the second year wood-rotting fungi, of which the polypores are most common, soften the sapwood, either generally or at least in scattered patches. The sapwood is usually not softened to a depth of more than 3 centimeters. The mycelia of fungi are often quite thick in the inner bark in logs that have not been entered by phloem-feeding insects. The bark is

always intact, but is punctured by the exit holes of buprestids, scolytids and cerambycids.

The phloem-feeding cerambycids *Romaleum atomarium* and *Graphisurus fasciatus* were still present. Larvae of a species of Dicera were found in some logs. Apparently the larvae of *Romaleum atomarium* require more than one year to complete their development. Two-year-old logs contained larvae which varied in size from mature to very small. This indicates that the females do not restrict their egg-laying to fresh logs. Larvae feed both on the inner bark and on rotten sapwood.

Several beetle larvae which bore in rotten wood were found for the first time. Apparently wood must first be attacked by fungi before these can enter. The most common species was the tenebrionid, *Alobates pennsylvanica*. It was observed that they were always burrowing in wood attacked by "white-rot" fungi. They were found in practically all logs examined. A related species *Merinus lacvis* was found only once. The adults of *Passalus cornutus* were observed in newly formed burrows in rotten patches of wood. *Reticulitermes flavipes* were present in logs in contact with the ground, where they were tunneling through the rotten wood on the underside of logs. The burrows of the platypodid, *Platypus quadridentatus*, were often numerous in stumps and were present in most of the logs. They form tunnels in the sapwood and heartwood in which a fungus grows that serves as their food. A predacious colytid, *Colydium lineola*, was found in their burrows.

The tenebrionids, *Uloma punctulata*, *Xylopinus saperdoides*, *Dioedus punctatus*, and *Scotobates calcaratus*, were present in about half of the logs examined. They were never present in great numbers in logs less than two years old, but seemed to be more characteristic of more advanced stages of decay in which there was rotten sapwood.

The carpenter ant, *Camponotus herculeanus pennsylvanica*, was found in about 10 per cent of the logs examined. It excavates the sapwood and heartwood to form places for its nests.

The subcortical fauna was similar to that of logs during the latter part of the first year, but more species were collected. The melandryid, *Synchroa punctata*, and the pyrochorid, *Dendroides bicolor*, were found under bark in logs where the phloem had been eaten out by phloem-feeders. In the moist frass under the bark a great variety of species was found. Many such insects feed on fungi, while others are predacious. Collembolans and mites were numerous. A rare insect, *Zorotypus hubbardi*, was found under bark. Both nymphal stages and adults of an aradid bug, *Mezira granulata*, were common. The food of this insect was not determined. Essig (1926) says the aradid are predacious, and Comstook (1930) says they are supposed to feed on fungi. Nymphs of a fulgorid, *Epiptera* sp., were found in small colonies feeding on a powdery looking fungus. Cockroaches were present under the bark of nearly every log.

Fly larvae of several species were present under the bark of every log that was moist. The number of individuals was often very great. They are probably an important source of food for many small predacious staphylinids, histerids, and other predacious species.

Typical predacious beetle larvae found were those of *Alaus oculatus*, *Chariessa pilosa emarginata*, and certain staphylinids and histerids. Larvae of *Alaus oculatus* as long as 3 cm. were found, and, although there were never more than two or three in a log, their effect on the population of various larvae must be considerable. Adults of certain staphylinids and histerids were found that are doubtless predacious. Several specimens of Chelonethida (pseudoscorpions) were found under bark. Usually only one or two were seen in a log. They are predacious, but, on account of their small size and their scarcity, cannot affect the community of animals in logs very much. Centipedes run through the litter on the forest floor and certain species are regularly found running over bark and into spaces under the bark. *Geophilus varians*, *Cryptops hyalina*, and *Linotaenia bidens* were common. They probably feed on various small larvae. *Geophilus varians* was once seen carrying a termite. *Scolopendra viridis* is a large species and was not as numerous as the small species. Usually only one or two were found in a log.

Third-Year Oak

Most logs between two and three years old no longer contain solid sapwood, but the heartwood is still solid. The bark is usually still intact. About 25 logs were examined, and the following groups of animals were represented by the numbers of species indicated: Insecta, 70; Chilopoda, 6; Diplopoda, 2; Chelonethida, 1; Acarina, 11 ±; Mollusca, 5; Annelida, 1. Insects were represented by the following orders: Coleomolida, 3; Zoraptera, 1; Isoptera, 1; Orthoptera, 1; Heteroptera, 1; Homoptera, 1; Coleoptera, 51; Hymenoptera, 6; Diptera, 4 ±; Lepidoptera, 1. The animals collected may be classified according to their known or probable food habits as follows: feeding on rotten sapwood, 20; feeding on fungi and rotten frass under bark, 50; predacious or scavengers, 25; on fungi in burrows in the heartwood, 1. The total number of species was 95.

About 25 species of animals were found in logs two to three years old that were not found in one- or two-year logs. Certain of these were characteristic of very rotten sapwood and heartwood. Such species were *Uloma punctulata*, *Dioedus punctatus*, *Scotobates calcaratus*, *Oylopinus saperdoides*, *Scolecocampa liburna*, and *Pseudolucanus capreolus*. Other species such as certain staphylinids, *Platypus quadridentatus*, *Eupsalis minuta*, *Euparius marmoreus*, *Chelanops* sp., *Tenebroides* sp., and certain oribatid mites possibly occur in younger logs, but they were not encountered.

The most characteristic wood-boring beetle larvae were those of *Alobates pennsylvanicus*. *Passalus cornutus* occurred more frequently than in second-

year logs. *Romaleum atomarium* was still present, but only large larvae were found. Other species feeding on rotten wood were those that were previously mentioned as being new entrants into logs in the second year. *Reticulitermes flavipes* was a common inhabitant of rotting wood, and often occurred in large colonies, in contrast to the smaller colonies present during the second year of decay.

The subcortical fauna was similar to that of two-year-old logs, but *Dendroides bicolor* and *Synchroa punctata* were present in greater numbers. The larvae of these insects were usually the first animals that were seen when the bark was pulled from a log.

In parts of logs where no phloem-feeder had been, there was often a thick mat of fungus mycelia, probably of wood-rotting fungi, between the bark and wood. In such places several species of fungus beetles were found feeding on the fungi. As they ate out the fungus hyphae they formed small places between the bark and wood very much as phloem-feeders do in solid wood. Species found were the adults of *Platydemia ruficornis*, *Haplocephala bicornis*, several unidentified coleopterous larvae, fly larvae, and the adults of staphylinids of the tribe Aleocharinae. In one instance a chelonethid, *Chelanops virginica*, was found eating a small larva. Small larvae that appeared from their structure to be predacious were also found. These were possibly staphylinids or histerids. The predacious larvae of *Alaus oculatus*, *Charissa pilosa marginata*, *Philonthus* sp., and other unidentified species that appeared to be predacious from their large heads and long sharp mandibles, were common under bark. Adults of several predacious staphylinids and histerids were found. Centipedes of several species were common. Ants were found in every log, either under the bark, or running over the log. They probably feed on small larvae and various animal remains (Wheeler, 1913). Chelonehtids were found rarely.

Logs Over Three Years Old

As mentioned previously the sapwood of an oak log is fairly well rotted by the end of the third year. Following this there seems to be a period of several years during which the sapwood disintegrates further and eventually both the bark and sapwood begin to weather away. It was not possible to follow these stages in logs of known ages. Thus, logs in which the heartwood had begun to rot were selected for study in order to learn the animals associated with this stage of decay. Some of the logs studied had patches of the bark remaining, and others that were probably older consisted of a mass of rotten heartwood, with various amounts of solid heartwood as a core. The observations were based on logs that appeared to have been solid when felled. Trees attacked by heart-rot before they were cut would naturally disintegrate more rapidly. The heartwood in the logs examined had been attacked by "red-rot" fungi. Rotten wood of this type could be crumbled with the hands.

Twenty logs were examined and 96 species of animals were collected. Various groups were represented by the following number of species: Insects, 68; Chilopoda, 4; Diplopoda, 4; Acarina, 9; Chelonethida, 1; Annelida, 1; Mollusca, 7; Vertebrata, 1. Insecta were represented by the following orders with the number of species indicated: Collembola, 3; Thysanura, 1; Orthoptera, 1; Isoptera, 1; Coleoptera, 48; Diptera, 5 +; Lepidoptera, 1; Hymenoptera, 8. All these animals may be classified according to their food habits as follows: feeding on rotting wood, 30; feeding on fungi, or disintegrated wood under bark or beneath logs, 39; predacious, 25; nesting in rotting wood, 1.

The most characteristic animals were those feeding on rotting wood. The presence of many of the species listed apparently depended on a coverage of bark which was often lacking. The rotten wood caterpillar, *Scolecampula liburna*, occurred in only two logs in which a small amount of sapwood remained. This is in contrast to its common occurrence in rotten sapwood in logs up to three years old. The scarabid, *Polymoecus brevipes* was found in large numbers in very rotten logs. In a log about 50 cm. in diameter and 10 meters long, it was estimated that there were about 150 larvae to the cubic meter. Larvae of another scarabid, *Trichiotinus bidens*, were found in two logs. The large larvae of a lucanid, *Pseudolucanus capreolus*, were found in nearly every log examined. In some cases they were under a log where they had formed small earthen cells. Another lucanid found as a larva was *Dorcus (brevis?)*. Only two were collected. Lucanids found as adults in rotting wood were *Ceruchus piceus* and *Platycerus quercus*. Larvae of the prionid, *Derobrachus brunneus*, varying in length from 1.0 to 7.0 cm. were found in rotting heartwood of eight logs. Larvae of *Xylopinus saperdoides* were common. Larvae of *Meracantha contracta* were found in very soft wood on the underside of logs. The small active larvae of an alleculid, *Hymenorus* sp. were common in heartwood attacked by "red-rot" fungi.

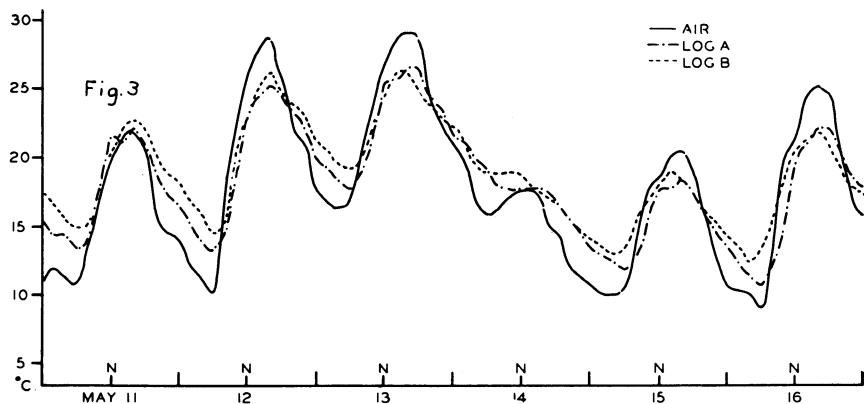
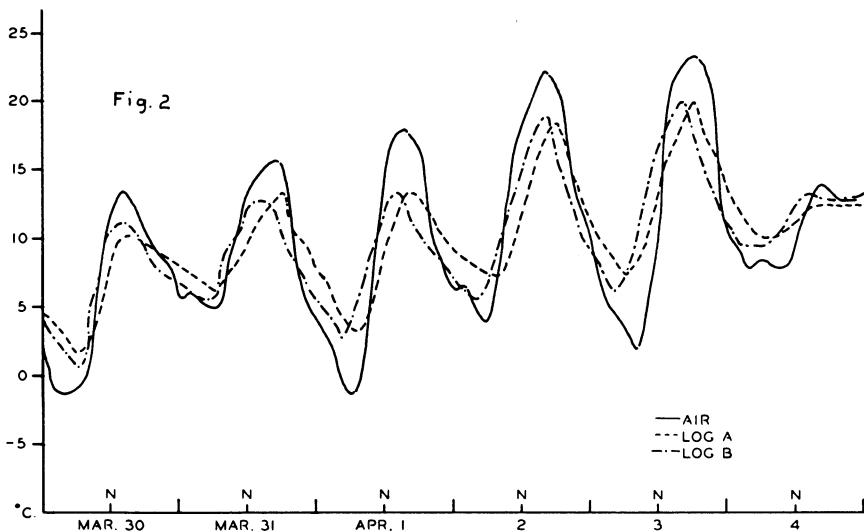
Probably the most important predacious animal was the larvae of an elaterid, *Alaus oculatus*. It will be noted that the presence of this species in logs of all stages has been mentioned. In the latter stages of decay it was observed feeding on *Pseudolucanus capreolus*. Adults and pupae were found in the burrows of *Derobrachus brunneus*. Probably it also feeds on the many larvae of *Polymoecus brevipes* that are often present, and on other large wood-boring larvae.

MICROCLIMATE

TEMPERATURE

The subcortical temperature in two-year-old pine logs exposed to the sunlight in August was considerably higher than air temperature (FIG. 4). The mean daily maximum temperature under the loose pine bark, 1 cm. thick, for the period August 3-9, 1937, was 43.2°C., whereas the mean daily maximum temperature in air for the same period was nearly 10°C. less. The

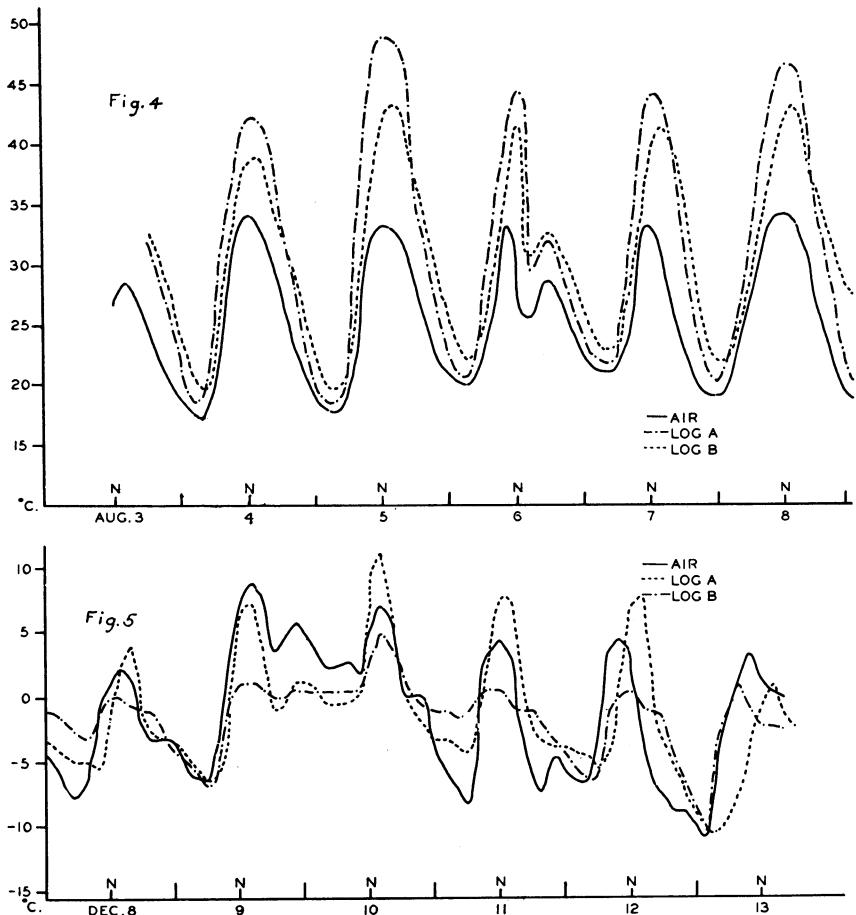
mean weekly temperature under the bark and in air for this period was 28.1 and 25.4°C., respectively, the difference being 2.7°C. The highest temperature recorded under loose pine bark was 48.9°C. when the air temperature was 33.3°C. The minimum daily temperature under loose bark in air was very nearly the same.



FIGS. 2-3. 2: Temperature record in a pine log about 30 cm. in diameter that was one year old. The bark was about 1.5 cm. thick. "Log A," temperature in the sapwood at a depth of 5 cm. from the bark on the upper side. "Log B," temperature in the sapwood of the same log at a depth of 2 cm. from the bark on the upper side.
3: Temperature record in an oak log about 30 cm. in diameter that was one year old. The log was lying north and south in the shade. The bark was about 1.0 cm. thick. "Log A," temperature under the bark on the top side. "Log B," temperature in the same log, 2.5 cm. deep in the sapwood on the top side.

In pine logs exposed to sunlight in December, the rise of subcortical temperature over air temperature was evident but not as pronounced as that in August. During this period the highest temperature recorded under bark

was 12.1°C . when the air temperature was 7.2°C . The temperature record for December 8-14, 1937 (FIG. 5) is representative of the type of records obtained from November 30 to December 28.



Figs. 4-5. 4: Temperature in pine log, about eight months old, lying north and south in full sunlight. The bark had been loosened by bark beetles and cerambycids, and was about 1.0 cm. thick. "Log A," temperature under the bark on the top side. "Log B," temperature under the bark of a pine log of the same age and in the same position. The bark was about 3.0 cm. thick. 5: Temperature in a pine log, exposed to sunlight. The bark was loose and about 2.5 cm. thick. "Log A," temperature under the bark on the top side. "Log B," temperature 2.5 cm. deep in the sapwood on the top side of the same log.

Temperature in all logs in shade fluctuated with air temperature in all seasons of the year, but the temperature under the bark or in sapwood of a log did not reach the maximum or minimum temperature recorded in air. The mean temperature in both air and in a log over a given period, however, was very nearly the same. The temperature record for the week March 30-

April 5 (FIG. 2), for example, shows that the mean maximum temperature under the bark of a two-year-old pine was 3°C. lower than that in air. During the same period the mean minimum temperature under the bark was 2.6°C. higher than in air. The temperature record obtained May 11-17 in a rotten oak log is also shown (FIG. 2) as an example of those obtained in logs in shade.

In records made of subcortical temperature in one-year pine logs in December, 1937, the daily minimum temperature under bark or 2.5 cm. deep in the sapwood, and in air were on some days very close together, while on other days they differed by several degrees. It will be seen in FIGURE 5 that on December 11, 1937, the minimum temperature 2.5 cm. deep in the log was — 1.5°C. while the minimum air temperature was — 8.9°C. The minimum temperature under the bark of the same log was at the same time about — 3.9°C. Two days later when the air temperature fell to — 11.1°C., the temperature both under the bark and 2.5 cm. deep in sapwood was — 10.5°C. During this time the thermograph bulbs in the log had not been disturbed. On December 9 there also was little difference in the minimum air temperature and the temperatures in the same log, the temperatures at both depths in the log and in air being about — 6.6°C.

AIR IN LOGS

Eleven samples of air taken from under the bark of oak and pine logs in October and December, 1937, showed from 0.24 to 1.83 per cent carbon dioxide by volume. These samples were taken by boring a hole through the bark and inserting a needle to draw out gases by the method previously described. It is probable that some contamination of the samples resulted. Another series of samples was collected in June, 1938, from a series of logs in which tubes had been rigidly emplaced for connection to the sampling apparatus. Percentages of carbon dioxide as high as 5.53 were found (Table 1). The decrease in the oxygen content of the samples from that of air was approximately equal to the increase in carbon dioxide content. The location of the ten tubes from which samples were taken follows :

TABLE 1. ANALYSIS OF AIR IN LOGS.

Log No.	CO ₂ %	O ₂ %	CO ₂ +O ₂ %	Log No.	CO ₂ %	O ₂ %	CO ₂ +O ₂ %	Log No.	CO ₂ %	O ₂ %	CO ₂ +O ₂ %
1	2.97	18.61	21.48	4	0.23	20.04	20.22	7	11.97	9.39	21.36
1	3.26	17.87	21.13		1.48	20.24	21.72		4.52	17.07	21.59
1	1.20	20.19	21.39		1.77	18.35	20.12		4.96	16.01	20.97
1	5.53	15.53	21.06	5	0.72	19.86	20.58	8	2.28	17.88	20.16
1	4.95	16.68	21.23		1.12	19.94	21.06		0.94	20.06	21.00
2	0.45		0.69	20.13	20.82	9	2.53	18.89	21.42
2	0.79	19.71	20.50	6	0.63	20.38	21.01		2.68	18.33	21.01
3	0.58	20.23	20.81		0.25	21.88	22.13	10	0.89	19.45	20.34
3	0.20	20.78	20.98		0.44	20.52	20.96		1.95		

No. 1—Under the bark on the top side of an oak log four years old and about 40 cm. in diameter. The sapwood under the bark was soft and the bark loose.

No. 2—Same log as No. 1. Tube ran through sapwood into the punky heartwood about 60 cm. from end of log.

No. 3—Same log as No. 1. Tube inserted to depth of about 30 cm. into the center of the end of log. All heart was rotten and punky. Passalus working around tube.

No. 4—Under bark on top side of a pine log one year old, about 25 cm. in diameter. Exit holes of buprestids and cerambycids were plugged for radius of about 10 cm.

No. 5—Hole bored into the end of a three-year-old pine log about 25 cm. in diameter. Sapwood was rather solid but had been attacked by fungi leaving pores through the wood.

No. 6—Tube under the bark of pine log one year old and about 30 cm. in diameter.

No. 7—Under bark and one inch into sapwood of a pine log three years old. Log about 75 cm. in diameter.

No. 8—Tube 30 cm. into the end of a pine log two years old.

No. 9—Tube inserted into a Passalus burrow under bark of an oak log about four years old. Log about 75 cm. in diameter.

No. 10—Same log as No. 9 on the top under the bark. The bark was loose and perforated by cracks and exit holes of beetles.

MOISTURE IN LOGS

The moisture content of the 69 logs tested varied widely during the spring and summer. Those that consistently had a low moisture content were small poles that were rotten and exposed to sun. Values for these logs ranged from 26 to 53 per cent. The moisture content shortly after rains was naturally greatest. Logs that were punky took up water quickly since the wood was very porous and the bark was either perforated in many places or lacking. Moisture content of such wood was as high as 372 per cent. Often various logs that had been cut only one year showed moisture contents up to 60 per cent after rains, and logs two years old contained as much as 198 per cent. Throughout the spring and summer of 1937 when samples were taken none were found that contained less than 50 per cent moisture except the pine poles previously mentioned. The frass under the bark of pine logs the first summer after they were cut contained from 102 to 293 per cent moisture.

These results are presented only to show the variation in moisture content of some representative logs from which collections were made and do not represent a comprehensive survey of logs under all conditions. Since most of the collections were made from logs in the forest it is to be ex-

pected that moisture contents found are higher than would be found in logs in open situations exposed to more sunlight.

TOLERATION OF HIGH TEMPERATURES

In the experiments on thermal death points at different relative humidities, the following larvae were investigated:

Cerambycidae	<i>Romaleum atomarium</i> (Drury)
	<i>Monochammus titillator</i> (Fab.)
	<i>Acanthocinus nodosus</i> (Fab.)
Buprestidae	<i>Chrysobothris</i> sp. (probably <i>femorata</i> Oliv.)*
Pyrochroidae	<i>Dendroides bicolor</i> (Newm.)

Larvae were collected one to three days before they were used, and kept at room temperature in one-ounce metal cans with some of the wood from which they were collected. To determine the amount of water lost, the weight of the feces deposited during an experiment was deducted from the total weight lost. In experiments on larvae of *Acanthocinus nodosus* and *Chrysobothris* sp., a Warburg apparatus was used. The other larvae were tested in jars in a water bath.

TABLE 2. RESULTS OF EXPOSING LARVAE OF *Chrysobothris femorata* TO VARIOUS TEMPERATURES AND HUMIDITIES FOR TWO HOURS.

HUMIDITY 10-15 PER CENT			HUMIDITY 95-100 PER CENT		
No. Larvae	Temp. °C.	Results	No. Larvae	Temp. °C.	Results
3	50	Alive	4	50	Alive
4	51	Alive	3	51	Alive
4	52	3 alive, 1 dead	4	52	2 alive, 2 dead
4	53	Dead	4	53	Dead

Chrysobothris sp. larvae (Table 2), collected on August 5 and 6, 1937, from the bark of white oak logs in which they had formed hibernating cells, survived at temperatures as high as 52°C. when the humidity was either 10-15 or 90-95 per cent. The average loss of water for four individuals under each of these conditions was 8.6 and 2.4 per cent respectively.

Larvae of *Monochammus titillator* (Table 4), collected August 9 and 12, 1937, from under pine bark survived a temperature as high as 50°C. when the relative humidity was 10-15 per cent, with an average loss of water for three individuals of 26.9 per cent. In humidities of 50 per cent larvae survived at 49°C., with an average water loss for three individuals of 17.7 per cent. In a saturated atmosphere larvae only survived temperatures as high as 44°C. with no loss of water.

* The larvae of *Chrysobothris* have not been sufficiently described to make accurate determinations possible. *Chrysobothris femorata* has been reared from several logs, and the larvae of that species appear to be similar to those used in these experiments.

Larvae of *Romaleum atomarium* (Table 3), collected from oak logs and stumps September 4 and 5, 1937, survived a temperature of 49°C. when the relative humidity was 10-15 per cent, with an average water loss for four individuals of 26.9 per cent. They survived temperatures of 46°C. when the relative humidity was 50 per cent, and lost 12.7 per cent of their body weight. In a saturated atmosphere, 45°C. was the highest temperature tolerated.

Acanthocinus nodosus (Table 5), collected from under pine bark September 14, 1937, endured temperatures as high as 46°C. when humidity was at 10-15 per cent, with an average loss of water amounting to 16.1 per cent. When humidity was 90-95 per cent, 44°C. was the highest temperature at which they survived, the corresponding water loss amounting to 1.7 per cent.

Larvae of *Dendroides bicolor* (Table 6), collected under bark of rotting oak logs, survived at temperatures as high as 41°C. when humidity was either 10-15, 50, or 100 per cent. Under these conditions they lost 19.1 per cent of their body weight by evaporation of water in 10-15 per cent humidity; 14.5 per cent at 50 per cent humidity; and 0.0 per cent in a saturated atmosphere.

TABLE 3. RESULTS OF EXPOSING LARVAE OF *Romaleum atomarium* TO VARIOUS TEMPERATURES AND HUMIDITIES FOR TWO HOURS.

HUMIDITY 10-15 PER CENT			HUMIDITY 50 PER CENT			HUMIDITY 95-100 PER CENT		
No. Larvae	Temp. °C.	Results	No. Larvae	Temp. °C.	Results	No. Larvae	Temp. °C.	Results
4	45	Alive	3	46	2 alive, 1 dead	8	43	Alive
3	46	Alive	2	48	Dead	4	45	Dead
4	48	Alive	4	49	Dead	2	46	Dead
4	49	3 alive, 1 dead	8	50	Dead			
8	50	Dead						

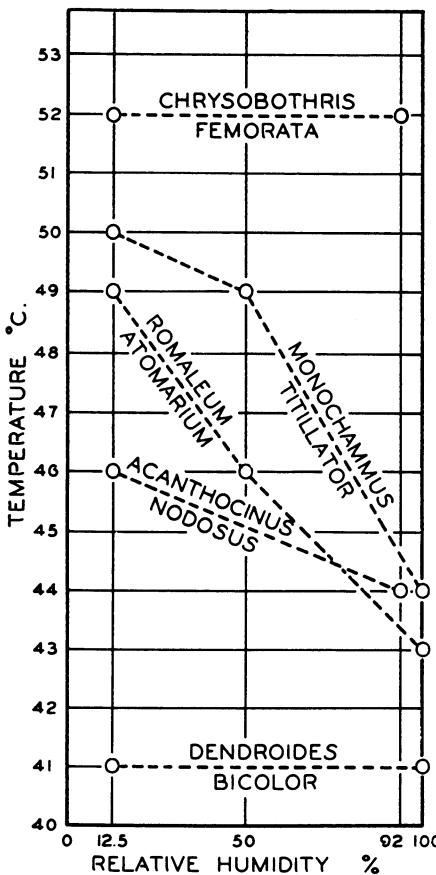


FIG. 6. Toleration of coleopterous larvae to high temperatures of two hours duration in atmospheres of different humidities. Each point represents the highest temperature tolerable.

TABLE 4. RESULTS OF EXPOSING LARVAE OF *Monochamus titillator* TO VARIOUS TEMPERATURES AND HUMIDITIES FOR TWO HOURS.

HUMIDITY 10-15 PER CENT			HUMIDITY 50 PER CENT			HUMIDITY 95-100 PER CENT		
No. Larvae	Temp. °C.	Results	No. Larvae	Temp. °C.	Results	No. Larvae	Temp. °C.	Results
4	44	Alive	2	46	Alive	8	43	Alive
3	46	Alive	3	49	Alive	4	44	2 alive, 2 dead
3	49	2 alive, 1 dead	3	50	Dead	2	49	Dead
3	50	2 alive, 1 dead	4	51	Dead	2	50	Dead
4	51	Dead						

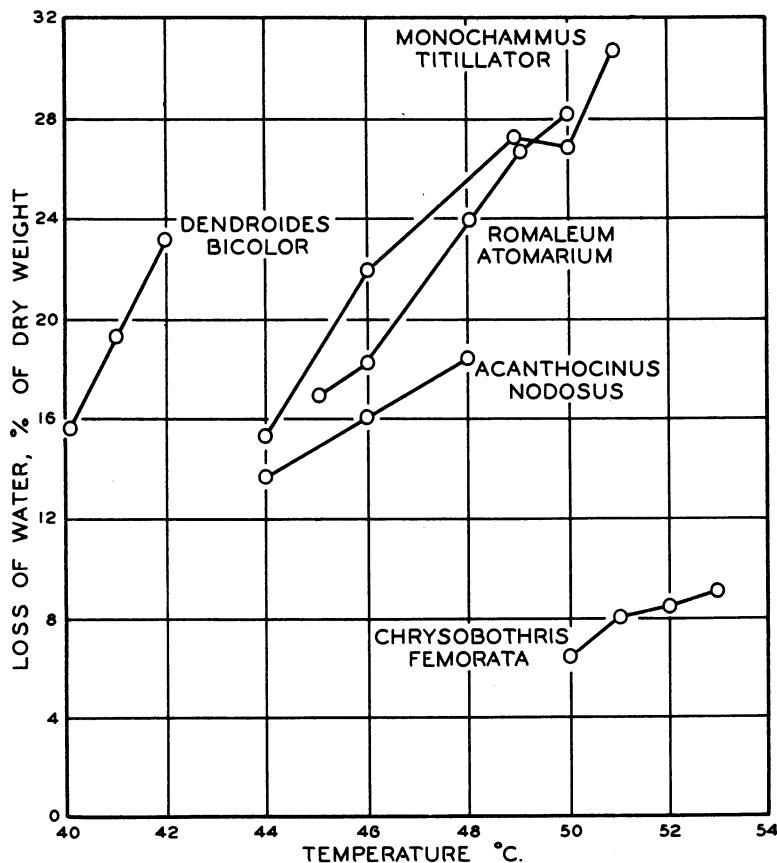


FIG. 7. Relation between temperature and the percentage body weight lost as a result of evaporation of water by various coleopterous larvae. Larvae were exposed for two hours in an atmosphere of 10-15 per cent relative humidity (Table 7).

TABLE 5. RESULTS OF EXPOSING LARVAE OF *Acanthocinus nodosus* TO VARIOUS TEMPERATURES AND HUMIDITIES FOR TWO HOURS.

HUMIDITY 10-15 PER CENT			HUMIDITY 50 PER CENT			HUMIDITY 95-100 PER CENT		
No. Larvae	Temp. °C.	Results	No. Larvae	Temp. °C.	Results	No. Larvae	Temp. °C.	Results
4	44	Alive	2	48	Dead	8	43	Alive
4	46	Alive				4	44	1 alive, 3 dead
4	48	Dead				4	46	Dead
						2	48	Dead

TABLE 6. RESULTS OF EXPOSING LARVAE OF *Dendroides bicolor* TO VARIOUS TEMPERATURES AND HUMIDITIES FOR TWO HOURS.

HUMIDITY 10-15 PER CENT			HUMIDITY 50 PER CENT			HUMIDITY 95-100 PER CENT		
No. Larvae	Temp. °C.	Results	No. Larvae	Temp. °C.	Results	No. Larvae	Temp. °C.	Results
3	40	Alive	3	40	Alive	3	40	Alive
3	41	Alive	3	41	Alive	3	41	Alive
4	42	Dead	2	42	Dead	3	42	Dead

It will be observed that *Chrysobothris* sp. with the highest thermal death point lost less water than any of the other species. Larvae of *Dendroides bicolor* lost more water than the other species in relation to the temperature to which they were subjected (Table 7, FIG. 7). Toleration of all larvae to high temperatures is presented in FIGURE 6.

TABLE 7. RESULTS OF EXPOSING LARVAE IN HUMIDITY OF 10-15 PER CENT AT VARIOUS TEMPERATURES FOR TWO HOURS.

Upper figure, temperature; lower figure, loss in body weight (in per cent) from evaporation of water.

<i>Chrysobothris femorata</i>	50° 6.3	51° 8.1	52° 8.6	53° 9.2	
<i>Monochammus titillator</i>	44° 15.2	45° 22.1	49° 27.3	50° 26.9	51° 30.7
<i>Romaleum atomarium</i>	45° 17.0	46° 18.6	48° 24.1	49° 26.9	50° 28.3
<i>Acanthocinus nodosus</i>	44° 13.9	46° 16.1	48° 17.5		
<i>Dendroides bicolor</i>	40° 10.3	41° 14.5	42° 14.7		

FOOD RELATIONS

In order to learn what foods were eaten by insects in logs, the gut contents of certain species were examined. Species that were obviously boring in wood were not examined. In some cases, it was doubtful as to whether

a species was predacious or feeding on fungi when it was found under bark, and it was to such species that more attention was given. In the following paragraphs the results of the examinations are given.

Tachymenis flavicauda Say (Carabidae), 10 adults. Fragments of mites and collembolans were found in the gut. The legs of mites of the families Uropodidae and Trombidiidae could be identified. Collembolan remains consisted of antennae, scales, parts of the furcula, and legs. This species is common under pine bark.

Tachyta nana (Gyll) (Carabidae), 10 adults. Contents of the gut of these carabids were similar to those of *Tachymenis flavicauda*. *Tachyta nana* is common under oak bark.

Cossonus corticola Say (Curculionidae), 8 adults. Collected from under pine bark where they are common. Fungus hyphae and spores were found in the gut.

Canosoma crassus Grav. (Staphylinidae), 5 adults. This staphylinid was common under oak bark. Only fungus hyphae and spores were found in the gut. Two individuals contained only round black spores. The others had about 50 per cent hyphae and 50 per cent spores of various shapes.

Platysoma lacontei Mars. (Histeridae), 10 adults. Found under oak bark. Food in the gut appeared to be entirely of animal origin. Individuals were confined with fly larvae with which they were associated under the bark. The fly larvae were eaten in every case. Two individuals ate six fly larvae in one day.

Ecritus exiguum (Er.) (Histeridae), 3 adults. These small histerid beetles were found under oak bark. Only black fungus spores were found in their guts.

Saprinus sp. (Histeridae), 6 larvae. The gut contents of these larvae showed that food was of animal origin. A few fungus spores and particles of wood were found in four specimens. It is probable that these were taken in with other food. *Saprinus* larvae were common under pine bark where there were many dipterous larvae. Three of them were confined with six of the dipterous larvae and at the end of 24 hours all of the latter had been eaten. The shriveled integuments of the fly larvae remained, showing that the soft parts of their bodies had been eaten.

Cylistix cylindrica (Payk) (Histeridae), 10 adults. Only an oily liquid, probably of animal origin, was found in the gut. The insects occurred under pine bark where there were many fly larvae. When confined with some of these fly larvae (probably *Lonchaea* sp.) they ate them readily.

Thanasimus dubius (Fab.) (Cleridae), 10 adults. Adults collected from pine that contained many scolytids under the bark. *T. dubius* was seen catching and eating adults of *Ips calligraphus* on logs. In the laboratory it would immediately attack and eat out the soft parts of the adults of that little

beetle placed with them. The gut contents of the ten adults collected from logs consisted entirely of animal matter.

Dendroides bicolor Newn. (Pyrochroidae), 20 larvae. Fungus hyphae and spores made up approximately 90 per cent of the gut contents. The rest consisted of particles of wood and liquid.

Ischiodontes sp. (Elateridae), 10 larvae. The larvae of this elaterid were found under pine bark. Only particles of wood with a few fungus hyphae and spores were seen in the gut contents.

Alaus, 10 larvae, from pines and oaks. (*Alaus myops* is found in pines and *A. oculatus* in oaks.) An oily chyme in which a few small particles of wood and fungus spores were sometimes found. Larvae brought to the laboratory ate any kind of larvae placed before them. In the field they were observed feeding on the larvae of *Monochammus titillator*, *Derobrachus brunneus*, *Pseudolucanus capreolus*, *Polymoecus brevipes*, *Alobates pennsylvanica*, and *Romaleum atomarium*.

Temnochila virescens (Ostomidae), 10 larvae. The gut contents consisted of an oily chyme, indicating that animal food had been eaten. A few particles of wood were found in some larvae. Observations on the feeding habits of these larvae show that they are general feeders. They were found in the pupal cells made in the sapwood by *Monochammus titillator* where the partially eaten larvae of that beetle gave evidence of their predatory habits. The larvae of *T. virescens* was also found in the pupal chambers formed by *Callidium antennatum* and *Chrysobothris* sp. in pine poles. In such cases it could be seen that the larvae of *T. virescens* had tunneled through the burrow of these borers, apparently to search them out and eat them. In certain empty pupal chambers that could not be accounted for by the emergence of the wood borers or by the attack of a parasite, a small burrow, apparently made by *T. virescens*, was seen leading from the frass left by the borer to its pupal chamber in the sapwood.

Brontes dubius Fab. (Cucujidae), 9 adults, 1 larva. Occurs under pine and oak bark. In both adults and larvae only fungus hyphae and spores were present.

Silvanus planatus Germ. and *S. imbellis* Lec. (Cucujidae), 15 adults. These cucujids are common under oak bark. In both species fungus hyphae and spores were found. Certain cucujids are supposed to be predacious, but apparently these are not, at least in the adult stage.

Uloma punctulata Lec. (Tenebrionidae), 5 adults, 2 larvae. Common in rotten pine wood. In both larvae and adults, rotten wood was in the gut.

Uloma imberbis Lec. (Tenebrionidae), 6 adults. A species similar to *U. punctulata*, but found in rotten oak. Only rotten wood was found in the gut.

Platydema subcostatum Lap. (Tenebrionidae), 6 adults. Found in groups under oak bark, feeding on patches of mold. Hyphae and spores were found in the gut.

Platydema ruficorne Stunn. (Tenebrionidae), 4 adults. Found under oak bark, feeding on fungi. Hyphae and spores were found in the gut.

Boros unicolor Say (Boridae), 2 larvae. The gut contents of the larvae examined consisted of particles of wood and fungus hyphae and spores. No estimates of the relative amounts could be made. It appeared that the particles of wood contained much of the fungus hyphae. Larvae occur under the bark of pine where they feed in the frass left by various phloem-feeders.

Synchora punctata Newn. (Melandryidae), 10 larvae. Gut contents consisted entirely of bits of wood intermeshed with fungus hyphae and spores. The relative amounts could not be estimated.

TESTS FOR CELLULASE

The gut contents of larvae of eleven species of wood-eating insects were tested for the presence of a cellulase by the methods previously described. Larvae were feeding in every case when they were taken from the logs for tests, except those of *Derobrachus brunneus*, which were collected in winter. They began to eat, however, after they were left in room temperature for several days. The following is a list of the species used, with the number of larvae investigated and the type of wood they ate:

Passalidae	<i>Passalus cornutus</i> Fab., 10. Feeds on rotten wood of various deciduous trees and rarely pine.
Lucanidae	<i>Pseudolucanus capreolus</i> L., 6. Feeds on rotting pine and deciduous trees.
Scarabidae	<i>Polymoechus brevipes</i> Lec., 15. Larvae collected from oak log rotted by "red-rot" fungi.
Cerambycidae	<i>Derobrachus brunneus</i> (Forst.), 12. Feeding in rotting pines and hardwood. Larvae were also found in the solid heartwood of a rotting oak log. <i>Rhagium lineatum</i> Oliv., 6. Feeds in phloem of pines. <i>Callidium antennatum</i> Newm., 8. Feeds in phloem of pines. <i>Romaleum atomarium</i> (Drury), 13. Feeds in phloem of oaks and in rotting oak wood.
Tenebrionidae	<i>Monochammus titillator</i> (Fab.), 12. Feeds in phloem of pines. <i>Acanthocinus nodosus</i> (Fab.), 8. Feeds in phloem of pines. <i>Alobates pennsylvanica</i> (Degeer), 12. Found in rotting oak.
Noctuidae	<i>Scolecocampa liburna</i> Geyer, 5. Found in rotting oaks.

The only positive test for a cellulase in this series of larvae was obtained with the gut contents of *Derobrachus brunneus*. The larvae were collected February 14, 1938, from a very rotten log. They had formed burrows in

the heartwood that was still hard. The juice from their gut had no apparent action on wood shavings or filter paper, but digested a section of lettuce midrib completely in four hours.

AMOUNTS OF WOOD EATEN BY *Callidium antennatum* AND *Chrysobothris* SP.
IN PINE

Examination of Frass

The frass in the burrows of both *C. antennatum* and *Chrysobothris* sp. was fine and tightly packed. Its predominant color was that of the sapwood. Scattered through the frass were dark brown particles that on closer examination proved to be fecal pellets. These pellets were the same color as the phloem, which was brown in a log that had dried out. When they were soaked in water and pulled apart with needles, it was found that they were made up of many fine particles of wood that were cemented together. These particles could be identified as phloem. Close examination of the lighter colored particles which made up the greater part of the frass showed them to be clean cut, individual chips of sapwood. Their size varied, being larger toward the end of the burrow where the mature larva was found.

AREA OF THE BURROW AND DRY WEIGHT OF LARVAE

The average dry weight of the phloem covering area of one square centimeter on shortleaf pine trees was found to be 0.0555 ± 0.0021 grams. This figure is based on ten samples taken from shortleaf pines, about 25 cm. in diameter, that had been cut for a week. Five samples were taken at one meter from the base of the tree and five at about 10 meters from the base.

All the larvae of *Callidium antennatum* examined had constructed their cells in the sapwood and had completed their feeding period. The areas of the ten burrows examined ranged from 22.6 cm.^2 to 60.7 cm.^2 The dry weights of the larvae from the same burrows ranged from 0.0158 gm. to 0.0422 gm. Their wet weight ranged from 0.0584 gm. to 0.1512 gm., the percentage of body weight lost in drying varying from 49.36 to 79.75 per cent. The estimated amount of wood eaten by the larvae ranged from 1.26 ± 0.10 to 3.37 ± 0.26 grams (FIG. 8). Expressed in terms of grams of wood per gram of larvae the amounts consumed varied from 75.60 ± 6.0 gms. to 79.81 ± 6.2 gms., the average being 77.9 ± 3.2 gm.

The areas of the five burrows made by larvae of *Chrysobothris* sp. ranged from 6.97 cm.^2 (an immature larva) to 25.74 cm.^2 The larvae weighed before drying 0.0178 gm. (an immature larva) to 0.1014 gm. After being dried they weighed from 0.0048 to 0.0260 gms. The estimated amount of wood eaten ranged from $0.39 \pm .03$ gms. to $2.06 \pm .16$ gms. (FIG. 8). The amount of wood eaten expressed as grams of dry wood per gram of dry larva ranged from 75.07 ± 5.8 to 50.56 ± 6.3 , averaging 79.0 ± 3.1 grams.

The estimated amount of wood consumed by the larvae of both species was proportional to the areas of the burrows (FIG. 8). It will be noted that the amount of wood eaten per gram of larva fell within a narrow range in the larvae of both species. If a population of *C. antennatum* is assumed in which mature larvae contain 68.4 per cent water (the average of the ten determined) then an area of one square foot (929 cm.² or 0.0929 m.²) of log, having a phloem layer comparable to that determined in this experi-

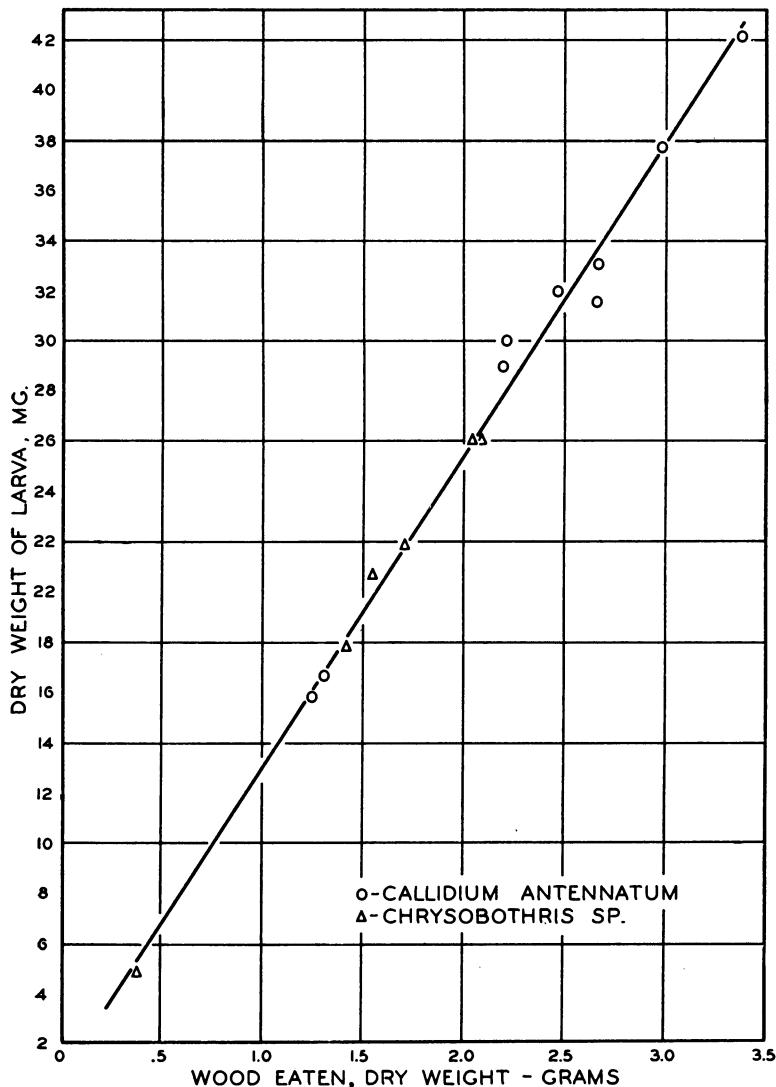


FIG. 8. The relation between the dry weight of larvae of *Callidium antennatum* and *Chrysobothris* sp. to the calculated amount of dry phloem that they consumed.

ment, would have the potentiality of producing 2.2 grams of larvae (wet weight) if all the available phloem were utilized. Assuming the average wet weight of a mature larva to be 0.1 grams this would give 22 individuals to the square foot.

None of the log from which larvae were collected showed starch in the sapwood with the potassium iodide test. The inner bark (cambium) layer, however, showed an abundance of starch as evidenced by the deep blue-black color produced. These observations were confirmed by microscopic examination of thin sections of wood treated with iodide solution. Large blue granules of starch could be seen in certain cells of the phloem while none could be found in the sapwood. Special attention was directed to parenchyma cells of rays and resin ducts in the sapwood which are known to be storage cells, but in no case was starch found. A freshly cut pine log was examined in March, 1938, and did show a small amount of starch in the parenchyma cells of the rays and resin ducts. Thus the previous findings only apply to the logs examined and are not to be taken as representing the conditions to be expected in any pine log. In no case was starch found in fecal pellets that had been picked from the frass and treated with iodide solution.

ANALYSIS OF WOOD

Samples of living phloem from three shortleaf pine trees (*Pinus echinata*) cut in November, 1937, contained an average of 5.02 per cent (dry weight) starch. Duplicate determinations were made on three samples with the following results: (1) 4.82 and 4.97 per cent, (2) 4.86 and 5.21 per cent, and (3) 5.10 and 5.18 per cent.

DISCUSSION

SUCCESSION

Pine. There is a succession of animals in pine logs similar in nature to that described by Adams (1915) and Blackman and Stage (1924). The first animals entering a log are cerambycid, burprestid, and scolytid beetles. All of these animals feed on phloem. It has been shown that scolytids and certain cerambycids aid the entrance of wood-rotting and other fungi in logs (Leach, Orr, and Christensen, 1937). The activity of these animals leaves a space under the bark more or less packed with chewed-up wood, part of which has been through the gut of some larva. Apparently such conditions are favorable for the growth of various fungi other than those that contribute to wood decay. These phloem-feeding animals therefore help to change the condition of a log so as to make it attractive to a large number of species that feed on fungi and decaying wood. Most of the members of the phloem fauna in pines complete their life cycle in one season or less. By the end of the first summer after a pine log is cut, there is usually little or none of the phloem remaining. This is only the case if a log is not exposed to unusual

conditions, such as being split and racked where it can be dried out rapidly. Logs in contact with the ground or in partial shade invariably contain many insects feeding on phloem. During the second year the sapwood begins to become softened and species that feed on such wood enter. The subcortical fauna is still very much the same with the addition of certain species such as *Dendroides bicolor* and *Boros unicolor*. During the third year additional species enter the sapwood, which by this time is often punky in places. The bark on small logs has often fallen off. Where it remains, the subcortical fauna typical of the first and second year is present, but represented by fewer species. After the sapwood has become punky throughout, fewer species are found in it, and species characteristic of intermediate stages of decay are absent, or are only rarely found. One species found in such wood, *Dero-brachus brunneus*, is able to digest cellulose. The final stages in the decomposition of the wood, in which it becomes a part of the soil has not been studied, but it is reasonable to assume that insects characteristic of the soil fauna (termites, etc.) replace those found only in rotten wood.

Oaks. The succession of animals in oak logs is essentially the same as that in pine logs in that the same ecological groups of animals are involved. There is first a phloem-feeding fauna that prepares the way for the entrance of a subcortical fauna living on decayed wood and fungi. In oak logs the entrance of a subcortical fauna is not entirely dependent on the phloem-feeders as it appears to be in pine. The bark of oak logs may become loosened sufficiently for the entrance of some insects merely by the drying of the phloem layer. Species feeding on solid wood, on wood in early stages of decay, and on punky wood succeed each other. Some species such as *Passalus cornutus* are among the first to enter a rotting log and remain until it is beginning to fall apart. Certain species such as *Uloma imberbis* and *Polymoecus brevipes* appear to select wood attacked by "red-rot" fungi while other species such as *Alobates pennsylvanica* appear to select wood attacked by "white-rot."

Oak logs in the punky stage of decay contain more species of animals and more individuals than does the corresponding stage in pine. The length of time required for the transformation of pine and oak logs from a solid log to a stage where they become mixed with the litter of the forest floor was not determined exactly. It appears, however, from the observations made on pine and oak logs three to four years old, that the decay of the former is much more rapid. The time required will naturally be influenced by the size of the log and the conditions to which it is exposed. Oaks have a relatively large amount of heartwood which is resistant to decay; pine logs contain relatively less heartwood. Thus, the decay of sapwood in a pine log affects a greater part of the log than would a corresponding amount of decay in the sapwood of oaks. Oak logs up to 60 cm. in diameter that had been dead over five years still contained solid heartwood. It appears that slowness of the decay of the large amount of heartwood in an oak log makes

for a suitable habitat for animals feeding in rotting wood for several years after sapwood and bark have decayed and weathered away.

While comparable ecological groups of animals occur in both pine and oak logs, the species are, for the most part, different. Closely related species of the same genus *Uloma punctulata* and *Uloma imberbis* occur in pine and oak respectively. In the genus *Alaus*, *A. myops* occurs in pines and *A. oculatus* occurs in oak. Both of these species are predacious and feed on a variety of wood-boring larvae. It is therefore difficult to understand why the two species should have a specific preference for a coniferous or a deciduous tree. Probably the answer is not to be found in specific wood preferences of the larvae, but in a strongly fixed oviposition response of the females to either a coniferous or a deciduous tree. Possibly *Alaus myops* and *A. oculatus* arose from xylophagous forms that had developed a preference for a particular host tree. Oviposition response of the female to a particular type of tree conceivably might have remained even after the larvae no longer fed on wood. *Xylopinus rufipes* was found only in pine and *X. saperdoides* only in oak. The small carabid, *Tachymenis flavicauda*, occurs in pine and a similar species, *Tachytta nana*, is found in oak. Both species feed on mites and collembolans.

Certain species are not restricted to either pine or oaks. About 25 species were found that occur in both types of trees. These include species feeding on rotting wood, on fungi under the bark, and on other insects. The large eletarid larvae *Orthosetethus infuscatus* occurs in rotten logs of both types of trees. *Derobrachus brunneus* also bores in both rotten pine and oak logs. Ants and centipedes are not restricted to one type of tree. Termites are equally common in both types of logs. *Brontes dubius* and certain staphylinids occur under the bark of both pines and oaks, where they feed mainly on fungi. *Dendroides bicolor* and *Synchroa punctata* may occur in both pines and oaks, but they are more commonly found in oaks. *Passalus cornutus* feeds typically in oaks and other deciduous trees, and rarely occurs in pine. Apparently no generalizations can be made concerning the species common to both types of logs. Weiss (1920a) has shown that certain fungi are attractive to more insects than others. Possibly a difference in the fungal flora of pine and oak logs may explain the preference of certain fungus-feeding insects for either pine or oak logs. Predators such as centipedes are of general occurrence both in litter and in logs and would not be expected to show a preference for particular species of trees.

Adams (1915) says that, in general, the fauna of rotting logs of different species of trees tends to become the same as they grow older. This is doubtless true of deciduous logs, but can hardly be applied to both deciduous and coniferous trees. While certain species are common to both rotten pine and oak logs, most of the species which feed on rotting wood are different.

When pine and oak logs have fallen apart, and are becoming part of the humus layer of the forest, probably more animals would be common to both.

Members of the phloem-feeding fauna are apparently the only animals whose activity prepares the way for succeeding animals.

Shelford (1911) says: "Ecological succession is the succession of ecological types (physiological types, modes of life) over a given point or locality due to changes in environmental conditions at that point. From this point of view we have nothing to do with species except as names are necessary." In a forest habitat the significant environmental changes which affect succession in a log are those caused by fungi and, to a lesser extent, the action of animals. The change is both chemical and mechanical and is probably most significant because of its relation to food requirements of animals. Logs are not everlasting habitats, but eventually merge with an adjacent habitat, the humus of the soil.

MICROCLIMATE

Temperature. Records of temperatures under the bark of logs exposed to sunlight in summer show that solar radiation has a marked effect on the subcortical temperature. The results obtained are similar to those reported by various other workers (Craighead 1920, Graham 1925, Patterson 1930, and Gottlieb 1928). High temperatures in logs exposed to the sun were shown by Graham (1925) to be of significance in shortening the time required for development of beetles. Subcortical temperatures may also be fatal to bark beetles, and advantage has been taken of this fact in control methods for certain bark beetles attacking pines (Patterson, 1930).

The subcortical temperatures recorded under pine bark on clear days in December show that solar radiation may raise the subcortical temperature above air temperature in winter. The effect of solar radiation in winter, however, is not as great as in summer. Certain animals living under bark such as collembolans, carabids, staphylinids, and dipterous larvae are not inactive all winter in the Duke Forest. All of these insects were active under bark when the subcortical temperature was above 7 to 10°C. In logs exposed to the sun the effect of solar radiation in raising the subcortical temperature as much as 5°C. above air temperature, enables such insects to be much more active.

The fluctuation of temperature in logs in shade with air temperature is to be expected since a log is of course subjected to changes in air temperature. The lag of temperature at various depths in logs accounts for the failure of log temperature to reach the maximum and minimum air temperatures, since the daily maximum and minimum air temperatures do not usually last more than an hour. When air temperature was fairly constant over a period of several hours, as it sometimes was in winter, temperatures in logs had time to come into equilibrium with air temperature. It is not likely that the maximum and minimum temperature under the bark of logs in the

shade and the maximum and minimum temperature of air differ sufficiently to be of great significance to animals living in such places during the summer, spring, and fall. The significance of the differences in the minimum and maximum temperatures under bark in winter and in air is questionable. From the records obtained on the days when air temperature was below 0°C. it appears that bark may sometimes offer protection to animals from sudden drops in temperature of short duration (FIG. 5), but low temperatures lasting as much as three to four hours are also reached under bark. There are many insects that hibernate under bark and crevices in logs. The protection afforded by bark to hibernating insects is thus very slight. Logs are probably more important as hibernacula on account of their high moisture content and the fact that they afford protection to various arthropods from birds, than on account of protection from low temperatures.

It was thought before temperature records were made that perhaps rotting logs would have a significantly higher temperature than air, because of the activity of bacteria and other fungi or because of auto-oxidative processes. In none of the records obtained can any such effect be shown. Any heat produced in the logs from these causes was not enough to raise the mean temperature of a log significantly above the mean air temperature. The disintegration of a log is a rather slow process, requiring several years, therefore heat produced by the activity of bacteria, fungi or auto-oxidative processes is probably conducted outward as fast as it is produced.

MOISTURE CONTENT OF LOGS

In all the logs from which collections were made, except certain pine logs that had been split and racked, the moisture content was well above that which would be expected to obtain in air-dry wood. Hawley and Wise (1926) give data to show the relationship between the moisture content of wood in equilibrium with atmospheres of different relative humidities at 24°C. While they state that the details of the relationship are not well worked out, especially at the extreme ranges of humidity, their results can be taken as approximately correct. According to their data, wood absorbs 33 per cent of its weight of water in a saturated atmosphere at 24°C. No work seems to have been done on the equilibrium that would be obtained between wood of different moisture contents and dry air. It is reasonable, however, to assume that when wood is in equilibrium with a saturated atmosphere, any air space in the wood would also be saturated. If wood contained more water than that which it would absorb from a saturated atmosphere, the humidity of air spaces in the wood should undoubtedly be close to 100 per cent since there is nothing to prevent water in the wood from exerting its normal vapor pressure. It seems safe to conclude therefore that wood containing as much as 50 per cent moisture would raise the humidity of a small, closed air space to the saturation point, provided of course, the volume of air be not too much greater than the volume of wood. Since most of the logs from which

samples of wood were collected contained 50 per cent or more water, any air space in such logs, as those made by insects, should be expected to be at or near to the saturation point at all temperatures.

As there is a lack of knowledge on the relation of wood moisture to humidity of air spaces in the wood, conclusions as to the humidity of the atmosphere in which *Callidium antennatum* and *Chrysobothris* sp. live cannot be drawn from the results of this research. The water content of the wood in which they live (relatively dry pine logs) was found to be as low as 26 per cent. According to data given by Hawley and Wise (1926) this corresponds to the amount of water contained in wood in equilibrium with an atmosphere of 95 per cent relative humidity. It seems likely that such a sample of wood would maintain a humidity in its contained air spaces greater than the usual atmospheric humidity, and would be free from the variations occurring in atmospheric humidity.

From the data obtained it appears that logs that have been attacked by wood-rotting fungi are capable of containing more water than freshly cut logs. This can be explained by the fact that the fungi break down and remove part of the wood, leaving more spaces to hold water.

Moisture is undoubtedly of great significance to many animals living in logs. Relative humidities of less than 100 per cent are fatal to many collembolans (Davies, 1928). Soft-bodied nymphs of many species of mites living under bark are probably similar to collembolans in their requirements for moisture. Larvae of *Dendroides bicolor*, which are typical subcortical animals, were shown by the writer to be sensitive to low humidites. The common observation that dry logs do not contain many wood borers also indicates that moisture in logs is important. Fidler (1936) showed that the moisture content of the soils was of great importance to the larvae of a scarabid. Not only do they require an atmosphere of saturated humidity, but also soil containing more water than would be necessary to maintain a saturated humidity in soil air. It seems probable that larvae of scarabids and lucanids living in logs might have similar reactions to the moisture content of wood.

CARBON DIOXIDE IN LOGS

The data on the presence of carbon dioxide in air under the bark and in wood of logs indicates that the composition of the atmosphere in which log-dwelling animals live may be quite different from the normal composition of air. The scope of the data collected is not great enough to determine the conditions under which carbon dioxide would be most abundant or the maximum amounts that might be expected. It does seem that greater amounts should be obtained during warm weather when the activity of bacteria and fungi would be greater, and that the greatest amount should be expected where fungus growth is most abundant. Many openings in the bark should also be expected to increase ventilation and thus influence the amount of

carbon dioxide found under the bark. High temperatures and wind would be expected to cause a greater diffusion of carbon dioxide from a log, since these factors are of importance in the ventilation of soil (Keen, 1931). The effect of carbon dioxide in the concentration found, or in higher concentrations that might be present, on insects living under bark or in the wood of logs, has not been studied to the writer's knowledge.

Carbon dioxide is important in controlling the respiration of some insects. It has been shown that *Dixippus morosus* responds to carbon dioxide with an increased rate of respiratory movement. This response shows two maxima, one between 0.0 and 1.0 per cent carbon dioxide and the other at about 25 per cent. Hazelhoff (1935) found in experiments with *Periplaneta* and many other insects, that in concentrations of 2 to 3 per cent, carbon dioxide causes opening of the spiracles and at 10 per cent, induces respiratory movement. It would be interesting to know if animals living in logs are so affected. If they are, it would be even more important that they remain in an atmosphere of high humidity, since evaporation of water occurs largely through the spiracles when they are open (Mellanby, 1935).

TOLERATION OF HIGH TEMPERATURES

The results of the experiments show that *Chrysobothris* sp. had the highest thermal death point of any of the larvae investigated and that its death point was not influenced by relative humidity. Compared with the other larvae its loss of water was considerably lower. In any experiment where insects are subjected to a fatal combination of relative humidity and temperature there is a question as to which of these factors actually cause death: i.e., is death due to heat or to desiccation or to a combination of the two? There are considerable data on the limits of desiccation of insects, all of which indicate that considerably more water can be lost by insects without fatal results than was lost by the larvae in this experiment. The meal worm, *Tenebrio molitor*, has been investigated by several authors, who show that more than 50 per cent of its body weight can be lost without loss of vitality (Hall 1922, Buxton 1930, Mellanby 1934). Therefore, it seems most likely that death of *Chrysobothris* sp. was due to the effects of heat alone. These results are similar to those reported by Mellanby (1932) on fleas and meal-worm larvae, in which he shows that the thermal death of these forms is also unaffected by humidity for short periods of time. Graham (1924) reports the thermal death point of *Chrysobothris dentipes* adults as varying from 45 to 52°C., but did not give the method by which he arrived at these figures. The larvae used in the writer's experiments agree with the upper limit he reports, but they did not show such variation.

The resistance of *Chrysobothris* sp. to desiccation is similar to that of species living in dry material, although not as marked as in the case of *Tenebrio molitor*. Since *Chrysobothris* sp. forms its hibernating cell in the relatively thin, dry bark of oak, usually less than one-half inch from the

surface, it is to be expected that it would be subjected at times to low humidities. The relative humidity surrounding insects in such cells in wood is not known, and it would not be safe to draw conclusions as to the humidity of the air around the larva from the dryness of the wood. Fidler (1936) has shown that chafer larvae (Scarabidae) form an earthen cell around themselves in which they are able to maintain a higher humidity than that of the surrounding atmosphere. If *Chrysobothris* sp. can maintain a relative humidity in the atmosphere surrounding it which is greater than that which would naturally be produced from moisture in the wood, it can do so only by a constant evaporation of moisture from its body, since there is no impervious material lining the cells. The moisture in the air around the larva would be absorbed by the wood when the moisture content of the latter became lower than that which it would contain at the relative humidity around the larva. This follows from the fact that wood absorbs a definite amount of water from the atmosphere at different humidities, and reaches a moisture equilibrium with the atmosphere at a particular humidity (Hawley and Wise, 1926).

The ability of *Chrysobothris* sp. to withstand high temperatures and low humidities is significant in view of its habits. It is well known that most species of the Buprestidae are thermophilic forms, mating and laying their eggs in places exposed to the sun. Graham (1925) showed that the larvae of *Chrysobothris dentipes* occurred only on the top side of pine logs in the sun where the subcortical temperatures were highest. The writer's observations, made while collecting from both pine and oak logs, are in accord with Graham's experimental work. *Chrysobothris* sp. lays its eggs in timber exposed to the sun and its young, by virtue of their adaptations to high temperature and low humidity, are able to live in situations that are intolerable to many other insects.

Monochamus titillator, *Romaleum atomarium*, and *Acanthocinus nodosus* may be considered together since they gave similar results. It is apparent from the results obtained with these species that humidity had an effect on their thermal death point. The larvae of each of these species were able to survive a higher temperature in an atmosphere of low humidity than in a saturated atmosphere or one 90-95 per cent saturated. This phenomenon has been encountered by other workers using different species of insects. Mellanby (1935) reviewed the literature on the subject and based his explanation of the phenomenon on the fact that the body temperature of an insect is lowered in a dry atmosphere by the evaporation of water from its body (Necheles 1924, Mellanby 1932). He points out that only larger insects (above 100 mg.) are able to be cooled enough in this way to affect their thermal death points. The results of the writer's experiments can be explained on the same basis. The fatal temperature in a saturated or nearly saturated atmosphere probably represents more closely the intensity of heat that a larva is able to withstand. At temperatures above this fatal limit a

larva in a dry atmosphere is able to keep its body several degrees cooler than its surroundings for short periods of time by the evaporation of water.

The relation of *Monochammus titillator*, *Romaleum atomarium*, and *Acanthocinus nodosus* to high temperature may be correlated with the conditions in which they live. They are normally found only where the wood is moist and where the humidity of the air around them is probably always near the saturation point. Furthermore they are not found in parts of a log where the subcortical temperature is likely to be as high above the air temperature as it is in the parts inhabited by *Chrysobothris*.

The thermal death point of the larvae of *Dendroides bicolor* is not affected by humidity. This can be explained by the fact that they have a large surface area in relation to their weight, because of their small size, and thus absorb more heat per unit of body weight than do larger forms. In addition, the amount of water that can be evaporated from their bodies is not sufficient to maintain their body temperature below that of their surroundings for a very long time. The larvae of *Dendroides bicolor* are found under the bark of pine and oak logs that have been dead longer than a year, and in which the bark has been loosened from the sapwood by various phloem feeders. They are never found on the top side of logs exposed to the sun, but are only in situations where the temperature under the bark rises but little above the air temperature and where the humidity is near saturation. They are active, and the looseness of the bark makes it possible for them to migrate to a part of the log where conditions are favorable.

NUTRITION OF WOOD BORERS

From the results of the tests for starch in the phloem being eaten and the feces produced by *C. antennatum* and *Chrysobothris* sp., it is concluded that they are able to digest and remove starch from the phloem that they eat. That both species feed for the most part, if not exclusively, on the phloem is shown by the results of the examination of their feces and the frass in the burrows. The significance of this selection of the thin layer of phloem that lies between the cork bark and the xylem, appears to be a difference in the nutritive value of xylem and phloem. At least one of these differences is the greater amount of starch in the phloem. Since the phloem layer becomes quite thin when a log dries out, a larva feeding in it would have to gnaw out a burrow either in the cork bark or in the xylem to accommodate its increase in size as it grew older. This explains the uneaten frass dug from the xylem. Apparently the xylem plays no part in their nutrition.

Since the dry weight of the larvae of *Callidium antennatum* and *Chrysobothris* sp. is correlated with the area of their burrows and the calculated dry weight of phloem that they eat, the two species must have approximately an equal amount of growth on an equal amount of wood. Whether the phloem in the various logs from which larvae were collected had the same nutritive value or not is not known. It seems probable, however, that if they had

differed greatly, a greater difference in the relation between the dry weight of individual larvae and the area of their burrows, and thus in the amount of wood eaten, would have been obtained. It will be observed in Fig. 8 that the relation between the dry weight of a larva and the amount of wood it ate is fairly constant for every individual.

The amount of starch in the phloem of the logs in which larvae of *C. antennatum* and *Chrysobothris* sp. were found is not known and can only be inferred from the analysis of phloem from similar trees cut in November of the following year. These samples had an average starch content of 5 per cent. It is doubtful that from these results it can be safely assumed that the same percentage of starch obtained in logs containing larvae of *C. antennatum* and *Chrysobothris* sp. The reason for this is that no detailed knowledge is available for the seasonal variation of starch in pines in North Carolina or, in fact, at any place in the United States to the writer's knowledge. Pines are classified by Busgen (1931) as "fat trees" because they store large amounts of a fatty material as well as starch. Studies made in Europe by Antevs (quoted by Busgen, 1931) show that there is a conversion of starch to fat; high temperatures, the reverse. Other factors that may affect the amount of starch are the season and the number of years since a seed crop was borne (Busgen, 1931). It is thus clear that, until much more data are obtained, predictions of the amount of starch in pines cannot be made. It is therefore impossible, from the results obtained in the present study, to come to any very definite conclusions as to the amount of starch consumed by *C. antennatum* and *Chrysobothris* sp. with the phloem they ate.

The phloem-feeding cerambycid larvae tested for a cellulase were *Monochamus titillator*, *Acanthocinus nodosus*, *Callidium antennatum*, *Rhagium lineatum*, *Romaleum atomarium*. None of these larvae showed a cellulase in their gut contents nor did they possess intestinal protozoa or bacteria that could be considered as playing a part in their nutrition. The possibility of the presence of mycetomes, however, has not been excluded, but the work of Mansour and Mansour-Bek (1934a, 1934b) has placed any digestive function of these bodies very much in doubt. Cellulose digestion by the larvae investigated seems, therefore, rather improbable. If utilization of cellulose by the larvae is excluded, the question arises as to what substances in the phloem serve as their source of carbohydrate. Fungi can be excluded because the larvae often begin their burrows in weakened or recently dead trees in which there is little or no fungal growth. It is generally recognized that living phloem is richer in starches, sugars, and proteins than the xylem (Busgen, 1931). The possibility that insect larvae might be able to subsist entirely on the stored starches, sugar, and protein in the phloem is apparent. The author has shown that the living phloem of shortleaf pine contained as much as 5 per cent starch in November and that the larvae of *Callidium antennatum* living on pine phloem remove starch from the wood

they eat. Mansour and Mansour-Bek (1934a) showed that the larvae of a cerambycid could live in wood containing 3.9 per cent starch without attacking the cellulose. Parkins (1936) found that the larvae of species of *Lyctus* depended on starch in wood for their source of carbohydrates. It is, therefore, probable that the starches and sugars in phloem can furnish the necessary carbohydrates for *Callidium antennatum*. While it has not been shown that the other phloem-feeding larvae investigated digest the starch, it seems likely that they would. It has often been assumed that insects living in wood possessed remarkable digestive powers, because they were believed to be living on cellulose. It has only been in recent years that attention has been called to the fact that many insects may live on materials in wood other than cellulose. In fact, cellulose-digestion in insects has been shown for only a few species (Mansour and Mansour-Bek, 1934b). It is probably significant that there are many insects that attack the phloem of trees as soon as they are dead or even when they are in a weakened condition, in view of the fact that phloem contains more protein, starches and sugars than xylem.

The absence of a cellulase in the larvae of insects feeding in rotten wood (*Passalus cornutus*, *Pseudolucanus capreolus*, *Polymoeus brevipes*, and *Scolecocamp liburna*) does not necessarily mean that they are unable to derive nourishment from cellulose. The presence of symbiotic protozoa and bacteria must be taken into consideration. Wiedemann (1930) showed that certain scarabid and lucanid larvae contain bacteria in their gut that digested part of the cellulose in the wood ingested by the larvae. He also found that these beetle larvae digested part of their intestinal bacteria and thus were able to benefit from their presence. Wiedemann did not find cellulase in the larvae he investigated. The scarabid *Polymoeus brevipes* and *Pseudolucanus capreolus* are similar to the larvae investigated by Wiedemann (1930) in that they feed on rotting wood, possess intestinal bacteria in great numbers, lack cellulase, and belong to genera closely related to the genera studied by Wiedemann.

How the other species of rotten-wood feeding larvae investigated obtain available carbohydrates from their food is not known. The results of the writer's experiments show that they do not secrete a cellulase. Whether these species depend on intestinal symbionts or derive carbohydrates from other sources remains to be determined. No symbiotic protozoa were found in the gut of *Alobates pennsylvanicus*. The writer has observed that *Alobates pennsylvanicus* was always found in wood in which "white-rot" fungi were growing. The possibility is suggested that their nutrition is in some way associated with the type of decay of the wood. Recent work by Boswell (1938) has shown that certain fungi attacking pine, break down cellulose into hexose, and pentose compounds much more rapidly than these compounds are utilized by the fungus. It therefore seems quite possible that certain types of rotting

wood might contain enough digestible carbohydrates, other than cellulose, to supply the needs of an insect feeding on the wood.

The presence of a cellulase in the gut of *Derobrachus brunneus* is of particular interest. The larvae of this species are some of the largest of the cerambycids. They feed in both rotten pine and oaks. In pines they were observed feeding on wood in a very advanced stage of decay, so rotten, in fact, that it could be easily torn to pieces with the hands. In oaks they were observed feeding in the solid heartwood of a rotten log that had been dead about five years. In other oak logs, they were feeding in sapwood attacked by a "white-rot" fungi. While it can not be definitely stated the cellulase found is secreted by these larvae, it is probable that this is the case, since no intestinal protozoa or bacteria were found in their gut that could account for the presence of cellulase.

GENERAL DISCUSSION OF FOOD RELATIONS

Several ecological groups of animals characteristic of logs may be separated on the basis of their food habits:

(a) Wood-boring insects, chiefly the larvae of Coleoptera and Hymenoptera. Certain forms are characteristic of sound wood, while others are found feeding only on rotten wood.

(b) Associated with these xylophagous species are parasitic Hymenoptera and Diptera, and certain predaceous beetles that are stenophagous and are thus similar to parasites.

(c) Another group consists of predaceous species that are general feeders, such as *Alaus oculatus*.

(d) A fauna distinct from the xylophagous insects includes those feeding on fungi, or relying on their presence in rotting wood. These are chiefly beetles, dipterans, mites, and collembolans. These also have parasites and predators, that are regularly associated with them.

(e) A secondary fauna associated with logs are predatory species that are general feeders such as certain carabids, centipedes, spiders, and ants that visit logs in the course of their hunts for food in the forest floor.

(f) Other species incidentally associated with logs are species that find suitable nesting or hiding places in rotten wood such as bees and wasps. Other species hibernate under bark and in the wood that are not otherwise found there, such as hornets, wasps, and lizards.

This classification is essentially that given by Brues (1927).

Sound wood is eaten by a large number of insects that apparently are able to derive all their food from the stored products in wood. Other insects are able to live on wood as a result of the activities of symbiotic protozoa or bacteria in their guts, while still other species, such as the cerambycid *Derobrachus brunneus* have developed the ability to digest cellulose (Mansour and Mansour-Bek, 1935).

Brues (1927) points out that xylophagous Coleoptera, Hymenoptera, and Lepidoptera constitute part of what may be considered a primitive fauna that has long been characteristic of wood. Xylophagous Hymenoptera and Lepidoptera, in particular, are some of the more primitive members of these orders, and Brues considers that these orders probably arose from ancient lignivorous forms.

Certain parasitic groups living today, such as the Oryssidae, show close affinities to phytophagous Hymenoptera and are thought to have been derived from primitive xylophagous Hymenoptera. If such is the case, it is significant that today the Oryssidae are ecto-parasites of buprestid larvae living in wood.

In many cases it is not possible to be certain whether insects eating rotting wood derive their food substance from fungi in the wood or from the wood itself. Certain species feeding on rotting wood such as *Dendroides canadiensis* and *Synchroa punctata* undoubtedly are dependent on fungi (Payne, 1931). The gut contents of other species show that they probably feed exclusively on fungus spores and hyphae. Certain insects found under bark, such as species of Staphylinidae, Tenebrionidae, Cisidae, and Melandryidae have also been reported as feeding on the fruiting bodies of various wood-rotting fungi, particularly of the genus *Polyporus* (Weiss, 1920).

One of the striking things about the fauna of logs is the important part played by predaceous species in controlling the number of xylophagous and mycetophagous forms. This has been commented on by Fiske (1907) in discussing the enemies of wood-boring Coleoptera. He pointed out that wood-boring insects, as compared to external feeders, had a relatively small variety of parasites. Certain predaceous species are stenophagous, as Fiske (1907) and Brues (1927) pointed out. The clerid *Thanasimus dubius* feeds almost entirely on bark beetles, both in its larval and adult stage. The carabids, *Tachyta nana* (Gyll) and *Tachymenis flavicauda* Say, probably get most of their food by preying on mites and collembolans. Further, certain Histeridae, such as *Cylindrichus cylindrica* are probably predaceous on fly larvae. In contrast to such predators are those such as an ostomid, *Temnochila vivescens*, and the elaterids, *Alaus myops* and *A. oculata* which feed on a variety of xylophagous larvae.

SUMMARY

1. During the period from September, 1936 to February, 1938 about 280 logs, 155 pines and 125 oaks, were examined in the Duke Forest, Durham, North Carolina.
2. There is a succession of animals in pine and oak logs from the time they are cut until they disintegrate.
3. Insects feeding in the phloem of pine and oak logs during the first year after they are cut prepare the way for the entrance of fungi and a subcortical fauna including mycetophagous and predaceous species. A sub-

cortical fauna in oaks may enter spaces formed between the bark and wood by the shrinkage of sapwood. The environmental changes in logs leading to a succession of wood-feeding animals appear to be largely those caused by fungi.

4. Subcortical temperatures under the loose bark of pine logs exposed to sunlight in summer rose as much as 11°C. above air temperature when the latter was 33°C.

5. Temperatures under the bark and at various depths in sapwood of logs fluctuate with air temperatures in all seasons of the year with a lag depending in part on the depth in the log at which temperatures are taken. Animals under bark probably receive little protection from low temperatures in winter in the Duke Forest. It is suggested that for many animals logs are more important as hibernacula because of their moisture content rather than the protection they afford from low temperatures, though logs do moderate extreme and rapid changes.

6. Temperatures in rotting logs were not perceptibly affected by heat that might have been produced by fungi or other organisms, or by possible auto-oxidative processes within the wood.

7. Samples of air taken from under bark and from rotting wood of logs contained as much as 5.53 per cent (volume) carbon dioxide, and oxygen concentration as low as 15.53 per cent (volume).

8. The highest temperature of two hours duration tolerable to larvae of *Chrysobothris* sp. (probably *femorata* Oliv.) taken from oak logs, was 52°C. regardless of the relative humidity in which they were exposed. Toleration of *Chrysobothris* sp. to such high temperature may be correlated with the fact that it lives on the top side of oak logs exposed to the sun.

9. The highest temperature of two hours duration tolerable to *Romaleum atomarium*, *Monochamus titillator*, and *Acanthocinus nodosus* was 49°, 50°, and 46° respectively, when exposed in air with a relative humidity of approximately 10-15 per cent. With relative humidity of 100 per cent they could only tolerate temperatures of 44°, 44°, and 43°C., respectively. The explanation offered for this phenomenon is that the cooling effect of evaporation of water from a larva in dry air undoubtedly lowers its body temperature below that of its surroundings.

10. The highest temperature of two hours duration tolerable to larvae of *Dendroides bicolor* was 41°C. in humidities of both 10-15 and 90-95 per cent. It is considered that their small size prevents them from being able to lose enough water by evaporation to maintain a lower body temperature than their surroundings.

11. Loss of water from larvae tested for toleration to high temperatures was proportional to the temperatures at which they were exposed, when relative humidity was 10-15 per cent.

12. Of the larvae tested, those of *Chrysobothris* sp. were most resistant to

desiccation, and those of *Dendroides bicolor* least resistant. The percentage of body weight lost by evaporation from larvae of *Romaleum atomarium*, *Monochamus titillator*, and *Acanthocinus nodosus* was intermediate between that of *Chrysobothris* sp. and *Dendroides bicolor*. The difference in the larvae investigated with respect to their resistance to desiccation may be correlated with the conditions of moisture in the logs in which they live.

13. The average dry weight of the phloem covering one square centimeter of area on shortleaf pines was found to be 0.0555 ± 0.0021 grams.

14. The amount of starch in three samples of living phloem collected from shortleaf pine in November was 5.02 per cent of the dry weight of the sample.

15. The larvae of *Callidium antennatum* and *Chrysobothris* sp. feed on the phloem of pine poles containing as little as 26 per cent water. They eat little, if any of the sapwood which they dig out in making their burrows. In poles which contained larvae the sapwood contained no starch, but the phloem contained enough starch to be turned blue-black by iodine.

16. Larvae of *Callidium antennatum* and *Chrysobothris* sp. remove starch from the phloem they eat.

17. The areas of the burrows that had been formed by ten larvae of *Callidium antennatum* and four larvae of *Chrysobothris* sp. up until they had formed pupal chambers, were determined. The areas of the burrows measured were proportional to the dry weights of the larvae that had made them. From the average dry weight of the phloem covering one square centimeter of surface on shortleaf pine, the amount of phloem that had probably been consumed by larvae of both species was calculated. The dry weights of phloem probably consumed were proportional to the dry weights of the larvae. The average amount of phloem (dry weight) that had been eaten by a larva (dry weight); for *Chrysobothris* sp. it was 77.1 ± 3.1 grams.

18. The gut contents of five larvae feeding on rotting wood and five larvae feeding on phloem were tested for the presence of a cellulase with negative results. Cellulase was found in the gut contents of the larvae of *Derobrachus brunneus*, which feeds in solid and soft rotting wood.

19. Larvae of beetles feeding on phloem of logs less than one year old are probably able to derive all their essential food from products stored in the cells of the phloem without digesting cellulose.

20. The gut contents of 22 species of insects of doubtful food habits were examined. Some were found to be predaceous, others fed on fungus hyphae and spores, rotting wood, or both.

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APPENDIX

In the following lists the animals collected from pine and oak logs are given. The numerals immediately following the scientific name refer to the ages of logs from which the species was collected; next follows the location on or in the log where it was usually found; next follow the stages in life history that feed in the log; then the relative abundance of the species, whether common, occasional, or rare; and finally the food eaten. In the latter, the asterisk following the food means that the observation was made by the author. The food of certain species has been inferred from a knowledge of related species. An asterisk following a reference means that it refers to a related species.

I. ANIMALS COLLECTED FROM PINE LOGS

Collembola

Entomobrya sp.; 1, 2, 3, 4; under bark in rotten wood; all; decayed wood, fungi.

Pseudachorutes sp.; 1, 2; under bark; all; occasional; decayed wood, fungi.

Isotoma sensibilis Tlb.; 1, 2, 3, 4; under bark in rotten wood; all; common; decayed wood, fungi.

Entomobrya ligata Nic.; 1, 2, 3, 4; under bark in rotten wood; all; common; decayed wood, fungi.

Tomocera flavescens Tlb. var. *Americanus* Schott; 1, 2; under bark; all; common; decayed wood, fungi.

Entomobrya corticola Nic.; 1, 2, 3, 4; under bark in rotten wood; all; common; decayed wood, fungi.

Isoptera

Reticulitermes flavipes Koll.; 2, 3; rotting wood; all; common; sapwood*.

Orthoptera

Parcoblatta sp.; 1, 2, 3, 4; under bark, under logs; all; common; omnivorous, Blatchley (1920).

Heteroptera

Undetermined; 1; under bark; all; common; predaceous on scolytids*.

Homoptera

Epiptera sp.; 1; under bark; all; rare; fungi.*

Coleoptera

- Galerita bicolor* Drury; 1, 2, 3; on log under bark; adult; occasional predacious, Forbes (1883).
- Clivina* sp.; 2, 3, 4; on log under bark; adult; occasional; phytophagous, Blatchley (1910)*.
- Tachymenis flavicauda* (Say); 1, 2, 3, 4; under bark; adult larva; common; Collembola mites*.
- Atheta* sp.; 2, 3; under bark; adult larva; occasional; fungi?
- Erchomus ventriculus* Say; 1, 2; under bark; adult larva; common; fungi?
- Nudobius cephalus* (Say); 1, 2; under bark; adult larva; common; predacious?
- Alcocharinac* gen. sp.; 1, 2, 3, 4; under bark in rotten wood; adult larva; common; fungi?
- Saprinus* sp.; 1, 2; under bark; adult larva; common; predacious*.
- Platysoma parallelum* Say; 1, 2; under bark; adult larva; common; predacious*.
- Platysoma parallelum* Say; 1, 2; under bark; adult larva; common; predacious*.
- Plegaderus* sp.; 1, 2, 3; under bark in rotten wood; adult larva; occasional; fungi*.
- Cylistix cylindrica* (Payk.); 1, 2; under bark; adult larva; common; predacious probably fly larvae*.
- Platysoma lecontei* Mars.; 1, 2, 3, 4; under bark in rotting wood; adult larva; common; predacious*.
- Platros floralis* Melsh.; 1; under bark; larva; rare; predacious*.
- Thanasimus dubius* Fab.; 1; under bark on log; adult larva; common; bark beetles*. Fiske (1907).
- Cymatodera* sp.; 2; under bark; larva; occasional; predacious? Weiss (1922)*.
- Copidita thoracica* Fab.; 3; rotting wood; larva; common; rotting wood*.
- Boros unicolor* Say; 1, 2; under bark; larva; occasional; fungi, rotting wood*.
- Dendroides bicolor* Newn.; 1, 2; under bark; larva; common; fungi*, rotting wood.
- Alaus myops*; 1, 2, 3, 4; under bark in rotting wood; larva; common; predacious*, general beetles.
- Ischiodontus* sp.; 1, 2; under bark; larva; common; rotting wood*.
- Orthostethus infuscatus* Germ.; 3, 4; rotting wood; larva; common; rotten wood*.
- Melanotus* sp.; 1, 2, 3, 4; under bark in rotting wood; larva; common; rotten wood*.
- Elater verticinus* Beauv.; 1, 2, 3, 4; under bark in rotting wood; common; rotten wood*.
- Megapenthes limbalis* (Hbst.); 2, 3; under bark; larva; occasional; rotten wood*.
- Drapites* sp.; 1, 2, 3; under bark; larva; common; rotten wood?
- Buprestis lineata* Fabr.; 1, 2; phloem, sapwood; larva; common; phloem, sapwood*.
- Buprestis* sp.; 1, 2, 3; phloem, sapwood; larva; common; phloem, sapwood*.
- Chalcophora* sp.; 1; phloem; larva; common; phloem*.
- Chrysobothris* sp.; 1; phloem; larva; common; phloem*.
- Temnochila virescens* (Fab.); 1; under bark; larva adult; common; predacious* general feeders.
- Tenebroides collaris* Sturm.; 1; under bark; adult larva; common; predacious*.
- Rhizophagus cylindricus* (Lec.); 1; under bark; adult larva; occasional; predacious on scolytid*.
- Brontes dubius* Fab.; 1, 2, 3; under bark; adult larva; common; fungi*.
- Mycetophagus pini* Zieg.; 1, 2; under bark; adult larva; occasional; fungi, Weiss (1922)*.
- Colopterus semitectus* Say; 1; under bark; adult larva?; common; sap, Blatchley (1910)*.
- Stelidota geminata* Say; 1; under bark; adult larva?; common; sap, Blatchley (1910)*.
- Pycnomerus sulcicollis* Lec.; 2; under bark; larva; common; predacious?
- Colydiidae* sp.; 2; under bark; larva; predacious?

- Penthelispa haematodes* Fab.; 2; under bark; adult larva; common; predacious?
- Penthelispa reflexa* Say; 2; under bark; adult larva; common; predacious?
- Synchita* sp.; 2, 3; rotten wood; larva; common; rotting wood*.
- Uloma punctulata* Lec.; 3, 4; rotten wood; adult larva; common; rotten wood*.
- Xylopinus rufipes* (Say); 2, 3, 4; rotten wood; larva; common; rotten wood*.
- Scotobates calcaratus* (Fab.); 3, 4; rotten wood; larva; common; rotten wood*.
- Alobates barbata* (Knoch); 2; under bark; only adults found; occasional; probably hibernating.
- Bolitotherus cornutus* (Panz); 1; under bark; adult larva?; occasional; fungi*.
- Hypophloeus parallelus* Melsh.; 1; under bark; adult larva?; occasional; predacious? Schwartz (1889)*.
- Platydema flavipes* Fab.; 1, 2, 3; under bark; adult larva; common; fungi*.
- Hypulus concolor* (Lec.); 2; rotting wood; larva; occasional; rotten wood*.
- Stephanopachys rugosus* Oliv.; 1, 2; sapwood; larva; common; sapwood*.
- Passalus cornutus* Fab.; 3, 4; rotting wood; adult larva rare; rotten wood*.
- Pseudolucanus capreolus* (L.); 3, 4; rotting wood; larva; rare; rotten wood*.
- Derobrachus brunneus* (Forst.); 4; rotting wood; larva; occasional; rotten wood*.
- Asemum moestum* Hald.; 1; phloem, sapwood; larva; common; phloem, rotting sap-wood*.
- Rhagium lineatum* Oliv.; 1; phloem; larva; common; phloem*.
- Xylotrechus sagittatus* (Germ.); 1; phloem; larva; rare; phloem*.
- Callidium antennatum* Newn.; 1; phloem; larva; common; phloem*.
- Acanthocinus obsoletus* (Oliv.); 1; phloem; larva; common; phloem*.
- Acanthocinus nodosus* (Fab.); 1; phloem; larva; common; phloem*.
- Eupogonius tomentosus* Hald.; 1; phloem; larva; rare; phloem*.
- Monochammus titillator* (Fab.); 1; phloem; larva; common; phloem*.
- Leptura* sp.; 2; 3; rotten wood; larva; present; rotten wood*.
- Rhyncolus* sp.; 1, 2, 3; under bark; adult larva; rare; probably fungi.
- Cossonus corticola* Say; 1, 2, 3; under bark; adult larva?; common; fungi*.
- Pissodes memorensis* Germ.; 1; phloem; larva; common; phloem*.
- Pachylobius picivorus* Germ.; 1; phloem; larva; rare; phloem*.
- Hylobius pales* Hbst.; 1; phloem; larva; common; phloem*.
- Platypus flavigornis* Fabr.; 1; sapwood; adult larva; common; fungi in its burrow.
- Ips grandicollis* Eichh.; 1; phloem; adult larva; occasional; phloem*.
- Ips calligraphus* Germ.; 1; phloem; adult larva; common; phloem*.
- Xyleborus fitchi* Hopk.; 1; sapwood; adult larva; occasional; fungi*.
- Orthotomicus caelatus* (Eichh.); 1; phloem; adult larva; common; phloem*.
- Pityophthorus annectens* Lec.; 1; phloem; adult larva; occasional; phloem*.
- Pityophthorus pullus* Simm.; 1; phloem; adult larva; occasional; phloem*.
- Dendroctonus valens* Lec.; 1; phloem; adult larva; common; phloem*.
- Dendroctonus tenebrans* (Oliv.); 1; phloem; adult larva; common; phloem*.

Diptera

- Forcipomyia* sp.; 2; under bark; larva; rare; unknown.
- Chironomidae* (undetermined); 3, 4; rotten wood; larva; common; fungi? Curran (1934)*.
- Sciara coprophila* Lint.; 1, 2; under bark; larva; occasional; reared from dead cerambycid.
- Cecidomyidae* (undetermined); 3, 4; rotten wood; larva; common; fungi? Harris (1923)*.
- Xylopaagus fasciatus* Walker; 1; under bark; larva; occasional; predacious on *Rhagium lineatum**.

- Dolichopodidae* (undetermined); 2, 3, 4; rotten wood; larva; occasional; fungi? Curran (1934)*.
- Phoridae* (undetermined); 1, 2; under bark; larva; common; predacious; Curran (1934)*.
- Lonchaea* sp.; 1, 2; under bark; larva; common; bacteria or fungi, Curran (1934)*.
- Theresia monohammi* (Ins.); 1; under bark; larva; common; parasite of *Monochammus titillator*.
- Sarcophaga repax* Walker; 1; under bark; larva; common; parasite of *Monochammus*.

Hymenoptera

- Sirex migricornia* Fab.; 1; sapwood; larva; occasional; sapwood.
- Oryssus* sp.; 1; under bark; larva; common; parasite of *Chrysobothris* sp.
- Atanycolus* sp.; 1; under bark; larva; rare; parasite host unknown.
- Coeloides pissodis* Ashm.; 1; under bark; larva; common; parasite of *Pissodes nemorensis*.
- Coeloides* (striatus Prov.); 1; under bark; larva; occasional; parasite host unknown.
- Coeloides* sp.; 1; under bark; larva; occasional; parasite host unknown.
- Pristaulacus resutovorus* (Westw.); 1; under bark; larva; occasional; parasite unknown.
- Trypoxylon clacatum*; 2, 3; nests in cerambycid burrows; larva; common; probably spiders or insects.
- Halictus* (Chloralictus) sp.; 4; nests in rotten wood; larva; common; poiren.
- Canponotus herculeanus* (*pennsylvanicus* DeG.); 1, 2, 3; nests in sapwood or bark; adults and larvae; common; predacious and scavengers, Wheeler (1913).
- Crematogaster lineota* Say; under bark; adults; common; scavengers, Wheeler (1913).
- Leptinothorax curvispinosus* Mayr.; 1, 2, 3, 4; under bark; adults; common; scavengers, Wheeler (1913).
- Ponera coarctata* (*pennsylvanica* Emery); 1, 2, 3, 4; under bark; adults; occasional; scavengers, Wheeler (1913).
- Lasius umbratus mixtus* Nyl.; 1, 2; under bark; adults; occasional; scavengers, Wheeler (1913).

Annelida

- Lumbricidae* (undetermined); 3, 4; under bark in rotten wood; all stages; common; rotten wood*.

Mollusca

- Polygyra thyriodus* Say; 4; under log in rotten wood; adults; occasional; rotten wood fungi?
- Euconulus chersinus* Say; 2, 3; under bark; adults; common; rotten wood fungi?
- Zonitoides arboreus* Say; 2, 3, 4; under bark; adults; common; rotten wood fungi?
- Philomycus carolinensis* (Bosc.); 3, 4; in rotten wood; adults; occasional; rotten wood fungi?

Myriapoda

- Cambala annulata* Say; 3, 4; under logs in rotten wood; adults; common; rotten wood*.
- Fontaria coriacen* Koch; 2, 3, 4; under logs in rotten wood; adults; common; rotten wood*.
- Polydesmus serratus* (Say); 4; under logs in rotten wood; adults; common; rotten wood*.
- Geophilus varians* McNeil; 1, 2, 3, 4; under bark; adults; common; predacious.
- Linotaenia bidens* (Woods); 1, 2, 3, 4; under bark; adults; common; predacious.
- Cryptops hyalina* Say; 1, 2, 3; under bark; adults; common; predacious.
- Bothropolys multidentatus* Newport; 1, 2, 3; under bark; adults; occasional; predacious.

Chelanops oblongus; 1, 2; under bark; all stages; common; predacious* small larvae probably mites.

Chelanops virginnae; 1, 2; under bark; all stages; common; predacious.

Chelifer cancroides; 1, 2; under bark; all stages; common; predacious.

Acarina

Uropoda sp. (several species); 1, 2, 3, 4; under bark; all; common; unknown.

Trachyuropodidae (undetermined); 1; under bark; all; unknown.

Parasitus sp.; 1, 2; under bark; all; common; certain species are probably predacious.

Dendrolaelaps sp.; 1, 2; under bark; all; common; certain species are probably predacious.

Pergamasus sp.; 1, 2; under bark; all; common; certain species are probably predacious. Several undetermined species; 1, 2, 3, 4; under bark; all; common; certain species are probably predacious.

Tyroglyphidae (undetermined); 2, 3; under bark; all; common; certain species are probably predacious.

Allothrombium pulvinus Ewing; 2; under bark; all; occasional; predacious?

Orabatidae (several undetermined spp.); 2, 3; under bark; all; occasional.

Vertebrata

Plethodon glutinosus (Green); 4; under logs in rotten wood; adult; occasional; probably various insects.

II. ANIMALS COLLECTED FROM OAK LOGS

Collembola

Entomobrya ligata Nic.; 1, 2, 3, 4; under bark in rotten wood; all; common; fungi and rotten wood? Essig (1926)*.

Lepidocyrtus cyaneus Tlb.; 1, 2, 3; under bark in rotten wood; all; common; fungi and rotten wood? Essig (1926)*.

Isotoma sensibilis Tlb.; 1, 2, 3, 4; under bark in rotten wood; all; common; fungi and rotten wood? Essig (1926)*.

Pseudistoma sensibilis Tlb.; 1, 2, 3; under bark in rotten wood; occasional; fungi and rotten wood? Essig (1926).

Pseudachorutes sp.; 2, 3; under bark; all; occasional; fungi*.

Neosmithirus clavatus (Banks); 2, 3, 4; under bark; all; rare; fungi?

Thysanura

Machilis variabilis Say; 2, 3, 4; under bark; adult; common.

Isoptera

Reticulitermes flavipes Koll.; 2, 3, 4; sapwood; all; common; rotting wood*.

Zoraptera

Zorotypus hubbardi Caudell; 2, 3; under bark; all; rare; fungi?

Orthoptera

Parcoblatta sp.; 1, 2, 3, 4; under bark; all; common; omnivorous? Blatchley (1920)*.

Heteroptera

Mezira granulata Say; 2, 3, 4; under bark; all; common; predacious? Essig (1926).

Systelloderus biceps; 2, 3; under bark; all; common; predacious?

Homoptera

Epiptera sp.; 2, 3; under bark; all; occasional; fungi*.

Coleoptera

Tachyta nana (Gyll); 1, 2, 3, 4; under bark in rotten wood; all; common; mites and collembola*.

Harpalus pennsilvanicus (De Geer); 2; under bark; adult; rare; predacious, Forbes 1883)*.

Agonum (?punctiforme Say); 2; under bark; adult larvae?; rare; predacious?

Bolitobius cinctus Grav.; 4; rotten wood; all; common; predacious? Mank (1923)*.

Hesperus baltimorensis (Grav.); 4; rotten wood; all; common; predacious*.

Gastrolobium lecontei (Horn); 1, 2, 3; under bark; all; common; predacious*.

Conosoma crassus (Grav.); 1, 2, 3, 4; under bark in rotten wood; all; common; fungi*.

Thoracophorus costalis Er.; 1, 2, 3; under bark; all; occasional; scavenger? fungi.

Staphylinus violaceus Grav.; 3, 4; under bark in rotten wood; all; common; predacious*.

Tachinus fembriatus Grav.; 4; rotten wood; all; common; predacious? Mank (1923).

Coproporus ventriculus Say; 3, 4; under bark; all; common; scavenger fungi?

Trachysectes confluentus Say; 3, 4; under bark; all; common; fungi*.

Philonthus sp.; 1, 2, 3, 4; under bark; larvae adult? common; predacious Mank (1923)*.

Batrisodes? sp.; 4; rotten wood; larva adult? occasional; mites? Blatchley (1910).

Actium sp.; 4; rotten wood; larva adult? occasional; mites Blatchley (1910).

Acritus exiguum (Er.); 1, 2; under bark; all; common; fungi*.

Bacanius punctiformis Lec.; 2, 3; under bark; all; common; fungi?

Epierus regularis Beauv.; 2, 3, 4; under bark; all; occasional; fungi?

Epierus sp.; 2, 3, 4; under bark; all; fungi?

Platysoma carolinum (Payk.); 2, 3, 4; under bark in rotten wood; all; common; predacious*.

Platysoma lecontei Mars; 2, 3, 4; under bark in rotten wood; all; common; predacious*.

Chariessa pilosa Forst. sub-sp. *Marginata* Say.; 1, 2, 3; under bark; larva adult? common; predacious Felt (1906).

Mordellistena sp.; 2, 3; rotten wood; larva; rare; rotten wood*.

Glipodes sericans Welsh; 3; rotten wood; larva; occasional; rotten wood*.

Dendroides bicolor Dru.; 2, 3, 4; under bark; larva; common; rotten wood* fungi.

Elater nigricollis Hbst.; 2, 3, 4; under bark in rotten wood; larva; common; rotten wood*.

Orthostethus infuscatus (Germ.); 3, 4; rotten wood; larva; common; rotten wood*.

Deltometopus amoenicornis (Say); 4; rotten wood; larva; occasional; rotten wood*.

Alaus oculatus Linn.; 1, 2, 3, 4; under bark in rotten wood; larva; common; predacious*.

Melanopus sp.; 1, 2, 3; under bark in rotten wood; larva; common; rotten wood*.

Adelocera sp.; 2, 3; under bark in rotten wood; larva; common; predacious*.

Eleterinae (undetermined); 2, 3, 4; under bark in rotten wood; larva; common; rotten wood*.

Chrysobothris femorata (Oliv.); 1; phloem; larva; common; phloem*.

Agrilus sp.; 1, 2; phloem; larva; common; phloem*.

Dicerca sp.; 2; phloem; larva; occasional; phloem*.

Ptilodactyla sp.; 4; rotten wood; larva adult; rare.

Ptilodactyla serricollis Say; 2; rotten wood; larva adult; rare.

Rhysodes americanus Lap.; 4; rotten wood; larva adult; occasional; rotten wood.

Tenebroides sp.; 3; under bark; larva adult; rare; predacious.

Silvanus embellis Lec.; 1, 2; under bark; larva adult; common; fungi*.

Silvanus planatus Germ.; 1, 2; under bark; larva adult; common; fungi*.

Brontes dubius Fab.; 1, 2, 3, 4; under bark; larva; common; fungi*.

- Lachmophloeus* sp.; 1, 2; under bark; adult; common; predacious Schwartz (1889).
Megalodacne fasciata (Fab.); 1, 4; under bark; larva adult; occasional; fungi*.
Triplax thoracica Say?; 4; rotting wood; larva adult?; occasional; fungi*.
Mycetophagidae (undetermined); 4; rotting wood; larva adult?; common; fungi?
Coxelus guttulatus Lec.; 2; under bark; larva adult; occasional; predacious?
Penthelispa reflexa Say; 2, 3, 4; under bark; larva adult; common; predacious.
Synchita fuliginosa Melsh.; 2; rotting bark; larva adult?; common; rotting bark.
Solydium lineola Say; 3; burrows of *Platypus* sp.; larva adult; occasional predacious on scolytids Felt (1905).
Hymenorus sp.; 4; rotten wood; larva adult?; common; rotten wood.
Hoplocephala bicornis Oliv.; 2, 3; under bark; larva adult; common; fungi*.
Platydema subcostatum Lap.; 2, 3, 4; under bark; larva adult; common; fungi*.
Platydema ruficorne Sturm.; 2, 3, 4; under bark; larva adult; common; fungi*.
Platydema ruficolle Cast. and Brill.; 2, 3, 4; under bark; larva adult; common; fungi*.
Uloma imberbis Lec.; 3, 4; rotten wood; larva adult; common; rotten wood*.
Dioedus punctatus Lec.; 3, 4; rotten wood; larva adult?; common; rotten wood*.
Scotobates calcaratus (Fab.); 3, 4; rotten wood; larva; common; rotten wood*.
Merinus laevis Oliv.; 2; rotten wood; larva; rare; rotten wood*.
Xylopinus saperdoides (Oliv.); 3, 4; rotten wood; larva; common; rotten wood*.
Alobates pennsylvanicus (DeG.); 2, 3, 4; rotten wood; larva; common; rotten wood*.
Meracantha contracta (Beauv.); 4; rotten wood; larva; common; rotten wood*.
Strongylium crenatum Makl.; 4; rotten wood; larva; common; occasional; rotten wood*.
Synchroa punctata Newm.; 2, 3, 4; under bark; larva; common; rotten wood* fungi.
Phlocotrya vaudouere Muls.; 2, 3; rotten wood; larva; common; rotten wood*.
Cis sp.; 2; under bark; larva adult?; common; fungi; Blatchley (1910).
Pseudolucanus capreole (L.); 3, 4; rotten wood; larva; common; rotten wood*.
Platycerus quercus Web.; 4; rotten wood; larva adult? occasional; rotten wood*.
Ceruchus piceus (Web.); 4; rotten wood; larva adult? occasional; rotten wood*.
Dorcus (brevis Say?); 4; rotten wood; larva adult? occasional; rotten wood*.
Polymoecus brevipes Lec.; 4; rotten wood; larva; common; rotten wood*.
Cloetus globosus (Say); 4; rotten wood; larva adult? rare; rotten wood*.
Trichiotinus bidens Fab.; 4; rotten wood; larva; occasional; rotten wood*.
Phileurus valgus L.; 4; rotten wood; larva; rare; rotten wood*.
Passalus cornutus Fab.; 2, 3, 4; rotten wood; larva adult; common; rotten wood*.
Derobrachus brunneus (Forst.); 4; rotten wood; larva; common; rotten wood.
Leptura proxima Say; 4; rotten wood; larva; common; rotten wood.
Xylotrechus colonus (Fab.); 1; phloem; larva; common; phloem.
Romaleum atomarium (Drury); 1, 2, 3; phloem, rotten wood; larva; common; phloem.
Neoclytus scutellaris Oliv.; 1; phloem; larva; rare; phloem.
Graphisurus fasciatus DeG.; 1, 2; phloem; larva; common; phloem.
Eupsalis minuta Drury; 3, 4; rotten wood; larva adult? occasional; solid and rotten wood Felt (1905).
Euparius marmoreus Oliv.; 3; under bark; larva adult? occasional; fungi Blatchley (1916).
Platypus quadridentatus Oliv.; 3; in sapwood; larva adult; common; fungi* (Ambrosia).
Orthotomicus coelatus Eichh.; 1; under bark; larva adult; common; phloem*.

Lepidoptera

- Scolecocampa liburna* Geyer; 3, 4; rotten wood; larva; common; rotten wood*.

Diptera

- Megasselia* sp.; 1, 2; under bark; larva; common; predacious? Curran (1934).
Lonchaea sp.; 1, 2; under bark; larva; common.

Tipula trivittata Say; 4; rotten wood; larva; rare.

Teucholabis sp.; 4; rotten wood; larva; rare.

Palpomyia sp. (undetermined species); 3, 4; rotten wood; larva; common.

Mycetophilidae (undetermined); 2, 3, 4; rotten wood; larva; common; fungi Baumberger (1918).

Cecidomyiidae (undetermined); 3, 4; rotten wood; larva; common; micro-organisms? Baumberger (1918)*.

Dolycopodidae (undetermined); 2, 3, 4; rotten wood; larva; common; micro-organisms? Baumberger (1918)*.

Oscinella sp.; 4; rotten wood; larva.

Tachinidae (undetermined); 1; larva; common; parasite on *Romaleum atomarium*.

Hymenoptera

Tremex columba L.; 1, 2; sapwood; larva; occasional; sound wood*.

Atanycolus simplex (Cress.); 1; under bark; larva parasite; common; parasite of *Chrysobothris fermorata**.

Atanycolus sp.; 1; under bark; larva parasite; host unknown.

Atanycolimorpha n. sp.; 2; under bark; larvae parasite; in *Romaleum atomarium**.

Sparhius floridanus Ashm.; 1; under bark; larvae parasite; common; in *Chrysobothris fermorata**.

Doryctes n. sp.; 2; under log; larva parasite; from scarabid larva.

Augochlora pura Say; 4; rotten wood (nesting); larva adult; common; pollen*.

Vespula maculata (L.); under bark; occasional; not feeding, hibernating.

Camponotus herculeanus pennsylvanicus DeG.; 1, 2, 3, 4; under bark in rotten wood; larva adult; common, scavengers? Wheeler (1913).

Crematogaster lineolata Say; 1, 2, 3, 4; under bark in rotten wood; larva adult; common; scavengers? Wheeler (1913).

Leptothorax curvispinosus Mayr.; 1, 2, 3, 4; under bark in rotten wood; larva adult; common; scavengers? Wheeler (1913).

Ponera coarota pennsylvanica Emery; 1, 2, 3, 4; under bark in rotten wood; larva adult; common; scavengers? Wheeler (1913).

Proceratium croceum; 1, 2, 3, 4; under bark in rotten wood; larva adult; occasional; scavengers? Wheeler (1913).

Formica exsectoides Forel; 3; under bark in rotten wood; adults; occasional; scavengers? Wheeler (1913).

Pheidole sp.; 4; rotten wood; all adults; rare; scavengers, Wheeler (1913).

Annelida

Lumbricidae (undetermined); 3, 4; under bark in rotten wood; all; common; rotten wood*.

Mollusca

Strobilops aena Pilsbry; 3, 4; under bark; all; common; rotten wood fungi?

Polygyra fallax Say; 4; rotten wood; all; rare; rotten wood fungi?

Polygyra tridentata Say; 4; rotten wood; all; occasional; rotten wood fungi?

Polygyra thyroidus Say; 4; rotten wood; all; rare; rotten wood fungi?

Zonitoides arboreus Say; 2, 3, 4; under bark; all; common; rotten wood fungi?

Euconulus chersinus Say; 2, 3, 4; under bark; all; common; rotten wood fungi?

Retinella indentata Say; 2, 3, 4; under bark; all; common; rotten wood fungi?

Philomycus carolinensis (Bosc.); 3, 4; under bark in rotten wood; all; common; rotten wood fungi?

Myriapoda

- Cambala annulata* (Say); 3, 4; under bark; all; occasional; rotten wood?
Fontaria coriacea Koch; 4; under bark under log; all; rotten wood*.
Polydesmus serratus Say; 4; under bark under log; all; rotten wood*.
Spirostrephon lactarium (Say); 3, 4; under bark under log; all; rotten wood*.
Linotaenia bidens (Woods); 1, 2, 3; under bark; all; common; predacious.
Geophilus varians (McNeil); 1, 2, 3; under bark; all; common; predacious.
Scolopendra viridis Say; 2, 3, 4; under bark in rotten wood; all; common; predacious.
Cryptops hyalina Say; 2, 3, 4; under bark in rotten wood; all; common; predacious.
Otocryptops sexspinosis (Say); 2, 3, 4; under bark in rotten wood; all; rare; predacious.
Bothropolyx multidentatus Newport; 2, 3, 4; under bark in rotten wood; all; occasional; predacious.

Chelonethida

- Chthonius spinosus*; 1, 2; under bark; all; occasional; predacious.
Chthonius longipalpus; 1, 2; under bark; all; occasional; predacious.
Chelanops sp.; 3; under bark; all; occasional; predacious.
Chelanops dentatus; 4; under bark; all; rare; predacious.

Acarina

- Podothrombium* sp.; 4; under bark; all; occasional; predacious?
Allothrombium pulvinus Ewing; 4; rotten wood; all; common; predacious?
Zetes sp.; 3, 4; under bark; all; occasional; fungi?
Schelorabates sp.; 4; under bark; all; common; fungi?
 (Undetermined specimens); 3, 4; under bark; all.
Uropoda sp. several species; 1, 2, 3; under bark; all; common; saprophytic?
 (Undetermined species); 1, 2, 3; under bark; all; saprophytic?
Discopoma sp.; 1, 2, 3; under bark; all; saprophytic?
 (Undetermined species); 1, 2, 3, 4; under bark; all; saprophytic?
Pergamasus sp.; 1, 2, 3, 4; under bark in rotten wood; all; common; predacious?
Seilus sp.; 2, 3; under bark in rotten wood; all; predacious?
Megisthanus sp. 1, 2, 3, 4; under bark in rotten wood; all; common; predacious?
Dendrolaelaps sp.; 1, 2, 3; under bark in rotten wood; all; predacious?
 (Undetermined species); 1, 2, 3, 4; under bark in rotten wood; all.
Tyroglyphidae (undetermined species); 2; under bark; all; common.

Vertebrata

- Plethodon glutinosus* (Green); 4; rotten wood under logs; adults; occasional; predacious?