The Great Basin Naturalist

Published at Provo, Utah by
Brigham Young University

Volume XXIII June 14, 1963 Nos. 1-2

A REVISION OF THE BARK BEETLE GENUS *DENDROCTONUS* ERICHSON (COLEOPTERA: SCOLYTIDAE)[1]

Stephen L. Wood[2]

Abstract

This taxonomic revision of all known species of *Dendroctonus* is based on an analysis of anatomical and biological characters. Among the anatomical structures found to be of greatest use in characterizing species were the seminal rod of the male genital capsule, the surface features of the frons, and the features of the elytral declivity. Characters of the egg gallery, position and arrangement of egg niches and grooves, and the character and position of the larval mines provided features for field recognition of species that were equal to, if not superior to, anatomical characters.

Following the general discussion and key each of the fourteen species recognized is treated separately, including a synonymy with an extensive list of references, anatomical description of the adult male and female, type locality, hosts, distribution and a description of the life history and galleries. Figures of anatomical parts, gallery systems and geographical distributions are included.

The species treated and their synonymy were: (1) *brevicomis* Leconte (=*barberi* Hopkins); (2) *frontalis* Zimmerman (=*arizonicus* Hopkins, *mexicanus* Hopkins); (3) *parallelocollis* Chapuis (=*approximatus* Dietz); (4) *adjunctus* Blandford (=*convexifrons* Hopkins); (5) *ponderosae* Hopkins (=*monticolae* Hopkins, *jeffreyi* Hopkins); (6) *aztecus* Wood, new species; (7) *terebrans* (Olivier); (8) *valens* Leconte (=*beckeri* Thatcher); (9) *micans* (Kugelann); (10) *punctatus* Leconte (=*johanseni* Swaine); (11) *murrayanae* Hopkins (=*rufipennis* Hopkins, nec. Kirby); (12) *obesus* (Mannerheim) (=*rufipennis* Kirby, *similis* Leconte, *piceaperda* Hopkins, *engelmanni* Hopkins, *borealis* Hopkins); (13) *simplex* Leconte; (14) *pseudotsugae* Hopkins.

[1]This study was supported by a research grant from the National Science Foundation, number B-6532.

[2]Zoology and Entomology Department, Brigham Young University, Provo, Utah. Scolytoidea contribution no. 24.

Introduction

The genus *Dendroctonus* consists of thirteen American species that range throughout the coniferous forests from Guatemala to the northern limits of tree growth in Canada and Alaska, and one Eurasian species that inhabits spruce forests from northern France to Siberia. All species infest coniferous hosts, principally representatives of the genera *Pinus*, *Picea*, *Pseudotsuga* and *Larix*, where their aggressiveness has marked them as the greatest tree killers known. Fantastic losses of standing timber resources, conservatively estimated as averaging more than five billion board feet annually, have resulted from epidemics of these insects.

All species in the genus bore in the inner bark of the bole of the host where they feed primarily upon the phloem tissue. They generally attack only living trees larger than about eight inches in diameter, either standing or prostrate, that have been weakened by age, drought, or other ecological factors; however, vigorous, healthy trees are not immune from attack, particularly during an epidemic. Their success in overcoming a tree is partly due to their gregarious nature, and partly to their association with blue-stain fungi and yeast organisms which interfere with normal physiology of the host thereby assuring success of the bark beetle attack. All fourteen species, with the possible exception of *aztecus*, are widely distributed geographically but are rather limited in host range. All species, with the possible exception of *pseudotsugae* and *valens*, confine their attacks to a single genus of host tree, and usually to a limited group of species within that genus, except during epidemic outbreaks when almost any conifer may exhibit signs of attack.

History

As originally described by Erichson (1836:52), the genus *Dendroctonus* included five species listed in the following order: (1) *Bostrichus micans Kugelann*, (2) *Scolytus terebrans* Olivier, (3) *Dermestes piniperda* Linnaeus, (4) *Hylesinus minor* Hartig, and (5) *Hylesinus minimus* Fabricius without the designation of a type species. Later, Eichhoff (1864:25) divided the group and described the genus *Blastophagus* for *Dermestes piniperda* Linnaeus and *Hylesinus minor* Hartig, and the genus *Carphoborus* (Eichhoff 1864:27) for *Hylesinus minimus* Fabricius. Since that date there has been no question concerning the identity or validity of the name *Dendroctonus* and no synonyms or subgenera have been described. Everyone treating this genus since its description, however, has overlooked the fact that Westwood (1838:39) designated *Dermestes piniperda* Linnaeus as the type species of the genus *Dendroctonus* just two years after its description. Hopkins' (1909:5) designation of *Bostrichus micans* Kugelann as the types species is, therefore, technically invalid.

Latreille (1802:203) described the monobasic genus *Tomicus* with *Hylesinus piniperda* Fabricius, which by definition (Fabricius, 1801:392) was *Dermestes piniperda* Linnaeus, as the type species. Because of an unfortunate error in identification, Latreille's name *Tomicus* became associated with another genus (*Ips* DeGeer) for approximately a hundred years before the error was detected, but the correct usage of Latreille's name was never restored by European writers. Meanwhile, *Dermestes piniperda* Linnaeus was designated as the type species of *Dendroctonus* Erichson (1836) by Westwood (*loc. cit.*), of *Blastophagus* Eichhoff (1864) (nec. *Blastophagus* Gravenhorst, 1827, or *Blastophaga* Gravenhorst, 1829, order Hymenoptera), by Lacordaire (1866:360), and of *Myelophilus* Eichhoff (1878:400) (nec. *Myelophila* Treitschke, 1835, order Lepidoptera). Since all four genera have, by definition or subsequent assignment, *Dermestes piniperda* Linnaeus as the type species, they are objective synonyms of one another with *Tomicus* Latreille having priority by at least 34 years.

By strict application of the Law of Priority the name *Dendroctonus* is unavailable for use in designating the genus to which *Bostrichus micans* and its allies belong. However, because of its unquestioned, consistent usage for more than a hundred years, because of the voluminous published literature concerning it, because of the tremendous economical and biological importance of the species involved, and because the original generic description applies to *micans*, the first species listed by Erichson (with a five-segmented antennal funicle), and not to *piniperda*, the third species listed (with a six-segmented funicle), an appeal was made to the International Commission on Zoological Nomenclature (Wood, 1961) to exercise its plenary powers in order to conserve the name *Dendroctonus* Erichson, with *Bostrichus micans* Kugelann as the type species as designated by Hopkins (1909:5), and to invalidate Westwood's (*loc. cit.*) type designation of *Dermestes piniperda Linnaeus*. The recommended action has now been taken that permanently fixes the name *Dendroctonus* to the genus treated here, with *Bostrichus micans* Kugelann as its type (Opinions and Declarations Rendered by the International Commission on Zoological Nomenclature, Opinion No. 670, in press).

To *Bostrichus micans and Scolytus terebrans* that were included in the original diagnosis of the genus by Erichson, Zimmerman (1868:149) added his new species *frontalis*, and also cited *terebrans*. Leconte (1860:59) described *valens* and *similis* as new species, then later (1868:173) added *Hylurgus obesus* Mannerheim, *Hylurgus rufipennis* Kirby and described as new *punctatus* and *simplex;* he also listed *frontalis* and mentioned *valens* as a synonym of *terebrans*. Chapuis (1869:34) recognized *micans*, *valens*, *obesus* and *terebrans*, and described *parallocollis* as new. Leconte (1876:384-386) listed *terebrans* (=*valens*), *similis*, *rufipennis* (=*obesus*), *punctatus*, *simplex*, *frontalis* and a new species *brevicomis*. Dietz (1890) recognized *terebrans*, *rufipennis* (=*similis*), *simplex*, and *frontalis* (=*brevicomis*) and described *approximatus* as new to the genus. Blandford (1897:146-147) recognized *terebrans* (=*valens*), *parallelocollis*, *approximatus*, and his new *adjunctus*. In many, if not most of the above citations the specimens under consideration by the various authors did not belong to the species named, and each writer in attempting to clarify the classification of *Dendroctonus* only added to the confusion of species.

In a series of papers published between 1892 and 1909, and summarized in his monumental monograph of the genus, Hopkins (1909) presented a new classification in which he added as new the names *barberi*, *convexifrons*, *arizonicus*, *mexicanus*, *monticolae*, *ponderosae*, *jeffreyi*, *pseudotsugae*, *piceaperda*, *engelmanni*, *borealis* and *murrayanae*. He also recognized as valid the previously described species *brevicomis*, *frontalis*, *parallelocollis*, *approximatus*, *simplex*, *obesus* (=*similis*), *rufipennis*, *punctatus*, *micans*, *terebrans*, *valens* and *adjunctus*.

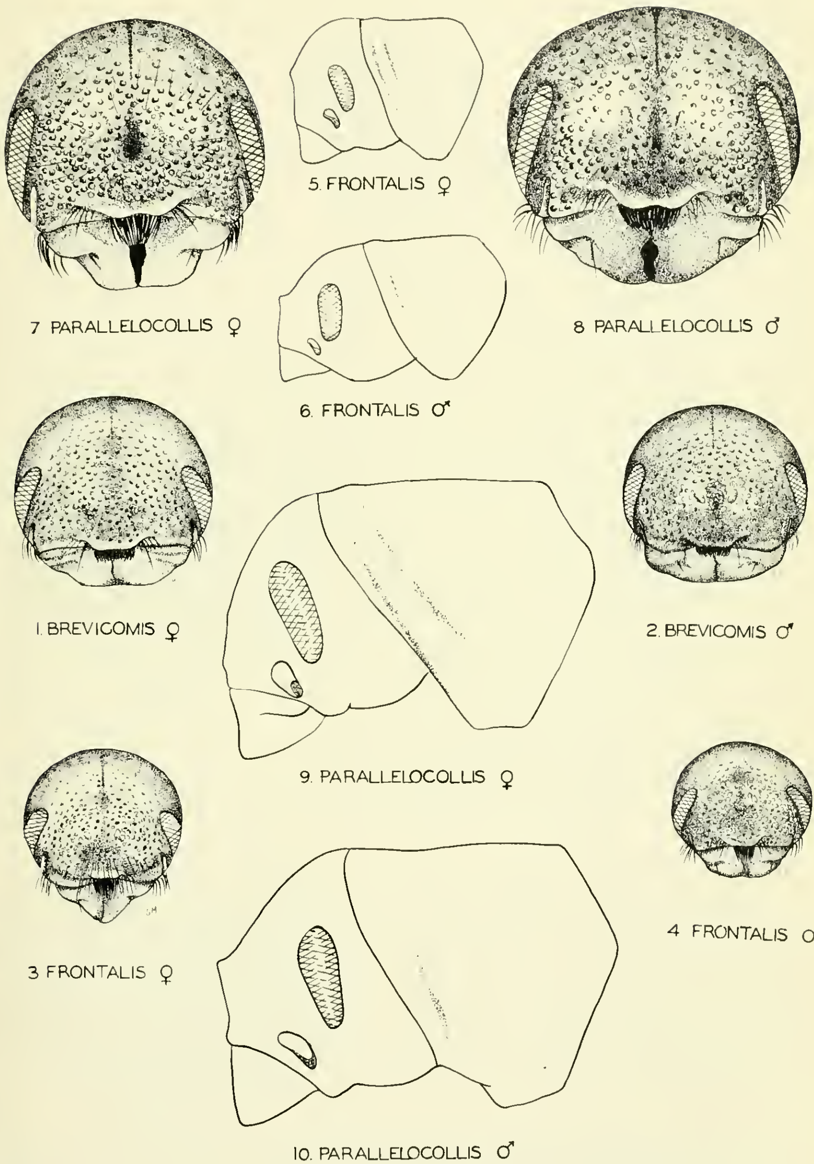
Alterations in the genus since the monograph by Hopkins include the addition of two names, *johanseni* by Swaine (1919:5E) and *beckeri* by Thatcher (1954:4), and the placement of *approximatus* as a synonym of *parallelocollis* by Schedl (1955:11), and of *beckeri* as a synonym of *valens* by Schedl (1955:15).

Discussion of Morphological Characters

General features.—Although characteristic of the various species in a general way, body size could be used only in conjunction with other characters because the smallest specimens of the largest species (*valens*) were almost as small as the largest specimens of the smallest species (*frontalis*). Body form ranged from moderately stout to rather slender, but differences were too slight and individual variation too great to distinguish between any but the extremes of body form. Mature body color was very characteristic of groups of species; for example, the first seven species listed in the key were uniformly black (or very dark brown), *valens* was a distinctive reddish brown, *micans* and *punctatus* a rather dark brown, and the last four species listed were very dark brown with much lighter reddish brown elytra. The vestiture was characteristic of one species only, *brevicomis*, where it was uniformly short.

Head.—The general surface sculpturing of the facial region was of extreme value and provided perhaps the most reliable external characters in establishing a workable classification of the genus. In general, the facial region is convex from the slightly elevated, smooth epistomal margin to the vertex, with a conspicuous epistomal process developed immediately above and overlapping the median portion of the elevated rim of the epistomal margin.

The epistomal process varied in width from a distance equal to one-fourth to one-half the distance between the eyes, with the lateral margins oblique and diverging from its horizontal apical portion towards its base by an angle as small as 20° in males of *valens* (Fig. 15) to one exceeding 80° in *pseudotsugae* (Fig. 23). In *aztecus*, *micans*, *simplex* and *pseudotsugae* the process was either transversely convex or flat with the lateral margins rather sharply rounded.



Figs. 1-4, 7-8. Cephalic aspect of head of *Dendroctonus* spp.: 1, *brevicomis* ♀; 2, *brevicomis* ♂; 3, *frontalis* ♀; 4, *frontalis* ♂; 7, *parallelocollis* ♀; 8, *parallelocollis* ♂.

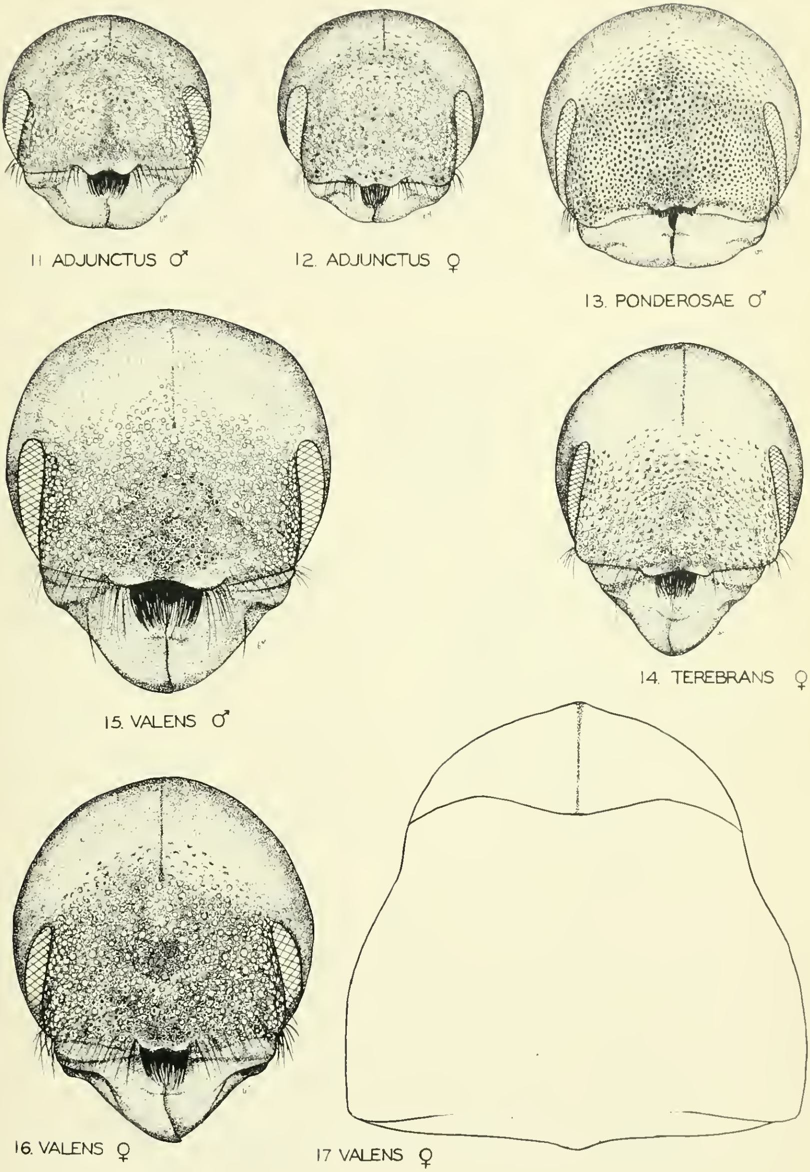
Figs. 5-6, 9-10. Lateral aspect of head and prothorax of *Dendroctonus* spp.; 5, *frontalis* ♀; 6, *frontalis* ♂; 9, *parallelocollis* ♀; 10, *parallelocollis* ♂.

In all other species the lateral arms were variously elevated thereby making the process transversely concave. In almost every species the epistomal process was somewhat wider with the lateral margins or arms, if elevated at all, more prominently elevated in the males than in the females. It should be emphasized that considerable individual variation in the size and shape of the epistomal process was apparent and could often be used with confidence only in combination with other characters.

The general contour of the facial region exhibited several consistent and reliable secondary sexual and interspecific variations. For example, in *brevicomis*, *frontalis*, *parallelocollis* and *adjunctus* (Figs. 1-12) a conspicuous median frontal groove below the upper level of the eyes was present with the areas lateral to it rather conspicuously elevated; both the groove and the elevations were more highly developed in the male than in the female. In the males of these species, except in *adjunctus*, the lateral elevations bear one or two dorsomedially directed, enlarged, almost hornlike tubercles. In *valens* (Fig. 16) and, to a lesser degree, in *terebrans* the female has a small median region elevated at the upper level of the eyes. In *punctatus*, *micans* and *murrayanae* there is a feeble median groove which on the lower third of the frons becomes a more or less definite median carina. In *ponderosae* there are remnants of a median groove at the upper level of the eyes and also on the lower half of the frons; in *aztecus* there is often a comparable, almost scarlike remnant of this impression on the lower half of the frons. In perhaps the majority of species the surface sculpturing, such as punctures and granules, appeared to be very slightly coarser in the female than in the male. In *punctatus*, *micans*, *murrayanae* and *obesus* (Figs. 18-21) the most minute details of surface features, the relative numbers of punctures and granules, offer the only really reliable method of separating species without resorting to dissection of the male genital capsule.

The eyes varied conspicuously in the genus from short and oval to long and slender. As illustrated by Hopkins (1909, fig. 15), however, the variation between individuals of the same species is so great that use of the eyes in classification at the species level is virtually impossible. The antennae are also exceedingly variable within a species and, consequently, were not utilized in this classification; this infraspecific variation probably was due more to variation in the way museum specimens dried than to variation in basic structure.

Prothorax.—The outline of the pronotum as seen from the dorsal aspect, although somewhat variable, offers useful characters in classification when used in combination with other features. The basal margin is somewhat bisinuate in all species; the lateral margins are arcuate to varying degrees in the different species and usually more or less converging anteriorly. In *aztecus* (Fig. 25) the transverse constriction just behind the shallowly emarginate anterior margin (Figs. 6, 10) is scarcely visible; in females of *brevi-*



Figs. 11-16. Cephalic aspect of head of *Dendroctonus* spp.; 11, *adjunctus* ♂; 12, *adjunctus* ♀; 13, *ponderosae* ♂; 14, *terebrans* ♀; 15, *valens* ♂; 16, *valens* ♀.

Fig. 17. Dorsal aspect of head and prothorax of *Dendroctonus valens* ♀.

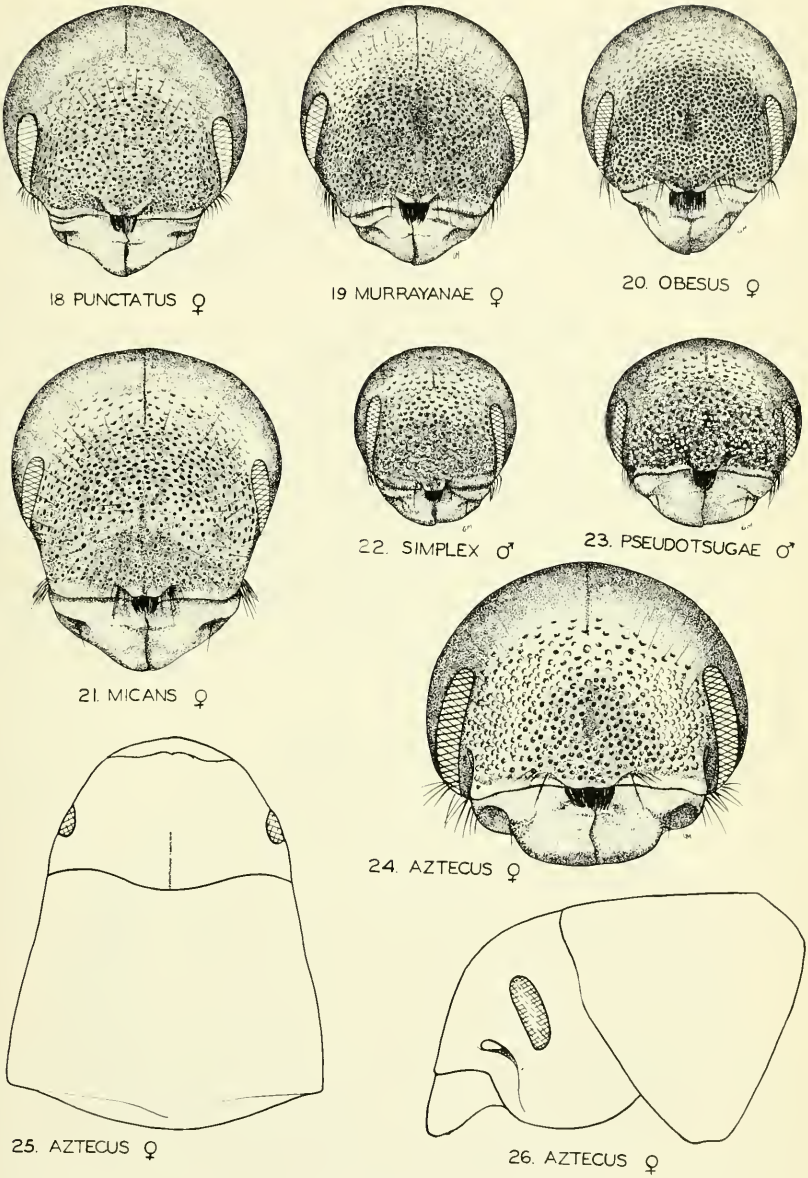
comis, *frontalis* (Fig. 5), *parallelocollis* (Fig. 9) and *adjunctus* the constriction is largely filled by an elevated callus; in the last nine species listed in the key the constriction is rather well developed.

The punctures on the disc of the pronotum vary considerably, both intra- and interspecifically. Because of their variability they were used only sparingly in separating species, this is in contrast to the great emphasis given pronotal punctures by Hopkins (1909:11, etc.). The proepisternal areas vary from punctured with very minute granules to rather coarsely granulate with the punctures almost entirely obliterated. Use of proepisternal characters was made only once in the key, with some reluctance, since the characters are seen with some difficulty unless the proper lighting conditions are employed.

Elytra.—The basic proportions of the elytra vary slightly, but do not reflect characters of value. There also is an increase in the average number of marginal crenulations at the base of each elytron from nine to twelve in the genus. This may have evolutionary significance, but appears too slight and too unreliable to use in diagnosing species.

The elytral striae and interstriae are of considerable value in recognizing species if used with sufficient caution. The interstriae vary from about equal width to more than twice the width of the striae. The striae and strial punctures vary somewhat in depth, but this feature is rather unreliable since lighting conditions may completely change the appearance of this character. The sculpturing of interspaces is rather variable within the genus and usually provides reliable characters for species diagnosis. In only one species, *simplex*, were simple, non-granulate interstrial punctures apparent on the disc. In *aztecus* some of the transverse crenulations on the disc were so coarse and long that they extended across striae and interstriae alike; in most of the species these crenulations varied within definite limits and were very useful when used with other characters in determining species.

Although conservatively sculptured the characters of the elytral declivity are, in many cases, the most easily observed and reliable external features available for the diagnosis of species. In *brevicomis* and *frontalis* (Figs. 27, 28) the second striae are straight and the second interspace is as wide as one and three; in *simplex* and *pseudotsugae* the second interspace is gradually narrowed and on at least the lower half is narrower than one or three; in all other species the second striae curve toward the suture at least near the elytral apex, causing an abrupt tapering of interspace two on less than the lower fourth of the declivity (Figs. 29, 30). Interspace two is at least shallowly impressed except in *frontalis*, *aztecus*, *murrayanae*, *punctatus* and *micans;* the first interspace is very strongly elevated in *simplex* and *pseudotsugae*, and rather weakly to not at all raised in the other species. The size of strial punctures and the sculpture of interspaces on the declivity usually are characteristic of species and offer excellent characters for diagnosis. In *obesus*,



Figs. 18-24. Cephalic aspect of head of *Dendroctonus* spp.: 18, *punctatus* ♀; 19, *murrayanae* ♀; 20, *obesus* ♀; 21, *micans* ♀; 22, *simplex* ♂; 23, *pseudotsugae* ♂; 24, *aztecus* ♀.

Figs. 25-26. Head and prothorax of *Dendroctonus aztecus*: 25, dorsal aspect; 26, lateral aspect.

murrayanae, *simplex*, *pseudotsugae*, and to a lesser extent in other related species, the interstrial granules on the declivity were greatly reduced or absent in the male, thereby providing a convenient, although not entirely reliable, means of distinguishing the sexes.

Legs.—The legs are rather characteristic of the genus, but present no consistent variations of sufficient magnitude to be useful in classification.

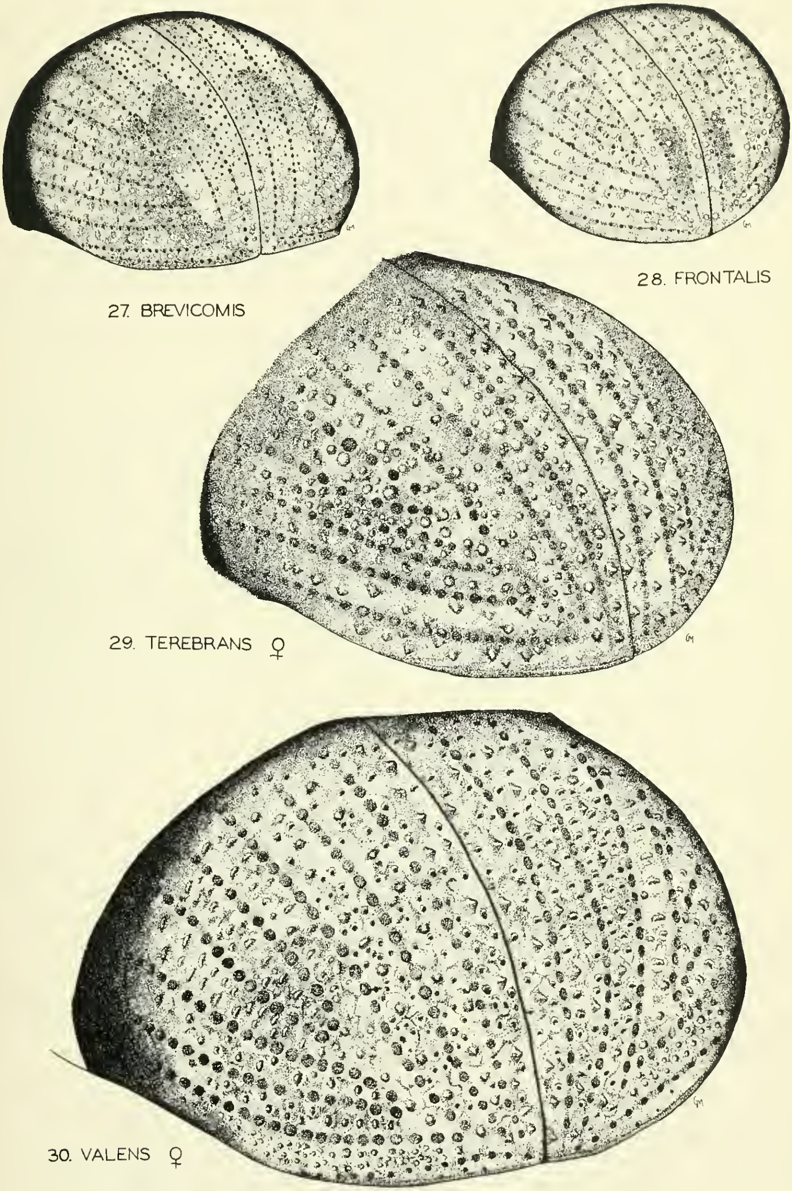
Male genitalia.—Although not suitable for rapid field identification, the characters of the genitalic capsule of the male (Figs. 31-42) included, in several cases, the only truly dependable method for recognizing species. When this study was initiated it was considered virtually impossible to separate *murrayanae*, *obesus*, *micans* and *punctatus* or to find sufficiently reliable evidence to place some of Hopkins' names in synonymy, because of the apparently tremendous individual variation involved, until genitalic characters were studied. When this was done the seemingly incomprehensible mass of variation fell into orderly patterns and very minute characters, particularly on the frons and declivity, which had been meaningless before, became useful and reliable means of diagnosing difficult species. The structure having taxonomic value was designated by Hopkins (1915:118) as the seminal rod.

Generic features.—Of the genera known to the writer, *Tomicus*, *Hylurgus*, *Pachycotes* and *Hylurgonotus* appear to be more closely allied to *Dendroctonus* than others. They share the symmetrical, more or less flattened antennal club; the finely faceted, entire eye; the absence of a presternal ridge between the coxae and the anterior margin of the prothorax; the bilobed third tarsal segments; the hairlike vestiture; and many other characters. In *Pachycotes* and *Hylurgonotus* (*brunneus* only) a distinct, though poorly developed epistomal process is evident, but both have the posterolateral ridge extending along the mandible acutely elevated; the other genera lack both characters; although the mandibular modification is apparent in *Hylurgus*. The male frons is noticeably impressed above in *Pachycotes*, *Hylurgonotus* and *Hylurgus*, almost imperceptibly so in *Tomicus*, and not all impressed in most *Dendroctonus*.

Discussion of Biology

Biology.—All species of *Dendroctonus* may pass the winter in almost any stage of development, however, some species are represented by a preponderance of one stage. In *adjunctus* and *ponderosae* the larval stage predominates, and in *simplex*, *pseudotsugae*, *terebrans* and perhaps *valens* the adult is the principal overwintering stage. In the other species one stage may be represented more commonly in hibernation than another, but not as disproportionately as those mentioned.

Flight activity for most species begins in the spring whenever daytime temperatures reach about 45° to 50°F., usually about April or May, and continues more or less without interruption until



Figs. 27-30. Dorsolateral aspect of elytral declivity of *Dendroctonus* spp.: 27, *brevicomis;* 28, *frontalis;* 29, *terebrans* ♀; 30, *valens* ♀.

late September or October. There are, however, conspicuous periods of increased flight activity that correspond with the emergence of overwintered young adults and of each new generation during the summer months. A notable departure from this usual pattern occurs in *ponderosae* where emergence ordinarily does not begin before late July and subsides by mid-September.

All species may, on occasion, attack standing, vigorous trees. Under normal endemic conditions, however, some species, noteably *parallelocollis*, *valens*, *terebrans*, *murrayanae*, *micans*, *punctatus*, *obesus*, *simplex* and *pseudotsugae*, prefer stumps or prostrate trees or logs. Others, such as *bervicomis*, *frontalis*, *adjunctus*, *ponderosae*, and possibly *aztecus*, seldom are found anywhere except in standing trees. Under endemic conditions the standing trees selected for attack ordinarily are either overmature, unthrifty, or weakened by disease, lightning, drought or other factors.

The pattern of attack on a particular standing tree usually is characteristic of the species. For example, *parallelocollis*, *valens*, *terebrans*, *murrayanae*, and possibly *punctatus* and *aztecus* ordinarily confine their attacks to the basal portion of the tree, seldom striking higher than two or three feet above the ground level. In *adjunctus*, *micans*, *obesus* and *ponderosae* (except on mature large trees) the attacks begins on the lower third of the bole and progresses upward; in *brevicomis*, *frontalis*, *pseudotsugae*, possibly *simplex*, and *ponderosae* (at least in overmature sugar pine) the attack begins in the upper midbole area and progresses upward and downward from that point. The attack, depending on the beetle population in a given area, may be concentrated into a few days, or it may extend over more than a year and involve two or more successive generations in some species if competing species do not occupy the available bark.

The individual attack is made by the female usually in a crevice of the bark. When the inner bark is reached and resin ducts are severed the tunnel may be invaded by quantities of pitch that must be removed as the burrow advances. The ability of the female to cope with this material is remarkable. The pitch and frass resulting from the excavation are pushed out of the entrance hole where they adhere to the bark forming a characteristic pitch tube. The presence of these pitch tubes or scattered frass ordinarily is the first indication that the tree is under attack. The size, color and general character of the pitch tubes may indicate the species of beetle making the attack.

Normally, about the time or shortly after the female reaches the phloem tissues she is joined by a male. If the male does not appear the gallery may be advanced, complete with egg niches or grooves until he does arrive, or it may be abandoned and a new attack started. Mating evidently first occurs within a few hours after the phloem tissues are reached; it evidently occurs in the first two or three centimeters of gallery where the gallery is shaped differently and wide enough to permit mating. Mating evidently oc-

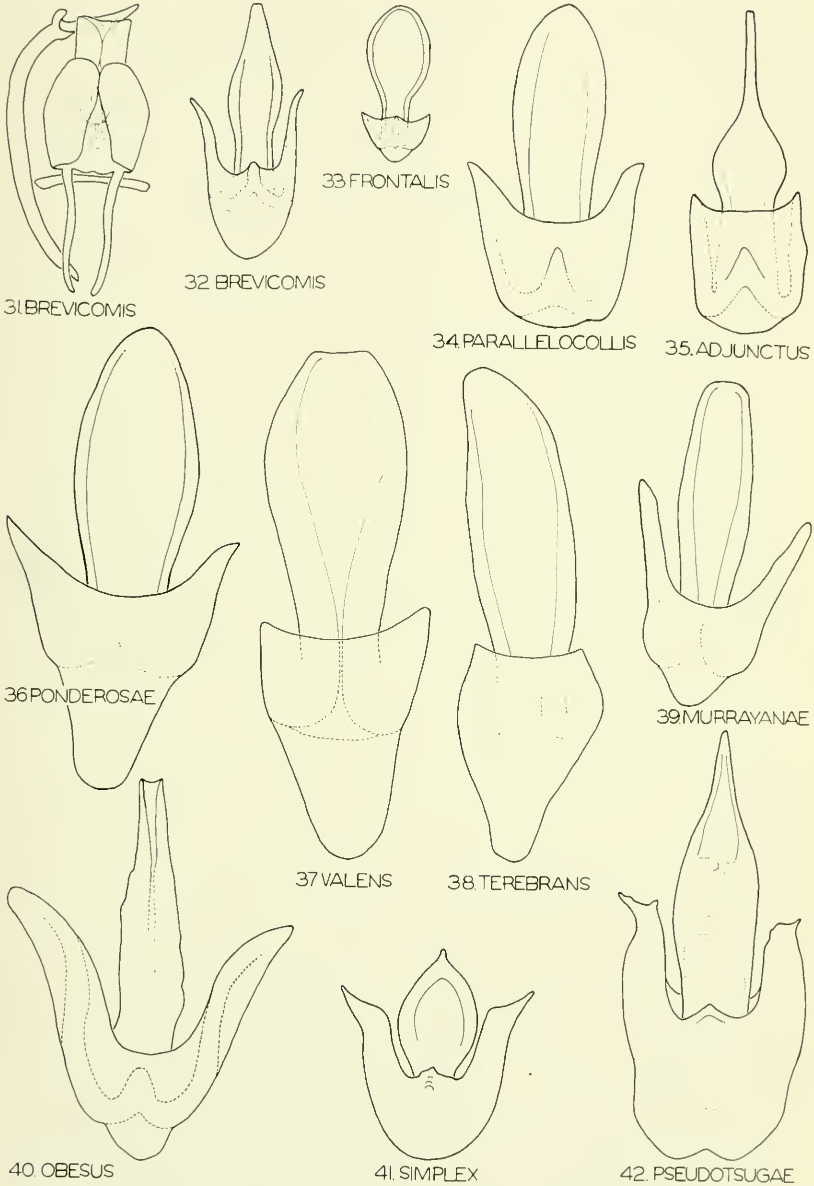


Fig. 31. Dorsal aspect of male genital capsule of *Dendroctonus brevicomis* with the internal position of the seminal rod indicated (posterior end up).

Figs. 32-42. Seminal rod of *Dendroctonus* spp.: 32, *brevicomis*; 33, *frontalis*; 34, *parallelocollis*; 35, *adjunctus*; 36, *ponderosae*; 37, *valens*; 38, *terebrans*; 39, *murrayanae*; 40, *obesus*; 41, *simplex*; 42, *pseudotsugae*.

curs repeatedly, since during this study it was observed in five species in galleries more than half complete. Following mating the male may abandon the gallery in search of another female, but more commonly he remains and takes over the function of removing frass and pitch from the tunnel, thereby permitting the female to concentrate on extension of the gallery and egg deposition. After the gallery is fairly well advanced the frass is packed in the lower or older regions of the gallery thereby closing the entrance tunnel. At any time during the development of the gallery the male may abandon the gallery by extending a ventilation tunnel, or he may remain until death. The female also may remain until death, or she may emerge from the completed gallery and make a second or even a third attack.

There is considerable variation in the character of the egg galleries among the various species of *Dendroctonus*. All are formed in the phloem tissues and scarcely, if at all, engrave the wood. In general they are more or less straight, linear, and follow the grain of the wood; however, in *brevicomis*, *frontalis*, *parallelocollis*, and *adjunctus* (Figs. 46, 47, 49, 51) they are strongly sinuate. In *brevicomis* the total lateral displacement[3] of a gallery usually is equal to or greater than the total longitudinal displacement; the whole complex forms an intertwining network of winding, branching galleries (Fig. 43). In *frontalis* the pattern is very similar to that of *brevicomis*, except that the total longitudinal displacement of one gallery usually exceeds its lateral displacement. Basically the galleries of *parallelocollis* are sinuate, forming a coarse branching and anastomosing criss-cross pattern entirely peculiar to this species. In *adjunctus* the total longitudinal displacement of a gallery is about three to four times greater than the lateral dispalcement; each successive curve, following the first large one, becomes smaller until the final part of the gallery may be virtually straight. In *valens* (Fig. 56), and to lesser extent in *terebrans*, certain parts or perhaps all of the gallery is expanded into a broad, flat cave from which the larvae mine, in congress, thereby enlarging the cave to an area that may cover several square feet of bark surface.

Placement of the eggs along the sides of the gallery varies considerably in the genus. In *brevicomis*, *frontalis*, *parallelocollis*, *adjunctus* and *ponderosae* the eggs always are placed individually in niches that are constructed alternately on the sides of the gallery. In *ponderosae* (Fig. 53) instead of individual niches alternating, from one to eight niches are formed on one side of the gallery then a comparable number are formed on the other. In *parallelocollis* (Fig. 49) the niches are formed in the sides of the gallery farthest from the cambium; the other four species mentioned above place

[3]Lateral displacement refers to deviations from or toward the main vertical axis of a gallery. For example, if the first turn of an egg gallery extends four centimeters to the right, then curves back to the imaginary vertical axis, the total displacement of that turn would be eight centimeters. If this gallery continued three centimeters to the left of the central axis and returned in making a second curve, the total lateral displacement of both turns would then be eight plus six, or 14 centimeters. Longitudinal displacement may be calculated in a similar manner by using a horizontal axis instead of a vertical one.

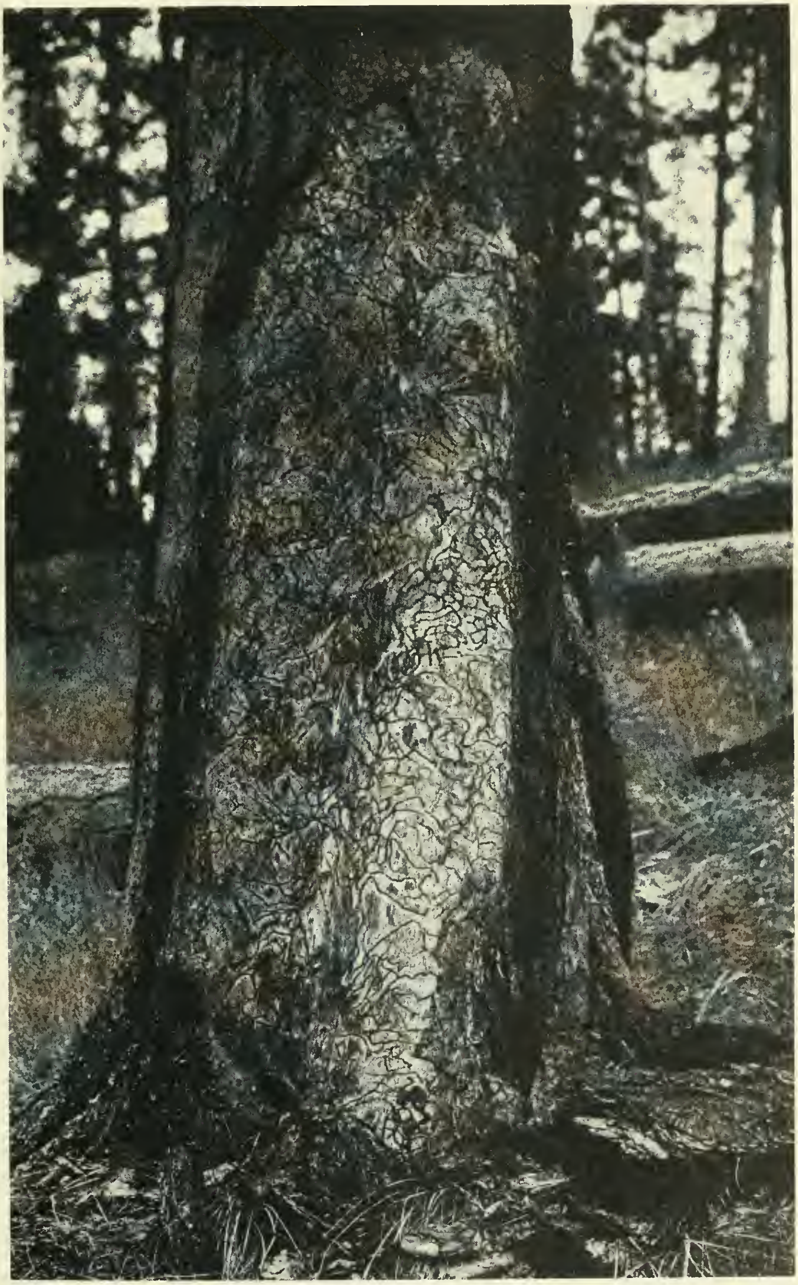


Fig. 43. Dead Ponderosa pine with bark peeled to expose egg galleries of *Dendrotconus brevicomis* (after Swaine, 1914).

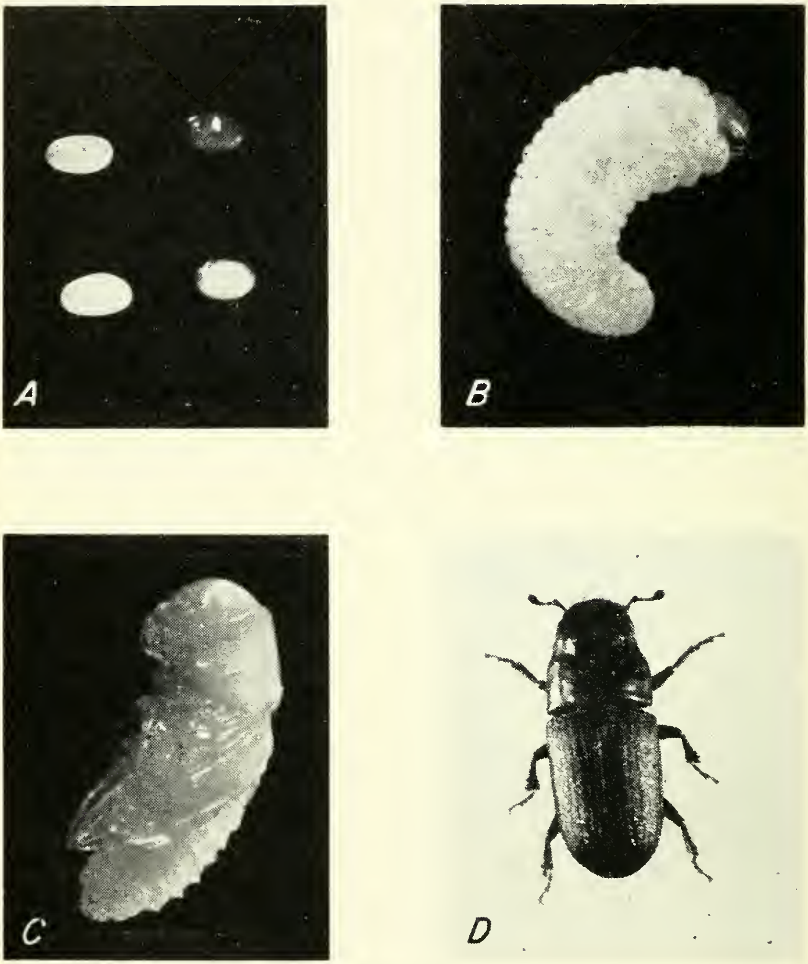


Fig. 44. Stages in the development of *Dendroctonus brevicomis*: A, eggs; B, larva; C. pupa; D, adult (after Miller and Keen, 1960).

their niches next to the cambium (Figs. 46, 47, 51, 53). The remaining species deposit their eggs in masses of about 20 or more in specially prepared grooves along the sides of the gallery. Ordinarily these grooves are placed alternately along the sides. In *pseudotsugae* (Fig. 63) and possibly in *simplex* (not observed), the eggs in each mass are oriented in a definite way; this habit of orienting or placing each egg in a special position did not appear to occur in other species. In *obesus* (Fig. 61) the characteristic habit was to place egg masses in grooves, but frequently some or even all of the eggs in a gallery were placed in individual niches; evidently this occurred most often when the beetle encountered unfavorable environmental conditions. The habits of *aztecus* were not observed.

The pattern of larval mines also varied among the different species in the genus. In *brevicomis*, *frontalis*, *parallelocollis*, *adjunctus* and, perhaps to a lesser extent, *ponderosae* and *simplex*, the larval mines are separate from one another and increase only slightly during the first and second instars. They then expand suddenly into an irregular feeding area where the last two larval instars occur. In *parallelocollis* (Fig. 49) the entire larval mine is between the inner and outer bark and is not exposed on the surface of peeled bark. In *brevicomis* (Fig. 46) and in about half of the *frontalis* (Fig. 47) mines the slender initial part of the larval mine is in contact with the cambium and exposed on peeled bark, the expanded portion in both species always is concealed in the inner or outer bark. (except *frontalis* in thin bark). In *adjunctus* (Fig. 51) and *ponderosae* (Fig. 53) the entire larval mine is in contact with the cambium and is exposed on the surface of peeled bark. In *terebrans*, *valens*, *micans*, *punctatus*, *murrayanae* (Fig. 59) and *obesus* (usually) (Fig. 61) the larvae feed in congress, forming a common cave for at least part of the larval period. In *terebrans* and *valens* this communal feeding continues until pupation, except for an occasional larva that forms a short individual tunnel just before pupation. In *murrayanae*, and presumably in *punctatus* and *micans*, the larvae feed in congress for six or eight centimeters when individual groups separate then later rejoin one another leaving islands of unexcavated bark in the feeding area; they may cover considerable distances in the process, but usually the larvae are in a common area by the end of their development. In *obesus* (Fig. 61) the larvae mine in congress for about the second and third instars when each separates from the others and constructs a separate mine, unless crowding is severe. In *pseudotsugae* (Fig. 63) the larvae construct individual mines that increase in width gradually throughout their length.

Pupation in all *brevicomis*, *frontalis* and *parallelocollis*, and in some *adjunctus* and *pseudotsugae*, takes place in the outer bark; in the remaining species it occurs at the end of the larval mine or in the frass of the common feeding chamber in the area of the cambium and is exposed on peeled bark.

The only species known to have a special overwintering habit is *obesus*. About half of the young adults emerge from the brood galleries and re-enter the base of their own or another brood tree or other suitable tree where they construct feeding tunnels. They emerge the following season to commence their attacks on new trees to begin another generation. This habit has not been reported in other species, but is suspected in *murrayanae* and perhaps in one or two other closely related species.

The number of generations each year varies from one to five or more. In *brevicomis* and *frontalis* three or more generations are common in the southern parts of their distributions, with fewer generations in cooler areas. In the other species one generation and a partial second generation is typical, except in the extreme southern areas where cool temperatures do not interrupt development, or in northern areas where one summer is not sufficient to complete larval development. In *ponderosae* one generation each year appears to be the rule in all areas, except in southern California where two and a partial third generation may occur.

Host specificity.—Under endemic conditions each species of *Dendroctonus* characteristically restricts its attacks to certain preferred species of coniferous trees. Each of the 14 species includes more than one host species in its preferred list; only two infest more than one host genus. Eight species normally attack only trees of the genus *Pinus;* these are *brevicomis*, *frontalis*, *parallelocollis*, *adjunctus*, *aztecus*, *ponderosae*, *terebrans* and *murrayanae*. Three species attack only trees of the genus *Picea;* these include *micans*, *punctatus* and *obesus*. One species, *simplex*, prefers only the species of *Larix*. The species of *Pseudotsuga* are preferred exclusively by *pseudotsugae*, except in northeastern British Columbia where *Larix* evidently is a normal host of endemic populations. The most unrestricted species in the genus is *valens;* it occurs most commonly in species of *Pinus*, but also is found in *Picea*, *Larix*, *Abies* and perhaps other genera of coniferous trees.

A phenomenon that has caused considerable controversy in the past and probably will continue to do so in the immediate future, occurs in several species. It is best illustrated by the distinctive, easily recognized *pseudotsugae*. Over most of its range the only host of this species is Douglas fir; understandably, it may also attack Big Cone spruce, *Pseudotsuga macrocarpa*, in areas where that host occurs. In northeastern British Columbia endemic populations evidently breed successfully in *Larix occidentalis*, although they presumably are unable to do so where both Douglas fir and Western larch occur together in other parts of the beetle's distribution. In *murrayanae* a similar situation presumably occurs in the Great Lakes area where Red pine (*Pinus resinosa*) and Eastern white pine (*Pinus strobus*) apparently are acceptable hosts of endemic populations; in all other parts of its distribution Jack pine (*Pinus banksiana*) or the virtually identical Lodgepole pine (*Pinus contorta*) are the only hosts. It is not impossible in this instance, however, that the Red pine and Eastern white pine infestations resulted from the overflow of an epidemic of this beetle in neighboring Jack pine. A similar, but much more complex problem appears to occur in *ponderosae*.

In *ponderosae* local endemic populations may exhibit a preference for any one of several hosts even though more than one of those on the preferred list may occur in mixed stands with the one actually selected in that area. For example, in certain parts of California Jeffrey pine (*Pinus jeffreyi*) is selected; in parts of Oregon and Washington it may be Western white pine (*Pinus monticola*); in parts of Idaho, Montana, Wyoming and Utah it may be Lodgepole pine; in parts of Colorado, Utah and the Black Hills it may be Ponderosa pine (*Pinus ponderosa*); in parts of Colorado, Utah, New Mexico and Arizona it may be Pinon pine (*Pinus edulis*); etc. Whether these preferences result from genetic differences in the local beetle populations, from competition between species attempting to occupy the same ecological niche, from differences in the host species, from differences in climate, or from other factors is uncertain. Experienced forest entomologists disagree concerning the behavior of endemic populations of this species in mixed stands of two or more of the preferred hosts. For example, it was reported by reliable, experienced workers that outbreaks of this species in Jeffrey pine did not spread into neighboring stands of Ponderosa pine. Other workers of equal reliability and experience reported that approximately equal numbers of the two host species were attacked when they occurred in mixed stands but that tradition required them to attribute the Ponderosa attacks to *Dendroctonus brevicomis*. Personal investigations conducted for very brief periods at each of three widely separated localities in the area in question, in three different seasons, have led me to the following conclusions for this particular area of controversy. First, in pure stands of Ponderosa pine at the lower elevations *ponderosae* ordinarily is not present, all beetle-killed trees appeared to be occupied by *brevicomis*; in pure stands of Jeffrey pine at higher elevations *ponderosae* has no competition from other aggressive species of *Dendroctonus* and, consequently, is present in all beetle-killed trees. At the higher elevations where mixed stands of the two hosts occurred both were attacked with approximately equal frequency by *ponderosae*, *brevcomis* occasionally was present in some of the Ponderosa pine trees. At the intermediate to lower elevations, rather near mixed stands of these hosts, both species of *Dendroctonus* occurred in the same Ponderosa pine trees, but *ponderosae* evidently occurred only in the lower third of the bole where its galleries were intermixed with those of *brevicomis*. It appeared that the colder winter temperatures encountered at the upper elevations, where mixed stands occurred, were a definite factor in retarding the development of *brevicomis* sufficiently that *ponderosae* could compete successfully in Ponderosa pine. At the lower elevations where mixed stands occurred it appeared that the temperature advantage enjoyed by *ponderosae* was absent and that the only reason this species was represented in Ponderosa pine at all was the nearby reservoir of Jeffrey pine where it enjoyed freedom from competition. In this area of California climatic factors appeared to be much more important than genetic factors. The principal California area considered here was in Lassen National Forest from Old Station to Black's Mountain south to Lassen Park; the elevation varied from about 3200 to about 7000 feet.

In the Uinta Mountains of Utah pure stands of Lodgepole pine occur in certain areas and pure stands of Ponderosa pine occur in others. Between the pure stands are areas where mixed stands of these trees are found. In the absence of usable published data, personal communication from local rangers and other Forest Service personnel familiar with the area indicate that some outbreaks of *ponderosae* occur in Lodgepole, but not in Ponderosa pine, and that other outbreaks occur in Ponderosa, but not in Lodgepole pine. Other workers reported that these outbreaks ordinarily sweep from one host species to the other. It was also reported that an attempt was made to rear beetles coming from one host species on the other host species, but was unsuccessful. Whether the failure resulted from genetic differences of the beetles or from faulty experimental procedure is unknown. Personal studies in these mixed stands indicated that beetles developing in an area where a mild outbreak in Lodgepole was in progress, were attacking Ponderosa pine. It appeared that a physiological adjustment requiring one or two successive generations was necessary before the normal survival rate of the brood was attained. The rate of survival of brood in the first Ponderosa pine trees attacked in this area was very low.

The above three paragraphs, although intentionally improperly documented to protect confidences, presents a phenomenon not adequately investigated; that is, host-restricted races may arise and behave as species in many respects. These possibly arise when temporarily altered factors of ecology, genetics, or other factors, permit the invasion of a host species different from that normally occupied in a given area. Whether this comes about from relaxed competition, from relaxed resistance of the host, or from other opportunities, the resulting gene flow from one population to another has the effect of preventing species formation. To effectively prevent species formation this need not occur more than once in numerous generations, nor must it occur in more than a few areas within the total distribution of the beetle species. The above example involving *pseudotsugae* appears to be a clear-cut example of a change in host selectivity. The lack of uninimity of opinion as to what occurs in populations of the apparently host-restricted races of *ponderosae*, particularly in view of my Uintah Mountain observations and the apparent absence of anatomical indicators of genetic change throughout its range, suggests a fertile field of research.

Infraspecific Variation

Morphological differences between species in *Dendroctonus* are, at best, rather poor and when complicated by tremendous individual variation the identification of specimens is made exceedingly difficult. Because of this, greater dependence in past years has been placed on locality and host data by specialists in identifying species than on specimens themselves. An analysis of this supposed hopelessly chaotic assemblage of variability appeared impossible until the reliability of genitalic characters in the male was established. Once their reliability was established genitalic characters served as a basis for sorting individual, sexual and geographic variations into comprehensible, predictable patterns and made possible the grouping of several populations, previously regarded as distinct, into recognizable species.

Individual Variation.—The greatest degree of individual variation was in size. Although it was actually demonstrated in only a few species it appeared that the largest specimen found in a particular species was almost exactly twice as large as the smallest specimen examined in that same species (2.5 and 5.0 mm. in *brevicomis*; 2.3 and 4.5 mm. in *frontalis;* 3.7 and 7.5 mm. in *ponderosae*; etc.). The size differences mentioned here possibly result from unusually favorable or unfavorable environmental conditions rather than genetic or other factors; in the three examples cited the largest and smallest individuals came from the same geographical area. Other variations in epistomal processes, antennae and eyes were treated and illustrated by Hopkins (1909:19-23) and were either avoided because of unreliability or were described in the systematic treatment of each species on the following pages.

Individual variations of present concern include usually reliable characters of taxonomic value that occasionally are altered or entirely missing in certain specimens. For example, the male declivity of *valens* ordinarily bears numerous fine, confused granules, but in an occasional specimen (fewer than five precent of the males) only a few median granules are present on each interspace with the locations of others marked by deep punctures. In other cases, an otherwise normal female of *obesus* (about two or three per cent) will have the punctures of the declivital striae two or three times as large as the interstrial punctures; and in males of *murrayanae* (about five percent of those from the west) the interstrial punctures of the declivity may be as much as half as large as the strial punctures. When odd examples such as these are encountered accurate identification may be possible only when they are associated with a long series of normal specimens.

Sexual Variation.—Secondary sexual characters are conspicuously developed in the species of *Dendroctonus.* As with most other genera in the subfamily Hylesininae, the posterior margin of the seventh abdominal tergum in the male bears a pair of closely set median stridulating processes that work against the roughened adjacent surface of the elytra. The squeaking noise of stridulation heard when a specimen is held next to the ear is a convenient field method of identifying males of all species in the genus. The absence of stridulation does not necessarily mean the specimen is a female, since males cannot always be induced to stridulate.

In *brevicomis*, *frontalis*, *parallelocollis* and *adjunctus* the frons has a median groove with the lateral areas elevated. This groove and the lateral elevations are much more highly developed in the males of these species than in the females and, in all but *adjunctus*, the lateral elevations of the males bear one or two pair of large, almost hornlike tubercles on their dorsomedian margins. In these same species the well developed transverse constriction found just behind the anterior margin of the pronotum in the male is largely filled by a conspicuously elevated transverse callus in the female (Figs. 5, 9). In *valens* (Fig. 16) and, to a lesser extent, in *terebrans*, the female frons bears a small, rather well developed median elevation at the upper level of the eyes. In all six species mentioned above, and other related species, the male frons is usually a little larger and more prominent and the female frons, pronotum and elytra are very slightly more coarsely sculptured.

In *pseudotsugae*, *simplex*, *obesus*, possibly *valens*, and to a much lesser extent *ponderosae*, *micans*, *punctatus* and *murrayanae*, the declivital tubercles on the elytra are moderately large in the female and smaller to entirely absent in the male. Field use has been made of this character in *obesus* giving about 90 percent accuracy; these tubercles would be much more reliable in determining the sex of *pseudotsugae* and *simplex*.

Geographical Variation.—Geographical variation was detected in five species. In each instance Hopkins (1909) employed these variations to characterize new species. Since they are minor, difficult to measure, and involve a minority of the population in any given area they were not used here to characterize geographical races.

Body size varied conspicuously in *ponderosae;* in general, specimens from the northwestern parts of its distribution (Washington and British Columbia) were distinctly smaller than those from the southern areas, particularly the southeastern parts of its distribution. However, there was a gradual transition in size through Idaho, Oregon and northern California. This variation was somewhat obscured by an ecological complication, since thin-barked pines which predominate as hosts of this species in the northwest normally produce smaller beetles than do hosts with thick bark. Size variations of less than one millimeter, associated with geographical location, involved populations of *obesus* east of eastern Alberta, of *brevicomis* from California to British Columbia, of *frontalis* from the United States, and of *murrayanae* from the western United States.

In *obesus* there was a greater tendency for fully mature (senile?) specimens to turn black with age in the western part of its range. Since this also occurs with *Trypodendron lineatum* (Wood, 1957:340), and possibly with other bicolored scolytid species, it may be caused by ecological factors. The frons of *obesus* also tended to be more densely granulate in western specimens, however, this character affected less than half of any series examined.

The frons varied conspicuously in *frontalis* from locality to locality. Almost every local population exhibited its own frontal characters which were consistent within that population. It was of interest, however, that one extreme variation in a series from Prescott, Arizona, also appeared in a West Virginia series.

The size of punctures on the pronotal disc varied tremendously between individuals of almost any local population, but variations apparently dependent on geographical origin were detected in two species. In *ponderosae* from central or southern California the pronotal disc commonly was uniformly, minutely punctured. These specimens always occurred with specimens tending to be more coarsely punctured. This character gradually faded from the population toward northern California. This variation was not associated with Jeffrey pine or any other host, as reported by Hopkins (1909). A somewhat similar variation in *murrayanae* probably occurs, but too few specimens were available to consider it fully.

Geographical variation in *brevicomis* involving the sculpture of the elytra was reported by Hopkins (1909). While his observations tend to be correct, it was observed that the most coarsely sculptured individual specimens of this species examined during this study came from northern California; the most finely sculptured came from western Chihuahua. Since this character cannot be measured with accuracy, and since definite patterns in the distribution could not be established using this character, it could not be employed to characterize geographical races. Somewhat similar variations were reported by Hopkins (1909) in *parallelocollis*, but may be attributed to the inadequacy of series available for study at that time.

Phylogeny

In treating the relationships of *Dendroctonus* to other genera of Scolytidae it is apparent that certain morphological and biological characters exist that might be useful in analyzing the lines of specialization observed within this genus. For example, only the most closely related of the genera allied to *Dendroctonus* have an evident epistomal process; elaborations of this structure within the genus would, then, appear to represent specialization of this character, and the absence of special modifications would appear to represent a primitive condition. Frontal grooves and tubercles and the specialized transverse callus of the pronotum are absent in allied genera, as well as in most species of *Dendroctonus;* therefore, their presence in *brevicomis*, *frontalis*, *parallelocollis* and *adjunctus* (groove only) evidently represents specialization. These four species also share the habits of constructing sinuate egg galleries and of placing their eggs in individual egg niches alternately on the sides of the gallery. The sinuate gallery is a departure from the typical straight, vertical hylesinine gallery, but the alternate placement of eggs definitely is primitive.

Among the largest species of the genus, increased size appears to be a departure from allied genera, hence is a specialization. Another specialization appears to be the reduction in size of the strial punctures on the declivity. In *pseudotsugae* and *simplex* extension of the epistomal process toward the epistomal margin and the deeper second declivital interspace are departures exhibiting specialization. The most striking specializations among the larger species, however, are biological; of special importance are the methods of egg deposition and of larval excavation. In all of these species the egg galleries basically are straight. Eggs are deposited in individual niches in *ponderosae* with niches placed in groups of one to eight first on one side of the gallery and then on the other. In the remaining species eggs are deposited in grooves along the sides of the egg gallery in batches of one to several dozen. In *pseudotsugae* and possibly *simplex* (not observed) each egg is oriented in a definite way; in the remaining species they are deposited at random without orientation. The larvae of *pseudotsugae* and *simplex* construct individual mines that seldom cross one another. In the remaining species observed during this study that share this method of egg deposition, the larvae feed in congress. This communal feeding continues in *obesus* until about the second instar when each larva constructs an individual mine that may cross and recross those of other larvae. In *valens* and *terebrans* communal feeding usually continues until pupation. In *murrayanae* groups of second instar larvae separate from one another, but reunite later into a common chamber. It is presumed that *micans* and *punctatus* share this latter habit, although neither was observed during this study.

When all morphological characters are considered *aztecus* undoubtedly is the most primitive species in the genus. The epistomal process, frons, prothorax, elytral declivity and absence of sexual differences match rather closely those of the hypothetical ancestor of the genus. It also bears a deceptive resemblance to *Hylurgus* or *Tomicus*. Unfortunately, the biology of *aztecus* was not studied in sufficient detail for use in a consideration of phylogeny.

On the basis of this study the following groups of closely allied species occur in the genus; they are listed in the order of increasing specialization, although the evolutionary relationships among the groups is uncertain.

1. *frontalis, brevicomis, parallelocollis.*
2. *aztecus, valens, terebrans.*
3. *adjunctus, ponderosae.*
4. *obesus, murrayanae, punctatus, micans.*
5. *simplex, pseudotsugae.*

It is clearly evident that *frontalis* and *brevicomis*, *valens* and *terebrans*, *murrayanae*, *punctatus* and *micans*, and *simplex* and *pseudotsugae* are geographical replacements of one another that developed in comparatively recent geological time. With the exception of *micans*, however, their distributions now overlap in some parts thereby removing all doubts concerning their specific identities. Although much more remote, it is also evident that *parallelocollis* arose in a similar manner from common ancestry with *frontalis-brevicomis*, *ponderosae* from *adjunctus* ancestry, and *obesus* from *murrayanae-punctatus-micans* ancestry. The structural bases for these conclusions are included in the key to species, and in the treatment of the various species.

Genus *DENDROCTONUS* Erichson

Dendroctonus Erichson, 1836, Archiv f. Naturgesch. 2(1):52; Ratzeburg, 1837, Die Forstinseketen, p. 217; Eichhoff, 1864, Berliner Ent. Zeitschr. 8:26;

Lacordaire, 1866, Genera des Coléoptères 7:360; Zimmerman, 1868, Tans. American Ent. Soc. 2:148; Leconte, 1868, Trans. American Ent. Soc. 2:172; Chapuis, 1869, Synopsis des Scolytides, p. 34 (1873, Mém. Soc. Roy. Sci. Liége (2)3:242); Leconte, 1876, Proc. American Philos. Soc. 15:384; Provancher, 1877, Fauna Ent. Canada 1:572; Lindeman, 1879, Bull. Soc. Imp. Nat. Moscou 54:53; Eichhoff, 1880 (1881), Die Europäischen Borkenkäfer, p. 125; Leconte and Horn, 1883, Coleoptera of North America, p. 523, Reitter, 1884, Verh. naturf. Ver. Brünn 33:53; Dietz, 1890, Trans. American Ent. Soc. 17:27; Blandford, 1897, Biol. Centr.-Amer., Coleoptera 4(6):146; Lovendal, 1898, De Danske Barkbiller, p. 86; Hopkins, 1899, West Virginia Agric. Expt. Sta. Bull. 56:392; Barbey, 1901, Scolytides l'Europe Central, p. 55; Hopkins, 1902, Proc. Ent. Soc. Washington 5(1):3; Formánek, 1907, Kurovici v Cechach a na Morave zyící, p. 21; Swaine, 1909, New York St. Mus. Bull. 134:95; Hopkins, 1909, U. S. Dept. Agric. Bur. Ent. Tech. ser. 17(1):1-64 (monograph); Hagedorn, 1910, Coleopterorum Catalogus 4:19; Hagedorn, 1910, Genera Insectorum 111:59; Reitter, 1913, Wiener Ent. Zeit. 32(Behheft):47; Saalas, 1914, Medd. F. et Fl. Fenn. 40:77; Hopkins, 1914, Proc. U. S. Natl. Mus. 48(2066):120; Hopkins, 1915, U. S. Dept. Agric. Bur. Ent. Tech. ser. 17(2):168; Blatchley and Leng, 1916, Rhyncophora or weevils of N. E. America, p. 652; Swaine, 1918, Dom. Canada Dept. Agric. Ent. Br. Bull. 14(2):60; Leng, 1920, Cat. Coleopt. America north of Mexico, p. 338; Blackman, 1922, Mississippi Agric. Expt. Sta. Tech. Bull. 11:56; Spessivtseff, 1925, Svensk Insektfauna 3:164; Spessivtseff, 1931, Opredelitel Korojedov, p. 86; Schedl, 1932, *in* Winkler, Cat. Coleopt. reg. palaearcticae, p. 1635; Dodge, 1938, Univ. Minnesota Agric. Expt. Sta. Tech. Bull. 132:26; Chamberlin, 1939, Bark and timber beetles of North America, p. 144; Schedl, 1940 (1939), Ann. Esc. Nac. Cienc. Biol. (Mexico) 1:339; Blackwelder, 1947, U. S. Natl. Mus. Bull. 185:784; Balachowsky, 1949, Faune de France 50:134; Stark, 1952, Fauna U.S.S.R. 33:184; Schedl, 1955, Zeitschr, angew. Ent. 38:7; Pfeffer, 1955, Fauna C.S.R. (Czechoslovakia), p. 121; Chamberlin, 1958, Scolytoidea of the Northwest, p. 64. Biol.: Smith, 1877, Shade trees . . . and Insects that infest them, p. 52; Cockerell, 1893, Trans. American Ent. Soc. 20:336; Judeich-Nitsche, 1895, Forstinsekten 1:445; Chittenden, 1899, U. S. Dept. Agric. Div. For. Ent. Bull. 18(5):55; Felt, 1906, New York St. Mus., Mem. 8, 2:337; Hopkins, 1909, U. S. Dept. Agric. Bur. Ent. Bull. 83(1):169; Herrick, 1910, Rur. New York, p. 896; Yates, 1910, Engineer News, p. 517; Craighead, 1928, Jour. For. 26(7):886; Inda, 1930, Mexico Forest. 8(8):173; Keen, 1938, U. S. Dept. Agric. Misc. Pub. 273:98; Shull, 1944, Idaho Expt. Bull. 252:5; Keen, 1949, U. S. Dept. Agric. Yearbook 1948:427.

Dendroctonus is not very closely allied to any known genus, but unquestionably is related to *Hylurgus* Latreille and *Tomicus* Latreille (=*Blastophagus* Eichhoff) of Europe and Asia, to *Pachycotes* Sharp of Australia and New Zealand, and to *Hylurgonotus* Schedl of South America. It differs from these genera, however, by the well developed, unique epistomal process (very poorly, narrowly indicated in *Hylurgonotus brunneus* Schedl and in *Pachycotes*), by the five-segmented antennal funicle, by the absence of a broad impression on the frons of the male (very feebly indicated in *Tomicus*), and by the strongly flattened antennal club.

Description.—Length 2.5-9.0 mm., 2.3-2.6 times as long as wide; body color dark brown to black, some species with reddish brown elytra.

Frons convex, with or without secondary sexual characters expressed as elevations, tubercles, etc.; epistomal margin laterally elevated, smooth, shining; epistomal process well developd just above elevated portion of epistomal margin, overlapping and extending almost to or flush with median portion of epistomal margin, its basal width equal to a distance one-fourth to one-half as great as distance between eyes, flat or transversely concave between its lateral margins (arms); surface varying from smooth and punctured in some species to densely granulate in others; vesiture hairlike, moderately long, fine, sparse, inconspicuous. Eye ovate, short and broad to rather long and narrow; entire; finely granulate. Antennal scape elongate, clavate; funicle five-segmented, increasing strongly in width from segment two to five, pedicle only slightly wider than two; club strongly flattened, subcircular in outline, with three weakly to strongly procurved sutures indicated only by setae.

Pronotum 1.2-1.4 times as wide as long, widest on basal third; sides feebly to moderately arcuate and more or less converging toward the broadly, shallowly emarginate anterior margin, with or without a prominent constriction just behind anterior margin; surface smooth and shining, with conspicuous, rather deep punctures of variable size more or less characteristic of each species; basal margin almost straight to bisinuate; lateral margins rounded. Vestiture hairlike, sparse to moderately abundant, short to rather long.

Elytra 2.1-2.5 times as long as pronotum; sides straight and subparallel on basal two-thirds, rather broadly rounded behind; scutellum rather small, somewhat depressed in basal notch between elytra; basal margins somewhat arcuate and bearing a row of about nine to twelve moderately large, raised, overlapping crenulations, with several smaller submarginal ones particularly on interspaces two and three; striae impressed or not, the punctures rather large and moderately deep; interstriae feebly to not at all convex, about one to two times as wide as striae, armed by variable transverse crenulations. Declivity rather steep, convex; variously sculptured. Vestiture hairlike; variable.

Type species.—*Bostrichus micans* Kugelann, subsequent designation (Hopkins, 1909:5) (cf. discussion of history above).

Key to the species of *Dendroctonus*

1. Frons with a rather deep, narrow median groove extending from just above epistomal process to upper level of eyes; if median impression obscure in male the lateral areas of frons rather strongly protubrant and usually armed by one or two tubercles (except *adjunctus*), if protubrance obscure in female then anterior constriction of pronotum with a transverse elevated callus (Figs. 5, 9) laterally and dorsally (obscure laterally in *adjunctus*); epistomal process very broad with the lateral margins prominently raised; smaller species 2.5-7.4 mm., in *Pinus* 2

Frons without a median groove or impression below upper level of eyes; lateral elevations of frons and transverse elevated callus of pronotum never present in either sex; epistomal process usually narrower and less prominent, the lateral margins raised or not; larger species 5.0-9.0 mm. (rarely as small as 3.7, or 3.4 in *simplex*), in *Pinus* and other conifers 5

2. Punctures and/or granules of second declivital interspace more abundant, confused; second declivital interspace as wide as one and three, not constricted apically (Fig. 27); smaller species, 2.5-5.0 mm. 3

Granules of second declivital interspace rather sparse and uniseriate; second declivital interspace narrower than one and three or strongly constricted apically (Fig. 30); larger species, 3.8-7.4 mm. 4

3. Declivital pubescence rather abundant and uniformly short, not longer than a distance equal to half the width of an interspace; transverse discal rugae on posterior half of discal interspaces almost never longer than half the width of an interspace; declivital striae usually not impressed, obscure; punctures of declivital interspaces more abundant and feebly if at all granulate (Fig. 27). .... *brevicomis* Leconte

Declivital pubescence less abundant, at least some hairs twice as long as width of an interspace; at least a few rugae on posterior half of elytral disc as wide as the interspace; declivital striae usually impressed, the punctures larger and distinct from those of interspaces; punctures of declivital interspaces less abundant and more coarsely granulate (Fig. 28) .... *frontalis* Zimmerman

4. Granules on declivital interspaces one and (usually) three more abundant, confused; transverse elevation of female pronotum very prominent laterally; male frons with prominent lateral tubercles (Figs. 7-10); larger, 4.5-7.4 mm.; stouter, 2.5 times as long as wide .... *parallelocollis* Chapuis

Granules on declivital interspaces one and three sparse, uniseriate; transverse callus of female pronotum obscure laterally; male frons without lateral tubercles (Figs. 11-12); smaller 3.8-6.0 mm.; more slender, 2.65 times as long as wide .... *adjunctus* Blandford

5. Declivital interspaces dull (minutely rugulose) or shining, if shining the punctures virtually all granulate in both sexes and strial punctures distinct and larger; epistomal process rather broad, the distance between eyes not more than 2.2 times its basal width; episternal area of prothorax more coarsely granulate, the punctures obscure or absent 6

Declivital interspaces smooth and shining, most of the punctures impressed, a few of them granulate in female; epistomal process rather narrow, the distance between eyes three or more times its basal width; episternal area of prothorax punctate, the granules minute or entirely absent 9

6. Surface of declivity opaque (usually rugulose); second declivital interspace impressed, usually flat, interspace one strongly and three weakly elevated; declivital interspaces usually uniseriately granulate and with scattered fine punctures .... *ponderosae* Hopkins

Surface of declivity usually shining, the second interspace not impressed and sutural interspace weakly if at all elevated; virtually all of the rather numerous punctures on declivital interspaces granulate, the granules close, confused 7

7. Epistomal process broad, flat, the margins not elevated (Fig. 24); strial punctures rather small and obscure, rugae of discal interspaces very coarse, many as wide as interspace, a few crossing striae; frons strongly evenly convex; pronotum gradually narrowed anteriorly, without an abrupt constriction (Figs. 25-26) .... *aztecus*, new species

Epistomal process broad, transversely concave, the margins strongly elevated (Figs. 14-16); strial punctures larger, never traversed by the smaller discal rugae; frons irregularly less strongly convex; pronotum feebly if at all narrowed anteriorly, with an abrupt constriction just behind anterior margin (Fig. 17) 8

8. Body color of mature specimens black; punctures on disc of pronotum rather coarse, those near lateral margin much larger; declivital tubercles usually larger, apparently more numerous (Fig. 29); southeastern United States .... *terebrans* (Olivier)

Body color of mature specimens reddish brown; punctures of pronotum not as coarse, those near lateral margin similar to those on disc; declivital tubercles usually smaller, apparently less numerous (Fig. 30); North America, except southeastern United States .... *valens* Leconte

9. Declivital striae weakly if at all impressed, the second apically curved toward sutural striae; declivital interspace one feebly elevated, two as wide or wider than one or three (except near apex); discal striae less than half as wide as interstriae; epistomal process usually transversely concave (except *micans*), rather broad, the lateral margins moderately oblique (less than 55° from the horizontal) (Figs. 18-21) 10

Declivital striae strongly impressed, the second straight; declivital interspace one strongly elevated, two weakly impressed and narrower than one and three; discal striae almost as wide as interstriae; epistomal process flat or convex, narrow, the lateral margins strongly oblique (about 80° from the horizontal) (Figs. 22-23) 13

10. Frons smooth and polished, with deep close punctures, but almost entirely without granules between punctures (Figs. 18, 21); strial punctures on declivity rather large, three or more times as large as those of interstriae 11

Frons rather finely granulate between the close, deep punctures (granules sometimes obscure in *murrayanae*) (Figs. 19-20); strial punctures on declivity usually minute, seldom more than twice as large as those of interstriae 12

11. Epistomal process flat; stouter, 2.3 times as long as wide; strial punctures more strongly impressed; larger, 6.0-8.0 mm.; northern Europe and Asia .... *micans* Kugelann

Epistomal process shallowly, transversely concave; more slender, 2.4 times as long as wide; strial punctures shallowly impressed; smaller, 5.4-6.5 mm.; northeastern North America to Alaska, in *Picea* .... *punctatus* Leconte

12. Frons coarsely, distinctly punctured, the granules between them usually isolated from one another, often very sparse (Fig. 19); male genitalia as figured (Fig. 39); from *Pinus* .... *murrayanae* Hopkins

Frons very closely, more coarsely granulate, the punctures usually obscure in central area (Fig. 20); male genitalia as figured (Fig. 40); from *Picea* .... *obesus* (Mannerheim)

13. Frons moderately protubrant, smooth with rather coarse, deep punctures (Fig. 22); punctures of pronotum rather large; discal interstriae with fine punctures interspersed with small rugae; smaller, 3.4-5.0 mm.; eastern North America to Alaska; from *Larix* .... *simplex* Leconte

Frons strongly protubrant, irregular, granulate, with rather fine, deep punctures (Fig. 23); punctures of pronotum rather small; discal interstriae without fine punctures dispersed among rugae; larger, 4.4-7.0 mm.; western North America; from *Pseudotsuga* and *Larix* .... *pseudotsugae* Hopkins

Dendroctonus brevicomis Leconte

Figs. 1-2, 27, 31-32, 43-46.

Dendoctonus brevicomis Leconte, 1876, Proc. American Philos. Soc. 15:384,386; Hopkins, 1902, Proc. Ent. Soc. Washington 5:3; Hopkins, 1909, U. S. Dept. Agric. Bur. Ent. Tech. ser. 17(1):81; Swaine, 1909, New York St. Mus. Bull. 134:96; Swaine, 1918, Dom. Canada Dept. Agric. Ent. Br. Bull. 14(2):62; Hagedorn, 1910, Coleopteroum Catalogus 4:20; Hagedorn, 1910, Genera Insectorum 111:60; Hopkins, 1915, U. S. Dept. Agric. Bur. Ent. Tech. ser. 17(2):211; Chamberlin, 1939, Bark and Timber Beetles of North America, p. 153; Chamberlin 1960, Scolytoidea of the Northwest, p. 68. BIOL.: Packard, 1887, U. S. Ent. Comm. Bull. 7:177; Packard, 1890,

U. S. Ent. Comm. Rept. 5:722; Hopkins, 1899, U. S. Dept. Agric. Div. Ent. Bull. 21:13; Hopkins, 1899, West Virginia Expt. Sta. Bull. 56:395; Hopkins, 1901, Proc. Soc. Prom. Agric. Sci. 22:66; Hopkins, 1902, U. S. Dept. Agric. Div. Ent., n. s., Bull. 37:21; Hopkins, 1903, U. S. Dept. Agric. Yearbook, 1902:281; Hopkins, 1904, U. S. Dept. Agric. Div. Ent. Bull. 48:18; Currie, 1905, U. S. Dept. Agric. Div. Ent. Bull. 53:74; Webb, 1906, U. S. Dept. Agric. Yearbook, 1905:632; Webb, 1907, U. S. Dept. Agric. Yearbook, 1906:515; Howard, 1907, U. S. Dept. Agric. Div. Ent. Rept., 1906:15; Hopkins, 1908, U. S. Dept. Agric. Yearbook 1907:162; Webb, 1908, U. S. Dept. Agric. Div. Ent. Bull. 58(2):17; Hopkins, 1909, U. S. Dept. Agric. Bur. Ent. Bull. 83(1):42; Hopkins, 1910, U. S. Dept. Agric. Bur. Ent. Bull. 58:59; Hopkins, 1910, U. S. Dept. Agric. Bur. Ent. Circ. 125:2; Hopkins, 1912, U. S. Dept. Agric. Bur. Ent. Circ. 143:5; Swaine, 1913, Ontario Ent. Soc. Rept. 43:90; Swaine, 1914, Dom. Canada Dept. Agric. Expt. Farms Bull. 17, ser. 2, Div. Ent. Bull. 7:13; Swaine, 1915, Canadian For. Jour. 11:89; Hopping, Proc. Soc. American For. 10:185; White, 1916, American Lumberman 2169 (Dec. 9):30; Burke, 1917, Proc. Ent. Soc. Washington 19:88; Hopkins, 1920, Sci. Monthly 8:504; Swaine, 1920, Agric. Gas. Canada 7:642; Chamberlin, 1920, Oregon Agric. Expt. Sta. Bull. 172:1-33; Chamberlin, 1920, Timberman 21(10):38; Chamberlin, 1920, Timberman 22(1):35; Miller, 1921, Timberman 23(1):40; Hopping, 1921, Canada Dept. Agric. Ent. Br. Circ. 15:9; Hopping, 1922, Canadian Ent. 54(6):129, 132; Boyce, 1923, U. S. Dept. Agric. Bull. 1140:1; Boyce, 1923, Timberman 24(7):157; Keen, 1923, American For. 29:689; Gibson, 1923, Canada Dept. Agric. Ent. Br. Rept., 1919:16; Patterson, 1923, Timberman 24(8):38; Elliott, 1924, Oregon St. For. Rept. 14:43; Felt, 1924, Manual of Tree and Shrub Insects, p. 250; Baker, 1924, American For. 30:599; Craighead, 1925, Jour. Forestry 23:341; Hopping, 1925, Jour. Forestry 23:932; Boone, 1925, Timberman 26(7):58; Caverhill, 1925, British Columbia Dept. Lands For. Br. Rept. 1924:E16; Snyder, 1925, Nature Mag. 5:311; Burke, 1926, Proc. Pacific Coast Ent. Soc. 2:57; Keen, 1926, Timberman 27(5):178; Evenden, 1926, Timberman 27(4):178; Miller, 1926, Jour. Forestry 24:897; Craighead, 1927, U. S. Dept. Agric. Circ. 411:6; Miller and Patterson, 1927, Jour. Agric. Res. 34:597; Patterson, 1927, U. S. Dept. Agric. Tech. Bull. 3:2; Person, 1928, Jour. Forestry 26:564; Keen, 1928, California Dept. Nat. Res. Div. For. Bull. 7:31; Keen, 1929, Pan-Pacific Ent. 5:108; Collingwood, 1929, American For. 35:652; Ebeling, 1929, California Countrym. 15(7):9; Nelson and Beal, 1929, Jour. American Phyto. Soc. 19:1101; Craighead, 1930, U. S. Dept. Agic. Misc. Pub. 74:5; Krauch, 1930, Jour. Forestry 28(8):1085; Hosmer, 1930, American For. 36:716; Miller, 1930, U. S. Forest Serv. Forest Worker 6(1):17; Anonymous, 1930, Mexican Agric. Formenta, Principales Plagas, p. 230; Struble, 1930, California Univ. Publ. Ent. 5(6):105; Marlatt, 1931, U. S. Dept. Agric. Bur. Ent. Rept. 1930:45; Craighead et al., 1931, Jour. Forestry 29:1004; Salmon and Baumhofer, 1931, Jour. Econ. Ent. 24:776; Blackman, 1931, New York St. Coll. For., Syracuse Univ. Bull. 4(4), Tech. Pub. 36:37, 45, 57; Keen, 1931, U. S. Dept. Agric. Yearbook 1931:428; Miller, 1931, Jour. Agric. Res. 43:303; Person, 1931, Jour. Foestry 29:696; Rumbold, 1931, Jour. Agric. Res. 43:851; Miller, 1933, Jour. Forestry 31:443; Marlatt, 1933, U. S. Dept. Agric. Bur. Ent. Rept. 1932:22; Marlatt, 1934, U. S. Dept. Agric. Bur. Ent. Rept. 1933:28; Heisley, 1933, U. S. Dept. Agric. Musc. Pub. 162:23; Salmon, 1933, California Agric. Mo. Bull. 22:136; Salmon, 1934, Jour. Forestry 32:1016; Beal, 1934, Jour. Econ. Ent. 27:1132; Weaver, 1934, Jour. Forestry 32:100; Doane et al., 1936, Forest Insects, p. 2, 9, 54, 68, 76, 78; Holst, 1936, Jour. Agric. Res. 53:513; Strong, 1936, U. S. Dept. Agric. Bur. Ent. Pl. Quar. Rept. 1935:23; Stump, 1936, California Highways Publ. Works Jour., April, p. 10, 26, 32; Keen, 1936, Jour. Forestry 34:919; Keen and Furniss, 1937, Jour. Econ. Ent. 30:482; Hopping, 1937, *in* Mulholland, British Columbia Dept. Lands For. Serv., p. 62; Hawley, 1937, Forest Protection, p. 91; Martin, 1937, American For. 43:122, 144; Stodieck, 1937, Nevada Ext. Bull. 84:10; Gordon, 1938, Proc. West. Shade Tree Conf. 5:69; De Gryse, 1938, Pulp and Paper Mag. Canada 39:27; Keen, 1938, U. S. Dept. Agric. Misc. Pub. 273:99; Keen, 1938, West Coast Lumberm. 65(6):48; Keen, 1939, Rocky Mtn. Conf. Ent. Rept. 15:5; Miller, 1939, Rocky Mtn. Conf. Ent. Rept. 15:4; Strong, 1939, U. S. Dept. Agric. Bur. Ent. Pl. Quar. Rept. 1938:21; Westveld, 1939, Appl. Silvicult. U. S., p. 472, 500; Coyle, 1940, Our Forests, p. 90; Johnson, 1940, Jour. Econ. Ent. 33:773; Person, 1940, Jour. Forestry 38:390; Ringle, 1940, Sci. American 162:348; Wheeler, 1940, California Cult. 87:636; Wallace, 1941, U. S. Dept. Agric. Sec. Rept. 1940:169; Yuill, 1941, Jour. Econ. Ent. 34:702; Annand, 1941, U. S. Dept. Agric. Bur. Ent. Pl. Quar. Rept. 1940:25; Annand, 1942 U. S. Dept. Agric. Bur. Ent. Pl. Quar. Rept. 1941:13; Craighead, 1942, Smithsn. Inst. Rept. 1941, Pub. 3665:368; Keen and Salman, 1942, Jour. Forestry 40:854; Orr, 1942, West Coast Lumberm. 69(4):42; Carter, 1942, Timberman 44(2):46; Annand, 1943, U. S. Dept. Agric. Bur. Ent. Pl. Quar. Rept. 1942:8; Furniss, 1943, Proc. West. For. Conserv. Assoc. 34:33; Keen, 1943, Jour. Forestry 41:249; Weaver, 1943, Jour. Forestry 41:8; Hall, 1944, Proc. West. For. Conserv. Assoc. 35:25; Annand, 1944, U. S. Dept. Agric. Bur. Ent. Pl. Quar. Rept. 1943:6; Miller, 1945, U. S. Dept. Agric. Bur. Ent. Pl. Quar. Ins. Pest Surv. 1944:14; Patterson, 1945, Univ. Washington Publ. Biol. 10:149; Furniss and Struble, 1946, U. S. Dept. Agric. Bur. Ent. Pl. Quar. Ins. Pest Surv. 1945:21; Hall, 1946, Timberman 48(2):54,62; Keen, 1946, Pan-Pacific Ent. 22:2; Bongberg, 1947, Timberman 48(7):128; De Gryse, 1947, Forest Ent. Canada, p. 3; Annand. 1947, U. S. Dept. Agric. Bur. Ent. Pl. Quar. Rept. 1945-46:21; Sand and Bryan, 1947, U. S. Dept. Agric. Farmers Bull. 1989:28; Anonymous, 1947, California Dept. Natl. Res. Div. For. 1946:8; Anderson, 1948, Jour. Econ. Ent. 41:596; Struble, 1948, Jour. Forestry 46:129; Anonymous, 1949, U. S. Dept. Agric. Bur. Ent. Pl. Quar. Ins. Pest Surv. 1948:19; Johnson, 1949, Jour. Forestry 47:277; Anonymous, 1950, U. S. Dept. Agric. Bur. Ent. Pl. Quar. Ins. Pest Surv. 1949:25; Keen, 1950, Jour. Forestry 48:186; Pearson, 1950, U. S. Dept. Agric. Monogr. 6:154; Beal, 1951, Proc. West. For. Conserv. Assoc. 41:59; Anonymous, 1951, U. S. Dept. Agric. Bur. Ent. Pl. Quar. Ins. Pest Surv. 1950:24; Anonymous, 1951, U. S. Dept. Agric. Bur. Ent. Pl. Quar. Ins. Surv. 1951(4):6; Johnson, 1951, Northwest Sci. 25:32; Whiteside, 1951, U. S. Dept. Agric. Circ. 864:1-11; Anonymous, 1952, U. S. Dept. Agric. Bur. Ent. Pl. Quar. Coop. Econ. Ins. Rept. 1(Sp. Rept. 4):91; Keen, 1952, U. S. Dept. Agric. Misc. Pub. 273:p.?; Keen, 1952, U. S. Dept. Agric. Yearbook 1952:688; Hoyt, 1953, U. S. Dept. Agric. Bur. Ent. Pl. Quar. Rept. 1951:40; Callaham, 1953, U. S. Dept. Agric. Bur. Ent. Pl. Quar. E. T. 311:1; Hoyt 1954, U. S. Dept. Agric. Bur. Ent. Pl. Quar. Rept. 1952:19; Orr, 1954, U. S. Dept. Agric. For. Serv. Intermtn. For. Range Expt. Sta. Rept. 1953:2; Lively, 1954, Nature Mag. 47:205; Ross, 1954, Canada Dept. Agric. For. Ins. Dis. Surv. Rept. 1953:142; Cowlin, 1955, U. S. Dept. Agric. For. Serv. Pac. N.W. For. Expt. Sta. Rept. 1954:34; Jemison, 1955, U. S. Dept. Agric. California For. Range Expt. Sta. Rept. 1954:30; Keen, 1955, U. S. Dept. Agric. Forest Pest Leaflet 1:1-4; Bailey, 1956, U. S. Dept. Agric. For. Serv. Intermtn. For. Range Expt. Sta. Rept. 1956:29; Buckhorn, 1956, U. S. Dept. Agric. For. Serv. Pacific N. W. For. Range Expt. Sta. Ochoco N. F. Rept. 1945-54:1; Jemison, 1956, U. S. Dept. Agric. California For. Range Expt. Sta. Rept. 1955:50; Whiteside, 1957, U. S. Dept. Agric. Pacific N. W. For. Range Expt. Sta. For. Ins. Condit. 1956:2, 17, 31; Moore, 1957, Jour. Econ Ent. 50:548; Price, 1957, U. S. Dept. Agric. Rocky Mtn. For. Range Expt. Sta. Rept. 156:99; Miller and Keen, 1960, Biology and Control of the Western Pine Beetle, 381 p.

Dendroctonus barberi Hopkins, 1909, U. S. Dept. Agric. Bur. Ent. Tech. ser. 17(1):85 (*new synonymy*); Swaine, 1918, Dom. Canada Dept. Agric. Ent. Br. Bull. 14(2):62; Hagedorn, 1910, Coleopteroum Catalogus 4:20; Hagedorn, 1910, Genera Insectorum 111:60; Hopkins, 1915, U. S. Dept. Agric. Bur. Ent. Tech. ser. 17(2):211; Chamberlin, 1939, Bark and Timber Beetles of North America, p. 155. BIOL.: Hopkins, 1909, U. S. Dept. Agric.

Bur. Ent. 83(1):49; Miller and Wales, 1929, Jour. Econ. Ent. 22:436; Craighead, 1930, U. S. Dept. Agric. Misc. Publ. 74:5; Blackman, 1931, New York St. Coll. For., Syacuse Univ. Bull. 4(4), Tech. Publ. 36:32; Craighead et al., 1931, Jour. Forestry 29:1008; Keen, 1938, U. S. Dept. Agric. Misc. Publ. 273:100; Beal, 1939, U. S. Dept. Agric. Farmers Bull. 1824:10; Pearson, 1950, U. S. Dept. Agric. Monogr. 6:154; Anonymous, 1951, U. S. Dept. Agric. Bur. Ent. Pl. Quar. Ins. Pest Surv. 1951(4):8; Anonymous, 1952, U. S. Dept. Agric. Bur. Ent. Pl. Quar. Coop. Econ. Ins. Rept. 1(Sp. Rept. 4):94; Orr, 1954, U. S. Dept. Agric. Intermtn. For. Range Expt. Sta. For. Ins. Condit. 1953:3; Price, 1955, U. S. Dept. Agric. Rocky Mtn. For. Range Expt. Sta. Rept. 1955:23; Price, 1956, U. S. Dept. Agric. Rocky Mtn. For. Range Expt. Sta. Rept. 1956:91, 97; Bailey, 1956, U. S. Dept. Agric. Intermtn. For. Range Expt. Sta. Rept. 1956:37; Yasinski, 1956, U. S. Dept. Agric. Rocky Mtn. For. Range Expt. Sta. Paper 23:1; Massey, 1961, Ann. Ent. Soc. America 54:354.

Dendroctonus brevicomis var. *barberi* Hopkins, 1905, Proc. Ent. Soc. Washington 7:147 (*nomen nudum*).

Dendroctonus arizonicus Hopkins, 1902, Proc. Ent. Soc. Washington 5:3 (in part; *nomen nudum*).

Dendroctonus brevicornis: Dietz, 1890, Trans. American Ent. Soc. 17:32.

Dendroctonus frontalis: Dietz, 1890, Trans. American Ent. Soc. 17:32 (in part).

Dendroctonus n. sp., Hopkins, 1904, U. S. Dept. Agric. Div. Ent. Bull. 48:42, 44.

This species is very closely related to *frontalis*, but is readily distinguished by the uniformly short declivital pubescence, by the less strongly impressed declivital striae, by the more numerous, more finely granulate punctures of the declivital interspaces, by the larger average size, and, in part, by the distribution.

Male.—Length 2.5-5.0 mm. (average about 4), 2.4 times as long as wide; mature color very dark brown.

Frons convex, with a pair of lateral elevations on median half just below upper level of eyes separated by a deep median groove, the summits of elevations armed at their dorsomedian margins by one or two prominent, somewhat dorsomedially oriented granules; epistomal margin elevated, its surface smooth and shining; epistomal process half (0.50 times) as wide as distance between eyes, its arms oblique (about 40° from the horizontal) and elevated, the horizontal portion about half its total width, transversely concave, overlapping and ending just above epistomal margin and bearing under its distal margin a dense brush of conspicuous yellowish setae; surface punctate-rugulose above eyes, more deeply punctured and subgranulate below. Vestiture, except epistomal brush, short, sparse, inconspicuous.

Pronotum 1.4 times as wide as long, widest on basal third; sides rather strongly arcuate on basal three-fourths, rather strongly constricted just behind the broadly, shallowly emarginate anterior margin; surface smooth with rather fine, shallow, close punctures on median third, becoming more finely punctured laterally; an indistinct median line apparent. Vestiture very short, rather sparse, inconspicuous.

Elytra 2.2 times as long as pronotum; sides straight and subparallel on basal two-thirds, rather broadly rounded behind; basal margins arcuate and bearing a row of about nine moderately large, raised, overlapping crenulations, with several smaller submarginal ones particularly on interspaces two and three; striae weakly impressed, the punctures rather small and shallow; interstriae about twice as wide as striae and armed by abundant, confused, small, transverse crenulations, each averaging about one-third the width of an interspace, never more than half as wide on posterior half of disc. Declivity moderately steep, convex with a feeble impression between first and third striae; strial punctures reduced in size; interstrial punctures ranging from finely granulate to not at all granulate, abundant, confused (about three to four irregular ranks across width of an interspace). Vestiture rather abundant, short, averaging about half as long as width of an interspace, never as long as its entire width.

Female.—Similar to male except lateral elevations of frons less prominent and unarmed, with median groove consequently less conspicuous; arms of epistomal process less strongly elevated; pronotal constriction largely filled by a prominent transverse elevated callus both laterally and dorsally; punctures of pronotal disc very slightly larger and deeper; transverse crenulations of elytral disc very slightly larger; and declivital granules much finer, only a few punctures with a minute granule on upper margins.

Type locality.—Middle California (Williams, Arizona, for *barberi*). The types of both descriptions were examined.

Hosts.—*Pinus ponderosa*, and *P. coulteri*. Rarely, particularly during epidemics, other species of *Pinus* may be attacked.

Distribution.—North America west of the Rocky Mountains from Chihuahua to British Columbia wherever the principal host tree, *Pinus ponderosa*, occurs.

Specimens from the following localities were examined (Fig. 45). ARIZONA: Carr Canyon, Chiricahua Mts., Coconino N. F., Crow King, "Deadmans Flat" (Coconino Co.), Flagstaff, Ft. Apache, "Fort Valley," Grand Canyon N. P., Groom Ck. (Prescott N. F.), Huachuca Mts., "Pleasant Valley," Prescott, San Francisco Mts., Santa Catalina Mts., Santa Rita Mts., Springerville, Walnut Canyon N. M., Williams, "Willow Rock," and Young. CALIFORNIA: Alta, "Atwell's Mill," Badger, Ballard, "Barton Flat" (San Bernardino N. F.), Bass Lake, "Battle Creek R. S." (Shasta Co.), "Bear Flat" (Warner Mt.), Berkeley, "Better Waller R. S.," Black's Mt., Blue Canyon, Blut Mt., Bray, Breckenridge Mt., "Buck Ck.," Burney, "Butte Ck. Basin" (Butte Co.), "Campbell Hot Springs," "Capanero Ck.," Carrville, Castella, Cayton, Cecilville, Cedar Grove (Kings Can. N. P.), "Cedar Ridge" (Glenn Co.), Chester, Cisco, "Clairsville," Coarsegold, Corte Madera, Crane Valley, "Cummings R. S. (Eldorado Co.), Cuyamaca Rancho St. P., Crystal Lake, "D. & H. Mill" (Madera Co.), Deep Creek, Diamond Springs, "Dixie Valley" (Lassen Co.), Dunlap, Elk Creek, "Figueroa Mt.," Fish Camp, Foresthill, Giant Forest, Hackamore, Happy Camp, "Harvey Valley" (Alameda Co.), Hayfork, "Hazel Green," Hobergs, Hot Springs, Idyllwild, Jackson Ck., Julian, "Kangaroo R. S.," Kaweah, Kaweah River, Kelsey, Kings Canyon, Klamath N. F., Kyburz, "Lagunas," Lake Almanor, Lake Arrowhead, "Little Humbug R. S.," "Little Yosemite," Long Barn, Lookout, Los Olivos, "Lumgray R. S.," Mather, McCloud, McLears Resort (Plumas Co.), Meadow Valley, Miami R. S., Milford, "Millwood," Miramonte, Modoc N. F., "Madrone Spring," Moffit Ck., "Mosquito," Mt. Hermon, "Nash Mine"

Fig. 45. Probable geographical distribution of *Dendroctonus spp.* with collection sites indicated: 1, *brevicomis* (circles); 2, *frontalis* (triangles).

(Trinity Co.), "Nigger Spring" (Lassen Co.). North Fork, N. Fk. Eel River, "Norton's Mill (Siskiyou Co.), "Norvell Flats" (Lassen Co.), "Oak Flat Camp" (Fresno Co.), "Onion Valley," Placerville, Plumas N. F., Pinecrest, Pinehurst, Pine Valley, "Pinoche R. S." (Mariposa Co.), Prattville, "Quintette," Santa Cruz, Shasta Springs, Sisson, Stirling City, Sugar Pine, "Summerdale," "Summit Lake" (Shasta Co.), Tenaya Lake, Three Rivers, Timber Mt., Tuolomne Meadows, Wawona, "Whitehall," White Hills, Willow Ranch, Wishon, Yosemite N. P., and Yreka. Colorado: Dolores, Ft. Garland, "Vallecito R. S." (La Plata Co.), Monte Vista, and Uncompahgre N. F. Idaho: Boise, Cedar Mt., Centerville, Couer d'Alene, Garden Valley, Kooskia, Moscow, Pioneer, Placerville, Smith's Ferry, Stites, and Troy. Montana: Missoula. Nevada: Las Vegas. New Mexico: Capitan Mts., Cloudcroft, Datil, Gloriela Mesa, Mescalero, Mimbres, Ruidoso, Santa Fe, Santa Catalina Mts., Zuni Mts., and Jermejo Park. Oregon: Ashland, Bend, Blue Mts., Bly, Burnt River, Chiloquin, Cold Springs, Colestin, Corvallis, "Dutch Ck.," Fremont N. F., Ft. Rock, Grants Pass, Jenny Ck., Joseph, Keno, Klamath Falls, Klamath Indian Res., Prineville, "Pringle Falls," Siskiyou Mts., Sisters, Sumpter, and Wallowa Mts. Texas: Big Bend and Davis Mts. Utah: Daves Hollow (Dixie N. F.), Escalante, Panguitch, Pin Hollow (Fish Lake N.F.), and Ashley N. F. Washington: Blue Mts., Buckeye, Chelan, Dayton, Kooskooskie, Northport, Pullman, and Toppenish. British Columbia: Aspen Grove, Little Shuswap Lake, "Midday Ck." in Indian Meadow, Midday Valley, "Spious Ck." Summerland, "Trepan Ck.," and "Trepanier Ck." Chihuahua Tres Rios.

Geographical variation.—Specimens from the eastern parts of the range of this species, Arizona, Utah and Colorado, tend to average slightly larger in size (less than 1 mm. larger); the elytral striae tend to be somewhat more deeply impressed; and the elytral crenulations tend to average slightly larger. These differences, however, are not sufficiently consistent in a long series from any particular locality to permit the recognition of distinct geographic races as was done previously by Hopkins (1909: 70). It is of interest to note that the smallest, most coarsely sculptured specimens came from northern California; the most finely sculptured specimens, from Chihuahua, had rather strongly impressed striae (equal to specimens from any other locality); and numerous specimens, particularly females, from Utah and Arizona cannot be distinguished from the average West Coast series. The Chihuahua series, particularly, exhibited every degree of morphological intergradation between extreme eastern and western populations.

Biology.—This species probably has destroyed more merchantable timber in North America than any other organism in historic time. Estimates indicate that approximately two billion board feet of standing timber have been destroyed annually since studies commenced over half a century ago.

Overwintering parent adults and brood may become active at any period when subcortical temperatures become sufficiently high, probably somewhere in the vicinity of 45° to 50° F. The dates at which favorable conditions for flight occur in the spring vary considerably from year to year and from locality to locality depending on exposure, altitude, latitude, weather, and other ecological factors. In general the first of the overwintering adults and brood emerge to attack new trees about the first of May. Attacks from these beetles ordinarily continue until the latter part of June. A paricularly early or late season, or a change in latitude north or south of the center of distribution may alter these dates by as much as a month. In the extreme southern limits of distribution it is possible that some flight activity may continue throughout the year. Because beetles do not emerge simultaneously, but do so slowly over a considerable period of time, and because of overlapping broods some flight activity continues throughout the summer season with periods of greatest flight activity coinciding with the emergence of each new brood. Flight activity is discontinued in October or November when daytime temperatures fall below 50°.

Trees selected for attack usually are living, standing and larger than 12 inches D.B.H. Prostrate trees are seldom attacked. In the absence of competing species the attack normally is distributed from the ground level upward to areas as small as four to eight inches in diameter where cork plates of the bark have formed. Younger bark of limbs or upper bole and of smaller trees where cork plates have not developed are rarely attacked. In the presence of competing species of *Dendroctonus*, particularly *adjunctus*, and to a lesser extent *ponderosae*, the area of attack by *brevicomis* is forced upward from the ground level a variable distance depending on the comparative abundance of competing species.

The attack usually begins in the upper midbole area of the host tree then progresses upward and downward. The attack is slow and continuous, without any sudden or concerted swarming of the beetles. Its duration is variable, evidently depending upon the population density of beetles in the area, upon resistance of the host, or upon climatic or other ecological factors peculiar to the season or locality. It may be completed in as little as seven days, or it may continue over the greater part of a year. Characteristically the attack will be concentrated on one particular tree until it is overcome, even when the beetle population is high, before an attack is started on a second nearby tree. There is no attempt to occupy all available bark; the density of individual attacks may be as low as an average of about five per square foot of suitable bark on a susceptible tree, or higher than 20 per square foot on a vigorous or resistant tree. In general, single tree attacks suggest an endemic condition, while group attacks suggest an epidemic condition.

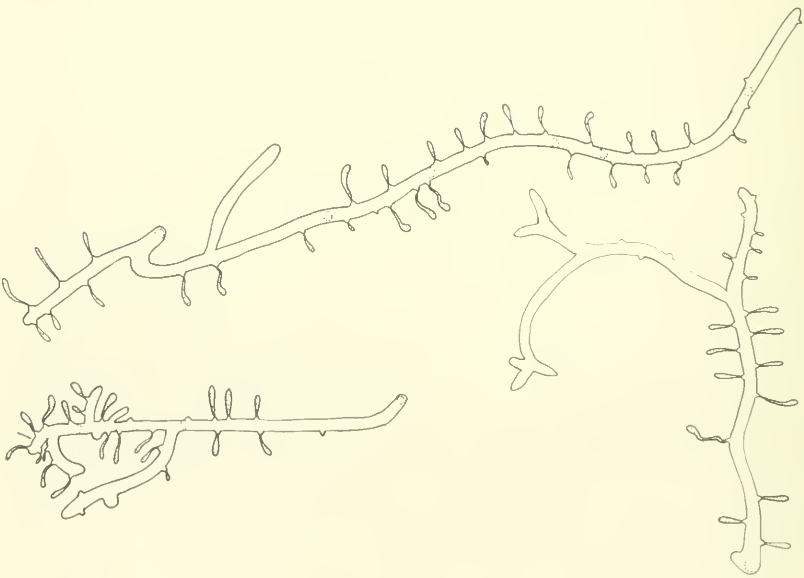


Fig. 46. *Dendroctonus brevicomis*: Egg galleries sinuate, predominantly transverse; egg niches large, placed individually on alternate sides of gallery; larval mines turn into outer bark and expand after a brief contact with the cambium.

The winding egg galleries (Figs. 43, 46) are constructed almost entirely in the inner bark or phloem tissues; they are in continual contact with and very lightly score or stain the woody or xylem tissues. Their total lateral displacement usually is equal to or greater than the total longitudinal displacement, although an occasional gallery may be decidedly longitudinal.

The diameter of an individual egg gallery is slightly greater than the width of a beetle; it averages approximately 35 cm. in length, although exact measurements of fully formed galleries are virtually impossible to obtain because of the tendency for the winding galleries to branch, to anastomose, and to cross and recross one another. It is not uncommon for more than one pair of beetles to occupy one gallery, usually each pair being found in different branches that use the same entrance hole. Presumably this habit has suggested a tendency toward polygamy to some workers, particularly when the male was late in arriving or failed to arrive at all.

The initial attack is made by the female, usually in a crevice of the bark. About the time she reaches the phloem tissues where the pitch begins to flow she is joined by the male who then assists her by pushing the excavated frass out of the entrance hole. Continuation of the parental or egg gallery is performed entirely by the female beetle. After several inches of gallery have been cleared and the frass ejected from the entrance hole, the male then packs the frass in the lower regions of the gallery thereby closing the entrance hole and tightly filling the gallery except for a few inches in the area where the beetles are working. It has been estimated that (Miller and Keen, 1960:16) about two-thirds of an inch of new gallery is formed each day. Mating occurs only after the female has been joined by the male, never on the surface of the tree before the attack begins. Although seldom seen, mating evidently occurs repeatedly, since it has been observed in various stages of gallery construction.

Ordinarily, but not always, the entrance tunnel is without a nuptial chamber or other means of turning around until the first ventilation tunnel or branch in the gallery is reached. Ventilation tunnels (indicated by dotted circles in Fig. 46) are placed at irregular intervals and are not always present. Their presence appears related to the stage of gallery construction, thickness of the bark, and activity of the beetles. Usually they are not constructed before the entrance hole is plugged by frass; they are less abundant or sometimes entirely absent in trees having comparatively thin bark; and they appear to be more numerous in galleries constructed by unusually active beetles. Seldom are they spaced at intervals less than five centimeters.

Oviposition ordinarily begins about eight days after the attack and continues for approximately 10 to 49 days (Miller and Keen, 1960:20), except when egg-laying is interrupted by winter in which case it is greatly extended. Although estimates of the number of eggs produced by a female based on the average number of eggs per inch of gallery have suggested a figure much higher, the highest number actually reported is 41 (Miller and Keen, 1960:19). Usually a majority of the eggs are deposited in the first third of the gallery, the number declining significantly in the final third.

Egg niches are symmetrical and ordinarily are constructed on the sides of the gallery, usually in direct contact with the cambium. They are broad and deep, the depth being equal to about one-fourth to one-third the diameter of the egg gallery. The deepest point is rounded, matching rather well the anterior profile of the parent beetle as seen from the dorsal aspect. Unfilled egg niches often cannot be distinguished from the beginning of a new branch of the gallery. The number and spacing of niches depends on many factors, but usually the minimum distance between eggs on a particular side of a gallery is one centimeter. When considering both sides of the gallery and the alternating placement of eggs this distance is reduced by half. Eggs are deposited individually in the niches; each niche is then filled by specially prepared frass packed to the original level or contour of the gallery.

Following the period of oviposition the gallery may be continued in an irregular feeding tunnel of somewhat greater diameter than usual until death of the parent bettle, or the beetles may construct an exit tunnel, often independent of one another, by extending one of the ventilation tunnels and emerge to attack another host tree. It has been estimated that as many as 50 percent of the parent beetles emerge to produce a second brood, and a few of these re-emerge to produce their third brood of the season (Miller and Keen, 1960:18). Of those beetles that re-emerge from the host males predominate significantly.

The incubation period has not been determined precisely. Available figures suggest that seven days are required for hatching under optimum conditions (Miller and Keen, 1960:20), presumably with longer periods required when less favorable conditions exist. The newly-hatched larvae mine the phloem next to the cambium for approximately one centimeter at right angles to the egg gallery. They then move into the inner bark and end their tunnels near the outer bark where an area is cleared for pupation. Under optimum conditions larval development may be completed in as little as 30 to 35 days (Miller and Keen, 1960:24); however, they do not develop at the same rate and some may require as much as 300 days to complete the larval stage of development. In the pupation cell the larva undergoes physiological changes to become a quiescent prepupa for about two to seven days before pupation occurs (Miller and Keen, 1960:30); mature larvae overwinter as prepupae, never as pupae. Under normal conditions about 6 to 20 days are required to complete the pupal stage (Miller and Keen, 1960:31), unfavorable conditions may extend this period. A maturation period between attainment of the adult stage and emergence from the host varies from 7 to 14 days (Miller and Keen, 1960:31), except in the spring months when it may be somewhat longer.

The number of generations each year is complicated by peculiarities of a particular season, by re-emergence of parent adults to produce a second or a third brood, and by overlapping generations. In the northern parts of its range one complete and a partial second generation appears normal, in southern California and in Arizona three complete and perhaps a partial fourth generation might be expected.

Dendroctonus frontalis Zimmerman

Figs. 3-6, 28, 33, 45, 47.

Dendroctonus frontalis Zimmerman, 1868, Trans. American Ent. Soc. 2:149; Leconte, 1868, Trans. American Ent. Soc. 2:173; Leconte, 1876, Proc. American Philos. Soc. 15:386; Dietz, 1890, Trans American Ent. Soc. 17:32 (part); Hopkins, 1902, Proc. Ent. Soc. Washington 5:3; Swaine, 1909, New York St. Mus. Bull. 134:96; Hopkins, 1909, U. S. Dept. Agric. Bur. Ent. Tech. ser. 17(1):90; Hagedorn, 1910, Coleopterorum Catalogus 4:20; Hagedorn, 1910, Genera Insectorum 111:60; Hopkins, 1915, U. S. Dept. Agric. Bur. Ent. Tech. ser. 17(2):211; Blatchley and Leng, 1916, Rhynchophora or weevils of North Eastern America, p. 653; Chamberlin, 1939, Bark and Timber Beetles of North America, p. 165. Biol.: Packard, 1890, U. S. Ent. Comm. Rept. 5:722; Hopkins, 1892, Poc. Ent. Soc. Washington 2:353; Hopkins, 1892, Science, July 29, 20:64; Hopkins, 1893, West Virginia Agric. Expt. Sta. Bull. 31:143, 32:213; Hopkins, 1893, Insect Life 5:187; Riley, 1893, Insect Life 6:140; Hopkins, 1893, Insect Life 6:126; Hopkins, 1894, Canadian Ent. 26:280; Lintner, 1894, Gardening 2:292; Hopkins, 1896, Canadian Ent. 28:250; Chittenden, 1897, U. S. Dept. Agric. Div. Ent. n. s., Bull. 7:67; Schwarz, 1898, Proc. Ent. Soc. Washington 4:81; Hopkins, 1898, Proc. Soc. Prom. Agric. Sci. 19:103; Hopkins, 1899, West Virginia Agric. Expt. Sta. Bull. 56:395; Hopkins, 1899, Proc. Ent. Soc. Washington 4:343; Hopkins, 1899, U. S. Dept. Agric. Div. Ent. Bull. 21:13, 14, 27; Lugger, 1899, Minnesota Agric. Expt. Sta. Bull. 66:315; Chittenden, 1899, U. S. Dept. Agric. Div. Foestry Bull. 22:55; Hopkins, 1901, U. S. Dept. Agric. Div. Ent. Bull. 28:pl. XII.; Hopkins, 1902, U. S. Dept. Agric. Div. Ent., n. s, Bull. 37:20; Hopkins, 1903, U. S. Dept. Agric. Yearbook 1902:270; Hopkins, 1903, Canadian Ent. 35:59; Hopkins, 1904, U. S. Dept. Agric. Div. Ent. Bull. 48:41, 44; Hopkins, 1904, U. S. Dept. Agric. Yearbook 1904:270; Hopkins, 1905 (1906), Proc. Ent. Soc. Washington 7:80; Currie, 1905, U. S. Dept. Agric. Div. Ent. Bull. 53:100; Felt, 1905, New York St. Mus., Mem., 8, 1:6; Webb, 1906, U. S. Dept. Agric. Yearbook 1905:632; Webb, 1906, U. S. Dept. Agric. Yearbook 1906:515; Zavitz, 1906, Ontario Ent. Soc. Rept. 36:126; Howard, 1906, U. S. Dept. Agric. Div. Ent. Rept. 1906:14; Hopkins, 1908, U. S. Dept. Agric. Yearbook 1907:163; Zavitz, 1908, U. S. Dept. Agric. Yearbook 1907:549; Fiske, 1908, Proc. Ent. Soc. Washington 9:24; Hopkins, 1908, Proc. Ent. Soc. Washington 9.131; Zavitz, 1909, U. S. Dept. Agric. Yearbook 1908:574; Hopkins, 1909, U. S. Dept. Agric. Bur. Ent. Bull. 58:58; Hopkins, 1909, U. S. Dept. Agic. Bur. Ent. Bull. 83:56; Hopkins, 1910, U. S. Dept. Agric. Bur. Ent. Circ. 125:1; Hopkins, 1911, St. Louis Lumberman, July 1, p. 669; Hopkins, 1911, U. S. Dept. Agric. Farmers Bull. 476, 15 p.; Mason, 1911, South. Lumberman, Sept. 30, p. 35; Hinds, 1912, Alabama Poly. Circ. 15; Mattoon, 1915, U. S. Dept. Agric. Bull. 244:35: Murphy, 1917, U. S. Dept. Agric. Bull. 544:27; Hopkins, 1919, American Lumberm. 2299:43; Hopkins, 1919, Sci. Month. 8:503; Boving and Champlain, 1921, Proc. U. S. Natl. Mus. 57:575; Hopkins, 1921, U. S. Dept. Agric, Farmers Bull. 1188, 15 p.; Blackman, 1922, Mississippi Agric. Expt. Sta. Tech. Bull. 11:58; Berckes, 1924, American Lumberm. 2554:80; Berckes, 1924, Lumberman 73(1025):10; Felt, 1924, Manual of Tree and Shrub Insects, p. 252; Howard, 1924, U. S. Dept. Agric. Bur. Ent. Rept. 1924:26; Middleton, 1924, U. S. Golf Assoc. Green Sec. Bull. 4:148; St. George, 1924, Lumber Trade Jour. 86(9):37; St. George, 1924, Proc. South. Logging Assoc. 14:79; Wyman, 1924, U. S. Dept. Agric. Forest Serv. Bull. 8(40):2; Anonymous, 1924, Natl. Lumberman 73:10; Craighead, 1925, Jour. Forestry 23:349; Craighead, 1925, Jour. Econ. Ent. 18:557; St. George, 1952, American Lumberm. 2607:50; Schoene, 1926, Virginia St. Crop Pest Comm. Quar. Bull. 7:4, 23; Beal, 1927, Jour. Forestry 25:741; Craighead, 1927, U. S. Dept. Agric. Circ. 411:9; Craighead, 1928, Jour. Foresty 26:886; Craighead and St. George, 1928, Forest Worker 4(2):11; St. George, 1928, Forest Worker 4(5):15; Nelson and Beal, 1929, Phytopathology 19:1101; St. George and Beal, 1929, U. S. Dept. Agric. Farmers Bull. 1586, 8 p.; St. George and Beal, 1929, South. Lumber Jour. 33(17):37; Bentley, 1930, Tennessee Bien. Rept. 1929:105; Craighead, 1930, U. S. Dept. Agric. Misc. Pub. 74:4; Craighead and St. George, 1930, Science 72:433; St. George, 1930, Jour. Econ. Ent. 23:826; Lutken, 1930, South Carolina Wkly News Notes 19:23; Marlatt, 1930, U. S. Dept. Agric. Bur. Ent. Rept. 1930:47; Rumbold, 1931, Jour. Agric. Res. 43:851; St. George, 1931, Forest Worker 7(6):16; Cary, 1932, Naval Stores Rev. 17:14, 18:14, 20, 19:14, 18; Moore, 1932, South Lumberm. 145(1833):21; Rumbold, 1932, Bull. Ecol. Soc. America 13(4):17; Beal, 1933, Jour. Forestry 31:329; Marlatt, 1933, U. S. Dept. Agric. Bur. Ent. Rept. 1933:29; Knull, 1934, Jour. Econ. Ent. 27:716; Beal, 1934, Jour. Econ. Ent. 27:1132; Nelson, 1934, Phytopath. Ztschr. 7:327; Caird, 1935, Bot. Gaz. 96(4):709; Bramble and Holst, 1935, Phytopathology 25:7; Craighead, 1935, U. S. Dept. Agric. Misc. Pub. 209:134; Holst, 1936, Jour. Agric. Res. 53:513; Holst, 1937, Jour. Econ. Ent. 30;676; Elliott and Mobley, 1938, South. For. 1938:332; Strong, 1938, U. S. Dept. Agric. Bur. Ent. Pl. Quar. Rept. 1937:17; Muesebeck, 1938, Proc. Ent. Soc. Washington 40:286; Ross and Mattoon, 1939, U. S. Off. Educ. Vocat. Div. Bull. 196:45; Bramble and Holst, 190, Phytopathology 30:881; Craighead, 1940, Phytopathology 30:976; Harrar and Ellis, 1940, Proc. Virginia Acad. Sci. 1:211; Harrar and Martland, 1940, Proc. Virginia Acad. Sci. 1:211; Mattoon, 1940, U. S. Dept. Agric Farmers Bull. 1671 (rev.):42; Page and Ruffin, 1940, Alabama Ent. Circ. 198:3; Hetrick, 1940, Jour. Econ. Ent. 33:554; Hetrick 1941, Proc. Ent. Soc. Washington 43:168; Carruth, 1941, Naval Stores Rev. 51(19):6; Friend, 1942, Yale Univ. School For. Bull. 49:144; Cruikshank, 1943, U. S. Dept. Agric. Misc. Pub. 533:58; Hetrick, 1943, South Planter 104(3):30; Nieland, 1943, Cit. Indus. 24(6):8; Anonymous, 1944, South Carolina Ext. Bull. 107:26; Beal and Massey, 1945, Duke Univ. School For. Bull. 10:82; Upton, 1945, Proc. Trans. Texas Acad. Sci. 28:100; Hoffman and Anderson, 1945, Jour. Forestry 43:436; O'Byrne, 1946, Virginia Ext. Circ. 403:1; Anderson, 1947, Texas For. Serv. Bull. 33:2; Barnhill, 1947, Alabama Ext. Handb. Alabama Agric. Ed. 4:221; Flory, 1947, South Carolina Ext. Bull. 107:26; Fronk, 1947, Virginia Agric. Expt. Sta. Tech. Bull. 108, 12 p.; Sand and Bryan, 1947, U. S. Dept. Agric. Farmers Bull. 1989:28; Underhill and Fronk, 1947, Virginia Agric. Expt. Sta. Rept. 1946:33; Anderson, 1948, Jour. Econ. Ent. 41:596; Gerhart and Ahler, 1949, Jour. Forestry 47:636; Hetrick, 1949, Proc. Assoc. South. Agric. Workers 46:93; Hetrick, 1949, Jour. Econ. Ent. 42:466; Anonymous, 1949, U. S. Dept. Agric. Bur. Ent. Pl. Quar. Ins. Pest Surv. 1948:20; Craighead, 1950, U. S. Dept. Agric. Misc. Pub 657:p?; Anonymous, 1950, Virginia Adv. Counc. Virginia Econ. Com. For., p. 25; Anonymous, 1950, Texas For. Serv. Circ. 26, 7p.; Folweiler, 1951, For. & People 1(3):10; Anonymous, 1951, U. S. Dept. Agric. Bur. Ent. Pl. Quar. Ins. Pest Surv. 1951(4):7; Anonymous, 1951, U. S. Dept. Agric. Bur. Ent. Pl. Quar. Ins. Pest Sum. 1950:24; Ford, 1951, North Carolina Res. Farm. 10(Prog. Rept. 2):3; Beal, 1952, Duke Univ. School For. Bull. 14:48; Hoyt, 1952, U. S. Dept. Agric. Bur. Ent. Pl. Quar. Rept. 1950-1:17; Cann, 1952, South Lumberm. 185(2321):150; Anonymous, 1952, U. S. Dept Agic. Bur. Ent. Pl. Quar. Coop. Econ. Ins. Rept. 1(4):89; Dyer, 1953, Georgia Agric. Ext. Bull. 578:8; Jones and Ford, 1953, North Carolina Ext. Serv. Folder 100, 6 p.; Barker and Nettles, 1954, South Carolina Ext. Circ. 239, 6 p.; Coyne, et al., 1954, Proc. Assoc. Agric. Workers 51:98; Jackson, et al., 1954, For. Dis. Ins. Georgia's Trees. p. 25; Lee, 1954, Jour. Forestry 52:767; Lee, 1954, Texas Forest News 33:5; Demmon, 1955. U. S. Dept. Agric. S. E. For. Expt. Sta. Rept. 1954:70; Bennett, 1955, Texas For. Serv. Circ. 43:2, 10; Flory, et al., 1955, South Carolina Agric. Ext. Serv. Bull. 116:10; Heller, et al., 1955. Jour. Foestry 53:483; Merkel, et al., 1955, South. Lumberm. 190(2389):60; Speers, et al., 1955, Proc. Assoc. South. Agric. Workers 52:100; Briegleb, 1955, U. S. Dept. Agric. South. For. Expt. Sta. Rept. 1954:66; Anonymous, 1955, U. S. Dept. Agric. Imp. For. Ins. 1954:14; Anonymous, 1955, U. S. Dept. Agric. South. For. Expt. Sta. Pest Rept.

nos. 6, 9; Bennett, 1956, U. S. Dept. Agric. South. For. Expt. Sta. Pest Rept. 10:3; Biegleb, 1956. U. S. Dept. Agric. South. For. Expt. Sta. Rept. 1955:49; Briegleb, 1956. U. S. Dept. Agric. S. E. For. Expt Sta. Rept. 1956:68; Denmon, 1956, U. S. Dept. Agric. S. E. For. Expt. Sta. Rept. 1955:71, 78; McArdle, 1956. U. S. Dept. Agric. For. Serv. Rept. 1953:3, 12; Merkel, 1956. Proc. Assoc. South. Agric. Workers 53:130; Merkel and Kowal, 1956, U. S. Dept. Agric. S. E. For. Expt. Sta. Paper 67:2; Clausen, 1956, U. S. Dept. Agric. Tech. Bull. 1139:67; Speers, 1956, Proc. Assoc. South. Agric. Workers 53:130; Walker, 1956, Georgia For. Res. Counc. Rept. 2:1, 6, 8; Nagel and David, 1956, Proc. N. Centr. St. Br. Ent. Soc. America 11:20; Davis and Nagel, 1956, Jour. Econ. Ent. 49:210; Nagel, et al., 1956, Jour. Forestry 55:894; Anonymous, 1956, U. S. Dept. Agric. Hort. Crops Res. Br. Pl. Dis. Rept. 241:220; Massey, 1957, Proc. Helminthol. Soc. Washington 24(1):29; Osgood, 1957, U .S. Dept. Agric. S. E. For. Expt. Sta. Paper 80, 19 p.; Anonymous, 1957, U. S. Dept. Agric. South. For. Expt. Sta. Pest Rept. 16:2; McCambridge and Kowal, 1957, U. S. Dept. Agric. S. E. For. Expt. Sta. Paper 76:2; Pechanec, 1957, U. S. Dept. Agric. S. E. For. Expt. Sta. Rept. 1956:39; Anonymous, 1957, U. S. Dept. Agric. South. For. Expt. Sta. Pest Rept. 17:1; Aldrich, 1958, Jour. Forestry 56:200; Heller, 1959, Photogram. Engin. 25:595; Anderson, 1960, Forest and Shade Tree Entomology, p. 218; Dixon and Osgood, 1961, U. S. Dept. Agric. S. E. For. Expt. Sta. Paper 128, 34 p.; Thatcher, 1961, Forest Entomology, p. 184.

Dendroctonus arizonicus Hopkins, 1902, Proc. Ent. Soc. Washington 5:3 (nomen nudum); Hopkins, 1909, U. S. Dept. Agric. Bur. Ent. Tech. ser. 17(1):95 (*new synonymy*); Hagedorn, 1910, Coleopterorum Catalogus 4:20; Hagedorn, 1910, Genera Insectorum 111:60; Hopkins, 1915, U. S. Dept. Agric. Bur. Ent. Tech. ser. 17(2):211; Chamberlin, 1939, Bark and Timber Beetles of North America, p. 158. Biol.: Hopkins, 1904., U. S. Dept. Agric. Bull. 48:42, 44; Hopkins, 1909, U. S. Dept. Agric. Bur. Ent. Bull. 83(1):72; Keen, 1939, U. S. Dept. Agric. Misc. Pub. 273:102; Anonymous, 1955, U. S. Dept. Agric. For Serv. For. Ins. 1954:9.

Dendroctonus mexicanus Hopkins, 1905 (1906), Proc. Ent. Soc. Washington 7:80 (preprint) (*new synonymy*); Hopkins, 1909. U. S. Dept. Agric. Bur. Ent. Tech. ser. 17(1):97; Hagedorn, 1910, Coleopterorum Catalogus 4:20; Hagedorn, 1910. Genera Insectorum 111:60; Hopkins, 1915, U. S. Dept. Agric. Bur. Ent. Tech. ser. 17(2):211; Chamberlin, 1939, Bark and Timber Beetles of North America, p. 145; Schedl, 1940 (1939), An. Esc. Nac. Cienc. Biol. (Mexico) 1:339; Johnston, 1942, Proc. American Sci. Congr. (State Dept., Washington), 8:245; Muesebeck, 1950, Jour. Econ. Ent. 43:125, 131; Perry, 1951, Unasylva (Mexico) 5:159; Becker, 1951, Zeitschr. angew. Ent. 33:186; Becker, 1952, Trans. Ninth Internatl. Congr. Ent. 1:582; Becker, 1954, Zeitschr. angew. Ent. 36:20; Becker, 1955, Zeitschr. angew. Ent. 37:11; Schedl, 1955, Zeitschr. angew. Ent. 38:10. Biol.: Hopkins, 1909, U. S. Dept. Agric. Bur. Ent. Bull. 83(1):74.

This species is very closely related to *brevicomis*, but is readily distinguished by the longer declivital pubescence, by the more strongly impressed declivital striae, by the more sparsely but more coarsely granulate punctures of the declivital interspaces, by the smaller average size, and, in part, by the distribution (Fig. 45).

Male.—Length 2.3-4.5 mm. (average about 3), 2.4 times as long as wide; mature color very dark brown.

Frons convex, with a pair of lateral elevations on median half just below upper level of eyes separated by a deep median groove, the summit of elevations armed at their dorsomedian margins by one or two prominent, somewhat dorsomedially oriented granules; epistomal margin elevated, its surface smooth and shining; epistomal process slightly wider than half (0.58 times) the distance between eyes, its arms oblique (about 40° from the horizontal) and elevated, the horizontal portion about half its total width, transversely concave, ending just above epistomal margin and bearing under its distal margin a dense brush of conspicuous yellowish setae; surface punctate-rugulose above eyes, coarsely, rather deeply punctured and subgranulate below. Vestiture, in addition to epistomal brush, rather long, sparse.

Pronotum 1.4 times as wide as long, widest on basal third; sides rather weakly arcuate on basal three-fourths, rather feebly constricted just behind the broadly, shallowly emarginate anterior margin; surface smooth with rather coarse, moderately deep, close punctures; punctures somewhat shallower and less abundant laterally but not reduced in size; a raised median line not apparent. Vestiture rather long, fine sparse.

Elytra 2.2 times as long as pronotum; sides straight and subparallel on basal two-thirds, rather broadly rounded behind; basal margins arcuate and bearing a row of about nine, moderately large, raised, overlapping crenulations, with several smaller submarginal ones particularly on interspaces two and three; striae rather strongly impressed, the punctures rather small, moderately deep; interstriae moderately convex, about one and one-half times as wide as striae and armed by a single very irregular row of rather coarse transverse crenulations, each averaging well over half the width of an interspace. Declivity moderately steep, convex; striae rather strongly impressed, the punctures only slightly smaller than on disc; interstriae convex, virtually all punctures rather coarsely, transversely tuberculate, arranged in an irregular single or partly double rank (never more than two ranks across an interspace). Vestiture rather abundant, rather long, length of most hairs equal to width of an interspace, a few twice as long.

Female.—Similar to male except lateral elevations of frons less prominent and unarmed, with median groove consequently less conspicuous; arms of epistomal process less strongly elevated; pronotal constrictions largely filled by a prominent transverse elevated callus both laterally and dorsally; punctures of pronotal disc very slightly larger and deeper; transverse crenulations of elytral disc very slightly larger; and declivital granules somewhat finer, a few punctures along edges of interspaces often without granules.

Type locality.—Carolina (Sacramento, Amecameca, Mexico, for *mexicanus;* Williams, Arizona, for *arizonicus*). The types of all three descriptions were studied.

Hosts.—*Pinus ayacahuite*, *echinata*, *glabra*, *lawsoni*, *leiophylla*, *montezumae*, *oocarpa*, *palustris*, *ponderosa*, *rigida*, *rudis*, *strobus*, *taeda*, *teocotl*, and *virginiana*. Records, presumably during epidemics, also come from *Picea excelsa*, and *rubens*.

Distribution.—North America south of a line drawn from New Jersey to central Arizona, south to Honduras.

Specimens from the following localities were examined (Fig. 45). ALABAMA: Calhoun and Montgomery. ARKANSAS: Hampton. ARIZONA: "Crook N. F.," Crown King, Flagstaff, Graham Mts., Hassayampa Lake, Jerome, Pine, "Pleasant Valley," Portal, Prescott, Prescott N. F., Rustler Park, Santa Catalina Mts., Sitgreaves N. F., Williams and Young. FLORIDA: Haw Ck., and Taylor Co. GEORGIA: Clyo, Demorest, and Thomasville. LOUISIANA: Singer, and Wilson. MARYLAND: Cumberland. NEW MEXICO: Bandelier N. M., Cloudcroft, and Mimbres. NORTH CAROLINA: Asheville, Biltmore, Black Mts., Boardman, Fletcher, "Mt. Graybeard," Pisgah Ridge, and Tryon. OKLAHOMA: "Western Indian Terr." PENNSYLVANIA: Mt. Alto. SOUTH CAROLINA: "Ben Quan," Clemson, Georgetown, and Pregnall. TENNESSEE: Ducktown. TEXAS: Beaumont, Call, Deweyville, and Kirbyville. VIRGINIA: Arlington, Auburn, Chase City, Cob Island, Glen Allen, Green Bay, King and Queen Co., Port Republic, and Virginia Beach. DISTRICT OF COLUMBIA: Washington. WEST VIRGINIA: Greenbrier, Hampshire, Hardy, Kanawha, Monongalia, Pendleton, Pocahontas, Raleigh, Randolph, Tucker, and Wood Cos. CHIAPAS: Huixtla. CHIHUAHUA: Tres Rios. DISTRITO FEDERAL: Mexico, and Tacubaya. HIDALGO: Jacala. MEXICO: Amecameca, Chapingo, San Rafael, Texcoco, and Tlalmanalco. MICHOACAN: "Michoacan." MORELOS: Cuernavaca, and Tlayacapan. PUEBLA: Texmelucan. TLAXCALA: *Tlaxcala*. ZACATECAS: Laguna Balderama. GUATEMALA: Godenez, and Santa Cruz del Quiche. HONDURAS: Olanchita, and Tegucigalpa.

Geographic variation.—Specimens from southern Mexico tend to average slightly larger in size (less than 1 mm. larger) and slightly darker in color than do those from the eastern United States. The frons varies conspicuously from area to area, but with no general trends in any direction. For example: a series from West Virginia has the frons very strongly protrubant; in series from neighboring areas the character is absent or nearly so, but reappears in a slightly modified form in one locality in central Arizona. These characters appear to characterize local populations and cannot be used to define geographic races.

Biology.—Estimates of the volume of timber destroyed annually by this insect are clouded by the difficulty of field identification in the southwestern United States and by the absence of such estimates for Mexico and Guatemala. Tremendous losses have been sustained, however, in the southeastern United States, Mexico and Guatemala which suggest the total damage resulting from activities of this insect may equal that of the Western Pine Beetle.

The winter is passed in all stages, including eggs, with larvae predominating. As with *brevicomis*, activity might resume whenever subcortical temperatures become favorable during or following the winter months. Because all stages overwinter and emerge from the host as they mature, there is an extreme overlapping of generations resulting in an almost continuous period of flight from April when the first flights of overwintering adults begin until December when activity ceases in the northern parts of the range. In southern Mexico and Guatemala it is expected that flight activity continues throughout the year without interruption. In any particular locality, however, there are periods of greatest flight activity that tend to coincide with the emergence of each new brood. According to Hopkins (1909b:62) a peculiarity of this species is its tendency to migrate considerable distances from the brood tree to begin a new attack; subsequent workers (Dixon and Osgood, 1961:6) also indicate that trees selected for attack may be either nearby or considerable distances from the point of emergence.

Trees selected for attack ordinarily are living, standing and larger than about six inches D.B.H. The attack usually is concentrated on the upper half of the bole, but may reach the ground level. The attack is slow and continuous; its duration depending on numerous factors such as the size and resistance of the host, the population density of beetles in the area, the climatic and other ecological factors peculiar to the area. The duration and pattern of attack on a host tree evidently are similar to those of *brevicomis.*

The egg galleries are almost entirely in the phloem tissues, not engraving, but staining the xylem slightly. They are winding,

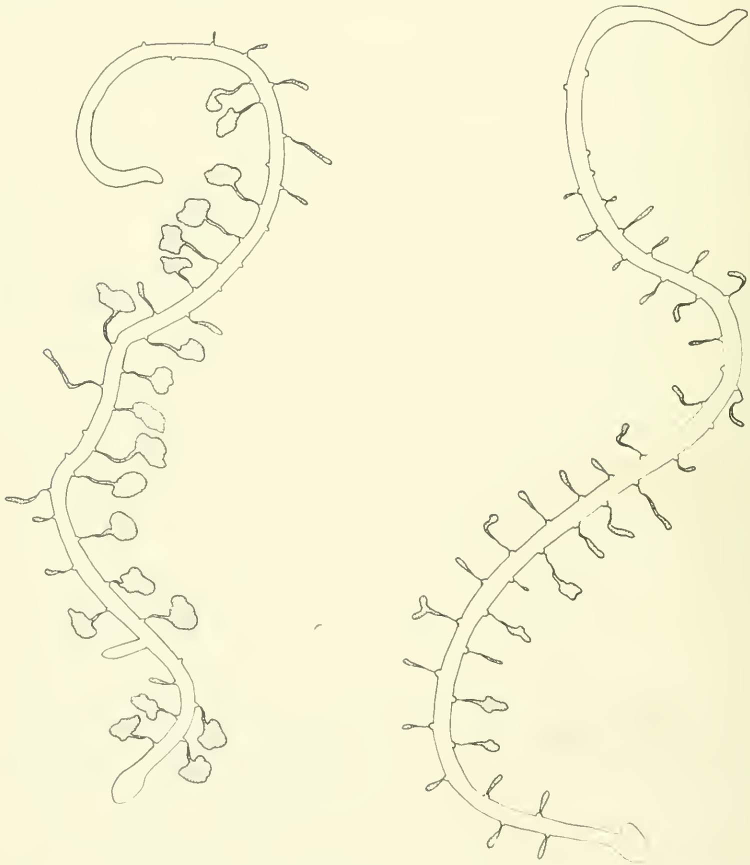


Fig. 47. *Dendroctonus frontalis*: Egg galleries sinuate, predominantly longitudinal; egg niches large, placed individually on alternate sides of gallery; larval mines may retain continual contact with cambium (left), or they may expand into outer bark (right).

elongate galleries (Fig. 47), often branching, anastomosing or crossing one another. The complicated interwoven series resembles rather closely that of *brevicomis*, except that there is a greater tendency for the galleries to be longitudinal; that is, for the total longitudinal displacement to exceed the total lateral displacement. The diameter of each egg gallery is slightly greater than the width of a parent beetle; in length they average approximately 30 cm., although the winding, complex character of the galleries makes accurate measurement virtually impossible.

As with other species of the genus, the initial attack is made by the female, usually in a crevice in the bark. The male joins the female about the time the pitch begins to flow; he then pushes the frass from the entrance hole while the female extends the gallery. After the gallery has been extended several centimeters he then packs the lower areas with frass thereby blocking the entrance hole, leaving only the area where the beetles are working free for their activities. The gallery may or may not have a nuptial chamber; ventilation tunnels may be spaced irregularly as in *brevicomis*. It has been reported (Dixon and Osgood, 1961:6) that extension of the egg gallery may occur at the rate of about 2.5 cm. per day.

Published data pertaining to the period of oviposition, egg production by individual females, and details of gallery formation are not sufficient for conclusive statements concerning them. The small amount of published information, however, permits the following comments.

Drawings, photographs (Hopkins, 1909b:58-68; Fronk, 1947:9; Dixon and Osgood, 1961:7; etc.), and limited personal observations of egg galleries indicate that egg niches are placed alternately along the sides of the gallery in contact with the cambium. They are symmetrical and about one-third as deep as the width of the gallery and slightly wider than deep. The spacing of niches appears variable, but evidently they may be as close as 6 mm., with an average of 17 mm. between niches on one side (accurate measurements should provide figures much lower than these). Eggs are deposited individually and each is packed in its niche with specially prepared frass to the original contour of the gallery.

Fronk (1947:10) found that under optimum conditions the eggs hatch in from 3 to 9 days, with an average of 5.5 days; unfavorable conditions such as occur during the winter evidently may lengthen the incubation period to several months. Each newly hatched larva mines the phloem in contact with the cambium, approximately perpendicular to the egg gallery. This mine of the first instar larva is of uniformly thin diameter for about one centimeter, or several times this length in an unfavorable environment (Hopkins, 1909: 61), it then widens abruptly into a short, irregularly oval area where the remaining larval instars are passed (Fronk, 1947:8). This enlarged area may be in contact with the cambium and visible on peeled bark, or in thick bark it may be entirely in the inner bark as in *brevicomis*. Toward the end of the fourth instar the larva bores into the outer bark where it clears a pupal chamber and enters the quiescent prepupal stage. The larval period under optimum conditions varies from 25 to 38 days and the pupal period about 8 to 11 days (Fronk, 1947:6); either or both stages might be lengthened several months by unfavorable conditions. In Virginia the lift cycle was completed under near optimum conditions in from 40 to 54 days (Fronk, 1947:7).

The number of generations completed in one year varies from 3 to 5 in the eastern United States; in Mexico and Guatemala the number undoubtedly is greater.

Dendroctonus parallelocollis Chapuis

Figs. 7-10, 34, 48-49

Dendroctonus parallelocollis Chapuis, 1869, Synopsis des Scolytides, p. 36 (1873, Mém. Soc. Roy. Sci. Liége (2)3:244).; Blandford, 1897, Biol. Centr.-Amer., Coleopt. 4(6):147; Hopkins, 1905 (1906), Proc. Ent. Soc. Washington 7:81; Hopkins, 1909, U. S. Dept. Agric. Bur. Ent. Tech. ser. 17(1):99; Hagedorn, 1910, Coleopterorum Catalogus 4:22; Hagedorn, 1910, Genera Insectorum 111:60; Hopkins, 1915, U. S. Dept. Agric. Bur. Ent. Tech. ser. 17(2):211; Chamberlin, 1939, Bark and Timber Beetles of North America, p. 144; Schedl, 1940 (1939), An. Esc. Nac. Cienc. Biol. (Mexico) 1:339; Schedl, 1955, Zeitschr, angew. Ent. 38:11. Biol.: Hopkins, 1909, U. S. Dept. Agric. Bur. Ent. Bull. 83(1):75; Muesebeck, 1950, Jour. Econ. Ent. 43:119, 131; Perry, 1951, Unasylva (Mexico) 5:159; Becker, 1951, Zeitschr. angew. Ent. 33:186; Becker, 1952, Trans. Ninth Internatl. Congr. Ent. 1:582: Becker, 1954, Zeitschr. angew. Ent. 36:20; Becker, 1955, Zeitschr. angew. Ent. 37:11.

Dendroctonus approximatus Dietz, 1890, Trans. American Ent. Soc. 17:28, 31; Blandford, 1897, Biol. Centr.-Amer., Coleopt. 4(6):147; Hopkins, 1905 (1906), Proc. Ent. Soc. Washington 7:81; Hopkins, 1909, U. S. Dept. Agric. Bur. Ent. Tech. ser. 17(1):101; Swaine, 1909, New York St. Mus. Bull. 134:95; Hagedorn, 1910, Coleopterorum Catalogus 4:19; Hagedorn, 1910, Genera Insectorum 111:60; Hopkins, 1915, U. S. Dept. Agric. Bur. Ent. Tech. ser. 17(2):211; Chamberlin, 1939, Bark and Timber Beetles of North America, p. 159; Schedl, 1940 (1939). An. Esc. Nac. Cienc. Biol. (Mexico) 1:322. Biol.: Schwarz, 1902, Proc. Ent. Soc. Washington 5:32; Hopkins, 1903, U. S. Dept. Agric. Yearbook 1902:281; Hopkins, 1903, Canadian Ent. 35:61; Hopkins, 1904, U. S. Dept. Agric. Div. Ent. Bull. 48:44; Hopkins, 1904, U. S. Dept. Agric. Yearbook 1904:281; Hopkins, 1905, U. S. Dept. Agric. Bur. Ent. Bull. 56:11; Burke, 1908, Proc. Ent. Soc. Washington 9:115; Hopkins, 1909, U. S. Dept. Agric. Bur. Ent. Bull. 83(1):77; Swaine, 1909, New York St. Mus. Bull. 134:95; Felt, 1924, Manual of Shade Tree and Shrub Insects, p. 251; Blackman, 1931, New York St. Coll. For., Syracuse Univ. Bull. 4(4), Tech. Pub. 36:30; Keen, 1938, U. S. Dept. Agric. Misc. Pub. 273:102; Beal, 1939, U. S. Dept. Agric. Farmers Bull. 1824:11; Muesebeck, 1950, Jour. Econ. Ent. 43:122, 131; Pearson, 1950, U. S. Dept. Agric. Monogr. 6:154; Anonymous, 1951, U. S. Dept. Agric. Bur. Ent. Pl. Quar. Ins. Pest Surv., Sup. 4:8; Anonymous, 1952, U. S. Dept. Agric. Bur. Ent. Pl. Quar. Coop. Econ. Ins. Rept. 1(4):94; Anonymous, 1954, U. S. Dept. Agric. For. Serv. For. Ins. Rept. 1954:10; Yasinski, 1956, U. S. Dept. Agric. Rocky Mtn. For. Expt. Sta. Paper 23:1.

Dendroctonus parallelocollis var. *approximatus*: Biol.: Fall and Cockrell, 1907, Trans. American Ent. Soc. 33:145.

This species is rather closely allied to *frontalis* and *adjunctus,* but is larger and more coarsely sculptured than either. From *frontalis* it may also be distinguished by the more nearly flattened declivital interspaces with the second weakly impressed, by the uniseriate, rounded granules on the second declivital interspace, and by the larger, more closely set crenulations of the elytral disc. From *adjunctus* it is also distinguished by the more strongly impressed declivital striae, by the interspacial granules being uniseriate only on declivital interspace two (rarely also on one) and much more closely spaced, by the much larger, more numerous crenulations of the elytral disc, and by the more prominent transverse pronotal callus of the female and large frontal, almost hornlike, tubercles of the male.

Male.—Length 4.5-7.4 mm. (average about 6.0), 2.5 times as long as wide; mature color very dark brown to black.

Frons convex, with a pair of lateral elevations on median half just below upper level of eyes separated by a deep median groove, the summit of elevations armed at their dorsomedian margins by one or two prominent, somewhat dorsomedially oriented tubercles; epistomal margin elevated, its surface smooth and shining; epistomal process slightly wider than half (0.57 times) the distance between eyes, its arms oblique (about 40° from the horizontal) and elevated, the horizontal portion about half its total width, transversely concave, ending just above epistomal margin and bearing under its distal margin a dense brush of conspicuous yellowish setae; surface punctate-rugulose above eyes, coarsely, rather deeply punctured and subgranulate below. Vestiture, in addition to epistomal brush, rather long, sparse.

Pronotum 1.4 times as wide as long, widest at base; sides feebly arcuate and converging very slightly to the almost imperceptable anterior constriction just behind the broadly, very shallowly emarginate anterior margin; surface smooth and shining, the punctures rather small, moderately deep, close (size, depth and arrangement variable in a series); a raised median line feebly indicated anteriorly. Vestiture sparse, inconspicuous; moderately long at sides.

Elytra 2.2 times as long as pronotum; sides straight and subparallel on basal two-thirds, rather broadly rounded behind; basal margins arcuate and bearing a row of about nine, moderately large, raised, overlapping crenulations, with several smaller submarginal ones particularly on interspaces two and three; striae weakly impressed, the punctures usually rather small and shallow with anterior margins raised, subcrenulate; interstriae about twice as wide as striae and armed by abundant, confused, transverse crenulations, each averaging at least half the width of an interspace, some as wide as an entire interspace on posterior half of disc. Declivity moderately steep, convex, with interspace two weakly impressed; striae narrowly, moderately impressed, the punctures smaller than on disc, distinctly impressed, one and two almost straight, three curving away from suture on upper half, toward suture on lower half; interspaces scarcely if at all convex, about equal in width (except for expanded portion of three), each bearing a series of moderately large rounded granules, those on one and three usually confused, uniseriate on two, usually with a few to many fine punctures in addition to granules; granules on interspace two separated from one another by an average distance equal to one-half width of the interspace. Vestiture not abundant, longer on sides and declivity, the longest setae about one and one-half times as long as width of an interspace.

Female.—Similar to male except lateral elevations of frons less prominent and unarmed, with median groove consequently less conspicuous; arms of epistomal process less strongly elevated; pronotal constriction largely filled by a prominent transverse elevated callus both laterally and dorsally; punctures of pronotal disc very slightly larger and deeper; transverse crenulations of elytral disc and declivital granules somewhat larger.

Type locality.—Mexico (Colorado for *approximatus*). The type of *approximatus* was studied; *parallelocollis* was based on Hopkins' material that was compared to the type.

Hosts.—*Pinus apacheca, arizonica, ayacahuite, chihuahuana, hartwegi, leiophylla, montezumae, patula, ponderosa, rudis,* and *teocotl.*

Distribution.—Central Utah and Colorado south to Honduras.

Specimens from the following localities were examined (Fig. 48). Arizona: Black Mesa F. R., Chiricahua Mts., Flagstaff, Fort Apache, Graham Mts., Grand Canyon N. P., Kaibab N. F., Paradise, Pine, Portal, Prescott, Rincon Mts., Santa Catalina Mts., Santa Rita Mts., Show Low, Tucson, and Williams. Colorado: Brookvale, Glen Haven, Las Animas, La Veta, Monte Vista, Palmer Lake. New Mexico: Capitan Mts., Carson N. F., Cloudcroft, Lincoln N. F., Santa Fe, and Sierra Blanca. Utah: Bryce Canyon N. P., Dixie N. F., Escalante, Kamas, Long Hollow, Panguitch, Panguitch Lake, and Pin Hollow in Fishlake N. F. Chihuahua: Chuichupa, and Tres Rios. Durango: El Salto, and Sierra Durango. Distrito Federal: Mexico. Mexico: Ixtaccihuatl. Michoacan: Jacona. Morelos: Jonacatepec. Oaxaca: Oaxaca. Puebla: Texmelucan. Tlaxacala: Tlaxacala. Vera Cruz: Jalapa and Vera Cruz. Guatemala: Quezaltenango, Santa Cruz del Quiche, and Tecpan. Honduras: San Pedro Sula.

Geographical variation.—Constant differences associated with geographical origin were not apparent. The features used by Hopkins (1909a:70) in establishing geographical races refer to individual differences that can be found in a long series from almost any locality throughout its range.

Biology.—This is not an aggressive species, consequently, damage caused by it is comparatively minor. It is a secondary enemy of pine, entering the host only after the tree has been overcome by the more aggressive species of *Dendroctonus* or of *Ips.*

Adults and larvae in all stages of development overwinter in their galleries at the base of the host tree, or, in the case of felled trees, on the lower side of the trunk next to the ground. They become active somewhat later than other species and usually extend their

Fig. 48. Probable geographical distribution of *Dendroctonus parallelocollis* with collection sites indicated.

old galleries for a period, with the adults resuming egg-laying activities, before emerging from the host. In the northern parts of the range the flight period begins early in June and continues until October, with the principal period of activity occurring in June and early July. In southern Mexico and Guatemala activity probably continues throughout the year without seasonal interruptions. Emergence from the host occurs gradually over a long period of time, consequently, large numbers of beetles are not in flight at the same time making a concerted attack on one tree by this species exceedingly difficult.

The trees selected for attack are those previously selected by and largely overcome by other species, or those felled more than six weeks prior to the attack. This species, usually occupies the basal portion of the bole from the ground level up to a height of six or eight feet; in the northern parts of its range, where it competes with *adjunctus* for space in the basal parts of the host, its galleries seldom extend more than two or three feet above the level of the ground. It also breeds in felled trees (Blackman 36:30), usually only on the lower side, particularly in those areas in contact with the ground. The smallest trees observed in which this species was breeding were 12 inches D.B.H., although this probably does not represent the minimum size acceptable to the species.

Ordinarily the attack is directed at the butt of the tree in areas of bark not occupied one to three weeks previously by other species. In an injured tree the attack may extend over a rather long period of time as successive generations slowly girdle it.

Basically the galleries (Fig. 49) are longitudinal and winding; they are coarser than those of associated species, particularly *adjunctus*, and present a strikingly different overall pattern. Branch galleries, many of which cross or join other galleries, are numerous, causing the entire network of galleries to form an apparently

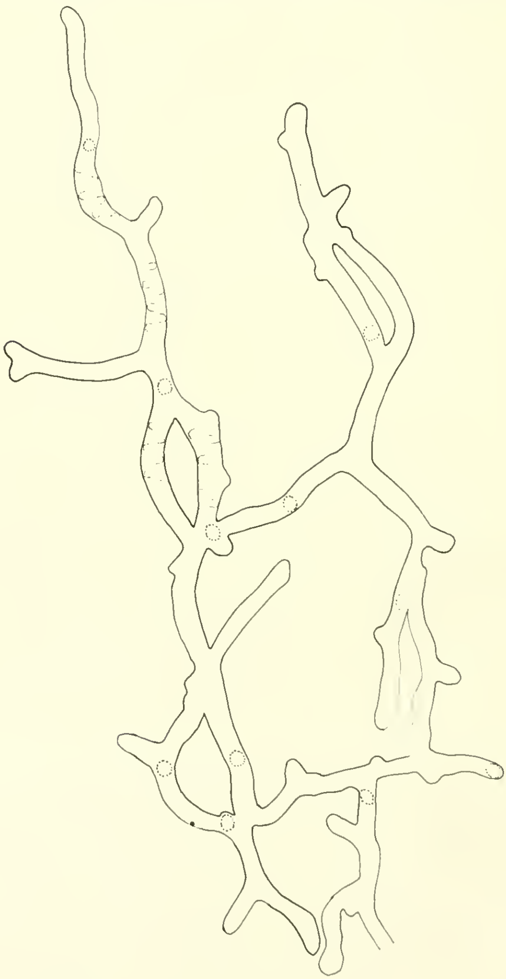


Fig. 49. *Dendroctonus parallelocollis*: Egg galleries form an apparent haphazard criss-cross pattern; egg niches large, placed alternately on gallery wall opposite cambium (upper left); larval mines entirely in outer bark, never exposed on surface of peeled bark.

aimless criss-cross pattern. As with other species the galleries are almost entirely in the inner bark, very faintly grooving or at least staining the cambium.

The egg galleries are rather coarse, averaging about 5 mm. in diameter. Gallery systems may be extensive, but because of their branching and anastomosing character it is virtually impossible to measure the work of individual beetles.

As with other species the initial attack is made by the female. Soon after she reaches the phloem tissues she is joined by the male. As with other species he then expels excess frass from the entrance hole or later packs the lower or more remote areas of the gallery with excess frass in order to keep clear the area where the female is working. Egg niches are very different from other species; they are not in contact with the cambium, but are located alternately on the sides of the wall farthest from the cambium. The niches are cup-shaped, larger than usual, and extend into the non-living portion of the bark. Each niche may contain, according to Blackman (1936:30), one to four eggs; not more than one egg per niche was found during this study. The larval mines are entirely in the bark, mostly in the outer bark, and do not contact the cambium at any time. Their length is variable and not easily measured, but evidently they are rather short. Pupal chambers are almost always in the outer bark.

Oviposition apparently begins about a week after the attack and probably continues over a substantially longer period than is the case with related species. The position of the egg niches and the possible deposition of several eggs in each makes it difficult to count with any degree of accuracy the number of eggs produced by any one female, since many of the eggs are destroyed by the observer's attempt to locate the niches. From the number of niches found, however, it is estimated that the number is not large, probably seldom exceeding 40 eggs per female. As with other species, a majority of the eggs apparently were deposited in the first third of the egg gallery. The exact spacing of egg niches, and the periods of incubation, larval and pupal development were not determined.

In the northern parts of its range one generation per year appears to be normal.

Dendroctonus adjunctus Blandford

Figs. 11-12, 35, 50-51.

Dendroctonus adjunctus Blandford, 1897, Biol. Centr.-Amer., Coleopt. 4(6):147; Hopkins, 1909, U. S. Dept. Agric. Bur. Ent. Tech. ser. 17(1):157; Hagedorn, 1910, Coleopterorum Catalogus 4:19; Hagedorn, 1910, Genera Insectorum 111:60; Chamberlin, 1939, Bark and Timber Beetles of North America, p. 144; Schedl, 1955, Zeitschr. angew. Ent. 38:8. Biol.: Johnston, 1942, Proc. Amer. Sci. Congr. (Washington, May 10-18, 1940) 8:245; Becker, 1951, Zeitschr. angew. Ent. 33:186; Becker, 1952, Trans. Ninth Internatl. Congr. Ent. 1:582; Becker, 1954, Zeitscher. angew. Ent. 36:20-61; Becker, 1955, Zeitschr. angew. Ent. 37:1.

Dendroctonus convexifrons Hopkins, 1909, U. S. Dept. Agric. Bur. Ent. Tech. ser. 17(1):87 (*new synonymy*); Hagedorn, 1910, Coleopterorum Catalogus 4:20; Hagedorn, 1910, Genera Insectorum 111:60; Chamberlin, 1939, Bark and Timber Beetles of North America, p. 158; Schedl, 1940 (1939), An. Esc. Nac. Cienc. Biol. (Mexico) 1:339. Biol.: Hopkins, 1909, U. S. Dept. Agric. Bur. Ent. Bull. 83(1):53; Felt, 1924, Manual of Shade Tree and Shrub Insects, p. 252; Blackman, 1931, New York St. Coll. For., Syracuse Univ. Bull. 4(4), Tech. Pub. 36:29; Keen, 1938, U. S. Dept. Agric. Misc. Pub. 273:102; Beal, 1939, U. S. Dept. Agric. Farmers Bull. 1824:11; Pearson, 1950, U. S. Dept. Agric. Monogr. 6:154; Anonymous, 1951, U. S. Dept. Agric. Bur. Ent. Pl. Quar. Ins. Pest. Surv., Sup. 4:8; Anonymous, 1952, U. S. Dept. Agric. Bur. Ent. Pl. Quar. Coop. Econ. Ins. Rept. 1(4):94; Anonymous, 1955, U. S. Dept. Agric. For. Serv. For. Ins. 1954:10; Yasinski, 1956, U. S. Dept. Agric. Rocky Mtn. For. Expt. Sta. Paper 23:1.

Dendroctonus approximatus: Dietz, 1890, Trans. American Ent. Soc. 17:31 (part); Schwarz, 1902, Proc. Ent. Soc. Washington 5:32 (part).

This species occupies a position between the two major groups within the genus, more or less compromising the characters of *parallelocollis* and *ponderosae*. Although the relationship is not close, it is allied to *parallelocollis*, but is readily distinguished by the more slender body form, by the more widely spaced, uniseriate granules on the first three declivital interspaces, by the more finely sculptured elytral disc, and by the absence of frontal tubercles in the male and more poorly developed transverse pronotal callus in the female. In many respects it is similar to *ponderosae* but may be distinguished by the more slender form, by the smooth, shining declivital interspaces, by the stronger median frontal groove, and, in the female, by the transverse pronotal callus.

Male.—Length 3.8-6.0 mm. (average about 5.2), 2.65 times as long as wide; mature body color rather dark brown.

Frons convex, with a pair of unarmed lateral elevations on median half just below upper level of eyes separated by a rather inconspicuous median groove; epistomal margin elevated, its surface smooth and shining; epistomal process half (0.50 times) as wide as distance between eyes, its arms oblique (about 40° from the horizontal) and elevated, the horizontal portion about half its total width, transversely concave, ending just above epistomal margin and bearing under its distal margin a dense brush of conspicuous yellowish setae; surface punctate-rugulose above eyes, more deeply punctured and subgranulate below. Vestiture, except epistomal brush, sparse, inconspicuous, rather long.

Pronotum 1.4 times as wide as long, widest on basal third; sides rather strongly arcuate on basal three-fourth, rather strongly constricted behind the broadly, shallowly emarginate anterior margin; surface smooth with rather fine, shallow, close punctures on median third, becoming more finely punctured laterally; an indistinct median line apparent. Vestiture rather sparse, long, becoming coarse laterally.

Elytra 2.5 times as long as pronotum; sides straight and subparallel on basal two-thirds, rather narrowly rounded behind; basal margins arcuate and bearing a row of about nine, moderately large, raised, overlapping crenulations, with several smaller submarginal ones particularly on interspaces two and three; striae weakly impressed, the punctures rather small and shallow; interstriae about twice as wide as striae and armed by rather abundant confused, transverse crenulations, each averaging about one-half the width of an interspace, a few almost as wide as the interspace on posterior half of disc. Declivity moderately steep, convex, with interspace two weakly impressed; striae weakly impressed, the punctures greatly reduced, one straight, two curving slightly toward suture on lower third, three diverging from suture on upper half, curving toward suture on lower third; interspace one slightly raised, two impressed and flat, three feebly convex, each bearing a uniseriate row of sparse, rounded or pointed granules and in addition several confused, minute punctures; granules on two separated from one another by an average distance equal to width of the interspace. Vestiture rather sparse, longer on sides and declivity, the longest setae about one and one-half or two times as long as width of an interspace.

Female.—Similar to male except lateral elevations and median frontal groove poorly developed; arms of epistomal process less strongly elevated; pronotal constriction with a feebly developed transverse elevated callus; punctures of pronotal disc very slightly larger and deeper; and transverse crenulations of elytral disc and granules of declivity very slightly larger.

Type locality.—Totonicapam, Guatemala (Williams, Arizona, for *convexifrons*). The type of *convexifrons* was studied; the type of *adjunctus* was compared to my material by R. T. Thompson.

Hosts.—*Pinus ayacahuite*, *chihuahuana*,, *montezumae*, *ponderosae*, *pseudostrobus*, *rudis*, and *tenuifolia*.

Distribution.—Southern Utah and Colorado south to Guatemala.

Specimens from the following localities were examined (Fig. 50). ARIZONA: Flagstaff, Fort Apache, Graham Mts., Grand Canyon N. P., Jacobs Lake, Kaibab N. F., Paradise, Rustler Park, Santa Catalina Mts., Show Low, and Williams. COLORADO: Durango, Ft. Garland, Las Animas Co., La Veta, Monte Vista, Rye, San Isabel N. F., and "Vallecito R. S." NEW MEXICO: Capitan, Carson N. F. Cloudcroft, Ft. Wingate, "Hermit Peak," Las Vegas, Lincoln N. F., Sierra Blanca Mts., and Vermejo. UTAH: Escalante, Long Hollow in Dixie N. F., Manti-LaSal N. F., Panguitch Lake, and Sanford Canyon. MEXICO: Nevado de Toluca, and Penuela La Gavia. GUATEMALA: Cerro Quemado, Chuchumatanes, Guatemala, La Esperanza, Las Trojadas, Montana de las Nubes, Poptum, Quetzaltenango, Sierra Maria Tecum, Tecpn, and Totonicapan.

Geographical variation.—Not observable in the limited material at hand.

Biology.—This species generally works in concert with other species of *Dendroctonus* to overcome a tree. Its galleries resemble, superficially at least, those of other species and, consequently, the resulting misidentifications have attributed much of the damage actually done by this species to others having more formidable repu-

Fig. 50. Probable geographical distribution of *Dendroctonus adjunctus* with collection sites indicated.

tations as tree killers. In the absence of an epidemic of other species it appears much more aggressive than the available literature would indicate, frequently initiating the primary attack on a tree.

Although any stage of development may be represented, the winter usually is passed as half grown larvae or as adults starting a new attack in the fall but without commencing oviposition. Larval development is resumed and egg deposition is started or resumed as soon as spring temperatures become sufficiently high. The brood, both young adults and larvae, completes its development and begins to emerge to seek new hosts in May or early June, usually several weeks after the emergence of *brevicomis* and *ponderosae.* Its habits of commencing attacks in the fall and the late emergence in the spring are important factors in the apparent lack of aggressiveness of this species, since the timing of its flight activity coincides with the period when other species have overcome host trees but have not yet occupied the lower portions of the bole. Although some flight activity occurs throughout the summer months, two periods of increased activity occur. The first is in May and early June, the second and greatest occurs between the latter part of August and the middle of October. The attack on a particular tree is spread over a considerable period of time and usually involves a relatively small population of this species.

Trees selected for attack are weakened standing trees larger than about ten inches D. B. H. Galleries have been observed in stumps, but not in prostrate trees or logs. In the absence of competing species the area of attack may extend from ground level to a height of about 10 or 12 feet. When competing species, particularly *pondero-*

sae, are present in large numbers this species may be restricted to less than the lower three feet of the bole.

The attack appears to begin in the upper parts of the area occupied by this species; that is, the bole about 4 to 12 feet above the ground level, with successively newer attacks occurring below this area until the level of the ground is reached. The attack may be completed in a few days when populations are high, or it may ex-

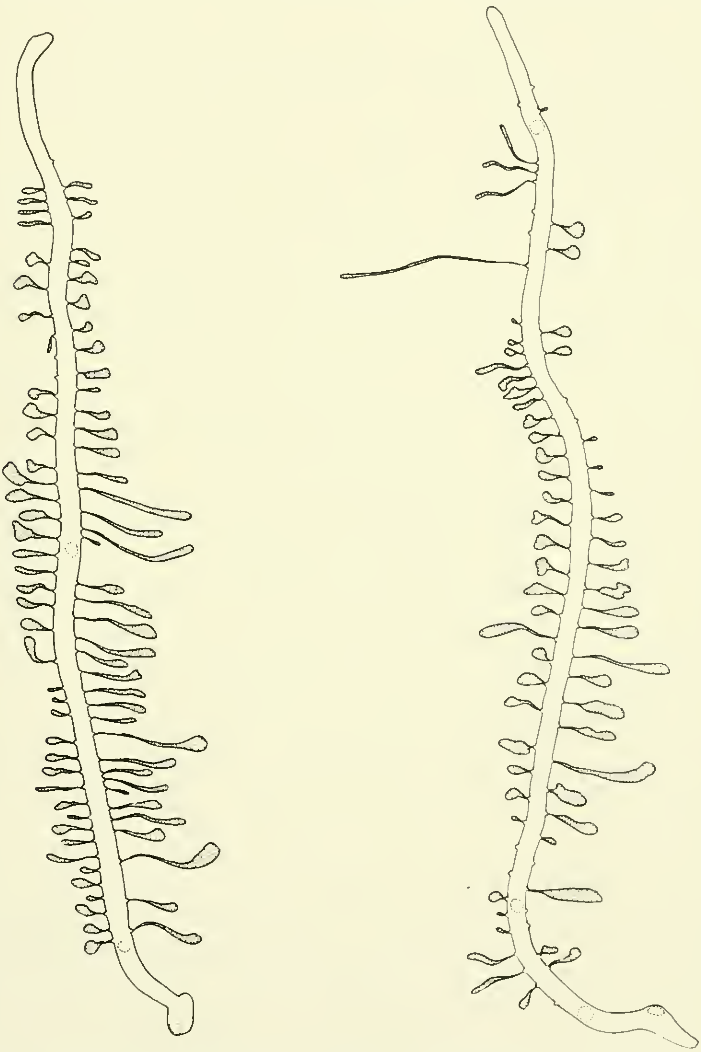


Fig. 51. *Dendroctonus adjunctus*: Egg galleries slightly to rather strongly sinuate (example at right about average); individual egg niches placed alternately on sides of gallery; larval mines transverse, usually in cambium but may extend into outer bark, seldom cross one another.

tend over the greater part of a year, particularly when the first attacks are made in the fall.

Egg galleries (Fig. 51) are sinuous and almost always extend upward from the entrance hole. As with other species of this genus they are almost entirely in the phloem, very lightly scoring or at least staining the wood. The total longitudinal displacement of an egg gallery usually is about three to four times as great as the total lateral displacement. Ordinarily the gallery extends horizontally either right or left from the entrance hole about four to seven centimeters then curves upward; about two to four broad sinuous curves are included in its vertical ascent. From the principal longitudinal axis of the gallery the first of these curves diverges about four to six centimeters, the remaining curves diverge about one-half to two centimeters from this axis. Of 36 egg galleries studied in the Panguitch, Utah, area during the last week of June, 1960, the average gallery length was 31 cm., the maximum was 89 cm.; the average width was about 4 mm. Although it appeared that an effort was made by the beetles to avoid doing so, galleries did cross or anastomose occasionally. Approximately one gallery in 25 descended vertically, evidently to avoid crowding or crossing neighboring galleries; more rarely one was primarily transverse. Branching or side galleries extending from the main egg tunnel were uncommon. When such branches did occur they usually did not exceed three centimeters in length and did not contain egg niches.

The initial attack is made by the female. As with other species this usually occurs in a crevis of the bark; ordinarily she is joined by the male about the time the entrance tunnel reaches the cambium. The male, as with other species, ejects frass from the entrance hole while the female extends the gallery. When sufficient working space is available he then packs the lower portions of the gallery with the excess frass.

Ventilation tunnels occur at irregular intervals; the minimum observed distance between two of them was 1.7 cm.; in trees having relatively thin bark they may be entirely absent. The average distance between ventilation tunnels in the 36 galleries measured for this study, was 5.2 cm. The first most commonly is placed within one centimeter, either above or below, the first egg niche; the average distance from the entrance hole to the first egg niche was 3.5 cm.

Egg niches are arranged alternately in the phloem on the sides of the gallery in contact with the cambium. Each is symmetrical, slightly deeper than wide and, compared to the foregoing species, is rather small. Each niche is very slightly larger than the egg it contains. The number and spacing of egg niches is variable; the minimum observed distance between two niches located on the same side of a gallery was 1.5 mm., the average distance was about 3.5 mm. The average number of egg niches in the 36 galleries mentioned above was 44.1; the maximum was 119. About one-tenth of the niches were located exactly opposite one another on the different sides of the gallery; this was a notable departure from the consistently alternate placement of niches in the preceding species where such an occurrence was exceedingly uncommon. Eggs are deposited individually in the niches; each niche is then filled by specially prepared frass to the original level of the gallery.

The period of incubation has not been determined precisely, but evidently it requires about a week under optimum conditions. The newly hatched larvae construct narrow tunnels in the cambium region perpendicular to the egg gallery. The larval mine extends about one to four centimeters along a straight to winding route, without increasing in diameter. It then expands abruptly into an oval to irregular feeding chamber approximately one-half to one centimeter wide and about one or two centimeters long. The entire larval mine usually is in contact with the cambium and is visible on the inner bark. Some of the larvae pupate in this chamber, however, most of them mine into the outer bark for pupation.

The number of generations may vary from one complete and a partial second generation per year to one generation in two full years (Hopkins 1909b:55). Although not reported, it appears possible that two generations might be completed in favorable years and localities in the southern parts of its range.

Dendroctonus ponderosae Hopkins

Figs. 13, 36, 52-53.

Dendroctonus ponderosae Hopkins, 1902, U. S. Dept. Agric. Div. Ent. Bull. 32:10; Hopkins, 1902, Proc. Ent. Soc. Washington 5:3; Hopkins, 1909, U. S. Dept. Agric. Bur. Ent. Tech. ser. 17(1):109; Swaine, 1909, New York St. Mus. Bull. 134:98; Hagedorn, 1910, Coleopterorum Catalogus 4:22; Hagedorn, 1910, Genera Insectorum 111:60; Hopkins, 1915, U. S. Dept. Agric. Bur. Ent. Tech. ser. 17(2):211; Swaine, 1918, Dom. Canada Dept. Agric. Ent. Br. Bull. 14(2):65; Chamberlin, 1939, Bark and Timber Beetles of North America, p. 156. Biol.: Hopkins, 1902, U. S. Dept. Agric. Div. Ent. Bull. 37:21; Hopkins, 1903, U. S. Dept. Agric. Yearbook 1902:275, 282; Hopkins, 1903, Canadian Ent. 35:59; Gillette, 1903, Colorado Agric. Rept. 24:118; Hopkins, 1904, U. S. Dept. Agric. Div. Ent. Bull. 48:41, 43, 44; Hopkins, 1905, U. S. Dept. Agric. Yearbook 1904:275, 281; Hopkins, 1905, Proc. Ent. Soc. Washington 7:147; Hopkins, 1905, U. S. Dept. Agric. Div. Ent. Bull. 56:10; Currie, 1905, U. S. Dept. Agric. Div. Ent. Bull. 53:100; Burke, 1906, Proc. Ent. Soc. Washington 7:4; Hopkins, 1906, Proc. Ent. Soc. Washington 7:147; Hopkins, 1906, Proc. Ent. Soc. Washington 8:4; Webb, 1906, U. S. Dept. Agric. Yearbook 1905:631; Webb, 1907, U. S. Dept. Agric. Yearbook 1906:515; Howard, 1907, U. S. Dept. Agric. Div. Ent. Rept. 1906:13; Hopkins, 1908, U. S. Dept. Agric. Yearbook 1907:162, 548; Hopkins, 1908, West Virginia Lumberm., Jan. 10:11; Hopkins, 1909, U. S. Dept. Agric. Bur. Ent. Bull. 58:59, 76; Hopkins, 1909, U. S. Dept. Agric. Bur. Ent. Bull. 83(1):90; Hopkins, 1909, U. S. Dept. Agric. Yearbook 1908:574; Hopkins, 1910, U. S. Dept. Agric. Bur. Ent. Circ. 125:2; Howard, 1910, U. S. Dept. Agric. Bur. Ent. Rept. 1909:21; Hopkins, 1912, U. S. Dept. Agric. Bur. Ent. Circ. 142:7; Butterick, 1912, Jour. Econ. Ent. 5:456; Swaine, 1913, Ontario Ent. Soc. Rept. 43:90; Brues, 1920, Insects and Human Welfare, p. 70; Miller, 1923, Timberman 26(2):50; Felt, 1924, Manual of Tree and Shrub Insects, p. 256; Craighead, 1925, Jour. Forestry 23:347; Craighead, 1927, U. S. Dept. Agric. Circ. 411:7; Nelson and Beal, 1929, Phytopathology 19:1101; Craighead, 1930, U. S. Dept. Agric. Misc. Pub. 74:4; Craighead et al., 1931, Jour. Forestry 29:1016; Blackman, 1931, New York St. Col. For., Syracuse Univ. Bull. 4(4), Tech. Pub. 36, 97 p.; Rumbold, 1931, Jour. Agric. Res. 43(10):848; Doane, Van Dyke, Chamberlin and Burke, 1936, Forest Insects, p. 80; Beal, 1937, U. S. Dept. Agric. Bur. Ent. Pl. Quar. E 403, 5 p.; Hanna, 1937, Western Farm Life 39(7):10; Davis, 1938, Colorado Bur. Pl. Ins. Control Rept. 1938:31; Keen, 1938, U. S. Dept. Agric. Misc. Pub. 273:106; Strong, 1938, U. S. Dept. Agric. Bur. Ent. Pl. Quar. Rept. 1937:18; Wygant, 1938, Rocky Mtn. Conf. Ent. Rept. 14:15; Beal, 1939, Rocky Mtn. Conf. Ent. Rept. 15:6, 13; Beal, 1939, U. S. Dept. Agric. Farmers Bull. 1824, 21 p.; DeLeon, 1939, Rocky Mtn. Conf. Ent. Rept. 15:13; Hester and Edwards, 1939, Colorado Bur. Pl. Ins. Control Rept. 1939:15; Stahl, 1939, Wyoming Stockm.-Farm. 45(7):p. ?; Wygant, 1939, Rocky Mtn. Conf. Ent. Rept. 15:14; Hester, 1940, Colorado Bur. Pl. Ins. Control Rept. 1940:8; Strong, 1940, U. S. Dept. Agric. Bur. Ent. Pl. Quar. Rept. 1939:23; Woodward, 1940, South Dakota St. Hort. Soc. Rept. 37:49; Annand, 1941, U. S. Dept. Agric. Bur. Ent. Pl. Quar. Rept. 1940:26; Isely, 1941, Methods of Insect Control, ed. 2, pt. 1, p. 102; Strong, 1941, American Yearbook 1940:492; Cook, 1942, Western Farm Life 44(10):4, 8; Craighead, 1942, Smithsn. Inst. Rept. 1940-41:368, 371, 378; Beal, 1943, Jour. Forestry 41:359; Wygant, 1945, U. S. Dept. Agric. Bur. Ent. Pl. Quar. Ins. Pest Surv. 1944:14; Poyner, 1946, Colorado Bur. Pl. Ins. Control Rept. 1945:24; Annand, 1946, U. S. Dept. Agric. Bur. Ent. Pl. Quar. Rept. 1945:30; Gates, 1947, Rocky Mtn. Conf. Ent. Rept. 18:7; Gates, 1947, Colorado Bur. Pl. Ins. Control Rept. 1946:28; Annand, 1948, U. S. Dept. Agric. Bur. Ent. Pl. Quar. Rept. 1947:26; Snyder, 1948, Colorado Bur. Pl. Ins. Control Rept. 1947:35; Anonymous, 1948, U. S. Dept. Agric. Bur. Ent. Pl. Quar. Ins. Pest Surv. 1947:17; Keen, 1950, Jour. Forestry 48:147; Pearson, 1950, U. S. Dept. Agric. Agric. Monogr. 6:154; Snyder, 1950, Colorado Dept. Agric. Rept. 1:75; Anonymous, 1950, U. S. Dept. Agric. Bur. Ent. Pl. Quar. Ins. Pest Surv. 1949:26; Beal, 1951, Proc. West. For. Conserv. Assoc. 41:58; Anonymous, 1951, U. S. Dept. Agric. Bur. Ent. Pl. Quar. Ins. Pest Surv. Sup. 4:6; Anonymous, 1951, U. S. Dept. Agric. Bur. Ent. Pl. Quar. Ins. Pest. Surv. 1950:24; Gates, 1951, Colorado Dept. Agric. Rept. 2:38; Hoyt, 1952, U. S. Dept. Agric. Bur. Ent. Pl. Quar. Rept. 1950:16; Massey et al., 1952, Jour. Econ. Ent. 45:861; Anonymous, 1952, U. S. Dept. Agric. Bur. Ent. Pl. Quar. Coop. Econ. Ins. Rept. 1(Sup. 4):92; Massey et al., 1953, Jour. Econ. Ent. 46:601; Knight and Wilford, 1954, U. S. Dept. Agric. Rocky Mtn. For. Range Expt. Sta. For. Ins. Cond. 1953:3; Orr, 1954, U. S. Dept. Agric. Intermtn. For. Range Expt. Sta. For. Ins. Cond. 1953:2; Price, 1955, U. S. Dept. Agric. Rocky Mtn. For. Range Expt. Sta. Rept. 1954:15; Mogren, 1955, Michigan Univ. Diss. Abs. 15:1477; Anonymous, 1955, U. S. Dept. Agric. For. Serv. Imp. For. Ins. 1954:8; Bailey, 1956, U. S. Dept. Agric. Intermtn. For. Range Expt. Sta. Rept. 1956:30, 33, 37; Ostmark and Wilford, 1956, U. S. Dept. Agric. Rocky Mtn. For. Range Expt. Sta. Paper 22:4, 13; Price, 1956, U. S. Dept. Agric. Rocky Mtn. For. Range Expt. Sta. Rept. 1955:21; Yasinski, 1956, U. S. Dept. Agric. Rocky Mtn. For. Range Expt. Sta. Paper 23:2, 5, 7; Knight and Yasinski, 1956, U. S. Dept. Agric. Rocky Mtn. For. Range Expt. Sta. Res. Notes 21, 4 p.; Hay, 1957 (1956), Ann. Ent. Soc. America 49:567; Price, 1957, U. S. Dept. Agric. Rocky Mtn. For. Range Expt. Sta. Rept. 1956:81, 84, 90, 99; Knight, 1958, For. Science 4:35.

Dendroctonus monticolae Hopkins, 1901, Proc. Soc. Prom. Agric. 22:67 (new synonymy); Hopkins, 1902, U. S. Dept. Agric. Div. Ent. Bull. 37:21; Hopkins, 1902, Proc. Ent. Soc. Washington 5:3; Hopkins, 1905, U. S. Dept. Agric. Bur. Ent. Bull. 56:11; Hopkins, 1909, U. S. Dept. Agric. Bur. Ent. Tech. ser. 17(1):105; Swaine, 1909, New York St. Mus. Bull. 134:97; Hagedorn, 1910, Coleopterorum Catalogus 4:22; Hagedorn, 1910, Genera Insectorum 111:60; Hopkins, 1915, U. S. Dept. Agric. Bur. Ent. Tech. ser. 17(2):211; Swaine, 1918, Dom. Canada Dept. Agric. Ent. Br. Bull. 14(2):65; Chamberlin, 1939, Bark and timber beetles of North America, p. 155; Chamberlin, 1959, Scolytoidea of the Northwest, p. 71. Biol.:

Hopkins, 1899, U. S. Dept. Agric. Div. Ent. Bull., n. s., 21:14, 26; Hopkins, 1904, U. S. Dept. Agric. Div. Ent. Bull. 48:19, 42, 45; Webb, 1907, U. S. Dept. Agric. Yearbook 1906:515; Hopkins, 1908, U. S. Dept. Agric. Yearbook 1907:162, 548; Burke, 1908, Proc. Ent. Soc. Washington 9:12, 115; Hopkins, 1909, U. S. Dept. Agric. Yearbook 1908:574; Hopkins, 1909, U. S. Dept. Agric. Bur. Ent. Bull. 58(5):59; Hopkins, 1909, U. S. Dept. Agric. Bur. Ent. Bull. 83(1):80; Hopkins, 1910, U. S. Dept. Agric. Bur. Ent. Circ. 125:2; Hopkins, 1912, U. S. Dept. Agric. Bur. Ent. Circ. 143:4; Hopkins, 1914, Ent. News 25:133; Brunner, 1914, U. S. Dept. Agric. Bull. 111:4; Swaine, 1914, Dom. Canada Dept. Agric. Expt. Farms Bull., ser. 2, 17:20, 26; Hewitt, 1915, Canada Dept. Agric. Div. Ent. Rept. 1915:29; Swaine, 1916, Can. For. Jour. 12:632; Hopkins, 1917, Jour. Econ. Ent. 10:92; Hopkins, 1919, Sci. Month. 8:506; Burke, 1919, Proc. Ent. Soc. Washington 21:123; Swaine, 1920, Agric. Gaz. Canada 7:642; Brues, 1920, Insects and human welfare, p. 69; Miller, 1921, Timberman 23(1):40; Hopping, 1921, Dom. Canada Dept. Agric. Ent. Br. Circ. 15:7, 11; Hopping, 1922, Canadian Ent. 54:129; Boyce, 1923, U. S. Dept. Agric. Bull. 1140, 7 p.; Boyce, 1923, Timberman 24(7):157; Gibson, 1923, Dom. Canada Dept. Agric. Ent. Br. Rept. 1919-20:16; Baker, 1924, American For. 30:599; Elliott, 1924, Oregon St. For. Rept. 14:43; Evenden and Hopping, 1924, Lumber World Rev. 47:12, 43; Felt, 1924, Manual of Tree and Shrub Insects, p. 255; Hopping, 1924, Canadian Ent. 56:126; Boone, 1925, Timberman 26(7):58; Caverhill, 1925, British Columbia Dept. Lands For. Br. Rept. 1924:E16; Craighead, 1925, Jour. Forestry 23:348; Evenden, 1925, American For. 31:593; Evenden, 1925, Timberman 26(11):63; Craighead, 1927, U.S. Dept. Agric. Circ. 411:5, 6, 8; Keen, 1928, California Dept. Nat. Res. Div. For. Bull 7:33; Craighead, 1930, U.S. Dept. Agric. Misc. Pub. 74:4; Patterson, 1930, U.S. Dept. Agric. Tech. Bull. 195, 19 p.; Evenden, 1930, Northwest Sci. 4:52; Marlatt, 1930, U.S. Dept. Agric. Bur. Ent. Rept. 1930:45; Patterson, 1930, U.S. Dept. Agric. Tech. Bull. 195, 19 p.; Cushman, 1931, Jour. Washington Acad. Sci. 21:301; Weir, 1931, Canada Min. Agric. Rept. 1930-31: 128; Craighead et al., 1931, Jour. Forestry 29:1009; Evenden, 1931, U. S. Dept. Agric. Yearbook 1931:391; Gibson, 1931, Jour. Econ. Ent. 24:575; Hastings, 1931, Outdoor Amer. 10(5):17; Morse, 1931, U. S. Dept. Agric. Yearbook 1931:430; Steiner, 1932, Jour. Agric. Res. 45:437; Marlatt, 1932, U. S. Dept. Agric. Bur. Ent. Rept. 1932:23; Marlatt, 1933, U. S. Dept. Agric. Bur. Ent. Rept. 1933:29; Richmond, 1933, For. Chron. 9:60; Salmon, 1933, California Agric. Month. Bull. 22:135; Swaine, 1933, Sci. Agric. 14:26; DeLeon, 1934, Canadian Ent. 66:51; DeLeon, 1934, Jour. Forestry 32:430; Twinn, 1934, Ent. Soc. Ontario Rept. 65:123; Weaver, 1934, Jour. Forestry 32:100; DeLeon, 1935, Ann. Ent. Soc. America 28:411; DeLeon, 1935, Ent. Amer. 15:59; Rust, 1935, Jour. Econ. Ent. 28:688; Thorne, 1935, Jour. Agric. Res. 51:131; Evenden, 1935, Idaho For. 17:12; Flint, 1935, Northwest Sci. 9(2):5; Strong, 1935, U. S. Dept. Agric. Bur. Ent. Pl. Quar. Rept. 1935:22; Hopping and Mulholland, 1937, For. Res. British Columbia 1937:62; Martin, 1937, American For. 43:122, 144; Bedard, 1938, Jour. Forestry 36:35; Twinn, 1938, Ent. Soc. Ontario Rept. 69:133; Keen, 1938, U. S. Dept. Agric. Misc. Pub. 273:102; Keen, 1939, Rocky Mt. Conf. Ent. Rept. 15:5; Evenden, 1939, Rocky Mtn. Conf. Rept. 15:12; Westveld, 1939, Appl. Silvicult. U. S., p. 398, 418; Evenden and Gibson, 1940, Jour. Forestry 38:271, 275; Ringle, 1940, Sci. American 162:348; Wheeler, 1940, California Cult. 87:636; Annand, 1941, U. S. Dept. Agric. Bur. Ent. Pl. Quar. Rept. 1940:26; Eaton, 1941, Jour. Forestry 39:710; Peirson, 1941, American For. 47:413; Smith, 1941, Jour. Econ. Ent. 34:10; Struble and Carpelan, 1941, man-Pacific Ent. 17:153; Yuill, 1941, Jour. Econ. Ent. 34:702; Craighead, 1942, Smithsn. Inst. Rept. 1940-41:368, 371, 378; Gardiner, 1942, Canada Min. Agric. Rept. 1941:55; Twin, 1942, Ent. Soc. Ontario Rept. 72:55; Struble, 1942, Pan-Pacific Ent. 18:97; Struble, 1942, Jour. Econ. Ent. 35:840; Brown, 1942, Canada Dept. Agric. Div. Ent. For. Ins. Serv. Rept. 6:8; Brown, 1943, Canada Dept. Agric. Div. Ent. For. Ins. Serv. Rept. 7:8; DeGryse, 1943, For. Chron. 19:142; Evenden et al., 1943, U. S. Dept. Agric. Circ. 664, 25 p.; Furniss, 1943, (Trans.)

West. For. Conserv. Assoc. 143:34; Gibson, 1943, Jour. Econ. Ent. 36:396; Offalax, 1943, For. Chron. 19:186; Twinn, 1943, Ent. Soc. Ontario Rept. 73:70; Twinn, 1943, Canada Ins. Pest. Rev. 21:8; Weaver, 1943, Jour. Forestry 41:8; Leech, 1944, Canada Dept. Agric. Div. Ent. For. Ins. Surv. Rept. 1943:63; Evenden and Struble. 1945, U. S. Dept. Agric. Bur. Ent. Pl. Quar. Ins. Pest. Serv. 1944:13; Leech, 1945. Canada Dept. Agric. Div. Ent. For. Ins. Serv. Rept. 1944:64; Hopping and Mathers, 1945, For. Chron. 21:98; Patterson. 1945, Univ. Washington Pub. Biol. 10:147; Annand, 1945, U. S. Dept. Agric. Bur. Ent. Pl. Quar. Rept. 1944:7; Annand, 1946, U. S. Dept. Agric. Bur. Ent. Pl. Quar. Rept. 1945:21; Furniss and Struble, 1946, U. S. Dept. Agric. Bur. Ent. Pl. Quar. Ins. Pest Surv. 1945:20; Gardiner, 1946, Canada Min. Agric. Rept. 1945:75; Leech, 1946, Canada Dept. Agric. Div. Ent. For. Ins. Surv. Rept. 1945:62; Mathers, 1946, Canada Ins. Pest Rev. 24:120; Anderson, 1947, U. S. Dept. Agric. Sec. Rept. 1947:140; Annand, 1947, U. S. Dept. Agric. Bur. Ent. Pl. Quar. Rept. 1946:34; DeGryse, 1947, Forest Entomology in Canada, p. 3; Gardiner, 1947, Canada Min. Agric. Rept. 1946:93; Leech, 1947, Canada Dept. Agric. Div. Ent. For. Ins. Surv. Rept. 1946:79; Richmond, 1947, Canada Ins. Pest Rev. 25:73; Sand and Bryan, 1947, U. S. Dept. Agric. Farmers Bull. 1989:28; Anonymous, 1947, California Dept. Nat. Res. Div. For. Ins. Cond. 1946:9; Anonymous, 1947, U. S. Dept. Agric. Bur. Ent. Pl. Quar. Ins. Pest. Surv. 1946:18; Anderson, 1948, Jour. Econ. Ent. 41:596; Annand, 1948. U. S. Dept. Agric. Bur. Ent. Pl. Quar. Rept. 1947:26; Hoffman and Merkel, 1948, Jour. Econ. Ent. 41:467; MacKay, 1948, Canda Dept. Agric. Div. Ent. For. Ins. Surv. Rept. 1947:93; Hopping and Beull, 1948, For. Chron. 24:141; Anonymous, 1948, U. S. Dept. Agric. Bur. Ent. Pl. Quar. Ins. Pest Surv. 1947:16; Anonymous, 1949, U. S. Dept. Agric. Bur. Ent. Pl. Quar. Ins. Pest Surv. 1948:19; McGuffin, 1949, Canada Dept. Agric. Div. Ent. For. Ins. Surv. Rept. 1948:105; MacKay, 1949, Canada Dept. Agric. Div. Ent. For. Ins. Surv. Rept. 1948:114; Evans, 1950. Canada Dept. Agric. Div. Ent. For. Ins. Surv. Rept. 1949:107; Gardiner, 1950, Canada Min. Agric. Rept. 1949:105; Keen, 1950, Jour. Forestry 48:146; Kenney et al., 1950, British Columbia Lands For. Serv. Rept. 1949:73; McGuffin, 1950, Canada Dept. Agric. Div. For. Ins. Surv. Rept. 1949:100; MacKay, 1950, Canada Dept. Agric. Div. For. Ins. Surv. Rept. 1949: 113, 121; Anonymous, 1950, U. S. Dept. Agric. Bur. Ent. Pl. Quar. Ins. Pest Surv. 1949:25; Beal, 1951, Proc. West. For. Conserv. Assoc. 41:58; Evans and Dyer, 1951, Canada Dept. Agric. Div. Ent. For. Ins. Surv. Rept. 1950:110; Hopping, 1951, For. Chron. 27:26; Kenney et al., British Columbia Dept. Lands For. Serv. Rept. 1950:63; McGuffin and Reid, 1951, Canada Dept. Agric. Div. Ent. For. Ins. Surv. Rept. 1950:99; Ross and Jones, 1951, Canada Dept. Agric. Div. Ent. For. Ins. Surv. Rept. 1950:113, 121, 123; Hopping, 1951, Ent. Soc. Ontario Rept. 81:74; Kolbe, 1951, Proc. West. For. Conserv. Assoc. 41:15; Anonymous, 1951, U. S. Dept. Agric. Bur. Ent. Pl. Quar. Ins. Pest Surv. Sup. 4:5; Anonymous, 1951, U. S. Dept. Agric. Bur. Ent. Pl. Quar. Ins. Pest Surv. 1950:24; Orchard et al., 1952, British Columbia Lands For. For. Serv. Rept. 1951:85; Ross and Jones, 1952, Canada Dept. Agric. For. Ins. Dis. Surv. Rept. 1951:109, 118; Anonymous, 1952, U. S. Dept. Agric. Bur. Ent. Pl. Quar. Div. For. Ins. Econ. Ins. Rept. 1(4):90; Clements, 1953, U. S. Dept. Agric. California For. Range Expt. Sta. For. Res. Notes 89, 5 p.; McGuffin, 1953, Canada Dept. Agric. For. Ins. Dis. Surv. Rept. 1952:116; Richmond, 1953, British Columbia Dept. Lands For. For. Serv. Rept. 1952:86; Ross and Jones, 1953, Canada Dept. Agric. For. Ins. Dis. Surv. Rept. 1952:132; Orr, 1954, U. S. Dept. Agric. Intermtn. For. Range Expt. Sta. For. Ins. Cond. 1953:2; Ross, 1954, Canada Dept. Agric. For. Ins. Dis. Surv. Rept. 1953:141; Kinghorn, 1955, Jour. Econ. Ent. 48:501; Reid, 1955, Canadian Ent. 87:316; Silver and Ross, 1955, Canada Dept. Agric. For. Ins. Dis. Surv. Rept. 1954:118; Struble and Johnson, 1955, U. S. Dept. Agric. For. Pest Leaflet 2, 4 p.; Anonymous, 1955, U. S. Dept. Agric. For. Serv. Imp. For. Ins. 1954:3, 7; Anonymous, 1955, U. S. Dept. Agric. Pac. N. W. For. Range Expt. Sta. For. Ins. Rept. 1954:26, 37; Gardiner, 1955, Canada Min. Agric.

Rept. 1954:16; Anonymous, 1955, For. Pest. Control Act. Comm. For. Ins. Cond. California 1954:6; Bailey, 1956, U. S. Dept. Agric. Intermtn. For. Range Expt. Sta. Rept. 1956:30, 37; Jemison, 1956, U. S. Dept. Agric. California For. Range Expt. Sta. Rept. 1955:5, 45, 50; Moreno Noriega, 1956, Fitofilo 9(15):20, 23, 25, 28, 31; Ostmark and Wilford, 1956, U. S. Dept. Agric. Rocky Mtn. For. Range Expt. Sta. Paper 22:5, 13; Price, 1956, U. S. Dept. Agric. Rocky Mtn. For. Range Expt. Sta. Rept. 1956:81; Silver and Ross, 1956, Canada Dept. Agric. For. Ins. Dis. Surv. Rept. 1955:94; Hay, 1957 (1956), Ann. Ent. Soc. America 49:567; Khan, 1957, Canadian Jour. Zool. 35:519; Whiteside, 1957, U. S. Dept. Agric. Pacific N. W. For. Range Expt. Sta. For. Ins. Cond. 1956:2, 13, 31, 43.

Dendroctonus jeffreyi Hopkins, 1909, U. S. Dept. Agric. Bur. Ent. Tech. ser. 17(1):114 (*new synonymy*); Hagedorn, 1910, Coleopterorum Catalogus 4:20; Hagedorn, 1910, Genera Insectorum 111:60; Chamberlin, 1939, Bark and Timber Beetles of North America, p. 159; Chamberlin, 1958, Scolytoidea of the Northwest, p. 72. Biol.: Hopkins, 1909, U. S. Dept. Agric Bur. Ent. Bull. 83:101; Hopkins, 1909, U. S. Dept. Agric. Yearbook 1909: 574; Hopkins, 1912, U. S. Dept. Agric. Bur. Ent. Circ. 143:5; Burke, 1919, Proc. Ent. Soc. Washington 21:123; Hopping, 1922, Canadian Ent. 54:130; Patterson, 1923, Timberman 24(9):156; Felt, 1924, Manual of Tree and Shrub Insects, p. 256; Craighead, 1927, U. S. Dept. Agric. Circ. 411:8; Keen, 1928, California Dept. Nat. Res. Bull. 7:37; Craighead, 1930, U. S. Dept. Agric. Misc. Pub. 74:5; Craighead et al., 1931, Jour. Forestry 29:1016; Keen, 1938, U. S. Dept. Agric. Misc. Pub. 273:107; Patterson, 1945, U. S. Dept. Agric. Bur. Ent. Pl. Quar. Ins. Pest Surv. 1944:14; Anonymous, 1947, California Dept. Nat. Res. Div. For. For. Ins. Cond. 1946:9; Anonymous, 1949, U. S. Dept. Agric. Bur. Ent. Pl. Quar. Ins. Pest. Surv. 1948:20; Anonymous, 1951, U. S. Dept. Agric. Bur. Ent. Pl. Quar. Ins. Pest Surv. Sup. 4:8; Anonymous, 1952, U. S. Dept. Agric. Bur. Ent. Pl. Quar. Coop. Econ. Ins. Rept. 1(Sup. 4):94; Anonymous, 1955, U. S. Dept. Agric. For. Serv. Imp. For. Ins. 1954:3; Anonymous, 1955, California For. Pest Control Act. Comm. For. Ins. Cond. 1954:6; Eaton, 1956, U. S. Dept. Agric. For. Serv. For. Pest Leaflet 11, 7 p.; Anonymous, 1957, U. S. Dept. Agric. Pl. Pest Control Div. Coop. Econ. Ins. Rept. 7:864.

This distinctive species appears to be more closely allied to *adjunctus* than to others in the genus, but is readily distinguished by the absence of lateral frontal elevations and a median groove, by the opaque surface of the elytral declivity, by the impressed declivital striae, by the stout body, and, in part, by the distribution (Fig. 52).

Male.—Length 3.7-7.5 mm. (average about 5.5; size evidently dependent on moisture conditions regulated by thickness of bark of host tree), 2.3 times as long as wide; mature body color black.

Frons convex from eye to eye, from vertex to epistoma, median line narrowly impressed above upper level of eyes, rather broadly protrubrant over an indefinite median area below upper level of eyes, often with remnants of a narrowly impressed median line; epistomal margin elevated, its surface smooth and shining; epistomal process half as wide (0.50 times) as the distance between eyes, its arms oblique (about 30° from the horizontal) and elevated along their median halves, the horizontal portion about half its total width, transversely concave, overlapping and ending just above epistomal margin and bearing under its distal margin a dense brush of conspicuous yellowish setae; surface punctate-rugulose above eyes, coarsely, rather deeply punctured and subgranulate below. Vestiture, in addition to epistomal brush, rather long, sparse, inconspicuous.

Pronotum 1.4 times as wide as long, widest at base; sides feebly arcuate, almost straight on basal two-thirds, converging slightly toward the well developed constriction just behind the broadly, shallowly emarginate anterior margin; surface smooth, shining, with very close, rather small, moderately deep punctures (variable), becoming granulose laterally; a median line feebly indicated, more prominent anteriorly. Vestiture scanty, usually evident only at sides.

Elytra 2.1 times as long as pronotum; sides straight and subparallel on basal two-thirds, rather broadly rounded behind; basal margins arcuate and bearing a row of about nine, moderately large, raised, overlapping crenulations, with several smaller submarginal ones particularly on interspaces two and three; striae weakly impressed. the punctures rather small, rather deep; interstriae about twice as wide as striae and armed by rather coarse, confused, transverse crenulations, each averaging about half the width of an interspace. Declivity rather steep, convex, with interspace two rather strongly impressed; striae rather narrowly impressed, the punctures smaller than on disc; striae one slightly, two rather strongly, three very strongly curved toward suture; interstriae usually at least slightly convex, minutely rugulose, dull, the punctures fine, confused, distinct to obscure or subgranulate; each interspace with a sparse, more or less definite median row of rather large granules. Vestiture scanty, longer and more conspicuous on declivity, longest setae slightly longer than a distance equal to width of an interspace.

Female.—Very similar to male, but evidently epistomal process less well developed, and elytral crenulations and declivital granules a little larger.

Type locality.—Spearfish, South Dakota (Kootenai, Idaho, for *monticolae;* and Little Yosemite, California, for *jeffreyi*). The types of all three descriptions were studied.

Hosts.—Pinus albicaulis, balfouriana, contorta, coulteri, edulis, flexilis, jeffreyi, lambertiana, monophylla, monticola, murrayana, ponderosa, and strobiformis. During an epidemic it was recorded from *Picea engelmanni.*

Distribution.—Southern British Columbia to the Black Hills of South Dakota. and south to northern Mexico.

Specimens from the following localities were examined (Fig. 52). ARIZONA: Chiricahua Mts., "Crook N. F.," Flagstaff, Fredonia, Kaibab N. F., and San Francisco Mts. CALIFORNIA: "Alder Ck.," Anthony Ck., Bass Lake, Bear Ck. R. S., Ben Lomond, Big Bear Lake, Big Bend, Big Meadows, Blacks Mt., Blue Canyon, Bray, Bunnel, Burnt Corral Meadows, Butte Lake, Carrville, "Cassidy Ridge," Cecilville, Chester, "Chiquito Basin," Clover Valley, Coulterville, Cow Ck., Crestline, Crocker R. S., Deep Ck., Dorrington, Duck Lake, Eagleville, Echo Lake, Eiler Lake, Facht, Fallen Leaf Lake, Favingers Camp, Fawn Ck., Floriston, Ft. Jones, Fulda, "Gasquet R. S.," General Grant N. P.,

Fig. 52. Probable geographical distribution of *Dendroctonus ponderosae* with collection sites indicated.

Gordon Meadow, "Grant Pk.," Grassy Lake, "Gray Meadows," "Gray Mesa," Hackamore, Haeckle's, Hat Ck., Hoffman, Hope Valley, "Huckleberry Meadow," Hume, Huntington Lake, Inyo Co., Idyllwild, "Kangaroo R. S.," Kern Co., King's Ck. Rd., Kyburz, Laguna Mt., Lake Almanor, Lake Arrowhead, Lake Ostrander, Lake Tahoe, Lake Valley R. S., Lamoine, "Leland Meadow," Lemon Canyon, Lion Meadow, "Little Kern," Little Shasta, Little Yosemite, Lloyd Meadows, Lookout, Lush Meadows, Mammoth, Mariposa Grove, Massack Mill, Mather, McCloud, "McCreary," Medicine Lake, Miami R. S., Middle Fk. Eel River, "Millwood," Mineral, Moffit Ck., Mohawk, Moraine, Mt. Brewer, Myers, Nevada City, North Fork, Norval Flats, Ockenden, Onion Valley, "Painted George," Pinecrest, Placerville, Plantation, Pollock Pines, Pyramid R. S., Robbers Ck., "Round Meadow," "Samson Flat," San Bernardino Mts., San Gabriel Canyon, "Saples Flat," "Scoffold," "Self R. S.," Sequoia N. P., Shaver, Sisson, "Snowline Camp," Soda Springs, "Soquel Basin," "Squaw Dome," Stirling City, "Summerdale," Summit Lake,. "Swaines," Tallac, Tenaya Lake, Three Rivers, Timber Mt., Tioga Rd., Trinity N. F., Wawona, "Willow Meadows," Willow Ranch, "Woodward Ck.," "Wright's Lake," Yreka, and Yuba Gap. Colorado: Bailey, Brookvale, Cascade, "Cat Mt.," Cuchetopa, Durango, Eagle, Elictra Lake, Estes P., Florissant, Ft. Garland, Glenwood Springs, Gunnison N. F., Gould, Green Mt. Falls, Hahns Pk., Husted, Idaho Springs, "Indian Ck.," Jones Ranch, "Kennedy Sta.," Larkspur, Las Animas, La Veta, Longs Pk., Manitou, Medicine N. F., Meeker, Monte Vista, Montrose, Montezuma N. F., "Ouray N. F.," Pogosa Springs, Palmer Lake, Pikes Pk., Pine, Pingre Pk., Poncho Springs, Porter, Saguache, San Isabel, San Juan Co., San Juan N. F., Uncompahgre N. F., "Ute Pass," Westcliffe, and White River N. F. Idaho: Cedar Mt., Centerville, Coeur d'Alene, Coeur d'Alene N. F., Collins, Kootenai, "Moscow Mts.," Sandpoint, Smith's Ferry, and Weiser. MONTANA: Apgar, Bigfork, Blackfeet Indian Res., Columbia Falls, Helena, "Iron Mt.," Lame Deer, Lewis and Clark N. F., Logan Pass, Lolo, Madison N. F., Missoula, Saltese, and Sula. NEVADA: Baker, Crystal Bay, Glenbrook and Las Vegas. NEW MEXICO: Gila N. F., Tres Ritos, and Vermejo P. OREGON: Ashland, "Auburn," Austin, Baker, Bly, Buck Lake, Cold Springs, Crater Lake N. P., Diamond Lake, Elk Ck., "Ferris Ranch," Grants Pass, Haines, "Highland Mine," Joseph, Keno, Klamath Falls, Klamath Indian Res., "Loves Sta.," Meryl Ck., North Powder, Ochoco N. F., Pinehurst, "Pokegama," Round Lake, Sparta, Sumpter, and Wallowa. SOUTH DAKOTA: Black Hills, Custer, Deadwood, Elmore, Hill City, Lead, Nemo, Piedmont, and Sylvan Lake. UTAH: Ashley N. F., Bryce Canyon N. P., Duck Lake, Escalante, Kamas, Logan Canyon, Manti-LaSal N. F., Panguitch Lake, Uintah and Ouray Indian Res., Wasatch Mts., and Wasatch N. F. WASHINGTON: Crescent Lake, Dayton, Fairfax, "Kamiak Butte," Longmire Spring, Metaline Falls, Moran, Mt. Rainier, Mt. Rainier N. F., Northport, "Pialschie," Pullman, Randle, Seattle, Spokane, Washington N .F., and White River. WYOMING: Bear Lodge in Black Hills N. F., "Downington," Elk Mt., Encampment, Fremont Lake, "Keystone," North Fork, and Wapiti. ALBERTA: Edmonton. BRITISH COLUMBIA: Adams Lake, Alleyne Lake, Arrowhead, Aspen Grove, Babine Lake, Blue River P. O., Big Loon Lake, Cowichan Lake, Downie Ck., Forester Ck., Frances Ck., Grand Forks, "Hope Mts.," Kamloops, Kootenay N. P., Little Fish Ck., Little Shuswap Lake, Midday Valley, Morrison Lake, Mud Lake, Na Kusp, "Nehalliston For.," Peachland, Princeton, Puntchesakut Lake, Revelstoke, Seymour Narrows, Shuswap Lake, Steamboat Mt., Sugar Lake, Sugarloaf Mt., Takla Lake, Tarnezell Lake, "Trepan Ck.," Trout Lake, Upper Arrow Lake, Whitetail Lake, Windermere, and Yoho N. P. BAJA CALIFORNIA: Sierra San Pedro Martir.

Geographical variation.—Specimens from the southeastern parts of the range tend to average considerably larger than specimens from the northwestern areas. The explanation for this, however, appears to be at least partly environmental rather than genetic, since most of the specimens from southeastern areas are from *Pinus ponderosa*, a host in which greater size is normally attained from all areas, while those from the northwestern areas are mostly from other host species. It was apparent after examining numerous series from the various host species that a particular average size was more or less characteristic of a host species. The average size in a particular tree appeared to be correlated with the average thickness of the bark of the host.

There are conspicuous differences in the size and depth of pronotal punctures in almost any series. In specimens from California they tend to average much smaller and shallower than from other areas. This variation in California appears to be associated with geographical origin, intensifying gradually from north to south (Lassen N. F. to the Yosemite area), rather than with host as reported by Hopkins (1909a:71), since large specimens with very small shallow punctures, the distinguishing features of Hopkins' *jeffreyi*, can be found in series from any host of this species in California.

BIOLOGY.—This has been referred to (Craighead et al., 1931: 1009) as the most destructive species of *Dendroctonus*. Estimates of losses in our timber resources due to this insect are scattered, conflicting and confused by the fact that this species has been known concurrently by three separate scientific names. Considering all factors, the average annual loss attributed to it since 1895 possibly may approach two billion board feet.

For the most part the winter is passed as second and third instar larvae, although a few parent adults may survive hibernation and a few larvae may reach the prepupal stage. Activity is resumed in the spring whenever temperatures become sufficiently high, probably about 50°F. A small fraction of the overwintered parent adults may resume egg laying activity in the spring, but usually most of them extend their galleries without ovipositing; very few of them re-emerge. Ordinarily by mid-June half of the immature stages have pupated (Blackman, 1931:14) and by mid-July most have matured. The young adult beetles do not emerge immediately from the brood tree, but enlarge the pupal chamber, often removing sufficient of the inner bark that their excavations join one another. One of these enlarged chambers may contain as many as 50 beetles. The period of flight is concentrated, seldom beginning before July 15 and rarely continuing later than August 25. In those areas of California where more than one generation occurs each year there may be notable departures from the usual activity cycle. Whether these deviations are the result of genetic or ecological factors is uncertain.

Trees selected for attack by endemic populations of this insect usually are overmature or weakened standing trees larger than six inches D. B. H. Windfalls or cull logs occasionally may provide favorable breeding places (Evenden, 1943:7), particularly when the bole is inclined. During epidemics the more vigorous, rapidly growing trees may be preferred (Beal, 1939:2), and coniferous host species not belonging to the genus *Pinus* may be attacked. Under endemic conditions the area of a particular tree attacked by this species may be restricted or forced upward from the base of the bole by such competing species as *adjunctus*, or downward from upper parts of the bole by *brevicomis*. Under endemic conditions in a given area the local population may exhibit a strong preference for one host species even though other acceptable host species may be intermixed. The preferred host in a given area may be Ponderosa, Lodgepole, Limber, Western white, Jeffrey or other pine species. In a given area during an epidemic any acceptable host, or sometimes any conifer, may be attacked, but following the epidemic the attacks may or may not be confined to the same host species originally favored. Climatic factors or competition usually re-establish the original conditions, however. These local races perhaps may indicate the existence of genetic factors that could lead to the formation of distinct species of beetles, but all available data suggests that the present stage of their evolution has not reached the point where geographical races (subspecies) can be recognized.

The attack evidently may follow either of two patterns depending on the age and vigor of the host tree and on the presence or absence of certain competing species of bark beetles. In mature sugar pine where aggressive competing species are virtually absent, the attack usually begins in the upper crown; the lower sections of the tree may then be attacked by one or more successive generations over a period of two or more years (Evenden, 1943:9). In younger trees of this and other species the attack usually begins at or near the base and extends upward. Compared to other species the attack is concentrated into a relatively short period of time. It coincides with the period of emergence from about July 15 to August 25, seldom requiring more than five weeks and possibly requiring as little as three or four days during an epidemic. The beetles strike the tree individually, not in dense swarms as some popular accounts of the attack might suggest. According to Blackman (1931:21) the number of entrance tunnels per square foot of bark surface of a successful attack on an average tree ranges from about four to nine. He also observed that the number of attacks was higher in trees where four to nine trees were killed in a group (5.90 per sq. ft.) than where only one to four trees were killed in a group (5.23 per sq. ft.

The vertical linear egg galleries (Fig. 53) usually are almost straight, although occasionally an environmental peculiarity may cause some to wind slightly. They are constructed primarily in the soft inner bark or phloem, continually in contact with the cambium and very lightly scoring the wood.

The diameter of an individual egg gallery is slightly greater than the width of the beetle which constructed it. Its length varies considerably, but evidently it depends more on enivronmental than on hereditary factors. In Lodgepole pine on the Wasatch National Forest in Utah, 35 egg galleries selected at random averaged 32.6 cm., the maximum length was 67.5 cm.; in Ponderosa pine on the Dixie National Forest in Utah, 35 egg galleries averaged 47.5 cm., the maximum length was 79.0 cm. Both series of measurements were made in drought areas in July 1960. In June of 1961 similar measurements made in Jeffrey pine on the Tahoe National Forest in California, averaged 41.7 cm. for 35 galleries, with the maximum length 66.0 cm. Measurable galleries in Ponderosa pine in California and Oregon and in Western white pine in Oregon gave comparable results, but were too few in number to provide reliable data. Presumably the character of galleries observed during a severe epidemic of this species in the Black Hills area led Hopkins (1909a: 112) to assume that a completely different species existed in that area as compared to an endemic Pacific Coast form which apparently constructed much longer galleries. Actually, under endemic conditions in comparable environments, the eastern, western, northern and southern populations appear indistinguishable when measurements, bark samples or photographs of gallery systems are compared.

The initial attack is made by the female, usually in a crevice of the bark. About the time she reaches the cambium tissues where the pitch begins to flow she is joined by the male who then assists her by pushing the excavated frass out of the entrance hole. Continuation of the egg gallery is performed entirely by the female

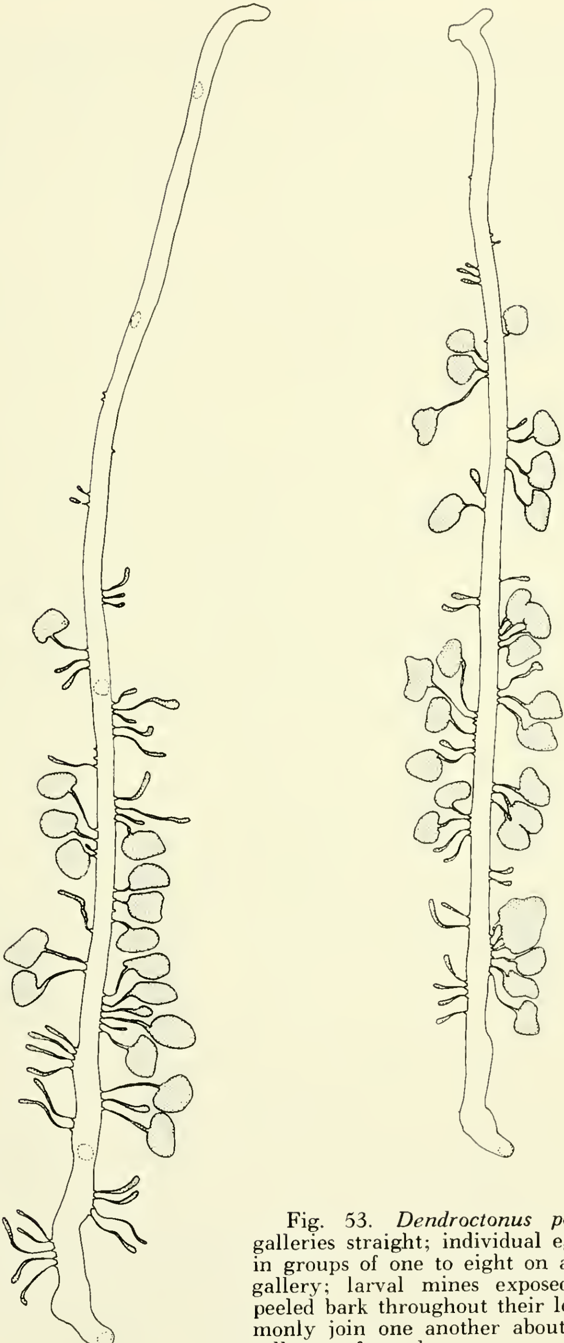


Fig. 53. *Dendroctonus ponderosae*: Egg galleries straight; individual egg niches placed in groups of one to eight on alternate sides of gallery; larval mines exposed on surface of peeled bark throughout their length, they commonly join one another about the time pupal cells are formed.

beetle. After several centimeters of gallery have been cleared and the frass ejected from the entrance hole, the male then packs the frass in the lower regions of the gallery thereby closing the entrance hole and tightly filling the gallery except for a few centimeters in the area where the beetles are working. It is not uncommon, following mating, for the male to leave the gallery, either before the entrance is blocked or through a ventilation tunnel, in order to join a second female.

From the entrance hole the gallery usually ascends diagonally about three to five centimeters before turning directly upward. In about half of the gallery systems studied this diagonal portion extended to the right of the entrance hole, about a third went to the left, and in the remainder the diagonal portion was absent. This oblique part of the tunnel ordinarily is more irregular in width than the remainder of the egg tunnel and ordinarily is sufficiently wide to permit turning or to act as a nuptial chamber. Ventilation tunnels usually are placed at irregular intervals along the egg gallery, but are not always present. Their presence appears to be related to the stage of gallery construction, to the thickness of the bark, and to the activity of the beetles. Evidently they are not constructed until after the entrance has been plugged. In thin barked Lodgepole pine 18 of the 35 galleries measured (see above) included ventilation chambers, of these 18 only three contained more than two ventilation tunnels, the maximum number was four in one gallery. In the relatively thick-barked Ponderosa pine 33 of the 35 galleries measured (see above) included ventilation tunnels and only three of the 33 included fewer than five; the maximum number in one gallery was 13.

The initial part of gallery construction progresses rapidly. Oviposition usually begins when the gallery is about one or two centimeters above the oblique portion, probably about four to five days after the attack. Egg-laying evidently continues until interrupted by cold weather. The eggs are deposited individually in comparatively small niches, although it is not uncommon for two eggs to be in one niche.

Egg niches are comparatively small, each is just large enough to accommodate an egg and a very small amount of specially prepared frass. The niches are both narrower and more shallow than those of the foregoing species. They are distributed in a pattern peculiar to this species, with alternating groups of one to eight niches placed along the sides next to the cambium. The size and spacing of these groups varies tremendously from gallery to gallery and even within the same gallery, depending upon the prevailing environmental conditions. Ordinarily about half of these "groups" consist of one niche each, seldom do they exceed five in number. It is not uncommon for one or two niches to occur opposite one of these groups, a departure from their strictly alternate arrangement. In a third of the galleries studied there were no niches in the upper or last half of the gallery; in an additional one-tenth there were none in the last third. When niches occurred in the terminal regions of the gallery it appeared, in many cases, that the adult female either abandoned the gallery prior to the onset of cold weather or died before or during the winter months.

Following oviposition the parent beetles may continue the gallery, often ending it in a somewhat irregular feeding tunnel, or they may abandon the gallery in order to commence a new attack. Evenden (1943:12) estimated that 10 to 30 percent of the parent adults from sugar pine and almost 100 percent of those from western white pine re-emerged in order to begin a second attack. These values appear to be higher than the estimated re-emergence rate observed during this study, but support the observation that there is a greater tendency for re-emergence to occur when the bark of the host tree is either comparatively thin or subject to rapid drying for various other reasons.

The length of the incubation period has not been determined precisely, but has been estimated by various workers to require about seven to ten days. The larval mines are continuously in contact with the cambium and are somewhat irregular, but usually their main axis tends to be perpendicular to the egg gallery. Their length varies considerably with the amount of moisture or crowding present. They may be only one or two centimeters in length, increasing very slightly in width before reaching the suddenly expanded irregular feeding area where the last two or three instars and pupation are passed, or they may extend 10 or 20 centimeters and increase substantially in width before the pupal cell is encountered. It is not uncommon to find both extremes in the same system of galleries. The larvae may pass the winter in any instar, but apparently second and third instar larvae predominate. Because of overwintering in this stage and, since only one generation occurs each year, the average length of the larval period is near 300 days. During the latter part of the larval period a pupal cell is cleared of the frass in the enlarged feeding area, still in contact with the cambium. Here the prepupal and pupal stages are passed, the latter evidently requiring about two to four weeks for completion. A maturation period of about one month usually follows the pupal stage before emergence occurs.

Dendroctonus aztecus, new species

Figs. 24-26, 54.

Dendroctonus adjunctus: Gibbson and Carrillo, 1959, Sec. Agric. Ganderia Foll. Misc. 9:141.

It is presumed that many of the records published as *adjunctus* since Blandford's description refer, at least in part, to this species.

Superficially this species appears to be more closely allied to certain species of *Blastophagus*, *Pachycotes*, *Hylurgus* and *Hylurgonotus* than to other species of *Dentroctonus* and, in many respects, appears to resemble the hypothetical ancestor of this genus. Although definitely more primitive, it is, however, rather closely allied to *terebrans* from which it differs by the flat epistomal process, by the more broadly, evenly convex frons, by the subcylindrical pronotum without a conspicuous anterior constriction, by the more coarsely sculptured elytral disc, and by the distribution (Fig. 54).

Male.—Length 5.5 mm. (paratypes 5.2-6.9), 2.65 times as long as wide; mature body color black.

Frons almost uniformly convex between eyes from vertex to epistomal process, with a small, rather indefinite median impression on lower third well above base of epistomal process; epistomal margin elevated, its surface smooth and shining; epistomal process slightly narrower than half (0.44 times) the distance between eyes, its lateral margins oblique (about 45° from the horizontal) and not at all elevated, the horizontal portion slightly more than half its total width, flat, overlapping and very slightly exceeding epistomal margin and bearing under its distal margin a dense brush of conspicuous yellowish setae; surface rather coarsely, closely, deeply punctured with rather abundant, isolated granules interspersed. Vestiture, in addition to epistomal brush, moderately long, sparse, inconspicuous.

Pronotum 1.2 times as wide as long, widest on basal half; sides weakly arcuate, almost subparallel on basal half, then converging gradually to the rather poorly developed transverse constriction just behind the broadly, shallowly emarginate anterior margin; surface smooth and shining with moderately small, close, rather deep punctures, becoming rather shallow laterally and very minutely granulate on lateral rim; a median line obscurely indicated anteriorly. Vestiture scanty, becoming more abundant, longer, and rather coarse anteriorly and laterally.

Elytra 2.3 times as long as pronotum; sides straight and subparallel on basal two-thirds, rather broadly rounded behind; basal margins arcuate and bearing a row of nine, moderately large, raised, overlapping crenulations, with several smaller submarginal ones particularly on interspaces two and three; striae weakly impressed, the punctures rather small and moderately deep; interstriae almost twice as wide as striae and armed by abundant, confused, transverse crenulations, each averaging about two-thirds the width of an interspace, a few wider than an interspace and sometimes crossing striae. Declivity steep, uniformly convex; striae one to three straight, the punctures almost as large as on disc; interstriae one to three about equal in width and bearing rather abundant, somewhat confused (usually arranged in widely staggered single row), moderately large tubercles. Vestiture much longer and more abundant on declivity, a few setae twice as long as width of an interspace.

Female.—Similar in all respects to male except pronotum evidently a little more coarsely punctured and the elytra somewhat more coarsely sculptured.

Type locality.—San Raphael, Mexico, Mexico.

Hosts.—*Pinus leiophylla* and *Pinus* sp.

Distribution.—Central Mexico (Sinaloa) to Guatemala (Fig. 54).

Type material.—The male holotype, female allotype and one paratype were taken at the type locality on September 11, 1949, from *Pinus leiophylla*, by J. P. Perry, Jr., collection no. 49-16028. Five paratypes were taken at Tlalmanalco, Mexico, on January 8 and April 16, 1950, from the same host, by the same collector; two paratypes were taken at Uruapan, Michoacan, Mexico, July 12; one paratype was taken 20 mi. N. E. Copala, Sinaloa, Mexico, by S. L. Wood, from *Pinus;* and eight paratypes are labeled "Guatemala, C. A., *Pinus*, Hopk. U. S. 9929 Gl."

Fig. 54. Probable geographical distribution of *Dendroctonus aztecus* with collection sites indicated (only two of the eight Guatemala records could be verified).

The holotype, allotype and seven paratypes are in my collection; the remaining paratypes are in the California Academy of Sciences and in the U. S. National Museum.

The Guatemala locations marked on the distribution map for this species are listed under *adjunctus*. At least some and possibly all of the series taken in Guatemala included this species: part of the series in question were unavailable for this study.

Geographical variation.—Not observed in the limited material at hand.

Dendroctonus terebrans (Olivier)

Figs. 14, 29, 38, 55.

Scolytus terebrans Olivier, 1795, Entomologie 4(Gen. 78):6.

Dendroctonus terebrans: Erickson, 1836, Archiv f. Naturgesch. 2(1):53; Lacordaire, 1866, Genera des Coleopteres 7:360; Zimmerman, 1868, Trans. American Ent. Soc. 2:149; Leconte, 1868, Trans. American Ent. Soc. 2:173; Chapuis, 1869, Synopsis des Scolytides, p. 35 (reprint of 1873, Mém. Roy. Soc. Sci. Liége, ser. 2, 3:243); Leconte, 1876, Proc. American Philos. Soc.

15:384; Schwarz, 1878, Proc. American Philos. Soc. 17:469; Hopkins, 1906, Proc. Ent. Soc. Washington 7:81; Hopkins, 1909, U. S. Dept. Agric. Bur. Ent. Tech. ser. 17(1):147; Provancher, 1877, Fauna Ent. Canada 1:572; Provancher, 1878, Fauna Ent. Canada 1(Add. et Cor.):13, 14; Schwarz, 1886, Ent. Americana 2:56; Schwarz, 1888, Proc. Ent. Soc. Washington 1:80; Dietz, 1890, Trans. American Ent. Soc. 17:28, 29; Blandford 1897, Biol. Centr.-Americana, Coleopt. 4(6):146; Hopkins, 1899, Proc. Ent. Soc. Washington 4:343; Smith, 1900, Cat. Ins. New Jersey, p. 364; Hopkins, 1905, Proc. Ent. Soc. Washington 7:81, 145, 147; Snow, 1907, Trans. Kansas Acad. Sci. 20(2):64; Swaine, 1909, New York St. Mus. Bull. 134:100; Blatchley and Leng, 1916, Rhynchophora or weevils of N. E. America, p. 654; Hagedorn, 1910, Colopterorum Catalogus 4:23; Hagedorn, 1910, Genera Insectorum 111:60; Hopkins, 1915, U. S. Dept. Agric. Bur. Ent. Tech. ser. 17(2):211; Beal and Massey, 1945, Duke Univ. School For. Bull. 10:80; Chamberlin, 1939, Bark and timber beetles of North America, p. 167. Biol.: Thomas, 1876, Nox. Ins. Illinois Rept. 1:146; Smith, 1877, Insects that Infest Shade Trees, etc., p. 55; Packard, 1887, U. S. Dept. Agric. Ent. Comm. Bull. 7:177; Packard, 1890, U. S. Dept. Agric. Ent. Comm. Rept. 5:721, 853; Hopkins, 1893, West Virginia Agric. Expt. Sta. Bull. 31:143, 32:213; Hopkins, 1894, Canadian Ent. 26:280; Hamilton, 1895, Trans. American Ent. Soc. 22:346, 378; Hopkins, 1899, U. S. Dept. Agric. Div. Ent. Bull. 21:27; Hopkins, 1899, West Virginia Agric. Expt. Sta. Bull. 56:392, 415, 421; Chittenden, 1899, U. S. Dept. Agric. Div. For. Bull. 22:56; Lugger, 1899, Minnesota Agric. Expt. Sta. Bull. 66:317; Felt, 1901, Forest, Fish and Game Comm. Rept. 7:480; Hopkins, 1901, U. S. Dept. Agric. Div. Ent. Bull. 28:pl. 12; Smith, 1901, Ent. News 12:92; Felt, 1902, U. S. Dept Agric. Div Ent. Bull. 31:64; Ulke, 1902, Proc. U. S. Natl. Mus. 25:36; Hopkins, 1902, U. S. Dept. Agric. Div. Ent. Bull. 32:10; Hopkins, 1904, U. S. Dept. Agric. Div. Ent. Bull. 48:pl. 7; Felt, 1906, New York St. Mus., Mem. 8, 2:333, 338, 342; Hopkins, 1909, U. S. Dept. Agric. Bur. Ent. Bull. 58:62; Hopkins, 1909, U. S. Dept. Agric. Bur. Ent. Bull. 83(1):146; Blackman, 1922, Mississippi Agric. Expt. Sta. Tech. Bull. 11:56; Felt, 1924, Manual of Tree and Shrub Insects, p. 262; Nelson and Beal, 1929, Phytopath. 19:1102; Craighead et al., 1930, U. S. Dept. Agric. Misc. Pub. 74:4; Craighead, 1935, U. S. Dept. Agric. Misc. Pub. 209:136; Adams, 1937, Arborists News 2(5):3; Friend, 1942, Yale Univ. School For. Bull. 49:145; Felt and Bromley, 1942, Jour. Econ. Ent. 35:170; Felt and Bromley, 1944, Jour. Econ. Ent. 37:213; O'Byrne, 1946, Virginia Agric. Ext. Circ. 403:1, 7; Anderson, 1947, Texas For. Serv. Bull. 33:7; Anonymous, 1951, U. S. Dept. Agric. Bur. Ent. Pl. Quar. Ins. Pest Surv. Sup. 4:8; Beal et al., 1952, Duke Univ. School For. Bull. 14:50; Hoyt, 1952, U. S. Dept. Agric. Bur. Ent. Pl. Quar. Rept. 1950-51:16; Anonymous, 1952, U. S. Dept. Agric. Bur. Ent. Pl. Quar. Coop. Econ. Ins. Rept. 1(Sup. 4):93; Cross, 1953, South. Lumberm. 187(2336):34; Hoyt, 1953, U. S. Dept. Agric. Bur. Ent. Pl. Quar. Rept. 1951-52:40; Lee and Smith, 1953, Proc. Assoc. South. Agric. Workers 50:105; Barker and Nettles, 1954, South Carolina Agric. Ext. Circ. 239(rev.):6; Hoyt, 1954, U. S. Dept. Agric. Bur. Ent. Pl. Quar. Rept. 1952-53:22; Jackson et al., 1954, For. Dis. Ins. Georgia's Trees, p. 26; Smith, 1954, South. Lumberm. 189(2369):155; Smith, 1954, Proc. South. Agric. Workers 51:100; Briegleb, 1955, U. S. Dept. Agric. South. For. Expt. Sta. Rept. 1954:68; Demmon, 1955, U. S. Dept. Agric. S. E. For. Expt. Sta. Rept. 1954:74; Flory et al., 1955, South Carolina Agric. Ext. Bull. 116:8; Lee and Smith, 1955, U. S. Dept. Agric. South. For. Expt. Sta. Res. Notes 76, 2 p.; Ostrow, 1955, Proc. Conf. For. Tree Improv. 3:104; Smith, 1955, Proc. South. Agric. Workers 52:99; Anonymous, 1955, U. S. Dept. Agric. For. Serv. Mor Imp. For. Ins. 1954:14; Bennett, 1955, Texas For. Serv. Circ. 43:2, 8; Bennett, 1956, U. S. Dept. Agric. South. For. Expt. Sta. For. Rptr. 10:10; Briegleb, 1956, U. S. Dept. Agric. South. For. Expt. Sta. Rept. 1955:50; Demon, 1956, U. S. Dept. Agric. S. E. For. Expt. Sta. Rept. 1955:74; Jordan and Dyer, 1956, Georgia Agric. Ext. Circ. 404, 12 p.; Merkel and Kowal, 1956, U. S. Dept. Agric. S. E. For. Expt. Sta. Paper 67:4; Walker, 1956, Georgia For. Res. Counc. Rept. 2:1, 3, 7;

Livingston et al., 1956, Alabama Rept. 64/65:55; Briegleb, 1957, U. S. Dept. Agric. South. For. Expt. Sta. Rept. 1956:67; McCambridge and Kowal, 1957, U. S. Dept. Agric. S. E. For. Expt. Sta. Paper 76:4; Pechanec, 1957, U. S. Dept. Agric. S. E. For. Expt. Sta. Rept. 1956:41; Smith, 1957, Jour. Econ. Ent. 50:241; Smith and Lee, 1957, U. S. Dept. Agric. For. Serv. For. Pest Leaflet 12, 7 p.; Anonymous, 1957, U. S. Dept. Agric. South. For. Expt. Sta. South. For. Rptr. 16:4.

This species is very closely related to *valens*, but is readily distinguished by the black body color, by the much larger punctures on the lateral areas of the pronotum, by the larger, more abundant declivital tubercles, and, in part, by the distribution (Fig. 55).

Male.—Length 5.0-8.0 mm. (average about 6.5), 2.3 times as long as wide; mature body color dark brown to black.

Frons rather evenly convex, with a shallow median impression about a third of distance from upper level of eyes to epistomal margin, very feebly elevated lateral to impression; epistomal margin elelevated, its surface smooth and shining; epistomal process broad, about half as wide (0.50 times) as distance between eyes, its arms oblique (about 30° from the horizontal), elevated only at median angles of arms, the horizontal portion about two-thirds its total width and broadly, transversely concave, overlapping and ending just above epistomal margin and bearing under its distal margin a dense brush of yellowish setae. Vestiture, in addition to epistomal brush, moderately long, sparse, inconspicuous.

Pronotum 1.4 times as wide as long, widest at base; sides weakly arcuate and converging very slightly toward the moderately strong constriction just behind the broadly, shallowly emarginate anterior margin; surface smooth and shining, the punctures moderately large, rather shallow, close, becoming two to three times larger in diameter near lateral margins; bottom or floor of each puncture irregularly reticulate; a partly impunctate, feebly raised median line indicated on posterior two-thirds; vestiture scanty, longer and more evident laterally.

Elytra 2.1 times as long as pronotum; sides straight and subparallel on basal two-thirds, rather broadly rounded behind; basal margins arcuate and bearing a row of about twelve moderately large, raised, overlapping crenulations, with several smaller submarginal ones particularly on interspaces two and three; striae weakly impressed, the punctures small and rather shallow; interstriae more than twice as wide as striae and armed by abundant, confused, transverse crenulations, each averaging about half the width of an interspace, a few about two-thirds as wide on posterior half of disc. Declivity rather steep, convex; strial punctures slightly smaller than on disc; interstrial punctures confused and all rather coarsely granulate, the largest forming a somewhat definite median row on each interspace. Vestiture moderately abundant, longer on declivity, longest setae slightly greater than a distance equal to width of an interspace.

Female.—Similar to male except a median frontal elevation evident at upper level of eyes; epistomal process less well developed; pronotal punctures very slightly larger; and discal crenulations and declivital granules a little larger.

Type locality.—Southern United States (probably Georgia). The concept of this species was based on Hopkins' material; the type was not studied.

Hosts.—*Pinus echinata, elliotti, palustris, rigida, rubens, serotina, strobus,* and *taeda.*

Distribution.—The United States south of a line drawn from New Jersey to eastern Texas.

Specimens from the following localities were examined (Fig. 55). ALABAMA: Aburn, Barton, Calhoun, "DeSoto S. P.," Grand Bay, Mobile and "Redland." ARKANSAS: Hot Springs. DELAWARE: "Delaware." DISTRICT OF COLUMBI(: "Taxoma." FLORIDA: Baker Co., Dunedin, Ft. Lauderdale, Gainesville, "Juniper

Fig. 55. Probable geographical distribution of *Dendroctonus* spp. with collection sites indicated: 1, *valens* (circles); 2, *terebrans* (triangles). Several additional records from southern Mexico and Guatemala have been published for *valens.*

Springs," Largo, Levy Co., Miami, Nassau Co., O'Leno S. P., Opa Locka, Tampa, and Winter Park. GEORGIA: Clayton, Cornelia, Ft. Valley, Kingsland, Myrtle, Thomasville, and Waverly. LOUISIANA: "Hart." MARYLAND: "Baden." NEW JERSEY: Clementon, Iona, "Lahaway," Lakewood, Mt. Misery, and New Brunswick. NEW YORK: Islip, Rockaway Beach and Bay Shore on Long Island. NORTH CAROLINA: Asheville, and Southern Pines. PENNSYLVANIA: Chinchilla. SOUTH CAROLINA: Chicora Place, Lumber, "New Landing," Pregnall, and Spartanburg. TEXAS: Austin. Call, Deweyville, Kirbyville, and Turlington. VIRGINIA: Ashland, "Camp Pickett," Falls Church, "Glen," and King. WEST VIRGINIA: Kanawah Station, Marion Co., Morgantown, Romney, "Roosevelt," and Crow.

Geographical variation.—Distinct differences correlated with geographical origin were not evident.

Biology.—This is a secondary enemy of pines, and less commonly, other coniferous trees; consequently, economic damage attributed to it is slight when compared to some of the other species of *Dendroctonus.*

Since this species has not been observed during the course of this study the following comments are based on personal observations made on two occasions a decade ago, and on the reports of Hopkins (1909b:147) and of Blackman (1922:57).

The principal overwintering stage is the adult, either in the bark of the brood tree or in newly started galleries of another host; they may also pass the winter as partly grown larvae. In the spring the adults became active in March or April and either begin or extend their new galleries as the period of oviposition commences. Overwintering larvae complete their development in the spring and evidently emerge from the brood tree prior to mid-July. The period of flight activity evidently continues more or less gradually from March to December. In the southern parts of its range activity may continue without interruption throughout the year .

Stumps more than four inches in diameter of recently cut trees, or of injured or weakened trees, are selected for attack. Their galleries ordinarily extend downward into the roots; occasionally they extend upward as much as two or three feet above the ground level, except in the southwestern parts of its distribution where they may extend more than 12 feet above the ground (Smith & Lee, 1957:3). Frequently the attacks are made in the vicinity of a wound at the base of the tree. Even though such attacks do not kill the host immediately they may interfere with normal growth, reduce vitality, thereby inviting other insect or disease causing agents to attack the tree.

The attack ordinarily begins at or just above the ground level, usually with only a few pairs of beetles participating. The female constructs the entrance tunnel and normally is joined by the male shortly after she reaches the cambium. If the amount of pitch encountered is excessive the gallery usually is extended upward, otherwise it is extended downward after ascending a centimeter or two. The egg gallery varies considerably in length, but seldom exceeds 30 centimeters. It may be linear, slightly wider than the beetle making it, or it may be branched; ordinarily it is irregularly widened at various places. As with other species, the male removes the frass from the working area, ejecting it from the entrance hole at first, then later packing it into the unused areas.

There are no individual egg niches. Groups of eggs are deposited rather loosely at one side of the gallery in one of the widened areas. These groups are then separated from the main areas of the gallery by a rather tightly packed partition of frass.

The periods of incubation and of larval development have not been precisely determined. The larvae do not construct individual tunnels, but work together in the phloem tissues in contact with the cambium, extending the cavity started by the parents. In some instances these cavities are said to cover several square feet of the inner bark (Blackman, 1922:58). These extensions by the larvae appear to wander aimlessly, favoring no particular direction. Larvae from eggs laid in the spring evidently pupate by mid-July and emerge in the fall. There is one complete and a partial second generation each year in most areas; two complete generations may occur in the extreme southern parts of its range.

Dendroctonus valens Leconte

Figs. 15-17, 30, 37, 55-56.

Scolytus terebrans: Harris, 1826, New England Farmer 5:169; Harris, 1862, A treatise on Some of the Insects Injurious to Vegetation, p. 56.

Hylurgus terebrans: (Biol.) Harris, 1841, A Report on the Insects of Massachusetts Injurious to vegetation, p. 72; Harris, 1842, A Treatise of Some of the Insects of New England which are Injurious to Vegetation, p. 72, 1852, p. 76; Fitch, 1858, Trans. New York St. Agric. Soc. 18:728; Harris, 1862, A Treatise on Some of the Insects Injurious to Vegetation, p. 86; Harris, 1863, A Treatise on Some of the Insects Injurious to Vegetation, Flint edition, p. 84; Thomas, 1876, Illinois State Entomologist Rept. 6:146; Smith, 1877, *in* Stewart, Shade Trees, Indigenous Shrubs and Vines, p. 52.

Dendroctonus terebrans: Zimmerman, 1868, Trans. American Ent. Soc. 2:149 (in part); Leconte, 1868, Trans. American Ent. Soc. 2:173 (in part); Leconte, 1876, Proc. American Philos. Soc. 15:385 (in part); Provancher, 1877, Faun. Ent. Canada 1:572; Dietz, 1890, Trans. American Ent. Soc. 17:29 (in part); Blandford, 1897, Biol. Centr.-Americana 4(6):146; Hopkins, 1899, Proc. Ent. Soc. Washington 4:343 (in part). Biol.: LeBaron, 1871, Prairie Farmer 42:p.?; Pachard, 1887, U. S. Dept .Agric. Ent. Comm. Bull. 7:175, 243 (in part); Pachard, 1890, U. S. Dept. Agric. Ent. Comm. Rept. 5:721 (in part); Hopkins, 1892, Science 20:64; Hopkins, 1893, West Virginia Agric. Expt. Sta. Bull. 31:143 (in part); Hamilton, 1895, Trans. American Ent. Soc. 22:346, 378; Wickham, 1896, Proc. Davenport Acad. Nat. Sci. 6:169; Wickham, 1896, Bull. Lab. Nat. Hist. State Univ. Iowa 3(4):170; Hopkins, 1897, West Virginia Agric. Expt. Sta. Rept. 6:41; Wickham, 1898, Bull. Lab. Nat. Hist. State Univ. Iowa 6(3):312; Hopkins, 1899, West Virginia Agric. Expt. Sta. Bull. 56:392, 415; Hopkins, 1899, U. S. Dept. Agric. Div. Ent. Bull., n. s., 21:14; Chittenden, 1899, U. S. Dept. Agric. Div. Ent. Bull. 22:56 (in part); Wickham, 1902, Bull. Lab. Nat. Hist. State Univ. Iowa 5(3):309; Felt, 1903, New York St. For. Comm. Rept. 7:480 (in part); Felt, 1906, New York St. Mus., Mem. 8, 2:342 (in part).

Dendroctonus valens Leconte, 1860, Pacific R. R. Explor. 5(2):59; Chapuis, 1869, Synopsis des Scolytides, p. 35 (1873, Mém. Soc. Roy. Sci. Liége

2, 3:243); Powell, 1904, Jour. New York Ent. Soc. 12:237; Powell, 1905, Jour. New York Ent. Soc. 13:5; Hopkins, 1905, U. S. Dept. Agric. Bur. Ent. Bull. 56:6, 11, 17; Hopkins, 1906, Proc. Ent. Soc. Washington 7:147; Hopkins, 1906, Proc. Ent. Soc. Washington 7:81; Swaine, 1909, New York St. Mus. Bull. 134:100; Hopkins, 1909, U. S. Dept. Agric. Bur. Ent. Tech. ser. 17(1):151; Hagedorn, 1910, Coleopterorum Catalogus 4:23; Hagedorn, 1910, Genera Insectorum 111:60; Hopkins, 1915, U. S. Dept. Agric. Bur. Ent. Tech. ser. 17(2):211 etc.; Blatchley and Leng, 1916, Rhynchophora or weevils of N. E. America, p. 577, 654; Swaine, 1918, Dom. Canada Dept. Agric. Ent. Br. Bull. 14(2):63; Chamberlin, 1939, Bark and Timber Beetles of North America, p. 167; Schedl, 1940 (1939), An. Esc. Nat. Cienc. Biol. 1:320, 323, 339; Schedl, 1955, Zeitschr. Angew. Ent. 38:14; Chamberlin, 1958, Scolytoidea of the Northwest, p. 78. Biol.: Hopkins, 1902, U. S. Dept. Agric. Div. Ent. Bull. 32:12; Gillette, 1903, Colorado Agric. Rept. 24:118; Hopkins, 1903, Canadian Ent. 35:61; Hopkins, 1904, U. S. Dept. Agric. Div. Ent. Bull. 48:19; Currie, 1905, U. S. Dept. Agric. Div. Ent. Bull. 53:74; Fall, 1907, Trans. American Ent. Soc. 33:218; Burke, 1908, Proc. Ent. Soc. Washington 9:115; Hopkins, 1909, U. S. Dept. Agric. Bur. Ent. Bull. 58:62; Hopkins, 1909, U. S. Dept. Agric. Bur. Ent. Bull. 83(1):153; Hopkins, 1912, U. S. Dept. Agric. Bur. Ent. Circ. 142:6; Swaine, 1913, Ontario Ent. Soc. Rept. 43:90; Swaine, 1914, Dom. Canada Dept. Agric. Expt. Farms. Ent. Bull., ser. 2, 17:20; Compere, 1915, California Hort. Bull. 4:574; Chamberlin, 1917, Canadian Ent. 49:323, 327; Chamberlin, 1918, Oregon Agric. Expt. Sta. Bull. 147:9; Blackman, 1919, Psyche 26:90; Herbert, 1919, Jour. Econ. Ent. 12:337; Hopping, 1921, Canada Dept. Agric. Ent. Br. Circ. 15:12; Hopping, 1922, Canadian Ent. 54:129, 130, 132; Graham, 1922, Minnesota Ent. Rept. 19:15; Blackman, 1922, Mississippi Agric. Expt. Sta. Tech. Bull. 11:22, 28, 58; Felt, 1924, Manual of Tree and Shrub Insects, p. 263; Hatch, 1924, Michigan Acad. Sci. Pap. 6:584; Trimble, 1924, Ann. Ent. Soc. America 17:384; Craighead, 1927, U. S. Dept. Agric. Circ. 411:4; Peirson, 1927, Maine For. Serv. Bull. 5:108, 121; Keen, 1928, California Dept. Nat. Res. Bull. 7:37; St. George, 1929, U. S. Dept. Agric. Farmers Bull. 1586:4; Craighead, 1930, U. S. Dept. Agric. Musc. Pub. 74:4; Blackman, 1931, New York St. Coll. For., Syracuse Univ. Bull. 4(4), Tech. Pub. 36:31; Burke, 1932, California Agric. Mo. Bull. 21:366; Walther, 1933, Jour. Econ. Ent. 26:828; Walther, 1933, Pan-Pac. Ent. 9:47; Kaston, 1936, Connecticut Agric. Expt. Sta. Bull. 387:645; Burke, 1937, Proc. Western Shade Tree Conf. 4:29; Brimley, 1938, North Carolina Dept. Agric. (Insects of North Carolina) :246; Dodge, 1938, Minnesota Agric. Expt. Sta. Tech. Bull. 132:28; Keen, 1938, U. S. Dept. Agric. Misc. Pub. 273:109; Beal, 1939, U. S. Dept. Agric. Farmers Bull. 1824:12; Wheeler, 1940, California Cult. 87:636; DeLeon, 1942, U. S. Dept. Agric. Bur. Ent. Pl. Quar. E-568, 4 p.; Felt and Bromley, 1942, Jour. Econ. Ent. 35:170; Evenden et. al., 1943, U. S. Dept. Agric. Circ. 664; Parr, 1943, Jour. Forestry 41:419; Felt and Bromley, 1944, Jour. Econ. Ent. 37:213; Beal and Massey, 1945, Duke Univ. School For. Bull. 10:81; Leech, 1945, Canada Dept. Agric. Div. Ent. For. Ins. Surv. Rept. 1944:66; Patterson, 1945, Univ. Washington Pub. Biol. 10:150; Anderson, 1947, Texas For. Serv. Bull. 33:7; Bruhn, 1947, Great Basin Nat. 8:21; Weidman nad Robbins, 1947, Jour. Forestry 45:428, 431; Muesebeck, 1950, Jour. Econ. Ent. 43:125, 131; Pearson, 1950, U. S. Dept. Agric. Monogr. 6:154; Craighead, 1950, U. S. Dept. Agric. Misc. Pub. 657:295; Evans and Dyer, 1951, Canada Dept. Agric. Div. Ent. For. Ins. Surv. Rept. 1950:110; Becker, 1951, Zeitschr. angew. Ent. 33:186; Lannon, 1951, Rhode Island Dept. Agric. Cons. Rept. 16:38; Perry, 1951, Unasylva 5:161; Whiteside, 1951, U. S. Dept. Agric. Circ. 864:3; Anonymous, 1951, U. S. Dept. Agric. Bur. Ent. Pl. Quar. Ins. Pest. Surv. Sp. Sup. 4:8; Beal, 1952, Duke Univ. School For. Bull. 14:50; Hoyt, 1952, U. S. Dept. Agric. Bur. Ent. Pl. Quar. Rept. 1950-51:16; Keen, 1952, U. S. Dept. Agric. Misc. Pub. 275:127, 142; Anonymous, 1952, U. S. Dept. Agric. Bur. Ent. Pl. Quar. Coop. Econ. Ins. Rept. 1(Sup. 4):93; Becker, 1954, Zeitschr. angew. Ent. 36:20; Knight and Wilford, 1954, U. S. Dept. Agric. Rocky Mtn. For.

Range Expt. Sta. Ins. Cond. 1953:4; Reid, 1955, Canadian Ent. 87:316, 323; Shenefelt and Benjamin, 1955, Wisconsin Agric. Ext. Circ. 500:84; Anonymous, 1955, California For. Pest Contr. Action Comm. For. Ins. Cond. 1954:7; Morena Noriega, 1956, Fitofilo 9(15):23, 35; Ostmark and Wilford, U. S. Dept. Agric. Rocky Mtn. For. Range Expt. Sta. Paper 22:6.

Dendroctonus beckeri Thatcher, 1954, Coleopterists Bull. 8:3. Biol.: Perry, 1955, Coleopterists Bull. 9:1.

This, the largest species in the genus, is very closely related to *terebrans*, but is readily distinguished by the reddish brown body color, by the smaller punctures in the lateral areas of the pronotum, by the smaller, less abundant declivital granules (Fig. 30) and, in part, by the distributions (Fig. 55).

Male.—Length 5.4-9.0 mm. (average about 8), 2.3 times as long as wide; mature body color reddish brown.

Frons irregularly convex, with a pair of lateral protubrances about a third of distance below upper margin of eye to epistomal margin, these protubrances separated by a broad, shallow, subconcave depression; epistomal margin elevated, its surface smooth and shining; epistomal process very broad, equaling about two-thirds (0.60 times) the distance between eyes, its arms oblique (about 20° from the horizontal), elevated only at inner angles of arms, the horizontal portion about two-thirds its total width, broadly concave, overlapping and ending just above epistomal margin and bearing under its distal margin a dense brush of yellowish setae. Vestiture, in addition to epistomal brush, moderately long, sparse, inconspicuous.

Pronotum 1.3 times as wide as long; sides weakly arcuate, almost subparallel, on basal two-thirds then moderately constricted just behind the broadly, shallowly emarginate anterior margin; surface smooth and shining, the punctures very close, rather shallow but sharply impressed, rather small but irregular in size, not larger laterally; an impunctate, feebly raised median line indicated on posterior three-fourths; vestiture scanty, longer and more evident laterally.

Elytra 2.2 times as long as pronotum; sides straight and subparallel on basal two-thirds, rather broadly rounded behind; basal margins arcuate and bearing a row of about twelve moderately large, raised, overlapping crenulations, with several smaller submarginal ones particularly on interspaces two and three; striae weakly impressed, the punctures rather small and deep; interstriae about one and one-half times as wide as striae and armed by abundant, confused, small, transverse crenulations, each averaging about one-third the width of an interspace, almost never more than half as wide on posterior half of disc. Declivity moderately steep, convex, with a feeble impression between first and third striae; strial punctures slightly smaller than on disc; interstrial punctures confused and finely to coarsely granulate, the largest granules forming an indefinite median row (in a few males only this median row of granules appears). Vestiture moderately abundant, longer on declivity, longest setae slightly exceed a distance equal to width of an interspace.

Female.—Similar to male except a median frontal elevation evident at upper level of eyes; pronotal punctures very slightly larger; and discal crenulations and declivital granules a little larger.

Type locality.—California (Totonicapan, Guatemala for *beckeri*). The types of both descriptions were studied. Hopkins did not state that the type of *valens* is a male.

Hosts.—*Pinus arizonica, chicuahuana, contorta, coulteri, echinata, edulis, jeffreyi, lambertiana, lawsoni, leiophylla, monticola, murrayana, oocarpa, ponderosa, pseudostrobus, radiata, resinosa, rigida, rudis, sabiniana, sylvestris, strobiformis, strobus tenuifolia,* and *virginiana, Abies concolor, Larix laricina, Picea canadensis, excelsa,* and *rubens.*

Distribution.—The coniferous forests of America north of Guatemala, except in the extreme southeastern United States.

Specimens from the following localities were examined (Fig. 55). ARIZONA: Apache N. F., Chiricahua Mts., Flagstaff, Ft. Apache Indian Res., Fredonia, Graham Mts., Grand Canyon N. P., McNary, Oak Ck. Canyon, Paradise, Portal, Prescott, Ramsey Canyon, Rincon Mts., Santa Catalina Mts., and Williams. CALIFORNIA: Alder Ck., "Alpine Ck." near Lake Tahoe, Arnold, Bass Lake, Bear Lake, Ben Lomond, Berkeley, Blancos Corral, Boulder Ck., Bray, "Burnt Corral," "BSA Camp" at Oakland, Camp Greenley, Camp Wolfboro, Carmel, Cedar Ridge, Chester, Cisco, Columbia, Cow Ck., Crane Valley, "Crooked Ck.," Crystal Lake, Cummings R. S., "Dark Canyon" in San Jacinto Mts., Del Monte, Devil's Garden, Dorrington, Dunsmuir, "Durley and Herrick Mine" in Plumas Co., Echo Lake, Eldorado, Fallen Leaf Lake, Fresno, General Grant N. P., Hackamore, Halls Flat on Black Mtn., Harvey Valley, Hat Creek, Hayfork, "Hazel Green," Herkey Ck. in San Jacinto Mts., Hobart Mills, Hope Valley, Huckleberry Meadow, Huntington Lake, Idyllwild, Inverness, Jackson, Jacumba, Jamesberg, "Jerome Mill," Julian, Junipero Serra Peak, Kelsey, Lake Co., Lake Arrowhead, Lake Tahoe, Lake Tenaya, "Lake McKenzie," Lamoine, Leavitt Meadows in Lassen Co., Little Yosemite, Lomo, Lone Pine, Loyalton, "Lumgray R. S." Madrone, Manzanita Lake in Lassen N. P., Mather, McCloud, McKenzie, Meadow Valley, Merced, Miami R. S., Milford, Millbrae, Miller Mt. Mill Valley, "Millwood," Mineral, Modoc N. F., Moffitt Ck., Mono Lake, Monterey, Mt. Hamilton, Mt. Hermon, Mt. Laguna, Mt. St. Helena, Nevada City, New Indria, North Fork, Oakland, Old Station, Onion Valley, Oriental, Orinda, Orinda Crossing, Pacific Grove, Palo Alto, Pebble Beach, Piedmont, Pinecrest, Pinehurst, "Pinogrande," Placerville, Plumas N. F., Point Areno, Pollock Pines, Quincy, "Quintette," Rattlesnake Ck., Riverside Co., Sacramento, Salinas, San Bernardino, San Bernardino Mts., "Sand Flat," San Francisco, San Jose, San Mateo, Santa Barbara Co., Santa Cruz, Santa Lucia Mts., Sequoia N. P., Shuteye, Shingle Springs, "Simpson Meadows," Sisson, "Snowline Camp" in Eldorado Co., Solano Co., Stanford, Stauffer, Stewarts Point, Stirling City, "Summerdale," "Sugarloaf Mt." in Los Angeles Co., Tallac, Three Rivers, Timber Mt., Truckee, Viola, Walkermine, Wawona, "Whitaker's Forest in Tulare Co., "Willow Meadow," Willow Ranch, Yreka, and Yuba Gap. COLORADO: Bailey, Cheyenne Mt., Estes Park, Ft. Garland, Douglas Co., Longs Peak, Manitou Park, "Mt. McClellan," Palmer Lake, Placer, "Powder River," Red Mt., San Isabel N. F., and Vallecito R. S. *in* LaPlata Co. IDAHO: Beaver Creek in Logan Canyon, Cedar Mt., Centerville, Coeur d'Alene, Farrogot, Grangeville, Grimes Pass, Harris Ridge, Moscow, Pioneerville, Priest River and Smiths Ferry. ILLINOIS: "Illinois." KANSAS: "Kansas." MAINE: Brunswick, Casco Bay, Limerick, Orono, Paris, Peak Island, and Portland. MASSACHUSETTS: Cambridge, Framingham, Lynn, and Stoneham.

Michigan: Grand Island, and Marquette. Minnesota: Aitkin, Cloquet, Duluth, Grand Rapids, Itasca Park, Olmsted, Plummer, Roseau Co., and Two Harbors. Montana: Helena, Missoula, and Sula. Nevada: Reno. New Hampshire: Durham, Manchester, and Webster. New Jersey: Lakehurst, Nilltown, and Newfoundland. New Mexico: "Bright Angel," Capitan, Capitan Mts., Carson N. F., Cloudcroft, Coolidge, "Culdridge," Ft. Wingate, Las Vegas, Lincoln N. F., Ruidoso, Sierra Blanca Mts., and Vermejo. New York: Hamburg, Ithaca, Syracuse, and West Point. North Carolina: Asheville, Balsam, Biltmore, and "Pink Beds." Ohio: Hocking Co. Oregon: Albany, "Anthony Ck.," Ashland, Aspen Lake, Baker, Bourne, Clover Ck., Cold Springs, Colestine, Corvalis, Crater Lake, Hood River, Joseph, Kerby, Klamath Lake, LaGrande, Mt. Hood, Prineville, Pringle Falls, Siskiyou Mts., "Slate Ck.," Sumpter, "Sutton Ck.," and Talent. Pennsylvania: Chambersburg, Milford, and Philadelphia. South Dakota: Black Hills, Custer, Deadwood, Elmore, Lead, and Spearfish. Utah: Ashley N. F., Escalante, Eureka, Kamas, Logan Canyon, Mammoth Mt., Navajo Mt., and Panguitch Lake. Virginia: Fredericksburg. Vermont: Fairlee. Washington: Blewett Pass, Buckeye, Dayton, Easton, East Satsop River, Fairfax, "Grass Prairie," "Half Moon," Malden, Metaline Falls, NewMan, Northport, Olympia, Pullman, Satus Ck., Seattle, Skakomish River, Skakomish, and Toppenish. West Virginia: Bretz, Cranesville, Crow, "Deckers Ck.," Hardy Co., Kanawha Station, "Mayfield Hill," Moorefield, Morgantown, Randolph, "Pallslow," Pendleton, Romney, "Roosevelt," and Tucker Mine. Wisconsin: Ashland, Bayfield, and Madison. Wyoming: "Lynn," Moskee, and Wyoming in Albany Co. Alberta: Athabasca Falls, Ft. Chipewyan, and Waterton Lakes N. P. British Columbia: Aspen Grove, Campbell River, Canford, Kamloops, Little Shuswap Lake, Midday Ck., Nicola, O'Kanagan Landing, Oliver, Peachland, Princeton, "Spious Ck.," Summerland, Trinity Valley, Vernon, Westwold. Northwest Territory: Ft. Smith. Nova Scotia: Kentville. Ontario: Ottawa, Prince Edward Co., Toronto, and Quitoico Pk. Quebec: Duparquet, Ft. Coulonge, Montreal, Saint Anne, and Saint Johns. Baja California: Sierra San Pedro Marlir. Chihuahua: Cerocahui, and Chihuahua. Distrito Federal: Mexico. Durango: El Salto. Hidalgo: Jacala. Mexico: Chalco, Ozumba Mt., and Tlalmanalco. Morelos: Cuernavaca. Puebla: Texmelucan. Guatemala: Cerro Quemado, Cuchumatenes Mts., El Baul, Guatemala City, Huehuetenanto, La Esperanza, Momostenango, Patzun, Panajachel, Quezaltenango, Totonicapan, and Uruapan.

Geographical variation.—Specimens from the northeastern parts of the range appear to be somewhat smaller than those from other areas; however, this may result from the limited material at hand, rather than actual population difference. The sexual differences of the frons appear to be more strongly developed in series originating in southern Mexico and Guatemala. There is also a tendency for the egg galleries of some specimens from those areas to be elongate and narrow; however, neither the sexual nor the gallery character is found in a majority of the population in those areas.

Biology.—In general, this is a secondary enemy of pine and spruce, but on occasion it attacks and kills apparently healthy trees. It usually works in conjunction with other more aggressive species and, consequently, comparatively little economic loss is attributed to it.

This species may overwinter either as young or mature adults or as partly grown larvae. There is an extreme overlapping of generations which is reflected by the fact that these insects may be seen in flight at any month of the year during their period of activity. In the northern parts of its range this period of activity evidently is from May to October; in the southern areas the species probably is active throughout the year.

Ordinarily stumps, injured, weakened or dying trees are selected for attack, although in some areas apparently healthy trees are selected. The attack usually is concentrated at or near the ground level at the base of the tree, but in some areas it may extend six or more feet above the level of the ground. Generally this species arrives quite some time after other species have attacked a particular tree.

The attack on any one tree ordinarily involves only a few pair of beetles of this species. It usually begins a few inches above the ground level then progresses above and below that point. It is not concentrated and, in fact, may involve two or more successive generations before the host succumbs.

The egg galleries (Fig. 56) of this species are exceedingly variable. The female, as with other species in the genus, constructs the entrance tunnel. After reaching the cambium region the tunnel extends upward for a short distance. If the amount of pitch encountered is excessive it may continue upward, if not, it may curve

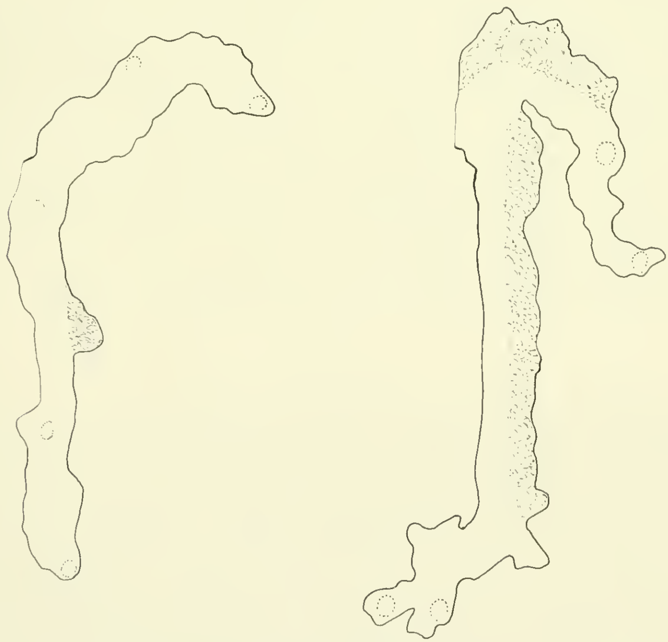


Fig. 56. *Dendroctonus valens*: Egg galleries broad, shape commonly resembling an inverted "J"; eggs placed in masses in grooves and packed in frass along sides of galleries (shaded areas above); larvae feed in congress often excavating large tabular areas in the inner bark (larval excavations not included).

downward into the roots. The egg gallery may be linear, slightly wider than the length of the beetle constructing it, or it may be branched or of a broad, irregular cave type. The linear pattern is more common in warmer parts of the range. In southern Mexico egg galleries exceeding 40 centimeters in length were not uncommon; however, it should be mentioned that broad cave-type excavations were found in the same tree with linear galleries as were all degrees of intergradation between the extremes. Usually one side of the gallery is expanded somewhat, either continuously or irregularly, for deposition of the eggs.

Oviposition in most areas of the United States evidently begins in late May or early June and continues throughout the warm months. Egg laying in northern or southern areas probably would begin earlier or later than this. The eggs are deposited along the far side of the expanded parts of the gallery, either loosely packed in frass or in layers, in groups of 10 to 40 or more. They are then covered with a more or less compact layer or partition of frass. There are no egg niches.

According to Swaine (1914:20) the larvae hatch in about ten days. They do not construct individual tunnels but mine in congress in the phloem next to the cambium in a general direction away from the egg gallery. Behind them the large flat cavity is filled by a reddish frass. The length of the larval period has not been determined precisely, but probably exceeds two months; it is suspected that in northern areas it may exceed a year. Pupal cells generally are formed in the frass, although occasionally a larva will construct a short individual tunnel in the phloem adjoining the common cavity where the pupal cell is formed. In the southern parts of its distribution there is one complete and at least a partial second generation each year; in the northern areas a generation evidently may require more than one year.

Dendroctonus micans (Kugelann)

Fig. 21

Bostrichus micans Kugelann, 1794, Schneider Magazin 5:523.

Dendroctonus micans: Erichson, 1836, Archiv Naturgesch. 2(1):53; Eichhoff, 1864, Berliner Ent. Zeitschr. 8:27; Chapuis, 1869, Synopsis des Scolytides, p. 35 (1873, Mém. Soc. Roy. Sci. Liége ser. 2, 3:243); Reitter, 1869, Verh. naturf. Ver. Brünn 8(2):p. ?; Lindemann, 1875, Bull. Soc. Imp. Nat. Moscou 49:213, 221; Lindemann, 1879, Bull. Soc. Imp. Nat. Moscou 54:73; Verhoff, 1896, Archiv Naturgesch. 62(1):124; Lovendal, 1898, De Danske Barkbiller, p. 87; Barbey, 1901, Scolytides l'Europe Centrale, p. 56; Hopkins, 1901, U. S. Dept. Agric. Bur. Ent. Tech. ser. 17(1):143; Hagedorn, 1910, Coleopterorum Catalogus 4:21; Hagedorn, 1910, Genera Insectorum 111:60; Reitter, 1913, Wiener Ent. Zeit. 32(Beiheft):47; Spessivtseff, 1913, (Practical keys to the bark beetles), p. 57; Spessivtseff, 1922, Medd. Skogsförsöksanstalt 19(6):465; Spessivtseff, 1925, Svensk Insektfauna 3:164; Pfeffer, 1932, Cat. Coleopt. Cechosloveniae 2:13; Schedl, 1932, *in* Winkler, Cat. Coleopt. reg. palaearcticae, p. 1635; Kurentzov, 1941, Bark-beetles of the Far East, U. S. S. R., p. 116; Balachowsky, 1949, Faune de France 50:134; Stark, 1952, Fauna U. S. S. R., 30:184; Pfeffer, 1955, Fauna C. S. R.

(Czechoslovakia), p. 121. BIOL.: Ratzeburg, 1861, Forstl. Bl. 2:64; Heyden, 1874, Jahrb. Nass. Ver. f. Naturk. 27-28:297; Eichhoff, 1880 (1881), Die Europäischen Borkenkäfer, p. 125; Altum, 1881. Forstzoologie 3(1):262; Henschel, 1885, Centralbl. f. d. g. Forsw. 11:534; Heyden, 1887, Ber. ü d. 60 Vers. deutsch. Naturf. u. Aerzte, p. ?; Altum, 1888, Zeitschr. Forst.-Jagdw. 22:242; Judeich and Nitche, 1895, Lehrbuch der mittel europäischen Forstinsektenkunde, p. 458; Severin, 1902, Bull. Soc. Centr. forestière Belg. 9:72, 145; Weber, 1902, Allg. Zeitschr. Ent. 7:108; Brichet and Severin, 1903, Bull. Soc. Centr. forestière Belg. 10:244; Baudisch, 1903, Centralbl. Forstw. 29:151; Bergmüller, 1903, Centralbl. Forstw. 29:252; Bergmüller, 1904, Forstl. Bl., p. 145; Quairière, 1904, Bull. Soc. Centr. Forestière Belg. 11:626; Nüsslin, 1905, Leitfaden der Forstinsektenkunde, p. 175; Quairière, 1905, Bull. Soc. Forstière Belg. 12:183; Quiévy, 1905, Bull. Soc. Centr. Forestière Belg. 12:334; Fuchs, 1906, Zeitschr. Forst.-Landw., p. 291; Formanek, 1907, Kurovci v. Cechach a na Morave zijící, p. 21; Pomerantzew, 1907, Ljaess, Shur. St. Petersburg 37:177; Tredl, 1907, Ent. Blätt. 3:11; Severin, 1908, Bull. Soc. Centr. Forestière Belg. 15:1; Hopkins, 1909, U. S. Dept. Agric. Bur. Ent. Bull. 83(1):141; Koch, 1909, Zeitschr. Forst.-Landw. 7:319; Chabrier, 19—, Mem. Mus. Hist. Nat. 6:470; Saalas, 1913, (reference ?), p. 77; Träghärdt, 1916, Skogsv. Tdjskr., p. 484; Saalas, 1917, Fichtenkäfer Finnlands 2:493; Kneiff, 1923, Mitt. Deutch. Denfrol. Ges., p. 246; Loos, 1925, Sudetendeutsche Forst.-Jagdztg. 25:53; Eulefeld, 1922, D. Forstz. 37:589; Koch, 1928, Bestimmungstabellen Ins. Fichte u. Tanne, p.?; Spessivtseff, 1931, Opredelitel Korojedov, p. 86; Torka, 1933, Ent. Blätt. 29:120; Roubal, 1942, Katalog Coleopt. Slovenska 3:258; Bioltchev, 1934, Lesov. Mis. 3(1):4; Pfeffer, 1943, Lesnická práce 22:181; Karpinski, 1948, Korniky ziem Polski, p. 96; Pfeffer, 1949, Lesnická práce 28:151; Gohrn, 1954, Det. forstl. Forsogsv. i Danmark 21:383.

Hylesinus (*Dendroctonus*) *micans*: Ratzeburg, 1839, Die Forst-Insekten 1:217; Kollar, 1858, Verh. Zool.-Bot. Ges. Wien 7:24; Willkomm, 1863, Thar. f. Jahrb. 15:249; Wahl, 1897, Zeitschr. Forst.-Jagdaw., p. 589; Eckstein, 1904, Zeitschr. Forst.-Jagdw., p. 243; Koch, 1909, Naturw. Zeitschr. Land-Forstw., p. 319.

Hylesinus micans: Geitel, 1862, Verh. Harz. Forstr., p. 21, 1867, p. 13; Gebbers, 1872, Verh. Harz. Forstr., p. 58; Ulrici, 1873, Zeitschr. Forst - Jagdw., p. 150; Glück, 1876, Zeitschr. f. Forst. - Jagdw. 8:385; Pauly, 1892, Zeitschr. Forst. - Jagdw., p. 257, 315, 351; Metzger, 1897, Münd. forstl. Hefte, p. 59; Obertreis, 1897, Zeitscher. Forst - Jagdw., p. 93; Schneider, 1897, Waldungen des Rheinlandes 12:382; F——, 1900, Deutsche Forst. - Zeit. 15:52; Esser, 1901, Wochenschr. Först., p. 286; Eckstein, 1904, Zeitschr. Forst. - Landw., p. 243; Methner, 1935, Wochenbl. Landesb. Pommern 2:216.

This is the only species in the genus occuring outside of the nearctic region. It appears to have reached Eurasia in comparatively recent times and is perhaps doubtfully distinct from the subarctic North American *punctatus*. This species may be distinguished from *punctatus* by the larger size and stouter form, by the flat epistomal process, by the smaller strial punctures, by the somewhat larger elytral crenulations, and by the distribution.

Male.—Length 6.0-8.0 mm. (average about 7), 2.33 times as long as wide; mature body color rather uniformly dark brown.

Frons convex, protruding very slightly in center area just below middle; epistomal margin elevated, smooth, shining; epistomal process a fourth (0.27 times) as wide as distance between eyes, its arms strongly oblique (about 55° from the horizontal) with margins sharply defined but not elevated, the horizontal portion about two-thirds its total width, flat, overlapping and ending just above epistomal margin and bearing under its distal margin a dense brush of yellowish setae; surface smooth and shining from vertex to epistoma, the punctures rather close, deep, coarse, sharp, with no indication of granules or tubercles. Vestiture fine, long, inconspicuous, rather sparse.

Pronotum 1.4 times as wide as long, widest at base; sides weakly arcuate and converging slightly anteriorly on basal half, then rather abruptly narrowed to a moderate constriction just behind the broadly, shallowly emarginate anterior margin; surface smooth and shining, the punctures rather coarse, close, deep, with a few very minute points interspersed; median line impunctate posteriorly; vestiture moderately abundant, fine and rather short on disc, longer and coarse laterally.

Elytra 2.5 times as long as pronotum; sides straight and subparallel on basal two-thirds, rather broadly rounded behind; basal margins arcuate and bearing a row of about twelve, moderately large, raised, overlapping crenulations, with several smaller submarginal ones particularly on interspaces two and three; striae weakly impressed, the punctures moderately large and deep; interstriae slightly more than twice as wide as striae and armed by abundant confused, small, transverse crenulations, each averaging about one-fourth the width of an interspace, never more than a third as wide on posterior half of disc. Declivity rather steep, convex, with the sutural interspaces slightly elevated; strial punctures almost as large as on disc; interstriae smooth, with numerous confused punctures less than one-third as large as those of striae, about a third of them minutely granulate on upper rim. Vestiture rather long and abundant; slightly longer on declivity, longest setae about one and one-half times as long as width of an interspace.

Female.—Similar to male except frons with a few minute granules between punctures (about one for each six punctures); punctures of pronotum and transverse crenulations of elytra a little larger; and declivital granules much larger.

Type locality.—Europe. The type was not studied.

Hosts.—*Picea excelsea;* less commonly from *Abies*, *Larix* and *Pinus*.

Distribution.—The coniferous forests of northern Eurasia from northern France to Siberia. About 150 specimens representing more than 50 localities were examined.

Geographical variation.—Not evident in the limited material at hand.

Biology.—This is a primary enemy of spruce forests in northern Europe and Asia where extensive damage has been inflicted at various times. Estimates of timber actually destroyed by this insect are not available.

Since the habits and work of this species were not observed during this study the following was summarized primarily from Eichhoff (1881:125-128) and from Severin (*in* Hopkins, 1909: 142-146).

The winter may be passed either as adults or as partly grown larvae. This indicates that there is an overlapping of generations as in related species. In central Europe the dates of oviposition indicate that the period of flight activity begins late in May or early in June and continues until about August, with the principal period of flight occurring in late June or early July.

Trees selected for attack may be either prostrate or standing; down trees are infested only on the under surface. The lower portion of the bole of standing trees may also be attacked, particularly if the tree is in a weakened condition, although young, vigorous, healthy trees may also be attacked during an epidemic. The pattern of the attack is not clear from available reports, but it is assumed that it progresses upward from the ground level.

The egg galleries tend to be vertical, although they are frequently curved and irregular in shape. They may be up to 20 cm. long, and usually are slightly wider than the beetle making the gallery; ordinarily they have two or three areas expanded on one side or the other. In each of these expanded areas groups of about 20 to 50 eggs are deposited and covered by or separated from the main part of the gallery by a layer or partition of frass. The first eggs are deposited in June and the last ones in September. Evidently one female may re-emerge and construct a second or a third set of galleries.

The larvae feed in congress, forming a large flat cavity in the phloem next to the cambium. There are no egg niches or individual larval mines. The larval period evidently requires at least two months for completion; it commonly continues over winter, pupation taking place during the early part of the following summer. Pupal cells are formed in the frass that fills the larval excavation. There may be one complete and a partial second generation each year.

Dendroctonus punctatus Leconte

Figs. 18, 57.

Dendroctonus punctatus Leconte, 1868, Trans. American Ent. Soc. 2:173; Leconte, 1876, Proc. American Philos. Soc. 15:384, 385; Schwarz, 1886, Ent. Americana 2:56; Hopkins, 1902, Proc. Ent. Soc. Washington 5:3; Hopkins, 1909, U. S. Dept. Agric. Bur. Ent. Tech. ser. 17(1):142; Swaine, 1909, New York St. Mus. Bull. 134:98; Hagedorn, 1910, Coleopterorum Catalogus 4:23; Hagedorn, 1910, Genera Insectorum 111:60; Hopkins, 1915, U. S. Dept. Agric. Bur. Ent. Tech. ser. 17(2):211; Blatchley and Leng, 1916, Rhyncophora or Weevils of Eastern North America, p. 654; Swaine, 1918, Dom. Canada Dept. Agric. Ent. Br. Bull. 14(2):65. Biol.: Packard, 1887, U. S. Dept. Agric. Ent. Comm. Bull. 7:177; Packard, 1890, U. S. Dept. Agric. Ent. Comm. Rept. 5:722; Hopkins, 1899. West Virginia Agric. Expt. Sta. Bull. 56:447; Hopkins, 1909, U. S. Dept. Agric. Bur. Ent. 83(1):139; Felt, 1924, Manual of Tree and Shrub Insects, p. 261.

Dendroctonus rufipennis: Dietz, 1890, Trans. American Ent. Soc. 17:28; Hamilton, 1894, Trans.American Ent. Soc. 21:35; Johnson, 1897, Pennsylvania Dept. Agric. Rept., p. 73.

Dendroctonus johanseni Swaine, 1919, Canadian Arctic Exped. Rept. 1913-1918, 3(E):5 (*new synonymy*); Van Dyke, 1924, Natl. Geographic Soc. Tech. Pap. 2(1):25; Swaine, 1933, Sci. Agric. 14(1):29; Chamberlin, 1939, Bark and Timber Beetles of North America, p. 165.

This species is very closely related to and perhaps doubtfully distinct from the Eurasian *micans*, but may be distinguished by the smaller size, by the more slender form, by the transversely concave epistomal process, by the larger strial punctures, by the smaller elytral crenulations, and by the distributions (Fig. 57). It is more likely to be confused with *murrayanae* and *obesus*, but may be distinguished by the uniformly brown color, by the smooth, polished frons which is deeply punctured but devoid of granules, and by the much larger punctures of the declivital striae.

Male.—Length 5.4-6.8 mm. (average about 6), 2.41 times as long as wide; body color uniformly brown to dark brown.

Frons convex, protruding very slightly at center just below middle; epistomal margin elevated, smooth, shining; epistomal process a third (0.32 times) as wide as distance between eyes, its arms strongly oblique (about 55° from the horizontal) and slightly elevated, the horizontal portion about two-thirds its total width, shallowly concave, overlapping and ending just above epistomal margin and bearing under its distal margin a dense brush of yellowish setae; surface smooth and shining from vertex to epistoma, the punctures rather close, deep, coarse, sharp, interspersed with a few very minute punctures, with no indication of granules or tubercles. Vestiture fine, long, inconspicuous, rather sparse.

Pronotum 1.4 times as wide as long, widest at base; sides weakly arcuate and converging toward the rather strong constriction just behind the broadly, shallowly emarginate anterior margin; surface smooth and shining, the punctures rather fine but irregular, close, deep, with a few very minute points interspersed; median line impunctate posteriorly; vestiture moderately abundant, fine and rather short on disc, longer and coarse laterally.

Elytra 2.5 times as long as pronotum; sides straight and subparallel on basal two-thirds, rather broadly rounded behind; basal margins arcuate and bearing a row of about twelve moderately large, raised, overlapping crenulations, with several smaller marginal ones particularly on interspaces two and three; striae weakly impressed, the punctures large and rather deep; interstriae about one and one-half times as wide as striae and armed by rather abundant confused, small, transverse crenulations, each averaging about one-fourth the width of an interspace, never more than a third as wide on posterior half of disc. Declivity rather steep, convex, with the sutural interspaces slightly elevated; strial punctures almost as large as on disc; interstriae smooth, with numerous confused punctures less than one-third as large as those of striae, about a third of them minutely granulate on their upper rims. Vestiture rather long and

Fig. 57. Probable geographical distribution of *Dendroctonus punctatus* with collection sites indicated.

abundant; slightly longer on declivity, longest setae about one and one-half times as long as width of an interspace.

Female.—So very similar to male that the sexes are recognized only with difficulty; female very slightly more coarsely sculptured, particularly declivital granules very slightly larger.

Type locality.—Northern New York (Sandstone Rapids, Coppermine River, Northwest Territories for *johanseni*). The type of both *johanseni* and *punctatus* were studied.

Hosts.—*Picea glauca, rubens,* and *sitchensis.*

Distribution.—The northern spruce forests from Alaska to New York and south along the mountains to West Virginia.

Specimens from the following localities were examined (Fig. 57). ALASKA: Circle, Haines Rd. (mi. 27), Rampart House, and Savonoski. NEW YORK: "N. Y." PENNSYLVANIA: Mt. Alto. WEST VIRGINIA: Randolph Co. ALBERTA: Cypress Hills, and McKenzie Highway (25th baseline). NORTHWEST TERRITORY: Aklavik, Ft. Smith, and Sandstone Rapids of the Coppermine River. ONTARIO: Frater. YUKON: Alaska Highway (mi. 1152) Carcross, Carmaks (mi. 8. Mayo Rd.), Rampart House, Watson Lake, Whitehorse, and Wolf Ck.

Geographical variation.—Not observed in the limited material at hand.

Biology.—This species evidently is rare in forests accessible to economic interests; consequently, it is not presently recognized by forest interests as an important species. Structurally and biologically it is so similar to *obesus* that field observers usually do not distinguish it from that species.

It is known to infest the lower bole and stumps of spruce from West Virginia to Alaska. Structurally it is almost indistinguishable from *micans* and is very similar to *murrayanae;* therefore, it is presumed that its biology is equally similar to these species. Collectors who took *punctatus* in two different areas of northern Canada and in Alaska suspected that at least two years were required to complete the life cycle in those areas; one year evidently is sufficient in the Great Lakes area and in the eastern United States.

Dendroctonus murrayanae Hopkins

Figs. 19, 39, 58-59.

Dendroctonus shoshone Hopkins, 1902, Proc. Ent. Soc. Washington 5:3 (*nomen nudum*).

Dendroctonus rufipennis: Hopkins, 1909 (nec. Kirby, 1837), U. S. Dept. Agric. Bur. Ent. Tech. ser. 17(1):138; Hagedorn, 1910, Coleopterorum Catalogus 4:23; Hagedorn, 1910, Genera Insectorum 111:60; Blatchley and Leng, 1916, Rhyncophora or weevils of Northeastern America, p. 655; Swaine, 1918, Dom. Canada Dept. Agric. Ent. Br. Bull. 14(2):64; Dodge, 1938, Minnesota Agric. Expt. Sta. Tech. Bull. 132:28; Chamberlin, 1939, Bark and Timber Beetles of North America, p. 152. BIOL.: Hopkins, 1909, U. S. Dept. Agric. Bur. Ent. Bull. 83(1):136; Vitzthum, 1926, Zool. Jahrb. Abt. Syst. Georgr. Tiere 52(5-6):407; Watson, 1931, Canadian Ent. 63:126; Swaine, 1933, Sci. Agric. 14:29.

Dendroctonus murrayanae Hopkins, 1909, U. S. Dept. Agric. Bur. Ent. Tech. ser. 17(1):140; Hagedorn, 1910, Coleopterorum Catalogus 4:22; Hagedorn, 1910, Genera Insectorum 111:60; Swaine, 1918, Dom. Canada Dept. Agric. Ent. Br. Bull. 14(2:64); Chamberlin, 1939, Bark and Timber Beetles of North America, p. 151, 164; Chamberlin, 1958, Scolytoidea of the Northwest, p. 77. BIOL.: Hopkins, 1909, U. S. Dept. Agric. Bur. Ent. Bull. 83(1): 138; Swaine, 1913, Ontario Ent. Soc. Rept. 43:89; Swaine, 1914, Dom. Canada Dept. Agric. Expt. Farms Bull., ser. 2, 17:28; Hopping, 1922, Canadian Ent. 54:130; Felt, 1924, Manual of Tree and Shrub Insects, p. 261; Craighead, 1927, U. S. Dept. Agric. Circ. 411:9; Keen, 1938, U. S. Dept. Agric. Misc. Pub. 273:109; Clapp, 1942, U. S. Dept. Agric. For. Serv. Rept. 1941:31; Patterson, 1945, Univ. Washington Pub. Biol. 10:150; Watts, 1948, U. S. Dept. Agric. For. Serv. Rept. 1947:27; Reid, 1955, Canadian Ent. 87:316.

This species is very closely allied to *punctatus* and *obesus* and is distinguished from them with considerable difficulty. From *punctatus* it differs by the more closely punctured, sparsely granulate frons (Fig. 19), by the more coarsely punctured pronotum, by the subequal size of strial and interstrial punctures of the declivity, by the reddish brown elytra with dark brown pronotum, and by the hosts. From *obesus* it differs by the distinctly punctured, finely, more sparsely granulate frons, by the male genitalia (Fig. 39), by the galleries (Fig. 59), and by the hosts.

Male.— Length 5.0-7.3 mm. (average about 6). 2.3 times as long as wide; body color dark brown, with reddish brown elytra.

Frons convex, protruding slightly on lower half; epistomal margin elevated, smooth, shining; epistomal process a third (0.32 times) as wide as distance between eyes, its arms strongly oblique (about 55° from the horizontal) and moderately elevated, the horizontal portion about two-thirds its total width, shallowly concave, overlapping and ending just above epistomal margin and bearing under its distal margin a dense brush of yellowish setae; surface shining from vertex to epistoma, the punctures very close, deep, coarse, about half of them with a small rounded granule on median or lower rim (usually). Vestiture fine, long, inconspicuous, rather sparse.

Pronotum 1.35 times as wide as long, widest at base; sides weakly arcuate and converging toward the rather strong constriction just behind the broadly, shallowly emarginate anterior margin; surface smooth and shining, the punctures rather fine, but irregular, close, deep; median line impunctate posteriorly. Vestiture moderately abundant, fine and rather short on disc, longer and coarse laterally.

Elytra 2.4 times as long as pronotum; sides straight and subparallel on basal two-thirds, rather broadly rounded behind; basal margins arcuate and bearing a row of about twelve moderately large, raised, overlapping crenulations, with several submarginal ones particularly on interspaces two and three; striae very weakly impressed, the punctures rather large and deep, usually decreasing in size toward base; interstriae slightly more than one and one-half times as wide as striae and armed by rather abundant, confused, small, transverse crenulations, each averaging about one-fourth the width of an interspace, never more than a half as wide on posterior half of disc. Declivity rather steep, convex, with the sutural interspaces slightly elevated; striae impressed, the punctures half as large as on disc, usually three times as large as those of interspaces (except in a few examples having unusually large interstrial punctures); interstriae almost smooth, subshining, the punctures rather abundant, confused (very irregularly three-ranked), the median series very finely granulate on upper rims. Vestiture rather long and abundant; slightly longer on declivity, longest setae about one and one-half times as long as width of an interspace.

Female.—Very similar to male except arms of epistomal process less strongly elevated, and declivital granules distinctly larger.

Type locality.—Keystone, Wyoming. The type was studied.

Hosts.—*Pinus banksianna, contorta* and *strobus.*

Distribution.—The Great Lakes area to Alberta, then south to Utah and Colorado.

Specimens from the following localities were examined. COLORADO: Jefferson, Kenosha Pass, and Wheeler Basin. IDAHO: Targhee N. F. MICHIGAN: Grand Island, and Whitefish Point. MINNESOTA: International Falls. MONTANA: Wisdom. UTAH: Logan Canyon and Wolf Ck. Pass. WYOMING: Bighorn Basin, Dubois, "Homestake," Keystone, Saratoga, and Shoshone N. F. ALBERTA: Banff, Cypress Hills, Edmonton, Hillsdale, Jasper N. P., and Lake Louise. BRITISH COLUMBIA: Stanley, and Wycliff. MANITOBA: Clear Lake Trail in Riding Mts. ONTARIO: Black Sturgeon Lake, and Frater.

Fig. 58. Possible geographical distribution of *Dendroctonus murrayanae* with collection sites indicated.

Geographical variation.—Specimens from the Great Lakes area average about 6.1 mm., those from the western half of the distribution about 5.7 mm. Those from the west also tend to have the pronotal punctures and the punctures of the declivital striae and interstriae very slightly larger. These differences are not sufficiently consistent, however, to warrant the recognition of distinct geographic races. It is possible that the apparent geographical differences are invalid, since one short series from Manitoba and another from Black Sturgeon Lake, Ontario, are intermediate in these characters and tend to obliterate any geographical distinctiveness.

Biology.—Ordinarily this is not an aggressive species, although available data indicate that it has contributed to bark beetle epidemics more commonly than published data would suggest and that it has killed healthy, vigorous Lodgepole pine. Because of the close superficial resemblance to *obesus* some losses actually caused by this species have been attributed to the destructive spruce beetle which supposedly infested Lodgepole pine. In all cases where specimens were preserved for study the "spruce" beetles infesting Lodgepole pine actually were this species.

The overwintering young and old adults and larvae in all stages of development become active when subcortical spring temperatures become sufficiently high, probably about 45° to 50°F. Flight activity probably does not begin before June at the high altitudes in Utah where Lodgepole pine grows. The earliest attacks observed during this study were found in the second week of July. Because of overlapping generations it is suspected that attacks probably continue from late June to early September.

Stumps, windfalls, overmature or weakened trees larger than about eight inches D. B. H. are selected for attack by this species: Trees dying from the attacks of *ponderosae* apparently provide a favorite breeding place for this species. In standing trees the attack seldom extends higher than about two feet above the level of the ground; in addition, it usually extends downward into the roots. In prostrate trees the lower side of the bole is preferred.

The attack evidently begins at or near the ground level at one side of the tree and progresses upward, downward, or around the tree from that point. At times two or more successive generations may be involved in progressively girdling a living tree. Ordinarily only a few pairs of beetles are involved in the attack on a particular tree.

The egg galleries (Fig. 59) are irregularly vertical, slightly wider than the beetle making them, with two or three irregular but shallow expanded areas along one or both sides; often short branch galleries may also be present. The galleries observed during this study averaged about 12 cm. in length; the longest ones were 20 cm. in length; they were constructed entirely by the female. As with other species they were excavated in the phloem in contact with the cambium. In a number of instances it was observed that the female excavated the complete egg gallery before the male appeared; evidently this is not a normal habit. In such instances there were no eggs or larvae in the gallery. When the male was present the lower part of the gallery was packed with frass thereby closing the entrance hole. Copulation was observed twice; in both instances it occurred near the middle of the gallery in one of the expanded areas.

In the Wasatch National Forest in Utah eggs were found during 1960 from July 12 to September 9; it was not determined whether or not these were the first or last eggs of the season. The eggs are deposited in the expanded areas in groups of about 20 to 50 or more. A more or less loose covering or partition of frass separates them from the main parts of the egg gallery. In the galleries observed, from one to three such groups occurred in each gallery.

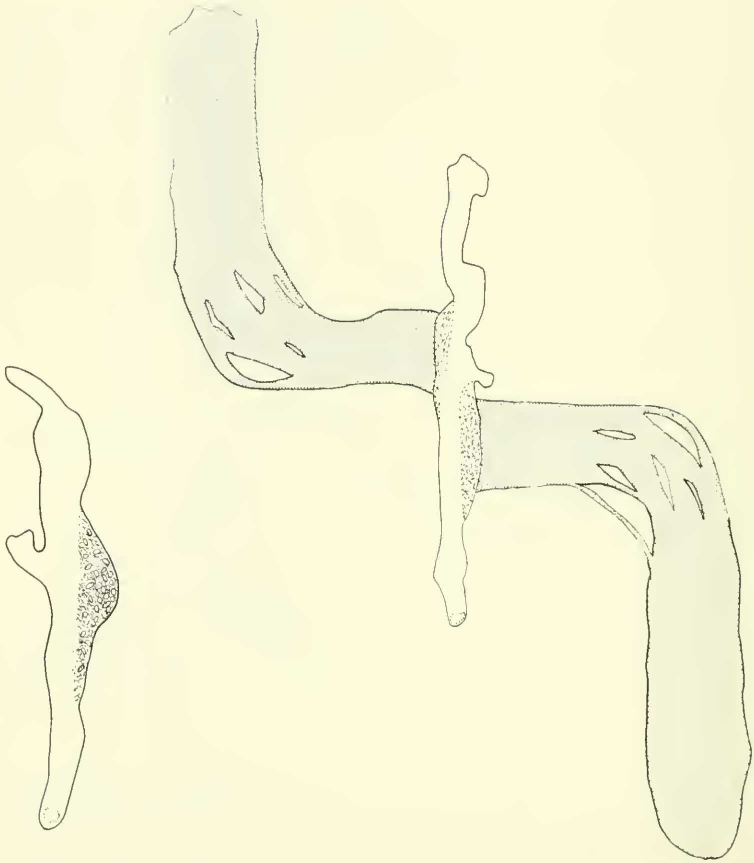


Fig. 59. *Dendroctonus murrayanae*: Egg gallery longitudinal, short, rather irregular; eggs deposited in irregular masses in egg grooves and packed in frass (left); larvae mine in congress, transversely through the second instar, then longitudinally as much as several feet. Characteristically islands of unexcavated bark remain at the angle where the larval mines turn.

Hatching time varied considerably with the season, but probably averaged about ten days in the galleries studied. There were no individual egg niches in any of the galleries. Evidently a female may re-emerge to construct a second set of galleries; this is supported by the fact that in September about a fourth of the galleries studied contained only the female, there were no adults present in an additional fourth.

The larvae feed in congress in a general transverse direction away from the egg gallery (Fig. 59). About six to ten centimeters from the egg gallery the excavated area turns either upward or downward and continues in that direction for an additional 20 to 30 cm. or more. It is characteristic of this species that just before or just after the vertical turn is made a few small groups of larvae become separated from the main body of larvae and mine independently for short distances before rejoining them. This leaves irregular islands of unexcavated phloem in the general cavity. When near maturity several of the larvae may construct short independent mines where pupation occurs; however, most of the pupal cells occur in the frass of the principal larval excavation. It appeared that the eggs laid in early July were represented by third and fourth instar larvae in September and probably did not mature until the following June; eggs laid in September evidently matured the following July. Evidently there may be one complete and a partial second generation each year in Utah. In the northern parts of the distribution it is possible that less than one complete generation occurs each year.

Dendroctonus obesus (Mannerheim)

Figs. 20, 40, 60-61.

Hylurgus obesus Mannerheim, 1843, Bull. Soc. Imp. Nat. Moscou 16:296; Mannerheim, 1852, Bull. Soc. Imp. Nat. Moscou 25:356; Mannerheim, 1853, Bull. Soc. Imp. Nat. Moscou 26:238.

Dendroctonus obesus: Leconte, 1868, Trans. American Ent. Soc. 2:173; Chapuis, 1869, Synopsis des Scolytides, p. 35 (1873, Mém. Soc. Roy. Sci. Liége, ser. 2, 3:243); Provancher, 1877, Fauna Ent. Canada 1:573; Provancher, 1878, Fauna Ent. Canada 5(Add. et Cor.):13; Schwarz, 1900, Proc. Washington Acad. Sci. 2:537; Hopkins, 1902, Proc. Ent. Soc. Washington 5:3; Hopkins, 1909, U. S. Dept. Agric. Bur. Ent. Tech. ser. 17(1):135; Swaine, 1909, New York St. Mus. Bull. 134:97; Hagedorn, 1910, Catalogus Coleopterorum 4:22; Hagedorn, 1910, Genera Insectorum 111:60; Swaine, 1918, Dom. Canada Dept. Agric. Ent. Br. Bull. 14(2):66; Chamberlin, 1939, Bark and Timber Beetles of North America, p. 151, 164; Chamberlin, 1958, Scolytoidea of the Northwest, p. 77. Biol.: Packard, 1877, U. S. Geol. Surv. Rept. 1875:589 (1877, Amer. Nat. 7:22); Hamilton, 1894, Trans. American Ent. Soc. 21:35; Hopkins, 1899, U. S. Dept. Agric. Div. Ent. 21:15, 21; Hopkins, 1902, U. S. Dept. Agric. Div. Ent. Bull. 37:22; Hopkins, 1903, Canadian Ent. 35:60; Hopkins, 1909, U. S. Dept. Agric. Bur. Ent. 83(1):132; Swaine, 1914, Dom. Canada Dept. Agric. Expt. Farms Bull. 7:33; Hewitt, 1915, Canadian Ent. Rept. 1915:30; Chrystal, 1915, Quebec Soc. Protec. Pl. Rept. 7:73; Chrystal, 1916, Agric. Gaz. Canada 3:796; Chrystal, 1916, Proc. Ent. Soc. British Columbia 9:65; Chrystal, 1917, Canadian Ent. Rept. 1915:44; Hopping, 1921, Canada Dept. Agric. Ent. Circ. 15:10; Hopping, 1922, Canadian Ent. 54:131; Felt, 1924, Manual of Tree and Shrub Insects, p. 260; Van Dyke, 1924, Natl. Geographic Soc. Tech. Pap. 2:25; Patterson, 1945, Univ. Washington Pub. Biol. 10:150; Annand, 1947, U. S. Dept. Agric. Bur. Ent. Pl. Quar. Rept. 1946-47:34; Anderson, 1947, U. S. Dept. Agric. Rept., sec. F., 1947:140; Anonymous, 1947, U. S. Dept. Agric. Bur. Ent. Pl. Quar. Ins. Cond. 1946:19; Anonymous, 1949, U. S. Dept. Agric. Bur. Ent. Pl. Quar. Ins. Cond. 1948:20; Richmond and Kinghorn, 1951, Forest Chron. 27:31.

Hylurgus rufipennis Kirby, 1837, *in* Richardson, Fauna Boreali Americana 4:195 (*new synonymy*); Mannerheim, 1853, Bull. Soc. Imp. Nat. Moscou 26:238; Peck, 1876, Trans. Albany Inst. 8:283, 301; Peck, 1879, New York St. Mus. Nat. Hist. Rept. 28:32; Packard, 1890, U. S. Dept. Agric. Ent. Comm. Rept. 5:814; Hough, 1882, Report on Forestry Submitted to Congress by the Commission of Agriculture, pt. 8:259.

Dendroctonus rufipennis: Leconte, 1868, Trans. American Ent. Soc. 2:173; Leconte, 1876, Proc. American Philos. Soc. 15:384, 385; Provancher, 1877, Fauna Ent. Canada 1:573; Provancher, 1878, Fauna Ent. Canada 5(Add. et Cor.):13, 14; Leconte, 1878, U. S. Geol. Geogr. Surv. Bull. 4:469; Schwarz. 1886, Ent. Americana 2:56; Dietz, 1890, Trans. American Ent. Soc. 17:28; Hopkins, 1898, U. S. Dept. Agric. Div. Ent. Bull. 17:69; Chittenden, 1898, U. S. Dept. Agric. Div. Ent. Bull. 18:96; Smith, 1899, New Jersey St. Bd. Agric. Rept. 27(Suppl.):364; Hopkins, 1899, West Virginia Agric. Expt. Sta. Bull. 56:349; Hopkins, 1899, Proc. Ent. Soc. Washington 4:343; Chittenden, 1899, U. S. Dept. Agric. Div. For. Bull. 22:56; Smith, 1900, Cat. Ins. New Jersey, p. 364; Hopkins, 1905, U. S. Dept. Agric. Bur. Ent. Bull. 56:6; Felt, 1906. New York St. Mus., Mem. 8, 2:753; Tredl, 1907, Ent. Blätt. 11:6. Biol.: Litner, 1885. New York St. Ent. Rept. 2:54; Fletcher, 1887, Rept. Minist. Agric., Append., Ent. Rept., p. 39, 40; Packard, 1887, U. S. Dept. Agric. Ent. Comm. 7:177; Packard, 1890, U. S. Dept. Agric. Ent. Comm. Rept. 5:721; Johnson, 1897, Pennsylvania Agric. Rept., p. 73; Harvey, 1898, Maine Agric. Expt. Sta. Rept. 13:176; Weed and Fiske, 1898, U. S. Dept. Agric. Div. Ent. Bull. 17:67; Howard, 1898, U. S. Dept. Agric. Div. Ent. Bull. 10:97; Hopkins, 1899, West Virginia Agric. Expt. Sta. Bull. 54:197, etc.; Johnson, 1901, Ent. News 12:92; Wickham, 1902, Bull. Lab. Nat. Hist. St. Univ. Iowa 5:309.

Dendroctonus similis Leconte, 1860, Pacific R. R. Explor. 5(2):59; Leconte, 1868, Trans. American Ent. Soc. 2:173.

Polygraphus rufipennis: Packard, 1890, U. S. Dept. Agric. Ent. Comm. Rept. 5:721.

Dendroctonus (*Polygraphus*) *rufipennis*: Cary, 1900, The Forester 6(3):52.

Dendroctonus piceaperda Hopkins, 1901, U. S. Dept. Agric. Div. Ent. Bull. 28:16 (*new synonymy*); Hopkins, 1902, Proc. Ent. Soc. Washington 5:3; Hopkins, 1902, U. S. Dept. Agric. Div. Ent. Bull. 32:21; Hopkins, 1902, U. S. Dept. Agric. Div. Ent. Bull. 37:22; Hopkins, 1903, U. S. Dept. Agric. Yearbook 1902:266, 270, 281; Hopkins, 1904, U. S. Dept. Agric. Div. Ent. Bull. 48:26; Hopkins, 1905, U. S. Dept. Agric. Yearbook 1904:266; Hopkins, 1905, U. S. Dept. Agric. Bur. Ent. Bull. 56:10, 11; Currie, 1905, U. S. Dept. Agric. Bur. Ent. 53:82; Felt, 1905, New York St. Mus., Mem. 8, 1:6; Felt, 1906, New York St. Mus., Mem. 8, 2:338, 379, 693; Burke, 1906, Proc. Ent. Soc. Washington 8:4, 5; Hopkins, 1906, Proc. Ent. Soc. Washington 8:5; Fall and Cockerell, 1907, Trans. American Ent. Soc. 33:218; Hopkins, 1907, U. S. Dept. Agric. Yearbook 1906:515; Hopkins, 1908, U. S. Dept. Agric. Yearbook 1907:160; Hopkins, 1909, U. S. Dept. Agric. Bur. Ent. Tech. ser. 17(1):126; Hopkins, 1909, U. S. Dept. Agric. Bur. Ent. Bull. 58:58, 75; Hopkins, 1909, U. S. Dept. Agric. Bur. Ent. Bull. 83(1):114; Swaine, 1909, New York St. Mus. Bull. 134:97; Hopkins, 1910, U. S. Dept. Agric. Bur. Ent. Circ. 125:2; Hagedorn, 1910, Coleopterorum Catalogus 4:22; Hagedorn, 1910 Genera Insectorum 111:60; Blatchley and Leng, 1916, Rhynchophora or weevils of North Eastern America, p. 653; Murphy, 1917, U. S. Dept. Agric. Bull. 544:27; Swaine, 1918, Dom. Canada Dept. Agric. Ent. Br. Bull. 14(2):62, 66; Brues, 1920, Insects and Human Welfare. p. 70; Peirson, 1923, Maine For. Serv. Bull. 1:25; Craighead, 1924, Dom. Canada Dept. Agric. Ent. Br. Bull. 25:39; Felt, 1924, Manual of Tree and Shrub Insects, p. 258; Swaine, 1924, Canada Dept. Agric. Pam. 48, 19 p.; Swaine, 1924, Pulp and Paper Mag. 22:567; Boutin, 1926, Nat Canadien 53:7; Craighead, 1927, U. S. Dept. Agric. Circ. 411:10; Peirson, 1927, Maine For. Serv. Bull. 5:118; Watson, 1928, Sci. Agric. 8:613; Craighead, 1930, U. S. Dept. Agric. Misc. Pub. 74:4; Swaine, 1930, Canada Dept. Agric. Div. For. Ins. Sp. Circ., 2 p.; Swaine, 1931, Canada Dept. Agric. Div. For. Ins. Sp. Circ., 4 p.; Balch, 1931, Forest Chron. 7:66; Peirson, 1932, Field Book of Destructive Forest Insects, ed. 2, p. 7; Balch, 1932, Nova Scotia Dept. Lands For. Rept. 1931:52; Balch, 1933, Nova Scotia Dept. Lands For. Rept. 1932:48; Swaine, 1933, Forest Chron. 9(4):12; Swaine, 1933, Sci. Agric. 14:14, 23; Twinn, 1933, Ontario Ent. Soc. Rept. 64:74; Twinn, 1934, Ontario Ent. Soc. Rept. 65:123; Balch, 1934, Pulp and Paper Mag. 35:680; Gobeil, 1935, Quebec Soc. Prot. Pl. Rept. 27:60; Dunn, 1936, Ontario Ent. Soc. Rept. 66:9; Nash, 1937, Massachusetts For. Pk. Assoc. Tree Pest Leaf. 14, 4 p.; Seavey, 1937, Maine For. Comm. Bien. Rept. 21:69; Dodge, 1938, Minnesota Agric. Expt. Sta. Tech. Bull. 132:27; Gobeil, 1938, Quebec Min. Terr. For. Serv. Ent. Bull. 2, 16 p.; Osborne, 1938, New York St. Conserv. Dept. Rept. 27:111; Chamberlin, 1939, Bark and Timber Beetles of North America, p. 164; Seavey, 1939, Maine For. Comm. Bien. Rept. 22:71; Gobeil, 1939, Nat. Canadien 66:71; McIntyre, 1939, Jour. Forestry 37:879; Nash, 1940, Massachusetts For. Pk. Assoc. Imp. Tree Pests 1940:70; Gobeil, 1941, Jour. Forestry 39:632; Gobeil, 1941, Pulp and Paper Mag. 42:730; Brown, 1941, Canada Dept. Agric. Div. Ent. For. Ins. Surv. Rept. 1940:8; Rendall, 1941, Maine For. Comm. Rept. 23:52; Balch, 1942, Nova Scotia Dept. Lands For. Rept. 1941:37; Balch, 1942, Jour. Forestry 40:621; Balch, 1942, Pulp and Pap. Mag. 43:900; Brown, 1943, Canada Dept. Agric. Div. Ent. For. Ins. Serv. Rept. 1942:6; Rendall, 1943, Maine For. Comm. Rept. 24:38; Parr, 1943, Jour. Forestry 41:420; Twinn, 1943, Canada Dept. Agric. Ins. Pest Rev. 21:8; Twinn, 1943, Ontario Ent. Soc. Rept. 73:70; Atwood. 1944, Canada Dept. Agric. Div. Ent. For. Ins. Serv. Rept. 1943:37; Balch and Hawboldt, 1944, Nova Scotia Dept. Lands For. Rept. 1943:51; Hawboldt, 1944, Canada Dept. Agric. Div. Ent. For. Ins. Serv. Rept. 1943:6; Atwood, 1945, Canada Dept. Agric. Div. Ent. For. Ins. Serv. Rept. 1944:8; Harrison, 1945, Nova Scotia Dept. Lands For. Rept. 1944:36; Reeks, 1945, Canada Dept. Agric. Div. Ent. For. Ins. Surv. Rept. 1944:6; Reeks, 1946, Canada Dept. Agric. Div. Ent. For. Ins. Surv. Rept. 1945:10; Reeks, 1946, Canada Dept. Agric. Ins. Pest. Rev. 24:26; Levesque, 1946, For. Quebecoise 11:529; DeGryse, 1947, For. Ent. Canada, p. 4; Hawboldt, 1947, Nova Scotia Dept. Lands For. Rept. 1945-46:36; Kennedy, 1947, Ontario Roy. Comm. For. Rept. 1947:117; Hawbolt, 1948, Nova Scotia Dept. Lands For. Rept. 1947:39; Reeks, 1948, Canada Dept. Agric. Div. Ent. For. Ins. Surv. Rept. 1947:14; Reeks, 1949, Canada Dept. Agric. Div. Ent. For. Ins. Surv. Rept. 1948:15; Hopkins, 1950. New York St. Conserv. Dept. Rept. 39:85; Hopkins, 1951, New York St. Conserv. Dept. Rept. 40:102; Anonymous, 1951, U. S. Dept. Agric. Bur. Ent. Pl. Quar. Ins. Pest Surv. Sp. Sup. 4:8; Reeks, 1953, Canada Dept. Agric. For. Ins. Surv. Rept. 1952:11; Shenefelt and Benjamin, 1955, Wisconsin Agric. Ext. Circ. 500:64; Marquis, 1956, U. S. Dept. Agric. N. E. For. Expt. Sta. Rept. 1955:10, 110; Price, 1956, U. S. Dept. Agric. Rocky Mtn. For. Range Expt. Sta. Rept. 1955:27; Forbes, 1956, Canada Dept. Agric. For. Ins. Surv. Rept. 1955:18; Forbes, 1957, Canada Dept. Agric. For. Ins. Surv. Rept. 1956:16.

Dendroctonus californicus Hopkins, 1902, Proc. Ent. Soc. Washington 5:3 (*nomen nudum*).

Dendroctonus dietzi Hopkins, 1902, Proc. Ent. Soc. Washington 5:3 (*nomen nudum*).

Dendroctonus wickhami Hopkins, 1902, Proc. Ent. Soc. Washington 5:3 (*nomen nudum*).

Dendroctonus piceaperda var. *engelmanni* Fall, 1907, Trans. American Ent. Soc. 33:218 (*nomen nudum*).

Dendroctonus engelmanni Hopkins, 1909, U. S. Dept. Agric. Bur. Ent. Tech. ser. 17(1):130 (*new synonymy*); Hagedorn, 1910, Coleopterorum Catalogus 4:20; Hagedorn, 1910, Genera Insectorum 111:60; Swaine, 1918, Dom. Canada Dept. Agric. Ent. Br. Bull. 14(2):65; Chamberlin, 1939, Bark and Timber Beetles of North America, p. 151, 161; Chamberlin, 1958, Scolytoidea of the Northwest, p. 75. Biol.: Hopkins, 1908, U. S. Dept. Agric. Yearbook 1907:161; Hopkins, 1909, U. S. Dept. Agric. Bur. Ent. Bull. 58:59; Hopkins, 1909, U. S. Dept. Agric. Bur. Ent. Bull. 83(1):126; Hopkins, 1909, U. S. Dept. Agric. Yearbook 1908:574; Hopkins, 1910, U. S. Dept. Agric. Bur. Ent. Circ. 125:2; Hopkins, 1912, U. S. Dept. Agric. Bur. Ent. Circ. 142:6; Craighead, 1927, U. S. Dept. Agric. Circ. 411:10; Keen, 1939, U. S. Dept. Agric. Misc. Pub. 273:126; Craighead and Brown, 1945, U. S. Dept. Agric. Bur. Ent. Pl. Quar. E-649:4; Patterson, 1945, Univ. Washington Pub. Biol. 10:149; Spencer, 1945, Green Thumb 2(1):9; Wygant, 1945, U. S. Dept. Agric. Bur. Ent. Pl. Quar. Ins. Pest Surv.

1944:14; Annand, 1945, U. S. Dept. Agric. Bur. Ent. Pl. Quar. Rept. 1944:20, 33; Annand, 1946, U. S. Dept. Agric. Bur. Ent. Pl. Quar. Rept. 1945:30; Bloch, 1946, Timberman 48(2):102; Anderson, 1947, U. S. Dept. Agric. Sec. Rept. 1946:140, 147; Annand, 1947, U. S. Dept. Agric. Bur. Ent. Pl. Quar. Rept. 1946:34; Massey, 1947, Rocky Mtn. Conf. Ent. Rept. 18:6; Anonymous, 1948, U. S. Dept. Agric. Bur. Ent. Pl. Quar. Ins. Pest Surv. 1947:17; Anonymous, 1949, U. S. Dept. Agric. Bur. Ent. Pl. Quar. Ins. Pest Surv. 1948:19; Annand, 1949, U. S. Dept. Agric. Bur. Ent. Pl. Quar. Rept. 1948:10; Corhart, 1949, American For. 55(3):14, 41; Wygant, 1949, U. S. Dept. Agric. Yearbook 1948:417; Bloch, 1950, Green Thumb 7(10):24; Bloch, 1950, Timberman 51(11):78, 80, 82, 84; Gardiner, 1950, Canada Min. Agric. Rept. 1949:105; Kenney, 1950, British Columbia Dept. Lands For. For. Serv. Rept. 1949:73; MacKay, 1950, Canada Dept. Agric. Div. Ent. For. Ins. Surv. Rept. 1949:114, 120; Mielke, 1950, Jour. Forestry 48:882; Nelson, 1950, Jour. Forestry 48:182; Watts, 1950, U. S. Dept. Agric. For. Serv. Rept. 1949:11, 40, 54; Anonymous, 1950, U. S. Dept. Agric. Bur. Ent. Pl. Quar. Ins. Pest Surv. 1949:25; Beal, 1951, Proc. West. For. Conserv. Assoc. 41:58; Bloch, 1951, Green Thumb 8:22; Prater, 1951, American For. 57(6):18; Ross and Jones, 1951, Canada Dept. Agric. Div. Ent. For. Ins. Surv. 1950:114, 121, 123; Sun, 1951, Proc. N. Cent. Sts. Br. American Assoc. Econ. Ent. 6:58; Anonymous, 1951, U. S. Dept. Agric. Bur. Ent. Pl. Quar. Ins. Pest Surv. Sp. Sup. 4:4; Anonymous, 1951, U. S. Dept. Agric. Bur. Ent. Pl. Quar. Ins. Pest Surv. 1950:23; Anonymous, 1951, U. S. Dept. Agric. Bur. Ent. Pl. Quar. Coop. Econ. Ins. Sp. Rept. 4:88; Anonymous, 1952, Timberman 53(12):96, 98, 100, 103; Evenden, 1953, Proc. Northw. Wood Prod. Clinic 8:56; Hoyt, 1953, U. S. Dept. Agric. Bur. Ent. Pl. Quar. Rept. 1951-52:68; Massey, Chishol, and Wygant, 1953, Jour. Econ. Ent. 46:951; Morse, 1953, Proc. Northw. Wood Prod. Clinic 8:56; Rettig, 1953, Proc. West. For. Conserv. Assoc. 43:50; Sommers, 1953, British Columbia Dept. Lands For. For. Serv. Rept. 1952:60; Yeager, 1953, Trans. N. Amer. Wildlife Conf. 18:596; Fitzgerald, 1954, American For. 60(1):24; Hoyt, 1954, U. S. Dept. Agric. Bur. Ent. Pl. Quar. Rept. 1952-53:20; Knight and Wilford, 1954, U. S. Dept. Agric. Rocky Mtn. For. Range Expt. Sta. Ins. Cond. 1953:2; Massey et al., 1953, Jour. Econ. Ent. 46:951; Massey and Wygant, 1954, U. S. Dept. Agric. Circ. 944, 35 p.; Nelson, 1954, Jour. Forestry 52:503; Schaeffer, 1954, Jour. Forestry 52:860; Vaux, 1954, Jour. Forestry 52:506; Bailey, 1955, U. S. Dept. Agric. Intermtn. For. Range Expt. Sta. Rept. 1954:40; Davidson, 1955, Mycologia 47:58; Love, 1955, Trans. American Geophys. Union 36:113; Price, 1955, U. S. Dept. Agric. Rocky Mtn. For. Range Expt. Sta. Rept. 1954:13, 17; Smith, 1955, Jour. Forestry 53:208; Thomson, 1955, Proc. British Columbia Ent. Soc. 51:45; Anonymous, 1955, U. S. Dept. Agric. For. Serv. Imp. For. Ins. 1954:5, 7, 9; Anonymous, 1955, U. S. Dept. Agric. Pacific Northw. For. Range Expt. Sta. Ins. Surv. 1954:26, 37, 39, 41, 43, 45; Anonymous, 1956, U. S. Dept. Agric. Pacific Northw. For. Range Expt. Sta. Ins. Surv. 1955:31, 40, 44, 46, 49; Knight, 1956, U. S. Dept. Agric. Rocky Mtn. For. Range Expt. Sta. Pap. 25, 12 p.; Ostmark and Wilford, 1956, U. S. Dept. Agric. Rocky Mtn. For. Range Expt. Sta. Pap. 22:2, 13; Price, 1956, U. S. Dept. Agric. Rocky Mtn. For. Range Expt. Sta. Rept. 1955:21; Yasinski, 1956, U. S. Dept. Agric. Rocky Mtn. For. Range Expt. Sta. Pap. 23:2; Bailey, 1957, U. S. Dept. Agric. Intermtn. For. Range Expt. Sta. Rept. 1956:31, 37; Brown, 1957, Canada Dept. Agric. For. Ins. Surv. Rept. 1956:74; Knight, 1957, Bull. Ent. Soc. America 3(3):27; Nagel, 1957, Jour. Forestry 55:894; Price, 1957, U. S. Dept. Agric. Rocky Mtn. For. Range Expt. Sta. Rept. 1956:81, 84, 86, 89, 92, 99; Whiteside, 1957, U. S. Dept. Agric. Pacific Northw. For. Range Expt. Sta. For. Ins. Cond. 1956:17, 34, 38, 40.

Dendroctonus borealis Hopkins, 1909, U. S. Dept. Agric. Bur. Ent.. Tech. ser. 17(1):133 (*new synonymy*); Hagedorn, 1910, Coleopterorum Catalogus 4:20; Hagedorn, 1910, Genera Insectorum 111:60; Swaine, 1918, Dom. Canada Dept. Agric. Ent. Br. Bull. 14(2):61, 66; Chamberlin, 1939, Bark and Timber Beetles of North America, p. 151, 163; Chamberlin, 1958, Scolytoidea of the Northwest, p. 68, 76. Biol.: Hopkins, 1909, U. S. Dept. Agric. Bur. Ent. Bull. 83(1):132; Hewitt, 1917, Dom. Canada Dept. Agric. Ent. Br. Rept. 1916:35, 37, 40; Hopping, 1921, Dom. Canada Dept. Agric. Circ. 15:10; Hopping, 1922, Canadian Ent. 54:131; Felt, 1924, Manual of Tree and Shrub Insects, p. 260; Van Dyke, 1924, Natl. Geogr. Soc. Tech. Pap. 2(1):25; Twinn, 1934, Ontario Ent. Soc. Rept. 65:123; MacKay, 1948, Canada Dept. Agric. For. Ins. Surv. Rept. 1947:93; MacKay, 1949, Canada Dept. Agric. For. Ins. Surv. Rept. 1948:114; Evans, 1950, Canada Dept. Agric. For. Ins. Surv. Rept. 1949:107; Evans and Dyer, 1951, Canada Dept. Agric. For. Ins. Surv. Rept. 1950:110; McGuffin and Reid, 1952, Canada Dept. Agric. For. Ins. Serv. Rept. 1951:98; Anonymous, 1952, U. S. Dept. Agric. Bur. Ent. Pl. Quar. Coop. Econ. Ins. Rept. Sp. Rept. 4:94; Brown, 1955, Canada Dept. Agric. For. Ins. Surv. Rept. 1954:104.

This species is very closely allied to *murrayanae* but is distinguished with difficulty by the more coarsely, closely granulate frons (Fig. 20), by the very distinctive male genitalia (Fig 40), by the galleries (Fig. 61), and by the hosts.

Male.—Length 4.4-7.0 mm. (average about 5.5), 2.3 times as long as wide; mature body color very dark brown with reddish brown elytra, old adults usually uniformly black.

Frons convex, protruding slightly on lower half; epistomal margin elevated, smooth, shining; epistomal process a third (0.35 times) as wide as distance between eyes, its arms rather strongly oblique (about 45° from the horizontal) and moderately elevated, the horizontal portion almost two-thirds its total width, shallowly concave, overlapping and ending just above epistomal margin and bearing under its distal margin a dense brush of yellowish setae; surface shining, the punctures very close, deep, rather fine, largely obliterated in central area by fine, abundant granules, at least one or two granules for each puncture in central area, less numerous in surrounding areas. Vestiture fine, long, inconspicuous, rather sparse.

Pronotum 1.4 times as wide as long, widest at base; sides weakly arcuate and converging toward the rather strong constriction just behind the broadly, shallowly emarginate anterior margin; surface smooth and shining, the punctures rather fine but irregular in size, close, deep; median line impunctate posteriorly. Vestiture moderately abundant, fine and rather short on disc, longer and coarse laterally.

Elytra 2.4 times as long as pronotum; sides straight and subparallel on basal two-thirds, rather broadly rounded behind; basal margins arcuate and bearing a row of about twelve moderately large, raised, overlapping crenulations, with several smaller submarginal ones particularly on interspaces two and three; striae very weakly impressed, the punctures rather large and shallow, usually decreasing slightly in size toward base; interstriae slightly more than one and one-half times as wide as striae and armed by rather abundant confused, small, transverse crenulations, each averaging about one-fourth the width of an interspace, never more than a third as wide on posterior half of disc. Declivity rather steep, convex, with the sutural interspaces slightly elevated; striae usually not impressed. the punctures minute, subequal in size to and often confused with those of interspaces; interstriae almost smooth, subshining, the punctures rather numerous, confused, the median series on each interspace very minutely granulate on upper rims. Vestiture rather long and abundant; slightly longer on declivity, longest setae about one and one-half times as long as width of an interspace.

Female.—Very similar to male except arms of epistomal process less strongly elevated, and declivital striae usually weakly impressed with the interstrial granules rather large and usually pointed.

Type locality.—Sitka Island, Alaska (Boreal North America for *rufipennis;* Oregon for *similis;* Camp Caribou, Maine, for *piceaperda;* Eagle, Alaska, for *borealis;* and Capitan, New Mexico, for *engelmanni*). All six types were studied.

Hosts.—All species of *Picea* within its range.

Distribution.—The spruce forests of North America from Alaska to Nova Scotia. south to Pennsylvania in the east and to the Mexican border in Arizona and New Mexico in the west.

Specimens from the following localities were examined (Fig. 60) ALASKA: Chichagof Isl., Circle, Eagle, Eklutna, Ft. Yukon, Homer, Juneau, Kenai Peninsula, Klutina Lake, Matanuska, Nutzotin Mts., Ruby, St. James Bay, Savonoski, Seward, Skaway, Tanana, and Yakutat. ARIZONA: Chiricahua Mts., San Francisco Peak. CALIFORNIA: Crescent City. COLORADO: Argentine Pass, Boulder, Clyde, Ft. Collins, Glenwood Springs, Gore Pass, Gunnison, Hahns Peak, Holy Cross Mtn., Leadville, "Leavenworth Valley," Meeker, New Castle, Ouray Peak, Pingree Pk., Rabbit Ears Pass, San Isabel N. F., Silver Plume, Steamboat Springs, "Twinn Sisters," and White River N. F. IDAHO: Beaver Ck. of Logan Canyon, Collins, and Lieber Ck. in Coeur d'Alene N. F. MAINE: Beaver Pond, Camp Caribou, Cupsuptic, and "Meadows." MICHIGAN: Grand Island, Isle Royal, Marquette, and Munising. NEW HAMPSHIRE: Colebrook, West Stewartstown, and Wonalancet. MINNESOTA: Itasco St. Pk., and International Falls. NEW MEXICO: Capitan Mts., Cloudcroft, Las Vegas, Pecos Wilderness Area, Sandia Mts.. Santa Fe Basin, and Sierra Blanca Mts. NEW YORK: Pleasant *Lake.* OREGON: Batterson, Cannon Beach, Cascade Head Expt. For., Coos Bay, Gold Lake, "Highland Mine," Hood River Meadows, Joseph, Marshfield, "Mt. Misery," Mt. Ashland, Santiam Pass. and Tolgate. PENNSYLVANIAS Ricketts. SOUTH DAKOTA: Black Hills N. F., and Spearfish Canyon. UTAH: Alta, Ashley N. F., Cedar Breaks N. M., Ephraim, Escalante, LaSal Mts., Logan Canyon, Lost Lake, Panguitch, Paradise Pk., Parowan Canyon, and Wolf Ck. Pass. WASHINGTON: Aberdeen, Easton, Fairfax, Hoquiam, Lake Wenatchee, Metaline Falls, Morse Ck., Mt. Rainier, Neah Bay, Parkway, Sappho, "Tieton R. S.," Wenatchee Lake, White Pass. White River. Winthrop, and Yakima. ALBERTA: Babine Lake, Banff, Calgary, Cypress Hills, Edmonton, Exshaw, Harlech, Jasper N. P., Kananskis For. Sta., Lake Athabasca, Lake Louise, Lesser Slave Lake, Nordagg, and Smoky Lake. BRITISH COLUMBIA: Aspen Grove, Babine Lake, Bloom Ck. Valley, Boundary Lake, Creighton Valley. Emerald Lake, Glacier, Lorna, Lower Post. Lumberton, Lumby. Ootsa Lake. "Paxton Valley." Priest River, Princeton, Queen Charlotte Islands, Salmo. "Seymour Ck.," Stanley, Trinity Valley, Vancouver. Vernon, Vermilion Summit on Banff Rd., Victoria, Ymir. and Yoho N. P. MANITOBA: Churchill, "Northern Manitoba," and Riding Mt. N. P. NEW BRUNSWICK: Nictor Lake and Fredericton. SASKATCHEWAN: "Northern Saskatchewan." NORTHWEST TERRITORY: Aklavik, Coppermine River, Ft. Norman, Ft. Smith. and Yellowknife. NOVA SCOTIA: Cape Breton Isl., and St.

Fig. 60. Probable geographical distribution of *Dendroctonus obesus* with collection sites indicated.

Peters. ONTARIO: Black Sturgeon Lake, Egg Lake in Algonquin Pk., Frater, Hearst, "Nighthawk Lake," North Bay, "Remi Lake," and Timmins. QUEBEC: Anticosti Isl., Cascapedia, Duparquet, and Gaspe Peninsula. YUKON: Teslin and Whitehorse.

Geographical variation.—Specimens from the eastern part of the distribution average about 0.2 mm. smaller than those from the west. A higher percentage of western specimens, particularly from Sitka spruce in British Columbia, are black in color (38 per cent); only an occasional eastern specimen was black. Whether this was due to the age of specimens at the time of collection, to climatic or other environmental factors, or to genetic factors is uncertain.

Biology.—This is the most destructive of the spruce inhabiting bark beetles. It is responsible for killing an estimated average of approximately one-third to one-half billion board feet of standing spruce timber each year. It is also reported to have inflicted substantial losses to Lodgepole Pine (Massey and Wygant, 1954:1), but this was not substantiated by an examination of the beetles collected from the infested pine trees (cf. *murrayanae*).

The spruce beetle may overwinter in any stage of development, but adults and half grown larvae predominate. Activity evidently begins in May when subcortical daytime temperatures reach about 45° to 50°F. The period of flight activity evidently begins late in May and continues until October, with two distinct seasonal peaks. The first of these is in June, and the second in late July to early September. Local climatic conditions or peculiarities of a particular season may accelerate or delay these peak periods a week or two and may also have a bearing on which of the two flight periods is greater. The first flight includes overwintered parent and young adults, the second primarily consists of beetles that mature from overwintered larvae.

Under endemic conditions the trees selected for attack consist of windfalls or other prostrate dying green trees or of overmature or weakened standing trees larger than about eight inches D.B.H. During an epidemic almost any spruce tree in the stand may be selected regardless of size or vigor. The attack usually begins on the lower third of the bole, except for the first two or three feet above the ground. It ordinarily progresses to include the upper bole and stump later in the season when the second flight occurs, if populations are not excessive. In prostrate trees only the lower half next to the ground is attacked. The upper bole smaller than eight inches in diameter and limbs generally are not subject to attack by this species. The attack is slow and continuous, without any sudden or concerted swarming of the beetles; its duration may vary from a few days to many months. depending on the population density of beetles in the area. upon the resistance of the host, or upon climatic or other ecological factors peculiar to the season or locality. The number of attacks per square foot of bark surface may be as high as 24. but averages between six and nine; the density of the attacks evidently is greater at the base of the tree and gradually decreases upward (Massey and Wygant, 1954:13).

The egg galleries (Fig. 61) are constructed by the female beetle mostly in the phloem tissues, but they engrave the wood more deeply than other species of *Dendroctonus*: the thinness of spruce bark may have some bearing on this habit. The egg galleries are vertical, almost straight, ordinarily with the lower one or two centimeters next to the entrance hole hooked diagonally to either the right or left. The average length of 13 cm. and the maximum length of 23 cm. for egg galleries observed during this study, made in 1960, in the Wasatch National Forest of Utah, agrees with that reported by Massey and Wygant (1954:13). The egg galleries are slightly wider than the width of the beetle making them and, in addition, there usually is an egg groove along the side next to the cambium about one or two millimeters deep. Ventilation tunnels are placed at irregular intervals, but are not always present.

Oviposition evidently begins less than a week after the attack; there is some question as to its duration because most of the beetles re-emerge to construct a second or third set of galleries. Massey

Fig. 61. *Dendroctonus obesus*: Egg gallery longitudinal, rather short; eggs deposited in irregular single or double rows in grooves (occasionally in individual niches as shown at upper left): larval mines usually independent through first instar, usually communal during second and sometimes third instars, usually independent but frequently crossing one another through final stages.

and Wygant (1954:15) reported a maximum of 144 eggs in one gallery; they also reported that there was an average of 20.5 eggs per inch of gallery (excluding the diagonal first inch). In the present study it was found that the number of eggs per inch of gallery where eggs occurred was equal to that found by Massey and Wygant, but this rate of deposition was seldom maintained for more than a third the length of the gallery. The largest number of eggs counted in one gallery during this study was 53 in an area where a small epidemic was beginning on the Wasatch National Forest.

There is considerable variation in the way eggs are deposited. In some galleries all or part of the eggs are placed individually in separate niches. These niches may be lengthened sufficiently to accommodate two or more eggs, or extended into elongate grooves as much as eight centimeters in length. The niches, or the more typical grooves, ordinarily are placed alternately on the sides of the egg tunnel in contact with the cambium. Ordinarily, individual niches are formed when the gallery enters a moderately unfavorable environment. Each egg or group of eggs is covered by a layer or partition of frass that separates them from the main gallery.

Following oviposition the gallery may be extended a short distance in an irregular feeding tunnel. When both parents are represented separate feeding tunnels may give the gallery a characteristic Y-shaped ending. Evidently most of the beetles re-emerge to form a second or third set of galleries.

At the high altitudes where this species occurs in Colorado incubation is thought to require three to four weeks (Massey and Wygant, 1954:16); it probably takes much less time in Pacific Coast areas where suitable hosts enable this species to live at or near sea level. The newly hatched larvae feed in the phloem in contact with the cambium, either individually or in groups, in a general direction at right angles away from the egg gallery. Ordinarily communal feeding is the rule during the second instar (Fig. 61). When about one-third grown all larvae form separate feeding tunnels that wind throughout the phloem frequently crossing one another. Some larvae that hatch from the first eggs deposited in June may become callow adults by October, however most of them overwinter as larvae and complete their development the following spring. Pupal cells are formed at the ends of the larval mines or in frass of a previously excavated area, either next to the cambium or entirely in the bark. The pupal period in the late spring or early summer may be completed in about 10 to 15 days (Massey and Wygant, 1954:17), however completion of this stage may take several months if pupation begins in the late fall and continues through the winter. A normal life cycle evidently requires from one to two years.

The low temperatures which prevail throughout much of the year in many areas where this species occurs may have a profound effect on the length of the life cycle of this insect. Collectors who took it in the McKenzie River area in northern Canada and in northcentral Alaska estimated that at least two years were required for larval development. The most remarkable adjustment this species has made to survive low temperatures, however, was reported by Massey and Wygant (1954:8) from studies conducted in Colorado. Many of the beetles emerged from brood galleries and went to the bases of trees, ordinarily a brood tree, where they reentered the host at or near the ground level. Here they passed the winter in feeding tunnels, then re-emerged in June or July to begin a new attack. It was estimated that about half of the beetles passed the winter in the same spot where they became adults; the remaining half included those beetles with the special overwintering habit. This hibernation habit has not been reported from other parts of the distribution of this species, nor has it been reported for any other species of *Dendroctonus;* almost certainly it is not restricted to the Colorado area, nor to this one species.

Dendroctonus simplex Leconte

Figs. 22, 41, 62.

Dendroctonus simplex Leconte, 1868, Trans. American Ent. Soc. 2:173; Leconte, 1876, Proc. American Philos. Soc. 15:384, 385; Provancher, 1878, Fauna Ent. Canada 5(Add. et Cor.):13, 14; Schwarz, 1886, Ent. Americana 2:56; Schwarz, 1888, Ins. Life 1:162; Dietz, 1890, Trans. American Ent. Soc. 17:28, 31; Hopkins, 1898, U. S. Dept. Agric. Div. Ent. Bull. 17:69; Hopkins, 1899, Proc. Ent. Soc. Washington 4:343; Hopkins, 1909, U. S. Dept. Agric. Bur. Ent. Tech. ser. 17(1):117; Swaine, 1909, New York St. Mus. Bull. 134:99; Hagedorn, 1910, Coleopterorum Catalogus 4:23; Hagedorn, 1910, Genera Insectorum 111:60; Blatchley and Leng, 1916, Rhynchophora or weevils of Eastern America, p. 653; Swaine, 1918, Dom. Canada Dept. Agric. Ent. Br. Bull. 14(2):62; Chamberlin, 1939, Bark and Timber Beetles of North America, p. 152, 162. Biol.: Packard, 1887, U. S. Dept. Agric. Ent. Comm. Bull. 7:177; Packard, 1890, U. S. Dept. Agric. Ent. Comm. Rept. 5:722; Harrington, 1891, Canadian Ent. 23:27; Hopkins, 1898, Proc. Soc. Prom. Agric. Sci. 19:104; Hopkins, 1899, West Virginia Agric. Expt. Sta. Bull. 56:392, 394; Felt, 1906, New York St. Mus., Mem. 8, 2:752; Fall and Cockerell, 1907, Trans. American Ent. Soc. 33:218; Hopkins, 1907, U. S. Dept. Agric Yearbook 1906:515; Hopkins, 1909, U. S. Dept. Agric. Bur. Ent. Bull. 83(1):103; Swaine, 1913, Ontario Ent. Soc. Rept. 43:89; Hewitt, 1917, Canada Dept. Agric. Ent. Br. Rept. 1916:36; Blackman and Stage, 1918, New York St. Coll. For., Syracuse Univ. 4(4), Tech. Pub. 10:39; Felt, 1924, Manual of Tree and Shrub Insects, p. 261; Peirson, 1929, Maine or. Serv. Bull. 5:79; Simpson, 1929, Canadian Ent. 61:274; Prebble, 1933, Canadian Ent. 65:145; Dodge, 1938, Minnesota Agric. Expt. Sta. Tech. Bull. 132:27; Weber, 1942, Minnesota Dept. Conserv. Statis Rept. 1941:79; McGuffin and Barker, 1947, Canada Dept. Agric. For. Ins. Surv. Rept. 1946:57; Anonymous, 1955, U. S. Dept. Agric. For. Serv. Imp. For. Ins. 1954:18.

The only species closely allied to this species is *pseudotsugae* from which *simplex* is distinguished by the much smaller size, by the less strongly protubrant, smoother but more coarsely punctured frons (Fig. 22), by the more coarsely punctured pronotum, by the larger punctures on the declivital interspaces, and by the distribution (Fig. 62).

Male.—Length 3.4-5.0 mm. (average about 4.2), 2.4 times as long as wide; mature body color dark brown, elytra often with a reddish cast.

Frons broadly convex, protruding somewhat on lower half, the inflated area arising abruptly just above the smooth, elevated rim of epistomal margin; epistomal process less than a third (0.30 times) as wide as distance between eyes, its arms very strongly oblique (about 80° from the horizontal) and usually not elevated, the horizontal portion about three-fourths its total width, flat, overlapping and apparently flush with epistomal margin (actually ending just above the slightly extended margin) and bearing under its distal margin a dense brush of yellowish setae; surface shining, smooth, with rather coarse, deep, very close punctures and a very few minute granules. Vestiture sparse, rather short, fine, inconspicuous.

Pronotum 1.4 times as wide as long; widest at base, sides weakly arcuate and converging toward the rather strong constriction just behind the broadly, shallowly emarginate anterior margin; surface smooth and shining, the punctures rather coarse, irregular in size, close, deep; median line narrowly impunctate posteriorly. Vestiture moderately abundant, fine and rather short on disc, longer and coarse laterally.

Elytra 2.5 times as long as pronotum; sides straight and subparallel on basal two-thirds, rather broadly rounded behind; basal margins arcuate and bearing a row of about ten rather large, raised, overlapping crenulations, with several smaller submarginal ones particularly on interspaces two and three; striae weakly impressed, the punctures rather large and deep, usually decreasing slightly in size toward base; interstriae less than one and one-half times as wide as striae and armed by an irregular row of transverse crenulations, each averaging about one-third the width of an interspace, a few half as wide on posterior half of disc, a few fine punctures interspersed with crenulations. Declivity rather steep, convex, with sutural interspace very strongly elevated and interspace two weakly impressed; striae rather deeply, narrowly impressed, the punctures greatly reduced; interstrial punctures rather coarse, numerous and confused on one, uniseriate on two and three; none of the punctures granulate. Vestiture rather coarse, slightly longer on declivity, the longest setae equal in length to about one and one-half times the width of an interspace.

Female.—Very similar to male except declivital interspaces with minute confused punctures and each with a median row of coarse, somewhat pointed tubercles, the tubercles spaced by a distance slightly less than width of an interspace.

Type locality.—Canada. The type was studied.

Hosts.—Larix laricina.

Distribution.—The eastern United States and Canada north of West Virginia west to northern British Columbia and Alaska.

Specimens from the following localities were examined (Fig. 62). ALASKA: College, Fairbanks, and McGrath. MAINE: Cupsuptic. MICHIGAN: East Lansing, Grand Island, Grand Ledge, Mackinac Isl., Marquette, Munising, Port Huron, and Seney. MINNESOTA: Carlton Co., Hennepin Co., Itasca St. Pk., Lake Itasca, Mille Lacs Co., Pine River, and St. Paul. NEW HAMPSHIRE: Pittsburg, and West Stewartstown. NEW YORK: Erie Co. WEST VIRGINIA: Cranesville. ALBERTA: Bilby, Edmonton, Mitsue, and Smith. BRITISH COLUMBIA: Wildmare Ck. NEW BRUNSWICK: Fredericton, and Nictor Lake. NEWFOUNDLAND: "Newfoundland." NOVA SCOTIA: Sydney. ONTARIO: Deili, Pine Springs, and Wooler. QUEBEC: Gaspe, Natashquan, and Ungara Bay.

Geographical variation.—Not evident in the material at hand.

Biology.—This species prefers dying or injured trees, and consequently, is not generally regarded as having major economic importance. However, it is known to have successfully attacked and killed healthy mature larch trees.

This species was not observed during this study; all comments which follow are based on Hopkins (1909b:103-106), Simpson

Fig. 62. Probable distribution of *Dendroctonus* spp. with collection sites indicated: 1, *pseudotsugae* (circles); 2. *simplex* (triangles).

(1929:274-279) and Prebble (1933:146). The galleries illustrated by Hopkins for this species are used as the basis for the qualified description of the galleries below. Since the placement of eggs in his figure lack detail, since the system appears to resemble that of the very closely related *pseudotsugae*, and because of the general phyletic position of *simplex* in the genus, it is presumed that egg grooves, not niches as illustrated, would normally be constructed by this species.

The principal overwintering stage is the young adult in the brood gallery, although it is not uncommon for some larvae to overwinter. Flight activity begins early in May and continues at a relatively low level until late August; the period of greatest activity apparently is from the last week of May to the second week of June. Adult beetles may re-emerge to construct a second or third set of galleries during the season, but none of their progeny leave the brood tree until the following spring.

Trees selected for attack include windfalls, snow breaks, stumps or other weakened or severely damaged material. The exact pattern of the attack and details of the galleries and habits have not been reported.

Hopkins (1909b:103) indicated that the galleries are vertical and slightly sinuate. Evidently they average about 20 to 25 cm. in in length. The eggs are deposited in groups of three to six or more, presumably in grooves rather than in individual niches. The larvae mine individually in continual contact with the cambium away from the egg gallery and without crossing one another. Evidently the larval mine increases only slightly through the first and second instars then expands suddenly into an irregularly oval feeding area where the last two larval instars, pupation and hibernation occur.

Oviposition ordinarily begins about the last week of May. The eggs hatch in about 11 days (Prebble, 1933:146) and complete larval development in approximately 27 days; about seven days are required for the pupal stage during the early summer months. Simpson found young adults in the first set of galleries completed during the season by August 1; in the second set of galleries young adults were present by September 17; larvae produced in the third set of galleries formed by these same parent adults passed the winter as larvae. The young adults produced in the first and second sets of galleries overwintered in those galleries and emerged the following May and early June. The overwintered larvae from the third set of galleries matured in June and emerged during July.

Dendroctonus pseudotsugae Hopkins

Figs. 23, 42, 62-63.

Dendroctonus similis: Leconte, 1876, Proc. American Philos. Soc. 15:385 (in part); Leconte, 1878, Bull. U. S. Geol. Geogr. Surv. 4:469; Packard, 1887, U. S. Dept. Agric. Ent. Comm. Bull. 7:177; Packard, 1890, U. S. Dept. Agric. Ent. Comm. Rept. 5:722; Dietz, 1890, Trans. American Ent. Soc. 17:30; Hopkins, 1899, West Virginia Agric. Expt. Sta. Bull. 56:392; Hopkins, 1899, U. S. Dept. Agric. Div. Ent. 21:10, 11, 21, 22, 26; Wickham, 1902, Bull. Lab. Nat. Hist. St. Univ. Iowa 5:310; Fall, 1907, Trans. American Ent. Soc. 33:218.

Dendroctonus pseudotsugae Hopkins, 1901, Proc. Soc. Prom. Agric. Sci. 22:67 (*nomen nudum*); Hopkins, 1903, Canadian Ent. 35:60; Hopkins, 1904, U. S. Dept. Agric. Div. Ent. Bull. 48:19, 45 (*nomen nudum*); Hopkins, 1905, U. S. Dept. Agric. Bur. Ent. Bull. 56:10, 11; Hopkins, 1906, Proc. Ent. Soc. Washington 8:4; Hopkins, 1909, U. S. Dept. Agric. Bur. Ent. Tech. ser. 17(1):121; Hagedorn, 1910, Coleopterorum Catalogus 4:22; Hagedorn, 1910, Genera Insectorum 111:60; Swaine, 1918, Dom. Canada Dept. Agric. Ent. Br. Bull. 14(2):62; Chamberlin, 1939, Bark and Timber Beetles of North America, p. 150, 159; Chamberlin, 1958, Scolytoidea of the Northwest, p. 73. Biol.: Swaine, 1914, Dom. Canada Dept. Agric. Ent. Br. Bull. 7:28; Brunner, 1915, U. S. Dept. Agric. Bull. 255:5; Chamberlin, 1917, Canadian Ent. 49:324; Chamberlin, 1918, Oregon Agric. Expt. Sta. Bull. 147:17; Hopping, 1921, Dom. Canada Dept. Agric. Circ. 15:10; Hopping, 1922, Canadian Ent. 54:131; Gibson, 1923, Canada Dept. Agric. Ent. Br. Rept. 1919-20:16; Felt, 1924, Manual of Tree and Shrub Insects, p. 258; Hofmann, 1924, U. S. Dept. Agric. Bull. 1200:53; Caverhill, 1925, British Columbia Dept. Lands For. Rept. 1924:E-17; Craighead, 1927, U. S. Dept. Agric. Circ. 411:11; Craighead, 1930, U. S. Dept. Agric. Misc. Pub. 74:5; Craighead, 1931, Jour. Forestry 31:1016; Hopping, 1932, Timberman

33(7):61; Bedard, 1933, Jour. Econ. Ent. 26:1128; Beal, 1935, Timberman 37(2):14; Furniss, 1936, Timberman 37(3):21; Furniss, 1937, Timberman 39(2):11; Bedard, 1937, Washington St. Coll. Res. Studies 5:103; Hopping, 1939, *in Mulholland*, Forest Resources of British Columbia, p. 62; Keen, 1938, U. S. Dept. Agric. Misc. Pub. 273:119; Beal, 1939, Rocky Mtn. Conf. Ent. Rept. 15:6; Furniss, 1941, U. S. Dept. Agric. For. Serv. Fire Contr. Notes 5:211; Hopping, 1942, Canadian Ent. 74:205; Kimmey and Furniss, 1943, U. S. Dept. Agric. Tech. Bull. 851:20; Patterson, 1945, Univ. Washington Pub. Biol. 10:149; Hopping, 1947, Canadian Ent. 79:150; Leech, 1947, Canada Dept. Agric. For. Ins. Surv. Rept. 1946:80; Leech, 1947, Canada Dept. Agric. Ins. Pest Rev. 25:63; Anonymous, 1947, California Dept. Nat. Res. Div. For. For. Ins. Cond. 1946:10; Mahaffay, 1948, American For. 54:64, 80; Anonymous, 1948, U. S. Dept. Agric. Bur. Ent. Pl. Quar. Ins. Pest Surv. 1947:17; MacKay, 1948, Canada Dept. Agric. For. Ins. Surv. Rept. 197:94; MacKay, 1949, Canada Dept. Agric. For. Ins. Surv. Rept. 1948:114; Bedard, 1950, U. S. Dept. Agric. Circ. 817, 10 p.; Evans, 1950, Canada Dept. Agric. For. Ins. Surv. Rept. 1949:106; MacKay, 1950, Canada Dept. Agric. For. Ins. Surv. Rept. 1949:114, 120; Anonymous, 1950, U. S. Dept. Agric. Bur. Ent. Pl. Quar. Ins. Pest Surv. 1949:26; Anonymous, 1950, U. S. Dept. Agric. Pacific Northw. For. Range Expt. Sta. Rept. 1949:52; Beal, 1951, Proc. West. For. Conserv. Assoc. 41:58; Evans and Dyer, 1951, Canada Dept. Agric. For. Ins. Surv. Rept. 1950:110; Kenney, 1951, British Columbia Dept. Lands For. For. Serv. Rept. 1950:63; Richmond and Kinghorn, 1951, For. Chron. 27:31; Ross and Jones, 1951, Canada Dept. Agric. For. Ins. Surv. Rept. 1950:114; Anonymous, 1951, U. S. Dept. Agric. Bur. Ent. Pl. Quar. Ins. Pest Surv. Sp. Sup. 4:7; Anonymous, 1951, U. S. Dept. Agric. Bur. Ent. Pl Quar. Ins. Pest Surv. 1950:25; Evans and Dyer, 1952, Canada Dept. Agric. For. Ins. Surv. Rept. 1951:108; Graham, 1952, British Columbia Lumberm. 36(7):52; Anonymous, 1952, U. S. Dept. Agric. Bur. Ent. Pl. Quar. Coop. Econ. Ins. Rept. 1(Sp. Rept.):92; Evans and Dyer, 1953, Canada Dept. Agric. For. Ins. Surv. Rept. 1952:130; Richmond, 1953, British Columbia Dept. Lands For. For. Serv. Rept. 1952:86; Richmond, 1953, British Columbia Lumberm. 37(5):42, 90, 92; Ross and Jones, 1953, Canada Dept. Agric. For. Ins. Surv. Rept. 1952:133; Wright, 1953, Proc. West. For. Conserv. Assoc. 43:153; Anonymous, 1953, U. S. Dept. Agric. Portland For. Ins. Lab. Rept. 1952:30; Evans and Silver, 1954, Canada Dept. Agric. For. Ins. Surv. Rept. 1953:139; Glascock, 1954, Proc. West. For. Conserv. Assoc. 44:45; Hoyt, 1954, U. S. Dept. Agric. Bur. Ent. Pl. Quar. Rept. 1952-53:21; Knight and Wilford, 1954, U. S. Dept. Agric. Rocky Mtn. For. Range Expt. Sta. Ins. Cond. Rept. 1953:4; Orr, 1954, U. S. Dept. Agric. Intermtn. For. Range Expt. Sta. Ins. Cond. Rept. 1953:1; Ross, 1954, Canada Dept. Agric. For. Ins. Surv. Rept. 1953:142; Bailey, 1955, U. S. Dept. Agric. Intermtn. For. Range Expt. Sta. Rept. 1954:41; Cornelius, 1955, Jour. Forestry 53:711; Cornelius, 1955, Proc. West. For. Conserv. Assoc. 45:50; Cowlin, 1955, U. S. Dept. Agric. Pacific Northw. For. Range Expt. Sta. Rept. 1954:31, 37; Evenden and Wright, 1955, U. S. Dept. Agric. For. Serv. For. Pest Leaf. 5, 4 p.; Fang and Allen, 1955, Jour. Econ. Ent. 48:79; Kinghorn, 1955, Jour. Econ. Ent. 48:501, 503; Silver and Ross, 1955, Canada Dept. Agric. For. Ins. Surv. Rept. 1954:117; Spaur, 1955, Oregon St. Bd. For. Bien. Rept. St. For. 1952-54:42; Anonymous, 1955, California For. Pest Contr. Act. Comm. For. Ins. Cond. 1954:6, 8; Anonymous, 1955, U. S. Dept. Agric. For. Serv. Imp. For. Ins. 1954:2, 4, 7, 10; Anonymous, 1955, U. S. Dept. Agric. Pacific Northw. For. Range Expt. Sta. For. Ins. Surv. 1954:23; Anonymous, 1956, U. S. Dept. Agric. Pacific Northw. For. Range Expt. Sta. For. Ins. Surv. 1955:27, 40; Bailey, 1956, U. S. Dept. Agric. Intermtn. For. Range Expt. Sta. Rept. 1956:29, 32; Chapman and Wilson, 1956, Jour. Econ. Ent. 49:427; Cowlin, 1956, U. S. Dept. Agric. Pacific Northw. For. Range Expt. Sta. Rept. 1955:34, 37; Gardiner, 1956, Canada Min. Agric. Rept. 1954-55:17; Hagenstein and Furniss, 1956, Proc. Soc. Amer. For. 1955:167; LeJeune, 1956, British Columbia Dept. Lands For. For. Serv. Rept. 1955:80; McArdle, 1956, U. S. Dept. Agric. For. Serv. Rept. 1955:12;

Lu and Bollen, 1956. Proc. Soc. Amer. Bact. 56:35; Ostmark and Wilford, 1956, U. S. Dept. Agric. Rocky Mtn. For. Range Expt. Sta. Pap. 22:5, 13; Phipps, 1956, Oregon St. Bd. For. Bien. Rept. St. For. 1954-56:29; Price, 1956, U. S. Dept. Agric. Rocky Mtn. For. Range Expt. Sta. Rept. 1955:21; Rudinsky and Vité, 1956, For. Sci. 2:258; Silver and Ross, 1956, Canada Dept. Agric. For. Ins. Surv. Rept. 1955:93; Walters, 1956, Canada Dept. Agric. Pub. 975, 11 p.; Yasinski, 1956, U. S. Dept. Agric. Rocky Mtn. For. Range Expt. Sta. Pap. 23:1, 3; Cowlin, 1957, U. S. Dept. Agric. Pacific Northw. For. Range Expt. Sta. Rept. 1956:25; Gibson, 1957, Jour. Econ. Ent. 50:266; Kahn, 1957, Canadian Jour. Zool. 35:519; Lu, 1957, For. Sci. 3:336; Price, 1957, U. S. Dept. Agric. Rocky Mtn. For. Range Expt. Sta. Rept. 1956:81, 84, 86; Silver and Ross, 1957, Canada Dept. Agric. For. Ins. Surv. Rept. 1956:81, 86; Vité and Rudinsky, 1957, For. Sci. 3:156; Whiteside, 1957, U. S. Dept. Agric. Pacific Northw. For. Range Expt. Sta. For. Ins. Cond. 1956:2, 5, 31, 43; Atkins and Chapman, 1957, Canadian Ent. 89:80.

This species is very closely allied to *simplex*, but may be distinguished by the larger size, by the more strongly protubrant, more finely punctured, subgranulate, irregular surface of the frons (Fig. 23), by the more finely punctured pronotum, by the finer punctures of the declivital interspaces, and by the distribution (Fig. 62).

Male.—Length 4.4-7.0 mm. (average about 5.5), 2.3 times as long as wide; body color very dark brown, with reddish brown elytra.

Frons broadly convex, protruding rather strongly on lower half, inflated area arising abruptly just above smooth, elevated rim of epistomal margin; epistomal process about a fourth (0.24 times) as wide as distance between eyes, its arms very strongly oblique (about 80° from the horizontal) and usually not elevated, the horizontal portion about three-fourths its total width, flat, overlapping and apparently flush with or exceeding epistomal margin and bearing under its distal margin a dense brush of yellowish setae; surface irregular, rather finely, closely punctured and becoming granulate on lower half. Vestiture sparse, rather short, fine inconspicuous.

Pronotum 1.4 times as wide as long, widest at base; sides weakly arcuate and converging toward the strong constriction just behind the broadly, shallowly emarginate anterior margin; surface smooth and shining, the punctures rather small, irregular in size, close, deep; median line narrowly impunctate posteriorly (usually); vestiture moderately abundant, fine and rather short on disc, longer and coarse laterally.

Elytra 2.5 times as long as pronotum; sides straight and subparallel on basal two-thirds, rather broadly rounded behind; basal margins arcuate and bearing a row of about ten rather large, raised, overlapping crenulations, with several smaller submarginal ones particularly on interspaces two and three; striae weakly impressed, the punctures rather large and moderately deep, usually decreasing slightly in size toward base; interstriae about one and one-half times as wide as striae and armed by abundant, confused, transverse crenulations, each averaging almost half the width of an interspace, a few two-thirds as wide on posterior half of disc. Declivity rather steep, convex, with sutural interspace very strongly elevated and interspace two weakly impressed; striae rather deeply impressed, the punctures half as large as on disc; interstrial punctures rather fine, abundant and confused on one and three, almost uniseriate on two; none of the punctures granulate. Vestiture rather coarse, slightly longer on declivity, the longest setae equal in length to about one and one-half times the width of an interspace.

Female.—Very similar to male except declivital interspaces with smaller punctures and each with a median row of very coarse, somewhat pointed tubercles, the tubercles spaced by a distance slightly less than width of an interspace.

Type locality.—Grants Pass, Oregon. The type was studied.

Hosts.—*Pseudotsuga taxifolia*, *P. macrocarpa*, and less commonly from *Larix occidentalis* and *Tsuga heterophylla*.

Distribution.—Western United States, Alberta and British Columbia.

Specimens from the following localities were examined (Fig. 62). ARIZONA: Chiricahua Mts., Flagstaff, San Francisco Mts., and Santa Catalina Mts. CALIFORNIA: Alameda Co., Alma, Bean Ck., Big Basin, Boulder Ck., Callahan, Camp Meeker, Chester, Coulterville, Dead Horse Summit in Siskiyou Co., Fieldbrook, Foresthill, Gaberville, Green Point, Guerneville, Hackamore, Half Moon Bay, Happy Camp in Siskiyou Co., Honda, Laguinitas, La Honda, Lights Ck., McCloud, Meadow Valley, Moffat Ck. in Siskiyou Co., Mohawk, Palo Alto, Placerville, Point Reyes, Quincy, Santa Cruz, Trinity Co., Upper Lake in Lake Co., Wrights, and Yellow Ck. COLORADO: Colorado Springs, Ft. Garland, Gunnison N. F., Moffat, Pagosa Springs, Palmer Lake, San Isabel N. F., San Juan N. F., and Saguache. IDAHO: Beaver Canyon in Nez Perce Co., Beaver Ck. in Logan Canyon, Henry's Lake, Kooskia, Kootenai, Pioneerville, Priest River, Sandpoint, Smiths Ferry, and Stites. MONTANA: Apgar, Belton, Bozeman, Columbia Falls, Fish Ck. Station, Kalispell, Lake McDonald, Middle Ck. in Gallatin Co., and Ovando. NEW MEXICO: Capitan, Cloudcroft, Santa Fe, Tres Ritos, and Vermejo Pk. OREGON: Ashland, Clover Ck., Cold Springs, Corvallis, Detroit, Dixie Pass, Elk Ck., Forest Grove, Grants Pass, Hood River, Jewell, Klamath N. F., MacDonald Forest, Mary's Peak, Mistletoe, Mt. Angel, Myrtle Point, Newport, Oregon Caves, Otis, Philomath, Pinehurst, Portland, St. Helens, Salmon River, Santiam N. F., Siskiyou Mts., Sumpter, Tillamook, Tiller, and Waldo. UTAH: Cache N. F., Logan Canyon, Panguitch, Parowan Canyon, Provo Canyon, and Sanford Canyon. WASHINGTON: Ashford, Buckeye, Curlew, Des Moines, Easton, Fairfax, Grays Harbor City, Hoodsport, Hoquiam, Kent, Keyport, La Grande, Longmire, Meredith, Metaline Falls, Monroe, Mt. Rainier N. P., North Bend, Northport, Orting, Payallup, Port Angeles, Port Williams, Pullman, Quinalt, Sappho, Satsop, Seattle, Shelton, Stimson Ck. in Mason Co., and Vancouver. ALBERTA: Waterton. BRITISH COLUMBIA: Australian, Babine Lake, Barriere, Bestwick, Boston Bar, Britain River, Buttle Lake, Campbell River, Canim Lake, Cowichan Lake, Cumberland, Fernie, Fraser River Valley, Grant Lake, Hamilton Lake, Kamloops, Kettle River Valley, Lac LaHache, Lillooet River Valley, Lumby, Macalister, Merritt, Nimpkish Valley, Okanagan Lake, Prince George, Quesnel, Seymour Narrows, Soda Ck., Trinity Valley, Upper Campbell Lake, Vancouver, Vernon, West Kettle River Valley, Williams Lake, Windermere Lake, and Wogs Lake.

Geographical variation.—Not evident in the material at hand.

Biology.—This is a primary insect enemy of Douglas Fir. Although estimates of damage inflicted by it are not available for all regions where it occurs, it probably is responsible for an average annual loss in excess of a half billion board feet of timber.

The winter is passed chiefly as young adults, although some larvae and parent adults also overwinter successfully. Flight activity may begin as early as the first of April and evidently continues at least until early September. Two principal periods of flight activity occur, the first during May or June is composed of overwintered young adults, the second during July or August is composed of beetles that overwintered as larvae and of parent adults re-emerging from their first set of galleries. The exact timing of each principal flight period may vary from locality to locality with altitude, latitude, exposure, peculiarities of a particular season, or other local ecological factors.

Ordinarily the material selected for attack includes stumps, windfalls, broken logs, or other injured or prostrate trees larger than eight inches in diameter. However, when populations are high or when assisted by draught, healthy, vigorous standing timber may be selected. The attack on a standing tree usually begins in the upper midbole area and progresses upward and downward from that point. In prostrate material, at least when the bark is relatively thick, the beetles attack the sides and upper surfaces as well as the lower. The attack is slow and continuous, without any sudden or concerted swarming of the beetles. Its duration is variable, evidently depending on the population density of beetles in the area, upon resistance of the host, or upon local climatic or other local ecological factors. It may be completed in a few days or it may continue for more than a year and involve two or possibly more successive generations.

The egg galleries (Fig. 63) are constructed almost entirely in the inner bark; they are in continual contact with the cambium and may very lightly score or at least stain the wood. They are straight or nearly so, and parallel the grain of the wood.

The initial attack is made by the female beetle in a crevice of the bark. Soon after beginning the attack she is joined by a male who takes over the function of removing frass from the entrance hole. Mating evidently occurs within a few hours after the cambium is reached. After the gallery has been extended several centimeters the male may pack the lower areas with frass thereby closing the entrance hole, or he may leave the gallery in search of another female. Most of the galleries are from about 12 to 30 cm. in length, but are known to exceed 90 cm. As with other species, ventilation tunnels are placed at irregular intervals, or they may be entirely absent. The maximum number of ventilation tunnels counted in more than a hundred galleries measured during this study was four; about 80 percent of the galleries had two ventilation tunnels.

Oviposition may begin within two or three days after the attack; according to Vité and Rudinsky (1957:157) the first eggs, under controlled laboratory conditions, may appear within 36 hours after the attack begins. Eggs evidently may be found throughout the

Fig. 63. *Dendroctonus pseudotsugae*: Egg galleries longitudinal, straight; eggs deposited in grooves, each oriented with its long axis perpendicular to egg gallery; larval mines usually independent, almost never cross, but may join one another during final stages of development.

period of summer activity until about early September. According to Chamberlin (1918:20) one female may produce as many as 160 eggs in one gallery; the maximum number counted during this study was 102 in a gallery only partly complete.

Eggs are deposited in grooves about two to four millimeters deep along the sides of the gallery, near but not necessarily touching the cambium. The grooves are placed alternately on the sides, without overlapping or without more than a few millimeters between the end of the groove on one side and the beginning of the next on the other side. The grooves vary considerably in length, they range from less than one to more than eight centimeters. The eggs are deposited in a single row in contact with one another and oriented with the long axis perpendicular to the egg gallery and more or less parallel to the cambium. It is presumed that the larvae emerge from the egg at the end farthest from the egg gallery. This habit of orienting the eggs is peculiar in the genus among the species observed personally during this study, and presumably is associated with the fact that the larvae construct independent mines, rather than working in congress as with other species that deposit masses of eggs in common grooves. The eggs are held in position by a rather thick layer or partition of coarse, fibrous frass that separates them from the egg gallery. Following the period of oviposition most of the females re-emerge to construct a second set of galleries.

The period of incubation varies considerably with various factors, particularly temperature. Vité and Rudinsky (1957:161) found, under controlled conditions, that it ranged from about 6 to 28 days. Under field conditions estimates of the incubation period range from 8 to 24 days. Under controlled conditions, Vité and Rudinsky (1957:161) found that larval development required about 19 to 72 days and the pupal period about 5 to 18 days. The larvae construct individual mines more or less perpendicular to the egg gallery and are in continual contact with the cambium area. They increase gradually in diameter and tend to fan out somewhat as they progress. Unless crowding occurs they normally do not cross one another. Near the end of larval development a pupal chamber may be cleared in the cambium area at the end of the larval mine, or the larva may bore out into the bark for a variable distance before pupating. The young adults overwinter in the brood galleries and emerge the following spring. Larvae that develop from eggs deposited in the fall may not mature before the onset of cold weather and, therefore, pass the winter as larvae. These larvae mature early in the following summer and may emerge in July or August, or, evidently, they may overwinter in the brood galleries (Bedard, 1950:9). There is one complete generation and possibly a partial second generation each year.

Material Examined

Although an exact count was not kept during this study, it is estimated that the number of specimens examined exceeded the following figures: *brevicomis*, 2000; *frontalis*, 400; *parallelocollis*, 500; *adjunctus*, 500; *ponderosae*, 2000; *aztecus*, 26; *terebrans*, 200; *valens*, 2000; *micans*, 150; *punctatus*, 200; *murrayanae*, 400; *obesus*, 5000; *simplex*, 300; *and pseudotsugae*, 2000. The distribution maps and records treated in the discussion of each species indicate where these species were collected.

The holotypes of species studied include: *brevicomis* Leconte, *barberi* Hopkins, *frontalis* Zimmerman, *arizonicus* Hopkins, *mexicanus* Hopkins, *approximatus* Dietz, *convexifrons* Hopkins, *ponderosae* Hopkins, *monticolae* Hopkins, *jeffreyi* Hopkins, *aztecus*

Wood, *valens* Leconte, *beckeri* Thatcher, *punctatus* Leconte, *johanseni* Swaine, *murrayanae* Hopkins, (*Hylurgus*) *obesus* Mannerheim, *piceaperda* Hopkins, *engelmanni* Hopkins, *borealis* Hopkins, *similis* Leconte, *simplex* Leconte, and *pseudotsugae* Hopkins. In addition, the types of *adjunctus* Blandford and of *rufipennis* Kirby were compared to my specimens by Dr. R. T. Thompson at the British Museum of Natural History. The types of *parallelocollis* Chapuis, *terebrans* Olivier, and of *micans* Kugelann were not examined; specimens of *parallelocollis* that were compared to the type for Hopkins were studied, however. Because *micans* is the only European species in the genus there was no problem with its identity.

Biological studies of the various species were conducted by myself in the following localities: *brevicomis* at Flagstaff, Prescott and Williams, Arizona, Dixie N. F., Salina and Ashley N. F., Utah, Plumas N. F. and Lassen N. F., California, and near Sisters, Oregon; *frontalis* at Prescott, Arizona; *parallelocollis* at Dixie N. F., Salina and Sanford Canyon, Utah, Prescott and Williams, Arizona, and Texmelucan, Puebla (Mexico); *adjunctus*, Dixie N. F., Sanford Canyon, and Panguitch, Utah, and Prescott, Arizona; *ponderosae*, Logan Canyon, Ashley N. F., Wasatch N. F., Salina, Panguitch, Sanford Canyon, La Sal Mts., and Dixie N. F., Utah, Flagstaff, Arizona, Fallen Leaf Lake, Lassen N. F., and Tahoe N. F., California, and Ochoco N. F., Oregon; *aztecus*, Coapala, Sinaloa (Mexico); *terebrans*, Kingsland, Georgia; *valens*, Logan Canyon, Ashley N. F., and Panguitch Lake, Utah, Lassen N. F., and Yreka, California; *murrayanae*, Logan Canyon, and Wasatch N. F., Utah; *obesus*, Santa Fe Ski Basin, New Mexico, Logan Canyon, Wasatch N. F., Ashley N. F., Dixie N.F., Utah, Gold Lake and Cascade Head Expt. For., Oregon; and *pseudotsugae*, Logan Canyon, and Sanford Canyon, Utah, Siskiyou Co., California, and Mary's Peak, Oregon.

The hosts and localities included in this study are restricted to those recorded for specimens examined during the study. When localities were not known to me and could not be located on available maps, the locality designation was placed in quotation marks. The scientific name of Douglas fir used here is *Pseudotsuga taxifolia*, as employed by R. J. Preston (1961, North American Trees, p. 63), not *P. menziesii* as currently employed in the checklist.

References to the vast quantity of literature treating *Dendroctonus* species is listed in the synonymies and is thought to be fairly complete to 1958 for all species except *micans*. About two-thirds to three-fourths of the articles listed were examined; mechanical problems made it impossible to examine all sources or to locate and review all recent articles. The disadvantages in this approach are obvious; undoubtedly some injustices and errors have resulted. Because no real taxonomic problem involved the European *micans*, an extensive effort to locate references to this species was not made. In treating the biologies of all species it was arbitrarily decided that when three principal authors who included original data in their reports agreed on a particular point, that point was considered as common knowledge, if it more or less agreed with my observations, and literature citations were not included. In a few instances where contradictory data were presented, all pertinent articles were studied and a decision was made as to the accuracy of the report.

Acknowledgement

The contributions and cooperation of numerous individuals and organizations have made possible the completion of this study. The writer is indebted to M. L. Prebble, Forest Entomology and Pathology Branch, Canada Department of Forestry, for providing in 1955 the initial stimulus and encouragement to undertake a revision of this difficult and important genus of forest insects. Appreciation is also expressed to the U. S. National Museum, to the Museum of Comparative Zoology, to the Museum Zoologicum Univesitatis (Helsinki), to the Canadian National Collection of Insects, to the Portland (Oregon), Berkeley (California), and Albuquerque (New Mexico) regional laboratories of the Forest Service, U. S. Department of Agriculture, to the University of California (Berkeley) and to the Oregon State University for making available facilities and/or specimens for this study. Special thanks are also due to J. B. Thomas (Sault Ste. Marie), George R. Hopping (Calgary), and D. A. Ross (Vernon), Forest Entomology and Pathology Laboratories, Canada Department of Forestry, for special notes and specimens; to R. W. Stark and David L. Wood, Department of Entomology and Parasitology, University of California (Berkeley), and to R. L. Furniss, Forest Service, U. S. Department of Agriculture, for council and direction in arranging field studies and especially for their kindness in reviewing the manuscript of this paper. Of the many forest rangers and entomologists contacted for direction and advice in locating local infestations, special mention should be made for the kindness and special assistance of Vern P. Yerkes, Cascade Head Experimental Forest (Otis, Oregon). Sincere thanks are also expressed to Donald E. Bright, Jr., to Jay B. Karren, and to Howard P. Shurtleff for the many weeks they spent gathering biological data throughout the western United States from 1960 to 1962, for this project. Appreciation is also expressed to the National Science Foundation for the financial aid necessary to conduct the field work that was so vital to this study.

Literature Cited

Beal, J. A. 1939. The Black Hills beetle, a serious enemy of Rocky Mountain pines. U. S. Dept. Agric. Farmers' Bull. 1824, 22 p.

Bedard, W. D. 1950. The Douglas-fir beetle. U. S. Dept. Agric. Circ. 817, 10 p.

Blackman, M. W. 1922. Mississippi bark beetles, Mississippi Agric. Expt. Sta. Tech. Bull. 11, 130 p., 18 pls.

Blackman, M. W. 1931. The Black Hills beetle. Bull New York St. Coll. For., Syracuse Univ. 4(4), Tech. Pub. 36, 97 p.

Blandford, W. F. H. 1895-1905. Family Scolytidae. Biologia Centrali-Americana, Coleoptera 4(6):81-298.

Chamberlin, W. J. 1918. Bark-beetles infesting the Douglas fir. Oregon Agric. Expt. Sta. Bull. 147. 40 p.

Chapuis, F. 1869. Snyopsis des Scolytides. Desoer: Liége. (Preprint of: 1873. Synopsis des Scolytides. Mém. Soc. Roy. Sci. Liége, ser. 3, 2:213-269.)

Craighead, F. C., J. M. Miller, J. C. Evenden, and F. P. Keen. 1931. Control work against bark beetles in western forests and an appraisal of its results. Jour. Forestry 29(7):1001-1018.

Dietz, W. G. 1890. Notes on the species of *Dendroctonus* of Boreal America. Trans. American Ent. Soc. 17:27-32.

Dixon, J. C. and E. A. Osgood. 1961. Southern pine beetle, a review of present knowledge. U.. S. Dept. Agric. For. Serv. S. E. For. Expt. Sta. Pap. 128, 34 p.

Eichhoff, W. 1864. Ueber die Mundtheile und die Fühlerbildung der europäischen Xylophagi sens. strict. Berliner Ent. Zeitschr. 8:17-46.

Eichhoff, W. 1878. Ueber die Borkenkäfer-Gattungen *Hylurgus* Latr. und Blastophagus Eichh. Stettiner Ent. Ztg. 39:399-400.

Eichhoff, W. 1881. Die europäichen Borkenkäfer. Springer: Berlin. 315 p.

Erichson, W. F. 1836. Systematische Auseinandersetzung der familie der Borkenkäfer (Bostrichidae). Archiv Naturgesch. 2(1):45-65.

Evenden, J. C., W. D. Bedard and G. R. Strubble. 1943. The Mountain pine beetle, an important enemy of western pines. U. S. Dept. Agric. Circ. 664, 25 p.

Fabricius, J. C. 1801. Systema Eleutheratorum secundum or-, denes, genera, species, adjectis synonymis, locis, observationibus, descriptionibus 2:384-395.

Fronk, W. D. 1947. The Southern pine beetle, its life history. Virginia Agric. Expt. Sta. Tech. Bull. 108, 12 p.

Hopkins, A. D. 1909a. Contributions toward a monograph of the scolytid beetles. I. The genus *Dendroctonus*. U. S. Dept. Agric. Bur. Ent. Tech. ser. 17(1):1-164.

Hopkins, A. D. 1909b. Practical information of the scolytid beetles of North American forests. I. Barkbeetles of the genus *Dendroctonus*. U. S. Dept. Agric. Bur. Ent. Bull. 83(1):1-169.

Hopkins, A. D. 1915. Contributions toward a monograph of scolytid beetles. II. Preliminary classification of the superfamily Scolytoidea. U. S. Dept. Agric. Tech. ser. 17(2):165-232.

Larcordaire, T. 1866. Famille LXIII. Scolytides. Histoire Naturelle des Coléoptères 7:349-398.

Latrielle, P. A. 1802. Histoire naturelle, générale et particulière des crustaces et des insects 3, 467 p. Paris.

Leconte, J. L. 1860. Report on insects collected on the survey. Reports of Explorations and Surveys for a Railroad Route from the Mississippi River to the Pacific Ocean 9(1):1-72, 2 pls.

Leconte, J. L. 1868. Appendix to Zimmermann's synopsis of the Scolytidae of America north of Mexico. Trans. American Ent. Soc. 2:150-178.

Leconte, J. L. 1878. Family IX. Scolytidae. *In* J. L. Leconte and G. H. Horn, The Rhynchophora of America north of Mexico. Proc. American Philos. Soc. 15:341-391.

Massey C. L. and N. D. Wygant. 1954. Biology and control of the Engelmann spruce beetle in Colorado. U. S. Dept. Agric. For. Serv. Circ. 944, 35 p.

Miller, J. M. and F. P. Keen. 1960. Biology and control of the western pine beetle. U. S. Department of Agriculture: Washington, D. C., 381 p.

Prebble, M. L. 1933. The larval development of three bark beetles. Canadian Ent. 65(7):145-150.

Schedl, K. E. 1955. Die Kiefern-Borkenkäfer Guatemalas. Zeitschr. angew. Ent. 38(1):1-48.

Simpson, L. J. 1929. The biology of Canadian bark beetles. Canadian Ent. 61(12):274-279.

Swaine, J. M. 1914. Forest insect conditions in British Columbia. Dom. Canada Dept. Agric. Div. Ent. Bull. 7. Expt. Farms. Bull., ser. 2, 17:1-41.

Swaine, J. M. 1919. The Coleoptera collected by the Canadian Arctic Expedition, 1913-18. Report of the Canadian Arctic Expedition 1913-1918, Insects 3(E), 27 p.

Thatcher, T. O. 1954. A new species of *Dendroctonus* from Guatemala (Scolytidae). Coleopterists' Bull. 8(1):3-6.

Vité, J. P. and J. A. Rudinsky. 1957. Contribution toward a study of Douglas fir beetle development. For. Sci. 3(2):156-167.

Westwood, J. O. 1838. Family Scolytidae. *In* Synopsis of the genera of British Insects, p. 39-40. Longman, Orme, Brown, Green and Longmans: London.

Wood, S. L. 1957. Ambrosia beetles of the tribe Xyloterini (Coleoptera: Scolytidae) in North America. Canadian Ent. 89(8):337-354.

Wood, S. L. 1961. An alternative proposal to the suggested validation of *Myelophilus* Eichhoff, 1878 (Insecta, Coleoptera). Bull. Zool. Nomencl. 18(5):319-321.

Zimmerman, J. O. 1868. Synopsis of the Scolytidae of America north of Mexico. Trans. American Ent. Soc. 2:141-149.