

Northernmost Occurrence of Bark Beetles and Their Hosts in the Nearctic

MALCOLM M. FURNISS

Study of bark beetles (Coleoptera: Curculionidae: Scolytinae) in the subarctic region of the New World has received little attention, due primarily to the inaccessible nature of the area and the lack of economic importance of the trees involved. Thus, even the diversity of scolytids in the far north remains to be surveyed systematically. However, in response to increasing attention given to the effects of climate change, I have gathered a listing of bark beetles known to occur in the northernmost tree locations in the Nearctic. Included is a discussion of their

biological characteristics that may adapt them to this environment. I hope that this information will stimulate systematic surveys and studies to determine their diversity, distinctive features, host relationships, and changes taking place through time.

Alaska

The biographic regions of Alaska reflect the great expanse of that state, extending over a wide range of latitude, longitude, and elevation. In broad terms, these regions are characterized by a relatively mild and moist coastal climate, particularly in the southeast and coastal south-central areas; an extensive drier, colder climate in interior and northern Alaska; and numerous mountain ranges that attain the highest elevation on the continent. Except for willows (*Salix* spp.), the species of Alaskan trees are somewhat more diverse in the coastal environment. Because species of Scolytidae are host-specific to a marked degree, their diversity reflects that of woody plant species that are needed and available for their existence. Warmer climate also enhances scolytid diversity by exerting less selective pressure, as is evident in tropical regions. Thus, more than half of the known Alaskan scolytid fauna occur in rather close proximity to the coast. Nonetheless, white spruce, *Picea glauca* (Moench) Voss, a tree that occurs widely in the interior and extending to the northern tree line, is host of more species of scolytids than any other tree species in Alaska (Furniss et al. 2002).

The boreal forest in interior Alaska extends northward to the south slope of the Brooks Range (Figs. 1 and 2).

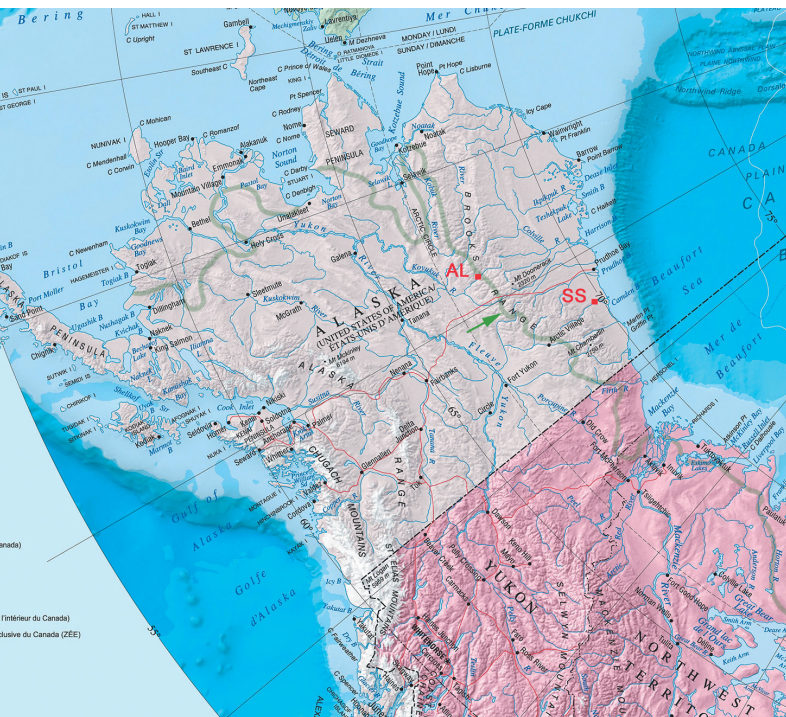


Fig. 1. Map of Alaska showing the tree line (green arrow) in the Brooks Range, and the locations of *Trypophloeus striatulus* at Shublik Spring (SS) and the species in Table 1 from Agiak Lake (AL). Map: Natural Resources Canada.

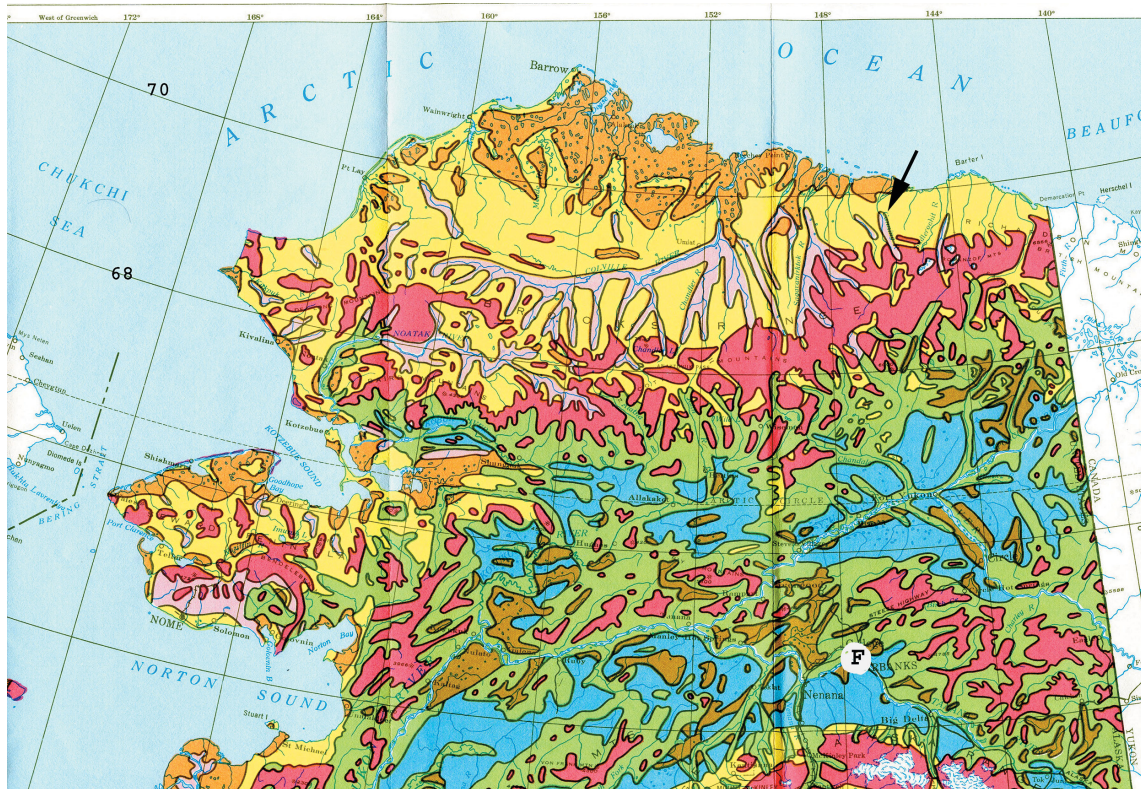


Fig. 2. Vegetative map of Alaska. Fairbanks is denoted by the letter "F"; the arrow denotes the locality of the collection of *Trypophloeus striatulus*. Red area is the non-forested crest of the Brooks Range. Green shows the extent of trees. Light pink areas denote the occurrence of willows on the North Slope surrounded by moist tundra (yellow). Viereck and Little 1972.

This mountain range rises to 2,749 m elevation on Mount Chamberlin (69° 16' 39" N); its crest runs east and west for about 1,100 km. The range is believed to be approximately 126 million years old. Temperatures here are rather extreme, commonly below minus 40° C in winter and above 30° C in summer. Other trees adapted to this northern area include *Picea glauca*, *Picea mariana*, *Betula papyrifera*, *Populus balsamifera*, and *Salix alaxensis* (Viereck and Little 1972). The latter willow species attains a maximum diameter of 18 cm and height of 9 m and is

considered by those authors to be a tree.

Fifty species of Scolytinae (23 species in the Hylesinini and 27 in the Scolytini) in Alaska have been compiled by Furniss et al. (2002). They belong to 23 genera (11 in Hylesinini and 12 in Scolytini). They infest 15 species of Alaskan trees, of which 10 are conifers (host to 47 species of Scolytinae) and five are angiosperms (host to 3 species of Scolytinae); all are native. The extent of their northward migration is limited by that of their tree hosts. For example, *Larix laricina*, host of *Dendroctonus*

Table 1. Bark beetles collected from *Picea glauca* at Agiak Lake, Alaska (Werner and Holsten 1984).

Hylesinini	Scolytini
<i>Carphoborus andersoni</i> Swaine	<i>Cryphalus ruficollis ruficollis</i> Hopkins
<i>Carphoborus carri</i> Swaine	<i>Crypturgus borealis</i> Swaine
<i>Dendroctonus punctatus</i> LeConte	<i>Dryocoetes affaber</i> (Mann.)
<i>Dendroctonus rufipennis</i> (Kirby)	<i>Dryocoetes autographus</i> (Ratzeburg)
<i>Hylurgops rugipennis rugipennis</i> (Mann.)*	<i>Ips borealis borealis</i> Swaine
<i>Phloeosinus pini</i> Swaine	<i>Ips perturbatus</i> (Eichhoff)
<i>Phloeotribus piceae</i> Swaine	<i>Ips tridens tridens</i> (Mann.)
<i>Polygraphus convexifrons</i> Wood	<i>Orthotomicus caelatus</i> (Eichhoff)
<i>Polygraphus rufipennis</i> (Kirby)	<i>Pityophthorus nitidus</i> Swaine
<i>Scierus annectans</i> LeConte	<i>Pityophthorus opaculus</i> LeConte
	<i>Scolytus piceae</i> (Swaine)

* First Alaska published record from *Picea glauca*

simplex LeConte, extends to about 67° N in the Koyuk River drainage, whereas *Picea glauca*, host of the greatest number of Alaskan scolytids, continues northward to tree line at about 69° N in the Brooks Range. Werner and Holsten (1984) reported 21 species of bark beetles attracted to pheromone-baited traps and spruce trap trees in a study at Agiak Lake in the Brooks Range at 68° 15' N (Table 1). Willows, however, are the most diverse woody vegetation in Alaska and display their adaptability by their occurrence along several North Slope rivers as far north as 70° N (Fig. 2). These willows vary in form from prostrate to the more tree-like *Salix alaxensis*, which is the primary host of *Trypophloeus striatulus* (Mannerheim).

Trypophloeus striatulus. I collected *Trypophloeus striatulus* at Shublik Spring (Fig. 1) on 24 July 1976 from *Salix alaxensis* (Andersson). The location is along the Canning River, North Slope of Alaska, 69° 27' 27" N; 146° 13' 15" W. This is the northernmost known record of a bark beetle in Alaska, inland of the Beaufort Sea by about 85 km and approximately 190 km north of the "tree line." Subsequently, I studied the biology of *T. striatulus* in *S. alaxensis* at 28 locations in Alaska (Furniss 2004). Most broods transformed to adults before fall, emerged, and excavated solitary chambers in the bark, where they overwintered before becoming sexually mature in spring. Emerged adults walked on the bark for protracted periods, lacking any disposition to fly. This behavior contributes to re-infesting the stem, downward, for several generations, thereby conserving a susceptible host (limited resource). A fungus, *Cytospora* sp., probably *chrysosperma* (Person) Fries, was present in stems infested by the beetles. Adults usually

chose a lenticel as a site for excavating a chamber, tapping the surface with their antennae, possibly attracted there by odor emitted by fungus-infected, underlying tissue. Egg galleries are primitive (cave-like). Eggs are exceptionally large, relative to the adult, and are laid in a cluster averaging about 20 per female. This is a relatively low number of eggs compared to many bark beetles and is another adaptive feature tuned to the limited host resource available in this environment. Larvae pass through 3 instars, feeding *en masse* in the first instar, then becoming solitary (Fig. 5C). Their mines contain almost entirely excrement, lacking fragments of phloem common in galleries of most bark beetles. Pupation occurs in a cell, excavated by the larva, which usually etches the xylem. A bird preys on overwintering larvae; otherwise the beetle has few natural enemies. An unidentified endoparasitic nematode occurs in the hemocoel of the abdomen in adult beetles. Commensals in galleries include several undescribed mites, and maggots of the dipterous family Sepsidae. The beetle was prevalent in feltleaf willow that had been browsed heavily by moose and in larger, older trees. A sister species, *Trypophloeus dejevi* (Stark), occurs near Nikkaluokta in Lapland, Sweden, on *Salix myrsinifolia*, and on Sakhalin island in North Russia (Lindelöw 2009).

Canada

Canada extends from the Atlantic to the Pacific Ocean and from 60° N to a varying northern tree line that extends to its northernmost point at approximately 69° N in the western provinces of the Yukon Territory and Northwest Territories. Canadian bark beetles can be divided into four major categories based on their

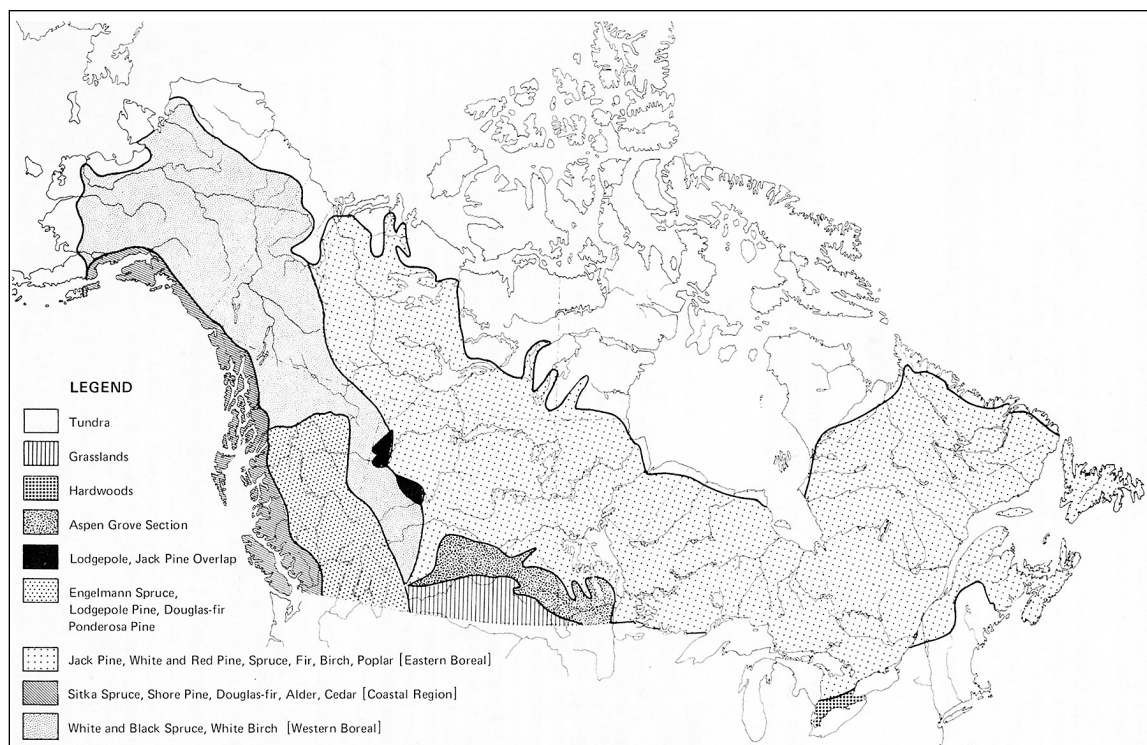


Fig. 3. Simplified forest classification of Canada and Alaska. Bright (1976).



Fig. 4. Location of collections of scolytids shown in Table 2. OC = Old Crow; A = Aklavik; SR = Sandstone Rapids. Map: Canada Department of Energy, Mines and Resources, 1970.

distribution: Transcontinental, Western boreal or montaine (extending to the Yukon Territory and interior Alaska), “Eastern boreal” (extending to the northern tree line in Northwest Territories), and Southern (Bright 1976, Fig. 3). The northernmost collections of Canadian scolytids are from the Yukon Territory and Northwest Territories (Bright 1976, Swaine 1919, Wood 1982). Tree species of this area mirror that of the tree line in Alaska and consist primarily of *Picea glauca* in the fringe area and willows along watercourses. Southward from the tree line, white spruce occurs in admixture with *Picea mariana*, *Betula papyrifera*, and *Populus balsamifera* (Little 1971). As in Alaska, *P. glauca* harbors the most bark beetle species in far northern Canada. In Table 2, all but *T. striatulus* infest that tree species. The Canadian bark beetle fauna numbers about 197 species (Bright 1976). Since that publication, an exotic species, *Tomicus piniperda* (L.) has become established in Canada, but is located far southward in pine.

Collecting in this remote northern area has been very limited (Fig. 4) and located mostly near the villages of Old Crow (67° 39' N) in the Yukon Territory and near Aklavik (68° 14' N) in the Northwest Territories. Old Crow (250 m elev.) has no road access and is in the upper Porcupine River drainage that flows into the Yukon River in interior Alaska. Aklavik (7 m elev.) is accessible by road seasonally and is located near the mouth of the great Mackenzie River that drains northwesterly from several western provinces. Amazingly, considering the winter conditions, Frits Johansen collected *Dendroctonus punctatus* LeConte (as *D.*

Table 2. Bark beetles collected from vicinities of Old Crow, Yukon Territory, and Aklavik and Sandstone Rapids, Northwest Territories, Canada.

Species & location	Date	Collector
Old Crow		
Hylesinini		
<i>Dendroctonus rufipennis</i> (Kirby)	vi-28-1981	D.E. Bright
Scolytini		
<i>Cryphalus ruficollis ruficollis</i> Hopkins	vi-28-1981	D.E. Bright
<i>Ips borealis borealis</i> Swaine	vi-28-1981	D.E. Bright
<i>Ips perturbatus</i> (Eichhoff)	vi-28-1981	D.E. Bright
<i>Pityophthorus opaculus</i> LeConte	vi-28-1981	D.E. Bright
<i>Pityophthorus recens</i> Bright	vi-28-1981	D.E. Bright
<i>Scolytus piceae</i> (Swaine)	vi-28-1981	D.E. Bright
Aklavik		
Hylesinini		
<i>Carphoborus andersoni</i> Swaine	1930-1932	O. Bryant
<i>Carphoborus carri</i> Swaine	v-25-1931	O. Bryant
<i>Dendroctonus rufipennis</i> (Kirby)	vi-12-1956	R.E. Leech
<i>Phleosinus pini</i> Swaine	1931	O. Bryant
Scolytini		
<i>Crypturgus borealis</i> Swaine	—	(Bright 1976)
<i>Ips perturbatus</i> (Eichhoff)	—	(Wood 1982)
<i>Ips borealis borealis</i> Swaine	vii-6-1973	Not on label
<i>Ips tridens engelmanni</i> (Mann.)	vi-18-1956	R.E. Leech
<i>Polygraphus rufipennis</i> Kirby	vii-6-1948	W.J. Brown
<i>Trypophloeus striatulus</i> (Mann.)	vi-29-1956	R.E. Leech
Sandstone Rapids		
Hylesinini		
<i>Dendroctonus punctatus</i> LeConte	ii-1915	F. Johansen
Scolytini		
<i>Pityophthorus nitidus</i> Swaine	ii-1915	F. Johansen
<i>Polygraphus rufipennis</i> Kirby	ii-1915	F. Johansen

johanseni Swaine), *Pityophthorus nitidus* Swaine, and *Polygraphus rufipennis* Kirby from white spruce below Sandstone Rapids (67° 30' N) in February 1915 during the Canadian Arctic Expedition of 1913-1918 (Swaine 1919). The site is near the mouth of the Coppermine River, which flows into the Coronation Gulf. The climate in all of these areas is subarctic.

Discussion

The scolytid species that have migrated with their hosts and adapted to the extreme northern environment since the last ice age have been collected at relatively few locations and mainly from white spruce, the most prevalent tree species. Remoteness of the northern areas and the lack of economic value of the trees have provided little incentive for extended surveys and study of scolytids there. However, with growing interest in climate change, additional species of bark beetles may be found in the higher latitudes in the future. The

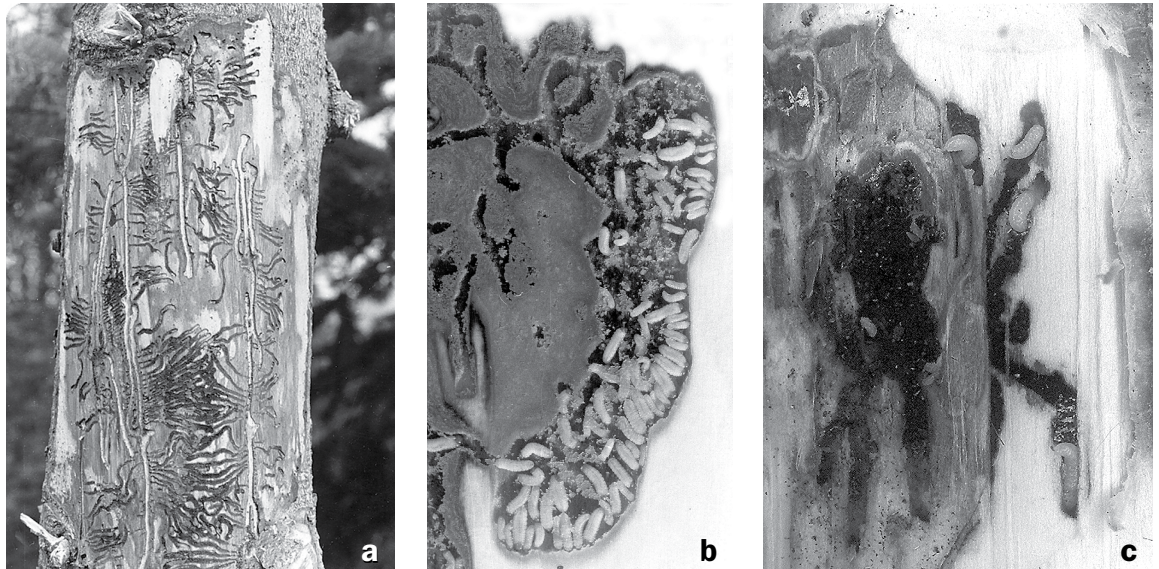


Fig. 5A. *Ips tridens engelmanni* galleries exposed by removing overlying bark. Overwintering adult broods congregate under bark near ground, where they are insulated by snow. Author photo.

Fig. 5B. Larvae of *Dendroctonus punctatus* aggregated along a feeding front in live spruce phloem. This species is adapted well to the northern environment by infesting the basal stem, where it is insulated by winter snow, and because a single mated female may establish a brood in a live tree without killing it, thus preserving it for more than one generation of beetles. Author photo.

Fig. 5C. *Trypophloeus striatulus* larvae that have mined in phloem away from their communal chamber (dark area) in preparation for pupating. The overlying bark has been removed. This bark beetle has several adaptive features that enable it to exist in willow in extreme northern Alaska (see text). Author photo.

distribution of scolytids in the north is only partially known and an effort is needed to establish the extent of their occurrence as a base line. For example, of the scolytid species known to infest white spruce in Alaska, the following were not collected at Agiak Lake (Table 1) but may occur there or elsewhere at some similar latitude: *Carphoborus intermedius*, *Phloeotribus lecontei*, *Scierus pubescens*, *Xylechinus montanus*, and *Cryphalus pubescens*. Also, the most northern location known for *T. striatus* in Canada is Aklavik, 68° 13' N; it likely will be found farther north, perhaps exceeding the northernmost record in Alaska.

Scolytids have several biological features (strategies) adapted to their colonization of hosts. One group utilizes attractant pheromones to aggregate flying adults in order to mass attack, overcome, and kill a host, aided by tree-pathogenic fungi. Their larvae mine separately. Another group does not aggregate as adults; a single mated female or a mating pair may successfully colonize a host. Their larval offspring overcome the host's defense by aggregating in a communal feeding chamber and may not kill their host, or may at least conserve it for more than one generation. Both of these strategies are represented by the scolytid species at the northern sites represented by Table 1 and 2. *Dendroctonus rufipennis* (Kirby) and *Ips tridens engelmanni* Swaine (Fig. 5A) are prominent examples of the former (Furniss et al. 1976, Ross et al. 2005). *Dendroctonus punctatus* LeConte exemplifies the other behavior, in which the larvae aggregate (Fig. 5B) (Furniss 1995). Larvae of *Trypophloeus striatulus* initially feed communally but form separate larval mines in which to pupate (Fig. 5C). Their offspring are disinclined to fly and re-infest their host

downward on the stem for more than one generation, thus preserving a susceptible resource. This behavior makes it well adapted to the far north, where feltleaf willow is of limited extent.

Some scolytids infest the basal stem, where the bark is thicker and insulated by winter snow. Representatives of this behavior are *D. punctatus*, *Hylurgops rugipennis rugipennis* (Mann.) and *D. rufipennis*. The latter attain the adult stage in their second year and migrate to near ground level, where they overwinter beneath the bark (Werner et al. 1977). This behavior of these species would provide a more favorable winter environment and presumably enhance their survival in years of sudden extreme freezing. However, this strategy is not a characteristic of most of the scolytids listed here and does not appear to be a selective factor in their presence. More important to them, perhaps, is the predisposition (killing) of their host by primary bark beetles such as *D. rufipennis* and *Ips* spp. Thus, I expect that as conifers creep northward as climate permits, the scolytids accompanying them may be those overwintering near ground. The pioneer conifer will likely be white spruce, accompanied first by *D. punctatus* that can establish a brood by a single female without the need to kill its host.

Acknowledgments

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- Mal Furniss** is co-chairman of the History Committee of the Western Forest Insect Work Conference and has contributed several articles to Heritage related to forest entomology. He was employed in 1950 by F. Paul Keen at Berkeley, who himself had been hired in 1915 by Andrew D. Hopkins, the father of forest entomology in America. Mal has studied bark beetles extensively in the field from Alaska to Mexico. He lives on the outskirts of Moscow, Idaho where he enjoys observing Nature's creatures and fostering their diversity.

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