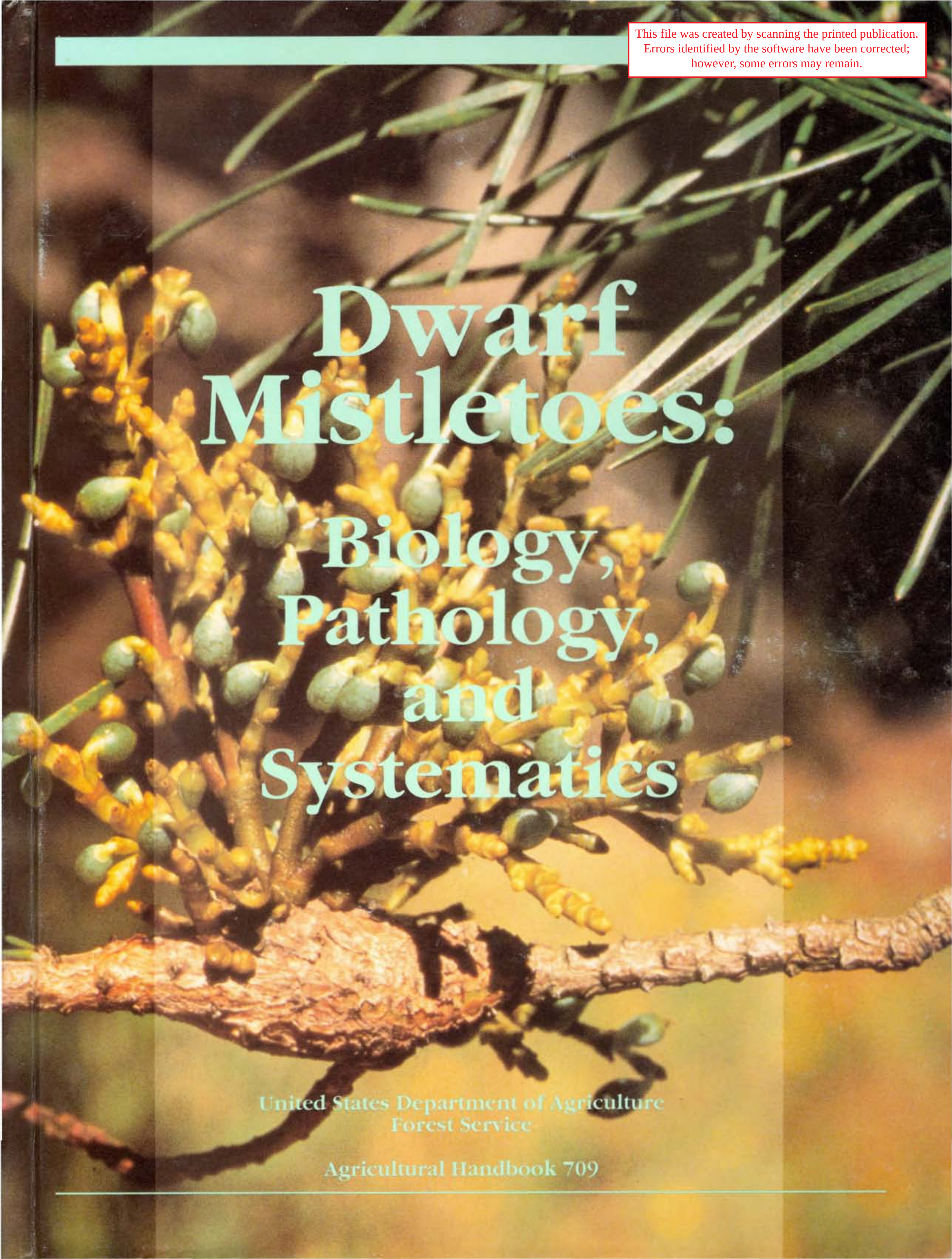

Dwarf Mistletoes: Biology, Pathology, and Systematics

United States Department of Agriculture
Forest Service

Agricultural Handbook 709

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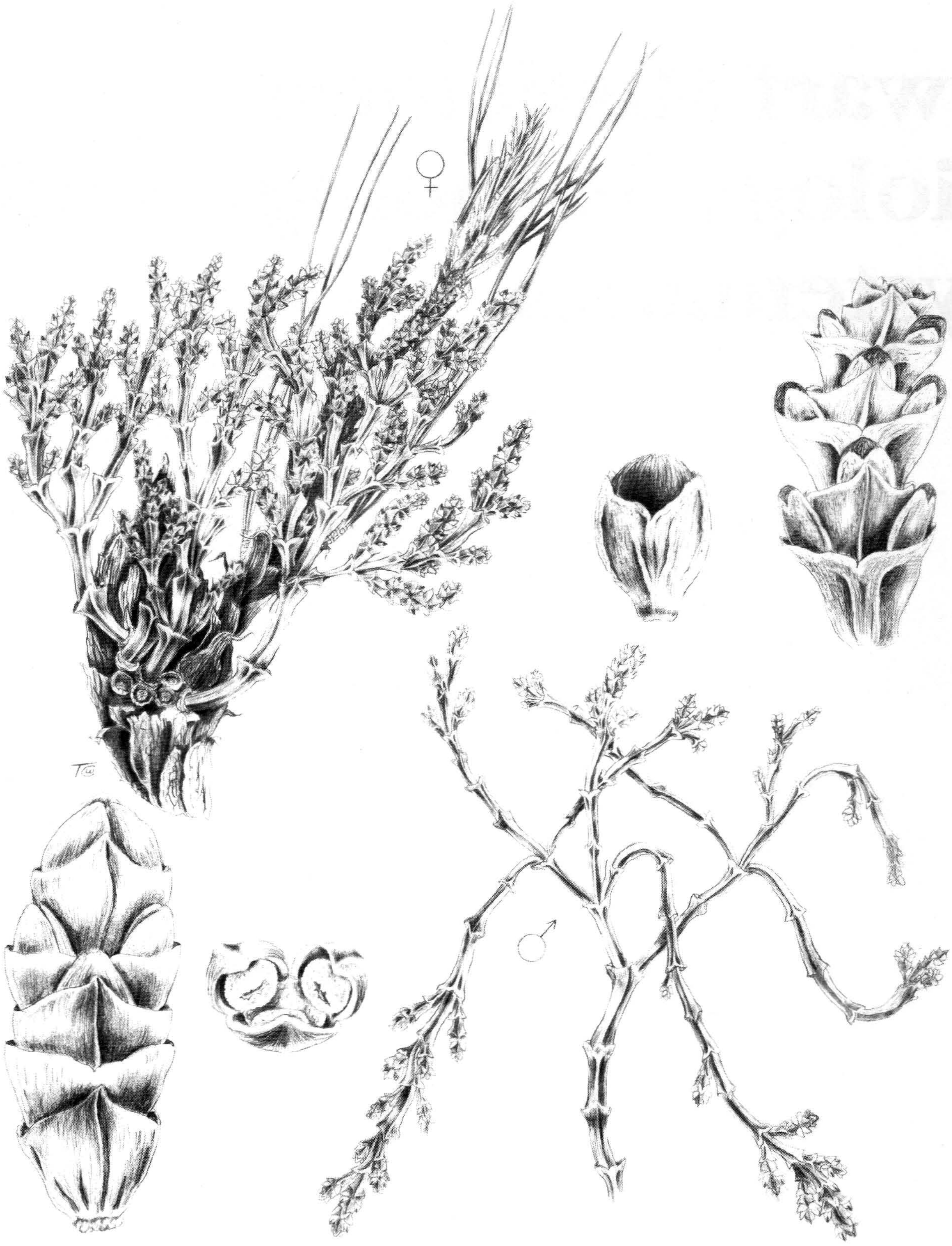

Arceuthobium hawksworthii

In Memory

Frank G. Hawksworth died on January 8, 1993, following heart surgery. He was known internationally as a forest pathologist, although his singular scientific passion was dwarf mistletoes. Frank's research spanned nearly four decades. He authored over 275 articles and reports, the majority of which concerned dwarf mistletoes. His enchantment with these fascinating plants never waned and his attention was not distracted.

Frank worked on this manuscript until the day he entered the hospital. He approached the study of mistletoes as a compositionist. He sought to understand the inter-relationships of species and thought of organisms as integral, functioning wholes. As an unusually acute observer, Frank possessed what taxonomists call "a good eye." His field studies were unrivaled and his comprehension of the literature was unsurpassed. Frank's outstanding knowledge, endless helpfulness, perennial good cheer, and his subdued but pervasive wit will be sorely missed. He is commemorated by *Arceuthobium hawksworthii* (a recently described species of dwarf mistletoe from Belize), *Phoradendron hawksworthii* (a mistletoe parasite of juniper in western Texas), and *Frankliniella hawksworthii* (a species of thrips associated exclusively with dwarf mistletoes).

Shortly before his death Frank sent me a reprint of a publication on the life of Lucy Bishop Millington, a nineteenth-century botanist of the Adirondack region of New York. In an accompanying note Frank commented "Shades of Durango in 1963?" He was referring to our discovery of five new species of *Arceuthobium* in a single day between Durango and El Salto, Mexico. He had marked a quote by Millington that described her emotions in 1871 when she realized that the decline and mortality of black spruce was caused by a then-undescribed mistletoe (now known as *A. pusillum*). Her reflections of that moment revealed a deep spiritual involvement with nature that elicited strong empathy in Frank. Perhaps her comments explain something of the fascination with discovery that motivates those with inquisitive minds. Few of us, however, would risk exposing the sensitivity necessary to acknowledge it.

> There is one day of my life marked with a white stone ... so few such days fall to the lot of man, that we do well to remember them. I drew nearer the secret heart of nature than ever before. I saw what human eyes had not seen before: I touched what none had touched before me. Though all the world may now look on, mine was the first delightful thrill of recognition ... in all one's lifetime scarce such a thing may happen again.
>
> Lucy Millington (1871a)

Del Wiens
Salt Lake City, Utah
June 1994

Dedication

For Peggy and Carol

Dwarf Mistletoes: Biology, Pathology, and Systematics

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Frank Goode Hawksworth
1926–1993

Preface

"So much has already been written on this genus [*Arceuthobium*] of the Loranthaceae that many readers will no doubt be surprised that there should be anything new to be said on the subject" (Johnson 1888). However, since then there have been more than 4,200 publications involving *Arceuthobium*! Following the appearance of our monograph—*Biology and Classification of Dwarf Mistletoes* (Arceuthobium)—in 1972, over 2,200 publications concerning the group have appeared and 18 new taxa have been described. The dwarf mistletoes also have been the subject of two symposia: "Control Through Forest Management" in Berkeley, California (Scharpf and Parmeter 1978), and "Dwarf Mistletoe Biology" in Fort Collins, Colorado (Hawksworth and Scharpf 1984).

Because our 1972 monograph is out of print, and because of significant new research on the genus, we decided that a completely new publication was in order. This new study not only expands the topics covered in the earlier version, but it also includes several new aspects: reproductive biology, host–parasite physiology, ecological relationships, biotic associates, pathological effects on host trees, and control. Dr. Brian W. Geils contributed to the chapter "Biotic Associates" (chapter 8). Drs. Clyde L. Calvin and Carol A. Wilson, Portland State University and University of California, Berkeley, have contributed two chapters: "Anatomy of the Dwarf Mistletoe Shoot System" (chapter 10) and "Endophytic System of *Arceuthobium*" (chapter 11). Dr. Daniel L. Nickrent, Southern Illinois University, contributed the chapter "Molecular Systematics" (chapter 15).

Abstract

Arceuthobium (dwarf mistletoes), a well-defined but morphologically reduced genus of the family Viscaceae, is parasitic on Pinaceae in the Old and New Worlds and on Cupressaceae in the Old World. Although conifer forests in many parts of the Northern Hemisphere are infested with dwarf mistletoes, those most commonly infested are in western North America and Mexico. In North America, *Arceuthobium* ranges from central Canada and southeastern Alaska to Honduras. Only *A. pusillum* occurs in eastern North America, and only *A. juniperi-procerae* is found in the Southern Hemisphere. *Arceuthobium bicarinatum* and *A. azoricum* are restricted to islands (Hispaniola and the Azores, respectively).

In this taxonomic revision, the 46 recognized taxa comprise 42 species—4 with 2 subspecies each, and 1 with 2 *formae speciales*. Eight species are known in the Old World and thirty-four species occur in the New. Natural hybridization and polyploidy are unknown and have resulted in a relatively clear, dendritic line of evolution. The genus is probably of early Tertiary origin and its closest relative is the genus *Notothixos*, which has tropical Asian and Australasian distribution. *Arceuthobium* presumably migrated to the New World before the Miocene Epoch. Intensive adaptive radiation occurred into the Pinaceae. Some of the species of *Abies, Picea, Tsuga, Larix,* and *Pseudotsuga* and 95% of the species of the *Pinus* are parasitized.

The morphological characteristics that delimit species of *Arceuthobium* are often cryptic and may be apparent for only short periods of the life cycle. Species and subspecies nonetheless differ in a number of discontinuous variables. Most species are sympatric with other members of the genus somewhere in their distribution and flowering periods often overlap, but species appear to be isolated reproductively.

In addition to systematic and descriptive information for each species, we review ecological relationships, biotic associates, physiology, anatomy, pathogenic effects, and methods of control for the *Arceuthobium.* Color pictures, distribution maps, and a list of specimens examined are provided.

Disclaimers

The use of pesticides is mentioned in this monograph but only for general information and not as an endorsement. Because of frequent changes in pesticide registration and labeling, the reader should check with State and local forest pathologists, county agricultural specialists, or State extension specialists to be sure the intended use of a pesticide is still registered. Remember that pesticides can be harmful to humans, domestic animals, desirable plants, and fish and wildlife if they are not handled or applied properly. Use all pesticides selectively and carefully, following the label directions. Follow recommended practices for the disposal of surplus pesticides and pesticide containers.

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Following Frank Hawksworth's death, Charles (Terry) Shaw provided broad and generous support for all phases of the project. The assistance of Brian Geils was critical for completion of numerous technical details, especially editing tables, figures, and appendices. Bob Hamre's deft editorial pen benefitted the text enormously. Sheila Ames rose to the challenge of an enormous bibliographical task, and Bonnie Speir withstood requests for continual revisions with remarkably good cheer. Mai Dailey assisted with correspondence and indexing. Joyce Patterson, Bernadette Velick, and Tracy Wager, provided the skillful illustrations that occur throughout the text. John Sprackling made especially significant contributions by assisting with herbarium work, phenological analyses, and preparation of the distribution maps.

We thank the curators of the many herbaria in North America, Central America, Europe, Asia, and Africa who allowed us to examine dwarf mistletoe collections. Also, we acknowledge the assistance of the many colleagues who collected specimens, provided data, reviewed various aspects of the manuscript, supplied photographs or drawings, assisted with numerical analyses and laboratory work, and performed many other courtesies.

The more than 60 colleagues who provided information during the preparation of the 1972 monograph are listed in that work. Many of those associates and numerous others also aided us in the preparation of this revision. In addition, we are grateful to the following individuals for their assistance in various aspects of the study—

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Biotic Associates

*Frank G. Hawksworth and Brian W. Geils**

Organisms associated with *Arceuthobium* include birds, mammals, insects, arachnids, and fungi. Most of the literature, however, is observational or anecdotal and widely scattered. Scientific names of birds and mammals mentioned here are listed in the appendix.

Birds

Except for the dwarf mistletoes (with their explosive fruits) and a few terrestrial root parasites, most mistletoe seeds are primarily dispersed by birds (Kuijt 1969a). Nicholls and others (1984) identified several types of bird–dwarf mistletoe associations: (1) long-distance dispersal of seeds, (2) use of shoots and fruits for food, (3) use of shoots and witches' brooms as foraging areas, and (4) use of witches' brooms for cover and nesting. Potential indirect effects of bird–dwarf mistletoe interactions are largely unstudied. Such effects include, for example, utilization of dwarf mistletoe–killed trees and those with dead tops by cavity–nesting birds, and openings in stand structure caused by dwarf mistletoe infestations.

Seed Dispersal

Birds have been implicated in long-distance dispersal of dwarf mistletoe seeds by several workers (Nicholls and others 1984, Weir 1916b, Zilka and Tinnin 1976). Kuijt (1963) discovered several isolated trees of *Pseudotsuga menziesii* infected by *Arceuthobium douglasii* in southern British Columbia that were about 80 km from the closest known source of infection. Weir (1916b) discovered seeds of *A. laricis* about 400 m from the closest infected larch trees. He surmised that the seeds were transmitted by high winds but mentioned that birds also may have been involved. Ireland (1926) found seeds of *A. occidentale* in an apple orchard about 1 km from the closest infested trees of *Pinus sabiniana.*

Only 3 studies quantify the frequency of isolated or "satellite" infection centers in otherwise mistletoe-free forests:

- Ostry (1978) studied *Arceuthobium pusillum* in 120-year-old *Picea mariana* stands in northern Minnesota and found 12 satellite infection centers in a 188-ha study area (0.06 centers/ha). The centers contained from 1 to >100 trees covering 0.51 ha; the most isolated infection center was 250 m from the nearest infection source.
- Hudler and others (1979) studied *Arceuthobium vaginatum* subsp. *cryptopodum* in 100- to 150-year-old *Pinus ponderosa* stands in Colorado and found 32 satellite infection centers in a 194-ha study area (0.16 centers/ha). Centers contained up to 175 trees covering 0.3 ha; the most isolated center was 450 m from the nearest infection source.
- Hawksworth and others (1987) studied *Arceuthobium americanum* in a 70-year-old *Pinus contorta* stand in Colorado and found 21 satellite infection centers in a 14.6-ha study area (1.4 centers/ha). Centers contained from 1 to 10 trees; the most isolated center was 65 m from the nearest infection source.

Although satellite centers are relatively scarce, the explosive mechanism of seed dispersal utilized by dwarf mistletoes enables them to intensify and spread rapidly from a newly established satellite center.

Nicholls and others (1984) made a thorough study of animal vectors of *Arceuthobium americanum* and reviewed the previous literature (table 8.1). They showed that animals, especially birds, act as long-distance dispersal agents of this dwarf mistletoe in Colorado. Unlike seeds of other mistletoes, those of *Arceuthobium* are destroyed if they are ingested (Hudler and others 1979). Thus, birds can only disperse seeds that accidentally adhere to their feathers and are subsequently deposited where infection is likely to occur (safe-site). Although such events are rare, a sufficient proportion of birds (27%) carried dwarf mistletoe seeds to make some such dispersal probable (Nicholls and others 1984). The gray jay was the most important seed vector for *A. americanum,* but other important resident species of birds were

* Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado.

TABLE 8.1 —Dispersal of seeds of *Arceuthobium* by birds

Arceuthobium	Location	Observation	Reference
A. americanum	CO	10 species of trapped birds had dwarf mistletoe seeds; gray jay was the most important vector	Hawksworth and others 1987 Nicholls and others 1989
A. americanum	MB, Canada	5 species of birds carried seeds	Punter and Gilbert 1989
A. pusillum	MN	7 species of trapped birds had dwarf mistletoe seeds; gray jay was the most important vector	Hudler and others 1974 Ostry and others 1983
A. pusillum	NFL, Canada	Gray jay was the most important vector	Singh 1982
A. tsugense	AK	Seeds found on feathers of Steller's jay	O'Clair and Armstrong 1985
A. vaginatum	CO	5 species of trapped birds had dwarf mistletoe seeds; pygmy nuthatch and mountain chickadee were the most important vectors	Hudler and others 1979
Arceuthobium spp.*	OR	4 species of birds carried seeds of 6 dwarf mistletoe species; Steller's jay was the most important vector	Zilka and Tinnin 1976

**A. abietinum, A. americanum, A. campylopodum, A. douglasii, A. laricis,* and *A. tsugense*

Steller's jay, mountain chickadee, and dark-eyed junco. Because dwarf mistletoe fruits mature in late summer, migratory birds such as warblers, robins, and hermit thrushes can also play a significant role in long-distance dispersal (Nicholls and others 1984).

Punter and Gilbert (1989) studied animal dispersal in *Arceuthobium americanum* on *Pinus banksiana* in southern Manitoba. They found no seeds on small mammals but observed seeds on 5% of the birds captured in mist-nets; gray jays and dark-eyed juncos were most common. A brown creeper, a red-breasted nuthatch, and a Swainson's thrush also carried dwarf mistletoe seeds.

Various bird species are implicated as dispersal agents for several dwarf mistletoe species. Gray jays are apparently the most important vectors for *Arceuthobium pusillum* in *Picea mariana* and for *A. americanum* in *Pinus contorta.* Steller's jays disperse several dwarf mistletoe species in the Pacific Northwest; nuthatches and chickadees are important for long-distance dispersal of *A. vaginatum* subsp. *cryptopodum* in Colorado (table 8.1). Birds, particularly the mistle thrush, have been suggested as long-distance vectors of *A. oxycedri* in France (Gerber and Cotte 1908) and Pakistan (Zakaullah and Badshah 1977), but quantitative data are lacking. Gorrie (1929) suggests that tits and finches are the primary long-distance dispersal agents of *A. minutissimum* in India.

Birds are very important for dispersal of dwarf mistletoe species that typically occur in isolated trees or in the tops of otherwise uninfected trees. This pattern is characteristic of the following dwarf mistletoes:

- *Arceuthobium minutissimum* on *Pinus wallichiana* in Pakistan (Hawksworth and Zakaullah 1985).
- *Arceuthobium occidentale* on *Pinus sabiniana* in California (unpublished data).
- *Arceuthobium cyanocarpum* on *Pinus flexilis* in the Rocky Mountains (Urban 1968, unpublished data).
- *Arceuthobium verticilliflorum* on *Pinus* spp. in Durango, Mexico (unpublished data).

Except for *Arceuthobium verticilliflorum,* seeds of these species are effectively dispersed by explosive fruit, although birds likely augment mistletoe spread. Because the large fruits of *A. verticilliflorum* are not explosively discharged, birds probably are the primary vectors of this species; their activity probably accounts for the widespread distribution of this mistletoe in the open-canopy stands where it commonly occurs. Dispersal agents for *A. verticilliflorum* have not been determined, but we suspect the gray silky-flycatcher because it feeds on the fruits of other mistletoes (particularly *Phoradendron* spp.) and is common in pine forests of the Sierra Madre Occidental (Sutton 1951).

Dwarf Mistletoes as Food

Birds in the United States that utilize dwarf mistletoes for food are summarized in table 8.2. Weir (1916b) noted house sparrows feeding on fruits of

TABLE 8.2 —Use by birds in the United States of *Arceuthobium* for food

Bird	*Arceuthobium*	Location	Reference
Blue grouse	*A. americanum*	WY	Skinner 1928
	A. campylopodum	WA	Boag 1963
	A. douglasii	AZ	Severson 1986, Lecount 1970
	A. douglasii?	OR	Crawford and others 1986
	A. douglasii	UT	Pekins and others 1987
	A. douglasii	WA	Standing 1960
	A. laricis	WA	Beer 1943
	A. sp.	?	Stewart 1944
	A. vaginatum	CO	Zwinger 1970
Ruffed grouse	*A.* spp.	ID	Wicker 1967a
	A. americanum	WY	Wagner 1968, Skinner 1928
Spruce grouse	*A. americanum*	WA	Zwickel and others 1974
"Grouse"	*A. douglasii*	MT	Weir 1916b
	A. laricis	MT	Weir 1916b
Phainopepla	*A. occidentale*	CA	First report
Black-capped chickadee	*A. americanum*	WY	Wagner 1968
House sparrow	*A. campylopodum*	ID	Weir 1916a
Mourning dove	*A. cyanocarpum*	ID	Urban 1968
Mountain bluebird	*A. cyanocarpum*	ID	Urban 1968
	A. vaginatum	CO	Evans and Evans 1991
Western bluebird	*A. vaginatum*	CO	Pinkowski 1981
Evening grosbeak	*A. vaginatum*	AZ	Hawksworth 1961a
American robin	*A. vaginatum*	CO	Zwinger 1970
Black-headed grosbeak	*A. vaginatum*	AZ?	Marshall 1957
Band-tailed pigeon	*A.* spp.	AZ, CA	Neff 1947

Note: A question mark indicates that species or location are unknown or inferred.

Arceuthobium campylopodum in Idaho, and Hawksworth (1961a) observed evening grosbeaks taking ripe fruits of *A. vaginatum* subsp. *cryptopodum* in Arizona. Phainopeplas feed on ripe fruits of *A. occidentale* in the Sierra Nevada foothills (W. J. Hawksworth, personal communication). The Antillean euphonia eats large quantities of *A. bicarinatum* fruits in the Dominican Republic (Etheridge 1971); tits and finches forage on fruits of *A. minutissimum* in India (Gorrie 1929). The song thrush ingests fruits of *A. oxycedri* in France (Gerber and Cotte 1908), and the mistle thrush feeds on this dwarf mistletoe in Pakistan (Zakaullah and Badshah 1977). In general, feeding on dwarf mistletoe shoots and fruits is uncommon for birds other than the euphonia in the Dominican Republic and the gray silky-flycatcher in Mexico.

A number of reports document feeding by grouse on dwarf mistletoes (table 8.2). Most of these reports are simply observational, but Severson (1986) notes that although blue grouse feed primarily on foliage of *Pseudotsuga menziesii,* 2 to 8% of the bird's diet is composed of *Arceuthobium douglasii.* The importance of such large birds as grouse for establishment of new mistletoe populations is unknown. Although ingested seeds would be rendered inviable, Zilka (1973) suggests that grouse roosting high in tree crowns would carry seeds externally that, once dislodged, would be washed down to young host shoots susceptible to infection.

Witches' Brooms as Nesting Sites and Cover

The dense and abnormally branched witches' brooms caused by dwarf mistletoe infection are commonly utilized by some birds for nesting sites. The often large systemic witches' brooms in *Pseudotsuga menziesii* that result from infection by *Arceuthobium douglasii* are often used as nesting platforms by several owls and accipiters (table 8.3). Approximately 25 to 30% of these raptors normally nest in witches' brooms. In eastern Oregon, however, 19 of 20 nests of long-eared owls were found in witches' brooms (Bull and others 1988). Ravens on the east side of the Cascades in Washington nest in witches' brooms (S. Martin, personal communication). Witches' brooms induced by *A. douglasii* are also commonly used for roosting cover by grouse (Martinka 1972, Stauffer and Peterson 1986, Weir 1916b). At least 10 passerine species have been found nesting in witches' brooms of various dwarf mistletoes (table 8.4).

TABLE 8.3 —Nesting by raptors in witches' brooms induced by *Arceuthobium*

Raptor	*Arceuthobium*	Location	Abundance*	Reference
Northern spotted owl	*A.* spp.	OR	3 of 18 nests in brooms	Forsman 1983
	A. spp.	OR	9 of 47 nests in brooms	Forsman and others 1984
	A. douglasii	WA	3 of 3 nests in brooms	Richards 1989
	A. douglasii	WA	11 of 29 nests in brooms	Irwin and others 1989
Mexican spotted owl	*A. douglasii*	NM	1 of 3 nests in brooms	Ligon 1926
	A. douglasii	NM	2 of 6 nests in brooms	Pederson 1989
	A. douglasii	AZ, NM	7 of 22 nests in brooms	Fletcher 1990
Great gray owl	*A. douglasii*	OR	10 of 49 nests in brooms	Bull and Henjum 1990
Long-eared owl	*A. douglasii*	OR	19 of 20 nests in brooms	Bull and others 1988
Great horned owl	*A. vaginatum*	CO	1 nest in broom	Reynolds, personal communication 1990
Cooper's hawk	*A.* spp.	OR	"common" in brooms	Reynolds 1979; Reynolds and others 1982
	A. douglasii	OR	20 of 31 nests in brooms	Moore and Henny 1983
	A. douglasii	OR	50–70% of nests in brooms	Moore and Henny 1984
Goshawk	*A. douglasii*	OR	5 of 34 nests in brooms	Moore and Henny 1983
Sharp-shinned hawk	*A. douglasii*	OR	3 of 25 nests in brooms	Moore and Henny 1983, 1984

*Relative abundance of nests for the raptor species that were found in witches' brooms.

TABLE 8.4 —Nesting by passerines in witches' brooms induced by *Arceuthobium*

Passerine	*Arceuthobium*	Location	Reference
American robin	*A. americanum*	CO	First report
	A. campylopodum	WA	First report
	A. vaginatum	CO	Bennetts and others 1992
	A. vaginatum	CO	Nicholls and others 1984
Gray jay	*A. pusillum*	MN	Warren 1899
Red crossbill	*A. vaginatum*	CO	Bailey and others 1953
House wren	*A. vaginatum*	AZ	Nicholls and others 1984
Mourning dove	*A. vaginatum*	CO	First report
Western tanager	*A. vaginatum*	CO	Bennetts and others 1992
Chipping sparrow	*A. vaginatum*	CO	Bennetts and others 1992
Hermit thrush	*A. vaginatum*	CO	Bennetts and others 1992
Cassin's finch	*A. vaginatum*	CO	Bennetts and others 1992
Pine siskin	*A.* spp.	OR	Zilka 1973

Dwarf Mistletoe Effects on Bird Habitat

Bennetts (1991) and Bennetts and Hawksworth (1992) studied relationships in central Colorado between infestations by *Arceuthobium vaginatum* subsp. *cryptopodum* in stands of *Pinus ponderosa* and the population dynamics of various bird species. The abundance of dwarf mistletoe in a stand was directly correlated with species diversity and bird density. They also demonstrated a strong positive correlation between incidence of dwarf mistletoe and the number of snags used by cavity-nesting birds. Severs and others (1991) reported a nearly three-fold increase in the density of cavity-nesting birds in stands severely infested by dwarf mistletoes over the density in comparable but uninfested stands.

Mammals

Literature involving mammal–dwarf mistletoe associations has been discussed in detail by Hawksworth (1975), Nicholls and others (1984), and Tinnin and others (1982).

Seed Dispersal

Red squirrels and flying squirrels are known to carry seeds of *Arceuthobium pusillum* in *Picea mariana* stands in Minnesota (Hudler and others 1974, Ostry and others 1983). In the first year of their studies, 20 seeds were found on mammals and birds—including 1 on a red squirrel and 10 on flying squirrels. In the following year, 25 seeds were found—all on red squirrels. Lemons (1978) studied the role of red squirrels as seed vectors of *A. campylopodum* in central Oregon. He found no seeds on squirrels in stands of *Pinus ponderosa* where dwarf mistletoe infestation was low, but about 50% of squirrels carried mistletoe seeds in severely infested stands. He observed that squirrels carried seeds for distances up to 150 m. Because squirrels groom seeds from their fur soon after becoming attached, he doubted they were important for establishment of new and distant infection centers.

The seed vectors of *Arceuthobium americanum* on *Pinus contorta* in Colorado were studied by Nicholls and others (1987b, 1989). Seeds were discovered on 4 species of mammals—least chipmunk (24 of 254 animals with seeds), golden-mantled ground squirrel (3 of 20 animals with seeds), red squirrel (1 of 15 animals with seed), and American marten (1 of 1 animal with seed). Although chipmunks and ground squirrels carried the most seeds, they are unlikely to initiate new infection centers because they spend most of their time on or near the ground and are therefore unlikely to deposit those seeds at infection safe-sites. Red squirrels are more effective animal vectors because they frequent tree crowns; but they have relatively small home ranges and are less likely than birds to effect long-distance dispersal.

Taylor (1935) studied porcupines in Arizona and discussed the possibility that they might disperse *Arceuthobium vaginatum* subsp. *cryptopodum.* Porcupines definitely feed on dwarf mistletoe shoots (see below), but we question the importance their role as an effective vector because (1) outer twigs with needles (safe-sites) are too small to support such large animals, and (2) resinous wounds on older tissues (where porcupines frequent) are unlikely infection courts (Hawksworth 1961a).

In Manitoba, Punter and Gilbert (1989) trapped 193 mammals in *Pinus banksiana* stands infested by *Arceuthobium americanum;* none of the animals (including least chipmunk, red-backed vole, deer mouse, and Franklin's ground squirrel) carried dwarf mistletoe seeds. Urban (1968) implicated various rodent species in the dispersal of *A. cyanocarpum* in the open stands of *P. flexilis* at Craters of the Moon National Monument in southern Idaho.

Dwarf Mistletoes as Food

Various mammals utilize dwarf mistletoe shoots as a dietary supplement, but none are dependent on them as a primary food source.

The red squirrel is the most thoroughly studied of all the mammals that forage on trees infected with dwarf mistletoe. It is most commonly associated with *Arceuthobium americanum* on *Pinus contorta* in British Columbia (Baranyay 1968, Wood and others 1985), Montana (U.S. Department of the Interior 1970), Wyoming (Wagner 1968), and Colorado (unpublished data). Small branches 6 to 13 mm in diameter are nipped off and the cortex consumed; in all areas observed, squirrels select mistletoe-infected twigs over uninfected twigs. In British Columbia, 90% of the mistletoe-infected branches over a 30-ha area were gnawed (Wood and others 1985). One of the earliest reports of dwarf mistletoes in North America mentions that this squirrel fed on *A. campylopodum* in the "Oregon Territory" (Hooker 1847). Rodents, presumably tree squirrels, in California feed on dwarf mistletoe cankers in true firs (Scharpf 1982).

Abert squirrels in northern Arizona feed nearly exclusively on the bark of young twigs of *Pinus ponderosa* (Keith 1965). Keith observed that these squirrels also feed on the inner bark of twigs infected by *Arceuthobium vaginatum* subsp. *cryptopodum* by removing the mistletoe shoots and outer bark, and consuming inner bark and associated endophytic system of dwarf mistletoe. Shaw and Hennon (1991) found that 22% of the infections caused by *A. tsugense* on young *Tsuga heterophylla* in southeast Alaska had been chewed by rodents. Wass (1976) reported rodent chewing on *A. tsugense* infections on *P. contorta* in British Columbia and noted their absence on similarly infected *T. heterophylla.* States and others (1988) found that foraging times of Abert squirrels on dwarf mistletoe and associated structures varied by season—1% in spring, 3% in summer, 5% in autumn, and 12% in winter. Stephenson (1975) reported that squirrels in Arizona consumed dwarf mistletoe shoots and fruits throughout the year, but mistletoe comprised less than 4% of the total diet. In southeastern Utah, however, dwarf mistletoe was rarely used for food (Patton and Vahle 1986).

Chipmunks eat the fruits and seeds of *Arceuthobium campylopodum* in Washington (Broadbooks 1958), those of an unidentified mistletoe in northern Idaho (Wicker 1967a), and those of *A. americanum* in Colorado (Nicholls and others 1984). Dwarf mistletoes, however, are probably not an important element in their overall diet.

Taylor (1935) commented that some porcupines in the Southwest are "excessively fond" of *Arceuthobium vaginatum* subsp. *cryptopodum* and prefer this plant to pine needles and inner bark during certain seasons. Winter foraging on dwarf mistletoe was restricted to only 20% of the porcupine population, but those individuals that did feed on mistletoe, did so extensively. In winter, spring, and summer, 20 to 25% of stomach contents was mistletoe shoots; in autumn, the amount rose to 65%. Certain trees of *Pinus ponderosa* in Colorado that are infested with *A. vaginatum* subsp. *cryptopodum* are also especially attractive to porcupines in winter; the ground under these trees is often littered with hundreds of porcupine fecal pellets comprised of fragments of dwarf mistletoe shoots. Johnson and Carey (1979) noted that, in one area of northern Colorado, dwarf mistletoe shoots made up about 25% of the porcupine fecal pellets. In the Pacific Northwest, *A. campylopodum* is such an attractive food for porcupines in autumn and winter that shoots of this dwarf mistletoe are used for bait to trap the animals (Hooven 1971, Lawrence 1957).

Deer forage opportunistically on dwarf mistletoes. Although shoots are high in nutritive value (Urness 1969), they are usually inaccessible. Shoots of *Arceuthobium vaginatum* subsp. *cryptopodum* have a digestibility ratio of about 50% and are high in nutrients—45 to 55% acid-detergent fiber, 0.15 to 0.25% phosphorus, and 5 to 7% crude protein (Urness 1969). Hawksworth (1961b) observed mule deer in northern Arizona feeding on shoots of *A. vaginatum* subsp. *cryptopodum* in green logging slash. Other observations of mule deer in several studies (Currie and others 1977) showed that this dwarf mistletoe contributed less than 1% to the total diet. Dried mistletoe shoots that had fallen to the ground were only eaten in April and constituted about 2.5% of that month's diet. Wright and Arrington (1950), in their study on mule deer of the northern Kaibab Plateau, reported that *A. vaginatum* subsp. *cryptopodum* contributed from a trace to 54% of the diet (overall average <1%). Leach (1956) and Leach and Hiele (1957) observed that *A. campylopodum* occurred in the stomach contents of California mule deer 10 to 25% of the time, but contributed only 1 to 2% of the volume consumed. Craighead and others (1973) report that *A. americanum* on *Pinus contorta* is an important, high-protein, winter food for elk in thermal areas of Yellowstone National Park.

Witches' Brooms as Nesting Sites and Cover

Farentinos (1972) found that, in Colorado, 10 of 40 nests of Abert squirrels were in witches' brooms of *Pinus ponderosa* induced by *Arceuthobium vaginatum* subsp. *cryptopodum*. Dwarf mistletoe was rare on the study site, and all large witches' brooms observed were utilized as nesting sites. Similar observations were reported near Allenspark, Colorado (Pollock 1981).

Red squirrels in Colorado nest in witches' brooms of *Pinus contorta* caused by *Arceuthobium americanum* (Hatt 1943). Patton and Vahle (1986) reported that 35% of red squirrel nests in an Arizona mixed conifer forest were found in witches' brooms. Nesting sites for red squirrels in eastern Oregon were found in brooms of *P. ponderosa* induced by *A. campylopodum* (Lemons 1978).

Witches' brooms of *Pinus contorta* induced by *Arceuthobium americanum* are frequently used by the American marten for nesting sites in California (Spencer 1987), Montana (Burnett 1981), and Wyoming (Campbell 1979, Hauptman 1979, Buskirk and others 1987). In northeastern Oregon, witches' brooms of *Pseudotsuga menziesii* caused by *A. douglasii* are often used by porcupines in winter for protection from snow and wind (Smith 1982). Flying squirrels on the east side of the Cascades in Washington also frequently utilize witches' brooms induced by *A. douglasii* for cover and nesting sites (S. Martin, personal communication). Lemons (1978) reports that witches' brooms of *Pinus ponderosa* caused by *A. campylopodum* are used as nesting sites by flying squirrels and bushy-tailed woodrats in eastern Oregon.

Dwarf Mistletoe Effects on Mammal Habitat

The indirect effects of dwarf mistletoe infection on stand opening—the production of dead branches and dying trees—have been studied in relation to abundance of mammals in *Pinus ponderosa* infested with *Arceuthobium vaginatum* subsp. *cryptopodum*. In certain years, dwarf mistletoe–infested stands in northern Arizona received significantly more use by mule deer than stands without dwarf mistletoe, but no long-term preferences were observed (Clary and Larson 1971). Both mule deer and elk in Colorado used infested stands more frequently than uninfested stands (Bennetts and others 1991).

Insects

The literature on insect–dwarf mistletoe associations was summarized by Stevens and Hawksworth (1970, 1984). They recognized 3 major types of association: (1) pollination (chapter 3), (2) predation of shoots, fruits, and seeds (this chapter), and (3) invasion of insects into trees weakened by dwarf mistletoe infection (chapter 12).

Predation of Shoots, Fruits, and Seeds

Many diverse species of insects feed on dwarf mistletoe shoots, fruits, and seeds (Stevens and Hawksworth 1970, 1984). Most are generalist feeders that only forage on dwarf mistletoes incidentally and opportunistically. For example, the grasshopper *Melanoplus devastator,* which usually feeds on herbaceous vegetation, destroyed more than 90% of the shoots of *Arceuthobium campylopodum* in a California plantation of *Pinus jeffreyi* (Scharpf and Koerber 1986). Also, the harvester ant, *Atta mexicana,* which is a generalist feeder, utilized shoots of *Arceuthobium durangense* in Sinaloa, Mexico (Nickrent 1988).

A number of insect species, including members of the Lepidoptera, Hemiptera, Coleoptera, and Thysanoptera, feed exclusively on dwarf mistletoes.

Lepidoptera

The thicket hairstreak butterfly, *Mitoura spinetorum* (Lycaenidae), is highly prized by butterfly collectors, and larvae are obligate feeders on dwarf mistletoe (fig. 8.1). The species occurs from southern British Columbia to central Mexico (Shields 1965). Larvae have been collected from 10 species of *Arceuthobium* (Stevens and Hawksworth 1970) and probably occur

Figure 8.1–Larvae of the thicket hairstreak butterfly, *Mitoura spinetorum*, feeding on a pistillate plant of *Arceuthobium americanum*; note how well late-instar larvae mimic mistletoe shoots.

on all North American species. Larvae are common enough in certain years to exert a minor degree of biological control but are usually too rare to significantly affect dwarf mistletoe populations. A related species, *M. johnsonii*, occurs on both subspecies of hemlock dwarf mistletoe—*A. tsugense* subsp. *mertensianae* in California and *A. tsugense* subsp. *tsugense* from Oregon to southern British Columbia (McCorkle 1962). McCorkle (Anonymous 1982) found in Oregon that 28 larvae completely destroyed 74% of 144 shoots of *A. tsugense* subsp. *tsugense*.

The most destructive larvae that feed on dwarf mistletoe are *Dasypyga alternosquamella* (Pyralidae) and *Filatima natalis* (Gelechidae) (Heinrich 1921). Little is known of the biology of these species, but both are apparently widespread in western North America and occur on several species of *Arceuthobium*. *Dasypyga alternosquamella* in British Columbia is extremely destructive to shoots of *A. americanum* (Reich 1992). Larvae of either species can destroy an entire crop of mistletoe shoots by mining larger shoots and consuming smaller shoots.

Hemiptera

The plant bug *Neoborella tumida* (Miridae) feeds on several species of dwarf mistletoes in the western United States and Mexico (Knight 1925, Stevens and Hawksworth 1970). *Neoborella tumida* is notable for its size and color mimicry of dwarf mistletoe fruits. Three other species of *Neoborella* that apparently also feed exclusively on dwarf mistletoes have been described from the western United States and Canada (Herring 1972, Kelton and Herring 1978). *Platylygus mexicanus* is reported from Durango, Mexico, on a "mistletoe" (presumably *Arceuthobium nigrum*) of *Pinus leiophylla* (Kelton and Knight 1970).

The spittle bug *Clastoptera distincta* (Cercopidae) is widespread on *Arceuthobium vaginatum* subsp. *cryptopodum* in Arizona, New Mexico, and southern Colorado, but it apparently does little damage. The spittle bug is also common in northern Arizona on *A. abietinum* f. sp. *concoloris*.

Coleoptera

The twig beetle *Pityophthorus arceuthobii* (Scolytidae) is apparently restricted to dwarf mistletoes in central Mexico. These beetles mine large shoots (frequently >3 cm at base) of both subspecies of *Arceuthobium globosum* (subsp. *globosum* and subsp. *grandicaule*) (Wood 1971, unpublished data). This twig beetle may also occur on other large-stemmed Mexican dwarf mistletoes such as *A. vaginatum* subsp. *vaginatum* and *A. durangense*.

Thysanoptera

Several species of thrips (Thripidae) are commonly associated with *Arceuthobium* (Stevens and Hawksworth 1970, 1984). Thrips are plant feeders, but the severity of their effects on dwarf mistletoe populations is not known. Most dwarf mistletoe–associated thrips have broad host ranges, but at least the species *Frankliniella hawksworthii* feeds exclusively on dwarf mistletoe (O'Neill 1970).

Mites and Spiders

Several species of mites (Mesostigmata and Trombiformes) occur on dwarf mistletoes (Stevens and Hawksworth 1970), but their effects are unknown. Most dwarf mistletoe–associated mites have broad host ranges, but at least 4 species appear to be exclusively associated with dwarf mistletoes—*Typhlodromus* *arceuthobius* (Pytoseiidae) on *Arceuthobium campylopodum* and *A. occidentale* in California (Kennett 1963); *T. pusillus* on *A. pusillum* in eastern Canada (Kennett 1963); *Paraphytopus arceuthobii* (Eriophiidae) on flowers of *A. campylopodum* and *A. occidentale* in California (Keifer 1952); and *Brevipalpus porca* (Tenuipalpidae) on several dwarf mistletoes in California, Arizona, Utah, and New Mexico (Pritchard and Baker 1958).

Spiders associated with dwarf mistletoes in northern Colorado were studied by Jennings and others (1989). They found 22 species in 18 genera associated with 3 species of dwarf mistletoe, but none was restricted to them. Of the 118 individuals collected, 65% were hunters and 35% were web spinners. The spider fauna varied considerably among *Arceuthobium americanum*, *A. cyanocarpum*, and *A. vaginatum* subsp. *cryptopodum*, but differences were apparently associated with their host trees (*Pinus contorta*, *P. flexilis*, and *P. ponderosa*, respectively) rather than with the dwarf mistletoe. Many of the spiders had *Arceuthobium* pollen adhering to their body setae, but it is unlikely that spiders are effective pollinators. Spiders may, in fact, hinder pollination by ensnaring pollen grains in their webs (Baker and others 1985, Jennings and others 1989) or by capturing pollinating insects.

Fungi

Many fungi are associated with dwarf mistletoes. They frequently kill shoots, fruits, and seeds directly; they may indirectly kill shoots by destroying the outer host cortex of a branch or by killing the entire branch. Heart rot fungi may also invade dwarf mistletoe swellings on the trunks of fir or hemlock trees (chapter 12).

Fungi on Shoots and Fruits

Several fungi infect shoots and fruits of *Arceuthobium* (Gilbert 1984, Kuijt 1963, Hawksworth and others 1977, Wicker and Shaw 1968). Many of these are saprophytic or weakly parasitic, but at least 8 species are parasitic and apparently restricted to *Arceuthobium* (table 8.5). Fungi that parasitize dwarf mistletoe-infected trees also may infect the dwarf mistletoe. For example, the brown felt blight fungus, *Herpotrichia juniperi*, which infects *Abies magnificae* in California, also parasitizes *A. abietinum* f. sp. *magnificae* (Scharpf 1986).

Sphaeria arceuthobii, long known as *Wallrothiella arceuthobii*, was recently transferred by Barr and others (1986) to *Caliciopsis*. *Sphaeria arceuthobii* was originally described by Peck (1875) as a parasite of *Arceuthobium pusillum* in New York and subsequently was found in northern Michigan (Wheeler 1900), but no additional records of the fungus on *A. pusillum* have been reported. The biology of *Caliciopsis* was studied by Weir (1915a), Dowding (1931b), Wicker and Shaw (1968), Kuijt (1969b), Parker (1970), and Knutson and Hutchins (1979). The fungus infects stigmas during anthesis; later, stigmas and apical portions of the fruit are replaced by a black mycelial stroma. Normal fruit development is prevented and infected fruits fail to produce seed (fig. 8.2).

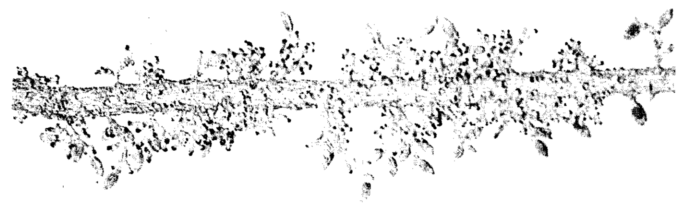

Figure 8.2 –Numerous aborted pistillate flowers of *Arceuthobium douglasii* infected by *Caliciopsis arceuthobii*. The fungus infects stigmas and apical portions of developing fruits, which are later aborted and transformed into prominent black mycelial stroma.

Caliciopsis arceuthobii is restricted to spring-flowering species of dwarf mistletoe (table 8.6) and is common on *Arceuthobium douglasii*, frequent on *A. americanum*, and rare on *A. vaginatum* subsp. *cryptopodum* (Hawksworth 1961b). In certain years, the fungus destroys more than 90% of the fruits of *A. douglasii* (Weir 1915c, Hawksworth and others 1977).

An 1,100-km disjunction (fig. 8.3) exists between populations of *Caliciopsis arceuthobii* in Oregon, Washington, and Idaho and those in Colorado, Arizona, New Mexico, and Mexico (Hawksworth and others 1977). We have been unsuccessful in spite of considerable effort over many years to collect the fungus within this distributional gap, and now believe it is a real discontinuity. Comparative studies on the biology and morphology of the northern and southern populations are needed. Wood (1986) gives a distribution map of *C. arceuthobii* in British Columbia.

TABLE 8.5 –Fungi parasitizing shoots of *Arceuthobium* in the New World*

Fungus	Location	Reference
Colletotrichum gloeosporioides (Melanconiales)	Canada, western US, & Mexico	Hawksworth and others 1968 Muir 1967, 1973a, 1977 Parmeter and others 1959 Scharpf 1964 Wicker 1967b Wicker and Shaw 1968 Wood 1986
Cylindrocarpon gillii (Melanconiales)	Canada, western US, & Mexico	Ellis 1939, 1946 Gill 1935 Kuijt 1963 Mielke 1959 Muir 1973a Wicker and Shaw 1968 Wood 1986
Cylindrocarpon sp. (Melanconiales)	southern Mexico	Hawksworth and others 1977
Caliciopsis arceuthobii (Sphaeriales)	Canada, US, & Mexico	Barr and others 1986 Dowding 1931 Hawksworth 1961 Hutchins 1974 Parker 1970 Peck 1875 Weir 1915 Wicker and Shaw 1968 Wood 1986
Alternaria alternata (Monilliales)	MB, Canada	Sutton 1973
Metasphaeria wheeleri (Sphaeriales)	CA	Linder 1938
Pestalotia maculiformans (Melanconiales)	WA	Wicker and Shaw 1968
Pestalotia heterocornis (Melanconiales)	Dominican Republic	Hawksworth and others 1977

*Updated from Hawksworth and others 1977.

TABLE 8.6 –Hosts and distribution of major fungal parasites of *Arceuthobium* in North America*

Arceuthobium	*Caliciopsis arceuthobii*	*Colletotrichum gloeosporioides*	*Cylindrocarpon gillii*
A. abietinum	US	US	
f. sp. *concoloris*	US	US	—
f. sp. *magnificae*	US	US	—
A. americanum	Canada, US	Canada, US	Canada, US
A. apachecum	US	US	—
A. blumeri	US	Mexico	—
A. californicum	US	US	—
A. campylopodum	US	US	—
A. cyanocarpum	—	US	—
A. divaricatum	US	US, Mexico	—
A. douglasii	Canada, US	Canada, US	Canada, US Mexico
A. laricis	US	US	—
A. microcarpum	US	US	—
A. monticola	—	US	—
A. occidentale	US	—	—
A. pusillum	—	—	Canada, US
A. siskiyouense	—	US	—
A. tsugense subsp. *tsugense*	Canada, US	Canada, US	—
A. tsugense subsp. *mertensianae*	US	US	—
A. vaginatum subsp. *cryptopodum*	—	—	US

*Updated from Hawksworth and others 1977.

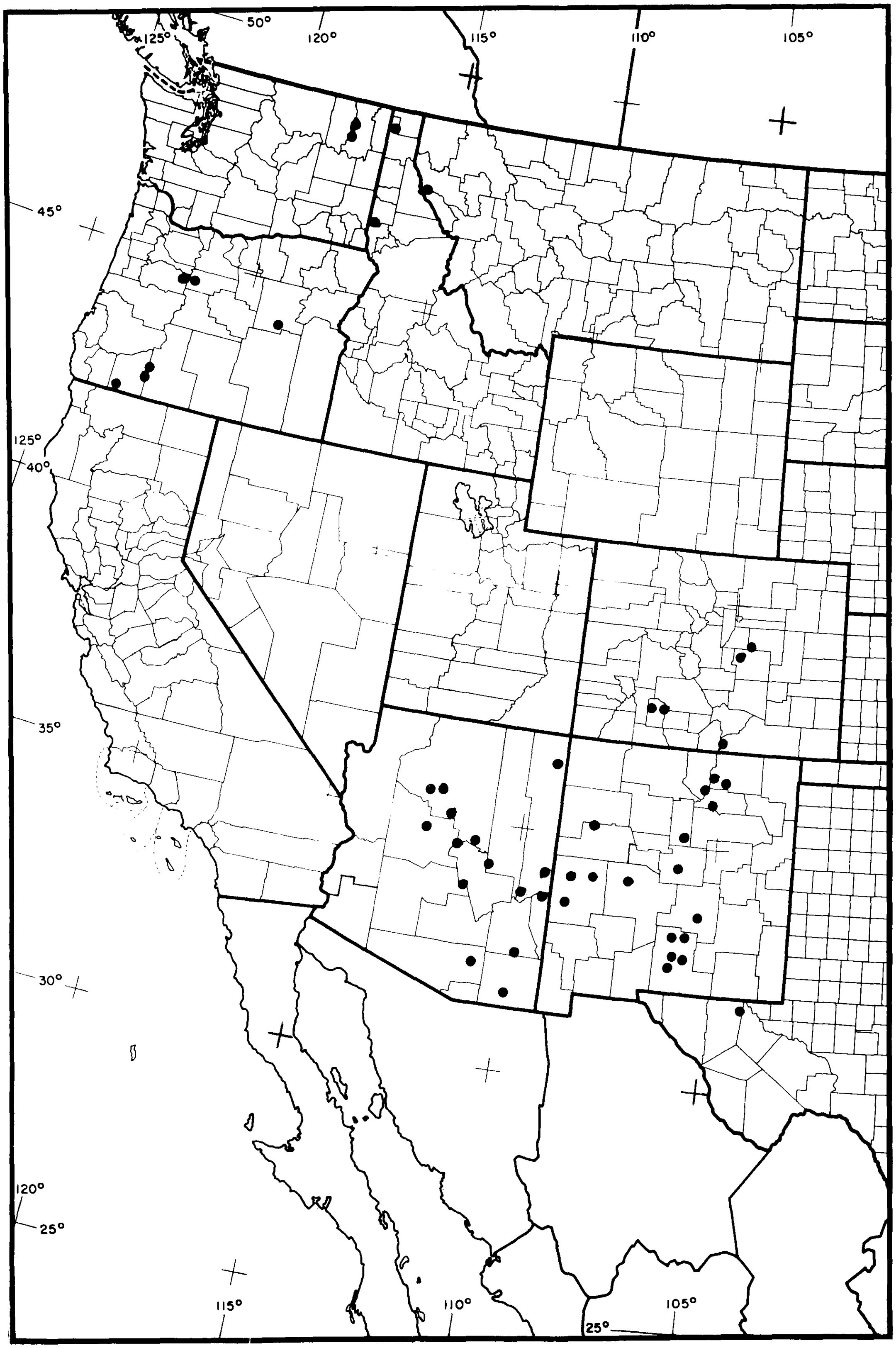

Figure 8.3 –Distribution of *Caliciopsis arceuthobii* on *Arceuthobium* in the western United States and Canada (updated from Hawksworth and others 1977 and Wood 1986).

Colletotrichum gloeosporioides is the most lethal and widespread pathogen of *Arceuthobium.* Weir recognized the fungus before 1920 as a serious parasite of dwarf mistletoes in the Pacific Northwest (Wicker and Shaw 1968). The biology and pathology of *C. gloeosporioides* were described in detail by Parmeter and others (1959). Infection first appears as small brown to black necrotic lesions on mistletoe shoots; lesions enlarge, coalesce, and ultimately cause dieback of shoots (fig. 8.4). The fungus affects most western species of dwarf mistletoe (table 8.6). Several observers report locating areas where a large portion of shoots have been killed by this pathogen. In California, Parmeter and others (1959) observed more than half of the shoots of *A. abietinum* killed; in Washington, Wicker (1967a) noted 24% of the shoots of *A. campylopodum* diseased; and in Alberta, Muir (1977) found more than half of the shoots of *A. americanum* affected. Muir (1967) and Wood (1986) describe the distribution of the fungus in western Canada; the distribution in the United States appears in figure 8.5.

Figure 8.4 –Dying shoots of *Arceuthobium abietinum* infected by *Colletotrichum gloeosporioides.* (R. F. Scharpf)

Cylindrocarpon gillii was studied in detail by Ellis (1946), but it was recognized as a serious shoot parasite of *Arceuthobium* by Weir before 1920 (Wicker and Shaw 1968). In fact, Weir described it as "*Fusarium campylopodii* sp. nov." in an unpublished manuscript. Ellis (1939) also originally thought that it was a *Fusarium,* but after detailed study he transferred it to *Septogloeum* (Ellis 1946). Muir (1973) classified it as *Cylindrocarpon.* Early infection of mistletoe shoots by *C. gillii* is characterized by small, yellowish white lesions. These lesions enlarge, coalesce, erupt through the epidermis, and expose conspicuous masses of white spores; shoot tissues distal to lesions die. The fungus is widespread and parasitizes most species of *Arceuthobium* in the western United States and western Canada (fig. 8.6 and table 8.6; Wood 1986). There are, however, few collections from Idaho, Montana, Nevada, or Wyoming. Mielke (1959) attempted to introduce the fungus on *A. americanum* in southern Idaho, but the population of the parasite became extinct within about 3 years.

Seed Fungi

Because seeds infected by mold will not germinate, molds can markedly effect populations of *Arceuthobium.* For example, Wicker (1967b) planted seeds of 6 dwarf mistletoe species and found that 32 to 60% of the seeds were killed by molds during the first winter (September to April) and an additional 6 to 11% in the following spring (April to June). Many species of fungi, yeasts, and bacteria were isolated from mistletoe seeds in the field (Wicker 1974a); the most common genera found were *Epicoccum, Stemphylium, Hormiscium, Phyllosticta,* and *Coniothyrium.* Carpenter and others (1979) and Shaw and Loopstra (1991) noted the loss to fungi of seeds of *A. tsugense* planted on *Tsuga heterophylla* in the wet coastal environment.

Canker Fungi

Many fungi invade the already diseased inner bark of host branches infected by dwarf mistletoe (dwarf mistletoe cankers). Some of these kill infected branches or prevent shoot formation by the dwarf mistletoe.

The canker caused by *Cytospora abietis* is common on firs parasitized by *Arceuthobium abietinum* in California and Oregon (Wright 1942; Scharpf 1969c, 1980, 1983a, 1983b; Scharpf and Bynum 1975; Filip 1984, Filip and others 1979). The fungus kills infected branches, thereby giving trees a ragged appearance due to "flagging" of afflicted branches (see fig. 16.7).

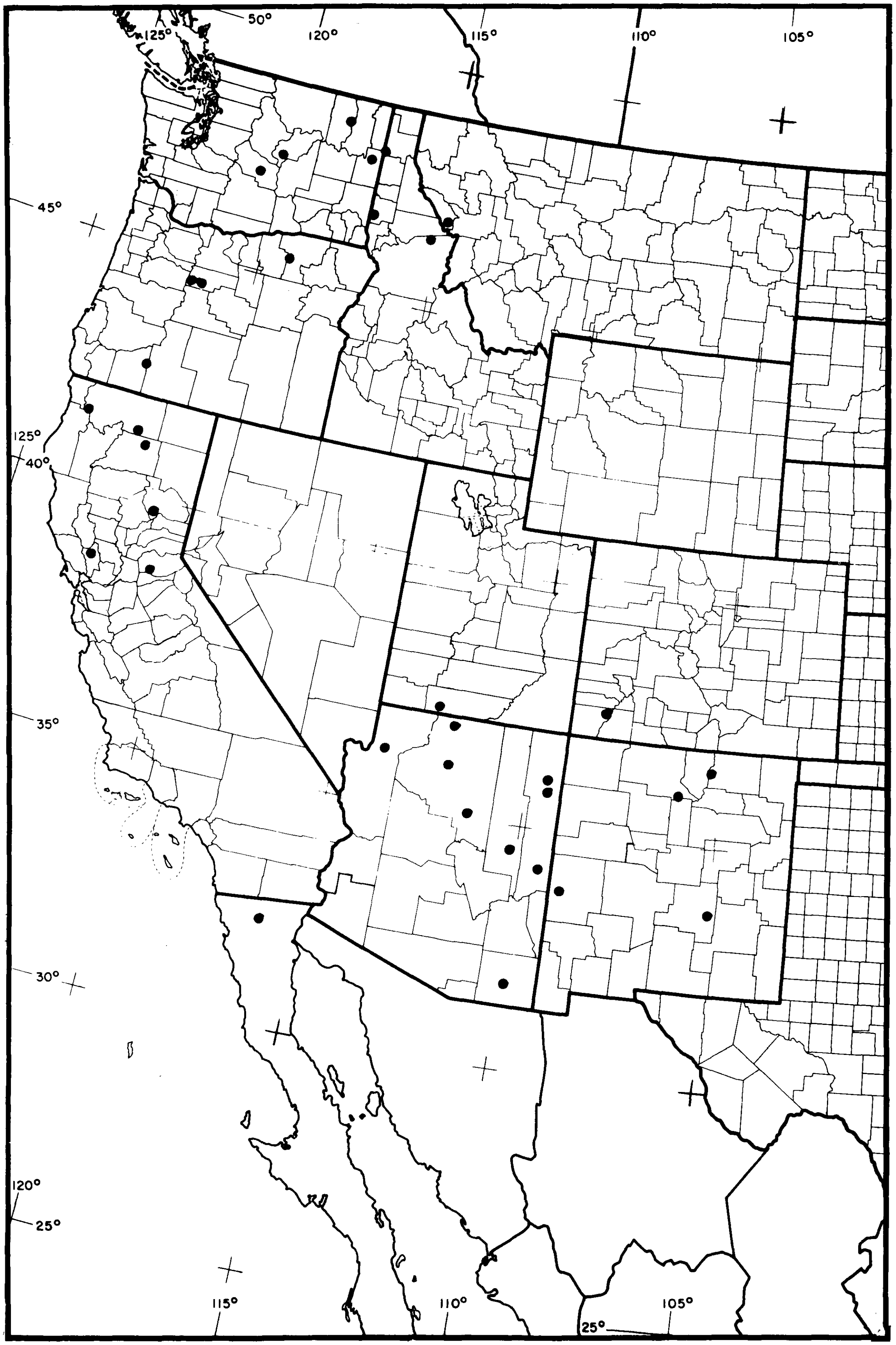

Figure 8.5 –Distribution of *Colletotrichum gloeosporioides* on *Arceuthobium* in the United States and northern Mexico (updated from Hawksworth and others 1977).

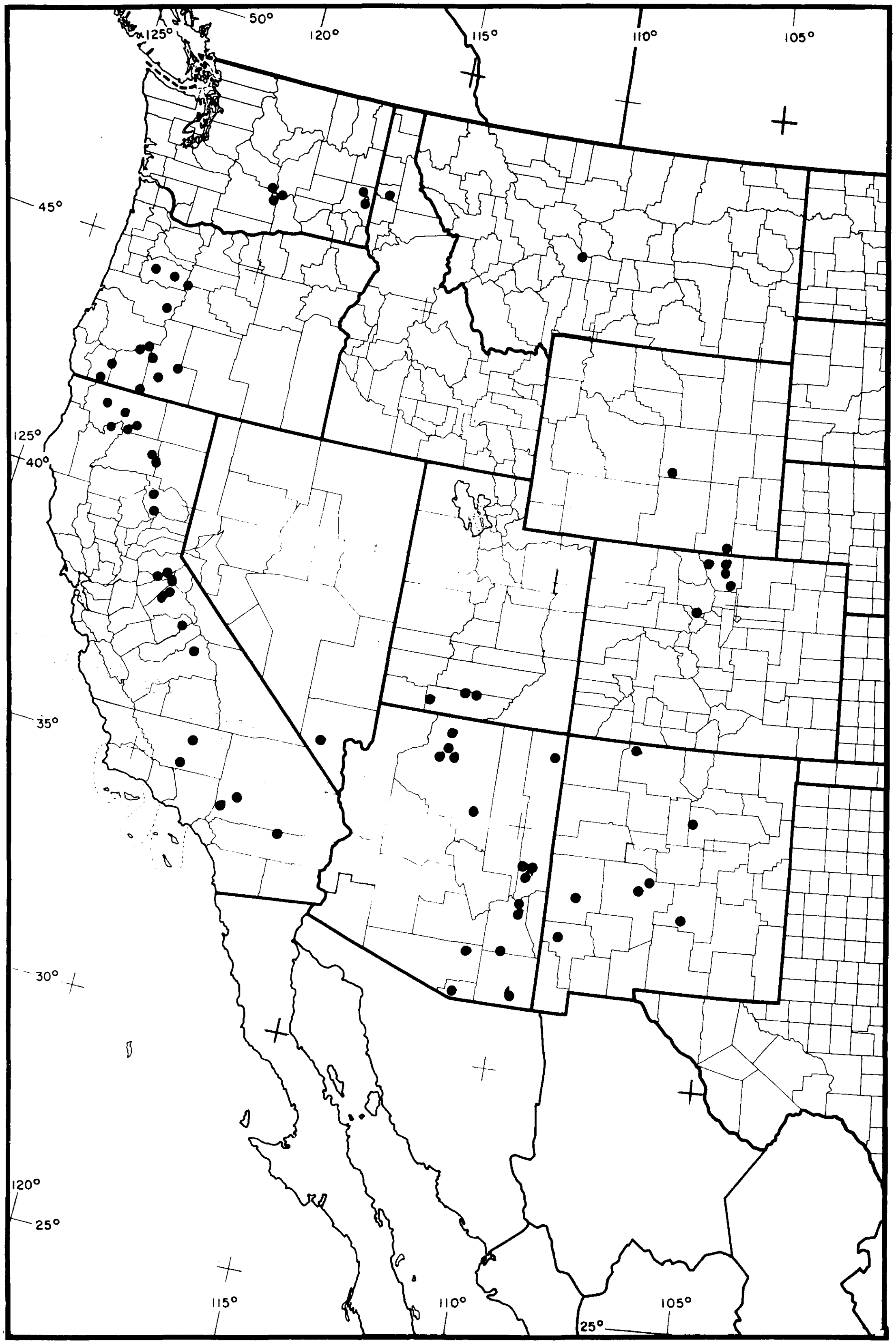

Figure 8.6–Distribution of *Cylindrocarpon gillii* on *Arceuthobium* in the western United States (updated from Hawksworth and others 1977).

Although the fungus is primarily associated with dwarf mistletoe-infected branches, it does occur on branches weakened from other causes as well. In California, 22% of mistletoe-infected branches were parasitized by the fungus, compared to only 4% of the non-mistletoe-infected branches (Scharpf 1969c).

More than 20 fungal species in coastal British Columbia are associated with the cankers caused by *Arceuthobium tsugense* infection of *Tsuga heterophylla* (Baranyay 1966; Funk 1973, 1979, 1981; Funk and Baranyay 1973; Funk and Smith 1981). The high incidence of fungi on this dwarf mistletoe is presumably due to the wet, cool climate characteristic of hemlock forests where the mistletoe is found. The most important of these fungi, *Nectria macrospora,* substantially reduces dwarf mistletoe shoot and fruit production (Funk and others 1973, Smith and Funk 1980).

A pathogenic syndrome termed "resin disease" is common throughout the central and northern Rocky Mountains on *Arceuthobium americanum* (Mark and others 1976). Several weakly parasitic fungi, primarily *Alternaria alternata* and *Aureobasidium pullans,* invade the outer cortex of the host tissue (*Pinus contorta*) adjacent to the dwarf mistletoe canker. A necrophylatic periderm layer develops, outer host tissue dies, and although the host branch remains alive, dwarf mistletoe shoot production ceases. The syndrome is occasionally abundant in some areas, usually killing nearly all mistletoe shoots.

A rust fungus, *Peridermium bethelii,* is associated with *Arceuthobium americanum* on *Pinus contorta* (fig. 8.7). It is common in the Rocky Mountains from southern Alberta to central Colorado, and is known from a single locality on the eastern slope of the California Sierra Nevada (fig. 8.8 and Hawksworth and others 1983). Hyphae infect not only the mistletoes' endophytic system but adjacent host tissues as well (Hawksworth and others 1983, Peterson 1966). Although the rust's life cycle has not been elucidated, observations of its patchy distribution within infested stands suggest that it does not have an alternate host but rather is transmitted directly from mistletoe canker to mistletoe canker. *Peridermium bethelii* kills mistletoe-infested branches but is too uncommon to exert significant biological control.

Several additional species of canker fungi are associated with dwarf mistletoe. *Nectria fuckeliana* is a pathogen in California of *Arceuthobium littorum* on *Pinus muricata* and of *A. abietinum* f. sp. *concoloris* on *Abies concolor* (Byler and Cobb 1972). Filip and others (1979) report that *Cytospora abietis, Cryptosporium pinicola,* and *Nectria macrospora* in Oregon are associated with cankers caused by *Arceuthobium abietinum* on *Abies grandis*. Funk (1984) observes that *Endothiella agregata* is associated with cankers on *Pinus contorta* induced by *Arceuthobium americanum* in British Columbia. *Sphaeropsis sapinea* in California causes necrosis and death of branches of *P. sabiniana* and *P. muricata* infected by *A. occidentale* and *A. littorum,* respectively (Hunt 1969).

Figure 8.7–A sporulating canker caused by *Peridermium bethelii* infecting *Arceuthobium americanum* on *Pinus contorta;* note white peridia and yellow spores erupting from a region of the branch within the already swollen mistletoe infection.