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TAXONOMY, PHYLOGENY, AND COEVOLUTION OF PINES AND THEIR STEM RUSTS

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ABSTRACT

We review and reinterpret major events in the evolution of pines and their stem rusts using information from their taxonomy, genetics, biogeography, and fossil history. Understanding of pine evolution has been significantly revised in the last 20 years. Pines appear to have evolved early in the Mesozoic and to have diversified and migrated throughout middle latitudes in the Northern Hemisphere supercontinent, Laurasia, by the end of the Mesozoic. By this time, the major subgenera had appeared (subgenus *Strobus*, oldest) as well as several early subsections, probably including at least *Cembroides, Gerardianae, Strobi, Canarienses, Pineae, Sylvestres, Ponderosae*, and *Australes*. In the early Tertiary, global climates changed and favored the spread throughout middle latitudes of angiosperm floras adapted to hot, humid conditions. These apparently fragmented and displaced pines into local cool dry refugia in polar latitudes, warm dry refugia at low latitudes, and scattered upland refugia at middle latitudes (e.g., present Rocky Mountains and Japan). Several subsections were split north and south. Some of these areas experienced intensive mountain-building, which created environmental heterogeneity that favored pine radiation and created secondary centers of origin (e.g., Mexico). Following the climatic deterioration at the end of the Eocene, tropical-adapted angiosperms were eliminated throughout middle latitudes, and pines replaced them. Radiations of subsections *Oocarpae, Sabinianae*, and *Contortae* and of many species within subsections seem to date to this period.

Rusts appear to be much older than pines, probably arising as autoecious species in the Carboniferous, with ferns and mosses as original hosts. Heteroecism evolved early, enabling rusts to remain specialized on primary hosts but to radiate on evolutionarily more advanced secondary hosts. The conifers were the first new host group, followed by primitive, then more advanced, angiosperm hosts. Estimated trends in angiosperm evolution and approximate dates of origins of pine lineages are used to infer trends in rust phylogeny. Groups of rusts sharing ancient angiosperm hosts also share old pine hosts, including *Cronartium ribicola, C. occidentale, C. quercuum, C. comptoniae*, and *C. flaccidum*. Putatively derived rusts (including secondarily autoecious species and special forms) *C. appalachianum, Peridermium filamentosum*, and *P. yamabense* share primary and alternate hosts that evolved more recently.

Quaternary climate oscillations affected the genetic structure of rusts as well as hosts. Rusts apparently followed their hosts during glacial and interglacial periods. Three distinctive and autoecious white pine rusts occur on nearby mountaintops in Japan and trace their origin to biogeographic events in the Quaternary.

Effective control of pathogens in introduced and endemic situations may depend on an understanding of genetic relationships among both rusts and hosts. Many biochemical tools are available that should be used to clarify some of these relationships.

DEDICATION

We dedicate this paper to the late William B. Critchfield, pine geneticist, systematist, and geographer, whose pioneering work set the stage for future attempts at unraveling the mysteries of pine evolution.

INTRODUCTION

The stem rusts of pine in *Cronartium*, *Peridermium*, and *Endocronartium* are some of the most ancient, ubiquitous, and destructive pathogens of forest trees. Increasing human interference over the past two centuries in these predominantly wild pathosystems has had disruptive and sometimes disastrous consequences. These have resulted from several types of disturbance: from introducing exotic pathogens onto native pines (as with white pine blister rust introduced into North America); from introducing exotic pines into areas of native pathogens (as with eastern white pine (*Pinus strobus*) into Japan); and from upsetting the ecological and genetic balance of endemic pathosystems (as in fusiform rust of southern USA pines). Furthermore, there are suggestions that pine-breeding programs, especially those that involve interspecific hybridization, may be creating bridges for new genetic combinations of native rusts of wider virulence.

If we are to mitigate the deleterious effects of human interference in pine-rust pathosystems and mount effective programs of rust resistance, we must understand the genetic structure of both hosts and pathogens. Information about the phylogenetic and taxonomic relationships of pines and rusts might eventually enable us to gauge the genetic amplitude of the different pathogens, to calculate the risk to domesticated forest crops, and to identify centers of origin for resistance genes. Leppik's (1959) cogent statement still applies: "...our most effective control measure, the breeding of rust-resistant varieties, depends ultimately upon our knowledge of the genetic constitution and phylogenetic relationships of the rusts involved" to which we add, most emphatically, their wild hosts as well. To this end, we review the taxonomy and phylogeny of pines and rusts and describe processes by which pine-rust pathosystems may have coevolved.

PINES

Classification and Taxonomy of Pines

History of Classification

Pines have been described and classified since Classical times. Theophrastus (370-285 B.C.), a pupil of Aristotle, wrote extensively about morphology, reproduction, and uses of pines in his *Enquiry into Plants* (Hort 1916; Abbe 1965; Mirov 1967). Using the Greek names *pitys* and *peuke*, Theophrastus described five Mediterranean pines that can be referred to as modern species. Subsequent Classical geographers and natural historians used Theophrastus' identifications and often mentioned these pines in their writings. Virgil (70-19 B.C.) first used the name *Pinus* to refer to pines in his two lyrical works, *Georgics* and *Eclogues* (Abbe 1965).

Although the name *Pinus* was quickly adopted, its circumscription varied, even into the time of the Linnean systematists. Tournefourt (1694) defined the genus narrowly, whereas Linnaeus (1753) included modern *Cedrus*, *Larix*, *Picea*, and *Abies* as well as pine in *Pinus*. The genus was quickly reduced again to Tournefourt's framework by Miller in 1754 (in Little and Critchfield 1969), who

segregated *Abies* and *Larix*. *Cedrus* and *Picea* were soon also removed, and the narrow definition of *Pinus* was widely accepted by the mid nineteenth century. By that time, pines were distinguished from other conifers by needle like leaves that were borne on short shoots in fascicles of two to five and that had a sheath of bud scales at the base of the fascicle (Spach 1842; Endlicher 1847; Carriere 1867).

Since the time of Linnaeus, over 40 serious systematic treatments of *Pinus* have appeared (reviewed in Mirov 1967; Little and Critchfield 1969; Price 1989). Many of these have relied on phenetic similarities of single traits or trait complexes (e.g., needle characteristics, Koehne 1893; Doak 1935; Jaehrig 1962; de Ferre 1965; cone characteristics, Klaus 1980, 1989; wood anatomy, Hudson 1960; van der Burgh 1973). In the last two decades, systematists have brought new biochemical and molecular tools to the study of pine classification, including analyses of terpenes (Mirov 1967), immunoglobins (Price et al. 1987), and DNA (Strauss and Doerksen 1990; Kossack 1989).

The most useful classifications are holistic and attempt to summarize and reconcile information from many types of traits. An evolutionary framework is implicit in ordering groups, and these systems are based on hypotheses about phylogenetic relationships and evolutionary transformations. George Russell Shaw (1914) was the first to apply this type of analysis to pines in his landmark synthesis, *The Genus Pinus*. Shaw used information on morphology of the shoots, leaves, ovulate and pollen cones, seeds, wood anatomy, bark, growth habit, habitat, and world distribution to classify the pines. Shaw divided the pines into two widely accepted sections, *Haploxylon* and *Diploxylon* (as named by Koehne 1893), based on the presence of one or two vascular bundles in the needle. He further distinguished four subsections and 13 unnamed groups.

Subsequently, several evolutionary systematists have modified Shaw's system. Pilger (1926) elevated *Haploxylon* and *Diploxylon* to subgeneric status and rearranged the ordering of some groups of *Diploxylon* pines. Pilger's classification was criticized for its overreliance on needle number (Duffield 1952; Mirov 1967), and Shaw's ordering of the groups was more widely retained. A major contribution to evolutionary ordering of species and higher taxa, especially within subgenus *Diploxylon*, came from the extensive artificial hybridization work of Duffield (1952). This information corroborated Shaw's system in many places but also indicated new groupings in several places. A French group of systematists (de Ferre 1965; Campo-Duplan 1950; Flous 1937; Gaussen 1960) studying morphology of juvenile forms, resin duct position, and especially pollen anatomy proposed a classification of pines that differed radically from Shaw's. The systematic interpretations of this group have not been widely accepted because they were not consistent with other kinds of data.

Genus Pinus: *Little and Critchfield (1969)*

The modern authority, following Shaw, is the classification of Little and Critchfield (Critchfield and Little 1966; Little and Critchfield 1969)[1]. Although retaining much of Shaw's reasoning and order, Little and Critchfield incorporated new types of systematic information based on genetic data, especially from contemporary studies on hybridization and biochemical variation. They also brought the nomenclature up to international code (Lanjouw 1966). Although there have been slight modifications and additions proposed subsequently (especially in little known groups such as the Mexican pines; see next

[1] We adopt the Little and Critchfield (1969) system and refer authority of pine names to them, although pines not included in their system are referenced.

section), Little and Critchfield's system is so widely accepted that we summarize it here intact except for a few recent updates.

Little and Critchfield (1969) divided *Pinus* into 3 subgenera, 4 sections, 15 subsections, and 94 species (Fig. 1). *P. longaeva* Bailey (1970) was not segregated by Little and Critchfield. The species occur throughout the Northern Hemisphere (one species crosses the Equator at Sumatra) in temperate regions and tropical mountains. Little and Critchfield added subgenus *Ducampopinus* with only a single species, *P. krempfii* of Vietnam, distinct from all other pines in its flattened leaves and absence of ray tracheids. Subgenus *Strobus* (= Shaw's *Haploxylon*) comprises 2 sections, 5 subsections, and 31 species distributed in North America and Eurasia; subgenus *Pinus* (= Shaw's *Diploxylon*) comprises 2 sections, 9 subsections, and 62 species (Fig. 1). Maps are in Little and Critchfield (1969). The two major subgenera are characterized by the following traits, with some exceptions:

	Pinus subgenus	
	Strobus	*Pinus*
Vascular bundle	Single	Double
Fascicle sheath	Deciduous	Persistent
Base of fascicle bracts	Not decurrent	Decurrent
Needles/fascicle	1-5	2-5
Staminate buds	Not preformed	Preformed
Spring shoots	Uninodal	Uni- or multinodal
Ray tracheids	Smooth walls	Dentate walls
Annual rings	Obscure	Distinct
Umbos on cone scales	Terminal and dorsal	Dorsal

The two major subgenera were further divided into two sections each. Within subgenus *Strobus*, section *Strobus* has two subsections with 19 species of mostly northern distribution in North America and Eurasia. Section *Parrya* has three subsections with 12 species: one distributed in central Asia, one in southwestern USA, and one in southwestern USA and Mexico. The following traits distinguish the sections:

	Subg. *Strobus*, sect.	
	Strobus	*Parrya*
Umbos on cone scales	Terminal	Dorsal
Needles per fascicle	5	1-5
Needle epidermis and hypodermis	Distinct	Similar
Conelet scales	Pointed	Rounded
Wood ray cells	Large pits	Small pits

Within subgenus *Pinus*, section *Pinea* is a heterogeneous group with three subsections and five species of mostly southern distribution in Mexico, the Mediterranean region, and central Asia. The section is not distinguished by a consistent set of traits from the other section in the subgenus. Rather, each subsection within *Pinea* has a unique set of subgenus *Strobus* traits that sets it apart within subgenus *Pinus* and lacks advanced traits found in section *Pinus*. Section *Pinus* is the largest in the genus, comprising six subsections in North America and Eurasia with 57 species distributed mostly in the south but a few far north. Distinguishing traits include:

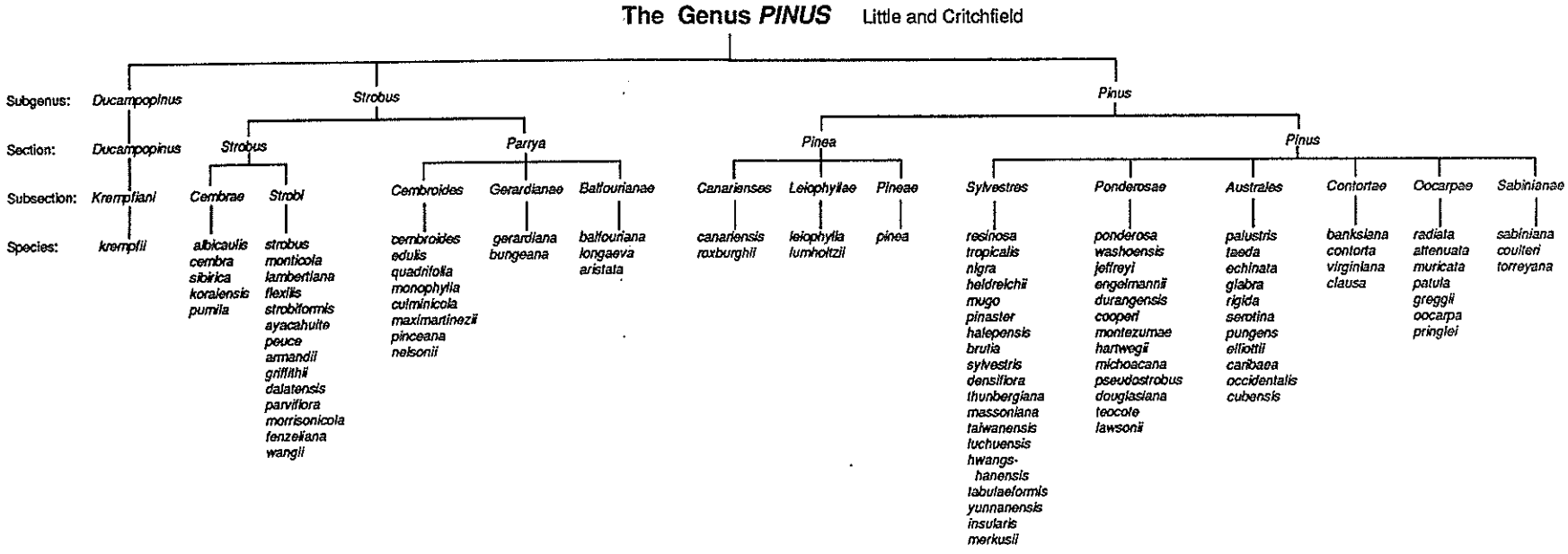

Figure 1. Taxonomy of the genus *Pinus* according to Little and Critchfield (1969), showing the species classed into subgenera, sections, and subsections.

	Subg. *Pinus* sec.	
	Pinea	*Pinus*
Subg. *Strobus* traits	Present	Absent
Seed wing long, dehiscent	Absent	Present
Spring shoots	Uninodal	Uni- or multinodal

Little and Critchfield further subdivided each section into subsections. Although they followed Shaw's subdivisions in many cases, they used evidence from modern studies on genetic relationships and hybridization to develop the subsections and classify species in subsections. In general, species within a subsection are able to hybridize, whereas crossability is reduced among species of different subsections (Critchfield 1975). This resulted in revisions, especially in section *Pinus*, where Shaw's reliance on cone morphology led to some uncorroborated classifications. Three subsections have bihemispheric distributions; the others are limited to North America or Eurasia.

Within subgenus *Strobus*, section *Strobus* is divided into two subsections (Fig. 1). Subsection *Cembrae*, the stone pines, comprises five species of high latitudes and high altitudes, four of which are in Eurasia and one is in western North America. *Cembrae* pines have cones and seeds uniquely adapted to disperal by alpine birds of the genus *Nucifraga*, which is the primary basis for their taxonomic segregation. The 14 species of subsection *Strobi*, the white pines, are distributed in northern Eurasia (8 species) and North America (6 species). The subsections are characterized by

	Subg. *Strobus*, sect. *Strobus* subsect.	
	Cembrae	*Strobi*
Cone dehiscence at maturity	Indehiscent	Dehiscent
Seeds	Wingless	Winged

Section *Parrya* within subgenus *Strobus* comprises three subsections (Fig. 1). Subsection *Gerardianae* has two species in south and east Asia; subsection *Balfourianae*, the foxtail pines, has two species (later divided into three species) restricted to high elevations in southwestern USA; and subsection *Cembroides*, the pinyon or nut pines, has eight species limited to semiarid regions of southwestern USA and Mexico. Plant exploration and genetic analyses of the little-known pines of Mexico continue to revise subsection *Cembroides*. Distinguishing traits of these subsections are

	Subg. *Strobus*, sect. *Parrya* subsect.		
	Gerardianae	*Balfourianae*	*Cembroides*
Needles per fascicle	3	5	1-5
Seeds	Large, rudimentary wing	Small, winged	Large, wingless

Each of the three subsections within section *Pinea* of subgenus *Pinus* (Fig. 1) is distinguished by unique retention of certain subgenus *Strobus* traits. Subsection *Pineae* is monotypic, containing *P. pinea* of the Mediterranean. Subsection *Canarienses* comprises two highly disjunct species, one of the

Canary Islands off northwest Africa and one of the Himalayas, and subsection *Leiophyllae* comprises two Mexican species. The subsections are characterized by

	Subg. *Pinus*, sect. *Pinea* subsect.		
	Pineae	*Canarienses*	*Leiophyllae*
Strobus traits	Seed with rudimentary wing (cf. *Gerardianae*)	Seed with undetachable long wing (cf. *Strobi*)	Leaf sheath deciduous (cf. *Strobus*)
Needles/fascicle	2	3	3-5

The six subsections of section *Pinus*, subgenus *Pinus*, contain 60% of the species in the genus and are distributed in nearly every pine habitat. *Sylvestres* is the largest subsection, containing 19 species--all in the Old World except *P. resinosa* and *P. tropicalis* of eastern North America. The remaining subsections are restricted to North America. Subsection *Contortae* comprises FOUR species distributed throughout northern and eastern North America. The 11 species of subsection *Australes*, the southern yellow pines, occur mostly in southeastern USA, with some on the Caribbean islands and adjacent Central America. Subsection *Ponderosae*, the western yellow pines, has 13 species in western USA, Mexico, and Central America; subsection *Oocarpae* has seven species in southwestern USA, Mexico, and Central America; and subsection *Sabinianae* has 3 species in southwestern USA. The subsections are distinguished by unique combinations of traits rather than single diagnostic characteristics.

Subg. *Pinus*, sect. *Pinus*, subsection:	
Sylvestres	Small symmetrical cones that open at maturity, prickle on cone scale
Ponderosae	Moderate to large symmetrical cones that open at maturity, prickle on cone scale, cones leave basal scales on branch
Australes	Symmetrical cones that open at maturity, prickle on cone scale, spring shoots multinodal
Sabinianae	Massive symmetrical cones with slow opening past maturity, cone scales terminate in long stout beak, seeds large, with thickened base of wing
Contortae	Asymmetrical cones that remain closed at maturity, two needles per fascicle, needles < 8 cm
Oocarpae	Asymmetrical cones that remain closed at maturity, mostly three needles per fascicle, needles > 8 cm

Recent Revisions and Unresolved Questions

Several areas of pine classification remain ambiguous, either because of confusing patterns of relationships or because the pines are little known. In the first category is the uncertain position of *P. krempfii*. The species is distinguished from all other pines by its flattened leaves and absence of ray tracheids. Discovered and described in 1921 (LeComte 1921), it has been placed in subgenus *Strobus* (then *Haploxylon*) (Pilger 1926), in a new subgenus *Ducampopinus* (Gaussen 1960), and elevated to an

independent monotypic genus *Ducampopinus* (Chevalier 1944; Buchholz 1951; de Ferre 1953). It is more commonly accepted to be in the genus *Pinus*, although whether it is a separate subgenus (e.g., Little and Critchfield 1969) or within *Strobus* (Florin 1931; Erdtman et al. 1966) is not clear. Despite its differences, *P. krempfii* has many subgenus *Strobus* (and especially section *Parrya*) traits--including single vascular bundle, deciduous needle sheath, base of fascicle bracts not decurrent, 2 needles per fascicle, cones with thin scales, dorsal umbos, and thin prickle--and wood resembling subgenus *Strobus*. Unfortunately, living tissue is extremely difficult to obtain, and none of the modern biochemical and molecular investigations have included this species.

Another species of uncertain affinity is the recently described *P. rzedowskii* Madrigal and Caballero (1969). A rare species limited to three populations in Michoacan, Mexico, it was originally placed in subsection *Balfourianae*. The species is haploxylon, has dorsal umbos on the cone scales (thus placing it in *Parrya*), has many *Cembroides* features, yet has an articulate seed wing found only in section *Pinus* and in *P. aristata* of subsection *Balfourianae*, and has several features found only in *P. canariensis* of subsection *Canarienses*. Klaus (1989) felt its combination of characteristics was distinct enough to warrant a new monotypic subsection *Rzedowskiae* within section *Parrya*.

There are several ambiguous areas of classification in section *Strobus*, subgenus *Strobus*. A general question is whether subsection *Cembrae* is a natural or polyphyletic group. Shaw (1914) segregated *Cembrae* from *Strobi* on the assumption that retention of seeds in the indehiscent cone (*Cembrae*) and dispersal of seeds by birds are monophyletic traits. This assumption has been investigated and defended by Lanner (1982, 1988, 1990) and challenged by Critchfield (1986). Critchfield reasoned that although the available evidence is highly discordant, it does not support the monophyletic origin of *Cembrae* traits.

A specific question within section *Strobus* is the relationship of *P. lambertiana*. Critchfield (1986) summarized the evidence for the apparent genetic isolation of *P. lambertiana* from its supposed closest relatives, the other western North American species of *Strobi*. The suggestion that it might not belong in subsection *Strobi* (Wright 1962) was dismissed by Critchfield (1986), but there is no good explanation for its close genetic relationship to Asian *Strobi* pines.

Subsection *Cembroides* has received much recent investigation. In the last two decades, a large amount of literature has accumulated on genetics and systematics of the pinyon pines (summarized in Passini et al. 1988; Zavarin 1990). Many new species and species complexes have been described, with as many as 16 species in the subsection. The relationships and ranks of many of these remain uncertain, although there is general agreement that there are three distinct groups within the subsection (Zavarin 1988): *Cembroidae* with most of the species, *Pinceanae* with *P. pinceana* and *P. maximartinezii*, and *Nelsoniae* with *P. nelsonii*.

In subgenus *Pinus*, ambiguities remain in determining the natural classification of subsection *Oocarpae* and its relation to pines in *Ponderosae* and *Australes* (reviewed in Millar 1986). Shaw's classification of these groups, which relied heavily on assumed evolutionary trends in cone serotiny, was significantly revised by later genetic and crossing data (Duffield 1952; Critchfield 1967). These authors recognized that closed cones had evolved independently at least four times among pines and were not reliable indicators of monophyly. Duffield (1952) transferred 9 of the 16 species in Shaw's *Insignes* to other groups, leaving 7 that constituted Critchfield and Little's (1966) subsection *Oocarpae*.

The *Oocarpae* subsection remains heterogeneous. Although some species cluster into natural groups (e.g., those in California), other members have disparate relationships both within the subsection

and to species in other subsections. Barriers to crossing exist among some Latin American and Californian members of *Oocarpae*, while hybridization is possible to one species of *Australes* and two species of *Ponderosae* (Critchfield 1967).

Several new classification systems for the genus have appeared since Little and Critchfield (1969). Van der Burgh (1973, with modifications in Farjon 1984) emphasized wood anatomy along with other morphological characteristics. He did not split the system into the traditional subgenera but recognized instead eight sections (two with haploxylon pines and six with diploxylon) with 15 subsections. In his figure (in Farjon 1984), he implies that the diploxylon pines arose independently from primitive haploxylon pines. Although many of the subsections are similar to Little and Critchfield, in some where they differ, van der Burgh's system does not conform to patterns of hybridization (Millar 1986).

Klaus (1980, 1989) developed an evolutionary classification that relies heavily on cone morphology of fossil and extant species, although he incorporated some other morphological features. His system borrows elements from both Little and Critchfield (1969) and van der Burgh (1973, in Farjon 1984) and has the two traditional subgenera, *Strobus* and *Pinus*, seven sections, and 13 subsections. The main changes are in the addition of a new subsection in section *Parrya*, *Rzedowskiae*, and the segregation of *P. resinosa* into a new subsection, *Resinosae*, in section *Pinus* (Klaus 1989).

Analyses of DNA polymorphisms (Strauss and Doerksen 1990; Kossack 1989) are consistent with the subgeneric and section divisions of Little and Critchfield (1969). Haploxylon and diploxylon pines are unambiguously distinct, with the two subgenera robustly monophyletic in their analyses. DNA analyses resolved relationships best at the level of subgenus through distinct subsections, whereas subsections within section *Strobi* and within section *Pinus* were not clearly separated.

Phylogeny and Evolution of Pines

The classification systems described above provide hypotheses about evolution by suggesting common origins for sets of species. They are static models, however, in that they do not indicate the complexity of evolutionary time, phylogenetic linkages, degree of relationships, evolutionary paths, or evolutionary trends. Our goal here is to provide a historical picture of pines as they evolved from a pre-*Pinus* ancestor to their modern diversity. The scenario we develop is speculative yet synthetic in that we attempt to integrate different kinds of evidence and build on recent models of others (e.g., Miller 1976; Axelrod 1986). When evidence was contradictory, we chose the most parsimonious solution.

There are three main lines of evidence useful for interpreting the history of pines. The first is genetic relationships among extant species. Degree of relationship is inferred from comparative studies of anatomy, morphology, physiology, biochemistry, and molecular biology, and from studies of natural and artificial hybridization. The fossil record is a second source. Although there are biases in what gets preserved and errors made in identification and interpretation, fossils provide direct evidence and dates for the occurrence of specific morphologies in specific locations and indirect evidence for reconstructing paleoclimates. A third source is biogeography. Present habitats and distributions of extant species as well as regional paleogeography and plate tectonics provide important clues to evolutionary history.

Origins of the Genus Pinus

Interpretation of the early evolution of the genus *Pinus* and the family *Pinaceae* has been significantly revised by comparative analyses of internal cone anatomy in fossil and extant species (Miller

1976, 1977, 1982, 1988; Stockey 1984). These studies identified four fixed traits of internal cone anatomy that distinguish pines from all other extant and fossil pinaceous genera (Miller 1976). A surprising result was that fossil cones having external anatomy of pines did not necessarily have the diagnostic internal pine characteristics. This was especially true of pinaceous remains from the Mesozoic (see Table 1 for geologic times), many of which had been previously identified as pines. Most of these were reclassified into two extinct pinaceous genera, *Pityostrobus* (Nathorst) Dutt (1916) (a highly diverse taxon, probably comprising several natural genera) and *Pseudoaraucaria* (Alvin 1957, 1960; Miller 1976). *Pityostrobus* is now recognized as the pool of variation out of which *Pinus* and other modern genera of the pine family evolved (Fig. 2).

Two further revisions followed from the studies of internal anatomy of fossils. One is that none of the modern pinaceous genera is as old as previously thought, with most genera having no or few

Table 1. Approximate ages and durations of geologic times in the history of the earth

ERA	Period	Epoch	Duration (millions of years)	Millions of years ago
Cenozoic	Quaternary	Holocene	Approximately the last 10 000 years	
		Pleistocene	2.4	2.5
	Tertiary	Pliocene	4.5	7
		Miocene	19.0	26
		Oligocene	12.0	38
		Eocene	16.0	54
		Paleocene	11.0	65
Mesozoic	Cretaceous		71	136
	Jurassic		54	190
	Triassic		35	225
Paleozoic	Permian		55	280
	Carboniferous		65	345
	Devonian		50	395
	Silurian		35	430
	Ordovician		70	500
	Cambrian		70	570
Precambrian			4030	4500

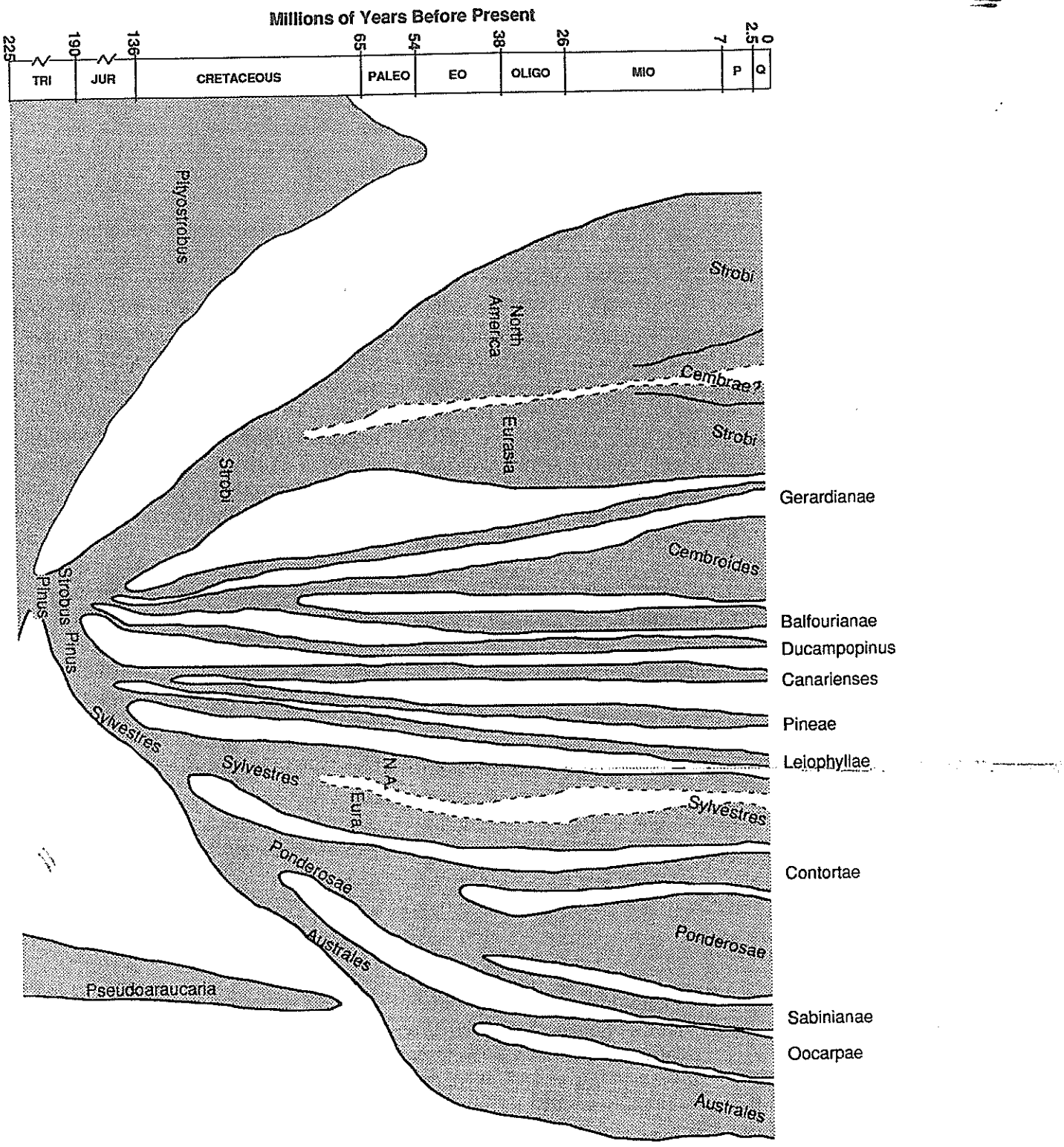

Figure 2. Hypothesized phylogeny of the pines, showing their origins from *Pityostrobus* in the Mesozoic and their divergence over geologic time into modern subgenera, sections, and subsections. Subsections that occur in North America and Eurasia are indicated. See Table 1 for geologic times.

remains from the Mesozoic. Previously, pines and other genera in the pine family were believed to have abundant fossil records extending into the Jurassic (summarized in Mirov 1967). The only modern pinaceous genus with a definite Mesozoic record is *Pinus*, which is known from a single species, *P. belgica*, found in Early Cretaceous (130 million years ago) sediments in Belgium (Alvin 1960) and from many species found in sediments of mid and late Cretaceous (Penny 1947; Miller 1976; Robison 1977; Blackwell 1984; Miller and Malinky 1986; Stockey and Ueda 1986; Stockey and Nishida 1986). *Pinus* is now considered to be the oldest genus in the pine family, whereas previously (Mirov 1967) it was thought to be the youngest.

The diversity of forms already present in Cretaceous pine fossils indicates that pines arose even earlier, in the Triassic or Jurassic (Miller 1976; Eguiluz Piedra 1985; Axelrod 1986) (Fig. 2). There is still mixed opinion as to whether the first pines were subgenus *Strobus* or *Pinus*. Early morphologists (Shaw 1914; Doak 1935) thought subgenus *Strobus* had many primitive traits relative to *Pinus* and shared by *Pityostrobus* and other modern pinaceous genera. These include high number of needles per fascicle, resin canal placement, cotyledon anatomy, thin cone scales, terminal umbos on the cone scales, cylindrical symmetric cones, primitive seed wings, uninodal spring shoots, small lateral ray pits of the wood, and thick-walled ray parenchyma in the wood. Contradicting this is the predominance of subgenus *Pinus* in the Cretaceous fossil record (Miller 1976; Axelrod 1986; Miller and Malinky 1986; Stockey and Nishida 1986; Stockey and Ueda 1986). Only fragmentary and questionable fossil evidence exists for subgenus *Strobus* in the Cretaceous (Jeffrey 1908; Stopes and Kershaw 1910; Penny 1947). Several new studies have suggested that pines of section *Parrya*, subgenus *Strobus*, were among the first lineages to evolve (van der Burgh, in Farjon 1984; Klaus 1989; Strauss and Doerksen 1990).

The center of origin of pines remains uncertain. At the beginning of the Mesozoic, the continents were still together in one land mass, Pangaea (Smith et al. 1981). By the early Jurassic, the northern continent, Laurasia, began to drift from the southern continent, Gondwanaland. Since the earliest pinaceous fossils (*Pityostrobus, Pseudoaraucaria*, and *Pinus*) were found at temperate middle paleolatitudes (Eguiluz Piedra 1985; Axelrod 1986) in eastern North America and western Europe, it is tempting but not conclusive to suggest that pines originated there. Regardless of where they arose, it is clear that pines spread rapidly at temperate paleolatitudes across Laurasia in the early and mid Mesozoic (Eguiluz Piedra 1985). By the Cretaceous, *Pityostrobus* and *Pinus* had reached both eastern and western extremes of the continent (California: Miller 1976; Japan: Stockey and Ueda 1986; Stockey and Nishida 1986) as well as many inland locations. These early migrations must have been accompanied by major genetic radiations, with subgenus *Pinus* diverging early and, like subgenus *Strobus*, spreading rapidly across Laurasia.

Cretaceous Evolution of Pines

The Cretaceous was a time of major radiation in *Pinus* during which all the sections and many subsections appear to have originated (Axelrod 1986). Compared with the present, the climate of the Cretaceous appears to have been warmer and drier, with seasonality at middle latitudes, although less latitudinal zonation and little topographic variability (Savin 1977; Hallum 1984; Axelrod 1986; Parrish 1987). These conditions were ideal for dispersal of pines. The breakup of Laurasia into North America and Europe (Smith et al. 1981), which began in the late Cretaceous (Fig. 3), created a barrier to migration that can be used to date the groups that now exist in both continents. Although there were transient connections between North America and Europe later during the Tertiary and Quaternary (discussed below), these were unlikely to be major routes of pine migration. Thus, monophyletic groups within the genus with major distributions in both North America and Europe must have evolved prior to the breakup

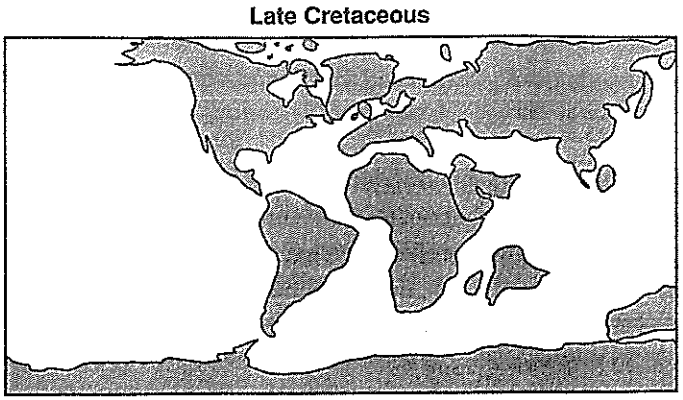

Figure 3. Generalized map of the continents during the Late Cretaceous. The supercontinent Pangaea began to break into Laurasia and Gondwanaland in the Jurassic. By the Late Cretaceous, Laurasia was beginning to split into North American and Eurasian continents. The Tethys Sea still formed the southern shore of Eurasia, and India had not yet collided with Eurasia.

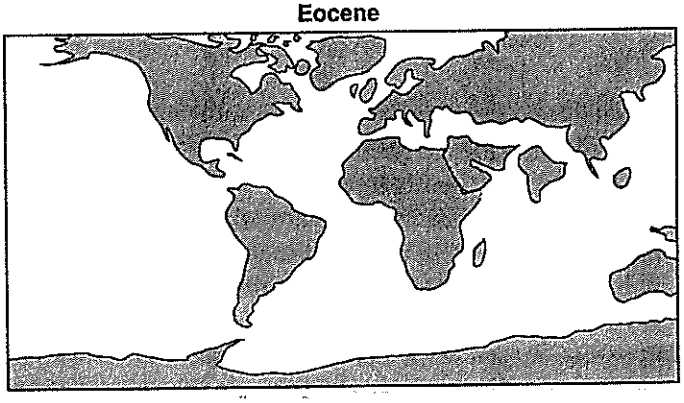

Figure 4. Generalized map of the continents during the Eocene. Although the North American and Eurasian continents were mostly isolated, land connections persisted transiently during the Eocene in the North Atlantic and Beringia. The Tethys Sea persisted throughout this epoch.

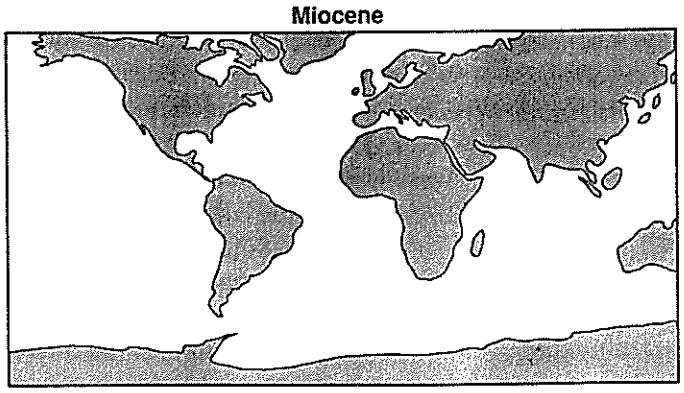

Figure 5. Generalized map of the continents during the Miocene. North America and Eurasia have assumed near-modern orientations and latitudes, the North Atlantic connection has been severed, and by the mid Miocene the Beringia connections also were severed.

of Laurasia. This dates the divergence of the two major subgenera prior to the Tertiary, which is corroborated by the existence of Cretaceous fossils of both subgenera. An ancient monophyletic origin for subgenus *Pinus* is supported by molecular data (Strauss and Doerksen 1990; Kossack 1989), and supported by patterns of hybridization (Critchfield 1975) and comparative morphology (Shaw 1914; Little and Critchfield 1969).

Several other lineages appear to have diverged soon after the origin of the subgenera (Fig. 2). Within the unusually diverse section *Parrya* are found traits otherwise only in subgenus *Pinus*, and in the diverse section *Pinea* are found traits otherwise only in subgenus *Strobus*. This suggests early origins for lineages in these sections before the subgenera had evolved other derived traits. Molecular (Strauss and Doerksen 1990; Kossack 1989) and cladistic (van der Burgh, in Farjon 1984) analyses confirm the early divergence times of the subsections within these sections. The little known *P. krempfii*, with its unique combination of traits, may also have arisen as a minor lineage from the early pine gene pool (Fig. 2) either distinct from the other subgenera (as suggested by evidence leading to Little and Critchfield's classification) or allied to subgenus *Strobus* (summarized in Erdtman et al. 1966; van der Burgh, in Farjon 1984). Despite the antiquity suggested for these clades within *Parrya, Pinea*, and *Krempfiani*, they either did not radiate early, or, if they did, many of the lineages went extinct without leaving a record. There is little hint of their presence in the known Cretaceous or early Tertiary fossil record, and many of the radiations within the subsections are considered to be recent events (discussed below).

Within each of the two major subgenera was a lineage that migrated widely prior to the end of the Cretaceous and left abundant evidence of early radiations. Pines of subsection *Strobi* and subsection *Sylvestres* probably evolved following the divergences of sections *Parrya* and *Pinea* (Fig. 2). The fact that DNA analyses resolved evolutionary distinctions among subsections within *Parrya* and *Pinea* but not among subsections within *Strobus* or *Pinus* points to the younger ages of the last two sections (Strauss and Doerksen 1990; Kossack 1989). Within their respective sections, *Strobi* and *Sylvestres* are characterized by fewer derived traits than the other subsections (Shaw 1914; Klaus 1980). Distribution of species in the subsections in both North America and Eurasia indicates that they evolved prior to the close of the Mesozoic. Many Cretaceous pine fossils including the oldest known, *P. belgica* (Alvin 1960), have traits that ally them to subsection *Sylvestres* (Penny 1947; Pierce 1957; Chaney 1954; Robison 1977; Stockey and Nishida 1986). They have been found in deposits in western Europe; eastern, central, and western North America; and Japan.

Subsections *Ponderosae* and *Australes* appear to be closely related (Shaw 1914; Duffield 1952; Gaussen 1960; Jaehrig 1962; de Ferre 1965; Klaus 1980). The evolutionary transformations of traits suggested by Shaw (1914) indicate these subsections to be derived from *Sylvestres*, with *Australes* having the most derived traits of the three subsections (e.g., multinodal spring shoots). Fossil cones allied to *Ponderosae* and *Australes* are the next most common pines after *Sylvestres* in the Cretaceous and early Tertiary record. *Ponderosae*-like cones have been found in both western and eastern North America (Penny 1947; Robison 1977; Stockey 1983, 1984), while *Australes*-like cones have been found in eastern North America (Blackwell 1984; Miller and Malinky 1986). During the late Cretaceous, an epicontinental seaway existed in central North America, effectively isolating the eastern and western regions floristically (Muller 1970; Eguiluz Piedra 1985). Consideration of all the evidence together suggests that a lineage of *Sylvestres* had migrated throughout North America by the mid Cretaceous and that *Ponderosae* evolved from this gene pool and also spread throughout North America. *Australes* may have evolved from an eastern lineage of *Ponderosae* or *Sylvestres*, subsequently diverging in isolation from western elements of these groups due to the epicontinental seaway. Extant *Ponderosae* occurs only in western North

America, Mexico, and Central America, while *Sylvestres* occurs only in eastern North America and the Caribbean (Little and Critchfield 1969).

Tertiary Evolution of Pine: Paleocene and Eocene

The transition from Mesozoic to Cenozoic eras (65 million years ago, Table 1) marked the beginning of a major upheaval in pine evolution that lasted 35 million years. It ended in the evolution of most modern subsections and of patterns of speciation within subsections[2] (Axelrod 1986). By the early Cenozoic, the breakup of Laurasia was well under way with North America and Eurasia isolated at all latitudes except for transient connections in the North Atlantic and Beringia (Tiffney 1985a, 1985b). The Cretaceous mid-continental seaway of North America shrunk in size through the early Tertiary: by the end of the Eocene, it existed only as a major bay penetrating the Gulf coast (Tiffney 1985a). The extensive southern border of Eurasia was formed by the Tethys Sea (Fig. 4) (Plaziat 1981) which included regions now along the Mediterranean, Himalayas (India had not yet collided with Asia), and southeast Asia.

Major continental movements were only part of the changes of the early Cenozoic. This period was also marked by dramatic changes in global climate (Wolfe 1975, 1978, 1985; Hsu 1983; Parrish 1987). Relative to the early-middle Cretaceous, the late Paleocene and early Eocene (and at least two other periods during the mid Eocene) had hot, humid, tropical conditions that were highly equable and aseasonal (Wolfe 1975, 1978, 1985; Buchardt 1978; Parrish 1987). The warm, wet periods lasted 5-10 million years each, and average annual temperatures fluctuated 7-10°C between warm and cool periods (Wolfe 1978). This climate extended in broad zones throughout middle latitudes in both Northern and Southern Hemispheres (Wolfe 1975, 1978, 1985). Within these zones, latitudinal changes in climate were much less exaggerated than at present, and tropical-subtropical conditions extended from 25° to 60-70° latitude (Wolfe 1985). The latitudinal gradient that did exist differed from the present pattern. In general, low latitudes were warm and dry, mid latitudes were tropical and subtropical, and high latitudes were cool and dry (Wolfe 1985; Parrish 1987).

This climate had an enormous effect on global floristics. By the early Eocene, mid to high latitudes were dominated by highly diverse angiosperm floras with species adapted to tropical conditions (reviewed in Wolfe 1975, 1978, 1985; Tiffney 1985a, 1985b; Wolfe and Upchurch 1986). Foliage and reproductive structures were as diverse and had similar adaptations (e.g., in leaf and fruit structure and shape) as in present Indomalaysian rain forests (Reid and Chandler 1933; Wolfe 1975; Tiffney 1985a, 1985b). Only a few nonpinaceous gymnosperms that were adapted to warm, humid conditions (e.g., *Taxodium, Glyptostrobus*) occurred in the drier of these floras. This cosmopolitan angiosperm flora has been called the boreotropical flora to indicate its tropical adaptations at boreal latitudes (Wolfe 1975). The greatest diversity of boreotropical fossils has been found in western and eastern North America, eastern Asia, and western Europe. Homogeneities in floristic composition among the regions have been explained by transcontinental migration across land bridges in the North Atlantic and Beringia (Tiffney 1985a, 1985b). During the hot, humid periods of the Eocene, these bridges were climatically and ecologically able to support boreotropical floras.

What happened to the pines during these periods of angiosperm evolution and dominance? In the Cretaceous, the distribution of pines at temperate, dry, middle latitudes resembled modern pine

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[2] Millar, C.I. Impact of the Eocene on the evolution of pines. (In preparation.)

biogeography. By the Paleocene and early Eocene, pines had virtually disappeared from these latitudes; in fact, there are scant pine remains from these periods at all (Wolfe 1987). Their distribution and subsequent evolution can be explained by postulating strategically located Eocene refugia.

The major climate changes that favored the evolution and spread of the boreotropical angiosperm flora during the three (or more) hot periods of the Eocene severely reduced the distribution of pines. Pines are ecologically poor competitors for angiosperms under tropical conditions (Bond 1989). Pines that occurred in habitats increasingly more tropical (= mid latitudes) at these times must have suffered widespread population extinctions and fragmentations. Cool-dry or warm-dry areas became refugia for existing pine populations or for populations that were able to migrate into them as global conditions warmed.

Three major regions in the Northern Hemisphere might have been pine refugia during the hot, humid periods of the Eocene: high latitudes, low latitudes, and dry inland areas at middle latitudes. There is no evidence for boreotropical floras above 70° north. Above these latitudes, there is evidence in North America and Eurasia for low diversity, cold and seasonally adapted coniferous-angiosperm flora (Wolfe 1972, 1978; Savile 1972; Kuc 1974; Norris 1982). Much of the area now under the Arctic Ocean may have been land in the early Tertiary (Wolfe 1985) and could have provided pine habitat. Early Tertiary pine pollen has been recovered from the Mackenzie Delta and Banks Island, Canada at 69-73°N. (Norris 1982) and in Spitsbergen, Norway, at 76-80°N. (Schweitzer 1974). The lower inclination postulated for the earth's axis during the Eocene (Wolfe 1978) would have permitted high enough light levels at high polar latitudes for plant growth.

Scattered evidence points to warm-dry regions in low latitudes (Wolfe 1975, 1978, 1985; Parrish 1987). The Mississippi embayment of North America supported dry subtropical angiosperm flora (Wolfe 1978), and there is evidence that elsewhere in the continent conditions were warmer and drier further south. Although parts of the Mexican and Central American isthmuses were transiently under water during the Mesozoic (Kellum 1944; Eguiluz Piedra 1985), they were elevated during the Eocene and may have provided pine habitat, although fossil deposits are almost absent from this period (Martin and Harrell 1957; Eguiluz Piedra 1985).

Low latitudes along the Eurasian Tethys Seaway, from the present Mediterranean basin across to southeastern Asia, may also have provided warm-dry habitats for pine refugia. There is evidence that despite abundant boreotropical floras at mid latitudes, low latitudes in Asia such as Borneo and Madagascar supported dry floras (Guo 1980).

Among the inland areas at middle latitudes that might have supported pines in the Eocene, inland western North America is best documented. An upland region extended from northern Nevada and central Idaho north to British Columbia (Axelrod 1966). Of the abundant early Eocene fossil floras from this region, pines are known from only a few locations and are within this upland region (summarized in Wolfe 1987). More fragmentary evidence suggests that areas of Japan may also have been refugia (Wolfe 1985).

This major fragmentation of pines during the Eocene had a great effect on their subsequent evolution. The restriction of pines to refugia explains the current pattern of north-distributed and south-distributed subsections and related species within subsections. Subsections that might have radiated from southern refugia in North America (Fig. 2) include *Cembroides, Leiophyllae, Australes, Sabinianae*, and *Oocarpae* (more on the last two below); *Contortae* radiated from northern refugia. In Eurasia (Fig. 2), subsections *Canarienses, Pineae, Gerardianae*, and *Krempfiani* may have been in southern refugia along the Tethys Seaway (recall India was not attached to the continent, and the area of present Nepal was

the southern edge of the continent). Some subsections may have been divided north and south by the Eocene boreotropical flora. For instance, in North American *Strobi* (Fig. 2), ancestors of *P. monticola* and *P. strobus* were in northern refugia; ancestors of *P. strobiformis*, *P. ayacahuite*, and *P. chiapensis* (*P. strobus* var. *chiapensis*) were in southern refugia. In Eurasia (Fig. 2), *P. parviflora* lineages were northern, and the other seven Eurasian *Strobi* lineages were southern (along the Tethys). In *Sylvestres*, the ancestral lineage of *P. resinosa* was in northern refugia, of *P. tropicalis* in southern North America refugia; ancestral lineages of *P. sylvestres*, *P. densiflora*, and *P. thunbergiana* were in northern Eurasian refugia, and lineages of the other 14 species were in southern refugia. Similar north-south patterns can be seen in species of *Ponderosae*. Inland areas of mid-latitude western North America may have served as refugia for subsection *Balfourianae*, for ancestral lineages of *P. flexilis* within *Strobi* and of *P. ponderosa*, *P. jeffreyi*, and *P. washoensis* within *Ponderosae*. The relation of these inland areas in western North America to southern refugia in Mexico is unclear.

In addition to the biogeographical effect that the Eocene had on pines and the divergence that arose due to isolation of lineages, some pine refugia had characteristics that actively promoted pine radiation. These areas became secondary centers of pine origin. The primary example is in Mexico and Central America, which is widely recognized as an area of high pine diversity and radiation. The late Eocene and Oligocene were times of enormous tectonic changes in this area (reviewed in Eguiluz Piedra 1985). Three main mountain ranges rose, and there was abundant volcanism associated with the uplifts. These events created a heterogeneity of habitats, microclimates, and soils favorable for pine divergence and speciation. Thus, two events contributed to make this area a center of pine origin and diversity: first, pines of diverse lineages were concentrated into Mexican refugia by global effects during the Eocene, and second, creation of environmental diversity favored speciation of pines in the area. Subsections *Cembroides*, *Oocarpae*, and southern elements of *Ponderosae* were especially affected by these events (Fig. 2). Similar events may have occurred in Japan, as indirect evidence of subsequent pine radiations suggests, but the fossil record of pines in the Eocene of Japan is not as complete and does not indicate as clearly as North America the sequence of events (Wolfe 1985).

Tertiary Evolution of Pines: Oligocene to Pliocene

The warm and humid tropical conditions of the Eocene came to a sudden end with a dramatic climatic deterioration called the terminal Eocene event (Wolfe 1978, 1985). The estimated drop in average global temperature was as much as 13°C, with conditions becoming cold, dry, and seasonal where they had been hot, humid, and aseasonal. Changes in inclination of the earth and patterns of air circulation (Wolfe 1978) led to latitudinal zonation that resembled the present. North America and Eurasia were completely severed in the North Atlantic, and the final Tertiary isolation of the two continents at Beringia occurred in the Miocene (Fig. 5). During the Oligocene, mountain-building of the early North American cordillera, Alps, and Himalayas commenced, and environmental gradients and heterogeneity were much greater than before (Wolfe 1985, Axelrod 1986).

The effect of these physical changes was equally dramatic on plants. In a short time, the boreotropical flora all but disappeared throughout the middle latitudes and was replaced by conifers and deciduous angiosperms. In one fossil sequence where successive chronological intervals are well preserved, the boreotropical flora was completely replaced by conifers in only one million years (Axelrod 1966). The widespread reappearance of conifers can be interpreted to mean that pines migrated from Eocene refugia and once again became widely distributed at middle latitudes.

The Miocene was a period of pine proliferation in the fossil record (Axelrod 1986). Relative to the climate of the terminal Eocene event, temperatures were somewhat warmer, with lower ranges in

annual temperature, approaching the general present conditions (Wolfe 1978). Mountain-building was active, creating orographic effects on climate, and elevational gradients. Mediterranean climates developed in some parts of the world. These were conditions that clearly favored pines, although the unusual floristic associates of pines compared with the present suggest that the ecological relationships were still quite different from modern ones. During the Miocene are found fossil pines with clearly modern alliances, and it seems safe to say that the lineages leading to most modern species or closely related species complexes had diverged by the late Miocene. A few subsections with derived traits, such as *Oocarpae* and *Sabinianae*, may have arisen late in the early Tertiary (Eguiluz Piedra 1985). There is little indication of their existence earlier, and they are related genetically to *Ponderosae* and *Australes* (reviewed in Millar 1986; Critchfield 1966) which may have been progenitor groups.

To this point, the evolution of subsection *Cembrae* has not been discussed. Since questions remain about the monophyly of *Cembrae*, the origin and evolution of its species is unclear. If monophyletic (as defended by Lanner 1990), its North American and Eurasian distribution suggests that it evolved before the breakup of Laurasia at the end of the Mesozoic. Alternatively, the single North American species, *P. albicaulis*, may have migrated from northeastern Asia to North America by way of Beringia land connections. That this land connection existed transiently into the Miocene (and in the Quaternary, see below) and was used as a plant corridor for angiosperms has been amply documented (Tiffney 1985a, 1985b). However, its ecological availability and use by pines is less certain. Through the warm periods of the Eocene, the latitudes of the land bridge were within the zone dominated by subtropical flora, and it probably could only have supported pine growth during later periods. If *Cembrae* is not monophyletic, individual species may have evolved independently from *Strobi* at various times. The highly derived morphology of the cone and the co-adaptation to dispersal by *Nucifraga* birds suggest that pines of *Cembrae* are recent lineages. Without further evidence, the question is unresolved.

Another candidate for transcontinental migration by way of Beringia is the lineage leading to *P. lambertiana* in subsection *Strobi*. If *Strobi* had a northern refugium at high latitudes in Asia, then the migrations south following the terminal Eocene event may have provided an opportunity for migration of a *P. lambertiana* lineage into North America. As described in an earlier section, *P. lambertiana* has unexpected genetic relationships to other members of the subsection. Although other geographically related *Strobi* species are able to hybridize, *P. lambertiana* does not cross with any of the western North American species of *Strobi* (Critchfield 1986). It does, however, cross with two Asian species of the subsection. Similarly, the resistance mechanism of *P. lambertiana* to white pine blister rust resembles that of Asian *P. armandii* more than that of other North American *Strobi* (Kinloch 1982). Finally, unlike other pines of the subsection, there is little evidence of *P. lambertiana* in the fossil record until later in the Tertiary (the relationship of *P. delmarensis* (Axelrod 1986) from the Eocene of San Diego to *P. lambertiana* is uncertain). This hypothesis and other explanations for the unusual relationships of *P. lambertiana* still need to be investigated.

The late Miocene and Pliocene had fluctuating climates of cool versus warm average global temperatures. Mountain-building continued and pines continued to flourish, although local distributions still differed from the present. Lineages leading to closely related species such as *P. longaeva--P. aristata*, *P. parviflora--P. pentaphylla--P. himekomatsu* (Saho 1972; Numata 1974), and species complexes in *Cembroides* most likely diverged during this time.

Quaternary Evolution of Pines

To this point, we have described how climate and tectonic change over vast periods of time may have guided major episodes in the evolution of pines, resulting in the patterns of diversity in the subtaxa we see today. The Quaternary Period, which began only about 2.5 million years ago, represents less than 2% of the time elapsed since the first appearance of pines in the fossil record. Yet it presents an opportunity to examine with finer focus the dynamics of population change that lead ultimately to speciation. Two lines of evidence complementary to each other and unique to this period make this possible: existence of fossil pollen and macrofossils that can be identified with contemporary species, and patterns of genetically determined geographic variation documented for the same species (Critchfield 1984).

The Pleistocene was an epoch of global spasms of great ice sheets advancing and retreating in rapid frequency over large areas of continental Europe, North America, and mountain ranges worldwide. Glacial episodes were followed by interglacial periods of shorter duration, of which the present Holocene epoch beginning about 10 000 years ago is but the latest. Paleontologists are uncertain how many times this cycle was repeated, but some estimates range from 16 to 18 (Bowen 1979). Although the changes in average global temperature between the glacial and interglacial periods (5-10°C for middle latitudes, Bowen 1979) were less than that inferred for the terminal Eocene event, the Pleistocene was unique for the rapid frequency of climatic changes. Sea levels lowered during the cold, dry glacials, opening up migrational routes between different continents and between continents and offshore islands through land bridges. For example, during glacial periods the Bering land bridge was transiently elevated, and Japan and Britain were connected to their continental mainlands. The reverse occurred during the interglacial periods.

Miki (1957) may have been the first to recognize and document, in the forests of Japan, two basic patterns that characterized the response of pines to the sudden and frequent oscillations in climate during the Pleistocene. The mountains of Japan, like those of North America, have a basically north-south orientation providing migratory escape routes to lower latitudes during colder climatic periods. During interglacials species adapted to warm, moist climates (Miki's type B: e.g., *P. densiflora, P. thunbergiana*), expanded in the lowlands and climbed in elevation, forcing competitors up to colder, harsher environments. When the climate reversed, cold-adapted species (type C: e.g., *P. koraiensis, P. pumila*) migrated to lower elevations and expanded in valleys, displacing type B species which were then relegated to small, isolated refugia where local environments were mild enough to allow survival until another cycle began. Type A (*P. fujiii, P. protodiphylla*, and *P. trifolia*, Miki 1957) did not have adequate variability to adapt and became extinct. Tsukada (1985) showed more comprehensively the drastic changes in composition of Japanese forests from glacial to interglacial phases. During the last full glacial, boreal conifers (including *P. koraiensis*) occupied most of the lowlands of the entire Japanese archipelago. Now these forests are largely broad-leaved, or mixed with conifers in the north; elsewhere, most of the conifers have been pushed to higher elevations.

The abrupt oscillations of climate and the resulting effects on pine distribution had drastic impacts on the genetic structure of forest populations. In addition to species extinction and reduction in genetic variation, one of the major consequences was reorganization and redistribution of genetic variation (Critchfield 1984, 1985). Populations that were fragmented continued their short-term evolution in isolation. If parts of the population mosaic were subjected to differential selection pressure or genetic drift as a result of going through a bottleneck, gene frequencies would change. When the cycle shifted and population fragments coalesced again, gene exchange resumed, and gene frequencies changed again. Transient races thus appeared and disappeared, in more or less constant flux. This rationale has been used to explain many of the anomalous patterns of variation found in extant conifer populations (e.g.,

Critchfield 1984, 1985; Kinloch et al. 1986; Millar et al. 1988). The microevolutionary processes of the Quaternary that may be read in the genetic structure of extant species give insight into events that might have preceded major radiations in the past and into incipient radiations of the future.

STEM RUSTS

Host parasite affinities and geographic distribution of pine hosts, their stem rusts in *Cronartium--Peridermium*, and secondary hosts in different dicotyledon families are summarized in Tables 2 and 3. With respect to host-parasite affinities, only endemic pathosystems are considered; we do not attempt to deal with relationships based on artificial inoculation or on behavior of introduced hosts or pathogens. Much of the same information is in both tables, but each emphasizes a different perspective. From the perspective of hosts (Table 2), it is noteworthy that subgen. *Strobusus* the oldest lineage, has only three rusts. Subsection *Strobi*, with 14 species on all Northern Hemisphere continents, has only one (*C. ribicola*)[3]; while three subsections (*Gerardianae, Balfourianae*, and *Krempfiani* in subgenus. *Ducampopinus*) have none. Subgenus *Pinus* hosts 80% of the stem rusts, and most of these are in North America. Six subsections host only one rust, while four subsections have five or more.

Like their hosts, the greatest diversity of the rusts is in North America (especially western North America) with 11 taxa, compared with 4 in Asia and 2 in Europe. Some rusts are confined to only one pine host subsection (or even a single species: e.g., *C. appalachianum* and *P. virginiana*), while others attack 3 or 4. Most have only one alternate host family, but *C. flaccidum* has 10. Four are autoecious; except for *P. harknessii*, these have relatively narrow host ranges.

Classification and Taxonomy of Stem Rusts

The pine stem rusts in *Cronartium--Peridermium* comprise about 15 species in *Melampsoraceae*, a small but taxonomically difficult group. In the opening statement to his monograph "The *Peridermium* Species on Pine Stems" Peterson (1967) declared "taxonomic knowledge of *Cronartium* is in a state of disorder." Having completed our own review, we feel this might still serve as an appropriate conclusion, but must acknowledge with gratitude that without that paper and its sequel on *Cronartium* (Peterson 1973) we would not have made this attempt. Our review follows his concept and nomenclature of the genus, modified only by developments since his papers were published.

To the uninitiated, confusion is apparent from the beginning, with three generic names for different members of a single natural group. *Cronartium* designates the sexual stage of heteroecious species on dicot hosts. *Peridermium* is the form genus used for the aecial stage on pine stems when the alternate host is unknown or does not exist. Some of these *Peridermia* were put into a new genus, *Endocronartium*, erected to accommodate those autoecious species considered to have an endo-type sexual cycle with meiosis (Hiratsuka 1969). We will not discuss *Endocronartium* here because interpretation of the cytogenetic data on which it is based is controversial (Epstein and Buurlage 1988; Gibbs et al. 1988) and will be addressed elsewhere in these proceedings (Hiratsuka 1990), and because the controversy is not relevant to our theme. Whatever their sexual behavior is it seems clear that the autoecious *Peridermia* have a polyphyletic origin, deriving by reduction from closely related heteroecious species.

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[3] Authorities for nomenclature in *Cronartium--Peridermium* are in Peterson (1967, 1973) except where indicated otherwise.

Table 2. Pine hosts of stem rusts in *Cronartium--Peridermium* and their geographic distribution

Pine host (Subg./ Sect.-Subsect.)	No. of species	Continent[a]	Stem rust
Ducampopinus	1	A	(None described)
Pinus			
Pinea			
Canarienses	2	E,A	*flaccidum*
Leiophyllae	2	NA	*conigenum*
Pineae	1	E	*flaccidum*
Pinus			
Australes	11	NA	*comandrae*, *comptoniae*, *conigenum*, *quercuum*, *strobilinum*
Contortae	4	NA	*appalachianum*, *comandrae*, *comptoniae*, *harknessii*, *quercuum*, *stalactiforme*
Oocarpae	7	NA	*comandrae*, *conigenum*, *harknessii*, *stalactiforme*
Ponderosae	13	NA	*arizonicum*, *comandrae*, *comptoniae*, *conigenum*, *filamenotosum*, *harknessii*, *stalactiforme*
Sabinianae	3	NA	*harknessii*
Sylvestres	19	A,E,NA	*comandrae*, *comptoniae*, *flaccidum pini*, *quercuum*
Strobus			
Strobus			
Cembrae	5	A,E,NA	*ribicola*, *yamabense*
Strobi	14	A,E,NA	*ribicola*
Parrya			
Balfourianae	3	NA	(None described)
Cembroides	8	NA	*occidentale*
Gerardianae	2	A	(None described)

[a] A = Asia, E = Europe, NA = North America.

Table 3. Stem rusts in *Cronartium--Peridermium*, their distribution, and their hosts

Rust species	Continent	Dicot host	Pine host (subsect.)
Cronartium			
appalachianum	eNA	*Santalaceae*	*Contortae*
arizonicum	wNA	*Scrophulariaceae*	*Ponderosae*
comandrae	NA	*Santalaceae*	*Australes*, *Contortae*, *Oocarpae*, *Ponderosae*
comptoniae	NA	*Myricaceae*	*Australes*, *Contortae*, *Ponderosae*, *Sylvestres*
conigenum	swNA	*Fagaceae*	*Australes*, *Leiophyllae*, *Oocarpae*, *Ponderosae*
flaccidum	E,A	(10 families)[a]	*Canarienses*, *Pineae*, *Sylvestres*
occidentale	swNA	*Saxifragaceae*	*Cembroides*
quercuum	A,NA	*Fagaceae*	*Australes*, *Contortae*, *Sylvestres*
ribicola	A	*Saxifragaceae* *Scrophulariaceae*	*Cembrae*, *Strobi*
stalactiforme[b]	NA	*Scrophulariaceae*	*Contortae*, *Oocarpae*, *Ponderosae*
strobilinum	seNA	*Fagaceae*	*Australes*
Peridermium			
filamentosum	wNA	autoecious	*Ponderosae*
harknessii	wNA	autoecious	*Contortae*, *Oocarpae*, *Ponderosae*, *Sabinianae*
pini	E	autoecious	*Sylvestres*
yamabense	A	autoecious	*Cembrae*

[a] *Acanthaceae*, *Asclepiadeaceae*, *Balsaminaceae*, *Gentianaceae*, *Loasaceae*, *Paeoniaceae*, *Scrophulariaceae*, *Solanaceae*, *Tropaeolaceae*, *Verbenaceae*.

[b] Invalidly published in *Cronartium*; *P. stalactiforme* Arth. & Kern.

Diagnostic traits separating these fungi are few, and none is completely satisfactory. One practical and descriptive way to group the pine stem rusts is by the type of disease or symptoms they cause. Four basic effects on hosts have been described (Peterson 1967):

- Stimulation of apical meristems (*C. conigenum, C. strobilinum*--the cone rusts) causes the host to proliferate pithlike tissue and primary vascular tissue (although lateral meristems are stimulated as well).

- Stimulation of lateral meristems (*C. quercuum, P. harknessii*) causes hosts to proliferate secondary tissues through hyperplasia, usually resulting in galls. Western gall rust (*P. harknessii*) also causes perennial cankers by eventually killing tissues from the center of the infection (primary gall) outward. The fungus continues to grow centrifugally, causing a series of secondary galls (ridges) before these, in turn, also become necrotic. Some of these infections remain viable for over two centuries (Peterson 1961).

- Stimulation lacking (*C. occidentale, C. ribicola, C. comandrae, C. appalachianum, P. pini, P. stalactiforme*). This largest group of stem rusts usually causes no direct stimulation of tissues, although hormonal imbalance may induce lateral buds not in direct contact with the pathogen to grow. Infections eventually result in cankers. *P. stalactiforme* does cause minor lateral meristem stimulation (as well as causing limb rust, see below), but its predominant symptom is an elongate canker.

- Systemic infection (*C. arizonicum, P. filamentosum, P. stalactiforme*--the limb rusts). These remarkable rust fungi infect their hosts systemically, proliferating in mature tracheids and penetrating radially into the xylem of large trees (Peterson and Shurtleff 1965). Infection is through a small twig, after which mycelium grows through a branch to the bole, up and down the bole, and back out into new limbs. Eventually infected branches die, giving the tree a window like appearance at mid crown. The mycelial thalli thus formed from single infections may be unique among parasitic fungi in their extension and biomass. Aecia of *C. arizonicum* and *P. filamentosum* have a distinctive long, tonguelike shape. These two species cause limb rust on all hosts they infect, but *P. stalactiforme* causes limb rust only on Jeffrey pine (*Pinus jeffreyi*), and then only from the central Sierra Nevada southward. On other host species and in other places, it causes cankers (Peterson 1968).

Because they do not unambiguously separate the causal fungi, symptoms cannot be the criteria for taxonomic classification. Peterson (1967, 1973) emphasized spore size and morphology, particularly the degree of aeciospore wall modification, but acknowledged their limitation in discriminating some species. Host specificity will sometimes separate morphologically similar species and is the basis for the subspecific designation of *forma specialis* (special form).

Several species with narrow host ranges or distinctive morphology are straightforward enough, such as *C. appalachianum*, *C. comandrae*, *C. comptoniae*, and *C. occidentale*. Others form complex taxa that have not been fully worked out. We will focus the remainder of our discussion on these.

C. ribicola *Complex*

Until relatively recently, *C. ribicola*, the white pine blister rust, was thought to be a fairly homogeneous species. Recognition of greater complexity began when young plantations of native Korean pine (*P. koraiensis*) in both Korea and Japan started coming under severe attack from blister rust (Yokota

et al. 1975; La and Yi 1976). Eastern white pine (*P. strobus*), planted as an exotic, also became heavily infected in Japan, although still not so badly as Korean pine. This was cause for some alarm because Korean pine had been highly resistant in European and North American trials. Moreover, most of these plantations were associated with infected *Pedicularis* alternate hosts (as opposed to *Ribes*), suggesting that the rust was *C. kamtshaticum*. This rust had long been known on scrophulariaceous hosts (*Pedicularis* and *Castilleja*) from the Kamchatka peninsula down through the Kuril Islands to northern Japan. Its connection to the aecial stage of *Peridermium kurilense* on *Pinus pumila* was presumed but never proven by artificial inoculation (Wicker and Yokota 1976). *C. ribicola* on *Ribes* had also been observed on the island of Hokkaido since the turn of the century. Inoculations conducted in Japan to clarify host relationships showed that aeciospore isolates collected from both *P. pumila* and *P. strobus* were complexly related (Yokota and Uozumi 1976). The isolates fell into one of three types: those that would infect

- both *Ribes* and *Pedicularis*, designated *C. ribicola* f. sp. *pedicularis*--this discovery undermined the basis for a separate species in *C. kamtshaticum*;
- *Ribes* only, designated *C. ribicola* f. sp. *ribicola*; and
- *P. pumila* only--an autoecious form, the first white pine-to-white pine stem rust discovered, subsequently named *Peridermium yamabense* Saho & I. Takahashi (Saho 1981).

No trials with *Castilleja* were reported. These findings prompted new international trials. In Germany, *Ribes*, but not *Pedicularis*, was successfully inoculated with isolates of *P. strobus*, whereas the converse was true in Korea with isolates from *P. koraiensis*, suggesting an additional type that only attacks *Scrophulariaceae* (Stephan and Hyun 1983). Hiratsuka and Maruyama (1976) reported successful inoculation of *Castilleja* with Canadian isolates from *P. monticola* and *P. albicaulis* in a single trial, but Hunt (1984) was unable to infect scrophulariaceous hosts in field tests in British Columbia.

Meanwhile, two additional races of white pine-to-white pine *Peridermia* infecting *P. pumila* on isolated mountain tops in Hokkaido and Honshu were found (Saho 1987). These could be distinguished from each other and the previously described *Peridermium yamabense* by a combination of characteristics, including nuclear number, type of aeciospore wart ornamentation, and germ tube branching. Struck by the similarity of one of these races (Kurikoma) to *Endocronartium* (= *Peridermium*) *pini* Y. Hiratsuka, Saho conjectured that it might be a *forma specialis* of the latter.

Little is known about the race in India on Himalayan blue pine (*P. griffithii*) and *Ribes*, but Peterson (1967) was emphatic on its morphological distinction in the aecial stage from both *Peridermium strobi* (= *C. ribicola*) and *P. kurilense* (= *C. kamtshaticum*, now considered part of *C. ribicola*: Yokota and Uozumi 1976). Much remains to be learned of the genetic amplitude of this complex.

C. flaccidum *Complex*

This complex is the most widespread of all pine stem rusts geographically (if one excludes *C. ribicola* artificially introduced into North America and Europe), ranging throughout Eurasia from Spain and Great Britain to Japan and the Philippines. It has the most alternate hosts, with members in ten different families (Table 3, Fig. 6), and has had more synonyms than any other *Cronartium* or *Peridermium*. This alone suggests its variability, which is extensive, but Peterson (1973) considered all the Eurasian *Cronartia* on *Sylvestres* hosts, including *C. delawayi*, *C. gentianum*, and *C. himalayense* conspecific in *C. flaccidum*. Van der Kamp's (1968) review concluded that the complex comprised at

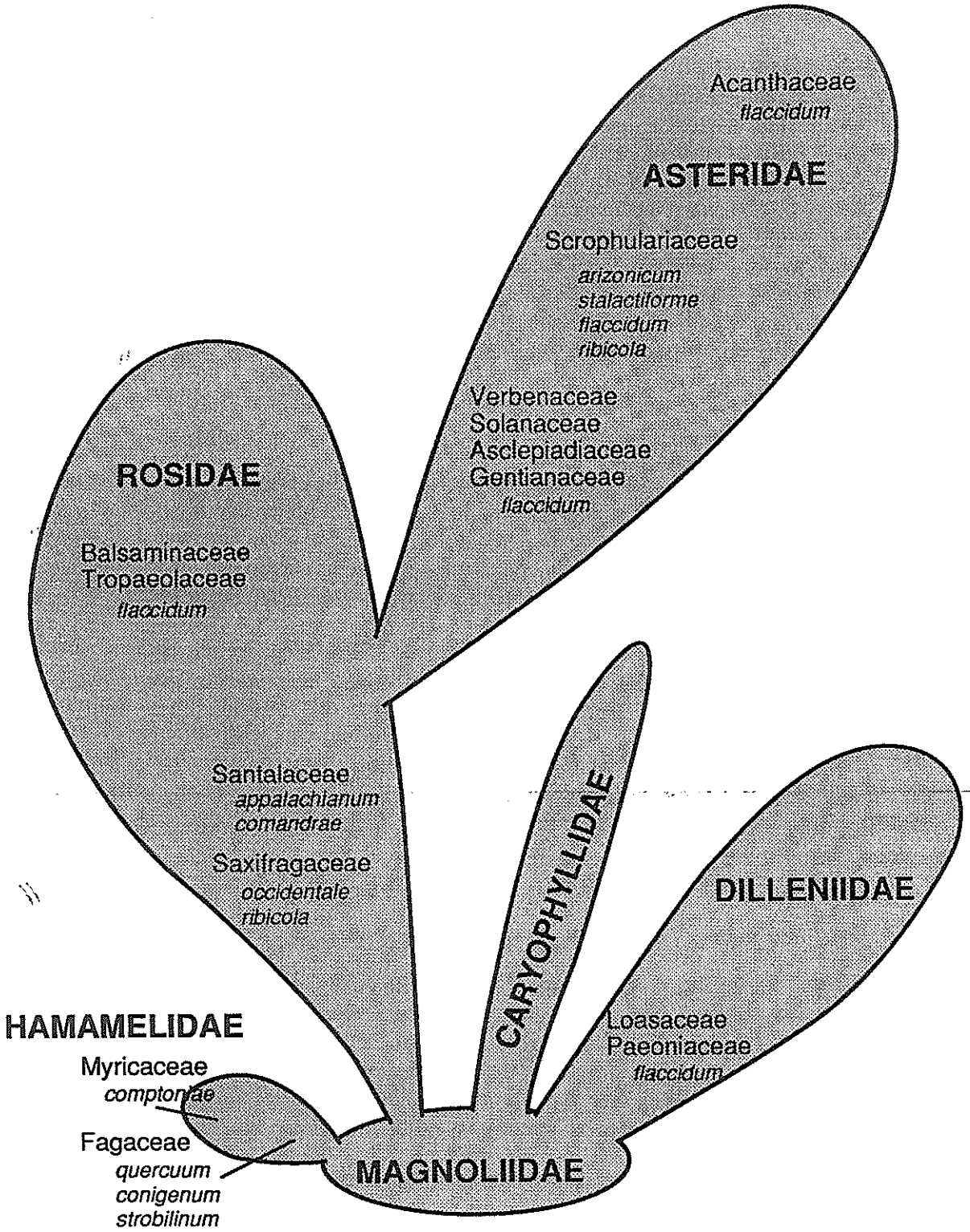

Figure 6. Alternate host families of pine stem rusts. Lobes indicate relative size of subclasses of dicots (bold type) in phylogenetic sequence from bottom to top (adapted from Cronquist 1968). Stem rusts in *Cronartium* are in italics.

least one race or special form that alternates to *Gentianum* and *Paeonia* but not other dicots; another that alternates to many dicotyledons (including *Paeonia*) but not *Gentianum*, and an autoecious form (*P. pini*).

Gibbs et al. (1988) described characteristics of this complex in Britain that further confused the picture. They examined nuclear and germ tube behavior of isolates from Scotland and England and were surprised to find that the long recognized autoecious *P. pini* in Scotland had binucleate, long, nonseptate germ tubes typical of heteroecious *Cronartia* (including *C. flaccidum*). Furthermore, the "Thetford" form from East Anglia had short, uninucleate, septate germ tubes typical of autoecious *Peridermia* (or *Endocronartium*, including *E. pini*: Hiratsuka 1968, 1969; Hiratsuka et al. 1966), yet some isolates had the ability to infest *Paeonia*! Other isolates apparently could infect pine directly. They concluded that there must be at least two races of *P. pini*, the Scottish long-tube form and Hiratsuka's (1968) short-tube form. They also raised again the issue of facultative heteroecism--the possibility that the same spore form of a rust can infect both primary and alternate hosts. This was first proposed by Meineke (1929) but never satisfactorily proved (Wagener 1964).

C. quercuum *Complex*

The gall-forming pine-oak rusts were formerly assigned to two species, *C. quercuum* of eastern North America and Asia (the only rust common to North America and Asia) and *C. fusiforme* of southern USA. There were few or no morphometric differences or an alternate host specificity to distinguish the two; distinction was based on gall shape (globose or fusoid) and unclear host specificities among southern and eastern species of pines in subsections *Australes* and *Contortae*.

Burdsall and Snow (1977) partially resolved the problem by relegating *C. fusiforme* to synonymy with *C. quercuum* and erecting four special forms (f. sp. *banksianae*, *echinatae*, *fusiforme*, and *virginianae*) based on data of host specificities. However, they did not deal with the form parasitizing Asiatic pines in *Sylvestres*. Peterson (1967) found no significant morphological differences between North American and Asian isolates, but Powers et al. (1988) reported many physiological, phenological, and morphological differences (see also Powers et al., 1990). The cone rusts (*C. conigenum* and *C. strobilinum*) are related to *C. quercuum* in having the same alternate hosts in *Quercus*; together, they are often known as the pine-oak rusts.

C. coleosporioides *Complex*

This diverse group of rusts on western North American hard pines causes very different diseases but is united in having common alternate hosts in *Scrophulariaceae* (or lacking alternate hosts, i.e., are autoecious). The group includes several limb rusts, a canker rust, and a gall rust. Inoculations of alternate hosts with aeciospores from some of the species produce morphologically distinct urediospores (Peterson 1973). Their inclusion in *C. coleosporioides* is thus a gross oversimplification. The limb rusts form a subcomplex on their own, which formerly were all described as three races of *P. filamentosum*:

- a heteroecious race (Coronado, named for the national forest where it was discovered) was recently described as *C. arizonicum* (Cummins 1984), and
- two autoecious races (Powell and Inyo), both with short septate germ tubes typical of autoecious species, can be distinguished from each other by morphological and phenological traits (Peterson 1968).

P. stalactiforme also causes a limb rust but only on Jeffrey pine and only in certain geographic areas. On lodgepole (*P. contorta*) and other pine hosts, it causes bark swelling and very elongate cankers. *P. stalactiforme* alternates to hosts in *Scrophulariaceae* and is clearly a distinct species but is not validly described in *Cronartium*.

P. harknessii, the western gall rust, is usually considered autoecious. Although several reports of alternation to *Scrophulariaceae* exist, most attempts to verify these claims experimentally have failed (Peterson 1967, 1973). This rust is highly variable, with one of the widest host ranges--four subsections of pine, (compared with only one for the *filamentosum* subcomplex--and one of the widest geographic distributions: from the Pacific to the Atlantic coasts and from sea level to over 3500 m elevation (Peterson 1960). An albino race is widespread in western North America on ponderosa pine (*Pinus ponderosa*) (Mielke and Peterson 1967). Symptomologically, *P. harknessii* has closer affinities with *C. quercuum* than its cohorts in *C. coleosporioides*.

Clearly, much remains to be done to resolve some of these taxonomic relationships, but new approaches are needed. Isozyme analysis is a promising technique that has long been available but only recently exploited (Vogler et al. 1988; Tuskan and Walla 1989; Powers et al. 1989). Starch gel electrophoresis is efficient because 20 or more marker loci can be analyzed simultaneously on many different isolates. Results in our laboratory have so far indicated a remarkable uniformity of structural genes within populations of the wide-ranging western gall rust (*P. harknessii*), making comparisons among populations unambiguous (Vogler et al. 1988). Initial comparisons of the few species we have examined show the same pattern of homogeneity within taxa and heterogeneity among taxa as in western gall rust (unpublished data). Similarly, Powers et al. (1989) obtained clear separation of five species as well as the four *formae speciales* of *C. quercuum*, using polyacrylamide gel electrophoresis. Tuskan and Walla (1989) found more variability than did Vogler et al. (1988) or Powers et al. (1989) within populations of *P. harknessii* and *C. quercuum* f. sp. *banksianae* in North Dakota and Minnesota but were able to separate the two species. These and other molecular techniques are promising and need to be pursued systematically for the genus.

Phylogeny and Evolution of Stem Rusts

Rusts are generally thought to be an ancient lineage whose original hosts were primitive plants, such as ferns and mosses, possibly arising in the warm, moist forests of the Carboniferous Period. At this time they were probably autoecious, with a relatively simple life cycle and a spore stage homologous with teliospores. A unique adaptation acquired early in rust evolution was heteroecism--the ability simultaneously to parasitize their original host as well as alternate, or secondary, hosts in completely different families of evolutionarily more advanced taxa. This intriguing paradox--of extreme specialization on the one hand, often requiring a matching gene-for-gene fit to hosts, coupled with such apparent promiscuity on the other--has been difficult to rationalize. Leppik (1967) coined the terms biological specialization and biogenic radiation for these opposing trends. Nevertheless, such radiation is usually not indiscriminate and is often confined to a single family or even species. *Cronartium flaccidum*, with its profusion of alternate hosts in ten dicot families, is a striking exception. Perhaps heteroecism, accompanied by acquisition of new spore forms adapted to seasonal climates, occurred in response to some drastic environmental change such as the colder, drier climate of the Permian Period (which also gave rise to the conifers). Together, these adaptations increased both the genetic and ecological amplitude of the lineage that became the aecial rusts, while retaining for them a secure base on their primary hosts until well established on secondary hosts.

The first major new host group was the conifers; extant fern-conifer pathogens are *Hyalospora*, *Milesina*, and *Uredinopsis*. From the conifers, rusts radiated successively to primitive, then more advanced dicots (meanwhile abandoning ferns, then conifers, as primary hosts), culminating with the dicot-monocot relationship where the overwhelming majority of species exist today. The process of radiation, establishment, and reradiation Leppik (1953) called "climbing the hologenetic ladder" of ecologically more opportunistic host species. Autoecious and microcyclic rusts are usually considered to be derived from heteroecious and macrocyclic parent species.

The theory of coevolution of rusts with their hosts is classic (Leppik 1953, 1967; Savile 1971; Hiratsuka and Sato 1982). It implies that the phylogenetic history of one member of the pair ought to reflect that of the other, although it has more often been used to deduce rust phylogenies from hosts than vice versa. It has considerable intuitive appeal and heuristic value but is not universally accepted; Hart (1988) recently concluded that host transfer was at least as frequent as cospeciation (coevolution) of rusts with hosts, based on cladistic analysis of 30 rust genera. The two concepts are not mutually exclusive, and we accept the classic view in our consideration of pine stem rust evolution. It is much easier to demonstrate at higher taxonomic ranks (classes, orders), but we assume that the same principles apply at lower levels as well--that is, that phylogenetically more primitive taxa of hosts harbor the more primitive rusts. Lack of a fossil record in *Cronartium--Peridermium* (as with most fungi) presently restricts our inferences to phylogenetic evidence in any case.

This evidence is recapitulated in Figures 6 and 7 for dicot and pine hosts, respectively. Dicot hosts of *Cronartium* are in four of six of the subclasses. Figure 6 shows subclass and family relationships in phylogenetic sequence (following Cronquist 1968) from primitive (bottom) to advanced (top). There are no hosts in the most primitive subclass (*Magnoliidae*) but there are in three of four directly derived lineages. Although most species are limited to a single host family (sometimes a single genus), there are groups of rusts that share common families in *Fagaceae* (3 species), *Saxifragaceae* (2), *Santalaceae* (2), and *Scrophulariaceae* (4). *C. comptoniae* stands alone in *Myricaceae*, but *C. flaccidum* is nearly ubiquitous, occurring in ten families (of 14 total) and in nine of these exclusively. These range from the most primitive (*Paeoniaceae*) to most advanced (*Scrophulariaceae*, *Acanthaceae*). At least two races, or *formae speciales*, are known on *Asteridae* hosts (see previous section), and perhaps more await discovery in the vast geographic and host range of this species complex. *C. ribicola* also has races or *formae speciales* in both relatively primitive (*Saxifragaceae*) and advanced (*Scrophulariaceae*) families.

The rusts in the *Fagaceae* group are undoubtedly related to each other, as are those in the *Saxifragaceae* and *Santalaceae* groups, by symptomology as well as primary hosts. A distinct exception is the very disparate group of rusts sharing scrophulariaceous hosts. These include limb and canker rusts on subgenus *Pinus* in western North America and canker rusts on subgenus *Strobus* in Asia and appear to represent a case of convergent evolution.

The evolutionary sequence of the stem rusts is shown against the phylogenetic background of their primary pine hosts in Figure 7. Correlated evolution again is assumed, and speciation events of rusts are approximately superimposed onto differentiation of host groups. We recognize that the scheme is oversimplified and often conjectural, with timing of speciation events having only relative value. Nevertheless, the evidence from primary and alternate hosts is reasonably consistent.

We must assume that the primordial *Cronartium* evolved before the major split of the main subgenera of pines (*Pinus* and *Strobus*), undoubtedly after the breakup of Pangaea into Laurasia and Gondwanaland but before the Laurasian split. This early progenitor followed subgenus *Strobus* as the ancestral *C. ribicola* and subgenus *Pinus* as the ancestral *C. flaccidum*. Both of these lineages persist, but

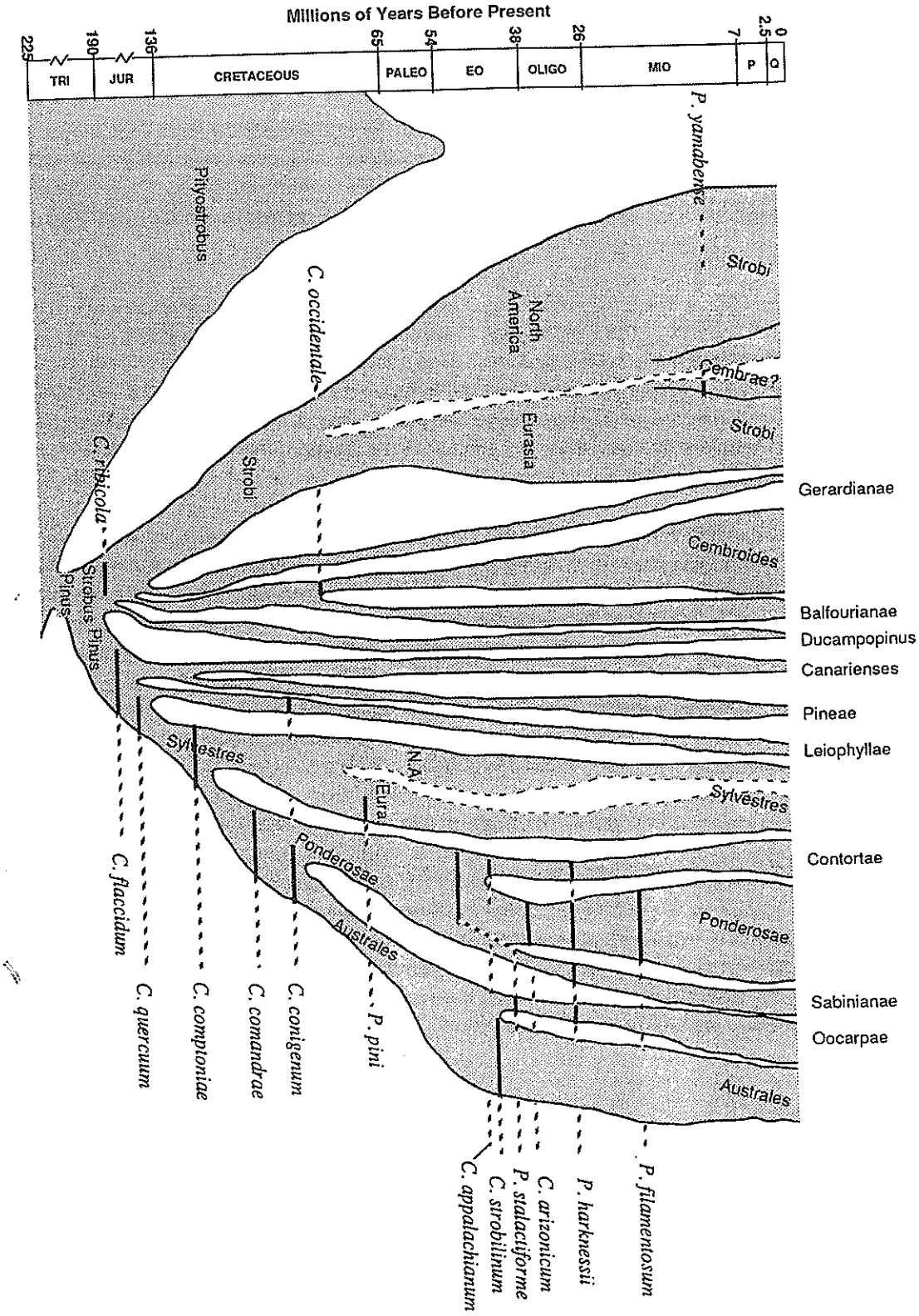

Figure 7. Hypothesized phylogeny of stem rusts in *Cronartium--Peridermium* (italics) **superposed on phylogeny of pine hosts** (cf. Fig. 2). Horizontal bars indicate relative order of differentiation of lineages leading to modern stem rust species, as inferred from present host-rust affinities and host phylogenetic histories.

all the other taxa split off along the way. Evidence supporting this is the relative antiquity of alternate hosts in *Ribes* and *Paeonia*, as well as the two primary hosts in *Strobi* and *Sylvestres*.

After the Laurasian split, the white pine rusts differentiated, along with their hosts, into *C. ribicola* on subsections *Strobi* and *Ribes* in Asia and *C. occidentale* on subsection *Cembroides* and *Ribes* in North America. Later in Asia, *C. ribicola* radiated to hosts in *Scrophulariaceae* as well, then later still split off an autoecious variant on *P. pumila*, if our chronology of the segregation of subsection *Cembrae* is correct (see Fig. 7).

Phylogeny of the hard pine (subgenus *Pinus*) stem rusts is more complex. Although *C. flaccidum* is ancient by the criteria of the antiquity of its primary host in *Sylvestres* (also *Canarienses* and *Pineae*) as well as one of its alternate hosts (*Paeonia*), it is anomalous in the diversity of alternate hosts it attacks and the relative phylogenetic youth of most of them. We can rationalize this if we assume that much of this radiation occurred later--for example, to the *Scrophulariaceae*. Why *C. flaccidum* did not follow North American members of *Australes* after the Laurasian split is unclear. *Peridermium pini* may have derived from *C. flaccidum* at some point after this time.

Pine-oak rusts were another early lineage preceding the Laurasian split. *C. quercuum* causes galls on species in subsection *Sylvestres* in Asia and *Australes* and *Contortae* in North America. Although nominally the same species at present, it seems unlikely that the stem rusts on these two continents will remain so because of recently described differences discussed earlier. Later offshoots from the ancestral *C. quercuum* were the cone rusts *C. conigenum* on western North American *Ponderosae* and *Leiophyllae* and eastern *Australes*, and *C. strobilinum* on *Australes* only. *C. comandrae*, with alternate hosts in *Santalaceae*, has the widest primary host range of pine stem rusts endemic to North America (Table 3), but a putatively derived species (*C. appalachianum*) is limited to a single pine species of both pine (*P. virginiana*) and alternate host (*Buckleya distichophylla* (Nutt.) Torr.).

Of the western group of North American rusts united by scrophulariaceous alternate hosts, *Peridermium stalactiforme* (a *Cronartium* without formal or valid description) might be ancestral to *C. arizonicum* because of its wider host range in *Contortae*, *Ponderosae*, and *Oocarpae*, compared with *Ponderosae* alone for *C. arizonicum*. The autoecious *P. filamentosum* complex probably derived from *C. arizonicum*. *P. harknessii*, the western gall rust, is problematical. It has the widest host range of any *Peridermium* (four western North American subsections), and it causes symptoms unlike *C. arizonicum* or any of the other limb rusts, even though it has been grouped formally in the *C. coleosporioides* complex because of dubious claims that it can occasionally infect species of *Scrophulariaceae*.

Centers of Diversity

Earlier we described how centers of genetic diversity can develop where the environment is variable enough over both space and time to reorganize (without exterminating) available genetic variability through natural selection. For pines, such secondary centers of speciation and diversity began to develop during the Eocene and continued through the Pleistocene in regions like the North American southwest (especially Mexico) and Japan, where the predominantly north-south topographic grain allowed plant populations to migrate with the ebb and flow of glaciers. These two situations contrast with northern Europe, where east-west mountain barriers restricted migration during glacial advances and led to reduced species diversity.

We may assume that a similar dynamic applies to the pine stem rusts and their alternate hosts as well. The pattern we see is different parts of the pathosystem alternately expanding and contracting

along environmental gradients in response to major climatic fluctuations over time. During this process, populations alternately become fragmented and continue their short-term evolution in isolation, only to reunite later, forming new combinations of variability. Since the last glacial ended so recently, it is not surprising that many anomalous and complex patterns of variation exist in extant populations.

Japan is an unusual center of diversity for many conifer rusts as well as their hosts. In Table 4, different pines, stem rusts, and alternate hosts are shown overlapping in elevation from near sea level to timberline. *C. quercuum* and *C. flaccidum* share a common pine host (*P. densiflora*), and *C. flaccidum* and *C. ribicola* share a common alternate host (*Pedicularis*). Approaching timberline, *C. ribicola* overlaps both *Pinus koraiensis* and *P. pumila* and also its presumed autoecious derivative, *Peridermium yamabense* on *P. pumila*. The existence of at least three distinct morphological and physiological races of autoecious white pine rusts on different mountaintops of both Honshu and Hokkaido (Saho 1987) is interesting. It suggests that perhaps the host populations never descended low enough in elevation during the full glacial to make contact with each other, remaining isolated as montane islands for longer than one glacial cycle, or that these rusts are capable of more rapid evolution (in any one glacial cycle) than might have been expected.

Are any of these rust populations exchanging genes? This question is critical to defining the genetic amplitude of these species and even to our concept of the species. It leads to broader questions that address taxonomic and evolutionary problems remaining for the pine stem rusts and that have important implications for domestication strategies for pine crops in jeopardy from these pathogens:

Table 4. Primary and alternate hosts of pine stem rusts (*Cronartium--Peridermium*) in the central mountain region of Honshu, Japan (adapted from Hama 1987 and Kakishima et al. 1984)

Primary host	Elev. (m)	Stem rust	Alternate hosts
P. thunbergiana	400-600	*C. quercuum*	*Quercus serrata, Q. dentata*
P. parviflora	500-900	None	
P. densiflora	500-1200	*C. flaccidum*	*Paeonia albiflora* f. *hortensis*, *P. obovata*, *P. suffruticosa* *Pedicularis resupinata* var. *caespitosa*
		C. quercuum	*Quercus serrata*, *Q. dentata*
P. koraiensis	1200-2600	*C. ribicola*	*Ribes sinanense* *Pedicularis euphrasioides*, *P. chamissonis* var. *japponica*, *P. resupinata*, *P. yezoensis*
P. pumila	2300-2900	*C. ribicola*	*Ribes sinanense* *Pedicularis euphrasioides*, *P. chamissonis* var. *japponica*, *P. resupinata*, *P. yezoensis*
		P. yamabense	None

- What is the genetic structure of stem rust species? That is, what is the magnitude of their genetic variation, how is it distributed geographically within and among populations (or among hosts), and how is it maintained?

- Is the sexual cycle really functional in heteroecious species? If so, is sexual behavior predominantly outbreeding or inbreeding?

- What are the genetic implications of autoecism, or endo-type sexual cycles? Does gene exchange occur among individuals and populations of these species, or have they arrived at evolutionary dead ends?

These questions are rooted in the phylogenetic history of these rusts and their hosts and can best be explored in centers of gene diversity such as Japan and western North America. Increased use of existing and emerging techniques of molecular biology will hasten their solution.

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