Phenetic and Phylogenetic Relationships Among Ten Species of *Dendroctonus* Bark Beetles (Coleoptera: Scolytidae)

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ABSTRACT Molecular genetic relationships among 10 species of *Dendroctonus* bark beetles were assessed using electrophoretic data from 18 gene loci. Cluster and distance Wagner analysis of these data showed a high level of similarity between *D. pseudotsugae* Hopkins and *D. simplex* LeConte, *D. valens* LeConte and *D. terebrans* (Olivier), and *D. adjunctus* Blandford and *D. approximatus* Dietz. These groupings correspond generally to groups identified in earlier studies using anatomical, cytogenetic, and behavioral characteristics. The distance Wagner tree indicated that *D. rufipennis* (Kirby), *D. adjunctus*, and *D. approximatus* are the most primitive species. *D. valens*, *D. terebrans*, *D. simplex*, *D. pseudotsugae*, and *D. frontalis* Zimmermann appear to be the most evolutionarily advanced of the species studied.

Dendroctonus Erichson (1836) is a widely distributed bark beetle genus infesting coniferous trees (family Pinaceae) throughout North America and in parts of Europe and Asia. In his monograph on the genus, Hopkins (1909) listed 24 species, including 12 that he described. *Dendroctonus* species classification was originally based on variations in anatomical, biological, and behavioral characteristics. As additional criteria and more populations were incorporated into systematic schemes for identifying bark beetles, some of Hopkins's 24 species were shown to be host races or geographic variants of single species and were subsequently synonymized (Wood 1963). The most recent revision of *Dendroctonus* (Wood 1982) includes 19 species, 17 restricted to North and Central America, and two Paleoarctic species, *D. micans* and *D. armandi* (Table 1).

Anatomical characters used in classifying *Dendroctonus* species include beetle size and color, and features of the head, pronotum, elytra, and male genitalia (Wood 1963, 1982). Biology, behavior, and host species are also important taxonomic characters. Wood (1963) used such characters to place *Dendroctonus* species into groups of closely allied species (Table 2). For example, frontal grooves and tubercles of the frons (more prominent in males) are present only in the group composed of *D. brevicomis*, *D. frontalis*, *D. mexicanus*, *D. vitei*, and *D. approximatus*. Behavioral characters such as form of egg galleries, position and arrangement of egg niches, aspects of larval mines and feeding, and pupation were also considered in grouping *Dendroctonus* species. *D. valens* and *D. terebrans* larvae, for example, feed communally, whereas *D. pseudotsugae* and *D. simplex* larvae construct individual mines seldom crossing each other. For this as well as other reasons, *D. valens* and *D. terebrans* are grouped together, as are *D. pseudotsugae* and *D. simplex*. Thomas (1965) concurred with Wood's species groups on the basis of larval and pupal anatomy.

Lanier (1981) was able to differentiate among karyotopes of all 14 *Dendroctonus* species he studied. Using chromosomal, morphological, and ecological evidence, Lanier suggested groupings that were very similar to those of Wood (Table 2). The only significant disparity was that Wood placed *D. adjunctus*, as a transitional species, with *D. ponderosae*, while Lanier interpreted *D. adjunctus* to be chromosomally intermediate between *D. ponderosae* and *D. brevicomis*, and placed it in a separate group.

Wood (1963) used certain anatomical and biological characters to rank the *Dendroctonus* species groups in an order of increasing specialization, relative to other Scolytidae. For example, increased body size, elaborations of the epistomal process, a five-segmented antennal funicle, and absence of a broad impression on the frons of the male appear to be specializations in *Dendroctonus*. Characters similar to those of the beetle, *Hylurgus*, which is believed to closely resemble the hypothetical ancestor of the genus, include the frons, prothorax, elytral declivity, and the absence of conspicuous anatomical differences between the male and female. Other characteristics, such as patterns of egg deposition and larval mining, were also used to distinguish between primitive and more specialized species.

Lanier (1981) also suggested an order of specialization for *Dendroctonus* species. *D. rufipennis*, *D. murrayanae*, *D. punctatus*, *D. simplex*, and *D. pseudotsugae* have the same chromosomal formula as the primitive scolytid, *Hylurgops rugipennis* subsp. *pinifex*, tribe Hylastini. Reduction

Table 1. Currently recognized *Dendroctonus* species (from Wood 1982)

D. armandi Tsai & Li
D. adjunctus Blandford
D. approximatus Dietz
D. brevicomis LeConte
D. frontalis Zimmermann
D. jeffreyi Hopkins
D. mexicanus Hopkins
D. micans (Kugelann)
D. murrayanae Hopkins
D. parallelocollis Chapuis
D. ponderosae Hopkins
D. pseudotsugae Hopkins
D. punctatus LeConte
D. rhizophagus Thomas & Bright
D. rufipennis (Kirby)
D. simplex LeConte
D. terebrans (Olivier)
D. valens LeConte
D. vitei Wood

of the chromosome number, in addition to behavior and ecology, were the basis of his phylogenetic ordering of the species groups.

Although Wood (1963) and Lanier (1981) placed the *Dendroctonus* species into nearly identical species groups, their postulated order of specialization for these groups differed. In fact, the two postulated phylogenies—one based largely on anatomy, the other on cytogenetics—are nearly opposite (Table 2). Based on anatomy, Group I, including *D. brevicomis*, is considered least specialized, and Group V, including *D. simplex* and *D. pseudotsugae*, is considered most specialized. However, chromosomal evidence indicates that species in Groups V and VI are more closely related to primitive scolytids, and Groups I and II, including *D. brevicomis*, are considered more specialized.

Electrophoretic analysis has been used extensively in recent years to estimate genetic relationships among populations, species, and closely related genera. Electrophoretic techniques have been developed for the study of several *Dendroctonus* species, including *D. ponderosae*, *D. brevicomis*, *D. frontalis*, *D. terebrans*, *D. jeffreyi*, and *D. pseudotsugae* (Anderson et al. 1979, 1983, Namkoong et al. 1979, Stock et al. 1979, Stock & Amman 1980, Sturgeon 1980, Florence et al. 1982, Higby & Stock 1982). The emphasis in most of these studies was on elucidating intraspecific relationships. Only two of the studies included species comparisons—*D. ponderosae* and *D. jeffreyi* (Higby & Stock 1982), and *D. frontalis* and *D. brevicomis* (Namkoong et al. 1979)—although mating tests have also been done between *D. pseudotsugae* and *D. simplex* (Furniss 1976) and the *D. ponderosae* complex (Lanier & Wood 1968).

Electrophoresis thus could provide additional criteria which, when integrated with existing knowledge of the anatomy, cytogenetics, and behavior of *Dendroctonus* species, might provide further insight into *Dendroctonus* evolution and

Table 2. *Dendroctonus* species-groups[a] based on anatomy, behavior (Wood 1963), and cytogenetic (Lanier 1981) characters

Anatomy	Cytogenetics	
Group I		
D. brevicomis[b]	*D. rufipennis*	Primitive
D. vitei	*D. murrayanae*	↓
D. frontalis[b]	*D. punctatus*	↓
D. mexicanus	*D. micans*	↓
D. approximatus[b]	—	↓
Group II		↓
D. adjunctus[b]	*D. pseudotsugae*	↓
D. ponderosae[b]	*D. simplex*	↓
D. jeffreyi	—	↓
Group III		↓
D. parallelocollis	*D. valens*	↓
D. terebrans[b]	*D. terebrans*	↓
D. valens[b]	*D. parallelocollis*[c]	↓
	D. rhizophagus[c]	↓
Group IV		↓
D. micans	*D. ponderosae*	↓
D. punctatus	*D. jeffreyi*	↓
D. murrayanae	—	↓
D. rufipennis[b]	—	↓
Group V		↓
D. simplex	*D. adjunctus*	↓
D. pseudotsugae	—	↓
Group VI		↓
—	*D. approximatus*	↓
—	*D. brevicomis*	↓
—	*D. frontalis*	↓
—	*D. mexicanus*	Advanced

[a] *D. armandi* was not included in these groupings.
[b] Species obtained for this electrophoretic study.
[c] Not studied cytologically, but placement inferred by Lanier (1981) from other characters.

speciation. Reported here is a molecular interpretation of phylogeny, based on electrophoretic data, of the five species groups proposed by Wood (1963) and Lanier (1981).

Methods

Twenty-two populations, representing 10 *Dendroctonus* species and all of the species groups recognized by Wood (1963) and Lanier (1981), were obtained for this study (Tables 2 and 3). *Alniphagus aspericollis*, a member of the tribe Hylesinini (considered more primitive than the closely related tribe Tomicini, which includes *Dendroctonus*), was also collected to aid in phylogenetic analysis. Species were identified by host tree, gallery pattern, and anatomical characteristics (Furniss & Carolin 1977, Wood 1982). A voucher collection containing four representative specimens of each species was deposited in the Entomology Museum at the University of Idaho.

Techniques and recipes used for starch gel electrophoresis of *Dendroctonus* enzyme systems were those described by Namkoong et al. (1979), May (1980), Sturgeon (1980), Florence & Kulhavy (1981), and Higby & Stock (1982). Gels were made

Table 3. Collection information for all populations

Species	Abbreviation	Collection site	Host	Collection/shipping date(s)
D. ponderosae	PON	Flaming Gorge, Utah	*Pinus contorta* Dougl.	1–26 July 1982
D. ponderosae	PON	Cariboo Forest Region, Williams Lake, British Columbia	*P. contorta*	27 Aug. 1983
D. adjunctus	ADJ	Escalante, Utah	*P. ponderosae* Laws.	8 Nov.–17 Dec. 1982
D. approximatus	APX	Escalante, Utah	*P. ponderosae*	1 June–17 Dec. 1982
D. brevicomis	BRV	Escalante, Utah	*P. ponderosae*	8 Nov.–17 Dec. 1982
D. brevicomis	BRV	Colville, Wash.	*P. ponderosae*	10 Nov.–5 Dec. 1982
D. brevicomis	BRV	Shasta County, Calif.	*P. ponderosae*	24 May 1983
D. brevicomis	BRV	Siskiyou County, Calif.	*P. ponderosae*	24 May 1983
D. rufipennis	RUF	Kenai Peninsula, Alaska	*Picea sitchensis* var. *lutzii* (Bong.) Carr.	16 June 1982
D. rufipennis	RUF	Fairbanks, Alaska	*P. glauca* (Moench) Voss	27 Sept. 1982
D. rufipennis	RUF	Kaibab National Forest, Ariz.	*P. engelmanni* Parry	26 Aug. 1982
D. rufipennis	RUF	Herkimer County, N.Y.	*P. rubra* Sarg.	3 Sept. 1983
D. frontalis	FRN	Saratoga, Tex.	*P. taeda* L.	19 June 1982
D. terebrans	TER	Rabun County, Ga.	*P. taeda*	14 June 1982
D. valens	VAL	Escalante, Utah	*P. ponderosae*	20 Dec. 1982
D. valens	VAL	Cortland County, N.Y.	*P. resinosa* Ait.	24 Aug. 1982
D. simplex	SIM	St. Lawrence County, N.Y.	*Larix laricina* (Du Roi) K. Koch	18 Aug. 1982
D. simplex	SIM	Kennebec County, Mass.	*L. laricina*	20–23 Aug. 1982
D. simplex	SIM	Fairbanks, Alaska	*L. laricina*	23 Sept. 1982
D. pseudotsugae	PSD	Weippe, Idaho	*Pseudotsuga menziesii* (Mirb.) Franco.	15 Mar. 1983
D. pseudotsugae	PSD	Priest River, Idaho	*P. menziesii*	13 Apr. 1983
D. pseudotsugae	PSD	Corvalis, Oreg.	*P. menziesii*	29 Apr. 1983
Alniphagus aspericollis	ALNI	Orofino, Idaho	*Alnus rubra* Bong.	15 Mar. 1983

from a 13% solution of hydrolyzed potato starch (a 50:50 mixture of Electrostarch lot no. 392 and Sigma Starch stock no. S-4501) and the appropriate gel buffer. From an initial screening of 25 enzyme systems, 13 enzyme assays (18 gene loci) that produced consistently interpretable banding patterns in all 10 species were selected for routine testing. *D. ponderosae* was used as a standard for each assay because electrophoretic variation in this species is best documented in the literature.

Electrophoretic data were analyzed using BIOSYS-1, a computer program developed at the University of Illinois at Urbana for analysis of allelic variation (Swofford & Selander 1981). Allele frequencies were calculated for all groups. Several genetic variability indices—including Nei's (1978) genetic identity (I) and genetic distance (D), and Cavalli-Sforza & Edwards's (1967) chord distance—were calculated from these frequencies. The latter two measures are based on a genetic model and estimate the mean number of electrophoretically detectable mutations (amino acid substitutions) per locus since the populations diverged from a common ancestor.

To compare amounts of genetic variation within and among species, percent polymorphism and average heterozygosity were calculated. When the frequency of the most common allele was ≤ 0.99 in at least one population, a locus was considered polymorphic (Nei 1975). Average heterozygosity, the average frequency of heterozygous individuals per locus, was calculated using the unbiased estimate based on conditional expectations (Leven 1949, Nei 1978).

Hierarchical cluster analysis of the electrophoretic data was done using the weighted pair-group method with arithmetic averaging (WPGMA). Results of this procedure reflect overall phenetic similarity among groups. Relationships among the species were also estimated using the distance Wagner procedure (Farris 1972), which produces a tree from the chord distance matrix values. This technique produces a branching network of ancestor/descendant relationships. Branch length is proportional to the amount of evolutionary change estimated to have occurred since the entities diverged. The distance Wagner tree, derived from electrophoretic data on the 10 *Dendroctonus* species and the more primitive scolytid species *A. aspericollis*, was rooted by the outgroup method (Farris 1972, Hennig 1966).

Results

Of the 18 enzyme-producing gene loci studied (Table 4), three (EST1, IDH2, and LAP1) were monomorphic for the same allele in all species; SOD was also monomorphic in all of the species studied, except in *D. frontalis* and *D. terebrans*, where it was fixed for a unique allele. Seven loci (AAT, ACP, CK, EST2, LAP2, PEP-la, and PGI) were polymorphic in all *Dendroctonus* species. The remaining seven loci were monomorphic in at least one species.

The esterase enzyme system was the most variable in *Dendroctonus*, as in other insect groups. In all species combined, seven esterase loci (four anodal and three cathodal) were seen. The esterase

Table 4. Allele frequencies at 18 gene loci, percent polymorphism (P), and average heterozygosity (H), in 10 *Dendroctonus* species and one related genus[a]

Locus	PON	ADJ	APX	BRV	RUF	FRN	TER	VAL	SIM	PSD	ALN1
AAT											
(*n*)	(334)	(68)	(62)	(72)	(142)	(58)	(73)	(59)	(217)	(194)	(40)
A	0	0	0	0	0	0	0.370	0	0.060	0.296	0
B	0.662	0.529	0.516	0.264	0.465	0.500	0.568	0.161	0.834	0.673	0
C	0.338	0.471	0.484	0.264	0.528	0.500	0.062	0.458	0.106	0.031	0
D	0	0	0	0.472	0.007	0	0	0.381	0	0	0
E	0	0	0	0	0	0	0	0	0	0	1.000
ACP											
(*n*)	(185)	(33)	(70)	(76)	(77)	(34)	(36)	(31)	(57)	(97)	(38)
A	0.265	0	0.221	0.079	0.351	0.132	0.097	0	0.079	0.129	0
B	0.243	0.470	0.600	0.809	0.513	0.515	0.708	0.952	0.754	0.443	0
C	0.492	0.530	0.179	0.112	0.136	0.353	0.194	0.048	0.167	0.428	1.000
CK											
(*n*)	(323)	(65)	(42)	(94)	(93)	(52)	(74)	(44)	(264)	(153)	(45)
A	0	0.023	0.036	0	0	0	0.196	0.955	0	0	1.000
B	0.989	0.631	0.464	0.926	0.898	0.154	0.257	0.045	0	0.016	0
C	0.011	0.338	0.405	0.074	0.102	0.538	0.439	0	0.498	0.111	0
D	0	0.008	0.095	0	0	0.298	0.108	0	0.491	0.873	0
E	0	0	0	0	0	0.010	0	0	0.011	0	0
EST-1											
(*n*)	(421)	(84)	(160)	(114)	(185)	(104)	(65)	(83)	(196)	(183)	(60)
A	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0
B	0	0	0	0	0	0	0	0	0	0	1.000
EST-2											
(*n*)	(399)	(63)	(83)	(63)	(85)	(105)	(57)	(70)	(195)	(148)	(60)
A	0.019	0	0	0.079	0	0	0	0	0	0.118	0
B	0.277	0.008	0.006	0.405	0.159	0	0	0	0.041	0.135	0
C	0.278	0.079	0.060	0.278	0.276	0	0	0.014	0.154	0.301	1.000
D	0.137	0.286	0.283	0.103	0.147	0.152	0	0.071	0.226	0.172	0
E	0.234	0.405	0.536	0.048	0.171	0.284	0.158	0.214	0.269	0.149	0
F	0.055	0.183	0.108	0.048	0.212	0.300	0.342	0.564	0.208	0.030	0
G	0	0.040	0.006	0.032	0.035	0.181	0.228	0.136	0.082	0.037	0
H	0	0	0	0.008	0	0.100	0.219	0	0.015	0.020	0
I	0	0	0	0	0	0.109	0.053	0	0.005	0.037	0
EST-4											
(*n*)	(291)	(86)	(94)	(79)	(108)	(100)	(64)	(78)	(200)	(183)	(40)
A	0.993	0.994	1.000	0.880	1.000	0	0	0.026	0	0	0
B	0.007	0.006	0	0.120	0	0	1.000	0.974	0	1.000	0
C	0	0	0	0	0	1.000	0	0	1.000	0	1.000
IDH-1											
(*n*)	(361)	(53)	(107)	(75)	(127)	(70)	(78)	(48)	(141)	(139)	(50)
A	0	0	0.065	0.053	0	0.021	0.897	0.917	0.028	0	0
B	0	0.849	0.790	0.360	0	0.979	0.103	0.073	0.950	0.014	1.000
C	1.000	0.009	0.117	0.233	0.795	0	0	0.010	0.021	0.960	0
D	0	0.142	0.028	0.340	0.157	0	0	0	0	0.025	0
E	0	0	0	0.013	0.047	0	0	0	0	0	0
IDH-2											
(*n*)	(297)	(85)	(62)	(79)	(91)	(27)	(65)	(61)	(80)	(145)	(50)
A	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0
B	0	0	0	0	0	0	0	0	0	0	1.000
LAP-1											
(*n*)	(135)	(38)	(35)	(75)	(73)	(40)	(15)	(12)	(115)	(115)	(50)
A	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0
B	0	0	0	0	0	0	0	0	0	0	1.000
LAP-2											
(*n*)	(175)	(62)	(71)	(85)	(121)	(56)	(20)	(19)	(144)	(143)	(30)
A	0	0	0	0	0	0	0	0	0.083	0.189	0
B	0.371	0.476	0.401	0.453	0.612	0.027	0.400	0.789	0.219	0.493	0
C	0.626	0.524	0.599	0.541	0.277	0.786	0.475	0.158	0.694	0.304	1.000
D	0.003	0	0	0.006	0.112	0.188	0.125	0.053	0.003	0.014	0

Table 4. Continued

Locus	PON	ADJ	APX	BRV	RUF	FRN	TER	VAL	SIM	PSD	ALN1
MDH-1											
(*n*)	(377)	(74)	(84)	(141)	(176)	(112)	(91)	(68)	(226)	(199)	(50)
A	0	0.007	0	0	0.088	0	0	0	0	0	0
B	1.000	0.986	1.000	0	0.830	0.004	0.011	1.000	0.088	0.103	1.000
C	0	0.007	0	1.000	0.082	0.996	0.874	0	0.909	0.894	0
D	0	0	0	0	0	0	0.115	0	0.002	0.003	0
MDH-2											
(*n*)	(348)	(90)	(87)	(124)	(154)	(102)	(80)	(63)	(225)	(199)	(50)
A	1.000	0.011	0	0	0	0	0	0	0	0	0
B	0	0.983	0.994	1.000	1.000	1.000	0	0	0	0.005	0
C	0	0	0	0	0	0	0	0	1.000	0.990	0
D	0	0.006	0.006	0	0	0	1.000	1.000	0	0.005	0
E	0	0	0	0	0	0	0	0	0	0	1.000
ME											
(*n*)	(478)	(77)	(108)	(134)	(135)	(110)	(81)	(66)	(203)	(186)	(50)
A	1.000	0	0	0	0.437	0	0	0	0	0	0
B	0	0	0	0	0.404	0	0	0.803	0	0	0
C	0	0.084	0.028	0.056	0.159	0.023	0.778	0.197	0	0.995	0
D	0	0.916	0.972	0.869	0	0.977	0.222	0	0	0.005	0
E	0	0	0	0.075	0	0	0	0	1.000	0	1.000
MPI											
(*n*)	(300)	(67)	(87)	(122)	(187)	(79)	(78)	(42)	(125)	(190)	(50)
A	0	1.000	1.000	0.967	0	0	0	0.024	0	0	0
B	1.000	0	0	0	0.045	1.000	0	0	0	0.095	0
C	0	0	0	0.029	0.936	0	0.955	0.214	0.892	0.879	0
D	0	0	0	0.004	0.019	0	0.045	0.738	0.108	0.026	0
E	0	0	0	0	0	0	0	0.024	0	0	1.000
PEP-g1											
(*n*)	(420)	(78)	(101)	(130)	(155)	(86)	(55)	(56)	(163)	(132)	(49)
A	0	0.904	0.975	0.985	0.952	0	1.000	0.920	0	0	0
B	0.932	0.096	0.025	0.015	0.048	0	0	0.080	1.000	0.792	−0.408
C	0.068	0	0	0	0	0.791	0	0	0	0.201	−0.378
D	0	0	0	0	0	0.209	0	0	0	0.008	−0.214
PEP-1a											
(*n*)	(235)	(69)	(26)	(65)	(98)	(45)	(32)	(44)	(191)	(123)	(50)
A	0.017	0.891	0.788	0.008	0.929	0	0	0.977	0	0.012	0
B	0.832	0.109	0.212	0.985	0.071	0	0	0.023	0.966	0.675	0
C	0.151	0	0	0.008	0	0	0.031	0	0.034	0.313	0
D	0	0	0	0	0	0.933	0.969	0	0	0	1.000
E	0	0	0	0	0	0.067	0	0	0	0	0
PGI											
(*n*)	(404)	(61)	(130)	(102)	(170)	(124)	(71)	(53)	(228)	(158)	(50)
A	0	0	0	0	0	0	0	0	0	0	0
B	0	0	0	0	0	0	0.204	0.321	0	0	0
C	0.009	0.033	0.402	0.265	0	0	0.655	0.642	0.029	0.025	0
D	0.978	0.680	0.677	0.108	0.988	0.512	0.141	0.038	0.836	0.959	0
E	0.014	0.270	0.254	0.603	0	0.456	0	0	0.129	0.013	0.920
F	0	0.016	0.027	0.025	0.012	0.032	0	0	0.007	0.003	0.080
SOD											
(*n*)	(421)	(84)	(160)	(100)	(185)	(104)	(65)	(83)	(196)	(183)	(60)
A	0	0	0	0	0	0	0	0	0	0	1.000
B	1.000	1.000	1.000	1.000	1.000	0	0	1.000	1.000	1.000	0
C	0	0	0	0	0	1.000	1.000	0	0	0	0
P	50	72	61	67	67	61	61	67	61	72	11
H	0.156	0.223	0.225	0.228	0.236	0.215	0.247	0.187	0.181	0.228	0.044

[a] For explanation of abbreviations, see Table 3.

system was most complex in *D. simplex*, *D. pseudotsugae*, *D. rufipennis*, *D. terebrans*, and *D. valens*, where overlapping banding patterns made genotypes at some esterase loci uninterpretable. Only three esterase loci (EST1, EST2, and EST4) were present and interpretable in all 10 species. Although bands for EST4 were missing in *D. frontalis* and *D. simplex*, null alleles (which occur frequently at esterase loci) were assumed present at this locus in those two species, and EST4 was included in the analyses.

Two or more populations were sampled in six

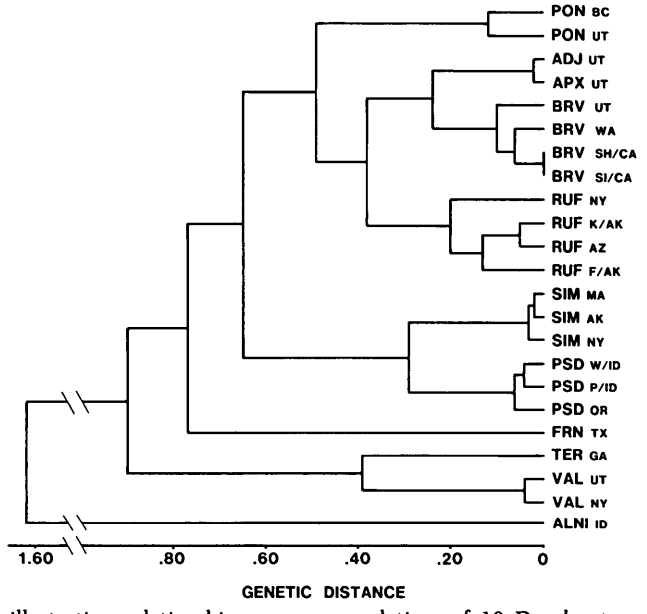

Fig. 1. Phenogram illustrating relationships among populations of 10 *Dendroctonus* species and the related scolytid, *Alniphagus aspericollis*. See Table 3 for meaning of abbreviations.

species (*D. ponderosae, D. brevicomis, D. pseudotsugae, D. rufipennis, D. simplex,* and *D. valens*). When populations were treated as separate groups and subjected to WPGMA cluster analysis, all populations within a species clustered together and below a genetic distance of 0.20 (Fig. 1). Intraspecific similarity was greatest in *D. simplex* and lowest in *D. rufipennis*.

Percent polymorphism ranged from 50% in *D. ponderosae* to 72% in *D. adjunctus* and *D. pseudotsugae* (Table 4). Over all species, the genus is polymorphic at an average of 64% of the loci. Average heterozygosity ranged from 0.156 in *D. ponderosae* to 0.247 in *D. terebrans*. Average heterozygosity over all *Dendroctonus* species was 0.213. *A. aspericollis* was considerably less heterozygous ($H = 0.044$) than any *Dendroctonus* species.

In pair-by-pair comparisons of genetic distance values, *D. adjunctus* and *D. approximatus* were most similar ($D = 0.004$), and *D. valens* and *D. frontalis* were least similar ($D = 1.497$) (Table 5). Average genetic identity over the entire genus was 0.568. In contrast, average genetic identity between *Dendroctonus* species and *A. aspericollis* was 0.186.

Discrete clusters of species (species groups) could be identified based on electrophoretic similarity (Fig. 1). Electrophoretic species groups identified by both the WPGMA and distance Wagner techniques were *D. valens* and *D. terebrans; D. pseudotsugae* and *D. simplex*; and *D. adjunctus* and *D. approximatus*. In the WPGMA analysis, *D. ponderosae* and *D. frontalis* were not as closely related to other species included in the study. However, based on ancestor/descendant relationships (the distance Wagner tree, Fig. 2), rather than phenetic similarity (WPGMA, Fig. 1), *D. frontalis* appeared more closely related to *D. brevicomis*.

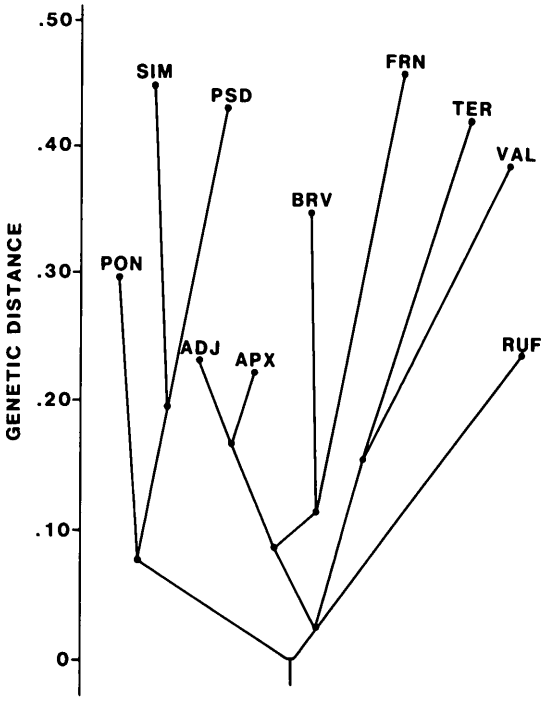

Fig. 2. Distance Wagner tree suggesting evolutionary relationships among 10 *Dendroctonus* species. See Table 3 for meaning of abbreviations.

Table 5. Nei's (1978) genetic distance (below diagonal) and Cavalli-Sforza and Edwards's (1967) chord distance (above diagonal) values for 10 *Dendroctonus* species

Species[a]	PON	ADJ	APX	BRV	RUF	FRN	TER	VAL	SIM	PSD
PON	—	0.547	0.548	0.588	0.457	0.695	0.758	0.672	0.607	0.546
ADJ	0.565	—	0.099	0.384	0.407	0.586	0.660	0.566	0.605	0.633
APX	0.568	0.004	—	0.388	0.414	0.587	0.659	0.564	0.601	0.630
BRV	0.656	0.249	0.246	—	0.492	0.609	0.633	0.629	0.593	0.588
RUF	0.361	0.228	0.237	0.431	—	0.672	0.660	0.548	0.612	0.557
FRN	1.074	0.663	0.658	0.675	0.984	—	0.584	0.756	0.592	0.657
TER	1.461	1.034	1.018	0.846	0.879	0.671	—	0.527	0.649	0.590
VAL	1.013	0.621	0.619	0.901	0.565	1.497	0.496	—	0.672	0.642
SIM	0.700	0.785	0.777	0.720	0.778	0.655	0.918	1.126	—	0.426
PSD	0.578	0.958	0.932	0.765	0.615	0.998	0.638	0.916	0.305	—

[a] For explanation of abbreviations, see Table 3.

Discussion

Results of distance Wagner and WPGMA analysis were consistent at high similarity levels; in both, *D. terebrans* and *D. valens*, *D. pseudotsugae* and *D. simplex*, and *D. adjunctus* and *D. approximatus* grouped together. In the distance Wagner tree, however, *D. frontalis* was grouped with *D. brevicomis*, a relationship that corresponds more closely to that identified in earlier studies. The distance Wagner tree also suggests that *D. frontalis* is more specialized than *D. brevicomis*. Cytogenetic evidence tends to support this relationship. Thus, both within- and between-group variation in level of specialization seems to occur.

Distance Wagner analysis suggests that *D. adjunctus*, *D. approximatus*, and *D. rufipennis* are the most primitive species, and that *D. simplex*, *D. pseudotsugae*, *D. frontalis*, *D. terebrans*, and *D. valens* are among the more evolutionarily advanced species in the genus. These results support Wood's (1963) contention that *D. adjunctus* and *D. approximatus* are among the least specialized species within the genus, and that *D. simplex* and *D. pseudotsugae* are among the most specialized, as well as Lanier's (1981) suggestion that *D. rufipennis* is one of the most primitive *Dendroctonus* species, and *D. frontalis* one of the most advanced.

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