Genetic Variation Among Mountain Pine Beetle (*Dendroctonus ponderosae*) (Coleoptera: Scolytidae) Populations from Seven Western States

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ABSTRACT Genetic characteristics of mountain pine beetles from 15 sites in seven western states were compared using electrophoresis. A high level of genetic similarity was observed among all groups, including those from areas previously considered separate ranges of *D. monticolae* (=*ponderosae*) and *D. ponderosae*.

THE MOUNTAIN PINE beetle, *Dendroctonus ponderosae* Hopkins, exhibits variations in morphology, behavior, and physiology over its extensive range. Morphological variation is seen in size differences in beetles from different localities and in the surface sculpturing of various body parts. There are also apparent differences in host selection among populations. While this insect attacks most species of pines in western North America, beetle populations in mixed pine stands may concentrate on one host species (Baker et al. 1971, Wood 1963). This diversity is reflected in the taxonomic history of the mountain pine beetle. Hopkins (1902) proposed the name *D. ponderosae* for a bark beetle attacking ponderosa pine in the Black Hills of South Dakota. In 1905, Hopkins described *D. monticolae* from specimens taken from western white pine at Kootenai, Idaho. Later, Hopkins (1909) extended the host list of *D. monticolae* to several additional pine species in the northwestern states and California. The ranges of Hopkins' (1909) Black Hills beetle (*D. ponderosae*) and mountain pine beetle (*D. monticolae*) are shown in Fig. 1.

In 1909, Hopkins also described the monophagous Jeffrey pine beetle (*D. jeffreyi*), which was coincident with the range of Jeffrey pine in California and adjacent parts of Oregon and Nevada. Hopkins recognized that these three species shared characteristics which placed them close together in his classification. In 1963, Wood synonymized the three species under *D. ponderosae*. Later studies (Smith 1965, Lanier and Wood 1968) lead to reinstatement of *D. jeffreyi* as a separate species. A recent genetic comparison of Jeffrey pine beetle and mountain pine beetle from California supports their separate species designations (Higby and Stock 1982).

While Lanier and Wood's (1968) investigations generally confirmed the synonymy of *D. monticolae* and *D. ponderosae*, interest in the existence and status of infraspecific groups continues. Electrophoretic studies of mountain pine beetles in local areas have begun to elucidate population relationships at the genetic level (Stock and Guenther 1979, Stock and Amman 1980, Sturgeon 1980). Recent studies of mountain pine beetle population dynamics permitted our acquisition of beetles from a larger portion of their range. Here we report results of our genetic comparison of these groups, specifically aimed at identifying the level of genetic variation over the species as a whole and determining if any genetic differences occur between beetles from the two general areas previously considered to be occupied by *D. monticolae* and *D. ponderosae*.

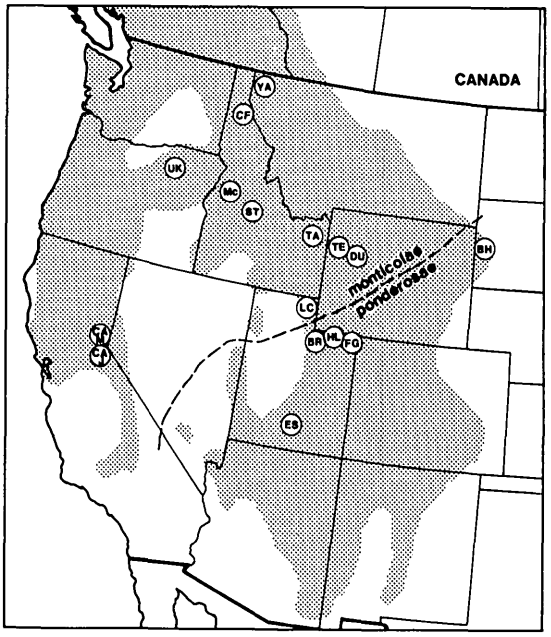

Fig. 1. Approximate distribution of mountain pine beetle in the western United States (shaded area) and locations of 15 mountain pine beetle populations and one Jeffrey pine beetle population from which electrophoretic data were obtained for this study. Division between what was earlier considered *D. monticolae* and *D. ponderosae* is indicated by a broken line.

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Table 1. Location, source stand, and population characteristics of 15 mountain pine beetle and 1 Jeffrey pine beetle collections

Species[a]	Code	Location	Host[b]	Source stand composition	Population characteristics
MPB	Ukiah (UK)	Umatilla Co., Oreg.; 15 mi W of Ukiah in Umatilla N.F.	LP	LP with some PP	Epidemic (high density) since 10–12 years ago.
MPB	Clark Fork (CF)	Shoshone Co., Idaho; Coeur d'Alene N.F.	LP	Mixed LP, western larch, Douglas-fir, cedar, and western white pine	Low density for many years. Last outbreak in area was in early 1960's.
MPB	Sawtooth (ST)	Custer Co., Idaho; Sawtooth N.F.	LP	Pure LP	Low density since the 1930's but was increasing at this localized site near Alturas Lake.
MPB	McCall (McC)	Adams Co., Idaho; Payette N.F.	LP	LP with few PP	Low epidemic level since about 1977.
MPB	Yaak (YA)	Lincoln Co., Mont.; Kootenai N.F.	LP	LPP with few western larch and Douglas-fir	Epidemic since 1977 and is the first large outbreak for existing stands in this area.
MPB	Targhee (TA)	Fremont Co., Idaho; Targhee N.F.	LP	Pure LP	Had been epidemic for about 4 years but now declining.
MPB	Dubois (DU)	Fremont Co., Wyo.; 20 mi NW Dubois in Shoshone N.F.	LP	Pure LP with some aspen near open areas	Epidemic.
MPB	Teton (TE)	Teton Co., Wyo.; Bridger-Teton N.F.	LP	Pure LP	Had been epidemic during the 1960's, but now very low density; only one tree found infested.
MPB	Logan Canyon (LC)	Cache Co., Utah; Wasatch-Cache N.F.	LP	LP with few subalpine fir, Douglas-fir, and aspen	Low epidemic level for past 10 years.
MPB	Bear River (BR)	Summit Co., Utah; Wasatch-Cache N.F.	LP	Pure LP	Declining following a large outbreak started in 1970.
MPB	Hoop Lake (HL)	Summit Co., Utah; Wasatch-Cache N.F.	LP	LP with few subalpine fir	Epidemic since 1981.
MPB	Flaming Gorge (FG)	Daggett Co., Utah; Ashley N.F.	LP	About 75% LP and 25% PP with few Douglas-fir, subalpine fir, and aspen	Epidemic since about 1980; increase started in 1976.
MPB	Escalante (ES)	Garfield Co., Utah; Dixie N.F.	PP	PP with few Douglas-fir, aspen, and blue spruce	Epidemic since 1978.
MPB	Black Hills (BH)	Lawrence Co., S.D.; Black Hills N.F.	PP	Pure PP	History of continuing high-density outbreaks.
MPB	CA-M[c]	Near Lake Tahoe in northern California	PP	Mixed LP and PP	Moderate density.
JPB	CA-J[c]	Near Lake Tahoe in northern California	JP	Mixed LP and PP	Moderate density.

[a] MPB, Mountain pine beetle (*Dendroctonus ponderosae*); JPB, Jeffrey pine beetle (*D. jeffreyi*).
[b] LP, Lodgepole pine (*Pinus contorta* var. *latifolia*); PP, ponderosa pine (*P. ponderosa*).
[c] From Higby and Stock (1982).

Methods

Mountain pine beetles were obtained from 14 sites (Table 1, Fig. 1): one in Oregon, four in Idaho, one in Montana, two in Wyoming, five in Utah, and one in South Dakota. In addition, genetic data from mountain pine beetles and Jeffrey pine beetles from California, reported by Higby and Stock (1982), were included so that a species comparison could be made.

Upon emergence, adult beetles were frozen at −20°C until electrophoresis was done. Methods for electrophoretic analysis of mountain pine beetle isozymes are described by Higby and Stock (1982). Gels were made from a 13% solution of hydrolyzed potato starch (Electrostarch lot no. 307) and the appropriate buffer. Relative mobilities of loci and allozymes at individual loci, and common banding patterns are given in Stock and Amman (1980).

Observed genotype frequencies were compared to values derived from random-mating (Hardy-Weinberg) expectations. Contingency χ^2 tests, based on the observed number of each allele at a locus, were used to compare gene frequencies at a locus between sites. To compare overall genetic composition among sites, Nei's (1972) genetic identity and genetic distance values were calculated using data from all loci, monomorphic and polymorphic. To aid visualization of relationships among groups, a dendrogram was constructed us-

Table 2. Allele frequencies, Hardy-Weinberg χ^2 values, and average heterozygosity for 15 mountain pine beetle populations and 1 Jeffrey pine beetle population

Species		MPB →															JPB
State		OR	ID	ID	ID	ID	MT	WY	WY	UT	UT	UT	UT	UT	SD	CA	CA
Site		UK	CF	ST	MC	TA	YA	DU	TE	LC	BR	HL	FG	ES	BH	CA	CA
Year		1979	1979	1980	1980	1980	1980	1980	1980	1980	1980	1980	1980	1980	1979	1980	1980
Host		LP	LP	LP	LP	LP	LP	LP	LP	LP	LP	LP	LP	PP	PP	PP	JP
Locus Allele																	
AAT1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.04	0.28
	2	0.47	0.60	0.50	0.59	0.61	0.51	0.66	0.57	0.66	0.65	0.66	0.61	0.66	0.48	0.55	0.59
	3	0.53	0.40	0.50	0.41	0.39	0.49	0.34	0.43	0.34	0.34	0.34	0.39	0.35	0.52	0.40	0.13
	4	—	—	—	—	—	—	—	—	—	0.01	—	—	—	—	—	—
	n	51	31	29	45	80	69	62	75	88	87	60	543	100	94	364	402
	χ^2	7.0**	2.1	1.7	0.7	0.1	0	2.7	0.3	0.1	1.0	1.3	2.8	0	2.0	19.3*	83.6**
AcP	0	—	—	—	—	0.01	—	—	—	—	—	—	—	—	—	—	—
	1	—	—	0.66	0.71	0.56	0.62	0.70	0.73	0.68	0.75	0.72	0.64	0.78	—	0.65	0.94
	2	—	—	0.34	0.29	0.43	0.38	0.30	0.27	0.32	0.25	0.28	0.36	0.22	—	0.35	0.06
	n	—	—	76	55	79	89	87	82	66	59	73	540	83	—	206	494
	χ^2	—	—	0.3	0.8	8.8**	11.1**	0.8	3.84*	1.7	5.7*	1.3	0	0	—	0.1	18.6**
EST1	1	0.02	0.03	0.02	0.04	0.02	0.01	0.02	0.03	0.02	0.02	0.05	0.01	0.01	—	0.08	0.10
	2	0.38	0.45	0.30	0.40	0.33	0.45	0.33	0.29	0.29	0.36	0.47	0.41	0.03	0.17	0.38	0.46
	3	0.26	0.33	0.35	0.27	0.34	0.22	0.31	0.28	0.31	0.21	0.22	0.23	0.08	0.13	0.27	0.41
	4	0.18	0.11	0.19	0.20	0.08	0.12	0.08	0.10	0.09	0.11	0.03	0.13	0.52	0.41	0.12	0.02
	5	0.11	0.08	0.14	0.07	0.22	0.16	0.26	0.30	0.29	0.29	0.23	0.22	0.33	0.27	0.12	—
	6	0.05	0.11	0.01	0.02	0.01	0.04	—	—	0.01	0.01	—	—	0.03	0.02	0.02	—
	n	87	46	81	56	96	113	97	99	100	94	97	586	89	128	618	521
	χ^2	2.0	7.4	9.5	2.3	18.2	17.3	9.8	28.4**	3.1	20.8*	5.2	9.5	0.8	3.4	195**	28.9**
LAP2	1	0.04	0.05	0.14	0.05	0.06	0.05	0.08	0.06	0.01	0.03	0.02	0.05	0.06	0.32	0.25	0.23
	2	0.59	0.68	0.60	0.61	0.56	0.56	0.51	0.62	0.57	0.46	0.61	0.74	0.54	0.28	0.42	0.57
	3	0.36	0.27	0.26	0.34	0.38	0.39	0.41	0.32	0.41	0.51	0.38	0.21	0.41	0.40	0.32	0.20
	n	48	11	79	48	77	95	80	91	88	61	90	348	81	60	483	460
	χ^2	0.6	1.2	10.7*	6.4	6.4	11.6**	10.8*	2.4	2.5	5.6	2.8	14.4**	2.0	25.3**	59**	39.5**
PEP	1	0.94	0.97	0.98	0.99	0.99	0.96	0.96	0.99	0.98	0.95	0.88	0.97	0.99	0.99	0.98	0.95
	2	0.06	0.03	0.02	0.01	0.01	0.04	0.04	0.01	0.02	0.05	0.12	0.03	0.01	0.01	0.02	0.05
	n	79	51	85	49	100	110	99	100	96	94	100	584	84	115	595	553
	χ^2	0.43	0	0.1	0	0	1.4	0.9	2.2	0.2	0.1	8.8	1.9	0	0	0.5	11.7*
PGI	0	—	—	—	—	—	—	—	—	0.01	—	—	—	—	—	—	0.33
	1	0.98	0.96	0.99	0.97	0.99	0.95	1.0	1.0	0.99	1.0	1.0	0.99	0.99	1.0	0.93	0.57
	2	0.02	0.04	0.01	0.03	0.01	0.05	—	—	—	—	—	0.01	0.01	—	0.07	0.10
	n	66	40	85	57	100	115	90	100	100	100	100	598	101	124	542	549
	χ^2	0	0	0	0	0.2	0	0	0	0	0	0	2.0	0	0.01	0	7.3**
IDH	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1.0
	2	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	—
MDH2	1	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	—
	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1.0
Avg heterozygosity		11.2	10.3	12.7	11.8	12.7	13.2	12.4	12.1	12.1	12.1	11.9	11.9	11.0	11.1	14.2	13.8

χ^2 Values were significant at the 95% level (*) and at the 99% level (**). Data shown are for six polymorphic loci and two monomorphic loci diagnostic for Jeffrey pine beetle versus mountain pine beetle. Ten monomorphic loci (AAT2, AGP1, AGP2, AGP3, EST2, EST3, LAP1, MDH1, TO, and CK) were identical in all populations.

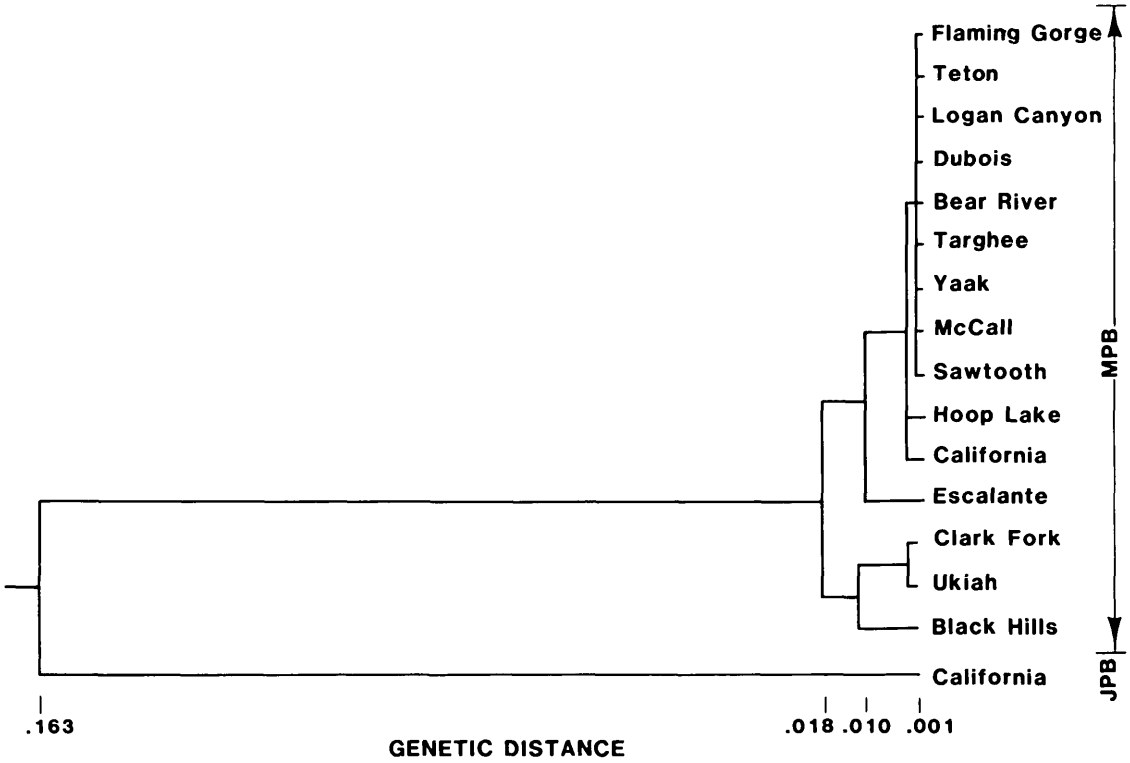

Fig. 2. Genetic relationships among 15 mountain pine beetle populations and one Jeffrey pine beetle population estimated using electrophoretic data from 6 polymorphic and 12 monomorphic loci.

ing genetic distance values and an International Mathematics and Statistics Language (IMSL) computer subroutine called OCLINK. Average heterozygosity was calculated according to the method of Nei (1975) to give an estimate of overall genetic diversity in each group.

Results and Discussion

Genotype and allele frequency data were obtained from 18 enzyme-producing gene loci in the 14 beetle populations. Six loci—aspartate aminotransferase 1 (AAT1), acid phosphatase (AcP), esterase 1 (EST1), leucine aminopeptidase 2 (LAP2), peptidase (PEP), and phosphoglucose isomerase (PGI)—were polymorphic in at least one population. Polymorphic loci were defined as those in which the frequency of the common allele was less than 0.99 in at least one population. Allele frequencies at these loci, plus corresponding frequencies from the California mountain pine beetle and Jeffrey pine beetle groups, are shown in Table 2.

Table 3. Nei's genetic identity values for 15 mountain pine beetle populations and 1 Jeffrey pine beetle population, calculated using electrophoretic data from 6 polymorphic and 12 monomorphic loci

	UK	CF	ST	MC	TA	YA	DU	TE	LC	BR	HL	FG	ES	BH	CA-M	CA-J
UK	—															
CF	0.998	—														
ST	0.981	0.980	—													
MC	0.981	0.981	0.999	—												
TA	0.981	0.982	0.997	0.998	—											
YA	0.982	0.981	0.997	0.999	0.998	—										
DU	0.977	0.978	0.996	0.997	0.998	0.997	—									
TE	0.978	0.978	0.998	0.998	0.998	0.997	0.999	—								
LC	0.978	0.978	0.996	0.997	0.999	0.996	0.999	0.999	—							
BR	0.975	0.974	0.993	0.996	0.996	0.996	0.999	0.997	0.998	—						
HL	0.977	0.978	0.994	0.997	0.996	0.997	0.998	0.997	0.998	0.998	—					
FG	0.980	0.981	0.997	0.999	0.998	0.998	0.998	0.999	0.998	0.995	0.998	—				
ES	0.967	0.963	0.987	0.989	0.986	0.985	0.989	0.990	0.990	0.990	0.984	0.987	—			
BH	0.989	0.983	0.973	0.971	0.972	0.972	0.970	0.970	9.969	0.969	0.964	0.968	0.972	—		
CA-M	0.978	0.978	0.997	0.997	0.997	0.997	0.997	0.995	0.995	0.995	0.994	0.995	0.985	0.974	—	
CA-J	0.817	0.824	0.846	0.849	0.843	0.844	0.849	0.848	0.847	0.846	0.849	0.847	0.834	0.804	0.850	—

A single variant creatine kinase (CK) allele was observed, in addition to the common allele, in the Sawtooth, McCall, and Yaak populations, but because of the rarity of this allele, the CK locus was considered monomorphic and was not included in Table 2. Eleven other loci—isocitrate dehydrogenase (IDH), AAT2, α-glycerophosphate dehydrogenase 1, 2, and 3 (AGP1, AGP2, and AGP3), EST2 and EST3, LAP1, malate dehydrogenase 1 and 2 (MDH1 and MDH2), and tetrazolium oxidase (TO)—were monomorphic in all groups, although IDH and MDH2 were fixed for a different allele in the Jeffrey pine beetle and are considered diagnostic for that species (Higby and Stock 1982).

In most cases, observed genotype frequencies conformed to expectations for random-mating populations (Table 2). The only consistent exception was in the California mountain pine beetle and Jeffrey pine beetle groups, where a deficiency of heterozygotes resulted from pooling several subsamples of each species from nearby host stands.

When pair-by-pair comparisons were made among all groups at individual loci, California mountain pine beetles, Jeffrey pine beetles, and South Dakota mountain pine beetles were most different from other groups, especially at the AAT1 and LAP2 loci. As in earlier studies, the esterase locus varied most among groups, showing significant differences in about 80% of all pair-by-pair comparisons.

Average heterozygosity varied from 10.3 to 14.2% (Table 2). Nei's genetic identity values ranged, among mountain pine beetle populations, from 0.963 to 0.999 and, between mountain pine beetles and Jeffrey pine beetles, from 0.804 to 0.850 (Table 3). Relationships among groups are shown in Fig. 2. The high level of genetic similarity observed among mountain pine beetle collections in this study, and the relatively much lower level of similarity between the Jeffrey pine beetle and the mountain pine beetle, support the current single-species interpretation of *D. ponderosae*, the mountain pine beetle. No genetic differentiation is apparent between beetle samples taken in the geographic ranges originally described for *D. ponderosae* and *D. monticolae* (Fig. 1).

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References Cited

Baker, B. H., G. D. Amman, and G. C. Trostle. 1971. Does the mountain pine beetle change hosts in mixed lodgepole pine and whitebark pine stands? U.S. Dep. Agric. For. Serv. Res. Note INT-151.

Higby, P. K., and M. W. Stock. 1982. Genetic relationships between two sibling species of bark beetle (Coleoptera: Scolytidae), Jeffrey pine beetle and mountain pine beetle, in northern California. Ann. Entomol. Soc. Am. 75: 668–674.

Hopkins, A. D. 1902. Insect enemies of pine in the Black Hills Forest Reserve. U.S. Dep. Agric. Div. Entomol. Bull. 32 (New Series).

1905. The Black Hills beetle. U.S. Dep. Agric. Bur. Entomol. Bull. 56: 1–24.

1909. Contributions toward a monograph of the scolytid beetles. I. The genus *Dendroctonus*. U.S. Dep. Agric. Bur. Entomol. Tech. Bull. 17: 1–164.

Lanier, G. N., and D. L. Wood. 1968. Controlled mating, karyology, morphology, and sex-ratio in the *Dendroctonus ponderosae* complex. Ann. Entomol. Soc. Am. 61: 517–526.

Nei, M. 1972. Genetic distance between populations. Am. Nat. 106: 283–292.

1975. Genetic variability in natural populations, pp. 127–174. *In* Molecular population genetics and evolution. North Holland research monographs, frontiers of biology, vol. 40. American Elsevier Publishing Co., Inc., New York.

Smith, R. H. 1965. A physiological difference among beetles of *Dendroctonus ponderosae* (=*D. monticolae*) and *D. ponderosae* (=*D. jeffreyi*). Ann. Entomol. Soc. Am. 58: 440–442.

Stock, M. W., and G. D. Amman. 1980. Genetic differentiation among mountain pine beetle populations from lodgepole pine and ponderosa pine in northeast Utah. Ibid. 73: 472–478.

Stock, M. W., and J. D. Guenther. 1979. Isozyme variation among mountain pine beetle (*Dendroctonus ponderosae*) populations in the Pacific Northwest. Environ. Entomol. 8: 889–893.

Sturgeon, K. B. 1980. Evolutionary interactions between mountain pine beetle, *Dendroctonus ponderosae* Hopkins, and host trees in the Colorado Rocky Mountains. Ph.D. dissertation, University of Colorado, Boulder.

Wood, S. L. 1963. A revision of the bark beetle genus *Dendroctonus* Erichson (Coleoptera: Scolytidae). Great Basin Nat. 23: 1–117.

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