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Patterns of genetic variation of the genus *Capsicum* (*Solanaceae*) in Mexico

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Abstract: The evolutionary relationships of 186 accessions of *Capsicum* from Mexico were studied through enzyme electrophoresis. A total of 76 alleles representing 20 genetic loci coding for nine enzyme systems were observed and the allelic variations of enzymes were studied for geographical distribution. Allele frequencies were used to estimate the apportionment of gene diversity within and between populations and to construct a dendrogram based on a similarity matrix containing NEI genetic distances. – The gene diversity estimates suggest that the structure of *Capsicum* populations in Mexico consists of predominantly homozygous genotypes presumably due to a self-pollinated breeding system and population bottlenecks. Significant genetic differentiation was found mainly between populations of differing geographical regions. – Based on the results of this study, three species of domesticated *Capsicum* can be identified in Mexico, *C. annuum* var. *annuum, C. chinense*, and *C. pubescens*. Semidomesticated and wild forms include two species, *C. frutescens* and *C. annuum* var. *glabriusculum*. A sharp geographical division results between the latter species; *C. frutescens* was collected exclusively in the southeastern states of Oaxaca, Chiapas, and Tabasco; whereas wild and semidomesticated forms from the rest of the country are *C. annuum*. Based upon the similarity of enzyme genotypes of semidomesticated and wild forms, the primary center of domestication of cultivated *C. annuum* was estimated to be the region comprising the states of Tamaulipas, Nuevo Leon, San Luis Potosi, Veracruz, and Hidalgo in eastern Mexico. A possible second center of domestication is suggested to be localized in the state of Nayarit, western Mexico.

Capsicum (*Solanaceae*) is a New World genus with approximately 27 species. Of these, *C. annuum, C. frutescens, C. chinense, C. baccatum*, and *C. pubescens* are domesticated (Genetic Resources of *Capsicum* 1983). This genus has its center of origin in South America, where 22 of the species are endemic (HUNZIKER 1979).

The basic chromosome number of all the *Capsicum* species is $x = 12$ except for *C. ciliatum* (H. B. K.) O. K. and an undetermined species from Brazil whose basic chromosome number are $x = 13$, and a tetraploid domesticated *C. annuum* accesion (PICKERSGILL 1977). The generic limits of *Capsicum* include all the forms with free,

glabrous filaments, campanulate and rotate to subrotate corollas, smooth and toothed calyx margins, two- or more loculed fruits, pulpy or non-pulpy berries, and non-pungent or pungent berries with the pungent material, capsaicin, confined to the placenta (ESHBAUGH 1970; PICKERSGILL, pers. comm.).

Various taxonomic studied of the Mexican *Capsicum* have recognized different species. MUNOZ & PINTO (1966) mentioned the five domesticated species listed above. However, in a recent study, the number of commercially cultivated species were reduced to three: *C. pubescens, C. chinense*, and *C. annuum* (LABORDE & POZO CAMPODONICO 1984). *Capsicum pubescens* is found only in some regions of high altitude and low temperatures as Pinal de Amoles, Queretaro; La Villita, Michoacan; and La Grandeza, Chiapas. *Capsicum chinense* is reportedly restricted to La Peninsula de Yucatan (LABORDE & POZO CAMPODONICO 1984). *Capsicum annuum* is found throughout the country and shows great morphological variation. *Capsicum annuum* is the only species considered to be native to Mexico. *Capsicum chinense* and *C. pubescens* are thought to have been introduced from Cuba and South America, respectively (LABORDE & POZO CAMPODONICO 1984).

Several wild forms of *Capsicum,* thought to be *C. annuum* (Genetic Resources of *Capsicum* 1983), can be found in almost every state of Mexico. In order to differentiate between these and the domesticated species, they have recently received the varietal names of either *minimum* (MILLER) HEISER (HEISER 1964), *aviculare* (DIERB.) D'ARCY & ESHBAUGH (D'ARCY & ESHBAUGH 1972), or *glabriusculum* (DUNAL) HEISER &PICKERSGILL (HEISER & PICKERSGILL 1975).

The evolutionary relationships of species in the genus *Capsicum*, specifically the more closely related species of *C. annuum, C. chinense,* and *C. frutescens,* have been examined by other workers through three different approaches: karyotype analyses, numerical taxonomic analysis, and chemotaxonomic studies. Karyotype analyses disclosed that domesticated types for these three species varied in the size, position, and number of satellites, and in chromosome morphology. For instance, in domesticated *C. chinense* and *C. frutescens* there are one pair of acrocentric chromosomes and eleven pairs of metacentric chromosomes, whereas the domesticated *C. annuum* may have one or two pairs of acrocentric chromosomes. The wild counterpart of the latter species has been found to have six different chromosome karyotypes distributed geographically along Latin America, with four of these karyotypes confined to Mexico (PICKERSGILL 1971).

Numerical taxonomic analysis based on quantitative and qualitative morphological characters determined that domesticated *C. annuum, C. chinense,* and *C. frutescens* can be easily distinguished from one another, despite parallel evolution under cultivation for such traits. On the other hand, the wild forms of these species cluster closely and show little divergence from one another, making them difficult to classify as separate species (PICKERSGILL & al. 1979).

Finally, chemotaxonomic studies based on enzyme electrophoresis indicate that this group forms an allozymically indistinguishable group of populations (JENSEN & al. 1979) or a single "polytypic" species inasmuch as the highest NEI genetic distance between species was 0.09 (MCLEOD 1977, MCLEOD & al. 1979).

The objective of this study was to further explore the pattern of genetic diversity and the phylogenetic relationships among wild, semidomesticated, and domesticated forms of *Capsicum* from Mexico, where an extensive collection has been carried out (Genetic Resources of *Capsicum* 1983; LABORDE, unpubl.).

Methods and materials

***Capsicum* accessions.** 192 accessions of *Capsicum* were included in the study, of which 186 were obtained from Mexico by collecting seeds from domesticated, semidomesticated, and wild forms. The domesticated class was composed of improved and land race varieties; the semidomesticated forms came from family gardens but were probably selected from wild peppers; and the wild types were sampled directly in their natural habitats or bought at nearby market places (LABORDE, unpubl.). Seed samples of these collections are maintained at Unidad de Recursos Geneticos, INIA-CIAB; Celaya, Guanajuato, Mexico. Site of collections, elevation, longitude, latitude, sampling technique, and collectors, are presented in Table 1; the sites of collection can be seen in Fig. 1. Each accession was treated as an operational taxonomic unit (OTU) to avoid any a priori bias of systematic affiliations.

12 accessions from outside Mexico were used as references or "outgroups" for the evolution of the Mexican accessions. They included two undetermined *Capsicum* species, one from Costa Rica (BG 2688) and the other (BG 0003) from Peru; *C. annuum* var. *annuum* CA 133 cv. R-Naky, a mild variety grown in southern New Mexico; *C. chinense* CA4, a domesticated type collected by Dr P. G. SMITH in Peru, and FL 0013 (PI 439420), *C. chacoense* FL 0007 (PI 260434), *C. praetermisum* FL 0008 (PI 439528) and FL 0009 (82 C 217), *C. baccatum* var. *baccatum* FL 0010 (PI 439399), *C. baccatum* var. *pendulum* FL 0011 (PI 267729), and *C. frutescens* FL 0012 (PI 208738) and FL 0014 (McIhanny Select

Fig. 1. *Capsicum* collecting in various Mexican states. AGS Aguascalientes; CAMP Campeche; CHIH Chihuahua; CHIS Chiapas; GDO Durango; GRO Guerrero; HGO Hidalgo; JAL Jalisco; MICH Michoacan; NAY Nayarit; NL Nuevo Leon; OAX Oaxaca; PUE Puebla; Q ROO Quintana Roo; QRO Queretaro; SLP San Luis Potosi; SON Sonora; TAM Tamaulipas; TAB Tabasco; VER Veracruz; YUC Yucatan; ZAC Zacatecas

Table 1. Summary of collection data for the Mexican accessions of *Capsicum*. [1] AAG A. AGUILLON, G.; AGM ARTURO GUERRERO, M.; ASR ARTURO SAMANIEGO, R.; CS C. SANDOVAL; FCR FRANCISCO CARDENAS, R.; HH HUMBERTO HURTADO; JALC JOSE A. LABORDE, C.; JDR JUAN D. RUIZ; JLA JOSE L. AGUILAR; LHR LUIS HERNANDEZ RIVERA; ML MANUEL LAGARDA; OPC OCTAVIO POZO, C.; RGC R. GARCIA CALDERON; RS RICHARD SPELLENBERG; SMH SALVADOR MONTES HERNANDEZ. * FL 0004 "Esmeralda"; FL 0005 "Linea Experimental #7"

No.	No. of access.	Source	Degree of domestication	Site of collection	State	Elevation (m)	Longitude	Latitude	Sampling technique	Collectors[1]
1	BG 3238	original	wild	El Basapo	Sonora					JALC
2	BG 3235	original	wild	El Pajarito	Sonora	389	109°40′	29°50′	mass	JALC
3	BG 3233	original	wild		Sonora					JALC
4	BG 3232	original	wild		Sonora					JALC
5	BG 3231	original	wild	El Pajarito	Sonora	389	109°40′	29°50′	mass	JALC
6	BG 3230	original	wild	El Pajarito	Sonora	389	109°40′	29°50′	individual	JALC
7	FL 0001	original	wild		Sonora				mass	LHR
8	BG 3229	original	wild	El Colador	Sonora	677	109°40′	29°50′	mass	JALC
9	BG 3228	original	wild	El Colador	Sonora	677	109°40′	29°50′	individual	JALC
10	BG 3227	original	wild	El Colador	Sonora	677	109°40′	29°50′		JALC
11	BG 3225	original	wild	La Montosa	Sonora				mass	JALC
12	BG 3222	original	wild	La Cieneguita	Sonora					JALC
13	BG 3220	original	wild	Alamos	Sonora	389	108°50′	27°00′	mass	JALC
14	BG 3217	original	wild	Alamos	Sonora	389	108°50′	27°00′	mass	JALC
15	BG 3215	original	semicultivated	Alamos	Sonora	389	108°47′	27°02′	mass	JALC
16	BG 3213	original	wild	Tapizuelas	Sonora	389	108°57′	26°45′	individual	ASR
17	BG 3212	original	wild	Tapizuelas	Sonora	389	108°54′	26°40′	individual	JALC
18	BG 3211	original	wild	Tapizuelas	Sonora	389	108°54′	26°40′	individual	JALC
19	BG 3210	original	wild	Tapizuelas	Sonora	389	108°54′	26°40′		JALC
20	BG 3209	original	wild	Tapizuelas	Sonora	389	108°54′	26°40′	individual	JALC
21	BG 3207	original	wild	Tapizuelas	Sonora	389	108°54′	26°40′	mass	JALC
22	BG 3195	original	wild	Los Tanques	Sonora	389	108°50′	27°15′	mass	
23	BG 3194	original	wild	Los Tanques	Sonora	389	108°40′	27°15′	individual	
24	BG 3191	original	wild	Agua Salada	Sonora	389	108°48′	27°18′	mass	

25	BG 3190	original	wild	Agua Salada	Sonora	389	108°48′	27°18′	individual	ASR
26	BG 3189	original	wild	Naranjo	Sonora	389	108°47′	27°18′	mass	ASR
27	BG 3188	original	wild	Naranjo	Sonora	389	108°47′	27°18′	individual	
28	BG 3187	original	wild	Tamayuco	Sonora	389	108°47′	27°18′	mass	
29	BG 3186	original	wild	Camotes	Sonora	389	108°47′	27°18′	individual	ASR
30	FL 0003	original	semicultivated	Navojoa	Sonora				individual	RS
31	BG 2800	original	wild	Navojoa	Sonora					ML
32	BG 3326	original	wild		Sonora					JLA
33	FL 0002	original	wild	Batopilas	Chihuahua				individual	RS
34	BG 2797	original	semicultivated		Nayarit					CS
35	BG 2796	original			Nayarit					
36	BG 2794	original	semicultivated		Nayarit					
37	BG 2786				Nayarit					
38	BG 2778				Nayarit					
39	BG 2676	original	semicultivated		Nayarit		105°46′	22°21′		FCR
40	BG 2769	original	semicultivated		Nayarit					
41	BG 2764				Nayarit					
42	BG 2756	original	semicultivated		Nayarit					
43	BG 2750				Nayarit					
44	BG 2747	original	semicultivated		Nayarit					
45	BG 2737	original	semicultivated	La Presa	Nayarit	11	105°12′	21°48′	individual	
46	BG 2736				Nayarit					
47	BG 2733				Nayarit					
48	BG 2732	original	semicultivated	La Presa	Nayarit	11	105°12′	21°48′	individual	CS
49	BG 2729	original	semicultivated	La Presa	Nayarit	11	105°12′	21°48′	individual	CS
50	BG 2728				Nayarit					
51	BG 2727	original	semicultivated	La Presa	Nayarit	11	105°12′	21°48′	individual	CS
52	BG 2725	original	semicultivated	La Presa	Nayarit	11	105°12′	21°48′	individual	CS
53	BG 2724				Nayarit					
54	BG 1669	increased	semicultivated	Santiago Ixcuintla	Nayarit	11	105°13′	21°49′	mass	JALC
55	BG 1668	original	semicultivated	Santiago Ixcuintla	Nayarit	11	105°13′	21°49′	mass	JALC
56	BG 1662	original	semicultivated	Autan	Nayarit	2	105°17′	21°17′	mass	JALC
57	BG 1661				Nayarit					

Table 1 (continued)

No.	No. of access.	Source	Degree of domestication	Site of collection	State	Elevation (m)	Longitude	Latitude	Sampling technique	Collectors[1]
58	BG 1658	original	semicultivated	Autan	Nayarit	2	105°17′	21°32′	mass	JALC
59	BG 1657				Nayarit					
60	BG 1650	original	semicultivated	Sentispac	Nayarit	11	105°13′	21°49′	mass	JALC
61	BG 1649				Nayarit					
62	BG 1648				Nayarit					
63	BG 1645	original	semicultivated	Botadero	Nayarit	11	105°13′	21°49′	mass	JALC
64	BG 1644				Nayarit					
65	BG 1642	increased	semicultivated	El Limon	Nayarit	14	105°28′	22°24′	mass	JALC
66	BG 1638	original	semicultivated	Tecuala	Nayarit	14	105°28′	22°24′	individual	JALC
67	BG 1635	original	semicultivated	Tecuala	Nayarit	14	105°28′	22°24′	mass	JALC
68	BG 1629				Nayarit					
69	BG 1628	original	semicultivated	Quimichis	Nayarit	14	105°28′	22°24′	mass	JALC
70	BG 1624				Nayarit					
71	BG 1623				Nayarit					
72	BG 1622				Nayarit					
73	BG 1617				Nayarit					
74	BG 1616	increased	semicultivated	Novillero	Nayarit	14	105°28′	22°24′	mass	JALC
75	BG 1670	original	semicultivated	Plan de Barrancas	Jalisco	800	104°11′	21°02′	individual	JALC
76	BG 1671	increased	semicultivated	Plan de Barrancas	Jalisco	800	104°11′	21°02′	mass	JALC
77	BG 1690	original	wild	El Poblado	Jalisco	35	105°16′	19°56′	mass	JALC
78	BG 1693				Jalisco					
79	BG 1694				Jalisco					
80	BG 1697	original	wild	Chamela	Jalisco	35	105°16′	19°56′	mass	JALC
81	BG 1699	original	wild	El Paraiso	Jalisco	35	105°16′	19°56′	mass	JALC
82	BG 1700	original	wild	El Paraiso	Jalisco	35	105°16′	19°56′	mass	JALC
83	BG 1702	original	wild	El Rebalsito	Jalisco	35	105°16′	19°56′	mass	JALC
84	BG 3575	original	wild	Tepec	Jalisco	1 450	103°38′	20°00′	mass	SMH
85	BG 3576	original	wild	Tepec	Jalisco	1 450	103°38′	20°00′	individual	SMH
86	BG 3577	original	wild	Tepec	Jalisco	1 450	103°38′	20°00′	individual	SMH

87	BG 0038	original	cultivated	Autlan	Jalisco	1 003	104°25′	19°42′		AGM
88	BG 0039	original	cultivated	Autlan	Jalisco	1 003	104°25′	19°42		AGM
89	BG 0050	increased	cultivated	Autlan	Jalisco	1 003	104°25′	19°42		AGM
90	BG 0924	increased	cultivated	San Cristobal	Jalisco	1 888	102°18′	21°53′	mass	AAG
91	BG 0939	increased	cultivated	La Muralla	Jalisco	1 942	101°55′	21°22′	mass	AAG
92	BG 0952	original	cultivated	Yahualica	Jalisco					
93	BG 0998	original	semicultivated	Tomatlan	Jalisco					HH
94	BG 3291	increased	cultivated	Matamoros	Jalisco	2 844	101°35′	21°52′	individual	AGM
95	BG 3355	increased	cultivated	Autlan	Jalisco	1 003	104°25′	19°42′		RGC
96	BG 1755	original	cultivated	La Villita	Michoacan	1 755	101°28′	19°14′	mass	JALC
97	BG 3302	original	semicultivated	El Tahuasal	Michoacan	50	102°20′	17°59′	mass	JALC
98	BG 3306	original	cultivated	Miguel Aleman	Guerrero		98°30′	16°30′	individual	JALC
99	BG 3307	original	cultivated	Miguel Aleman	Guerrero		98°30′	16°30′	individual	JALC
100	BG 3308	original	cultivated	Miguel Aleman	Guerrero		98°30′	16°30′	individual	JALC
101	BG 3309	original	cultivated	Miguel Aleman	Guerrero		98°30′	16°30′	individual	JALC
102	BG 3312	original	semicultivated	El Chumascadero	Oaxaca		97°30′	16°00′	mass	JALC
103	BG 3313	original	wild	Pochutla	Oaxaca	280	96°31′	15°44′	mass	JALC
104	BG 3317	original	wild	Margaritas	Chiapas	55	93°00′	15°33′	mass	JALC
105	BG 3318	original	semicultivated	Excuintla	Chiapas	110	92°40′	15°19′	individual	JALC
106	BG 3321	original	wild	Tenochtitlan	Chiapas	28	92°28′	15°10′	individual	JALC
107	BG 3324	original		Motozintla de Mendoza	Chiapas		92°14′	15°22′	mass	JALC
108	BG 3328	original	cultivated	La Grandeza	Chiapas	1 227	92°14′	15°22′	mass	JALC
109	BG 1844	original	wild	General Teran	Neovo Leon		99°40′	25°15′	mass	JALC
110	BG 1850	original	wild	Montemorelos	Nuevo Leon				mass	JALC
111	BG 1852	original	wild	La Maquina	Nuevo Leon		100°02′	25°00′	mass	JALC
112	BG 3476		wild		Nuevo Leon					
113	BG 1854	original	wild	La Maquina	Nuevo Leon		100°02′	25°00′	mass	JALC
114	BG 1855	increased	wild	La Maquina	Nuevo Leon		100°02′	25°00′	mass	JALC
115	BG 1809	original	wild	Chamal Viejo	Tamaulipas	348	99°21′	22°52′	mass	JALC
116	BG 1811	original	wild	La Puente	Tamaulipas	348	99°21′	22°51′	mass	JALC
117	BG 1812	original	wild	La Puente	Tamaulipas	348	99°21′	22°51′	mass	JALC
118	BG 1813	increased	semicultivated	La Puente	Tamaulipas	348	99°21′	22°51′	mass	JALC
119	BG 1814	original	wild	Librado Rivera	Tamaulipas	348	99°21′	22°51′	mass	JALC

Table 1 (continued)

No.	No. of access.	Source	Degree of domestication	Site of collection	State	Elevation (m)	Longitude	Latitude	Sampling technique	Collectors[1]
120	BG 1817	original	wild	Libio Guerra	Tamaulipas	348	99°21′	22°51′	mass	JALC
121	BG 1822	original	wild	El Mante	Tamaulipas	186	99°00′	22°40′	mass	JALC
122	BG 1823	original	semicultivated	El Mante	Tamaulipas	186	98°59′	22°40′	mass	JALC
123	BG 1834	original	wild	Llera de Canales	Tamaulipas	291	99°00′	23°25′	mass	JALC
124	BG 1837	original	cultivated	Llera de Canales	Tamaulipas	291	99°00′	23°25′	individual	JALC
125	BG 1840	original	cultivated	Llera de Canales	Tamaulipas	291	99°00′	23°25′	individual	JALC
126	BG 1787	original	semicultivated	Ahuacatlan	San Luis Potosi				mass	JALC
127	BG 1789	original	cultivated	Arroyo Seco	San Luis Potosi				mass	JALC
128	BG 1795	original	semicultivated	Nescuayo	San Luis Potosi	200	98°50′	21°20′	mass	JALC
129	BG 1798	original	semicultivated	Tampacan	San Luis Potosi	200	98°50′	21°20′	mass	JALC
130	BG 1799	original	semicultivated	Tampacan	San Luis Potosi	200	98°50′	21°20′	mass	JALC
131	BG 1800	original	semicultivated	Tampacan	San Luis Potosi	200	98°50	21°20′	mass	JALC
132	BG 1801	original	semicultivated	Tampacan	San Luis Potosi	200	98°50′	21°20′	mass	JALC
133	BG 1804	original	semicultivated	San Martin Chalchi.	San Luis Potosi	40	98°40′	21°20′	mass	JALC
134	BG 1511	original	cultivated	San Vicente Tancua.	San Luis Potosi	40	97°47′	21°40′	mass	OPC
135	BG 1512				San Luis Potosi					OPC
136	BG 1513				San Luis Potosi					OPC
137	BG 1514				San Luis Potosi					OPC
138	BG 1515				San Luis Potosi					OPC
139	BG 1516				San Luis Poitosi					OPC
140	BG 1519	original	semicultivated	Atotonilco El Grande	Hidalgo	2 138	98°40′	20°16′	mass	OPC
141	BG 1520	increased	cultivated	Atotonilco El Grande	Hidalgo	2 138	98°40′	20°16′	mass	OPC
142	BG 1521	increased	cultivated	Atotonilco El Grande	Hidalgo	2 138	98°40′	20°16′	mass	OPC
143	BG 1523	increased	cultivated	Cuacuila	Puebla	1 472	98°03′	28°11′	mass	OPC
144	BG 1534		cultivated		Puebla					OPC
145	BG 1535		cultivated		Puebla					OPC
146	BG 1536		cultivated		Puebla					OPC
147	BG 1606		cultivated		Puebla					
148	BG 0912		cultivated	Amoles	Queretaro					JDR

149	BG 3295		cultivated	Queretaro	Queretaro	1 865	100°21′	20°38′		
150	BG 3241		cultivated	San Jose De Lourdes	Zacatecas	2 249	102°50′	23°11′		
151	BG 2528		cultivated		Guanajuato					
152	BG 2529		cultivated		Guanajuato					
153	BG 0639		cultivated		Guanajuato					
154	BG 1875		cultivated	Felipe Angeles	Durango	1 910	103°56′	24°01′		
155	BG 0947		cultivated	El Liano	Aguascalientes					
156	BG 3415		cultivated	Paplanta	Veracruz					
157	BG 3425		cultivated		Veracruz					
158	BG 3444		cultivated	Paplanta	Veracruz					
159	BG 3457		cultivated		Veracruz					
160	BG 2801	original	wild	Teapa	Tabasco	50	93°00′	17°30′	mass	JALC
161	BG 2802	original		Teapa	Tabasco	50	93°00′	17°30′	mass	JALC
162	BG 2805	original	wild	Palenque	Chiapas	60	91°58′	17°30′	individual	JALC
163	BG 2808	original	wild	Tapijualapa	Tabasco	60	92°47′	17°28′	mass	JALC
164	BG 2811	original	wild	Tapijualapa	Tabasco	60	92°47′	17°28′	mass	JALC
165	BG 2814	original	wild	La Aurora	Tabasco	60	92°50′	17°40′	mass	JALC
166	BG 2815	original	wild	La Aurora	Tabasco	60	92°50′	17°40′	mass	JALC
167	BG 2816	original	wild	La Aurora	Tabasco	60	92°50′	17°40′	mass	JALC
168	BG 1746	original	wild	Ichek	Campeche		89°56′	19°42′	mass	JALC
169	BG 1747	original	wild	Ichek	Campeche		89°56′	19°42′	mass	JALC
170	BG 1717	original	semicultivated	Temax	Yucatan	25	88°55′	21°10′	mass	JALC
171	BG 1721	original	semicultivated	Buctzotz	Yucatan	15	88°50′	21°12′	mass	JALC
172	BG 1724	original	wild	Sucila	Yucatan	12	88°20′	20°30′	mass	JALC
173	BG 0569	original	cultivated		Yucatan					JALC
174	BG 1725	original	wild	Puerto Morelos	Quintana Roo		86°50′	20°54′	mass	JALC
175	BG 0101		cultivated							
176	BG 1506		cultivated							
177	BG 1507		cultivated							
178	FL0004*		cultivated							
179	FL0005*		cultivated							

Tabasco), a variety grown in Louisiana. Except for the two undetermined *Capsicum* species, the remaining ten accessions undoubtedly rank as species, as documented elsewhere (SMITH & HEISER 1951 b; ESHBAUGH 1968, 1970, 1976, 1980; HEISER & PICKERSGILL 1969; Genetic Resources of *Capsicum* 1983). In addition, some diagnostic descriptions of *Capsicum* spp. were used, including flower color, presence or absence of calyx constriction, and seed color, as suggested by the International Board for Plant Genetic Resources standard format (Genetic Resources of *Capsicum* 1983).

Habitat. The habitat description that follows is summarized from the field notes, and limited mainly to those occupied by wild *Capsicum* (LABORDE, unpubl.).

In Sonora (Fig. 1) wild *Capsicum* populations are usually found near streams or step hills where moisture is available. When the populations are distributed over the hills, they associate with *Prosopis* spp. ("auct. non. mesquite") and *Quercus* spp. ("auct. non. encino"). The soil types occupied are normally either light-deep soils near streams and step hills or "tepetate" (high calcium content) and rocky ones on hills. The plant heights in these native habitats vary from 0.8 m to 1.3 m.

Jalisco (Fig. 1) is a state characterized by xeric conditions in more elevated areas and tropical conditions along the Pacific Coast. in drier regions, wild *Capsicum* populations form associations with *Acacia* spp. ("auct. non. huizache") and *Opuntia* spp. ("auct. non. nopal") whereas in tropical areas small populations consisting of 10 – 20 plants are dispersed inside the dense forests. In contrast to xeric populations, individuals from the tropical region seem to have an indeterminate growth pattern, their intermixed branches being as long as 2.5 m.

Some regions of the states of Michoacan, Guerrero, Oaxaca, Chiapas, and Tabasco (Fig. 1) are mostly characterized by tropical climate. Populations of *Capsicum* are found here in association with *Physalis* in Michoacan and Oaxaca or localized inside *Coffea* and *Musa* plantations in Chiapas and Tabasco. The growth habit seems to be more determinate. Plants heights can vary from 1.5 m to 1.8 m.

In La Peninsula de Yucatan, which includes the states of Campeche, Yucatan, and Quintana Roo (Fig. 1), *Capsicum* populations can be found growing in rocky soils with open vegetation or in deep soils with a dense evergreen vegetation. In the latter habitat, the individuals have intermixed, 3 m-long branches.

In eastern Mexico two regions with different habitat conditions can be identified. The region of Las Huastecas, which is composed by part of the states of Tamaulipas, San Luis Potosi, Hidalgo, and Veracruz, is characterized by tropical climate, with plant heights up to 1.7 m. The regions in northern Tamaulipas and Nuevo Leon are more xeric, and plants collected there were usually shorter than 1.0 m. A difference between the *Capsicum* collected from these regions and those from tropical Jalisco and La Peninsula de Yucatan is that the former have a more determinate growth habit.

Other relevant characteristics of population biology include seed dormancy and seed dispersal mechanisms. Herbarium seeds have been found to germinate after 12 years, suggesting that seed dormancy might be a survival mechanism. Thus, the individuals composing a colony can be the result of different zygotic generations.

Seed dispersal mechanisms, though not fully studied in this species, are thought to be by either water, wind, or birds. Wind and water dispersal might be enhanced by the presence of the *S* gene (SMITH 1951 a), which allows the easy separation of the ripe fruit from its pedicel, and by fruit which is light and rounded when completely dried. The presence of this species near streams or at step hills might be due to water dispersal. Even though bird dispersal is widely suggested as the main dispersal mechanism, it has not yet been conclusively proved. Birds are strongly attracted by the red fruits, a situation requiring that field collections should be timed close to ripening to avoid preharvesting by birds. Bird dispersal is also suggested by the common finding of small populations of peppers at the base of trees used by birds.

Electrophoresis. Leaf extracts were surveyed for the following enzymes: aconitase, ACO (E.C.4.2.1.3); isocitrate dehydrogenase, IDH (E.C.1.1.1.42); malate dehydrogenase, MDH (E.C.1.1.1.37); 6-phosphogluconate dehydrogenase, 6-PGDH (E.C.1.1.1.44); phosphoglucomutase, PGM (E.C.2.7.5.1.); phosphoglucoisomerase, PGI (E.C.5.3.1.9); peroxidase, PRX (E.C.1.11.1.7); shikimate dehydrogenase, SKDH (E.C.1.1.1.25); and triose phosphate isomerase, TPI (E.C.5.3.1.1). Seed extracts were surveyed only for phosphoglucomutase and phosphoglucoisomerase. The extraction buffer was 1.5% Glutathione in 0.1 M Tris-HCl pH 8.5. All the enzymes were resolved in 11% starch gels; the first five using the histidine buffer system (VALLEJOS & TANKSLEY 1983) and the last four with the tris-citrate buffer system (RICK & al. 1977). Enzyme staining protocols were according to VALLEJOS (VALLEJOS 1983). The mean number of individuals sampled per accesion was 14 plants (Range = 56).

Genetics. Extracts from the inbred lines *C. annuum* var. *annuum* (CA 133) and *C. chinense* (CA 4) were used as controls in gels to detect enzyme polymorphism, and the numbering of alleles within a locus was made according to the order they were detected. The genetic and linkage relationships of genes encoding PGM, PGI, IDH, 6PGDH, and SKDH have already been described (TANKSLEY 1984). For the other enzymes (ACO, MDH, PRX, and TPI) loci were assigned according to their probable homology with enzyme loci in tomato (*Lycopersicon esculentum*) a species from the same family, *Solanaceae,* and for which much information is available on isozyme genetics (RICK 1983; TANKSLEY & LOAIZA-FIGUEROA, unpubl.). The genetics and linkage relationships of these additional loci in pepper is the subject of another report (LOAIZA-FIGUEROA & TANKSLEY, unpubl.).

Analysis. Using the genotypic information for the isozyme loci, allelic frequencies were calculated for each accession and a dendrogram based on NEI's genetic distance (NEI 1972) was developed for the 192 OTUs' (Fig. 4). Other calculated estimates of genetic differentiation total gene diversity within populations (Hs), gene diversity between populations (Dst), inter- to intrapopulational gene diversity ratios (Rst), and coefficient of gene differentiation (Gst) (NEI 1973, 1976).

Results and discussion

Enzyme variation and geographical distribution. A total of 76 alleles representing 20 loci coding for nine enzymes were discerned in this study. The geographical distribution of polymorphic loci is depicted in Fig. 2. The various enzymes and their alleles are reviewed in the following paragraphs.

Aconitase (ACO). Two loci with three alleles each were resolved for this enzyme (Fig. 3 a).

Aco-1. Most of the accessions were fixed for the $Aco\text{-}1^1$ allele. The exception was an accession from La Costa de Jalisco, which was polymorphic for both the $Aco\text{-}1^1$ and $Aco\text{-}1^2$ alleles. $Aco\text{-}1^2$ was the predominant allele in BG 1755 from Michoacan. $Aco\text{-}1^3$ was present in both BG 1755 and BG 3328.

Aco-2. $Aco\text{-}2^1$ was the predominant allele throughout Mexico. BG 1755 and BG 3328 were fixed for the alternate allele $Aco\text{-}2^2$. $Aco\text{-}2^2$ was also detected in four wild accessions from Sonora, Tabasco, La Peninsula de Yucatan, and Las Huastecas. $Aco\text{-}2^3$ was the most common allele in the wild accessions from Sonora and the coast and most elevated parts of Jalisco. $Aco\text{-}2^3$ was also localized, though more restricted, in one accession (BG 1717) from La Peninsula de Yucatan as well as in six wild accessions from southern Tamaulipas northwards to central Nuevo Leon.

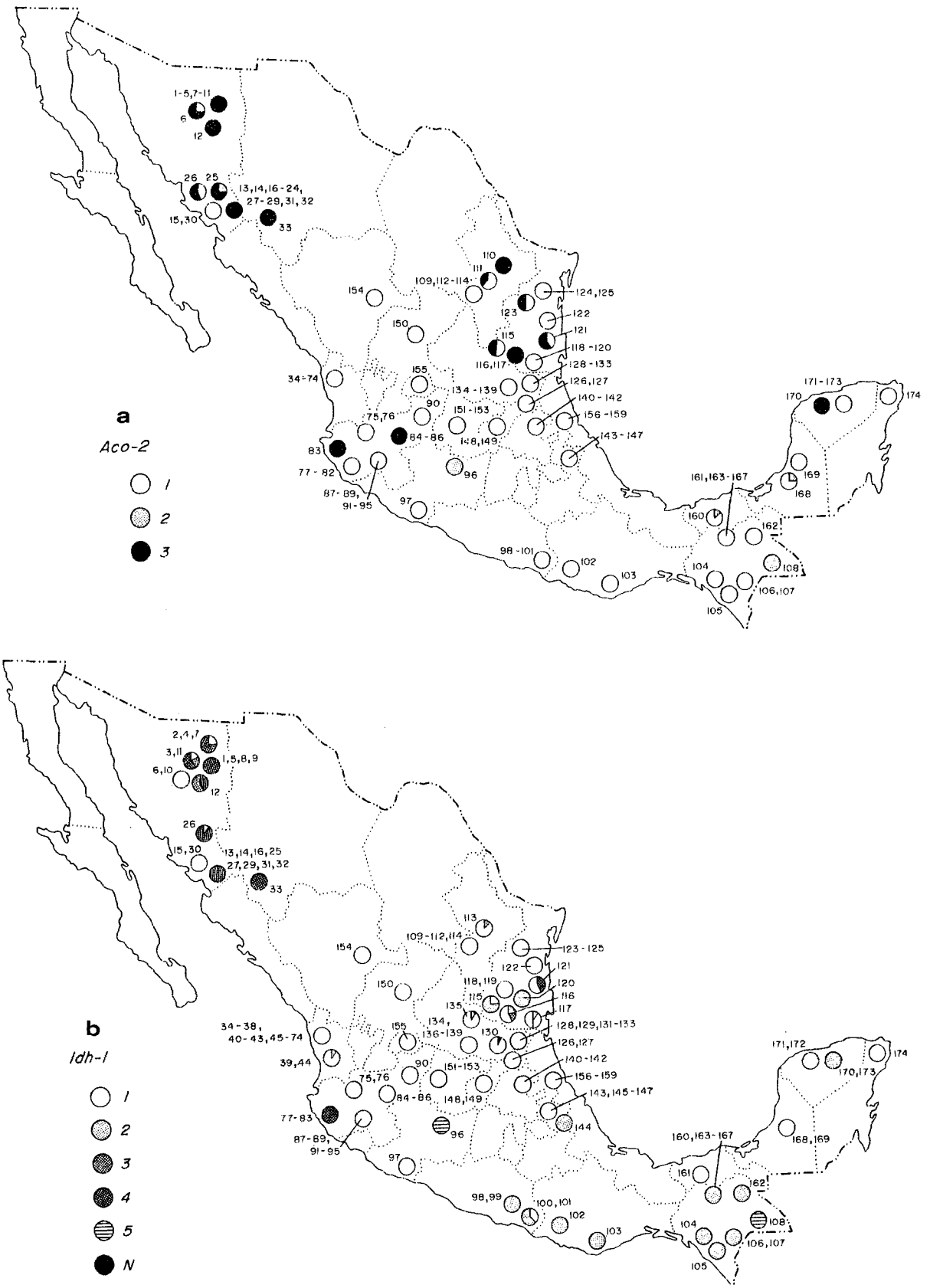
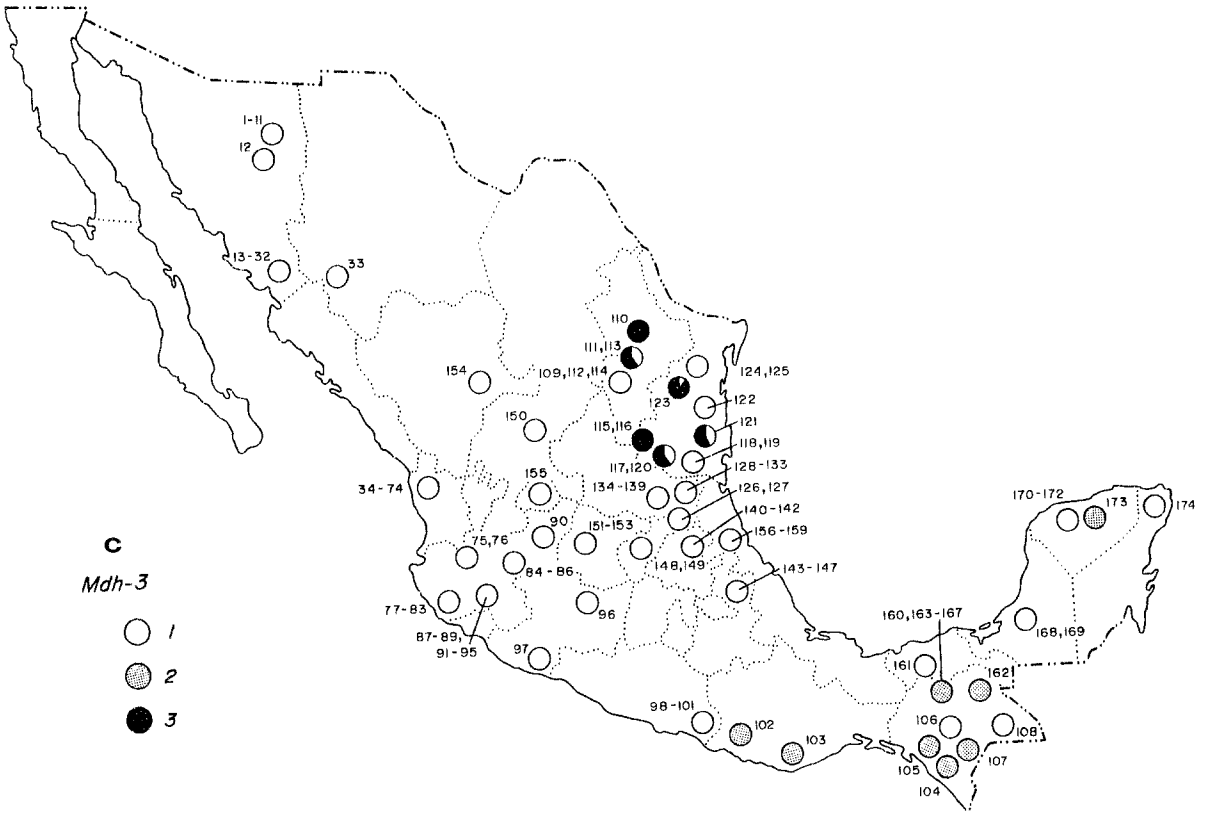


Fig. 2*a—l*. Geographical distribution of alleles at twelve enzyme loci in 174 *Capsicum* accessions from Mexico. Symbols under the enzyme locus represent alleles and those within the map describe frequencies. *a Aco-2; b Idh-1; c Mdh-3; d Pgi-1; e Pgm-1; f Pgm-2; g Pgm-3; h 6-Pgdh-1; i 6-Pgdh-2; j 6-Pgdh-3; k Skdh-1; l Tpi-2*. Because of space limitations on the map, polymorphic populations from a geographical region were depicted by a single symbol, representing the pooled allele frequency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128-133
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151-153
156-159
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84-86
143-147
77-83
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160,163-167
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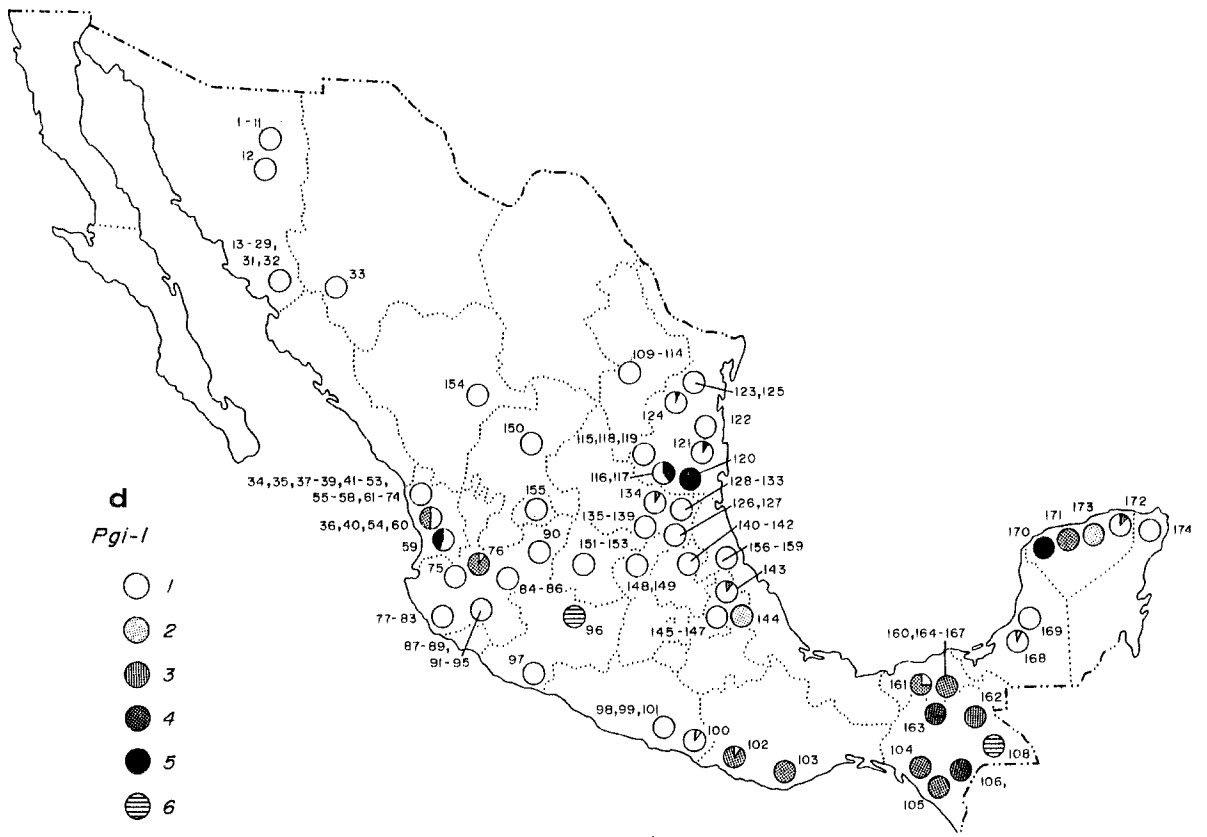
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Pgi-1
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122
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115,118,119
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116,117
128-133
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55-58,61-74
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77-83
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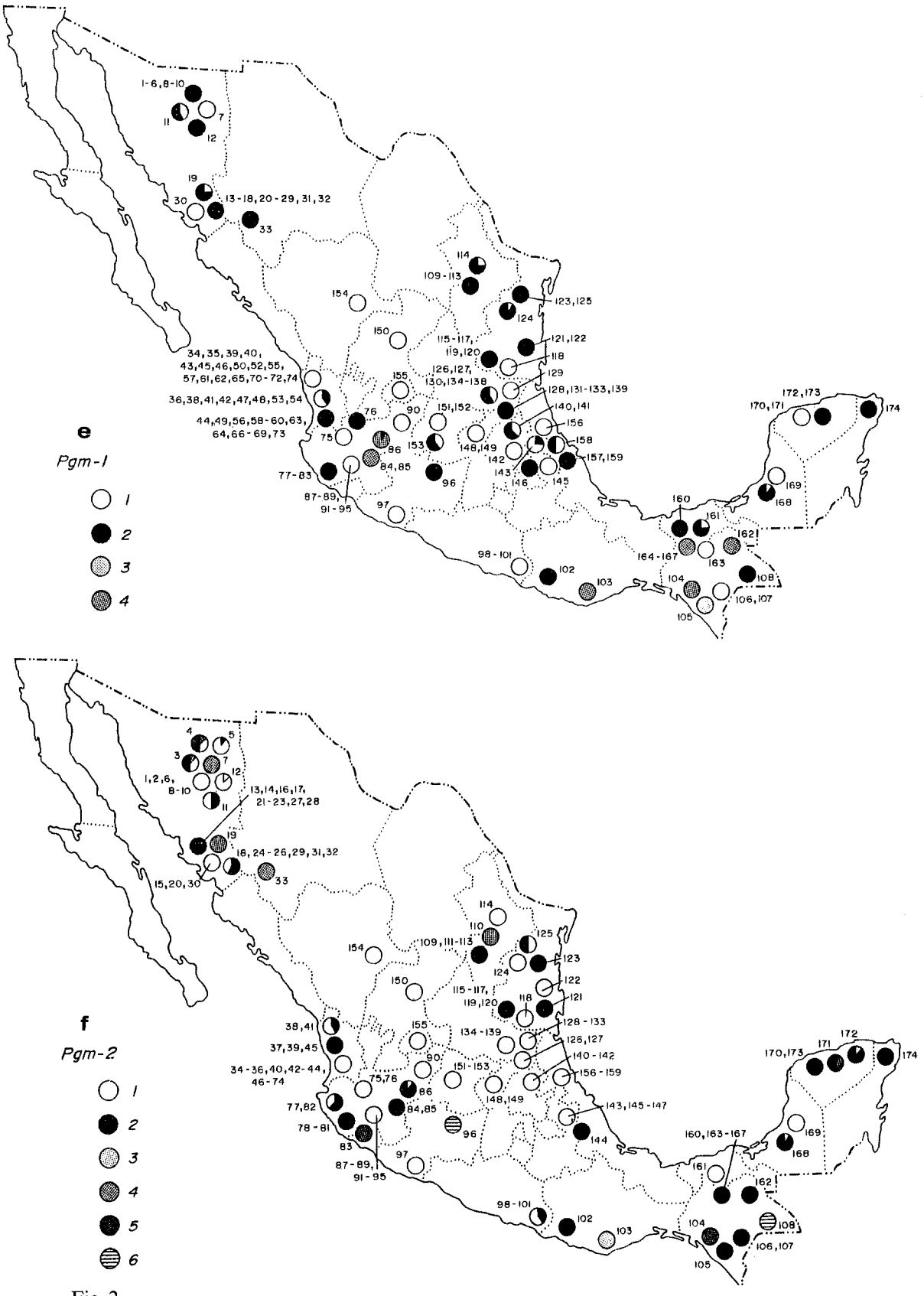
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Pgm-1
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11
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109-113
154
123,125
124
150
115-117,
119,120
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57,61,62,65,70-72,74
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140,141
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156
44,49,56,58-60,63,
64,66-69,73
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84,85
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77-83
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146
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87-89,
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172,173
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164-167
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106,107
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f
Pgm-2
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5
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7
12
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8-10
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87-89,
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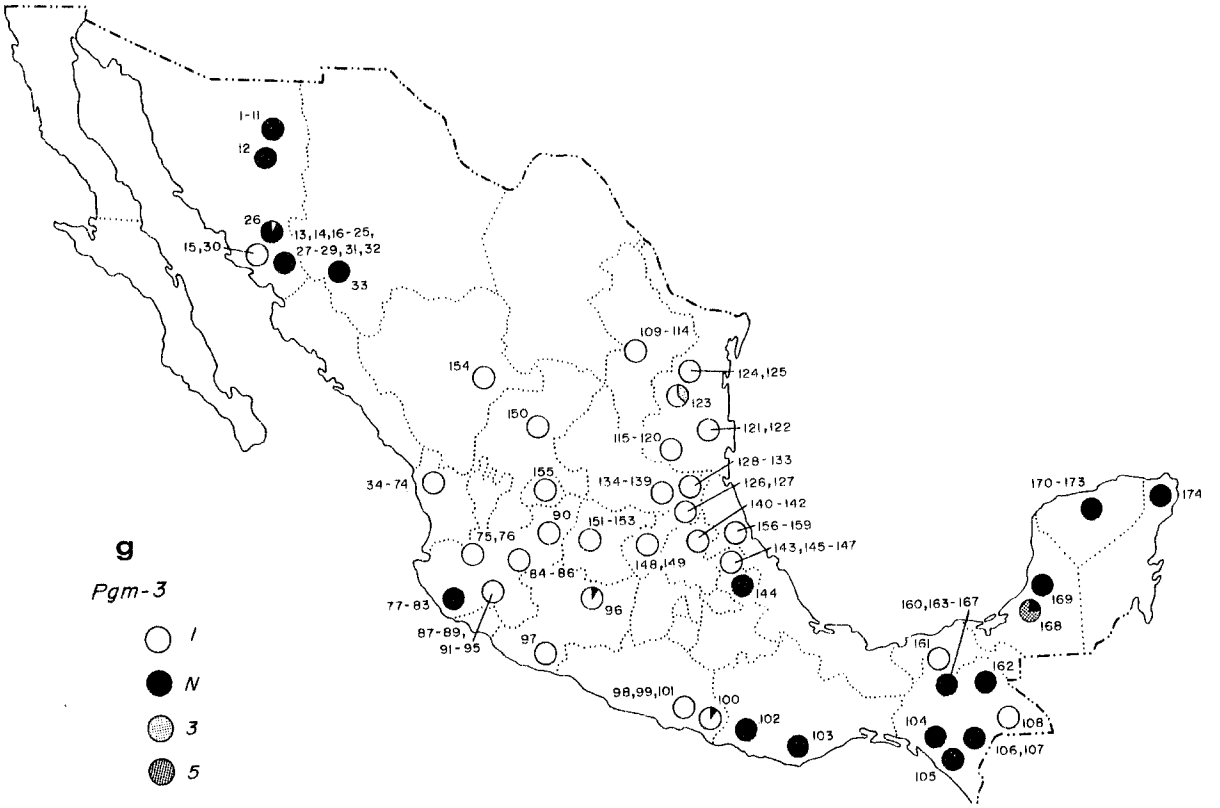
Fig. 2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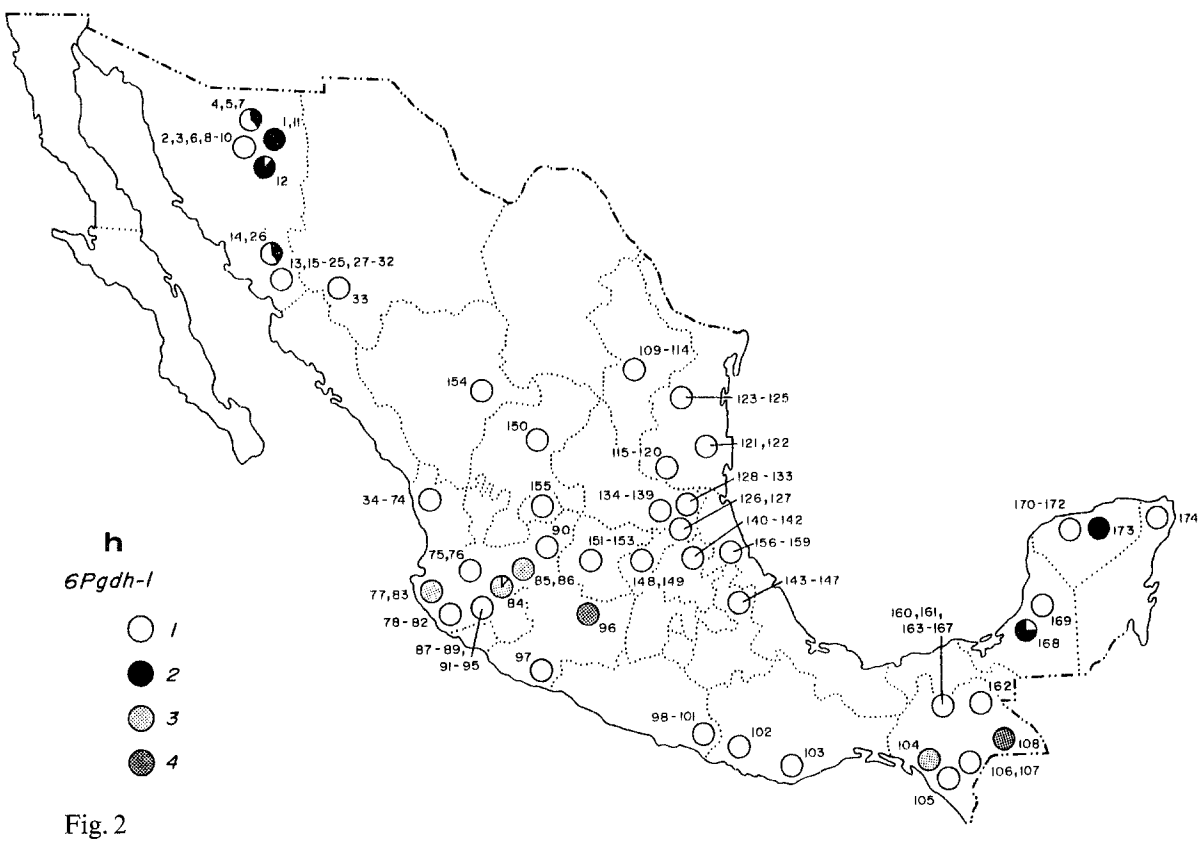
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Fig. 2

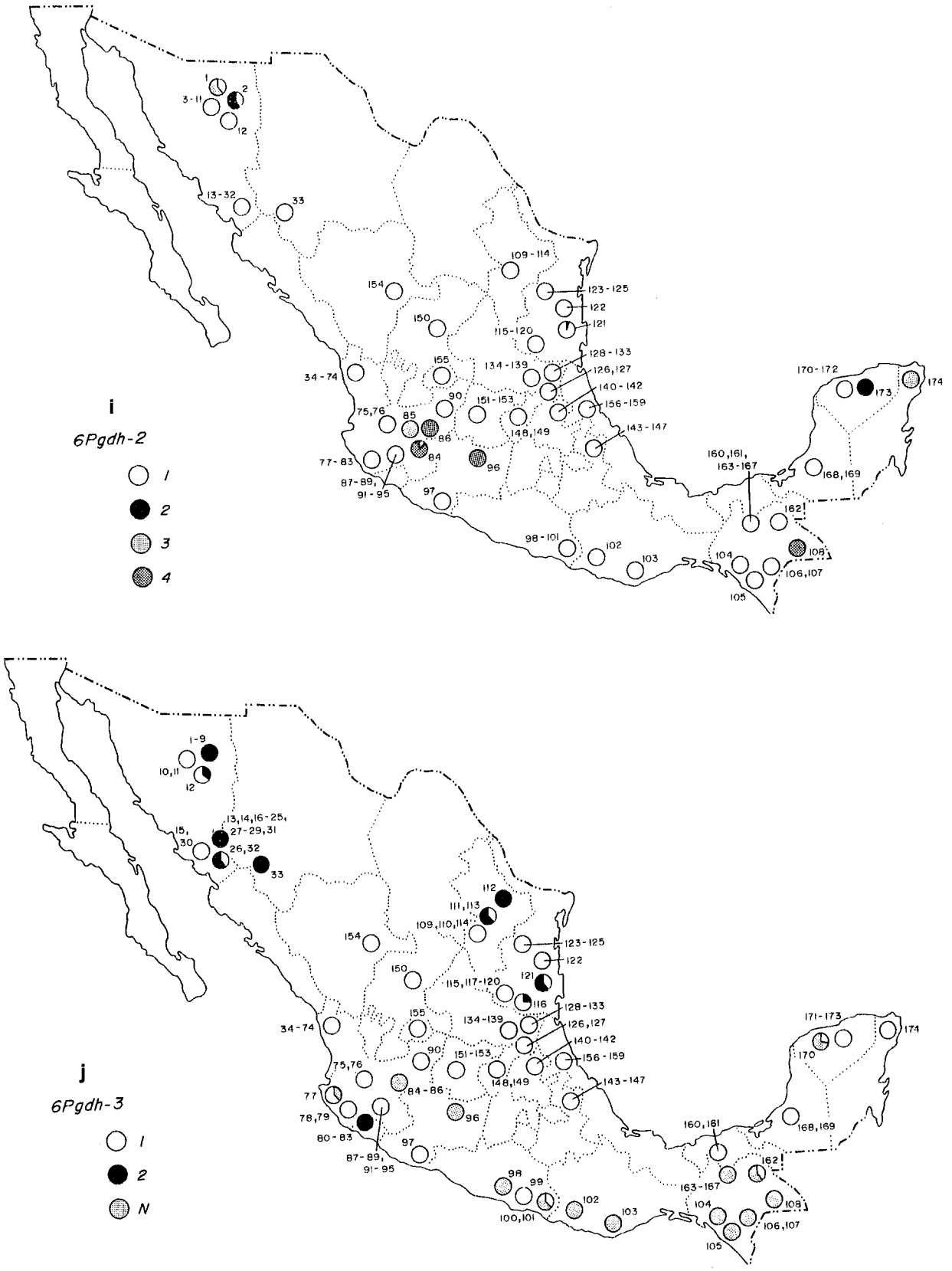
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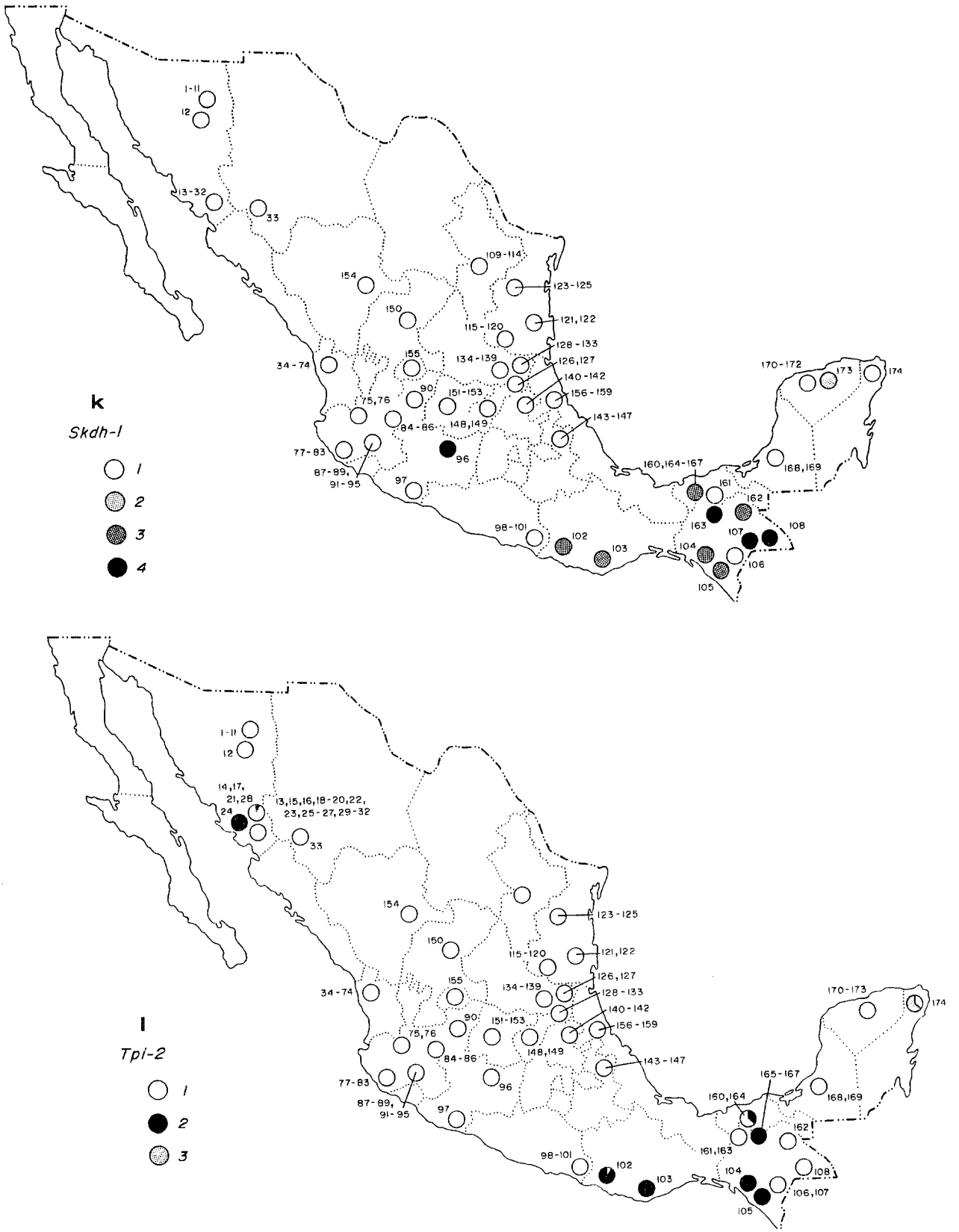
Fig. 2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Skdh-1
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151-153
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168,169
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174
l
Tpi-2
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14,17,
21,28
24
13,15,16,18-20,22,
23,25-27,29-32
165-167
170-173

Fig. 2

Isocitrate dehydrogenase (IDH). One locus with six alleles was found to be responsible for this enzyme (Fig. 3 b). *Idh-1*^{1} represented 66.77% of the total variation in the Mexican accessions and was found in most regions surveyed. *Idh-1*^{4} accounted for 19.06% of the total variation observed. This allele was fixed in all of the accessions from La Costa de Jalisco as well as in most of the accessions from Sonora. *Idh-1*^{2} accounted for another 11.86% of the total variation and was restricted mainly to Guerrero, Oaxaca, Chiapas, and Tabasco.

The other alleles, constituting 2.29% of the total variation, showed regional localizations. *Idh-1*^{3} was observed in six accessions from the northwestern (Sonora) and northeastern (Nuevo Leon and Tamaulipas) ranges. *Idh-1*^{5} was found in three accessions: BG 1812 from southern Tamaulipas; and BG 1755 and BG 3328, which were fixed. Finally, *Idh-1*^{n} (null allele, no activity) was only observed in one accession, BG 1799 from Las Huastecas, with a frequency of 0.071.

Malate dehydrogenase (MDH). Four loci were resolved for this enzyme (Fig. 3 c).

Mdh-1. Three alleles were found for this locus with only two (*Mdh-1*^{1} and *Mdh-1*^{2}) being present in the Mexican accessions. *Mdh-1*^{1} was fixed in all the accessions analyzed, except BG 3235 whose frequency was of 0.33. *Mdh-1*^{2} was found in two accessions, BG 0569 from La Peninsula de Yucatan and BG 3235 from Sonora.

Mdh-2. Of the two alleles resolved for this locus, *Mdh-1* was the most common allele in all regions surveyed. *Mdh-1*^{2} was observed in three accessions from southern to northern Tamaulipas with a frequency varying from 0.10 to 0.5.

Mdh-3. Four alleles for this locus could be distinguished. *Mdh-3*^{1} is distributed in three general regions. The first region comprises Sonora, Nayarit, Jalisco (upper and coastal regions), Michoacan, and Guerrero in which *Mdh-3*^{1} is fixed in all the accessions sampled. The second region is La Peninsula de Yucatan where this allele is again fixed in all but one (BG 0569) of the accessions surveyed. The third region is the eastern range of the genus and, in contrast to the aforementioned areas, the frequency of *Mdh-3*^{1} varied from 0.2 to 1.0. The exceptions for these regions were Tabasco and Chiapas where only two accessions, BG 2802 and BG 3321, where fixed for *Mdh-3*^{1}.

Mdh-3^2 was the predominant allele in accessions from Oaxaca, Chiapas, and Tabasco. *Mdh-3*^{3} was restricted to the region extending from southern to northern Tamaulipas to central Nuevo Leon, where its frequency never fell below 0.5.

Mdh-4. Of the three alleles resolved for this locus, *Mdh-4*^{1} was the most common in all of the Mexican accessions. *Mdh-4*^{2} was confined to four accessions from Mexico, BG 3321 and BG 3324 from Chiapas, as well as BG 1721 and BG 1724 from La Peninsula de Yucatan. *Mdh-4*^{n} (null allele) was fixed in BG 1755 and BG 3328.

Phosphoglucoisomerase (PGI). The zone of activity corresponding to *Pgi-1* (TANKSLEY 1984) was resolved into six alleles (Fig. 3 d). *Pgi-1*^{1} summed up 85.5% of the total variation and was omnipresent in most of the regions studied. *Pgi-1*^{3} was also high in frequency (0.877) and, though dispersed in some other regions, the major concentration was situated in accessions from Guerrero, Oaxaca, Chiapas, and Tabasco. *Pgi-1*^{4} was confined to and fixed in three accessions from Chiapas, BG 2808, BG 3321, and BG 3324. *Pgi-1*^{5} was observed in seven accessions, the major concentration was seen in five accessions from Tamaulipas. *Pgi-1*^{2} was seen in three accessions, BG 0569, BG 1534, and BG 1746. *Pgi-1*^{6} was fixed in BG 1755 and BG 3328.

Phosphoglucomutase (PGM). As discussed by TANKSLEY (1984), the activity of this enzyme is coded by three loci (Fig. 3 e).

Pgm-1. Four alleles were ascertained for this locus. *Pgm-1* was in the highest frequency (0.547) and was the only allele in all but four accessions from Sonora and La Costa de Jalisco. Next in occurrence was $Pgm\text{-}1^1$, accounting for 39.22% of the variation, and observed in the majority of the areas examined. $Pgm\text{-}1^3$ was observed in BG 3318 from Chiapas. $Pgm\text{-}1^4$ was observed in ten accessions; seven from Chiapas and three from Jalisco.

Pgm-2. Six alleles could be distinguished for this locus. $Pgm\text{-}2^1$ accounted for 62.0% of the variation and was observed in most of the regions scanned. $Pgm\text{-}2^2$, with 31.9%, was dispersed through out the range of the genus. With the other alleles, representing 5.9% of the total variation, some regional localizations could be detected. $Pgm\text{-}2^2$ occurred in two accessions, one from Chiapas and the other from La Peninsula de Yucatan. $Pgm\text{-}2^4$ was concentrated in the northwestern (7 accessions) and northeastern (1 accession) ranges. $Pgm\text{-}2^5$ was observed in three accessions each from Michoacan (BG 1755), Chiapas (BG 3317), and La Peninsula de Yucatan (BG 1721). Finally, $Pgm\text{-}2^6$ was observed in BG 1755 and BG 3328.

Pgm-3. Five alleles were resolved for this locus. $Pgm\text{-}3^1$ and $Pgm\text{-}3^n$ (null allele) were the most common. The former was the predominant allele in most of the accessions from Nayarit and Las Huastecas and was fixed in most of the domesticated types. This allele was also detected in three accessions (FL 0003, BG 3189, and BG 3215) from Sonora and one (BG 2802) from Tabasco.

The presence of $Pgm\text{-}3^n$ was found in accessions from four different regions. In Sonora this allele appeared in 31 out of 34 accessions, with frequencies ranging from 0.85 to 1.0. In La Costa de Jalisco it was fixed in all the accessions surveyed as well as in those from Oaxaca, Chiapas, and most of La Peninsula de Yucatan.

The remaining *Pgm-3* alleles were considered rare. $Pgm\text{-}3^3$ was observed in only one accession, BG 1834, from northern Tamaulipas with a frequency of 0.3. $Pgm\text{-}3^5$ was detected in BG 1746 from La Peninsula de Yucatan with frequency of 0.75.

Peroxidase (PRX). Three loci where resolved for this enzyme. The variability observed for this loci was the lowest of any enzyme loci studied.

Prx-1. $Prx\text{-}1^1$ was observed in most of the accessions surveyed, with frequencies ranging from 0.86 to 1.0. $Prx\text{-}1^2$ was resolved in BG 1755 (Michoacan) and BG 1822 (Tamaulipas), with a frequency of 0.38 and 0.019, respectively. $Prx\text{-}1^3$ appeared in BG 1822 with a frequency of 0.019. Finally, $Prx\text{-}1^4$ was observed in two landrace varieties from Las Huastecas, BG 1523 and BG 1534, whose respective frequencies were 0.13 and 1.0.

Prx-2. All populations were fixed for $Prx\text{-}2^1$. Thus, this locus represents the most conservative of all the enzyme loci surveyed.

Prx-3. Most of the accessions (179) analyzed were fixed for $Prx\text{-}3^1$. The remaining twelve accessions were fixed for $Prx\text{-}3^2$. Seven of these collections were localized in the states of Oaxaca, Chiapas, and La Peninsula de Yucatan. The only exception for the distribution of the latter allele is one accession, BG 3217, from Sonora.

6-Phosphogluconate dehydrogenase (6-PGDH). Two loci coding for this enzyme have been previously reported (TANKSLEY 1984). During this project an additional *6-Pgdh* locus, *6-Pgdh-3,* was observed (Fig. 3 f).

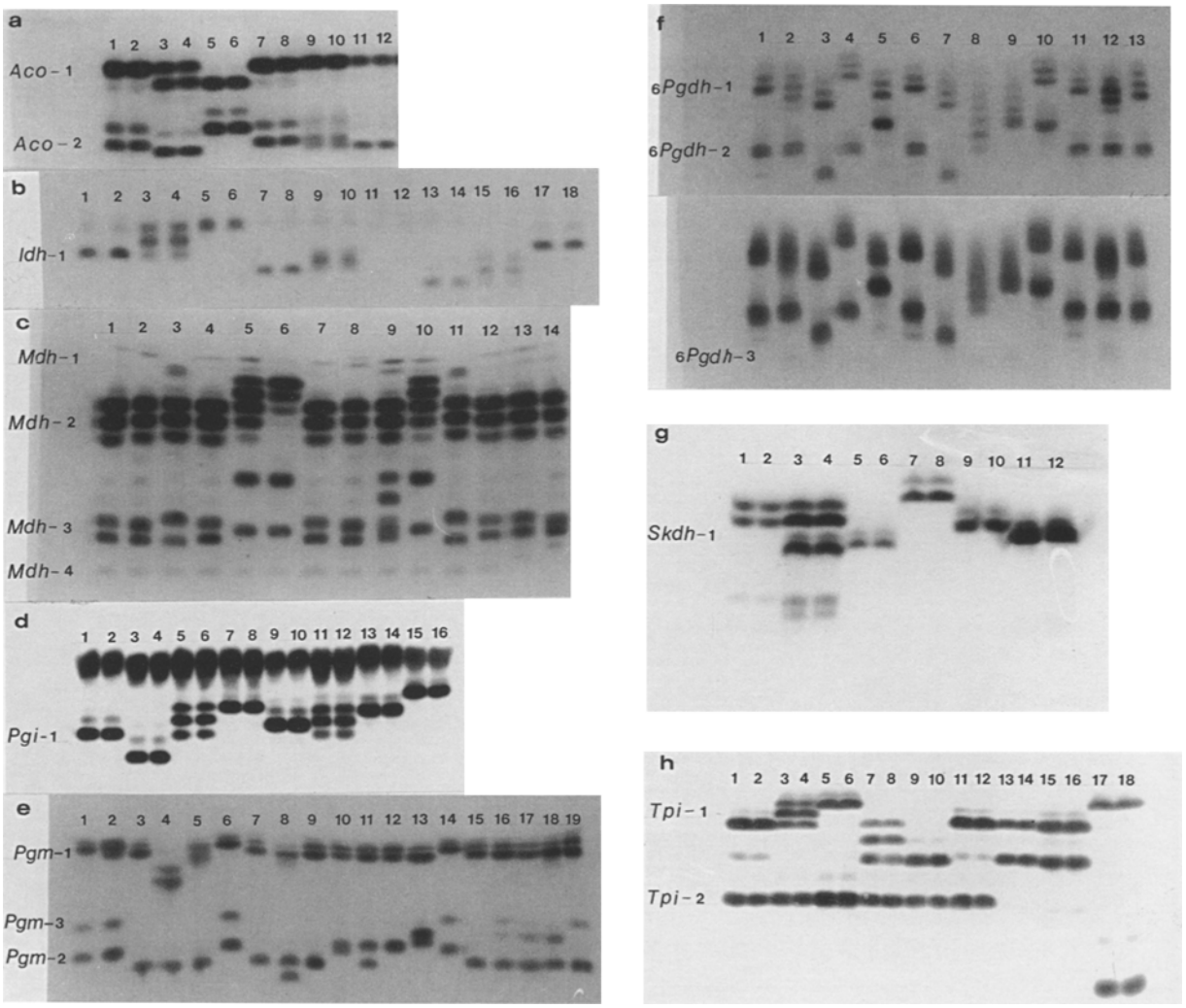

Fig. 3. Phenotypes of alleles at enzyme loci in *Capsicum*. **a** *Aco-1*: *1* and *2* homozygous *1/1; 3* and *4* heterozygous *1/2; 5* and *6* homozygous *2/2*. *Aco-2*: 5 and 6, homozygous *1/1; 7* and *8* heterozygous *1/2;* 9 and 10 heterozygous *1/3; 11* and *12* homozygous *3/3*. **b** *Idh-1*: *1* and *2* homozygous *1/1; 3* and *4* heterozygous *1/2; 5* and *6* homozygous *2/2; 7* and *8* homozygous *3/3; 9* and *10* heterozygous *1/3; 11* and *12* homozygous *n/n; 13* and *14* homozygous *4/4; 15* and *16* heterozygous *1/4; 17* and *18* homozygous *5/5*. **c** *Mdh-1*: *1* homozygous *1/1; 2* homozygous *2/2; 3* homozygous *3/3*. *Mdh-2*: *4* homozygous *1/1; 5* heterozygous *1/2; 6* homozygous *2/2*. *Mdh-3*: *7* homozygous *1/1; 8* homozygous *2/2; 9* heterozygous *1/3; 10* homozygous *3/3; 11* homozygous *4/4*. *Mdh-4*: *12* homozygous *1/1; 13* heterozygous *1/2; 14* homozygous *2/2*. **d** *Pgi-1*: *1* and *2* homozygous *1/1; 3* and *4* homozygous *2/2; 5* and *6* heterozygous *1/3; 7* and *8* homozygous *3/3; 9* and *10* homozygous *4/4; 11* and *12* heterozygous *1/5; 3* and *14* homozygous *5/5; 15* and *16* homozygous *6/6*. **e** *Pgm-1*: *1* homozygous *1/1; 2* heterozygous *1/2; 3* homozygous *2/2; 4* homozygous *3/3; 5* homozygous *4/4*. *Pgm-2*: *6* homozygous *1/1; 7* homozygous *2/2; 8* heterozygous *2/3; 9* homozygous *4/4; 10* heterozygous *1/5; 11* heterozygous *2/5; 12* homozygous *5/5; 13* homozygous *6/6*. *Pgm-3*: *14* homozygous *1/1; 15* homozygous *n/n; 16* heterozygous *1/2; 17* homozygous *3/3; 18* homozygous *4/4; 19* homozygous *5/5*. **f** *6-Pgdh-1*: *1* homozygous *1/1; 2* heterozygous *1/2; 3* homozygous *2/2; 4* homozygous *3/3; 5* homozygous *4/4*. *6-Pgdh-2*: *6* homozygous *1/1; 7* homozygous *2/2; 8* heterozygous *1/3; 9* homozygous *3/3; 10* homozygous *4/4*. *6-Pgdh-3*: *11* homozygous *1/1; 12* homozygous *2/2; 13* homozygous *n/n*. **g** *Skdh-1*: *1* and *2* homozygous *1/1; 3* and *4* heterozygous *1/2; 5* and *6* homozygous *2/2; 7* and *8* homozygous *3/3; 9* and *10* homozygous *4/4; 11* and *12* homozygous *5/5*. **h** *Tpi-1*: *1* and *2* homozygous *1/1; 3* and *4* heterozygous *1/2; 5* and *6* homozygous *2/2; 7* and *8* heterozygous *1/3; 9* and *10* homozygous *3/3*. *Tpi-2*: *11* and *12* homozygous *1/1; 13, 14, 15,* and *16* homozygous *2/2; 17* and *18* homozygous *3/3*

6-Pgdh-1. Of the four alleles discovered for this locus, *6-Pgdh-1*^{1} represents the most common allele. It appeared fixed in almost every region, except for Sonora where its frequency ranged from 0.15 to 1.0. *6-Pgdh-1*^{2} was localized in eight accessions from Sonora with a frequency ranging from 0.10 to 1.0. The only exception for this geographical distribution was BG 1746 and BG 0569 from la Peninsula de Yucatan. The former had a frequency of 0.75 for *6-Pgdh-1*^{2}, the latter, 1.0. *6-Pgdh-1*^{3} was found in four collections from Jalisco and one from Chiapas. *6-Pgdh-1*^{4} was typical in BG 1755 and BG 3328.

6-Pgdh-2. Of the four alleles resolved for this locus, *6-Pgdh-2*^{1} was present in 172 of the Mexican accessions surveyed. *6-Pgdh-2*^{2} was observed in three accessions: BG 3235 from Sonora, BG 1822 from southern Tamaulipas, and BG 0569 from La Peninsula de Yucatan. The same pattern was observed for *6-Pgdh-2*^{3}, which was present in three collections (BG 3238, BG 3576, and BG 1725), each from a different region. *6-Pgdh-2*^{4} was distinctive in BG 1755 and BG 3328.

6-Pgdh-3. Of the three alleles resolved for this locus, *6-Pgdh-3*^{1} was present in almost every region. *6-Pgdh-3*^{2} and *6-Pgdh-3*^{n} (null allele) showed a geographical trend. *6-Pgdh-3* was quite common in Sonora (northwestern Mexico) and also detected in four accessions (BG 1811, BG 1822, BG 1852, and BG 1854) from the northeastern distribution of the genus. The exception to this geographical trend was four collections (BG 1697, BG 1699, BG 1700, and BG 1702) from La Costa de Jalisco (western Mexico). The presence of *6-Pgdh-3*^{n} was mainly confind to accessions from Oaxaca and Chiapas, except for four accessions (BG 1690, BG 3575, BG 3576, and BG 3577) from Jalisco and one (BG 1717) from La Peninsula de Yucatan.

Shikimate dehydrogenase (SKDH). Of the five alleles resolved for the single locus coding for this enzyme (Fig. 3 g), four were present in the Mexican accessions. *Skdh-1* was detected in almost every region. Regional localization and fixation were characteristics for the remaining zymotypes. *Skdh-1*^{2} was found in BG 1534 and BG 0569 from Las Huastecas and La Peninsula de Yucatan, respectively. *Skdh-1*^{3} was observed in ten out of fifteen collections surveyed from Oaxaca, Chiapas, and Tabasco. *Skdh-1*^{4} was present in BG 2808, BG 3324, and BG 3328, from Chiapas, as well as BG 1755 from Michoacan.

Triose phosphate isomerase (TPI). Two loci were found coding for this enzyme (Fig. 3 h). The most anodal band corresponds to *Tpi-1* whereas the most cathodal one to *Tpi-2*.

Tpi-1. *Tpi-1* was present in every collection surveyed, with a frequency ranging from 0.16 to 1.0. *Tpi-1*^{2} was observed in one accession, BG 1822 from southern Tamaulipas, with a frequency of 0.03. *Tpi-1*^{3} was present in BG 1657 and three collections (BG 1724, BG 1725, and BG 1746) from La Peninsula de Yucatan. *Tpi-1*^{4} was restricted to three accessions (BG 3213, BG 3188, and BG 2800) with a frequency ranging from 0.50 to 0.54. *Tpi-1*^{5} was only observed in BG 3230 from Sonora.

Tpi-2. *Tpi-2*^{1} was present in all but seven of the Mexican collections studied. *Tpi-2*^{2} was observed in two different regions. In Sonora the frequency of *Tpi-2*^{2} varied from 0.10 to 1.0 in five accessions whereas in Oaxaca and Chiapas it ranged from 0.12 to 1.0 in nine collections studied. *Tpi-2*^{3} was confined to La Peninsula de Yucatan, with a frequency of 0.66 in BG 1725.

Table 2. Total gene diversity (HT), gene diversity within populations (Hs), total gene diversity between populations (Dst), inter- to intrapopulational gene diversity ratio (Rst), and coefficient of gene differentiation (Gst) for three categories of *Capsicum*. Those accessions on which either a wild, semicultivated, or cultivated category was known were included in these estimations of gene diversity

Category	No. of access.	No. of loci	HT	Hs	Dst	Rst	Cst
Cultivated	50	20	0.176	0.012	0.163	13.346	0.930
Semicultivated	42	20	0.077	0.007	0.070	9.048	0.900
Wild	71	20	0.282	0.025	0.256	10.040	0.909

Gene diversity analysis. Gene diversity analysis, defined as the frequency of heterozygotes expected under Hardy-Weinberg equilibrium, measures the partitioning of genetic variation within and among populations (NEI 1973, 1977). Estimates of total gene diversity, gene diversity within populations, total gene diversity between populations, inter- to intrapopulational gene diversity ratio, and coefficient of gene differentiation are given in Table 2. The best estimate of gene diversity is obtained when a large number of loci is surveyed (NEI 1978). AYALA (1982) indicated that estimates of gene diversity change little as the number of loci exceeds 20. Therefore, the total number of loci, 20, ascertained in our study may give a representative value for these estimates.

The total gene diversity (HT) for domesticated, semidomesticated and wild *Capsicum* was 0.176, 0.077, and 0.282, respectively. These values represent the average heterozygosity expected if all populations were pooled together and mated randomly (NEI 1973). Following NEI's approach for the study of genetic differentiation of population (NEI 1977), HT for every category was partitioned into intrasubpopulational and intersubpopulational components. In other words, this method allowed the estimation of inter- and intrasubpopulational genic variations with respect to the entire genome as well as a model of the genetic structure of populations (NEI 1977) of the genus *Capsicum* in Mexico.

The intrasubpopulational gene diversities (Hs) in domesticated, semidomesticated, and wild accessions were 0.012, 0.007, and 0.025, respectively. These estimates represent the average expected heterozygosity within each population (Table 3). Hence, in terms of genetic variability, the most variable populations were the wild ones, followed by the domesticated, and semidomesticated types. The low level of expected heterozygosity indicates that the genetic structure of populations from all three categories mostly consists of similar genotypes.

The low level of genetic variation present in the semidomesticated accessions indicates the presence of bottlenecks, or drastically reduced population sizes, during the history of the population. As was mentioned previously, these accessions came from small family gardens and in many cases may have derived from single plants selected in the wild. PICKERSGILL & HEISER (1976) pointed out that small gardens place a severe limit on space and number of individuals in an area. Thus rare alleles and rare combinations can be lost.

The intersubpopulational gene diversity (Dst) were 0.256 for wild types, 0.163 for domesticated accessions, and 0.070 for semidomesticated collections. Using Hs and Dst estimates, inter- to intrasubpopulational gene diversity ratios (Rst) were

Table 3. Mean heterozygosity in wild, semicultivated, and cultivated populations of *Capsicum*. Those accessions on which either a wild, semicultivated, or cultivated category was known were included in this estimation. – *a C. chacoense; b* and *c C. praetermisum; d C. baccatum* var. *baccatum*; *e* and *f C. pubescens*; *g, j,* and *m C. chinense*; *h C. baccatum* var. *pendulum; i* and *k C. frutescens; l C. annuum* var. *annuum*

Access.	Mean	Access.	Mean	Access.	Mean	Access.	Mean
Wild							
BG 1697	0.000	BG 1809	0.044	BG 3186	0.014	BG 3190	0.038
BG 3213	0.025	BG 3230	0.030	BG 3321	0.000	BG 3476	0.000
BG 3575	0.025	FL 0001	0.033	FL 0002	0.000	BG 3577	0.018
BG 1699	0.000	BG 1702	0.000	BG 1724	0.028	BG 1725	0.036
BG 1811	0.065	BG 1817	0.016	BG 1834	0.055	BG 1852	0.072
BG 1854	0.036	BG 1855	0.019	BG 2808	0.000	BG 2814	0.014
BG 2815	0.000	BG 2816	0.000	BG 3187	0.019	BG 3188	0.025
BG 3191	0.019	BG 3194	0.000	BG 3195	0.000	BG 3207	0.015
BG 3209	0.000	BG 3211	0.023	BG 3212	0.009	BG 3217	0.023
BG 3220	0.000	BG 3228	0.000	BG 3229	0.000	BG 3231	0.032
BG 3235	0.070	BG 3313	0.000	BG 3317	0.000	BG 3576	0.000
FL 0007[a]	0.000	FL 0008[b]	0.000	FL 0009[c]	0.025	FL 0010[d]	0.000
BG 1690	0.047	BG 1700	0.045	BG 1746	0.091	BG 1812	0.098
BG 1814	0.000	BG 1822	0.133	BG 1844	0.000	BG 2800	0.047
BG 2805	0.025	BG 2811	0.023	BG 3189	0.098	BG 3233	0.040
BG 3326	0.033	BG 1747	0.000	BG 1850	0.000	BG 2688	0.000
BG 2801	0.022	BG 3210	0.019	BG 3222	0.070	BG 3225	0.077
BG 3227	0.000	BG 3232	0.054	BG 3238	0.023		
Semicultivated							
BG 0998	0.000	BG 1519	0.019	BG 1638	0.000	BG 1645	0.000
BG 1658	0.000	BG 1662	0.000	BG 1668	0.000	BG 1670	0.000
BG 1801	0.000	BG 1804	0.000	BG 1823	0.000	BG 2725	0.000
BG 2727	0.000	BG 2729	0.000	BG 2732	0.022	BG 2747	0.005
BG 2756	0.007	BG 2769	0.023	BG 2797	0.000	FL 0003	0.000
BG 1616	0.000	BG 1628	0.000	BG 1642	0.000	BG 1669	0.035
BG 1671	0.004	BG 1717	0.021	BG 1721	0.049	BG 1795	0.000
BG 1813	0.025	BG 1635	0.000	BG 1650	0.024	BG 1787	0.018
BG 1799	0.032	BG 2676	0.002	BG 2737	0.000	BG 2794	0.041
BG 3215	0.000	BG 3302	0.000	BG 3318	0.000	BG 0003	0.000
BG 1798	0.000	BG 1800	0.000				
Cultivated							
BG 1534	0.000	BG 1535	0.000	BG 1536	0.000	BG 1506	0.014
BG 1507	0.024	BG 2528	0.000	BG 3415	0.000	BG 3444	0.025
FL 0004	0.000	FL 0005	0.000	BG 0952	0.000	BG 1755[e]	0.022
BG 3328[f]	0.000	BG 0569	0.000	BG 1520	0.024	BG 1521	0.000
BG 1837	0.034	BG 3309	0.034	BG 0101	0.039	BG 3306	0.025
FL 0011[h]	0.000	FL 0012[i]	0.000	FL 0013[j]	0.077	FL 0014[k]	0.000
BG 1511	0.037	BG 1840	0.025	BG 3308	0.080	BG 3312	0.024
BG 1789	0.025	BG 3307	0.025	BG 0038	0.000	BG 0039	0.000
BG 0050	0.000	BG 0639	0.024	BG 0912	0.000	BG 0924	0.000
BG 0939	0.000	BG 0947	0.000	BG 1523	0.000	BG 1606	0.000
BG 1875	0.000	BG 2529	0.000	BG 3241	0.000	BG 3291	0.000
BG 3295	0.000	BG 3355	0.000	BG 3425	0.000	BG 3457	0.000
CA 133[l]	0.000	CA 4[m]	0.000				

calculated for each category. These Rst values were 13.346 in domesticated, 10.040 in wild, and 9.048 in semidomesticated accessions. The high Rst value in domesticated accessions can be due to the fact that six different species participated in the total gene diversity ratios, whereas only four and at least one species participated in those of the wild and semidomesticated accessions, respectively (Table 3). In general, these gene diversity ratios suggest that gene differentiation has occurred in each of the three categories, domesticated, semidomesticated, and wild. To test this hypothesis, coefficients of gene differentiation were calculated for each group.

The coefficients of gene differentiation (Gst), which estimate the proportion of genetic diversity between populations (NEI 1976), were 0.930, 0.900, and 0.909 for domesticated, semidomesticated, and wild accessions, respectively. WRIGHT (1978) noted that Gst is a weighted average of the fixation index, Fst, which is the reduction in heterozygosity of a population due to random genetic drift. Fst has a theoretical minimum of zero (alleles in common) and a theoretical maximum of one (fixation for alternative alleles). Using HARTL's (1981) qualitative interpretations of the coefficients of gene differentiation, the results of this test suggest that the three collection categories have undergone high amounts of genetic divergence among their populations. That is, of the total variation found within these categories, about 90% is due to genetic differences among collections and roughly 10% is ascribable to alleles in common.

Evolutionary relationships. The evolutionary relationships of populations from the genus *Capsicum* in Mexico are expressed in terms of standard genetic distance between two populations, which measures the accumulated allelic substitutions per locus among the pair of populations (NEI 1972). The mean standard genetic distance in domesticated, semidomesticated, and wild accessions were 0.2234 ($S^2 = 0.0841$), 0.0836 ($S^2 = 0.0187$), and 0.3344 ($S^2 = 0.0529$), respectively. Although the domesticated category was composed of six recognized species, its genetic distance was lower than in the wild category, in which four recognized species were included.

One way to find evolutionary relationships in a group of taxa is through inspection of the clusters produced by a clustering technique such as the unweighted pair group method, UWPGM (SNEATH & SOKAL 1973), applied to the matrix of genetic distances. The result of the clustering technique is portrayed on a dendrogram. NEI (1978) pointed out that the reliability of the clusters of the dendrogram depends on the difference of genetic distance among populations, their level of

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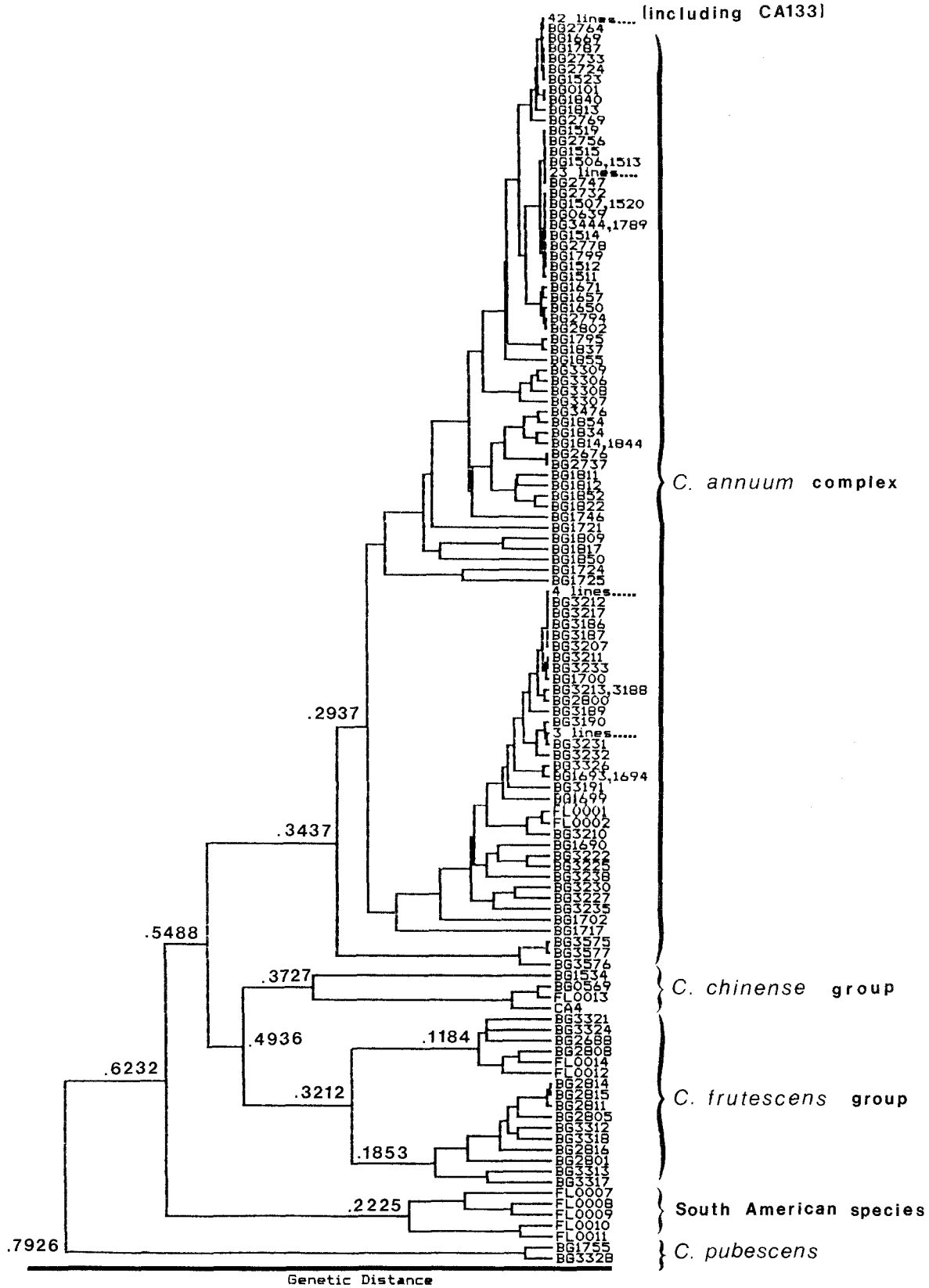
Fig. 4. NEI genetic distance values among different clusters of *Capsicum* accessions. Populations included in the dendrogram under the names "42 lines", "23 lines", "4 lines", and "3 lines" had the same phenotype for the 20 loci described in this study: 42 lines (BG 0998, BG 1535, BG 1623, BG 1668, BG 1670, BG 2725, BG 2797, BG 2528, BG 3415, FL 0004, FL 0005, BG 0952, BG 1521, BG 1642, BG 3302, BG 0003, BG 1622, BG 1624, BG 1648, BG 1649, BG 1661, BG 1747, BG 1798, BG 2728, BG 2736, BG 2750, BG 2796, BG 0038, BG 0039, BG 0050, BG 0912, BG 0924, BG 0939, BG 0947, BG 1606, BG 1875, BG 2529, BG 3241, BG 3291, BG 3295, BG 3355, CA 133); 23 lines (BG 1536, BG 1638, BG 1645, BG 1658, BG 1662, BG 1801, BG 1804, BG 1823, BG 2727, BG 2729, FL 0003, BG 1616, BG 1628, BG 1635, BG 3215, BG 1516, BG 1617, BG 1629, BG 1644, BG 1800, BG 2786, BG 3425, BG 3457); 4 lines (BG 1697, BG 3194, BG 3195, BG 3220); 3 lines (BG 3209, BG 3228, BG 3229)


42 lines..... (including CA133)
BG2764
BG1669
BG1787
BG2733
BG2724
BG1523
BG0101
BG1840
BG1813
BG2749
BG1519
BG2756
BG1515
BG1506,1513
23 lines.....
BG2747
BG2732
BG1507,1520
BG0639
BG3444,1789
BG1514
BG2778
BG1799
BG1512
BG1511
BG1671
BG1657
BG1650
BG2724
BG2802
BG1795
BG1837
BG1855
BG3309
BG3306
BG3308
BG3307
BG3476
BG1854
BG1834
BG1814,1844
BG2676
BG2737
BG1811
BG1812
BG1852
BG1922
BG1746
BG1721
BG1809
BG1817
BG1850
BG1724
BG1725
4 lines.....
BG3212
BG3217
BG3186
BG3187
BG3207
BG3211
BG3233
BG1700
BG3213,3188
BG2800
BG3189
BG3190
3 lines.....
BG3231
BG3232
BG3326
BG1693,1694
BG3191
BG1696
FL0001
FL0002
BG3210
BG1690
BG3222
BG3225
BG3238
BG3230
BG3227
BG3235
BG1702
BG1717
BG3575
BG3577
BG3576
BG1534
BG0569
FL0013
CA4
BG3321
BG3324
BG2688
BG2808
FL0014
FL0012
BG2814
BG2815
BG2811
BG2805
BG3312
BG3318
BG2816
BG2801
BG3313
BG3317
FL0007
FL0008
FL0009
FL0010
FL0011
BG1755
BG3328
.2937
.3437
.5488
.3727
.4936
.1184
.6232
.3212
.1853
.2225
.7926
C. annuum complex
C. chinense group
C. frutescens group
South American species
C. pubescens
Genetic Distance

heterozygosity, the sample size, and and the number of loci surveyed. The data presented here sufficiently fill all four requirements.

Three major groups can be seen in the dendrogram in Fig. 4. The first group is composed of BG 1755 and BG 3328, two *C. pubescens* accessions, which are divergent from the other accessions by allelic substitutions at 79% of the loci. The small genetic distance (D = 0.0483) between the two accessions in this group is due to differences in allelic frequencies at the *Aco-1, Pgm-3,* and *Prx-1* loci.

The second division is formed by the S. American species *C. chacoense* (FL 0007), *C. praetermisum* (FL 0008 and FL 0009), and domesticated and wild *C. baccatum* (FL 0010 and FL 0011). The first two species diverged from each other by a genetic distance of 0.1400 and both diverged from *C. baccatum* by a genetic distance of 0.2225. The wild and domesticated *baccatum* were poorly differentiated (D = 0.0483). The evolution among these taxa has already been discussed by MCLEOD & al. (1979) and the data presented here roughly coincide with their findings.

The third division is formed by the complex *C. annuum-frutescens-chinense* of domesticated, semidomesticated, and wild forms. The largest mean genetic distance found among clusters of this complex was D = 0.5488. Two main subdivisions can be ascertained which correlate with geographical and morphological differentiation, and the presence or absence of *Pgm-3,* which apparently resulted from a *Pgm-2* duplication (TANKSLEY 1984).

Capsicum chinense (CA 4 and FL 0013) and *C. frutescens* (FL 0012 and FL 0014) formed the first subdivision, as well as all the collections from Oaxaca, Chiapas, and Tabasco. *Capsicum chinense* and *C. frutescens* are not members of a single group (D = 0.4936), but *C. chinense* and *C. frutescens* groups can be discerned. Thirteen out of fourteen collections from southern Mexico clustered in the *C. frutescens* group and none of them clustered in the *C. chinense* group. Three of those collections, BG 2808, BG 3321, and BG 3324, were closely related, in roughly 12% allelic substitutions, to the two *C. frutescens* accessions (FL 0012 and FL 0014) used in this study. The accession BG 3324 was the only one showing calyx constriction. The remaining ten accessions diverged in approximately 32% allelic substitutions, and it can be noted that some divergence (D = 0.1853) has occurred between them. Other features of these accessions are their greenish corolla and the lack of the *Pgm-3* locus. Two cultivated accessions clustered in the *C. chinense* group, and one, BG 0569 from La Peninsula de Yucatan, was closely related to the control *C. chinense* (CA 4) used in this study. The other accession, BG 1534 (Puebla), even though not closely related (D = 0.3727), had alleles in common with CA 4 in 14 out of 20 loci. The accession BG 1534 was white flowered and did not show a calyx constriction.

The second group (named as the *C. annuum* complex because the other control, CA 133, is included here) is also highly heterogeneous Three clusters can be identified. The first cluster is produced by BG 3575, BG 3576, and BG 3577. These accessions represent a group of wild peppers coming from regions of high altitude (1455 m) in Jalisco, possessing the *Pgm-3* gene and a greenish corolla. These three accessions were the only non-pungent ones from all the accessions analyzed.

The second and third clusters diverged in approximately 29% allelic substitutions. The former is made up by all the wild accessions from La Costa de Jalisco (western Mexico) to Sonora (northwestern Mexico). All of these collections have

a greenish flower and lack the *Pgm-3* duplication. The only exception to this trend is BG 1717 from La Peninsula de Yucatan. It is a white-flowered population, however it still lacks the *Pgm-3* duplication.

The third cluster represents all of the wild, semidomesticated and domesticated collections from eastern Mexico. In addition, it included the domesticated types from all over the country as well as the semidomesticated and domesticated forms concentrated in Nayarit, western Mexico. Its divergence from the other clusters is shown by the fact that this group is white-flowered (except BG 1535, a purple-flowered semicultivated accession) and possesses the *Pgm-3* duplication. Other exceptions are BG 1721, BG 1724, BG 1725, BG 1746, and BG 1747 from La Peninsula de Yucatan. Although these collections are white-flowered, three of them did no show the *Pgm-3* duplication. It is also noteworthy that three semidomesticated accessions, BG 3215 and FL 0003 from Sonora and BG 2802 from Tabasco, are in this group. The former were collected from populations in the wild; the latter was introduced from eastern Mexico to be sold in a market place in southern Mexico (LABORDE, unpubl.).

Two points on the evolution of the genus *Capsicum* in Mexico can be addressed from the data presented: (1) relationships of the Mexican *Capsicum* to other previously defined *Capsicum* species; and (2) region of domestication of *C. annuum*.

Using the controls CA 4 and CA 133 as well as the species from outside Mexico as references, the domesticated species in Mexico are found to include three species: *C. pubescens, C. chinense,* and *C. annuum* var. *annuum*. Two accessions, BG 1755 and BG 3328, belong to the first species, and both exhibited the morphological characteristics of the species, including purple flowers and black seeds (Genetic Resources of *Capsicum* 1983, HEISER & SMITH 1948). Two accessions, BG 0569 and BG 1534, are identified as *C. chinense*. Only BG 0569 showed the key morphology of the species, such as calyx constriction and greenish corolla (SMITH & HEISER 1957, Genetic Resources of *Capsicum* 1983) as found in the control CA 4. The remaining domesticated accessions can be classified as *C. annuum* var. *annuum* because of their close relationship with the CA 133 control. Thus, these results agree with the classification cited elsewhere (Genetic Resources of *Capsicum* 1983, LABORDE & POZO CAMPODONICO 1984).

The semidomesticated and wild accessions were previously classified as one variety in *C. annuum, C. annuum* var. *glabriusculum* (Genetic Resources of *Capsicum* 1983). According to the genetic distance values in Fig. 4, major genetic differences exist among the accessions, making possible the identification of two species: *C. annuum* var. *glabriusculum* and *C. frutescens*. We should note that a general taxonomic missunderstanding is wide spread. "Bird peppers", "piquines", or the numerous vernacular names the wild small peppers are called can be *frutescens* or *annuum*. The results of this study demonstrate sharp geographic and genetic differentiation between these species in Mexico; *C. frutescens* was collected exclusively in the southeastern states of Oaxaca, Chiapas, and Tabasco. Semidomesticated and wild accessions from the rest of the country were closely affiliated with *C. annuum*.

The geographical distribution pattern of the wild forms allows further insights into the evolution of *Capsicum* in Mexico. Genetic distance values between clusters of geographic populations in the dendrogram suggest that genetic differentiation is correlated with geographic isolation and is consistent with studies of other organisms (AYALA & al. 1974). Such a model is observed in allopatric populations

of *C. annuum* var. *glabriusculum*. The northeastern and northwestern ranges of this species are as far as 900 km distant from one another and are separated by an arid region known as La Altiplanicie Mexicana, in which this species is not distributed. This isolation seems to have persisted for a long time and perhaps it has allowed little or no migration between those geographic populations. As a consequence, genetic differentiation has occurred at a rate of 29 allelic substitutions per 100 loci. A similar model of differentiation can be applied to wild populations of the *C. frutescens* group. Even though these populations are not so well separated geographically as those of *C. glabriusculum*, they have evolved into two subgroups genetically differentiated by approximately 32% allelic substitutions.

NEI (1976) computed genetic distance values in various organisms, including rodents, lizards, fish, and *Drosophila,* and suggested that genetic distance values between subspecies range from 0.02 to 0.20. AYALA & al. (1974), working with the *Drosophila willistoni* group, suggested that, on the average, 23 alleleic substitutions per every 100 loci can be considered the amount of genetic differentiation that occurred between subspecies in this group. These values are comparable in magnitude with genetic distances found in the *C. annuum* complex and the *C. frutescens* group.

Nevertheless, before any conclusions can be drawn on recognizing subspecies in those two taxa, further analysis, such as karyotype studies and breeding relationships between geographical populations, should be made to support the classification of subspecies within the genus *Capsicum* in Mexico. Thus far, this substitution of alleles constitutes a good argument against the proposal that these species form an allozymically indistinguishable association or a single polytypic species (MCLEOD 1977, JENSEN & al. 1979, MCLEOD & al. 1979); and preliminary morphological evaluation (LOAIZA-FIGUEROA & TANKSLEY, unpubl.) suggests that accessions from any given geographical region of Mexico are morphologically distinguishable. Moreover, it is suggested that *C. annuum* and *C. frutescens* should be considered native to Mexico, for both species possess centers of diversity in this country.

Finally, our data are in agreement with PICKERSGILL's (1971) proposal that the center of domestication of *C. annuum* is situated in eastern Mexico. We suggest the region comprising the states of Nuevo Leon, Tamaulipas, San Luis Potosi, Hidalgo, and Veracruz. This was the only region in which domesticated, semidomesticated, and wild accessions possessed the *Pgm-3* duplication and whitish corolla characteristics of virtually all cultivated *C. annuum*. This was also the only area in which wild accessions were found that showed very close affinity with the *C. annuum* var. *annuum* (CA 133) control. PICKERSGILL (1971) based her proposal upon karyotype analysis and upon archaeological record of chili peppers and other crops, including corn, beans, and squash among others, in Mexico (FLANNERY 1973).

Our data also suggest that a possible second center of domestication can be situated in western Mexico, in the state of Nayarit, where semidomesticated and domesticated accessions presented the same *C. annuum* characteristics described above. Unfortunately, wild accessions from this specific region were not available to critically evaluate our hypothesis. However, if the semidomesticated accessions we tested were selected directly from the local wild populations, it is very likely that the "true" *C. annuum* characteristics are also occurring spontaneously in the wild.

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