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THE CHAPARRAL VEGETATION IN MEXICO UNDER NONMEDITERRANEAN CLIMATE: THE CONVERGENCE AND MADREAN-TETHYAN HYPOTHESES RECONSIDERED[1]

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A comparative study between an unburned evergreen sclerophyllous vegetation located in south-central Mexico under a wet-summer climate, with mediterranean regions was conducted in order to re-analyze vegetation and plant characters claimed to converge under mediterranean climates. The comparison considered floristic composition, plant-community structure, and plant characters as adaptations to mediterranean climates and analyzed them by means of a correspondence analysis, considering a tropical spiny shrubland as the external group. We made a species register of the number of species that resprouted after a fire occurred in 1995 and a distribution map of the evergreen sclerophyllous vegetation in Mexico (mexical) under nonmediterranean climates.

The Tehuacán mexical does not differ from the evergreen sclerophyllous areas of Chile, California, Australia, and the Mediterranean Basin, according to a correspondence analysis, which ordinated the Tehuacán mexical closer to the mediterranean areas than to the external group.

All the vegetation and floristic characteristics of the mexical, as well as its distribution along the rain-shadowed mountain parts of Mexico, support its origin in the Madrean-Tethyan hypothesis of Axelrod. Therefore, these results allow to expand the convergence paradigm of the chaparral under an integrative view, in which a general trend to aridity might explain floristic and adaptive patterns detected in these environments.

Key words: chaparral; convergence; evergreen; mexical; Mexico; sclerophyll; Tehuacan Valley; vegetation.

The evergreen sclerophyllous vegetation consists mostly of low-stature shrubs and trees (1–3 m high) and broad-leafed sclerophyllous species with 40–100% coverage by woody vegetation. This ecosystem has been associated typically with mediterranean climates with warm, dry summers and cool, wet winters (Griesebach, 1872; Cain, 1950; Naveh, 1967; Specht, 1969; Thrower and Bradbury, 1977; Cody and Mooney, 1978; Di Castri, 1981). It receives different names according to the five different regions of the world where it grows, including "chaparral" in California, "fynbos" in the Cape Province of South Africa, "matorral" in Chile, "maquia" in the Mediterranean basin, and "mallee" in the south and south-western Australia (Cody and Mooney, 1978). Although these regions occupy <5% of the earth's surface, they harbor almost 20% of the known vascular plants of the world (Cowling et al., 1996). These plant communities, except the Chilean matorral, have also been traditionally characterized by fires. Resprouting ability by means of lignotubers, burls, etc., has been considered an adaptation to these disturbances (Naveh, 1974).

Under the view of the "superorganism" or Clementsian paradigm, this ecological system has been analyzed extensively in a comparative manner for more than three decades. Originally, all the studies were focused on testing plant community-level convergence, assuming that under a similar climate these communities will evolve towards convergent solutions, including a maximum efficiency flow of energy and nutrients (Barbour and Minnich, 1990). Since then, a significant number of studies testing convergence have been published in the literature, including different mediterranean-climate regions (Naveh, 1967; Mooney and Dunn, 1972; Parsons, 1976; Pignatti and Pignatti, 1985; Cowling and Witkowski, 1994, among others).

Although the convergent viewpoint has played an important role in promoting comparative studies among mediterranean-type ecosystems focused on plant physiology (Mabry and Difeo, 1973), plant anatomy (Kummerow, 1973), phenology (Kummerow, 1983), floristics (Pignatti and Pignatti, 1985; Arroyo et al., 1995), life history (Armesto, Vidiella, and Jiménez, 1995; Zedler, 1995), seed dispersal (Milewski and Bond, 1982: Hoffmann and Armesto, 1995), and vegetation (Parsons and Moldenke, 1975; Parsons, 1976; Naveh and Whittaker, 1979; Cowling and Campbell, 1980), this conceptual framework has limited the approach in which the sclerophyllous vegetation can be integrally viewed and understood. For example, paleobotanical evidence has been underestimated, although many studies of the paleobotanical development of the chaparral have been described in different publications by Axelrod (1950, 1958, 1973, 1975, 1977, 1989), emphasizing that a significant number of chaparral genera are represented in Tertiary floras and

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in many cases the living species are very similar to the fossils. These records provide reliable evidence that sclerophyllous vegetation, which is distributed all over the world, constitutes a reminiscence of the Madrean-Tethyan sclerophyllous vegetation that occupied a subhumid belt across much of North America-Eurasia region by the middle Eocene. This vegetation had originated from alliances in older laurophyllous forests that adapted to a spreading dry climate (Axelrod, 1977). In North America, the Madro-Tertiary Geoflora appeared on the drier borders of the North American tropics by the Middle Eocene and probably occupied much of the southwestern United States and adjacent Mexico by the end of the Oligocene, and it expanded its range north and southward, as well as east and westward in response to expanding dry climate conditions during the Miocene epoch (Axelrod, 1958). Similar processes occurred in the Northern Hemisphere and also explain many of the broad floristic changes in the actual mediterranean-type ecosystems of the Southern Hemisphere (Rundel [1981] for Chilean matorral, but see Arroyo et al. [1995] for a different hypothesis on the origin of Chilean sclerophyllous vegetation; Specht [1981] for Australian Mallee and Linder, Meadows, and Cowling [1992] for South African Fynbos).

Since the seminal model of Mooney and Dunn (1970), proposing that in the mediterranean-type climates, fire, drought, high temperatures, rainfall unpredictability, and mineral deficiencies have selected resprouting evergreen sclerophyllous shrubs as the predominant growth form, most of the studies were designed to test for this evolutionary convergence. Therefore, the central idea of the model relating to the existence of an evergreen sclerophyllous vegetation with mediterranean climate has remained untouched, even though much evidence of its presence in nonmediterranean climates all over the world should also be considered to expand the model. For example, Muller (1939) described the western montane chaparral in the summer rain area of Nuevo Leon (Mexico) where the floristic composition and growth form are strongly similar to the California chaparral. Axelrod (1975) reported the presence of sclerophyllous taxa in areas of summer and winter precipitation (Arizona-New Mexico, eastern Mediterranean), summer rain and winter drought (eastern Mexico, northwestern India), and well-distributed rainfall throughout the year (northern coast, Turkey). Accordingly, Vankat (1989) claimed for a revision of the Mooney and Dunn's (1970) long-standing paradigm, after finding different responses in seasonal patterns of stem-water potentials between Arizona (with summer rainfall) and California chaparrals. Barbour and Minnich (1990) reviewed the IBP and post-IBP literature on chaparral to assess the degree of convergence among the five mediterranean-type ecosystems and found so many differences among vegetations that they questioned the convergence paradigm. In addition, phylogenetical and historical effects have also been accounted for the explanation of the evolution of plant traits of mediterranean plants (Blondel and Aronson, 1995). For example, Herrera (1992) found that the life history traits such as flowering biology and seed dispersal of southern Spain are better explained by means of historical processes described by some authors (i.e., Axelrod, 1975; Pignatti, 1978; Pons, 1981; and Palamarev, 1989) than by similar (convergent) selection pressures under a Mediterranean climate. Keeley (1995) supports this explanation due to the remarkable similarity in seed germination, dispersal, and seedling recruitment patterns observed in California and Mediterranean species of *Quercus*, *Rhamnus*, and *Prunus*.

The presence of the evergreen sclerophyllous vegetation in Mexico under a tropical climate of summer rains has been reported by different authors (Muller, 1939, 1947; Miranda and Hernández, 1963; Axelrod, 1975, 1989; Rzedowski, 1978). Taking into consideration the information from these studies, it is possible to assume that the sclerophyllous vegetation in Mexico might be a relict of the Madro-Tertiary Geoflora that constitutes the principal element of the Mexican chaparral (named here mexical) in nonmediterranean climates and that its current patchy distribution probably responds to a gradual trend toward increased dryness during the Tertiary and Quaternary (Axelrod, 1958). If the sclerophyllous vegetation in Mexico exhibits the same plant characters associated with the chaparral vegetation under mediterranean climates, this would allow analysis of what factors have contributed to similar plant traits dominating under different climates. At the same time, and considering that fire has not played an important ecological factor in the Tehuacán mexical (only a 1-ha fire occurring in 1995 has been reported in the study zone for >50 yr), the resprouting ability of plants and characters in plants that have been referred as adaptations to fire need to be reconsidered.

This paper is the first attempt to assess a comparison of the evergreen sclerophyllous vegetation located in south-central Mexico (Tehuacán Valley), with other mediterranean regions of the world. The aim of this study is to test whether the characters at the community and population level that have been claimed to converge under mediterranean climates all over the world are the same as those in the plant communities and populations of the Tehuacán Valley under nonmediterranean climate. We try to determine common environmental characteristics between mediterranean and nonmediterranean climates to explain the patterns observed. We consider: (1) floristic composition and the plant community; (2) plant characters that have been considered as adaptations to mediterranean climates, including fire as an ecological factor; and (3) distribution of the mexical under nonmediterranean climates and a general description of the vegetation including dominant woody genera, maximum height of vegetation, presence of evergreen and sclerophyllous species, altitudinal range, and type of climate.

MATERIALS AND METHODS

Study site—The semiarid Tehuacán-Cuicatlán valley is located between the states of Puebla and Oaxaca, Mexico (17°39′–18°53′N, 96°55′–97°44′W). It covers 10 000 km^2 including several intermountain valleys (Fig. 1). Climate is semiarid with an average annual precipitation around 400 mm and a drought period in the middle of the summer rain season (Fig. 2). This region owes its aridity to the rain shadow produced by the Eastern Sierra Madre (Villaseñor, 1990; Dávila et al., 1993).

The evergreen sclerophyllous vegetation in the valley (mexical) is located in an altitudinal belt along the mountain chains of Puebla and

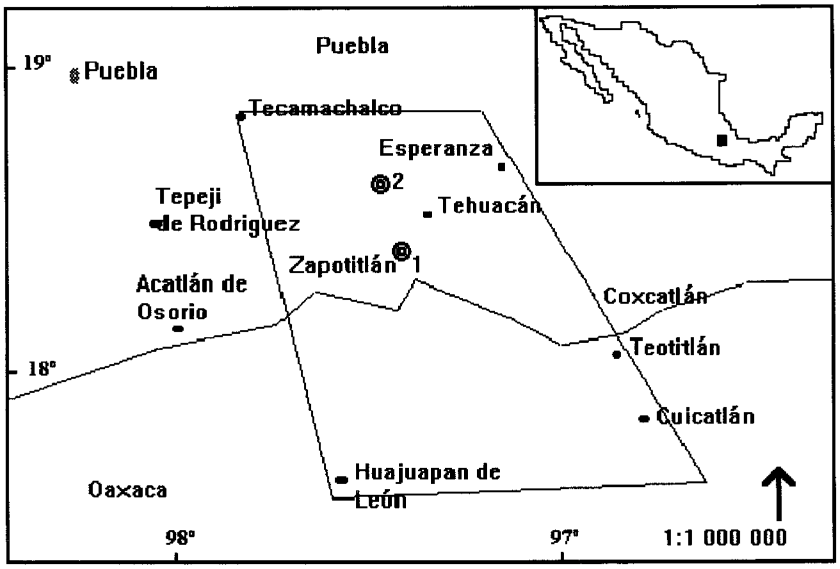

Fig. 1. Location of sites. The area of the Tehuacán Valley is delimited by the continuous line (located between 17°39′ and 18°53′N and between 96°55′ and 97°44′W). Site 1 = Cerro Viejo and Site 2 = Cerro Zotoltepec. The irregular line represents the state boundary between Puebla and Oaxaca states.

Oaxaca, ranging from 1950 to 2500 m a.s.l. The two study sites are located along two mountains named Cerro Viejo (18°15′N, 97°26′W) and Cerro Zotoltepec (18°38′N, 97°27′W; Fig. 1). The nearest climatic station (Tecamachalco) reports 611.5 mm and 17.7°C mean annual temperature (García, 1988). The area corresponds to the central part of a Cenozoic continental basin originating from an arm of the Cretaceous sea (Brunet, 1967), comprising calcareous mountains that reach up to 2900 m a.s.l.

Vegetation sampling—At Cerro Viejo and Zotoltepec a total of 15 Canfield lines of 50 m each per locality (Mueller-Dombois and Ellenberg, 1974) were used to describe the vegetation. From these lines, the following data were obtained for each woody species: relative cover, maximum and minimum height, and frequency (%) as the proportion of times each species was found in the 15 lines. From these data the Relative Dominance Index (R.D.I) per species was obtained, such that R.D.I. = relative cover (%) × frequency (%) × relative density, where relative density = number of individuals/50 m^2. A total of three 1000-m^2 quadrats (50 × 20 m) were used to determine the mean number of species in the Tehuacan mexical, in order to compare them with other mediterranean regions reported by Cowling et al. (1996).

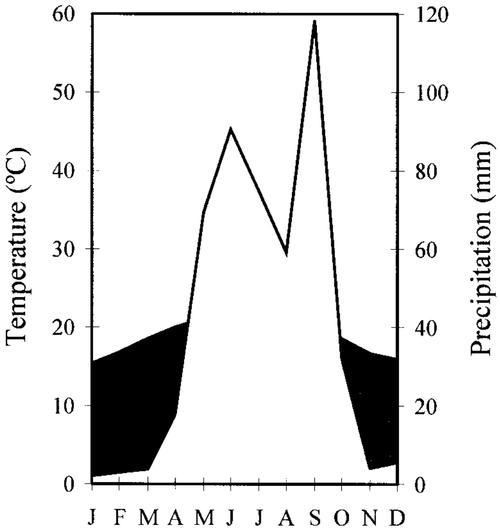

Fig. 2. Ombrothermic diagram of the Tehuacán city climate.

Structural comparison with Mediterranean-type vegetation—The characters of the dominant woody species from different Mediterranean-climate areas were collected from the Specht (1988) databook. The importance of the species within their communities studied was confirmed from the following studies: Wilson and Vogl (1965), Hanes (1977), and Mooney et al. (1977) for the Californian chaparral; Mooney et al. (1977) and Rundel (1981) for the Chilean matorral; Beadle (1981) and Specht (1981) for the Australian mallee; and Tomaselli (1981), Quezel (1981), and Romane and Terradas (1992) for the Mediterranean Basin vegetation represented in France, Spain, and Greece. Data on South Africa fynbos are lacking. Fourteen characters regarding plant form, photosynthetic organs, and leaf characteristics were used in the comparative analysis. These three main groups characterize typical mediterranean traits. Every character was scored as binary to avoid the low frequency of rare characters. Characters and character states were scored as follows: (1) renewal buds {1 = microphanerophyte, 0 = nanophanerophyte}, (2) plant height {1 = 25–100 cm, 0 = 100–1000 cm}, (3) crown diameter {1 = <100 cm, 0 = >100 cm}, (4) photosynthetic organs {1 = leaves, 0 = phyllodes, cladodes, both leaves and stems absent}, (5) leaf size {1 = subleptophyll to nanomicrophyll (<0.10–12.25 cm^2), 0 = microphyll to mesophyll (>12.25–180.3 cm^2), (6) leaf length {1 = <1–2 cm, 0 = 2–20 cm}, (7) leaf width {1 = <1–5 mm, 0 = 5–50 mm}, (8) leaf angle {1= mainly horizontal, <45° with respect to the horizon, 0 = mainly vertical, >45° with respect to the horizon}, (9) leaf margin {1 = entire, 0 = serrate/toothed, lobed/deeply dissected, rolled, recurved/revolute, grooved/incurved}, (10) leaf consistency {1 = malacophyll, 0 = semisclerophyll, sclerophyll}, (11) leaf tomentosity {1 = nonhairy, 0 = lower side hairy, upper side hairy, both sides hairy}, (12) leaf seasonality {1 = evergreen, 0 = summer and winter deciduous}, (13) leaf color {1 = all green, 0 = all glaucous, all white, green and white, glaucous and white}, (14) stem number {1 = single, 0 = several}.

The role of the characters was weighted by means of the number of species scored in each area and then ordinated by a Simple Correspondence Analysis (Greenacre, 1984). As a reference, the spiny shrubland

Table 1. Summary of vegetational measurements obtained by the line intercept in the study areas (E = evergreen, D = deciduous).

Area Species	Percent cover	Height max.	Height min.	Relative frequency	Relative dominance	Leaf seasonality
Cerro Viejo						
Quercus sebifera	24.92	2.90	0.10	100.00	646.29	E
Citharexylum oleinum	8.52	3.50	0.15	88.87	56.41	E
Rhus virens	7.46	2.00	0.20	88.87	90.91	E
Garrya ovata	7.29	3.50	0.20	66.63	44.88	E
Dasylirion serratifolium	6.70	2.00	0.35	100.00	47.79	E
Havardia elachistophylla	5.95	0.80	0.05	100.00	54.51	D
Ageratina espinosarum	5.02	2.00	0.30	55.53	69.11	D
Quercus obtusata	4.82	4.00	3.50	33.33	9.64	E
Brahea nitida	4.22	6.00	0.15	55.53	36.83	E
Comarostaphylis polifolia	4.04	1.40	0.14	55.53	49.76	E
Salvia candicans	3.68	1.00	0.10	88.87	55.18	E
Krameria cytisoides	3.20	1.30	0.50	55.53	8.66	E
Litsea glauscescens	2.80	1.10	0.18	55.53	3.71	E
Ceanothus greggii	2.77	1.80	0.50	44.43	19.29	E
Bouvardia longiflora	1.98	0.70	0.20	33.30	0.91	D
Phylanthus subcuneatus	1.56	1.00	0.16	22.20	6.90	D
Dodonaea viscosa	1.51	2.40	0.50	33.33	7.04	E
Nolina longifolia	1.17	2.00	0.40	33.33	5.45	E
Rhus standleyi	1.08	1.10	0.25	66.63	2.05	E
Others	79.76					
Total	105.2					
Cerro Zotoltepec						
Quercus sebifera	32.20	4.32	0.60	100.00	774.32	E
Ageratina espinosarum	22.99	2.40	0.28	100.00	542.35	D
Amelanchier denticulata	22.51	2.50	0.33	83.30	794.29	E
Rhus virens	12.89	3.40	1.10	83.30	79.29	E
Forestiera rotundifolia	11.90	2.76	0.46	83.30	137.88	D
Salvia candicans	11.09	1.64	0.12	100.00	199.68	E
Salvia thymoides	10.85	1.30	0.08	83.30	224.06	E
Garrya ovata	7.68	4.10	1.05	66.65	79.64	E
Lindleya mespilioides	7.48	4.48	0.66	50.00	64.81	E
Mimosa lacerata	7.26	3.02	0.53	83.30	44.05	D
Citharexylum oleinum	6.92	2.52	0.30	100.00	46.01	E
Dodonaea viscosa	4.33	3.95	0.70	50.00	37.50	E
Others	29.23					
Total	187					

vegetation adjacent to mexical was considered in the analysis, which is typical of arid climates, located near the Tehuacán mexical, at 18°20′N, 97°27′W, with an altitude ranging from 1380 to 1800 m a.s.l. (Osorio et al., 1996) and an average annual rainfall around 425 mm (Dávila et al., 1993; Valiente, 1991). The inclusion of this external group into the analysis was considered necessary to test the similarity with the Tehuacan mexical situated within the same region just below the altitudinal belt of the sclerophyllous vegetation. A total of 121 dominant species were included in the analysis: 28 for the Tehuacán region, 18 for the Tehuacán spiny shrubland, 23 for the Californian chaparral, 13 for the Chilean matorral, 24 for the Mediterranean Basin, and 15 for the Australian mallee. The analysis was run in SAS version 6.03 (SAS Institute, Cary, NC).

In each of the localities, coal remnants were searched in soil profiles (up to 10 m deep) in order to detect wildfire evidence in the past. Resprouting ability was assessed by unearthing the roots and examining for presence of lignotubers, burls, or rhizomes. In addition to this, field observations were made in order to ensure that disturbed plants resprouted. These included a record of the species that resprouted after the 1-ha fire that occurred in 1995.

The distribution of the mexical—A distribution map of the mexical was undertaken, using bibliographic information published mostly in Mexico for the last 50 yr. In addition, the information contained in vegetation maps (scale 1:1 000 000) published by INEGI (1981) was also used to construct a 1:4 000 000 map showing the distribution of the mexical.

RESULTS

The sclerophyllous vegetation of the Tehuacan Valley consists of 225 species of seed plants. In both study sites, the plant coverage is 100%, although in some places in the same localities, it is ∼40–60%. Vegetation is predominantly constituted by shrubs (47%), ephemerals (39.2%), camaephites (10.8%), and trees (7.41%) with heights ∼2 m tall, although some tree species can reach up to 4 m tall. In both sites, *Quercus sebifera* Trel. (Fagaceae) is the dominant species and most of the species observed are evergreen and sclerophyllous (Table 1), whose leaf angles with respect to the horizontal axis are >45°. Plants mostly have several stems that originate from the base or close to it. The data obtained shows that 96.4% of the species resprout. All these characters (leaf angles, basal branching, and resprouting), are similar to the mediterranean plant traits considered in the comparison (Table 2).

No fire evidence, measured as coal remnants, were found in soil profiles. In the burned area during June

Table 2. Morphological attributes reported for species of mediterranean-type ecosystems (Hanes, 1971; Specht, 1988) and from this study for the Tehuacán mexical and the spiny shrubland. Numbers indicate % of species bearing the morphological trait: leaf seasonality: 0 = summer and winter deciduous, 1 = evergreen; leaf consistency: 0 = semi-sclerophyll, sclerophyll, 1 = malacophyll; leaf angle: 0 = mainly vertical, 1 = mainly horizontal; photosynthetic organs: 0 = phyllodes, cladodes, both leaves and stems, absent, 1 = leaves; leaf size: 0 = microphyll (12.25 cm^2)–mesophyll (180.25 cm^2), 1 = subleptophyll (<0.10 cm^2)–nanomicrophyll (12.25 cm^2); stem number: 0 = several, 1 = single; sprouting stems: 0 = no, 1 = yes.

Zone	Leaf seasonality		Leaf consistency		Leaf angle		Photosynthetic organs		Leaf size		Number of stems		Resprouting stems	
	0	1	0	1	0	1	0	1	0	1	0	1	0	1
Tehuacan mexical	18	82	79	21	93	7.1	3.6	96	11	89	93	7.1	3.6	96.4
Tehuacan spiny shrubland	89	11	0	100	39	61	0	100	5.6	94	44	56	77.7	22.3
California chaparral	35	65	74	26	70	30	4.3	96	13	87	87	13	50	50
Chile matorral	38	62	54	46	0	100	7.7	92	15	85	69	31	24.4	75.6
Mediterranean Basin	0	100	79	21	92	8.3	0	100	0	100	38	63	62.5	37.5
Australia mallee	0	100	100	0	67	33	6.7	93	6.7	93	60	40	69.3	30.7

1995, a total of 14 species resprouted: *Ageratina spinosarum* (A. Gray) R.M. King & H. Rob. (Asteraceae), *Amelanchier denticulata* (Kunth) Koch (Rosaceae), *Comarostaphylis polifolia* (Kunth) Zucc. ex Klotzsch (Ericaceae), *Citharexylum oleinum* (Benth.) Moldenke (Verbenaceae), *Croton hypoleucus* Schltdl. (Euphorbiaceae), *Gochnatia smithii* B.L. Rob. & Greenm. (Asteraceae), *Havardia elachystophylla* A. Gray ex S. Watson (Mimosaceae), *Lindleya mespilioides* Kunth (Rosaceae), *Quercus sebifera* Trel. (Fagaceae), *Rhus standleyi* Barkley (Anacardiaceae), *Rhus virens* Lindh., *Salvia aspera* Mart. & Galeotti (Lamiaceae), *Salvia candicans* Mart. & Galeotti, *Xerospirea hartwegiana* (Rydb.) Henr. (Rosaceae). Reproduction from seeds was recorded only for *Croton hypoleucus*, *Gymnosperma glutinosum* (Spreng.) Less (Asteraceae), *Ceanothus gregii* A. Gray (Rhamnaceae), and *Phytolacca icosandra* L. (Phytolaccaceae).

Some of the genera of the mexical have the same species or close relatives of those present in the mediterranean-type ecosystems of California, i.e., *Arbutus*, *Ceanothus*, *Garrya*, *Juniperus*, and *Rhus* (Table 3). In addition, the mexical has some genera that are present in different mediterranean ecosystems of Chile, the Mediterranean Basin, or Australia (i.e., *Rhus*, *Juniperus*, *Arbutus*, *Comarostaphylis* (= *Arctostaphylos*), *Quercus*, *Salvia*, *Acacia*, *Stevia*, *Lithospermum*, *Linum*, *Aristida*, etc. (Table 4).

Plant diversity is 90 ± 6 species of vascular plants per 1000-m^2 sample in the study zones.

Vegetation structure: comparison with mediterranean-climate areas—The first axis of the correspondence analysis carried out to discriminate among the geographical areas studied explains 57.9% of the variance, whereas the second axis indicates 16% (Fig. 3). The main plant characters explaining the first axis are (1) leaf seasonality, (2) leaf consistency, and (3) leaf angle. Along this axis, the Tehuacán mexical is ordinated closer to the mediterranean-climate areas than to the tropical external group or spiny shrubland. The character states that are common to the mexical and the mediterranean-climatic areas are (1) evergreen, (2) sclerophyllous or semisclerophyllous, (3) leaves with nearly vertical angles. The mediterranean-climatic areas that are more similar in this axis to the Tehuacán mexical are the Chilean matorral and the Californian chaparral.

The main plant character explaining the second axis is the number of stems, with a load factor of 0.78. This axis runs from multistemmed plants in the upper part of it, to single-stem plants in its lower part. Along this axis, the Tehuacán mexical is ordinated again close to the Chilean matorral and the Californian chaparral.

Geographical patterns of the mexical—The distribution of the mexical is highly concentrated along the different mountain chains of the country (Fig. 4), including the Mexican states of Aguascalientes, Coahuila, Chihuahua, Durango, México, Guanajuato, Guerrero, Hidalgo, Jalisco, Nuevo León, Oaxaca, Puebla, Querétaro, San Luis Potosí, Tamaulipas, Tlaxcala, and Zacatecas. In all cases, the mexical is located along the rain-shadowed (dry) aspects of the mountain chains, which include the Sierra Madre Oriental, Sierra Madre Occidental, Neovolcanic belt, and Oaxacan mountains. Altitudinally the mexical ranges between 1700 and 2800 m a.s.l. (Fig. 4; Table 5). In all cases, the mexical occupies an interme-

Table 3. Some identical and closely related taxa in sclerophyllous vegetation in subhumid Madrean North America and central México. * = fossil occurrence (Axelrod, 1975).

Taxa	California	SW United States	NE México	Tehuacán Valley	NW Oaxaca
Arbutus	*menziesii*	—	*xalapensis*	*xalapensis*	*xalapensis*
Arctostaphylos	*pungens*	*pungens*	*pungens*	*pungens*	*pungens*
Ceanothus	*greggii*	*greggii*	*greggii*	*greggii*	*greggii*
Garrya	*elliptica* *(*masoni* Pliocene)	—	*ovata*	*ovata*	*ovata*
Garrya	*(*axelrodi* Miocene Nevada)	—	*ovata*	*ovata*	*ovata*
Juniperus	*californica*	*monosperma*	*deppeana*; *mexicana*	*deppeana*	—
Karwinskia	*(*californica,* Miocene and Pliocene)	—	*humboldtiana*	*humboldtiana*	*humboldtiana*
Rhus	*(*sonorensis,* Miocene)	*virens*	*virens*	*virens*	*virens*
Rhus	*(*tehachapiensis,* Miocene)	*chondroloma*	—	*chondroloma*	*chondroloma*

Table 4. Common genera between mediterranean-type ecosystems and the Tehuacán mexical.

Family of seed plants	Tehuacán Valley mexical	California chaparral	Chilean matorral	Mediterranean Basin	Australian mallee
Agavaceae	*Yucca*	x			
Anacardiaceae	*Rhus*	x		x	
Cupressaceae	*Juniperus*	x		x	
Ericaceae	*Arbutus*	x		x	
Ericaceae	*Comarostaphylis*	x		x	
Fagaceae	*Quercus*	x		x	
Garryaceae	*Garrya*	x			
Lamiaceae	*Salvia*	x		x	
Rhamnaceae	*Ceanothus*	x			
Rosaceae	*Amelanchier*	x		x	
Rosaceae	*Cercocarpus*	x			
Scrophulariaceae	*Penstemon*	x			
Mimosaceae	*Acacia*		x		
Asterasceae	*Gochnatia*		x		
Asteraceae	*Baccharis*		x		
Lamiaceae	*Satureja*		x	x	
Asteraceae	*Stevia*			x	
Boraginaceae	*Lithospermum*			x	
Convolvulaceae	*Ipomoea*			x	
Crassulaceae	*Sedum*			x	
Oleaceae	*Fraxinus*			x	
Linaceae	*Linum*			x	x
Poaceae	*Aristida*				x
Sapindaceae	*Dodonaea*				x

diate position between oak and pine forests (above), and the xerophitic communities (below). The mexical ranges from arid to dry-temperate climates (Table 5), which corresponds to types Bs and Cw, respectively, according to García (1973). The vegetation for all the states where descriptions are available (Table 5) is dominated by evergreen, sclerophyllous shrubs with few tree representatives. Finally, a significant number of genera are common among the different mexical localities and with different mediterranean-type ecosystems of the world (Table 5).

DISCUSSION

Mediterranean-type vegetation is characterized by >40% woody canopy coverage and one-layered vegetation formed by woody, sclerophyllous, and evergreen subshrubs and herbs located in the canopy breaks (Barbour and Minnich, 1990). These features, at the community level, have been found in the mexical under the nonmediterranean climate in the Tehuacán Valley and also can be observed in all the mexical vegetation types along the principal mountain chains of Mexico. Its presence in Mexico under tropical climate of summer rains has been reported by different authors (Muller, 1939, 1947; Shreve, 1939; Le Sueur, 1945; Miranda, 1948; Martin, 1958; Miranda and Hernández, 1963; Rojas-Mendoza, 1965; Rzedowski, 1966, 1978; Rzedowski and

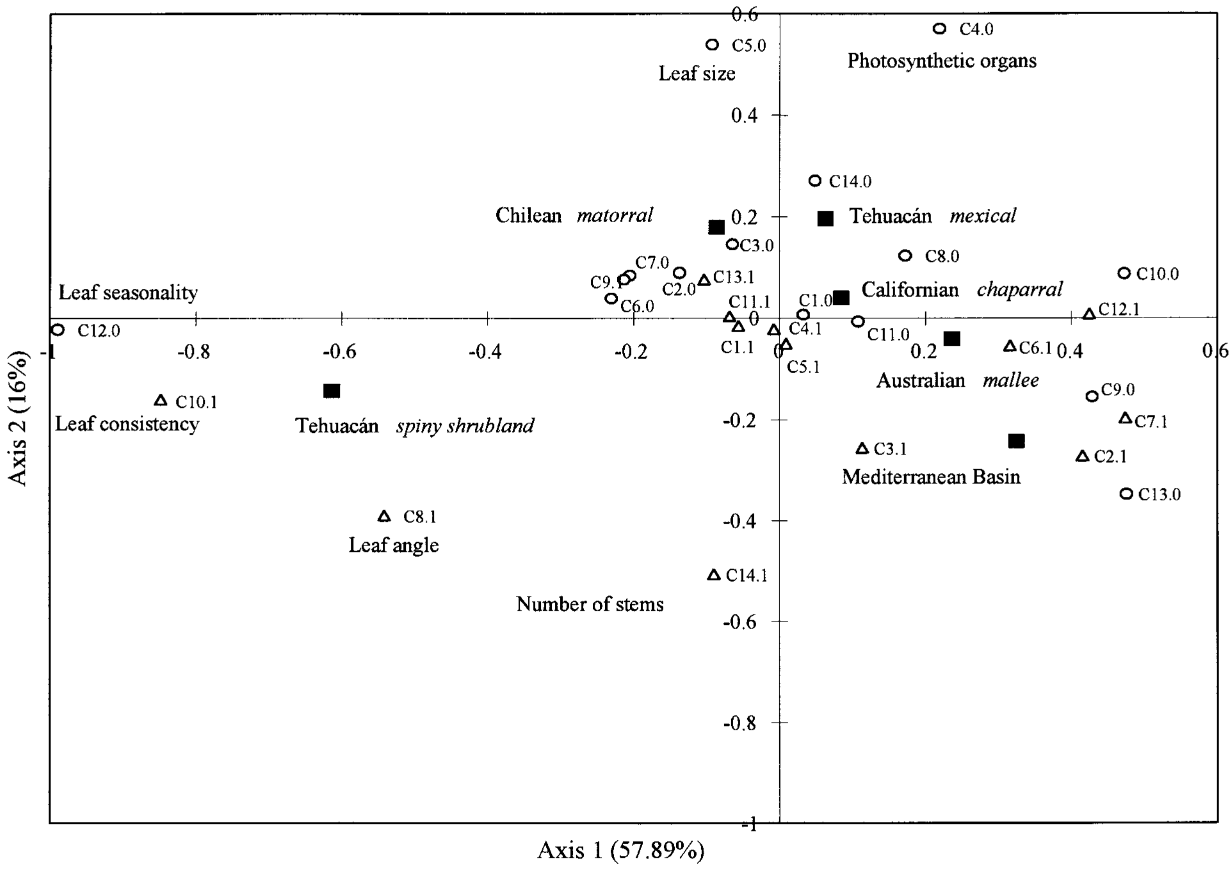

Fig. 3. Correspondence analysis graph of the structural comparative analysis between the Tehuacán mexical and the mediterranean-type ecosystems of California, Chile, Australia, and the Mediterranean Basin. The Tehuacán spiny shrubland was used as an outgroup. The first axis explains 58% of variance and the second axis explains 16% of variance. See Materials and Methods for codes of characters and character states.

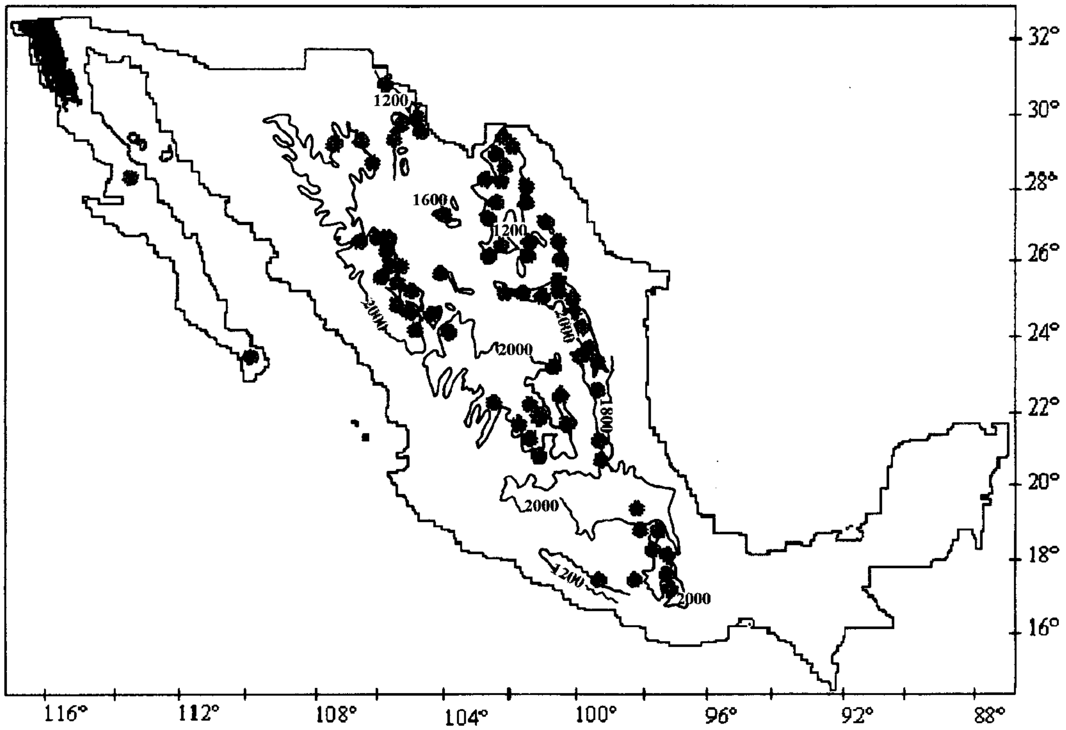

Fig. 4. Distribution of the mexical (dotted marks) under wet-summer climates in México. Altitude lines are in m a.s.l. The black delimited zone in the North West of Mexico indicates the chaparral distribution under mediterranean climate.

Mac Vaugh, 1966; González-Quintero, 1968; Puig, 1970; Axelrod, 1975, 1989; Cruz-Cisneros and Rzedowski, 1980; Hiriart, 1981; García, 1983), however, this is the first time in which its similarity in different mediterranean zones has been assessed. Therefore, not considering the mediterranean climate as an explanation for the development of evergreen sclerophyllous vegetation in Mexico, a common character between the mediterranean climate and our study sites is seasonal drought with almost seven dry months. Sclerophylly has been associated with water stress, damage avoidance by herbivores, and soil oligotrophy (Turner, 1994). Preliminary observations reveal that mexical soils are shallow and because of the well-developed petrocalcic horizon the mexical has low levels of nitrogen and phosphorus (Hennessy et al., 1983).

The correspondence analysis shows two different groups. The first corresponds to the areas of evergreen sclerophyllous vegetation (Chilean matorral, Tehuacán mexical, Californian chaparral, Australian mallee, and Mediterranean Basin vegetation) and the second to the Tehuacan spiny shrubland. Both groups have been differentiated on the basis of leaf seasonality, consistency, and angle. In all five evergreen, sclerophyllous vegetation areas of the analysis, the character states "evergreen" and "sclerophyllous" and "vertical leaf angles" were dominant. In contrast, in the Tehuacan spiny shrubland the character states "deciduous," "malacophyllous," and "horizontal leaf angles" were the dominant traits. Two of these discriminatory characteristics (evergreen and sclerophyllous) correspond to those found by Barbour and Minnich (1990) as consistently similar among the five mediterranean-type ecosystems. The other factor, steep leaf angles, has been reported as an adaptation of Mediterranean sclerophyllous plants to reduce radiation absorption during extended drought periods (Ehleringer and Comstock, 1989; Valiente-Banuet et al., unpublished data). Within chaparral ecosystems, limited water represents a major stress affecting plant performance and since leaf temperatures usually increase plant water stress, steep leaf angles contribute to a reduction in leaf solar radiation absorption (Smith and Ullberg, 1989). In the Tehuacan mexical, 93% of the species present leaf angles ranging between 45° and 90° with respect to the horizontal axis, which suggests that evergreen-sclerophyllous species are responding mainly to water stress.

Considering the second axis in the correspondence analysis, the number of stems is a significant discrimination factor. This character can be considered as an architectural characteristic related to resprouting ability, and it is represented by a significant number of species in the Chilean matorral not so frequently observed in other mediterranean regions. Mediterranean-type ecosystems have been matched with natural fires and therefore typical features of shrubs, such as lignotubers and burls at the root crown/stem base, have been associated with postfire resprouting ability (James, 1984; Kummerow and Ellis, 1989). These woody structures and resprouting ability are present in the shrubs of the Tehuacan mexical where there is no evidence of periodic fire, indicating that their presence can be better considered as an ancient preadaptation to fire inherited from ancestors belonging to laurophyllous forests (Axelrod, 1975). Actually, the fact that in the Tehuacán mexical a significant number of species resprouted after a fire in 1995 suggests a similar response to fire when compared with mediterranean

Table 5. Environmental and vegetation characteristics of mexical under wet-summer climates.

Mexican state (Source)	Altitude (m a.s.l.)	Climatic type (García, 1973)	Dominant woody genera	Vegetation height range (m)
Chiapas (Miranda, 1952)	1530	Cb	*Quercus, Dodonaea, Rhus, Amelanchier, Harpalyce, Ximenia, Xylosma, Ilex, Ternstroemia, Garrya.*	2–4
Coahuila (Muller, 1947)	>2000	between Bs and Cw	*Quercus, Garrya, Rhus, Cercocarpus, Microrhamnus, Berberis, Cowania, Arctostaphylos, Ceanothus, Amelanchier, Arbutus, Fraxinus, Rhus, Nolina, Dasylirion, Yucca.*	0.30–0.60
Distrito Federal (Rzedowski, 1954)	2500–2800	Cw	*Quercus, Eupatorium, Baccharis, Buddleia, Lamourouxia, Arbutus, Salvia.*	1–3
Guanajuato (Quero, 1977)	2300–2600	Cw_0–Cw_1	*Quercus, Arctostaphylos, Baccharis, Acacia, Garrya, Bursera, Cowania, Dasylirion, Dodonaea, Arbutus, Prunus, Alnus, Galium, Dahlia, Ageratina, Lobelia, Ribes, Salvia, Senecio, Mimosa, Acacia, Amelanchier, Eysenhardtia, Forestiera, Lippia, Opuntia.*	1–4
Hidalgo (González-Quintero, 1968; Hiriart, 1981)	2150–2300	Bs	*Quercus, Agave, Amelanchier, Arbutus, Arctostaphylos, Baccharis, Bouvardia, Buddleia, Ceanothus, Dasylirion, Ageratina, Lamourouxia, Salvia, Stevia, Rhus, Berberis, Clethra, Juniperus, Krugiodendron, Leucaena, Lindleya, Litsea, Mimosa, Myrtus, Pistacia, Vauquelinia, Wimmeria, Croton, Lippia, Tecoma, Thryallis, Zexmenia.*	0.20–3
México (Rzedowski et al., 1964)	>2000		*Quercus, Nolina, Agave, Bouvardia, Dalea, Dasylirion, Ageratina, Helianthemum, Havardia, Rhus, Verbesina.*	0.20–2
Nuevo León (Muller, 1939; Rojas-Mendoza, 1965)	2000–2800	BSk'w	*Quercus, Rhus, Cercocarpus, Arctostaphylos, Ceanothus, Arbutus, Cowania, Yucca, Nolina, Pinus, Juniperus, Garrya.*	0.30–1.5
Oaxaca (Cruz-Cisneros and Rzedowski 1980; García, 1983)	2000–2450	Cw_0–Cw_1	*Rhus, Lindleya, Arctostaphylos, Juniperus, Quercus, Pinus, Amelanchier, Arbutus, Ceanothus, Cercocarpus, Dodonaea, Fraxinus, Garrya, Leucaena, Mimosa, Havardia, Salvia, Satureja, Sphacele, Stevia, Tecoma, Vauquelinia.*	1–4
San Luis Potosí (Rzedowski, 1966)	>2000	between Bs and Cw	*Quercus, Amelanchier, Arbutus, Arctostaphylos, Cercocarpus, Garrya, Rhus, Salvia, Yucca, Brahea, Casimiroa, Citharexylum, Gochnatia, Persea, Havardia, Hesperozygis, Myrtus, Dodonaea, Ageratina, Forestiera, Fraxinus, Ptelea, Rhumnus, Sophora, Vauquelinia.*	1.5–3
Tamaulipas (Martin, 1958; Puig, 1970)	>1700	Between Bs and Cw	*Quercus, Arbutus, Yucca, Cercocarpus, Bauhinia, Pinus.*	±1.8

zones (Keeley, 1992). Particularly, *Ceanothus gregii*, a common species in the California chaparral, recruits seedlings after fire both in California (Keeley, 1992) and in the Tehuacán mexical. Therefore, resprouting ability has recently been considered not as an adaptation, but a pre-adaptation to fire with an evolutionary origin based on the response of the plants to herbivory (López-Soria and Castell, 1992). For this reason, resprouting ability has been associated with ancient woody groups abundant in Chile, under a nonextreme climate (Arroyo et al., 1995). Mexical vegetation, developed probably under the mildest climate among all the studied sites, maintains also many old woody tropical lineages (i.e., *Acacia*, *Amelanchier*, *Arbutus*, *Bursera*, *Ceanothus*, *Cercocarpus*, *Comarostaphylis*, *Garrya*, *Karwinskia*, *Leucaena*, *Litsea*, *Quercus*, *Rhus*, *Satureja*, etc.), which are fossil representatives of the pre-Pliocene period. Mexical vegetation contains the highest percentage of resprouters (94.7%; present study), followed by Chile (75.6%; García-Fayos, unpublished data), whereas the more extreme climate areas of California and Mediterranean Basin only contain 50 and 64% of resprouter taxa, respectively (Hanes, 1971; García-Foyas, 1991). These data support the hypothesis that under less extreme climates, the maintenance of older woody resprouter lineages takes place. This hypothesis is reinforced by the fact that in the other mediterranean-type ecosystems, belonging to the Mediterranean Basin, the older tropical woody lineages suffered extinction processes, whereas the group of seeders diversified (Herrera, 1992).

An evolutionary convergence explanation can be claimed at this point, without invoking group selection. However, the results of this study show that the same traits that have been thought to converge under mediterranean climate are also developed among plants under tropical and nonmediterranean climate. Consequently, it seems that the present climate is not an important factor in the evolution of the plant traits studied, which is also supported by the fact that plants of the Tehuacan spiny shrubland living under the same tropical climate of the Tehuacán mexical, but in drier areas and below the 1900 m of altitude, differ completely in these characteristics. In contrast, the Tehuacan mexical plants are much more similar to mediterranean-type vegetation, even though they are established in a tropical climate.

The mexical vegetation can be considered as a relict of the Madro-Tertiary Geoflora, whose patchy distribution might be the result of the expanding dry climate during the Miocene epoch (Axelrod, 1958). For example, Axelrod (1975) reports genera such as *Acacia*, *Gochnatia*, *Baccharis*, *Satureja*, *Stevia*, *Lithospermum*, *Yucca*, *Rhus*, *Juniperus*, *Arbutus*, *Comarostaphylis*, *Quercus*, *Garrya*, *Salvia*, *Ceanothus*, etc., which are present both in Mexico and California, and some of them are also present in the Mediterranean Basin and the Chilean matorral. The presence of these genera in both zones with summer-wet climates of Mexico and the mediterranean regions of the world supports the origin of the mexical in the Madrean-Tethyan sclerophyllous vegetation, which occupied a subhumid belt across much of North-America-Eurasia by the middle Eocene and originated from alliances in older laurophyllous forests that adapted to spreading into dry climate (Axelrod, 1977). Actually, the mexical is distributed entirely along the dry parts of the mountain chains produced by the rain shadow of the Eastern and Western Sierras Madre and Neovolcanic belt, as well as the Oaxacan mountains. In all the cases, below the altitudinal limit of the mexical, different types of xerophitic shrublands are found, whereas above the mexical, oak and pine forests are always present if the altitude is above 2500 m. This patchy distribution of the mexical along the main mountains of Mexico perhaps had a wider distribution than today. Indeed, during the Pliocene, California chaparral had a wider distribution than it does today, occupying areas now desert or covered with broadleaved evergreen forests (Axelrod, 1973). The gradual development of regional differences in the distribution of seasonal rainfall and in temperature relations as drier climates developed (Axelrod, 1973) probably accounted for its actual patchy and relict distribution along the Mexican mountains. Undoubtedly, the recent formation of important mountain chains such as the Sierra Madre Occidental, no more than 5 million years B.P. (Cserna, 1989), provided areas for spread of mexical. Indeed, the fossil record indicates that the summer rainfall regime from Arizona to Texas and southward into Mexico approximates the conditions under which chaparral-type vegetation occurred during most of its recorded history, which can be traced back into the Oligocene (Axelrod, 1973). Therefore, the mediterranean climate is not old (Axelrod, 1973), and therefore sclerophyllous species that now typify the mediterranean areas are survivors of a richer flora that persisted in Mexico under summer-wet climates. This accounts for the phenological patterns reported for mediterranean regions. Plant phenology is one of the processes that have been thought to converge among the mediterranean-climate areas. In response to hot and dry summers and mild and wet winters, plant communities around the mediterranean ecosystems show similar phenological patterns consisting of a marked flowering peak at the spring season (Arroyo, 1988). This indicates that species responded to a mediterranean climate that developed gradually since the late Cenozoic (Axelrod, 1973). In contrast, the mexical community has shown a different phenological pattern. Data (unpublished) taken over one year revealed that a marked flowering peak is shown neither in the spring nor in any other season. In contrast to the marked seasonality in mediterranean communities, mexical showed a constant flowering percentage across the four seasons.

The prevalence of Tertiary genera in Mexico, which now are extinct in some mediterranean regions of the Mediterranean Basin (Herrera, 1992), probably is due to more benign and nonextreme climatic conditions in Mexico, such as has been suggested for Chile by Arroyo et al. (1995). If so, it might help to explain both the high and similar plant diversity encountered in 1000 m^2 in the Tehuacan mexical (90 ± 6 species), with respect to the Chilean matorral (100 ± 15 species), and the prevalence of resprouter species in both sites. As Herrera (1992) pointed out, the extinction of these taxa allowed the diversification of seeders during Quaternary. In Mexico, nothing is known about diversification of taxa during the Quaternary, however, it is possible that if this phenomenon really occurred, the high diversity shown in the Tehuacán mexical can be related to the presence of a mixture of Tertiary and Quaternary species, with the predominance of species from the Tertiary.

In summary, the similarities found in this comparative study between the mexical and the mediterranean regions indicate that the mexical represents the same vegetation that traditionally has been considered only associated with mediterranean climates. In addition to classical views of evergreenness and sclerophylly as adaptations to environmental constraints, such as oligotrophy, water stress, and herbivory, this study allows us to expand the convergence paradigm. Therefore, these ecological systems should be better understood under the integrative view of the Madrean-Tethyan hypothesis proposed by Axelrod (1958, 1975) in which a paleoclimatical trend to aridity might explain many of the floristic and ecomorphological patterns detected in these environments. At the same time, once the mediterranean climate developed gradually after the late Cenozoic in the five different mediterranean regions, taxa under a summer-wet climate gradually adapted physiologically to the new conditions.

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