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VEGETATION AND COMMUNITY TYPES OF THE CHIHUAHUAN DESERT

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ABSTRACT

A classification of plant communities of the Chihuahuan Desert Region, inclusive of all montane habitats is presented. A total of 16 intergrading communities is recognized including eight Desert Scrub and Woodland communities: Chihuahuan Desert Scrub (with 5 facies), Lechuguilla Scrub, Yucca Woodland, *Prosopis-Atriplex* Scrub, Alkali Scrub, Gypsophilous Scrub, Arborescent Cactus Scrub, and Riparian Woodland; three Grassland communities: Grama Grassland, Sacaton Grassland, and Tobosa Grassland; a Chaparral community: Montane Chaparral; and four Montane Woodland communities: Juniper-Pinyon Woodland, Oak Woodland, Pine Woodland, and Mixed Fir Forest. Representative species in each are listed.

RESUMEN

Se Presenta una clasificación de comunidades de plantas de la región del Desierto de Chihuahua, incluyendo todos los habitats montañosos. Un total de 16 comunidades son reconocidas, incluyendo ocho comunidades de bosque y matorral: Matorral del Desierto de Chihuahua (con cinco facies), Matorral de Lechuguilla, Bosque de *Yucca,* Matorral de *Prosopis-Atriplex,* Matorral Halófilo, Matorral Yesófilo, Matorral de Cacto Arborescente, y Bosque Ribereño; tres comunidades de pastizal: Pastizal de Tobosa, Pastizal de Grama, y Pastizal de Sacatón; una comunidad de chaparral: Chaparral Montés; y cuatro comunidades de Bosque Montés: Bosque de Junípero-Piñon, Bosque de Encino, Bosque de Pino, y Bosque de Coníferas Mixtas. Se enumeran especies representativas de cada comunidad.

Vegetation in the Chihuahuan Desert Region, which we outline in the maps (Garcia 1976) accompanying the Gazetteer of the Chihuahuan Desert Region by Henrickson and Straw (1976), varies from a Desert Scrub in the Chihuahuan Desert proper to diverse non-desert vegetation types including Chaparral, Pinyon-Oak, and Oak, Pine and Fir woodlands or forests at progressively higher elevations in montane areas. We divide the Chihuahuan Desert Region into three regions following Morafka (1977). The northern Trans-Pecos Region, north of the Rio Grande consists of basins (800–)1100–1500 m in elevation with scattered, igneous-rock and limestone ranges including the igneous-rock Davis Mountains (2560 m), Chisos Mountains (2390 m), Chinati Mountains (2360 m), Quitman Mountains (1980 m), the limestone Sierra Tierra Viejas (1860 m), and Glass Mountains (1880 m), and the geologically mixed Franklin Moun-

tains (2190 m) as well as a series of smaller ranges. The region has some internal drainage but mostly drains through the Rio Grande and Pecos rivers.

The Mapimian Region extends through eastern Chihuahua and Coahuila from the Rio Grande to the transverse extension of the Sierra Madre Oriental in southern Coahuila. The region has a range and basin topography with basins 700–1200(–1400) m in elevation, many with internal drainage with small to large ephemeral lakes, some receiving rivers originating in the adjacent Sierra Madre Occidental. Most of the ranges are limestone and extend only 700–1200 m above the plains but some high ranges occur including the limestone Sierra de la Madera (3023 m), Sierra de la Menchaca (2818 m), Sierra del Carmen (2731 m), Sierra San Marcos del Pino (2645 m), Sierra Mojada (2380 m), Sierra de Paila (2370 m) and Sierra Jimulco (3135 m).

South of this region is the high plateau, the Altiplano Mexicano, which forms the Saladan Region. This region extends through parts of Zacatecas and San Luis Potosí and is a large, mostly igneous-rock, partly limestone area of moderate relief with internally draining basins from 1550–2100 m elevation with scattered, often small, dry lakes, no rivers, and only a few high ranges as the igneous-rock Sierra Astillero (3195 m) in northern Zacatecas and the Sierra de Catorce (3060 m) in northern San Luis Potosí.

This physical setting provides topographic diversity with an elevation range from about 500–3195 m, with igneous-rock, limestone, gypsum parental materials that provide a variety of substrates varying from mountain ridges, slopes, canyons to alluvial fans, fine-textured basins, saline playas, gypsum flats, silaceous and gypsum dunes as well as freshwater springs, seeps, and rivers covering some 13° (ca 1500 km) of latitudinal range that provides for a wide diversity of habitats. This is presented in a climate characterized by warm summers, cool winters, with associated periods of freezing and occasional snows during the winter months, with about 69 to 90% of the rainfall coming during the hottest summer months between May and October, with measured average rainfalls of 156–34 mm in the bolsons, recorded to 425 mm at higher elevations and unknown amount on the higher mountains and with rainfall also varying greatly from year to year.

We here present a brief description of the vegetative cover over this diverse region (Table 1). We recognize a series of often strongly intergrading plant community-types. These are designated by a combination of physiognomically, floristically, and physiographically derived names simply to provide for convenient communication. Many species occur throughout the Desert Scrub vegetation zone, varying in abundance and stature in different community-types. Other species range well outside the

TABLE 1
OUTLINE OF PLANT COMMUNITIES OF THE CHIHUAHUAN DESERT REGION

I. Desert scrub and woodlands
  A. Chihuahuan Desert Scrub (Matorral Desierto Micrófilo with 5 phases or facies).
    1. *Larrea* Scrub (Gobernadoral, *Larrea-Flourensia* Scrub).
    2. Mixed Desert Scrub (Chaparrillo).
    3. Sandy Arroyo Scrub (Matorral de Arroyos).
    4. Canyon Scrub (Matorral de Cañon).
    5. Sand Dune Scrub (Matorral de Dunas or Medanos).
  B. Lechuguilla Scrub (Lechuguillal, Matorral Desierto Rosetófilo con *Agave lechuguilla*).
  C. Yucca Woodland, *Dasylirion* Scrub or Woodland (Izotal, Sotolal, Matorral Desierto Rosetófilo).
  D. *Prosopis-Atriplex* Scrub (Mezquital).
  E. Alkali Scrub (Matorral Halofitico).
  F. Gypsophilous Scrub (Matorral Gipsofilo).
  G. Cactus Scrub (Matorral Crassicaule, Matorral Cilíndrico Crasicaule, Garambullal).
  H. Riparian Woodland (Bosque Ripario).

II. Grasslands
  A. Grama Grasslands (Navajita or Pastizal de Grama).
  B. Sacaton Grassland (Zacatonal).
  C. Tobosa Grassland (Pastizal de Tobosa, Bajo con Tobosal).

III. Chaparral
  A. Montane Chaparral (Chaparral Montano).

IV. Montane woodlands
  A. Juniper-Pinyon Woodland (Bosque de Enebros y Piñones).
  B. Oak Woodland (Bosque de Encinos).
  C. Pine Woodland (Pinares).
  D. Mixed Fir Forest (Bosque Mixto de Abetos).

Chihuahuan Desert Region. We support Gleason's (1926) individualistic concept of plant communities stressing that each species or genotypically distinct subgroup of a species has a certain range of habitat tolerances and will be expected to occur wherever environmental extremes do not exceed these tolerances providing they can be dispersed to these localities. An outline of our system is presented in Table 1 showing eight communities in a Desert Scrub and Woodland vegetation, three Grassland, one Chaparral, and four Montane Woodland communities.

Other treatments covering portions of the Chihuahuan Desert Region have been published by Shreve (1939) for Chihuahua, Muller (1939, 1947) for Nuevo León and Coahuila, Gentry (1957) for Durango, Marroquín et al. (1964) for the Mexican portion of the Desert, Rzedowski (1957, 1966) for arid portions of San Luis Potosí and Zactaceas and for San Luis Potosí. Morafka (1977) and Medellin-Leal (1982) present brief discussions of vegetation throughout the Chihuahuan Desert Region and Brown et al. (1979) and Brown (1982), present, in a digitized format, vegetation series and associations as part of their biotic communities of the American Southwest. The Secretaría de Programación y Presupuesto, Instituto Nacional de Estadística, Geografía e Informática is publishing comprehensive geographical data for each state that includes discussions of vegetation and series of maps on vegetation, geology, climate, hydrology, soils, and potential land uses. These are presently available for Coahuila, Nuevo León, and Zacatecas.

It is important to realize that man's activities have been strongly altering portions of the Chihuahuan Desert Region for years (York and Dick-Pettie 1969). Sheep, goat, and cattle grazing has occurred in some areas for over four centuries. Grasslands have been overgrazed allowing shrub encroachment. Montane forests have been completely cleared away from some ranges (e.g., the Sierra Mojada in west-central Coahuila) to provide beams for mines, vigas for houses, and charcoal for ore processing. Indigens have moved their camps from spring to spring undoubtedly dispersing seeds.

RESULTS

I. *Chihuahuan Desert Scrub and Woodlands.*—Much of the Chihuahuan Desert is covered with a low scrub vegetation mostly 0.5–2 m tall ranging from a relatively species-poor *Larrea*- or creosote bush-dominated scrub on gently sloping plains to a more species-rich Mixed Desert Scrub on upland rocky bajadas. Other species are concentrated in relation to edaphic factors. Here we recognize a series of six often intergrading community-types, some with several distinct phases. A roughly estimated cover for each vegetation type is expressed as a percentage of the total Chihuahuan Desert Region area.

A. Chihuahuan Desert Scrub: (Mattoral Desierto Micrófilo, with 5 phases or facies) ca 70%.

Larrea tridentata, Flourensia cernua, Acacia neovernicosa, Parthenium incanum, Jatropha dioica, Fouquieria splendens, Opuntia leptocaulis, O. kleiniae, O. imbricata, O. phaeacantha, O. rufida, Opuntia spp., *Euphorbia antisyphilitica, Krameria erecta, Prosopis glandulosa, P. laevigata, Leucophyllum minus, L. laevigatum, L. candidum, Tiquilia greggii, Calliandra eriophylla, Dalea formosa, Cordia parviflora, Viguiera stenoloba, Lippia graveolens, Aloysia wrightii, Koeberlinia spinosa, Mimosa binucifera, Acacia greggii, Lycium berlandieri, L. pallidum, Parthenium ar-*

gentatum, Echinocactus horizonthalonius, Condalia lycoides, Sericodes greggii, Senna wislizeni, Agave lechuguilla, A. scabra, Yucca torreyi, Y. filifera, Bouteloua ramosa, B. trifida, and species of *Ephedra, Mimosa, Buddleja, Mammillaria, Corypantha, Echinocereus, Lophophora, Dyssodia, Zinnia, Chameasaracha, Menodora, Tiquilia, Pectis, Croton, Zaluzania, Muhlenbergia, Scleropogon, Bothriochloa, Erioneuron, Aristida, Tridens, Setaria, Enneapogon, Lycurus,* etc.

The Chihuahuan Desert Scrub is the basic matrix community-type throughout the Chihuahuan Desert Region. Several distinct phases can be recognized. These phases often contain many of the same species, but in different relative abundances.

1. *Larrea* Scrub (Gobernadoral, *Larrea-Flourensia* Scrub) ca 40%.

A *Larrea* Scrub or Creosote Bush Scrub phase occurs on extensive areas of intermontane arid alluvial or outwash plains and bajadas that are dry most of the year. In these areas *Larrea tridentata* (creosote bush or gobernadora) is either quantitatively or at least visually dominant. These areas may have either sandy or commonly clayish soils but are generally of uniform texture. Many species listed above occur only as scattered individuals on these often monotonous plains (see Fig. 1). Increased diversity is commonly encountered in deeper soils and along minor drainages where the frequency of *Flourensia cernua, Acacia neovernicosa, Leucophyllum* spp., *Prosopis glandulosa, P. laevigata, Cordia parviflora, Acacia greggii, Anisacanthus* spp., and many other species commonly increase locally.

Some authors, as Rzedowski (1957) and Brown (1982), distinguish separate *Larrea, Larrea-Flourensia, Larrea-Prosopis, Acacia neovernicosa-Larrea,* or *Larrea-Flourensia-Yucca filifera* associations to reflect the diversity encountered in this community type. As these associates become more important *Larrea* scrub blends into the following phase.

2. Mixed Desert Scrub (Chaparrillo) ca 25%.

A more diversified Mixed Desert Scrub phase of the Chihuahuan Desert Scrub occurs both on slopes and on limestone and calcareous-bedded volcanic ash above the *Larrea*-dominated scrub. Here *Larrea* is often more sparse and accompanied by an often high diversity of associated species. Usually no single species is dominant over a broad area, rather the vegetation conforms to a mosiac with species composition shifting with slope, exposure, and substrate (see Fig. 2). This phase blends completely into the Lechuguilla-dominated community.

3. Sandy Arroyo Scrub (Matorral de Arroyos) ca 2%.

A distinct phase of this Desert Scrub occurs along sandy arroyo margins. In these habitats a different assemblage of species is characteristic including: *Fallugia paradoxa, Brickellia laciniata, Celtis pallida, Chilopsis linearis, Acacia berlandieri, A. greggii, Forestiera angustifolia, Juglans microcarpa, Pistacia texana, Baccharis salicifolia,* etc.

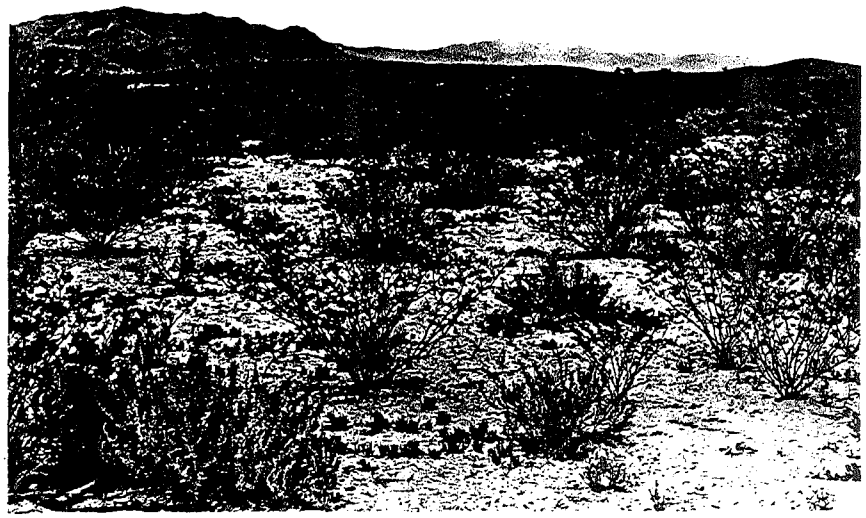

FIG. 1. A phase of *Larrea* Scrub near La Vibora in clayish plains east of Sierra Mojada in west-central Coahuila with *Larrea tridentata, Atriplex acanthocarpa, Cordia parviflora, Prosopis glandulosa,* etc.

4. Canyon Scrub (Mattoral de Cañon) ca 2%.

In rocky canyon habitats another distinct assemblage of species is encountered including: *Diospyros texana, Fraxinus greggii, Clematis drummondii, Condalia warnockii, C. fasciculata, Ungnadia speciosa, Vauquelinia angustifolia, Leucaena retusa, Berberis trifoliolata, Rhus microphylla, Sophora secundiflora, Mascagnia cana, Eysenhardia texana, Lippia graveolens, Notholaena sinuata, Pellaea* spp., *Selaginella* spp., etc.

5. Sand Dune Scrub (Matorral de Dunas or Medanos) ca. 1%.

A fifth phase of the Chihuahuan Desert Scrub occurs in sand dunes that develop on the leeward side of large dry lakes that receive sand in the inflowing waters. Large dune complexes occur in the extreme western portion of Trans-Pecos, Texas, northward into New Mexico, near Samalayuca, Chihuahua, just south of Cd. Juarez, and smaller dunes occur on the margins of dry lakes throughout the Chihuahuan Desert Region. These dunes have a relatively sparse vegetative cover of *Larrea tridentata* mixed with some characteristic dune species or psammophytes as *Psorothamnus scoparius, Artemisia filifolia, Yucca elata,* and *Prosopis glandulosa,* etc.

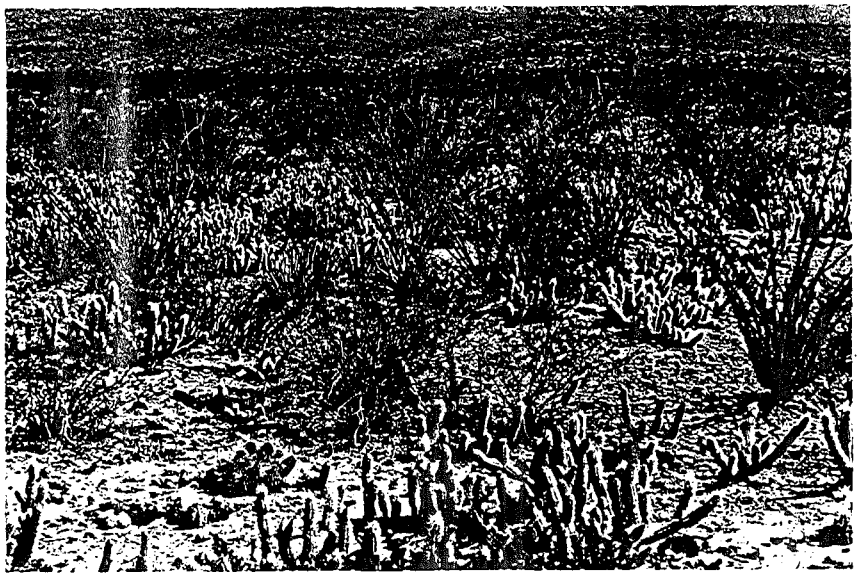

FIG. 2. Mixed Desert Scrub in limestone-derived plains 8 mi. west of Cuatro Cienegas, Coahuila, with *Larrea tridentata, Fouquieria splendens, Opuntia* (*Grusonia*) *bradtiana, Agave lechuguilla,* etc.

In the larger dune complex, as near Samalayuca, the dunes may be so mobile that shrub vegetation has little opportunity to establish. In rainy years many grasses and forbs appear among the shrubs, including *Penstemon ambiguus, Heliotropium convolvulaceum,* and species of *Abronia, Croton, Palafoxia, Cordylanthus,* etc.

During the summer flowering season many annual and perennial herbs develop in the understory of the *Larrea* and Mixed Desert Scrub areas. These include a number of C4-annual species as *Aristida adscensionis, Allionia incarnata, Tidestromia lanuginosa, Erioneuron pulchellum,* and species of *Euphorbia, Pectis, Boerhaavia, Amaranthus,* etc. Additional C3-annuals include *Oligomeris linifolia,* and *Bahia absinthifolia.* Perennial herbs include species of *Croton, Chamaesaracha,* and in some areas *Scleropogon brevifolius, Nyctaginea capitata,* and others.

We have then in the Chihuahuan Desert Scrub a series of species whose local abundance varies according to habitat. The plains are often dominated by *Larrea tridentata,* as topography increases on the alluvial fans, species diversity greatly increases. On extrusive-igneous-rock the *Larrea* Scrub often intergrades with a degraded Grama Grassland. On limestone or calcareous-bedded volcanic-ash substrates *Larrea* Scrub may intergrade into more species-rich community-types as the Mixed Desert Scrub or the *Agave lechuguilla*-dominated scrub. This transition is very gradual with *Larrea* remaining as a component in all these phases.

B. Lechuguilla Scrub (Lechuguillal, Matorral Desierto Rosetofilo con *Agave lechuguilla*) ca 7%.

Agave lechuguilla, Hechtia scariosa, Parthenium argentatum, P. incanum, Fouquieria splendens, Acacia neovernicosa, Tiquilia greggii, Jatropha dioica, Zexmenia brevifolia, Euphorbia antisyphilitica, Viguiera stenoloba, Dalea formosa, Calliandra eriophylla, Eysenhardtia parvifolia, Buddleja marrubifolia, Mortonia scabrella, Morntia spp., *Chrysactinia mexicana, Aloysia* spp., *Ephedra* spp., *Brickellia* spp., *Dalea* spp., *Opuntia leptocaulis, O. kleiniae, O. phaeacantha, O. rufida, Echinocereus stramineus, E. pectinatus, Ariocarpus fissuratus, A. retusis, Thelocactus bicolor, Yucca carnerosana, Y. torreyi, Y. filifera, Dasylirion* spp., *Agave falcata, Notholaena sinuata, Pellaea* spp., *Selaginella lepidophylla, Erioneuron pulchellum, Bouteloua* spp., *Muhlenbergia* spp., etc.

Many areas suitable for the mixed phase of Chihuahuan Desert Scrub, i.e., on more exposed, well drained limestone alluvial slopes and ridges have instead dense stands of *Agave lechuguilla,* a rosette species that spreads by rhizomes often forming dense patches. The erect leaves rise 2–6 dm above ground level and have very sharp terminal and marginal spines. Associates include the above listed species, all of which also occur in adjacent communities as does lechuguilla itself. This community could just as well be considered another phase of a microphyllous Chihuahuan Desert Scrub in that it grades completely into that community, but it differs in composition and has traditionally been recognized as a distinct community.

Lechuguilla Scrub is best developed on limestone substrate but also occurs on igneous-rock substrates. The effect of basic limestone and acidic igneous-rock substrates on plant distribution is of some interest. Whittaker and Niering's (1968) quantitative studies of vegetative cover on limestone versus igneous-rock substrates in the Santa Catalina Mountains in southeastern Arizona showed that vegetative cover on limestone was rather consistently more xerophytic than that on igneous-rock substrates at comparable elevation and exposure. They record shifts of oak-pine forests and woodland on diorite to *Cercocarpus*-dominated scrub on limestone. They also found shifts of open oak woodlands and desert grasslands on diorite to desert grasslands and desert scrub respectively at comparable elevations and exposures on limestone. They noted a general trend of xerophytic species ranging into higher elevations on limestone—they are usually replaced by more mesic species on igneous-rock substrates. Rzedowski (1955), using floristic methods, recorded similar vegetation changes

between rhyolite and limestone substrates in a series of locations in San Luis Potosí, recording shifts from cactus-mesquite scrub (equal to his Matorral Crasicaule) on igneous-rock-derived soils to a limestone desert scrub (equal to his Matorral Desierto Rosetófilo) on limestone-derived soils. Other comparisons of his show changes in species compositions between oak woodlands and grasslands between igneous-rock and limestone substrates. Similar shifts in vegetation or species composition can be observed between igneous-rock and limestone substrates throughout the Chihuahuan Desert but this has not been well studied. Likewise the causal factors associated with the change from rather uniform stands of *Larrea* on deep, fine-textured alluvial soils to the more mixed shrub composition on rockier soils and mixed shrub-leaf-succulent stands on rocky limestone outcrops also have not been analyzed. Whittaker and Niering (1968) consider the principal cause of xeric nature of rocky limestone habitats to be associated with drying soils affected by drainage through subsurface cracks and fissures.

While many species occur on both limestone and igneous-rock substrates, providing their moisture requirements are met, other species tend to favor, and some appear to be restricted to one substrate or the other. As rocky limestone substrates are so common through much of the Chihuahuan Desert Region, many Chihuahuan Desert species are often considered restricted to this substrate. Some of these (*Fenderella, Mortonia,* and *Buddleja*) occur on limestone outcrops well outside the Chihuahuan Desert Region as far west as the Mojave Desert of California where they are often considered disjunct Chihuahuan Desert elements. We would suggest they are more correctly considered calciphytic elements.

C. *Yucca* Woodland, *Dasylirion* Scrub or Woodland (Izotal, Sotolal, Bosque de Palma, Matorral Desierto Rosetófilo) ca 5%.

Yucca carnerosana, Y. faxoniana, Y. torreyi, Y. rostrata, Y. filifera, Dasylirion leiophyllum, D. texanum, Agave lechuguilla, A. falcata, A. striata, Hectia scariosa, Acacia berlandieri, A. constricta, Aloysia wrightii, Euphorbia antisyphilitica, Jatropha dioica, Chrysactinia mexicana, Forestiera angustifolia, Fouqueria splendens, Gochnatia hypoleuca, Gymnosperma glutinosum, Lippa graveolens, Parthenium argentatum, P. incaum, Leucophyllum canescens, L. laevigatum, L. frutescens, L. minus, Mimosa biuncifera, Condalia warnockii, C. fasciculata, Rhus microphylla, R. virens, Randia pringlei, Ungnadia speciosa, Zexmenia brevifolia, Larrea tridentata, Viguiera stenoloba, Opuntia phaeacantha, O. tunicata, O. leptocaulis, O. kleiniae, O. stenopetala, Opuntia spp., *Echinocereus pectinatus, Echinocactus horizonthalonius, Senecio douglasii,* and species of *Mammillaria, Corypantha, Ferocactus, Epitelantha, Bouteloua, Eragrostis, Enneapogon, Setaria, Heteropogon, Croton, Menodora, Euphorbia, Notholaena, Pellaea, Polygala, Selaginella,* etc.

FIG. 3. Yucca Woodland on limestone slopes on the northern edge of the Sierra de la Madera in central Coahuila, with *Yucca faxoniana, Gymnosperma glutinosum, Fouquieria splendens, Parthenium incanum, Viguiera stenoloba,* and species of *Opuntia, Lycium, Buddleja, Senecio, Agave, Acacia, Fraxinus,* etc.

The larger arborescent rosette-leaved yuccas (izotes) and dasylirions (sotols) are among the most conspicuous and picturesque elements in the Chihuahuan Desert Region (Fig. 3). Where they occur in large numbers they visually, though rarely quantitatively, dominate the landscape causing these areas to be designated as distinct communities of Izotal, Sotolal, Bosque de Palma, etc. In the Chihuahuan Desert Region extensive areas of Izotal or Sotolal occur on limestone hills and slopes above the Desert Scrub zone up to Montane Chaparral. *Yucca canerosana,* or its scarcely distinct phase *Y. faxoniana,* or in other areas *Dasylirion leiophyllum* or *D. texanum* are conspicuous elements among a highly variable grass-shrub-dominated understory, most of which continues into the Mixed Desert Scrub at lower elevations. Some of these areas, particularly those dominated by *Dasylirion* have high concentrations of grasses and could as well be considered Desert Grasslands rather than Desert Scrub. This zone is of interest because of its species diversity and the variety of plant associations encountered. In many areas the conspicuous *Yucca* or *Das-*

ylirion species are of reduced frequency or drop out altogether leaving their Desert Scrub associates.

Other *Yucca* species can also form conspicuous associations. *Yucca torreyi* occurs scattered in the *Larrea* and Mixed Desert Scrub almost throughout the desert. A race of *Y. treculeana* is conspicuous among the gypseous dunes of the Cuatro Cienegas Basin. *Yucca elata* occurs commonly in sandy arroyos and in transitions from desert to grassland as well as in some dune areas. The only area where large yuccas have appreciable coverage is in the Saladan Region in northern Zacatecas and San Luis Potosí where the gigantic *Yucca filifera* (izote, palma) may form relatively dense stands to 8 m in height in association with *Larrea tridentata* and its associates. This formation has been called an Izotal or Bosque de Palma but it could as well be included as a phase of *Larrea* Scrub.

Local or extensive stands of large sawleaf-rosettes of *Dasylirion* species (sotol) often occur in the Mixed Desert Scrub and Montane Chaparral usually on steeper calcareous slopes. Such stands can be called Sotalal. They share many of the same associates with Izotal.

D. *Prosopis-Atriplex* Scrub (Mezquital) ca 5%.

Prosopis glandulosa, P. laevigata, Atriplex canescens, Lycium berlandieri, L. pallidum, L. torreyi, Ziziphus obtusifolia, Z. lloydii, Opuntia inbricata, O. kleiniae, Opuntia spp., *Agave scabra, Ericameria triantha,* with *Larrea tridentata, Flourensia cernua, Sporobolus* spp., *Muhlenbergia* spp.

In deep, fine alluvium, especially where more or less fresh water is available at depths of 3–10 m, and sometimes in low areas where water briefly stands as well as near shallow arroyos, in alluvial fans and bajadas, the Desert Scrub grades into a taller scrub or short woodland at least visually dominated by mesquite (*Prosopis glandulosa* over much of the Chihuahuan Desert Region or *P. laevigata* in the Saladan Region) mixed with representatives of the species noted above. Most of these shrubs tend to be taller (2–4 m) and they may occur in greater densities than shrubs of the true Desert Scrub. This density may be related to availability of water. Thus Mezquital habitats are less xeric than Desert Scrub habitats and may be considered at least in part non-desert. Where salinity increases this grades into Alkali Scrub. Mesquite also may be an important component of Desertic Scrub particularly along the eastern boundary of the Chihuahuan Desert Region.

E. Alkali Scrub (Matorral Halofítico) ca 2%.

Atriplex acanthocarpa, A. canescens, A. obovata, Allenrolfea occidentalis, Sesuvium verrucosum, Suaeda suffrutescens var. *detonsa, S. palmeri, S. nigrescens, Distichlis spicata, Sporobolus wrightii, S. spartinae, Limonium limbatum, Ariocarpus kotschoubeyanus,* etc.

The internally drained basins of the Chihuahuan Desert Region have small to large, nearly flat bottoms where diverse combinations of chlorides, carbonates, and sulfates accumulate. During dry seasons these become concentrated through evaporation only to be diluted and partially dissolved again during the season of rain when runoff often produces extensive shallow lakes that persist for days or weeks. Only certain especially adapted halophytic plants can exist in such habitats. As in gypsum flats, saline habitats are dispersed like islands through the Chihuahuan Desert Region providing the isolation that enhances evolutionary change. Henrickson (1977) notes that 25 of 40 recorded halophytic species are endemic to the Chihuahuan Desert Region including three endemic genera *Meiomeria, Reederochloa,* and *Pseudoclappia,* the latter also occurring on gypsum. In less saline areas, there is gradation to *Prosopis-Altriplex* Scrub, or Sacaton Grassland to Tobosa Flat community-types. Saline habitats can also occur over gypsum substrates giving saline-gypsum habitats.

F. Gypsophilous Scrub (Matorral Gipsõfilo) ca 2%.

Tiquilia hispidissima, T. gossypina, Petalonyx crenatus, Isocoma gypsophila, Ericameria triantha, Machaeranthera gypsophila, M. restiformis, Atriplex reptens, Fouquieria shrevei, Dalea filiformis, Euphorbia astyla, Dicranocarpus parviflorus, Dyssodia gypsophila, and species of *Garillardia, Nama, Anulocaulis, Selinocarpus, Drymaria, Flaveria, Nerisyrenia* as well as *Larrea tridentata, Acacia neovernicosa, Viguiera dentata, Gymnosperma glutinosum, Gutierrezia* spp., etc.

Local to extensive deposits of gypsum (hydrated calcium sulfate, rarely associated with its anhydrite form, sleenite) occur scattered throughout the Chihuahuan Desert Region. The gypsum deposits, like limestone, were formed by precipitation from and/or evaporation of ancient seas and probably have been exposed in the region since early Tertiary times. Physically, gypsum deposits are recognized only with experience. Chihuahuan Desert Region deposits may consist of extensive pure gypsum flats or hills or they may be bedded with limestone. The deposits tend to be white, tan or grayish, and resemble clay or marl. They may be superficially compact but are generally friable and often emit a distinctive hollow ringing sound when pounded or stamped upon. But the easiest way to recognize gypsum is by the characteristic assemblage of obligate, or near obligate gypsophylic plant species that are restricted to these outcroppings. The scattered island-like gypseous outcroppings tend to have a very open plant cover consisting of those species that can tolerate the high sulfate conditions. Though some annuals occur on gypsum, most of the flora consists of perennial shrubs or herbs. Some gypsophilous species differ from non-gypsophilous relatives in their distinctive cespitose habit. As gypsum can hold water to some degree, development of an extensive root

system allows utilization of this resource. The gypsum habitat is thought to be a refugium for those plants that can tolerate the soil. As noted above, some of these species occur only on gypsum, but most are facultative and also can occur on adjacent soil types. Of great interest is the number of endemic species (about 70) restricted to gypsum in the Chihuahuan Desert Region. This includes members of four endemic genera restricted to gypsum (*Dicranocarpus, Marshalljohnstonia, Petalonyx, Strotheria*) and other genera mostly restricted to gypsum (*Anulocaulis, Selinocarpus, Nerisyrenia, Sartwellia, Pseudoclappia,* etc.). A listing of putatively facultative and obligate gypsophiles is given by Powell and Turner (1977). Some obligate gypsophiles, i.e., *Dicranocarpus* appear to occur in almost all the gypsum deposits; other gypsophilic species are restricted to one or a few deposits. This community intergrades with *Larrea* Scrub phase of Chihuahuan Desert Scrub and with the Sacaton Grassland and occasionally with Saline Flats providing a restrictive saline-gypseous habitat.

G. Arborescent Cactus Scrub (Matorral Crasicaule, Matorral Cilíndrico Crasicaule, Garambullal) less than 1%.

Myrtillocactus geometrizans, Stenocereus pruinosus, Prosopis laevigata, Acacia constricta, Yucca filifera, Mimosa spp., *Gymnosperma glutinosum, Jatropa dioica,* in other areas *Opuntia streptacantha, O. leucotricha, O. microdasys,* and various species of *Agave, Opuntia,* and grasses.

The Arborescent Cactus Scrub has two distinct phases in the Chihuahuan Desert Region, both restricted to the Saladan area in Zacatecas and San Luis Potosí and both occurring on igneous-rock derived soils. There are a few, scattered, relatively flat or gently sloping areas at about 1700 m elevation in San Luis Potosí (as near Los Bocas) about 40 km north of Cd. San Luis Potosí and along the southwestern edge of the Chihuahuan Desert Region that support stands of the conspicuous candelabriform cacti *Myrtillocactus geometrizans* (garambullo) sometimes mixed with the allegedly introduced *Stenocereus pruinosus* (pitayo) 4–6 m tall. Both of these species have their main distributions south of the Chihuahuan Desert Region. *Myrtillocactus* occurs as scattered individuals in a broad area in the southern Chihuahuan Desert Region in a Mixed Desert Scrub and only rarely does it occur in concentrated stands.

A second phase of Arborescent Cactus Scrub occurs along the southern border of the Chihuahuan Desert Region in Zacatecas and San Luis Potosí where arborescent "tuna" cacti are often conspicuously dominant. The prominent cacti include *Opuntia leucotricha* (nopal duraznillo) and *O. streptacantha* (nopal cardon), which are often 2–4 m tall, and the shorter *O. robusta* (nopal tapon). These plants are of considerable economic importance as they provide nutritious fruits known as tunas (both colorado and verde). They can also be cut for stock forage but usually they grow

so densely as to critically reduce pasturage available to livestock. The extensive exploitation and intensive human management and disturbance in these areas leads to the supposition that they may represent parts of an essentially anthropogenic agroecosystem, even though the species involved are indigenous to this general region. Animal exclosure plots have shown that grasses quickly recover when grazing is removed (S. Meyer, pers. comm.). This phase of Arborescent Cactus Scrub occurs between the Chihuahuan Desert Scrub to the east and grasslands to the west. Many of the understory plants in this phase of Cactus Scrub are characteristic of the desert scrub but basically we exclude most of this phase of cactus scrub from the Chihuahuan Desert Region.

H. Riparian Woodland (Bosque Ripario) less than 1%.

Salix gooddingii, Salix spp., *Chilopsis linearis, Prosopis glandulosa, P. pubescens, Fraxinus velutina, Populus fremontii, Baccharis salicifolia, Phragmites australis,* and the introduced *Tamarix ramosissima* and *Arundo donax.*

Riparian Woodlands are well developed along a few portions of the Rio Grande, Rio Conchos, and other permanent rivers that cross the Chihuahuan Desert Region. The above listed species often occur in narrow galleries or in some places rather broad thickets along the rivers. However, in many areas along these rivers, Riparian Woodland is very poorly developed. Where marginal mesic habitats occur, certain herbaceous species may be encountered, such as species of *Sabatia, Samolus, Eleocharis,* etc. Unfortunately in many areas native species are being displaced by the introduced vigorous *Tamarix ramosissima* and *Arundo donax.*

II. *Grasslands.*—Grasslands occur within the Chihuahuan Desert Scrub as local stands of Sacaton Grasslands and Tobosa Grasslands, and as local or extensive stands of Grama Grasslands that continue well outside the limits of the Chihuahuan Desert Region proper.

A. Grama Grasslands (Navajita or Pastizal de Grama) ca 5%.

Bouteloua gracilis, B. curtipendula, B. eriopoda, B. chasei, Bothriochloa alta, B. saccharoides, Lycurus phleoides, Stipa eminens, Aristida glauca, Muhlenbergia monticola, Muhlenbergia spp., with *Mimosa binucifera, Buddleja marrubifolia, Acacia constricta, Yucca elata, Zinna* spp., etc.

Grama grasslands cover large gentle to moderate slopes of coarse sandy soils derived from extrusive igneous rocks, usually rhyolite or andesite, and are most extensive in a zone west of the Chihuahuan Desert Region along the lower eastern margin of the Sierra Madre Occidental at 1300–1900 m. They reappear at similar altitudinal zones in the Chihuahuan Desert Region in archipelagic fashion on large to small, island-like igneous-rock mountain-masses such as the Davis Mountains of Trans-Pecos Texas, the Sierra Maderas del Carmen of northern Coahuila and many

smaller igneous-rock masses scattered within the Chihuahuan Desert Region such as the Sierra del Rancheria in Chihuahua. The main grasses are *Bouteloua gracilis, B. curtipendula,* and *B. eriopoda,* but a great many other species are present, as are forbs. The plants usually cover at least three-fourths of the ground-surface and rise to about 3–5 dm (up to 1 m following late summer and early fall rains). The Grama Grasslands intergrade downslope with *Larrea* Scrub. At contacts between limestone and igneous rocks there can be a dramatic and rather sharp contact between Grama Grasslands on igneous rocks and other community-types such as Mixed Desert Scrub or Lechuguillal or Sotalal on calcareous substrates. This kind of contact does not depend on the relative position on the slope and illustrates a high level of edaphic control of vegetation cover.

When overgrazing and subsequent erosion seriously deplete the humic soil and bring the hardpan or parent rock near the surface the grassland yields to what can be called a Degraded or Desert Grassland facies with the invasion of many kinds of spindly shrubs. This shrubby formation can at times somewhat resemble in both physiognomy and species-composition the Mixed Desert Scrub community, but often has appreciable quantities of *Opuntia imbricata, Agave lechuguilla, Yucca elata, Condalia ericoides, Rhus microphylla,* species of *Dasylirion, Dalea, Mimosa,* and even clumps of *Prosopis glandulosa* and *Larrea tridentata.* Near arroyos, *Aloysia gratissima, Fallugia paradoxa, Celtis pallida,* and *Prosopis glandulosa* are conspicuous elements.

A subtype of Grama Grassland with *Bouteloua chasei,* occupies a relatively small (ca 150 km^2) gypseous limestone karstic basin, the San Roberto Basin in Nuevo León at about 1700 m and also occurs in a similar limited area in extreme northern San Luis Potosí. These areas have a number of other endemics as well.

B. Sacaton Grassland (Zacatonal) ca 2%.

Sporobolus airoides, S. wrightii, Prosopis glandulosa, Atriplex canescens, A. obovata, A. acanthocarpa, Lycium berlandieri, L. torreyi, Suaeda spp., etc.

Sacaton Grasslands occur in scattered localities in deep calcareous alluvial deposits near arroyos and in intermontane habitats along the margins of *Prosopis* communities or mosaically intertwined within mesquite where large tussocks of *Sporobolus airoides* often dominate the landscape. Possibly this community-type should be considered a phase of the Mezquital for most of the species are shared. Often species are present from the *Larrea* Scrub phase of Desert Scrub as well. It sometimes appears that the soils supporting the *S. airoides* may be slightly more saline on the average than those supporting the nearby *Prosopis* and *Atriplex* but

we have no confirmation that this is correct. It should be noted that tussocks of *S. airoides* occur scattered in other community-types such as Grama Grassland and *Prosopis-Atriplex* Scrub, etc., where salinity is certainly low.

C. Tobosa Grassland (Pastizal de Tobosa, Bajo con Tobosal) ca 2%.

Hilaria mutica with *Scleropogon brevifolius, Sporobolus airoides, Prosopis glandulosa, Hoffmanseggia glauca,* etc.

In some enclosed basins with internal drainage and on flats in the northern Chihuahuan Desert Region south to central Chihuahua and Coahuila, where salts do not accumulate to appreciable levels, the fine-textured alluvial clay soils support extensive stands of tobosa grass (*Hilaria mutica*). Texas ranchers call these areas Tobosa Flats. They are usually almost pure, monospecific stands of tobosa grass and can incorporate hundreds of hectares of almost unbroken grassland with the culms rising usually only about 3–5 dm. Since the plants primarily reproduce by rhizomes, the possibility exists that a stand 0.5 km^2 or more may represent only a single clone. Tobosa grass can also occur on upland mesas, hills, and rocky substrates as well as on gypsum. Tobosa Flats may intergrade downslope with Alkali Flats and upslope with Mezquital or occasionally they intergrade into *Larrea*-dominated phase of Desert Scrub and Grama Grasslands.

III. *Montane Chaparral.*—The middle and often upper slopes and lower canyons of the mountain ranges throughout much of the Chihuahuan Desert Region are covered with a more mesic Chaparral vegetation. Many of the species also occur in Chaparral vegetation on the adjacent Sierra Madre Oriental or Occidental.

A. Montane Chaparral (Chaparral, Chaparral del Montano) ca 5%.

Quercus pungens, Q. invaginata, Q. hypoleucoides, Q. pringlei, Q. imbricata, Q. hypoxantha, Q. potosina, Cercocarpus montanus var. *glaber, C. m.* var. *paucidentatus, C. fothergilloides* var. *mojadensis, Fraxinus greggii, Rhus virens, R. aromatica, Garrya ovata, G. wrightii, Ceanothus fendleri, C. greggii, Berberis trifoliolata, Lindleya mespiloides, Arctostaphylos pungens, Ptelea trifoliolata, Sophora secundiflora, Chrysactinia mexicana,* and species of *Mimosa, Salvia, Eupatorium, Agave, Nolina, Dasylirion,* grasses, etc.

The Grama Grassland on igneous rock, the Mixed Desert or Lechuguilla or Izotal Scrub on limestone substrates throughout the Chihuahuan Desert Region grade upward into a complex and species-rich Montane Chaparral community on mountain slopes. The vegetation consists of shrubs 1–2 m tall with relatively small, hard-textured, usually persistent or semideciduous leaves. Depending on exposure, Chaparral can be very dense or open with a grass-dominated understory. The component species ex-

tend into Juniper-Pinyon zones and many species continue up to Pine or Oak Woodlands.

IV. *Montane Woodlands.*—Only the larger ranges in the Chihuahuan Desert Region contain Pinyon and true Oak, Pine or Fir forests. For the most part these community-types are relatively species poor.

A. Juniper-Pinyon Woodland (Bosque de Enebros y Piñones) ca 1%.

Pinus edulis var. *edulis, P. cembroides, P. remota, P. johannis, Juniperus erythrocarpa, J. deppeana, J. pinchotii, Rhus aromatica, Ceanothus fendleri, Chrysactinia mexicana, Fraxinus cuspidata, F. greggii,* and species of *Quercus, Nolina, Opuntia, Dasylirion, Agave, Salvia, Bouteloua, Stipa, Sporobolus, Muhlenbergia, Sorghastrum,* etc.

Juniper-Pinyon Woodland occurs on scattered higher mountains throughout the Chihuahuan Desert Region mostly above the Montane Chaparral zone or on dry exposed slopes in the same altitudinal zone as Chaparral generally between 1300 and 2400 m. The understory associates are generally the more xeric-tolerant Chaparral species and grasses.

B. Oak Woodland (Bosque de Encinos, Encinal) less than 1%.

Quercus gravesii, Q. glaucoides, Q. grisea, Q. emoryi, Q. muhlenbergia, Q. pringlei, Q. hypoxantha, Q. intricata, Q. invaginata, Pinus cembroides, Juniperus flaccida, J. erythrocarpa, Prunus mexicana, P. serotina, Rhamnus betulifolia, Garrya ovata, G. wrightii, Fraxinus cuspidata, Ptelea trifoliolata, Lonicera albiflora, Acer grandidentatum, Salvia regla, Arbutus xalapensis, and species of *Nolina, Agave, Vitis,* grasses, etc.

Those same mountains that are high enough to support Juniper-Pinyon Woodland usually have at about the same altitudinal zone but within more sheltered canyons or relatively mesic northern slopes an Oak Woodland or sometimes an Oak-Pine Woodland with trees rising 3–6(–10) m in height. The Oak Woodland grades into Juniper-Pinyon Woodland or Scrub or Chaparral on more exposed slopes and upward to Mixed Conifer-Oak Woodlands.

C. Pine Woodland (Pinares) less than 1%.

Pinus ponderosa var. *scopulorum, P. arizonica* var. *stormiae, P. strobiformis, Quercus greggii, Q. hypoleucoides, Q. gravesii, Cupressus arizonica, Arbutus xalapensis, Acer grandidentatum, Tilia* sp., *Agave potrerana, Prunus serotina,* and species of *Salvia, Garrya, Ceanothus, Rubus, Nolina, Carex,* and various grasses.

True Pine Woodlands occur only in higher flats and slopes of a few mountain ranges. In Texas they occur in the Davis and Chisos mountains; in Coahuila in the Sierra Maderas del Carmen, Sierra Santa Fe del Pino, Sierra de la Madera, and Sierra de San Marcos del Pino; in Zacatecas the Sierra del Astillero and Sierra de Mazapil near Concepcion del Oro. In

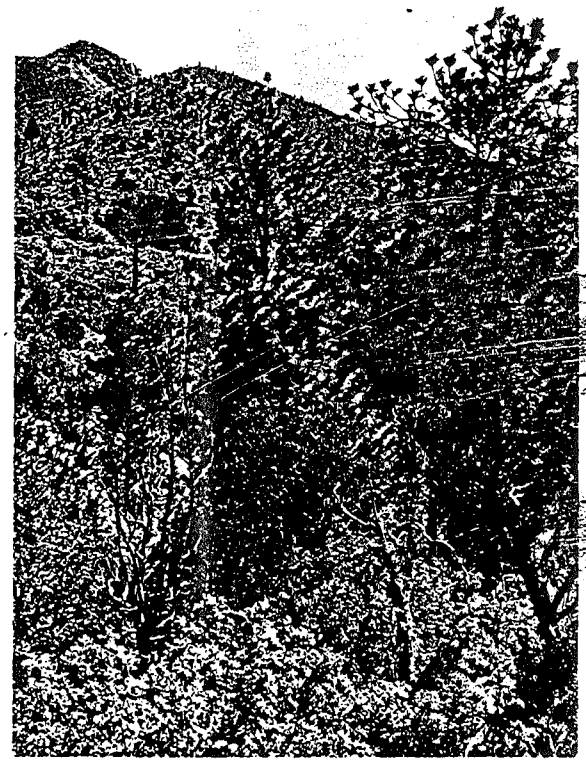

FIG. 4. Pine Woodland on the marginal slopes of the central valley in the Sierra Santa Fe del Pino in north-central Coahuila with *Pinus arizonica* var. *stromiae, Pinus cembroides, Quercus glaucoides, Q. gravesii,* and an understory of Chaparral species.

most of these ranges the Pine Woodland occurs as a mixed Oak-Pine Woodland or Forest (Fig. 4). These taxa also extend down into mesic north-facing canyons. Other mountains that one would expect altitudinally to have pine forests do not. This may be due to their orientation to prevailing moisture-carrying winds or in some cases due to past removal of forests by man within historic times as in the Sierra Mojada.

D. Mixed Fir Forest (Bosque Mixto de Abetos) less than 1%.

Pseudotsuga menziesii, Abies durangensis var. *coahuilensis, Pinus arizonica* var. *stormiae, P. ponderosa* var. *scopulorum, P. strobiformis, Cupressus arizonica, Quercus greggii, Q. rugosa, Q. sideroxyla, Cornus sto-*

FIG. 5. Mixed Fir Forest on the north side of the limestone Sierra de la Madera in central Coahuila with *Abies durangensis* var. *coahuilensis, Pseudotsuga menziesii, Quercus greggii,* etc.

lonifera, Holodiscus dumosus, Arctostaphylos pungens, Agave potrerana, and species of *Nolina, Lonicera, Physocarpus, Rosa, Salix, Carex, Stipa,* and other grasses.

True Fir Forest with both *Abies* and *Pseudotsuga* occurs only in two ranges in the Chihuahuan Desert Region. Rather extensive stands occur in the Sierra Maderas del Carmen in northern Coahuila (about 80 km^2) and on the north slopes of the Sierra de la Madera (Fig. 5) in central Coahuila (about 20 km^2). In both ranges the firs extend from about 2500–3000 m elevation and occur mixed with pines and oaks to form a Mixed Fir Forest. Both are subject to commercial logging.

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ER: The scene on the cover was photographed by Harry Gordon in Big Bend National k, Brewster County, Texas. Sue Peaks and Sierra del Caballo Muerto are in the background a Chihuahuan Desert indicator plant—lechuguilla (*Agave lechuguilla*) in the foreground.

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