En: Ramammorthy, T.P., J. Fa, R. Bye y A. Lot (Eds.). 1993. *The biological diversity of Mexico: origins and distributions*. Oxford University Press.

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Conservation-Oriented Analysis of Mexican Butterflies: Papilionidae (Lepidoptera, Papilionoidea)

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Mexican Papilionoidea is composed of five families, over 20 subfamilies, about 50 tribes, 400 genera and just over 2,200 species. A conservation-oriented analysis of Mexican Papilionidae is presented here. Brief historic accounts of taxonomic and biogeographic aspects of the study of the family are given. Pertinent data from other families, mainly Pieridae and Nymphalidae, have been incorporated where appropriate to reinforce conclusions regarding areas of endemism and species richness. Several biogeographic patterns are identified. The southwestern part of the Nearctic region, mainly the United States and Mexico, are indicated as areas supporting relictual elements of the group. The various levels of diversity in the group (Lepidoptera) in the country, including many endemic taxa, suggest that Mexico has been an active center of speciation at both specific and transspecific levels. Fifty-seven species of Papilionidae are recognized in Mexico; species endemism is over 10%. Tropical deciduous and montane cloud forests are notably rich in Papilionidae. Among the areas richest in Papilionidae in Mexico are Los Tuxtlas (Veracruz) and Sierra de Juárez (Oaxaca), but areas richest in endemic taxa are border areas between the states of Morelos and Guerrero followed by Cañón del Novillo (Tamaulipas). Northern Mexico is generally poorer in butterflies than southern Mexico. The problems in the conservation biology of Mexican butterflies are discussed: habitat destruction resulting from man's activities and unrestricted commercial trade in Lepidopterans seem to be among the primary causes. The need for comprehensive studies is empahsized, and suggestions are offered for conservation and management of these diverse populations.

Mexico contains important biogeographic provinces that are species-rich, are high in endemics, contain primitive or plesiomorphic groups, and embrace zones of relictual biota. This chapter discusses these aspects in relation to butterflies, with the aim of evaluating the diversity of the Papilionidae of Mexico. After the Coleoptera, the Lepidoptera, of which

Table 4.1. Transspecific taxa in Mexican Papilionidae through time

Year	Tribe	Subtribe	Genus	Subgenus	Species Group
1758[1]	1	1	1	None	1
1836[2]	1	1	1	None	7
1879–1901[3]	2	2	2	None	12
1906[4]	2	2	2	None	16
1940[5]	2	2	2	None	—
1944[6]	4	5	4	None	—
1961[7]	5	5	6	Yes	17
1983[8]	5	6	9	Yes	17
1987[9]	5	6	6	Yes	—
This report	5	6	12	None	17

See text for details.
[1]Linnaeus; [2]Boisduval; [3]Godman & Salvin; [4]Rothschild & Jordan; [5]Hoffmann; [6]Ford; [7]Munroe; [8]Hancock; [9]Miller.

the Papilionidae is part, is the richest order, comprising roughly 200,000 species worldwide. Approximately 25,000 of them, including many paleoendemics and neoendemics, are found in Mexico, thus making it one of the countries with the highest diversity, along with Brazil and Indonesia. The Mexican Papilionidae family is composed of about 57 taxa. Its small size lends itself to an analysis of diversity. For comparative purposes, data from other families, particularly Pieridae and Nymphalidae, have been included in this study. Collins and Morris (1985) provided an excellent introduction to the biology and conservation of Papilionidae that has served as an invaluable background for the present survey. A brief historical review of the study of the family precedes discussion on the diversity of the family in Mexico.

Knowledge of diversity and of the nature of endemism are critical in conservation-oriented studies. Diversity, which has eluded definition, is conceptualized differently by authors with varying backgrounds. It should have greater biological significance, reflecting the evolutionary histories of organisms of an area; but it is usually equated with species richness (Rosenzweig, 1975; Wilson, 1988; other contributions in this volume). Discussions of diversity lay much emphasis on the term endemism, but there is some disagreement on its use. It is used here to suggest a restricted distribution. Taxa may be paleoendemic or neoendemic. In this chapter, those that are centered in Mexico or have their major distribution in the country are considered quasiendemic. Conservation biology generally stands to benefit from discussions of the interrelation of centers of endemism (Nelson, 1983; Patterson, 1983), as they may be useful when assigning priority to areas in need of conservation. In Mexico, conservation biology is intimately associated with preservation of the habitats of the

Table 4.2. Species and subspecies recognized in Mexican Papilionidae through time

Year	Species	Species indicated	Subspecies indicated
1758[1]	4	0	0
1836[2]	29	11	11
1879–1901[3]	49	41	41
1906[4]	53	43	55
1940[5]	52	52	65
1966[6]	57	51	62
1975[7]	57	47	57
1978[8]	59	58	71
1981[9]	44	41	52
1984[10]	62	62	70
1988[11]	57	57	82

See text for details
[1]Linnaeus; [2]Boisduval; [3]Godman & Salvin; [4]Rothchild & Jordan; [5]Hoffmann; [6]D'Almeida; [7]Tyler; [8]Díaz & De la Maza; [9]D'Abrera; [10]Beutelspacher; [11]LLorente & Luis.

monarch butterflies, *Danaus plexippus*, which migrates southward by the millions to overwinter in the central Mexican state of Michoacán, draping the firs and pines near Angangueo, among other places.

HISTORY

The history of taxonomic studies of this family in Mexico is summarized in Tables 4.1 and 4.2. Table 4.1 presents the gross taxonomy of Papilionidae accepted in ten relevant studies listed chronologically. The rank of subfamily has not been included as there has been no significant change at this level since the work of Rothschild and Jordan (1906). Recognition of transspecific taxa has increased over time except at the level of subgenera. In the case of monotypic groups (e.g., *Baroniini*), the intermediate subgroups (*Baroniini* and *Baroniina*) have been included. Table 4.2 lists, sequentially, species and subspecies recognized in 11 studies. The "recognized species" here include those whose original descriptions did not provide localities or areas of distribution in Mexico. "Species indicated" and "subspecies indicated" include those whose distribution in Mexico has been provided in the cited works. In cases where subspecies have not been designated by an author, one has been included for each indicated species. Figure 4.1 depicts the early surge in recognized and indicated species which, after a steady climb during the nineteenth century, stabilized at 58 ± 3 around the beginning of the 1960s. Although species concepts have varied among

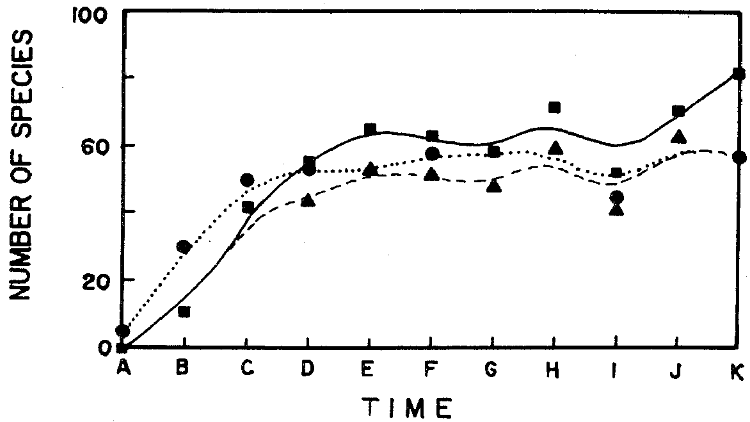

Figure 4.1. Species numbers of Papilionidae recognized over time. Circles, recognized species; Squares, indicated species; Triangles, indicated subspecies.

authors, recognition of specific groups (species or subspecies) has remained approximate (Fig. 4.1). The number of infraspecific taxa accepted by authors during the period 1975–1990 has stayed at 72 ± 8.

The difference in the number of species in the recognized or indicated categories in Table 4.2 reflects the changing perceptions of distribution of taxa across time (Fig. 4.1). Linnaeus (1758) and Boisduval (1836) provided general and vague distribution data. Godman and Salvin (1879–1901) assigned the collection localities to countries. The growth of knowledge of geography is clearly reflected in the contribution of Rothschild and Jordan (1906), who give altitudinal data as well as more precise localities. Two contributions that have added to our knowledge of Mexican Papilionidae are those of Hoffmann (1940) and Beutelspacher (1984). The former used administrative divisions and altitudinal zonation for providing distributional data, and the latter's data were accompanied by reliable distributional maps. This chapter, which builds on these earlier studies, incorporates the use of modern electronic techniques available today to analyze data from various sources (see below).

It is possible that 90–95% of species and subspecies of Mexico's Papilionidae have already been documented. Further exploration of little-studied areas, detailed analysis of geographic variation of disjunct populations of some species, and the study of the reproductive biology of others may reveal the remainder. There are few descriptive ecological studies of the Papilionidae in Mexico. Whereas knowledge of some species, e.g., *Baronia brevicornis*, may be deemed adequate, that of others (various endemic or quasiendemic species whose principal distribution is Mexican and those that have differentiated at subspecific levels mainly in Mexico) is meager and known only through museum samples or collections. Examples include *Parides alopius, Pyrrhosticta diazi, P. abderus, Priamides rogeri, P. erostratinus,* and *Pterourus alexiares*. In some cases information on their likely host plants is lacking. The above observations generally stress the need for field and laboratory studies in Mexican groups.

MATERIALS AND METHODS

Data were compiled from museum collections, catalogs, and literature. Collections in the Allyn Museum (Florida) and the Natural History Museum of New York, which house two of the most important collections from Mexico (Hoffmann and Escalante) provided valuable information. Their holdings cover over 50 years of sustained collections from many parts of Mexico. Historic collections of Welling, Hubbell, Wind, Holland, and Miller are housed in these museums as well. In Mexico, the collections of L. González and that of the Zoology Museum at UNAM were consulted. The data from the Holland Catalogue (MS) with information on northern Mexico, otherwise scarce, were included. The samples were all checked for taxonomic accuracy. Literature related to distribution, host plants, and life cycles of the Papilionidae of Mexico exceeding 100 entries was compiled.

A capture screen was designed for the dBASE III plus software program for analysis of data. Data relating to 15 areas (genera, species, subspecies, sex, day, month, year, state, municipality, locality, vegetation type, collector, altitude, number of individuals, and collection code or number of bibliographical reference) were compiled from the samples and bibliographical references. The ecological and geographical data were thus integrated. Lists were made for areas, states, and other parameters of distribution (vegetation types, altitude); and maps were generated from the data base. Areas of richness were determined from the above analysis. Phylogenetic factors (plesiomorphic and apomorphic groups and their interrelations) were taken into consideration in this exercise. The genealogical relations put forward by Durden and Rose (1978), Hancock (1983), Igarashi (1984), and Miller (1987) were also used.

RESULTS

Table 4.3 presents the classification of the Papilionidae of Mexico accepted here. It recognizes three subfamilies, five tribes, six subtribes, 12 genera, 57 species, and 82 subspecies. Of these groups, one monotypic subfamily, six species, and 28 subspecies are endemic; another 28 subspecies, which are restricted to the Mesoamerican region, are considered quasiendemics. The species and subspecies endemisms are 10.5% and 34.1% respectively. This fact, along with the high number of quasiendemics and the presence of important plesiomorphic elements and paleoendemics, suggests that the diversity of Papilionidae of Mexico is unique.

A preliminary analysis of the endemism of the Mexican Pieridae reveals similar percentages and biogeographical characteristics. The same can be seen for Hesperiidae, Nymphalidae, and Lycaenidae. The species ende-

Table 4.3. Classification of Mexican Papilionidae

Baronia brevicornis brevicornis Salvin	E
B. brevicornis rufodiscalis W. & M.	E
Parnasius phoebus ssp?	
Protesilaus marcellus Cra.	
P. philolaus Boi.	Q*
P. oberthueri R. & J.	Q*
P. epidaus epidaus Do.	Q*
P. epidaus fenochionis G. & S.	E
P. epidaus tepicus R. & J.	E
P. phaon Boi.	
P. branchus Do.	Q*
P. belesis belesis Bat.	Q*
P. belesis occidus Vaz.	E
P. thymbraeus thymbraeus Boi.	Q*
P. thymbraeus aconophos Gray	E
P. agesilaus neosilaus Hopffer	Q*
P. agesilaus fortis R. & J.	E
P. macrosilaus macrosilaus Gray	Q*
P. macrosilaus penthesilaus Felder	E
Eurytides marchandi marchandi Boi.	
E. marchandi occidentalis Maza et al.	E
E. lacandones lacandones Bat.	
E. calliste calliste Bat.	Q*
E. salvini Bat.	Q*
Battus philenor philenor Linnaeus	
B. philenor orsua G. & S.	E
B. philenor ssp?	
B. philenor acauda Oberthr	E
B. polydamas polydamas Linnaeus	
B. laodamas copanae Reakirt	Q
B. laodamas procas G. & S.	E
B. eracon G. & S.	E
B. belus varus Kollar	Q
B. belus chalceus R. & J.	E
B. lycidas Cramer	
Parides alopius G. & S.	Q*
P. montezuma Westwood	Q*
P. photinus Do.	Q*
P. photinus ssp.?	
P. erithalion sadyattes Druce	Q
P. erithalion polyzelus Felder	Q
P. erithalion trichopus R. & J.	E
P. lycimenes lycimenes Boi.	
P. lycimenes septentrionalis M. & D.	E
P. iphidamas iphidamas Fabricius	
P. sesostris zestos Gray	Q
P. childrenae Gray	
P. eurimedes mylotes Bat.	Q
Pterourus esperanza Beu.	E
P. palamedes leontis R. & J.	E

Table 4.3. (cont.)

P. glaucus glaucus Linnaeus	
P. alexiares alexiares Hopffer	E
P. alexiares garcia R. & J.	E
P. rutulus rutulus Lucas	
P. multicaudatus Kirby	
P. pilumnus Boi.	Q*
P. eurymedon Lucas	
Pyrrhosticta victorinus victorinus Do.	Q*
P. victorinus morelius R. & J.	E
P. victorinus ssp.	
P. diazi Rac. & Sbo.	E
P. garamas garamas Geyer	E
P. garamas ssp?	
P. abderus abderus Hopffer	E
P. abderus electryon Bat.	Q*
P. abderus baroni R. & J.	E
Heraclides thoas autocles R. & J.	
H. cresphontes Cra.	
H. ornythion Boi.	Q*
H. ornythion ssp.	
H. astyalus pallas Gray	Q
H. astyalus occidentalis Br. & Fau.	E
H. androgeus epidaurus G. & S.	Q
H. androgeus ssp?	
Troilides tolus tolus G. & S.	Q*
T. tolus mazai Beu.	E
Priamides pharnaces Do.	Q*
P. anchisiades idaeus Fabricius	
P. rogeri Boi.	Q*
P. erostratus erostratus Westwood	Q*
P. erostratus vazquezae Beu.	E
P. erostratinus Vas.	E
Papilio polyxenes asterius Stoll	
P. polyxenes coloro Wright	
P. bairdii Edwards	
P. zelicaon zelicaon Lucas	
P. zelicaon nitra.	
P. indra pergamus Edwards	
P. indra ssp?	

This classification is based on the contributions of Hancock (1983) and Miller (1987), and the taxa are phylogenetically arranged from plesiomorphic to apomorphic. Nevertheless, for the arrangement of genera in Papilionini a greater number of genera representing distinct groups of species are recognized, so the distinct wing patterns, the host plant, and the patterns of distribution stand out, reflecting the geneological relation in this tribe. Subgenera are not recognized. The same criteria have not been applied in Leptocircini, where the genus *Protesilaus* contains distinct groups of species that are relatively homogeneous among themselves. The availability of names is being examined by K. Brown (personal communication). The question mark (?) in front of names suggests the possibility of an unnamed subspecies as well as suggesting the need for additional studies to confirm its occurrence in

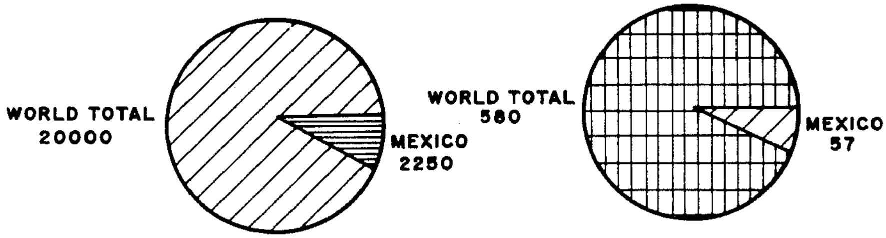

Figure 4.2. World and Mexican totals of Papilionoidea (left) and Papilionidae (right).

mism in Pieridae is over 10% and in the other families somewhat below this figure (see Fig. 4.8, below). Among the endemic species of the Pieridae are *Lieinix neblina, Euchloe guaymasensis, Eucheira socialis, Falcapica limonea, Heliochroma crocea, Prestonia clarki,* and *Neophasia terlooti.*

Figure 4.2 illustrates the representation of Papilionoidea in Mexico in relation to the rest of the world. Papilionidae consists of four subfamilies. Of them, Baroniinae and Papilioninae occur in Mexico. The presence of Parnasiinae is doubtful. Praepapilioninae, which is extinct, is known from the Colorado fossils of the Middle Eocene. Baroniinae, which is endemic to southern and southeastern Mexico, is monotypic and has more plesiomorphic characters than *Praepapilio*. Papilioninae is represented by three of the four subtribes (Miller, 1987): Leptocircini, Troidini, and Papilionini.

The generic and subgeneric concepts have differed among authors (Hancock, 1983; Miller, 1987; Miller & Brown, 1981). A less conservative taxonomy adopted here recognizes 10 genera in Papilioninae: *Protesilaus, Eurytides, Battus, Parides, Pterourus, Pyrrhosticta, Heraclides, Troilides, Priamides,* and *Papilio.*

Papilionidae consists of 580 species worldwide of which about 10% are found in Mexico (Fig. 4.2). Figure 4.3, which provides a comparison of species richness in various countries in North America (Nearctic region, Mesoamerica, and the Antilles), clearly suggests that Mexico is the richest. Collins and Morris (1985) have pointed out that Mexico holds tenth place in the world in terms of numbers of species and seventh in endemics (Figs. 4.4 and 4.5). However, the many quasiendemics recognized among Mexi-

Table 4.3. (cont.)

Mexico. The supraspecific classification precedes the species enumeration. There are three subfamilies, five tribes, six subtribes, 12 genera, 17 species groups in Papilioninae, 57 (+1?) species, 82 (+7?) subspecies.

PAPILIONIDAE. Baroniinae: Baroniini; *Baronia*. Parnasiinae: Parnasiini; *Parnassius*. Papilioninae: Leptocircini; *Leptocircina, Protesilaus, Eurytides.* Troidini; *Battina, Battus, Troidina, Parides.* Papilionini; *Pterourus, Pyrrhosticta, Heraclides, Troilides, Priamides, Papilio.*

E, endemic; Q, quasiendemic or mesoamerican (with an additional area in Central America). The asterisk indicates that species is considered in this category.

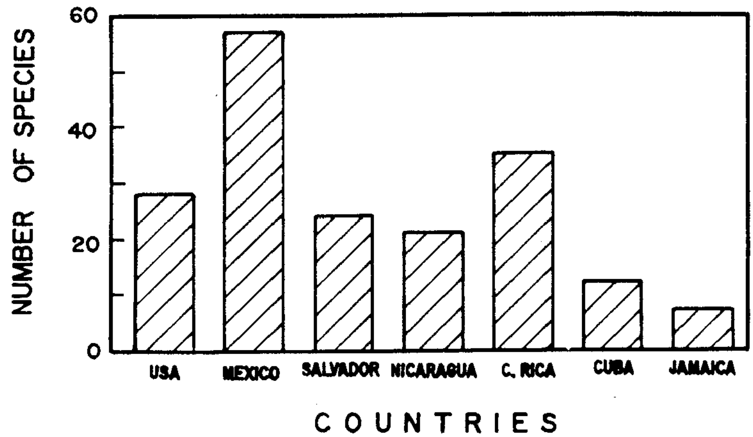

Figure 4.3. Numbers of species of Papilionidae in Mexico and adjacent countries. After Collins & Morris, 1985.

can taxa here would rank the country even higher with respect to the exclusivity of its lepidopteran fauna (Table 4.4). The presence of habitats of relictual biota of various plesiomorphic species and paleoendemics in Mexico (e.g., *Baronia brevicornis, Parides alopius,* and *Pterourus esperanza*) further supports this claim. Thus Mexico is among the richest and most diverse countries for butterflies, together with Indonesia, the Philippines, China, Brazil, Madagascar, and India. Table 4.4 and Figures 4.6 and 4.7 give the number of species, endemics, and quasiendemics and their respective percentages. In the Antilles the number of species is low, but endemism is relatively high. Forty-seven percent of the Papilionidae of Mexico are

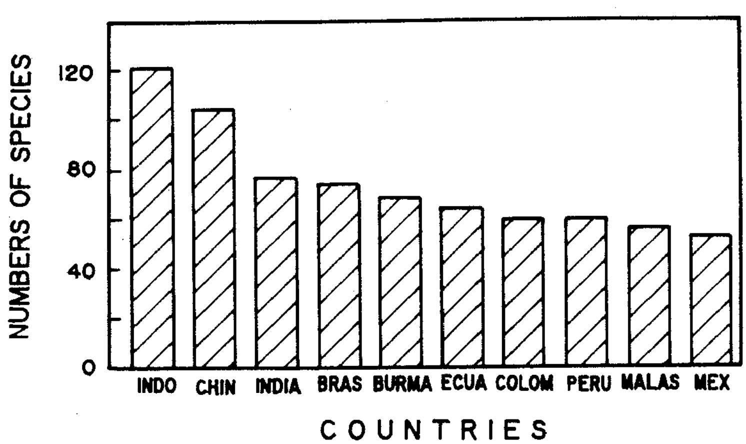

Figure 4.4. Numbers of species of Papilionidae for countries with the greatest diversity in the family. After Collins & Morris, 1985.

Table 4.4. Endemics and quasiendemics in Mexico and adjacent countries

Country	Total species	Endemics No.	Endemics %	Quasiendemics No.	Quasiendemics %
United States	28	1	3.6	8	28.5
Mexico	57	6	10.5	21	36.8
Salvador	24	0	0	0	0
Nicaragua	21	0	0	0	0
Costa Rica	35	0	0	0	0
Cuba	12	4	33.3	2	16.7
Jamaica	7	3	42.8	0	0

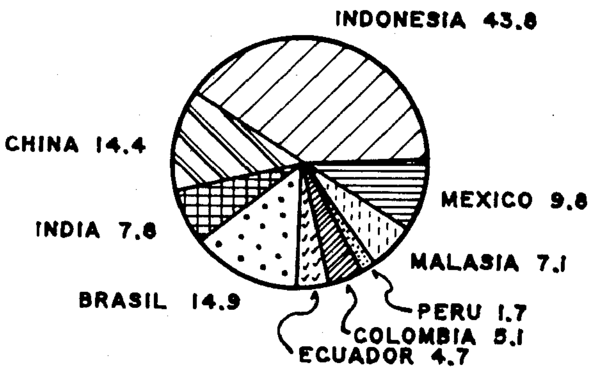

Figure 4.5. Endemism (percentages) of Papilionidae for countries with the greatest diversity in the family. After Collins & Morris, 1985.

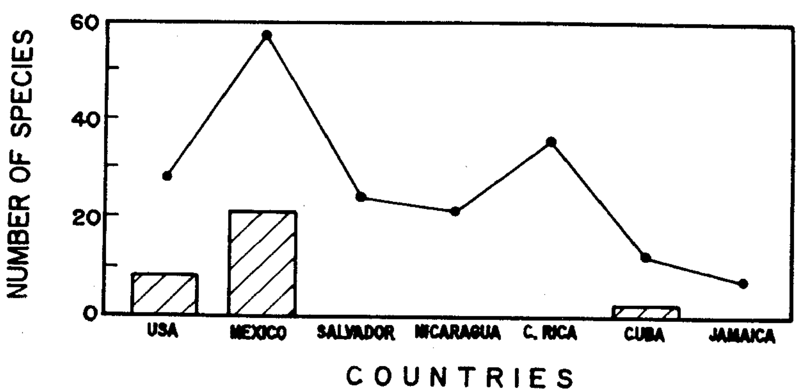

Figure 4.6. Numbers of species and endemics in Mexico and adjacent countries. Bars indicate endemics.

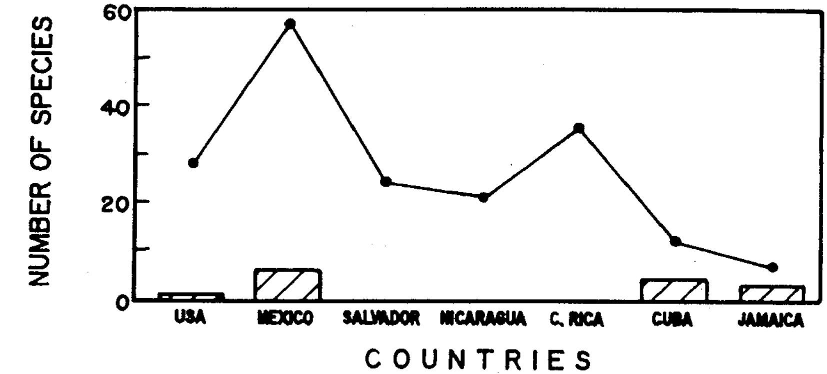

Figure 4.7. Numbers of species and quasiendemics in Mexico and adjacent countries. Bars indicate quasiendemics.

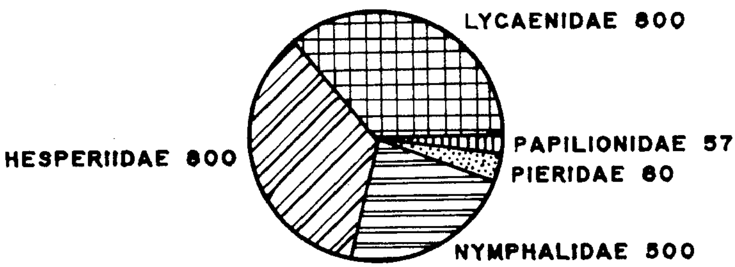

Figure 4.8. Approximate numbers of species in various families of Papilionoidea.

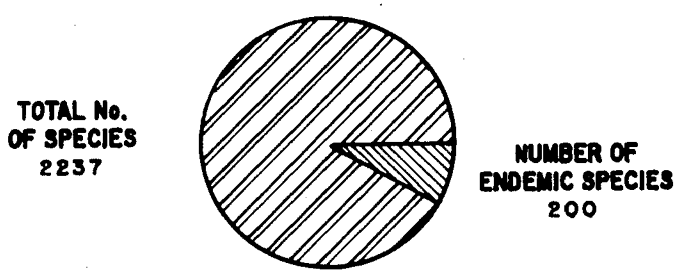

Figure 4.9. Approximate number of endemics in Papilionoidea in Mexico.

endemic and quasiendemic, making Mexico one of the most important countries in the region.

Figure 4.8 provides estimates of species numbers in families of Papilionoidea for Mexico from which a preliminary evaluation of endemism by family was obtained. The two estimates, integrated in Figure 4.9, give a total of 9.4% endemism for the Papilionoidea of Mexico. Like Papilionidae, other Lepidopteran families in Mexico have sets of genera or groups of plesiomorphic species that inhabit (like the paleoendemics) areas of relictual biota, principally xeric and mesic areas of medium and high mountains (500–1,500 m and 1,800–3,000 m above sea level, respectively). Examples include *Aegiale, Heliocroma, Prestonia, Eucheira, Lieinix, Anetia, Bolboneura, Cyclogramma, Manataria, Paramacera, Cyllopsis, Megisto, Pindis, Anemeca, Microtia, Caria, Apodemia, Emesis, Calephelis,* and *Eumaeus.* These supraspecific taxa have evolved mainly in the Mexican Transition Zone as defined by Halffter (1976, 1987).

PHYLOGENETIC CONSIDERATIONS

Durden and Rose (1978) were the first to report two fossil species of Praepapilioninae (*Praepapilio colorado* and *P. gracilis*). These fossils from the Middle Eocene (48 Ma) of Colorado present more apomorphic characters than the endemic Baroniinae of Mexico which indicates that generic and suprageneric differentiation in Papilionidae may date back to the Eocene-Paleocene (Miller, 1987). Differentiation of the families of Papilionoidea, then, may be placed at least in the Upper Paleocene.

The contributions of Ford (1944), Ehrlich (1958), and Munroe (1961) followed by the phylogenetic analysis and classifications of Hancock (1983), Igarashi (1984), and Miller (1987) form the basis for discussion of the evolutionary history of the Papilionidae. These studies suggest that the ancestral morphology of the group had its origins in *Baronia brevicornis.* The polarization of character states in the cladistic analysis of transspecific taxa in the Papilionidae has its plesiomorphic origins in *Baronia.* This genus, however, exhibits specializations.

Munroe (1961) considered the Parnasiinae and the Papilioninae as sister subfamilies. Only Papilioninae is found in Mexico, as the report of *Parnasius phoebus* ssp. in Tamaulipas is suspect. Its presence (if found) would be a marginal distribution of an apomorphic taxon of Parnasiinae. The genealogical relations of the Papilioninae tribes were little understood until the work of Hancock (1983) and Miller (1987). Hancock recognized three tribes and Miller four; all of Hancock's tribes and three of Miller's are found in Mexico (Tables 4.1, 4.3).

Of the ten generic groups recognized in Leptocircini by Miller (1987), only the most plesiomorphic occur in Mexico. In the case of *Protesilaus,* groups of plesiomorphic species of Mesoamerican evolution and derived species with a southern affinity are found. The *Eurytides* are apomorphic groups with a southern affinity except for, perhaps, *E. salvini* and *E. calliste,* which could be considered Mesoamerican.

The two subgroups of Troidini are the monotypic *Battina* and *Troidina.* The latter subtribe is composed of ten generic groups, of which only one—Parides, apomorphic within the subtribe—is present in Mexico. However, there are sets of plesiomorphic species of Mesoamerican evolution and derived groups with a southern affinity. *Battina* presents a similar case with two groups of species. In both subtribes taxa of Mesoamerican evolution are less numerous than those of a southern evolution.

The only phylogenetic analysis of Papilionini taxonomically less conservative in approach (Hancock, 1983) recognizes 11 generic groups. It is based on criteria that better express phylogenetic and biogeographic aspects in the classification of the tribe. These criteria, applied at world level, recognize over 20 generic groups in the Papilionini. Six generic groups of this tribe are found in Mexico (Table 4.3). In the cladogram of Hancock (1983), most plesiomorphic groups (*Pterourus, Pyrrhosticta, Heraclides, Troilides*, and *Priamides*) and one of the most apomorphic (*Papilio*) may be seen. These species groups are of Mesoamerican evolution (*Pterourus* and *Pyrrhosticta*), southern evolution (*Heraclides, Troilides*, and *Priamides*), and a section of *Papilio*, which is Nearctic.

BIOGEOGRAPHIC PATTERNS AND ORIGINS

Various lineages in Mexican Papilionidae display biogeographic patterns described by Halffter (1976, 1987); they include the following groups.

1. Paleoamerican (*Baronia*)
2. Mesoamerican (the several groups of species of Papilionini genera)
3. Nearctic (*Papilio*)
4. Neotropical (several Troidini and Leptocircini)

The lack of fossil evidence and genealogical studies impedes the interpretation of chronological relations of different clades. Nevertheless, paleo- and neoendemics in several communities are recognized, which is significant. *Baronia* is a good example. Its two subspecies occur in the lower deciduous tropical forests, one in southern Mexico (Balsas Basin) and the other in western Mexico (inland Chiapas), and suggest an old vicariant process for the communities. The levels of differentiation of these populations, however, do not warrant their recognition as species. *Parides alopius*, with a similar distribution, occurs in colder climates of higher altitudes and latitudes. The age of these elements in both communities may date back to the Paleocene. *Pterourus alexiares* sspp. and *P. esperanza* may represent elements of two groups of species that have converged into a community composed of groups of northern, southern, and local origins. These communities, which have remained as relict populations in montane cloud forests at least since the Oligocene, may have experienced vicariant processes comparable to *Pyrrhosticta abderus* and *P. victorinus*, during this time. Various groups of subspecies of neotropical affiliation may have differentiated during the Pleistocene, possibly in the tropical wet and humid forest refugia in southern and southeastern Mexico (e.g., *Eurytides marchandi occidentalis, Battus laodamas procas, Parides erithalion trichopus, Battus eracon*, and *Parides lycimenes septentrionalis*). The first three have their vicariants in the coastal areas of the Gulf of Mexico. Halffter (1976) has provided further examples from Papilionoidea and has also described other patterns. Additional examples may be seen in Dismorphini (LLorente, 1983; LLorente

& Luis, 1988). Some of the oldest paleoendemics found in montane cloud forests and tropical deciduous forests (sensu Rzedowski, 1978) may possibly have closer genealogical relations with relicts of the Greater Antilles (Cuba and Hispaniola). Examples include *Pterourus*, *Heraclides*, and *Parides* in Papilioninae, *Anetia* in Danainae, and *Prestonia*, *Heliocroma*, and *Apodemia* in other Papilionoidea groups.

It is possible that the time and degrees of differentiation of several Papilionidae of the region are related and may coincide with the geological ages of the areas. *Baronia* in the Cretaceous areas of southern and western Mexico and *Pterourus esperanza* in mountains may date back to the Eocene-Oligocene. The various biogeographical provinces of Mexico that link Nearctic and Neotropical regions, thus acting as a corridor or barrier for their biotic elements, and the presence of disjunct areas of extreme climates (xerics and mesics) seem to have generally provided for the high degree of speciation in these areas (Hancock, 1983; LLorente, 1983).

It is difficult to suggest a "center of origin" for any group with certainty, and the exercise is shrouded in controversy (Croizat et al., 1974; Nelson, 1978, 1983; Patterson, 1983). The problem is compounded if the group in question is of great age, as is the case with the families and subfamilies of Papilionoidea. The unpredictability of the differential extinction of species and clades often invalidates some criteria for locating centers of origin, e.g., more plesiomorphic groups, more diversified groups (Collins & Morris, 1985). Several areas of origin proposed for the Papilionidae by Shields and Dvorak (1979), Hancock (1983), and Collins and Morris (1985) are debatable. It is noteworthy that Miller (1987) did not find biogeographical patterns in the cladograms of areas as a function of a vicariant model based on tectonic plates, which may suggest that unrecognized extinction for some areas has made it difficult to interrelate centers of paleoendemics. For the present, Hancock's (1983) suggestion that the family and its more plesiomorphic groups may have originated in Laurasia seems reasonable (Collins & Morris, 1985). The present distribution of the Praepapilioninae, Baroniinae, and the primitive groups of Papilioninae (*Pterourus* and *Battus*) and Parnassinae (*Archon* and *Sericinus*) points to the southwest of the Nearctic region (United States and Mexico) as the most probable place of origin for the family.

The latitudinal gradients of species richness in the butterflies pointed out by Slansky (1972) and Scriber (1973a) have been observed in other continental areas (Collins & Morris, 1985). The higher diversity encountered toward the tropics has led to the characterization of the Papilionidae as "preeminently tropical" (Collins & Morris, 1985). The diversity that prompts such generalizations may be due not only to greater diversification there but also to a probable lower rate of extinction in these latitudes.

ENDEMISM AND RICHNESS

Of the 57 species, 25 have ample regional or continental distributions. Six species and 28 subspecies are endemic to the country (Table 4.3). The

Table 4.5. Distribution of endemics of Mexican Papilionidae in physiographic provinces

Taxa	1	2	3	4	5	6	7	8	9
Baronia brevicornis brevicornis		X							
B. b. rufodiscalis			X						
Protesilaus epidaus fenochionis	X	X				X			
P. e. tepicus					X				
P. belesis occidus	X				X				
P. thymbraeus aconophos	X	X					X		
P. agesilaus fortis	X	X					X		
P. macrosilaus penthesilaus	X			X	X	X	X		X
Eurytides marchandi occidentalis	X					X			
Battus philenor orsua								X	
B. p. acauda						X			
B. laodamas procas	X	X				X			
B. eracon		X				X			
B. belus chalceus						X			
B. e. trichopus	X	X				X			
Parides lycemenes septentrionalis				X			X		X
P. esperanza				X					
P. palamedes leontis					X				
P. alexiares alexiares					X				
P. a. garcia					X				
Pyrrhosticta victorinus morelius	X	X				X			
P. diazi		X							
P. abderus abderus				X	X				
P. a. baroni	X					X			
Heraclides astyalus occidentalis						X			
Troilides tolus mazai		X				X			
Priamides erostratus vazquezae		X				X			
P. erostratinus					X				
Total	10	11	1	4	8	13	4	1	2

1) Sierra Madre del Sur; 2) Balsas Basin; 3) Chiapan Interior; 4) Sierra de Juárez; 5) Sierra Madre Oriental; 6) Pacific Coastal Plain; 7) Yucatan Peninsula; 8) Islas Marias; 9) Gulf Coastal Province.

geographic areas with the highest number of endemic taxa are tropical deciduous forests of southern and western Mexico, the mesic areas of the Sierra Madre Oriental, the Sierra de Juárez, the Sierra Madre del Sur, and the Pacific Coastal Plains, particularly the last, which has 53% of the endemic subspecies.

Table 4.5 gives the distribution of endemic taxa in their recognized physiographic areas: Sierra Madre de Sur, Balsas Basin, Chiapan Interior, Sierra de Juárez, Sierra Madre Oriental, Pacific Coastal Plains, Yucatán Peninsula, Islas Marias, and Gulf coast.

The endemic elements of Papilionoidea of northern Mexico, particularly those associated with desert areas, are also found in southern areas of the

Figure 4.10 Areas of high endemism of Papilionidae in Mexico. 1. Durango-Sinaloa border. 2. Cañón del Novillo, Tamaulipas. 3. Sierra de San Juan, Nayarit. 4. Southern parts of Sierra Madre de Oriental. 5. Morelos. 6. Cañón de Zopilote, Guerrero. 7. Sierra de Atoyac, Guerrero. 8. Sierra de Juárez, Oaxaca. 9. Inland Chiapas.

United States. Some endemic taxa of Hesperiidae, Pieridae, Nymphalidae, and Lycaenidae can frequently be found associated with the Valley of Tehuacán-Cuicatlán, semiarid areas of Querétaro and Hidalgo, or in thorn scrub areas of Sonora-Sinaloa and in the Peninsula of Baja California. However, data pertaining to these taxa are too incomplete to provide a synthetic picture of their endemism.

Generally, areas of endemism of other Papilionoidea families coincide with those of Papilionidae; there are, as mentioned above, other zones of endemism in xeric areas in these families. These coincidences in various groups of Papilionoidea suggest biogeographic patterns that may have been reached through shared historical processes. Figure 4.10 shows areas of high endemism for the Papilionidae of Mexico that include representative populations of quasiendemic taxa. Three notable biogeographic patterns of endemic and quasiendemic Papilionidae of Mexico, associated with a pattern of vicariant diversification, are discernible. These three areas can be divided into subpatterns.

1. Modern pattern along the coastal areas. This pattern is characterized by specifically or subspecifically differentiated populations along the coastal strips, e.g., *Protesilaus epidaus* (subspecific northern and south-

Table 4.6. Number of species of Papilionidae in Mexican states

State	No. of species
Baja California Norte	7
Baja California Sur	6
Sonora	7
Chihuahua	7
Coahuila	3
Nuevo León	23
Tamaulipas	24
Sinaloa	17
Durango	10
Zacatecas	2
San Luis Potosí	27
Nayarit	23
Jalisco	28
Aguascalientes	6
Guanajuato	9
Querétaro	7
Hidalgo	19
Colima	26
Michoacán	24
México	21
Distrito Federal	8
Tlaxcala	0
Guerrero	31
Morelos	24
Puebla	31
Veracruz	41
Oaxaca	40
Chiapas	41
Tabasco	28
Campeche	11
Yucatán	21
Quintana Roo	21

ern populations along the Pacific coast) or *Dismorphia amphiona* (LLorente, 1983).

2. Mesomontane pattern. In this pattern of elements restricted to montane cloud forests, the disjunct populations found in the large physiographic areas (e.g., Sierra Madre Occidental, Sierra Madre del Sur, Sierra Madre Oriental-Sierra de Juárez, and the mountains of Chiapas) are often subspecifically differentiated, e.g., members of *Pterourus alexiares*, *Pterourus esperanza*, and *Pyrrhosticta abderus*.
3. Xeric-relictual pattern. This pattern is made up of relictual elements associated with areas of tropical, deciduous forests and pine-oak

Table 4.7. Papilionidae in various areas of Mexico

Area	No. of species	Percent of species in the area	Percent of species in the country
Monterrey	16	69.5	28.0
Cañón del Novillo	21	87.5	36.8
Sierra de San Juan	20	87.0	35.1
Huasteca Potosina	16	59.3	28.0
Patla-Necaxa	26	84.0	45.6
San Nicolás Tolentino	16	76.2	28.0
Tepoztlán-Yautepec	20	83.3	35.1
Teocelo	20	48.8	35.1
Yanga-Tuxpango	25	61.0	43.9
Sierra de Atoyac	20	64.5	35.1
Sierra de Juárez	31	77.5	54.4
Los Tuxtlas	29	70.7	50.9
Boca del Chajul	26	63.4	45.6

forests of southern and western Mexico. Included are *Baronia brevicornis* and *Parides alopius*.

The ecological characterization of some of the historic elements in these patterns is similar to that described by Halffter (1976) in his patterns of dispersion (typical Neotropical pattern, Montane Mesoamerican pattern, and Paleoamerican pattern).

Table 4.6 lists the states of Mexico and the number of species found in each. The highest numbers of species are found in the southeastern states of Veracruz and Chiapas, with 41 each. Oaxaca, with 40, is a close second. These species account for 72% of the total in Mexico. The states of Guerrero and Puebla have the next highest number of species with 31 each. The northern states have fewer Papilionidae. They usually number less than ten as is the case in Baja California Norte, Sonora, Chihuahua, Durango, Zacatecas, and Coahuila. The northeastern states of Nuevo León and Tamaulipas have 23 and 24 species respectively. Numbers range from seven to 27 in the eastern states of San Luis Potosí, Querétaro and Hidalgo. In the central states (México, Morelos) there are more than 20. The Yucatán Peninsula has between 11 and 21 species. The states rich in species are also those whose vegetation is varied. It is of interest that this factor is independent of surface area. For example, Chihuahua is more than 30 times larger than Colima but has fewer than one-third its species.

The states with tropical forests and cloud forests are the most species-rich, particularly those with more mesic climates along the coastal strips, from Chiapas to Sinaloa on the Pacific side to Tabasco and Tamaulipas on the Gulf. Morelos, México, and Puebla in central Mexico with this type of vegetation have a considerable number of species. The paucity of

Figure 4.11. Papilionidae in Mexico: areas where the group has been studied. 1. Monterrey. 2. Cañón del Novillo. 3. Sierra de San Juan. 4. Huasteca Potosina. 5. Patla-Necaxa. 6. San Nicolás Tolentino. 7. Tepoztlán-Yautepec. 8. Teocelo. 9. Yanga-Tuxpango. 10. Sierra de Atoyac. 11. Sierra de Juárez. 12. Los Tuxtlas. 13. Boca del Chajul. See Table 4.7 for details.

Papilionidae in Zacatecas, Coahuila, and Tlaxcala may be due to the fact that these states have been generally undercollected. Table 4.7 lists the 13 best known geographic areas (Fig. 4.11) for the Papilionidae of Mexico.

The ten richest areas in terms of species and endemism of Papilionidae (in Mexico) are north to south and west to east: (1) Cañón del Novillo; (2) Durango-Sinaloa border; (3) Sierra de San Juan; (4) Sierra de Atoyac; (5) some parts of Morelos bordering Guerrero state; (6) Barranca de Patla; (7) Los Tuxtlas, Veracruz; (8) Sierra de Juárez; (9) inland Chiapas; (10) Boca de Chajul.

Most available studies on the biology of Papilionidae, such as mimicry, foraging, and gradients of diversity, do not include Mexican species or populations. The only reliable studies are those of Vázquez from the 1950s and the more recent efforts of Paul Spade. However, the lack of information for Mexican taxa is significant when compared with those of the United States or Central America. Often even their original host plants are not known. *Pterourus multicaudata*, *P. alexiares*, *P. pilumnus*, and *P. esperanza* are examples. These mostly Mexican species are poorly known, while *P. glaucus*, which is shared with the United States, is well known in scientific literature. There are no Mexican counterparts to studies of De Vries (1987) and Young (1985) and Muyshondt and Muyshondt (1975) concerning the biology of Papilioninae in Costa Rica and El Salvador. Studies of the Papilionidae of Mexico have until now focused more on aspects of variation, taxonomy, and biogeography. It is encouraging that, of late, Mexican Papilionidae has been attracting the attention of scholars, e.g., Leptocircini, *Baronia*, (K. Brown, unpublished data).

It is essential to have systematic information on the biology of the endemic and quasiendemic taxa, especially in areas of species richness or in relict areas. It is well known that various Papilionidae thrive in areas subject to perturbation by man. *Baronia brevicornis*, whose host plant is *Acacia cymbispina* ("cubata"), flourishes in disturbed and abandoned areas of the tropical deciduous forests. It has been observed that plantations of avocado (*Persea* spp.), orange and other citrus (*Citrus* spp.), and "chirimoya" (*Annona* spp.) promote population increases in *Pyrrhosticta, Heraclides, Priamides*, and *Protesilaus* in various parts of Mexico. This knowledge is key to the restoration of species through reforestation measures.

Aspects of ecology cannot be generalized for all the Papilionoidea from studies of Papilionidae, as the phytophagic interrelations differ from one family to another and are often monophagic or oligophagic. The reproductive strategies and life histories are also likely to be different so far as patterns are concerned. Some of the differences that have been noted include the foraging behavior of the groups: for example, the caterpillars of Papilionidae feed mostly on trees, whereas those of other family groups feed on creepers and annual plants. Adult Papilionidae rely on nectar for sustenance or feed on dissolved salts in moist earth, whereas other groups of Papilionoidea feed on decomposing (exuded or fermented) organic material. Of late, several genera of Pieridae and Nymphalidae have been the subjects of study, i.e., *Enantia, Eucheira, Hamadryas*, and *Bolboneura*, among others.

DIVERSITY AND ITS CONSERVATION

Data on maintenance of diversity in Mexican Papilionidae are presently lacking and urgently needed. It may be assumed safely that the diversity includes a set of delicate interrelations in specific habitats. Any disturbance in this balance of nature leads to possible extinctions. Destruction or alteration of habitat through deforestation, livestocking, intensive agriculture, urbanization, and industrialization are the greatest threats not only to the preservation of diversity of butterflies (Collins & Morris, 1985) but to whole biotic communities.

Commercial trade poses a significant threat to the diversity of Mexican butterflies. First, the trade does not discriminate among rare, restricted, threatened, or paleoendemic species. The problem is acute, as capture of samples frequently involves a long chain of local traders usually hired by middlemen working for collectors, businessmen, or museums. Uninformed children and adults are hired to indiscriminately collect such samples, as has been observed in Oaxaca, Chiapas, Veracruz, and Guerrero. An intense educational effort on the nature of this trade (actual worth of samples, rarity of species, and so on) which in part is international, may remedy the situation. The Appendix provides the contrast in prices. Second, the exporter has one or two itineraries he follows regularly for some years that include a minimum of two or three areas per itinerary (Escalante and González, pers. comm.), placing him at the top of a pyramid of major depredation. Alarmingly, some work, under the umbrella of "scientific" societies or conservation agencies, involves this type of trade depredation in covert ways, often with vulnerable or endangered species. To date, there is no effective legislation or regulation, illustrated by the fact that, following the law of supply and demand, the prices for butterflies in Mexico are much lower than those in other neotropical countries, which indicates a constant supply.

Habitat preservation is essential for further study of the biology of these organisms, as it may lead to a better understanding of the mechanisms by which diversity is preserved, as well as alternative ways to conserve these biota.

DISCUSSION AND CONCLUSIONS

Mexico has been an important theater of speciation for butterflies, as suggested by the specific and transspecific endemism in the group. Endemism in Mexican Papilionoidea is roughly 9%, which is a good index of comparison to the Lepidoptera in the country (25,000 species). Tropical and deciduous forests, semiarid zones, and in some cases pine-oak and montane cloud forests are centers of paleoendemism for butterflies and moths. The areas of high endemism for the Papilionoidea are tropical and montane cloud forests of the Balsas Basin, Sierra Madre del Sur, Pacific Coastal Plain, and Sierra Madre Oriental–Sierra de Juárez. The species-rich areas are tropical and montane cloud forests in southern, southeastern, and western Mexico. About 25% of Mexican Papilionidae are found in some of these areas (Fig. 4.11). Generally, areas with pronounced topographic, climatological, and vegetational heterogeneity have high numbers of Lepidoptera. The most species-rich areas, with the greatest number of endemics are montane cloud forests in the oldest mountains and in the coastal strips of southern Mexico between 500 to ,1600 m (Sierra de Juárez, Sierra de Atoyac, and Sierra de Chiconquiaco). Disturbed vegetations, rather than virgin ones, seem to harbor higher numbers of Papilionidae; but the degrees of disturbance are not known in terms of the proportion of each type of area, which might explain the maximum richness and permanence.

Despite what has been studied, there are gaps in our knowledge, which is generally evident in phylogenetic studies. Biological understanding of various plesiomorphic species are preliminary. Aspects of population dynamics of species and communities of Papilionidae are poorly known.

Anthropogenic factors contribute greatly to habitat alterations in species-rich areas, among which are intensive slash-and-burn agriculture, deforestation, cattle-raising, trade in wild biota, urbanization, and industrialization. These practices continue to take a heavy toll on a great genetic richness. Fortunately, there are areas that can be recovered and restored in the species-rich states of Guerrero, Oaxaca, and Chiapas. Conservation and study of diversity should go hand in hand, so the construction of a system of protected areas will be accompanied by ecological, biogeographic, taxonomic, and genetic research.

Acknowledgments

We thank Drs. Lee D. Miller (Sarasota, Florida) and Frederick Rindge (Natural History Museum, New York) for facilities to study collections in their institutions. Dr. Jorge Soberon was an important early participant in the study. Isabel Vargas (Papilionidae) and Teresa Lilejhoult (Pieridae) helped variously in data collection and areographic studies. Alejandro Peláez and Jorge Moreno provided assistance with the use of dBASE III plus. Luis González Cota provided unpublished data and allowed access to his private collection. Isolda Luna, in addition to processing various versions of the Spanish text, reviewed them. Dr. K.S. Brown critically read and made valuable suggestions on an earlier version. Alejandro Martínez M. helped with photography. CONACyT of Mexico and PSPA of the Universidad Nacional Autónoma de Mexico and the Facultad de Ciencias of the same university provided financial assistance. Finally, we thank T.P. Ramamoorthy and Marguerite Elliott for help with the preparation of this chapter in English.

APPENDIX

Price list for Mexican butterflies (Papilionidae)[a]

Papilionidae	Cost				
	$0.50–2.00	$2–30	$30–150	$150–1,500	>$1,500
Baronia brevicornis (rare[b])	*				
Parnassius phoebus	*	*			
Protesilaus marcellus	*	*			
Protesilaus philolaus	*	*			
P. oberthueri					
P. epidaus	*				
P. phaon	*				
P. branchus	*	*			
P. belesis	*				
P. thymbraeus	*	*			
P. agesilaus	*				
P. macrosilaus	*				
Eurytides marchandi	*	*			
E. lacandones	*	*			
E. calliste		*			
E. salvini		*			
Battus philenor	*				
B. polydamas	*	*			
B. laodamas	*	*			
B. eracon		*			*
B. belus	*				
B. lycidas	*	*			
Parides alopius		*			
P. montezuma	*	*			
P. photinus	*				
P. erithalion	*	*			
P. lycimenes	*	*			
P. iphidamas	*				
P. sesostris	*	*			
P. childrenae		*			
P. eurymedes	*				
Pterourus esperanza (vulnerable[b])					*
P. palamedes	*	*			
P. glaucus[c]	*	*			
P. alexiares				*	*
P. rutulus	*	*			
P. multicaudatus[c]	*	*			
P. pilumnus		*			
P. eurymedon	*	*			
Pyrrhosticta victorinus[c]	*	*			
P. diazi					*
P. garamas[c]		*			
P. abderus		*	*		

Appendix (cont.)

	Cost				
Papilionidae	\$0.50–2.00	\$2–30	\$30–150	\$150–1,500	>\$1,500
Heraclides thoas		*			
H. cresphontes[c]	*	*			
H. ornythion	*	*			
H. astyalus[c]	*				
H. androgeus	*	*			
Troilides tolus	*	*			
Priamides pharnaces	*				
P. anchisiades[c]	*				
P. rogeri	*	*			
P. erostratus	*		*		
P. erostratinus					
Papilio polyxenes	*	*			
P. bairdii		*			
P. zelicaon	*	*			
P. widia		*			

Asterisks in more than one of the price columns indicate price fluctuation due to demand in the market or to forms, sexes, or subspecies that have distinct prices.
[a]Compiled from De la Maza (1978), Collins & Morris (1985), and several private lists from European and United States businesses.
[b]Conservation category following IUCN.
[c]Usually grown in captivity.

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