ORIGINS AND RELATIONSHIPS OF MEXICAN AND ANTILLEAN PAPILIONOIDEA (LEPIDOPTERA)

By WILLIAM P. COMSTOCK
and E. IRVING HUNTINGTON.
The American Museum of Natural History. New York, N. Y., U. S. A.

INTRODUCTION

The survey of a living fauna is but a glimpse, a snapshot as it were, of a dynamic organization of creatures. We can observe, collect, preserve and group specimens. We can compare, correlate and tabulate our findings and with the collaboration of many students, create a static classification of some particular group of organisms at the present time level. It is soon borne in upon us how complex is the picture if we consider these organisms from a dynamic rather than from a static viewpoint. Then we realize that the interrelationships are multifarious in space and time. One living creature can exist only as a part of the whole complex of life. The present and the past are equally involved. Where did this individual come from which we nominate as an example of a species? What were its progenitors? What gave the race capacity for survival? The field broadens. We extend our researches into the revealed facts of geology, paleogeography, paleoclimotology, paleobotany, paleontology. The possibilities are intriguing!

Geology tells us that the inanimate earth is mobile. Mountains uplift and are leveled again and again in geologic time. Volcanism plays its part. Climates change from oceanic to continental, wet or dry. Ice ages intervene, effecting great changes of sea level, making land where once there were shallow seas; greatly modifying climate. Paleogeography reveals to us vast changes in continental outlines between the past and present. The fossil record tells us of past life.

The work of many paleontologists and paleobotanists has given us a moving picture of the fauna and flora of the past. Evolution is revealed.

The fauna of the earth is directly or indirectly phytophagous; it always has been. But mammals, birds and insects are particularly dependent for food on modern flora, the angiosperms or flowering plants. The period of origin of the Angiospermae has not been revealed by the geological record. They appear fully formed, as Athena from the head of Zeus, in the Mesozoic Era at the beginning of the Cretaceous Period, a time as distantly remote from the beginning of the Cenozoic Era as that time is from the present. Although transitional forms of the angiosperms are lacking, they are thought to have been derived from the cycads which preceded them and flourished in the early Mesozoic; they also bore flowers. Sago palms are surviving cycads.

MESOZOIC AND CENOZOIC ERAS

The Mesozoic was an era of mild, moist, equable climate enduring approximately two hundred million years, this climate persisting into the Cenozoic Era, despite great orogeny and changes of continental outline in North and Central America. A characteristic condition of the Mesozoic world was the wide distribution of some genera and even species of fauna and flora. Many species seem to have been cosmopolitan. The close of the Mesozoic Era brought an event which must have had a profound effect on the distribution of species in the Americas. The Laramide revolution, one of the greatest orogenies of all time, extending from Alaska to Central America, marked the inception of the Rocky Mountains. Concurrently the Andes uplifted, Central America became elevated somewhat and North and South America were connected by land.

Early in the Cenozoic Era, tropical and subtropical climates prevailed far to the north of their present extent. Eocene forests in the state of Washington were much like those of Panama today. In North America, the western coastal areas were lower and an oceanic climate influenced a much more extensive inland region than at present. A great embayment from the Gulf of Mexico covered the Mississippi Valley region with a shallow sea. The connection between North and South America appears to have existed during the early part of Eocene time. Available evidence suggests that a warm, moist, uniform climatic condition persisted throughout a vast region in the

Americas. It may be postulated that the Eocene biota was fairly stable, that species were widely distributed and that there was less variety of species.

A world-wide, complex ecology maintained sixty million years ago at the beginning of the Cenozoic Era. Living organisms of every phylum existed much as they do in the present. Organisms had evolved vastly at this time level. Conditioning for modern life had arrived; many now existing organisms then lived, while their primitive progenitors had already largely disappeared.

The Cenozoic was an era of change as the fossil records show. During its sixty million years the horse evolved from a small four-toed mammal to its present stature. It was an era of great advancement for the mammals. Their food supply was adequate with widespread grasscovered plains in North America. The flora remained more static, and insect evolution apparently more nearly kept pace with the flora.

Throughout western North America during Cenozoic time mountain chains were uplifting, the continental connection with South America was severed in the Eocene and later further disrupted. The climate of North America progressively but very gradually became continental. The waters of the Mississippian embayment receded producing a central continental region which was cooler and dryer but semitropical floral elements persisted for a long time. Shifting isotherms, as indicated by the fossil flora, record the climatic change. Tropical flora retreated to the south and with it the tropical fauna. The population pressure was toward the south, toward Mexico and the Antilles, with the way open from North America.

During the major part of Cenozoic time different conditions prevailed to the south of Mexico. Continuous land connection did not exist with South America between early Eocene and late Pliocene. The land was broken into a series of islands, not inhibiting completely a biotic interchange, but certainly greatly retarding it. Climatic conditions were quite probably favorable to tropical flora and fauna throughout the regions of northern South America and Central America. The influence of a cooling and dryer climate did not operate in this region as it did in the north.

The existence of the Antilles as land masses during all of Cenozoic time is much disputed, but their permanence from late Miocene to the present is generally accepted. The existence of a land bridge between the Antilles and Central America has been frequently and

variously postulated. Although geological evidence for such a bridge has not been found, it has been regarded by many students as a biological necessity and hence its creation. For a butterfly fauna no such necessity exists. In fact, the composition of the Antillean butterfly fauna is a strong argument against the existence of a land bridge as is later explained.

Consider the region of the Gulf of Mexico in the living present; an extended continuous continental mass offset by large oceanic islands; moist and dry climates from tropical to subtropical and to temperate in the great continent to the north. Its lands possess a varied ecology suited to many forms of life. The region is conditioned to maintain a fauna and flora of great diversity.

The basic explanation of the origin of the present Mexican and Antillean butterfly faunas lies in the ecological conditions existing during the Cenozoic Era in North America. During the Cenozoic, northern Mexico was an integral part of the North American continent, even as it is today. It was the most southern part of that continent and it was the natural refuge of a fauna requiring tropical or semi-tropical habitats which could no longer maintain itself to the north. Following the Pliocene Period, with the establishment of land connection in Central America, South American biotic elements entered the Mexican gulf region. This southern butterfly fauna is well represented today. It is well established in Mexico south of the Isthmus of Tehuantepec and spreads to the north in both the coastal regions of the Pacific and the Gulf of Mexico, there extending beyond the Rio Grande. The fauna of northern origin is still dominant in northern Mexico, both in the coastal regions and on the central plateau.

CENOZOIC BUTTERFLIES

Having considered briefly the broad background in time, some of the fauna living in the Cenozoic Era may be regarded in more detail. Weighing the available evidence, it seems reasonable to assume that butterflies not only existed in early Cenozoic time but that they were very similar to those now living. The earliest known American butterfly fossils are mid Cenozoic and are from the Miocene deposits of Florissant, Colorado. These fossils show that the butterflies of that horizon had evolved to the point where they had some of the structural characteristics of present day species. Corresponding fossils found in European deposits of about the same age possess the

same characters, showing that a similar fauna existed in the holarctic region at about the same time. These species of fossil butterflies can be definitely placed in existing families and their relationships to species of existing genera are obvious. Some of these fossil species belong in the family Nymphalidae and their structure is significant. The wings are sufficiently well preserved to indicate their size and shape and also their venation. Among these Nymphalid species, two differing characteristics may be observed in the branching of the radial veins of the fore wings. In one example, the first and second radial veins depart from the main radial stem above the discal cell. In the other, only the first radial vein arises in this manner; the second radial originates at the apex of the discal cell or distad of it.

The phylogenic significance of this structural difference in vein positions is brought out by an examination of existing species of Nymphalidae. The living genera, the world over, are about equally divided into two groups based on the positions of the first two radial veins of the fore wings. There can be little question of the great antiquity of the family Nymphalidae. It probably originated in the Mesozoic Era if consideration is given to the time element involved to bring about the well-established, differing structures appearing in mid Cenozoic species and their apparent holarctic distribution of that time.

While the fossil Nymphalidae furnish the most detailed information concerning the similarities existing between extinct and living species, resemblances are to be found in other families. There are fossil species wich are obviously referable to the Papilionidae, Pieridae, Satyridae, Libytheidae and Lycaenidae. These examples indicate the antiquity of the Papilionoidea and their generally slow rate of evolution throughout the Cenozoic Era.

PRESENT BUTTERFLIES

The genera of the Papilionoidea, as listed in the catalogue of the Mexican Lepidoptera prepared by Professor Carlos C. Hoffmann (1940), are used as a basis of comparative study. One hundred and eighty-six genera in ten families are known from Mexico. The fauna has a wellbalanced representation in all families with an admixture of northern and southern species represented in the genera. In total, the fauna presents a unified picture of continuity linking northern and southern forms adapted to the ecology of a region with varied climatic conditions. The balanced fauna is characteristically continental.

Contrasting greatly with the Mexican Lepidopterous fauna is that found in the Antilles, either as a whole or in its various island units. Of the ten families of Papilionoidea found in Mexico, eight appear in the Antilles, Brassolidae and Morphidae being unrepresented. In the Antilles only forty-eight genera are found, less than one-third of the genera occurring on the mainland. The number of species is greatly reduced, hardly ten per cent of the number listed for Mexico. The insular fauna is not only impoverished but unbalanced.

The families Papilionidae, Pieriade and Nymphalidae are the best represented in the Antillean fauna, both in number of genera and number of species. Next in importance is the family of small butterflies, the Lycaenidae. These are represented in the Antilles by thirty-six species compared with two hundred and ten in Mexico. Many of the species of Lycaenidae in the Antilles are endemic. An opposite condition is found with the Riodinidae, numerous in genera on the continent but with only one species in a continental genus existing in the Antilles. The family Satyridae, with eighteen genera in Mexico, none of which occur in the Antilles, has an Antillean endemic genus **(Calisto)** with eighteen species. The following table presents the relative numerical values:

NUMBER OF GENERA OF FAMILIES OF PAPILIONOIDEA

	Mexico	Antilles
Papilionidae	2	1
Pieridae	24	10
Danaidae	22	4
Satyridae	18	1
Brassolidae	4	0
Morphidae	1	0
Nymphalidae	57	25
Libytheidae	1	1
Riodinidae	41	1
Lycaenidae	16	5
Total Genera	186	48

The present fragmentary and unbalanced representation of the Papilionoidea in the Antilles, the ocurrence in all families of endemic species in the Antilles, as well as species which have subspecific representatives both on the continet and in the Antilles, all point to the permanence of the separation of the islands and the creation of a fauna built up from waif species. Species arrived in the islands sporadically over a very long time. The endemic species are probably representative of the early arrivals which became established. Subspecies could be representative of species of later arrival which have not evolved to such an extent as to become completely differentiated from their continental relatives. Over all, this pattern of the Antillean population is obscured by cosmopolitan species which move about more frequently, and by repeated reinvasion by individuals of species already established. This interchange was and is in both directions but dominantly from the mainland to the islands. As in the past, it continues today aided by the modern means of communication introduced by man.

The water barriers of the present can not be greatly different from those existing in the past between individual islands or the islands and the mainland. Similar conditions must have controlled during mid Cenozoic time between Mexico and South America. The spread of fauna was restricted. While the water barriers still restrict the spread of populations to the Antilles, these barriers have disappeared throughout Central America.

The Papilionoidea of the Antilles are definitely related to the fauna of Mexico but are divided into two groups. One group, the more ancient fauna, is related to the older northern fauna of Mexico which is considered to have reached the islands in Cenozoic times while population movements from the north were in progress; the other faunal group, representative of South and Central American species, is assumed to have reached the Antilles adventitiously during and after Pliocene time with the arrival in Central America and Mexico of many southern species.