THE MONARCH BUTTERFLY

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Illustrated by the author,
unless otherwise stated

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IN CO-OPERATION WITH THE
LIFE SCIENCES DIVISION, ROYAL ONTARIO MUSEUM
THE MONARCH BUTTERFLY
To

MISS HILDA WHITE
for her enthusiastic assistance which made the preparation of the manuscript possible

and

DR. C. B. WILLIAMS
for his pioneer studies of insect migration and for his helpful suggestions and friendship over the years
IN THE Monarch hutterAy goes back to my childhood, when I first became fascinated by the study of moths and butterflies. There were many factors involved in the study of these beautiful creatures which I found appealing. The search for caterpillars led to many a thrilling adventure as I combed the woods, examining every growing plant from lichens to tall trees for a discovery that would add a new species to my collection. Rearing the caterpillars provided an absorbing occupation at home, where my collection of rearing bottles teetered precariously on a row of rickety shelves attached to our garden fence. Collecting moths meant that on summer nights, preferably when a storm was threatening because then the moths were more active, I would make the rounds of my sugar trees which were baited with a heady mixture of apple sauce, sugar, and molasses, prodding the darkness with my torch in quest of the various moths that had come to feed.

Preparing and arranging the specimens in my collection occupied weekend and after-school hours. Making drawers, cutting glass, and lacquering pins were all part of the enjoyment. Proudly I arranged the specimens on pins in neat rows that resembled an array of aeroplanes preparing for formation flight, and then displayed them to my friends and relatives for admiration.

During the long winter months my spare time was spent waiting for the cocoons and chrysalids to hatch and reading many interesting and informative books about insects. I read and re-read the meticulous observations and colourful descriptions of Henri Fabre, who represented to me all that was admirable in a great naturalist. Maynard’s Manual of the North American Butterflies was my constant companion, its pages so worn that they had to be repaired with adhesive tape. Harold Bastin’s Insects, Their Life Histories and Habits and Packard’s A Guide to the Study of Insects revealed new horizons. A wealth of material awaited my eager enquiry and I revelled in the works of Comstock, Holland, Harris, Howard, Kirby, and Say.

It was during this period of active reading that I learned of the mystery surrounding the movements of the Monarch butterfly. Did it go south for the winter, or did it hibernate? Because some authorities believed that it hibernated, I searched diligently throughout the winter trying to find at least one dormant specimen. I found Angle-wings, Mourning Cloaks, and
Red Admirals, but not a single Monarch. That, however, did not rule out the possibility that I had missed one because the ice prevented me from turning over a particular log, or that the hibernating spot was in the hollow of a tree which was out of my reach.

Although I eventually turned to collecting deer flies (Tabanidae) and later grasshoppers and crickets (Orthoptera), the question: Where does the Monarch butterfly go in the winter? continued to intrigue me. It haunted me through my undergrad days and dogged my thoughts through Graduate School. It was in the latter at the University of Toronto that I encountered Professor A. G. Huntsman, whose painstaking enquiry and resolve persistence in obtaining factual data made me regard him as a modern version of Socrates. Whenever I proposed a solution to a certain problem, Professor Huntsman would meet my hypothesis with the same factual approach. Invariably he forced me to answer the questions, What are your facts? On what data do you base this conclusion? These questions remained with me and are the basis of the programme outlined in this book.

While enrolled in the Graduate School, I became attached to the staff of the Royal Ontario Museum as a lecturer. These were the lean years of the great depression and Museum funds were sadly lacking. My income was microscopic and there was no financial support available for work on the Monarch butterfly. Therefore I carried on the investigation after hours, with the able and enthusiastic assistance of my mother.

During my war service, 1940-45, I was able to turn my position as a meteorological officer attached to the Royal Canadian Air Force to good advantage through the kind co-operation of Dr. Andrew Thompson. I made surveys of populations of the Monarch butterfly in the various parts of Canada where I was posted, and the excellent training which I received in meteorology made it possible for me to analyse the data on the movements of the Monarch butterfly in terms of weather conditions.

In 1950 the late Robert Fennell, then Chairman of the Museum Board, became interested in the work on the Monarch butterfly and suggested that a portion of the annual budget be used to further my investigations. An enlarged programme was thus made possible.

Up to this point I had been carrying on the work almost single-handed, but I received assistance from an unexpected source. In 1951 my wife, who was keenly interested in the project, wrote an article about the tagging of Monarch butterflies which kindled the interest of many naturalists and professional biologists who read it. As a result, I was deluged with offers of assistance from people all over the United States and Canada. These volunteers, who number over three hundred, are the “co-operators” whose observations and experiments have proved to be so valuable in this report. The size of the project, augmented by volumes of mail, interviews, and press
releases, grew to such proportions that it became necessary to employ a full-time research assistant. I was most fortunate in obtaining Miss Hilda White who used her genius for organization to its fullest extent and devoted herself wholeheartedly to the project; her diligence and persistence hastened immeasurably the publishing of this report.

The processing of the data, as presented in this report, has taken three years to complete. Various factors involved in the life cycle of the Monarch butterfly have been included also, in part for the interest of the ardent naturalist, and in part to add further data on insect life in general and on butterflies in particular.

The problem originally was to answer the question: Does the Monarch butterfly south in the fall and remain there all winter? Considered superficially the question seems simple, but it becomes more and more complex as it is studied and there is no single, simple answer. The main problem is an intricate interweaving of many subsidiary questions. I have dealt with many of these, some of which are directly related to the original query and others only indirectly so.

Thirty-four years have elapsed since I first considered this problem, and now I have decided to bring together the data at my disposal and upon these to base a few tentative conclusions. I should like to make clear that this work represents only a beginning in this field of research and I hope that the data presented here will serve to stimulate inquiry and provoke questions which will be investigated by students of the future.
It is with considerable pleasure that I express my most profound thanks to all those who, over the years, have given so freely and so enthusiastically of their time and thought to this study. It would be extremely difficult to name those who are most deserving of special mention because so many people contributed to this project in so many different ways; for example, Mrs. L. Wylie and her father (the late Mr. Harry Stiles), Miss Ruth Haigh, and Mrs. L. W. Hobbs submitted voluminous reports, detailed and accurate, concerning their experiments and observations; Mr. Lloyd Beemer organized local groups of co-operators and thus increased immeasurably the number of tagged butterflies from which many valuable returns were made; Mr. Paul Beard supplied me with live specimens, collected during the winter months from the overwintering colony in the Monterey Peninsula of California; Miss Ivy LeMon publicized our programme by radio, television, and newspaper not only augmenting our list of co-operators but also drawing public attention to our project; and Mrs. C. L. Duane, owner of Butterfly Trees Lodge in Monterey, made our stay in this region enjoyable and assisted us in many ways to carry out our investigation of tagging methods on overwintering populations. I trust that in listing the names of all those who participated in this study and in giving full credit for their individual contributions throughout the text they will feel that they are sharing with me the pleasure of having contributed to the knowledge of a most fascinating insect.

I wish to acknowledge the kindness of the Canadian Aero Service Corporation for permission to reproduce their excellent relief map upon which our release-recovery lines were plotted.

My sincere thanks are extended to Mr. Hugh Halliday, whose nature photographs are so well known throughout North America, and to Mr. Terry Shaw, for permitting me to use their photographs illustrating the metamorphosis of the Monarch butterfly.

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INTRODUCTION

Much has been written about the supposed migratory habits of the Monarch butterfly and I should like to outline briefly some of the conflicting ideas that have been presented, not as a critical review of the opinions of others, but rather to emphasize the reason why I began the study of the Monarch butterfly. Most naturalists today are of the opinion that the Monarch butterfly moves from the northern breeding grounds to the southern parts of the continent, there to remain until the return of higher temperatures in the following spring. However, in the literature of the past, it has been suggested that hibernation takes place within the breeding area. Dr. Scudder, in *Fruit Children of the Air*, states that "woodmen sometimes, in cleaving open a tree, will discover a little colony of hibernating butterflies, as has been done in the case of the Monarch." The noted entomologist C. V. Riley was of the opinion that "the archippus butterfly hibernates within hollow trees and in other sheltered situations," and that such butterflies prefer to hibernate in the southerly timber regions until the following spring when "a small portion of these butterflies that have survived awake from their winter torpor and fly to the prairies, there to lay their eggs upon the milkweed." Mr. J. Alston Moffat, in his article "Anosia Archippus, Yet Again" which appeared in a report to the Entomological Society of Ontario in 1900, states that there is "altogether insufficient direct evidence to warrant the assumption that the autumnal swarms migrate from the more northern parts of its summer range in America, to the south in order to winter there."

Dr. Scudder was of the opinion that "it is not improbable that it [the Monarch butterfly] is as regular a migrant as the birds, returning southward in the autumn," although he pointed out that such a conclusion "is certainly not proven." Holland, in *Butterfly Book*, states that the Monarch butterfly does not hibernate but migrates southward there to remain during the winter, returning the following summer in a "wave of migration." However, Dr. Klotz in his recent *Field Guide to the Butterflies* states that "perhaps a few adults or pupae hibernate in the north."

If there was disagreement on the question of southern migration, there was still more uncertainty about the possibility of a return migration. Those who maintained that the Monarch butterfly did migrate southward in the fall did not, for the most part, believe that the same individuals returned to the breeding grounds the following spring. Clarence M. Weed, in *Butterflies Worth Knowing*, states that in the spring or early summer the Monarch
INTRODUCTION

butterflies move northward until they find milkweed plants and here lay their eggs; this would indicate a return migration of the same individuals. The Comstocks, in *How to Know the Butterflies*, state that the “mother butterfly follows the spring northward as it advances as far as she finds milkweed sprouting; there she deposits her eggs, from which hatch individuals that carry on the journey, and in their turn lay their eggs as far north as possible. Thus generation after generation pushes on until late in the season we hear of them as far north as Hudson Bay.”

In many textbooks and popular books on entomology the Monarch butterfly is discussed not only because it is such a well-known butterfly, but also because of its possible migratory habits. Almost as many authors claim that it is a true migrant as voice the opinion that it is not. And there are many that avoid declaring their opinions one way or the other or emphasize the need for more accurate information.

In 1930 *The Migration of Butterflies* by Dr. C. B. Williams was published. This monumental volume synthesized a great mass of observational data and, together with other shorter papers and popular articles, was responsible for stimulating studies on insect migration and drawing the attention of entomologists to the need for accurate observations and the publication of such under a clearly defined title. In order to obtain as much factual data as possible on the migration of the Monarch butterfly, the present study was initiated.

F. A. Urquhart
PART I

GENERAL DISCUSSION
CHAPTER ONE

MILKWEED

The question: Is the Monarch butterfly of economic importance? has often been asked. If the larva of the Monarch Butterfly feed upon a plant of agricultural importance, it would be considered of economic importance as an insect pest. There are certain economic uses for the milkweed, but they are of slight commercial value. In the Monterey Peninsula, however, particularly at Pacific Grove, the Monarch butterfly is of direct economic value, because there are certain areas within the peninsula where many thousands of them overwinter on the tall Monterey Pines (Plate I). Such spectacular displays are of considerable interest to tourists and many thousands of them visit Pacific Grove for the express purpose of seeing the Monarchs. John Steinbeck, who is a native of this area, describes these concentrations in Sweet Thursday—he may be forgiven the popular but erroneous conclusion that the butterflies feed upon the pine sap and, at times, become inebriated with this potent brew.

The City of Pacific Grove considered the Monarch butterfly sufficiently important to the economy of the area to pass the following Ordinance.

CITY OF PACIFIC GROVE

PROTECTION OF BUTTERFLIES

ORDINANCE No. 352

AN ORDINANCE PROVIDING FOR THE PROTECTION OF THE MONARCH BUTTERFLIES DURING THEIR ANNUAL VISIT TO THE CITY OF PACIFIC GROVE

The council of the city of Pacific Grove do ordain as follows:

SECTION 1. It shall be unlawful, and it is hereby declared to be unlawful for any person to molest or interfere with in any way the peaceful occupancy of the Monarch Butterflies on their annual visit to the City of Pacific Grove, and during the entire time they remain within the corporate limits of said City, in whatever spot they may choose to stop in; provided, however, that if said Butterflies should at any time swarm in upon or near the private dwelling house or other buildings of a citizen of the City of Pacific Grove in such a way as to interfere with the occupancy and use of said dwelling and/or other buildings, that said Butterflies may be removed, if possible to another location upon the application of said citizen to the Chief of Police of this City.

SECTION 2. Any violation of this Ordinance shall be deemed a misdemeanor and shall be punishable by a fine of not more than Five Hundred Dollars ($500.00), or by imprisonment in the County Jail of Monterey County for not more than six (6) months or by both such fine and imprisonment.
SECTION 3. This Ordinance is hereby declared to be urgent, and shall be in effect from and after its final passage. The following is a statement of such urgency: Insomuch as the Monarch Butterflies are a distinct asset to the City of Pacific Grove, and cause innumerable people to visit said City each year to see the said Butterflies, it is the duty of the citizens of said City to protect the Butterflies in every way possible, from serious harm and possible extinction by brutal and heartless people.

PASSED AND ADOPTED BY THE COUNCIL OF THE CITY OF PACIFIC GROVE, this 16th day of November, 1938, by the following vote:

AYES: COUNCILMEN: (Mayor) Fiddes, Norton, Calbraith, Burton.
NOES: COUNCILMEN: Lee, Matthews.
ABSENT: COUNCILMEN: Solomon.
APPROVED: Nov. 16, 1938.

WILLIAM FIDDES,
Mayor of said City.

ATTEST:
ELGIN C. HURLBERT,
City Clerk.

The seed floss of Asclepias syriaca was at one time used by the colonists of New England for stuffing pillows and cushions, and the seeds of this plant were sent to England by Governor John Winthrop in 1670. It was later transmitted to the European continent and became abundant in parts of southern France, Corsica, and Dalmatia. By the middle of the nineteenth century Asclepias syriaca and Asclepias incarnata were cultivated freely throughout Europe. There have been various attempts to bring the plant into full commercial use in England, France, Germany, and Russia, but, as far as the author is aware, without success. The stem fibres of Asclepias have been suggested as a substitute for flax and hemp. Milkweed latex has been mentioned repeatedly as a possible source of rubber in temperate latitudes. During World War II the seed floss proved to be the best substitute for kapok in the manufacture of life jackets. Both the stem fibre and the floss have been suggested as stock for papermaking. Dr. Woodson points out that the more or less poisonous character of nearly all species, which makes Asclepias a dangerous pest in cattle and poultry areas, is a serious drawback to its possible use as a crop plant.

Since the larvae of the Monarch butterfly feed upon the leaves of various species of milkweed, the distribution of breeding populations is determined, to a great extent, by the presence or absence of this particular plant. Also, the abundance of any one or more species of milkweed in a given area decides the potential density of a given population of Monarch butterflies. The importance of this family of plants is obvious.

The true milkweed belongs to the genus Asclepias, the term being derived from a Greek word meaning swallow-wort, and, according to one authority, there are more than one hundred species of it in North America. With the exception of tropical and subtropical species, all are perennials and those found in North America are erect. They are rather coarse herbs with a milky
1. a, cluster of plants from a main vegetative centre referred to as a perennial caudex; b, cluster of plants referred to as a clone; c, fruit in the form of a swollen pod; d, flowers occur in dense, close, terminal, or lateral clusters.
juice, and the leaves are arranged alternately or in opposite clusters. The margins of the leaves are smooth, although they may possess a slightly wavy margin that gives the impression of being broadly toothed. The flowers occur in dense, close, terminal, or lateral clusters (Fig. 1) and the corolla is deeply five-parted, the segments of each part pointing downward at the time of flowering. Situated above these segments is a crown of five hooded structures. The fruit is a long swollen pod (Fig. 1) which is packed with small oval brown seeds, each one of which is attached to a tuft of silky material. When ripe, the pod breaks open and the seeds, attached to the tufts of silk, are carried away by the wind.

There are, apparently, no true rhizomatous species of the milkweed in North America but some species, such as *Asclepias syriaca*, produce long roots that have vegetative centres (Fig. 2), similar to the eyes found in

![Figure 2. Some species produce long roots that have vegetative centres.](image)
potatoes, which will produce clusters of plants known as clones (Fig. 1). Throughout the summer months these vegetative centres produce individual or small clusters of plants that reach a height of six to eight inches. To find out how fast such a clone would grow, a stick was placed upright beside one of them in the month of August and by the end of October it was found that the plant had increased its height by only one-and-a-half inches. On the other hand, clusters of plants from a main vegetative centre, known as a perennial caudex (Fig. 1), may reach a height of four to five feet during the summer period. Some of these plants, as for example in _tuberosa_, may attain a very great age for herbaceous perennials and the shrubby thickets of _subulata_ are frequently over a century old.

Many species of milkweed grow in dense clumps in a particular part of a field because perennial shoots are derived from the common elongated roots passing from one cluster of plants to another. The fact that the plants tend to grow in dense masses is of significance in the survival of the larvae, as will be discussed later.

Owing to disease, or perhaps to the fact that a plant may be growing in a soil not suitable to it, some plants are noticeably less vigorous in their growth than others and do not present a luxuriant foliage. Such small, stunted plants usually possess leaves that are thin in texture and yellow in colour. They do not appear to be confined to a particular field or part of a

![Image of diseased plants]

Figure 3. Diseased plants that are noticeably less vigorous in their growth possess thin, yellow leaves.
field and it is not unusual to find healthy plants and markedly diseased plants growing side by side.

Certain milkweed plants produce flowers and finally seeds in the course of a single summer, whereas others do not. Plants growing from a small vegetative centre do not usually produce flowers and seeds, but plants growing from a perennial caudex grow to a large size and eventually produce abundant flowers and large seed pods. Sterile and fertile plants may be found growing side by side.

In areas where the milkweed plants have been cut down in midsummer or late summer, an abundance of small shoots will arise from the gemmiferous roots. These plants have comparatively small leaves which are narrow and a yellowish-green as compared with the broader and darker green of the larger plants.

Towards the end of July and continuing throughout August and into September, in the northeastern United States and Canada, the milkweed plant produces large flower clusters. These flowers produce a great deal of nectar and also give off a very strong and fragrant perfume. This combination attracts a great many different kinds of insects, particularly certain species of flies and bees, and it is not unusual to find many insects trapped in the flowers of the milkweed. If you grasp one of these trapped insects, and pull it gently to remove it from the flower, you will notice that a pair of small yellow pollen sacs is attached to one or more of its tarsi (feet). The entire structure, consisting of two pollen sacs attached to a central body,
Upper row, left to right: egg; head of larva protruding through hole in side of egg; 1st instar larva eating egg-shell.
Middle row, left to right: variation in amount of black pigment in larva; mass of fatty tissue within abdominal cavity of butterfly; head of cremaster being secured to button of silk while pupa is still held by larval skin.
Lower row, left to right: pupa; field of tall flowering milkweed in foreground and cut over area in background; ovipositing female Monarch flying across field of small milkweed plants.
PLATE II

Colour variation of female Monarch butterflies from various parts of South America, showing occurrence of D. p. megalippe (wing tip black with white spots).

Top row, left to right: Honduras; Costa Rica; Virgin Islands.
2nd row, left to right: Dominican Republic; Colombia; Cuba.
3rd row, left to right: Puerto Rico; Northern Brazil; Peru.
4th row, left to right: British Guiana; Venezuela; Dominican Republic.
5th row, left to right: Ontario, Canada; Ontario, Canada; Ontario, Canada.
known as a pollinium (Fig. 4). A pollinium consists of two completely enclosed packages of pollen grains which are united by a yoke-like process extending from each package to a common body which is known as the gland or corpusculum. This gland is dark brown in colour and of a horny texture. It is somewhat compressed and the inner surface of it is smooth and entire, but the outer surface has a narrow slit passing almost completely through it from the top to the bottom. This slit is of great importance in transporting the pollinia from one flower to another by insects visiting the flowerhead. The yoke-like processes, which are known as translator arms or retinacula, are usually elaborately ringed or fluted. They are ordinarily yellow in colour and horny in texture and are attached at one end to the gland and at the other to the tip of the pollinium sac.

When an insect is attracted to the flower in its pursuit of nectar, it may accidentally thrust the tarsus of one of its legs into the narrow, vertical slit of the pollinium gland. If the insect is large, such as a wasp or bee, it is able to pull the gland with the attached pollinium sacs free from the Bower. However, if the insect is small it is unable to do so and becomes firmly trapped.

When a bee or other insect alights on the flower of another milkweed plant the tarsus bearing the pollinium sacs may slip into the narrow space between the two contiguous anther wings, thus placing the pollinium sac into its destined chamber. The stigmatic chamber into which the pollinium sac is placed is composed of the lateral margins of the anthers themselves, except at the very tip where a small area of the true stigma is exposed. Within two or three hours the pollen tubes start to emerge and when in contact with the stigma the tubes penetrate it very quickly. The pollen tubes pass through the stigma head to the cavity of the carpel, each tube seeking an ovule. It is in this way that cross-fertilization in the milkweed plant is effected.

As the seeds develop, the pod begins to form. At first the pod is a small, globular structure attached to a comparatively large stem and surrounded by the dead or dying flowers in which fertilization did not occur. As the pod becomes larger, it assumes an elongate form. In some species the pod may be long and slender, and in others rather swollen. The outside may be smooth or covered with soft spine-like processes.

The species of Asclepias are distributed among three centres of dispersal, temperate to tropical North America, subtropical South America, and southern and eastern Africa. Of these, the North American and the African are by far the largest, including over one hundred species each. The South American consists of twelve differentiated species.

The species of Asclepias found in North America are adapted to a wide range of environment, although they are essentially subtropical plants and
only a few species extend to elevations over two thousand metres or are found as far north as the extreme southern parts of Manitoba, Saskatchewan, and central Ontario and Quebec. Most of the species prefer rather open dry woods, glades, barrens, and plains, although there are a number of desert species found in the southwestern United States and Mexico. Broadly speaking, species of *Asclepias* may be found throughout the United States and certain parts of southern Canada from the Atlantic coast to the Pacific coast, and throughout Mexico and Central America. It should be borne in mind, of course, that this does not indicate the prevalence of any particular species. Although there are more species west of the Mississippi (Texas alone has thirty), there are greater numbers of a particular species (e.g., *syriaca*) east of the Mississippi.

The ancestral home of the genus *Asclepias* in North America is in the Appalachian and Ozark highlands—Palaeozoic land masses upon which the genus may well have been represented in some form as early as Cretaceous. Dr. Woodson states that: “The strong similarity and slight degree of differentiation of the populations in those areas may be a reflection of their great age as well as the relative geologic and ecologic stability of their habitats. The rather slight differences between them may be due in large part to the Pleistocene ice sheets to the north, and to the south the intervening Mississippi embayment, and later its alluvium to which few species of *Asclepias* have proved themselves adaptable.” When Cretaceous seas drained from the Rocky Mountain area, the western portions of the United States and of Mexico gradually received various species of *Asclepias* which immigrated from the east, mostly from the Ozarks and from Florida. It is believed that this immigration took place during the Pleistocene.

Dr. Woodson states that the numerous African species do not appear to coincide with the genus *Asclepias*, and he points out that if he were able to undertake a revisionary study of the African species as a whole he would find an entirely different array of genera or subgenera.

As yet, we do not know whether the larva of the Monarch butterfly will feed upon all species belonging to the genus *Asclepias*. From our own observations and from information received from our co-operators, however, larva are known to feed upon the following species: *A. purpurascens*, *A. incarnata*, *A. tuberosa*, *A. amplexicaulis*, *A. syriaca*, *A. tomentosa*, *A. carrasavorum*, *A. eriocarpa*, *A. speciosa*, *A. fascicularis*, *A. verticillata*, *A. lanceolata*, *A. exaltata*, *A. sulcifrontii*.

*Asclepias syriaca* is the most abundant and ubiquitous species of milkweed found around the Great Lakes, and the one upon which most of the eastern population is known to feed. It is a very sturdy plant. The main stem is straight and thick—in many plants it may measure 18 mm. (3") in diameter at the base. The leaves are thick, dark green, and those located near the base
Milkweed

may exceed seven inches in length. The flower head is large and varies in
colour from white to light purple. The white flower individuals have been
placed in the form "leucantha," and although they have slightly longer hoods,
nevertheless in a single field a complete gradation from white to light
purple may be found.

It is not unusual to find uncultivated and ungrazed fields of many acres
supporting a dense growth of this common milkweed. Although it is most
abundant and grows most luxuriantly in rich clay loam, it also grows suc-
cessfully in dry sandy areas. The common milkweed is encountered through-
out the area surrounding lakes Ontario, Erie, and Michigan in pasture fields,
roadside, margins of woodlots, high banks of creeks and rivers, lake shores,
dry sandy uplands, and low-lying meadows.

A. syriaca is one of the first field plants to make its appearance in spring
and early summer. From May 26 to May 28, 1956, the author made a survey
of the lakes region and found that along the north shore of Lake Ontario,
from Toronto to Hamilton, the plants were, on an average, two inches high.
In the vicinity of the Niagara Peninsula they were eight inches high.
Throughout the Peninsula of Point Pelée they were, on an average, fourteen
inches high. There is thus a considerable difference in the growth rate in
spring in a north-south direction. By June 3 the plants in the vicinity of
Toronto had grown to an average height of twelve inches, a good indication
of the rapid rate of growth within a given area.

Figure 5. In late fall seed pods are found on naked stems.
In the vicinity of Toronto, flowers appear by June 1 and continue to appear throughout July and the first two weeks of August. The first flowers to appear are terminal, but the stem continues to grow beyond these flowers and to put out additional flower clusters resulting in a lateral arrangement of clusters.

Seed pods first appear during the first week of July and continue throughout August and September. Pods appear first on the lowest flower clusters, since these were first to make their appearance. A single plant may possess large seed pods, small seed pods, and a fresh flower cluster all at the same time.

As the plant reaches maturity, the lower leaves turn yellowish-green and drop from the plant, and in late fall it is not unusual to find a plant with large seed pods containing ripe seeds on a naked stem (Fig. 5). With the advent of frost all of the leaves fall from the plant, although in protected areas a few plants, usually those that did not produce seed pods or flowers, may be found bearing a few green leaves at the summit.

A list of the various species of Asclepias found in each state of the United States, Mexico, and each province of Canada, is given in Part II, chapter vii.
Egg

The egg of the Monarch butterfly, which is about the size of the head of a pin, is one of the most exquisite objects in nature, particularly when viewed through a magnifying glass or microscope (Plate 1). One writer has compared it to a "priceless gem cut by a master craftsman," and it does indeed have a gem-like appearance. Each facet, of which there may be from twenty-six to thirty-seven in a row extending from near the pointed apex to the base, is four-sided, the sides being formed by a thickening of the shell of the egg. These thickenings form vertical (from base to apex) and transverse ridges. There are twenty-two to twenty-five vertical ridges, and a large number of transverse, varying from five hundred to nine hundred.

When the egg is first deposited it is creamy-yellow at the base and pale cream, almost white, at the apex but as the embryo develops within the egg, the contents change from pale cream to creamy yellow to light grey and finally to dark grey prior to the hatching of the minute larva (Plate 1).

It was found that it was most difficult to remove an egg from a leaf without damaging it, and so the section of the leaf bearing the egg was cut away with a pair of scissors.

During midsummer (August) when temperatures range from 70°F. to 90°F., the egg develops rapidly. A period of three to four days elapses between the time when the egg was deposited and the hatching of the larva. In early summer (June and early July) and late summer (September and October) a longer period is required, varying from four to six days. Eggs kept at 65°F. took from eight to twelve days to develop. The rate of development of the embryo varies with temperature; development is rapid at high temperatures and slow at low temperatures.

Larva

Hatching

The egg turns dark grey in colour when it is close to the time of hatching and under a strong magnifying glass or a microscope the black head of the larva (Plate 1) can be clearly seen through the transparent egg-shell moving restlessly back and forth. The first evidence that the larva is about to emerge
is the appearance of an irregular transverse slit which widens gradually as the larva cuts the shell, finally forming an irregularly-shaped hole with ragged edges. The shiny black head of the larva soon makes its appearance through the hole (Plate I). Some larvae remain quiescent within the egg-shell after the exit hole has been made, the shiny black head protruding from the opening, while others crawl from the egg as soon as the hole is large enough to permit escape. After emerging, the larvae eat all or part of the empty shell (Plate I).

In the course of the rearing experiments it was found that certain characteristics distinguished individuals one from the other. For example, one larva would tend to be rather sluggish and take its time about crawling forth from the comfortable, though cramped, confines of the egg-shell; having finally emerged it would move slowly away, stopping frequently to elevate the thoracic region of its body and waving back and forth indecisively; it would not bother to consume all of the egg-shell, although it would return to it in a slow and contemplative manner. Another larva, in marked contrast, would rapidly chew its way out of the egg-shell and, shortly after emerging, devour the shell and crawl rapidly away to a particular leaf there to take up residence for the first stage of its life cycle. Such individual variation seems to continue throughout larval life. Individuals that were most active on hatching continued to show marked activity as compared to their more lethargic brothers and sisters.

After raising many hundreds of caterpillars I soon learned to recognize individual larvae, although the differences were so slight that it would be difficult to describe them. I sometimes named certain individuals (Mary, John, Bill, etc.) more because I was accustomed to naming pet animals than because of the scientific value of such a procedure. But it was this interest in the individual that led to separating the more active from the more sluggish, and which revealed that this difference continued throughout life and explained, in part, the difference in the time taken for the larvae to reach maturity when raised under identical conditions.

First Instar (Fig. 6)

By instar is meant the period between hatching from the egg and the molting of the larval skin and the periods of time between two successive molts. A larva newly hatched from the egg would be in the first instar until it shed its skin for the first time. A larva in the second instar is one which has shed its skin once and so on. These various stages, or instars, can be recognized by examining colour markings, presence (or absence) and arrangements of hairs, and the length of the front pair of feelers on the head and the three segments of the body to which the true, claw-like legs are attached (Fig 6).
FIGURE 6. Various larval instars. a, 1st instar; b, 2nd instar; c, 3rd instar; d, 4th instar; e, 5th instar.
The larva is, naturally, very tiny when it first emerges from the egg-shell, being between 1.7 and 2.0 mm. with an average length of 1.9 mm. It is light in colour (greyish-white being perhaps as close a description as possible) with the exception of the head and legs. The head is a shiny black with the exception of a slight ring around the base of the antennae and at the base of the mouth parts, and it possesses a few long hairs.

The prothorax (the portion of the body bearing the first pair of legs) is light in colour with the exception of a pair of small triangular dark spots bearing a cluster of long hairs. The spiracle (breathing pore) is small, round, and light in colour. Adjacent to the spiracle is a small, oval pigmented area, bearing two long hairs. The prothorax extends ventrally to form a fleshy process between the head and the first pair of legs.

The mesothorax (the portion of the body to which the second pair of legs are attached) bears a pair of fleshy dorsal tubercles which are slightly pigmented and which become more elongated with the growth of the caterpillar, eventually forming the feeler-like processes (mesothoracic filaments), so characteristic of the larva of the Monarch butterfly. Each tubercle bears a long hair. Immediately beneath the tubercle are two long hairs surrounded by a V-shaped pigmented area.

The metathorax (the portion of the body bearing the third pair of legs) has four long hairs and an elongated, slightly pigmented area.

Second Instar (Fig. 6)

One of the most characteristic differences between larvae of the first instar and those of the second is the appearance of two pairs of elongated yellow bands surrounding a central triangular spot on the head. Immediately beneath the triangular central spot is a transverse light brown marking. These markings remain constant throughout the larval period. Second instar larvae are decidedly stouter than those of the first instar and they are very light in colour.

The triangular spot on the prothorax is more elongated than in the first instar and there is a definite indication of a dark band extending beyond the spiracle. The spiracle has a dark border which contrasts with the lighter background of the larva. The ventral tubercle is much smaller in size and not so acutely pointed. There is also a tendency for the first pair of legs to become comparatively smaller and to assume a position closer to the head. The large hairs that were located in the vicinity of the triangular spot have now disappeared as have also the two large hairs that were associated with the spiracle.

The mesothoracic filaments, which in the first instar were small and oval in shape, have become more elongated and, when viewed under the microscope, there is a slight indication of what would appear to be segmentation.
The long hairs which protruded from the mesothoracic filaments in the first instar have disappeared. A faint brownish band now extends from the base of the mesothoracic process down to and including the basal segment of the legs. The mesothorax is sparsely covered with a number of very short hairs, together with a sprinkling of small, irregular pigmented spots.

The long hairs associated with the metathorax of the first instar have disappeared in the second instar. A narrow light brown band extends from the back of the caterpillar down to and including the basal segments of the legs.

Third Instar (Fig. 6)

In this instar the prothorax shows one obvious change, namely, that the pigmented triangular area, which was present in the first and second instar, has become greatly elongated and extends down in a thin line to a point beyond the spiracle. In addition, the spiracle has assumed an oval shape rather than a round shape, and has a very heavy contrasting border. The ventral fleshy tubercle is still present but is small.

The mesothoracic filaments have become more elongated and irregular in outline. It will be noted that if the filament is placed along the back of the larva it will extend to a point beyond the front portion of the metathorax. The light brown band is now more marked.

There is very little change in the characteristics of the metathorax but it will be noted in reference to Figure 6 that the body is sparsely covered with minute hairs and irregular pigmented spots.

Fourth Instar (Fig. 6)

The broad pigmented band is now very obvious on the prothorax in this instar and completely surrounds the spiracle extending from the back of the larva to and including the under-surface near the base of the first pair of legs. The first pair of legs tend definitely to be closer to the head. The ventral tubercle is no longer apparent. There is a slight indication of two secondary pigmented bands on the back associated with creases which in turn are associated with the segmentation of the body.

The mesothoracic filaments have become elongated and extend to a point immediately behind the metathorax. Although not indicated in the drawing, there is still a tendency to segmentation of these filaments which is very obvious under the microscope. The pigmented band has become very broad and extends to the base of the legs. In addition, a large secondary pigmented band has appeared near the posterior portion of the metathorax, together with a third pigmented band associated with the intersegmental fold.

With the exception of an additional thin pigmented band, very little change has taken place in the metathorax.
Fifth Instar (Fig. 6)

The fifth instar marks the final growth period of the larva. It is in this instar that the final colour pattern is established. In the previous instars the bands, with the occasional exception, tend to be light to medium brown in colour and the over-all colour of the larva is definitely pale. In the fifth instar, however, the pigmented bands are very dark in colour in comparison with the others, and there is also a slight variation in pigmentation from light to dark cream, which imparts a secondary banding effect.

The dark band of the mesothorax has become much broader. The legs have come close to the base of the head. The mesothoracic filaments have become greatly elongated, and now extend well beyond the posterior portion of the metathorax which still exhibits a segmented appearance. The colour bands have become very broad, and the two secondary bands mentioned in the fourth instar have joined to form a common band, which gives the appearance of a dark area surrounding two lighter islands of a paler colour.

There is also a broadening of the secondary band in the intersegmental fold between the mesothorax and the metathorax.

There is a decided increase in the amount of pigmentation in the metathorax. The primary band has become much broader and has joined at its base with the secondary band which, in turn, joins ventrally to the bands associated with the first segment of the abdomen.

In all, the final instar displays the characteristics of the Monarch butterfly larva, in which there are alternate bands of dark brown (black) and light cream and yellow which when viewed carefully present an intricate pattern rather than a definite regular banding. There is a considerable amount of variation in the width of the black bands, which, in extreme cases produces the effect of a black larva with narrow yellow bands (Plate 1).

Moulting

The following account of the moulting process was submitted by two operators, Mrs. L. Wylie and Mr. H. F. Stiles.

Although one speaks lightly of a series of moults, each moulting is a rather serious operation for the caterpillar and takes hours. Of all the transformations that occur in the life cycle certainly the moulting seems to be the one most difficult to achieve. It is a long, laborious operation.

For some reason it is generally not observed and out of all the caterpillars raised has been observed but twice. From measurements it appears there are four moults, maybe five, in the life of the caterpillar before the chrysalis is formed. These occur somewhere around the 5th, 9th, 12th and 14th days. The early days in the life of the caterpillar show rather slow growth, but after the eighth day the rate of growth greatly increases. If a human grew in proportion to the Monarch caterpillar he would end up a person thirty-five to forty feet tall.

The first sign of the moulting occurs when the caterpillar suddenly appears to
EGG—LARVA

become indifferent to life. Generally it seeks the under side of some surface and
lies immobile for some hours. Then with the anal prolegs and the four pairs of
regular prolegs fixed to the surface it lowers its body just in front of the front set
of prolegs at an angle of about 30 degrees, with its head upward.

In this position it lies for hours. There is often a series of slight convulsions in
which the caterpillar raises the front part of its body and some strain seems to
pass through the whole of it. It gradually loses its brightness of color starting from
just back of the antennae and working back. The skin seems to gradually loosen
or wrinkle. Here it lies for ten hours or longer, quiet at times, at other times
racked with slight convulsions. During this period it is extremely sensitive to
jarring, reacting to the slightest jar by suddenly raising its head. Even someone
walking seems to bother it.

After hours in this position it spins a web into which it fastens its true legs.
Then, with this action, a pulling starts; the old skin works back, then suddenly
there is a violent action, the caterpillar lets go with the entire front end, and with
a wild waving and twisting of the entire body frees itself from the old skin.

Now the caterpillar rests—it apparently needs it. The new skin is loose and in
folds looking badly wrinkled. Shortly it moves away. In one case it returned and
devoured the cast skin. In the other it paid no attention to it.

Two hours later, having filled out the new skin, it becomes active and goes
about feeding.

The above observations may be further amplified by those of Dr. Samuel
Siddler:

My attention was attracted one morning to one of these caterpillars while
molting its skin; it had been stationary at least twenty-four hours; and now first
began swaying its body from side to side, falling over so far that the thoracic
filament of the upper side became perpendicular, and then drawing itself forcibly
back to an opposite position; the muscular effort caused a considerable indentation
along the falling side of the swaying larva at the point where the white band
widens, and at which muscles are attached. The motion was repeated about once
in three seconds and continued for nearly three-quarters of an hour; now and then
the larva would violently shake its filaments or strain forward the front of the
thoracic segments, thus gradually detaching the old skin from the new; at last,
after remaining quiet, as if to gather strength for a final effort, it began to make
violent contortions, especially about the thoracic regions, which at first seemed
infeebled, but suddenly the integument parted between the head and body, and,
by the movements of the larva, passed backward over the new skin, slipping
over the whole body at once and leaving a little empty pellicle at the hinder
extremity. The skin was with difficulty removed from the filaments, especially
from one whose tip had been bent in the former stage, and which only parted
after strong exertions, the fresh filaments lay limp along the back until they were
gradually drawn forward, the tip clinging to the moist body until the last; but
they did not regain their full elasticity for some time. The remaining process
scarcely lasted a minute; the head, however, still remained attached and was only
removed after repeated lateral abrasions and violent efforts with the front legs.
After these efforts, the insect remained quiet, resuming the same attitude, with
bent head, which it had taken before molting, awaiting undoubtedly the harden-
ing of its integuments, and it was nearly two hours before the colors of the head
became bright and fixed; the larva then first devoured all the old pellicle, except the head, and afterward moved off in search of daintier diet.

Rate of Growth and Food Consumption

The rate of growth of the larva of the Monarch butterfly is prodigious. When newly hatched the larva weighs .54 milligrams; it increases in weight to 1.50 grams (1500 milligrams) in the short space of fifteen days. This is an increase of two thousand, seven hundred times its original weight. To accomplish this seemingly fantastic rate of growth the larva consumes enormous quantities of milkweed leaves, as those who have kept such insects in captivity will testify. The periods of feeding are erratic. A particular leaf being eaten may be completely consumed in the short period of four minutes, followed by a pause lasting from fifteen minutes to two hours before a second leaf is chosen. The amount of leaf devoured and the time taken to do so varies with the size of the leaf and the size of the larva. Feeding may take place during the night as well as the day, although the latter is more usual. Larvae deprived of food during the day will feed throughout the night. Larvae that have been given an ample supply of food during the day and have been kept in a warm place, or have had the rearing tube exposed to the direct rays of the sun will, in most cases, not feed during the night. The higher the temperature the more active the larvae become and hence if the rearing tube is kept in a warm place or exposed to the direct rays of the sun a greater amount of food is consumed in a given length of time. It follows that larval feeding upon milkweed growing in the open mature more rapidly than those feeding upon milkweed growing in shaded areas, such as the margins of wooded areas. However, larvae are rarely found in shaded areas. In one particular field that supported an extensive growth of milkweed, two hundred and sixty-five larvae were found on the plants in the exposed portions and three were found on plants growing along the margin of a small woodlot at one end of the field. This distribution of the larvae is correlated with the egg laying habits of the adult; the female butterfly chooses plants growing in the open in preference to those growing in the vicinity of trees.

The rate of growth is directly related to temperature: the higher the temperature the more rapid the growth rate and, conversely, the lower the temperature the slower the growth rate. It follows that the growth rate is more rapid in midsummer (July and August) than in early and late summer (May and June—September and October). During the warm days of July and August when air temperatures may reach 90°–100°F, larvae may reach maturity in ten days. In May and June it may take fourteen to seventeen days to reach maturity. In September and October, with particular reference
to October, it may take twenty days or more. Larvae placed in a refrigerator set at 45°F. took thirty-eight days to reach maturity.

**Miscellaneous Observations**

*Playing Possum*

A rather peculiar habit of the larva and one which does not seem to have any protective value is that of "playing possum" (Fig. 7). When a larva at any stage of its development is molested it will immediately loosen its grasp upon the surface of the leaf, curl up as if to protect the under-surface of the body, and fall to the ground, there to remain for a period varying from a few seconds to five-and-a-half minutes. This habit is more common to larvae in the first three instars than in the last two. It is also more apt to take place if the larva is on the upper surface of the leaf compared to the under-surface or margin. When the larva in the fourth or fifth instar has a firm grasp on the side of the leaf or the stem it is more apt to jerk the thoracic portion of the body from side to side than to play possum. It is possible that larvac in the early stages of development may be liable to attack from predacious insects and the trick of falling to the ground might have some protective...
value although such a trick appears to be detrimental rather than beneficial to survival.

Not all larvae play possum; on one occasion a specimen 4 cm. in length (in the fifth instar) refused to do so nor would a much smaller specimen of 1.3 cm. (in the third instar). A still smaller specimen, less than 1 cm. in length finally played possum after repeated goading with the tip of a lead pencil.

Of those larvae that did play possum when touched, some did so repeatedly while others did so only once or twice. For example, a particular specimen that was fully developed and nearing the pupation period, remained in a curled-up position for a period of five-and-a-half minutes; when it started to crawl away it was prodded again with a lead pencil and immediately curled up, remaining in this position for one minute. This was repeated nineteen times, after which it refused to play possum. A second specimen remained curled up for three-and-a-half minutes, and repeated the act seventeen times. A third specimen remained inactive for five seconds, repeated the act for twenty-five seconds, and then refused to do so. With such meagre information we can only conclude that the peculiar act of playing possum is subject to individual variation and does not seem to be correlated with the age of the larva.

After dropping to the ground in playing possum, the larva must find the host plant again. That the larva has difficulty in regaining its source of food was first discovered as a result of the following experience: in pursuit of a clearer understanding of the life cycle of the Monarch butterfly about one acre of our property was devoted to the cultivation of milkweed (A. syriaca). In order to obtain an abundant supply of eggs and larvae, an ovipositing female was placed in one of our large cages and the cage was placed over a stand of milkweed. Later, when the cage was removed, a count of 146 larvae was made on three stalks in one particular stand. Two days later, only 23 larvae could be found. As I was examining the plants for possible insect predators, my collie became interested and joined in the search. Delighted with this sport, he wagged his tail vigorously and by accident hit the plant I happened to be examining. Twelve of the larvae on the plant played possum and fell to the ground. For two hours I watched what happened to the larvae that fell upon the ground. Only two of them regained the plant from which they had fallen and one located a small plant five feet away. The remainder dispersed in all directions. Perhaps some of them found other milkweed plants while others perished.

That the larvae might not be able to find another milkweed plant when dislodged from the primary one incited my interest, and a few simple experiments were devised which showed that the larvae have considerable
difficulty in finding the host plant again and apparently do so by a trial and error method (see chapter viii).

Cannibalism

If a number of larvae are placed upon the leaf of a milkweed plant, within a very short space of time they will have distributed themselves over the plant—one to a leaf when possible. However, under crowded conditions such as in rearing vessels or cages, in the absence of sufficient food it is not unusual to have one larva eat another, attacking the posterior portion of the victim’s body as if the presence of faecal material had stimulated the reaction. If pupae, particularly newly formed ones, are present in the same cage with starved larvae, they will be attacked and partly eaten. Nor is it unusual for newly hatched larvae to consume portions of adjacent unhatched eggs. On the whole, however, cannibalistic behaviour seems to be abnormal and takes place only under the conditions described above.

Larval Migration

During the second or third instar the larvae move from the leaf upon which they have been feeding to other leaves of the same plant or they may leave the plant in search of other plants. Thus small larvae are found on the tender, small leaves of seedling plants, whereas large larvae are found on larger plants. This tendency to migrate was demonstrated by placing first instar larvae on milkweed plants growing in pots that were placed on the window-sill. Many of the second and third instar larvae left the plant to carry out the molting process on any adjacent object on the window frame; such migrants were unable to find their way back to the potted plants.

As in the case of playing possum, this migrating habit might be a factor in reducing the population in those areas where milkweed plants are widely spaced. In most fields, however, milkweed (A. syriaca) tends to grow in rather dense stands and, therefore, such migrating larvae would not experience difficulty in finding another plant. None the less, there are species of Asclepias which do not grow in dense stands, and there are also fields containing milkweed plants which have been mowed, resulting in the production of many widely-spaced, small milkweed shoots. The females choose these smaller milkweed shoots upon which to deposit their eggs, rather than the larger plants with tougher leaves. In investigating the ovipositing habits of the females, it was found that 20 per cent of the small milkweed shoots had one or more eggs glued to their leaves. Yet, three days later, when one would expect to find many larvae on these small shoots, the percentage had dropped to 2 per cent. Whether or not this absence of larvae is due entirely or in part to the habit of playing possum it is impossible to state. No pre-
FIGURE 8. Above, characteristic holes made by first instar larva; below, the membrane of the leaf consumed leaving some of the veins intact.
dacious insects were found on the plants. A few live larvae, however, were found crawling on the ground and six dead larvae were found, three of which were being attacked by ants. Our co-operators in other localities experienced a similar situation, namely, that of finding many eggs, but, at a later date, few larvae. Perhaps the habit of playing proums, together with the migratory habit combine to expose the larvae to the numerous insectivorous ground animals and these are responsible for the marked reduction in the population.

*Feeding Habits*

Although the majority of first instar larvae remain on the underside of the leaf, it is not unusual to find them on the upper surface. They feed on one or other side of the midrib of the leaf, usually at a distance between the midrib and the margin. The membrane of the leaf is consumed, leaving the veins and in some cases the veinlets intact, thus producing a series of holes, some of which are divided by the veins that have not been consumed (Fig. 8). It would appear that the mandibles of these small larvae are not capable of penetrating tougher portions of the leaf and it is therefore understandable why the female butterfly deposits her eggs on young, tender leaves of the plant.

In the fourth and fifth instars the larvae have become quite large and much more sluggish. They tend to remain on the under-surface of the leaf, although the occasional specimen may be found on the top of the leaf, particularly at night or during dull cloudy weather. A habit was observed in these instars which had not been noticed in others, namely, that of chewing the midrib of the leaf and crawling out to the far end of the leaf, causing it to bend. Only the occasional larva was observed doing this, and so far there is no adequate explanation for it. Although the amount of leaf tissue consumed in the first, second, and third instars is considerable, it is not nearly as great as the amount consumed in the fourth and fifth instars, since these are the periods when the growth rate is greatest.

*Larvae of Different Instars Occurring at the Same Time*

During August and September larvae in the first and fifth instars frequently will be found at the same time in the same field and occasionally on the same plant. This is because eggs are deposited at various times throughout the breeding season and hence larvae will be present in various instars at any given time. This is discussed at length in future chapters.
CHAPTER THREE

PUPA

FORMATION

When the larva has reached full development it leaves the milkweed plant, upon which it has been feeding, in search of a suitable location for changing from the larval to the pupal stage. Immediately prior to this it consumes enormous quantities of food in a relatively short period of time.

The nomadic period is a restless and active one. A larva that has left the host plant becomes agitated when forced to return to it. The rate at which the larva crawls away from the plant seems to be directly related to the number of times its journey has been forcibly reversed and the agitation increases with each return. The reason for this restlessness is that the pupa is developing within the outer skin, or exoskeleton, and a suitable place must be found for the suspension of the pupa before development has reached the stage when the larva is no longer able to crawl.

The distance travelled from the host plant varies considerably, partly because some larvae tend to wander around in circles more than others and partly because of physical obstructions. Pupae have been collected two hundred feet distant from the nearest milkweed plants and, on the other hand, the occasional pupa has been found on the underside of the leaf of a milkweed plant. In the latter case, after numerous observations, it was concluded that the larva does not pupate on the underside of a leaf of the same plant upon which it has been feeding but has probably wandered from one plant to another. The presence of a pupa on a milkweed leaf is rare as is evidenced by the fact that for a total of sixty-three pupae found in a one-acre field only four were collected from the underside of milkweed leaves.

Pupae may be found in a great variety of places: on the underside of logs (those that are not lying flat upon the ground but are held up at one end by some other object); limbs of trees; the under-surface of the leaves of various kinds of plants; the under-surface of the horizontal timbers of fences; and eaves and window-sills of buildings. Indeed, almost any object which gives support and shelter may be selected.

After choosing a particular site, the larva becomes much slower in its movements than during the wandering period. It moves slowly from place to place, frequently rearing the front portion of its body, as if investigating its chosen environment to avoid the possibility of any object touching the
newly formed soft pupa. This exploratory period may last for two or three hours but ends when the larva begins to lay down a thin layer of silk over the surface of the support.

The formation of a mat of silk is done slowly and deliberately. Under a strong magnifying glass it is seen that the silk fibres are rather coarse, and irregularly spaced (Fig. 9). Towards the centre of the area the fibres are massed more closely together, finally forming a dense patch approximately 25 sq. mm in area, with a mass of fibres forming a slight elevation referred to as the “button.” In preparing the mat of silk and the button the larva takes numerous, and at times lengthy, rest periods. Once the button has been formed the larva remains inactive, lying over the mat of silk, head and thorax inclined inwards, for a period of an hour or more. Following this rest period, the larva grasps the button of silk firmly with the anal prolegs, which are armed with a circle of strong, curved spines that become entangled in the silken fibres, holding it firmly to the silk.

In the course of rearing experiments it was observed that occasionally a larva would become dislodged from the button of silk. In some cases the larva would crawl back to the top of the cage and form a second button and once again become suspended. In other cases the larva, once dislodged,
THE MONARCH BUTTERFLY

was unable to climb up the wall of the cage and would enter the pupa stage while lying upon the floor. This invariably led to the formation of a badly distorted pupa, which produced a butterfly likewise distorted. The question immediately arose as to why some of the larvae were able to go through the process of forming the button of silk a second time, while others were not. To answer this question I interrupted the larvae at various times during the process of making the mat and button and finally becoming suspended. If the larva was removed from the mat of silk it would immediately form a new one. This was repeated four times with a single larva. If the larva was removed after forming a button, it would immediately form a new mat and button. This was repeated twice with a single larva. If the larva was removed after becoming suspended from the button of silk, it would make feeble attempts to crawl up the side of the cage, finally lying inert on the bottom, there to transform into the pupa.

This peculiarity can readily be explained. When the larva has reached its full development, anatomical changes begin to take place within its body. The pupa does not appear miraculously. It is a steady development, the rate of which varies with the temperature—the higher the temperature the more rapid the rate of development. During the process of metamorphosis the larva must find a suitable location, spin a mat of silk and a button, and, finally, in an inverted position allow the final metamorphosis to take place. Each phase of this metamorphic development must be accomplished in a set period of time. The larva cannot control the rate of bodily changes or arrest any one of them. The urge to leave the host plant is associated with certain anatomical changes; when this part of the metamorphic processes has been completed, it is followed by others that lead to the spinning of a silken mat. The larva often leaves the host plant well in advance of the changes that lead to final suspension from the button of silk, and in some cases the larva may travel a considerable distance before locating a suitable pupation site. As the end of the nomadic period approaches, the larva will display a marked increase in activity if it has been unable to locate a suitable place. The same agitation is displayed by larvae dislodged from the mat of silk. Having prepared the mat of silk and button, the larva may wait some considerable time before suspension.

In the inverted position the larva assumes a U-shape (Fig. 10), the head and thoracic region bent inward and the abdominal portion curved. As development proceeds the larva becomes more elongate, assuming a J-shape. Accompanying this elongation is a decided difference in colour, the bright yellow bands becoming more translucent and light blue-green in colour. This marks the final stage of the metamorphosis from larva to pupa and at this stage the pupa has formed within the larval skin.
The next step is the removal of the skin from the pupa (Fig. 10). A marked swelling occurs in the thoracic region causing the skin to break immediately behind the head. The swelling continues, causing the skin to be pushed towards the posterior end of the body as the entire pupa gradually emerges. The spines of the prolegs turn outwards, not inwards, and therefore the spines remain embedded in the silk so long as a pressure forces them outwards. When the skin has been pushed back to the point of attachment to the button of silk, shrinkage causes the spines to be retracted, and this, together with the active gyration of the pupa, eventually dislodges the spines from the silk. The fluid located between the larval skin and the pupa fills up the space between the spines, thus decreasing the depth of attachment since less of the spine is free.

The cremaster, or pupa stalk, is removed from inside the shrivelled skin and embedded firmly into the silk of the button (Plate 1). The larval skin still remains attached to the pupa and the button of silk but by its active gyration, the pupa eventually dislodges the skin and it falls to the ground, leaving the newly formed pupa intact.

Prior to carrying out this study, I had concluded that the purpose of the gyration was only to embed the knob of the cremaster firmly into the silk fibres, but by careful observation and a few simple experiments this con-
Figure 11. Cremaster of pupa showing club-like spines of the knob.

Figure 12. Drawings of spines of knob of cremaster showing the range of variation in shape.
elusion was found to be invalid. It was found that the pupa gyrate almost continuously until the larval skin has been dislodged, and then for a very short period after. On examining the knob of the cremaster under a hand lens, I found that its club-like spines (Fig. 11), were firmly embedded before the active gyrations commenced and that the embedding of the knob of the cremaster was accomplished slowly, carefully, and deliberately. An examination of the illustration showing the spines of the cremaster (Fig. 12) will indicate how perfectly they have been designed, like so many small button-hooks, for becoming readily attached to the pad of silk. The active gyrations commence after the cremaster has been made secure; if such gyrations commenced before the cremaster was firmly attached the pupa would have been dislodged. Therefore it seems obvious that the active gyrations of the pupa are not to embed the spines of the cremaster into the button of silk, but to dislodge the useless larval skin.

The question as to why it is necessary for the pupa to dislodge the larval skin arises. A rather simple experiment seemed to supply the answer. The skin was held against the pupa by gently inserting a very fine insect pin through the larval skin, after it had been pushed back and the cremaster freed and embedded, and into the cardboard of the top of a box from which the pupa was suspended. It was found that the larval skin became partly embedded in the pupal skin (Fig. 13), because the pupa when first formed is very soft and there are deep furrows between the legs, antennae, wings, and abdominal segments. These furrows disappear as the pupa contracts but an object placed in them will become embedded. Of ten specimens in which the larval skin was held against the pupa, the skins of four became embedded and of these only one produced a slightly distorted butterfly; the other three were normal. Thus, failure to dislodge the larval skin may cause distortion of the butterfly or death of the pupa if the thin pupal skin is ruptured, or it may, if deeply embedded in the thoracic region (Fig. 13 d), prevent the proper emergence of the butterfly, if the skin or some foreign object becomes slightly embedded, particularly in the abdominal region (Fig. 13 e), no apparent harm results.

In a later series of experiments it was found that if the skin of the pupa was damaged, for example, by being pierced by a sharp spine or tarsal claw, then the pupa would in some cases fail to develop and in others produce distorted butterflies; if, however, the pupal skin was not damaged, as was the case in Figure 13 e, then a perfectly formed butterfly would emerge.

Semi-exarate Pupa

The term semi-exarate pupa is used to apply to that stage in development between the larva and the fully formed pupa. It is somewhat grub-like in
FIGURE 13. a, a strand of silk caught behind the thoracic region prevented the pupa from dislodging the skin; b, d, two experimental pupae in which the skin became embedded; c, a thread placed loosely around the pupae in the semi-exarate stage produced this distortion; e, a thread placed against the abdominal region, while the pupa was in the semi-exarate stage, caused the thread to become completely embedded.
appearance (Fig. 14). The thoracic and abdominal segments are well defined, each segment being swollen and marked off by deep folds in the region of the intersegmental folds. The wing buds, which are small in comparison with the more elongate abdominal region, are swollen and extend above the rest of the body. The head, mouth parts, and legs have the appearance of being free appendages because each is individually delineated, like a ploughed furrow; hence the choice of the word "exarate" which is derived from the Latin \textit{exaratus} meaning "ploughed up." One of the most striking features of the semi-exarate pupa is the presence of a deep sulcus (channel-like depression) located between the two sections of the mouth parts (modified galea which unite to form the proboscis).

The semi-exarate pupa is soft to touch and a slight pressure can readily break the thin exoskeleton, causing a greenish body fluid to exude. It is in this stage that the Monarch butterfly is most vulnerable, not to predators or parasites but to the possibility of being struck by foreign objects, falling to the ground, or having the claws or spines of the larval skin pierce the thin skin.

\textbf{Fully Formed Pupa (Plate I)}

The exoskeleton of the semi-exarate pupa becomes firmer; the abdominal segments become retracted; the wings, legs, antennae, proboscis, and head gradually become less swollen; the depressions between the various structural units become shallower; and finally the smooth, wax-like mature pupa is formed (Plate I). The process of changing from semi-exarate pupa to mature pupa takes from twelve to nineteen hours.

As its development progresses, and particularly in the later stages, the pupa turns first dark green and later dark brown. Within a relatively short time after discoloration has set in, the bright orange wings of the butterfly
Figure 15. Emergence of butterfly from the pupa.
with their characteristic dark markings can be seen clearly through the transparent skin of the pupa (Fig. 15). Finally the pupa splits open and the butterfly emerges. The time taken for its development is from nine to fifteen days. As will be demonstrated later, temperature plays a direct role in time of development and low temperatures can delay development for many days.

For convenience in describing the various parts of the pupa (Fig. 16), I have divided it into the following regions: appendicular region, being that part occupied by the head, antennae, legs, and mouth parts; alar region, being that part occupied by the wings (note that the second pair of wings appears as small strap-like structures behind the first pair of wings); pronotal region, being a small area that appears to be divided into two parts and somewhat resembles in shape the broad wings of a moth and is located immediately behind the head; and the abdominal region, which occupies the region located between the wings and the cylindrical, segmented portion extending from the tips of the wings to and including the cremaster.

If the pupa is placed with the appendicular region downwards, the following broad regions may be designated: ventral region being that part facing downwards; dorsal region being that part facing upwards; lateral regions being those parts facing to the sides. With the pupa in this position and the head pointing away from the observer, the left side is to the left of the observer and the right side to the right.

As shown in Figure 16, the following parts may be clearly seen in the appendicular region: head; first pair of legs, which are very short and attached to the prothorax; second pair of legs, which extend to three-quarters the length of the ventral region; antennae, the segments of which are distinct, extending the entire length of the ventral region; and the proboscis, composed of two separate units occupying the central portion.

Immediately following the pronotal region is a large swollen portion to which the front pair of wings is attached; this is the mesonotum. Following this is a narrower segment, the metanotum, to which the second pair of wings is attached; as pointed out above, these wings are only partly visible and appear as a narrow band along the margins of the broad pair of wings. At each side of the pronotum, next to the front margin of the mesonotum, is a thoracic spiracle (breathing pore).

The abdominal region is composed of six well-defined segments, segments 4-9, as well as three incomplete segments on the dorsal surface located between the metanotum and a distinct line of gold spots. Abdominal segment 4 is hidden in the ventral portion by the wings. Abdominal segments 5, 6, 7, and 8 are ring-like. The ninth segment bears the cremaster as well as two black tubercles on the ventral surface. The genital orifice is marked by a slight depression between the two arms of the cremaster. A pair of
Figure 16. Parts of the pupa: a, dorsal view; b, ventral view; c, ventral view showing the position of gold spots and line of fracture (heavy line); d, dorsal view showing position of gold spots and line of fracture (heavy line).
well-developed elongate spiracles is located on abdominal segments 4, 5, 6, and 7. On the outside margins of the second and third abdominal segments are well-developed spiracles, one pair to each segment.

The cremaster (Fig. 11) is a blunt spine-like structure located at the posterior end of the pupa. For the sake of description, it may be conveniently divided into three parts: knob, shaft, and base. The knob, which is the portion that becomes attached to the button of silk, is slightly larger in diameter than the shaft. Numerous spines resembling minute button-hooks are its most characteristic feature. Some of the spines are broadly curved and possess comparatively large hooks; others are straight and possess comparatively small hooks; and still others are slender, straight, and without hooks (Fig. 12). Being rounded at the apex, these spines are ideally suited for hooking onto the strands of silk contained in the button. It is therefore a simple procedure for the pupa to thrust the spines into the mass of loose silk and, by a gentle rotating motion, to cause each spine to become entangled. The shaft of the cremaster is roughly two millimetres in length. It is narrowed immediately behind the head and gradually becomes broader towards the base. It is heavily chitinized and shiny black in colour. The base is broad, somewhat resembling an inverted wine glass, attached to which is a pair of pigmented bars, which I have termed the arms of the cremaster.

The cremaster is, of course, confluent with the rounded base of the pupa.

One of the most attractive features of the mature pupa of the Monarch butterfly is the presence of a definite number of shiny, gold spots. I have given them names in keeping with their position in relation to the various parts of the pupa as described above (Fig. 16). There are two pairs of gold spots associated with the compound eyes which I have designated as ocular spots and, to distinguish one pair from the other, the large elevated pair located near the centre I have termed the median ocular spots, and the smaller flat pair which are located near the side of the head, the lateral ocular spots. The large pair located at the junction of the first pair of wings to the body I have designated as the lateral ulnar spots, the small pair as the median ulnar spots, and the pair located on the wings as the alar spots. If the exoskeleton is removed from the ventral region when the butterfly is ready to emerge, it is found that the median ocular spots are located on the inside margin of the compound eyes and the lateral ocular spots on the outside margin. There are two pairs of gold spots on the mesonotum, one pair near the centre, which I have termed median notal spots, and one pair near the outside margin, the lateral notal spots. On the posterior margin of the third abdominal segment is a row of rounded tubercles joined by a band of gold spots. Each tubercle has a dark central pigment spot joined to a dark anterior band. There are twenty-two to twenty-six tubercles of variable size. I have termed the band of gold spots the abdominal spots.
The reason for the golden quality of the spots may readily be ascertained by the following examination. Using a fine scalpel or a cutting edge having a fine, sharp point, remove by dissection one of the gold spots from the body of the pupa; place the gold spot in a shallow vessel containing water; working under a microscope, or strong magnifying lens, turn the gold spot upside down—that is, with the concave part that faced the inside of the pupa upward and the convex outer part downward; using two fine pins or needles, hold the spot firmly with one needle and scratch the inner surface of the spot with the other needle. You will observe that there is a yellow pigmented layer on the outside followed by a series of plate-like scales each of which, when scratched away, glistens in the water like a minute diamond. Light falling upon the spots is reflected from these plates through the pigmented area, thus imparting a lustre that resembles metallic gold.

As yet, we do not know what particular function is served by these ornamental spots. A pupa from which I had removed one of the median ocular spots produced a normal adult butterfly. In a second case one of the uhar spots was removed with apparently no damage to the mature butterfly. A pupa, the gold spots of which were covered with wax, produced a butterfly whose wings failed to expand. Another pupa, the gold spots of which were covered with an opaque paint, produced a normal butterfly. I am of the opinion that these spots are not purely ornamental but that they perform a definite function. They may act as light receptors that delay emergence of the adult butterfly during periods of adverse weather conditions. This suggestion is, however, hypothetical, and is not supported by accurate and detailed experimentation.
In the course of rearing many hundreds of Monarch butterflies, it was noticed that they tended to emerge from the pupae during the daylight hours, particularly at noon. Each day adults would be removed from the rearing cages in which they had emerged and, after we had chosen those that were to be used for certain experiments, the remainder were tagged and released. In the early morning there would be only a few adults clinging to the sides and roof of the rearing cages, but by noon there would be a great many. Separating and tagging was usually done in the afternoon, so that at such times the cages were nearly emptied of butterflies—except for those that had emerged so recently that the wings were too soft to handle. In the late afternoon relatively few butterflies emerged. It would appear that the butterflies emerge from the pupae between 7 A.M. and 3 P.M., with the largest number emerging between 9 A.M. and 1 P.M.

One would expect maximum emergence to take place during midday because at that time incident radiation and air temperature is at a peak and the rate of development is greater than during the night when there is no incident radiation and air temperature is at a minimum. This simple assumption raises one question, however. If development was more rapid during the day and less at night, would one not expect to find a few butterflies emerging during the night, having almost completed their development during the previous day? But rarely does a Monarch butterfly emerge during the night. Presumably some light-perception mechanism controls the rate of development, allowing more rapid development on bright, sunny days, less on cloudy days, and virtually no development during periods of darkness.

The advantage to the newly emerged butterfly in having a few bright, sunny, warm hours in which to develop is obvious. The Monarch is a rather helpless creature when it first emerges. The wings are soft and cannot be used for flight; hence the butterfly is unable to escape the attacks of various predatory animals. Strong winds may dislodge a newly emerged butterfly from its support and, if it falls to the ground, its wings are unable to develop properly. Therefore it is necessary for the Monarch butterfly to develop as rapidly as possible after emerging from the pupa.
The Monarch butterfly rarely emerges from the pupa during periods of rain. This obviously is of advantage to the survival of the species, because during periods of high humidity the wings would remain limp for a longer period of time, and gusty winds, which often accompany periods of inclement weather, might dislodge the butterfly from its support, causing it to fall to the ground. It is difficult to understand, however, how the delay in emergence is accomplished. One might think that during periods of rain it is usually cloudy and cool and hence it is simply the retarding effect of low temperature on the rate of development. However, on one occasion during a prolonged period of rain lasting three days, and with air temperatures above 70°F., no butterflies emerged in our rearing cages. It would appear from this that temperature is not the controlling factor. Perhaps lack of sunlight or extreme moisture conditions are responsible. With regard to sunlight as a possible controlling factor, many of our specimens emerged on cloudy days, although not nearly as many as on clear days, but unfortunately the degree of cloudiness was not taken into consideration. With regard to rain as a possible factor, one of our co-operators reported an experiment in which he delayed emergence of the butterfly by sprinkling it continuously with water. From the above discussion we can conclude only that some factor or factors appear to operate in retarding emergence during periods of unfavourable weather conditions and in hastening emergence during periods of favourable conditions.

When the mature butterfly is ready to emerge, the pupa skin breaks open. Casually observing the emergence of the butterfly one might think that the fracturing of the pupal skin is a haphazard process, but close observation reveals that the skin of the pupa breaks open along a set of well-defined lines of fracture (Fig. 16). To describe this process as accurately as possible it is necessary to apply terms to the various parts of the pupal skin, following a terminology and divisional system similar to that given in the previous chapter for describing the completely formed pupa, in which appendicular region was the term applied to that region occupied by the head, antennae, mouth parts, and legs; alar region to that occupied by the wings; pronotal region to that occupied by the pronotum; and abdominal region to that occupied by the segments of the abdomen, including the cremaster.

If we examine the empty pupal skin after the adult butterfly has emerged, the regions as outlined above are very well marked. There is an elongate, somewhat triangular plate that covered the appendicular region; there are two small quadrangular plates that fall away from the remainder of the pupal skin when the butterfly emerges, which together covered the pronotal region; there are two large, somewhat quadrangular plates that covered the alar region; and finally a cylindrical plate, one portion of which extends towards the head end of the pupal skin, that covered all of the abdominal
PLATE III

Colour variation of male Monarch butterflies from various parts of South America, showing occurrence of *D. p. megalype* (wing tip black with white spots).

Top row, left to right: Panama Canal; Dominican Republic; Dominican Republic.

2nd row, left to right: Virgin Islands; Nassau (Bahamas); Venezuela.

3rd row, left to right: Columbia; Colombia; Colombia.

4th row, left to right: Puerto Rico; Northern Brazil; Peru.

5th row, left to right: Ontario, Canada; Ontario, Canada; Ontario, Canada.
Variation in colour of male butterflies in one locality (upper three rows) and female butterflies (lower three rows).
region. We can designate the plates of the pupal skin as follows and proceed to outline the lines of fracture.

*Appendicular plate* (a single plate), being that portion of the pupal skin that covered the appendicular region.

*Alar plates* (two plates), being that portion of the pupal skin that covered the alar region.

*Pronotal plates* (two plates), being that portion of the pupal skin that covered the pronotal region.

*Abdominal plate* (a single, cylindrical plate), being that portion of the pupal skin that covered the abdominal region.

It is very difficult to follow the line of fracture by examining the empty pupal skin, because the alar plates roll back as the butterfly emerges and, in addition, secondary folding takes place as the skin dries out; incidentally, the "rolling back" of the alar plates is accomplished by a downward and inward motion rather than an upward and outward one. It is, therefore, easier to follow the lines of fracture by examining a pupa at the moment when the butterfly is emerging than by examining the skin after it has been shed.

The first indication that the butterfly is preparing to emerge is shown by a split in the pupal skin in the centre of the pronotal region, dividing this small plate into two separate pronotal plates. This is the *first* line of fracture. Following this, a fracture occurs in the centre of the mesonotum and metanotum, constituting the *second* line of fracture. The latter is followed almost immediately, and perhaps concurrently, by fractures on each side of the appendicular region; these considered separately constitute the *third* and *fourth* lines of fracture. The pronotal region, which was divided into two separate plates by the first line of fracture, is now divided completely from the remainder of the pupal skin by a fracture at the front or anterior end, and the back or posterior end; these considered separately constitute the *fifth* and *sixth* lines of fracture. The appendicular plate is now free from the rest of the pupal skin, except for a slight area of attachment to the abdominal plate at its narrowest, or posterior end. The pronotal plates are completely free from the remainder of the pupal skin. It is at this point that a leg, or antenna, will appear. In most cases a leg, one of the mesothoracic pair, is thrust forth and paws the air seeking to establish contact with the outside surface of the pupal skin. This is followed by the second mesothoracic leg. Concurrently the head appears through the opening made by the complete removal of the pronotal plate. At this point the butterfly, with frequent rest periods, attempts to extricate itself from the pupal skin. A *seventh* line of fracture takes place extending from the posterior end of the median line of fracture of the mesonotum and metanotum, along the anterior margin of the first abdominal segment to the right and left of the median line, and
then posteriorly along the outside margin of the metathoracic wings to the posterior margin of the third abdominal segment in the vicinity of the conspicuous line of gold spots.

By the time the seventh line of fracture has been completed, the butterfly has succeeded in grasping the sides of the pupal case with the sharp sickle-like claws of the mesothoracic legs. The alar plates, having been reduced to two slender, partly rolled, somewhat shrivelled, skin-like structures, assist the butterfly in obtaining a firm grasp on the pupal skin. The butterfly then pulls the thorax and abdomen free and remains suspended from the now empty pupal case. The time taken for the butterfly to emerge, from the first fracture of the pupal case, varies from one-and-a-half to three-and-a-half minutes with an average emergence time, based on twenty-four observations, of one minute and twenty-one seconds.

The newly emerged butterfly has small, fleshy wings and a rather plump abdomen. The legs seem to be unusually long, this illusion being due to the softness of the integument which permits the legs to extend straight out; as the integument hardens, the muscles of the legs cause them to become flexed, thus giving the impression of becoming shorter. If a section of the
margin of the wing is cut off at this stage with a pair of scissors, a drop of clear, green fluid will form all along the cut edge (Fig. 17). Therefore, the body fluid passes between the upper and lower membranes of the wing and not along the veins alone. The drops become larger as the body of the butterfly pulsates, indicating that this action pumps the body fluid into the expanding wing. If the membrane of the wing is squeezed, a bubble containing this greenish body fluid will form, further indicating that the fluid is not confined to the veins of the wing. By inserting a needle or fine pin into the bubble, the body fluid will exude and, by rupturing the membrane, the upper membrane can easily be peeled away from the lower one, thus demonstrating that the wing is composed of two membranes separated in this formative stage by a space containing body fluid.

Within a period of ten to twenty minutes the wings reach their maximum size (Fig. 15). The pumping action continues, accompanied by a back and forth movement of the wings. A drop of brown fluid is discharged which is the waste products stored within the body of the butterfly during development within the pupa.

Depending on temperature and weather conditions, the butterfly remains clinging to the pupal skin for a period of two to seventeen hours. Specimens kept in rearing cages could, when alarmed, attempt flight within two or three hours after emergence. The flight, however, was of short duration.

It is during this formative period that the wings may become twisted or develop poorly if they are not allowed to hang in a vertical position: one pair of wings may be perfectly formed and the other pair distorted; or any one of the four separate wings may become distorted. Shrews and mice may attack the butterfly, particularly if the pupa was situated close to the ground, with the result that the wings are frayed and torn at the margins. That this damage took place during the emergence period is evident from the glazed appearance of the wing, due to the exudation of body fluid in the vicinity of the torn parts. This can be easily demonstrated by seizing the wing during the formative period with a pair of forceps and rupturing the wing membrane much as a shrew or mouse would do. Wings torn after the formative period is over do not show this glazed appearance or distortions in the damaged area.

For many years I had observed that far more butterflies with distorted wings occurred in the late fall than during the summer and early fall, and I had noticed also that such damaged specimens were more abundant after a severe frost than before it. I concluded that cold temperatures were responsible. It was during the summer of 1956, when most of our rearing experiments were carried out, that the true explanation for such distortions was found. With the advent of low temperatures, and particularly freezing temperatures, the leaves fall from the plants. Pupae fastened to such leaves
would fall to the ground and if the emerging butterfly was unable to find a suitable support, or if such a support was located near the ground or close to surrounding objects, the wings would become distorted.

The metamorphosis of any insect involves an extremely complicated series of developments. Of the many changes that must take place to transform a worm-like larva that feeds upon the leaves of plants into a winged creature that feeds upon the liquid nectar of flowers, the development of the wings is most spectacular. The wings begin their development within the body of the Monarch larva when it is only five or six millimetres in length. By the time the larva has reached a length of an inch or more, the structures which will eventually produce the final wings of the butterfly may be seen by carefully removing one side of the outer wall of the body of the larva. The first pair of wings are located in the region occupied by the second pair of legs (mesothorax) and the second pair of wings are located in the region occupied by the third pair of legs (metathorax).

The entire body cavity of the larva is lined with a row of cells that are located just beneath the hard outer skin (exoskeleton). This layer of cells is termed the hypodermis, or hypodermal layer. The word hypodermis is derived from the Greek word "hypo" meaning "beneath" and the Latin word "dermis" meaning "skin." Hypodermal cells are, therefore, the body cells located beneath the skin and from them the wing buds are derived.

The wing buds may be compared to the four fingers of a glove; the main part of the glove being the body of the caterpillar and the four fingers the two pairs of wing buds, one pair located on each side of the body. If a section of a wing bud were cut away so that we could examine the inside of it, diagrammatically it would look something like Figure 18 a. Very little space separates the upper and lower layers of cells. This is the condition existing before the larva enters the pupal stage.

Development of the wing buds, as well as other morphological changes, takes place very rapidly between the mature larval stage and suspension of the larva, culminating in the final appearance of the pupa. When the larva changes into the pupa, the wings expand to approximately sixty times their former area. If a section of the wing bud of the pupa is cut away (Fig. 18 b), the hypodermal cells are found to be more elongate, rather than being columnar, and each cell has an elongated process that is attached to a fine membrane known as the basal membrane or groundmembrane. The cavity in the centre is filled with body fluid or haemolymph. The accompanying drawing is diagrammatic; actually, the front pair of wing buds lie above the second pair and hence in cutting through one wing bud one would, of necessity, cut through the one beneath it. Notice that in the drawing there is a thick layer of chitin of the outer cuticula of the pupa which is absent in the first drawing because the chitin has not formed at that stage.
ADULT

FIGURE 18. Drawings illustrating various stages in the development of the wing; a, section through wing bud in its early stage of formation; b, development of wing within the pupa; c, development of scales from hypodermis; d, further development of wing scales.
Figure 19. Drawings illustrating various stages in the development of the wing scales; a, scale and scale ridges; b, scale and associated hypodermal fibres; c, hypodermal fibres between upper and lower wing membranes; d, structure of wing scale.
As development proceeds, certain cells of the hypodermis become modified, increase in size, and project above the others (Fig. 18 c), the projections bending towards the outer edge of the wing; at the same time a space, filled with body fluid, develops between the chitinous cuticle and the hypodermal layer.

At a later stage the walls separating each of the hypodermal cells appear to break down, so they can be distinguished one from the other only in the presence of the nuclei. Coincident with further development of the projections and apparent disappearance of the cell walls of the hypodermis, the hypodermis becomes folded (Figs. 18 d; 19 a). The hypodermal cells with the elongated projections (later to become scales) are located on the crest of each fold, as shown in the illustration. The hypodermal projections are actually broad and thin—they appear to be thread-like in the drawings because the latter represents a section through the projection. The projections of the hypodermal cells which were attached to the grundmembran disappear—a few remnants are shown in the drawing.

The hypodermal cells secrete a chitinous cover which eventually will be the wing membrane. The projections on the crest of each fold also secrete a chitinous cover which will form the scales on the wings. Therefore each row of scales on the wing of the butterfly represents a ridge or crest.

The next step is the formation of bundles of fibres (Fig. 19 b and c) extending from the upper to the lower membrane of the wing. In the accompanying drawing the hypodermal cells are seen to have become elongated and to have penetrated the upper and lower grundmembran. These hypodermal cells occur in groups extending from the trough of the upper surface to the trough of the lower surface of the wing.

When the butterfly first emerges from the pupa, the wings are small and thick. As mentioned previously, body fluid is pumped into the wing under pressure that forces the wing to expand. This expansion is not a stretching of the membrane of the wing; it is simply a flattening out of the ridges, somewhat after the manner of the expansion of the air chamber in an accordion. If the wing did not possess the bundles of hypodermal fibres holding the upper and lower surfaces of the wing together, then, of course, the wing would expand like a paper bag filled with water. If the wing is squeezed shortly after the butterfly emerges from the pupa then the hypodermal fibres become damaged, allowing the wing to expand and thus forming a bubble.

Once the wing scale has been formed over the hypodermal projection, the protoplasm of the wing-scale cell withdraws and as it does it leaves behind a series of chitinous pillars (Fig. 19 d). These chitinous pillars hold the two surfaces of the scale together. When the wing scale is filled with protoplasm, it appears transparent; when the protoplasm withdraws, its
place is presumably taken by air and becomes white. The chitin upon the outer surface of the scale (i.e., the surface which is away from the wing membrane) develops well-marked striae, whereas the lower surface is usually unstriated and flat (Fig. 19 d). The presence of these striae, in some species of butterflies, imparts beautiful iridescent colours to the wing by light diffraction. Those scales which are destined to be white are now fully formed and will undergo no further changes. Those scales which are destined to become pigmented become filled with body fluid which, by chemical changes, produces the variety of colours found upon the wing. The subject of the chemical and physical nature of the pigments in the scales is rather long and involved and hence is omitted from further consideration.

**Flight Habits**

At first glance, the flight of the Monarch butterfly would appear to be rather aimless and lacking in control. Actually, the Monarch is capable of a great deal of flight control and can alter its forward speed and direction at will. The characteristics of the flight of the Monarch butterfly may be divided into five flight patterns, each one being distinct and initiated and maintained by a fairly well-defined set of circumstances or stimuli. These are as follows: (1) gliding flight; (2) cruising flight; (3) speed flight; (4) pre-nuptial flight; (5) social flight.

**Gliding Flight (Fig. 20 a)**

The broad wings make it possible for the Monarch butterfly to take advantage of vertical air currents to maintain height when travelling close to the ground. This leisurely flight pattern is adopted when the butterfly is seeking suitable nectar-bearing flowers. It is characteristic of the local breeding population, particularly the resident adults. The speed of this flight varies considerably depending upon wind direction.

**Cruising Flight (Fig. 20 b)**

The wings of the butterfly are capable of considerable movement in a vertical plane from completely closed wings held above the body to within 30 degrees of the vertical beneath the body. In addition, as the air presses against the broad plane of the wing, the apical portion of the front pair of wings is capable of bending slightly, thus increasing the forward speed. In cruising flight, the wing passes through approximately 30 degrees of arc, as shown in the accompanying figure. It is a leisurely flight interrupted by gliding. It is used when the butterfly is feeding, passing from one flower to another, or during migration. The speed, based on fifteen observations taken by motor car, is 11 miles per hour. It is the normal or usual flight when con-
ditions necessitate movement from one place to another without any strong stimulation.

**Speed Flight (Fig. 20 c)**

When a butterfly is alarmed, the wings beat rapidly and pass through a vertical arc of 120 degrees. The degree of arc can be seen by observing a butterfly fluttering against a window pane, the rapidly moving wings showing as a blurred image through the entire movement.

It is most difficult to ascertain the speed of the Monarch butterfly during speed flight. On one occasion, in calm weather, a Monarch butterfly in speed flight, but not maximum speed, kept abreast of the car when the speedometer was registering between 20–25 m.p.h. A speed of 30 m.p.h. would not
be an excessive estimate of maximum speed and when assisted by a tail wind the butterfly's maximum speed could be much greater. Speed flight, from our observations, is carried out under strong stimulation, such as escaping from danger or attempting to get back on an original direction of flight, and may be demonstrated by releasing a captured butterfly.

Prenuptial Flight

When a male pursues a female, she will fly in an ascending spiral, pursued by the male. This usually takes place if the female is ready for mating, otherwise a zig-zag speed flight is employed by the female to elude the male. The vertical distance to which the male and female may rise varies considerably. At times the female will break away from the spiral flight and elude the male by speed flight. Occasionally two males may adopt the prenuptial flight, but in this case the flight is much more rapid and erratic, each male trying to get in front of the other. Such flights are usually of short duration, each party dropping to earth again after a short interval.

Social Flight

Of all the flight patterns none is as interesting to observe as that which I have termed social flight. With a combination of gliding and cruising flights, two or more butterflies will follow each other in a wide circle in a horizontal plane. Such a flight usually occurs during migration when the butterflies are flying at a height of one hundred feet or more. As the butterflies follow each other they drift with the prevailing wind. Butterflies which have been caged for a few hours and then released will exhibit this flight pattern. Speed flight takes them rapidly to some height where, as if conversing one with the other, they form the circle. It is because of this resemblance to a social gathering that the term "social" was used. Undoubtedly the butterflies are attracted to each other for purely social reasons, since at this particular time during migration the reproductive organs (at least in the females) are undeveloped. The Monarch butterfly tends to be gregarious during migration and the association of a number of butterflies during flight is not uncommon.

Sex Ratio

If Monarch butterflies have been collected in an area that has an abundance of flowering plants, more males than females will probably have been captured. Likewise, when the southward migration commences in late summer, again more males than females are found. However, if a number of eggs are collected, or obtained by placing a female in a cage with some milkweed plants, and raised from larvae through to mature butterflies, then just as many females as males are found. The reason for this seeming contra-
diction is that the males tend to remain in the areas where there are flowering plants while the females, occupied in depositing their eggs on small milkweed plants, do not. Hence, the ratio of males to females depends upon where the butterflies were collected. In late summer females may remain in a given northern locality depositing their eggs while the males, not so occupied, move southward. Hence, in certain localities, more males than females will be found at the beginning of the migration, while later, when both sexes are taking part, as many females as males will be found. Therefore, although the sex ratio is actually equal, under certain conditions there may be more of one sex than the other.

Mating Habits

One portion of a particular field where many of our field observations were made was cut so as to form a sod of short grass (Plate I). Scattered through this portion of the field were many small milkweed plants ranging in height from small seedlings less than two inches high to larger plants of not more than eight inches high. There were no flowering plants in this part of the field. A small creek flowed through the other portion, thus preventing mowing, with the result that there was a profusion of tall flowering plants and a luxuriant stand of flowering milkweed.

Prior to 1956 many hundreds of specimens were captured in this field, a return tag placed on the wings, and the butterflies liberated. There was a marked difference in the number of males and females tagged—99 per cent were males. All of the specimens were captured in the portion of the field where the flowering plants were growing.

In the summer of 1956, to carry out the rearing experiments involved in a certain study, eggs had to be collected. Only a few eggs were found on the leaves of the large milkweed plants, and these were located on the small calyx-like leaves surrounding the flowers. On July 26, 1956, a few Monarch butterflies were seen flying close to the ground in the portion of the field where the grass had been mowed. An examination showed that all the specimens in this part of the field were females and were busily engaged in laying their eggs upon the small milkweed plants.

The female Monarch butterfly, having been engaged in egg laying for periods up to four hours, flew to the adjacent portion of the field to feed. Here she would encounter a male that had been lying in wait, resting with wings partly opened, on the broad leaves of one of the surrounding hawthorn bushes.

When the female came into view, the male would immediately give chase. At times the female, perhaps seeking other areas for egg laying, would increase her speed and thus, on a zig-zag flight, elude her pursuer. At other
times the female would fly vertically in small circles closely followed by the male who seemed to be attempting to get in front of her. Eventually the pair would come to rest upon a broad leaf of milkweed or hawthorn. The female, with wings closed or but slightly open, would occasionally extend her proboscis as if attempting to feed. The male, with wings moving gently up and down, would strut beside and at times in front of her. Eventually taking up a position beside the female, the male would bend his abdomen in a lateral direction in such a manner as to bring the tip of it into contact with the tip of the abdomen of the female, the latter remaining still with wings closed. Using his well-developed jaw-like abdominal claspers, the male was able to obtain a secure grasp of the female, his hold upon the female being so strong that, when alarmed, he was able to take to wing carrying the female suspended beneath him (Fig. 21). It is not known for what length of time the male and female remain so united, but on one occasion such a pair was found an hour and a half later on the same tree and in the same position.

While holding the female firmly by means of his abdominal claspers, the male inserts his long needle-like aedeagus into the ductus copulatrix of the female and deposits a spermatophore (sperm-containing sac) into the bursa copulatrix, where it remains until the sperm are needed for fertilizing the eggs as they pass down the oviduct.
The above sequence, however, is not always completed. On many occasions the mating flight has been observed to the point where the male and female were resting side by side on a leaf, but when the male attempted to thrust his abdomen beneath the wings of the female the latter would snap her wings open several times in quick succession, at the same time arching her abdomen upwards, thus avoiding the claspers of the male. Why this reaction should take place is difficult to explain. Perhaps the scent exuded by the male may entice the female to rest but a different set of stimuli are involved in actual copulation. When the female reacts in this manner the male will strut in front of her opening and closing his wings, perhaps in an attempt further to mollify the female.

On each of the hind wings of the male there is a small black swelling. This is the scent receptor (Fig. 38). It consists of a small oval chamber with a slit-like aperture opening towards the abdomen. The roof of the chamber is covered with broad black scales. The interior of the chamber is lined with small, black scales, which, without the aid of a microscope, resemble black dust and have been so described. These minute black scales fit into goblet-like structures termed poscula. There are also a few scattered hair-like scales that fit into broad saucer-like structures termed patellae. In the base of the posculum and patella is a minute pore which penetrates the thin skin-like chitinous membrane. Beneath this is located a white, waxy substance that is produced from a fluid that enters the wall of the receptor through a minute channel between it and the adjacent wing vein.

If the tip of the abdomen of the male is squeezed, a pair of yellow glands, that are covered with long hairs, will be extruded (Fig. 38). These are the anal scent glands which exude a very sweet flower-like aroma rather like that of spiraea. A clear, yellow fluid collects on the surface of the gland and if a drop of it is placed at the opening to the scent receptor it is absorbed by the receptor. The scent receptors are like small blotting papers, constructed to hold the scent-producing fluid for a longer period of time than would be the case if the fluid were exposed directly to the warm, dry, summer air.

The male pursues the female when she is seeking food in the nectar of flowers and, by extruding his anal scent-producing glands surrounds the female with this aroma while they are in flight. Stimulated to feed, she follows the male to a suitable resting place. It is interesting to note here that the author has never observed a mating flight on windy days except in protected areas. This is reasonable since a stray breeze would dissipate the aroma and thus fail to entice the female. Having come to rest upon the leaf, the male continues to surround the female with the flower-like scent, which at times causes her to uncoil her proboscis. The male seeks, with the tip of his abdomen, the tip of the abdomen of the female. In order to obtain a firm hold with his abdominal claspers he must withdraw the anal glands, and
when he does so the source of the aroma is immediately cut off. The female might, as a result, take flight, particularly when the male seeks to grasp her. It is at this stage that the scent receptors apparently come into play. The male, prior to attempting copulation, transfers some of the scent-producing fluid to the scent receptors, which continue to produce the aroma until grasping has been accomplished.

Many species of butterflies possess modified clusters of scales or hairs upon the wings or body which act in a manner similar to the scent receptors described above; they are by no means confined to the Monarch butterfly. The structure involved varies from a simple group of wing scales that are but slightly modified, to a scent receptor similar to that of the Monarch butterfly but to which has been added a slight concave cup-like depression at the entrance to the receptor which receives the drop of fluid from the anal glands. This cup-like depression is in some cases devoid of scales, thus assuring the passage of the fluid into the receptor rather than among the scales of the wing in front of the entrance to the receptor.

When the drop of fluid is placed at the entrance to the receptor of the Monarch, the scales are so arranged that the fluid flows into the chamber. Here it coats the many minute black scales which, in turn, conduct the fluid into the patellae and poscula where it passes through the minute pores into the absorbing layer beneath. It is a most ingenious structure for holding and at the same time slowly disseminating a flower-like aroma, as a result of which fertilization of the eggs is assured.

De Niceville observed that "The males (Euploeaiceae) may often be observed patrolling a small aerial space, with the end of the abdomen curled under the body toward the thorax, and with the two beautiful yellow anal tufts of long hairs distended to their fullest extent at right angles to the body." Müller noted that in D. crippus "a very small portion of the wing, close to the orifice of the sexual cavity, was entirely denuded of scales as if they had been repeatedly rubbed away by introducing something into the slit." In this species, the area referred to is slightly concave, forming a cup-like depression which perhaps receives the drop of fluid from the anal glands and hence is a further specialization of that found on the wing of the Monarch butterfly. In some butterflies a patch of scales on the hind wings may be covered by a similar patch on the underside of the front wings; such an arrangement would assist in preventing rapid volatilization of the scent-producing fluid until it was needed. This would account for the presence of a strong odour when the wings were separated. Finally, the present interpretation may explain many of the observations which have been made relative to the mating flight (as in the case of the graylings) of many species of butterflies, the presence of hair and scale clusters on parts of the body, and
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the presence or absence of odours during certain seasons of the year and under certain conditions as here outlined.

OVIPOSITION

Once the ovaries have developed and mating has taken place, the female deposits her eggs upon the leaves of the milkweed plant. She does not deposit an egg on any leaf of any plant indiscriminately but, on the contrary, displays a considerable amount of selectivity. As if aware that the very small larva hatching from the egg would require a tender leaf for its first meal, the female deposits the eggs upon the tiny leaves of small milkweed plants. These plants, which are usually three to eighteen inches in height, bear leaves which are a soft, yellow-green in colour, with thin epidermis and a thin layer of pubescence on the under-surface and are in contrast to the blue-green leaves with thick epidermis and thick pubescence of the older leaves of the mature plants. Even to man's taste, the small leaves are similar to the young leaves of a lettuce plant. Rarely will the female deposit her eggs upon a milkweed plant that has a row of clusters or has "one to see; if she does the egg will be found glued to one of the small narrow leaves surrounding the flower head.

The female not only chooses small tender leaves for her offspring, but she also avoids unhealthy plants (Fig. 3), such as those that are attacked by a virus disease that turns the leaves yellow, and those infested with aphids which cluster together in dense masses on the underside of the leaf causing it to curl. Such plants are obviously unhealthy, and hence we would expect the female to reject them, but other plants which, to the human eye, seem to be devoid of disease may also be avoided. In some cases such healthy plants have been found to bear an egg deposited by a previous female, but in other cases there appears to be no reason for the rejection.

In choosing a particular plant the female first employs sight to direct her to it. Flying slowly, in gliding flight, she weaves back and forth across the field within a few inches of the top of the vegetation (Plate I). Occasionally a plant may be covered by surrounding tall grass, but the female will crawl slowly down the grass eventually reaching the plant and, having deposited an egg or having rejected the plant, crawl back again. It is during such a performance that the wings often become tattered and torn. Having sighted a plant she approaches it slowly, flying into the gentle breeze which assists in retarding her forward motion, with her two pairs of long legs (the first pair are very short and are held closely against the front part of the thorax) extended. Fluttering, in hovering flight, she gently touches the leaf of the plant with the tarsi of her mesothoracic legs, or she may alight momentarily.
It is through the sensory organs of the tarsi of the legs that the leaf is examined for its suitability as food for the future larva. If the leaf is acceptable, she bends her abdomen under it so that the tip of the abdomen comes in contact with the lower leaf membrane close to the central rib of the leaf (Fig. 23). A yellow, wax-like egg is extruded (Plate 1), the blunt base foremost, together with a mucilage-like secretion which firmly cements the egg, in an upright position, to the leaf. Rarely does the female Monarch butterfly deposit her eggs on the top surface of the leaf except under caged conditions; when she does so it is usually on the small leaves surrounding the flowerhead. Occasionally she may accidentally deposit her egg upon the leaf of an adjacent plant that is not a milkweed; this happens in the following manner. Alighting upon a small milkweed seedling, having examined the leaf with her tarsi, she bends her abdomen until the tip of it touches the surface of the leaf. If in so doing the tip of the abdomen happens to come into contact with the leaf of another plant, she will deposit an egg.

1To test the sensitivity of the tarsal sense organs perform the following simple experiment. Soak a piece of cloth in a weak solution of honey and water; holding a Monarch butterfly by the wings, folded together, bring it close to, but not touching, the cloth. You will observe that the butterfly displays no positive reaction. Now extend one of the mesothoracic pair of legs and place the tarsi on the saturated cloth; you will observe that the butterfly extends its proboscis in preparation for feeding (Fig. 22).
Figure 23. Females ovipositing.
upon it. This may be easily demonstrated by placing a leaf, or a piece of paper, in contact with the tip of the abdomen when the female is in the act of ovipositing (Fig. 24).

![Image](image_url)

**Figure 24.** Female depositing an egg on a piece of paper while held so that the tarsi are resting on the leaf of the milkweed plant.

Many plants may be examined before the female finally chooses a particular one. When the decision has been made, the process of bending the abdomen and depositing an egg is accomplished rapidly, taking between three to five seconds to complete. She then continues her flight upwind to another suitable plant.

How many eggs a female is capable of laying is not known and would be difficult to ascertain. However, more than four hundred eggs have been counted in the ovaries of a single female. Depending upon the rate of development of the eggs and the longevity of the female, it is quite likely that under ideal conditions a single female is capable of laying more than four hundred eggs.

**Number of Generations**

In late summer and fall the Monarch butterflies move south to their overwintering quarters and at such times they may be extremely abundant. The numbers fluctuate from one year to the next. When abundant, Monarchs
will be found feeding upon the nectar of flowering plants or clinging in
groups of many hundreds to the branches of the trees chosen as an overnight
roosting site. They may be seen flying across the highways or passing in a
steady stream over the roofs of houses. In years of abundance, they are
among the most striking and ubiquitous members of the insect world in
North America.

The journey from the northern breeding grounds, which occupy that portion
of North America roughly between latitudes 32° N. and 48° N., to the over-
wintering quarters, along the coast of the Gulf of Mexico, Mexico, and the
Pacific coast of California, covers many hundreds of miles. There are many
dangers in this long journey, of which the most important are violent rain
and wind storms—it is a common sight to see countless thousands of dead
and dying Monarch butterflies strewn for many miles along the shore of a
large lake following a severe storm. The result is that of the many millions
of Monarch butterflies that start on the southward journey only a few of
them will reach the final destination.

Having reached the overwintering sites, the danger of storms is still a
major factor in their survival. In some respects the danger is greater, because
violent wind storms of hurricane velocity sweep along the sub-tropical
shores of North America. If such a storm should strike a colony established
on the pine trees in a particular area of the coast, they may be shaken from
their precarious resting places and hurled to the ground to become victims
of the many species of insectivorous animals, or carried out to sea where,
with wings broken, they will finally fall into the water. The danger is much
greater when violent wind storms follow the passage of a severe cold front
with temperatures below 40° F.; under these conditions the butterflies are
completely helpless since they are unable to fly, their muscles immobilized
by the cold.

For those that survive there still remains the long trip north again, to
which is added the hazard of encountering below freezing temperatures
which are common in spring and early summer. An unusually warm period
in March and early April may draw the butterflies to a latitude in which
they may be caught in a mass of sub-freezing polar air that may last for
several days. None the less, a few of the original millions that journeyed
southward complete the round trip and return to their northern breeding
grounds.

The Monarch butterfly produces many generations during the summer
months, the number varying with latitude. This explains why many millions
of butterflies are by late summer ready to journey southward in the fall,
when only a few returned to the breeding grounds in the spring.

In the course of investigations, the fully developed ovaries of female
Monarch butterflies were examined and the number of mature and develop-
There was an average of 420 eggs (or potential eggs) per female. If we assume that every egg deposited hatches and eventually produces a mature butterfly, working on a round figure of 400 eggs per female (of which half are females), there would be sixteen million butterflies in the third generation from the migrant female that returned in the spring. This figure is, of course, inaccurate because not all of the eggs hatch and only a small percentage of the larvae reach maturity as adult butterflies. What the percentage of survival in nature is, we do not know. Even if a loss of 50 per cent is assumed, however, there would still be eight million butterflies resulting from the return of a single female. The Monarch butterfly has very few predators and parasites and hence the production of great numbers in one season is possible.

Of the Monarch butterflies that leave their overwintering sites to journey northward, some travel short distances before laying their eggs while others travel long distances. Those that travel but a short distance, naturally will deposit their eggs earlier than those travelling a longer distance. Therefore more generations are produced in the southern portions of the breeding range than in the northern portions, or in the case of the western populations more generations are produced along the coast of California than in the mountainous interior to the east. Also the cold weather in late summer stops further reproduction in the northern parts of the breeding range earlier than in the southern parts.

As a result of the many rearing experiments carried out in various localities in the United States and Canada, we now know how long it takes to complete the cycle from the egg to the sexually mature adult. Knowing when the first migrants return in the spring and when the last migrants leave in the fall, the possible number of generations in various parts of the breeding range can be estimated and it has been found that it varies from one to two generations in the north to three or four in the south. The most northern range is roughly latitude 48° N., and the most southern latitude 28° N., with an average range between 32° N. and 48° N.

The number of individuals found in a population in a given geographic area is not the result of the generations produced by the original migrant. The picture is more complicated. When the mature butterflies of the first generation, which were derived from eggs deposited by the returning migrants, appear in June or July, they spread out over the countryside in quest of new breeding grounds. Observations made on flights at this time indicate that there is a definite tendency to extend northward. For example, let us imagine that on May 15 a migrant female returns to Columbus, Ohio, to a field in which the early shoots of milkweed are growing, and there deposits a great many eggs. Approximately thirty-three days later (June 17) adults of the first generation will make their appearance. These individuals
Figure 25. In late August, larvae in all stages of development may be found.

are conspicuous because they are brightly coloured, particularly the males. Some of these first generation adults may remain for many days in their home site, but the majority of them will emigrate to other fields to the north, northeast, and northwest. Some of them may journey as far north as Toledo, others northeast to Cleveland, and others northwest to Lima. The exact distances of such movements are as yet unknown.

There is thus a mixed population in a given area during the month of June which consists of late migrants, newly emerged first generation, and immigrants of the first generation from farther south. In any given field in the breeding area brightly coloured first generation butterflies mingle with migrants and immigrants. The population of the second generation in a given locality will be mixed with offspring of the first generation immigrants and offspring of the migrants (that is, first generation residents). Further immigration takes place in July and August, but by this time all migrants have died, leaving only the offspring of the various generations. During August and September there may be a mixture of tattered and faded butterflies, freshly emerged and brightly coloured butterflies, eggs, larvae (in every stage of development [Fig. 25]) and pupae. It is quite likely that all
butterflies found in the northern fringes of the breeding range are immigrants (not migrants) from farther south.

The annual dates for the spring migrants are approximately as follows:

Southern portion (lat. 32° N.–37° N.): March–April
Central portion (lat. 37° N.–42° N.): April–May
Northern portion (lat. 42° N.–48° N.): May–June

The number of generations for each portion is approximately as follows:

Southern portion: 3 or 4 generations
Central portion: 2 or 3 generations
Northern portion: 1 or 2 generations
CHAPTER FIVE

GENERAL CONSIDERATIONS

SPECIES AND SUBSPECIES

At the present time the Monarch butterfly is known by the scientific name *Danais plexippus*. The scientific name *plexippus* will remain constant from now on by virtue of a recent ruling of the International Commission on Zoological Nomenclature which reads as follows: “The Commission agreed to use their plenary powers to direct that the trivial (or specific) name *plexippus* Linnaeus, 1758 (as published in the binomial combination *Papilio plexippus*) should be applied to the American species figured as *Danais plexippus* by Holland (W. J.), 1931, in the Butterfly Book as figure 1, plate 7; to place the trivial name *plexippus* Linnaeus, 1758 in the official list of specific trivial names in Zoology.”

When a species has a very wide geographic range, certain anatomical differences are noticeable at the various extremes of the range. The Monarch butterfly has such a range, extending from the tip of South America to the southern borders of Canada. In an attempt to find some morphological character, or characters, which might distinguish the North American population from the northern and southern South American populations, we examined the male genitalia but could find no significant differences. The shape of the claspsers seemed, on first consideration, to offer a structural difference, but on examining specimens from various localities we found that this character exhibited a wide range of variation. The terminal portion of the claspettes (gnathos) seemed to offer a degree of variation, but when considered on a large geographical scale, this character likewise was of no significance.

The specimens which were examined from South America south of the Amazon drainage system have one obvious character that distinguishes this population from any of the others, namely, the absence of a black band on the posterior margin of the front pair of wings. When other characters, such as colour, markings, and size, are taken into account there is a marked difference between this population and the one found in the northern parts of South America. In order that we may discuss this South American population without resorting to a cumbersome descriptive statement a third scientific name has been attached to *Danais plexippus*, namely, *erippus* (Plate VI). The South American population then is given the scientific
terminology *Danalis plexippus crippus* and we refer to it as a subspecies. The distinguishing characteristics outlined above, however, plus the facts that *Danalis plexippus crippus* appears to be geographically isolated and, unlike the northern population but similar to the North American one, is migratory, in our opinion establish *crippus* as a species rather than as a subspecies. Although the locality records of this species are not numerous, it appears to be limited to South America south of the equator. Most of the records are from the coastal region, mainly because there have been no collections made in relatively uninhabited areas of the Amazon drainage. It is found in southern parts of Peru, southern Brazil, Bolivia, Paraguay, Chile, Uruguay and Argentina (Fig. 43). Much more intensive collecting is necessary to define the northern limit more accurately.

The population found in the northern half (north of the Amazon drainage) is extremely variable and, with our present limited knowledge, it is impossible to assess its correct taxonomic position. The individuals from this population possess the black band on the posterior margin of the front pair of wings as do the individuals from North America, and they are darker in colour than the specimens found south of the Amazon. That the subspecies found in the humid tropical regions of South America are darker in colour than the ones found in North America and southern South America conforms to Gloger’s Rule. There is another slight difference in colour between the specimens from North America and those from northern South America: the large light spots at the apex of the front pair of wings are of a creamy colour in the former and decidedly white in the latter; there is also a tendency in the latter for the apex of the front pair of wings to be black in colour, with the exception of the spots, whereas the specimens from North America have a light reddish-brown area surrounded by black. The word “tendency” is used because many specimens from northern South America, and particularly from the islands in the Caribbean close to the mainland, were examined in which the light brown area was present. Thus, there seems to be a difference, although it is slight, between the population in northern South America and the population in North America, and the subspecific name *megaliptae* has been applied to the South American one. These specimens, therefore, have the scientific name of *Danalis plexippus megaliptae*. Until further information is available, particularly life history studies and cross-breeding experiments, it is perhaps advisable to continue to consider this population as a subspecies of *plexippus*.

This form ranges from the equator northward to Panama, Venezuela, British Guiana, Surinam, French Guiana and the islands of the Caribbean. More intensive collecting is necessary to establish the northern limits in Central America. The occasional specimen has been collected along the Gulf coast from Texas to Florida and the Florida Keys.
The population in North America, unlike its relatives south of the Amazon drainage system, possesses a black band on the posterior margin of the front pair of wings and, in contrast to the population north of the Amazon, creamy colored spots on the apical portion of the front pair of wings. In keeping with a three-name system, this North American Monarch is termed *Danaus plexippus plexippus*. It ranges from Mexico and the Gulf states of North America northward to the southern borders of Canada. It has been introduced into many parts of the earth and has been collected, as an accidental migrant, in many parts of the world (Fig. 43).

Clark (1941) gives the range as follows:

- Trinidad; Cuba; Peru; from Costa Rica (San José and Juan Vinas), the Gulf coast, and southern Florida northward through North America to Vancouver Island, the Northwest Territories, the Red River Valley, Fort Providence (west of Great Slave Lake), Lake Athabaska, the western shore of Hudson Bay, Moose Factory (on southwestern James Bay), southern Quebec, and Nova Scotia; Bermuda; the Canary and Cape Verde Islands; casual in the British Isles and western Europe; also, as a relatively recent immigrant, from the Hawaiian Islands and eastern Polynesia westward to the Andaman Islands, southward to northern New Zealand and eastern and southern Australia, and northward to Formosa.

Williams *et al.* (1942) give the range as follows:

The northern form *plexippus* is almost completely dominant in the whole of North America, Mexico, Central America to about the level of Nicaragua, and the Bahama Islands. It is also found in Cuba, Jamaica, Haiti and some of the Virgin Islands along with the intermediates. It is this North American form which appears to have spread over most of the world and all the specimens I have seen from the Pacific Islands, from Australia and New Zealand, from the Azores and Canary Islands in the East, and all but one of the British-caught specimens are of this type.

As is the case with many species of insects, the Monarch butterfly exhibits marked variations in color and size. Some are more brilliantly colored than others (Plate IV); some are very small and some unusually large (Plate V); some have more black pigment in the scales which tends to obliterate the white spots along the margin of the wing; and so on. At least one writer has suggested, based upon the measurements of wing length, that there are different populations in various parts of North America but we have failed to find any such significant differences. Since migration takes place over a large area and encompasses all localities in which Monarch butterflies occur, the author sees no reason for assuming differences in population.

In discussing the presence of an organism in a given area, the following questions must be answered: (1) is it a permanent resident (meaning, does it occur in this particular area, in one form or another, for twelve months of the year, and has it done so throughout historical times)? (2) if it is not a
permanent resident, was it introduced accidentally by man or by some natural force, or does it occur in this area for some months of the year and in another area for the remainder of the year? The answers to these questions will determine the various categories under which the geographical distribution of the organism must be discussed, namely (a) breeding range; (b) overwintering range; (c) accidental range; and (d) permanent resident range. The first two categories are considered when an organism is a migrant. The third category can apply to any organism. The fourth category applies to the more sedentary species. Since Danaus plexippus plexippus is a migrant we must consider its geographical distribution under the categories of breeding range and overwintering range, and since it has been carried to other parts of the earth, we must also consider its accidental range.

It is necessary to emphasize that there are no clear-cut boundary lines in the distribution of a species. One can only refer to distribution, for the most part, in terms of relative abundance to the point of non-existence. Thus, in the centre of the range a given species is most abundant, becoming less abundant towards the periphery of the range, and dwindling to complete absence, often because of insurmountable objects such as large bodies of water, uninhabitable deserts, and so on.

**Breeding Range**

As a general rule, one may state that the breeding range of the Monarch butterfly is directly correlated with the presence of the host plant, milkweed. There are many species of milkweed in North America, which occur in Mexico, the United States, and as far north as the more southern parts of Canada. But the number of species found in various parts of North America varies greatly, as does the abundance of a particular species in any given area. For example, Asclepias syriaca grows in dense masses, covering several acres of ground in many instances, in the vicinity of the Great Lakes. Such a luxuriant growth of the host plant supports a large population of larvae and, since such growth continues throughout the entire summer period, successive generations have an endless supply of food; thus, a great number of adult butterflies are ready to take part in the movement southward. Therefore, although the breeding range of the Monarch butterfly in North America may be given as Mexico and the United States to southern Canada, this does not specify the more concentrated areas, such as mentioned above.

There are two concentrated breeding areas for the Monarch butterfly, one of which is located in the Salinas and San Joaquin valleys of California, and the other, a much larger area, in the northeastern United States and southern Canada, from approximately 32° N. to 48° N. latitude and from 95° W. longitude to the Atlantic Coast (Fig. 78). The Monarch butterfly
does, of course, breed in other areas in North America, but to a much more
limited extent because, although there are many species of milkweed, none
of them grow in such great profusion as in the areas of concentration.

There is another factor which has a direct bearing on the abundance of
larvae in a given area. When the Monarch butterflies return to the breeding
grounds the ovaries are, in most cases, undeveloped, and the milkweed
shoots, even in the more southern parts of the continent, are small in size.
Therefore certain areas, particularly those situated near the overwintering
localities, are omitted. For example, a female Monarch leaving an over­
wintering locality at Alligator Point in Florida may fly as far north as
Kentucky or Indiana before the eggs have developed sufficiently in the
ovaries for oviposition. Hence, the presence of larvae in the southern states
in early summer and midsummer is rare.

Overwintering Range

In late summer and early fall the Monarch butterfly moves southward,
eventually reaching the overwintering localities (Fig. 78). In some areas
where the temperature exhibits marked fluctuations (cold nights and warm
days) the overwintering areas may be well defined and marked by special
roosting sites or "butterfly trees." Roosting sites are characterized by a mass
concentration of butterflies on a particular group of trees in a particular
area. In other areas, where the temperatures remain consistently high, there
are no particular roosting sites; the overwintering population roosts as indi­
viduals over a relatively wide area, seeking separate nocturnal roosts and
being active during the day.

The overwintering area is located along the Gulf states from St. Peters­
burg, Florida, westward to and including Mexico, thence northward along
the Pacific coast as far north as Monterey, California. From the data which
we now have, butterfly trees are located at Lighthouse Point south of
Tallahassee in northern Florida, and at various localities in California from
Santa Monica north to Monterey. Scattered overwintering populations
occupy the remainder of the region as outlined above.

Accidental Range

As a result of storms in late summer and early fall, usually associated
with strong polar outbreaks and resulting squall lines, the occasional speci­
men may be carried away from its normal range. Although the breeding
range is fairly restricted in North America, specimens of the Monarch butter­
fly have been collected at such distant points as Alaska, Great Slave Lake
in the Northwest Territories of Canada, and Moosonee in northern Ontario.
The Monarch butterfly has also been found in various lands in the South
Pacific, on the Canary and Cape Verde Islands, in Great Britain, and western Europe. In certain islands of the South Pacific, where species of *Asclepias* (or perhaps closely related genera) are found, some of them introduced to the islands by man, the Monarch butterfly has become established, as for example in Australia, New Zealand, and Hawaii. These immigrations or accidental occurrences, are due in part to the advent of intensive and rapid trade by ships and aeroplanes. We have ample evidence in support of such a conclusion both from historical records and from biological evidence, as outlined in chapter X. The continued extension of its range over shorter distances of a few hundred miles, as from island to island, is well within the realm of possibility. When Monarch butterflies are on islands they are more likely to fly out over the ocean, going from one island to another, and during periods of inclement weather settle on a ship at sea. In this way gravid females can be carried to distant lands and, in the presence of milkweed, initiate a new population.

It is highly probable that eventually the Monarch butterfly will become permanently established in many areas throughout the world when suitable species of milkweed have been wilfully or accidentally introduced into new areas. A case in point may be mentioned here. Until two years ago the larva of the Monarch butterfly was unknown in the vicinity of Fort William, a city north of Lake Superior, although on rare occasions adult butterflies were seen. A resident introduced the milkweed plant into his garden. The following year Monarch butterfly larvae were found on the plant. The same situation may occur in any area where conditions are favourable for the growth of the milkweed and where a gravid female is present. If the milkweed plant became established in Great Britain or western Europe, the Monarch butterfly quite probably would also become established there, as it has in Australia, New Zealand, Hawaii, and elsewhere.

**Fluctuations in Number**

Many species of animals fluctuate in numbers from year to year. Such fluctuations are most noticeable among those species which, because they are preyed upon by many other species, depend largely upon their numbers for survival as, for example, the rabbit, lemming, and meadow mouse. Although the Monarch butterfly is not preyed upon to any great extent, it does depend upon great numbers in order to survive. The Monarch butterfly, as was noted previously, travels great distances from the northern breeding grounds to the southern overwintering grounds. In the course of such travels it is exposed to many dangers, and must establish large numbers each year to maintain the species. It is not surprising, therefore, to find that the number of Monarch butterflies fluctuates greatly.
In 1950 and 1951 the Monarch butterfly reached a peak in numbers. During the fall migration the trees in certain areas along the north shore of Lake Ontario were festooned with countless thousands of Monarch butterflies as they came to rest for the night. Fields of goldenrod and asters seemed to be covered with a moving orange blanket. In 1952 there were fewer of them on the roosting sites and only the occasional specimen was seen in the same fields. In 1953 I was unable to find any roosting colonies on the same trees and, after searching for the better part of a day, I captured only three specimens. In this year the Monarch butterfly was so rare that we discontinued our tagging programme. In 1954 many more specimens were tagged and a few clusters, numbering a dozen or so, were located on the trees growing along the shore of Lake Ontario. In 1955 there was a great increase in numbers and by 1956 the trees were once again covered with Monarch butterflies. In 1957 there was a noticeable drop in numbers, although some correspondents reported a slight increase. In the summer of 1958 the numbers had been so reduced that in some areas the Monarch was considered rare. These observations seem to indicate that there is a cycle of six or seven years, with a sudden drop in a period of two years, and a slower rise for the following four or five years. If this is true, we would expect a peak to occur again in 1962 or 1963.

The cause of a sudden decrease in numbers is not known definitely. The Monarch butterfly does not appear to suffer from attacks by parasites, predators, or disease. It is, however, defenseless against unfavorable weather conditions. Being a cold-blooded invertebrate animal, it is unable to maintain a uniform body temperature and cold temperatures will completely immobilize it, or under certain conditions prove lethal. At temperatures below 50°F the Monarch butterfly has difficulty in flying, and at temperatures below 40°F it is unable to move.

In 1958, exceptionally cold temperatures prevailed during the spring and early summer over most of the North American continent, with below freezing temperatures in Florida and adjacent Gulf states. This prevented the returning females from reaching the normal breeding grounds, and those that had succeeded in flying north during short periods of mild weather were caught in the freezing polar air and, no doubt, perished. Hence, the breeding population, by then greatly reduced in number, was confined to the more southern parts of the breeding range where the food available is considerably less than in the more northern parts. In addition, the cold temperatures retarded development, thus reducing the number of generations. We may conclude therefore that weather conditions are the most important factors in controlling the numbers of Monarch butterflies and causing periodic fluctuations and that the cycle is an irregular one in which the balance is between the biotic potential and weather conditions.
The Monarch butterfly, compared with other species of insects, is relatively immune from attack by parasites and predators. Only three species of parasitic flies (Fig. 26) have been reared from larvae and pupae and, in the northern parts of the breeding range, the degree of parasitism has been found to be under 2 per cent. The occasional larva or pupa may be attacked by an unknown disease, but this is a rare occurrence.

Many predators will feed upon the larvae or adults, but none to any great extent. The catbird, black phoebe, and blackbilled cuckoo have been known to feed upon the adult butterfly on rare occasions. A newly emerged butterfly may be attacked by a mouse or shrew, and a few species of predacious insects, such as pentatomid bugs and larvae of aphid lions, may attack the small larvae (Plate VII and Fig. 27). I have occasionally found a Monarch butterfly caught in the strong web of the yellow garden spider (Argiope aurantia). Collectively, such predation reduces the population only to a small degree.

**Batesian Mimicry**

While collecting butterflies and moths in the forests of South America many years ago, H. W. Bates, an outstanding student of Lepidoptera, became interested in the numerous species of butterflies belonging to different
Figure 27. Above, body of butterfly eaten by ants; below, butterflies whose bodies have been devoured by mice and shrews.
families which closely resembled each other in size, shape, colour, and mode of flight. He concluded that the species which possessed a strong odour were not eaten by birds and that other species that did not possess this protection evaded their predators because they resembled their more fortunate and distant relatives. This theory became known as the Batesian Theory of Protective Mimicry and has been applied to many instances of close resemblance. The theory has not been confined to the insect world. Many examples have been suggested for mammals and birds. In every case, according to this theory, a single species is protected by mimicry while other species of the same genus have survived without such protection. That animals have gained protection from their predators by resembling some object in their environment is not difficult to accept. Many insects, such as the mantids and phasmids, resemble twigs and leaves and perhaps gain a certain amount of protection by such camouflage. A beetle that looks like the bark of a tree upon which it is resting, or a butterfly with closed wings which resembles the leaf of a tree or bush are, perhaps, protected. Whether such protection is as important to the survival of the species today as it was thousands of years ago is a question worthy of consideration. Perhaps certain arboreal lizards in past ages were more numerous than they are today and hence, although insects may be protected from attack by birds at the present time, such predators as birds may not have been responsible for the development of such protective resemblances.

Such protective resemblance is, in many cases, most striking; but there is one point to be borne in mind, namely, that such resemblances apply to what may be termed constants in nature. A stick insect may resemble the twig of a tree or bush, but not the twig of a particular species of tree or bush. A mantid may resemble a cluster of leaves, but not the leaves of a particular species of tree or bush. There have been twigs and leaves in nature for many thousands of years and hence such objects may be considered constants when considered collectively. A particular species, however, has changed through the ages and it would be difficult to imagine a particular species of insect evolving so as to continue to resemble the leaf of a particular species of tree or bush which we assume is also evolving. It is likewise difficult to imagine a species of insect that resembled another species of insect when, through the ages, both have been evolving.

The theory of protective mimicry has been applied to the Monarch and Viceroy butterflies. The resemblance in this case is so striking (Plate VIII) that it has been used as one of the outstanding examples in support of the theory which, in this particular case, presupposes that the Monarch butterfly is distasteful and the Viceroy tasteful to birds. A bird, having attempted to eat a Monarch butterfly, "learns" that it is distasteful and therefore when it sees a Viceroy butterfly it does not attempt to eat it. In this way, the
Viceroy gains protection from birds, which the Batesian theorists consider the most important group of predators and a principal factor checking survival of the Viceroy as a species.

In popular books and textbooks the idea has been advanced that the reason the Monarch butterfly is distasteful is because the larva is distasteful, and the larva is distasteful because it feeds upon the bitter leaves of the milkweed plant. Except for the very coarse leaves of the milkweed plant, which taste bitter, we have found that the small leaves of the milkweed plant, the preferred food of the Monarch butterfly larva, are not distasteful, nor is the larva or the adult (Urquhart, 1958). This, of course, does not indicate distastefulness or the reverse in so far as birds are concerned.

As a boy, I accepted the theory as applied to the Monarch and Viceroy butterflies. I concluded that the Monarch butterfly was bitter to taste since the milkweed plant, upon which the larva fed, must be bitter because of the thick glue-like fluid that exuded from an injured leaf or stem. On the other hand, I felt that the Viceroy would have a sweet, nut-like flavour. The ultimate authority—the printed word—stated that such was the case.

It was after graduation from the University that the subject of the distastefulness of the Monarch butterfly again aroused my interest. In carrying out investigations on the migration of the Monarch butterfly the problem of the Viceroy-Monarch mimicry arose. I decided to taste a Monarch butterfly, and, much to my surprise, found that it had no taste.

Some time later, I attended a meeting where the subject of Batesian mimicry was being discussed. The chairman related that he had been visiting in Massachusetts in late summer when the Monarch butterflies were moving southward along the Atlantic coast. A friend remarked on the supposed distastefulness of the Monarch butterfly and, to prove the point, captured one and tasted it. The chairman stated that the butterfly had proved to be extremely distasteful and asked the audience if anyone had ever tasted a Monarch butterfly. I raised my hand. "Was it not very bitter?" he enquired. "It had no taste at all," I replied. "Perhaps your taste mechanism does not respond to the secretions of the Monarch butterfly; such peculiarities of taste perception are inherited, you know." I quietly agreed to this possibility.

Two weeks later a reporter from a well-known news magazine called at my office for an interview, which resulted in a short well-written account of my little experiment. A second magazine published a lengthy article on the subject of mimicry decrying my attack on the validity of the Batesian theory. Other newspapers, unaware of the significance of the original story, presented accounts that hinted at poor professors finding it necessary to enrich their low-vitamin diet by eating live butterflies.

Having gained such unsavoury notoriety, I decided to delve into the
literature. I found that there were many hundreds of examples in support of the theory, which included flies that looked like bees; beetles that had the appearance of Lilliputian alligators; butterflies that mimicked toads; butterflies that belonged to different families resembling one another, and so on. Rare was the book or scientific publication that, in the true light of research and investigation, questioned the theory and tried to find substantiating data. The universal conclusion presented was that to man they look similar and therefore they must appear so to their predators. Few authors questioned whether such species would look alike to a bird, a lizard, or a snake, and yet if a Monarch butterfly is shown by experimentation to be palatable to man, the point is immediately raised that it may be unpalatable to a bird. Thus the theory is founded on the basis of one of the five senses of man (sight) and maintained despite the antagonistic results of another (taste). Those, such as Dr. Mcatee, who have investigated in great detail the dietary habits of birds concluded that there was no evidence in support of the theory, and recent experimental work, using caged birds, rejects rather than supports the theory.

The theory of protective mimicry has been so widely advertised in textbooks and in school curricula that some biological supply houses have arranged special displays on this subject for use in visual education. Occasionally an insect from Europe is used with one from North America to illustrate protective mimicry; it is difficult to understand what benefit is gained by a European insect mimicking a North American species. A recent publication issued by one of the more reliable biological supply houses objected strongly to this procedure, and in so doing pointed out that the theory is an anthropomorphic one and should be more clearly substantiated by accurate and intensive field observations together with a continuation of studies on the dietary habits of birds.

To determine what factors brought about changes in a particular species is impossible. To try to explain why the Viceroy resembles the Monarch butterfly in colour and colour pattern, and yet another species of the same genus, the Banded Purple, does not, is likewise impossible (Plate VIII). If we assume that the Viceroy owes its survival to the fact that it evolved, in some mysterious manner, so as to resemble the Monarch butterfly closely, then we must look for some different explanation to account for the survival of the Banded Purple. It has been suggested that the Banded Purple is distasteful to birds and hence does not require the protection offered by protective mimicry. If so, why did the Viceroy not mimic its closest relative, the Banded Purple?

I am of the opinion that the Batesian theory of protective mimicry is untenable, and I would offer a different explanation to account for such close resemblances. Such an explanation is, of course, hypothetical and, like that
of protective mimicry, must be subjected to careful examination, accumulation of data, experimental proof, and criticism.

If the Darwinian theory of the origin of species by natural selection is correct, then we may assume that the Viceroy and Monarch butterflies have changed in keeping with the changing conditions on the earth's surface. It is possible that when the present colour and colour pattern of the Viceroy and the Monarch evolved they acted as camouflage against groups (classes) of predators abundant in the particular habitat where the species lived. Perhaps the groups concerned were amphibians and reptiles rather than birds. This suggestion is offered because most insectivorous reptiles and amphibians are attracted to a moving object and will ignore one that remains motionless. As the Viceroy and Monarch butterflies continued to evolve and in so doing were able, owing to physiological changes, to move into more remote habitats, the need for such camouflage was no longer necessary, but since colour and pattern were not detrimental to survival, they have persisted to the present day. A similar explanation might be applied to other species of insects. Such a theory allows for a rational explanation for survival based on the origin of species by natural selection in which protective resemblance to a constant factor in nature is the main criterion. Thus, in so far as shape and colour pattern are concerned, the theory of protective resemblance holds true. A beetle that resembles a piece of bark is protected; a spider that resembles the yellow anthers of a flower can lie in ambush; the larva of a geometrid moth resembles a twig; a butterfly, with wings closed, resembles a leaf of a tree and, in flight, a leaf tossed by the wind; and so on. The question of whether or not such resemblances evolved to protect the insect from detection by birds, amphibians, reptiles, or other insectivorous animals is impossible to answer. It would appear, however, from the work of Dr. McAttee, that birds are not the significant predators. That the Monarch butterfly is distasteful to birds has never been demonstrated. If every fledgling of the many species of birds had to learn that such was the case, the population of Monarch butterflies might be seriously depleted. It would appear from my observations, those of my colleagues interested in observing the habits of birds, and from published accounts dealing with the analysis of the stomach contents of birds, that butterflies are rarely attacked. We must conclude that there is something, other than taste, involving the flight of butterflies that renders them immune from attack by birds. It is only during mass flights or when butterflies have been disabled and flutter helplessly on the ground that many specimens may be found which indicate attack by birds.

The above discussion does not discount the idea that some insects have evolved a secretion which, to some predators, is distasteful. Certain pentatomid bugs are known to possess such a defensive mechanism, However,
the protection is not necessarily against birds as much as against amphibians and certain species of insectivorous reptiles. Given a distasteful insect, a chameleon or frog will discharge it without injury. A bird, on the other hand, tends to mutilate the specimen.

Warning colours, particularly red, have been proposed under a theory of “warning colouration.” The work carried out by Dr. McAttee, however, does not lend support to this theory. We do know, however, that certain species of animals are able to detect wave-lengths of light outside man’s visual spectrum, and we also know that certain species of animals are blind to certain colours of man’s visual spectrum. It is conceivable that although a certain colour, such as red, is obvious to man it may not be obvious to certain predatory animals. For example, when we offered newly emerged goldenrod gall flies to our chameleon she was quite unconscious of their presence. No attempt was made to follow their movements as they crawled over the leaves. When we introduced a spider, however, the chameleon focused both eyes upon its prey and with lightning rapidity her tongue shot out and captured it. It is possible that a given species of insect may, through natural selection, have evolved a colour which rendered it invisible to some of its predators, and at the same time evolved a distastefulness as a protection against others. It does not necessarily follow that the one is dependent upon the other, or that a learning process is involved.

With regard to insects, I would propose that, in keeping with the origin of species by natural selection, in the evolution of certain colours, colour patterns, and forms, the principle involved is that of protective resemblance to a non-specific constant in nature; that other colours of that part of the spectrum which renders the insect more or less invisible to its predators evolved; and that distastefulness evolved, independent of any other changes, as a protection against predators that possessed well-developed gustatory organs.


C H A P T E R S I X

MIGRATION

Definition of Terms

Cahn (1925) defines migration as "A periodic passing from one place to another." He breaks this major classification into two subclasses, daily movements and seasonal movements. The daily movements are feeding movements or reaction to light, and seasonal movements are related to breeding.

Thomson (1926) states:

To deserve the description "migrating" in its strict sense, movements need not necessarily have a very great geographical amplitude, but at least they must involve a definite change of locality. They must be purposive in that the change of scene is associated with some definite advantage which serves as its raison d'être and there must be return movements to the original area. They must be periodic in that they correspond to some recurrent change either in the environmental conditions themselves or in the animal's reaction thereto. True migrations are changes of habitat, periodically recurring and alternating in direction, which tend to secure optimum environmental conditions at all times.

Williams (1930) takes exception to Thomson's definition:

To my mind this definition insists too much on the teleological aspect of migration, and it would be impossible to refrain from using the word migration to describe a change of habitat until the critical observer was convinced that optimum conditions had been reached thereby. Further, I am inclined to disagree with the requirement that "there must be return movement to the original area." In the first place this would prevent the use of the word migration for the well-known movements of lemmings and locusts . . . . The definition of migration that appears to suit best the conditions as found in mammals, birds and insects is as follows: "migration is a periodic, more or less unidirectional, continued movement, assisted by the efforts of the animal, and in a direction over which it exerts a control, which results in the animal passing away from its previous daily field of operations." "In cases where the animal is carried a long distance by agencies beyond its control the use of the term "involuntary migration" is not desirable and should be replaced by "involuntary distribution" or "dispersal."

Heape (1931) defines four types of movement common to many species of animals. When a population of a species of animal moves from one place to another without a return movement, this may be an emigration or an immigration depending on whether the animals are moving out of a particular locality (emigration) or into a particular locality (immigration). If the population moves in random fashion from one locality to another, the move-
ment is termed nomadism. If a population moves from point A to point B and back again to point A, it is migration.

We have become accustomed to interpret the word “migration” in terms of the migration of birds when the birds fly back and forth annually between the breeding grounds and the overwintering grounds. In late summer the barn swallow moves southward to its overwintering grounds and in the spring it moves northward to its breeding grounds. This is one type of movement to which the term “migration” has been applied. In the breeding grounds the swallow leaves the nest to obtain food for its young and returns to the nest again. This is quite a different movement and yet it is a return although vague in direction and encompassing a wide area. The term nomadism has been suggested for this type of haphazard movement. When the swallows prepare for their southward flight they gather together in flocks during the afternoon, remain so grouped together during the night, and disband the following morning in order to obtain food. This constitutes still another type of movement. Arriving in the overwintering quarters they disperse over a wide area, moving from place to place. This rather aimless movement is of a somewhat different type, though slightly so, from that found in the breeding area. There are, then, four types of movement. Should the word migration be applied to all of them? Is it possible to arrange a classification of movement that would allow an adequately descriptive term for each of them?

There are, of course, many other types of movements, such as the congregation of snakes in a particular area in preparation for hibernation; the movement of frogs to a pond in spring; and so on. Species of salmon on the west coast of North America return to the rivers and, having spawned, die. This is in part similar to the movements of birds, in that it constitutes a return trip, but it is a slightly different type of movement since it occurs but once for each individual. Occasionally, for reasons that are not very clear, certain species of animals may suddenly appear in numbers, far beyond their normal geographical area, where conditions are not suitable for their survival. For example, the migratory locust, owing to factors involved in population density, will move in dense masses from one area to another. The sharp-tailed grouse of North America will move, under certain ill-defined conditions, far south of its normal range. The Norwegian lemming is a classic example of a mass exodus. These freak occurrences, which seem to follow an ill-defined cycle, constitute a quite different type of movement. The word movement may be used as a collective term and hence is the major or all-embracing one. Any motion of an animal may be referred to as a movement. This term may be divided into three major categories: involuntary dispersal, nomadism, and migration. An organism may be carried to a different locality by forces beyond its control, for example, a bird carried
by a strong wind, an insect carried on a drifting log, or a butterfly carried on a ship. Such accidental movements may be termed involuntary dispersal as suggested by Williams. An animal may move aimlessly from place to place, as for example: a herd of antelope grazing, a flock of starlings feeding, or ants foraging. Following the suggestion of Heape, the term nomadism may be applied to this type of motion. Nomadism may carry a population of animals over a very great area and, in some cases, this type of movement may be the only one exhibited.

An animal may move in one direction, as a more or less continuous movement, assisted by the efforts of the animal and under its control resulting in the animal passing away from its previous field of operation, as, for example, the flight of the swallow southward, the movement of the Norwegian lemming, and the migratory grasshopper. This kind of movement may be termed a migration.

How many variations there are of the migratory movement will only be known as the result of research over a period of many years. At present, however, we may acknowledge three major groups: emigration, immigration, and remigration. If individuals of a particular species of animal leave an area and invade another, we may term this moving-out type of migration an emigration and the moving-in type of migration an immigration. Emigration is therefore defined as “the movement of an organism in one direction out of a given area, as a more or less continuous action, under the control of the organism, resulting in the organism passing away from its previous field of operation with no return.” Immigration is defined as “the movement of an organism in one direction into a given area, as a more or less continuous action, under the control of the organism, resulting in the organism passing away from its previous field of operation with no return.” Remigration presents a back and forward movement and is defined as “the periodic movement of an organism in one direction, as a more or less continuous action, under the control of the organism, resulting in the organism passing away from one field of operation to another with a return to the original field of operation.” It will be noted that the definition for remigration is the one which, in ornithology, is applied to the word migration. Remigration has been used also in the sense of “a movement of a portion of a species population from one locality to another with a return movement to the original locality by different individuals of the species.” This is a most unfortunate use of the term because the prefix “re” has no significance in the definition as given. It is perhaps an attempt to change the original meaning of the word migration so as to preserve its significance in ornithology.

Remigration may be divided into two groups: daily remigration and annual remigration. For example, a species of bird may roost during the night in one particular area and feed during the day in another. In the
morning the birds leave their roosting grounds and journey to the feeding grounds and in the evening they return again to the roosting grounds. This is a daily remigration. In the late summer and fall, the Monarch butterflies leave their northern breeding grounds and journey southward, where they remain during the winter months, returning north the following spring. This is an annual remigration.

The following chart is presented as a basis for a more exact system of subdivisions that may be devised by future workers.

\[
\begin{array}{ccc}
\text{Involuntary dispersal} & \text{Migration} & \text{Nomadism} \\
\text{Emigration} & \text{Immigration} & \text{Remigration} \\
\text{Daily remigration} & \text{Annual remigration} \\
\end{array}
\]

According to the above discussion and classification, the Monarch butterfly is an annual remigrant. This term defines exactly the type of movement involved in the case of the Monarch butterfly only at the species level, because not all members of the breeding population take part in annual remigration. When the Monarch butterfly returns to the breeding grounds one or more generations may be produced, but not all of them move south in the fall. The early generations perish after mating and laying their eggs, and only the late generations migrate. The entire population of the species does not, therefore, take part in the annual remigration. To complicate our terminology further, we know that some of the Monarch butterflies which have spent the winter in the southern parts of North America move north and deposit their eggs which produce a generation that in turn moves northward.

To distinguish the types of annual remigrants we could use qualifying words such as species, when our discussion is on the species level only, and population, when our discussion is on the population level. This gives a rather cumbersome trinomial terminology such as annual species remigration and annual population remigration. Perhaps, as a result of further studies on the movement of animals, a more complicated, although less cumbersome, system may evolve.

**Purpose of Annual Remigration**

A Monarch butterfly leaves its breeding grounds in late summer or fall and journeys southward to escape the lethal low temperatures of winter and
MIGRATION 1

The complete absence of food. Having remained in the southern parts of the continent, under favourable temperature conditions and with adequate food, it returns to the northern breeding grounds when warm temperatures arrive. This explanation of the purpose of annual remigration is very simple but, we must admit, completely anthropomorphic. How does a Monarch butterfly know that by journeying southward it will escape cold temperatures and lack of food? How does it know when warm temperatures have returned to the breeding grounds? At present no finite teleological explanation is possible.

Some species of insects overwinter in the egg stage, some in the larval stage, others in the pupa stage, and still others in the adult stage. There are a number of species of butterflies which overwinter in the adult stage in a dormant condition, such as the Mourning Cloak, species of Angle Wings, and the Red Admiral. The Monarch butterfly escapes the cold of winter by flying southward, even though it is possible for it to withstand freezing temperatures. We can conclude only that the Monarch butterfly exists today because, during the course of its evolution, an instinct to migrate became a part of its physiological inheritance. What chromosome contains this peculiar gene and how it operates, we do not know. We can conclude only that the habit of migrating is as much a part of the species Danaus plexippus as is its colour, its morphology, and its anatomy.

Fall Migration

In North America during the months of July and August the Monarch butterfly is commonly seen along the sides of roadways, pasture fields, meadows and in flower gardens. The life of the Monarch butterfly at this time of the year seems to be one of leisure—gliding from flower to flower on seemingly motionless wings. Direction does not appear to be very important and as many will be seen flying in one direction as in another. Larvae are common on the milkweed plants at this time, and now and then a bright green pupa may be found suspended from a window ledge or the branch of a bush or small tree.

As the summer heat of August fades into the cool of September there is a decided change in the flight habits of the Monarch butterflies. With the exception of the nuptial flight, all types of flight are still apparent but the flight seems more purposeful—towards a movement in a more decided southerly direction. Instead of visiting the flowers in the garden and then flying off in any direction, butterflies approach from the north and having fed move southward to sample other flowers en route. Those flying well above the ground, at a height of fifteen or twenty feet, move slowly in gliding or cruising flight in a southerly direction.
The southerly movement is more apparent in late August and September but the full migration actually starts in July. Casual observation does not disclose this fact because only a few, in comparison with the numbers resident in a given area, take part. As more and more individuals start to move southward we become increasingly aware of the migration, which reaches a climax in numbers in September and rapidly comes to an end in October.

The southward flight appears to be initiated by sudden changes in temperature although it is conceded that decreasing hours of daylight may be a contributing factor. The critical temperature seems to be approximately 55°F.

Monarch butterflies move southward at a time when food, in the form of nectar, is most abundant. In late summer and fall the fields and meadows are ablaze with the color of fall flowers, and the milkweed plants have large and succulent leaves. If the Monarch butterfly is unable to withstand the cold of winter by hibernation, the importance of vacating the northern climate is understandable. If the butterfly must continue to feed upon the nectar of flowers, the importance of seeking a warmer climate where flowers can be found is unquestioned. In order to discover if the Monarch butterfly and the various immature stages in its development were able to withstand cold temperatures a number of rather simple tests were carried out. It was found that the larvae and newly formed pupae were readily killed by freezing temperatures. Pupae which had developed so that many of the structures of the adult butterfly had formed and fat had been deposited in the tissues were less susceptible, while the adult butterflies recovered from exposure to temperatures well below the freezing point. With the last, however, exposure to low temperatures for long periods of time proved fatal. Thus although the larvae and pupae would not likely survive the cold of winter, the adults might possibly do so if the exposure was not for a long period of time. The fat deposited in the body of the butterfly lowers the freezing point of the body fluid thus allowing survival after exposure to low temperatures. As a result of tests carried out on the necessity for food in survival, it was found that Monarch butterflies must have continued access to a supply of nectar and, further, that the fat found in the tissues is apparently not available to the butterfly as a source of nourishment until the following spring when the return flight northward takes place.

One of the characteristic features of the southward flight is the establishment of overnight roosting sites (Plate IX). These sites may be one or more of a group of trees, usually located near a large body of water and particularly on peninsulas that point in a southerly direction. During periods of maximum abundance many thousands of Monarch butterflies may cling to the branches of the tree. With wings closed they resemble clusters of dead brown leaves, but in the morning when the first rays of the sun fall upon
them they spread their wings, presenting to the observer an unforgettable sight—a tree ablaze with the colour of thousands of butterfly wings. When the body temperature is such as to permit the full action of the wings they drift away, a few at a time, and continue their leisurely flight southward.

During the day, when the sun is shining and the air temperature may be well above 55°F, the Monarch butterflies proceed southward. As evening approaches and the sun’s rays gradually diminish in intensity, the air becomes cooler. If the butterflies did not come to rest they would eventually become paralyzed with the cold and fall to the ground, there to become prey to their numerous ground-inhabiting enemies—ground beetles, ants, mice, shrews, and numerous other insectivorous animals. (To test whether or not a Monarch butterfly could survive if forced to remain on the ground in a state of suspended animation, ten were placed on the grass at the margin of a small woodlot. The following morning only the wings remained [Fig. 27].) It is imperative, therefore, that the Monarch butterfly seek a suitable shelter from the cold evenings of late summer and fall.

If the evening is warm (above 55°F.) the Monarch butterflies tend to spread out over the branches of a tree or form small scattered clusters. If the evening is cold they form more dense clusters and if a brisk breeze is blowing they form large dense clusters. The density of the clusters and the numbers involved seem to be correlated with atmospheric temperature and weather conditions. If the branches of a tree which have only a few small clusters on them are shaken, the butterflies are readily dislodged and will fall to the ground like so many dead leaves. If the branches of a tree that have large, heavy clusters are shaken, the butterflies are not readily dislodged. A slender twig with but a few butterflies resting on it will vibrate violently when shaken, the butterflies will be tossed violently from side to side, and thus dislodged. A slender twig that is laden with butterflies will not vibrate violently when shaken but will tend to sway back and forth; the butterflies will not be tossed violently from side to side and will not be so readily dislodged. Furthermore, when exposed to a wind, each butterfly in a dense cluster is protected by its neighbours, so that the entire cluster rather than the individual is subjected to the storm.

Throughout the migration, Monarch butterflies come to rest in the evening, remain at rest throughout the night, then continue on their journey the following day. They are found singly or in small groups upon trees and bushes bordering fields, ravines, rivers, and creeks. They do not always come together in dense masses. Roosts involving great numbers are usually located in the vicinity of large bodies of water such as along the Atlantic coast, the Pacific coast, the shores of the Great Lakes, and the Gulf of Mexico. Occasionally observations of such mass gatherings have been recorded inland in some of the southern states where, owing to a sudden increase in
numbers in a particular area in conjunction with the passage of a severe cold front, the butterflies have gathered together in great numbers. Great numbers have been recorded passing through a certain area, such as Eagle Pass, Texas, and they may under adverse weather conditions form congregations on small bushes and trees, or under normal weather conditions spend the night in scattered groups.

It has been observed repeatedly that certain trees are chosen as a roosting site. These trees have one factor in common, namely, that the leaves are of a form that allows the butterfly to cling to them most easily and securely. Trees having leaves with slender petioles or deeply serrated margins are usually chosen, largely because of the structure of the tarsal claws. The tarsi of the Monarch butterfly do not possess adhesive pads and hence they are unable to cling to the plane surface of the leaves of the tree. The ability to remain suspended from a given object depends entirely upon the sharply pointed, sickle-shaped tarsal claws, and a Monarch butterfly while resting hangs with legs up and wings down (Fig. 28). It is important that the butterflies maintain a secure hold upon the leaves of the tree during low night temperatures, particularly if a strong wind is blowing. The sickle-shaped tarsal claws can be placed over the narrow petiole of the willow leaf, or the deeply notched margin of the maple leaf, and in this way the butterfly can remain suspended even if completely immobilized by cold temperatures. Pine trees are an ideal roosting site, because the tarsal claws can maintain a firm hold on the needles (Fig. 28).

If a group of trees is located on the migrating route where great numbers are most likely to occur and if these trees or a group of them have the characteristics described above, they will be chosen year after year. If a tree that formed a roosting site is removed, the butterflies will choose the next most suitable tree. If all of the trees except those that are not suitable are removed, they will choose suitable trees in a different locality entirely. This process has occurred over the past twenty years in the vicinity of Toronto, Ontario, where trees have been progressively removed in order to make room for buildings and roads. I have spent many hours watching the first arrivals choose as their roosting site a large silver maple and adjacent willows, discarding the broad-leaved basswoods, oaks, and chestnuts. They fluttered from one leaf to another on the basswood and occasionally one came to rest momentarily, then passed on to the oak, and finally settled on the most suitable willow. They chose the leeward side of the tree and, having settled, spread their wings as a signal to the late arrivals. Soon the leeward side of the tree seemed to be covered with restless butterflies, some with wings partly exposed and vibrating, some fluttering from one group to the other, and others, seemingly more exhausted than the rest, remaining with closed wings as if asleep. As the air cooled, those on the outside fringes...
of the tree would flutter to the more protected areas and come to rest as close as possible to their companions. The density of the individual congregations would depend upon the strength of the wind and the amount of the drop in temperature. Choice of a given roosting site thus seems to be based upon the geographical location of the site, the degree of protection offered against the wind, and the characteristics of the foliage of the trees involved.

A migrating butterfly, on encountering a height of land, wooded area, or a city of tall buildings, as a general rule will increase the height of flight while still maintaining a southerly direction. However, if a passage (such as a city street, a broad roadway through a wooded area, or a river valley) is available which does not necessitate a change in direction, the butterfly will continue to fly close to the ground. For example, my office window faces a broad street that runs northeast-southwest. When abundant, the Monarch butterflies may be seen flying across the lawns, visiting the flowers in the gardens while maintaining their direction southward. However, on another street running east and west, I rarely find a Monarch close to the ground, but looking up into the sky see them drifting over, taking advantage of the air currents to keep them aloft while slowly drifting southward. In a similar
manner they may follow river valleys and mountain passes. That they will fly to considerable heights to overcome a mountain barrier is evidenced from reports of specimens seen and collected at heights of 11,000 feet above sea level. Normally, however, the butterflies fly close to the ground, rarely above 15 feet.

Monarch butterflies tend to avoid strong winds and will accumulate in great numbers if faced with one. In 1939, while tagging butterflies along the shore of Lake Ontario near Toronto, I observed Monarch butterflies attempting to avoid the wind by clinging to the leeward side of the willow branches. But the wind was so gusty that strong up-currents were produced which at times dislodged the resting butterflies and hurled them into the air. Some were carried northward to distances beyond sight but most were able, by taking advantage of down-currents, to regain a position close to the ground, flitting from one small bush to another, and finally returning to their former position on the larger willow bushes. Now and then a strong gust would carry the butterflies over the lake, thus accounting for the many water-soaked or broken-winged Monarch butterflies cast up by the waves. From casual observation erroneous conclusions might have been deduced, because at times it would appear that the Monarch butterflies travelled north in a strong wind and at times they seemed to fly south against the wind. The majority, however, were seeking refuge on the leeward side of the bushes awaiting the return of better flying conditions.

Monarch butterflies appear to have an antipathy to large bodies of water. I have observed many hundreds of Monarch butterflies following the shoreline of Lake Ontario and only occasionally has one attempted to fly out over the water, and that usually when a gentle northerly wind was blowing. At times, having reached the southerly point of the mainland, they may fly considerable distances over water in order to follow the shoreline at a more distant point. It is quite likely that the Monarch butterflies may be carried far out to sea by strong northerly winds, and, if the shoreline lies in a northeast-southwest or northwest-southeast direction, the butterflies thus carried away from the mainland may fly in a more direct southerly direction, thus increasing their distance from the mainland. This might account for the many reports of Monarch butterflies seen many hundreds of miles from land.

The southward migration of the Monarch butterfly may be visualized as a retreat from that part of North America extending from the Atlantic coast in the east to the Pacific coast in the west, and from approximately the American-Canadian border in the north to the Gulf of Mexico in the south, to the coastal areas of the Gulf of Mexico, the Pacific Ocean, and the mainland of Mexico and adjoining territories (Fig. 78). We now know, as a result of our tagging programme, that Monarch butterflies move southward to
these regions and that those inhabiting the northeastern part of the United States and the southern parts of the eastern provinces of Canada in many cases reach Mexico, where they overwinter.

If female Monarch butterflies are collected in late summer in a field where milkweed is growing and where larvae in various stages of development may be found, some will be found to contain well-developed eggs although others do not. If the females had been examined in midsummer all of them would have contained eggs—except, of course, the recently emerged individuals. With the advent of cold temperatures all the Monarch butterflies move southward. Females that possess mature eggs will deposit them en route, thus accounting for the presence of larvae in parts of southern North America in late summer and fall after a complete absence during midsummer. There is, apparently, one interesting difference in the habits of female butterflies in which the ovaries have remained undeveloped and those in which eggs are ready to be laid: the former are found on the roosting sites but the latter are not. Female butterflies collected from the roosting sites have undeveloped ovaries, but many of the females resting individually on trees or bushes in the vicinity of fields containing milkweed plants contain ripe eggs. Females containing ripe eggs may be found, however, on overwintering roosting sites.

**Tagging Method**

In our research it was necessary to follow the routes taken by many individual Monarch butterflies. This could only be done by using some distinctive marking system so that the migrant could be followed from one place to another. After years of trials and failures we finally developed a method that permitted us to follow the mean route taken by a single individual for nearly two thousand miles. The history of the development and final success of this method is described at length in chapter 22.

**Overwintering**

If you were to take a motor trip in January from Fort Myers, Florida, to New Orleans, Louisiana, you would most likely make the following observations with regard to the presence or absence of Monarch butterflies. From Fort Myers to Sarasota you would probably not see any Monarch butterflies, although people living in this particular area might inform you that they are occasionally seen, and periodically may occur in considerable numbers. In the vicinity of Sarasota you would see an occasional specimen fluttering from one flower garden to another, and towards evening they would be seen settling upon the trees for the night. Following the direction of flight, it soon becomes obvious that they are not travelling in any particular direction.
Indeed, they act more like the early generations that we find in the breeding grounds. This, we may assume, is an overwintering, nomadic population that most likely remains in the area throughout the winter months awaiting the retreat of the cold weather in the north.

Such nomadic overwintering Monarch butterflies will be seen from Sarasota to Gainesville, but as you pass along the shores of Apalachee Bay, and particularly if you are a mile or so inland, you become aware that the Monarch butterflies are flying in a westerly direction, and at Lighthouse Point you will find a small (approximately 1,500) overwintering, roosting population. It is also apparent that the number of Monarch butterflies seen flying freely is greatly reduced. Along the northern shore of Apalachee Bay you may not encounter a single specimen. You notice, too, that there is a decided drop in temperature, particularly in the morning, and freezing temperatures are not unusual.

From Lighthouse Point to Pensacola there is a pronounced rise in minimum temperatures, which becomes apparent as you approach the Gulf coast of Louisiana. You also encounter more active, free-flying Monarch butterflies, particularly in the region of Mobile Bay. These non-roosting individuals behave in a manner similar to those at Sarasota, Florida.

A motor trip in January from San Francisco to Los Angeles, California, would yield the following. At Berkeley, across the bay from San Francisco, you will experience cold, damp weather. Temperatures regularly drop below freezing during January. From San Francisco to Salinas you will probably not encounter any Monarch butterflies, but in certain years you may find them clustered upon trees in great numbers at Stinson Beach or Palo Alto. From Salinas to Pacific Grove on warm sunny days you may see the occasional specimen feeding upon the nectar of flowers growing in nearby gardens, very much as around Apalachee Bay, Florida. At Pacific Grove in three distinct localities, namely, Butterfly Trees Lodge, Millar's Lodge, and Washington Park, large Monterey pines are literally covered with countless thousands of overwintering Monarch butterflies (Plate IX). This is similar in many respects to the situation at Lighthouse Point where temperatures are low, the atmosphere is humid, and the butterflies are found on pine trees. From Pacific Grove to Morro Bay only the occasional Monarch butterfly will be seen, but there are a number of localities where large roosting colonies will be found. From Morro Bay to Los Angeles the number of Monarch butterflies seen progressively increases as they did from Lighthouse Point to New Orleans.

There is, therefore, a similarity between the activity and occurrence of Monarch butterflies along the coast of the Gulf of Mexico and the Pacific coast of California, during the month of January. Such a similarity may be due to the fact that cold air masses flow southeastward from the extreme
northwest. The leading edge of this mass of cold polar air will extend across
the continent from south of Pacific Grove eastward along the shore of the
Gulf of Mexico across northern Florida, and from there northeastward into
the Atlantic Ocean. Hence most of the North American continent becomes
covered with cold air. As it moves southeastward, the colder portions of it
touch northern California, causing the freezing temperatures at San Fran-
cisco, and the eastern edge causes temperatures to become much colder in
the eastern portions of the Gulf of Mexico coast as compared to the western
portions. In chapter xii a weather map showing the position of this cold air
mass, which represents a high pressure area, illustrates the manner in which
such distant points as San Francisco and Lighthouse Point would have low
temperatures owing to the southeastward flow of the cold air (Fig. 78).

We may conclude from our observations and consideration of the meteo-
rological maps that Monarch butterflies overwinter along the Gulf coast and
the Pacific coast either as free-flying, non-roosting individuals in those areas
unaffected by polar air mass outbreaks, or as roosting colonies in those areas
affected by polar air mass outbreaks.

We know that the Monarch butterflies also occur as free-flying, non-
roosting individuals in Mexico largely because of the absence of polar air
mass outbreaks, for the most part, in this area.

The Japan Current along the Pacific coast and the Gulf Stream in the Gulf
coast area both modify the polar air. Such warm water currents are most
effective when the air circulating around the high pressure area passes over
them. This is not so likely in the cold areas mentioned above, since the cold
air masses are moving away from the Pacific Ocean and to the northeast
away from the Gulf of Mexico.

The overwintering roosts are most spectacular and, since they receive
such a great deal of publicity, it is popularly believed that all Monarch
butterflies overwinter in this manner. If it were possible to count the number
of free-flying, non-roosting Monarch butterflies living in Mexico, the southern
parts of California, and the western shores of the Gulf of Mexico, and to
compare this number with the numbers found on roosting sites, we would
quite likely find that the former would far outnumber the latter.

During the cold of the morning the butterflies overwintering on trees
remain inactive, hanging in great clusters like bunches of dead leaves. If you
shake the branches of the trees vigorously when the temperature of the air
is below 50°F, they will be dislodged and drift to earth, there to remain as
if dead, or moving in but a feeble manner because their muscles, numbed by
the cold, refuse to respond. When the temperature rises above 60°F, a few
hungry individuals will leave the roosting colony to feed upon the nectar
found in the flowering plants growing in nearby gardens and towards
evening return again to the protection of the pine trees.
When temperatures rise above 70°F, the colony becomes active. This is usually in late February, although it may not occur until March. Gradually the colony breaks up, and usually by the middle of March only a few stragglers remain. The females are the first to leave, because their eggs have started to develop and they must reach the northern breeding grounds as soon as possible.

It is not unusual to find Monarch butterflies mating during the winter months (January and February), more frequently in late February than in early January. Although the eggs do not develop to any appreciable extent until late February, the occasional female may have well-developed eggs at any time from late fall to early spring. These females are the survivors of a late fall ovipositing population. With the advent of cold air, oviposition terminates and some females, still holding two or three dozen fully formed eggs, join the roosting colony for the winter months. I have found that such eggs would not hatch even though, on dissection after they had been laid, there was evidence of mating having taken place. Eggs laid after the colony had disbanded in early spring would hatch.

Some Monarch butterflies, by choice or chance, establish roosting sites where cool temperatures prevail, while others fly freely where warm temperatures prevail. If a roosting site is to be established, because of low temperatures the factors involved are probably the same as those described for the overnight roosting sites during the southward flight. At present we can only speculate as to what factors decide the final disposition of the Monarch butterflies throughout the overwintering range. Eventually, by continuing a programme of tagging, we may find the answer. By tagging we have found that the line of migration in the fall is quite definitely to the southwest, although for short distances of two or three hundred miles, it may be south or southeast. From San Francisco southward the coastline of North America is oriented northwest-southeast. When the Monarch butterflies reach the Pacific coast they may be averse to flying southeastward and, repelled also by the open water of the Pacific Ocean, congregate in this area, those in the north forming roosts and those in the south remaining free-flying. Those from the plains region might reach the Pacific coast of Mexico or California (travelling over the mountains) depending upon the trajectory of flight. The following are a few examples, based upon the information we now have as a result of our tagging programme, illustrating the dispersal in the overwintering areas.

Suppose an individual leaves the breeding grounds in locality A (Fig. 29). Flying in a southwesterly direction it would eventually arrive on the Pacific coast at point B in the area of San Francisco. Here it may remain at an overwintering roost or proceed slightly farther south to Pacific Grove. If we assume that there is an antipathy to flight in an easterly direction, it may be concluded that this individual will remain in the general area of
A Monarch butterfly leaving the breeding area C and flying southwestward would reach area D where temperature conditions are such that roosting sites are not established and hence this individual would be observed flying actively in this vicinity. A change in flight direction from southwest to more southerly would explain why an individual leaving the breeding grounds at area E would arrive on the Pacific coast of Mexico and, perhaps, remain free-flying in the northern half of Mexico. A specimen tagged at point G was recovered at point H, which is what we would expect if the hypothesis of a general southwesterly flight is accepted. A more southerly flight from area I would explain the occurrence of populations in area J and, since temperatures in this area repeatedly drop to freezing or near-freezing, we would expect to find roosting sites in this area, which, as we have seen, is the case. It is quite likely that intensive search in area J will disclose the occurrence of other roosting sites besides the one at Lighthouse Point.

There will, of course, be a number of trajectories varying from slightly west of south to southwest, and hence individuals from the same geographic area will not necessarily arrive at the same overwintering grounds. Winds, particularly strong winds, play an important role in altering the flight direction. Since wind direction varies from day to day, so the effect upon the flight direction varies, and therefore two individuals departing from the same field a few days apart may have entirely different trajectories, especially if a frontal system, accompanied by marked changes in wind direction, passes through the area.

We may assume, from the information we now have, that populations travelling through the area of the Rocky Mountains follow the valleys so long as such valleys are oriented in a south to southwesterly direction; otherwise, they fly over the lower range of mountains.

Spring Migration

The time of departure from the overwintering sites varies from north to south, and from year to year. In the more northern parts of the overwintering range departure is much later than in the southern parts. Monarch butterflies overwintering in Mexico may start their return journey in January reaching southern Texas in February and central and northern Texas in March, while overwintering colonies are still clinging to the Monterey pines in Pacific Grove in northern California. In certain years warm temperatures in late winter may cause an early migration—reports of spring migrations during the last week of February have been received for northern California. In other years in the same area departure may be postponed until late March. It may be generally stated that spring migration in most localities begins in the last week of February, with migrants passing northeastward over the southern and western parts of North America in March.
From the results of recoveries from our tagging of overwintering colonies in California it would appear that spring migrants travel northeastward (Fig. 79). Unfortunately most of the recoveries from such tagging operations have been for relatively short distances and hence it cannot be stated with certainty that a Monarch butterfly that journeyed from Ontario in Canada to Mexico will return by the same or a similar route.

It has been suggested that the returning migrants travel northward but a short distance, deposit their eggs and die. The resulting generation then proceeds northward, and so on. If such were the case, we would expect to find a large population of larvae in the southern parts of the continent in early spring, and we would expect to find fresh, brightly coloured specimens in the central and northern parts of the continent in spring and early summer. However, only a few larvae have been reported for the southern localities, particularly southern Texas, in spring, and the adults found in central and northern localities in May and early June are obviously old and worn, and in colour are the same as those found in the overwintering localities in late winter (Plate X). Finally, the time taken for the complete development of a Monarch butterfly from egg to adult would not be sufficient to account for the presence of faded specimens found in northern localities in early May. It would appear therefore that some, if not all, migrants return to the breeding grounds in spring and early summer, followed by first generation butterflies in June and early July. The change in colour intensity among specimens collected in early spring, early summer, and midsummer is clearly shown in the accompanying colour plate (Plate XI).

During the fall migration, the flight of the Monarch butterfly is leisurely—I have referred to it as “cruising.” In contrast to this, the flight of the spring migrants is swift. With rapidly beating wings—a type of flight I have termed “speed”—the female rarely pauses to sip nectar from early spring flowers. Approaching an isolated building, one that could be circumnavigated quite easily and would be by a fall migrant, she flies without hesitation over the building rather than change course. As evening approaches she comes to rest alone upon a small bush or tree rather than in roosts as do the fall migrants.

In the afternoon the female Monarch butterfly may be seen flying from one small milkweed plant to another, pausing just long enough to curve her slender abdomen beneath the leaf to deposit a small conical egg. Such ovipositing females were followed in late spring in a meadow, where milkweed plants had grown to a height of eight to twelve inches, near the town of Durham, Ontario. Gliding from one milkweed plant to another, sometimes pausing to deposit an egg and at other times rejecting the plant as unsuitable, the females oviposited without cessation for periods up to thirty-five minutes. Clinging to the leaves of a plant, usually not a milkweed plant, a female would rest for periods up to twelve minutes before once again
starting to deposit her eggs. Occasionally, after such a respite, the female would leave one section of the field and fly to another section or to a remote field before laying more eggs. Throughout there was an air of urgency about her activities.

By mid-June, females with tattered wings may be seen fluttering feebly from one milkweed plant to another, resting only for brief periods. The life span of the migrant over, a new generation of Monarch butterflies fills the depleted ranks of those that ventured southward in the fall. Generation after generation, as we have seen, soon give rise to many thousands of Monarch butterflies that will in turn leave the breeding grounds to spend the winter months in warmer climates.
PART II

RESEARCH DATA AND REFERENCE MATERIAL
## CHAPTER SEVEN

### MILKWEED

**List of Milkweed Species Recorded for the Provinces of Canada, the States of the United States, and Mexico**

**Canada**

<table>
<thead>
<tr>
<th>Province</th>
<th>Species</th>
</tr>
</thead>
<tbody>
<tr>
<td>British Columbia</td>
<td>(1 species)</td>
</tr>
<tr>
<td>Manitoba</td>
<td>(6 species)</td>
</tr>
<tr>
<td>Quebec</td>
<td>(2 species)</td>
</tr>
<tr>
<td>New Brunswick</td>
<td>(1 species)</td>
</tr>
<tr>
<td>Nova Scotia</td>
<td>(1 species)</td>
</tr>
<tr>
<td>Ontario</td>
<td>(10 species)</td>
</tr>
<tr>
<td>Saskatchewan</td>
<td>(2 species)</td>
</tr>
</tbody>
</table>

**United States**

<table>
<thead>
<tr>
<th>State</th>
<th>Species</th>
</tr>
</thead>
<tbody>
<tr>
<td>Alabama</td>
<td>(14 species)</td>
</tr>
<tr>
<td>Arizona</td>
<td>(26 species)</td>
</tr>
<tr>
<td>State</td>
<td>Species</td>
</tr>
<tr>
<td>---------------------</td>
<td>-------------------------------------------------------------------------</td>
</tr>
<tr>
<td>Arkansas (12 species)</td>
<td><em>incarnata</em></td>
</tr>
<tr>
<td></td>
<td><em>perrinis</em></td>
</tr>
<tr>
<td></td>
<td><em>verticillata</em></td>
</tr>
<tr>
<td></td>
<td><em>tuberosa</em></td>
</tr>
<tr>
<td>California (17 species)</td>
<td><em>cuaronae</em></td>
</tr>
<tr>
<td></td>
<td><em>pecticulata</em></td>
</tr>
<tr>
<td></td>
<td><em>linaaria</em></td>
</tr>
<tr>
<td></td>
<td><em>verticillata</em></td>
</tr>
<tr>
<td>Colorado (16 species)</td>
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</tr>
<tr>
<td></td>
<td><em>subverticillata</em></td>
</tr>
<tr>
<td></td>
<td><em>pumila</em></td>
</tr>
<tr>
<td></td>
<td><em>hallii</em></td>
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<tr>
<td></td>
<td><em>speciosa</em></td>
</tr>
<tr>
<td>Connecticut (10 species)</td>
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</tr>
<tr>
<td></td>
<td><em>verticillata</em></td>
</tr>
<tr>
<td></td>
<td><em>tuberosa</em></td>
</tr>
<tr>
<td></td>
<td><em>exallata</em></td>
</tr>
<tr>
<td>Delaware (12 species)</td>
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</tr>
<tr>
<td></td>
<td><em>verticillata</em></td>
</tr>
<tr>
<td></td>
<td><em>tuberosa</em></td>
</tr>
<tr>
<td></td>
<td><em>rupa</em></td>
</tr>
<tr>
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<td><em>incarnata</em></td>
</tr>
<tr>
<td></td>
<td><em>perrinis</em></td>
</tr>
<tr>
<td>Florida (20 species)</td>
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<tr>
<td></td>
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</tr>
<tr>
<td></td>
<td><em>verticillata</em></td>
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<tr>
<td></td>
<td><em>tuberosa</em></td>
</tr>
<tr>
<td></td>
<td><em>lanceolata</em></td>
</tr>
<tr>
<td></td>
<td><em>amplexicaulis</em></td>
</tr>
<tr>
<td>Georgia (20 species)</td>
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<td></td>
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<tr>
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<td><em>tuberosa</em></td>
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<td></td>
<td><em>rupa</em></td>
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<td><em>lanceolata</em></td>
</tr>
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<td></td>
<td><em>exallata</em></td>
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<tr>
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<tr>
<td></td>
<td><em>spectaculum</em></td>
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<tr>
<td></td>
<td><em>subtuberosa</em></td>
</tr>
<tr>
<td></td>
<td><em>verdazula</em></td>
</tr>
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</table>
### MILKWEED

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<thead>
<tr>
<th>State</th>
<th>Species Count</th>
<th>Species Details</th>
</tr>
</thead>
<tbody>
<tr>
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</tr>
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</tr>
<tr>
<td>Iowa</td>
<td>15 species</td>
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</tr>
<tr>
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<td>13 species</td>
<td><em>A. incarnata</em>, <em>A. perennis</em>, <em>A. verticillata</em>, <em>A. tuberosa</em>, <em>A. exaltata</em>, <em>A. amplexicaulis</em>, <em>A. syriaca</em></td>
</tr>
<tr>
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<td>9 species</td>
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<tr>
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</tr>
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<td></td>
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<td>Wisconsin</td>
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<td>Wyoming</td>
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<tr>
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</table>
The following key may help to identify the seventeen most abundant species found in the United States east of the Mississippi drainage and in the eastern provinces of Canada:

1. Flowers orange; leaves irregularly arranged (not opposite); juice not milky: N.H., Ont., Minn., and southward  
   \[ A. tuberosa \]
   Flowers not orange; leaves opposite; juice milky  
   2

2. Flowers bright red or purple; leaves opposite and usually broad  
   3

Flowers greenish, yellowish, white, or greenish purple; leaves opposite or whorled  
   6

3. Flowers small (\(\frac{3}{4}\)" wide and \(\frac{3}{4}\)" long); hoods 2-3 mm. long and equal to the anthers; veins ascending; swamps; N.B., westward and southwest  
   \[ A. incarnata \]
   Flowers large (\(\frac{3}{4}\)" wide and \(\frac{3}{4}\)" long); hoods 6 mm. long and exceeding the anthers; veins of the leaves transverse  
   4
4. Dry ground; underside of leaves pubescent; dark purple flowers: N.H. to Ont. and Minn., and southward
   A. purpurascens
   Wet, pine barrens; underside of leaves without pubescence; flowers red or reddish purple
   5
5. Flowers red; leaves elongate and tapering towards base and apex; slight petiole; wet pine barrens on the coast; N.J. to Fla. and west to Texas
   A. lanceolata
   Flowers reddish-purple; leaves rounded or heart-shaped at the base and tapering to an acutely pointed apex; petiole absent; distribution and habitat similar to lanceolata
   A. rubra
6. Seed pods covered with soft spines and with a fine, silky pubescence (only apex of pod with soft spines in sullivantii) 7
   Seed pods smooth or slightly pubescent, without soft spines
   9
7. Entire plant smooth (slight indication of spines at apex of seed pod); leaves with slightly heart-shaped base; rich soil; flowers decidedly purple as compared to those in "8": Ont. to Minn., Neb. to Kansas A. sullivantii
   Pubescent; base of leaves oval; rich soil or margins of streams; flowers greenish purple to white
   8
8. Flowers greenish purple to white: rich and sandy soil; N.B. to Sask., and westward
   A. syriaca
   Flowers purplish: margins of streams; Minn. to Ark. and westward
   A. speciosa
9. Stem of seed pod curved downwards, but seed pod erect or nearly so 10
   Stem of seed pod erect (not curved) 14
10. Single cluster of flowers on a naked, terminal stem (peduncle) 11
    More than one cluster of flowers 12
11. Leaves with heart-shaped, clasping base; flowers greenish-white: sandy woods and fields; N.H. to Neb. and southward
    A. amplexicaulis
    Leaves with obtuse base; flowers greenish purple: dry ground; Wis., Ind., and Ia.
    A. meadii
12. Leaves mostly pubescent; hoods of flowers two or three times the length of the anthers: prairies and oak openings; Ill., and Wis., to S. Dak., and Minn.
    Leaves mostly smooth; hoods approximately equal to length of anthers 13
13. Pedicels (stems of individual flowers) few, well separated and equal to length of flowerhead stem (peduncle); corolla lobes greenish; hoods white: moist soil; N.E. to Minn. and southward to Ga. and Ark.
    A. phytolaccoides
    Pedicels numerous and crowded together; pedicels longer than peduncle; peduncle pubescent; corolla lobes white; hoods purplish or reddish; dry woods; L.I. to Ind. and southward to Fla. and westward to La.
    A. variegata
14. Leaves broad
   Leaves narrow to filiform

15. Flowers pale pink: dry woods and hills; N.H. to Ont. and Minn., southward to N.C. and Ark.  
   A. quadrifolia

   Flowers white: low, moist soil; Ind. to Mo., Fla., and Tex.  
   A. perennis

16. 3-9 dm. high; few branches; leaves arranged in a whorl: prairies and open woods; Mass. to Sask. and southward  
   A. verticillata

   1-1.5 dm. high; many branches from a woody base; leaves arranged in a spiral: dry plains; Ia. and Neb. to Cal. and N. Mex.  
   A. punila

**Species Upon Which Larvae Have Been Reported Feeding**

The following communications, dealing with the milkweed as the food plant of the larva of the Monarch butterfly, have been received.

I have found caterpillars on blue nightshade plants often, but not as regularly as milkweed. [J. Hagar, Rockport, Texas.]

[Author's Note: It is doubtful whether or not this is a species of Solanum.]

... regarding the narrow-leaved milkweed. It is a definite fact that the Monarch larva feed on this. For years I collected them on no other plant. Around Livermore Valley, Central Valleys. Salinas Valley, etc. this is the only milkweed. When you get up to 3000 feet elevation in the foothills of the Sierras and higher ranges along the coast, the broad-leaved takes over. No narrow-leaved plants are found in the Monterey area. [R. G. Wind, Pacific Grove, Cal.]

May I say with absolute certainty that larvae were found on both the broad-leaved milkweed and the narrow, lanceolate-leaved milkweed. . . . The larvae are found in Redwood City as late as December on the lanceolate-leaved milkweed. Over the week-end of Sept. 4-5 I went to the high Sierra Nevada Mts. After leaving the floor of the central valley and ascending to the 3000 feet elevation, the lanceolate-leaved milkweed gave way to the broad-leaved, the latter continuing to the 5000-6000 feet elevation. Altitude definitely determines the type of milkweed. In Yosemite Park there is a broad-leaved type with deep purplish, brown blossoms in contrast to the white flowers found in Carmel Valley. [P. Beard, Monterey, Cal.]

At Dufferin Island in the Niagara River, just above the falls, I found three Monarch caterpillars. . . . There was none of the common milkweed around, so they were feeding on swamp milkweed. In this part of the country [Niagara Falls, Ontario] swamp milkweed is not the food plant, or at least I have never found Monarch caterpillars on anything else except the regular [common] milkweed. The third and largest caterpillar had a choice of swamp milkweed and common milkweed. He ate equal amounts of each. . . . [Ruth Haigh, Niagara Falls, Ont.]

[Author's Note: The milkweed species referred to by Miss Haigh were identified as A. incarnata and A. syriaca.]

We caught the worms off the hollyhock and they turned into Monarch butterflies. [S. Johnston, Albuquerque, N. Mex.]

[Author's Note: We believe that the butterfly reared from the caterpillars taken from the hollyhock plant was wrongly identified.]
We observed the first larva July 10, 1955, and shortly thereafter we collected the specimen of *A. speciosa.* [E. D. Freeland, Mineral, Cal.]

Seven specimens were reared from caterpillars feeding on *fuchias* captured June 20. [E. A. Stoner, Benicia, Cal.]

[Author's Note: The validity of this identification has not been checked.]

The caterpillar feeds upon different species of *Asclepias,* although it shows a wonderful dislike to the peke milkweed (*A. phytolaccoides*). Larvae furnished with this plant would wander about their breeding cages day after day, and would eventually die rather than touch it; in the north it generally appears to confine itself to *A. cornuta* [syracusa] but has been found on *A. purpurascens* and *A. incarnata,* in the south and in Missouri, it also feeds on the butterfly weed, *A. tuberosa,* *A. amplexicaulis,* *A. tomentosa,* and *A. curassavica,* and has been taken in Cuba by Dr. Gundlach on *A. nivea.* It has been discovered, too, on the neighboring genus *Apocynum—A. androsaemifolium* and according to Coquillett feeds also on *A. aspera.* [S. Scudder, Butterflies of the Eastern U.S. and Canada, 1, Nymphalidae.]

The attached box contains a sample of the vine which seems to serve as the principal food plant for the Monarch in this area. It is certainly a member of the *Asclepiadaceae.* The Monarchs oviposit freely on it, and in preference to a species of *Asclepias* which grows in the same area. The *Asclepias* does serve as a secondary food plant. [J. P. Knudsen, Decatur, Ala.]

[Author's Note: This plant was identified as *Gonolobus laevis.*]
CHAPTER EIGHT

EGG—LARVA

Rearing Methods

The following methods were employed to rear larvae from the time of hatching from the egg to the complete development of the adult butterfly. To obtain a sufficient number of eggs, ovipositing females were placed in large screened cages (3' X 3' X 4') which were closed at the top and open at the bottom so that they could be placed over milkweed plants (Fig. 30). A sheet of canvas was spread over the top of the cage because it was found that when the butterflies were exposed to the direct sunlight for long periods of time they did not live as long, nor did they lay as many eggs. A variable number of female butterflies were placed in a cage at one time. The milkweed plants were examined every other day and the leaves bearing eggs were removed.

Once the egg has been deposited upon the leaf of the milkweed plant it is most difficult to dislodge it without breaking the shell, because it is glued to the leaf by a secretion produced by the female at the time the egg was laid. In the course of our experiments, it was necessary to remove the eggs from the milkweed plants and place them in plastic containers for observation. At first we attempted to lift the egg from the surface of the leaf by placing the sharp edge of a scalpel at the base of the egg next to the leaf surface and pressing gently so as to cut through or break the adhering surfaces. This method was not satisfactory because many eggs were broken or damaged. A number of other methods were tried but we finally resorted to removing, with the aid of a pair of small scissors, a section of the leaf bearing the egg. This gives some indication of the strength of the relatively insoluble adhesive that so firmly glues the egg to the leaf.

The eggs collected on each day were given a catalogue number, and the approximate time of oviposition was noted in the field records. In many cases the eggs were removed immediately after they were deposited by the female, and in this way an accurate record was obtained of the time taken for development. The eggs were placed in small, square plastic containers (2" X 2" X 1") and observations were made at regular intervals during the day until they hatched. The time of emergence, the changes which took place in the colour from hatching to active crawling, the rate of development, and behaviour were all recorded.
Figure 30. a, rearing tubes held in an orange crate; b, large rearing cage; c, small screen cage; d, rearing tube; e, large cage placed over milkweed plants.
When the larvae hatched they were removed from the plastic containers and placed in small vials which were plugged at the open end with cotton wool. Only one larva was placed in each vial. It was found that by using a fine camel's hair brush dipped in water the minute larvae could be picked up without injury. The rate of development of the larvae to the completion of the first instar, and any changes that took place in colour, size, and morphology were recorded.

When the larvae entered the second instar they were placed in glass tubes (18" in length and 2½" in diameter), which were closed at each end with cheesecloth (Fig. 30). Each tube was numbered (according to the original catalogue number), with a grease pencil or a paper label held in place by an elastic band. The tubes were arranged vertically in orange crates and kept out of doors in a shaded corner of a small woodlot. During periods of rain, a sheet of canvas was thrown over the tubes to prevent damage to the larvae. Notes on the development of the larvae within the tubes were made daily. The tubes were cleaned and fresh milkweed leaves supplied daily. To obtain preserved material of a definite age, some of the larvae were removed at specified times and preserved in 70 per cent alcohol.

Small screen cages (12" X 4" X 4") were used to compare the rate of development of the larvae under normal atmospheric conditions with those in the closed glass tubes (Fig. 30). These small cages were used also for observations on the rate of development of the pupae, which were suspended from the silks of the cage by inserting a piece of fine wire through the silk mat and then attaching the free end of the wire to the screen. In this way distortion of the butterfly as the result of emerging in a smaller, closed vessel was prevented.

Larvae were collected at various times throughout the summer months from milkweed plants growing in fields. These specimens were placed in large screened cages which were tightly sealed by twisting the edges of the wire screen together (Fig. 30). This was done to retain any parasites which might emerge. This same type of cage was used in investigations concerning the effect of cold temperatures upon the larvae, pupae, and butterflies in late summer. As many as 200 larvae could be handled in one cage (Fig. 31), and although they were crowded, their rate of development compared favourably with that in the rearing tubes and smaller rearing cages.

Mr. C. A. Anderson of Dallas, Texas, kindly submitted the following account of the rearing method which he has used so successfully.

In the spring, I collect the eggs in the fields. The eggs are placed in half-gallon milk cartons covered by a piece of cloth held in place by a rubber band. When the larvae are one week old, they are placed in corrugated paper boxes (18" X 18" X 12"). A panel is cut out on one side of the box and the opening is covered with a sheet of plastic cemented on. A door (4" X 4") is cut in one end
of the box. The sides and the bottom of the door are cut. The top part is not cut and it serves as the door hinge. A piece of scotch tape attached to the bottom side of the door serves as a handle. The rough edges of the corrugated paper will serve as a latch and hold the door shut.

The box is turned upside down and fitted over two or three layers of pieces from corrugated paper boxes. These layers are nailed to a piece of board. Two six-penny nails are pushed through the edges of the box at the bottom. The nails catch a hold between the layers of corrugated paper nailed to the board. This makes it possible to move the box around without spilling the contents. Several layers of newspapers are fitted over this improvised bottom. When cleaning is necessary, the nails are removed, the box lifted up, the old newspapers with the larvae removed, clean pieces of newspaper put over the bottom, the larvae placed on the paper with fresh leaves, the box replaced and the nails inserted.

Twenty larvae are placed in each cage. Should disease break out or a tachnid fly invade the cage, the loss will be confined to twenty instead of spreading through the whole colony.

The cages are checked morning and evening. The plastic fronts enable one to determine readily the conditions within the cages.

The milkweed is brought in from the fields. It is stored in bushel baskets in the garage. Old newspapers are soaked in buckets. Into the bottom of the basket goes a layer of wet newspapers, then a four-inch layer of milkweed, a layer of wet newspapers on top of it, repeating until the basket is full. When properly packed, the milkweed will keep for one week in a daily temperature range of 70 degrees to 90 degrees. Five hundred ten-day-old larvae consume a bushel basket of milkweed in 24 hours.
Weight

Using a finely adjusted chemical balance it was found that from ten eggs the average weight of an egg was .54 mg.

Size

H. F. Stiles, Grand Rapids, Michigan, reports as follows: "The egg when laid is almost pure white. It is conical in shape. In size it is about \( \frac{3}{4} \) mm. by \( \frac{3}{4} \) mm., or about 1.50 inch by 1.32 inch. It is a beautiful egg—almost as if sculptured. About eighteen ribs run from the apex to the base, and crosswise between these main ribs are numerous cross ribs."

Measurements were made with the aid of a ruled microscope eyepiece and all measurements were made to the nearest .07 mm. Length refers to the distance from base to apex. Width refers to the greatest width, which is approximately half-way from the base.

<table>
<thead>
<tr>
<th>Number of Eggs</th>
<th>Length</th>
<th>Number of Eggs</th>
<th>Width</th>
</tr>
</thead>
<tbody>
<tr>
<td>15</td>
<td>1.12</td>
<td>2</td>
<td>.77</td>
</tr>
<tr>
<td>20</td>
<td>1.19</td>
<td>23</td>
<td>.84</td>
</tr>
<tr>
<td>14</td>
<td>1.26</td>
<td>20</td>
<td>.91</td>
</tr>
<tr>
<td>3</td>
<td>1.33</td>
<td>4</td>
<td>.98</td>
</tr>
<tr>
<td>2</td>
<td>1.40</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

**Average Length:** 1.20

**Average Width:** .87

Number of Cells per Row

The number of cells in a given vertical row is determined by the length of the row; therefore a branched row will have fewer cells than an unbranched one. Some error enters in counting the small cells at the apex. Only cells that seemed to be continuous with the row considered are included. For sixty-five complete rows the following counts were obtained.

<table>
<thead>
<tr>
<th>Number of Rows</th>
<th>Number of Cells per Row</th>
</tr>
</thead>
<tbody>
<tr>
<td>6</td>
<td>26</td>
</tr>
<tr>
<td>12</td>
<td>28</td>
</tr>
<tr>
<td>8</td>
<td>29</td>
</tr>
<tr>
<td>7</td>
<td>30</td>
</tr>
<tr>
<td>6</td>
<td>31</td>
</tr>
<tr>
<td>8</td>
<td>32</td>
</tr>
<tr>
<td>6</td>
<td>34</td>
</tr>
<tr>
<td>6</td>
<td>35</td>
</tr>
<tr>
<td>6</td>
<td>37</td>
</tr>
</tbody>
</table>

**Average Number of Cells per Row:** 32
Branched Ridges

The rows of cells may occur in a single row from base to apex, or two shorter rows may meet to form a branched or forked arrangement. The branching may occur near the apex, near the base, or at variable distances in between. The number of forked ridges varies from one egg to another. The following are counts based on ten eggs chosen at random.

<table>
<thead>
<tr>
<th>Number of Eggs</th>
<th>Number of Forked Ridges</th>
</tr>
</thead>
<tbody>
<tr>
<td>6</td>
<td>5</td>
</tr>
<tr>
<td>3</td>
<td>6</td>
</tr>
<tr>
<td>1</td>
<td>8</td>
</tr>
</tbody>
</table>

**Average number of forked ridges:** 6

The number of cells in each branch of the fork will vary according to the length of the branch being considered.

Number of Longitudinal Ridges

The number of longitudinal ridges will exhibit marked variation at various places on the egg. Counts made near the apex will have fewer ridges than counts made near the base because of the occurrence of branches near the base. The following counts were made near the base of the eggs to include all branches.

<table>
<thead>
<tr>
<th>Number of Eggs</th>
<th>Number of Ridges</th>
</tr>
</thead>
<tbody>
<tr>
<td>9</td>
<td>21</td>
</tr>
<tr>
<td>18</td>
<td>22</td>
</tr>
<tr>
<td>8</td>
<td>24</td>
</tr>
</tbody>
</table>

**Average number of ridges:** 22

Apex

At the apical end of each row of cells there are a number of small irregularly shaped cells, followed by still smaller cells which finally merge with an indefinite opaque centre. A cap-like appearance (micropyyle) is thus given to this portion of the egg.

From the Literature

The following information has been recorded by Scudder (1889).

Egg (64.1) very pale amber green, becoming grayish before hatching. Vertical ribs twenty-two in number about .1 mm. apart in the middle, the intervals smooth and glistening, broken by bands .012 mm. in width, giving the egg somewhat the appearance of being overlaid with a thick layer perforated by regular meshes which are the cells between them, so the largest part of the egg these cells are about .08 mm. in breadth and .025 mm. in height, being quadrangular with rounded sides. Summit of the egg about .1 mm. in diameter (67.4) not at all sunken but gently convex, the outside cells about .01 mm. in length, and the micropyple proper .05 mm. in diameter. Height of egg usually about 1.2 mm. and the breadth .85 mm.
The following information has been recorded by Walker (1886).

The egg is laid singly, on the under-side of the leaves of various species of Asclepias... It is about one-twentieth of an inch long by one-thirtieth in diameter, in shape nearly cylindrical for half its length, then tapering to a somewhat obtuse point, and with a flat base; its form may perhaps best be compared to one of the projectiles for modern rifled guns, known as "Pallister shot." Its surface is sculptured with about 22 strongly carinate longitudinal ribs, between which is a rather larger number of more delicate transverse ridges, and its colour is a pale-greenish yellow.

**Time Taken for Development of Egg**

Hatching times from oviposition to the complete emergence of larva were recorded at room temperature, 62° F.–78° F., with the following results.

<table>
<thead>
<tr>
<th>No. of eggs</th>
<th>Hatching time in hours</th>
</tr>
</thead>
<tbody>
<tr>
<td>25</td>
<td>106</td>
</tr>
<tr>
<td>50</td>
<td>112</td>
</tr>
<tr>
<td>10</td>
<td>122</td>
</tr>
</tbody>
</table>

**Average time:** 111 hrs. (4.6 days)

Five eggs were placed out-of-doors and exposed to the direct rays of the sun. Two of them hatched in 82 hours and three in 94 hours. The average time was 89 hours (3.7 days).

Ten eggs were placed in a refrigerator held at 42° F. At the end of ten days these were removed. No hatching had taken place but all ten eggs hatched at a later date; unfortunately, the time interval was not recorded.

Miss Ruth Haigh of Niagara Falls, Ontario, reported as follows: "Two eggs that I did see deposited were watched for the day they hatched. One took four days and the other five."

With summer temperatures, therefore, hatching takes place in approximately four days. Low temperatures will retard development and increase the hatching time whereas high temperatures will accelerate development and decrease the hatching time.

**Larva**

Mrs. L. Wylie and Mr. H. F. Stiles submitted the following excellent account of the hatching process and the reactions of the newly emerged larva.

**July 12, Thursday:**

5.01 p.m. Head emerged from egg case.
5.06 p.m. Caterpillar 3/32" long was completely free from case.
5.09 p.m. Caterpillar returned to case and started eating it.
5.25 p.m. Case half eaten and caterpillar rested until—
5.27 P.M. Ate and rested by spells until—
5.40 P.M. Case % eaten. Caterpillar left shell and started crawling but remained close (1/16") to case at all times. Several stretches, turns, and twists, and then rested alternately until—
5.43 P.M. Became entirely quiet until—
5.55 P.M. Stretched a bit a few times, remained quiet again until—
5.59 P.M. Stretched again. Quiet until—
6.01 P.M. Returned to case but did not eat any of it. Remained until—
6.17 P.M. When it started to move, apparently aimlessly about, but remaining always on bud mass until—
6.22 P.M. Began eating balance of egg case.
6.42 P.M. Finished all of egg case except small cup at base, promptly left and for first time crawled onto another bud from that on which egg case was located. Crawled over three more buds and disappeared at—
6.45 P.M. into bud mass.
At this time caterpillar was entirely white except for shining black head, and a few fine black hairs.
No further observations until—
7.55 P.M. Caterpillar in same place on bud stem within bud mass.
10.45 P.M. In approximately same spot. Dark spots showing on body.

July 13, Friday:
Fed all day on stem of one bud and in almost same position. Seemed to eat only outer layer of stem. Excreta noticed for first time toward evening.
At 11.00 P.M. faint stripes began to show on sides.

July 14, Saturday:
Saturday morning caterpillar seemed to have increased in length to 3" but no signs of molt. Stripes now faint across back but more apparent on sides.
Fed during day in approximately same area but on different stems—remained within bud mass.

July 15, Sunday:
Sunday morning caterpillar now had distinct but light colored stripes around sides and back.
Fed in same area.
Sunday night 10.00 P.M. for first time color was noticed, body began to take on a yellowish green color. Stripes much more distinct and complete.

Scudder (1889) records the following:
On escaping from the egg, the caterpillar completely devours the shell and then attacks the leaf, eating a slender hole often entirely through it, and when it has done feeding returns to the concealed side of the leaf; if it is still erect, to the inner, that is the upper, side, if extended horizontally, to the lower surface. If, however, it has been born late in the season on a flower, it attacks the flowers themselves and eats down into the ovaries at first, not attacking the leaves until later. The caterpillar eats voraciously, and ordinarily matures rapidly.

When the time for eclosion approaches, the black head of the larva may be seen through the transparent shell moving back and forth. The following observations taken from my notes will give some idea of the time taken and the method employed during eclosion:
12.00 P.M.: First indication of a minute slit-like opening in the egg-shell approximately one-third from the top of the egg.

12.10 P.M.: Continuous chewing movement has produced an elongated slit equal in measurement to the width of the head of the larva.

12.20 P.M.: During the past 10 minutes no apparent larval movement.


1.30 P.M.: During past hour the larva would chew for short periods followed by longer periods of inactivity.

2.25 P.M.: The slit now enlarged to form an irregular hole smaller in size than the head of the larva.

2.30 P.M.: Vigorous activity, hole still further enlarged.

2.35 P.M.: Larva emerged.

When the larva has reached full development within the egg, it would appear that some considerable time is necessary for the chitinous mouth parts to harden enough to penetrate the shell of the egg. The apparent activity prior to the appearance of the first slit-like opening is perhaps an attempt to penetrate the egg-shell. Following such movement, the larva remains within the shell relatively inactive waiting for further hardening of the mouth parts. This takes approximately two hours at room temperature (74°F.). It is probable that the time period would be considerably shortened at higher temperatures.

After emerging from the egg-shell, the larva varies in activity from complete immobility to marked activity, as shown by Mr. Stiles. In our rearing experiments it was observed that the larvae did not always consume the entire egg-shell. The following counts were made:

Egg-shell intact except for small exit hole: 12
Egg-shell partly eaten: 16
Egg-shell completely devoured, except for basal plate: 19

Therefore of 47 eggs, only 19, or approximately 41 per cent, were completely devoured.

Observations by other authors seem to give the impression that the larvae always consume the egg-shells before beginning to feed on the leaf of the host plant; we thought, therefore, that perhaps the above result was due to the newly hatched larvae being confined to a small space. To check these results, counts were made of eggs hatched out-of-doors. The following counts were made:

Egg-shell left intact, except for small exit hole: 18
Egg-shell partly eaten: 8
Egg-shell completely devoured, except for basal plate: 6

Therefore of 32 eggs, only 6, or 18.7 per cent were completely devoured.
Such counts, however, simply indicate that the larvae do not always consume the egg-shell. The lower count in nature of egg-shells completely consumed is perhaps due to the difficulty of recognizing the very minute basal plate of the egg as compared with the more obvious unconsumed egg-shell. Also, in nature the larvae were free to wander away from the leaf after hatching, while in our experiments the larvae were confined to a small plastic box.

Eggs retained for life history studies were glued in rows on a filing card which was placed in a plastic rearing box. Each egg could be identified by the catalogue number written beneath it. The eggs were glued close together, a space of approximately 4 mm. separating them in each row, the rows being approximately 14 mm. apart. This method, although facilitating keeping notes and recording periods for each phase of development, resulted in the destruction of some of the unhatched eggs which were partly devoured by the newly hatched larvae from other eggs. The unhatched eggs were probably destroyed by larvae that had wandered away from the partly devoured egg-shells from which they had emerged, returning to unhatched eggs rather than to their own egg-shell. The importance for the ovipositing female to deposit a single egg upon a leaf is suggested from these observations.

Observations carried on continuously for a period of five hours revealed a few interesting habits of the newly hatched larva. The larva under observation hatched at 12.00 o'clock and immediately after eclosion was transferred to the surface of a small, terminal leaf. A newly emerged larva is so very small that it crawls, with apparent difficulty at first, on top of the fine leaf hairs. Hence the first food consists of these minute hairs. Feeding on the leaf hairs commenced twenty minutes after eclosion and only a few hairs were consumed. One hour and fifteen minutes after eclosion, the larva had consumed enough hairs in a small area (about the size of the head of a pin) to form a dimpled depression on the surface of the leaf. After consuming the leaf hairs in this area the larva wandered off, investigating, as it were, the entire surface of the leaf, only to return to the same area to feed again. This time the larva was able to penetrate beneath the surface of the leaf. The habit of returning to the original feeding site accounts for the close proximity of the holes made by first instar larvae on a small leaf.

The lengths of newly hatched larvae were measured, being read to one-tenth of a millimetre with the aid of a ruled measuring disc in a microscope.

<table>
<thead>
<tr>
<th>No. of larvae</th>
<th>Length</th>
</tr>
</thead>
<tbody>
<tr>
<td>4</td>
<td>1.7</td>
</tr>
<tr>
<td>6</td>
<td>1.8</td>
</tr>
<tr>
<td>32</td>
<td>1.9</td>
</tr>
<tr>
<td>8</td>
<td>2.0</td>
</tr>
</tbody>
</table>

Average Length: 1.9 mm.
**Rate of Development**

Some of our co-operators submitted data concerning the length of time between hatching and pupation of the larva of different geographical localities.

**R. Yunick of Schenectady, New York:**

<table>
<thead>
<tr>
<th>No. of larvae</th>
<th>Time in days</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>15</td>
</tr>
<tr>
<td>2</td>
<td>17</td>
</tr>
<tr>
<td>1</td>
<td>18</td>
</tr>
<tr>
<td>2</td>
<td>19</td>
</tr>
<tr>
<td>4</td>
<td>20</td>
</tr>
<tr>
<td>1</td>
<td>22</td>
</tr>
<tr>
<td>2</td>
<td>23</td>
</tr>
<tr>
<td>1</td>
<td>24</td>
</tr>
<tr>
<td>1</td>
<td>25</td>
</tr>
</tbody>
</table>

Average Time of Development: 20 days

**Mrs. Belle Johnston of Mount Clemens, Michigan:**

<table>
<thead>
<tr>
<th>No. of larvae</th>
<th>Time in days</th>
</tr>
</thead>
<tbody>
<tr>
<td>4</td>
<td>13</td>
</tr>
<tr>
<td>1</td>
<td>14</td>
</tr>
<tr>
<td>9</td>
<td>15</td>
</tr>
<tr>
<td>16</td>
<td>16</td>
</tr>
<tr>
<td>11</td>
<td>17</td>
</tr>
<tr>
<td>3</td>
<td>18</td>
</tr>
<tr>
<td>2</td>
<td>19</td>
</tr>
</tbody>
</table>

Average Time of Development: 16 days

**Miss Ruth Haight of Niagara Falls, Ontario:**

<table>
<thead>
<tr>
<th>No. of larvae</th>
<th>Time in days</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>11</td>
</tr>
<tr>
<td>1</td>
<td>12</td>
</tr>
<tr>
<td>7</td>
<td>13</td>
</tr>
<tr>
<td>5</td>
<td>14</td>
</tr>
<tr>
<td>10</td>
<td>15</td>
</tr>
<tr>
<td>4</td>
<td>16</td>
</tr>
</tbody>
</table>

Average Time of Development: 14 days

**Mrs. J. Senghas, Mount Clemens, Michigan:**

<table>
<thead>
<tr>
<th>No. of larvae</th>
<th>Time in days</th>
</tr>
</thead>
<tbody>
<tr>
<td>6</td>
<td>12</td>
</tr>
<tr>
<td>41</td>
<td>13</td>
</tr>
<tr>
<td>17</td>
<td>14</td>
</tr>
<tr>
<td>3</td>
<td>15</td>
</tr>
<tr>
<td>1</td>
<td>16</td>
</tr>
<tr>
<td>1</td>
<td>17</td>
</tr>
</tbody>
</table>

Average Time of Development: 13 days

**Mrs. L. W. Hobbs of Lathrup Village, Michigan:**

<table>
<thead>
<tr>
<th>No. of larvae</th>
<th>Time in days</th>
</tr>
</thead>
<tbody>
<tr>
<td>2</td>
<td>10</td>
</tr>
<tr>
<td>1</td>
<td>13</td>
</tr>
<tr>
<td>1</td>
<td>16</td>
</tr>
<tr>
<td>1</td>
<td>17</td>
</tr>
<tr>
<td>1</td>
<td>18</td>
</tr>
</tbody>
</table>

Average Time of Development: 14 days

Mrs. Lester Luxenber of Philipsburg, Pennsylvania, obtained an average time of development of 13.1 days based on the rearing of 130 larvae.
THE MONARCH BUTTERFLY

The rearing experiments on which these conclusions were based were carried out during July and August. Those giving a high average time of development were observed in mid or late August to September; those giving a low average in July and early August. During August and September at a time when the weather was unreasonably cool we carried out some experiments in the shade of a woodlot so that there was very little incident solar radiation falling upon the rearing tubes. The following results were obtained:

<table>
<thead>
<tr>
<th>No. of larvae</th>
<th>Time in days</th>
</tr>
</thead>
<tbody>
<tr>
<td>3</td>
<td>16</td>
</tr>
<tr>
<td>4</td>
<td>17</td>
</tr>
<tr>
<td>2</td>
<td>19</td>
</tr>
<tr>
<td>3</td>
<td>20</td>
</tr>
<tr>
<td>3</td>
<td>21</td>
</tr>
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<td>2</td>
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</tr>
<tr>
<td>8</td>
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<td>25</td>
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<td>1</td>
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</tr>
<tr>
<td>3</td>
<td>27</td>
</tr>
<tr>
<td>1</td>
<td>28</td>
</tr>
</tbody>
</table>

AVERAGE TIME OF DEVELOPMENT: 21 + days

Under the same conditions but during July and August we obtained the following results:

<table>
<thead>
<tr>
<th>No. of larvae</th>
<th>Time in days</th>
</tr>
</thead>
<tbody>
<tr>
<td>30</td>
<td>13</td>
</tr>
<tr>
<td>12</td>
<td>14</td>
</tr>
<tr>
<td>4</td>
<td>15</td>
</tr>
<tr>
<td>2</td>
<td>16</td>
</tr>
</tbody>
</table>

AVERAGE TIME OF DEVELOPMENT: 13 + days

Attempts were made to rear the larvae in tubes exposed to the direct rays of the sun but because of the difficulty of controlling the deposition of moisture on the surface of the glass, which interfered with the moulting process, the test was discontinued.

The following data were obtained for the weight of the egg and the weight of the larva at various stages in its development according to the age in days. Weights were obtained by means of a torsion balance and finely adjusted chemical balance.

<table>
<thead>
<tr>
<th>No. of specimens</th>
<th>Age in days</th>
<th>Weight—mg</th>
<th>Av. weight—mg.</th>
</tr>
</thead>
<tbody>
<tr>
<td>10</td>
<td>eggs</td>
<td>5.4</td>
<td>.54</td>
</tr>
<tr>
<td>10</td>
<td>2</td>
<td>26</td>
<td>2.5</td>
</tr>
<tr>
<td>4</td>
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<td>50.2</td>
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</tr>
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<tr>
<td>3</td>
<td>15</td>
<td>4500</td>
<td>1500</td>
</tr>
</tbody>
</table>
FIGURE 32. Rate of development (by weight) of larvae.
The larvae entered the pupa stage on the sixteenth day. The rapid rate of growth, particularly after the tenth day, is clearly shown in the graph plotted from the above data (Fig. 32).

Since the rate of development depends on the temperature to which the larva is subjected, and since the air temperature will vary from day to day, week to week, and month to month, the rate will depend to a great extent on the particular period of summer when the observations are made. The air temperature will vary for different localities within a given area. Cooler temperatures will prevail in shaded areas as compared with exposed areas. Temperatures over open sand areas will be warmer than over grassy areas. Temperatures, in so far as the body temperatures of the larvae are concerned, will vary according to the amount of incident radiation, and larvae exposed to the direct rays of the sun will have a higher body temperature than those in the shade. Adverse weather conditions also play an important role in retarding the growth rate. Prolonged periods of cloudy, rainy weather will retard the growth of the larvae even more than vegetative shade.

Although it is not possible to state that larvae develop more slowly in June than in July, and in July than in August (for June in a particular year may have an average temperature higher than that of July or August), it can be stated that larvae in May, early June, late September, and October usually have a slower rate of development than those in late June, July, and August.

In addition to the effect of temperature on the rate of growth, there is also an inherent, and perhaps inherited, variation among larvae from the same or different parents. Larvae reared under exactly the same conditions (in the same rearing tube) may show a difference of as much as five days in the rate of development. The fastest rate of growth which we recorded was eleven days and the slowest was twenty-nine days. Under laboratory conditions, of course, the eleven-day period could be reduced by maintaining optimum temperatures night and day, and the twenty-nine-day period could be extended by subjecting the larva to minimum temperatures night and day. In the present report, however, we are dealing with natural temperature conditions because such temperatures are the ones that govern the natural growth rate of the larvae and hence may be used to estimate dates of arrival and departure and the number of generations in a given area.

Playing Possum

When a larva curls up and drops from the host plant, as a result of being alarmed, it may remain on the ground for several minutes before crawling away. If alarmed again it may or may not play possum. The following data were obtained for the period of quiescence after each stimulation and the
number of such periods to saturation for a particular specimen. Stimulation was caused by probing with a blunt lead pencil. Saturation was reached when, regardless of the number of stimulations, the larvae no longer played possum.

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The above data are plotted in Figure 33.

![Figure 33. Quiescent period plotted against number of stimulations.](image-url)
The above data are plotted in Figure 34.

Relocating the Food Plant

If the larva has fallen to the ground as a result of being disturbed, it must find the milkweed plant upon which it was feeding or discover a new plant. We had observed in the field that the larvae apparently experience some difficulty in relocating the food plant; the following series of experiments was therefore carried out. A leaf of the food plant was placed upon a sheet of paper and larvae of various instars were placed at varying distances from the leaf. As the larva crawled over the surface of the paper its direction of travel was marked by a pencil line. The following results were obtained (Figs. 35 and 36; the figures are plotted to scale from the original tracings).

It was observed that larvae of the first instar appear to be positively phototropic, and larvae of subsequent instars do not appear to be affected by light intensity.

Re-discovery of the host plant appears to be mostly by accident. If larvae were placed with the rear of the body touching the leaf and the front of the body directed away from it, they moved away from the food supply (Fig. 36). If larvae were placed so that they were facing the leaf, they had no difficulty in finding the source of food if the distance from the leaf to the heads of the larvae was less than two inches. That larvae were unable at times to find the host leaf is demonstrated in Figures 35 and 36. In Figure 36a, specimens (2) and (3) were apparently able to crawl directly to the food plant, and yet specimen (1) was unable to do so. That finding the leaf was due, for the most part, to random movement, is demonstrated in
Figure 36 b, the larva started away from the leaf, even though the hind part of the body was touching it, and then returned to the leaf by an aimless, circuitous route—this is further emphasized in Figure 35 c.

Finding the food plant out-of-doors also appears to be by random movement, as shown in Figure 36 d and e. In Figure 36 e larva 1 came within a few inches (8" and 14") of each plant but still appeared to be unable to locate either of them.

The following observation was submitted by Mr. F. A. Stricker of Kitchener, Ontario:

On a field trip, July 12, I sat down to enjoy a smoke and noticed a plexippus...
Figure 35. Tracings of larval movements in seeking milkweed leaves: a, 1st instar larvae are affected by light source; b, larva failed to locate leaf; c, after circuitous route, larva eventually located leaf; d, larva failed to locate leaf.
larva, about half grown, crawling through the grass. It travelled about six feet in the time it takes to smoke a cigarette. Searching the area I located four milkweed plants about twenty feet from the place I first noticed the larva. No other plants were in the immediate area. This larva was crawling into the wind and away from the plants. Placing the larva one foot from the plant and upwind from it, it turned and crawled away from the plant. This was repeated five times with the same results. I then placed the larva downwind from the plant. It turned and found the plant. But it was still travelling in its original direction.

**FIGURE 36.** Tracings of larval movements in seeking milkweed leaf: a, of three larvae, two located leaf and one failed to do so; b, larva placed so as to have posterior end of body touching leaf, crawled away from it and failed to locate it; c, larva, oriented as in "b" succeeded, by circuitous route, in locating leaf; d, experiment under field conditions with milkweed plants indicated by small circles; three of the larvae located plant 1, and one larva located plant 3; e, experiments under field conditions with plants located in positions "left" and "right": both larvae moved south to the plants on the right and one succeeded in finding it, while the other moved to the north but was unable to locate plants on the left; larva 2 was unable to locate plants.
Mrs. L. Luxenberg of Philipsburg, Pennsylvania, submitted the following pertinent observation:

In my field trips I am amazed by the marked decrease in the number of surviving larvae. I have marked plants and revisited them daily but it is difficult to find any larvae. . . . I found a potter wasp dragging a freshly killed larva.
The process of pupa formation can be divided into four phases: nomadic, silk mat, button, and suspension.

**Phase 1: Nomadic**

During this phase the larva seeks a suitable place for final suspension of the pupa and is marked by a decidedly negative phytotaxis.1 This was borne out by the following simple experiment. Ten larvae, which had reached full development, were placed on ten separate milkweed plants. Within fifteen minutes all of them had crawled to the ground and moved away from their respective plants. After they had travelled a short distance from the plants they were picked up and returned to them. This procedure was repeated five times with the same results. The time taken to leave the plant, after being replaced, varied considerably—some larvae crawled to the ground almost immediately while others remained for periods up to one hour before leaving the plant.

**Phase 2: Silk Mat**

Having chosen a suitable location, the larva forms a silk mat on the under-surface of the object from which the pupa is to be suspended (Fig. 9). The area of the silk mat varies according to the nature of the surface: on a glass surface the area varied from 300 sq. mm. to 1125 sq. mm. with an average area of 875 sq. mm.; on a rough surface, such as cardboard, the area varied from 240 sq. mm. to 700 sq. mm. with an average area of 425 sq. mm.

The following observations were made during this phase.

1.15 p.m. August 17: Larva began formation of silk mat; head and thoracic regions moving slowly back and forth and raised to a height of ten to twenty millimetres at frequent intervals; viewed through a magnifying glass, a thread of silk could be seen extending from the mouth to the surface of the box lid; outer silk fibres laid down first; frequent periods of inactivity varying from six seconds to four-and-a-half minutes.

1 I have used this term as a combination of the Creek phyton, plant, and *taxis*, orientation; the latter (*taxis*) is now commonly used when expressing motion towards or away from, such as positive and negative phototaxis.
THE MONARCH BUTTERFLY

4 P.M.: Larva beginning to place a greater number of strands in the central area; its motions decidedly slower. When viewed through a magnifying lens, the mat of silk was seen to be composed of a layer of rather coarse strands irregularly arranged so as to form an open network.

5 P.M.: Button of silk being formed. Time taken for this phase was 3 hrs., 45 min.

Phase 3: Button

Having completed the silk mat, the larva proceeds to form the button by adding a great many strands of silk, one on top of the other, in a small central area, until an obvious pile of loose strands has been made.

The following time observations were recorded during this phase.

5 P.M.: Button of silk being formed; button consists of many irregular strands placed loosely one above the other and, because of the combined density of the strands, it is more conspicuous than the remainder of the mat of silk; each strand is of varying thickness and in some cases the strand is decidedly flattened, which causes it to curl, thus keeping the individual strands well separated rather than becoming closely matted together.

5.45 P.M.: Button of silk formed; larva resting with head held over button; at irregular intervals head is raised and a strand of silk produced.

6.30 P.M.: Motion of larva much slower; body shorter, the intersegmental folds completely hidden, head bent downwards; body more translucent, the yellowish green of the developing pupa now visible through the exoskeleton.

7 P.M.: Position now reversed; anal prolegs fastened to button; through magnifying lens, slight pulsations of prolegs could be seen causing curved spines to become enmeshed in silk strands of the button.

7.30 P.M.: No change.

8 P.M.: Suspensión. Time taken for this phase was 3 hours.

Phase 4: Suspension

8 P.M.: Larva quite suddenly released its hold on the mat of silk and became suspended from the button by means of the curved spines of the anal prolegs.

8 A.M. August 18: During the previous twelve hours the larva remained in a U-shape, the head, thoracic region, and first third of the abdominal region curved ventrally; exoskeleton translucent, showing the yellow-green of the underlying pupa.

8.30 A.M.: Larva more elongate—J-shape; slightly more swollen in vicinity of thorax as compared to rest of body.

11.45 A.M.: Exoskeleton breaking immediately behind the head.

12.00 P.M.: Pupa completely exposed; larval skin at base of cremaster; pupa gyrating vigorously.

12:05 P.M.: Larval skin falls away. Time taken for complete appearance of pupa was 16 hours. The complete process for production of pupa, in this particular case, took 22 hours.
1:30 P.M.: During the past hour and a half the abdomen contracted; wings became confluent with the body and legs; antennae and mouth parts became more solidly joined to the main body of the pupa; pupa still soft and spots yellow in colour.

5:30 P.M.: Very little change.

9:00 A.M. August 19: Gold spots now formed.

Approximately 21 hours were taken for the complete formation of the pupa from the initial semi-exarate pupa stage.

**Experiments Interrupting Sequence of Phases**

To test whether or not the larva was capable of retracing each phase, the following experiments were conducted. Ten minutes after the larva began forming the mat of silk it was removed and placed in another rearing tube. The larva crawled to the top of the tube and began once again to form the mat of silk. This operation was repeated four times. After the fourth interruption, only a small mat was formed consisting of relatively few strands, and the button of silk was rapidly constructed. The first two interruptions did not seem to interfere unduly with the process of constructing the mat. There was a marked increase in activity after the third, further emphasized after the fourth. The experiment was discontinued at this point.

A larva which had completed the mat of silk and had begun to construct the central portion was removed to another rearing tube. It climbed to the top of the tube, made a very small mat consisting of a few strands, and began to construct the button. It was removed again to another rearing tube. Once again a mat of a few strands and a complete button were formed.

The larva used in the preceding experiment was removed to another rearing tube after the button had been completely formed and the larva had remained in a quiescent state with the thoracic region held over the button for a period of one hour. It was unable to climb up the wall of the glass tube. It was placed on a piece of cardboard that was sparsely covered with strands of silk laid down by other larvae. The larva remained clinging to the strands of silk for one hour and ten minutes. It did not attempt to construct a button and finally entered phase 4, the curved spines holding on to four strands of silk.

A larva which had entered phase 4 (within 3 minutes of suspension) was removed and placed in a rearing box. It was unable to climb the sides of the box and entered the pupa stage on the floor.

These experiments seem to indicate that since metamorphic changes are taking place in the larva each phase is dictated by the degree of change. Time periods for each phase vary with temperature—the higher the tem-
perature the shorter the period, and vice versa. Whether or not lack of sufficient food would interfere with such a sequence of events has not yet been clearly demonstrated. Larvae in the last instar in which the amount of food available was greatly reduced failed to produce an undersized pupa. It is possible, however, that a combination of correct temperature and lack of sufficient food may produce the small adults which occur in early summer in the southern states and in late summer and fall in the northern states and Canada.

**Observations Submitted by Co-operators**

The following observations were submitted by Mr. H. F. Stiles of Grand Rapids, Michigan:

When mature the caterpillar crawls to the spot chosen for the chrysalis. This spot is one protected from the winds and if possible under some protection from the rain. In a 24" square screened breeding cage eight out of twenty caterpillars hung in the southwest corner almost touching one another, and here they were protected from the prevailing southwest winds. Two hung at about the middle of the west side, still well protected, and only one hung near the center. The others hung in a protected spot on strips of bark. The balance hung on leaves of milkweed plant. It is interesting to note that only seven out of twenty remained to hang on plants.

It is not uncommon for it to lie absolutely immobile for one to three hours. Then it begins to spin a mat of silk. This varies in size but averages about 3" × 1", generally being a little longer one way than the other. It varies greatly in density, being thin on the edges and thicker toward the center. After completing this first stage it builds, in the approximate center of the mat, a mound or tuft of silk. This is about 1" to 2 mm., or .075 of an inch across at the base and about the same in height. It is roughly conical in shape and appears in most cases to lean slightly to one side. This mound is most carefully built by placing layer on layer of silk. When the mound is completed the caterpillar fastens it firmly by strands of silk passed around and over it with the outer ends covering the entire mat previously woven.

Completed, the caterpillar turns around so that his tail end is at and over the mound. Then when the exact position is finally found, the caterpillar grasps the silken mound with his anal prolegs and is ready to hang. The prolegs clamp tightly and solidly on and in the silken mound.

He may lie for hours fastened to the mound but sometimes only for minutes. Then he drops his body down, first in almost the shape of a "U", but soon drops still further to the characteristic 'T' shape.

In the early stages there is little movement, sometimes a partial uncurling and recurling. As time passes convulsions seem to seize the body and it appears the caterpillar is straining to hasten the process. Occasionally there is a serious convolution with twisting and writhing. As the time approaches for the transformation to the chrysalis the skin loses its brightness, the color, especially at the lower end, fades and becomes lifeless; the antennae are emptied and hang limp.

As the split starts on the back a little above the head a continual writhing takes
place, and with each expansion the skin of the caterpillar is forced upward toward the tail. It moves slowly but unless one is watching closely he will miss an interesting part. When the skin is well worked up almost to the tail, yet while still attached to the caterpillar, there suddenly appears on the back side close to the top or rear end a small black organ about the size of a heavy thread and about 5 inch long. This is called the “cremaster.” It waves in what appears an aimless manner but actually the movement is definite. It seeks a spot on the silk mound, attaches itself, and is the thread by which the chrysalis is hung. This takes only about two seconds. A few more writhings of the body and the now useless skin of the caterpillar is shaken loose and drops. All the above from the first split of the skin to shaking loose of the skin takes place in 4 to 6 minutes, an average of 5 minutes.

Mr. F. A. Stricker of Kitchener, Ontario, reports as follows:

After the larva has completed its “last supper” it expels the body wastes, and wanders about until it finds a suitable place to form a pupa. Only one of my larvae chose its host as a final resting place. After locating such a site it begins to spin a silken mat, but not until it searches the immediate area for obstacles which might hinder the formation of the chrysalis and the emerging adult. The larva succeeds in searching the area by hanging on with its prolegs and leaning downward, and searching in all directions, changing its position from time to time until a complete circle has been searched. Then, completing the silken mat, it rests, horizontally, for a period of time varying from several hours to two days, before attaining the inverted position. The larva usually drops in late afternoon or early evening, changing to a pupa around noon of the following day. Just before the larva sheds its striped coat, for the last time, the anterior portion becomes quite plump and loses its characteristic button-hook shape, to hang straight downward. The larval skin splits and gently rolls upward until the cremaster is free. When the cremaster is secure the exuvia falls free. Now the pupa is in the transition stage, and it remains in this stage for several hours before assuming a shiny green appearance with gold spots. [Mr. Stricker submitted also the following data:]

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We attached weights to find out the various strengths of the attachment of the chrysalis.

At 15 ounces the silken mat pulled loose

" 2x " tuft " from the mat

" 16% " cremaster broke

We were unable to pull the cremaster from the silken tuft, as a break occurred at any place but at this point.

The following data were obtained from Mrs. Bette Johnston of Mount Clemens, Michigan.
Average number of hours from the time the larva inverted to the shedding of the skin was 16 hours. This average was based on 23 observations.

Shortest number of hours—3 hours
Longest number of hours—25 hours

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<td>1</td>
<td>21</td>
</tr>
<tr>
<td>3</td>
<td>22</td>
</tr>
</tbody>
</table>

Average temperature during the above observations was 72°F. All observations were indoors.

The following data were submitted by Miss Ruth Haigh of Niagara Falls, Ontario.

<table>
<thead>
<tr>
<th>Time taken from splitting of skin</th>
<th>Time taken for cremaster to become attached to button</th>
<th>Time taken for larval skin to drop</th>
<th>Complete time for pupa formation</th>
</tr>
</thead>
<tbody>
<tr>
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<td>5</td>
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</tbody>
</table>

AVERAGES: 3 min. 15 sec. 16 sec. 55 sec. 10 hrs.
The following data were submitted by Mrs. L. W. Hobbs of Lathrup Village, Michigan.

<table>
<thead>
<tr>
<th>Time taken from inverted position to formation of pupa</th>
<th>No. of specimens involved</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hrs. Min.</td>
<td></td>
</tr>
<tr>
<td>8 - 10</td>
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<td>10 - 12</td>
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<td>12 - 14</td>
<td>6</td>
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<tr>
<td>14 - 16</td>
<td>8</td>
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<tr>
<td>16 - 18</td>
<td>11</td>
</tr>
<tr>
<td>18 - 20</td>
<td>16</td>
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<tr>
<td>20 - 22</td>
<td>15</td>
</tr>
<tr>
<td>22 - 24</td>
<td>8</td>
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<tr>
<td>24 - 26</td>
<td>7</td>
</tr>
<tr>
<td>26 - 28</td>
<td>3</td>
</tr>
</tbody>
</table>

Average Time: 18 hrs. 25 min.

If the figures supplied by Mrs. Hobbs are divided into intervals of two hours, the following data are obtained:

<table>
<thead>
<tr>
<th>Time taken in hours</th>
<th>No. of specimens involved</th>
</tr>
</thead>
<tbody>
<tr>
<td>6 - 10</td>
<td>9</td>
</tr>
<tr>
<td>10 - 12</td>
<td>2</td>
</tr>
<tr>
<td>12 - 14</td>
<td>6</td>
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<tr>
<td>14 - 16</td>
<td>8</td>
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<tr>
<td>16 - 18</td>
<td>11</td>
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<td>18 - 20</td>
<td>16</td>
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<tr>
<td>20 - 22</td>
<td>15</td>
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<td>22 - 24</td>
<td>8</td>
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<tr>
<td>24 - 26</td>
<td>7</td>
</tr>
<tr>
<td>26 - 28</td>
<td>3</td>
</tr>
</tbody>
</table>

It will be seen from this that the mean is approximately twenty hours, which is slightly above that reported by others, but within one or two hours
of the average from other data. We cannot explain the large number for the period 8-10 hours.

DESCRIPTION OF FULLY FORMED PUPA

The following description of the fully formed pupa was submitted by H. F. Stiles.

The chrysalis chosen for this description was an average one which was approximately four days old. When "back" is referred to, it is the side of the chrysalis which was the back of the caterpillar, and when "front" is referred to, it was the lower or leg side of the caterpillar.

This chrysalis was 11.7 mm. or .468 inch across at widest part, which is at line of gold dots described later. It was 11.7 mm. or .468 inch from front to back. The diameter at the base before tapering rapidly away is from front to back 10 mm. or .396 inch, and from side to side at same point exactly the same dimensions. The diameters being the same is odd but since measurements were with micrometer they are exact. The length is 25 mm. or 1.009 inches, measuring from base to cremaster to bottom tip. What appears to be a cup is marked by a row of golden dots described later on the back. At the center of the back this row of dots is 78 mm. or .295 inch from the top, and at the middle of the side 8 mm. or .320 inch from the top.

On the back near the base there is a slight bulge which ends a little less than ½ up. On the front side starting about one half down the cap is a cleavage line which continues around and down the side. It is this point where the chrysalis splits for the butterfly to emerge.

As described above, there seems to the naked eye to be a row of golden dots at the base of the cup and running around to the center of each side. This actually is a continuous band of gold with a silvery band below, and on this silvery band are black splotches. This can be seen with a 10-power glass but to the naked eye produces the effect of a series of dots.

Beside the row of dots at the base of cup there are six other golden dots on the body of the chrysalis. Two, one on each side, low on the sides, and two, one each side of the center line on the back somewhat higher than the side ones—and finally, two more, one on each side between the others described above.

The body of the chrysalis seems to be divided into twelve zones by slight depressions in the case, the top six above the line of golden dots being quite regular, those below being irregular.

On each side under 10-power glass 6 slits can be seen, four above the row of golden dots and two below.

On top of the chrysalis on the back is a small black triangle close to the base of the cremaster and on the front side are two rows of dots, the first pair being separated and protruding, but the last two pairs being connected and joined to base of cremaster which is also black. These last pairs are quite flat.

The cremaster is about 1 mm. or .040 inch in diameter, 25 mm. or .096 inch in length. It is shining jet black as are the markings around it, as described above.

The top end of the cremaster is covered with pointed mushroom-shaped hooks and it is these which become embedded in the silk and thus firmly support the chrysalis.
When the larval skin has been shed, the form of the pupa is somewhat grub-like; the abdomen is large and obviously segmented with deep intersegmental folds; the wings are small and extend above the body of the pupa; the legs, mouthparts, and antennae give the appearance of being partly exarate; there is a deep well-developed sinus between the gales. We have termed this metamorphic stage the "semi-exarate pupa." Some considerable time is taken for the semi-exarate pupa to become fully formed.

Weight
Using a chemical balance, it was found that four fully mature pupae weighed 5.42 gms. The average weight is therefore 1.35 gms. The range of weights varied from .78 gms. to 1.36 gms. The .78 gm. pupa was an exceptionally small one and was not included among the four used to obtain an average figure.

Development from Fully Formed Pupa to Emergence of Imago
The time taken for the various phases of development up to the formation of the fully developed pupa was presented above. The following data conclude this set of observations, giving the time taken from the fully formed pupa to the emergence of the imago.

<table>
<thead>
<tr>
<th>Time</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>7.00 A.M. Aug. 20</td>
<td>Thoracic portion grey in colour</td>
</tr>
<tr>
<td>11.00 A.M. Aug. 21</td>
<td>Entire pupa dark brown in colour</td>
</tr>
<tr>
<td>7.00 A.M. Aug. 22</td>
<td>Reddish colour of wings visible</td>
</tr>
<tr>
<td>11.00 A.M. Aug. 23</td>
<td>Wings clearly visible</td>
</tr>
<tr>
<td>8.30 A.M. Aug. 25</td>
<td>Imago emerged</td>
</tr>
</tbody>
</table>

Approximately thirteen days were taken for complete development within completely formed pupa.

The time taken from the full development of the pupa to emergence of the imago was as follows.

<table>
<thead>
<tr>
<th>No. of specimens</th>
<th>Time in days</th>
</tr>
</thead>
<tbody>
<tr>
<td>4</td>
<td>11</td>
</tr>
<tr>
<td>3</td>
<td>12</td>
</tr>
<tr>
<td>8</td>
<td>13</td>
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<tr>
<td>12</td>
<td>14</td>
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<td>9</td>
<td>15</td>
</tr>
<tr>
<td>6</td>
<td>16</td>
</tr>
<tr>
<td>2</td>
<td>17</td>
</tr>
</tbody>
</table>

Average rate of development: 14 days
PLATE V
Variation in size of Monarch butterfly females (left) and males (right)—slight reduction.
Species and subspecies of *Danaus*: from southern North America and South America.

Top row: left, *D. p. gilippus* (♂, ♀); right, *D. g. hermippus* (♂, ♀).

2nd row: left, *D. g. abeaster* (♂, ♀); right, *D. g. niveus* (♂, ♀).

3rd row: left, *D. g. herminice* (♂, ♀); right, *D. c. eristalis* (♂, ♀).

4th row: left, *D. c. terhan* (♂, ♀); right, *D. c. montecusum* (♂, ♀).

5th row: left, *D. c. cleophae* (♂, ♀); right, *D. j. manicenius* (♂, ♀).

6th row: left, *D. s. erginus* (♂); right, *D. crippes* (♂, ♀).
The following data were submitted by Miss Ruth Haigh of Niagara Falls, Ontario.

<table>
<thead>
<tr>
<th>No. of specimens</th>
<th>Time taken</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
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<td>1</td>
<td>10</td>
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<tr>
<td>1</td>
<td>15</td>
</tr>
<tr>
<td>8</td>
<td>12</td>
</tr>
<tr>
<td>2</td>
<td>14</td>
</tr>
</tbody>
</table>

Average rate of development: 11 days, 2 hrs., 53 min.

The following data were submitted by Mrs. L. G. Senghas of Mount Clemens, Michigan.

<table>
<thead>
<tr>
<th>No. of specimens</th>
<th>Time taken in hours for semi-exuviate pupa to pupa</th>
<th>Time taken in days for complete development of imag</th>
<th>No. of specimens</th>
</tr>
</thead>
<tbody>
<tr>
<td>37</td>
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<td></td>
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</tr>
<tr>
<td>1</td>
<td>17</td>
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<td>1</td>
</tr>
</tbody>
</table>

Average: 11 hrs., 42 min.

The following data were submitted by Mrs. Bette Johnston of Mount Clemens, Michigan.

<table>
<thead>
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<th>No. of specimens</th>
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<td>5</td>
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<tr>
<td>2</td>
<td>14</td>
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</table>

Average: 11.2 days
The following data were submitted by Mrs. L. W. Hobbs of Lathrup Village, Michigan.

<table>
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<th>No. specimens</th>
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<th>No. specimens</th>
<th>Time</th>
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<tr>
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</tr>
</tbody>
</table>

Average: 12 days, 18 hrs.

The following data were submitted by Mr. L. Beamer of Meaford, Ontario.

<table>
<thead>
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<th>No. specimens</th>
<th>Time taken in days</th>
<th>No. specimens</th>
<th>Time taken in days</th>
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</thead>
<tbody>
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<td>11</td>
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<td>35</td>
</tr>
<tr>
<td>15</td>
<td>24</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Average: 23.9 days
The time of development of the imago, from the data submitted by Mr. Beamer, is approximately twice that for other localities. Mr. Beamer explains the reason for this as follows: "I believe that the temperature factor plays a great part in the time of development of the pupa. All of those that I have reported were reared in a hen house and, therefore, were shaded most of the time. It was never very warm in the daytime, particularly in September, and was decidedly cool at night. When I brought the chrysalids into our glassed-in front porch, development was much more rapid."

The data obtained from our rearing experiments gave an average of 14.7 days, which is longer than that of the other co-operators further south, but shorter than Mr. Beamer's.

The above data seem to indicate that the rate of development varies with latitude as well as with the ecological situation.

The following information is given by Scudder (1889):

Mr. Gosse in writing of the metamorphosis of this species says (Letters from Alabama, 1867):

"The change of form which the evolved pupa undergoes is most conspicuous in the suspended butterflies; and I have never seen it more remarkable than in this of the archippus, although I have observed the metamorphosis of many species... In this case the abdominal segments were at first much elongated, being distinctly separable, as in the caterpillar; those of the thorax, on the contrary, were contracted, while the wings were small, thick and wrinkled; their extremities being free; for a purpose we shall soon discover. The whole skin was soft, moist and pulpy, and the color bright green, with alternate yellow bands. In a few hours, the abdominal segments had contracted into the form of a smooth, blunt cone, all traces of the divisions being lost, except where a fine line, scarcely perceptible, marked their position; the thoracic segments had much lengthened, and the wings now occupied the half of the entire length; their tips, which before were free, had stretched beyond their first boundary, far over the abdomen, and were now fixed in the general outline. The whole surface was become tense, hard and glossy, and the hue a uniform greenish white."
CHAPTER TEN

ADULT

EMERGENCE FROM PUPA AND SUBSEQUENT DEVELOPMENT

Time of Day when Emergence from Pupa Takes Place

Our observations that there is a definite tendency for maximum emergence of butterflies from pupae during midday have been corroborated by our co-operators. The following data concerning the time of day when the imago emerged were submitted by Mrs. L. W. Hobbs of Lathrup Village, Michigan.

<table>
<thead>
<tr>
<th>No. of specimens</th>
<th>Time of emergence</th>
</tr>
</thead>
<tbody>
<tr>
<td>4</td>
<td>6-7 A.M.</td>
</tr>
<tr>
<td>13</td>
<td>7-8 A.M.</td>
</tr>
<tr>
<td>13</td>
<td>8-9 A.M.</td>
</tr>
<tr>
<td>21</td>
<td>9-10 A.M.</td>
</tr>
<tr>
<td>11</td>
<td>10-11 A.M.</td>
</tr>
<tr>
<td>20</td>
<td>11-12 A.M.</td>
</tr>
<tr>
<td>14</td>
<td>12-1 P.M.</td>
</tr>
<tr>
<td>9</td>
<td>1-2 P.M.</td>
</tr>
<tr>
<td>7</td>
<td>2-3 P.M.</td>
</tr>
<tr>
<td>2</td>
<td>3-4 P.M.</td>
</tr>
<tr>
<td>2</td>
<td>4-5 P.M.</td>
</tr>
<tr>
<td>1</td>
<td>5-6 P.M.</td>
</tr>
<tr>
<td>1</td>
<td>6-7 P.M.</td>
</tr>
<tr>
<td>3</td>
<td>7-8 P.M.</td>
</tr>
</tbody>
</table>

This information was plotted to form the following histogram (Fig. 37) which shows maximum emergence occurring between 8 A.M. and 1 P.M. Mrs. Bette Johnston of Mount Clemens, Michigan, submitted the following data.

<table>
<thead>
<tr>
<th>No. of specimens</th>
<th>Time of emergence</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>4-5 A.M.</td>
</tr>
<tr>
<td>5</td>
<td>5-6 A.M.</td>
</tr>
<tr>
<td>0</td>
<td>6-7 A.M.</td>
</tr>
<tr>
<td>2</td>
<td>7-8 A.M.</td>
</tr>
<tr>
<td>0</td>
<td>8-9 A.M.</td>
</tr>
<tr>
<td>4</td>
<td>9-10 A.M.</td>
</tr>
<tr>
<td>4</td>
<td>10-11 A.M.</td>
</tr>
<tr>
<td>9</td>
<td>11-12 A.M.</td>
</tr>
<tr>
<td>7</td>
<td>12-1 P.M.</td>
</tr>
<tr>
<td>3</td>
<td>1-2 P.M.</td>
</tr>
<tr>
<td>5</td>
<td>2-3 P.M.</td>
</tr>
<tr>
<td>1</td>
<td>3-4 P.M.</td>
</tr>
<tr>
<td>1</td>
<td>4-5 P.M.</td>
</tr>
<tr>
<td>0</td>
<td>5-6 P.M.</td>
</tr>
<tr>
<td>1</td>
<td>6-7 P.M.</td>
</tr>
</tbody>
</table>
Figure 37. Histograms showing number of butterflies emerging from the pupae at various times; upper figure from Hobbs data; lower figure from Johnston data.
THE MONARCH BUTTERFLY

The histogram (Fig. 37) presents a form similar to that shown for the data presented by Mrs. Hobbs and shows the peak of emergence between 9 A.M. and 3 P.M.

Effect of Temperature and Humidity on Emergence from Pupa

During periods of cool, rainy weather imagos rarely emerged. In a cage containing sixty-four pupae no imagos emerged during a three day period of rain, but on the fourth day, with clear sky and warm sunshine, twenty-eight emerged. Similar observations have been reported by one of our co-operators, Mr. H. F. Stiles of Grand Rapids, Michigan.

The time elapsing before the butterfly emerges is highly variable depending on temperature, humidity, and actually whether it is raining or not. If it is rainy and wet outside with its resulting humidity and coolness, there is no emergence, but if you transfer some of the chrysalids into a heated room, in a few hours, although nothing happens to those left outside, those inside start to emerge. Warm with an electric light, such as a photo lamp, and the time of emergence is greatly reduced. Refrigerate some and they will lag behind even those left outside.

Mr. Stiles found that if pupae, which had been exposed to outdoor temperatures for a few hours, were transferred to warm temperatures the adult butterflies emerged in “far less time” than those left at outdoor temperatures. When a caterpillar was placed in warm temperature and allowed to pupate under these conditions the time for emergence was reduced from an average of 324 hours to 151 hours.

Concerning the effect of moisture the following report from Mr. Stiles is significant: “A pupa was allowed to hang until almost at the point of emergence; it was then removed to outdoors and kept sprinkled with fine mist. After 36 hours it still had not emerged. The sun at this time was shining and the spray was stopped; immediately the pupa was dry, the butterfly emerged.”

Development after Emergence from Pupa

Mr. Stiles has submitted the following observations:

Although the full wing expansion seems to be complete in from twelve to eighteen minutes, careful measurements show that expansion is not complete until about thirty-five to forty minutes have passed. After the early rapid expansion of the wings occurs, the pumping action continues. Of those timed it appeared a pumping cycle took place about every twenty seconds and lasted about twelve seconds.

The physical reactions of this cycle were as follows: The wings were brought together at the wing tips and compressed against the body and at about this time the butterfly’s abdomen was curled out and exposed between the body side of the wings. This position was held a few seconds and at the same time, besides pressure being exerted on the body by the wings, there was some internal action.
Finally, the body assumed its normal position, and the wings were separated; this was followed by a period of rest of twenty seconds' duration. As above stated this series of cycles continued for approximately twenty to thirty minutes after the first rapid expansion, or a total of thirty-five to forty minutes after the emergence of the butterfly.

At about this time the butterfly ejects four or five drops of a brownish liquid. This may be repeated in another minute or two. It was noted where the second emission of the liquid occurs that the pumping action continues after the first. Immediately this final ejection of the fluid occurs the pumping action ceases and almost immediately the butterfly spread its wings for the first time.

Even after this operation is complete and the butterfly has assumed its final form, the wings and body must dry and harden. During perhaps a period of three hours the butterfly, clinging to the now empty chrysalis, keeps flexing its wings. Opening them and closing them, they become harder and stiffer and gradually gaining strength. Suddenly without warning the butterfly flies away.

Miss Elsie L. Stebbins of San Francisco, California, submitted the following observations.

Last Tuesday morning, Sept. 11, I arrived at the office just as the Monarch in the jar on my desk was climbing down out of the chrysalis. It was 9.05 A.M. The wings were very short. As soon as the insect was free of the chrysalis it balloon ed its abdomen at intervals.

9.10 A.M. Made rather gay movements, turning around, unrolling curled proboscis a bit, or rather loosening the coil while keeping it curled.

9.11-9.12 A.M. Wings had gained five inches in length. Note: right wing seemed to be five inches longer than the left one at this point.

9.14 A.M. Wings had become same size as each other and measured almost two inches long.

9.16 A.M. Wings by this time were folded forward over the under side of the abdomen, hiding abdomen. A second later they flipped back, then forward, meeting across abdomen again.

9.17 A.M. Made first fee ble attempt at stretching wings out a bit and pressing them together. Stretched them only a little more than five inches apart and then placed them together; did this twice in a minute.

9.19 A.M. Wings now twenty-five inches long. Moved mouth parts hastily.

9.21 A.M. Partially unrolled proboscis. Wiggled mouth parts [aborted prothoracic legs] again. Feelers, about five inches in length, which had been lying straight along back were raised five or so upward, that is, away from body.

9.24 A.M. Wings are not increasing in size now. Butterfly curled abdomen upwards. Turned around slightly, rotating on end of old chrysalis to which it still clung.

9.28 A.M. Tried to rotate body.


9.35 A.M. Butterfly seemed more or less at a standstill but bent legs, moved mouth parts, closed wings once in a while, then opened them almost fifteen inches.

9.44 A.M. A drop of brown liquid was produced. Still clinging to chrysalis.

9.51 A.M. Three more drops of brown liquid descended in quick succession.

10.04 A.M. Wings now almost twenty-four inches long.

10.16 A.M. No motion.
10.20 A.M. Butterfly moved from chrysalis to cloth from which chrysalis suspended.

10.21 A.M. Stretched wings 1½" apart. Then 2 or 3 inches apart. I lifted the lid of the coffee jar from which the cloth and chrysalis were suspended, and the butterfly crawled half way out on edge of lid. Then stretched almost fully out. Put him back in jar.

10.24 A.M. No motion.

10.38 A.M. Upon being disturbed slightly, started stretching wings again.

11.39 A.M. Wings same size as last measured. Was very quiet in bottle until I raised lid, when stretched wings frequently to fullest. Noticed feelers were now perpendicular instead of lying along back.

11.49 A.M. Upon being disturbed slightly, started stretching wings again.

11.59 A.M. No motion.

12.00 P.M. After returning from lunch, put the butterfly into an upside-down wastepaper basket of wire and he started walking around on the green blotter the basket was inverted upon. Then started climbing up the wires, working wings vigorously all the while. He stopped to rest at the top of his new "cage" and dropped another spot of brown liquid.

1.40 P.M. Had not tried to fly at all. When ruler was pointed at him he finally fluttered quickly from the top of the basket to half-way down on the other side.

3.29 P.M. When disturbed he not only fluttered to bottom of wastebasket and climbed up to top, but looked around him half-way up, moving his head from side to side decisively.

3.50 P.M. Flew from top of "cage" to the bottom—then half-way up. Left butterfly in basket over night at office.

8.30 next morning. Upon arriving at office found butterfly fluttering in the basket.

The following data concerning the time taken for imago, after leaving the pupal skin, to complete its development, were submitted by F. A. Stricker of Kitchener, Ontario.

<table>
<thead>
<tr>
<th>No. specimens</th>
<th>Time taken for development of imago after leaving pupal skin (Min.)</th>
</tr>
</thead>
<tbody>
<tr>
<td>5</td>
<td>13</td>
</tr>
<tr>
<td>6</td>
<td>14</td>
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<tr>
<td>5</td>
<td>15</td>
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<tr>
<td>4</td>
<td>16</td>
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<td>7</td>
<td>17</td>
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<td>8</td>
<td>18</td>
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<tr>
<td>5</td>
<td>19</td>
</tr>
<tr>
<td>10</td>
<td>20</td>
</tr>
<tr>
<td>4</td>
<td>21</td>
</tr>
</tbody>
</table>

Average: 17 min.

These data, of course, refer only to the time taken for the wings to reach maximum size; they do not refer to the period up to the first flight. Mr. Stricker reports that "The maiden flight is taken two to five hours after emergence."

Miss Ruth Haigh of Niagara Falls, Ontario, submitted the following detailed observations on the time elapsing between the first fracture of the
ADULT 145

pupal skin and the complete emergence of the imago, and also the time lapse from emergence to the full wing development.

<table>
<thead>
<tr>
<th>From first fracture</th>
<th>From emergence to fully formed wings</th>
</tr>
</thead>
<tbody>
<tr>
<td>No.</td>
<td>Min.</td>
</tr>
<tr>
<td>1</td>
<td>45</td>
</tr>
<tr>
<td>1</td>
<td>50</td>
</tr>
<tr>
<td>2</td>
<td>55</td>
</tr>
<tr>
<td>3</td>
<td>1</td>
</tr>
<tr>
<td>1</td>
<td>10</td>
</tr>
<tr>
<td>3</td>
<td>1</td>
</tr>
<tr>
<td>1</td>
<td>20</td>
</tr>
<tr>
<td>1</td>
<td>54</td>
</tr>
<tr>
<td>2</td>
<td>1</td>
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<tr>
<td>1</td>
<td>41</td>
</tr>
<tr>
<td>2</td>
<td>45</td>
</tr>
<tr>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>AVERAGE: 1 min. 17 sec.</td>
<td></td>
</tr>
</tbody>
</table>

After the imago has reached its full development, as measured by wing development, there is a considerable lapse of time before the wings become sufficiently hardened to allow flight to take place. Mrs. L. W. Hobbs of Lathrup Village, Michigan, has submitted the following time observations.

<table>
<thead>
<tr>
<th>No. specimens</th>
<th>Time from complete wing development to first flight</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>1 30</td>
</tr>
<tr>
<td>1</td>
<td>30</td>
</tr>
<tr>
<td>4</td>
<td>2 30</td>
</tr>
<tr>
<td>8</td>
<td>2 30</td>
</tr>
<tr>
<td>12</td>
<td>12 30</td>
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<tr>
<td>18</td>
<td>18 30</td>
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<tr>
<td>18</td>
<td>18 30</td>
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<tr>
<td>16</td>
<td>16 4</td>
</tr>
<tr>
<td>8</td>
<td>8 30</td>
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<tr>
<td>5</td>
<td>5 30</td>
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<tr>
<td>3</td>
<td>3 30</td>
</tr>
<tr>
<td>4</td>
<td>4 30</td>
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<tr>
<td>2</td>
<td>2 30</td>
</tr>
<tr>
<td>1</td>
<td>1 30</td>
</tr>
<tr>
<td>1</td>
<td>1 30</td>
</tr>
<tr>
<td>AVERAGE: 3 hrs. 53 min.</td>
<td></td>
</tr>
</tbody>
</table>

It should be emphasized that it may take as long as seventeen hours before the imago is capable of strong or sustained flight. The following observations emphasize this fact:

Sept. 9 4.55 P.M.: Imago emerged from pupa skin
5.35 P.M.: Wings have reached full length
7.30 P.M.: Wings soft, capable of short flight when disturbed
8.00 P.M.: Wings soft; capable of sustained flight

Sept. 10 9.00 A.M.: Wings still soft but, when released, flew out of sight

It is not unusual to find a Monarch butterfly, in the field, capable of flying a considerable distance and yet the wings may be very soft; in the face of a still breeze such individuals seek protection among the vegetation.

Causes of Wing Distortion after Emergence from Pupa

The occasional pupa may be dislodged from its support and fall to the ground. To test the effect of such an accident on the emerging imago, thirty pupae were placed on the floor of a rearing cage at various distances from the sides. The pupae in all cases were well formed and did not appear to suffer any apparent damage from being in contact with the floor of the cage.

It was found that the amount of distortion of the butterfly varied with the distance from the sides of the cage; those farthest away from the sides suffering the greatest amount of distortion. The reason for this is as follows:

When the butterfly emerges from the pupal skin, the entire body is very soft; the wings begin to expand immediately on emergence and, regardless of the position of the butterfly, continue to do so; as the butterfly crawls over the floor of the cage in an attempt to reach the sides, the wings fall loosely and thus expand irregularly. A pupa situated close to a side of the cage allowed the emerging imago to secure a firm hold, with the wings expanding in a vertical direction and thus eliminating distortion. An imago emerging far from the sides of the cage would have a considerable distance to travel, thus giving a greater amount of distortion to the expanding wings.

These observations may be correlated with the great number of imagos with distorted wings which are found in the late fall when pupae attached to deciduous leaves fall to the ground.

Relative Abundance of Males and Females

In the course of our rearing experiments, a record was kept of the number of males and females for two hundred specimens. It was found that there were 102 females and 98 males, or approximately a 1:1 ratio. Collecting in the field gave conflicting results, varying from 68 males and 1 female in one area, to 32 females and no males in another. To examine the reason for this discrepancy, observations were carried out over a period of three years during mating and oviposition.

The particular field chosen was ideally suited for studying this problem (Plate I). It was approximately twelve acres in area, of which approximately seven acres were hay-cropped and five acres left in a pseudo-natural state (there was a limited amount of grazing). The cropped area consisted of cut grass, small pasture plants, and milkweed shoots. The uncropped area sup-
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ported a dense growth of grass, milkweed, and tall flowering plants. Observations were made in the central portion of each section. The results for recorded specimens were, 128 females and 12 males in the hay-cropped area; 86 males and 42 females in the uncropped area. With respect to the males and females present in the uncropped area, variation in relative numbers occurred throughout the day. The following counts for one day indicate the variation that occurred in the uncropped area:

<table>
<thead>
<tr>
<th>Time</th>
<th>Males</th>
<th>Females</th>
</tr>
</thead>
<tbody>
<tr>
<td>8 A.M.--10 A.M.</td>
<td>12</td>
<td>0</td>
</tr>
<tr>
<td>10 A.M.--12 A.M.</td>
<td>8</td>
<td>3</td>
</tr>
<tr>
<td>12 A.M.--4 P.M.</td>
<td>14</td>
<td>8</td>
</tr>
</tbody>
</table>

The following counts for one day were made in the cropped area:

<table>
<thead>
<tr>
<th>Time</th>
<th>Males</th>
<th>Females</th>
</tr>
</thead>
<tbody>
<tr>
<td>8 A.M.--10 A.M.</td>
<td>0</td>
<td>42</td>
</tr>
<tr>
<td>10 A.M.--12 A.M.</td>
<td>0</td>
<td>36</td>
</tr>
<tr>
<td>12 A.M.--4 P.M.</td>
<td>0</td>
<td>12</td>
</tr>
</tbody>
</table>

As explained in chapter IV, if counts are made in a field, or portion of a field, where flowering plants are absent but small milkweed are abundant, then more females will be recorded than males, because of the oviposition habits of the females. If counts are made in a portion of a field where flowering plants are abundant and at a time when females are ovipositing in another part of the field, then more males will be recorded than females. The increase in proportion of females to males in such an area will vary throughout the day, depending upon the feeding periods of the females. If the field supports a mixture of flowering plants and small milkweed plants than there will be approximately as many males as females. We may conclude therefore that the ratio of males to females is 1:1, but that this ratio will vary according to ecological conditions and the feeding-ovipositing habits of the females.

MATING HABITS

Field Observations

During the breeding season the males pursue the females and, at times, will pursue other butterflies. We have recorded pursuit of the following species of butterflies: Speyeria aphrodite; Nymphalis antiopa; Vanessa atalanta; Limenitis arthemis; Limenitis archippus; Papilio glaucus; Papilio polyxenes. Although there were many species of butterflies present in the field under observation, only the larger species that were in direct fight over the field were pursued. Males were also recorded as pursuing a chipping sparrow, a song sparrow, a leaf, and a piece of paper—the latter two objects blown by a dust devil.
Julius Meyer (1879) records the following observation with respect to the pursuit of a humming-bird by a Monarch butterfly which was resting beneath the flower of an *Asclepias*:

Scarcely had I observed it [humming-bird] than out rushed the butterfly and furiously attacked the bird, which in an instant sought safety in precipitate flight, followed closely by the insect till lost to view in the distance. Amazed at so strange a spectacle, I stood upon the spot, gazing in the direction where they had disappeared for some five minutes or more, when to my surprise and pleasure I saw the butterfly coming back, which, when near the flower flew in a wide circuit around it, as if to ascertain whether another enemy had taken possession of it or not. Then lessening its flight it finally ventured upon the flower again; but being much agitated walked nearly all over the plant repeatedly until it finally settled upon its chosen place for its nightly rest.

*Examination of the Scales*

The accompanying drawings (Fig. 38) of the various scale configurations were made by using a microscope equipped with a camera lucida and hence represent fairly accurate outlines as well as being of the same magnification. The scales on the membrane of the wing are oval in shape, and the apices smoothly rounded or slightly serrated or notched. The scales on the veins of the wing are elongate. The scales located on the top of the so-called scent gland are similar in shape to those found on the wing membrane, but they are much more numerous and form a dense mass. Approaching the slit-like opening to the gland the scales of the wing membrane become more elongated and those possessing serrated or notched apices tend to become more numerous. Within the cavity of the gland the scales are much smaller, black in colour and with slight to decidedly serrated apices. These small black scales have been referred to as "scent scales" or *androconia*. In addition to these numerous and closely arranged black scales, there are also a few hair-like scales.

*Examination of Scent Glands*

By embedding the portion of the wing bearing the scent gland taken from a freshly killed specimen (not a preserved one) in paraffin, it is possible to make a transverse section through it so as to view the parts in relation to each other. This is shown in the accompanying illustration taken from a camera lucida drawing (Fig. 39). The membrane of the wing, located next to the second cubitus vein (1) is folded in such a manner as to form a pocket with a narrow slit-like opening (2). There is a small opening (3) between the cavity of the second cubitus vein and the cavity which is enclosed by the upper and lower wing membranes (4) and now forming the roof of the gland. The chitinous membrane (5) of the roof of the gland is of the same thickness as that of the adjacent vein, and it remains thick until after it has
Figure 38. Scales 1–6 from wing membrane near opening to scent receptor; 7–8 from exterior roof covering of scent receptor; 9–11 from central area of wing; 12 from top of wing vein; 13–15 from inside of scent receptor.
Figure 39. A, transverse section through scent receptor of right rear wing (explanation of numbers given in text); B, left lateral view of male Monarch showing position of tip of abdomen in relation to scent receptor; C, structures located within the cavity of the scent receptor; D, anal scent gland partly extruded; E, anal scent glands fully extruded.
curved into the cavity of the gland, at which point (6) it becomes extremely thin—so thin, in fact, that it is difficult to detect in gross section. This flap-like portion may be referred to as the lip. This very thin membrane forms the wall (7) of the receptor cavity. It will be noted that it becomes thick again just prior to union with the wing membrane (8).

Attached to this thin membrane and with peg-like bases that penetrate it, are numerous small black scales set into goblet-like structures that might be termed poscoclula from the Latin, meaning a goblet (Fig. 39). There are also a few hair-like scales that are set into minute pores located in the centre of saucer-like structures that might be termed patellae from the Latin, meaning a saucer. Many of these patellae do not possess scale-like hairs. The thin membrane lying between the poscoclula and the patellae is thrown into shallow irregular folds.

A fluid which appears to originate in the second cubitus vein passes through the minute opening (3) and fills the cavity (4) where it becomes transformed into a white, spongy, wax-like substance. If the second cubitus vein, or the roof of the gland, is punctured with a fine pin, the fluid will flow out and, on coming in contact with the air, will form a white, wax-like covering on the pin identical to that found on the floor of the gland. If the gland taken from a live male is dissected under the microscope it is quite easy to remove the white, waxy substance from it. If this substance is placed in chloroform it immediately dissolves, exhibiting no apparent cellular structure.

**Position of Scent Glands on the Wing**

Although there are many places on the front and hind wings where the scent glands might have been located, it is interesting to note that they are on the upper surface of the hind wings in a position such that they can readily be touched by the apex of the abdomen, as indicated in the accompanying illustration drawn to scale (Fig. 39). The scent gland, which is a pocket-like structure, has a slit-like opening that faces the abdomen. If the abdomen of the male is squeezed gently, so as to cause the anal glands to be partly extruded, the cluster of hairs can be made to brush past the slit-like opening by bending the abdomen sideways when the wings are partly spread, or by bending the abdomen upwards when the wings are folded together vertically.

If the tip of the abdomen is squeezed, a drop of clear yellow liquid can be forced from the anal scent gland. Using a dissecting pin, the drop may be transferred from the anal scent gland to the entrance to the scent gland. Within a few seconds the drop will pass into the pocket, being directed by the scales at the entrance, and be absorbed. Dissection of the gland indicates that the black scales within have become coated with the fluid and that it was partly absorbed by the wax-like material beneath.
It is a pleasure to submit the following hitherto unpublished paper by T. H. Priddle of Calgary, Alberta. It is included in the present work because Mr. Priddle’s observations are similar in many respects to those presented for the Monarch butterfly and hence indicate a pattern of behaviour which may be common to many species of Lepidoptera.

Until comparatively recent times little has been written concerning the habits of courtship and mating of butterflies. Perhaps the most constructive suggestion in this field was the one made that male butterflies possess a certain area of loosely attached scales capable of producing a sex-stimulating odour. Each species was considered to have its own peculiar odour which would stimulate only a female of the same species, thus ensuring that correct pairing was achieved. My own observations, however, do not support this theory, and the following is an attempt to review this, perhaps the most important and interesting phase in the insect’s life, from a rather different viewpoint. The subject is not one which lends itself readily to description in print and for convenience I have found it necessary to deal with the various aspects separately before considering the picture as a whole.

Male Activity

With respect to sex activity, males can be divided into two groups: Group 1 comprising those families in which the male seeks a mate at rest, and group 2 in which the male can locate a female only while on the wing. To simplify matters, I have selected the small cabbage white and the small tortoiseshell as illustrative examples of each group. Strictly speaking, although the small white quite definitely belongs to the herbage-searching group, many males do find their mates on the wing. However, I consider this as only a minor deviation and therefore, in view of its suitability in all other respects, have chosen this species in preference to more rigidly governed species such as the marbled white, which is of local distribution and therefore not so readily studied as can be the small white.

1) The small white may be seen at almost any time of day endlessly patrolling the vegetation, usually following the line of least resistance and hesitating to surmount obstacles which rise sharply to any height. Evidence indicates that, although moving objects are readily discerned, its definition even at close quarters is poor. Yellowing leaves, fragments of white paper, and even small white flowers, will momentarily provoke sexual excitement as witnessed by its rapidly hovering flight as it pauses to investigate. Other males of its own species, on the wing, serve only as a temporary distraction and, once identification is established, each returns to its endless quest. Male activity normally increases with age and of course is influenced by temperature variations, and the daily peak is reached during the late afternoon and early evening.

2) The small tortoiseshell usually selects some elevated vantage point, perhaps a leaf in a hedgerow, or often a spot on a warm brick wall or fence post. In open country a barren patch of sun baked earth may be utilized. With wings outstretched it will often rest for long spells, apparently enjoying the warm sun, rising occasionally to patrol its territory, but always returning anon to its favoured position. In fact, it is waiting, patient and ever alert, for a female to pass by. As the position of the sun changes, so does the insect reorientate itself, ensuring that the sun is always behind it. Thus the presence of a butterfly passing from behind, and in the sun’s glare, is always “telegraphed” ahead by its shadow. One might expect butterflies of this group to possess good vision. However, the fact that
small birds such as sparrows are pursued with the same zeal that a female of the species would command, indicates that it is little better than that of their fellows of the preceding group.

The Virgin Female

It cannot be said that the virgin female shows any tendency to locate a mate. On the contrary, males are pointedly avoided wherever possible. Of the vast numbers of female whites to be observed at the vegetable plot on a warm summer day, few, if any, are virgin. They are more likely to be flushed from some conceal ing foliage, the flowering broad bean being a favourite, from which excursions for food are made with caution. The female tortoiseshell, like others of this group, is certainly less prone to the skulking habits of the white. However, as the males are not capable of pressing their attentions while the female is at rest, it is conceivable that camouflage is unnecessary.

The Fertilized Female

As soon as a female has been fertilized her main task is to locate the larval food plant and deposit the eggs. Egg-laying commences as soon as the sun has warmed the air sufficiently for activity to begin, and carries on at a steady pace until shortly after noon, when the females make their way to suitable cover such as waste ground, where they quietly rest and occasionally feed. Should the commencement of warm sunny conditions be postponed until noon or later, the egg-laying period is invariably curtailed, depending largely on the rate of temperature increase. There can be little doubt that the disappearance of the females, which is quite sudden, is noticed by the males, as the extreme tenacity with which the occasional passing female is pursued contrasts sharply with the half-hearted attention paid prior to mid-day.

The Act of Pairing

Pairing usually takes place once in the lifetime of a female, although a male may take several mates if the opportunities arise. To achieve union it is necessary for the male to adopt a position immediately alongside the female, which rests with wings closed. The male then curves the tip of its abdomen laterally to meet the sex organs of the female which, normally concealed within the abdomen, are protruded when the insect is stimulated. The pincher-like extremities of the male's abdomen are used to grip the female.

Stimulation of a female white at rest is generally of short duration, the male simply hovering directly overhead for a few seconds before alighting. When initial contact is made in flight, a more lengthy procedure is observed. The male takes up a position below and slightly to the rear of the female, and changes its pattern of flight to a short and erratic zig-zag design, which is quickly imitated by the female. The sweep of this pattern becomes more and more pronounced, the couple moving in union with the female now leading, until, after they have chosen a suitable resting-place, the gyrations become smaller and smaller until the couple alight. Invariably the pair makes a short flight immediately after pairing, the female hanging head down with wings closed, thus, on alighting again, the insects are facing in opposite directions. With this particular species while paired only the male uses its wings.

A female tortoiseshell passing through the territory of a male is pursued with extremely rapid and direct flight. The male does not make any apparent effort to
overtake the female, and the pair will often fly considerable distances with the male always just a few inches behind, this despite the fact that the speed of the female varies constantly. Eventually the female settles, in most cases in the open, either on the ground or on low herbage. She may settle with wings either closed or pressed flat. Usually at this stage they will be opened out. The male never hovers over the female, but settles a few inches behind her, and with wings outspread can be seen to be trembling quite violently. Inevitably the male approaches the female, slowly and hesitantly. If during this time she has closed her wings, the first movements of the male will induce her to open them again. Still the male advances until in some cases I have known it to tread upon the female's wings. Then quickly she flutters into the air to alight at a short distance, where the whole procedure is repeated. Eventually the pair adopt a brief zig-zag pattern of flight close to suitable low cover. The female alights and threads her way carefully through the plant stems and comes to rest, with the male close in attendance. Union is achieved with both insects pointing head down, and both are almost incapable of movement, even when agitated—a fact which probably explains the desire of the female to seek a place of concealment.

The Anti-male Device

It has already been stated that a female normally takes but one mate in her lifetime. However, in the course of her egg-laying duties she will certainly meet many males each intent on securing her, and evidently some method of identification must be used to ensure that she may be allowed to carry out her task with a minimum of interference. This I have termed the "anti-male" device. A female white on being approached by a male while she is at rest, immediately depresses her wings fully, and, in the event of her being settled upon a grass blade or narrow stem, may even cause the outer edges of the wing tips to touch. At the same time, the abdomen is elevated to the vertical position, and as in the case of a virgin female, the sex organs can be seen protruding from the abdomen. Usually the male balks at this display and moves on. However, at peak "male activity" periods, he may alight and attempt to achieve union, which, due to the lack of vertical flexibility of his abdominal extremities, he is wholly unable to do. In desperation he may force the female into flight, attempting to induce her to adopt the mental flight pattern. She reacts by pointing almost vertically upwards, and with a hovering, laboured flight ascends slowly in a gentle arc. Pairs often rise to a considerable height in this manner, but always the male is forced to admit defeat and to fall earthward, the female remaining aloft for a few moments before following. Butterflies of the group which make contact only in the air have no need for the resting device described, and it is therefore never exhibited; but, allowing for the different mode of flight, which is much more direct and rapid, they observe the same procedure in the air.

Mutual Identification

It is obviously necessary for males to be able to differentiate not only between virgin and fertilized females of the same species, but also between their own sex and other species. The male always endeavours to adopt a position below and to the rear of the female; thus when two males meet in flight with each trying to arrive at the same position in relation to the other, the pattern quickly evolves into a wild "over and under" type. The participants quickly realize this error and soon go their separate ways. Should a male white at rest be approached by another, be
ADULT responds with a rapid shuffling wing motion, outwards and slightly forward, which
is always quickly understood by the investigator. Female butterflies generally
keep to themselves. The only exception deserving comment concerns the older
fertilized females. Frequently when two of them meet at the larval food plant,
one will pursue the other with a shallow imitation of the male pattern. After a
short time the roles may be reversed, but these antics are always of short duration.
Certainly a female nearing the end of her reproductive capacity is noticeably more
masculine in demeanour. I have noted occasions when a female having at first
discouraged a male with the fertilized flight reaction, impulsively pursed him
when he sought to break off the encounter, only to give the same negative
reaction when interest was renewed.

Behavior in Captivity
Unfortunately the majority of our butterflies are most uncooperative in captivity.
The cabbage white is one exception to this rule and if handled frequently and
considerately will become quite indifferent to the observer. This species was
therefore chosen as the subject of one or two simple experiments to test a theory
of visual flight pattern stimuli and reaction which had been formed from field
observations. The following facts emerged:
1) The change from virgin to fertilized flight pattern is quite sudden and
irrevocable. Females were separated from their mates at varying intervals, and the
longest period of mating after which the virgin flight pattern could still be induced
was thirty minutes, although some gave the fertilized reaction after only five or ten
minutes. Normally of course mating lasts some four to five hours, and it is of
interest to note that the ovaries, previously soft and small, become grossly enlarged
and feel quite hard to the touch during this short period.
2) Within the confines of a jar a female will respond to either male or female
activity without distinction. Furthermore, a reaction can be obtained by rubbing
two fingers together immediately over a female to simulate the hovering flight of
a male.
3) If a female is separated from a male by a sheet of glass a reaction is still
obtained, providing that the insects are in close proximity.
4) A number of males confined in a jar with a single female precipitate no
reaction by movement other than flight activity. It is important to note that
immediately such activity ceases the female adopts the normal resting posture
once more. Assuming that the "scent scales" theory is correct, one might suppose
that a number of males confined in a jar would sufficiently saturate the atmosphere
to induce a constant reaction from the female.
5) The "scent scales" of the male are easily shed and therefore older males
possess fewer in number, yet owing to their greater activity and more controlled
flight these produce a more rapid and positive reaction even when further from the
female. I would add that the experiments were repeated on many occasions, fresh
insects being used each time. As the reactions of the fertilized females are more
readily observed, these were used mainly, virgin females being used only once
as a check. It is not possible to induce a male after it has been handled to adopt
the hovering flight normally associated with stimulation at rest. The "flight activity"
referred to is merely that produced by agitation.

Conclusion
I feel that already the evidence is sufficient to warrant serious consideration of
the physical pattern and response behaviour pattern which I have endeavoured
to trace. Unfortunately I have not as yet been able to experiment with "deodorised" males, though this would seem to be the most conclusive test. Many observers are able to distinguish family groups and even individual species by their flight characteristics. It is my opinion that the subtle difference in both rate of wing beat and wing action itself is the identifying and stimulating factor. It will have been noticed that many closely allied forms have, in addition to similar markings, also similar characteristics of movement. One might therefore expect mutual stimulation to occur between these species, as indeed it does. The illustrative examples used in this text probably serve as the best examples. I have noticed male tortoiseshells going through the preliminary nuptials with female red admirals, commas, and peacocks, and the small white frequently with the green-veined white, and large cabbage white. These encounters seldom get beyond the early stages and never have I seen the participants even approach the act of union, although the Nymphalidae, having a more prolonged period of courtship, probably have the greatest difficulty in finding that an error has been made.

It is my hope that these notes may stimulate some further research into this matter and that perhaps these findings may be verified independently.

Discussion

Housman (1951) made a rather careful examination of the scent organs of the Monarch butterfly and his conclusions may be summarized as follows: The scent organ of the Monarch butterfly is a slightly elevated black pouch about three millimetres in length and one-and-one-half millimetres in width; the dark scales which cover it are similar to those found in the dark areas of the wing. The cavity of the sac is lined with tiny black overlapping scales which are much smaller and more delicate than the surface scales and more heavily pigmented, and are termed scent scales or androconia. The inner wall of the sac itself is thin, yellowish, and with regularly arranged circular areas, so-called scent cups; each scent cup is covered with a thin cuticle bearing a minute central pore from which extends an extremely narrow, hair-like scale, similar to a seta. Fitted into such pores are the scale stalks or pedicels in contact with the unicellular gland cells of the epidermis; in areas between the cups are pits in which the pedicels of broader scales are located. These two types of scales give off characteristic odours and would account for the term scent scales and for reference to the sac as a scent gland or an area of "sensory scales." Secretions from specialized gland cells escape in the regions of the pedicels to coat the surfaces of the scales, and thus these modified insect hairs serve as outlets for all secretions. The secreting substance has a faint, fragrant odour likened to the sweet milkweed blossoms; it may serve, in function, as a sex stimulant in that it is attractive to the opposite sex. This author does not indicate how he was able to detect the presence of a secretion on the scales or pin-point the origin of the aroma.

Longstaff (1912) translated Fritz Müller's papers dealing with hair tufts, felted patches, and similar structures on the wings of male Lepidoptera. The following statement concerning Danaus gilippus and D. erippus is sig-
significant in the present discussion: "It is not possible to detect any odour arising from the wings of the males of either of the two species found in the Province of S. Catharina. . . . If one strongly compresses the abdomen, there is exerted on each side of the last segment a finger-shaped membranous tube with closed apex, which is covered with dark hairs, erected as the tube passes out of the abdomen, and exhaling at the same time a somewhat strong odour in \textit{D. crippus}, and one less strong though still perfectly distinct in \textit{D. gilippus}." The author further points out that it "appears extremely unlikely that such a function [namely the production of scent] would be exercised by a cavity communicating with the air only by a narrow slit, and, in addition, having apparently no mechanism on the wing by means of which it could be opened."

Doubleday \textit{et al.} (1846) pointed out that in some males of \textit{D. crippus} a small portion of the wing, close to the orifice of the sexual cavity, is denuded of scales as if they had been repeatedly rubbed away by introducing something into the slit.

Some authors have suggested that the glands may be rudimentary in function because of the development of the abdominal scent glands, and others that the substance produced by the glands is transferred to the tip of the male abdomen (Müller, 1871).

In many species of \textit{Lepidoptera} there are no sexual pouches similar to those found in the danaids, but there are patches of modified scales or hairs on various parts of the wings or, in some cases, on the thorax. \textit{Epicalias acontius} possesses a felt-like patch of scales on the lower surface of the front wings which, when at rest, lies over a similar patch on the upper surface of the hind wings. \textit{Myrcella orias} males possess a similar felt-like patch on the upper surface of the hind wings. In the \textit{Ithomysis} a tuft of long hairs is located near the front margin of the hind wings of the males which apparently emits a vanilla-like odour. In \textit{Prepona}, one of the Nymphalinae, there is a similar tuft of black hairs on the hind wings of the males. The males of \textit{Thaumantis}, a genus of Morphinae, have similar tufts of hair on the upper surface of the hind wings near the base. In species of \textit{Antirrhea}, one of the Satyrinae, the males are said to produce a strong odour from a patch of scales located on the hind wings at the anterior base of the upper surface, which is covered by the fore wings and protected by a covering mane of pale buff hairs. \textit{Stichophthalma} (Morphinae) has a patch of modified scales and an erectile wisp of hairs on the hind wings of the male. A species of \textit{Ageronia} (Nymphalinae) possesses two large brown spots situated between the wings, where they oppose each other; this appears to be associated with emitting a scent. In \textit{Leptalis} (Pierinae) there is a patch of scales associated with producing a scent on the portions of the front and hind wings which conceal each other. In the case of \textit{Melete} the odour is
most pronounced when the wings are opened; when the wings are closed the odour is retained. It is interesting to note that, according to Scudder (1889) Aurivillius “looks askant at the so-called scent scales described by Fritz Müller because he could detect no odour from Mancipium brassicae even though large androconia were present.” Barth (1957) describes “odoriferous organs” situated in the intersegmental membranes of the eighth and ninth abdominal segments in Metalobosa cuprea and similar glands as well as “glandular areas” on the posterior edge of the dorsal surface of the hind wings of Ilice fasciata. Although the author is of the opinion that the scales on the wings are glandular he does not indicate the presence of glandular tissue nor does he demonstrate that a secretion of any kind is produced by such areas. He indicates, however, the presence of a large darkly staining body associated with each scale, which he terms a gland cell (druesenzellkern) which is located in the matrix beneath the glandular scale both in the wing glands and in the scales of the abdominal glands of I. fasciata. The space beneath the scale, which the author has termed a “sektetsammelraum,” might be just as easily interpreted as a lacuna into which a secretion may accumulate, having been directed by the scale from the outside inwards. Likewise, the “strahlenfigur” may direct the secretion throughout the matrix rather than from the matrix to the lacuna and hence to the outside.

From the above it would appear that the anal glands of the male produce a secretion which has a flower-like aroma, but there seems to be little evidence to support the suggestion that a secretion with a flower-like aroma is produced by the wing scent glands and/or scent scales. If such scales did produce an aromatic secretion, it would be difficult to explain the reason for the presence of two such mechanisms, namely, anal glands and androconia.

We have observed that the female does not appear to be attracted to the male by some pleasant aromatic perfume, but that the male pursues the female. We have pointed out, and it has been suggested by others, that the wing scent glands are placed so as to allow contact with the scent glands at the tip of the abdomen of the male, and we have demonstrated that a secretion from the anal glands is absorbed by the wing scent glands. In so far as the Monarch butterfly is concerned, then, the so-called scent glands of the wing are, perhaps, scent receptors that receive the odoriferous fluid from the anal glands which is absorbed through the pores at the bases of the poscula and patellae into the spongy matrix beneath.

**OVIPosition**

When the female deposits her eggs upon the leaves of the host plant, a considerable amount of selectivity is exercised. As will be indicated in the
following data, only healthy plants are chosen; small plants are preferred to large plants, and small leaves are preferred to large leaves (Fig. 40). In addition, the egg is usually deposited on the underside of the leaf in a fairly restricted area.

In a pasture field that was quite heavily grazed there was a mixture of tall milkweed plants possessing flower heads and small seed pods, second growth plants between one and two feet in height, and a great many seedling or gemmiferous plants 3"-8" in height. The observations were made in August at a time when the first early summer generation had passed and
butterflies were not commonly seen. A careful examination of every leaf on
a selected number of milkweed plants was made, with the following results.

400 plants possessing flowers, and seed pods in some cases, yielded
1 larva.

200 plants without flowers or seed pods and of medium height yielded
2 eggs and 1 larva.

400 small plants less than one foot in height yielded 74 eggs and 12
larvae.

In September a second count was made of large and small plants. At this
time larvae and adults were abundant. The following results were obtained:

200 large plants possessing small seed pods yielded 33 larvae but no
eggs.

200 small plants yielded 3 larvae and 12 eggs.

The larvae found on the large plants were in the third to fifth instar.

The larvae found on the small plants were in the first to second instar.

It would appear that the larvae migrate from the small to the large plants,
and oviposition is, for the most part, on the small plants.

The following observations on this subject were submitted by our co­
operators.

Observations seem to indicate that early in the season the eggs are laid in the
majority of cases on the top of the milkweed plant, often on the tight, undeveloped
bud masses, often on the leaflets immediately adjacent to the bud masses, and
seldom on the larger leaves. As the season progresses and bud masses loosen, eggs
are no longer found in these locations, but are laid on the main leaves. The eggs
then are to be found almost anywhere on the leaves of the plant. [H. F. Stiles.]
I collected 14 larvae that were half to full grown and all of them were found singly on milkweeds a foot or less in height. [L. Beanier.]

Statistics were kept on 100 eggs found between July 26 and August 3; 62% were found on 54 plants with no flowers or seed pods; 33% were found on 16 plants in flower; 5% were found on 3 plants with tiny pods. [Mrs. B. Johnston.]

Mrs. J. Senghas found that out of a total of 97 eggs and first instar larvae collected, 37 were found on plants more than one foot in height and 60 were found on plants less than one foot in height. Mrs. L. W. Hobbs found that out of a total of 58 eggs collected, 48 were on seedling or second growth plants, 4 on flower buds and 6 on medium-sized plants.

To obtain eggs for rearing experiments, a number of females were placed in a large rearing cage inverted over a milkweed plant. As the eggs were removed, observations were recorded as to the number of eggs found on the leaves of the upper half as compared to the lower half of the plant and the position of the eggs on the leaf.

For a total of 250 eggs, 38 were found on the upper surface and 212 on the lower surface, or 15 per cent on the upper surface and 85 per cent on the lower surface. In one of our rearing cages, out of a total of 250 eggs, 182 were located on the leaves of the upper half of the plant as compared to 68 on the leaves of the lower half, or 73 per cent on the upper half and 27 per cent on the lower half.

Observations made while collecting eggs in the fields seemed to indicate that there was a definite tendency for the female to deposit the egg near the base of the leaf. Dividing the leaf into three sections, namely, apical third, middle third, and basal third, the following data were recorded from field observations for a total of 39 eggs: basal third, 27 or 69 per cent; middle third, 9 or 23 per cent; apical third, 3 or 8 per cent.

The following observations on this subject were recorded by our co-operators:

It appears that approximately 25% of the time [the eggs] will be found on the upper surface of the leaf, and 75% on the under side of the leaf. It appears that as the season progresses, more and more the eggs are laid on the under side of the leaves, until by mid-August no eggs were found on the upper surfaces. [H. F. Stiles.]

Mrs. J. Senghas found that out of a total of 48 eggs collected, 40 were found on the lower surface and 8 on the upper surface of the leaf, or approximately 83 per cent on the lower surface and 17 per cent on the upper surface. Mrs. Bette Johnston reports that "97% were found on the under side of the leaf, and 3% of the eggs were found on the top side of the leaf." Mr. E. McDonald collected 18 eggs all from the under-surface of the leaf.

Numerous field observations have indicated that two eggs are rarely found upon the same leaf. Also, eggs are not deposited upon leaves infested
with aphids or on leaves of unhealthy plants (those apparently attacked by some sort of virus disease that causes stunting of leaf growth and development of a yellowish colour).

The female apparently uses her tarsi for selecting a suitable plant and leaf upon which to deposit her eggs. She can be observed flying close to the vegetation, with legs outstretched, occasionally touching a particular weed, until a suitable milkweed plant is found. That the female will deposit an egg on any leaf surface, so long as she is grasping the milkweed plant, was indicated by gently placing the leaf of a foreign plant between the tip of the abdomen of the female and the milkweed leaf (Fig. 24). When the tip of the abdomen touched the foreign surface an egg was deposited. A gravid female was held near a milkweed plant without any response. When the second pair of legs touched the plant, the abdomen was immediately arched in the characteristic oviposition attitude, and an egg was deposited. A gravid female was placed on a potted clover plant and the tip of her abdomen was touched by a milkweed leaf. There was no response but when the butterfly was placed on the milkweed leaf, she deposited an egg upon the stem of the clover plant.

Field observations supported the above records: on one occasion an ovipositing female came to rest upon a small (5") milkweed plant next to a large dandelion plant, a leaf of which extended beneath the leaf of the milkweed plant upon which the female was located; the female deposited her egg upon the leaf of the dandelion plant.

A female was observed ovipositing and the time interval in seconds between two successive egg deposits was recorded. The female would alight upon many plants without depositing an egg, even though she curved her abdomen under the surface of the leaf and remained in this position for two or three seconds. If on examining the leaf an egg was found, then the time interval to the finding of the next egg was recorded.

<table>
<thead>
<tr>
<th>Time interval in seconds</th>
<th>Frequency of eggs deposited</th>
</tr>
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<tbody>
<tr>
<td>20</td>
<td>1</td>
</tr>
<tr>
<td>45</td>
<td>9</td>
</tr>
<tr>
<td>60</td>
<td>16</td>
</tr>
<tr>
<td>80</td>
<td>4</td>
</tr>
<tr>
<td>90</td>
<td>2</td>
</tr>
</tbody>
</table>

From these data it is seen that the average time interval is 59 seconds, and that the most frequent time interval is 60 seconds.

Following the above series of observations, the female came to rest for a period of ten minutes, during which time she remained with her wings partly spread; upon being alarmed, she flew to a group of small plants and in another three minutes had deposited two more eggs. She then came to rest again and at the end of twenty minutes flew away.
Not only did the female deposit her eggs upon small plants exposed in the open field, but she also sought out small plants that were completely surrounded by tall grass. In order to deposit her eggs upon such plants, it was necessary for her to crawl through the grass. It is quite likely that much damage was done to the wings as a result.

When the female comes to rest upon a milkweed plant, she bends her abdomen in an arc so that the tip comes into contact with the under-surface of the leaf (Fig. 23). Depending upon the position of the thorax on the upper surface of the leaf, the abdomen may reach a distance of 2 to 19 mm. The length of the abdomen of fifty females was measured, giving an average length of 17 mm. If half of the abdomen is curved beneath the leaf the egg would be deposited at a distance of 8-9 mm. On numerous occasions, however, more than three-quarters of the length of the abdomen was placed...
beneath the leaf, thus allowing the egg to be placed closer to the central area near the midrib. In most cases, the female will grasp the leaf near the base because a firmer hold can be obtained on the petiole of the leaf or on the main stem in the case of small plants. This accounts for the egg being placed near the basal third of the leaf. Eggs found on the small leaves surrounding the flower head are, in most cases, located on the upper surface. This is explained by the fact that the female grasps the surrounding small leaves or flower cluster, hence the tip of the abdomen touches the upper surface of the leaf.

In the accompanying frequency graph, the number of eggs is plotted against the distance from the margin of the leaf where the eggs were deposited (Fig. 41). The range varied from 0 (or from the margin of the leaf) to 23 mm., with the maximum frequency between 5 mm. and 18 mm.

Observations on the time required for oviposition, when the tip of the abdomen came into contact with the leaf, varied from 2 to 5 seconds, with an average time of 3.2 seconds.

The flight pattern of the ovipositing female is characteristic: the legs are extended; the wings are not completely spread; the flight is slow, regular, and within a few inches of the top of the vegetation. In a given direction, flight is altered from side to side of the mid-line, as shown in the accompanying diagram (Fig. 42). In this manner a complete reconnaissance of the field is made. In the majority of cases, flight during oviposition was carried out against the wind. This slows down the forward rate of movement and thus permits a more exact survey.

![Diagram of flight pattern of ovipositing Monarch butterfly.](image)
That the females tend to remain in a particular field for some considerable time is indicated by the fact that an ovipositing female was tagged on August 4 and was recovered in the same field on August 16. On another occasion, however, a female tagged at 10 A.M. was recovered at 12 noon but intensive collecting over a period of four hours failed to recover it a second time.

Mr. C. A. Anderson, who has reared many thousands of Monarch butterflies, has informed us that mating takes place seven days after emerging from the pupa; oviposition commences the day following mating; males and females have a life span of forty days in captivity; and that a female in captivity will lay 100 eggs on the first day, 125 on the second day, and 75 on the third.

Mr. R. H. Rogers reported mating taking place the day following emergence from the pupa: "The very next day after releasing nos. 1705-6-7 [Aug. 9], which had hatched on Aug. 8, they were still around the milkweed patch. One of the tagged butterflies mated with one of the other tagged ones."

Number of Generations

The number of generations that may occur in any given area depends upon: (1) the time of return of the migrant female in spring and early summer; (2) the prevailing temperature during the breeding season; and (3) the time-span of the breeding season.

A female returning in April or early May to the central area of the United States will produce an earlier brood of larvae than one returning to Canada in late May or early June. Warm temperatures in early spring will produce earlier breeding records than will cold temperatures and warm summers will produce more generations than cold summers. If warm temperatures prevail into fall and early winter, more generations will be produced than if cold temperatures prevail because the time-span of the breeding period is determined by the temperature condition in the spring and fall.

First Appearance of Adults

The following information was received from our co-operators from various parts of the United States and Canada with respect to the earliest dates when Monarch butterflies were observed:

Mrs. J. Hagar of Rockport, Texas, reported collecting a female on April 24, a male on April 27, a male on May 2, a female on May 12 and a female on July 8. "The July female was a battered specimen but still flying. I was unable to find any in June and August and only the single specimen in July."

S. H. Clark of Palacios, Texas, writes as follows: "I saw 3 Monarchs here on March 17th. They were feeding on the blossoms of the chinaberry tree and they
were the first I had noticed since last fall. They became quite numerous by March 29th and I could see dozens of them at a time. From March 30-31 only a few scattered individuals were to be seen. It seems as if they had moved on.”

E. Schuchard of San Antonio, Texas, reports the following first occurrences: March 26, 1 specimen; April 5, 5 specimens; April 10, 2 specimens.

Mrs. D. A. Crossley of Brownsville, Texas, writes as follows: “[On April 14] my husband made a trip to central Texas. He found literally hundreds of them flying across the road, into windshields, just everywhere. They had reached the country up around Austin.”

Lawrence S. Dillon of College Station, Texas, reports as follows: “I am forwarding a Monarch captured while feeding on spirea on March 17, the only one observed. However, on March 7 a specimen was observed sailing northward on a steady warm south wind, going too fast for capture.”

C. A. Anderson of Dallas, Texas, reports as follows: “The females appeared March 27 and remained for two days.”

Mr. Bryant Mather of Jackson, Mississippi, reports seeing Monarch butterflies on March 8 and 27, and copulating pairs on April 2.

L. Harris of Atlanta, Georgia, reports as follows: “On March 17 Mrs. Harris was in New Orleans and observed Monarchs flying about in the yards and grounds in the suburbs. On March 18 she drove along the Gulf of Mexico to Mobile, Alabama, and saw a few Monarchs along the way, including some on the famous Bellingrath Gardens near Mobile. After leaving Mobile and heading northward toward Atlanta she did not see any more Monarchs.”

John Symmes of Atlanta, Georgia, reports as follows: “Have made 22 collecting trips and have observed only 2 Monarchs. The first was collected on April 20 and was somewhat worn. On June 5 I saw one at Albany, Georgia. The following year Mr. Symmes reported collecting specimens on April 10 and June 7.

P. Kight of Stone Mountain, Georgia, reports Monarch butterflies on March 7 and 9, also on April 21 and 23.

Mrs. A. P. Ryland of Pine Bluff, Arkansas, reports as follows: “My son, George, who lives thirty miles below Pine Bluff, saw a number of Monarchs on March 27... He said the butterflies looked worn, as if they had been blown about.”

Mr. Paul Beard of Mendota, California, reports: “In this particular vicinity Monarchs return from hibernation around the middle of April, though a few individuals arrive earlier.”

Miss Helen Kimball reports collecting a “battened” female Monarch butterfly on March 3 at Davis, Yolo County, California, and seeing two at Folsom, California, on March 19.

Mrs. C. H. Oliver of Yosemite National Park, California, saw two Monarch butterflies on May 29. On May 29 Monarch butterflies were observed passing through Arch Rock, California. On June 12 Mrs. Oliver reported “Monarchs are all over the Valley now and are laying their eggs.” On April 24 of the following year Mrs. Oliver saw 9 Monarch butterflies on the road from Fresno to Yosemite National Park.
Mrs. R. E. Vollrath of San Marino, California, reports tagging Monarch butterflies on May 12.

The following observations were submitted by Mrs. Frank Throm of Overland Park, Kansas:

- April 26: 3 seen flying north; weather was clear; milkweed plants were sprouting, some of them were 2–3 inches tall.
- May 9: 6 seen flying north; wind was from the south at 30 mph; temperature was 84°F.
- May 10: 9 seen flying north; wind from the south at 20 mph; temperature was 93°F.
- May 13: Tagged 2 males
- May 15: 2 seen—tagged 1 male
- May 16: Tagged 6 males
- May 17: Tagged 3 males
- May 19: Tagged 2 males
- May 20: Tagged 9 males, 1 female

"Except for one specimen collected May 19, all of them were worn and torn. I have never seen so many Monarchs here in the spring."

Ezra Day of Salt Lake City, Utah, reports seeing a Monarch butterfly on June 9.

D. W. Davis of Logan, Utah, reports as follows: "Monarch butterflies were first noticed during early July in the Logan area. At this time they were rather scarce."

Frank M. Young of Bloomington, Indiana, saw Monarch butterflies on May 31.

D. H. Thomas of Columbus, Ohio, reports seeing one Monarch butterfly on May 30.

H. C. Kemp of Jefferson, Ohio, reports seeing Monarch butterflies on June 8.

L. E. Egan of Hastings, Nebraska, reports seeing Monarch butterflies from April 30 to May 15.

Tom Fergus of Des Moines, Iowa, reports a classmate finding a "damaged" Monarch butterfly on May 31 and states further that the Monarch butterflies do "not arrive in any great numbers until the middle of June." At a later date he reports capturing a specimen on May 26.

Robert Stone of McKeesport, Pennsylvania, reports as follows: "During the months of May and June I saw five Monarchs. . . . They did not seem inclined to stop any place. The only place they did land was on the slag they used for the road bed."

R. Yunick of Schenectady, New York, reports as follows: "I saw my first Monarch on June 13, at Collin’s Park in Scotia, N.Y."

P. van der Vlugt of Canyon City, Oregon, reports as follows: "On June 2 I saw the first Monarch of the season hovering over the iris beds."

Mrs. L. W. Hobbs of Lathrup Village, Michigan, reports collecting the first specimen on May 29, and a second one on May 31. She further reports that these specimens were "light in color and quite battered."
Mrs. Paul A. Elliott of Muskegon, Michigan, reports as follows: "The first one I saw here was on May 27, and at East Jordan, Michigan (200 miles north) I saw one on May 28."

Mrs. L. G. Senghas of Mount Clemens, Michigan, reports that the first Monarch butterfly was seen on May 26.

Mrs. E. Spricker of Waukesha, Wisconsin, reports: "The first Monarchs that any of us saw this year were on May 30. I saw 4, and the children reported having seen some too. All of them were found feeding on lilac blossoms."

A. H. Moock of Milwaukee, Wisconsin, reports seeing Monarch butterflies feeding on lilac blossoms on May 30.

F. R. Arnold of Chippewa Falls, Wisconsin, states: "They come through here on their northward trek commencing the last week of May and continuing to the middle of June."

Miss Ruth Haigh of Niagara Falls, Ontario, tagged many Monarch butterflies from June 6 to July 22 on nearly every day throughout this entire period, indicating a continuous appearance of migrant and resident individuals.

Mrs. J. R. Glynn of Limehouse, Ontario, reported tagging a female Monarch butterfly on June 14, and pointed out that the specimen was "washed out" in appearance.

In the vicinity of Toronto (village of Highland Creek) I have recorded the following early arrivals: May 21 (2 seen); May 23 (1 collected); May 24 (3 seen). On June 5 a specimen, flying directly north, flew the length of my garden about 4 feet above the ground and upon reaching the house flew up and over the top of it rather than around it. I followed it for 150 yards until it reached a schoolhouse, where once again it flew over the building and continued due north out of sight.

T. McDonald of Port Hope, Ontario, reports seeing a few rather faded specimen on May 30.

At Varney, Ontario, on June 11, many were seen and collected; females were laying eggs.

L. Beamer of Meaford, Ontario, reported seeing two Monarch butterflies on May 25.

W. Krivda of Riverton, Manitoba, reports seeing the first Monarch butterflies on June 10.

It would appear that the returning migrants reach the southern parts of the continent in March and April; the central parts in April and May; and the more northern parts in May and June. This schedule of arrival will, of course, vary from year to year depending upon temperature conditions.

First Appearance of Eggs and Larvae

Mrs. E. Reed of Conroe, Texas, wrote on May 7: "The eggs and larvae are now on the milkweed plants."
PLATE VII

Sample of Monarch butterflies that have been attacked by birds or mice and shrews: a faded (or glazed) appearance in the vicinity of the injury would indicate that the attack occurred while the wings were soft. Such injuries could be caused by mammals (particularly mice and shrews), birds, amphibians, reptiles, and insects.
PLATE VIII

Protective mimicry: \textit{upper row}, Monarch; \textit{centre row}, Viceroy; \textit{lower row}, Banded Purple. The tagged Monarch butterflies travelled a distance of over a thousand miles without any appreciable damage to tag or specimen.
B. Mather of Jackson, Mississippi, reports collecting larvae on April 27.

A. Renfro of Santa Barbara, California, wrote on June 22: “During the last month I raised 2 Monarchs. The caterpillars shed their skins and became pupae on June 4 and 5 and emerged from the pupae on June 14 and 16.”

Paul Beard of Mendota, California, reported on May 21: “Today, on my way home from the San Joaquin River area, I captured several Monarchs which were so brilliant (in color) that I am sure they must have just emerged. In this particular vicinity Monarchs return from hibernation around the middle of April, though a few individuals arrive earlier. Larvae develop on the milkweed until well into October.”

Mrs. G. H. Oliver collected larvae and eggs at Yosemite National Park, California, on May 19.

Miss Helen Kimball of Napa County, California, writes: “On May 22 I found ten full-grown caterpillars which pupated two days after they were collected.”

Mrs. F. Throm of Overland Park, Kansas, collected larvae on May 22, and pupae on May 26.

D. W. Davis of Logan, Utah, writes: “The milkweed plants are growing well. On May 28 I located one larva killed by a fungus disease on the leaf of a milkweed plant. This larva was slightly over $\frac{1}{2}$ inch long.”

David Chen of Bethesda, Maryland, writes: “I collected 25 Monarch caterpillars on May 12. They were in the second [instar] and were found in one location of about 75 sq. ft. That gave me the idea that female Monarchs might have arrived here as early as the beginning of May. First adult emerged on June 1.”

D. W. Bouton of Endicott, New York, reports collecting a half grown larva on July 1.

Mrs. L. W. Hobbs of Lathrup Village, Michigan, collected eggs and larvae at Northville and Birmingham, Michigan, on June 5, 6, and 8, and reports eggs and larvae as being plentiful between June 10 and July 1. Pupae were found as early as June 25, and an adult emerged on July 7.

Mrs. L. C. Senghas of Mont Clemens, Michigan, collected eggs on May 28, and with respect to a second generation she wrote on July 15: “We seem to have started another brood of Monarchs following a period of 16 days when there were very few Monarchs.”

P. van der Vlugt of Canyon City, Oregon, collected larvae during the latter part of June.

L. Beamer of Meaford, Ontario, collected 3 nearly full grown larvae on July 1, and the adults emerged from the pupae on July 17.

C. S. Queich of Transcona, Manitoba, writes: “Four larvae were brought to me on July 5. They entered the pupa stage between July 10-15, and all emerged between July 25-Aug. 5.”

From our observations, the earliest oviposition records were May 22 at Point Pelee, Ontario, and May 28 near Kitchener, Ontario. Monarch butter-
flies are of common occurrence and ovipositing occurs during the first two weeks of June in the vicinity of Durham, Ontario.

It may be concluded, therefore, that larvae occur in the southern parts of the United States in late April and May; in the central parts in May and early June; and in the northern parts of Canada in late May and June to early July.

Last Appearance of Adults and Larvae

The following data were received from our co-operators regarding the latest dates when Monarch butterflies and larvae were observed.

R. Deonison of Sault Ste. Marie, Ontario, reports: "The last Monarch I saw was on September 4."

L. Beamer of Meaford, Ontario, reports seeing the last Monarch butterfly on November 9.

Mrs. W. Pendziak of Kingston, Ontario, reports that the last Monarch butterfly seen was on September 28.

Mrs. J. R. Glynn of Limehouse, Ontario, writes: "October 26 was the last day I saw a Monarch flying."

Miss Ruth Haigh of Niagara Falls, Ontario, reports: "I saw the last Monarch butterfly on October 7; it was not flying in any definite direction."

N. Sibley of Whitmore, Michigan, reports the last appearance of the Monarch butterfly on October 21.

K. L. Clark of Mason, Michigan, writes: "I found a newly hatched male Monarch, just out and drying its wings, on November 1. It surprised me because our first hard frost had been on September 20, and we had several hard frosts between September 20 and November 1."

Mrs. L. W. Hobbs of Lathrup Village, Michigan, reports: "I looked in vain for a single specimen to appear on October 21 and 23, after tagging four on October 16. Observed no specimens between October 16 and 28 and observed only one on October 28."

Mrs. C. W. Johnson of North Kingstown, Rhode Island, reports that the last Monarch butterfly seen was on October 10.

H. C. Kemp of Jefferson, Ohio, writes: "I observed the last Monarch here on November 8."

Mrs. E. W. Fleming of Bay Village, Ohio, writes: "We caught a live Monarch on November 5—the latest date we have ever had."

Mrs. Lester Lundenberg of Philadelphia, Pennsylvania, writes: "The last Monarch I saw was on October 19. This was several days after a severe frost and night temperatures of 29°F."

F. Young of Bloomington, Indiana, reports seeing a Monarch butterfly flying southward west of Worthington, Indiana, on November 11, and one on November 14 in Bloomington.
D. Manger of Paoli, Indiana, reports seeing the last Monarch butterfly on October 19.

Mrs. F. Thron of Overland Park, Kansas, reports seeing the last Monarch butterfly on November 17. She writes also: "A friend from Bartlesville, Oklahoma, reported seeing five Monarchs on the streets of her town on November 20."

R. E. House of Asheville, North Carolina, writes: "Migrants were seen as late as November 20th passing thru the high mountain gaps. The weather had already been below freezing with snow."

Mrs. G. H. Oliver of Yosemite National Park, California, reports that the Monarch butterfly is absent after September 15.

A. T. Edwards of Santa Monica, California, reported on December 12 that he had found many caterpillars and pupae. These were later sent to us for identification. During October, November, and December Mr. Edwards collected over 300 larvae. On January 30 Mr. Edwards sent 3 larvae and 2 pupae to us which had been collected on January 20.

L. Schellbach of Grand Canyon, Arizona, collected caterpillars on October 31. He wrote that the last butterfly seen and tagged was on November 4.

Mrs. H. Beasley of Lindale, Texas, reports seeing the last Monarch butterfly on November 4.

Mrs. E. Reed of Conroe, Texas, wrote on July 11: "I haven't seen a Monarch since the last of May. Some Monarchs stay all winter. I have found caterpillars and chrysalids in April. In September and October the Monarchs are here in great numbers."

S. H. Clarke of McAllen, Texas, writes: "My sister, who lives in the lower Rio Grande Valley, wrote that a few Monarchs showed up about two weeks ago. On October 18 I saw one Monarch and on October 19 I saw several hundreds, but they were very scattered—seeing one or two every 5 or 6 minutes."

From the records of our observations near Toronto, Ontario, the following data are significant: The last Monarch butterfly seen was on October 22, although the last butterfly emerged in our rearing cages on November 2. A severe frost on October 9 killed two larvae that were in the act of entering the pupa stage, and most of the pupae. Of fourteen survivors, the wings of the butterflies were in some cases distorted on emerging and in all cases flight was impossible. On October 18 we made an extensive survey of the milkweed stands in our study fields and found all had been killed by severe frost; the presence of a few green plants near our house kept reared specimens living to November.

It may tentatively be concluded that the last appearance of Monarch butterflies depends upon low temperatures, which in the northern parts of the breeding range varies from late September to mid-October. A few butterflies emerging from sheltered situations such as the corners of houses, barns, etc., could survive the first freezing temperatures and thus account for the reports of Monarch butterflies in late October and early November.
Also, pupae and larvae are more likely to be killed if located close to the ground in low-lying situations than in more elevated situations, owing to the lower temperatures near the ground during periods of first frost. The observations submitted by the co-operators indicate, as we would expect, that as the Monarch butterflies move southward the last appearances will occur at progressively later dates until, in the region of the Gulf states, they will be found in varying degrees of abundance throughout the winter months.

**Breeding Records in Southern Areas**

If a Monarch butterfly breeds close to its overwintering site then we should expect more generations there than in areas many miles distant. Before estimating the number of generations, based on the data presented above, it is necessary thoroughly to examine the breeding habits of the Monarch butterfly in the extreme southern portions of its range. The following information has been received from our co-operators: Mrs. D. A. Crossley of Brownsville, Texas, writes in a number of consecutive letters, as follows:

During the last part of November the children found numerous caterpillars in the school yard. The caterpillars were put into jars with leaves from the host plant. They promptly went into the pupa stage. About the second week of December the butterflies emerged. On January 20 a whole crop of Monarchs emerged and were released. From the third to the tenth of February the children found more caterpillars, although not as numerous as earlier. The first emerged on February 15. We have had another batch of caterpillars which began Feb. 26 and has continued through today (March 4). Since March 20 I haven’t seen any more here. From the first week of June until September 34 we saw no Monarch butterflies.

One of the pupae sent to us by Mrs. Crossley was that of *D. cresimus*. The pupae taken in January were *D. plexippus*. It is possible that there is a confusion in identification, since Mrs. Crossley wrote concerning the caterpillars found in February “This time there are four differently marked caterpillars on the same host plant.”

Mrs. J. Hagar of Rockport, Texas, reports that there are no Monarch butterflies in her area during June, July, and August. She reports, however, finding caterpillars on December 6 which entered the pupa stage and emerged on December 26.

Anthony Inglis, Fisheries Research Biologist with the Gulf Fishery Investigations at Galveston, Texas, submitted the following excellent report on the breeding activities and presence of adults in his area:

From the time I started tagging Monarchs near the end of February (26/2/57) until I stopped on the first of April (two tagged 1/4/57) I successfully tagged 44 males and 47 females. Of those tagged and released, one was recaptured on two subsequent occasions 10 and 15 days after tagging, four were recaptured once from 3 to 4 days after tagging. Of the total number of Monarchs tagged, 22 were raised from larvae of varying
ADULT

During the course of tagging efforts, I found numerous Monarch larvae and eggs which I attempted to raise at home. I tagged and released 22 adult butterflies which were incubated in cages and put at home. My efforts to rear the adults from larvae began on March first when I brought in three large caterpillars, one of which immediately pupated during the three or four hour period from the time of capture and when I took it home. However, my success was relatively low, probably less than 5, due to a heavy infestation of a parasite.

The numbers of Monarch butterflies began to increase about the end of February, reaching a peak around the end of March and beginning of April, coinciding with the advent of warmer spring weather. By the end of May and early part of June, the number of Monarchs was considerably less, though I still counted six to a dozen or so flying about each day during the hottest part of the summer. They again began to reappear in large numbers in late September, reaching a peak about the middle of October. This year cold weather has set in considerably earlier than last, and whereas in 1956 there were large numbers of them through the end of November, I have seen a very few during this month just ending.

Mr. Inglis also reports: “On January 1st I found one large Monarch larva and one Monarch egg which hatched next day.”

Professor L. S. Dillon of College Station, Texas, reports as follows: “The Monarch is quite conspicuously absent in the vicinity of College Station from July 1 until September 1. I have for two summers had two graduate students in the field studying butterfly populations and neither they nor myself and my wife have observed any during these two months. After the first of September, however, a few Monarchs per day may be observed.”

Mrs. S. S. Ruisell of Stamford, Texas, writes as follows: “At present [November] we have three Monarch chrysalids which we expect to emerge within a week. Monarch butterflies are in abundance during August, September, and the first of October. The last Monarchs seen here and the last emerging from chrysalids were just before Nov. 25.”

Miss Ruth Neal of Everglades, Florida, writes: “I have never seen the Monarch butterfly in this region during the summer months.”

E. Christensen of Homestead, Florida, writes: “No one locally has any information about overwintering colonies. Monarch butterflies occur in south Florida the year round and seemingly in about uniform numbers with no indication of seasonal fluctuation such as would be produced with an influx of migrants.”

A. G. Jackson of Miami, Florida, writes: “I have made weekly surveys of the surrounding countryside, approximate radius of 100 miles, during September, October and November. Only on rare occasions have I seen one in September. From Miami to Everglades City, to Everglades Park then to Flamingo I have failed to find one Monarch during the winter months.”

F. Butcher of Miami, Florida, writes: “I do not recall having encountered a single specimen of this insect in the Miami area during the past six or seven years. During the same period my students have not included it in their general collections.”
H. F. Strobecker of Coral Gables, Florida, writes: "Certainly the Monarch is not at any time (to my knowledge, which covers about 10 years) a conspicuous feature of the south Florida fauna. In our small collection of butterflies there are four specimens—three taken in October and one in March."

J. P. Knudson of Sarasota, Florida, writes as follows: "In March of 1953 during a visit to Sarasota I collected Monarchs flying in company with *berenice* at Myakka State Park. The interesting point is that both *berenice* and the Monarchs were very fresh and dwarf specimens. This would indicate that the Monarchs had been breeding in south Florida in January and February and may suggest the presence of a sedentary race in the south Florida area."

A. N. Tissot of Gainesville, Florida, writes: "No specimens of Monarchs have been noticed since late in the winter or very early in the spring (latter part of February or some time in March). While I cannot say with certainty that no caterpillars of this species are present in this part of Florida, I very seriously doubt that any could be found here now (June 21)."

P. S. Hill of Jacksonville, Florida, writes as follows:

In the late fall and early winter the Monarch butterfly breeds the most. They breed naturally in both winter and summer in the area where I have observed them. They are not abundant in the larva stage during the months of May, June and July. They are more abundant in the late summer than in the early summer. My observations have taken place only in St. Augustine, Florida, and in Jacksonville, Florida. I have no information as to how soon the female lays her eggs after emergence from the chrysalid.

The milkweed in leaf was found by me in St. Augustine, Florida. Upon moving to Jacksonville, Florida, I brought up several of the milkweed plants and planted them in my yard. With constant transplanting of new, small plants and emptying the milkweed pods in the immediate area, I formed a stable milkweed leaf hedge. After three years (December 1956) there was the largest number of Monarch chrysalids I have ever seen. At one time we must have had six dozen, all in this stage of development. This was in the early part of January 1957. Many of these I brought inside the studio and they had hung on my sausage. They were in the caterpillar stage when brought inside the studio. A male Monarch was born on January 16, 1957, in the early morning. He had a wing spread of four and one half inches. He became tame, was fed daily on sugar and water from an eye dropper. Died on March 19th, 1957, at the age of 54 days.

The following excerpts from a report submitted by J. P. Knudson of Decatur, Alabama, indicate that fall migrants may oviposit in the southern states giving rise to a fall generation following a period of absence in the summer.

In late July a careful search was made of the *Asclepias* plants along Baker's Creek for any traces of the early stages of the Monarch. No ova or larvae were found and, of equal interest, there was no indication that any larvae had fed on any of the plants earlier in the season. Weekly searches of the plants during the month of August gave similar negative results. On August 31 a few Monarchs were observed, and one female was seen ovipositing on the vine-like plant later identified as *Empanelia albida*. On September 2 a careful search revealed many ova and some first generation larvae. About 25 ova were collected for rearing purposes. On September 3 a careful search of the host plants disclosed only four larvae, one mature and the others very small. On October 3, a final search produced a single half-grown larva. By the end of September the *Asclepias* plants were in poor condition. The majority were turning yellow, and many had already dropped most of their leaves. During June, July and August Monarch butterflies were either absent or extremely rare in the Decatur area. The first specimens was sighted on August 30. The following day five specimens were seen, and throughout September Monarchs were to be seen in small numbers. All the specimens observed
early in the month were worn and dull brown in color. Toward the end of the month these worn specimens began to be replaced by fresh bright ones. Monarchs remained abundant during the period between October 20 and November 1.

John Symmes of Atlanta, Georgia, reports that there were no Monarchs in his area between June 7 and August 18, and further that he has never collected a larva.

Mr. L. Harris of Atlanta, Georgia, corroborates Mr. Symmes' report.

Only three of our co-operators have recorded finding larvae along the Gulf coast south of latitude 32° N. during the months of March, April, May, and June. Some of our co-operators, for the same latitude, report the presence of larvae in November and December, although not abundant. It would seem then, that, with a few exceptions, the Monarch butterfly does not breed to any appreciable extent in the southern part of the continent south of latitude 32° N.

General Conclusions

From the above data it may be concluded that:
(1) The breeding range of the Monarch butterfly is between latitude 32° N. and latitude 48° N. approximately. (2) The migrant females arrive in the southern parts of the breeding range in late March and April; in the central parts in April and May; in the more northern parts in May and June. (3) Breeding is completed by late September in the northern sections, and by October in the southern sections of the breeding range.

March is taken as the earliest breeding date and October 20 as the latest breeding date within the southern section then, assuming an average rate of development from egg to adult as being 33 days, and allowing 7 days to reach sexual maturity there is a possibility of three to four generations, assuming, of course, that optimum temperature conditions prevailed throughout the breeding period.

In the northern parts of the breeding range from May 20 to September 20, there would be a possibility of two to three generations. Therefore, in the most southern parts of the breeding range four generations are possible, in the central parts of the breeding range three generations are possible, and in the northern parts of the breeding range two generations are possible. There are possibilities beyond these limits, however. South of the breeding range it is possible that a small breeding colony may exist giving five generations; and north of the breeding range it is possible that only a single generation exists.

As pointed out in chapter VI, a female containing fertile ova may fly southward depositing her eggs en route, thus accounting for late broods in the southern states, such as Texas and Mississippi, after a period of complete absence in the summer. Females migrating northward may likewise deposit
eggs in early March, thus accounting for the early broods in the southern states.

The following is a probable schedule of generations for the more southern portions of the breeding range:

- Returning migrants: April 15
- First appearance of members of first generation: May 18
- First appearance of sexually mature females of first generation: May 25
- First appearance of members of second generation: June 27
- First appearance of sexually mature females of second generation: July 4
- First appearance of members of third generation: August 6
- First appearance of sexually mature females of third generation: August 13
- First appearance of members of fourth generation: September 15
- First appearance of sexually mature females of fourth generation: September 22

The following is a probable schedule of generations for the more northern portions of the breeding range:

- Returning migrants: May 28 (I use this date since it presents a more accurate picture than the average for a wider area south of the Great Lakes)
- First appearance of members of first generation: June 30
- First appearance of sexually mature females of first generation: July 7
- First appearance of members of second generation: August 9
- First appearance of sexually mature females of second generation: August 16
- First appearance of members of third generation: September 18
- First appearance of sexually mature females of third generation: September 25

If these schedules are, within limits, an accurate presentation of the number of generations within a given geographic area, then the observations made by our co-operators should fit the schedule with respect to the occurrence of the first appearance of eggs, larvae, and pupae.

According to the schedule for the more northern portions of the breeding range of the eastern population, the female migrants return in the latter part of May. We should expect to find eggs in late May and early June; we should expect to find mature larvae and pupae in late June and early July. That this schedule, based upon early adult records and rearing experiments, is accurate is corroborated by the observations submitted by our co-operators.

L. Beamer of Meaford, Ontario, collected mature larvae on July 1.

Mrs. L. G. Sengbus of Mount Clemens, Michigan, collected eggs on May 28.
Mrs. L. W. Hobbs of Lathrup Village, Michigan, collected eggs on June 6.

D. W. Bouton of Endicott, New York, collected a half-grown larva on July 1.

In the central states, from Maryland west to Kansas, we would expect to find eggs, larvae, and pupae at an earlier date, and in the extreme southern portion of the range near latitude 33° N. we would expect to find the early stages in April. This is substantiated by the observations presented previously in this chapter.

Concerning the probability of five generations beyond the southern portions of the breeding range, Mr. C. A. Anderson of Dallas, Texas, reported to us as follows: "In years when I have remained at home throughout the summer, I have bred the Monarchs in captivity through five generations. Reared in captivity, they bred from the first of April to the middle of January. The fifth generation appeared as strong as did the first."

**Comparative Numbers During Breeding Season**

It might be assumed that the Monarch butterflies are of rare occurrence in the spring and early summer, owing to the relatively few returning migrants, and that there is a gradual increase in numbers throughout the summer culminating in a peak of abundance in late summer and early fall. This, however, is not an accurate conclusion. In the northern part of the breeding range, with which we are most familiar, there is a definite scarcity of adults during the period from July 15 to August 15. This observation, made repeatedly over many years, is corroborated by Mr. L. Beamer of Meaford, Ontario, who wrote to us as follows: "From July 23 till August 22 Monarchs were relatively scarce. From this time till September 1 there was a marked increase in their numbers, reaching its peak on the dates August 31 to September 4 inclusive."

The reason for this disparity in numbers may be explained as follows: The Monarch butterflies enter the Canadian region during the month of June and the occasional specimen arrives in late May. At this time a few females may be seen ovipositing throughout June and into the first two weeks of July. The odd first generation female from the central and southern portions of the breeding range also makes its appearance. By mid-July ovipositing has been completed and the females have died. From July 15 to August 15 the larvae are present on the milkweed plants, but the adults are relatively scarce. With the advent of the new generation, together with further breeding, the numbers increase through August and September. Also, as discussed previously, individuals from the north begin to move southward, thus augmenting the numbers of the local populations.
CHAPTER ELEVEN

GENERAL CONSIDERATIONS

Danaus Plexippus

Danaus

Danaidae Lutr., Syst. Buff., siv. 108 (1805)
Danaus Lutr., Gen. Const. iv., iv: 201 (1809)
Aunis Huhn., Verz. bek. schmett., iv: 16 (1818)
Danaus Crol., Encycl. meth., ix: 172 (1819)

Plexippus


It is, perhaps, difficult to apply Linne's original description, which appears in the tenth edition of Systema Nature, to the Monarch butterfly which we find in North America. The description reads: "P.D. alis integerrimis fulvis: venis nigris dilatatis, margine nigro punctis albis." This would, broadly speaking, apply. However, Linne adds: "Adae primores fascia alba ut in sequente, cui similis," the following species being chrysippus, which, as Barnes and MacDunnough (1917) point out, does not apply at all to the North American form but does to the Asiatic. From diagnostic consideration, rather than from reference to locality, one would be led to consider the Fabrician name archippus as correct for the North American species and plexippus for the Asiatic species. This has led to a good deal of controversy and a variety of specific names.

The name Danaus plexippus is the scientific name now applied to and accepted for the Monarch butterfly in North America. However, the specimen in Dr. Holland's illustration is not one belonging to the North American population. It is a South American form which has been placed as a subspecies of plexippus, namely, D. plexippus megalippe. Dr. Holland made an error in terming this specimen plexippus. The error is excusable because we still do not know what should be designated as species or subspecies in South America and there is still much confusion concerning whether certain populations in South America are sufficiently distinct to warrant specific rank or are but geographical races that warrant subspecific designations.
C. B. Williams et al. (1942) summarize the opinions on the various subspecies as follows.

1. North American
   Race: Clark, Fehr, Talbot

2. Intermediate
   Subspecies: nigrippus, megalippus

3. Tropical American
   Subspecies: megalippus

4. South American
   Subspecies: crippus

Williams et al. accept for purposes of description the nomenclature of Clark. In a later publication by Clark (1941), megalippus is substituted for nigrippus. In addition, Clark describes two new subspecies, tobagi and portoricensis. We then have, according to Clark, the following subspecies of plexippus as follows: Danaus plexippus plexippus; Danaus plexippus megalippus; Danaus plexippus tobagi; and Danaus plexippus portoricensis.

The distribution of these various subspecies may be summarized as follows:

1. Danaus plexippus plexippus: North America, south of latitude 50° N., and Central America (Fig. 43).
2. Danaus plexippus megalippus: Brazil, north of the Amazon; Guianas; Venezuela; Colombia; Ecuador; Peru; West Indies.
3. Danaus plexippus crippus: Brazil south of the Amazon; to north Patagonia; west to Bolivia and the Argentine.
4. Danaus plexippus tobagi: Island of Tobago, British West Indies. I am of the opinion that this is a local color variety of megalippus. I have collected specimens in Trinidad which are definitely megalippus, and it is difficult to imagine that a small adjacent island would hold a distinct subspecies.
5. Danaus plexippus portoricensis: Known only from the island of Puerto Rico. Clark describes this "new subspecies" as follows: "Resembling D. p. megalippus from the Guianas but smaller, the fore wing less than 45 mm. long; pair of white spots just beyond the end of the cell in the fore wing absent; two preapical spots small and pale yellowish; no white spots in the black border of the hind wing." When we consider that the only additional specimen examined was one male received from the Brooklyn Museum, and that the diagnostic features presented are those which exhibit considerable variation within a population, it is difficult to accept this subspecies as having any validity.

We are of the opinion that tobagi and portoricensis are color variations of megalippus and are not of significance to the population. It is to be
Figure 43. Geographical distribution of the three subspecies of *Danusa plectippus*.
expected that a collector may become overly enthusiastic about a particularly well-marked specimen, and, if he has only one or two such specimens, he may propose a subspecific name for his discovery without giving due consideration to population and geographic distribution. Hence, such names as *tobagi*, based on a specimen from the Island of Tobago in the British West Indies, and *portoricensis*, based on two specimens from Puerto Rico, do not clarify the taxonomic and distributional problems but, on the contrary, confuse the issue.

A study should be made of the variations existing in the population of South America and, once such a study has been made, proper nomenclature would assist in presenting a clearer understanding of the species as a whole. Until such time as a study is made, and it must be done carefully and fully, including the biology as well as the taxonomy, the author is of the opinion that we can accept only the three populations as outlined above. In the present study, however, we are concerned only with the population in North America, *Danaus plexippus plexippus*.

Species and subspecies of the genus *Danaus*, other than *D. plexippus*, found in parts of southern North America, the Caribbean Islands, and South America are illustrated in Plate VI. There are four species: *D. gilippus*, *D. eresimus*, *D. erippus*, and *D. kleophile*. There would appear to be certain differences in color among various populations of *gilippus* and *eresimus*, and hence five subspecies of *gilippus* and four of *eresimus* have been recognized, and are included in Plate VI. It should be borne in mind, however, that the differences existing between the various subspecies of a species are slight and hence identification on the basis of an illustration of a single specimen is difficult. Indeed the whole population complex of the species is such that recognition of subspecies changes depending upon the material available and the conclusions of the specialist.

We may divide the above species into two major groups.

**Group I**

In which the scent receptors of the male are small and narrow; the light spots on the apical portion of the front pair of wings are buff or yellow in colour; the cell of the hind wing is long; general ground colour is orange with a slight brownish tinge particularly in the female; and the larva has two pairs of fleshy appendages. Included in this group are the following species: *Danaus plexippus*, *D. cleophile*, *D. erippus*.

* Danaus plexippus: as described in the present work and occurring in North America.

* Danaus cleophile Godt.: this is the smallest of the American species. The pale spots at the apical portion of the front wings are bright yellow in colour—more obvious in the male than in the female; the black area at the apex of the front wings is more extensive—more obvious in the males; black
band on the hind margin of the front pair of wings does not extend across the entire width of the wing. This species occurs in the West Indies, particularly Haiti, Cuba, and Jamaica.

\textit{D. criippus} Cr.: This species is similar to \textit{D. plexippus} in many respects, because the front wings are long and tend to be acutely pointed, and the light spots on the apex of the front wings are buff or cream in colour. It differs from \textit{plexippus} in that it lacks a black band on the hind margin of the front pair of wings and in that the veins on the under-surface of the hind wings are broadly marginated with white. It has been considered a subspecies of \textit{D. plexippus} but because of the marked differences in colour pattern and its geographical distribution, being found in South America south of the Amazon drainage, it is quite likely, as Seitz (1924) has suggested, a distinct species.

\textbf{Group II}

In which the scent receptors of the male are large and oval; the light spots on the apical portion of the front pair of wings are white; the cell of the hind wing is short; general ground colour is light to dark brown with a slight tinge of orange; and the larva has three pairs of fleshy appendages. Two species are included in this group: \textit{Danaus gilippus} and \textit{Danaus erebus}.

The variation existing within each of these species is such as to make an accurate identification rather difficult. However, there are two characteristics that may serve to identify them: (1) \textit{D. gilippus}, and its subspecies, has a relatively short cell on the hind wings which, in contrast to \textit{erebus}, makes the two veins originating from the apex of the cell appear short—the corresponding veins in \textit{erebus} are longer. (2) The veins on the underside of the hind wing of \textit{gilippus} are marginated with white scales; such scales are absent in \textit{erebus}. The presence of such scales imparts a fuzzy appearance to the veins of \textit{gilippus} in contrast to the definite outline of those of \textit{erebus}. These are the only differences which I have found to be constant. I could find no marked differences in genitalia. Other differences may exist or future studies may disclose a complexity of populations under a single species.

The following subspecies of \textit{Danaus gilippus} have been recognized: \textit{D. gilippus gilippus} Cr.: three additional white spots, of which one is V-shaped, present on the front wings and four on the hind wings; comparatively dark in colour; the scent receptors of the male contrastingly dark; occurs in South America, especially at the coast near Rio de Janeiro and Bolivia.

\textit{D. gilippus nivosus} Godm.: three additional white spots, of which one is V-shaped, present on the front wings and four on the hind wings, but the spots are larger than those of \textit{gilippus} and those on the hind wings are
very faint owing to the much lighter ground colour; the scent receptors of the male are less contrasting than *gilippus* owing to the presence of white scales which imparts a grey colour tone; occurs in northern Peru.

*D. gilippus jamaicensis* Bat.: this race is slightly smaller than *cleothera*; the ground colour is almost uniformly yellow-brown with contrastingly dark wing margins; the thorax is dark brown in contrast to the yellow-brown of the abdomen—particularly in the female; the scent receptors of the male are covered with gray scales with a margin of dark brown scales on the side adjacent to the wing vein. In general appearance it resembles *nivosus*, but it is much smaller and the white spots are also very small.

*D. gilippus hermippus* Fldr.: similar to *gilippus*, but is darker in colour and the additional spots on the front and hind wings are absent; the band on the margin of the hind wings is contrastingly dark, almost completely obliterating the white spots; occurs in Colombia.

*D. gilippus cleothera* Godt.: similar to *hermippus* but much lighter in colour; white spots evident on the dark band of the hind wings; smaller in size; front wings do not taper as much towards the apex; occurs in Mexico, Central America, and the Antilles.

*D. gilippus berenice* Cram.: this is the most distinctive race; the ground colour tends to be uniformly dark brown; the light spots on the front wings are very small; the dark band on the hind wings obliterates the white spots; the margin of white scales of the veins on the underside of the hind wings is very distinct; occurs from the Gulf states of North America, throughout the West Indies, northern South America as far south as southern Brazil.

It is most difficult to separate the subspecies of *Danaus eresimus*. I have been unable to find any clear demarcation between any of these populations; any colour differences appear to be of degree rather than of kind, nor do they seem to be any well-defined geographical limitations. When a sufficient number of specimens have been collected in many localities throughout the entire range of the species it may be found that we are dealing with a cline varying from the small, dark, brightly marked *erginus* of Peru to the lighter, less brightly spotted *montezuma* and *eresimus* to the north.

*D. eresimus erginus* Godm. and Salv.: comparatively small; front wings dark brown particularly towards the apex; white spots large and contrastingly bright; light markings on the underside of the rear wings show through to the upper surface, giving the appearance of a broad, diffuse light band; white spots on black band of rear wings distinct; occurs in Peru.

*D. eresimus tethys* Farb.: larger than *erginus*; front wings lighter in colour; white spots smaller and less distinct; light markings on the underside of the rear wings do not show through to the upper surface; single row of small white spots on the black band of the hind wings, the second row being obliterated; occurs in the Antilles.
**D. erosinum montezuma** Tal.: similar to *tehyg*; only distinguishing characteristics are the presence of a dark band near the apex of the front wings and the white spots are smaller; occurs in Central America and the Gulf coast of Texas.

**D. erosinum erosinum** Cram.: lighter in colour than *montezuma*; black band near apex of front wings present; black band on hind wings tends to obliterate completely the rows of white spots; occurs in the northern parts of South America and the Gulf coast of North America; commonly found in Venezuela.

**Geographical Distribution of Danaus plexippus plexippus**

**Breeding Range**

From approximately 32° N. latitude in the east and 30° N. latitude in the west to 48° N. latitude. There are a few scattered populations south of 32° N. latitude but, as far as our rather intensive investigations have disclosed, there are none north of 48° N. latitude, except in the extreme southern portion of Manitoba and Saskatchewan. Larvae have not been recorded for Newfoundland, the eastern half of Nova Scotia, or central Quebec. Larvae are apparently rare in the southern parts of the Prairie Provinces of Canada, with the exception of Manitoba in the vicinity of Brandon and Winnipeg. We have been unable to obtain any larval records for Vancouver Island, British Columbia, or Alberta.

The following are a few of the observations made by our co-operators concerning the relative scarcity of the Monarch butterfly in certain areas.

Across the Dakotas, Montana and Idaho I saw two Monarchs. I saw one Monarch in Oregon until we hit the coastal range, when we found a few beds of milkweed and with it many more Monarchs. [A. Moeck.]

I have caught Monarchs in Baker and Grant Counties in eastern Oregon but I have never seen them in large numbers. Several miles up Canyon Creek from John Day we see the occasional Monarch, but there is no milkweed within several miles. I sometimes see several Monarchs in the mountains while riding after cattle. [Pete van der Vlugt.]

As of yet I have not observed the Monarch in any stage in this locality [Bridgeport, Washington]. [G. F. Tiegt.]

Vancouver Island is away outside the migration route. To the best of my knowledge, only a single specimen has been taken here. Asclepias seem to grow only in the extreme northeast part of B.C. Jones in his check list of the B.C. Lepidoptera gives the range of *D. plexippus* as southern B.C. I consider this a serious error as it conveys the idea of a much wider range in B.C. than is actually the case. [R. Guppy.]
Now, about the Monarch butterflies: they were here [Bolsoo, B.C.] some years ago, but I haven't seen a single one for many years (probably 10 or 12). I have only one record July 2, 1944, and I expect it is one of the last I caught. [There is] no milkweed in the Okanagan. [H. R. Foxlee.]

I have collected one perfect specimen, Aug. 25/56. The Monarch butterfly is very rare in this locality. [W. Lacusta, Furness, Saskatchewan.]

I have seen only two Monarchs in the banding season, one on June 17/56 and the other on Sept. 19/55. [C. H. Herber, Daival, Saskatchewan.]

I have never seen any swarms of Monarchs in this area, and when they first appear they are fresh. [Later, Mr. Quelch reported the Monarchs as being more abundant than usual and that some worn ones were collected.] [C. S. Quelch, Transcona, Manitoba.]

From June 26/55 over a period of 8 weeks, covering 7000 miles, I saw not a single Monarch. As we headed home across Minnesota we saw four soaring across the Highway. [The states covered were North Dakota; Colorado; Wyoming; Idaho; Oregon; Washington; Kootenay Valley, B.C.; Alberta; Montana; North Dakota; Minnesota; Michigan. The first Monarch were seen in Minnesota.] [A. Moreck.]

I have seen only one Monarch in this area during the present summer, which may be due to the apparent absence of the milkweed plant of any species in the Santa Cruz County [California]. [A. Glade.]

I am very poorly situated to be of any assistance. In the nine years I have collected here, I've seen not more than five Monarchs and caught two. [D. Eff, Boulder, Colorado.]

As usual here at the foot of the Rockies, Monarchs were scarce. Locally, until the beginning of September, not over six Monarchs were seen. We took a trip during the last three weeks of June west in Colorado to Craig, then north through western Wyoming to Yellowstone, then to Sun Valley and Twin Falls, Idaho, and back via Salt Lake City and western Colorado. We saw five Monarch. [D. Eff, Boulder, Colorado.]

During my summer travels in the Colorado Highlands I failed to observe Monarch butterflies. [H. H. Nagel, Fort Collins, Colorado.]

Monarch butterflies were very scarce in this locality. We saw only two—one at 7,500 feet elevation on Oct. 11, and the other on Oct. 13 between 9,000 and 9,500 elevation. [C. A. Shields, Penasco, New Mexico.]

On Aug. 17 I was called upon to judge the Insect Exhibits in the H.H. Club fair for Bernalillo County, New Mexico. One of the collections contained a male Monarch butterfly which was collected in Albuquerque on Aug. 8, 1955, in flight near a drainage ditch. As yet I have not observed the insect in this area. [C. L. Massey, Albuquerque, New Mexico.]

We have now found the larvae of the Monarch feeding on our native milkweed plant and also entering the chrysalis stage on October 6 here at Grand Canyon, Arizona. [Previously, Mr. Schellbach reported that eggs and larvae had not been found in this area.] [L. Schellbach, Grand Canyon, Arizona.]
... here in the Cumberland Mountain section of Tennessee we haven't seen one butterfly this spring, and less chance of caterpillars and eggs. Also, seldom are any milkweed plants found here. [E. H. Swartley, Alpine, Tennessee.]

I live well out on the plains in the Arkansas valley which I have found is a flyway for insects. . . . The population of Monarchs isn't too large here. [N. Marston.]

I did not see a single Monarch here during the summer. [J. Coe, Foley, Alabama.]

I have not seen any large numbers of A. plexippus in Alabama. [L. V. Jorgenson, Decatur, Alabama.]

Overwintering Range

As a result of rather intensive investigation through the medium of correspondence and three expeditions, it would appear that the North American migratory population overwinters either in roosting sites or as a scattered population over a wide area (such as in Mexico). Only one eastern roosting concentration has been located, at Lighthouse Point near Apalachicola in northern Florida. This is a relatively small population and will probably be destroyed because of the removal of trees for building purposes. Western roosting populations have been located at various points along the California coast from Monterey to Los Angeles (Pacific Grove, Carmel, mouth of Palo Colorado Canyon, Big Sur, Hot Springs, Cambria, Morro Beach, and Santa Monica). There are three other possible sites, namely, Pt. Reyes, Stinson Beach, and Bolinas, but material evidence (in the form of photographs) has not been obtained.

By far the greatest number of individuals overwinter in scattered populations. In the east, individuals in flight may be found in Florida from Tampa northward along the Gulf coast and westward through the Gulf coast of Alabama, Mississippi, Louisiana, and Texas. Our information shows that the greatest concentration of the scattered populations is to be found in Mexico. In the west, individuals in flight may be found throughout the winter months along the coast of California from San Diego to Santa Maria. Although information is lacking for Baja California on the Pacific coast of Mexico, it is highly probable that scattered populations exist in this area. We have reason to believe that the scattered populations do not extend south of latitude 16° N. in Central America nor, except in very rare instances, are they to be found on the islands of the Caribbean.

Accidental Range

It is quite likely that, over a period of many years, a number of extralimital observations and captured specimens may be recorded. With our present limited knowledge of relative abundance such accidental records are not considered part of the distributional pattern. However, in a letter received from Mrs. B. Jaquith of Toronto, Ontario, an enthusiastic naturalist
and an accurate observer, evidence based on observational records is presented in support of considering a population in Alaska. Species of milkweed occur in this area, and Mrs. Jaquith observed many adult Monarch butterflies that were brightly coloured, as if newly emerged.

Concerning the range extension of Danaus p. plexippus into other parts of the earth, Walker (1886) has given the following information:

Of late years this range, great as it is, has extended in a wonderfully steady and rapid manner across the whole breadth of the Pacific Ocean, and far into the Malay Archipelago. Anosia plexippus, unobserved by the early voyagers to the Sandwich Islands, is now abundant and firmly established there. In the Marquesas Islands, where it is now the commonest butterfly, I was informed by a Roman Catholic missionary, who had resided forty years on the island of O. Hiva-Oa (Dominica) that he distinctly remembered seeing the first specimens about the year 1860, certainly so conspicuous an addition to the very limited insect-flora of these islands could not have been long overlooked. In the Society Islands (Tahiti and Eimeo) and the Cook and Heevey groups (Mangai'a, Rarotonga, Aitutaki and Aitu) I saw both the butterfly and its food-plant Asclepias curassavica in plenty, and the latter, indeed, is a pest to cultivation in some of the islands. The insect has even reached the remote little island of Oparo or Ràp-i, far away to the southward, but I could not meet with it at Pitcairn Island, nor did any of the inhabitants, to whom I showed specimens, recognise it as existing there.

Mr. G. F. Mathew, R.N. (to whom I am greatly indebted for some most interesting notes on the butterfly as observed by him during his recent cruise in H.M.S. "Eagle", as well as a full list of localities, given further on) informs me that Anosia plexippus is found throughout the Samoan, Friendly, and Fiji Islands, and is especially abundant in the latter group, which he regards as perhaps its headquarters (at the present time) in the Western Pacific. It appears also to have reached the North Island of New Zealand, as well as Norfolk Island. In New Caledonia, where it has been long established, it became very abundant some years ago, but is now comparatively scarce, owing, as suggested by Mr. E. L. Layard to Mr. Mathew, to the destruction of nearly all its food-plant by the larvae. We first hear of its occurrence in Australia in 1870, when Mr. Miskin (Ent. Mo. Mag. vol. viii, p. 17) records its appearance in Queensland; it now seems to have spread throughout all the warmer parts of this great island, and even to Hobart Town (Tasmania) in lat. 42° S. In the New Hebrides, Solomon Islands, New Guinea, and other islands in that part of the Pacific, it appears to be now firmly established and not rare; but it was not seen by Mr. Mathew at the Gilbert, Ellice, and Marshall Islands, nor at the Carolines, though he noticed the Asclepias at the latter group, and Mr. Scudder (Psyche, vol. i, p. 81) records the occurrence of young larvae at Ponapé Island (Carolines) on some "milk-weeds" (Asclepias) which had been accidentally introduced. Dr. Semper has recorded the butterfly from Celebes, and Mr. W. F. Kirby informs me that it has been found in Java.

Starting from the eastern coast of America, we find Anosia plexippus throughout the West Indies in company with some curious local forms of the genus; and it has long been established in the Bermudas, 650 miles from the coast of the United States. Two examples, now in the collection of Messrs. Salvin and Godman, were taken in 1864 in the islands of Faval and Flores respectively, but I cannot ascertain that any have since been found in the Azores, nor did I see the insect when there
in October, 1880. It does not seem to have reached Madeira, though Asclepias curassavica has found its way to that island.

The first record of the occurrence of *A. plexippus* in Britain is in 1876 (Ent. Mo. Mag., vol. xiii, p. 107) a specimen having been taken by Mr. J. T. D. Llewelyn at Neath in South Wales, on September 6th of that year. This is now in the British collection at the Natural History Museum, South Kensington, and is a very fine example of the ordinary North American type. Another was taken at Hayward's Heath, Sussex, in the autumn of the same year (Entomologist, vol. ix, p. 267). In September, 1877, a specimen was captured by M. Crassul in La Vendée (Petites Nouvelles Entomologiques, II, pp. 253, 254), the only record I can find of its occurrence on the European continent. A specimen is recorded by Mr. J. Jenner Weir (Entom. vol. xix, p. 12), as having been taken near Soulland, Kent, on September 21st, 1881; but the number seen and caught last year far exceeds all that have been previously noted. A round dozen, at least, have been recorded from our southern counties. Cornwall contributing quite half the number, though Devon, Dorset, and the Isle of Wight have also been favoured with the visits of the imposing stranger. (Ent. Mo. Mag., vol. xxii, pp. 134, 161, 211; Entomologist, vol. xviii, p. 305).

The same author is of the opinion that the seed of the milkweed was carried from the New World to other places through the medium of commerce, and thus "the first great gap of 2550 miles in extent (measured from the nearest point of the American continent) may have been bridged over by the plants." With regard to the Monarch butterfly, however, the author tends to favour the theory that the combination of its "migratory propensities" assisted by strong winds might conceivably carry the species to foreign lands and, in proposing this solution, he puts forth evidence with regard to swarms being found at sea 200 miles from the nearest land. Williams (1958) also supports this theory. Records of other species of butterflies found at sea are presented in support of this contention. This, according to Walker, is perhaps a plausible explanation in so far as the crossing of the Pacific Ocean is concerned, but the explanation for the presence of the Monarch butterfly in Great Britain and western Europe is not as readily explained. "The same remarks may apply to its dispersal across the Atlantic; but owing to the much more stormy character of this ocean, and the less steady winds, the chances of the butterfly crossing a given extent of ocean in safety are less favourable."

In a leaflet (no author designated) issued by the Australian Museum (1886) it is stated that the Monarch butterfly was first seen in Queensland in 1870. It is now well established in Australia, where the larvae feed upon *A. fruticosa*, *A. curassavica*, and *A. rotundifolia*. Eggs are laid in February.

We are indebted to Dr. A. Musgrave, Curator of Entomology of the Australian Museum, for the following information concerning the presence of the Monarch butterfly in Australia.
The Wanderer butterfly, as Danaus plexippus L. is known in Australia, was first recorded from this continent by W. H. Miskin (1871) and his observations are based on specimens seen about Brisbane and at Rockingham Bay during the year 1870.

He states, "The sudden appearance this season, and for the first time, of this fine insect in Queensland, has caused much speculation among our local entomologists. What seems most extraordinary is the fact of its appearance in such large numbers, and of its being so widely distributed. I cannot ascertain that a single specimen was observed last season, or ever before in the colony."

Professor Frederick McCosh of the University of Melbourne was among the first to record (1873) the first appearances of the butterfly at Lord Howe Island (collected December 1870), Clarence River (1871), and Melbourne (April 1872).

This butterfly is very common in Eastern Australia as the late Dr. C. A. Waterhouse (1932) points out in his book, and "specimens may be taken at almost any time of the year in the warmer parts." He further points out, "It has spread rapidly in Australia and is still extending its range. It has not yet been recorded from Tasmania, but as its foodplant is growing at Launceston, it will soon be found there."

So far as Tasmania is concerned he seems to have overlooked an earlier reference by J. J. Walker (1886) who, in addition to giving Australian records, notes it also from Hobart Town, Tasmania. In 1908 A. C. Pearse records the butterfly from Launceston, Tasmania, where it was collected by Mrs. H. W. Hodges.

In South Australia, in the National Parks, Danaus plexippus may be seen flying about in hundreds, according to Womersley (1936).

Reference to J. J. Walker, who made many of his observations while serving as Engineer-Commander in the Royal Navy on the Australian Station, shows that he was particularly interested in the geographical distribution of the Wanderer and its migrations, and several papers published in 1914 and 1915 give much information on the appearance of the insect in Australia and its spread in Australia, the Pacific and elsewhere.

Though the insect is common in Eastern Australia, occurring in Queensland, New South Wales, Victoria, and South Australia, and though the life-history is familiar to most entomologists, we find that little has been recorded of the number of broods in the States cited.

One of the most recent accounts of the life history of the insect in Australian scientific literature is that given by the late Mrs. Edith Coleman (1939) from observations made in Victoria (Melbourne) and therefore in the southern part of Australia. She writes, "There are at least three broods, probably more, for one finds on the foodplant, at the one period, eggs as well as larvae in every stage of development up to pupation point, Pupation takes place in 14–20 days, the pupal stage lasting 15–20 days, the variation in time being, doubtless, dictated by weather vagaries."

The Monarch butterfly reached the Hawaiian Islands about 1845. Scudder (1889) writes:

At any rate we have the direct statement of Dr. Luther H. Gulick who was born upon the islands, that in 1852, after eleven years' absence, he returned to the
islands, and his brother drew his attention to the fact that Asclepias had been introduced during his absence and had already become a troublesome weed; that his brother had noticed that wherever the milkweed appeared there also Anosia made its advent, a butterfly unknown until after the milkweed had been introduced.

With regard to the spread into Caroline Islands in Micronesia, Scudder writes:

He [Dr. Gulick] was for some time a resident of Ponape, and the butterfly was first seen by him in the year mentioned [1857], not long after he had discovered several young milkweeds which had sprung up in earth in which various other plants had been brought from the Hawaiian Islands in a Wardian case. The plants were brought in a missionary vessel which sailed from Honolulu, and on its way to Ponape touched only at Apaian of the Gilbert Islands and Eon of the Marshall group, and at Kunai... It is evidently impossible that in a voyage consisting in the whole of fifty-four days, the insect in any stage or stages could have been transported in the Wardian case itself, for it easily undergoes all its transformations in warm regions in a month or five weeks at most. If the butterflies were introduced at that time, as there is every reason to believe from Dr. Gulick's accounts, there seems no other supposition possible than that an impregnated female flew into the hold of the vessel while lading at Honolulu, and was carried perforce to Ponape; or, possibly, a pair of butterflies. It would certainly be absurd to suppose that a gravid female could have flown over two or three thousand miles of ocean, and in addition have appeared in Ascension Island almost simultaneously with a few plants of Asclepias. As the butterflies pass the entire winter in hibernation and then lay eggs in the spring, there is nothing in any way really surprising in Dr. Gulick's statements, unless it be impossible for an impregnated female to live in enforced hibernation a couple of months without laying; when it would be necessary to suppose a pair to have been transported, which would of course be more extraordinary.

Granting our explanation to be just, it is highly probable that it was from this single ancestor, or pair, that the swarms which have now spread over the entire South Seas, in many of which it is the commonest butterfly known, have sprung. Our knowledge of the period and extent of this later distribution we owe largely to Professor Semper, who states that the butterfly was first seen in 1863 by Captain Ruchan, one of numerous collectors of the Museum Godeffroy, on the islands of the Tonga or Friendly group, again nearly another 2000 miles from Ponape. The first specimens actually obtained was secured in 1866 on Niulafon, one of the islands of this group, and in the same year larvae were discovered on Asclepias curassavica, a plant now spread quite as far as the Annam. We now begin to be able to record in part the rapidity of its spread; for it was first seen in Tutuila, one of the islands of the neighboring Samoan group, in 1867, but upon Upolu and Savaii, islands of the same Samoan group, distant at the nearest some fifty miles, not until 1869. Yet in Upolu it became one of the commonest butterflies in 1870. It was not until 1868 that it was discovered at Tongahalu, one of the southern of the Tonga Islands, but in the same year it was seen in the open sea five hundred nautical miles to the southeast. In 1869 it had appeared at Bora-bora, one of the Hauru Islands, five hundred miles or more away. In 1870 to 1872 it was found on Hushine and Tahiti of the Society Islands, again five
hundred miles or more distant. So far the account of Professor Sempé.

But MI'.

James J. Walker, who sailed in the South Seas in 1883 and found Anosia nearly everywhere one of the commonest butterflies, states that he was informed at the Marquesas Islands, which lie to the northeast of the Society Islands, again at the distance of some five hundred miles, by a Roman Catholic missionary residing there forty years, that he distinctly remembered seeing the first specimen there about the year 1860, it should be noted that the Marquesas Islands are nearly as distant in a southeasterly direction from the Hawaiian Islands as the Carolines are to the southwest. Mr. Walker also found the butterfly on the Harvey and Society Islands and at Oparo, one of the Andaman group, in 28° south latitude, though it had not then reached Pitcairn Island, which lies much farther east and somewhat farther north. These statistics indicate its movements from the Caroline Islands in an easterly and southeasterly direction, but it has also left its marks by the way, in a southward extension from this route of travel. For it has reached Waigiou, New Britain, New Ireland, New Guinea, the Louisiade Islands, every part of Solomon and New Hebrides groups, the Duke of York Island, the Loyalty and Fiji Islands, New Caledonia, Norfolk Island, the northern island of New Zealand, the entire eastern coast of Australia, from Cape York southward even as far as Hobart Town in Tasmania. It reached Lord Howe Islands in 1870, Clarence River on the opposite coast of Australia in 1871, Melbourne in 1872 and has now extended even to Ceylon, and according to Kirby, to Java.

It thus appears that it now possesses a territory in the Pacific Ocean of at least 110° of longitude and 65° of latitude. But this is by no means all. It has moved also in some strange way in the opposite direction from the American continent. It has long been known in the Bermudas as one of the extremely few butterflies to be found on that island. Specimens now in the collection of Godman and Salvin were taken in 1864 in the islands of Fajal and Flores, but it seems not to have been since recorded from the Azores. It has, however, made its appearance on the continent of Europe at LaVendée on the Atlantic coast of France, and a number of instances of its capture in England have been signalized within the last ten years. These instances are so numerous and recorded for so many different years that it would seem highly probable that the butterfly has been endeavouring to maintain a foothold ever since 1876 when the first instance of its occurrence was recorded. The first specimen was found at Neath in South Wales in September, a second one in Sussex in the same month, and a third at Hayward’s Heath in October. In 1877 one was taken at Poole Harbor. In this year also a specimen was taken upon the continent. It did not appear again till 1881 when a specimen was taken in Kent in September. Again in 1884 one was taken in the Isle of Wight. In August and September, 1885, nine specimens were taken in the counties of Dorset, Devon, Cornwall, and the Isle of Wight. It was again taken in 1886 in the south of England, in Guernsey, at Gibraltar, and in Portugal.

I have spoken of this extension of its natural regions as one due to commercial agencies, because it would seem that the distance to which the insect has been carried must be due to something more than its very remarkable powers of flight. The fact that the butterfly has been seen flying at sea five hundred miles from land is a sufficient proof of the latter, and we should be far from questioning its power to compass with so very great difficulty one-half the extreme distances to which we know it has been carried without power of alighting. But that this should occur with a female heavily with eggs (and no other supposition would permit us to understand its subsequent propagation in the regions visited) is past
creden ce; more especially as we have in the instance of its transport from the
Hawaiian Islands to the Caroline group an almost certain proof of the method of
its transport, through artificial aid. The alighting of one of these butterflies laden
with fertile eggs upon some part of a vessel or within its hold would by no means
be a strange occurrence; and this is all that is necessary to explain its transport
over the wider regions. That, having once established itself in one of the Micro
nesian Islands, it could easily spread over the whole of Polynesia through the
insect's ordinary power of flight will not be questioned. But that this has taken
place not only within historic times, but within the last twenty or thirty years, as
has been shown by Semper, is an almost direct proof that its first introduction to
the South Seas was by artificial means; for if it could be brought about solely by
the power of flight of the insect, aided by the natural currents of the air, it would
have happened long ago; and the fact that the insect has been able to establish
itself wherever it chose when it got a foothold and that it has not until a very
recent period so established itself, are sufficient proofs that commercial agencies,
so much more abundant in later times than formerly, have been the great means
of introducing these butterflies to the islands of the Pacific. It is highly probable
that it owed its first introduction to the Hawaiian Islands to similar agencies, and
that its appearance in Europe is due to the same cause.

Larvae feeding upon milkweed growing in the vicinity of docks and
railway yards could conceivably enter the pupal stage attached to packages,
particularly crated material, destined for foreign lands. Barring accident, and
assuming that the crate was kept in a cool place such as the hold of the ship,
the adults might not emerge until twenty days later, a period of time that
would permit transporting by ship over long distances.

In severe wind storms it is possible that Monarch butterflies may be
carried out to sea. A ship would be to such Monarch butterflies an island
of refuge and, since they remain inactive during periods of stormy weather,
and particularly strong winds, they would remain quiescent in protected
parts of the ship and thus be carried considerable distances. Coastal winds
blowing over the ocean would tend to keep the Monarch butterflies inactive.
On reaching the mainland they would become active again or, while at sea
and during a period of calm, they might make their presence known. In this
connection the following observation is worthy of note. During a period of
maximum abundance when the Monarch butterflies were migrating south
ward, a small sailing vessel eight miles from the Canadian shore on Lake
Ontario attracted a great many Monarch butterflies. A strong wind was
blowing and the butterflies sought shelter in various parts of the vessel, out
of the wind. The sailing vessel crossed Lake Ontario, covering a distance of
forty-two miles, and the butterflies remained on the vessel throughout the
trip. Two specimens, both females, were found fluttering against the cabin
window the following day. If a female Monarch was transported in this
manner, and if on reaching a distant land milkweed plants were present,
then a population would arise. If this land mass were within a short distance
of other land masses it is highly probable that the spread might continue by

direct flight. As has been shown in the present work, females may possess

fertilized eggs during the southward migration, and fully matured ova can

be found in overwintering individuals throughout the winter months.

Since Monarch butterflies remain inactive, seeking shelter on the leeward

side of trees and bushes, during stormy weather and high winds, the chance

of their flying away from land and over large bodies of water is remote. It

has also been shown in the present work that Monarch butterflies are

repelled by large bodies of water and tend to move around rather than over

them.

If, as has been suggested, Monarch butterflies may be carried to great

heights, it is necessary to bear in mind that flight is impaired at temperatures

below 50°F. and at a temperature of 40°F., or lower, the Monarch is unable

to fly. In storms which usually accompany the passage of a cold front

temperature would be most effective in prohibiting flight. If a flight took

place from North America to the British Isles it would be necessary for the

Monarch butterflies either to fly night and day or, since they tend to become

inactive during periods of darkness, to rest upon the surface of the ocean.

To test whether or not a Monarch butterfly could rest upon the surface of

water and take wing again, the following simple experiment was carried

out. Two Monarch butterflies were placed upon the surface of the water

with the wings held together over the back of the specimen so that only

the thorax and abdomen touched the water. When released they took wing

and flew away without difficulty. Two specimens were then placed on the

surface of the water, the wings outspread and held so as to be in contact

with the surface. When released they too flew away. Finally, five specimens

were held together by the wings and immersed in the water to a depth of

eighteen inches. When released under the water, four of them rose quickly

to the surface and flew away, but one specimen with a broken wing tip was

unable to do so (Fig. 44). To test the possible effect of fractured wings in

this connection, the wings of five specimens were fractured (the apical

portion of the right front wing only) and five were left intact. The five

fractured specimens were unable to take wing from the surface of the water

and the five undamaged specimens experienced no difficulty. Seitz (1906)

states: "I very often saw plexippus at sea flying at a very considerable height

and observed that it could settle on the surface of the water with the wings

expanded and rise again without difficulty into the air." The length of time

that the Monarch butterfly could rest on the surface of the ocean without

saturating the hairs of the body and thorax, and thus making flight from the

surface of the water difficult or impossible, has not yet been ascertained.

After many years of careful observations we have found that during the

fall migration the Monarch butterflies fly south or southwest. Even if they
Figure 44. Monarch butterflies immersed in water to a depth of sixteen inches floated to the surface and flew away (a, b, c); if the wing is fractured it is unable to fly from the surface of the water (d); specimens were tagged (c) for migratory flight records.
were carried out to sea from the eastern coast of North America by a strong wind, it is difficult to accept the possibility of flight northeast to the British Isles.

Travelling in direct flight from the New England coast to the south coast of England, the butterflies would cover a distance of approximately 3,000 miles. The fastest rate of travel recorded from the return of our tagged specimens is eighty miles per day. Therefore it would take approximately forty days to cover this distance and our experiments have shown that deprived of nourishment a Monarch butterfly will die in ten to fourteen days.

It would appear that over great distances, such as that from North America to the British Isles, the Monarch butterfly is transported, at least for much of the distance, by man. As mentioned earlier, adults may seek refuge in various parts of the ship while the latter is lying at anchor near shore, or larvae and/or pupae may accidentally be taken on board with crated merchandise. The former seems most plausible for the following reason. During the southward migration the Monarch butterflies gather together in great numbers during periods of cold inclement weather. Such weather follows the passage of cold frontal systems that are often associated with strong winds and hence rough seafaring weather. Butterflies moving down the Atlantic or Pacific coasts encountering cold weather, will seek shelter and if they happen to be flying off the coast-line would conceivably seek it in various parts of the ship. Such stowaways would probably remain on the ship during its voyage since, in the first place the butterflies are averse to flights over large bodies of water, and in the second place tend to remain quiescent during stormy periods. If such a vessel should enter a zone of comparative calm and warm air temperatures, the butterflies might leave the vessel and start southward over many miles of ocean. With the approach of darkness they would seek shelter and might land upon another vessel at sea, thus accounting for the observations recorded by Williams (1958).

**FLUCTUATIONS IN NUMBERS FROM YEAR TO YEAR**

That the numbers of Monarch butterflies fluctuate over a period of years is evident from the reports which we have received from our co-operators and from personal observations during the past twenty-two years. The following observations were received from our co-operators across the continent.

**Rare Occurrence** 1953

1... made about daily searches all over Lincoln County and on many of the islands off the coast of Maine. There were no Monarchs to be found. [E. Ford, Newcastle, Maine.]
It was only on a few occasions that I saw the butterflies this year. [T. McDonald, Port Hope, Ontario.]

It was a very poor season. In all, I saw two Monarchs in our garden. Careful search and re-search of hundreds of common milkweed plants turned up no caterpillars at all—only two eggs. [Mrs. L. G. Senghas, Mount Clemens, Michigan.]

There were hardly any Monarch butterflies this fall. [Mrs. W. F. Doucette, Mount Clemens, Michigan.]

I took my tags to New Jersey and instead of the swarms found there last year I found only a few. [Mrs. L. W. Hobbs, Lathrup Village, Michigan.]

Although I made a number of field trips in search of them, I was unable to capture a single Monarch. I think the Monarch migration through this area must have been in unusually small numbers this year. [J. Wayland-Smith, Oneida, New York.]

We saw no Monarchs, either at Schenectady or at Lake George. [Mrs. E. S. Betz, Schenectady, New York.]

The butterflies were practically non-existent in this area, and I was able to tag only three. [Mrs. J. H. Mullin, Greenport, New York.]

During the late summer and autumn I saw so few Monarchs that I was unable to tag one. [E. Yarrow, Bronx, New York.]

In 1952 and 1953 there have been actually 110 Monarchs at Fire Island, N.Y., although in 1950 and 1951 there appeared to be very substantial numbers. [J. J. Shapiro, New York, New York.]

Concerning the lack of Monarch butterflies in 1953, we noticed that there were also fewer of several other insects as well. The drought caused the milkweed plants to become so dry that one small caterpillar had to crawl over a whole plant in order to find enough fresh leaves. [Mrs. T. L. Fish, East Lee, Massachusetts.]

E. L. Tripp of Framingham, Massachusetts, saw only one Monarch throughout the entire season.

I was unable to do any banding owing to the scarcity of butterflies. I saw only one in August. There has been a noticeable scarcity of milkweed butterflies during the past few years here in Massachusetts. [A. R. Lewis, East Hampton, Massachusetts.]

I was not able to tag a single Monarch butterfly. I had 26 nine-year-olds looking too, and absolutely none! It was impossible to locate one (pupa). [Miss A. Penay, Bridgeport, Connecticut.]

We have found this a very poor year for Monarchs. [Mrs. E. W. Fleming, Bay Village, Ohio.]

I saw only one Monarch this fall. [D. L. Nicholas, Bel Air, Maryland.]

1954

I observed only three Monarchs the whole summer, around the end of August. I did not observe any larvae or other stages. [G. F. Tiedt, Bridgeport, Washington.]
During the entire season I saw but two Monarchs. [E. J. Ford, Newcastle, Maine.]

Monarchs were not only scarce during the tagging period, they have been decidedly scarce all summer. During September our students collected only one Monarch; I have not seen a single larva or chrysalis this season. [L. Beamer, Mecaford, Ontario.]

I was out looking several times and so were our Grade 13 Zoology students. We only sighted two specimens. [A. Wylhs, Ripley, Ontario.]

This year there were very few butterflies to be seen in this area. There have been no caterpillars in Port Hope that I have seen for two years. [T. McDonald, Port Hope, Ontario.]

These last two years there have been few Monarchs seen, only in spring and fall. We have found neither eggs nor larva. [Miss Ruth Haux, Niagara Falls, Ontario.]

Monarchs were few and not often seen during the summer. I have never seen a year of so few Monarch butterflies and caterpillars. [H. F. Stiles, Grand Rapids, Michigan.]

Monarchs were very much less numerous than usual. [B. W. Smith, Oneida, New York.]

Our hunt for Monarchs was almost futile this year. [Mrs. E. S. Betts, Schenectady, New York.]

There was a marked scarcity of Monarchs in this area in the early part of summer, with infiltration of only an occasional one into August and September. [D. H. March, Alfred, New York.]

At home I saw no Monarchs. This is the second year in a row. I did find one caterpillar in the second week of September. [D. W. Boutil, Endicott, New York.]

There did not seem to be very many Monarchs around. I spent quite a bit of time looking for caterpillars in areas containing milkweed—however, not one caterpillar was seen. [Mrs. R. F. Mohr, White Plains, New York.]

This year there were very few Monarch butterflies in Scarsdale. [Mrs. M. J. Goell, Scarsdale, New York.]

Saw very few Monarchs this summer. [Miss E. Yarrow, Bronx, New York.]

For some reason I am unable to understand, the last three years have been abominably poor years for Monarchs in my area of Fire Island. [J. J. Shapiro, New York, New York.]

Monarchs were rather scarce again this year. They disappeared entirely after hurricane Hazel. [C. Bradway, Bridgetown, New Jersey.]

During the past three years we had a pathetically small number of Monarchs. [Mrs. K. L. Seelbach, Cleveland Heights, Ohio.]

From Oct. 11-14 during very warm, sunny weather I saw not a single Monarch in Houston. [Mrs. L. Luxenberg, Philadelphia, Pennsylvania.]
I did not see a single Monarch all season. [J. J. Johnson, McDonald, Pennsylvania.]

The Monarch butterfly has been scarce in the Indiana Dunes for the past two summers. [Mrs. T. Carter Harrison, Chesterton, Indiana.]

We have had very few Monarchs here this season. [Mrs. A. P. Hyland, Holly Grove, Arkansas.]

Monarch butterflies were very scarce in this locality. We saw only two—one 7500 feet elevation and the other 9500 feet elevation. [Mrs. C. A. Shields, Pensaco, New Mexico.]

This past season I did not find even one Monarch. In past years I have seen literally thousands at my country home on Lake Pontchartrain. [Mrs. J. W. Townsend, New Orleans, Louisiana.]

More Abundant Occurrence

In 1954 there were indications, in certain parts of the United States and Canada, that the Monarch butterfly was becoming more abundant. This trend increased in 1955, as the following reports from our co-operators show.

1954

Butterflies were more plentiful than last year, but not as many as 1952. [Mrs. L. G. Senghas, Mount Clemens, Michigan.]

There seemed to be quite a few more butterflies this year than last. [Mrs. W. F. Dossette, Mount Clemens, Michigan.]

I was more successful than in previous years. [Mrs. L. W. Hobbs, Birmingham, Michigan.]

This year’s supply of Monarchs was much better than that of 1953, but not what it has been in the past. [Mrs. Lester Luxenberg, Philipsburg, Pennsylvania.]

The Monarchs were fairly plentiful this year. [R. A. Stone, McKeesport, Pennsylvania.]

1955

I am of the opinion that Monarchs were much more abundant in New England than for many years. [E. Ford, Newcastle, Maine.]

Monarchs were more plentiful than last year, during June and September, . . . I think Monarchs were more numerous here early in the season than in average years. [Mrs. E. W. Staufacher, Monroe, Wisconsin.]

Throughout this district there has been a considerable increase in the number of butterflies over the past two years. [S. Culham, Stavner, Ontario.]

Right around the village here the butterflies appeared to be present in more numbers than in 1954. [A. Wylds, Ripley, Ontario.]

Adults, in the latter part of September, were very common compared to the past three seasons. [P. A. Striecker, Kitchener, Ontario.]
The Monarch butterfly population has increased over last year in my vicinity. [K. L. Clark, Mason, Michigan.]

During the past summer Monarchs were only slightly more common than during the preceding three summers. This year the Monarchs were most prevalent the first two weeks of August. [H. F. Breckerhoff, Exeter, New Hampshire.]

Migrating butterflies were much more numerous here this fall than in either of the two previous years. [R. Wayland-Smith, Oneida, New York.]

During the summer Monarchs were quite plentiful in the area as compared to previous years. [H. Yunick, Schenectady, New York.]

For the first time in three years I have spotted some Monarchs but they were few. [D. Bouton, Endicott, New York.]

This summer seemed to make up for the scarcity the previous few summers. There were not only many Monarchs in our section, but other butterflies which I had not seen for some time. [Miss E. Yarrow, Bronx, New York.]

I found Monarchs to be fairly abundant in eastern Massachusetts during August and September of this year. [C. N. Potter, East Holliston, Massachusetts.]

The following are reports received from our co-operators during these years. 1955

The Monarch was very abundant here this year. [H. C. Kemp, Jefferson, Ohio.]

They were plentiful this year. I counted over 100 and banded 35 from August 25 to October 15. [Mrs. J. Mullen, Greenport, New York.]

Monarchs have been common here this summer. [Mrs. W. F. O’Brien, Melrose, Massachusetts.]

Around September 18th the Monarchs were very abundant. Besides the adults flying I found large numbers of larvae. [R. W. Hildreth, East Holliston, Massachusetts.]

The Monarchs are plentiful here at present. I have seen 20-30 in one afternoon. [H. Birkbahn, Coal Valley, Illinois.]
We seem to have an abundance of the adult butterfly around Gilmore City. [Miss D. Sabo, Gilmore City, Iowa.]

I found a great increase in the number of Monarchs this year over last year. [J. Rankin, Cedar Rapids, Iowa.]

1956

During the summer there was a tremendous increase of migrating Monarchs over the past three years. Every day I was travelling I could expect to see 5 or 6 or more in contrast to one or two which might be seen in a week in previous years. I began tagging three years ago and I have noticed a general uprising in the numbers each year. [S. Colham, Stayner, Ontario.]

... on September 1st the Monarchs were so plentiful along the highway between Barrie and Midhurst that they slowed traffic almost to a walk. [L. Beamer, Meaford, Ontario.]

There has been a decided movement with many more butterflies than for several years. [N. O. Sibley, Whittemore, Michigan.]

It appears that 1956 is going to be an all-time record year for Monarchs. I have observed far more this year during July than during the whole season last year. [Mrs. L. W. Hobbs, Lathrup Village, Michigan.]

I feel sure that this year is proving that the Monarch butterflies are in abundance. [Mrs. E. W. Fleming, Bay Village, Ohio.]

I tagged 100 Monarchs and could have tagged many more. On September 15 & 16 the trees around my school were filled with Monarchs. I have never seen so many at one time in this vicinity. [H. Birkhahn, Coal Valley, Illinois.]

The Monarch butterflies were very plentiful here this year. The butterflies seemed to come in waves all summer. [H. C. Kemp, Jefferson, Ohio.]

This year we have had a phenomenal number of Monarchs. In all the years we have worked on the survey the Junior Curators and I have never run across so many Monarch butterflies, caterpillars and eggs. In one hour I collected 91 eggs. Other years I spent hours in the field with very little success. We were just flooded with Monarchs this summer. [Mrs. E. W. Fleming, Bay Village, Ohio.]

In the northern part of the lower peninsula of Michigan Monarchs were very thick, and on Mackinac Island on September 15th there were thousands of them. [D. H. Thomas, Columbus, Ohio.]

I saw 167 individuals this season as compared with 49 in 1955. [Mrs. C. W. Cottrell, Cambridge, Massachusetts.]

I have found Monarchs very abundant this year, especially the fall brood. [C. N. Potter, East Holliston, Massachusetts.]

During the latter part of August great numbers were to be seen on the south shore of Long Island Sound. [Mrs. J. H. Mullen, Greenport, New York.]
GENERAL CONSIDERATIONS

Last week-end I was at Cape May, New Jersey. There were Monarchs everywhere. At any time I could see a dozen and once in a while as many as 50. The natives there said that on September 13 they were just hanging thick on the golden rod and other food plants. [Mrs. C. S. Miskelly, Bradford, Vermont.]

Monarch butterflies have become quite numerous around Logan during the past ten days or so. I can't speak for many years back in Utah, but they are certainly numerous in the state this year and several people have commented as to the abundance. [D. W. Davis, Logan, Utah.]

The building of Monarch butterflies has taken an upswing during the past few days due to the influx of a tremendous number of migrating butterflies. [P. F. Spangle, Sulphur, Oklahoma.]

Abundant? Yes! After August 15 they began to be seen more often, more so, I would say, than I have ever observed before. [L. Schellbach, Grand Canyon, Arizona.]

In October my trees were covered with Monarchs. [Mrs. S. S. Russell, Stamford, Texas.]

The fall 1956 migration was the best I have ever seen. The flights at their maximum were so heavy that accounts reached the local newspapers. [L. S. Dillon, College Station, Texas.]

1957

I cannot remember ever having seen Monarchs so common in this locale. [F. A. Stricker, Kitchener, Ontario.]

On some days as many as 2000 passed by Port Hope. [T. McDonald, Port Hope, Ontario.]

... great quantities of Monarchs and, it seemed to me, more milkweed than usual. [Miss Ruth Haigh, Niagara Falls, Ontario.]

There are thousands this summer. [Mrs. E. W. Fleming, Bay Village, Ohio.]

Monarchs were quite abundant here—more so than during the past two years. [D. L. Niehans, Bel Air, Maryland.]

Less Abundant Occurrence

Although some of our co-operators considered the 1957 population equal to or greater in number than the 1956 one, most of them agreed that there were fewer in 1957 than there had been in 1956.

This has been a poor year for Monarchs. I have reared and tagged only forty, although in 1956 I reared hundreds. [P. van der Vlugt, Canyon City, Oregon.]

There was a slight decrease in numbers. [S. Culham, Stayner, Ontario.]

They were certainly not as plentiful as last year. [Mrs. J. R. Glynn, Limehouse, Ontario.]

The movement of adult butterflies has been much lighter than a year ago. The marked migration I observed at Tawas last September has been non-existent this year. [N. O. Sibley, Whittmore, Michigan.]
The season here was very poor as compared to the past two years. We did not locate a butterfly tree or see any great mass movement. [Mrs. P. A. Elliott, Muskegon, Michigan.]

They did not seem to be in numbers this year. [F. R. Amhol, Chippewa Falls, Wisconsin.]

They were very scarce in Wisconsin this year. They are generally quite common in the fall but this was not the case this year. [W. E. Sieker, Madison, Wisconsin.]

D. Bouton of Endicott, New York, reported Monarchs to be less abundant; all summer he reports seeing only 15 individuals.

Mrs. J. H. Mullen of Greenvale, New York, saw only 9 Monarchs and tagged but 4 of them. She concludes that the mass D.D.T. spraying was responsible.

We estimate the number of Monarchs to be one-third the number of last year. [D. H. Thomas, Columbus, Ohio.]

There were not as many butterflies as I had anticipated. [R. A. Stone, McKeesport, Pennsylvania.]

There were not as many this summer. I saw only 20. [Mrs. C. W. Zellman, Lake View, Iowa.]

The Monarch butterfly population was not particularly heavy this year, although there were a number of butterflies flying in the fields in northern Utah. [D. W. Davis, Logan, Utah.]

I might report that the number of Monarchs observed and reported in this area has been unusually small this year. [H. F. Brown, Norman, Oklahoma.]

During the summer of 1958, all co-operators agreed that the Monarch butterflies were scarce. In 1956 we had anticipated this scarcity and had alerted co-operators to the necessity of tagging as many as possible during the summer of 1957. The result was that many returns were obtained which would not otherwise have been procured.

1958

I also cannot understand why there were no Monarchs this year in this region. I did not see or band one this year. [G. H. Herber, Duval, Saskatchewan.]

I have not seen a single Monarch this year. [C. S. Quech, Transcona, Manitoba.]

We were unable to tag any Monarchs. We sighted only four during the season. [Dr. C. A. Ellis, Fredericton, New Brunswick.]

Unfortunately this year I tagged only two Monarchs. I seem to have missed any mass migration if there was one. [Glen R. Downing, Minneapolis, Minnesota.]

I don't suppose I saw more than eight Monarchs all summer, and no eggs or larvae, in spite of a fair amount of searching. [Mrs. L. G. Sengbus, Mount Clemens, Michigan.]

I saw only four Monarchs the whole summer. . . . Although I searched milkweed
RESULTS THIS YEAR WERE VERY DISAPPOINTING, BUT I GUESS THIS WAS TRUE COUNTRY WIDE. [MRS. L. W. HOHNS, LAITHROP VILLAGE, MICHIGAN.]

THIS WAS THE FIRST SEASON IN YEARS THAT WE HAVE NOT HAD MONARCHS IN OUR GARDEN—THOUGH USUALLY FEW IN NUMBER. [MRS. R. S. RAYNER, SOUTH PORCUPINE, ONTARIO.]

ALL SUMMER Long, WHILE WORKING FOR LANDS AND FORESTS I WAS BESIDE A LARGE FIELD OF MILKFLOWER... I SAW ONLY TWO MONARCH BUTTERFLIES. [H. DENISON, SOULT ST. MARIE, ONTARIO.]

LIKE OTHERS IN THIS PROJECT, LAST SUMMER I WAS UNABLE TO END MONARCHS. ONLY ONE APPEARED. [FRED S. ARMSTRONG, DEEP RIVER, ONTARIO.]

I AM RETURNING ALL THE TAGS, AS THERE WERE NO MONARCHS TO BAND. [LLOYD BEAMER, MEAFORD, ONTARIO.]

THIS YEAR THE MONARCH “JUST WAS NOT WITH US”. [H. JOHNSON, PETERBOROUGH, ONTARIO.]

ON AUGUST 3 I SAW THE FIRST BUTTERFLY AND AFTER THAT ONLY ON A FEW OCCASIONS DID I SEE ANY AT ALL... IN MID-SEPTEMBER THERE WERE ABOUT 100 FLYING QUITE HIGH PAST WILLOW BEACH, ONTARIO. IN ALL OF THE USUAL PLACES NO BUTTERFLIES COULD BE FOUND AND ON ONLY ONE OCCASION DID I SEE A CATERPILLAR. [T. MCDONALD, PORT HOPE, ONTARIO.]

WAS ABLE TO TAG ONLY ONE MONARCH ON AUGUST 18, AND SAW ONLY ABOUT TEN ALL SUMMER. [ALLAN MCNAUGHT, MONKTON, ONTARIO.]

APPEARENTLY THIS WAS A MONARCH-FREE SEASON. [MRS. M. LOVESY, TORONTO, ONTARIO.]

WE SAW ONLY FOUR AND THAT WAS FAIRLY EARLY IN THE SEASON. [MRS. J. M. GLYNN, LIMEHOUSE, ONTARIO.]

THE FIRST ONE TAGGED ON JULY 24 WAS THE FIRST ONE SEEN THIS YEAR. NO EGGS OR LARVAE WERE FOUND UNTIL AUGUST. NO BUTTERFLIES WERE SEEN AS LATE AS OCTOBER. [MISS RUTH HAIGH, NIAGARA FALLS, ONTARIO.]

THEY HAVE BEEN VERY SCARCE THIS SEASON. I WOULD BE SAFE IN SAYING THAT I HAVE NOT NOTICED OVER 3 OR 4 THE WHOLE SEASON. OTHER YEARS THEY HAVE BEEN VERY PLentiful IN OUR COUNTY OF NORFOLK AS WELL AS ON LONG POINT. I HAVE NEVER HEARD OF ANY PERSON SEEING THEM ANYWHERE ALONG LAKE ERIE THIS SEASON. [JOHN W. ALLAN, PORT ROWAN, ONTARIO.]

THE MONARCH WAS ALMOST ABSENT FROM THIS LOCALITY IN THE 1958 SEASON. [F. R. ARNOLD, CHIPPEWA FALLS, WISCONSIN.]

THIS WAS A VERY POOR YEAR—HAVED ONLY A SINGLE CHANCE TO TAG ONE MONARCH. [L. GRIEWISCH, GREEN BAY, WISCONSIN.]

I DON’T THINK I SAW MORE THAN A HALF DOZEN OR SO THE WHOLE YEAR. [W. E. SIEKER, MADISON, WISCONSIN.]

I PERCEIVED BUT AN APPROXIMATE DOZEN MONARCHS ALL SUMMER... I DIDN’T SEE THE FIRST ONE TILL ABOUT AUGUST. [MRS. K. W. FUGE, JEFFERSON, WISCONSIN.]
Throughout the entire summer I saw only two Monarchs. Neither I nor my friends were able to discover any caterpillars although they usually are fairly abundant.

[Stephen Gauss, Marblehead, Massachusetts.]

No Monarchs seen on Sanctuary this past summer. [Mrs. H. Underhill, Princeton, Massachusetts.]

The first Monarch I saw was a rather beaten female on July 20 in Barre, Mass. From my own observation, the western part of the state seems to be having a good year, but since I returned to Medford, Aug. 16, I haven’t seen one. . . . It looks like a bad year for the eastern part of Massachusetts. [Eric Johnson, Medford, Massachusetts.]

Indeed it was a poor year for Monarch butterflies. [Mrs. C. M. Williams, Lexington, Massachusetts.]

I spent most of the summer in the field in several New England areas and saw no Monarchs at all. [Richard W. Hildreth, East Holliston, Massachusetts.]

I found this a very scanty year for Monarchs. I was only able to tag four that I raised from eggs late in the season. [Mrs. C. W. Johnson, North Kingston, Rhode Island.]

We saw very few Monarchs here in Exira. [Miss Maxine Wells, Exira, Iowa.]

This year truly was a very poor year for the Monarch butterfly. [Robert A. Stone, McKeesport, Pennsylvania.]

This year I have not seen any Monarch butterflies on the move. [Joseph Woodburn, Jr., Philadelphia, Pennsylvania.]

Other years the Monarchs have been so numerous here, especially in October. But this year very few have been seen, and I have spent a lot of time out in fields with my net. I carried it in the car nearly every time I was on the road, watching fields and gardens. [Mrs. W. A. Lair, Landenberg, Pennsylvania.]

The few Monarchs I saw this fall were too wary or flying too high to catch. Late one afternoon during the migration period, I counted about a dozen flying from tree top to tree top, apparently preparing to settle for the night. Other than that they were few and far between. [J. W. Bracher, Cleveland, Ohio.]

We have had very few Monarchs this summer. This fall there have been very few too. Now is about the time of the big exodus and we’ve had only about 15 to band. [Mrs. E. Fleming, Bay Village, Ohio.]

This year I have caught only three—and seen a like number that got away. [Glen Feinlitz, Vermilion, Ohio.]

There were not too many Monarchs this year. If I had not raised 40, I doubt if I could have tagged my 50 for the year. [H. Birkhahn, Rock Island, Illinois.]

This year has been nearly a complete failure. . . . My bus driver reported seeing two Monarchs in late September, and I personally saw one Monarch in September, and that was it. [A. L. Brandhorst, Denver, Colorado.]

The Monarchs were late in appearing this year, the first being seen during the week of May 11.
GENERAL CONSIDERATIONS

I did not see any Monarchs this summer until Aug. 21. My husband and I searched milkweed patches in pastures and on roadsides during May and June and were unable to find a single larva. [Mrs. F. Throm, Overland Park, Kansas.]

Mrs. Throm has a report from friends near Deepwater, Missouri, saying there was no fall migration there.

I did not tag a single butterfly and saw not more than a dozen during the entire spring, summer or fall. [Mrs. D. Dreese, Arlington, Virginia.]

Monarch butterflies were rarely seen in the Blue Ridge Parkway last summer. [D. H. Robinson, Roanoke, Virginia.]

Monarchs have not been plentiful in my area this year. [E. A. Stoller, Benicia, California.]

Visited overwintering site at Stinson Beach and found only about 1/10 the normal number of butterflies. Where in previous years the branches were covered, the largest cluster seen had only approximately 200. [Mrs. Helen K. Court, Berkeley, California.]

I will admit that we don’t have as many as I have seen some years, but we have them in our grove by the hundreds. . . . I had people from Pacific Grove here last week and they said we have a lot more than they have up their way. [A. A. Crosbie, Cayucos, California.]

The situation here has been rather confusing. Last spring (1958) there were virtually no Monarchs in the trees in either Washington Park or in Palo Colorado Canyon (10 miles south). . . . However, there was the usual abundance of them at Milar’s Lodge. In November 1958, there were many of them at Milar’s, but not so many by Jan. 1, 1959. On Jan. 18, 1959, I visited Palo Colorado Canyon and saw not over 150 total. In November 1958 I visited Washington Park and could not find one. Sometime in November or December, 1958, a friend of mine saw thousands hanging in the trees at Natural Bridge State Park, just south of Santa Cruz. That is on the coast just north of here. [Paul Beard, Morro Bay, California.]

Monarchs are at least as plentiful as in previous years, if not more so. All the usual congregating places are swarming with them. Also, in my movements south along the coast almost to San Diego County, I have seen many in flight and several obvious swarming places. All reports from co-workers confirm this. [Nelson Baker, Santa Barbara, California.]

The clusters this year have been about normal, although I have noticed that they have been spread over a larger number of trees; however, this distribution may be caused by the very summery winter we have had.

The Monarchs arrived here about two weeks later than usual, but once they started arriving it took them less time to arrive than it usually takes. [Harold Ornabys, Ventura, California.]

In general I would say that there were approximately twenty per cent fewer butterflies at Death Valley in 1958 than in 1957. [M. B. Ingham, Death Valley, California.]

The Monarchs were late arriving and few in number. Where at times I’ve counted 30, this year I saw exactly 3, and haven’t seen a single one for several weeks now. [Miss D. E. McElwee, Oceanside, California.]
Monarchs have been very scarce this fall. They began coming over in late October, the first to be seen by the writer. I saw several flying southward, at 100 or more feet in one group. . . . There were approximately 100 Monarchs observed by the writer this fall, with fewer than a dozen low enough to reach. . . . In contrast with this fall, the writer observed a flight of several thousands in September 1957, and one dead tree was literally covered with Monarchs. [J. F. Combs, Beaumont, Texas.]

E. Schuchard of San Antonio, Texas, writes that the Monarchs did not appear on their pecan trees as usual.

I did not observe any Monarchs in this vicinity from the first week of February until the last week of March. However, since the last week of March (1958) the Monarch population has steadily increased and is now about at the early March level of last year. [Anthony Inglis, Galveston, Texas.]

[Miss Hilda White reported for Eagle Pass, Texas during the period from October 18 to November 9, 1958.] The Monarchs were not here in quantities as in previous years. At the airport, where last year they covered the trees, there were none—I never saw more than 10 flying over at any time.

At Maverick County Cemetery we were able to band about 850, but with more difficulty than one could have handled 8000 last year. They had to be single captures, as we saw only one cluster with as many as twenty in it, and it was too high to be reached by any of our nets.

Butterflies came in very small numbers, flying at great height without stopping. [Professor H. M. Hernández, Nueva Rosita, Coahuila, Mexico.]

The drop in numbers in 1958 was extremely well marked. Roosting sites, which in previous years had held such great numbers of Monarch butterflies that it was possible to tag many thousands of specimens, now held the occasional one or small groups of three or four. Larvae were extremely difficult to find and occurred only in late summer. No early migrants were observed in Ontario the first adults were found in August.

The weather conditions prevailing over North America during the spring and early summer are of interest in this connection. East of the Rocky Mountains the summer of 1958 was one of abnormal rain, overcast skies, and cool temperatures. Freezing temperatures occurred in the Gulf states from late February through March, April, and May. According to the O600 map of April 30, temperatures of 40°–50°F. existed in the southern states, with temperatures as low as 48°F. in southern Texas. Temperatures of 20°–25°F. occurred in northern Florida and the Gulf states in late February. Meteorologists have explained the unusually cold temperature as follows. The band of planetary winds which flows eastward across the North American continent at 10,000 to 40,000 feet ordinarily stays quite far north in summer, allowing the warm air to flow freely northward. During the spring and summer of 1958, however, the band of planetary winds moved southward, allowing the cold polar air to dominate the weather over most of the continent.
GENERAL CONSIDERATIONS

As a result of this cold weather, the returning migrant Monarch butterflies were unable to reach the breeding grounds and it is quite likely that the temperatures of 15°–20°F proved fatal to many of those caught in the more northern portions of the breeding grounds in late spring. Not only would such cold temperatures prove fatal in some instances, but the time required for development would be prolonged as well, thus reducing the possible number of generations. We therefore conclude that unfavourable weather conditions are primarily responsible for the reduction in numbers of the Monarch butterfly.

PARASITES AND PREDATORS

Parasites

Gillette (1888) reported obtaining fifty specimens of a new species of *Pteromalus* from a single Monarch butterfly chrysalis. The specimens were sent to Howard who described the species and gave it the name *archippe*.

Walker (1886) states that of the numerous Monarch butterfly larvae which he had reared, he had not bred an "ichneumon fly or any other parasite." He points out, however, that Riley records a dipterous fly, *Muscina* (Tachina) *archippe*, Riley, as a parasite of the larvae of the Monarch butterfly.

Scudder (1889) records Riley as stating that an ichneumon fly was reared from the Monarch butterfly "but nothing more is known of it." Eggs sent to Scudder from West Virginia produced several specimens of *Trichogramma intermedium*.

In the course of our rearing experiments a few parasites were obtained and a few others sent to us from our co-operators. The following species of dipterous parasites were examined and identified: *Achaetoneura schizurae* (Town.); *Achaetoneura archippe* (Will); *Exorista* sp. (In a letter, C. W. Sabrosky states: "some might call this *E. larvaenum* (L.) as it is often identified in this country, but there are some differences that make me hesitate to place a species name on it.")

No hymenopterous parasites were obtained from the rearing of over two thousand specimens, nor were any sent to us by our co-operators. In August, 1961, however, a number (approximately fifty) of ichneumon flies were found flying about a large rearing cage that contained two hundred larvae. These parasites were quite definitely attempting to gain access to the cage. Specimens were collected and sent to G. S. Walley, who identified them as *Temelucha recta* (Prov.). Not a single specimen was found inside the cage, and hence it cannot be concluded that this species is a parasite of the larva of the Monarch butterfly. Concerning the genus *Temelucha*, Mr. Walley reports as follows: "There are no host records in the literature of *Temelucha recta*, but the genus *Temelucha*, as far as is known, confines its
parasitism to microlepidoptera, and therefore I suspect the Monarch butterfly would not be a suitable host. All the specimens you sent are males, and these would probably be interested either in searching for females or possibly food material."

From the above information we may conclude that only three species of dipterous parasites are definitely known to attack the larva of the Monarch butterfly. There may be at least one egg parasite and perhaps one ichneumon larva parasite.

**Degree of Parasitism**

During the summers of 1955 and 1956, when the Monarch butterflies were most abundant, parasitism was high in some areas and low in others. The following reports were received from our co-operators:

Caterpillars collected for rearing purposes were found, in most instances, to be parasitized and died before entering the chrysalis stage. From the bodies of the caterpillars emerged white pupae (larvae) or grubs. These entered a brown pupal case. [L. Schellbach, Grand Canyon, Arizona, 1956.]

I have been raising caterpillars and so far out of twenty chrysalids five have shown signs of parasites. [P. Beard, La Honda, California, 1955.]

There seems to be a high rate of parasitism in Monarchs in Carmel Valley this year. Of several dozen chrysalids and larvae collected there this summer, fully 75% were with parasites. We found the same percentage (75%) of black parasitized chrysalids hanging on the milkweed as were eventually found to be parasitized from the larvae collected and reared. Last year the reverse was true. [P. Beard, Monterey, California, 1956.]

Practically all of our specimens were parasitized in the caterpillar stage. [A. Stein, Monticello, New York, 1956.]

I handled and raised no more than 25 caterpillars. I noticed that one out of every five had been [parasitized]. [E. Yarrow, Bronx, New York, 1956.]

During the caterpillar stage it seems rather susceptible to attack by parasites. During the summer of 1955 this was especially noticeable, and half of all caterpillars not raised in a cage were infected. Most lived to maturity and the parasitic grubs showed up only after the caterpillar had hung, and in one case after the chrysalis had formed the grubs emerged from the chrysalis. [H. F. Stiles, Grand Rapids, Michigan, 1956.]

I am sending . . . quite a collection of casualties among those larvae that I have been raising. The numbers seem to be quite high, many more than among those I raised last year. [Mrs. L. W. Hobbs, Lathrup Village, Michigan, 1957.]

Mrs. L. G. Sengbus of Mount Clemens, Michigan, reported larvae collected at Point Pelee, Ontario, on September 16, 1956, as being "heavily parasitized, and a total of 30 larvae of the parasite emerged from 10 Monarch butterfly larvae." These were sent to Mr. C. W. Salovský who identified them as Archaeoteneura archippicona.
Of approximately two thousand larvae, that were collected in the field in southern Ontario during the summer of 1956, only twenty-two were parasitized. This would indicate a low percentage of parasitism for this area.

**Unidentified Parasitism or Disease**

Occasionally an egg is found to be diseased. There may be a swelling on one side near the apex, which later turns into a hirsute growth resembling a mould, and at other times the egg turns black in colour and eventually becomes hard and dry.

The occasional larva will die without any appearance of having been parasitized, the entire body cavity becoming filled with a brownish fluid. Dissection does not indicate the presence of larval parasites.

It is not uncommon for a pupa to turn dark in colour. Such pupae, when dissected, exhibit a condition similar to that described above for the larva.

**Predators**

Very few animals are known to prey to any great extent upon the Monarch butterfly in any of its various stages. The occasional observation of predation has been submitted by our co-operators, and such occurrences have been mentioned in the literature.

I witnessed a pair of catbirds make continual passes at an adult Monarch in flight. They were unsuccessful. It was near a thicket where the birds were living, perhaps nesting. [B. Johnston.]

The other [Monarch butterfly] came out of the chrysalis very slowly and, after about two hours I put him on a butterfly weed. I saw a cuthird come down and pick him off. [I. LeMon.]

Mrs. L. G. Senghas collected an aphid-lion (Chrysopidae) feeding on a "medium-sized" Monarch butterfly larva.

On Sept. 18 I found a chrysalis attached to a milkweed plant. Ants had entered it and devoured the butterfly shortly before it was to emerge. [D. L. Mauger.]

Walker (1914) states that "like all the Danaidae, the insect, in all its stages, appears to be distasteful to every living creature. Although small insect-eating birds are wonderfully numerous at Callao, the larvae are untouched by them."

An article that appeared in Sonderling (bulletin of the Monterey Peninsula Audubon Society, vol. xiii, no. 4) states: "Natural Bridges Beach State park was carefully explored, and drowsy Monarch butterflies were located on two long branches of eucalyptus. Contrary to previous published reports, a bird was watched devouring a Monarch. A Black Phoebe captured the insect in the air and carried it to the branch of a tree. Here he made his characteristic clicking note and jerked his tail frequently while finishing his meal to the last bright wing-tip."
Mr. William Carrick, a nature photographer living in Toronto, Ontario, photographed a black-billed cuckoo feeding a Monarch butterfly larva to its nestlings.

During the first two weeks of January, 1955, we banded a thousand Monarch butterflies at Lighthouse Point, Florida. Observations prior to tagging revealed no indications of predation. However, on the morning on which the tagging operation was carried out, an unidentified bird picked up specimens bearing tags and flew away. The Monarch butterflies, at this particular time, were immobilized by the low temperatures. When the tag had been applied to the wing, the specimen was placed on the sand in the bright sunlight. The warm sand and the warm rays of the sun raised the body temperature of the butterfly so that it could fly back to the roosting site from which it had been removed. It was while the butterfly was struggling to fly that it was seized and carried off. We came to the conclusion at the time that the bright white tag on the wing attracted the attention of the bird.

Mr. Lucien Harris of Atlanta, Georgia, in company with Mr. H. L. Stoddard of Thomasville, Georgia, visited the locality at a later date and found that most of the population had been devoured. Many wings were found upon the ground—the bodies having been removed. Although most of the right front wings had tags, many had not, which indicated that the predatory bird in question did not confine its attacks to the tagged specimens. Concerning this incident Mr. Harris writes:

I explored the area and my finding of banded wings (and unbanded wings too) under myrtle bushes directly beneath horizontal perches in those bushes indicated that a number of birds (perhaps of the same species, such as the catbird) had captured and fed on the Monarchs after de-winging them. In addition to Monarch wings I found dragonfly wings, moth wings and grasshopper wings. It is my belief (and also Mr. H. L. Stoddard’s) that when the normal food supply becomes relatively scarce in January and February the Monarchs are eaten by birds when more desirable food is unavailable or scarce.

The above observations are the only evidence we have of Monarch butterflies being eaten by birds after twenty-one years of study and observations.

We observed that if a disabled Monarch butterfly remained on or close to the ground during the night the following day the body had been removed. We found, by setting small break-back traps, that the deer mouse, Peromyscus maniculatus, seemed to be responsible. We found also that a dead Monarch butterfly placed upon the ground was devoured by ants.

A shrew was observed tearing the wings of a Monarch butterfly that had recently emerged from the pupa and was resting, wings limp, upon the branch of a small bush located close to the ground. Monarch butterflies have been found on a number of occasions in the web of the common garden spider, Argiope aurantia. Various species of predacious Hemiptera, such as...
**Phymata rosea**, have been observed feeding upon the larva. None of the predators of the Monarch butterfly are of great significance, however, and do not control the population to any significant extent.

**Batesian Mimicry**

Bates (1862), who first proposed the theory of protective mimicry, was aware of the importance of physical factors in the environment producing similarities in the appearance of two species and he used this to explain how mimicry might be brought about: "It is perhaps true that the causes which produce a close or mimetic analogy cannot operate on forms which have not already a general resemblance, owing to similarity of habits, external conditions, or accidental coincidence."

McAttee (1932) after exhaustive studies on food preference in birds, based on stomach analysis, concluded that "the phenomena classed by theorists as protective adaptations have little or no effectiveness."

Manders (1911) points out that on the islands of Bourbon and Mauritius "there are no butterfly-eating birds . . . so that the cases of mimicry occurring there cannot be due to their influence." He points out that a trained observer can distinguish mimetic butterflies at a distance of twenty or thirty feet and hence a bird, which depends upon its powers of observation, would be able to distinguish them at a considerably greater distance. Drongos feed largely upon *Euploea* and hence a *Papilio* mimicking them obtains no protection in the vicinity of these birds.

Punnett (1915) presents a most convincing argument against the acceptance of the theory of protective mimicry. He points out that relatively few birds have been observed to prey habitually on butterflies, while some of those that do so show no discrimination between what according to theory should be pleasant to eat and what should not be pleasant. "Birds," he states, "are expected to bring about those marvellously close resemblances that sometimes occur by confusing the exact mimicking pattern with the model, while at the same time eliminating those which vary ever so little from it."

To credit such discrimination and yet, at the same time, suppose that birds are "fooled" by the resemblance can only be explained, according to this author, by assuming that "some birds do the rough work, others do the smoothing, and others again put on the final polish." Punnett lists the following objections to this theory: the difficulty of finding the appropriate enemy; the non-appearance of intermediates when the extreme forms are crossed; the relative scarcity of mimicry in the male sex; the existence of polymorphism among females of a species. Discussing the permutations and combinations of colour pattern within two groups of distantly related butterflies, Punnett accounts for similarities without involving a theory of mimicry as necessary for survival.
Franz H. Schweitzer (1936) is of the opinion that the view that some groups of insects have a repulsive odour or taste and serve as models for the palatable mimics is purely anthropomorphic since we cannot know the character of the odour to and the taste perception of the insect-eaters themselves. He points out that even for man the taste and odour of these insects living in the tropics was not actually tested until after the turn of the century and that the famous model Danais chryssippus is completely tasteless with no sharpness or bitterness. His conclusion concerning the supposed repulsive taste of the Danaidaeae and Acraeaeae is that it is a biological error that should be struck from science.

Wallace (1867) was one of the most ardent adherents to a theory of protective mimicry. Many of the examples which he gives belong in the category of protective resemblance to objects which are, in general appearance, static in nature, as for example the leaf of a plant (not a particular species), the bark of trees (not a particular species), and so on. Even the example of a tree frog mimicking a beetle (not a particular kind of beetle) might be accepted as protective resemblance, although the author does not indicate what protection is afforded by such resemblance. His weakest argument in favour of mimicry is indicated by the following passage: "If a bird began by capturing the slow-flying conspicuous Heliconidae and found them always so disagreeable that he could not eat them, he would after a very few trials leave off catching them at all, and this whole appearance, form, colouring, and mode of flight, is so peculiar, that there can be little doubt birds would soon learn to distinguish them at a long distance, and never waste any time in pursuit of them." Recalling Punnett's objection, it is difficult to understand how a bird "began" capturing a heliconid and then "learned" it was distasteful. If such were the case it is more difficult to understand how the heliconid developed an unpleasant taste. Further, each new generation of birds would have to learn and, in the process, many heliconids would perish.

Remington (1957) states that there are a number of biologists who find it difficult to accept the theory and attributes this to "an ignorance of the huge literature on mimicry, most of it published outside the Americas." However, he indicates a degree of doubt when he states "Danain butterflies... probably all are very distasteful to birds" (italics mine). He emphasizes the need for experimentation: "In view of the importance of experimental tests of mimicry hypotheses, it is disappointing that little carefully designed and statistically analyzed experimentation has been carried out on insect edibility to birds and the educability of birds offered mimics and models." In concluding his paper, the author points out that the entire subject is in need of investigation and re-evaluation.

That butterflies are attacked by many species of animals is unquestioned.
The problem of survival by mimicry has, however, centred around the predatory habits of birds. It is of interest, at this point, to consider the gustatory senses of birds in comparison with the olfactory and visual senses. Gurney (1922) cites an experiment in which strong-smelling substances, such as asafoetida, essence of anise, and oil of lavender were mixed with food given to turkeys, and it was found that, although some of the food did not contain such substances, no preference was shown. Even when prussic acid was tried they remained indifferent, although its strong fumes caused them to stagger. Wallace (1955) states that only the primitive kinds of birds possess good olfactory organs. Taste discrimination, which so often is correlated in part at least with smell, is an uncertain attribute in birds. Hann (1953) maintains that these senses of smell is poorly developed in birds, a fact borne out by the structure of the nose and the behavior of birds. On the other hand, almost every book on ornithology dealing with the anatomy and behavior of birds emphasizes the remarkable development of the organs of hearing and sight.

Although many species of insects have a disagreeable odor to man, we do not know that they have a disagreeable odor to predators. An ill-smelling histerid beetle will be devoured, without hesitation, by a lizard. However, the example of the Viceroy-Monarch butterfly has been used so extensively as a remarkable example of "protective mimicry" that the original theme of distastefulness and palatability to birds has been lost, and changed to the effect on the gustatory senses of man.

In tropical South America, and perhaps in other tropical regions, many species of Lepidoptera, moths and butterflies, have a strong odor to man. Longstaff (1912) deals with these various odors and compares them to the odors of "cockroach," "musk-rat," "rabbit-hutch," and "musty dung," none of which are agreeable to man. Unfortunately the author did not taste these various species: "I must confess that no enthusiasm has so far availed to bring me to the point of chewing a butterfly." Had he done so, he might have been surprised to find that although the butterflies possess a peculiar odor, this does not necessarily indicate unpalatability.

When collecting in the forests of Trinidad we were aware of the strong odor possessed by many species of butterflies and moths. Of the butterflies tasted, none could be classified as unpalatable if by this word we mean a bitter or obnoxious taste. One must bear in mind that what may be objectionable to one person may be pleasant to another. The fact remains that we are dealing with unpalatability to birds, not unpalatability to man. Therefore, since birds have no way of communicating their reactions directly, we can only ascertain the truth by careful field observations devoid of anthropomorphic interpretations.

It would be of distinct advantage to carry out controlled experiments, but
caged birds are obviously not good subjects for experimentation, and their reactions under such artificial conditions do not give the best indications of their reactions under natural conditions. Also, experiments carried out for a given species of bird are not indicative of the reaction for all species. Mander (1911) is of this opinion when he states that he is extremely doubtful as to any real value accruing from experiments on caged birds, whether nestlings or adults. No one believes that all butterflies taste alike, and some may be more palatable than others. He emphasizes the artificiality of such procedure by stating that "caged birds fed upon butterflies even with other insect food would no doubt learn in time to distinguish the different kinds, but this procedure to my mind begs the question, as it assumes that butterflies are an ordinary article of food in the wild state, a proposition regarding which the evidence here brought forward does not altogether support."

McAtee (1932) is of a similar opinion: "It has been demonstrated that behaviour of captive animals toward food is not a reliable indication of what wild individuals of the same species would do in the presence of the same food. In other words, since the feeding habits of an animal in captivity may vary widely from its known habits in the natural state, there is no avoiding the conclusion that the results obtained under experimental conditions do not indicate the part the animal might play in natural selection. [Such experiments] having no certain value in themselves, they must be checked up with definite knowledge of the natural food habits."

Since birds have been considered to be the important predators of butterflies, experiments have been carried out by Finn (1895), Jones (1932), Carpenter (1921, 1942), and others, in an attempt to ascertain whether or not a model is unpalatable to birds and that the mimic thus gains protection. Recently Brower (1958a) investigated the possible unpalatability of Monarch butterflies and the protection offered to the supposed mimic, the Viceroy, by experiments using the Florida Brush Jay. In the discussion the author states: "As the data showed, the Monarch was unacceptable on sight alone at some time to all the experimental birds. The theory that models are unpalatable and that their color pattern is a sign of unpalatability is thus supported." Certainly, the Monarch butterfly was not unpalatable, because in the text the author states:

All four birds reacted in their initial trial with the Monarch by killing or pecking the butterfly. This suggests either that the four experimental birds had not had experience with Monarchs in the field prior to capture, or, if they had experienced Monarchs in the wild, they had not remembered the unpalatability of Monarchs on sight alone under the cage conditions. That the lesson of unpalatability was never finally learned in the course of the experiments is seen in the repeated lapses... into pecking or killing a Monarch after several trials during which the Monarch was not touched. On the basis of sight alone, E-4 was outstanding in its failure to remember for more than two successive trials that the Monarch was unpalatable.
If the Monarch butterfly survives because it is unpalatable to birds, this experiment would not indicate it. The conclusion by the author that "the Viceroy is more edible than the Monarch, but less edible than the non-mimetic butterflies" is, we believe, valid. It would be improved by substituting the following statement: Florida Brush Jays under caged conditions prefer to eat paralyzed or dead specimens of *Papilio glaucus* and *P. palamedes* in preference to paralyzed specimens of the Viceroy; and they prefer to eat paralyzed Viceroy butterflies rather than paralyzed Monarch butterflies. The last conclusion in Brower's summary is as follows: "Three of the four experimental birds remembered to reject a Monarch and a Viceroy on sight alone, after a period of over two weeks had elapsed since their last experience with these butterflies." No importance was attached to the reaction of the fourth experimental bird, which was an important disclosure, because it indicated that unpalatability of a given species of insect varies throughout a predatory species of animal.

The work done by McAtee on a careful analysis of stomach contents still remains the most exact data on what the feeding habits of various species of birds are under natural conditions, and as this author has so ably demonstrated there is no evidence substantiating the theory of Batesian mimicry.

Voluminous as the literature may be it is filled with what appear to be examples of Batesian mimicry with no substantiating data. A species of fly may resemble a species of wasp; this does not indicate survival due to mimicry, however, because if we accept such an anthropomorphic interpretation we would have to explain why the vast majority of species of flies that do not look like wasps have succeeded in surviving. It is also necessary to bear in mind that the face of the earth, its fauna and flora, has passed through many and various phases. Species and families of living organisms that once dominated the earth have become extinct. Perhaps a given colour pattern may have evolved to harmonize with the landscape, thus giving protection to the species against a certain type of life dominant at that time, and when the landscape changed and the predatory species vanished, the colour pattern of the butterfly remained, since it was not of selective significance.

We are of the opinion that far more observational evidence is needed before we can accept as fact the value of the Batesian theory of protective mimicry for survival. In our field observations of the Monarch and Viceroy butterflies over the past twenty-two years, the evidence seems to be in favour of rejecting rather than accepting the theory.

**Integumental Anatomy**

We are deeply indebted to Dr. Paul R. Ehrlich of the University of Kansas for permitting us to reproduce here much of his original research as pub-
lished in the *Science Bulletin of the University of Kansas* (1958). It is included in the present work because we wish to bring together in one volume as much information as possible on the Monarch butterfly.

**THE HEAD**

(Figure 45)

The most prominent features of the hypognathous head are the compound eyes; they are approximately hemispherical and their combined width is almost one half that of the entire head. The sclerites of the frontal portion of the head between the eyes are termed here, collectively, the face. The homologies of these sclerites are uncertain, but it seems unlikely that the terminology used by Michener (1952), which is based on that of DuPorte (1946), reflects the true situation. The nomenclature employed here for the facial sclerites is based on DuPorte’s more recent work (1956). The central area of the face is occupied by the large protuberant roughly circular *frontocep palp* sclerite. This structure is bounded above by a sulcus connecting the inner margins of the antennal sockets, the *transfrontal suture*. This suture is only weakly in evidence externally, but is represented by a fairly strong ridge internally. Dorsolaterally the sclerite is bounded by the antennal sockets, at the edges of which it is infolded to form strong ridges along the lower parts of the sockets. These ridges connect with the ridge of the transfrontal suture and each bear on its lateral end a small dorsal projection, the *antennifer*, which is an articulation point for the scope of the antenna. Laterally the frontocep palp sclerite is bounded by the curved *laterofacial sutures*, which contain the prominent anterior tentorial pits and run from the dorso lateral edges of the labrum up to the ventral margins of the antennal sockets. These sutures, although not extremely prominent externally (they lie at the base of the forward thrust plate of the frontocep palp sclerite), are represented internally by large ridges which are major strengthening features of the forward wall of the head. Approximately the lower fifth of the frontocep palp sclerite is separated from the main portion by a transverse heavily sclerotized band, designated here the *clypeal band*.

Below the frontocep palp sclerite and separated from it by a weak *clypeal suture* is a small transverse sclerite, the *labrum*. The labrum has on its ventrolateral edges cylindrical projections called *pilifiers*, each of which bears a row of bristles on its inner edge.

The anatomical facts presented by DuPorte (1956, pp. 113–114, fig. 4) have been confirmed by dissection by the present author. The validity of DuPorte’s interpretation of these facts rests in large part on the answers to some of the more basic questions of insect morphology. These questions, concerning the value of musculature and innervation as morphological landmarks, the significance of the position of the anterior tentorial pits and their relationship to the so-called epistomal and frontogena l sutures, and the strictness with which interordinal homologies of facial sclerites or areas can be drawn, cannot be taken up in this paper.

The areas between the laterofacial sutures and the inner margins of the eyes are known as the *paraocular areas* (Michener, 1944). Near the ventral limit of each paraocular area, behind and slightly lateral to the pilifier, is a small protuberance, the *mandibular rudiment*.
The antennae, situated at the dorsolateral margins of the frontoclypeal sclerite, are long (each being more than three times as long as the head is wide) and clubbed. The basal segment, or scape, of each antenna is relatively large, ringlike, and wider anteriorly than posteriorly. It has on its anterodorsal edge a small
articulatory process. The second segment, or pedicel, is a simple ring approximately one-half the size of the scape. The remainder of the antenna is the flagellum, which in the monarch is composed of 43 segments. The segments increase very gradually in length, and the diameter of the antenna gradually becomes slightly greater from the proximal end of the vicinity of segment 30. In this region the width of the segments (and, of course, of the whole antenna) rapidly increases, while the length of the segments is somewhat reduced. The greatest width is reached in the vicinity of segments 39 and 40, while segments 41, 42 and 43 become progressively narrower. The resultant club is somewhat more than one sixth the length of the antenna.

The ventral surface of the head between the eyes is occupied by the proboscisial fossa, which is very shallow in this species. The maxillae occupy most of the anterior section of the fossa. Most prominent are the galeae, which are greatly elongated, concave mesally, and grooved together to form a tube through which liquid food is drawn by the sucking pump. Supporting the galeae, and extending laterocaudally from them, are the stipites, each bearing a small tubercle directly behind and slightly lateral to the galea, the maxillary palp. Each stipite is infolded
and longitudinally divided into two sections by an area of light sclerotization (shown by heavy stippling in figure 45). The inner margins of the stipites are bilobed. Behind each stipe is a small, triangular sclerite, the cardo. The central and posterior parts of the fossa are occupied by the somewhat triangular labial sclerite, which bears caudally the large sockets of the labial palps. An invagination along the mid-line of the sclerite produces an internal ridge, the labial apodeme. The anterior rim of each palpal socket has two short articular processes. The anterior parts of the walls of the proboscidial fossa, lateral to the maxillae, are the hypostomal areas. Projecting forward from their sockets at the rear of the labial sclerite and up across the face are the large, three-segmented labial palps. The middle segment of each palp is the longest; the distal one is the shortest. All segments are essentially cylindrical, but the distal one is terminally produced into a point.

The posterior surface of the head is broken centrally by a large opening, the foramen magnum, which is bisected by a transverse bar, the tentorial bridge. At the lateral ventral corners of the bridge are two depressions, the areas of articulation of the cervical sclerites. Along its dorsal and dorsolateral margins the foramen is bordered by the postocciput. This sclerite is well defined dorsally by the arched postoccipital suture, but the suture is indistinct laterally as it runs down to the posterior tentorial pits. The latter portions of the suture are shown as dotted lines in figure 46. The ventral border of the foramen is the main portion of the labial sclerite behind the sockets of the palps; the ventrolateral borders consist of thin

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**Figure 47.** Danaus plexippus. a, lateral view of head; b, antenna.
upward growths of the posterior corners of the labial sclerite. The suture separating this portion of the labial sclerite from the occiput is called here the \textit{paralabial suture}. Internally the dorsal portion of the postoccipital suture is represented by a strong ridge, while the lateral portions can be detected only as areas of heavy sclerotization. The labial suture is, however, represented by a rather strong ridge, at least in the ventral two thirds of its length.

Lateral to the labial and postoccipital sutures, and covering the greater portion of the caudal surface of the head capsule, is the \textit{occiput}. Approximately the inner one third of the occiput on each side of the foramen is separated from the remainder by two arcuate, heavily sclerotized streaks, the \textit{transoccipital bands}.

In the center of the dorsal surface of the head is the \textit{vertex}, an area delimited by the \textit{transfrontal suture} anteriorly, the antennal sockets anterolaterally, and the \textit{temporal suture} laterally and caudally. The temporal suture is represented internally by a rather strong ridge, but both the suture and the ridge are indistinct near the antennal sockets and in the center of the caudal portion. Lateral to the temporal suture, and running parallel to it from the antennal sockets to the postoccipital suture, is the \textit{paratemporal suture}, represented internally by a ridge which is not as distinct as that of the temporal suture. On the dorsal surface of the head the area between the two sutures is here called the \textit{temporal area}; on the caudal surface of the head there is a U-shaped depression between the temporal suture and the paratemporal and postoccipital sutures, called here the \textit{temporal fossa}.

Within the fossa are two reniform areas (outlined with dotted lines in figure 46a) in which there are a great many setae. These areas, possibly sensory, may be the \textit{chelaeformata} of Jordan (1923).

It should be noted here that the homologies of the various features of the dorsal and caudal surfaces of the head capsule are much confused by the presence of secondary sclerotizations. The above interpretation has been necessarily arbitrary, in an attempt to arrive at names which can be employed throughout the comparative work which will follow this paper.

The \textit{tentorium} consists of the posterior tentorial bar already described and two simple anterior arms running between the anterior and posterior tentorial pits. The anterior arms are somewhat thicker anteriodly than posteriorly. Between the anterior arms in the front of the head and attached to the cranial wall near the lower edge of the labrum is a fibrous ventral part of the sucking pump. The structure is roughly semicircular and is made up principally of the \textit{hypopharynx} (see Schmitt, 1938). The dorsal portion of the pump is not sclerotized and does not concern us here.

The compound eyes are separated from the head capsule by thin \textit{ocular diaphragms}. These are membranous disks perforated by large oval openings (long axis dorsoventral) through which pass the optic nerves. The diaphragms each have a small sclerotized area bordering the opening.

\section*{Thorax}
(Diagrams 48-57)

\textbf{Pronotum:} The pronotum is much smaller than either of the segments of the prothorax. The \textit{pronotum} is considered to be divided into three parts, a curved roughly triangular \textit{dorsal plate}, and two flat, dorsomedially fused \textit{lateral plates}. The dorsal plate is pointed at its posterior end, the beaklike point being curved ventrally and articulated with the prescutum of the mesothorax. The fused portions
of the lateral plates form a Y-shaped structure which articulates with the dorsal plate at the tips of the arms of the Y, the crotch of the Y is membranous. Just above the lateral plates of the pronotum and forward of the cephalic margin of the dorsal plate are the large, roughly hemispherical patagia. These well-sclerotized paired structures are the most conspicuous features of the dorsum of the prothorax. The ventral ends of the lateral plates of the pronotum are fused to the dorsal ends of the propleura, which in turn are fused with one another mid-ventrally, the fusion being indicated by a faint discrimen. Between the ring formed by the lateral plates of the pronotum and the propleura and the foramen magnum of the head is the membranous cervix. Bridging this cervical membrane lateroventrally on each side are the cervical sclerites. They are T-shaped, and each has a circular sclerotic pad bearing numerous setae on the stem of the T; the pads are called here cervical organs. The stem of the T articulates internally with the lateral extremity of the tentorial bridge and the upper arm of the T externally with the dorsal part of the cephalic margin of the propleura. Just forward of the line of fusion of the propleura, but not cut by the discrimen, is a narrow mid-ventral sclerite projecting into the cervix, called the presternum.

Internally the discrimen is represented anteriorly by a very weak inflection and caudally by a small intercoxal lamella. Lateroventrally on the rim of the coxal socket is the pointed pleural articulation of the coxa. Externally the discrimen may be traced between the bases of the coxae as a mid-line marking the base of the intercoxal lamella; it ends at the caudal margin of the coxal sockets at the oval furcasternum. In the center of the furcasternum can be seen a dark area repre-
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senting the furcal pit. Internally the furcasternum is produced into a heavily sclerotized two-pronged furca, which is joined to the pleuron by a plate which is to a large extent transparent, the furcal lamella.

Bridging the pro-mesothoracic intersegmental membrane midventrally is a narrow sclerite, the prothoracic spinasternum. The spinasternum tapers to a point anteriorly where it joins the furcasternum of the prothorax, and gradually widens posteriorly, so that where it meets the mesothoracic katepisternum it is nearly as wide as the furcasternum. The caudal end of the spinasternum is notched so that it joins the katepisternum at two points with a membranous triangle between them. Near its middle the spinasternum is deeply invaginated along with the adjacent membrane, forming an internal projection, the spina.

mid-laterally in the pro-mesothoracic intersegmental membrane is the first spiracle. The upper half of the anterior border of the spiracular opening is occupied by the narrow anterior spiracular sclerite, which bears near its ventral end a long apodeme. The entire posterior border of the opening is made up of the bandlike posterior spiracular sclerite, which has a small apodeme at its lower end.

Mesothorax: The mesonotum occupies the greater part of the dorsum of the pterothorax. It is divided into three sclerites, the prescutum, scutum and scutellum. The smallest of these, and the most anterior, is the prescutum. It is curved strongly ventrally in front where it articulates with the pronotum, and bears on its antero-ventral margin the thin bilobed first phragma. Arising from the lateral margins of the first phragma and hanging free in the body cavity are a pair of phragmal arms. Each lower lateral angle of the prescutum is produced into a long, slender process or presural extending latero-caudoventrally to just in front of the tegular arm. The suture between the prescutum and scutum is represented internally by a weak ridge.

![Diagram of Drosophila mesothorax](image-url)
The mesoscutum is the largest sclerite of the thorax. The lateral edges of the anterior part of the scutum are produced into sloping plates, the suralarcs. Internally each suralarc is separated from the main part of the scutum by a strong ridge, the scutal ridge, which runs from the posterior margin of the prescutum to the posterior margin of the scutal incision. The scutal incision is a deep notch in the lateral edge of the scutum just behind the suralarc. From the scutum just behind the incision a plate, the adnotale, projects forward forming a lateral border for the posterior part of the incision. The first axillary sclerite articulates with both the suralarc and the adnotale, which together make up the anterior notal wing process. Separating the scutum from the smaller mesoscutellum is the inverted V-shaped scuto-scutellar suture. The suture is represented internally by a strong ridge. Projecting forward and laterally from the end of the scuto-scutellar suture is a horizontal shelf, the postalar plate, the posterior portion of which is membranous. The anterior mesal part of the plate is in the form of a sclerotic arch which is continuous with the caudal part of the adnotale (this arch is hidden by the scutum in figure 28). The anterolateral corner of the postalar plate is produced as the posterior notal wing process, to which is fused the fourth axillary
sclerite. Behind the membranous part of the plate is a thin sclerotic strip, and mesal to this strip is the base of the membranous axillary cord. Lateral to the plate and mesal to the axillary cord a rounded process of the postalar portion of the epimeron projects through the membrane. This process is partially fused to the sclerotic part of the postalar plate.

Figure 52. Danaus plexippus. Dorsal view of thorax. Broken line represents outline of left tegula, removed to show structures beneath it.

A narrow membranous area separates the postnotum (the phragma-bearing plate) from the mesoscutellum. The second phragma is very large and somewhat triangular in lateral view, with dorsal and ventral angles posteriorly and a mid-lateral angle forward. The anterior angles are paired, and each articulates with the mesoscutum in the socket of a protuberance of the ventral edge of the scutum immediately behind the caudal end of the adnotale, the phragmal articulation. Dorsally, at the rear of the phragma, are two prominent triangular projections, the phragmal processes, whose tips serve for muscle attachment. The surface of the phragma itself displays a fairly complex pattern of ridges and varying sclerotization. Some major features of this pattern are a lightly sclerotized, anteriorly re-
The more prominent features of the sternopleural region of the mesothorax are the episternum, epimeron and coxa. The mesepisternum consists of a large katepisternum with a tiny anepisternum nestled between the dorso-caudal corner of the katepisternum and the ventral side of the basalarium. Approximately the lower third of the katepisternum is separated from the rest of the sclerite by the prescocal suture, which runs from the pleural suture to the anterior margin of the katepisternum at the point where it is joined by the prothoracic spinasternum. This part of the katepisternum is called here the sternopleurite. Immediately in front of the coxa the sternopleurite is traversed by the marginopleural suture, which runs from the pleural suture to the discriminum. The internal marginopleural ridge is strongest where it merges with the pleural ridge, becoming progressively weaker until it meets the base of the lamella of the discriminum. Internally the prescocal suture forms a strong ridge, the priscocmal ridge, which is continuous with the thickened upper edge of the lamella of the discriminum. Above the prescocal suture the katepisternum is separated by a vertical suture, the pre-episternal suture, from a narrow anterior sclerite, the pre-episternum.
The pre-episternal suture is represented internally by the pre-episternal ridge. This ridge is rather small at its origin near the anterior part of the precoxal ridge, but becomes increasingly prominent as it curves dorsally and merges with the pleural ridge.

![Diagram of thorax and base of abdomen](image)

**Figure 54. Donaus pleippus. Ventral view of thorax and base of abdomen.**

Mid-ventrally the sternopleurites unite in a suture, the *discrimen*, whose inflection forms the very high transparent lamella of the *discrimen*. The base of this lamella, in the form of two narrow strips of the sternopleurites, extends backward between the bases of the coxae to the ventral articulations of the coxae. Posteriorly the lamella of the *discrimen* merges into the mesothoracic furca, which arises from the *discrimen* above the coxal articulations. The furca, when viewed in caudal aspect, is roughly Y-shaped, the arms of the Y (the secondary furcal arms) fusing with the ventrocaudal corners of the prealar portions of the epimera. Running from the pleural ridges to the anteromesal parts of the secondary arms are the tendonlike primary furcal arms. The furca is a complex structure exhibiting varying
Figure 55. Danaus plexippus. Mesal (internal) view of right half of mesopleuron and sternum and prothoracic sternum. Posterior portion of epimeron omitted.
Figure 56. *Danaus plexippus*. Mesal (internal) view of right half of metapleuron and sternum and base of abdomen.
degrees of sclerotization in different areas. Major features are three thin rounded lamellae projecting posteriorly from the main stem of the furcal and from near the lateral borders of each of the secondary arms.

The mesepimeron is divided into two parts, an anterior prealar portion and a posterior postalar portion. The dorsal edge of the prealar portion curves strongly downward near the middle, leaving a relatively large area between it and the ventral side of the subalar. Near the dorsal part of the anterior border of the epimeron a small plate is separated from it, the pre-epimeron. The prealar portion is separated from the dorsocaudal corner of the prealar section by a line. The anterior end of this portion is inflected and curved downward into the body cavity as an apodeme and upward as a process which penetrates the two membranes mesal to the axillary cord and emerges lateral to the postalar plate. Externally the postalar portion of the epimeron appears as a long strip which fuses caudally with the dorsal part of the postnotum.

Between the epimeron and the episternum is the deeply inflected pleural suture. The internal manifestation of this suture, the pleural ridge, is the most prominent feature of the mesal wall of the mesothorax. Near its dorsal limit, at the point of attachment of the primary furcal arms, the ridge is produced mesocaudally into a small plate. The inflection producing this plate is responsible for the formation of the pre-epimeron, although the deep inflection of the pleural suture in this area makes the exact method of its formation difficult to determine. Narrow strips of the anepisternum and epimeron, carrying with them the pleural suture, project dorsally between the basalar and subalar areas as the pleural wing process. From this process just mesal to the can dorsal corner of the basalar a tubular internal process projects anteriorly behind the basalar, the tegular arm. The arm terminates just in front of the basalar in two lobes, one mesal to the other, whose surfaces are external. Articulating with the lateral lobe of the arm is the large lobed tegula. The smaller lower lobe of the tegula curves beneath the leading edge of the wing.

In the region of the pleural coxal articulation the pleural ridge becomes a quite complex structure as it is joined by the precoxal ridge, the marginopleural ridge, and the ridges formed by the inflected dorsal and anterior margin of the meron. The coxa (which is discussed here because it is an integral part of the thoracic capsule) consists of two sclerites, a relatively narrow anterior eucosta (Madden, 1944, not Michener) and a bulbous posterior meron. The nature between the two (the coxal suture) seems to be a line suture, with the internal ridge representing the inflection of the border of the meron alone. The dorsomesal border of the eucosta is inflected and produced into the relatively large eucostal apodeme. The caudo-ventromesal part of the coxa is membranous, containing one round sclerotic island, the coxal sclerite. A small caudomesal lip of the upper part of the meron, the precoxal sclerite, is separated from the rest of that structure by the postcoxal suture, which is represented internally by a weak ridge continuous with the inflected border of the meron. At the top of the coxal suture there is a tiny sclerite, a lip of the meron beyond its inflected edge, the basicoxite.

Above the episternum in front of the pleural wing process is a roughly diamond-shaped plate, the basalar. Internally a triangular cavity occupies the central part of the sclerite. A large, for the most part lightly sclerotized apodeme is attached by an almost transparent tendon to the anterior corner of the basalar. Above the epimeron, and separated from it by a considerable expanse of membrane, is the other epipleurite, the large elongate subalar. Internally the subalar has a con-
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**Figure 57.** Danaus plexippus. a, posterior view of mesothorax, tergum omitted (the line marked by short cross lines represents attachment of mesometathoracic intersegmental membrane). b, posterior view of metathorax (line of metathorax-abdominal intersegmental membrane indicated on left half of figure only).
cavity anterointerioventrally, and bears a conspicuous winglike apodeme projecting from its mid-section into the body cavity.

In the meso-metathoracic intersegmental membrane close to the upper part of the pyriform portion of the epimeron, is the second spinucle. It is bordered in front and behind by fringed, lightly sclerotized plates, the anterior and posterior spinocorollar sclerites.

Metathorax: In the metanotum the metascutum is divided into two lateral portions by the metascutellum. The scutocutellar ridge is very strong and wall-like, dividing the bulging upper part of the metanotum into three compartments. The anterior notal wing processes are merely small projections of the anterolateral walls of the scutum, while the posterior notal wing processes are long slender projections from the posterior part of the scutum. The scutal ridge is present in the same position as in the mesoanotum, but is, of course, much shorter. There is no scutal incision. A thin membranous area separates the complex metasternum dorsally from the metascutellum. The salient features of the postnotum are a ventrally truncated heart-shaped area at the mid-line of the dorsum, and the phragma which is divided into two arms, each tipped with a flat oval plate, which project into the body cavity from near the lateral extremities of the postnotum. The whole postnotum is so well fused with the tergum and epimeron laterally that its limits are difficult to ascertain.

As can be seen from the figures, the positions of the various sclerites of the metathoracic pleural and sternal areas are very similar to the positions of the homologous sclerites of the mesothorax, although their shapes are quite different. Therefore only major differences will be discussed here. The anepisternum is a small but well-defined sclerite just above the shoulder of the katepisternum. It bears numerous bristles, and although it is closely associated with the basalar and pleural wing process it is separated from each by a distinct line suture. The precocxal suture is absent, leaving the katepisternum as an undivided sclerite. There is an insignificant pre-episternum, which does not continue ventrally to the level of the coxa. The meson is sharply reduced in favor of the epimeron.

Internally the metathorax presents quite a different aspect from the mesothorax. The lamella of the discrimin is arched, arising at the base of the pre-episternal ridge and terminating at the base of the furca. The top of the lamella is thickened as in the mesothorax, and there are two short pointed thickenings in the base of the lamella. There is, of course, no precocxal ridge. The exocoxal apodeme has on its dorsum a small tubercle to which a muscle is attached. The metafurca is entirely different from the mesofurca. Its most prominent feature is a forward thrust structure, shaped somewhat like an arrowhead when seen in dorsal aspect, which overhangs the lamella of the discrimin. The posteriorly projecting secondary arms are fused together ventrally forming a V-shaped trough which becomes progressively shallower caudally. The arms are thin and are broadly fused to the epiphyses which are curved medially and form the caudal border of the thorax beneath the attachment of the abdomen. The transparent, tendon-like primary furcal arms arise near the base of the furca and attach to a plate which seems to be an outgrowth of both the pleural ridge and the epimeron just posterior to it. There is, however, no obvious pre-epimeron. The regular arm and tegula are absent.

The basalare is much smaller than that of the mesothorax, and bears on its inner surface a relatively large blunt basalare apodeme. The subalar is small and seems to be merely an external manifestation of a sclerotic cup to which the subalar muscle is attached.
The prothoracic legs of *Danaus*, as in all other so-called "four-footed butterflies," are greatly reduced. The 
profemur is long (approximately the same length as the 
profemur) and grooved on its lateral face. The male 
tarsus is simple (not divided into tarsomeres) while that of the female is club-shaped and divided into four 
tarsomeres, a long proximal one, and three compressed distal ones. On the caudal 
side of the distal end of the first three tarsomeres are paired spines. These are 
complemented by lobes on the caudal side of the proximal end of the last three 
tarsomeres which bear bundles of setae which cup around the bases of the spines.

The meso- and metathoracic legs are similar in both sexes. In specimens which 
have the scales intact, however, there is a small brush of narrow setalike scales 
somewhat more than halfway up the medial side of the tibia of the mesothoracic 
leg. This is absent in the metathoracic leg. The tibiae of the mesothoracic and 
metathoracic legs in the females bear numerous spines, while there are only a few 
scattered spines in the males. The spines of the proximal tarsomere are also more 
prominent in the female.
In the pretarsus, the unguifer (the dorsal plate to which the tarsal claws or ungues are articulated) is only slightly sclerotized. The most prominent feature of the ventral side of the pretarsus is the large flat unguisotractor plate. This plate is tapered internally into a long thin apodeme, the unguisotractor tendon. Just in front of the unguisotractor plate, between the basal parts of the claws, is a small, membranous lobe, the empodium. Just dorsal to the empodium is a small lightly sclerotized protuberance, the protilium. Lateral to the unguisotractor plate are two membranous lobes, the pulvilli. The ungues are not notched, and are abruptly hooked terminally and thickened basally.

**Figure 59. Dana sp. a, detail of distitarsus of pterothoracic leg of female. b, ventral view of pretarsus of pterothoracic leg.**

**Wings and Wing Bases**

(Figures 60-62)

The areas of the wing articulations present an extremely complex picture. Each area consists of two membranes and associated sclerotic plates; an upper membrane connecting the dorsum of the wing with the tergum, and a lower membrane connecting the venter of the wing with the pleurites. These membranes are called the upper and lower alary membranes respectively.

In these membranes are found a series of plates which are among the most important structures of the wing articulation, the axillary sclerites. In the mesothorax there are four axillary sclerites. The first axillary is visible only from the upper side. It is roughly Y-shaped, with the base of the Y articulating with the adnotale, the anterior arm with the suralar mesally and the second axillary laterally, and the posterior arm with the second axillary. The second axillary is bilobed when viewed from above. The medial lobe articulates with the first axillary mesally and the third axillary posterolaterally, the lateral lobe is narrowly fused to
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Figure 60. Danaus plexippus. a, dorsal view of mesothoracic wing base, wing held horizontal; b, lateral view of mesothoracic wing base, wing held vertical.
its anterolateral corner. Distally the lateral lobe is in contact with the complex basal sclerotizations of veins Sc, R, Cu and 2V. Beneath the upper alary membrane both lobes of the second axillary send plates ventrally which fuse into a blunt process. This process articulates with the pleural wing process, a small portion being exposed ventrally.

The third axillary is V-shaped, with the distal arm of the V lying in the upper membrane and appearing from above as a slightly arcuate oblong sclerite. The
proximal arm projects ventromesally between the membranes from the caudal end of the distal arm. A small portion of it penetrates the lower membrane and can be seen as a narrow strip above the subalar. The muscle of the third axillary sclerite is attached to the crotch and proximal arm of the V. The fourth axillary lies in the upper membrane and is fused to the posterior notal wing process, from which it is differentiated by a constricted area. Its distal end lies under the flap of membrane enclosing the third axillary muscle and works against the proximal arm of the third axillary.

In front of the first and second axillary sclerites is the pointed basal process of the subcosta (Sc), which articulates with the suture and the anterior arm of the first axillary. On the ventral side the base of the fused Sc + R is expanded into a bilobed sclerite, the radial plate.

In the metathorax there are only three axillaries, the fourth axillary being absent. The pattern of the sclerites is similar to that of the mesothorax, although their shapes are quite different. The first axillary is long and thin, with the posterior arm of the Y reduced to a mere bulge. The second axillary is very irregular and is fused anteriorly with the basal process of the Sc. Near the lateral edge, the second axillary bears a ventral process which penetrates the lower alar membrane, producing a rather large, ventrally exposed sclerite which articulates with the pleural wing process.

The third axillary is shorter than that of the mesothorax, and the muscle is smaller. It is more triangular than V-shaped. The portion visible from above is oblong, and the anterior and posterior ends of this portion are inflected ventrally and fused together to form a process which penetrates the lower membrane. The muscle is attached to the upper posterior angle of the rough triangle thus formed. The posterior notal wing process articulates with the caudomedial side of the lower apex of the triangle.

Just medial to the base of Sc + R, and projecting anteriorly is a large costal sclerite. On the underside a bilobed radial sclerite is present.

Figures of the wing venation are presented for completeness and for orientation in connection with the figures of the wing bases. The venation of the Monarch has been figured numerous times before, and nothing new is added here. The system of naming the veins is adopted from Klots (1951) with the substitution of anal veins for “anal veins.”

Abdomen
(Figures 62–64)

Pregenital segments: Because of the modification of the eighth sternum of the male into pseudovalves, it can be said that there are seven pregenital abdominal segments in both sexes of Danausplexippus. The first abdominal segment is highly modified, as in most higher insects, for articulation with the metathorax. The anterior part of tergum 3 is membranous. The sclerotic portion of the tergum is dorsocaudally bulged, giving a pouchlike effect. Its caudal margin slightly overhangs the second abdominal tergum. On each side of the first tergum, near its margins, is a deep inflection, the tergal groove. The heavy internal ridge of this inflection is called the tergal brace. The anterolateral corners of the tergum are produced laterally into small protuberances, the tergal lobes. The first abdominal sternum (sternum 1) is almost completely membranous, only a small posterior sclerotic portion remaining which is fused to sternum 2. This portion of the
Figure 62. Donax pleiippus: a, lateral view of male abdomen; b, wing venation.
sternum is also fused to a thin process of the postero-lateral corner of the tergum, the postspiraicular bar. Just in front of this point of fusion another thin process is emitted by the sternum which crosses the pleural area below the first abdominal spiracle and terminates just below the tergal lobe (not fusing with it). This process is called the prespicaular bar. The abdominal spiracles are all similar to the first thoracic spiracle but the abdominal anterior spiracular sclerites resemble the thoracic posterior spiracular sclerites and vice versa. There are brushes of bristles extending externally and caudally from the anterior spiracular sclerites of the abdomen.

The first, second, and third terga and sternae are fused together and lack intersegmental membranes. From the 3–4 intersegmental area onward there is an increase in the amount of intersegmental membrane and the resultant amount of possible overlap of segments. The size and shape of pregenital segments 2–7 can be seen in figure 62a. None of them bear significant internal processes.

Male genital segments: The eighth tergum is somewhat reduced. The eighth sternum is fairly normal, though lightly sclerotized, for the first one fourth of its length. Its caudal portion, however, is heavily sclerotized and inflated, forming a U-shaped structure below and around the genitalia proper. The extreme caudal portions of the sternum extend beyond the pleural membrane as hollow bidomed protuberances. These eighth sternal structures have the appearance of paired valves, and are called here pseudovalves, following Viette (1948). It should be noted that Klots (1956) is in error regarding Viette’s term as applying to enlargements of the ninth sternum (probably a lupana valvula).

Between the eighth and ninth sternae there is on each side an invagination of the intersegmental membrane which contains a hair pencil. The ninth sternum is a narrow U-shaped sclerotic band, termed by taxonomists the vinculum. Midventrally, it bears a blind tubular apodeme directed anteriorly, the sacculus. Articulated to the lateral arms of the vinculum are the paired valvae, morphologically probably the gonocoxites of the ninth segment. Each valva bears a sharp elongate caudoskeletal process. The ninth tergum which in most Lepidoptera makes up the major portion of the heavily sclerotized tegumen is membranous. The region of the tenth tergum is occupied by two fairly lightly sclerotized lateral lobes, termed collectively the uncus. There is no sign of a gnathos, or any other sclerotization of the tenth sternum. A membrane closes the rear end of the abdominal cavity, running from the bases of the valvae and the vinculum to the uncus and anus. This terminal membrane is referred to as the diaphragma. The anus is situated in the lobe of the membrane which separates the parts of the uncus. The diaphragma is pierced roughly in its center by the long, slender heavily sclerotized aedeagus. The eversible cone of membrane around the aedeagus is termed the anellus. The only sclerotization in the diaphragma proper is a roughly triangular juxta lying below the aedeagus and presumably helping to support it.

Female genital segments: Although it is not properly a genital segment, it should be mentioned that the seventh sternum is somewhat modified to extend up and around the anterior borders of the sinus vaginalis. The sinus vaginalis is a conspicuous cavity in the ventral side of the abdomen, just caudal to the seventh sternum. The sinus contains two sclerotic plates, a large anterior deeply incurved lamella antevaginalis, and a smaller posterior lamella postvaginalis. The two lamellae are joined laterally and enclose a small membranous area in the center of which is the receptive opening, the ostium bursae. Internally the heavily sclerotized ductus bursae leads from the ostium to the large membranous corpus bursae. In
Figure 63. Danausplexippus. a, mesal view of fourth abdominal spiracle; b, ventral view of apex of male abdomen; c, lateral view of male genitalia proper (setae of valvae omitted); d, mesal view of right pseudovulva (setae omitted), hair pencil and sternum 9; e, posterior view of male genitalia proper (setae omitted).
Figure 64. Danaus plexippus. a, lateral view of apex of female abdomen; b, lateral view of apex of female abdomen showing internal structures; c, ventral view of apex of female abdomen.
the wall of the corpus bursae is a pair of spined signa, joined by a yoke at the anterior end of the corpus. The corpus, ductus and ostium bursae together comprise the bursa copulatrix. The lamella antevaginalis is a structure of the 7-8 intersegmental membrane and can be differentiated from the seventh sternum, while the lamella postvaginalis, also presumably intersegmental in origin, cannot be distinguished from the eighth sternum. The eighth tergum is divided into two lateral plates, its dorsum being membranous.

The only well-sclerotized structures beyond the eighth segment are two lateral plates fused to the papillae anales, which bear the apophyses posteriores, strongly sclerotized paired apodemes which project forward into the body cavity. These plates are considered to represent the ninth tergum. The papillae anales are lightly sclerotized setose lobes on either side of the membranous bulge of the anal area. They are presumably derived from the ninth or tenth terga or both. Just below and anterior to the papillae is a small lightly sclerotized area which may be a remnant of the ninth or tenth sternum or both. The anus and oviporus, the former above and behind the latter, lie between the papillae. The ninth and tenth segments can be retracted within the eighth so that only the tips of the papillae can be seen, or they may be completely extruded so that the bulging lightly ridged membrane around the anus protrudes between the papillae.

Reproductive System

Female (Fig. 65)

The reproductive organs of the female may be divided into two groups, one concerned with receiving and storing the male sex cells (copulatory organs) and the other with the production of the female sex cells together with fertilization (ovulatory organs).

Copulatory Organs. These consist of a cylindrical, heavily chitinized tube, or duct, and a large sac-like structure. The tube, ductus copulatrix, receives the long, needle-like penis of the male. The ductus copulatrix is constricted, and is not so heavily chitinized at the point of entrance into the bursa copulatrix (Fig. 66); a heavily chitinized valve is located at the entrance to the bursa which, when closed, would prevent the escape of the seminal fluid. The bursa copulatrix is a large organ (approximately 4 mm. long and 3 mm. wide) that is capable of considerable expansion when filled with spermatophores (Fig. 66). When viewed from above it is somewhat pear-shaped, being broad in the central region, rounded at the anterior end, and constricted at the posterior end. To one side of the entrance of the ductus copulatrix is the slender ductus seminalis. Two dark bands, one on each side of the bursa, are most conspicuous; when viewed under the microscope, these bands present an irregular rhomboidal configuration or pattern (Fig. 66a). When the bursa is opened, it is seen that these dark bands are the bases of numerous large, small, and minute teeth which are heavily chitinized (Fig. 66c). The teeth of each band are arranged into two smaller bands, the teeth pointing in the opposite direction from a median line which
Figure 65. Female reproductive organs.
is located along the lateral margins of the bursa. The teeth are of medium size near the line of demarcation, larger in the central portion, and small to minute distad of the median line. Well developed longitudinal muscles are associated with the bursa. The channel leading to the entrance of the ductus seminalis can be clearly seen in the wall of the bursa, located adjacent to the valvular mechanism of the ductus copulatrix. The ductus seminallis gradually becomes wider to form the bulb seminalis, which in turn becomes slightly narrower, although not conspicuously so, to form the ductus receptaculi.

**Figure 66. a, bursa copulatrix; b, rhomboidal configuration of dark bands of bursa; c, arrangement of teeth within the bursa.**

**Ovulatoy Organs.** These consist of the ovaries, oviducts, seminal receptacle, and accessory glands. There are two ovaries, each composed of four ovarioles. Owing to the presence of a great mass of fatty tissue, it is most difficult to remove the ovaries from the surrounding tissue, particularly undevolved ones. Most successful dissection was carried out with partly developed ovaries. In removing the excess fatty tissue and surrounding trachea, some of the accessory organs may have been destroyed and hence are not indicated in the accompanying drawing. The undeveloped ovariole is a long slender tube consisting of a fine hair-like terminal filament which broadens into a granular area, the germarium (where ova develop), and then becomes progressively broader as it approaches the junction with the other ovarioles. The ovarioles, as shown in the accompanying drawing, are arranged in pairs. In life, of course, the ovarioles are arranged close together and, since each ovariole is longer than the length of the abdomen,
they are folded back so as to form a more or less compact mass. In the accompanying drawing each organ has been separated so as to show more clearly the structure involved. The four ovarioles join in a common duct, the paired oviduct, and these in turn unite to form the common oviduct. The vestibulum is a rather large swollen structure into which the following ducts lead: the common oviduct, the ductus receptaculi, the duct leading to the bulb seminalis, and the duct leading to the colletorial glands. The ductus receptaculi is slender and twisted; it becomes slightly inflated distal to form the receptaculum seminis which is relatively short. Attached to, and forming part of, the receptaculum seminis is a very long, slender, and much twisted gland, the glandula receptaculi. The colletorial glands are small, twisted organs connected to a common duct leading into the vestibulum.

The basal origin of the ductus seminalis and the fact that there is a separate opening into the bursa makes it difficult to correlate the various structures in conformity with that worked out so explicitly by M. J. Norris (1932) for Ephesia and Plodia. If the base of the bursa, which in Ephesia and Plodia leads directly and broadly into the vagina since there is but a single opening in this case, is analogous to the slender duct as found in the Monarch butterfly then it would be termed the ductus bursae instead of the ductus seminalis. However, as we have shown, the entrance to this duct is well marked as a relatively deep channel in the wall of the bursa leading from the lamina dentata and hence we are of the opinion that this duct is analogous to the slender duct identified by Norris as the ductus seminalis, which in Plodia and Ephesia originates in the region of the lamina dentata. The ductus bursae would then be analogous to what we have termed the ductus copulatrix, a terminology which we consider more aptly describes its function in the Monarch butterfly and other species in which the copulatory duct is distinct from the opening to the vagina. The gland which Norris terms “accessory” is analogous to what we have termed the colletorial glands.

The remaining structures are similar in all respects to what Norris has described, with the possible exception of a terminal filament at the apex of the ovariole which Norris states “appears to be absent in all the Lepidoptera.”

Male (Fig. 67)

It is extremely difficult to remove the male reproductive organs from preserved specimens because preservatives such as alcohol and formaldehyde tend to secure the fat firmly to the tracheal branches. At the same time the organs themselves become brittle making removal virtually impossible. Using live or freshly killed material it was found that the reproductive organs could be removed much more easily than those from preserved specimens.

The accompanying drawing (Fig. 67) was constructed from eight separate drawings, using a camera lucida, the organs being held in water during
examination to prevent possible distortion. The *vasa deferentia*, *accessory glands*, and *tubular gland* are much folded and twisted in their natural position within the body cavity, but for the sake of clarity they were stretched out and held in place by pins. In this way lengths of the structures and the variations in circumference may be compared more readily; also, if any portion of the reproductive organs are removed during gross dissection they may readily be identified by comparison with the accompanying drawing.

The *testis* is a large (2.4 mm. diam.) organ, the most conspicuous one of the entire internal anatomy because it is bright maroon or purplish-red in
colour. Holding the testis in place, as well as supplying it with oxygen, are a number of tracheae which break up into minute tracheoles that radiate throughout the outer wall imparting a most characteristic appearance to this organ. Two large tubes (the *vasa deferentia*) originate from the posterior margin of the testis. These tubes are tightly twisted around each other near their points of origin which at first glance gives the impression of being a large single tube instead of paired tubes. The *vasa deferentia* are conspicuously swollen for approximately one-quarter of their length, forming what Norris has termed the "funnels of the *vas deferens*." The *vasa deferentia* rapidly become more slender after leaving the funnels and are almost thread-like at the point of attachment to the *vesicula seminalis*. In the description of the male organs for two species of moths of the genera *Ephestia* and *Plodia* Norris designates a swollen area distal of the funnels as the *vesicula seminalis*, and large paired organs, similar to those here described, as paired glands, pointing out, however, that there is some difference of opinion with respect to this terminology. We were unable to locate any such swollen area and the paired glands of Norris were filled with spermatozoa; hence we concluded that these glands must be the *vesiculae seminalis*. The *vesiculae seminalis* are broadly united distal and free proximal. They are, in the natural position, so closely pressed one against the other that they appear to be a single organ, but by careful dissection and removal of the tracheae and fatty tissue it is seen that they are paired organs. They are large, white in contrast to the surrounding yellow fatty tissue, slightly U-shaped, broad at one end and tapering at the other. As a continuation of the tapered end are two long, twisted thread-like accessory glands. The *vasa deferentia* enter the *vesiculae seminalis* at the points of constriction or bases of the accessory glands. A single tube, the tubular gland, which is also the ejaculatory duct since the sperm pass down this tube towards the *aedeagus*, originates at the point of attachment of the *vesiculae seminalis*. The tubular gland varies markedly in thickness throughout its length, more than is indicated in the accompanying drawing. The thickened areas are marked off by a more slender portion of the tube as well as by knot-like contortions. Norris describes four distinct regions: (1) the upper or first gland containing a secretion composed of club-shaped masses radiating out from the cells; (2) the second gland containing a transparent secretion from which the outer wall of the spermatophore is formed; (3) the third gland containing a mass of irregularly shaped clear globules or crystals; and (4) the lower gland forming a reservoir of finely granular, opalescent secretion. The *ductus ejaculatorius* is a relatively narrow duct which is surrounded by circular muscle and at its distal end it becomes much broader, forming the *bulbus ejaculatorius* which has very thick muscular walls and is attached firmly to one side of the heavily chitinized *aedeagus*. 
Although it is not our intention to discuss at length the formation of the spermatophore and the transference of it to the bursa of the female, nevertheless there is one factor involved which does have a bearing on the subject of copulation as it relates to migration. To appreciate the possible significance of this factor it is necessary to review Norris’ observations with respect to the formation of the spermatophore and the processes involved during copulation. According to Norris the sequence of events in the formation of the spermatophore are as follows:

1. The secretion of the lower gland flows into the bursal cavity and hardens into a gelatinous mass;
2. The secretion of the second unpaired gland flows into the ductus ejaculatorius and vesica where it hardens from without inwards and is consequently moulded to the form of the ductus;
3. The secretion of the upper gland flows into the ductus;
4. The sperm is liberated into the ductus;
5. The secretion of the accessory glands is mixed with the sperm.

Norris further points out that if a female is killed fifteen minutes after the beginning of pairing the bursa is found to contain a gelatinous, opalescent mass which is the secretion of the lower gland as outlined above. If the female is killed thirty minutes after copulation the male and female will remain united and the vesica can be seen in the bursa. The sac of the spermatophore does not, however, contain any sperm at this stage. After forty minutes the sac of the spermatophore contains sperm. It would appear, therefore, that it may take an hour or more after the initiation of copulation for the spermatophore to be formed and introduced into the bursa.

The acceptance or rejection of copulation in so far as the female is concerned is dependent, according to Norris, upon the presence or absence of

Figure 68. Digestive, nervous and vascular systems: ph, pharynx; sd, salivary duct; sg, salivary gland, oe, oesophagus; fr, food reservoir; st, stomach; mt, malpighian tubules; si, small intestine; c, colon; r, rectum; a, anus; h, heart; ao, aorta; ac, aortal chamber; b, brain; sug, subesophageal ganglion; ag 1-4, abdominal ganglia.
sperm in the receptaculum seminis. If such is the case, it is possible that the female would copulate even though the ovaries were undeveloped. This reaction has been observed repeatedly and evidence of copulation has been found by dissection. In females that have undeveloped ovaries one may find that the **bursa** contains a gelatinous secretion from the lower gland and nothing else. This is a common occurrence in the Monarch butterfly. It is also possible that a male may copulate even though the sperm are not developed. Again, only a gelatinous secretion from the lower gland will be found in the bursa. It is possible for copulation to take place even when the reproductive organs in both sexes are undeveloped or, what is perhaps a more accurate statement, when there are no viable eggs or sperm.

**Digestive, Vascular, and Nervous Systems** (Fig. 68)

The following information has been taken from Burgess (1880).

**Digestive System**

**Pharynx.** The round pharynx is enclosed in a muscular sac and occupies much of the lower part of the head. Five principal muscles are attached to it: namely, two dorsal, two lateral, and one frontal, the latter being a paired muscle closely united. There is also a feeble muscle attached to the ventral surface. The sac has two principal muscle layers, an outer composed of longitudinal fibres and an inner composed of transverse fibres. The floor, or **hypopharynx**, is convex on each side of a median furrow, and the convex areas are covered with small papillae. The cuticular layer of the hypopharynx is very thick, while that lining the superior wall of the pharynx is thin and is thrown into slight transverse ridges. At the anterior border of the pharynx is a triangular muscular flap, the epipharynx, which overlies the opening into the proboscis and serves as a closing valve.

**Salivary Gland.** The salivary gland consists of two convoluted tubes which are located on either side of the oesophagus. The glandular portion of these tubes is about 40 mm. long and the more slender anterior and non-glandular portion, or duct, is about 12 mm. long. The two tubes unite in a common duct opening into the pharynx just below the hypopharynx.

**Oesophagus.** The oesophagus is a slender, thin-walled tube leading from the pharynx through the thorax and into the abdomen, at the base of which it opens into the food reservoir.

**Food Reservoir.** The food reservoir, which has been referred to as the "sucking stomach," is a large bladder-like sac occupying the upper part of the anterior half of the abdomen. Its wall is composed of longitudinal and transverse muscles. On the upper, interior surface, and particularly along the median line, are long hair-like processes that have broad corrugated
bases and pointed apices. Although the food reservoir is often found to contain nothing but air, Newport (1834) states that it is filled with food after feeding.

Stomach. The stomach is a straight tube lying along the ventral region of the abdomen from the second to the fifth abdominal segments. The walls are thick and composed of muscular and glandular layers.

Malpighian Tubules. These are six in number, three located on each side of the stomach, which unite to form a common duct which opens into the posterior end of the stomach.

Small Intestine. The small intestine is a narrow tube arising from the posterior end of the stomach, then passing backward, then upward and forward and then backward again, thus forming an "S" shape in the fifth and sixth abdominal segments.

Colon. The small intestine passes into the colon in the dorsal region of the sixth abdominal segment. The colon is somewhat pyriform in the female and longer and more cylindrical in the male. It is covered with numerous small glands.

Rectum. The colon narrows posteriorly and is followed by the short, cylindrical rectum, which in turn opens into the anus which is located on the ninth abdominal segment.

Vascular System

The heart is a small tube lying under the dorsal wall of the abdomen. It is held in position by triangular sheets of muscle (alarly muscles). There are two sets of muscular fibres running spirally in opposite directions. Slight constrictions divide the heart into a number of segments corresponding to those of the abdomen. It narrows anteriorly to form the aorta which passes between the right and left sets of thoracic muscles, and then under the suture between the mesoscutum and scutellum, and then expands so as to form a large, bulbous chamber (aortal chamber) which is held in position by fibrous connective tissue. The anterior end of this chamber bends downward and at the same time becomes narrower so as to form a slender tube. This tube passes backward and downward until it reaches the first part of the aorta; it then bends sharply forward again just above the oesophagus into the head and through the oesophageal nerve collar. The walls of the aorta are provided with muscular fibres arranged in spiral layers similar to the arrangement found in the heart.

Nervous System

The brain is located immediately above the oesophagus and gives rise to the optic and antennal nerves. The suboesophageal ganglion is connected to the brain by a pair of nerve commissures which form a collar-like arrange-
ment through which the oesophagus passes. The nerves of the mouth parts arise from the suboesophageal ganglion. There are two ganglia located in the thorax, two of the original three thoracic ganglia having been fused. Nerves to the legs and wings originate in the thoracic ganglia. The second to the sixth abdominal segments each contain a ganglion, which gradually increase in size posteriorly. A small ganglion, the frontal ganglion, lies in front of and below the brain hemispheres, with which it is connected by a recurved cord on either side. Posteriorly it gives off a single median cord, the nervus recurrens, which passes backward over the oesophagus and through the oesophageal nerve-collar. A pair of ganglia also lie behind the brain hemispheres, connected with the nervus recurrens. The latter runs backward over the oesophagus, innervating it and the dorsal vessel. On reaching the stomach it divides into three branches, which run over and on either side of this organ. Small branches are also given off to the food reservoir.
CHAPTER TWELVE

MIGRATION

Fall Migration

In chapter VI the use of the word “migration” is discussed and its meaning defined.

Date of Commencement of Flight

In order to obtain data on the possible dates of commencement of the southward migration for various parts of North America, our co-operators were asked to record observations of the increase in abundance of Monarch butterflies in their localities and to record the direction of flight. The following information was obtained for the Eastern, Central, and Western sections of North America.

Eastern

ALABAMA

During October the total number of specimens that passed through this area must have been very large. Only once was a tagged specimen recaptured at a later date . . . apparently the butterflies moved steadily enough that (virtually) all tagged specimens had moved out of the area before tagging operations began on the following day. The direction of Monarch migration through our area has proved rather difficult to determine with assurance. On several occasions the butterflies were observed moving steadily westward along the river bank and across Baker’s Creek. An average of one or two specimens per minute passed the point during each observation period. These specimens flew directly and purposefully, in marked contrast to the leisurely flight of the Monarchas feeding in the fields. At no time, however, did we notice anything like a mass movement of the butterflies in swarms (or even in hundreds). . . . In summary it appears that such evidence as we have points to a generally westward movement for the Monarchs in this area. . . .

During almost the entire month of October the specimens observed and tagged were in fine fresh condition. Beginning in late October and during early November we noted an ever increasing proportion of worn or battered specimens among our catch.

The decline in numbers and ultimate disappearance of the Monarchs from our area was almost dramatically rapid. When we resumed tagging with a fresh supply of labels on November 1, the peak of abundance was already past. Even so we managed to tag 16 specimens in 45 minutes. On November 2, we were able to tag only 11 butterflies in an hour. A cold rainy period then intervened, and when on November 7 we were again able to look for Monarchs only two
could be located in an hour's time. Further searching on later dates did not disclose any additional specimens.

The Monarchs which passed through here were quite evenly divided with respect to sex. [John P. Knudsen, Decatur.]

We have noticed single specimens . . . going on due westward [October]. Monarchs seem to have been following the river south of where they were seen, in October.

[Oct.] Thousands hanging on trees near WALA transmitter on highway. Seems they make their appearance each year, but not usually in such large crowds.

So far as I can learn from inquiring in all directions the Monarch migration did not rest on Mobile Causeway or in our locality this fall. A migration of Monarchs was seen in flight near Foley following the Bon Secour River Oct. 14. [Mrs. James Coe, Foley.]

CONNECTICUT

For almost thirty years . . . the Monarchs have been annual visitors—covering two pine trees on the island . . . the Monarchs usually visit us early in September . . . I believe that they remain about a week . . . . They cling quite low to ten-foot pines. [Leonard D. Weil, Outer Island, Stony Creek.]

GEORGIA

Each fall we have what might be termed a light but fairly steady southward migration. Apparently, when they reach the Gulf of Mexico along the coast of Florida they build up in rather large numbers . . . . Mr. E. V. Komarek tells me that he sees them each fall when he goes to the coast below Tallahassee.

On Oct. 4, Atlanta was visited by Monarchs travelling south. The first time in years that there were enough Monarchs in downtown Atlanta to be noticed by the citizens. [Lucien Harris, Atlanta.]

Tagged 61 Monarchs Aug. 26–Oct. 19. Was not able to tag any during summer. [Paul Right, Stone Mountain.]

In the southern part of S.C. and the northern part of Georgia we saw the greatest numbers of flying Monarchs. These were never observed in 'swarms' but appeared to be flying singly; however the stream was so constant that scarcely five minutes would elapse without seeing one or more. All were headed due south. From our very limited observation, it would appear that the crest of the migrating wave had just about reached the Georgia line by Sept. 13. [Robert A. Greene, Concord, S.C., to Jessup, Ga. (338 miles).]

ILLINOIS

They landed here in my yard Sept. 11; in the next six days we tagged 50. They left Sept. 18, early in morning. [Mrs. Jacob Rodell, Fidelity.]

INDIANA

Twenty-five, all flying in southwest direction, on Sept. 23. [Donald Mauger, Paoli.]
KANSAS
On Sept. 16 tagged 12 at Trimbles Lake, although Overland Park area revealed none. The large numbers seen at Trimbles Lake suggests that most Monarchs took a route east of here, a few drifted through in October. After Sept. 10, most Monarchs were seen flying southward. [Mrs. F. Throm, Overland Park.]

MAINE
Aug. 27–Sept. 11. Migrating Butterflies seemed to maintain a fairly consistent proportion to the number of birds migrants, with a high of 75 on Sept. 10. [Nourse Mazzeo, Matinicus Rock in the Gulf of Maine.]

MASSACHUSETTS
Aug. 28–Sept. 6, 5 Monarchs flying south. Sept. 2–Oct. 5, 11 Monarchs banded, feeding or resting. Nov. 3, 1 Monarch going in a southeasterly direction, 50 to 200 feet high, at 2:30 P.M. [David Miner, Barre.]

Sept. 24, watched 150–200 Monarchs flying along the beach. On same day at Drumlin Farm in Lincoln... observed about 150 Monarchs settling down on low shrubbery just before dusk. Sept. 29, about 150 seen migrating at Nantucket. [Bull. Mass. Audubon Soc., Gooseberry Island.]

On Sept. 29, at Nantucket, on the ocean side, Mrs. Emery of our MAS staff saw a steady migration all day, perhaps in all 150. Later in the day, she saw between 75 and 100 hanging on the cedar trees, perhaps resting for the night. At Gooseberry Island, near Westport, on Sept. 25 there were between 150 and 200 Monarchs. On one clump of beach goldenrod there were 35 alone. [Mrs. Ivy LeMon, Nantucket.]

On Sept. 25, just as it was beginning to get dusky... between 150 and 200 Monarchs rose off the grass to about 5 feet in height, and settled down further away. [Miss Ivy LeMon, Lincoln.]

MICHIGAN
Aug. 30. The butterflies seemed to be migrating over Lake Michigan either from nearby islands or the upper peninsula or Wisconsin, as they came in over the water from the northeast, touched the beach briefly (when we caught them) and then continued up over the hill in a southeasterly direction. We must have seen over a hundred... I have never seen so many Monarchs in one area before. They were not in a swarm, but rather a steady procession following the same direction. [Mrs. L. W. Hobbs, Birmingham.]

Our cottage was on the lake shore. In the late summer on my way through the yard I saw many Monarch butterflies formed like a blanket from the top of a small fruit tree to the ground. I must have disturbed them as they all took off to the lake front, flying south. [Mrs. H. Cipriani, Glenn.]

On Sept. 2 we saw our first Monarchs in any quantity—an evening flight all south bound and in which a dozen to fifty were always in the sky. I had never seen them travelling at such heights, the majority flying at about 200 feet, a few nearer 300 feet, and some even higher. One in particular I sighted and made
a triangulation and estimated at close to 500 feet... the flight referred to was following the shore of Lake Michigan going almost due south against a SSW wind of estimated 15 mile velocity. The flight lasted till sundown, a period of about 2 hours. Perhaps the height at which they flew was due to wind currents, for it was evident those close to the ground had more difficulty.

The big flight occurred Sept. 4, when we saw them in great numbers all headed south. The ones we now see are all young, fresh butterflies. [Harry F. Stiles, Grand Rapids.]

The limited observations possible seemed to indicate that the butterflies drift down the lake shore to Huron Point, where they tend to cluster. Quite a few take off across the water from a nearby beach, heading in the direction of Detroit.

I had a report of noticeable migration of Monarchs at Muskegon, on Sept. 4, flying south along the shore of Lake Michigan. At Huron Point (Lake St. Clair, south of mouth of Clinton River) they were reported "in the hundreds" on Sept. 7, and "in the thousands" on Sept. 8, but on Sept. 9 I saw only a few scattered individuals there. [Mrs. L. G. Seibaud, Mount Clemens.]

Situated as we are here in Muskegon on Lake Michigan, we get a great flight and sometimes heavy concentrations of Monarchs during the fall months, especially October. Occasionally the insects spend the night on cottonwood trees along the shore in heavy assemblies. [Mrs. Paul A. Elliott, Muskegon.]

On Sept. 4 Fire Officer Bert MacGregor observed a migration in his back yard—some flying 30-50 feet, all travelling in a west-southwest direction. Counted 54 butterflies in 5 minutes.

Sept. 8. More butterflies at Tawas than inland—no definite migrations, seemingly. General southwesterly direction.

Sept. 12. Still many Monarchs—appeared to move in groups—moving in a general southwest direction, but not high or in direct flight.

There seemed to be many more Monarchs at Tawas City area than 16 miles west inland from Lake Huron... am inclined to believe that butterflies have a flyway at Tawas along lake shore there. [N. Sibley, Tawas City.]

MISSISSIPPI

Large congregations are frequently seen late in September and early in October, moving south. [Bryant Mather, Jackson.]

NORTH CAROLINA

These butterflies [5 specimens sent, collected October] flying through Tunnel Cap were part of a mass movement southward extending over a probable 2-week period, flying steadily southward, sometimes against a wind at 10 m.p.h., Sept. 25–Oct. 5. [Arthur A. Henderson, Maggie.]

On Sept. 27 four of us observed a great number of Monarchs flying south through a gap in the ridge known as Tunnel Cap. They were observed from 10.30 A.M. till 2.30 P.M. The first three hours of observation we estimated they were crossing at the rate of 10,000 per hour. The last hour the flight had slowed to 2000 per hour. The day was overcast and there was a brisk wind from the
THE MONARCH BUTTERFLY

SSE. The Monarchs were quite low as they crossed the gap, which is 4480 feet in elevation. As soon as they crossed the gap they were able to glide downwards and southward, using the air currents. Coming across the gap they had to fly hard. Flight continued through Oct. 5. Since then there have been a few observed. There were considerably fewer crossing the gap towards the end of this period, but still kept up a rate of several thousand per hour. Wet, foggy weather seemed to slow them down. [Robert E. Howe, Asheville.]

OHIO

There was a migration, but it was in August. We had a very hot spell towards the end of August. Many Monarchs passed through our territory, but they were flying so high that no one could catch them. They did not seem to alight anywhere as there were no eggs or larvae to be found after this flight. [Mrs. E. W. Fleming, Bay Village.]

ONTARIO

The Monarchs always fly over our hilltop situated between Georgetown and Acton, just off No. 7 Highway, in a westerly direction. When we went to the Exhibition at Toronto we must have seen 40 or more going west, and at the Exhibition itself I noted many more flying in the same direction. Oct. 20 was the last day I saw a Monarch flying... it was flying in a southwest direction, as they all have been over our hillside this year. [Mrs. J. R. Glynn, Limehouse.]

On Sept. 24–25 the migration went through. They were large butterflies, not like the small ones I had raised. There were as many or more than 15 in 22 minutes, and never did I see two flying close together. They flew high, swiftly, and directly south. For a week after we saw one or two a day, flying low and tending to flit around. [Miss Huth Haigh, Niagara Falls.]

While watching hawks on Sept. 23, saw Monarchs passing over. We estimated for the five hours they passed steadily at rate of 40 a minute—making 12,000 in five hours. Time 1:30-6:30 P.M.; gentle southwest wind, and they were flying into it. They had been passing before we got there and still going when we left. [J. L. Bailie and Lister Sinclair, Scarborough Bluffs.]

PENNSYLVANIA

The migration started out this year as if it would be very heavy. On Sept. 15 we made the most tagging, and from then the migration suddenly ceased. [Robert Stone, McKeesport.]

While working along the Delaware River from Aug. 26–30, I observed a great number of Monarch butterflies... General direction flying out over the Delaware River was southeast. Approximate number observed in five days was 400... Probably more than this were going by Observation Point. [Joseph J. Woodburn Jr., Philadelphia.]

SOUTH CAROLINA

On Oct. 17, it was interesting to observe a small but definite migration... all flying steadily southward, in spite of a rather brisk cross-wind blowing from the
east. They were flying low, a few feet above the ground, none were high in the air. The line of flight was less than a half-mile wide—about a dozen or so were seen in 3 or 4 minutes. [Lucien Harris, west of Columbia.]

TENNESSEE

On Sept 22 I stood at Newfound Gap (5048 feet) and watched Monarchs fly southward in a steady flight at approximately 6 a minute. . . . They apparently had been flying at a higher altitude and we could see them high above us, for the day was bright and clear, and then we could see them start downward and come through the pass. At Indian Gap, only one mile from Newfound Gap, we found a somewhat similar but smaller flight. [Lucien Harris, Great Smoky Mountains.]

On Oct. 4th I saw the Monarchs migrating over Nashville. Looking eastward from a window on the 10th floor Monarchs could be seen high above the tall buildings as well as flying low over the roof tops. This flight was travelling in a southeasterly direction. On any clear day this fall Monarchs could be seen flying southward. [Lucien Harris, Nashville.]

My son reported seeing numbers flying high in Memphis, in mid-October. [Mrs. A. P. Byland, Memphis.]

VIRGINIA

In late August and early September all flew in a west or southwesterly direction. [D. Dreese, Arlington.]

WISCONSIN

On Sept. 25 and 28 and Oct. 9, I saw from one to three flights each day. There were from 10 to 15 up to 100 at a time flying a little east of due south about 50 to 100 feet above the tree tops. Most of them were sighted around noon or a little earlier. [Frank C. Webb, Kenosha.]

Between Sept. 1 and 6, in a three hour period an estimated 2000 Monarchs were sighted over Billy Mitchell Field, on shore of Lake Michigan. They were flying from 5 to 100 ft. high and due south. [Ralph Washichek, Wauwatosa.]

Central

ARKANSAS

On Nov. 1 saw large numbers of Monarchs hanging on willow trees along an irrigation ditch . . . next morning they were gone. [At Grady.]

On Oct. 13 driving from Cody to McChee (80 miles round trip) counted 265 Monarchs flying about 10 feet from the ground—all flying southwest. They have been floating by here in small numbers all of October and part of September, always travelling southwest. [Mrs. A. P. Byland, Pine Bluff.]

LOUISIANA

In past years about August 15th I have seen literally thousands at my country home on Lake Pontchartrain—they actually seemed to light on the lawn for a rest
of from 24 to 48 hours before taking off in flight across the lake (approximately 25 miles), then they could be seen on the New Orleans side of the lake flying in a southerly direction. [MRS. J. W. Townsend, New Orleans.]

MANITOBA

Monarchs seldom appear here until July or August. I have never seen any swarms of Monarchs in this area and when they first appear they are fresh. Monarchs are quite common this year, and I have tagged fifty the last of July. I told you in a previous letter I had never seen a worn Monarch here, but I have to retract that, as I saw several earlier in the year—the ones I am getting now are all very fresh. I have tagged three days in one week in the same spot and have not yet caught a specimen I previously tagged; looks as if they move out quite promptly. [C. S. Quelch, Transcona.]

OKLAHOMA

A few Monarchs were seen from April on through the summer, small numbers apparently breeding within the area. . . . Monarchs appeared in large numbers October 1, with a cold front moving southward. Rainy days, strong winds, cold spells beginning October 22, after which few Monarchs were seen. Tagged 44 October 6–21. [Harley P. Brown, Norman.]

The banding of Monarchs has taken an upswing during the past few days [Sept. 28] due to the influx of a tremendous number of migrating butterflies. The present migration started in late August and in the past week the migration has reached its height. I watched a series of flights and they appeared to originate to the northeast. This might be because the butterflies were following the course of a small creek into this area. [Paul F. Spangle, Sulphur.]

From my observations in Oklahoma where I lived for years, we could see them nearly all summer and also observe their preparation for migration, being bunched by the thousands in one tree or bush. Just what time of the year this took place I cannot definitely say but no doubt it was in August. [A. L. Brandhorst, State of Oklahoma.]

OREGON

During the middle of August south of Bend, Oregon [some friends] drove through six miles of clouds of Monarchs, all headed south. They claimed that they had to stop and have their radiator cleaned out there were so many caught on and in the car and literally covered the highway. They were flying low as though forced down through atmospheric conditions. [Co-operator, Bend.]

TEXAS

Butterflies passing a fixed point across area 100 feet wide, flying southwest.

Sept. 26

8 to 10 A.M.—75 per min.
10 A.M. to 1 P.M.—1 per min.
1 P.M. to 3 P.M.—gradually increased to 5 per min.
3 P.M. to 5 P.M.—5 per min.
5 P.M. on—decreased abruptly to nil
Sept. 28 8 A.M. — 1 per min.
10 A.M. — 3 "
11 A.M. — 2 "
1 P.M. — 2 "
3 P.M. — 2 "
5 P.M. — 2 "
Sept. 29 8 A.M. — 0.6 per min.
10 A.M. — 1.0 "
1 P.M. — 0.2 "
Sept. 30 wind from south—few, but not enough to count
Oct. 1 wind from south—none observed
Oct. 2 a few seen
Oct. 3 wind from south. A small number seen going southwest high (100 ft. in air)
Oct. 4 new norther arrived, bringing inclement weather
Oct. 5 wind from north
8 A.M. — 1.2 per min.
3 P.M. — 1.2 "
3:30 P.M.—3 "
5 P.M.—3 "
Oct. 8 10:45 A.M.—5.2 per min.
1:45 P.M.—3 "
Oct. 18 10:40 A.M.—2.2 per min.

The above is last observation recorded, the number after that decreasing to a rate that was too low to be counted. [L. S. Dillon, College Station.]

The Monarch has been seen in this area since about the first of October. As soon as I received your letter I asked all of my biology students to be on the look-out for it and I have had some favorable results. Our search for the Monarchs has extended some twenty miles north of Eagle Pass along the Rio Grande. At one point about seventeen miles from Eagle Pass a swarm of Monarchs was seen that numbered in the thousands. The mesquite trees were so heavily covered with this insect that there was hardly room for one more Monarch. On the same day, Oct. 20, at a point about twelve miles from Eagle Pass, another swarm of the Monarchs was seen. This group, however, numbered only about 1000 or 1500.

Great swarms have been seen on the willows growing along the banks of the Rio Grande. It has not been determined how long these insects have remained there, since they are constantly arriving in great numbers.

As to the direction of flight of the Monarch butterfly, the majority are going directly into Mexico. There are a few, however, that are following a direction down the river. It may be that these cross the river at a point further south.

According to what I have seen I would say that Eagle Pass is very definitely on the Monarch's flyway. [Arturo Garcia, Eagle Pass.]

Oct. 11 to Nov. 9, 1958. The Monarchs were not there in quantities as in previous years. At the airfield where last year they covered the trees there were none—I never saw more than ten flying over at any time I was there.

At Maverick County Cemetery we were able to band 850, and I collected 25 females.
The minimum temperatures ranged from 44°F to 69°F. It was only when the night temperatures were in the 50's that there was any clustering, and the largest cluster I saw was one of 20—the others had from 5 to 15 in a cluster. Practically all of the clusters were in huisache trees (a species of mimosa) and occasionally in mesquite, which were then losing their leaves. As a rule, unless it had been a very warm day, they began to form clusters about 4:45 P.M. In one huisache where we saw them clustered most often, they were always on the north side about 20 feet up, but on one mesquite tree where there were clusters a few times it was always on the west side, but it was protected by tall trees on the south.

The small clusters generally stayed until about 7:30 or 8:00 A.M. One morning a large cluster stayed until 10 A.M. There was very little wind while I was there, a great part of the time not a leaf stirred, and when a slight breeze did come it was from the north or northwest as a rule. The morning that I saw the most clusters, however, the wind was a little south of east.

The Monarchs always came in from the north, and if continuing on west directly south. One day, however, after continuous rains, and with the wind north by a little west, they came in from the east.

One day when I tagged only three, they were all females flying low as though searching for milkweed; I followed a fourth and it alighted on low milkweed and I saw its abdomen curved under the leaf, but when I pulled up the plant I could not find an egg—the plant was covered with mud from the rain.

I saw nearly full-grown larvae and one about 4 inch long. [Miss Hilda White, Eagle Pass.]

Bernstein (1917) reports seeing swarms of Monarch butterflies on large mesquite trees east of Eagle Pass late in October. They remained until the following day when nearly all of them left within an hour or so.

The Monarch is very abundant down here at this time [Nov. 16] and if my memory is correct it was just about as abundant last year.

On Nov. 2, while I was hunting above High Island (about 30 miles northeast of Galveston) I noticed a steady flow of Monarchs flying in almost a due westerly direction. I counted them against time and got an average of one per minute over a period from sunrise, 6.34 A.M. until 7:30 A.M. Of course they were not spaced one each minute, but rather seemed to come in pulses with 7–10 individuals in 5 minutes, then a period of 5–8 minutes with none. They were flying 5 to 30 feet above the ground. [Anthony Inglis, Galveston.]

Oct. 8. There is a general migration towards the south and a few points east of south. At night I found a good treeful of them by the water's edge in a creek on my place. [R. K. Williams, Harper.]

The end of 3rd week in October, at Garner State Park, north of Uvalde, on a river with cypress growing along the banks. Butterflies among the trees were thousands of Monarch butterflies—many were hanging on the tree trunks and branches. We visited there several times during the year, but never saw a Monarch at any other time. [Mrs. H. I. Shaffer, Hondo.]

On Oct. 27, while in Laredo, my husband and I happened to pass a hospital garden in which Monarch butterflies were clustered so heavily they weighted down the tips of the tree branches. We asked a neighbor about the unusual crowd. She shrugged her shoulders as though the matter were commonplace, and re-
marked that the butterflies came only at certain times of the year. [Mrs. R. L. Stockmeyer, Laredo.]

The Monarchs appeared here singly and in small numbers several days ago, but to-day (Oct. 20) they are here in great numbers; several hundreds can be seen at a time as they fly in a leisurely fashion through the streets of the town. Their direction is generally west-southwest, which is the direction of the coast line here. [S. H. Clark, Palacios.]

In Rio Grande City on Oct. 23, in a grove of Australian pine there were thousands and thousands of Monarchs hanging on every twig and stem and leaf, on dozens of large and smaller trees. On the way down in October we saw thousands on the road, all winging their way in the same general direction, south and southwest. [Herman Wilhelm, Rio Grande City.]

The fall months find the oak trees and wayside weeds full of the migration. The butterflies that hatch on the milkweeds here are never as numerous as the hordes going through. A big migration in the oak trees in our yard is now on [Oct. 29]. I am astonished at the ratio of males to females (out of 50 banded, only 11 were females).

The caterpillars appear first in early spring, late March, early April. I have never seen Monarchs during our summer, May, June, July, August. A few show up by middle September. I don't know of any heavy wintering location around here.

This year we had a splendid migration. The first came Oct. 6, then a long lapse and on Oct. 21 they covered the whole town. Next day, Oct. 22, not a dozen were seen and those were not stopping. [Mrs. Jack Hagar, Rockport.]

On Oct. 12 some Monarchs arrived and settled in the customary place on pecan trees. On Oct. 15 it rained all morning and Monarchs stayed on the bamboo all day—quite a large cluster. No more Monarchs from Oct. 18 on. [Ernst Schuchard, San Antonio.]

In October my trees were covered by Monarchs. They were here in different flights over several days. [Mrs. S. S. Russell, Stamford.]

MEXICO

While talking to a man about the Monarch butterfly I learned that he had been hunting in Mexico during the month of October. They decided to make camp, and within a very short time he was able to see a very large swarm of the Monarch butterfly. This man told me that this group of Monarchs was approximately three-fourths of a mile wide and three hours long. According to him the Monarchs kept flying directly south. He was able to take a picture of part of the swarm in flight; however, he said that he could have taken a much better picture if he had thought about it sooner. The picture, which I am enclosing, was taken when nearly all of the Monarchs were past him. [Arturo Garcia, in Mexico, forty miles south of Quemado, Texas.]

[Translated from Spanish.] The Monarch butterfly (Danaus plexippus) has been seen in this locality in quantities during September and October during migration, north to south. [Professor H. M. Hernandez, Nueva Rosita, Coahuila.]
The Monarch Butterfly

[Translated from Spanish.] Mr. Gustavo Glueckeri is an entomologist . . . and in the last 12 years in this region he has observed the migration of Danaus Plexippus, but during the years 1953 to 1957 this phenomenon has increased so that the butterfly has been much more numerous. The migration occurs principally from October to December. He does not know where they continue in their course.

[Dr. J. R. Acedo, Universidad de Sinaloa, Culiacan, Sinaloa, 24° 30' N.]

Since long time ago we have been observing here in Monterrey the flying of these butterflies in large numbers going southeast. This usually happens each year at the end of October and the beginning of November. As far as we know these butterflies do not overwinter in our surroundings, probably because the temperature is cold in the winter time.

As a matter of fact a migration has been seen farther south in Mexico and a paper published. I am transcribing the summary in English:

[Dr. Paulino Rojas M., Universidad de Nuevo Leon, Monterrey, Nuevo Leon.]

[Translated from Spanish.] They have been migrating from north to south every year. On one occasion during November the migration of a large group was observed in Cuidad el Maiz, San Luis Potosi. In October they were also seen in migration through Ciudad del Maiz, San Luis Potosi. [Dr. Roberto Llamas, Universidad Nacional, Mexico City.]

On November 3rd friends of mine were at Horsetail Falls, on the outskirts of Monterrey, Mexico. They reported that they saw Monarch butterflies around there. [Ernst Schuchard, Monterrey.]

Through the kindness of Dr. E. Murray-Aaron I am able to record that in 1890 the late Sir Rider Haggard observed a flight of thousands of Monarchs towards the south in Orizaba, Mexico. Dr. Aaron met him a few days later and confirmed the identification from some specimens that he had captured. [Williams (1942).]

Western Arizona

In September all the Monarchs we have seen and captured have been fresh specimens; no fair or poor ones among them. They appear as if freshly emerged. This intrigues me. We have never noticed any larvae or chrysalis on the species of milkweed growing here.

Up to October 4, no good flight records were recorded—no doubt due to the forested rims of the Canyon. There seemed to be a trend south and southwest, but there were not sufficient good observations to definitely say that this is so. Worth of note was the fact that all specimens captured were fresh specimens—up to the present we have not encountered any battered specimens that would show long flights or heavy buffeting.

"Abundant?" Yes, after August 15 they began to be seen more often. More so, I would say, than I have observed before.
You ask also: "Would you rather favor the idea that the Monarchs move directly southward and overwinter along the Gulf coast?" Again, I cannot definitely say. However, this seems to me to be the logical idea, for travelling from here north along U.S. Hwy 89 to Salt Lake City, Utah, and return I have seen Monarchs along this north and south route this fall. This highway follows the north and south valleys that are between mountain ranges and seems to me to make for an ideal flight route. [Louis Schellbach, Grand Canyon.]

CALIFORNIA

Oct. 16 I was in the Loma Linda area and noted a strong migration (about 10 per hour past a determined point) moving in a due east-west direction from the east. These were flying rather high to be caught with a net, and as they weren't intending to stop, I was able to band only one. The Monarchs have been passing through La Sierra (suburb of Arlington) in numbers that could be considered a weak migration, especially Oct. 23-Nov. 5. On Oct. 29 I had opportunity to be out in Joshua Trees National Monument. At a point just below the Bernadino-Riverside county line in the central portion of the park I observed two specimens flying west southwest.

While in La Jolla the 3rd Nov. I noticed a strong migration (comparable to that of Pacific Grove) which apparently was centred on some local point. . . . I was on a formal field trip and was unable to . . . find their nucleus. . . . I insert this with the hope that it may help a little as to their most southern extent before returning north. [Albert Grable, Arlington.]

My most significant observation of the fall months was considerable numbers of Monarchs flying leisurely north at roof top elevation. This was a warm day with little wind and consisted of more than usual numbers of individuals throughout the day, but puzzling to me was the northward flight. [E. A. Stoner, Benicia.]

I took a trip as far south as the border to San Diego, a matter of 125 miles, Monarchs all the way, flying along the coast passing northward at the rate of 1 or 2 every few minutes and at a height of 75 to 100 feet in the air. At the border they are coming up from Mexico, their flight is directly north and not from the east. [A. T. Edwards, San Diego.]

I have sent you three female Monarchs and one male. . . . I caught these between 29 Sept. and 2 Oct. I caught them flying in the general direction of southeast.

Dec. 3, the Monarchs are flying in a south and south-westward direction. [Dudley Tomlin, Santa Cruz.]

During October and November I was able to observe them on the wing from about 10 a.m. until sundown. There was no mass flight but a steady stream passing a given point at the rate of 6 to 10 per minute all day long—the sense of direction was noticeable, the oncoming specimens would follow a tract not varying more than a few yards. It was fairly open country—they followed the coast line, saw very few over the ocean. The rate of speed was about 6 to 8 miles per hour, and nothing seemed to distract them from their purpose.

The first general appearance of the migration occurs here about Oct. 10. They come from the south flying north. There is a roost at Pacific Grove, but that is
about 400 miles north of here. Most of the specimens I have taken at this time of the year [October] are in good shape and color and fat, and their food plant has long dried up from the hot summers down here yet they look like freshly emerged specimens. [Arthur Edwards, Santa Monica.]

COLORADO

They were all either heading west, or south mostly in a westerly direction, from July 27–Oct. 16 saw 18 . . . I am convinced that most of the ones hatched in northern Colorado migrate west to the Pacific in September, whereas the Laramie Plains in south Wyoming would be logical route—for there the Rockies level out to a mere plateau of around 7500 to 8000 feet, but according to my report no doubt I was wrong in my calculations. Enclosed letter from C. R. de Foliart, Dept. Entomology, University of Wyoming: "Southern Wyoming would appear to be a logical migratory route to the West, but in the five years I have been here I have observed very few Monarchs. Possibly they follow the North Platte River Valley through eastern Wyoming, but I have observed very few more in the Platte Valley than I've seen on the Laramie Plains. I would be unable to say whether those observed were eventually headed south or west. On the average, I have seen not more than a dozen or two in any one fall." [A. L. Brandhorst, Denver.]

In August I noticed no distinct migrational movements—seems to indicate that the migration in this area doesn’t occur until late September or October. . . . Practically none were seen up to 1st August when they started hatching from chrysalids. During the latter part of August and the first of September very few were seen, and never in groups, usually a single flying over an alfalfa field. [Norman Marston, Hartman.]

NEVADA

We are in an area of migration and they are very common hereabouts in the spring, summer and fall. In fact, they are one of the earliest butterflies and one of the latest that we see. They do breeds here in considerable numbers and I have raised them from narrow-leaved milkweed (Asclepias mexitcana) on several occasions. . . . I have never seen them moving in bands, in either the spring or the fall, in spite of the fact that they are quite common. . . . They don’t appear to be heading in any particular direction since you only see singletons, and they appear to be heading in various directions. . . . All I can say on the migration of Monarchs in this area is that they definitely do migrate since we never find any of them hibernating. I would feel fairly certain that their migration must be pretty much north and south in this area since they are faced with the Sierra Nevada Mountains on our west and would find it easier to go directly south. This, however, is speculation only, and if they do fly across the Sierra and join the well known migratory masses of the California coast it would be an interesting thing to know. [Ira La Rivers, Director, Dept. of Biology, University of Nevada, Reno.]

NEW MEXICO

I have noticed large numbers of Monarchs in this area around Nov. 1. I have noticed them in previous years, but never in such great numbers as the last two years. We frequently see bushes containing twenty to twenty-five Monarch butter-
Left: Monarchs congregating during southward movement. Right: Overwintering colony in Monterey Peninsula, California.

Male Monarch–tag attached to right wing

PLATE IX
Specimens collected from overwintering roosts in California from early winter to spring. A gradual fading in color is indicated from bright orange (upper left) in early winter to dull orange (lower right) in the spring (abdomens removed for ovary examination).
flies per bush. These butterflies stay here two to three weeks. [D. C. Badger, Hobbs.]

NEW MEXICO AND ARIZONA
I observed them on numerous occasions at Santa Fe, N.M., Flagstaff, Arizona, and possibly a dozen in Albuquerque, N.M., throughout September and October. [Calvin L. Massey.]

OREGON
On September 15 the fall asters were literally weighted down with them. These were no doubt migrating.
On October 10th we saw the last one of the season. [Pete van der Vlugt, Canyon City.]

UTAH
July 3rd. 29 butterflies have been tagged so far this season. . . . So far this season I have not seen any caterpillars, but I believe there are a few around if sufficient time were spent looking for them.
August. I can't speak for many years back in Utah, but they are certainly numerous in the state this year. [Donald W. Davis, Logan.]

UTAH AND ARIZONA
I also saw Monarchs Sept. 2, 3, 4 & 5 at Mt. Pleasant, Ridgefield, Arizona, and Kanab, Utah. . . . All were very much faded and tattered and very much so at Kanab, just above the Arizona border. [Co-operator.]

WASHINGTON
I have never seen a Monarch in the Puget Sound district. . . . Evidently they fly east of the Cascade Range. [Alfred Renfro, Bellevue.]

One may conclude from these observations that in the eastern section the flight commences in August with a peak movement in September; in the central section the flight commences in September with a peak period in October; and in the western section the flight commences in August in the northern states and the butterflies appear in numbers in the southern states in October, with the exception of the coastal states where the flight time coincides with that of the eastern section. Broadly speaking, the population from the northern breeding localities moves southward, augmenting the numbers in the southern states and thus giving rise to a peak movement at a later date: September in provinces of Canada and the northern states, and October in the southern states. The marked difference between the peak flight in the central section and that in the eastern section is because there is a very weak breeding population in the central states and hence the peak flight is dependent upon the arrival of the eastern populations as they move southwestward.
To obtain a more accurate date for the commencement of flight in the eastern section, observations were made on flight direction for eight compass directions in July and August. A field 180 acres in extent, containing many wild flowering plants and milkweed and located along the shore of Lake Ontario, was chosen for this purpose. The number of specimens observed flying in a given direction was noted. From July 1 to July 21, there was no apparent significant flight direction. On July 22, however, out of twenty-six specimens observed twelve flew in a definite southwesterly direction. On July 26, forty-six out of sixty-two were observed flying steadily in a southwesterly direction. By August 6 there was a definite southward trend. These observations would place the commencement of flight at approximately July 22.

The recoveries of tagged specimens given in Table I are of immediate significance.

### TABLE I

<table>
<thead>
<tr>
<th>Tagged at</th>
<th>Date</th>
<th>Recaptured at</th>
<th>Date</th>
<th>Approximate distance in miles of flight in southerly direction</th>
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<td>July 28</td>
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<td>Lafayette, Ohio</td>
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From these observations, it may be concluded that the southward flight commences between July 17 and July 22. Whether or not this date would vary from year to year has yet to be ascertained. It is interesting to note that the flight southward commences approximately one month after the summer solstice.

**Establishment of Roosting Sites**

In the vicinity of the Great Lakes roosting sites are usually large willow trees, although congregations have been found on Manitoba maple, silver maple, and cedar. It was thought that either sight or odour was responsible in attracting the butterflies to a given roosting site. To test this, a roosting site consisting of a group of trees (silver maple, willow, Manitoba maple, and cedar) located at one side of a large grassy field was chosen. This particular site proved ideal because Monarchs moving southward approached...
The lake and could be observed flying westward along the shore or attempting to fly southward over the lake, and during the evening reversing their direction (flying north instead of south or southwest) in order to locate a suitable roosting site. The observations were recorded diagrammatically, together with any pertinent observations, and are summarized in Figure 69.

Path "b" represents the butterflies that were moving westward following the lake shore; path "a" those that had passed this particular site and were returning to it; and path "c" those that were moving in a southerly direction from the north. The slight difference in the paths indicated is because the diagrams are based on two separate sets of observations and each path represents the mean path followed.

It seems, then, that the Monarchs are attracted, by sight, to a group of trees (particularly indicated in path "a"); that upon arriving at a particular group of trees a selection is made as to the most suitable and that once the tree has been selected a position is chosen on the leeward side.

This pattern of selection was checked on many occasions, and it would appear that the Monarch butterflies have remarkably acute vision. It is also apparent that a considerable amount of selection is exercised in choosing a suitable resting site protected from strong winds.

Effect of Low Temperatures on Initiating Roosting. Although southward migration commences between July 17 and July 22 roosting does not usually take place until August and reaches its peak, in so far as numbers on a given roosting site are concerned, in mid or late September. After a number of
Figure 70. Number of Monarch butterflies on roosting site correlated with date, minimum temperatures, and occurrence of cold frontal passage.
years of collecting many thousands of butterflies from various roosting sites, it was found that the largest number always coincided with a rapid drop in minimum nocturnal temperature. With the passage of a cold air mass resulting in clear skies and maximum radiation at night the numbers of butterflies increased very markedly. It appeared, therefore, that low temperatures might be responsible for initiating roosting. Throughout August and September frequent observations were made on the presence of Monarchs on a particular roosting site situated close to my home. The information obtained is presented in the accompanying chart (Fig. 70) in which the number of butterflies observed on the roosting site is given on the right side of the chart, and the dates are indicated on the left side of the chart. Minimum temperatures, taken from the monthly meteorological summaries issued by the Meteorological Branch of the Canadian Department of Transport, are given at the top of the chart, with a reading from left to right indicating the degree of drop in temperature. On August 13 one specimen was found on the tree (the previous year five specimens had been found on it on August 15). Observations were made before August 12, but there were then no butterflies on the trees; this negative information has not been included in the chart. After September 28 there were very few Monarch butterflies present and observations were discontinued. This sudden drop in numbers was due to freezing temperatures which destroyed pupae and larvae.

The periods of the passage of cold fronts, which are directly correlated with rapid drops in minimum temperatures, are indicated. However, earlier cold fronts were mild in that there were no heavy storms or strong winds with them. Later the cold fronts were accompanied by strong winds and heavy rain. The cold front of September 23 was accompanied by strong winds, heavy rain, and a severe drop in minimum temperatures which, a few miles north of Toronto, dropped to below freezing.

From an examination of the chart there appears to be a correlation between the passage of a cold front, which produced minimum temperatures below 55°F., and the presence of Monarchs on the roosting site. On only one occasion prior to September 12 did the minimum temperature drop below 55°F., on July 6 when a minimum temperature of 53°F. was reached. On that occasion no weather was associated with the passage of the front and the maximum speed of the wind did not exceed 12 m.p.h. The chart indicates that there was a slight urge to form roosts from August 12 to September 4, with a maximum of twelve specimens on September 3. It will also be noted that there was very little weather associated with the fronts, and wind velocity did not exceed 17 m.p.h. The cold front that passed on September 4 had a great deal of rain and winds of 20 m.p.h. with gusts to 35 m.p.h. Following the passage of this front the number of Monarchs on the roosts rose rapidly. The sudden appearance of many butterflies may be
explained as follows. As the cold front slowly advances southward the mature butterflies move southward ahead of it; eventually it overtakes the migrating butterflies, particularly if a large body of water such as Lake Ontario intervenes, and they remain in a particular area until the return of warmer weather. For example, a specimen tagged on September 14 was recovered in the same area on September 21. With the change from the cold air mass to a warm air mass, the number of roosting specimens decreases very rapidly. Four hundred specimens were observed on September 7; eight on September 13. With the return of warm air the tendency to roost is not as strong as during periods of colder air; the return of warm air and improved weather conditions would allow the population that was held up owing to cold air to move southward, depleting the population in a particular area; and, finally, the cold air would tend to slow down development, so that there would be fewer adult butterflies taking part in migration. As a result of the change to a warm air mass, from September 19 to September 22, development of larvae and pupae was rapid, stimulated perhaps by the effect of the previous cold air.

In the absence of data from other localities in North America one can only tentatively conclude that roosting is initiated by the occurrence of low temperatures following the passage of a cold front. If this conclusion is correct, then roosting should take place only in the provinces of Canada and those states of the United States which are affected by polar outbreaks to a marked degree. We have found that overwintering roosts occur in localities where the temperatures are known to drop frequently below 50°F. That falling temperatures, or change of air mass is responsible for establishing roosts in localities much farther south than Ontario, is evidenced in the following report received from Mr. C. A. Anderson of Dallas, Texas:

Just at dusk on October 26, 1954, a large cloud of Monarchs appeared on the horizon in the north. They were approximately 100 feet up and as they came closer they appeared like a gigantic, brown carpet moving rapidly along. They were riding a Texas "norther" coming down at 15 miles an hour. They took on somewhat the appearance of a swarm of bees with the exception that they appeared levelled off at the top and bottom. As they passed over the northern part of the city, it was apparent that they were lowering and that they would stop over for the night. They were hardly out of sight before the telephone started ringing. The word was that butterflies were settling down in trees near the Dallas Country Club. It was dark before we reached the location. Four large hackberry trees had been selected as the stop-over place. They were protected from the north wind which only touched their tops. With the aid of flashlight, it became evident that the insects were seeking protection from the cold wind. Not a single butterfly was to be seen in the top parts of the trees touched by the wind. The other parts of the trees were weighted down by Monarchs packed as closely together as they could get. They were immobile. They could be picked up and moved. They stayed where they were placed.
At daybreak the following morning, the temperature was 52 degrees. The day was clear and bright with a light north wind still blowing. As the sun warmed their location, the Monarchs commenced to flex their wings. At nine o'clock, they began to take off in two's and three's heading south. At one o'clock the trees were bare.

In the course of our investigations one particular observation was so striking that it is here recorded. On September 22, 1957, a number in excess of 1000 Monarchs was found on the roosting site. Many were captured and placed in cardboard containers. When a roosting colony is disturbed the uncaptured specimens, unless immobilized by the temperature, usually fly away. On this particular morning, however, the butterflies, although the minimum temperature had been 57°F, and at the time of collecting had risen to 62°F, refused to leave the roost. They would fly but a short distance from the tree, and immediately circle back and settle in small groups near the top of the tree out of reach of the net. The sky was slightly overcast with cirrostratus clouds; the wind was approximately 7 m.p.h. To us there was very little indication of an impending storm. The collecting was carried out at 7.00 A.M. By 11.00 A.M. the sky was overcast with altocumulus clouds, by 1.00 P.M. strong winds, up to 25 m.p.h., and thunderstorms swept the area. Meteorological reports indicated rapidly falling barometric pressure during the night and morning period—the only meteorological factor that might have been affecting the Monarch butterflies at the time the observations were made. In the absence of more observations of this nature it is not possible to conclude that when the barometric pressure falls the Monarchs remain on the roosting site protected from inclement weather conditions, although such a conclusion might be drawn from the above observation.

The density of roosting congregations of Monarch butterflies seems to be directly correlated with temperature. During periods of low temperatures the butterflies roost close together in dense masses, but during periods of higher temperatures (usually above 60°F.) they spread out over the roosting site. The following observation is taken from my notes for September 10, 1957: "A warm front passed through the Toronto region yesterday, with rain and rapidly rising temperatures associated with it. This morning there were more butterflies than yesterday (when they were relatively scarce) but they were more difficult to capture because they were more active. As soon as the net touched the branches of the tree they would immediately take to wing. The clumps were more diffuse. They were scattered over the branches of the tree, with their wings partly spread, in marked contrast to yesterday morning when they clung to the branches, close together, their wings folded."

That cold air may impede development and reduce the numbers taking
part in the southward movement is indicated by the following observations taken from my field notes for 1956: "On Sept. 7 Monarch butterflies were numerous. On Sept. 8 they were about half as abundant as on the 7th, and on the 9th they were relatively scarce. The weather has been unusually cold during this period."

When a Monarch butterfly has emerged from the pupa and the wings have expanded and become rigid enough to sustain flight it does not immediately fly southward. In the course of our rearing tests we found that newly emerged specimens, having been tagged and liberated, would fly in almost any direction close to the ground, employing a gliding or cruising flight. Specimens that had issued from the pupae for periods of from one to six days were liberated in groups of ten. Those of the first day flew aimlessly, visiting flowers in the garden. Of those that had emerged two days before, only one flew southward. Those that had emerged from three to six days before flew in a southerly direction. From this it would appear that there is an "exploratory period" lasting from one to three days after emergence from the pupa.

In the course of our tagging programme it was sometimes necessary to hold specimens in the rearing cages for a few days until enough time was available for tagging. In many cases, butterflies that had been held in the cages for periods in excess of two days would fly to the nearest flowers to feed rather than fly directly southward. As was pointed out earlier, Monarch butterflies must feed during migration and, according to our tests, if deprived of food will die within a period of ten days.

Effect of Low Temperatures on Terminating Migration

The Monarch butterfly breeds from June to October in most parts of the United States and southern Canada; they may continue to breed as late as January in California and begin breeding in March in the southwestern United States. Low temperatures appear to be responsible for terminating all breeding activity. This was borne out in the fall of 1956 when, following the passage of a cold front with resulting freezing temperatures, out of a total of two hundred and sixty-four pupae in our rearing cages, one hundred and forty-eight were destroyed. Of those surviving, sixty emerged and produced normal butterflies but the remainder after emerging from the pupae and drying their wings were unable to fly. (Mr. E. McDonald of Port Hope, Ontario, recorded a similar observation: "During cold weather, from Sept. 30 to Oct. 17, a few Monarch butterflies that we saw here were very much smaller in size. Also, the last four butterflies to hatch out during the cold weather in October were unable to fly.") Out of a total of forty-eight larvae only one survived the cold. The milkweed plants were killed and hence food was no longer available. The one remaining larva was kept alive for three
weeks without any visible change in size, although it was fed fresh milkweed leaves collected from a plant which, being located close to a heated building, had survived the freezing temperature.

Thirty larvae that were killed by the low temperatures were dissected and it was found that the body fluid was in a very thin liquid state with no indication of fat deposition. Some of the pupae had a similar lack of fat, while others had a considerable amount. It would appear that larvae and newly formed pupae were destroyed because the body fluid had a relatively high freezing point, and the more mature pupae survived owing to the presence of fat and hence a lower freezing point of body fluid.

To test the effect of low temperatures, ten pupae were placed in a refrigerator at 38°F on October 17. On November 1, one of them was removed and a perfectly formed butterfly emerged on November 3. On November 3 two specimens were removed; one emerged and the other turned dark in colour, with no emergence. On November 29 the remaining seven were removed. Five turned dark in colour with no emergence; the remaining two developed so that the butterfly could be seen distinctly within the pupa case, but they failed to emerge.

As noted above, butterflies that emerged during freezing temperatures were unable to fly. To test the effect of low temperatures on mature butterflies, the following experiments were carried out. Ten adult Monarchs were placed in the refrigerator at a temperature of 24°F for twelve hours. When the butterflies were liberated they flew away, with no apparent ill effects. Ten specimens were exposed to a temperature of 22°F for twenty-four hours. All recovered without any apparent ill effects. Ten specimens were exposed to a temperature of 20°F for twenty-four hours; two died. Of the remainder all exhibited ill effects in that they were unable to sustain flight and appeared to have lost the use of their legs. Five specimens were placed in the refrigerator at 8°F for six hours; all failed to recover. Ten specimens were placed in a wire cage and exposed for two days to outdoor temperatures ranging from a maximum of 34°F to a minimum of 10°F. When taken indoors six failed to recover. The four that recovered exhibited the same ill effects described above.

It was noticed during the refrigeration tests that if the specimens were not placed in waterproof containers they died within a very short period of time. It was assumed that this was due to the drying effect of the refrigerator and therefore all the specimens discussed above were placed in sealed waxed paper containers.

Although the above tests are by no means conclusive, they indicate that the pupae are more susceptible to low temperatures than are the adults; that the adults can withstand below freezing temperatures for short periods of time, but that prolonged periods are either fatal or produce paralysis.
Low temperatures therefore stop further breeding activity and hence are responsible for terminating the southward migration.

Characteristics of Flight During the Southward Migration

General Flight Characteristics. In chapter IV a discussion of the flight habits of the Monarch butterfly was presented in which the variations in flight pattern were divided into gliding, cruising, speed, prenuptial, and social flights. During the southward migration observations were made on the characteristics of flight and were compared to those made during the summer breeding season. With the exception of the prenuptial flight, all the variations described were present. The southward migration is, with rare exceptions, a slow, rather casual drifting movement characterized by periods of gliding, cruising, sudden bursts of speed, and, what is perhaps most characteristic, a social flight involving two or more individuals, as previously described.

When a roost breaks up in the early morning, it is not with a sudden movement of butterflies in mass, like a flock of blackbirds. Rather, the butterflies drift slowly and casually away from the tree, a few at a time, until all have taken wing. Only when the tree is shaken violently so as to dislodge the butterflies has a mass movement away from the roost been observed.

Direction of Flight. To test the direction of flight at various hours of the day and under various wind conditions, Monarchs that had been collected at a roosting site and tagged were liberated in groups of ten by throwing them into the air and then observing the direction of flight. Without exception, and for each set of eighty observations, all flew in a southerly direction—either southeast, south, or southwest. In the morning the tendency was to the southeast, and in the afternoon to the southwest. If a wind was blowing the direction was altered; for example, ten specimens liberated at 11 A.M. in a north wind all flew directly south, whereas on the previous day at the same hour but under calm conditions all flew in a southeasterly direction. With a southwesterly wind at 4 P.M., ten were recorded as flying south. A south wind increased the tendency to fly east in the morning and west in the afternoon. A northerly wind increased the tendency to fly directly south.

In the course of the tests a rather interesting observation was made. The specimens were collected from a maple tree. These specimens, in a state of stupor due to the cold, were placed in large cardboard cartons and transported to my home about a mile north. They were later liberated and some of them were found on the same tree on the following day, having flown back to the same field and chosen the same roosting site.

All of the specimens used in the tests were tagged. Some of the specimens did not fly very far before coming to rest again upon the ground, and were returned to us by our neighbours. Those liberated in the morning were
returned by our neighbours to the east, and those liberated in the afternoon were returned by our neighbours to the west.

To find out whether or not the antennae might possibly play a role in flight direction, the following simple tests were carried out. Thirty specimens were liberated in groups of ten. Ten were liberated without amputating the antennae; ten had one antenna amputated; ten had both antennae amputated. The tests were carried out at 11.00 A.M. with clear sky and almost calm wind conditions. The results were as follows: Antennae not amputated: all flew SE or ESE. One antenna amputated: all flew SE or ESE. Both antennae amputated: two flew S; four flew W; four flew NE.

The tests were repeated with the same results for specimens with the antennae not amputated and those with one antenna amputated. When both antennae were amputated, three flew S; two flew E; three flew NW; and two flew in erratic circles, eventually landing in pine trees about a hundred feet from the point of liberation. It would appear then that the antennae play a part in flight orientation and perhaps in direction as well.

Effect of Strong Winds. The above tests were carried out when winds were less than 10 m.p.h. and when the sun was shining. Although according to Williams (1949) flight continues southward regardless of cloud condition, our observations would seem to indicate that the Monarch butterflies tend to rest during periods of inclement weather when cloudy conditions prevail.

The possible effect of strong winds and cloudy, inclement weather are indicated in the following observations taken from my field notes for September 19, 1957:

Temperature 50°F. and many butterflies present on the roosting site; cold front approaching the area, and a strong southwest wind blowing; sky is overcast and threatening rain; rain commenced at 10 A.M.; Monarch butterflies had taken up a position the evening before on the east side of the tree but the strong southwest wind was blowing them off the branches and many hundreds of them were found clinging to the tall grass and small bushes near the ground. We liberated our morning catch in the screened porch, and after flying against the screen for a short time, much to our surprise they came to rest in clusters at the corners of the porch, where they remained inactive for the rest of the day. In order to test whether or not the butterflies could fly against a strong wind, 200 of them were tossed into air in groups of ten. Without exception, all were blown northward, being unable to fly against the wind. Some of them were caught in strong down currents and carried to the ground where they remained clinging to the grass. The following day many of them were found still clinging to the grass and low bushes where they had remained during the previous day and throughout the night.

Effect of Heights of Land. The following reports for mountainous regions are of interest regarding the height to which a Monarch butterfly will fly upon encountering topographic obstructions.

The Peak Highway through Lassen Volcanic National Park crosses a pass at an
elevation of 8,512 feet. This mountain pass is in a north-south direction and several times, during August and September, Monarch butterflies were observed at this pass travelling southward. [E. D. Freeland.]

Over the week-end of Sept. 4–5, 1955, I went to the high Sierra Nevada Mountains. After leaving the floor of the central valley and ascending to the 3000 ft. elevation, the narrow-leaved milkweed gave way to the broad-leaved, the latter continuing to the 5000–6000 ft. elevation. We camped in the little town of Mineral King (5000–9000 ft.) and hiked up to the 11,000 foot altitude. Monarch adults were flying at all of these elevations, but were noticeably fewer the higher we went. I am now convinced that the Monarchs could cross the Rockies and the High Sierra. [Paul Board.]

Over the central business section of Toronto 268 separate observations were made on the height of flight. Of this number 234 were flying at the height of 100 feet or more; the remainder flew close to the ground over lawns in gardens and parks. It would appear that on approaching an area of tall buildings, owing in part perhaps to vertical air currents, the height of flight is increased. Similar observations were made over wooded areas; the flight, however, was of the gliding and cruising type.

From these observations it would appear that Monarch butterflies will fly at considerable heights above sea level, depending on topography and artificial obstructions, but, for the most part, they remain within a few feet of the ground level. Strong winds may carry them to greater heights, but such cases would be exceptional.

Effect of Bodies of Water. On encountering a large body of water, the variations in height of flight are rather characteristic. The following observations are taken from my field notes:

Toronto, Sept. 23, 1939, 2 P.M. Monarch butterflies unusually abundant along the lake shore; a very strong south wind causing large breakers; many dead and partly drowned specimens washed up on shore; most of the butterflies had come to rest on the leeward side of small willow bushes that were between four and eight feet in height, but a great many were attempting to fly against the wind, out over the water, some of them flying to a considerable height before returning to the shore again. It would appear that the unusual abundance at this time occurring on small willow bushes was due to the strong wind.

Scarboro, Sept. 18, 1956, 4 P.M. Monarch butterflies migrating along the Bluffs [Lake Ontario], although the majority were moving in a southwesterly direction following the shore line, the occasional specimen would attempt to fly out over the Lake [the Bluffs are about 200 feet above water level]. A gentle southerly breeze, about 10 m.p.h., was blowing. The Monarchs, on leaving the Bluffs, would begin to fly higher and higher, as if attempting to find an offshore or northerly breeze to assist in the crossing, finally returning to land, still at a considerable height, then dropping down to ground level to continue in a southwesterly direction following the shore line.

Toronto, Sept. 14, 1957, 2 P.M. [This particular site, known locally as "Cherry Beach" forms a rounded peninsula separated by a channel from one of the islands]
Monarch butterflies were seen in goodly numbers feeding upon the flowers of the New England aster and goldenrod and flying westward along the lake shore, until they reached the apex of the peninsula at which point the flight was altered both in character and direction, from a gliding motion, with but slight visible movement of the wings, to a more rapid beat of the wings causing an increase in speed; the direction changed from westerly to northwesterly in a direct line from the peninsula across the channel to the island on the opposite side; one would conclude that the butterflies could see the island and were flying toward it.

It would seem that the Monarch butterflies display a certain amount of antipathy towards large bodies of water and that only when assisted by an off-shore wind will they attempt to cross one to continue on an unaltered flight. This is borne out by the returns of tagged specimens which had followed the shoreline. Strong winds undoubtedly do carry the butterflies out over large bodies of water and, when confronted by a long peninsula pointing southward, such as Point Pelee on Lake Erie, they will fly over an expanse of water rather than reverse their migration route or alter it to a northerly direction. When a strong wind is blowing it is not unusual to find large congregations of Monarch butterflies on such peninsulas, torn between the desire to fly south rather than north, and reluctance to fly over the water against the wind. The occasional specimen, rapidly beating its wings, will venture forth followed by others. Beal (1941) made frequent observations of the flight of the migrating Monarchs from Point Pelee and concluded that the flight over the lake took place against the wind as often as with it. The normal condition, however, from my observations and from the returns of tagged specimens, is that a tail wind will cause more flights across the large bodies of water than a head wind. Regardless of wind, the majority of the migrating population hold to the shoreline so long as the latter is oriented in a southerly direction.

That the Monarch butterflies do tend to follow the shoreline, rather than venture over large bodies of water, has been illustrated by Shannon (1916) (Fig. 71): To shed some light upon the forces that the insects face, I chose what I hoped would become a favorable post for observation. It was a sand-bar lying west-by-east along the southern Long Island coast; the west end of Coney Island. This place was chosen because the butterflies, as they move southward in the northeastern part of the United States, and reach the southern Long Island coast, are confronted by the ocean. Therefore, they are forced to turn westward to reach an overland route to the south. Rarely, a flock may venture directly southward over the wide waters. I have received one report of such a flock seen fifteen miles at sea. It is likely, however, that few of these ventures ever regain the land. Even the vast majority, which cautiously follow the westward and landward route, are forced to pass over lesser water barriers. Few such hurdles could be more dangerous to the fliers than the one that confronts them at the west end of Coney Island, where spread the wide waters of lower New York Bay.
Mr. L. Beamer of Meaford reports that on July 25, 1957, "Monarch butterflies were seen crossing Lake Erie." Mr. Beamer also records that Mr. George Irving has seen many Monarch butterflies, flying high, crossing Lake Erie at a distance of fifteen miles from the Canadian shore.

On numerous occasions Monarch butterflies have been seen crossing Lake Ontario and it is a common experience to have them land, in large numbers, on various small crafts and large lake boats. Mr. T. D. Muir reported the
following observation: “One evening, early in August, at a distance of 25-30 miles from Toronto (en route to Charlotte) we overtook a flight of Monarch butterflies some 200 feet up and moving southerly. The general impression was of a group instinctively drawn on towards some distant goal. A few of them landed on deck and one stayed aboard until we landed at Prescott.”

McDade (1957) recorded the following observation: “Our course was roughly parallel, but slightly divergent, to the coast of Long Island and about 15 miles off shore. Numerous Monarch butterflies were seen, about 30 per hour. Their general line of flight was southwesterly.”

Tagging Method

Williams (1958) states that the first recorded attempt to mark insects, in order to trace their movements, was that of Atkinson in 1796. This was published in the Transactions of the Linnean Society of London for 1804. In this instance the Indian silk-raisers put marks on the wings of male silkworm moths (Phalaena paphia), each district being represented by a distinctive mark. As a result of this, male moths were traced for distances up to one hundred miles.

Various methods of marking butterflies have been attempted, from time to time, as follows: (1) Making distinctive incisions in the wing (Shannon, 1917); (2) Arrangements of coloured spots (Meber, 1926); (3) Spraying with various types of dyes and other coloured materials (Cory, 1934; Meber, 1926); (4) Letter and number printed in red dye on the wing (Fletcher, 1936); (5) Gluing a label to the wing with Canada balsam (Fletcher, 1936); (6) A colour splash on one wing and a label glued to the other (Williams, 1958); (7) Stamped number on the rear wing (Anderson).

For many years Mr. C. A. Anderson of Dallas, Texas, has been carrying out a programme of marking Monarch butterflies by this last method. He kindly submitted the following description of it together with a few critical statements concerning its success.

The butterflies are kept in the cages until their wings are dry. They are then removed and marked. A rubber stamp and a good quality of check-protector ink are used for this purpose. The under sides of the wings are stamped with the same number consisting of a letter followed by one or two digits. For instance F 29 might be used. Each insect receives a different number. Great care is taken in stamping the wings so that they are not damaged in any way. After marking, the insects are placed in a screened porch and their action noted. Should there be any that have impaired flying ability, they are removed. The date of release and the numbers of the butterflies are carefully recorded.

At the time of release of my butterflies each spring, I send a post card to interested persons in the Americas and other parts of the world. The recipient is alerted to the fact that marked butterflies may come his way. The response is always gratifying.
The following is a sample of the card issued by Mr. Anderson for 1955.

**On The Wings of The Monarch Butterfly**

With: C. A. Anderson

3209 Centenary

Dallas 25, Texas

**SUBJECT:** Monarch butterflies, reared, branded and released in Texas.

**QUESTION:** Where do they go from here?

**YOUR PART:** Please report all marked butterflies you observe.

Once again we come with our numbered wings heading north. Many thanks for all the splendid reports we received in 1954 from so many friends in the American and other parts of the world. Special thanks go to our good friends of the Fourth Estate. A hearty welcome to the new friends who join us for the first time this year.

The Monarchs chose to route their southward journey over the Dallas area last fall. On October 24, they came spread along a twenty-mile front. When the flight ended that evening, an estimated 1,011,000 had flown over.

Just as dusk on October 24, the wind shifted to the north with a velocity of fifteen miles an hour. It brought in a huge cloud of Monarchs riding ahead of a cool front. The cloud changed into the shape of a tremendous, brown, moving carpet of unusual design.

A signal from somewhere designated a group of majestic huckleberry trees as the resting place for the night. Down came the magic carpet and in a matter of moments every twig was bent by the weight of the beautified butterflies. They took off in small groups the next morning. Before noon, the trees were bare.

**FIGURE 72.** Card issued by Mr. C. A. Anderson to inform naturalists of his "branded" Monarch butterflies.

Concerning the results of this method Mr. Anderson writes as follows:

I realize that the chances of any of my Monarchs being observed are remote indeed. When one considers the vast expanse of our country and the many hazards encountered by a butterfly coupled with the fact that a butterfly can fly his whole route without coming near human beings, the few thousands that I release are as nothing. A whole year may go by without a single authentic report. To me this is not discouraging in view of all factors involved.

The remarks about captured, marked butterflies are carefully checked. A good many of these reports prove to be fabrications on the part of someone seeking publicity. Others have captured butterflies that were not Monarchs, with natural or accidental markings. It often happens that a butterfly comes in contact with a newly painted object and gets a paint spot or streak on its body or wing. It happens occasionally that a butterfly is killed or dies and its wings come in contact with a sales slip or other ticket containing numbers, the rain or the dew moistens the numbers and they are transferred to the butterfly's wings. This makes a pronounced marking.

Except for the method used by Williams and his colleagues, in which the label informs the person capturing the tagged specimen where to send it, none of the above methods has produced the desired results since the method of marking does not ensure the return of the specimen.
In the early stages of our studies in 1938 and 1939, we attempted to use a combination of dyes and oil paint. It was a relatively simple matter, using a spray gun, to spatter many hundreds of butterflies as they clung to the branches of their roosting site. But we received none of these colourful specimens back from distant points. We then attempted applying a number to the wing. This was a tedious job and met with the same lack of success as the dye method. It soon became apparent that it was not sufficient to make the marked specimen distinctive—it had to bear some sort of label that would inform the person collecting the specimen what to do with it.

If one is dealing with only a few specimens Williams’ method of affixing the label to the wing “with enough adhesive to soak through the scales and to attach both scales and label” to the wing, is perhaps possible. It has been our experience, however, that when tagging many hundreds of specimens glue tends to get coated over the labels, the specimens, and the hands of the tagger, and a considerable amount of time is used in applying the adhesive. There was the added disadvantage that once the label had been applied (with difficulty) to the wing it was necessary to wait until the glue had “set,” otherwise there was a danger that it would fall off.

In order to avoid the use of a liquid adhesive we attempted to use a gummed label. A set of printed labels was prepared on light-weight paper that had a water-soluble glue on one side. After a few attempts to place this label on the wing we realized that it was necessary to remove the scales and so a patch of scales was removed from the upper surface of the hind wings and the label glued to the wing surface. We found, however, that this interfered with the motion of the wings because the veins, being elevated above the plane surface, caused the edges of the label to stick up, thus catching on the rear margin of the front wings. It was obvious from this that it would not be possible to place the label on the under-surface of the front wings, since the protruding edges would catch on the front edge of the hind wings. We then tried placing the tag on the upper surface of the front wings, and although this appeared to solve the problem, it was found that if the specimens were allowed to flutter about in a cage the labels worked loose and fell from the wing. We concluded that the vibration of the wing membrane loosened the glue.

By accident one of the labels, which measured 17 mm. in length and 7 mm. wide, became bent and the thought occurred to us that it might be bent over the leading edge of the wing. We attached it to the wing in this manner and found that it simplified the application, as well as making the label cling more firmly to the wing membrane. Many butterflies were tagged in this manner and a few of them were returned from distances up to forty miles. Because the glue of such labels was water-soluble, however, moisture destroyed the adhesive property of the glue. A waterproof paper
proved equally unsuccessful because when the glue became dry it tended to bend the label, causing it to fall from the wing.

As a result of a series of experiments, in which the tagged butterflies were kept in wire cages and allowed to flutter about for various lengths of time, I found that the labels would not adhere to the wing membrane. In some cases, perhaps because the label was glued to itself along the bent edge, the label remained on for as long as two days. With this in mind, an attempt was made to punch a hole through the area of the discal cell and glue the label to itself through this hole. A stiff piece of paper or light cardboard was placed under the wing and a paper punch was used to perforate both the card and the wing membrane. The purpose of the card was to stiffen the delicate wing membrane in order to prevent it from being torn. The procedure then was as follows. The butterfly to be tagged was held in the left hand, the right front wing was pushed forward and the card placed on the under surface of the wing. The punch was placed over the leading edge of the wing in a position that would result in a neat round hole being cut in the area of the discal cell. The moistened gummed label was placed over the leading edge of the wing, having first been bent in half so that the glued surfaces faced each other, and glued to each other through the hole. Many hundreds of specimens were tagged in this manner and the returns were most gratifying, some of them having travelled for distances up to 800 miles. Within a very short period of time, however, many co-operators reported that during periods of inclement weather the tag would become damp and fall from the wing. It was not until the winter of 1954 that we learned how true these reports were. At this time we had the very good fortune to attend a meeting of the American Association for the Advancement of Science, held at Berkeley University in California and we took advantage of this opportunity to visit the Monterey peninsula where we were able to observe and tag many thousands of overwintering butterflies. On one particular day we were able to tag one thousand Monarch butterflies, using the method outlined above. During the evening it started to rain and throughout the night there was a continuous light drizzle and heavy fog. When we visited the area the following day we found the ground beneath the trees where the butterflies were roosting littered with our small white tags.

On returning, we began to investigate what type of adhesive might possibly be used in place of the water-soluble glue. A number of business establishments were contacted and my colleagues in chemistry were approached for advice in solving the problem. It was suggested that a label similar to that commonly used to fix a price label to glass merchandise might be suitable because such labels adhere firmly to a smooth glass surface. As a result of correspondence with the firm that manufactured these labels, a tag was produced which would cling to the smooth surface of the wing
membrane, after the scales had been removed, by applying a slight pressure between the thumb and index finger, and which when bent in half would fit into the area of the discal cell (Plate IX). This label was treated with a waterproof solution and a chalk layer upon which instructions could be printed. The paper used was a dull litho-coated material with a 60 lb. basis weight. The paper was .0035 inches in thickness and .005 with the adhesive. The adhesive was a latex basis type bearing the trade name "perma-grip." The labels, numbered consecutively, were in sheets of fifty, as illustrated in Figure 73.

The manufacturers of this type of label have branch offices throughout the world and information concerning the purchase of this material may be obtained through the Avery Adhesive Label Corp. Ltd., 48 Haas Road, Rexdale, Ontario, Canada.
Placing the tag on the wing does of course add a slight amount of extra weight to it; but as long as the weight is kept close to the body of the butterfly the amount to be lifted by the wing is greatly reduced. This is illustrated in the accompanying diagram (Fig. 74), where $T'$ is the tag placed at the apex of the wing $W$, and $T''$ is the tag placed near the base of the wing close to the body $b$. The distance the weight must be lifted in position $T'$ is much greater than in $T''$ and hence the weight at position $T'$ is much greater than at $T''$. A comparison may be made between lifting a weight on the end of a long pole and lifting a similar weight without the pole or at the base of the pole near the hand. So far as the weight of the labels which we have been using is concerned, the following comparison with the weight of the butterfly is of interest. Ten butterflies (five males and five females) weighed 4.10 gms; hence the average weight of one butterfly is 0.41 gms. The weight
of fifty of our labels was .68 gms; the average weight of each label is therefore .01 gms. Hence the weight of a label is approximately 1/40 the weight of the butterfly.

Because the label is easy to apply, it can be done very quickly. It eliminates the use of liquid glues, and by bending the tag over the edge of the wing, a narrow margin of the glued surfaces are brought together, thus further assisting in holding the tag to the wing. Having the tags arranged on a sheet assists in typing individual numbers on each tag, and at the same time is an automatic record of the tags used on a particular day. The chalked surface of the label holds a deep impression of the number so that if the ink should be washed away the impression of the stamped number can be detected by examining the tag beneath the low power of a microscope.

The specimen to be tagged is held in the left hand. The thumb and index finger of the right hand removes the scales from both the upper and lower surfaces of the wing in the vicinity of the discal cell by a gentle stroking motion. A label is removed from the sheet, bent in half so that the adhesive surface of each half faces the other, and placed over the cleared area of the wing. A gentle pressure between thumb and index finger secures the label to the wing and the specimen is released. Approximately ten seconds of time is required to place the tag on the wing of a captured specimen.

That the above method has proved successful is evidenced by the many returns which we have had, up to a distance of nearly two thousand miles. We have also been able to tag butterflies with one wing broken across the costal area, the label holding the wing together much as a splint does a broken bone. Recoveries from over a hundred miles have been made of such damaged specimens.

Since there was a possibility that this tag could be used for marking other species of butterflies, it was applied to the following without any apparent effect on flight: Speyeria cybele, Speyeria aphrodite, Limenitis arthemis, Limenitis archippus, Papilio glaucus, Papilio polyxenes. Tags of the same size were placed on the wings of the following species, and although they were able to fly it appeared that flight efficiency had been decreased: Polygonia comma, Polygonia interrogationis, Vanessa atalanta, Vanessa cardui, Colias eurytheme, Colias philodice. These species were tested again using one-half the label size and it was found that flight was unaffected. The difference was not a matter of increased weight but rather that the edge of the larger label on the underside of the front wing interfered with the action of the right hind wing. The size of the tag used for other species, therefore, should be determined by the size of the discal cell because the free edges of the label should not extend beyond the inner margin of the cell; otherwise the anterior margin of the hind wing will tend to catch on
the free edge if it is turned upwards by the veins. A specimen of *Lycaena thoas* flew unhampered with a tag one-quarter the size used for the Monarch butterfly.

The tags were also tested on dragonflies. It was found that when the tag was placed on the front wing, flight was seriously affected; when placed on the front edge of the hind wing, flight was but slightly affected. The motion of the wings of a dragonfly is different from that of a butterfly, and hence the tagging method would have to be altered accordingly; further experiments on size and placement of such tags would be necessary for those insects in which flight depends upon the rapid vibration of the wings.

**Organization of Tagging Programme.**

In the early stages in the development of our tagging programme (1938) only relatively few specimens were tagged in one locality (Toronto). At this time the tag was attached to the wing with a water-soluble glue—it was not until sixteen years later that it was found that a water-soluble glue would not hold the tag to the wing during periods of wet weather. These early attempts also disclosed, of course, that the number of recaptures was directly related to the number tagged—the greater the number tagged the greater the chances of recovery.

Realizing the difficulties involved in following a complete flight route from one point to another (many hundreds or perhaps thousands of miles apart), it was decided to organize a team of co-operators throughout North America. To obtain such a team, in 1952 an article dealing with the migration of the Monarch butterfly was published in *Natural History*—a magazine produced by the American Museum of Natural History. A request for assistance was included in the article and as a result a team of seventy co-operators was obtained. As tagged specimens began to appear in various towns and cities throughout the United States and Canada, the investigation was reported in various newspapers and in this way brought to the attention of biologists and naturalists. Within a short period of time more than two hundred co-operators living in various parts of the United States and Canada were assisting in tagging Monarch butterflies. The distribution of those assisting our investigations is indicated in the accompanying map (Fig. 75).

Since many thousands of butterflies were being tagged at various times by so many individuals, the following system was devised to eliminate any possibility of duplication of numbers which would lead to an erroneous flight record. Each state of the United States and each province of Canada was indicated on the tag by a specific combination of letters. For example: O for Ohio, ON for Ontario, C for California, and so on. Each co-operator
was given a specified set of numbers. For example, a co-operator living in Ontario might be given two hundred tags bearing the numbers ON 1 to ON 200 inclusive; another co-operator in the same province might have the numbers ON 201 to ON 400 inclusive. The name and address of the co-operator were entered on a small filing card (5" x 3") together with the numbers of the tags sent to him. A typical filing card for one of our co-operators is shown in Figure 76.

![Beamer, Lloyd
Box 56,
Meaford, Ont.
1956 ON 1-50
ON 251-750
ON 851-1850 (ReId 1465-1850)
1957 ON 1-50
ON 751-950
ON 1201-1500
ON 3101-3450 3279
1958 ON 454-950 ReId - no Monarchs](image)

When a tagged specimen was captured it was mailed to our institution. The person sending it would give information on date and place of capture. Having the number and letter designation, we would then write to the person who had tagged the specimen informing him of the recapture, together with the name and address of the person who had found the specimen. The person finding the tagged specimen would be told where it had been tagged and given a brief explanation of the purpose of the tagging, together with the name and address of the person who had tagged the particular specimen. In this way we were able to increase the number of co-operators, because the person finding the tagged specimen often became interested in the project.

In order to obtain many returns it was necessary to tag thousands of specimens. Although it is possible to capture and tag specimens found feeding upon the nectar of flowers in gardens and fields, it takes a good many hours to tag a few specimens in this way. It was found that in order to tag many Monarchs in a short period of time, it was essential to locate a roosting site. This was done by following the flight of specimens in the
late afternoon, particularly those individuals that were flying in a northerly rather than in a southerly direction. Since the specimens become immobilized at temperatures below 50°F, the roosting site would be visited just prior to sunrise. The butterflies would remain massed together on the branches of the tree and it was a simple matter to use a large net to cover the cluster and then, by shaking the branch, cause them to fall into the net. They were then removed from the net and transferred to large cardboard cartons which were equipped with a trap-door arrangement on the top so that when the butterflies were placed in the box the door could be closed. By this method it was possible to collect as many as two thousand specimens in half an hour. With rising temperatures the butterflies would become active and, flying about in the box, would damage their wings. To overcome this, the butterflies were liberated in a large screened area ($20' \times 10' \times 8'$). The tagging operation could then be carried out in a leisurely manner. After the butterflies were tagged they were collected in groups in the screened area and liberated through the doorway. Tests on direction of flight were carried out in conjunction with this tagging programme.

During periods of cloudy weather, when temperatures remained low, it was possible to tag the specimens directly from the cardboard box in which they remained relatively inactive; this was the procedure used when tagging at the overwintering colonies in Florida and California.

The average time taken to tag a captured specimen (from the moment it is taken in the hand, the scales removed, and the tag fixed to the wing) is 11 seconds. In a period of four hours, 1,110 specimens were tagged, averaging 13 seconds for each specimen. The difference between the two figures was owing to fatigue: the first few specimens may take less than 11 seconds; over 500 specimens may take more than 13 seconds for each specimen. That we were able to tag so many specimens in a short period of time is responsible for the excellent flight returns listed in Table II.

**DISCUSSION OF FALL MIGRATION**

The most significant flight records have been traced on the accompanying map (Plate XII). These lines (referred to as “release-recovery lines”) indicate a point-to-point flight route. The locality where the specimen was tagged is indicated by a black bead at the north end of the line, and the locality where the tagged specimen was recovered is indicated by a black bead at the south end of the line. The flight line is indicated by a black thread connecting each point. A casual examination of this map would indicate a definite southwest migration route. Yet if we examine the short recovery records, particularly those in the list that were not plotted on the map, it is obvious that the direction of flight, although maintaining a southerly direction, may be south or southeast.
### TABLE II
Recoveries of Tagged Monarch Butterflies*

<table>
<thead>
<tr>
<th>Date of tagging</th>
<th>Place of tagging</th>
<th>Date of recovery</th>
<th>Place of recovery</th>
<th>Approx. distance</th>
<th>Direction</th>
</tr>
</thead>
<tbody>
<tr>
<td>8:56</td>
<td>Lighthouse Pt., Fla.</td>
<td>8:56</td>
<td>Lighthouse Pt., Fla.</td>
<td>8:56</td>
<td></td>
</tr>
<tr>
<td>8:56</td>
<td>Lighthouse Pt., Fla.</td>
<td>8:56</td>
<td>Lighthouse Pt., Fla.</td>
<td>8:56</td>
<td></td>
</tr>
<tr>
<td>8:56</td>
<td>Lighthouse Pt., Fla.</td>
<td>8:56</td>
<td>Lighthouse Pt., Fla.</td>
<td>8:56</td>
<td></td>
</tr>
<tr>
<td>8:56</td>
<td>Lighthouse Pt., Fla.</td>
<td>8:56</td>
<td>Lighthouse Pt., Fla.</td>
<td>8:56</td>
<td></td>
</tr>
<tr>
<td>8:56</td>
<td>Lighthouse Pt., Fla.</td>
<td>8:56</td>
<td>Lighthouse Pt., Fla.</td>
<td>8:56</td>
<td></td>
</tr>
<tr>
<td>22-01</td>
<td>Monterey, Calif.</td>
<td>Apr. 4:54</td>
<td>40 m. E. of Sacramento, Calif.</td>
<td>160 m.</td>
<td>N</td>
</tr>
<tr>
<td>1-57</td>
<td>Pacific Grove, Calif.</td>
<td>Jan. 3:57</td>
<td>Pacific Grove, Calif.</td>
<td>142 m.</td>
<td>N</td>
</tr>
<tr>
<td>16-57</td>
<td>Cayucos, Calif.</td>
<td>Feb. 27:57</td>
<td>Morro Bay, Calif.</td>
<td>2 m. S of Morro Bay, Calif.</td>
<td>110 m.</td>
</tr>
<tr>
<td>16-57</td>
<td>Morro Bay, Calif.</td>
<td>Mar. 15:57</td>
<td>Morro Bay, Calif.</td>
<td>2 m. N of Morro Bay, Calif.</td>
<td>20 m.</td>
</tr>
<tr>
<td>17-57</td>
<td>Monterey, Calif.</td>
<td>Apr. 4:52</td>
<td>Monterey, Calif.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>17-57</td>
<td>Pacific Grove, Calif.</td>
<td>Apr. 6:57</td>
<td>Patterson, Calif.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1st week of</td>
<td>San Carlos, Calif.</td>
<td>July 6:57</td>
<td>Grand Canyon Village, Ariz.</td>
<td>600 m.</td>
<td>SE</td>
</tr>
<tr>
<td>Mar. 52</td>
<td>Pacific Grove, Calif.</td>
<td>between Apr. 21-27-52</td>
<td>Auburn, Calif.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>2-57</td>
<td>Pacific Grove, Calif.</td>
<td>between Apr. 21-27-52</td>
<td>Auburn, Calif.</td>
<td>162 m.</td>
<td>NE</td>
</tr>
</tbody>
</table>

*We received thirty-nine returns for which no date of liberation was given on the tag and which were recovered in the same areas in which they had been liberated.

[290]
<table>
<thead>
<tr>
<th>Date of tagging</th>
<th>Place of tagging</th>
<th>Date of recovery</th>
<th>Place of recovery</th>
<th>Approx. distance</th>
<th>Direction</th>
</tr>
</thead>
<tbody>
<tr>
<td>2/27</td>
<td>Morro Bay, Calif.</td>
<td>Mar. 18/57</td>
<td>Pacific Grove, Calif.</td>
<td>105 m</td>
<td>NW</td>
</tr>
<tr>
<td>3/56</td>
<td>Morro Bay, Calif.</td>
<td>between Apr. 24-27/56</td>
<td>Paco Roble, Calif.</td>
<td>19 m</td>
<td>NE</td>
</tr>
<tr>
<td>3/57</td>
<td>Monterey, Calif.</td>
<td>before May 10/57</td>
<td>Monterey, Calif.</td>
<td>175 m</td>
<td>N</td>
</tr>
<tr>
<td>3/57</td>
<td>Pacific Grove, Calif.</td>
<td>Apr. 25/57</td>
<td>Yuba City, Calif.</td>
<td>120 m</td>
<td>N</td>
</tr>
<tr>
<td>3/57</td>
<td>Monterey, Calif.</td>
<td>Apr. 23/57</td>
<td>Fresno, Calif.</td>
<td>110 m</td>
<td>NE</td>
</tr>
<tr>
<td>27/57</td>
<td>Cayucos, Calif.</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>May 8/57</td>
<td>Conroe, Texas</td>
<td>June 5/7</td>
<td>near De Queen, Ark.</td>
<td>205 m</td>
<td>N</td>
</tr>
<tr>
<td>19/58</td>
<td>Conroe, Texas</td>
<td>May 20/58</td>
<td>Conroe, Texas</td>
<td></td>
<td></td>
</tr>
<tr>
<td>June 7/57</td>
<td>Chippewa Falls, Wis.</td>
<td>before June 15/57</td>
<td>Bloomer, Wis.</td>
<td>15 m</td>
<td>N</td>
</tr>
<tr>
<td>29/56</td>
<td>Coal Valley, Ill.</td>
<td>July 8/56</td>
<td>Coal Valley, Ill.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>July 2/56</td>
<td>Meaford, Ont.</td>
<td>Oct. 18/56</td>
<td>Galveston, Texas</td>
<td>1320 m</td>
<td>SW</td>
</tr>
<tr>
<td>6/57</td>
<td>Meaford, Mass.</td>
<td>July 20/57</td>
<td>Manchester, N.H.</td>
<td>46 m</td>
<td>NW</td>
</tr>
<tr>
<td>7/58</td>
<td>Lathrup Village, Mich.</td>
<td>July 26/56</td>
<td>Madison Heights, Mich.</td>
<td>12 m</td>
<td>E by 1 m. S</td>
</tr>
<tr>
<td>11/56</td>
<td>Mason, Mich.</td>
<td>before Aug. 8/56</td>
<td>Saginaw, Mich.</td>
<td>65 m</td>
<td>N</td>
</tr>
<tr>
<td>11/56</td>
<td>Stamford, Ont.</td>
<td>July 28/56</td>
<td>Saginaw Falls, N.Y.</td>
<td>8 m</td>
<td>SE</td>
</tr>
<tr>
<td>11/57</td>
<td>Lathrup Village, Mich.</td>
<td>July 21/57</td>
<td>Livonia, Mich.</td>
<td>8 m</td>
<td>SW</td>
</tr>
<tr>
<td>11/57</td>
<td>Lathrup Village, Mich.</td>
<td>July 26/57</td>
<td>Oak Park, Mich.</td>
<td>2 m</td>
<td>SE</td>
</tr>
<tr>
<td>12/56</td>
<td>Lathrup Village, Mich.</td>
<td>July 19/56</td>
<td>Detroit, Mich.</td>
<td>7 m</td>
<td>S</td>
</tr>
<tr>
<td>12/56</td>
<td>San Carlos, Calif.</td>
<td>Aug. 25/56</td>
<td>Lassen Volcanic National Park, Mason, Mich.</td>
<td>216 m</td>
<td>NE</td>
</tr>
<tr>
<td>18/57</td>
<td>Woodbridge, N.Y.</td>
<td>Aug. 11/57</td>
<td>Mountain Dale, N.Y.</td>
<td>1 m</td>
<td></td>
</tr>
<tr>
<td>15/56</td>
<td>Mason, Mich.</td>
<td>before Aug. 7/56</td>
<td>Toronto, Ont.</td>
<td>84 m</td>
<td>SE</td>
</tr>
<tr>
<td>19/56</td>
<td>Meaford, Mass.</td>
<td>before Aug. 10/57</td>
<td>Phoenix, N.Y.</td>
<td>110 m</td>
<td>SE</td>
</tr>
<tr>
<td>21/56</td>
<td>Medford, Ont.</td>
<td>before Aug. 7/56</td>
<td>Detroit, Mich.</td>
<td>5 m</td>
<td>NE</td>
</tr>
<tr>
<td>25/57</td>
<td>Detroit, Mich.</td>
<td>before Aug. 6/57</td>
<td>Lacayette, Ohio</td>
<td>132 m</td>
<td>SW</td>
</tr>
<tr>
<td>26/56</td>
<td>Bay Village, Ohio</td>
<td>Aug. 19/56</td>
<td>royal Oak, Mich.</td>
<td>7 m</td>
<td>S</td>
</tr>
<tr>
<td>26/56</td>
<td>Lathrup Village, Mich.</td>
<td>before July 31/56</td>
<td>Providence, R.I.</td>
<td>49 m</td>
<td>SE</td>
</tr>
<tr>
<td>Date of tagging</td>
<td>Place of tagging</td>
<td>Date of recovery</td>
<td>Place of recovery</td>
<td>Approx. distance</td>
<td>Direction</td>
</tr>
<tr>
<td>----------------</td>
<td>-----------------------</td>
<td>------------------</td>
<td>-------------------</td>
<td>-----------------</td>
<td>-----------</td>
</tr>
<tr>
<td>29, 35</td>
<td>Niagara Falls, Ont.</td>
<td>Oct. 21, 35</td>
<td>Niagara Falls, Ont.</td>
<td>1/2 m.</td>
<td></td>
</tr>
<tr>
<td>29, 55</td>
<td>N. Stamford, Ont.</td>
<td>July 28, 55</td>
<td>Stamford, Ont.</td>
<td>7 m.</td>
<td>NW</td>
</tr>
<tr>
<td>31, 56</td>
<td>Cambridge, Mass.</td>
<td>Aug. 10, 56</td>
<td>Lexington, Mass.</td>
<td>7 m.</td>
<td>SW</td>
</tr>
<tr>
<td>31, 56</td>
<td>Logan, Utah</td>
<td>Aug. 8, 56</td>
<td>Logan, Utah</td>
<td>32 m.</td>
<td>W</td>
</tr>
<tr>
<td>31, 56</td>
<td>Yankton, Mass.</td>
<td>7</td>
<td>Stowe, Mass.</td>
<td>32 m.</td>
<td></td>
</tr>
<tr>
<td>Aug. 2, 58</td>
<td>Barre, Mass.</td>
<td>Aug. 15, 58</td>
<td>Stonington, Conn.</td>
<td>75 m.</td>
<td>S</td>
</tr>
<tr>
<td>2, 58</td>
<td>Barre, Mass.</td>
<td>Aug. 4, 58</td>
<td>Barre, Mass.</td>
<td>6 m.</td>
<td>SW</td>
</tr>
<tr>
<td>3, 57</td>
<td>Marblehead, Mass.</td>
<td>Aug. 10, 57</td>
<td>Lynn, Mass.</td>
<td>6 m.</td>
<td>SW</td>
</tr>
<tr>
<td>3, 57</td>
<td>Marblehead, Mass.</td>
<td>Aug. 18, 57</td>
<td>Lynn, Mass.</td>
<td>6 m.</td>
<td>SW</td>
</tr>
<tr>
<td>3, 57</td>
<td>Marblehead, Mass.</td>
<td>Aug. 30, 56</td>
<td>Lexington, Mass.</td>
<td>18 m.</td>
<td>S</td>
</tr>
<tr>
<td>3, 57</td>
<td>Marblehead, Mass.</td>
<td>Aug. 13, 58</td>
<td>Marblehead, Mass.</td>
<td>2 m.</td>
<td>S</td>
</tr>
<tr>
<td>4, 56</td>
<td>Monroe, Wis.</td>
<td>Aug. 6, 56</td>
<td>Monroe, Wis.</td>
<td>100 ft.</td>
<td>S</td>
</tr>
<tr>
<td>7, 57</td>
<td>Detroit 24, Mich.</td>
<td>Aug. 21, 57</td>
<td>St. Clair Shores, Mich.</td>
<td>7 m.</td>
<td>S</td>
</tr>
<tr>
<td>7, 57</td>
<td>Detroit 24, Mich.</td>
<td>Aug. 12, 57</td>
<td>Detroit 5, Mich.</td>
<td>3 m.</td>
<td>SW</td>
</tr>
<tr>
<td>8, 57</td>
<td>Detroit 24, Mich.</td>
<td>Aug. 13, 57</td>
<td>Detroit 24, Mich.</td>
<td>7 m.</td>
<td>S</td>
</tr>
<tr>
<td>8, 57</td>
<td>Detroit 24, Mich.</td>
<td>Aug. 10, 57</td>
<td>Detroit 24, Mich.</td>
<td>3 m.</td>
<td>SW</td>
</tr>
<tr>
<td>8, 56</td>
<td>Logan, Utah</td>
<td>Aug. 25, 56</td>
<td>Logan, Utah</td>
<td>5 m.</td>
<td>S</td>
</tr>
<tr>
<td>8, 57</td>
<td>East Greenwich, R.I.</td>
<td>Aug. 31, 57</td>
<td>Wickford, R.I.</td>
<td>7 m.</td>
<td>S</td>
</tr>
<tr>
<td>10, 57</td>
<td>Highland Creek, Ont.</td>
<td>Aug. 17, 57</td>
<td>Highland Creek, Ont.</td>
<td>3 m.</td>
<td>S</td>
</tr>
<tr>
<td>11, 57</td>
<td>Niagara Falls, Ont.</td>
<td>Aug. 22, 57</td>
<td>Niagara Falls, Ont.</td>
<td>5 m.</td>
<td>S</td>
</tr>
<tr>
<td>Aug. 11, 57</td>
<td>Detroit, Mich.</td>
<td>Aug. 14, 57</td>
<td>Detroit 24, Mich.</td>
<td>3 m.</td>
<td>SW</td>
</tr>
<tr>
<td>12, 57</td>
<td>Bay Village, Ohio</td>
<td>Aug. 12, 57</td>
<td>Westlake, Ohio</td>
<td>5 m.</td>
<td>S</td>
</tr>
<tr>
<td>13, 57</td>
<td>Detroit 24, Mich.</td>
<td>Aug. 20, 57</td>
<td>Green Point, Detroit 36, Mich.</td>
<td>80 m.</td>
<td>W by S</td>
</tr>
<tr>
<td>14, 58</td>
<td>Danvers, Mass.</td>
<td>Aug. 17, 58</td>
<td>Danvers, Mass.</td>
<td>200 m.</td>
<td>SE</td>
</tr>
<tr>
<td>15, 57</td>
<td>Bay Village, Ohio</td>
<td>Aug. 15, 57</td>
<td>Bay Village, Ohio</td>
<td>200 m.</td>
<td>SE</td>
</tr>
<tr>
<td>16, 57</td>
<td>Detroit 24, Mich.</td>
<td>Aug. 19, 57</td>
<td>Detroit 9, Mich.</td>
<td>200 m.</td>
<td>SE</td>
</tr>
<tr>
<td>16, 57</td>
<td>Detroit 24, Mich.</td>
<td>Aug. 17, 57</td>
<td>Detroit 24, Mich.</td>
<td>200 m.</td>
<td>SE</td>
</tr>
<tr>
<td>16, 57</td>
<td>Detroit 24, Mich.</td>
<td>Aug. 20, 57</td>
<td>Detroit 24, Mich.</td>
<td>200 m.</td>
<td>SE</td>
</tr>
<tr>
<td>17, 56</td>
<td>Little Compton, R.I.</td>
<td>Aug. 17, 57</td>
<td>Brickyard, Detroit 24, Mich.</td>
<td>80 m.</td>
<td>W by S</td>
</tr>
<tr>
<td>17, 56</td>
<td>Bay Village, Mich.</td>
<td>Aug. 21, 57</td>
<td>Chicago, Ill.</td>
<td>200 m.</td>
<td>S</td>
</tr>
<tr>
<td>17, 57</td>
<td>Bethel, Maryland</td>
<td>Aug. 18, 57</td>
<td>Bethel, Maryland</td>
<td>200 m.</td>
<td>S</td>
</tr>
<tr>
<td>17, 57</td>
<td>Bay Village, Ohio</td>
<td>Aug. 19, 57</td>
<td>Olmstead Falls, Ohio</td>
<td>6 m.</td>
<td>S</td>
</tr>
<tr>
<td>Date tagging</td>
<td>Place of tagging</td>
<td>Date of recovery</td>
<td>Place of recovery</td>
<td>Approx distance</td>
<td>Direction</td>
</tr>
<tr>
<td>------------</td>
<td>--------------------------</td>
<td>-----------------</td>
<td>---------------------------</td>
<td>----------------</td>
<td>-----------</td>
</tr>
<tr>
<td>18/57</td>
<td>Toronto Island, Ont.</td>
<td>Aug. 23/57</td>
<td>Toronto Island, Ont.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>18/57</td>
<td>Toronto Island, Ont.</td>
<td>Aug. 23/57</td>
<td>Toronto Island, Ont.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>20/57</td>
<td>Meaford, Ont.</td>
<td>Aug. 28/57</td>
<td>Cortland, Ohio</td>
<td>225.0 m</td>
<td>S</td>
</tr>
<tr>
<td>20/57</td>
<td>Bay Village, Ohio</td>
<td>Aug. 30/57</td>
<td>Bay Village, Ohio</td>
<td></td>
<td>S</td>
</tr>
<tr>
<td>21/57</td>
<td>Meaford, Ont.</td>
<td>before Aug. 28/57</td>
<td>between Meaford and Toronto, Ont.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>22/57</td>
<td>Meaford, Ont.</td>
<td>Aug. 24/57</td>
<td>Wansbeekening Bay, Penetang, Ont.</td>
<td>30.0 m</td>
<td>NE</td>
</tr>
<tr>
<td>24/56</td>
<td>Bay Village, Ohio</td>
<td>Sept. 9/56</td>
<td>Rocky River, Ohio</td>
<td>4.0 m</td>
<td>E</td>
</tr>
<tr>
<td>24/56</td>
<td>Port Hope, Ont.</td>
<td>Aug. 21/56</td>
<td>Port Hope, Ont.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>25/56</td>
<td>Toronto Island, Ont.</td>
<td>Sept. 2/57</td>
<td>Detroit 35, Mich.</td>
<td>3.0 m</td>
<td>NW</td>
</tr>
<tr>
<td>26/56</td>
<td>Meaford, Ont.</td>
<td>Sept. 9/55</td>
<td>Crefeld, Maryland</td>
<td>520.0 m</td>
<td>SE</td>
</tr>
<tr>
<td>26/56</td>
<td>Bay Village, Ohio</td>
<td>Aug. 28/56</td>
<td>Bay Village, Ohio</td>
<td></td>
<td></td>
</tr>
<tr>
<td>28/56</td>
<td>Framington, Mass.</td>
<td>Sept. 1/56</td>
<td>Seabrook Beach, Y. H.</td>
<td>57.0 m</td>
<td>NE</td>
</tr>
<tr>
<td>30/55</td>
<td>Bay Village, Ohio</td>
<td>Oct. 2/55</td>
<td>Parkwood, Ariz.</td>
<td>115.0 m</td>
<td>S</td>
</tr>
<tr>
<td>30/56</td>
<td>Bay Village, Ohio</td>
<td>Sept. 7/56</td>
<td>Bay Village, Ohio</td>
<td></td>
<td></td>
</tr>
<tr>
<td>31/56</td>
<td>Bay Village, Ohio</td>
<td>Sept. 6/56</td>
<td>Middleburg Heights, Ohio</td>
<td>4.0 m</td>
<td>S</td>
</tr>
<tr>
<td>31/56</td>
<td>Meaford, Ont.</td>
<td>before Sept. 11/56</td>
<td>East Redstone, Ont.</td>
<td>80.0 m</td>
<td>SE</td>
</tr>
<tr>
<td>Sept. 1/37</td>
<td>Point Pelee, Ont.</td>
<td>before Sept. 8/57</td>
<td>Point Pelee, Ont.</td>
<td>55.0 m</td>
<td>SE</td>
</tr>
<tr>
<td>1/37</td>
<td>Point Pelee, Ont.</td>
<td>Sept. 8/57</td>
<td>Willard, Ohio</td>
<td>430.0 m</td>
<td>E</td>
</tr>
<tr>
<td>1/37</td>
<td>Point Pelee, Ont.</td>
<td>Sept. 1/57</td>
<td>Point Pelee, Ont.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>2/56</td>
<td>Bay Village, Ohio</td>
<td>Oct. 13/56</td>
<td>Celina, Tenn.</td>
<td>394.0 m</td>
<td>SW</td>
</tr>
<tr>
<td>2/57</td>
<td>Meaford, Ont.</td>
<td>Oct. 25/57</td>
<td>Old Saybrook, Conn.</td>
<td>450.0 m</td>
<td>S</td>
</tr>
<tr>
<td>3/55</td>
<td>Meaford, Ont.</td>
<td>Sept. 3/55</td>
<td>Blaine, Ont.</td>
<td>9.0 m</td>
<td>SW</td>
</tr>
<tr>
<td>3/55</td>
<td>Bayley's Harbor, Wisc.</td>
<td>Sept. 6/55</td>
<td>West Bend, Wisc.</td>
<td>130.0 m</td>
<td>S</td>
</tr>
<tr>
<td>Sept. 3/56</td>
<td>Meaford, Ont.</td>
<td>Oct. 18/56</td>
<td>Galveston, Texas</td>
<td>1020.0 m</td>
<td>SW</td>
</tr>
<tr>
<td>3/56</td>
<td>Bay Village, Ohio</td>
<td>Sept. 9/56</td>
<td>Bay Village, Ohio</td>
<td></td>
<td></td>
</tr>
<tr>
<td>6/57</td>
<td>Highland Creek, Ont.</td>
<td>Sept. 8/57</td>
<td>Toronto 33, Ont.</td>
<td>10.0 m</td>
<td>SW</td>
</tr>
<tr>
<td>Date of tagging</td>
<td>Place of tagging</td>
<td>Date of recovery</td>
<td>Place of recovery</td>
<td>Approx. distance</td>
<td>Direction</td>
</tr>
<tr>
<td>----------------</td>
<td>-----------------</td>
<td>-----------------</td>
<td>------------------</td>
<td>-----------------</td>
<td>-----------</td>
</tr>
<tr>
<td>6/57</td>
<td>Meaford, Ont.</td>
<td>Sept. 9/57</td>
<td>Toronto, Ont.</td>
<td>85 m.</td>
<td>SE</td>
</tr>
<tr>
<td>7/56</td>
<td>Port Hope, Ont.</td>
<td>Sept. 9/56</td>
<td>Rochester, N.Y.</td>
<td>64 m.</td>
<td>SE</td>
</tr>
<tr>
<td>7/56</td>
<td>Highland Creek, Ont.</td>
<td>pred. Oct. 1/56</td>
<td>Deering, Mo.</td>
<td>772 m.</td>
<td>SW</td>
</tr>
<tr>
<td>7/56</td>
<td>Highland Creek, Ont.</td>
<td>Sept. 8/56</td>
<td>Beamsville, Ont.</td>
<td>47 m.</td>
<td>S</td>
</tr>
<tr>
<td>8/56</td>
<td>Highland Creek, Ont.</td>
<td>Sept. 10/56</td>
<td>Buffalo, N.Y.</td>
<td>90 m.</td>
<td>S</td>
</tr>
<tr>
<td>8/56</td>
<td>Highland Creek, Ont.</td>
<td>Sept. 9/56</td>
<td>Shadyside, N.Y.</td>
<td>43 m.</td>
<td>S</td>
</tr>
<tr>
<td>8/56</td>
<td>Highland Creek, Ont.</td>
<td>Sept. 9/56</td>
<td>9 m. east of Olcott Beach, N.Y.</td>
<td>42 m.</td>
<td>S</td>
</tr>
<tr>
<td>8/56</td>
<td>Highland Creek, Ont.</td>
<td>Sept. 9/56</td>
<td>Highland Creek, Ont.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>8/56</td>
<td>Mount Clemens, Mich.</td>
<td>before Sept. 13/56</td>
<td>Grove Point Woods, Detroit, Mich.</td>
<td>10 m.</td>
<td>SW</td>
</tr>
<tr>
<td>8/56</td>
<td>Sheenectady, N.Y.</td>
<td>Sept. 9/56</td>
<td>Scarborough, Ont.</td>
<td>4 m.</td>
<td>SW</td>
</tr>
<tr>
<td>10/55</td>
<td>Newagen, Maine</td>
<td>Sept. 14/55</td>
<td>Spry Beach, N.J.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>10/56</td>
<td>Highland Creek, Ont.</td>
<td>Sept. 17/56</td>
<td>S. Euclid, Ohio</td>
<td>212 m.</td>
<td>SW</td>
</tr>
<tr>
<td>10/56</td>
<td>Highland Creek, Ont.</td>
<td>Sept. 13/56</td>
<td>Long Branch, Ont.</td>
<td>23 m.</td>
<td>W</td>
</tr>
<tr>
<td>10/56</td>
<td>Highland Creek, Ont.</td>
<td>Sept. 15/56</td>
<td>Simcoe, Ont.</td>
<td>80 m.</td>
<td>SW</td>
</tr>
<tr>
<td>11/56</td>
<td>Highland Creek, Ont.</td>
<td>Sept. 15/56</td>
<td>Abb's St., Toronto, Ont.</td>
<td>17 m.</td>
<td>W</td>
</tr>
<tr>
<td>12/55</td>
<td>Green Bay, Wis.</td>
<td>Sept. 22/55</td>
<td>Green Bay, Wis.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>12/55</td>
<td>Green Bay, Wis.</td>
<td>Sept. 23/55</td>
<td>Chicago, Ill.</td>
<td>197 m.</td>
<td>S</td>
</tr>
<tr>
<td>12/57</td>
<td>Highland Creek, Ont.</td>
<td>Oct. 9/57</td>
<td>Liberty, Miss.</td>
<td>1060 m.</td>
<td>SW</td>
</tr>
<tr>
<td>13/56</td>
<td>Melrose, Mass.</td>
<td>Sept. 22/56</td>
<td>West Haven, Conn.</td>
<td>123 m.</td>
<td>SW</td>
</tr>
<tr>
<td>13/56</td>
<td>Highland Creek, Ont.</td>
<td>Sept. 19/56</td>
<td>Quakerstown, Pa.</td>
<td>310 m.</td>
<td>SE</td>
</tr>
<tr>
<td>13/56</td>
<td>Highland Creek, Ont.</td>
<td>Sept. 15/56</td>
<td>Oswego, N.Y.</td>
<td>135 m.</td>
<td>E</td>
</tr>
<tr>
<td>13/56</td>
<td>Highland Creek, Ont.</td>
<td>before Sept. 20/56</td>
<td>Little Falls, N.J.</td>
<td>355 m.</td>
<td>SE</td>
</tr>
<tr>
<td>13/57</td>
<td>Milwaukee, Wis.</td>
<td>Sept. 14/57</td>
<td>Milwaukee, Wis.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>13/57</td>
<td>Milwaukee, Wis.</td>
<td>Sept. 20/57</td>
<td>Piqua, Ohio</td>
<td>115 m.</td>
<td>S'</td>
</tr>
<tr>
<td>16/57</td>
<td>Point Pelee, Ont.</td>
<td>Oct. 12/57</td>
<td>Biloxi, Miss.</td>
<td>875 m.</td>
<td>SW</td>
</tr>
<tr>
<td>16/57</td>
<td>Point Pelee, Ont.</td>
<td>Oct. 10/55</td>
<td>Lindale, Texas</td>
<td>838 m.</td>
<td>SW</td>
</tr>
<tr>
<td>16/57</td>
<td>Milwaukee, Wis.</td>
<td>Sept. 16/56</td>
<td>Bendale Park, Toronto, Ont.</td>
<td>6 m.</td>
<td>W</td>
</tr>
<tr>
<td>17/55</td>
<td>Cherry Beach, Toronto, Ont.</td>
<td>Sept. 18/55</td>
<td>Kingway, Toronto, Ont.</td>
<td>6 m.</td>
<td>W</td>
</tr>
<tr>
<td>17/56</td>
<td>Highland Creek, Ont.</td>
<td>before Oct. 1/56</td>
<td>Cobourg, Ont.</td>
<td>50 m.</td>
<td>E</td>
</tr>
<tr>
<td>17/56</td>
<td>Highland Creek, Ont.</td>
<td>Sept. 18/57</td>
<td>Woodbine Race Track, Toronto, Ont.</td>
<td>9 m.</td>
<td>SW</td>
</tr>
<tr>
<td>17/57</td>
<td>Monroe, Wis.</td>
<td>Sept. 57</td>
<td>Belvidere, Ill.</td>
<td>48 m.</td>
<td>SE</td>
</tr>
<tr>
<td>18/57</td>
<td>Highland Creek, Ont.</td>
<td>Oct. 11/57</td>
<td>Niceville, Fla.</td>
<td>985 m.</td>
<td>SW</td>
</tr>
<tr>
<td>18/57</td>
<td>Highland Creek, Ont.</td>
<td>before Sept. 22/57</td>
<td>Mount Hamilton, Ont.</td>
<td>50 m.</td>
<td>SW</td>
</tr>
<tr>
<td>Date of tagging</td>
<td>Place of tagging</td>
<td>Date of recovery</td>
<td>Place of recovery</td>
<td>Approx. distance</td>
<td>Direction</td>
</tr>
<tr>
<td>----------------</td>
<td>----------------------------------</td>
<td>------------------</td>
<td>------------------</td>
<td>-----------------</td>
<td>-----------</td>
</tr>
<tr>
<td>18/57</td>
<td>Highland Creek, Ont.</td>
<td>before Sept. 27/57</td>
<td>Burlington, Ont.</td>
<td>45 m.</td>
<td>SW</td>
</tr>
<tr>
<td>18/57</td>
<td>Highland Creek, Ont.</td>
<td>Sept. 20/57</td>
<td>Scarborough, Ont.</td>
<td>5 m.</td>
<td>SW</td>
</tr>
<tr>
<td>18/57</td>
<td>Highland Creek, Ont.</td>
<td>Sept. 29/57</td>
<td>St. Catharines, Ont.</td>
<td>42 m.</td>
<td>S</td>
</tr>
<tr>
<td>18/57</td>
<td>Highland Creek, Ont.</td>
<td>Oct. 3/57</td>
<td>Rosse, Mts.</td>
<td>1060 m.</td>
<td>SW</td>
</tr>
<tr>
<td>18/57</td>
<td>Highland Creek, Ont.</td>
<td>Jan. 24/58</td>
<td>Estacion Cateore, San Luis Potosi, Mexico</td>
<td>1870 m.</td>
<td>SW</td>
</tr>
<tr>
<td>18/57</td>
<td>Highland Creek, Ont.</td>
<td>Sept. 21/57</td>
<td>Scarborough, Ont.</td>
<td>6 m.</td>
<td>S</td>
</tr>
<tr>
<td>18/57</td>
<td>Highland Creek, Ont.</td>
<td>Oct. 9/57</td>
<td>Atlanta, Ga.</td>
<td>710 m.</td>
<td>SW</td>
</tr>
<tr>
<td>18/57</td>
<td>Highland Creek, Ont.</td>
<td>Sept. 21/57</td>
<td>Scarborough, Ont.</td>
<td>5 m.</td>
<td>SW</td>
</tr>
<tr>
<td>19/56</td>
<td>Highland Creek, Ont.</td>
<td>Sept. 22/56</td>
<td>Ajax, Ont.</td>
<td>8 m.</td>
<td>E</td>
</tr>
<tr>
<td>19/56</td>
<td>Highland Creek, Ont.</td>
<td>Oct. 2/56</td>
<td>Arlington, Va.</td>
<td>370 m.</td>
<td>SE</td>
</tr>
<tr>
<td>19/56</td>
<td>Highland Creek, Ont.</td>
<td>Sept. 25/56</td>
<td>Royebank, Ont.</td>
<td>2 m.</td>
<td>SE</td>
</tr>
<tr>
<td>19/56</td>
<td>Highland Creek, Ont.</td>
<td>Oct. 6/56</td>
<td>Sharon, Pa.</td>
<td>197 m.</td>
<td>SW</td>
</tr>
<tr>
<td>19/56</td>
<td>Highland Creek, Ont.</td>
<td>Oct. 29/56</td>
<td>Boston, Ga.</td>
<td>812 m.</td>
<td>SW</td>
</tr>
<tr>
<td>19/56</td>
<td>Highland Creek, Ont.</td>
<td>Sept. 21/56</td>
<td>Lakeshore Road, Toronto, Ont.</td>
<td>1400 m.</td>
<td>SW</td>
</tr>
<tr>
<td>19/56</td>
<td>Highland Creek, Ont.</td>
<td>Dec. 27/56</td>
<td>Seguin, Texas (dead)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>19/57</td>
<td>Highland Creek, Ont.</td>
<td>Sept. 29/57</td>
<td>Charleston Heights, S. Carolina</td>
<td>770 m.</td>
<td>S</td>
</tr>
<tr>
<td>19/57</td>
<td>Highland Creek, Ont.</td>
<td>Sept. 28/57</td>
<td>Queen Elizabeth Highway and Martindale, Ont.</td>
<td>45 m.</td>
<td>S</td>
</tr>
<tr>
<td>19/52</td>
<td>Cherry Beach, Toronto, Ont.</td>
<td>Oct. 1/52</td>
<td>Long Branch, Ont.</td>
<td>7 m.</td>
<td>W</td>
</tr>
<tr>
<td>Sept. 21/56</td>
<td>Highland Creek, Ont.</td>
<td>Oct. 9/56</td>
<td>Atlantic City, N.J.</td>
<td>304 m.</td>
<td>W</td>
</tr>
<tr>
<td>22/22</td>
<td>Toronto Island, Ont.</td>
<td>Sept. 24/52</td>
<td>Aldershot, Ont.</td>
<td>304 m.</td>
<td>SE</td>
</tr>
<tr>
<td>22/22</td>
<td>Toronto Island, Ont.</td>
<td>Sept. 27/52</td>
<td>Lakeside, Ont.</td>
<td>304 m.</td>
<td>SE</td>
</tr>
<tr>
<td>22/32</td>
<td>Toronto Island, Ont.</td>
<td>Oct. 7/52</td>
<td>Long Branch, Ont.</td>
<td>304 m.</td>
<td>SE</td>
</tr>
<tr>
<td>22/35</td>
<td>Liberty Borough, Pa.</td>
<td>Oct. 25/55</td>
<td>Port St. Joe, Florida</td>
<td>1400 m.</td>
<td>SE</td>
</tr>
<tr>
<td>23/36</td>
<td>Benicia, Calif.</td>
<td>Sept. 27/56</td>
<td>Vallejo, Calif.</td>
<td>9 m.</td>
<td>W</td>
</tr>
<tr>
<td>22/36</td>
<td>Highland Creek, Ont.</td>
<td>Sept. 22/56</td>
<td>Hamilton, Ont.</td>
<td>22 m.</td>
<td>SW</td>
</tr>
<tr>
<td>22/36</td>
<td>Highland Creek, Ont.</td>
<td>Sept. 23/56</td>
<td>Queen St. E., Toronto, Ont.</td>
<td>22 m.</td>
<td>SW</td>
</tr>
<tr>
<td>22/36</td>
<td>Highland Creek, Ont.</td>
<td>Oct. 9/56</td>
<td>Flushing, L.I., N.Y.</td>
<td>300 m.</td>
<td>E to S</td>
</tr>
<tr>
<td>22/36</td>
<td>Highland Creek, Ont.</td>
<td>Oct. 11/56</td>
<td>Woodbine Race Track, Toronto, Ont.</td>
<td>9 m.</td>
<td>W</td>
</tr>
<tr>
<td>22/56</td>
<td>Highland Creek, Ont.</td>
<td>Oct. 31/56</td>
<td>Maple Leaf Ball Stadium, Toronto, Ont.</td>
<td>22 m.</td>
<td>SW</td>
</tr>
<tr>
<td>24/56</td>
<td>Toronto, Ont.</td>
<td>Sept. 24/56</td>
<td>Toronto, Ont.</td>
<td>6 m.</td>
<td>W</td>
</tr>
<tr>
<td>24/56</td>
<td>Carlaw Ave., Toronto, Ont.</td>
<td>Sept. 26/56</td>
<td>Fort York, Ont.</td>
<td>13 m.</td>
<td>W</td>
</tr>
<tr>
<td>Date of tagging</td>
<td>Place of tagging</td>
<td>Date of recovery</td>
<td>Place of recovery</td>
<td>Approx. distance</td>
<td>Direction</td>
</tr>
<tr>
<td>----------------</td>
<td>-----------------</td>
<td>-----------------</td>
<td>------------------</td>
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<td>-----------</td>
</tr>
<tr>
<td>Oct. 9 1956</td>
<td>Benicia, Calif.</td>
<td>Jan. 9 1957</td>
<td>Costa Mesa, Calif.</td>
<td>394 m.</td>
<td>SW</td>
</tr>
<tr>
<td>Oct. 21 1956</td>
<td>Benicia, Calif.</td>
<td>Nov. 2 1955</td>
<td>Santa Rosa, Calif.</td>
<td>205 m.</td>
<td>SW</td>
</tr>
<tr>
<td>Nov. 3 1956</td>
<td>Santa Rosa, Calif.</td>
<td>Dec. 12 1956</td>
<td>Benoist, Texas</td>
<td>(Dec. 23 1957) Benoist, Texas (dead)</td>
<td>SW</td>
</tr>
<tr>
<td>Dec. 13 1956</td>
<td>Benoist, Texas</td>
<td>Dec. 23 1957</td>
<td>Santa Rosa, Calif.</td>
<td>205 m.</td>
<td>SW</td>
</tr>
<tr>
<td>Jan. 2 1957</td>
<td>Benoist, Texas</td>
<td>Feb. 5 1957</td>
<td>Santa Rosa, Calif.</td>
<td>205 m.</td>
<td>SW</td>
</tr>
</tbody>
</table>
Specimens collected in spring and early summer through midsummer to fall showing faded condition in early summer (similar to those in overwintering areas) to brightly-coloured specimens in midsummer (row 4) and predominantly so in late summer (last row). Note faded specimen at end of row 4 which is an immigrant from a first generation to the south.
Release recovery lines for tagged Monarch butterflies, indicating a general northeast-southwest migration.
Supposing a specimen tagged at point A on Figure 77 is recovered at point B. on the accompanying map (Plate XII) it would be indicated by the release-recovery line A-B. This particular specimen may have flown south-eastward to the Atlantic coast, then southwest following the coast line to the base of Florida, then westward to the locality where it was recovered at point B. This example is extreme in that the actual flight direction describes a wide arc east of the release-recovery line. Yet the fact that this is a probable route is substantiated by numerous observations from our co-operators and by our personal observations along the Gulf coast and throughout Florida. It is quite likely that all variations exist between this extreme and a straight line flight.

The westward movement of the Monarch butterflies is apparent along the highways in the northern part of Florida and the Gulf coast. This movement begins in September and continues throughout October and November with
a lesser movement, in that fewer individuals take part, throughout December and January. That the Monarch butterflies move down the Atlantic coast in great numbers is well authenticated in the literature and through personal correspondence from our co-operators. The flight pattern (the summation of all release-recovery lines) indicates that the fall migration of the Monarch butterfly is southwestward.

As will be seen from the map, we have had no returns for tagged specimens in the plains region and the mountainous sections of western North America. The reason for this is that very few specimens have been tagged in these regions because they do not occur as abundantly in the plains and mountains as in the east; indeed, in most localities in these areas they are rare. The reason for this is perhaps due to the fact that the various species of milkweed do not grow in such dense masses in these regions as in the east. We are therefore dealing with a very small and scattered population in the plains and mountain region. A number of specimens, however, have been tagged by our co-operators, but with no recoveries. The failure to obtain recovery may be explained in part by the sparseness of human habitations and in part by the absence of extensive flower gardens to which the Monarch butterflies might be attracted. However, I am of the opinion that the flight pattern for the eastern part of North America as here outlined could be extended to include the plains and parts of the mountain regions. This conclusion is based upon numerous observations on flight directions submitted by our co-operators and from my observations. In brief, if at any one point in North America where the Monarch butterflies are known to occur an intensive programme of tagging were carried out, the flight pattern would be similar to that for the eastern part of the continent.

The breeding population of Monarch butterflies occupies the area roughly between latitude 32° N and latitude 48° N (extending across the continent from the Atlantic to the Pacific coast). The population is not of uniform density throughout. By far the most dense is in the area of the Great Lakes, from approximately 100° to 70° west longitude and from approximately 32° to 48° north latitude (Fig. 76). From an extreme density in the immediate vicinity of the Great Lakes the population gradually becomes less dense to the west, east, and south. A similar dense population, although not as extensive, is found in California; some of my colleagues believe that the dense overwintering populations found along the coast are derived from this limited breeding area. Between these two areas of dense population is a sparse population extending through the central United States and the mountain regions.

The above conception of the limits of the breeding area of the Monarch butterfly is based on hundreds of observations received from our co-operators and colleagues which are on file at the Royal Ontario Museum. It is to be
FIGURE 78. Progressive movements of the Monarch butterfly population from the breeding area (A), through September (B), October (C), November (D), to December (E); (F), distribution of polar air associated with high pressure areas, which may restrict overwintering sites.
THE MONARCH BUTTERFLY

understood, of course, that we are discussing a breeding range which does not take into account the appearance of adult butterflies found in areas remote from the food plant—such areas as Churchill, Manitoba, and Great Slave Lake in Alberta. Nor are occasional breeding ranges in the southern United States in early spring or during the winter months taken into account.

Assuming the validity of the breeding range as here set forth and with the clear understanding that it is not possible to define exactly any boundary lines (hence these of necessity must be arbitrary) we can now proceed to outline the full migration in the light of our present knowledge based on data received from our tagging programme and many hundreds of observations on flight direction and first and last appearances in numerous localities throughout North America, as previously recorded (Fig. 78).

During September the adult population from the breeding range moves southward expanding the area of prevalence, particularly towards the southwest. The butterflies completely vacate the more northern fringe of the range and in the southern states, from which they were absent during the summer months, the occasional specimen is recorded.

Between the beginning of this southward movement in September and the first week of October, during which time outbreaks of polar air have lowered temperatures to below freezing in many northern localities, there is a decided change in the distribution of the migrating population. The southwestward movement becomes most noticeable. Co-operators in parts of southern North America, who reported no Monarch butterflies during the summer months and only occasional specimens in September, report vast numbers of them in October. By mid-October the condition is as indicated in Figure 78. It should be emphasized that the migrating population from the plains and mountain regions augment the area of density to the south, causing it to extend westward more rapidly. The increase in abundance over a wider area in California and extending through Oregon and Washington is undoubtedly due to the individuals coming from the sparse populations throughout the mountain valleys and from the north and northeast.

South of latitude 28° N. in Florida co-operators report Monarch butterflies as being present but, even throughout the winter months, they never assume a density comparable to the other areas here recorded. During the winter of 1951 we made a survey of the Florida peninsula and found the conditions to be as our co-operators had informed us. It was not until we reached St. Petersburg and Tampa, touring northward from the Florida Keys, that we found and were able to tag a few hundred specimens. From Jacksonville to Tallahassee many Monarch butterflies were seen and, with few exceptions, they were flying westward. From Tallahassee westward they were common, with at least one mass congregation at Lighthouse Point.

By late December the reports, with the exception of those from Florida, would indicate that the Monarch butterflies have reached their overwinter-
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ing quarters along the Gulf coast and the south Pacific coast of North America. We have had a tagged specimen returned from central Mexico that was liberated at Toronto, Canada. We assume then that the population made up of free-flying individuals (not congregated on trees as in California and Lighthouse Point) occupies the area as outlined (Fig. 78).

In the chart for December the solid tone indicates the only two areas where the Monarch butterfly is known to congregate habitually on a roosting site (Fig. 78).

Overwintering

Williams (1949) states that: "The butterflies move steadily southward until, about the beginning of October, they begin to reach Florida in the east and Southern California in the west. Here they settle down on groups of evergreen trees, usually close to the sea, and spend the greater portion of the winter in a state of semi-hibernation, occasionally flying around in bright sunshine, but more usually hanging dormant on the trees. The same trees may be visited year after year, and the butterflies may be in such numbers as to appear as chestnut-brown patches against the dark green of the foliage."

Williams (1938) further states that: "There are no hibernating quarters yet recorded in the whole of the Gulf Coast and Mexican frontier between Florida and California. In the east, they undoubtedly carry on into Mexico. On the Gulf Coast we have not yet any evidence of their arrival from the north, and no records anywhere of any movements out to sea towards the West Indies and South and Central America." Williams (1938) also pointed out the apparent lack of mass abundance of Monarch butterflies in Tennessee, Alabama, Mississippi, Arkansas, and Louisiana, and he emphasized the importance of numerous observations in order to explain flight direction and hibernation quarters.

The areas with which we are most concerned here are those that have been reported as overwintering sites or are suspected of being so. These are: the Atlantic coast of Georgia and Florida; the Gulf Coast from Florida to Mexico; Mexico (perhaps parts of Central America); and the Pacific coast of Mexico and California. The following information, amplified by our personal investigations of the areas concerned, has been received from our co-operators.

Atlantic Coast of Georgia

It had been reported that the Monarch butterflies overwintered on trees located on Jekyll Island off the Atlantic coast of Georgia. Miss Hilda White, research assistant on the Monarch butterfly project, visited the island in February, 1957, and reported as follows: "In the latter part of February,
1957, while on Jekyll Island, Georgia, nearly every day I would see from one to three Monarchs flying around. I searched for an overwintering congregation and covered the whole island, but I was unable to find such a roost. One may conclude that a few Monarch butterflies remain in this area during the winter months but that they do not usually congregate in numbers on trees.

Atlantic Coast of Florida

During January, 1956, we carried out a survey of Florida to ascertain whether or not the Monarch butterflies overwintered in this area. We had received communications from Miami, Palm Beach, Daytona Beach, and Gainesville to the effect that the Monarch butterfly was not abundant, and in some years absent in one or all of these localities. We had, however, received information of their presence in Jacksonville. Throughout the survey of the central and some of the Atlantic coastal area, not a single Monarch butterfly was seen south of a line from Daytona Beach on the east to Tampa on the west. In the vicinity of Lake City, Gainesville, and Ocala a few were seen flying to the southwest. We were led to conclude that the Monarch butterflies that entered Florida did so on a southwest flight from the Atlantic coast which carried them across the northern third of the state but not southward through it. This would explain not only their scarcity in most of Florida but also their prevalence along the Gulf coast north of Fort Myers, with occasional migration into the Everglades as far south as Cape Sable.

Gulf Coast of Florida

The following information has been received concerning the presence of Monarch butterflies in this area. Indirect observations, such as reports from a person other than the original observer, are not included.

As far as I have been able to gather, the Monarch is never particularly common here. [C. P. Kimball, Sarasota.]

Several years ago at Englewood, 80 miles south of Tampa, I found a colony of Monarchs of several thousands. I found them on live oak trees on a peninsula between bay and gulf, where they stayed some weeks; then they disappeared. Some time after I found them in a ten acre grove of slash pine about two miles from the first place. I visited them, both day and night, and while most of the trees were tall we never found them in the high boughs, and some of the largest gatherings were so low we could touch them. On pleasant days almost all of them left the grove, though a few were always about and they returned before night, and not to the same trees, for if the wind was from the east they would be found on the west side of the grove, and when from the west they would be on the east side, and when there was no bad weather they were often found near the center of the grove. My companion estimated their number at about twice what I did— he estimated the number at 10,000. They disappeared suddenly and, as far as I know, never returned to the same grove. [W. F. Smith, Englewood.]
We have seen numerous Monarchs here (Captive) but no concentrations. In fact they are much like one would see in summer, not semi-dormant or concentrated on trees—but flitting from spot to spot. I would estimate I had seen perhaps 50 Monarchs. We spent a month in Florida, a week travelling about the Gulf coast and six weeks in the coastal area of Texas between Galveston and Brownsville. At no time in all this area did we observe or, on inquiry, learn of any wintering grounds of the Monarch butterflies that might be likened to the Montereý trees. I am quite satisfied the Monarchs do not hibernate in this area as they do in California. It may be possible they do further south, as Mexico for instance. However, numerous Monarchs apparently do winter there in much the same manner as they live in the north. One evening I followed two Monarchs and saw them resting on bushes for the night and at two widely separated spots. [H. F. Stiles, Captiva.]

Last week [Nov. 5] we were on Sanibel Island located just southwest of Fort Myers, Florida, in the Gulf. We saw a number of Monarchs on Sanibel Island and many more Monarchs on a small island just north of Sanibel Island, which is called Captiva Island. The Monarchs were so numerous on the northern half of Captiva Island that we decided to visit an area which had a small group of pine trees on the northern portion of the island near the grounds of a Motel and Lodge known as the Plantation. The trees are located just south of the entrance through a gate to the grounds of the plantation. From 5:15 p.m. to 6 p.m. when it became dark the Monarchs flew in from various parts of the island to roost in several of the Australian pine trees. The butterflies were not in dense clusters, but they did cling to the pines in the same manner that the Monarchs did at Alligator Point. The weather was moderate with the low at night around 60 and the high in the daytime around 75. The colony is a small one of a few hundred Monarchs and certainly not over 500.

Captiva Island is very small being less than a mile wide and about 8 or 10 miles long. We noted the remains of a number of Monarchs which had been killed by automobiles.

We travelled on down to the lowest tip of Florida on the West Coast and noted some Monarchs flying casually about. We were not at a favorable spot at any time to try to locate a roost except the one on Captiva Island. [Lucien Harris.]

As far as we are able to ascertain, the only locality where Monarch butterflies congregate on trees throughout the winter months is at Lighthouse Point (Alligator Point) on the Gulf coast south of Tallahassee. This particular area was first brought to our attention by Mr. Lucien Harris of Atlanta, Georgia:

Herbert L. Stoddard wrote to me as follows: "On Nov. 4, 1954, at Alligator and Bald Points I saw several thousands of Monarch butterflies densely clustered, out of the wind, on young pine saplings—thicker than leaves on the trees. Such gatherings were at several places over a 10 acre tract when temperatures were as low as 24° F." [Lucien Harris.]

Each year, about the 21st of October, they start to come in droves, and at night they stop to rest on the Spanish moss that hangs from our large oak trees. A very few of them stay all winter, and last winter we had a severe winter, that is for Florida, and I found some of them frozen, as we had snow and temperatures as
low as 20°F. We live on Perdido Bay, which is about 13 miles from Pensacola, and about ten miles from the Gulf of Mexico. [Mrs. C. B. Hartley, Pensacola.]

Bromley (1928) states that: "In January, 1924, during the writer's trip through the Everglades, between west Palm Beach and Lake Okeechobee, great numbers of Monarch butterflies were noted flying over the saw grass, alighting on flowers, etc. Mating was observed in several instances."

At Sarasota Monarch butterflies were relatively common in the city park. They were found flying from one flower garden to another and coming to rest in the evening on the leaves of various species of trees. They never occurred in masses—only individually. A careful search was made of the coastal area in this vicinity but we were unable to find any butterflies at all.

From Sarasota to Pensacola, individuals were seen flying along the roadway and, in nearly every case, they were moving westward or southwestward, particularly from Panacea to Pensacola. They appeared to be particularly abundant at Pensacola, and so an intensive search was made of the area but no roosting sites were revealed. From numerous inquiries through naturalists' clubs and the Coast Guard, we concluded that the Monarch butterfly over-winters along the Gulf coast of Florida as a small colony at Lighthouse Point and as free-flying individuals throughout the entire area from Fort Myers in the south to Pensacola in the northwest.

Gulf Coast from Mobile, Alabama, to Brownsville, Texas

We did notice on a peninsula south of Mobile, running east and west with Old Fort Morgan on the west end and Orange Beach on the east end, an unusually large number of Monarchs. [H. F. Stiles.]

I saw a lone Monarch sailing down the street on Christmas day and another one in January. [Mrs. J. C. Coe, Foley, Alabama.]

In recent years there have been very few Monarchs sighted. From the information I can gather from trappers and hunters, there are no Monarchs sighted clustering along the coast line. The Monarchs, in my opinion, do not winter along the Louisiana coast. [Mrs. J. W. Townsend, New Orleans, Louisiana.]

In our survey we found Monarchs to be common in January along the coast of Alabama and Mississippi, particularly in the vicinity of Mobile. No roosting sites were located and no reports were received of such occurrences. It would appear that the Monarch butterflies spend the winter as individuals throughout this area. Our survey did not extend beyond New Orleans, but we have received reports from our co-operators:

The Monarchs appeared here singly and in small numbers several days ago, but today (October 20) they are here in great numbers. [S. H. Clark, Palacios, Texas.] I noticed Monarchs quite frequently at Hagar's Cabins, Rockport—about the same in number as in the summer around Toronto, Ontario. There were no concentrations—single individuals only. A few were seen at San Benito, San José and Gulfport. [Mrs. E. Jaquith.]
[Mrs. Jaquith reported seeing individuals during the first two weeks of March at St. Francis, La., New Orleans, La., and Mobile, Ala.]

On December 12 Mr. J. F. Combs of Beaumont, Texas, tagged a Monarch butterfly. On December 27 he recaptured it in good condition, and released it again. He found the same specimen dead on January 31. He states: “It had apparently been dead several days, and we had experienced about two weeks of rain, flood, cold and occasional temperatures as low as 30°F.”

From the first week of June until Sept. 14 we saw none here. On Sept. 14 a Monarch hit the car windshield. From Oct. 21-28 a number of them were sighted. We have never seen butterflies congregated in large numbers on a tree or anything else in this locality. [D. A. Crosby, Brownsville, Texas.]

From the above survey it may be concluded that Monarch butterflies overwinter as individuals along the Atlantic coast of Georgia, on the Gulf coast approximately from Fort Myers in southern Florida to Brownsville, Texas. The exception is one roosting site at Lighthouse Point, Florida.

Mexico and Central America

From a consideration of flight records and returns of tagged specimens, it would appear that a major proportion of the population of Monarch butterflies overwinters in Mexico. This conclusion was further substantiated by reports of great masses of Monarch butterflies passing through Eagle Pass, Texas, which is on the flight route, as indicated on the flight map. Miss White carried out a tagging programme in this area in October, 1958, in the hope that it would be possible to follow the flight into Mexico. Miss White reports the following observations:

I was at Eagle Pass, Texas, from Oct. 11 to Nov. 9, 1958. The Monarchs were not as abundant as in previous years, and at the airfield, where last year they covered the trees, there was none. After seven days of rain, on Oct. 17 I saw Monarchs flying over at the rate of 60 in 10 minutes, all flying south at a height of from 40 to 200 feet. The peak of the migration seems to have been from Oct. 17 to 24.

The following reports concerning the presence of Monarch butterflies in Mexico have been received. Mr. John Arrn of Eagle Pass, Texas, saw a migration of Monarchs in Mexico at a locality forty miles south of Quemado, Texas, which was approximately three-quarters of a mile wide and took three hours to pass. Professor Hector Hernandez wrote that the Monarch butterfly was at Nueva Rosita, Coahuila, during September and October, migrating southward. He sent us a specimen which was captured in September, 1957. Dr. Jesus R. Acedo of the Universidad de Sinaloa wrote on January 10, 1958, that during his twelve years in the region of Culiacan, Sinaloa, Mr. Gustavo Gluecker, an entomologist, had observed the migration
of the Monarch and that they were much more numerous during the past five years. Dr. Roberto Llamas, Director of the Instituto de Biología, Ciudad Universitaria, Mexico, wrote that in October the Monarch butterfly was seen in migration going through Ciudad del Maíz, San Luis Potosí, and on one occasion in November the migration was observed at Cadereyta, Querétaro. Miss Hilda White reported seeing five Monarchs, all feeding on poinsettia blossoms, at San José Puruá in the state of Michoacán in February, 1958; another was seen at Intepec on the isthmus of Tehuantepec in February, 1958; and another at San Cristóbal in Chiapas in March, 1958. Dr. L. Vasquez of the University of Mexico reported the following localities and dates for specimens in their collection: Monterrey, Nuevo Leon, November 1944; Santa Catarina, Nuevo Leon, November 1944; Acambato, Michoacán, 2 specimens, November 1944; San Diego, Puebla, January 9, 1954; San Diego, Puebla, March 22, 1953. Rzedowski (1957) made an excursion to the Sierra Madre Oriental, in the region south of Ciudad del Maíz on October 27, 1956. In a closed valley between Lagunillas and Puerto del Hambre (about 15 km. S.S.E. of Ciudad del Maíz) at about 2 P.M. he saw on the western slope of the mountain individuals going southeast. They were flying more or less individually without forming large groups, sometimes in groups of perhaps three, about two to six metres above the ground. Between four to ten butterflies passed per minute. About 4 P.M. the flight started to diminish and finally ceased. At Puerto de Alaquines Rzedowski saw a large concentration on top of a mesquite tree. The tree was about eight metres high and most of its branches were completely covered by butterflies. Some hundreds or perhaps thousands were seeking refuge on one tree, although many other mesquite trees were close. About 500 metres further on there was another mesquite on which two to three hundred butterflies were already in a tranquil condition. On October 28 a flight was observed on a road east of Ciudad del Maíz. Rzedowski suggested that the flight was eastward, rather than southward because "the butterflies follow the Sierra Madre in order to get to the humid tropical regions which are in easiest reach."

In order to obtain as much information as possible about the presence or absence of the Monarch butterfly in Central America, letters were sent to various government departments and universities, with the following responses:

Central America

Honduras. Dr. Luis Landa of Tegucigalpa reported capturing on May 14, a specimen "on the banks of a river that runs through the centre of the city." This specimen was sent to us so that we were able to identify it definitely as the species found in North America.
El Salvador. Dr. A. Zilch reported collecting one specimen. His colleague, Dr. Felton, collected five specimens in January. Rufus H. Thompson of the Dept. of Botany of Kansas reported that: "I was in El Salvador September and November, 1957, and saw Monarchs but no aggregations."

Costa Rica. A. P. Skutch of San Isidro wrote that: "This butterfly occurs in this region in small numbers."

Panama. Martin Mynyihan, Resident Naturalist, of Balboa, stated that he had not seen the Monarch butterfly in the Panama area during the six months he had been resident there, nor was he able to find any authentic records of its occurrence.

It would appear then that the Monarch butterflies overwinter in scattered populations throughout most parts of Mexico (with the exception of Campeche and Yucatan), and the greatest concentration is possibly in the upper two-thirds. If the flight did continue through the southern portions of Mexico and Central America we would expect to receive reports of great masses of migrating Monarch butterflies, since the narrowness of the land would tend to have a funneling effect. This does not seem to be the case; therefore, the flight into and through Mexico is most likely in the states of Coahuila, Nuevo Leon, San Luis Potosi, Durango, and Zacatecas. It would appear from Gustavo Gluecker’s observations that the flight may continue over the Sierra Madre Occidental range to the Pacific coast.

California

Monarch butterflies are present in most parts of the coastal region of California throughout the winter months. We have received the following records concerning their presence and overwintering roosts. The records begin with the most northern at Bodega Bay and are arranged in order southward to the most southern record at Arlington.

On the rows of cypress just north of Bodega Bay, Monarch butterflies have overwintered for eight years, to my knowledge, and more than that according to the residents here. [C. B. Andreini, Santa Rosa.]

The Monarchs which overwinter in this area (Mill Valley) were mainly on orange trees and some on Monterey pines. There have been reports from various students of large numbers of butterflies overwintering on the Tiburon Peninsula area, which is on the edge of the San Francisco Bay. [A. McLean, Mill Valley.]

I wasn’t expecting anything quite like what I saw at Stinson Beach last Saturday [February 12]. Monarchs were so thick they looked like a large swarm of bees. [H. Kimball, Stinson Beach.]

In 1955 the first numbers of Monarchs arrived at Santa Cruz on Sept. 20. In 1956 the first arrivals were noticed on Sept. 15 and large numbers arrived on the 18th and 19th. The Monarchs leave the area when the first rains come around the first of November. [E. C. Udey, Santa Cruz.]
The 1953 migration has started (Oct. 7). There are several thousand butterflies already on the trees. The scouts started arriving three weeks ago, although on Aug. 28th several were seen flying over our golf course. [A. L. Duanes, Pacific Grove.]

The Monarchs are now coming by the thousands [October 20]. Did you know that we have a heavy migration of Monarchs coming in from the south each year as well as from the north? [R. G. Wind, Pacific Grove.]

While in Monterey I visited the Butterfly Trees at Pacific Grove on Sept. 19, but as the season was too early I did not see any butterflies. [T. Holmes, San Francisco.]

The Monarchs are already gathering in Pacific Grove [September 29] and they have been flying in for several weeks now. Practically all Monarchs are now on the trees [November 6]. [P. Beard, Monterey.]

I heard of a place close to Big Sur where they are overwintering. Another report north of Santa Barbara. [M. Slack, Louisville, Kentucky.]

Yesterday I went up to see the butterflies at Cayucos. They are located in a group of cypress trees running several hundred feet from highway 101, toward the east, in front of the home of A. A. Croslie. The butterflies were there in very high concentrations clustered extremely thickly on the cypress branches and scattered about on flowers, bushes and vines in the garden of his house. According to Mr. Croslie the butterflies come there every year. [A. B. Berghell, Morro Bay.]

The first two Monarchs were observed on Aug. 30 at Morro Bay. On Sept. 6 I saw two more. During the next few days Monarchs were observed from time to time, but the main migration did not seem to have arrived. On Sept. 16 Monarchs could be seen at any time but they were not flocking. On Sept. 21 Monarchs could be observed at the rate of one every 30 seconds. I would judge that the main migration had definitely arrived.

Here at Morro Bay the Monarchs are still in residence [January 17] in apparently as large quantities as before. [A. B. Berghell, Morro Bay.]

Several persons have reported that there are larger gatherings of Monarchs at Pismo Beach than at Pacific Grove. Droses of Monarchs have been winter visitors to a cluster of cypress trees one half mile south of Pismo Beach for many years. It has been reported that as far back as old timers can remember, Monarchs have been locating each winter from October to March in the same grove of trees. [C. E. Petterd, Pismo Beach.]

The tagging was done during the latter part of August and in September and October in a grove of redwood trees eight miles north of Santa Barbara where the Monarch gather each winter. All through the year, however, they seem to frequent this spot. [N. W. Baker, Santa Barbara.]

Twelve miles north of Santa Monica and about two miles inland toward the mountains (the Monarchs gather) on a small grove of about ten acres consisting of pine, palm and eucalyptus—the butterflies show no particular preference. They arrive late in October or early November, with the greatest concentrations toward the end of December. [A. T. Edwards, Santa Monica.]
The Monarch migration arrived here (Arlington) about three days ago (November 10) with some tagged specimens being recaptured after a week from tagging time. I believe from last year's experience though, that they will move on in a few days, or weeks at most.

There is not too much doing here now (January 7) in regard to the Monarchs, although there must be a roosting tree near here, as there are small numbers present. [A. Grable, Arlington.]

In addition to the localities mentioned above, reports of concentrations have been received from Carmel, the mouth of the Palo Colorado Canyon, Hot Springs, and Cambria.

During the last two weeks of December and the first week of January of 1954, we motored from San Francisco to Los Angeles along the coast, recording the presence or absence of Monarch butterflies. From San Francisco to Salinas no butterflies were seen. In the Monterey peninsula the occasional specimen was seen. At Pacific Grove a few were seen among the flowers at Butterfly Trees Lodge. On the Monterey pines at Millers' Lodge and Washington Park many thousands were seen on the trees. It is important to note that although many thousands of butterflies were present in the Monterey peninsula area, only a few were seen flying. Therefore, these observations are not indicative of the presence or absence of overwintering quarters, and the fact that we did not see a specimen from San Francisco to Salinas does not rule out the possibility of their presence. It is also important to note that during the survey a series of cold fronts passed through the district, lowering temperatures below freezing in the San Francisco area, and to a low of 38°F. in the Monterey peninsula. The temperature rarely rose above 60°F. during the day and hence the Monarch butterflies would remain on the roosting site. From Monterey to Los Angeles, Monarch butterflies were seen flying across the highway, with the greatest number seen in flight between Pismo Beach and Santa Barbara. These observations would show that in the northern part of California the Monarch butterflies establish roosting sites due to low temperatures while in the more southern parts, the Monarch butterflies remain active, since temperatures below 60°F. are not common.

It was noted that the Monarch butterflies enter the overwintering sites in the northern parts of California from the south as well as from the north. It is possible that migrants reaching the Pacific coast area in December may begin to move northward, or perhaps the presence of mountains on the east and south and the Pacific Ocean on the west restricts their motion to a northerly flight. As yet we have no indication of the origin of these migrants from the south.

Discussion of Overwintering Sites

The questions of why the Monarch butterfly overwinters in the areas outlined and why they remain relatively inactive in roosting sites in some
localities and not in others may be correlated with the direction of motion of the high pressure areas arising from the polar continental air mass from the northwest. Figure 78 shows the position of the high pressure areas for the 0600 meteorological map for April 30, 1958, which is fairly characteristic of the movement of high pressure air systems moving across the continent during the winter months. A mass of cold polar continental air flows southward from the northwest, and as it does so it also moves to the east. The trajectory of this heavy dome of cold polar continental air is, therefore, southeastward. Warmer air, in the meantime, moves in from the west or southwest, forming an area of lower pressure and isolating the dome of cold air from its point of origin. The dome produces, on its southern edge, an area of cold air which can be delineated from the warmer air mass in the south. This area, termed a “front” in meteorology, is indicated by a line with icicle-like marks on the south side, indicating that the cold air is continuing to move southward, and a line with oval raindrop marks on the north side, indicating that the front is beginning to move northward as a warm front.

In the latter case a low pressure area will develop, giving rise to a warm front to the east of the centre of the depression and a cold front to the west of the centre of the depression. It should be noted also that the wind blows around the centre of high pressure in a clockwise direction and that within the area of high pressure there may be ten or more degrees difference in temperature, from cold on the east side to warm on the west side. The wind becomes warmer as it moves from east to west around the dome of cold air.

Therefore, areas of the earth’s surface exposed to the fresh outburst of air from the east end of the dome of cold air will experience colder temperatures than those at the west end which are exposed to the more modified, and hence warmer, air. As the cold front pushes southward, the polar air not only becomes warmer, but a series of frontal depressions forms, moving from west to east and thus areas located below the line indicated on the map do not have low temperatures.

From the distributional map it will be seen that the overwintering areas for the Monarch butterfly are those areas which are beyond the range of the cold air masses, except for a narrow fringe along the Gulf of Mexico and the Pacific coast of California. These last two areas are moderated by proximity to the warm water of the Gulf of Mexico in one case and the warm water of the Japan Current in the other. It will be noted also that Monarch butterflies are found on overwintering roosting sites where the cold fronts are effective and where temperatures, as a result, repeatedly drop to freezing or near-freezing throughout the winter months. The fact that the only record of overwintering roosts along the Gulf coast is located at the eastern extremity may be explained by the fact that it is in this area that the less modified, and hence colder, polar air causes lower temperatures.
The reason why overwintering roosts are not found, as far as we now know, east of this particular locality is that Florida maintains a modified temperature owing to the warm air over the Gulf of Mexico. However, low temperatures are experienced repeatedly throughout the winter months from Lighthouse Point as far south as Tampa, and it is quite likely that semi-permanent overwintering roosts will eventually be found in parts of this area.

Choice of Overwintering Roosts

The factors influencing the roosting on the trees during the winter are the same as those described for overnight roosting during migration. These trees are chosen which offer the best protection from the wind, most likely the prevailing wind, and this would be decided to a great extent by the topography of the area. Evidence was presented earlier to the effect that Monarch butterflies choose a particular tree, or group of trees, because of the favourable situation that gives protection against inclement weather conditions, and because the foliage is of a type suitable for the sickle-like tarsal claws of the butterfly to grasp. A similar explanation was proposed by my colleague, Dr. Downes (1942) when he answered the question: "How are the autumn butterflies, which are separated by from one to several generations from the group resident in the preceding winter, able to find their way year after year to these few small places from points perhaps many hundreds of miles away?"

For twenty miles along the coast a little south of Pacific Grove and for ten miles in the neighbourhood of San Diego every suitable group of trees was examined; only fourteen possible sites were found, at ten of which at least a few Monarch butterflies were seen. There is no doubt that this is typical of the situation along the whole coast from San Francisco to below the Mexican line. The fact that they occur at almost every suitable locality had been previously overlooked, as in most cases the number of butterflies is very small. It would seem therefore that the butterflies reach any point on this long coast line and then collect at, or discover, practically all the groups of trees, remaining in numbers proportional to the suitability of the sites found. The migration is therefore merely to the coast, and not to particular small places.

Observations on Monarch Butterflies on Roosting Sites

According to the observations received from our co-operators the Monarch butterflies begin to arrive in their overwintering sites towards the end of September and early October and they begin to congregate on the roosting trees in early November. The species of trees chosen in California are Monterey pines, cypress, and eucalyptus with, from our observations, a decided preference for the Monterey pines.

In areas such as Pacific Grove, where the temperatures during the winter are quite low and strong most winds blow in from the Pacific Ocean, the
Monarch butterflies usually mass together on the side of the trees away from the ocean and hence protected from the wind. During a particular period of inclement weather we observed that the rain falling upon the trees would run off the cone-shaped festoons of butterflies in small rivulets and although the branches would sway in the breeze the butterflies were not dislodged. On warmer, sunny days a few butterflies would leave the roosting site, fly to nearby gardens to feed upon the nectar of flowers, and then return again. We found that ten days was the longest period we were able to keep Monarch butterflies alive under natural conditions of temperature and moisture; perhaps the same conditions apply to the overwintering Monarch butterflies. Whether or not such foraging butterflies would return to the same cluster has not been ascertained.

On warm sunny days some members of the roosting colony would open their wings (under unfavourable conditions they remained closed) exposing the body to the rays of the sun. The black scales and hairs covering the thorax and abdomen would, perhaps, increase the body temperature as a result of the incident solar radiation being absorbed by the black surface. Such individuals soon took to flight. Occasionally, a butterfly thus warmed up would fly about the roosting site, coming to rest again on a different part of the tree. This usually occurred when the sky was clear but the air temperature was cool. On warm days at temperatures near 60°F many individuals would be found feeding on the flowers in surrounding gardens.

**Colour Change**

When spring and fall specimens are placed side by side, the difference in colour is decidedly marked (Plate XI). Those collected in the spring are very light in colour, and those collected in the fall are much darker and richer in tone. It was thought that perhaps this fading process took place during the winter months and, to check this possibility, Mr. Paul Beard of Monterey, California, sent ten live specimens to us every week beginning on December 15 and continuing to March 15. It was found that specimens collected in March were light in colour, and those collected in December were darker. It was further observed that those collected in December were lighter in colour than those collected in the breeding area in September. This range of colour is illustrated in Plate X for which specimens were chosen at random throughout the winter months. Comparing specimens in Plate X with those in Plate XI, it will be noticed that the December specimens are lighter in colour. It will be noticed also that the specimens collected in the overwintering sites in March are similar in tone and colour to those collected in the breeding area in the spring. This supports the conclusion that the faded specimens found in the breeding range in the spring are those that left the overwintering localities.
Ovary Development

Downes (1942) examined the reproductive organs of the overwintering Monarch butterflies on the roosting sites and came to the following conclusions: (1) that ripe sperm occur in both testes and ducts very soon after emergence from the pupa and probably at all times during the winter until the spring migration; (2) that overwintering females emerge from the pupa in September with all the egg-follicles quite small and unripe and they develop slowly during the winter months, with the first appearance of ripe eggs forming on March 26 at Pacific Grove. He also shows that there is only a slight increase in size of the eggs until the end of February, followed by a stage of rapid growth in early March. He further points out that “growth during the winter months is more active than would appear from the table as it is being offset by an opposite process of egg degeneration, which continually destroys the largest follicles during this period.” Since migration commences in July in the northern parts of North America at a time when mated pairs, eggs, and larvae are abundant, one would conclude that gravid females would be found taking part in migration. To test this possibility, five hundred females, taken from a roosting site on September 18, were dissected. Not a single gravid female was found. The following summer, collections of females were made in August and September in fields where there was an abundant supply of milkweed and where eggs and larvae were found. Eighty-two out of one hundred females examined in August were gravid and twenty-two out of one hundred females examined in September were gravid. One hundred females taken from the roosting site were examined this same year, and not one of them was gravid.

Some females with ripe ova do move southward, however; this explains the presence of larvae in the southern and southwestern states during the fall, after their complete absence during the summer months.

In 1941 Beal found that females from the roosting site were full of fat, the bursa copulatrix was small and flat, and the ovarian tubes were thin and tapering. To test whether or not females with ripe ova might be found in the overwintering areas, particularly in those areas where roosting sites were established, arrangements were again made with Mr. Paul Beard to send to us males and females taken from the winter roosting sites on the Monterey Peninsula of California at intervals throughout the winter months. The results are shown in Table III.

It will be noted that from November 5 to March 12 only 2 of a total of 145 females contained eggs, and 63 showed evidence of mating having taken place. It is stated that the ovaries were partly developed in the females containing eggs on January 14 and February 13. By this is meant that the ovarioles were thin and that although eggs were present they did not form a gradual series from ripe eggs with well-developed shells to the early
**THE MONARCH BUTTERFLY**

**TABLE III**

<table>
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<tr>
<th>Date</th>
<th>No. examined</th>
<th>No. containing sperm sacs</th>
<th>No. containing mature eggs and developed ovaries</th>
<th>Date</th>
<th>No. examined</th>
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<th>No. containing mature eggs and developed ovaries</th>
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<td>5</td>
<td>5**</td>
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<td>Mar. 27</td>
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<td>8</td>
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*This female was kept alive for 18 days; on death, examination revealed 38 mature eggs and ovaries partly developed.

**Although the ovaries were well-developed there were no mature eggs.

†This female was kept alive and 14 eggs were laid on Feb. 22; the eggs were not viable and the ovaries were only partly developed.

germinal eggs. It would appear that the relatively few eggs found in the oviducts had been retained, while the ovaries with undeveloped eggs that did not possess shells had degenerated. The difference between the ripe eggs and undeveloped ovaries was well marked and in definite contrast to the well-developed ovaries of March 27.

It may be concluded that a small percentage of females develop ripe eggs during the fall migration and that these eggs are deposited along the migratory route. If only a few of the complete complement of eggs are laid, the remainder are held in the oviducts during overwintering in those areas where milkweed is absent and temperatures are low. The eggs are retained until the return of continuous clement weather and the appearance of milkweed plants during the spring migration. These would be responsible for the very early appearance of larvae in parts of California, Mexico, Texas, and the Gulf states, and would also explain certain winter populations in Texas and Florida where milkweed is found during most of the winter months. I agree with Downes (1942) that ripe ova appear in March and early April, but I would add that this applies not to the entire female overwintering population but only to a portion of it, the remainder developing ovaries throughout April and during the spring migration.

The female of February 13 deposited eggs on February 22 but they were not viable. These were probably the eggs left over from the previous fall which were not fertilized. The bursa of this female contained two spermato-
phores indicating that mating had taken place and hence it would appear
that the sperm does not remain viable throughout the winter.

Downes (1942) was aware that some females laid eggs during the winter
months and of the presence of females with mature eggs during the over-
wintering period when he wrote that "although in general the reproductive
condition of the butterflies is the same in both southern and northern
localities throughout the winter as shown by the undeveloped condition of
the San Diego females, exceptionally a southern female is found to be mature
during the winter months. Thus two specimens were bred on 4th April and
7th April, 1931, from eggs laid in the wild at Fullerton Orange Co., in
December 1930, and females taken after their arrival at overwintering places
near San Diego in November 1936 laid eggs after two weeks in captivity.
The migrating instincts of such unusual individuals are not known.

We received larvae and pupae from Mr. A. T. Edwards of Santa Monica,
California, during November, together with photographs showing milkweed
plants covered with larvae. In his letter of December 12, Mr. Edwards
reported that: "During the months of October, November and December
I took over 300 larvae in the Santa Monica mountains. I obtained 110 perfect
butterflies." P. S. Hill of Jacksonville, Florida, reported raising Monarch
butterflies in February. We received larvae and pupae from Mrs. D. A.
Crosley of Brownsville, Texas, on February 24, and Mrs. Crossley reported
larvae in large numbers from February 28 to March 4; none were found after
March 15 at Brownsville. These, however, were most likely progeny from
early spring migrants rather than full migrants or members of an over-
wintering population.

**Spring Migration**

The following information, giving the approximate date of departure from
overwintering areas where roosting sites have been established, has been
received.

**Florida**

Herbert Stoddard said he made three visits to Alligator Point, Florida, in late
March and the Monarchs had gradually disappeared. At about the same time a
few Monarchs were flying rather aimlessly about on his plantation, between
Thomasville and Tallahassee, Gads Co., Georgia, about sixty miles north of
Alligator Point. [Lucien Harris, Lighthouse Point.]

**California**

Last Sunday [February 16, 1958] I went out to Galeta, just west of town, with the
idea of doing some tagging, but the butterflies had left already, which is much
earlier than usual. [A. M. Johnson, Santa Barbara.]
Last year's gathering of Monarchs departed on March 29, 1954, not a single one remained after a two day departing. [C. E. Petterd, Pismo Beach.]

To our knowledge the migration from here occurred a little later this year than usual. We noticed the disappearance of the Monarch from the pine tree surrounding our house the latter part of April, 1955.

As nearly as I have been able to judge, the great majority of Monarch butterflies left Morro Bay March 21, 1956. There are still a few strays here, but the number observable within a given period of time, under as nearly the same conditions as possible of sunshine, wind and temperature, appears to have dropped off most rapidly on that date. The Monarchs were definitely mating for some time prior to leaving. This was first noticed on February 27, 1956. [A. R. Berghell, Morro Bay.]

During the latter part of February, 1955, approximately one Monarch per hour passed my house. They travelled in a due north direction and of six specimens caught all were males.

I got up early March 17 [1957], and was at Washington Park a half hour before sunrise, but there was not a single Monarch left on the trees. The last few weeks have been very warm. Today there was not one visible around town, whereas last week they were thick over the whole peninsula. The last ten Monarchs I sent you were collected early morning on the 13th and there were only a small fraction left on the trees at that date. On March 9th I observed a Monarch flying in Redwood City. My father-in-law reports that the first Monarch he observed on his farm near Talare, Cal. was March 14th. On March 17th at Partington Canyon I tagged six Monarchs. Monarchs were seen scattered all along the highway. Many were feeding on Oenothera bushes. [Paul Beard, Monterey.]

Mr. Duane asked me to let you know that the Monarchs are commencing to leave Pacific Grove today [February 13, 1957]. [L. D. Weil, Pacific Grove.]

I wasn't expecting anything quite like what I saw at Stinson Beach last Saturday [February 10, 1954]. Monarchs were so thick they looked like a huge swarm of bees. The weather was quite warm so some of the butterflies were flying around and others were sunning themselves on the trees and bushes. There were several mating pairs, but although the milkweed was leafed out I found no eggs or larvae. Only a few were still at Stinson Beach on February 25 and these were scattered all around the bay. [H. Kissball, Stinson Beach.]

During the middle of March we had a number of warm days and it was during these periods that the butterflies started to migrate. They seemed to travel in large numbers northward from here. [A. McLean, Mill Valley.]

They are not present in Benicia at the present time [June 14, 1955]. Migrating Monarchs have left entirely by April and breeding residents are not yet present. [E. A. Stoner, Benicia.]

The overwintering Monarchs at Bodega Bay start their return migration in February. [G. B. Andreini, Bodega Bay.]

On March 3 [1955], the first Monarch, a battered female was seen at Davis. On March 5 a large number of Monarchs were still in the cypress trees. On March 19, two Monarchs were seen at Folsom.

The first Monarch was seen in Davis (14 miles S.W. of Sacramento) on February 14, 1957. [H. Kimball, Davis.]
Downes (1942) states that the spring migration is spread over a considerable period. From captured females containing ripe ova, and others some distance from the California coast during April, he concludes that the spring migration is in progress in early April. Of particular significance are his observations on the sex-ratio of the overwintering colony at Pacific Grove: "from the beginning of March onwards the proportion of females decreases still further until very few could be found, while the males remained in thousands until at least 8th May."

**Observations During Spring Migration**

In early spring the Monarchs reach points rather distant from the overwintering localities. This fact would substantiate departure on the dates specified above as do the following observations.

On Feb. 16, 1957, we were probably four miles from land searching for fish when we saw several Monarchs flying 10 to 15 feet above the water. Neither before the 16th nor thereafter until March 15th were any more seen by us or by anyone from whom we enquired. [C. F. Beatty, Islamorada, Florida Keys.]

Four Monarchs were seen on March 16, two of which were badly battered. Most of these seen were on a steady move in a northerly direction as though there was some light migration from an overwintering area further south or southwest. [The following were seen on the dates specified] May 16, 1; May 26, 1; May 27, 4; May 31, 1. [N. O. Sibley, Zellwood, Florida.]

On March 7th a specimen was observed sailing northward on a steady warm south wind, going too fast for capture. [L. S. Dillon, College Station, Texas.]

I saw only one last fall after the one I caught and sent to you around Oct. 19, 1955. I hadn't seen any more until May 19, 1956, when I saw a faded one in my yard. I didn't see any more until I saw one on Aug. 22, 1956, and another Sept. 12, 1956. [Mrs. H. S. Beasley, Lindale, Texas.]

In the Dallas area, the Monarchs put in their appearance when the milkweed first sends up its sprouts. On the average, it occurs about the middle of March each year. A thin wave of Monarchs appears and for two or three days the females deposit their eggs and then are seen no more. Their wings are gray and frayed. [C. A. Anderson, Dallas, Texas.]

The Monarchs passed through Decatur early in the spring of 1956. We saw the first ones in early March and captured a copulating pair on the 17th of March. All the spring specimens were in a somewhat battered condition and were observed flying haphazardly as if in search of food. By the end of March and the first week in April, Monarchs had become scarce in this area and were not observed again until September. A few females were observed ovipositing on young milkweed shoots in early March and a single generation resulted from these eggs. This generation either died out or moved north, since there was not a continuity of individuals throughout the summer. [J. P. Knudsen, Decatur, Alabama.]

April 10, Black Jack Mt., Maretta Co., 1 Monarch seen; June 7, Albany, 1 Monarch seen. No more were seen until August 18. [J. Symmes, Atlanta, Georgia.]
In the spring of 1956 the following sight records were made of individual Monarchs flying in a northerly direction: March 17, 5 observed flying northward along the beach on Jekyll Island; March 17, 22 observed inland feeding and casually moving about on Jekyll Island, which might represent an overwintering colony on the island; March 18, 6 observed on Jekyll Island with morning temperature of 45°F; March 19, 1 observed flying northward at Douglas in southeast Georgia; April 7, 7 observed at intervals between Atlanta and La Grange; April 8, 1 observed near Dublin in central Georgia; April 9, 1 observed at Avondale Estates, near Atlanta. Some of the spring migratory females, incidentally, begin to lay eggs as they proceed northward. Paul Kight found a freshly emerged adult near Stone Mountain, Georgia, on May 13, 1957. Present day Georgia lepidopterists have observed that the Monarch butterfly becomes very rare or almost absent in June and July. [Lucien Harris, Atlanta, Georgia.]

My son brought me one he caught on April 3, 1955. He saw two on April 8. [Mrs. A. P. Ryland, Grady, Arkansas.]

Since receipt of your May 7 directive, we have only two sight records; one on May 28 at South River and one on June 26 at Park Headquarters, North Rim. [L. Schellbach, Grand Canyon, Arizona.]

I saw the first Monarch on July 7, 1955; the direction of flight seemed to be northerly. [E. R. Day, Salt Lake City, Utah.]

We found an interesting bit of information this spring, which was totally unexpected to us, and that was that we found a nearly full grown Monarch caterpillar at Paradise, Utah, late in April, 1957. [D. W. Davis, Paradise, Utah.]

I saw the first Monarch of the season, hovering over the iris beds, on June 2, 1956. In spite of heavy rains and hail storms it appeared in perfect condition and was last seen flying high in a westward direction. [F. van der Vlugt, Canyon City, Oregon.]

Lugger (1890) reported large numbers at St. Anthony Park, Minnesota, on May 28, at which time there were no milkweed plants. Although very few of them had torn wings; they looked bleached and had few scales upon their wings. On June 5 they had arrived at Perham, some two hundred miles northeast of Minneapolis. Eggs were found in St. Anthony Park on June 17. In 1889 they arrived at Fergus Falls, in the Red River Valley, on May 2, and were seen mating on May 26.

Mrs. B. Johnston of Mount Clemens, Michigan reported that: "Ten Monarchs were seen on May 30, 1957, and six eggs were found on May 31, 1957."

H. J. Shannon (1954) reported females and males seen flying north in May along the New Jersey coast. The females were flying close to the ground as if trying to find milkweed upon which to deposit the eggs. He found eggs on May 21.

Miss Ruth Haigh of Niagara Falls, Ontario reported as follows: "To-day [May 30, 1956] I captured a male Monarch butterfly. The temperature
was 80°F. There was a strong southwest wind blowing and the butterfly was travelling southeast. While writing this, I have just seen another Monarch.”

On April 8, 1958, Mr. Anthony Inglis of Galveston, Texas, sent us three Monarch butterflies which he had captured. One was a male which was dead on arrival. The two females deposited eggs on April 20, three of which hatched on April 28.

The Monarch butterflies begin to leave the overwintering sites in February and by the end of March all have departed, with the exception of a few isolated colonies or stragglers in April. They reach the breeding grounds in March in the more southern section, April in the central regions and May in the more northern regions. It is probable that the time of the departure varies from year to year owing to unfavourable weather conditions, and hence arrival in various parts of the breeding area will vary from year to year.

The returns from the tagging programme have been plotted on Figure 79. With one long flight exception, the spring migration apparently is in a northeasterly direction.

**General Observations**

From personal observations and from numerous reports which we have received, it would appear that: (1) overnight roosts are not established during the spring migration; (2) spring migrants rarely stop to feed upon the nectar of the spring flowers and further that they reach certain areas early in the spring before flowering plants are abundant; (3) the flight is direct, north or northeasterly, rather than meandering; (4) gravid females, as reported previously, may retain fully developed eggs for a considerable length of time before ovipositing; (5) males take part in the flight as well as females, although in the more northern parts of the breeding range males are rare; and (6) the fatty tissue is a fuel reserve for the spring migration because at this time there is a paucity of nectar-producing plants and the females take little, if any, time for feeding.

Once the spring migration is under way the female must reach the breeding grounds as quickly as possible, because the eggs begin to develop rapidly and must be deposited. The absence of overnight roosts during spring migration may be accounted for by the fact that physiological and ecological factors affecting the spring migrants are similar to those affecting the summer breeding population: increasing temperatures in the warm sector of the frontal depression and active mating and oviposition. It has been previously pointed out that the breeding population does not take part in overnight roosting.

On many occasions we have observed spring migrants approaching a building from the southwest, flying to the northeast with rapidly beating
Figure 79. Flight records for spring migration from California.
wings, and, not pausing to feed on the flowers of the spring dandelions or to go around the building, fly up and over the obstruction to continue in a direct line to the northeast on the north side. On reaching the breeding grounds, oviposition is carried out, again with obvious haste. A few days after oviposition has begun, the wings of the females become dry and brittle, resulting in a tattered appearance. The abdomen becomes thin and on dissection it is obvious that the fatty tissue has been greatly reduced. There also appears to be a change in the texture of the fatty tissue, from the bright yellow and somewhat fluid appearance during the fall migration to a dull straw colour and more solid appearance after oviposition.

It was noted that some of the ovipositing females found in Durham, Ontario, in June, were of a new generation and not migrants from overwintering quarters. This may be explained as follows. From the above reports it is seen that some females deposit their eggs in the more southern parts of the continent and others in the more northern. We have seen also that in the southern states, eggs, larvae, and newly emerged adults may be found in the spring and early summer but that they disappear in midsummer and are not seen again until the fall. The reason is that these early generations also fly northward and mingle with the late arrivals from the overwintering quarters. Therefore in the more northern parts of the breeding range, such as southern Ontario, many dull-coloured butterflies, that have returned from the overwintering areas are found, mixed with a few newly emerged, bright specimens, from new generations to the south that have moved northward.

Holland (1917) suspected that possibility of southern generations moving northward in the spring migration when he wrote: "This northern migration is accomplished thus: The mother butterfly follows the spring northward as it advances as far as she finds milkweed sprouting; there she deposits her eggs, from which hatch individuals that carry on the journey, and in their turn lay their eggs as far north as possible. Thus generation after generation pushes on until late in the season we hear of them as far north as Hudson Bay."
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