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INTRODUCTION

THE INSECTS that compose the superspecies *tullia* are quite variable. Apparently they are sensitive to environmental conditions and as a whole represent plastic and probably "young" species. The shuttling about that has been forced upon these insects in North America by the vacillation of the Pleistocene ice sheets has caused considerable differentiation among populations. When series from well-separated localities are studied they appear to represent sharply defined species and subspecies. That this is an illusion can be demonstrated by study of material from many localities across the continent. With the possible exceptions of *mixturata* Alpheraky in the subarctic and *subfusca* Barnes and Benjamin from Arizona there are no well-defined and clearly segregated forms of *tullia* in North America, yet there are definite trends in variation that are widespread and deserve recognition.

The problem that faces the taxonomist is when to stop in naming populations. I shall face this by avoiding it. There is an abundance of names available. To recognize any further segregates would necessitate recognizing literally dozens of them.

There seem to me to be four or five distinct groups of related forms comprising the superspecies in the Nearctic. The easternmost of these is best called *inornata* Edwards. Essentially this is a group of insects that are almost free of ocelli, lack light basal patches on the under side of the hind wings, and with rare exceptions are single brooded. Five names have been suggested for variants in this group. From east to west these are *mcisaaci*, *nipisiquit*, *quebecensis*, *inornata*, and *benjamini*.

In the Rocky Mountains and the Great Basin lives a group of *tullia* forms that may be characterized as ocellated, with two basal light patches on the under side of the hind wings and, although usually single brooded, with a second or partial second brood occurring more frequently than among *inornata*. The oldest name that is available for this group is *ochracea* Edwards. In it we find from south to north the insects called *fusca*, *furcae*, *brenda*, *mono*, *ochracea*, and *mackenziei*.

In California and invading the extreme western parts of the Great Basin and the southern part of Oregon is a small cluster of forms that have these characters in common: they are ocellated, very pale in color, and are clearly two brooded. This is *california* Westwood and Hewitson. Two other names are applied to these insects: *galactinus* and *eryngii*. The former seems to be merely a brood name; the latter may represent some degree of hybridization with the adjacent form, *ampelos*.

On the west coast, north of California, and in the basin-range region, there flies a group of forms that are without ocelli and lack the light basal patches on the under side of the hind wings. They are very much like *inornata* in this respect. However, at least the southern members of the group are double brooded, and all are much lighter in color. For the time being I prefer to hold them apart from the eastern moiety. The oldest name available in the group is *ampelos* Edwards. From south to north we find these named entities: *elko*, *ampelos*, *insulana*, *sweadneri*, and *columbiana*.

Lastly, in Alaska there flies the Asiatic insect *mixturata* Alpheraky. It lacks ocelli and the light basal patches and most certainly is single brooded. On the under side of the hind wings there are areas of strongly contrasting colors. *Yukonensis* may be identical with *mixturata*; *kodiak* is closely related to it.

Schwanwitsch's postulated ancestral *Coenonympha* is much like *C. haydeni* Edwards. This suggests that the presense of ocelli is more primitive than their absence. The geographic position of the most ocellated members of the superspecies in America, the southern periphery of the species range, tends to support Schwanwitsch's contention. Thus the *ochracea* moiety may lay claim to being the modern carriers of the more primitive characteristics of pattern. This claim must be shared with *california*. At this point it may be of interest to note that members of both these moieties are in all probability those least disturbed by the repeated movements of the continental ice sheets and alpine glaciers of the Pleistocene. There is no reason to believe that they had to make long treks to

maintain themselves in hospitable environments. It is possible that their present-day pattern of life parallels closely that of the ancestral invader that established the superspecies *tullia* in America.

If these ocellated insects are accepted as the modern representatives of ancestral *tullia* most nearly like that ancient one, then *inornata* generally lacking ocelli and the light basal patches may be considered a more modern development from the ancestral stock. Such a condition may have developed on this continent or it may have developed in Asia, and *inornata* may represent a more recent invasion than that of *ochracea* and *california*. A thoughtful consideration of all the factors leads me to believe that such an invasion must have been at least pre-Wisconsin, if not earlier. I can accept an invasion of *mixturata* during or since the Wisconsin ice sheet but of no other Nearctic *tullia*.

If we accept a pre-Wisconsin date for the advent of *inornata* in North America, the present insect has survived many vicissitudes. Today it occupies land that has been covered from once to three or four times by the continental glaciers. In fact there are relatively few places where *inornata* is now found that were not glaciated. In the light of recent evidence from carbon-14 datings, the southernmost areas now occupied by *inornata* have been free of ice for about 11,000 years and the northernmost areas for something less than half of that time. Because I do not agree with some students of the genus who are inclined to believe that *tullia* invaded North America after the last great retreat of the ice, I must consider that they are insects that were successful in following their habitat as it moved south and north with the flow and ebb of the ice sheet or sheets.

Paleobotany has revealed that the lower Mississippi Valley, as far south as Louisiana and central east Texas, and the Atlantic coastal plain of the southern states, harbored a forest that at the peak of the Wisconsin glaciation contained characteristic elements now associated with the Boreal Forest of Canada. It seems likely that this forest extended southward from no great distance in front of the ice, possibly not more than a hundred miles, to the Gulf coast and northern Florida. Thus the minimum distance traveled by the *inornata* moiety lies between 1200 and 1800 miles. Such southing and northing imposed upon the wanderers environmental strains that must have been rigorous in sorting out the individuals fitted to survive. No such pressures were brought to bear upon any of the western moieties. As a result the *inornata* moiety is capable of enduring much more environmental variation in its present range than are the others. The various expressions of *inornata* are at home from the cool humid maritime areas about the mouth of the St. Lawrence River to the warm dry prairies, whereas the neighboring *ochracea* moiety (except *mackenziei*, the history of which will be traced in another article) is restricted to the semi-arid warm areas.

COENONYMPHA TULLIA INORNATA EDWARDS

EAST OF THE Rocky Mountains from the border states northward to the upper reaches of the Mackenzie River and eastward to the Atlantic coast from northern New Brunswick to Newfoundland and Great Whale River on Hudson Bay is found a group of related forms of *tullia* that are best considered a single variable subspecies or weakly developed species, depending upon one's particular point of view. The *Coenonympha* found in this area by no means form a homogeneous population. They represent a series of intergrading populations. As more and more series are collected from different localities spread across the range of the insect it becomes increasingly difficult to separate what formerly appeared to be several valid subspecies.

The oldest acceptable name for this group of populations is *inornata* Edwards, published in 1861. It was not until 1928 that a second acceptable name was proposed. At that time McDunnough cut out the prairie populations under the name *benjamini*. In 1926 Barnes and Benjamin had given the name *quebecensis* to the eastern spruce forest insect, but this is better called *inornata* in the light of Edwards' description. Several years later, in 1935, dos Passos named very dark material from southwestern Newfoundland *mcisaaci*, and four years later, in 1939, McDunnough gave the name *nipisiquit* to material from an isolated colony at Bathurst, New Brunswick.

So long as the insect was known from scattered areas it appeared reasonable to accept all these names in a subspecific sense. Now with few long gaps in the distribution of samples available for study, it is increasingly evident that these names, except *nipisiquit*, are little more than way points in a series of east to west clines, and it is quite evident that the insect is continuously distributed from the Atlantic coast to the Rocky Mountains. Specimens from the geographic extremes are strikingly different, yet when the known material is arranged in geographic order from east to west one series grades imperceptibly into the next, and no clear division is evident.

This poses a nomenclatorial problem. The *inornata* moiety of *tullia* may be considered a single subspecies that is plastic and has responded in different outward ways to ecological variation in its range. Thus everything from the Rockies to Newfoundland would be called *Coenonympha tullia inornata* Edwards. If it were not for the Holarctic character of *tullia*, *inornata* could be accepted as a weakly defined species. If the moiety be accepted as a species (and it has been by such nomenclatorial specialists as McDunnough and dos Passos), then the various environmental expressions assume the position of subspecies. Either of these solutions fits the Rules. However, the simplest solution is not always the best one. The taxonomist is faced with the task of naming the recognizable plants and animals in such a way that the biologist can accurately designate the subject of his studies. At times the solution to this problem seems impossible. On the one hand the taxonomist is faced by the poly-dimensional variation of nature and on the other constrained to the two-dimensional view of the Rules of Nomenclature.

I am on just such horns of a dilemma in respect to *inornata*. As a biologist I want "handles" for the maritime, forest, and prairie segregates of *inornata*. Such names are useful. As a biologist I want a taxonomy that shows *mcisaaci*, *nipisiquit*, *inornata*, and *benjamini* to be more closely related to one another than they are to, say, *ochracea* and *furca* or to *california*. At the same time I want a taxonomy that shows that all these are but bits of a species that is Holarctic with Eurasian ramifications as complex as those found in the New World. As a taxonomist I want to stay within the tenets of the Rules, for I agree with the soundness of limiting names to trinomials.

Mayr has proposed a solution to this sort of situation that I find palatable. By considering *tullia* a superspecies I can call the eastern Canadian moiety *Coenonympha tullia inornata*. *Inornata* then is a nomenclatorial fraction of *tullia*, but it ranks as a simple species not a subspecies. Thus when I use the combination *tullia inornata* I am referring to a fraction of the Holarctic insect that ranges from the Rocky Mountains to the Atlantic coast of Canada. Such designation is necessary only when I am considering the Holarctic insect. When I am discussing the Nearctic

insect and desire more detailed taxonomic treatment my trinomial becomes *Coenonympha inornata inornata* for the spruce forest populations of the insect, *Coenonympha inornata benjamini* for the prairie populations, and so forth. Each of these is a subspecies of the species *inornata*, which in turn is a member of the superspecies *tullia*.

COENONYMPHA INORNATA MCISAACI DOS PASSOS

Coenonympha inornata mcisaaci DOS PASSOS, 1935, Canadian Ent., vol. 67, pp. 83–84.

TYPE LOCALITY: Doyles Station, Newfoundland.

COLLECTOR OF TYPE: Hugh McIsaac.

LOCATION OF TYPE: The American Museum of Natural History.

ORIGINAL DESCRIPTION: "♂ 34 mm. Primaries, upper side; disk ochraceous tawny[1]; costal, outer and inner margin light brownish olive. Secondaries, light brownish olive; inner margin, pale olive grey. Primaries, underside; basal area, sage green extending along coastal margin but shading into tea green at apex; inner margin, ochraceous tawny, the division between the discal and limbal areas being marked by an irregular line, light brownish olive on the inner side and pale olive grey on the outer side; outer margin, pale olive grey. Secondaries, sage green at base, tea green beyond the cell, which is outwardly defined by a pale olive gray angular mark, reappearing at the anal angle. Fringes of both wings on both sides, pale olive gray.

"♀ 33 mm. Primaries, upper side; cinnamon buff, darker at the base, the markings of the under side faintly showing through. Secondaries, clay color, the markings also showing through. Primaries, under side; similar to ♂ but paler, the band broader and more distinctly defined. Secondaries, similar to ♂. The mesial band, pale olive gray continuing almost to the anal angle. The upper and under sides of both wings are bounded by a faint narrow black line and are without ocelli. Fringes similar to ♂.

"Antennae, head and body, similar to *inornata*.

"54♂, 15♀, July 1–August 3. . . .

"Doyles Station, Newfoundland."

RANGE: Newfoundland and adjacent Quebec.

BIONOMICS: Nothing is presently known of the preparatory stages of *mcisaaci*. I doubt that there is any real difference between them and those of *inornata inornata*.

ECOLOGY AND HABITAT: I have only one note concerning the habits of this subspecies. I quote from dos Passos (p. 82): "Doyle's Station is about seven miles from the sea, twenty-five miles north of Port aux Basque, and not far from the Great Codroy River. The elevation is in the neighborhood of thirty feet. The country is fairly level. It is timbered with spruce, fir, cedar, alder and poplar. Most of the specimens were taken along the railroad track, in open fields, marshes and barren land."

From this scant information there seems to be little difference between the behavior pattern of *mcisaaci* and that of *inornata*.

The island of Newfoundland is divided neatly into two unequal parts, east and west, by most students of the area. The narrower and less extensive western portion is composed of an old range of mountains. Fernald, examining the area as a botanist, and Atwood, as a geographer, agree that at least the northern part of these low mountains were not glaciated in Pleistocene time. Although certain plant communities were able to survive the proximity of the Newfoundland glacier I am not at all convinced that the climate was warm enough for *Coenonympha* in these unglaciated mountains. The present range of *Coenonympha* in North America falls far short of the northern limits of trees and well below the altitude at which plant growth ceases in the Rocky Mountains. Thus I cannot believe that *mcisaaci* is a glacial relict on Newfoundland.

The eastern portion of Newfoundland, and by far the larger area of the two, has been severely glaciated. It is a rugged upland with patches of forest interspersed with areas of tundra. Fire has reduced the naturally scant forest over much of this inhospitable part of Newfoundland. The southeastern portion of the land, the Avalon Peninsula, is more friendly. There the larger part of the human population of the island is found. Curiously, this is about the least well known part of the island when it comes to insects. Collectors for the Canadian National Collection have at least sampled the west, north, and central parts of the island, which leaves the south and east to be studied in detail.

Halliday divided the island into two areas that approximately coincide with the glaciated and non-glaciated division when he

[1] Ridgway.

mapped the forests. Section 8 of the Arcadian forest includes the glaciated regions and section 9 the non-glaciated. Unfortunately neither of these regions was described by him in the text that accompanies his revised map. While his map shows the entire island to be included in forest regions much of the land lacks trees. Generally speaking, the southern quarter of the island is a great "moss-barren," much like the arctic tundra. The western highlands and scattered uplands in the interior are of the same nature. A careful consideration of the distribution of *mcisaaci* and of the moss-barrens suggests very strongly that the two are incompatible. That *mcisaaci* is not found in these barrens has not been proved, but wherever *mcisaaci* has been found the region is forested.

A recent and detailed study of the climate of Newfoundland by Hare sheds little light upon the distribution of the insect on the island. It seems most likely that nowhere on Newfoundland is the climate inimical to *mcisaaci*. Thus the distribution seems to be governed by the distribution of sufficient soil to support a forest and its associated limited grasslands. Our present incomplete knowledge of the distribution of the insect suggests that a vegetative season shorter than 110 days may not be long enough for the full development of *mcisaaci* in one year. Knowing that other arctic and subarctic Satyridae may take two years for development from egg to imago, I hesitate to say that a growing season of less than 110 days will prevent the occurrence of the insect. In fact I know that the insect is capable of existing in areas with a shorter growing season, viz., Great Whale River on Hudson Bay.

VARIATION

In common with other insular forms *mcisaaci* shows less variation than do the mainland forms except *nipisiquit*. This is understandable, as all known *nipisiquit* come from the same locality. I think I have seen a large part of the material that has been collected on the island, most of which is in the Canadian National Collection. The other large series that I have seen is dos Passos' series from the type locality of *mcisaaci*. In this study I have been greatly assisted by Mr. Paul Bruggemann who measured and noted the material in Ottawa.

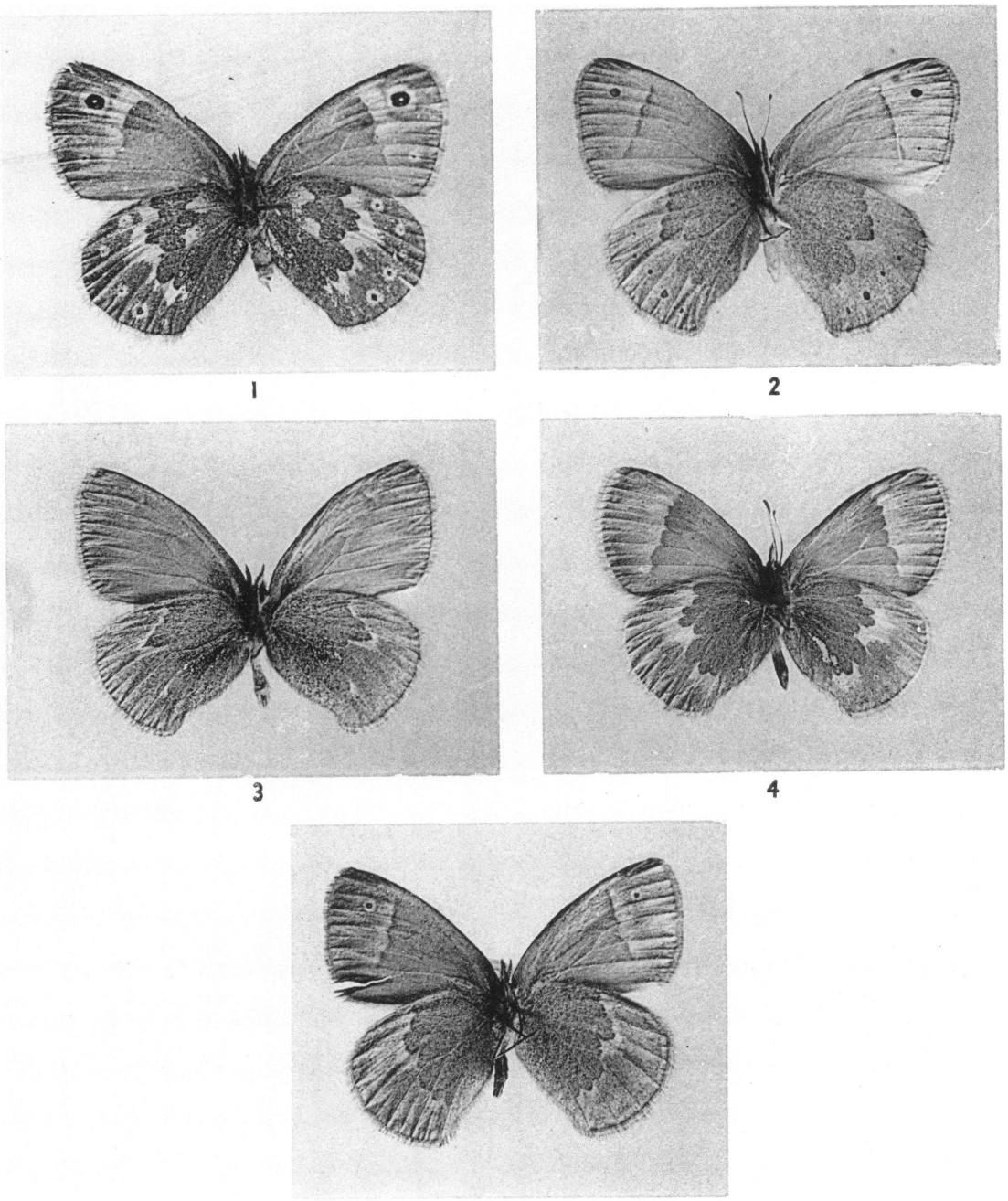
The five series studied in detail came from the following localities:

Saint Johns, St. Johns, latitude 47° 34′ N., longitude 52° 42′ W., on the Atlantic coast of the Avalon Peninsula in section 9 of the Arcadian Forest, predominantly spruce with pine and some hardwoods. The terrain has been glaciated. The mean annual temperature is about 41° F. (50 years' record). The mean annual precipitation is 53.8 inches (60 years' record). It is generally cloudy, and fogs are frequent. The daily variation in temperature is low, as might be expected from the proximity to the sea, being less than 20° F. Twenty-five males and nine females in the Canadian National Collection were studied. A few of these came from near-by New Melbourne.

Gander, Bona Vista, latitude 48° 57′ N., longitude 54° 34′ W., 482 feet above sea level, is in the interior northeast part of the island north of the lake bearing the same name. It is in section 9 of the Arcadian Forest (see St. Johns, above). The terrain has been glaciated. The mean annual temperature is about 39° F. (10 years' record). The mean annual precipitation is 39.7 inches (11 years' record). Cloudiness and fogs are frequent. The daily variation in temperature is low and on the average does not exceed 20° F. The material studied was collected by DiLabio and is in the Canadian National Collection. There are 18 males and six females in the series.

Doyles Station, St. Georges-Port au Port, latitude 47° 51′ N., longitude 59° 10′ W., about 40 feet above sea level, lies in the valley of the Great Codroy River on the southwestern point of the island. The forest is designated section 8 of the Arcadian Forest—spruce, pine, and hardwoods, with the spruce predominant. No meteorological data are available for Doyles Station, but the records for Saint Andrews, about 9 miles to the southwest, are these: mean annual precipitation, about 42 inches (7 years' record); mean annual temperature, about 40° F. (7 years' record). There is considerably less fog and cloudiness in this part of the island than along the east coast. The series studied consisted of 61 males and nine females, mostly in dos Passos' collection, where I was kindly allowed to study and measure the material.

Harmon Field (Stephanville), St. Georges-



Nearctic forms of *Coenonympha tullia*

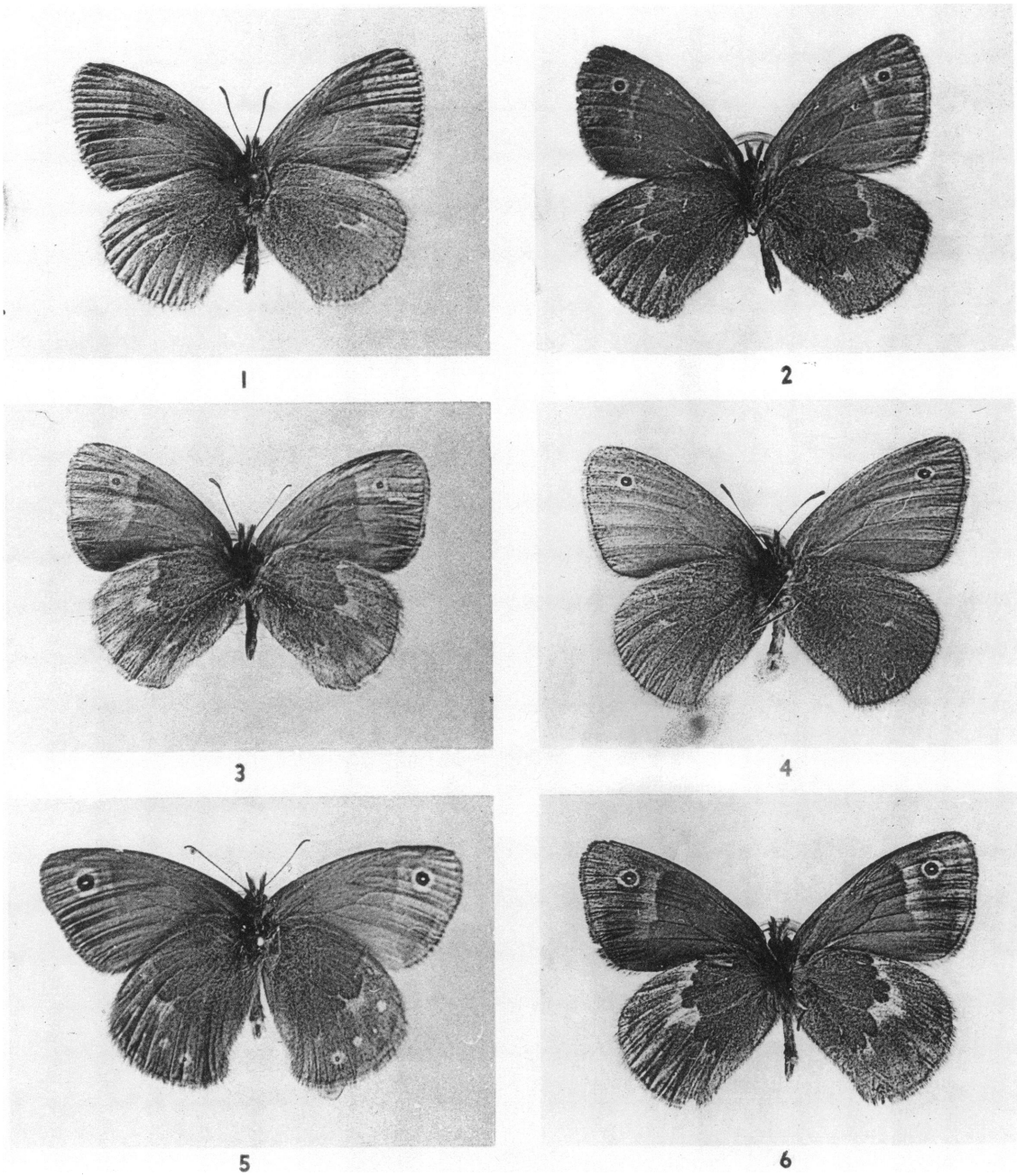
1. *Coenonympha tullia ochracea* Edwards. Under side of typical specimen from Daniel, Wyoming, 7000 feet, July 19, 1950, Clyde L. Glasgow, collector. Note characteristic ocelli and basal light patches on hind wing

2. *Coenonympha tullia california* Westwood and Hewitson. Under side of typical specimen from Calistoga, Napa County, California, August 10, 1930, R. G. Wind, collector. Note lack of contrasts and absence of basal light patches

3. *Coenonympha tullia ampelos* Edwards. Under side of typical specimen of *columbiana* McDunnough from Trail, British Columbia, June 6, 1953, Richard Fitch, collector. Note absence of markings on forewing and reduced markings on hind wing

4. *Coenonympha tullia mixturata* Alpheraky. Typical specimen from College, Alaska, 471 feet, June 11, 1940, Kay Huber, collector. Note strong contrasts and absence of ocelli and basal light patches on hind wing

5. *Coenonympha tullia inornata* Edwards. Under side of typical specimen from Shawbridge, Quebec, June 10, 1951, A. C. Sheppard, collector. Note well-developed rays and brown chevrons in submargin of hind wing



Variation among *Coenonympha tullia inornata*

1. *Coenonympha inornata mcisaaci* dos Passos. Under side of typical specimen from type locality, Doyles Station, Newfoundland, June 18, 1936, Hugh McIsaac, collector. The greatly reduced markings are characteristic of material from type locality

2. *Coenonympha nipisiquit* McDunnough. Under side of a representative specimen showing well-developed ocellus on forewing and broken ray on hind wing; Bathurst, New Brunswick, August 4, 1950, L. P. Grey, collector

3. *Coenonympha inornata inornata* Edwards. Under side of a rather pale male from Sand Lake, Ontario, June 30, 1926, F. P. Ide, collector, in the Canadian National Collection. Note light patches in submargin of hind wing

4–6. *Coenonympha benjamini* McDunnough. 4. Under side of typical specimen from Lethbridge, Alberta, June 24, 1929, J. H. Pepper, collector, in the Canadian National Collection. 5. Under side of an ocellate specimen from Calgary, Alberta, July 1, 1894, F. H. W. Dodd, collector, in the Canadian National Collection. Note absence of basal light patches and presence of brown chevrons on hind wing. 6. Under side of an almost immaculate specimen from Medicine Hat, Alberta, June 24, 1929, J. H. Pepper, collector, in the Canadian National Collection. Such specimens are more common among *benjamini* than among the eastern subspecies

TABLE 1

RADIUS OF LEFT FOREWING IN MILLIMETERS

	Males				Females			
	n	Mean	*S.D.*	*V*	*n*	Mean	*S.D.*	*V*
St. Johns	25	16.68	0.65	3.7	9	16.98	0.91	5.4
Gander	18	16.49	0.78	4.7	6	16.97	0.64	3.8
Harmon	58	17.37	0.49	2.8	4	17.92	—	—
St. Anthony	62	17.10	0.67	3.9	7	17.27	0.47	2.5
Doyles	61	16.36	0.89	5.4	13	17.03	0.96	5.6
All Newfoundland specimens	224	16.87	0.84	5.0	39	17.14	0.82	4.8
Bradore Bay, P.Q.	7	15.72	0.64	4.0	1	16.0	—	—

Port au Port, latitude 48° 32′ N., longitude 58° 33′ W., 44 feet above sea level, is located at the head of St. Georges Bay on the southwest coast of the island. The forest of the region is like that at Doyles, and the terrain has been glaciated. The mean annual temperature is about 40° F., and the mean annual precipitation is about 38 inches (8 years' record). The series studied contained 58 males and four females.

Saint Anthony, White Bay, latitude 51° 22′ N., longitude 55° 36′ W., about 45 feet above sea level, is situated on the east coast of Long Peninsula near its northern extremity. The Forest Classification Map of Canada includes all of the peninsula in section 8 of the Arcadian Forest. In the vicinity of Saint Anthony the forest consists of scattered clumps of black spruce in a tundra of lichens. The region was glaciated. Estimates of the mean annual temperature, about 35° F., and of the mean annual precipitation, about 35 inches, are based upon a broken record extending from 1944 to 1951. J. B. Wallis and B. S. Moore collected 62 males and seven females at the station. These are in the Canadian National Collection, as are those from Harmon Field.

Bradore Bay, Saguenay, latitude 51° 29′ N., longitude 57° 14′ W., near sea level, is situated in extreme eastern Quebec near the Labrador border on the Strait of Belle Isle. Some 10 to 12 miles to the north Bradon Hill rises to 1321 feet. The region is placed in the Northeastern Transition Section 13 of the Boreal Forest. There are no climatic data from this entire region. Halliday's description (1952, p. 17) reads: "The greater part of the peninsula of Labrador and Quebec, a high, well worn and flattened tableland rising somewhat to the east, is covered by a scant and poor forest growth. Climatic conditions are certainly more rigorous than in the southern parts, but another conditioning factor has been the denuding effect of glaciation, which has left large areas of bared Precambrian rocks, or very thin soils. There is a characteristic light cover of stunted black spruce and balsam fir, with scattered birch and jack pine. Shallow black spruce and tamarack swamps and treeless moors, where the vegetation takes on an alpine appearance, with abundance of white lichens, are common, the whole interspersed with many lakes. Where soil conditions are more favorable—as round some of the lakes, a much denser forest occurs."

The longest vegetative season, the period during which the mean air temperature is 43° F. or greater, occurs at Harmon Field, where it is 160 days, and the shortest at Saint Anthony, where it is 110 days.

VARIATION IN SIZE

My standard measure of size, used here, is the radius of the left forewing. This dimension is the most objective of all used in this study. The measurements were made to a tenth of a millimeter with a vernier caliper. The females are consistently but not significantly larger than the males (table 1).

VARIATION IN COLOR

Although there is some variation from specimen to specimen, the color of this subspecies of *inornata* is remarkably constant on the island of Newfoundland. The three mari-

TABLE 2

OCCURRENCE OF TRACES OF APICAL OCELLI

(For the number of specimens in each series, see table 1. Figures in italics not significant at the 1 per cent level of confidence.)

Station	Upper Side		Under Side	
	Males	Females	Males	Females
	% S.E.	% S.E.	% S.E.	% S.E.
St. Johns	*12.0 ±6.5*	*11.1 ±10.5*	*16.0 ±7.3*	*33.3 ±15.7*
Gander	0.00	0.00	*5.6 ±5.4*	*50.0 ±20.4*
Harmon Field	0.00	0.00	*6.9 ±3.3*	0.00
St. Anthony	0.00	0.00	14.5 ±4.5	*28.6 ±17.1*
Doyles Station	*6.6 ±3.3*	*15.5 ±10.0*	14.7 ±4.5	*15.4 ±10.0*
All Newfoundland specimens	3.1 ±1.2	*7.7 ± 4.3*	12.1 ±2.2	25.6 ± 7.0
Bradore Bay, P.Q.	0.00	0.00	0.00	0.00

time strains of *tullia* that I have seen in large numbers (*mcisaaci*, *nipisiquit*, and the subspecies on the British Isles) are all dark in color. *Mcisaaci* tends to be grayer than the others, while *nipisiquit* is redder. This is quite evident when long series are set adjacent to one another. The maritime strains are much darker than any of the mainland Nearctic strains. The one exception to this, which is really no exception, is the dark material found at Bradore Bay in Quebec. It is probable that as the north shore of the St. Lawrence estuary is explored a complete transition from the dark maritime strains to the much lighter material typical of most known series from eastern Canada will become evident. At present there is a gap of several hundred miles from which no *tullia inornata* have come. This is a critical region; it is where the true maritime climate gives way to an inland climate. In it lies the clue to the validity of *mcisaaci* as a distinct and well-separated subspecies.

The difference between the sexes does not seem to be so marked among *mcisaaci* as it is among either *nipisiquit* or *inornata*.

VARIATION IN APICAL OCELLI ON FOREWING

The Newfoundland strains of *inornata* are the least ocellated of all. On rare specimens a trace is found on the upper side, sometimes as an ill-defined light spot, less often as a small cluster of dark scales. More frequently ocelli or traces of them are found on the under side. Females show these marks about twice as often as do the males. (Table 2.)

VARIATION IN RAY ON UNDER SIDE OF FOREWING

The bi-colored buff and pink streak that lies just outside the cell is rather ill defined on most specimens of *mcisaaci*. In this respect *mcisaaci* differs markedly from the mainland strains, on which the ray is well defined. In addition to lacking definition this ray on the Newfoundland material tends to be a little shorter than on material from the mainland. Typical *mcisaaci* from Doyles Station is more like the mainland strains than it is like the other Newfoundland strains in the extent of the ray, but it is like the others so far as definition of the ray is concerned (table 3).

VARIATION IN RAY ON UNDER SIDE OF HIND WING

The irregular and angled streak of light scales across the disc of *tullia* on the under side of the hind wings is ill defined on *mcisaaci*. Thus the division between the darker inner part and the lighter outer part of the surface often is not clear. On *inornata* and *nipisiquit* the costal half of the ray generally is bold and rarely interrupted. On *mcisaaci* this portion of the ray is tenuous on many specimens. On considerably less than half of the specimens examined the ray extends posteriorly from its enlargement at the end of the cell, or it is broken between the cell and the inner margin of the wing. The reverse is true of both *nipisiquit* and *inornata*. Again the Doyles Station material is more like *in-*

TABLE 3

EXTENT OF RAY ON UNDER SIDE OF FOREWING

(For the number of specimens in each series, see table 1. Figures in italics not significant at the 1 per cent level of confidence.)

Station	To Cu_2 %	S.E.	To Cu_1 %	S.E.	To M_3 %	S.E.	To M_2 %	S.E.	Absent %	S.E.
MALES										
St. Johns	*4.0*	*3.9*	76.0	8.5	*16.0*	*.73*	—		*4.0*	*3.9*
Gander	—		88.9	7.4	*11.1*	*7.4*	—		—	
Harmon	—		60.3	6.4	32.8	6.2	*6.9*	*3.3*	—	
St. Anthony	*3.2*	*2.2*	75.8	5.4	21.0	5.2	—		—	
Doyles	52.5	6.5	37.7	6.2	*4.9*	*2.8*	*3.3*	*2.3*	*1.6*	*1.6*
All Newfoundland specimens	15.6	2.4	62.5	3.2	18.3	2.6	2.7	1.1	*0.9*	*0.6*
Bradore Bay, P.Q.	*28.6*	*17.1*	*42.8*	*18.8*	*28.6*	*17.1*	—		—	
FEMALES										
St. Johns	*33.3*	*15.7*	66.7	15.7	—		—		—	
Gander	*33.3*	*19.2*	66.7	19.2	—		—		—	
Harmon	—		75.0	21.6	—		*25.0*	*21.6*	—	
St. Anthony	—		100.0		—		—		—	
Doyles	76.9	11.7	*23.1*	*11.7*	—		—		—	
All Newfoundland specimens	38.5	7.9	59.0	7.9	—		*2.5*	*2.5*	—	
Bradore Bay, P.Q.	Yes		—		—		—		—	

TABLE 4

CONDITION OF RAY ON UNDER SIDE OF HIND WINGS

(For the number of specimens in each series, see table 1. Figures in italics not significant at the 1 per cent level of confidence.)

Station	Complete[a] %	S.E.	Broken[b] %	S.E.	M_3[c] %	S.E.	Fragmentary[d] %	S.E.
MALES								
St. Johns	—		32.0	9.3	*8.0*	*5.4*	60.0	9.8
Gander	—		33.3	11.1	*16.7*	*8.8*	50.0	11.8
Harmon	—		17.3	5.0	15.5	4.8	67.2	6.2
St. Anthony	—		*8.1*	*3.5*	56.4	6.3	35.5	6.1
Doyles	9.8	3.8	34.4	6.0	18.0	4.9	37.8	6.2
All Newfoundland specimens	*2.7*	*1.1*	22.3	2.3	26.8	3.0	38.2	3.3
Bradore Bay, P.Q.	*28.6*	*17.1*	*14.3*	*13.3*	*28.6*	*17.1*	*28.6*	*17.1*
FEMALES								
St. Johns	—		55.6	16.5	*22.2*	*13.9*	*22.2*	*13.9*
Gander	—		66.7	19.2	*16.7*	*15.2*	*16.7*	*15.2*
Harmon	—		*25.0*	*21.6*	—		*75.0*	*21.6*
St. Anthony	—		71.4	17.1	—		28.6	17.1
Doyles	38.4	13.5	*30.8*	*12.8*	*15.4*	*10.0*	*15.4*	*10.0*
All Newfoundland specimens	*12.8*	*5.3*	48.8	8.0	*12.8*	*5.3*	25.6	7.0
Bradore Bay, P.Q.	—		Yes		—		—	

[a] A recognizable band of light scales from the costal to the inner margin of the wing.

[b] Those specimens on which the irregular band is complete anterior to the cell but interrupted posterior to it.

[c] Those specimens on which the band is complete anterior to the cell but absent posterior to it.

[d] Individuals on which the band is represented by a spot on the costa, another at the end of the cell, and a third at the inner margin.

TABLE 5

PRESENCE OF SUBMARGINAL MARKS ON UNDER SIDE OF HIND WING

(Figures in italics not significant at the 1 per cent level of confidence.)

Station	*n*	Dark % S.E.	Light % S.E.	Both % S.E.	None % S.E.
MALES					
St. Johns	25	—	*16.0 ± 7.3*	—	84.0 ± 7.3
Gander	18	*11.1 ± 7.4*	*16.7 ± 8.8*	*11.1 ± 7.4*	83.3 ± 8.8
Harmon	58	—	10.3 ± 4.0	—	89.7 ± 4.0
St. Anthony	62	—	8.1 ± 3.6	—	91.9 ± 3.5
Doyles	14	—	57.2 ± 13.2	—	34.7 ± 13.2
All Newfoundland specimens	177	*1.1 ± 0.8*	14.7 ± 2.7	*1.1 ± 0.8*	83.1 ± 2.8
Bradore Bay, P.Q.	7	—	*14.3 ± 13.3*	—	85.7 ± 13.3
FEMALES					
St. Johns	9	—	—	—	100.0
Gander	6	—	—	—	100.0
Harmon	4	—	*25.0 ± 21.6*	—	75.0 ± 21.6
St. Anthony	7	—	*28.6 ± 17.1*	—	71.4 ± 17.1
Doyles	9	—	44.4 ± 16.5	—	55.6 ± 16.5
All Newfoundland specimens	35	—	20.0 ± 6.8	—	80.0 ± 6.8
Bradore Bay, P.Q.	1	—	Yes	—	—

ornata than it is like the rest of the Newfoundland material. (Table 4.)

VARIATION IN SUBMARGINAL AREAS ON UNDER SIDE OF HIND WING

No trace of ocelli was found on any Newfoundland specimen. This is the same as the condition found on *nipisiquit* and *inornata* from eastern Canada. The other marks that frequently occur in this area are light or dark chevrons. These are pronounced on both *inornata* and *nipisiquit*. The light patches may be related genetically to the ocelli that are found on many subspecies of *tullia*. They are less frequently sharply defined than are the dark brown chevrons. From studies on other subspecies the two do not seem to be genetically related.

When I was taking notes on *mcisaaci* in dos Passos' collection I neglected to record the occurrence of these marks, so inconspicuous are they on this subspecies, which accounts for the smaller number of specimens recorded in table 5. Only my own Doyles Station material is included.

COENONYMPHA INORNATA NIPISIQUIT MCDUNNOUGH

Coenonympha inornata nipisiquit McDUNNOUGH, 1939, Canadian Ent., vol. 71, p. 266.

TYPE LOCALITY: Bathurst, New Brunswick.

COLLECTOR OF TYPE: J. McDunnough.

LOCATION OF TYPE: Canadian National Collection, Ottawa, Ontario, Canada.

ORIGINAL DESCRIPTION: "Male. Characterized, as compared with typical *inornata* from the Quebec Laurentians and northern Ontario, by the deep brown color of the upper side shaded with smoky brown broadly along the outer margin of primaries and on nearly the whole of secondaries. The fringes are deep smoky, paling on the secondaries to gray below the apex of wing. Beneath, the primaries are deep brown shaded with greenish gray apically and narrowly along costa and down the outer margin toward anal angle; the irregular creamy oblique band is prominent and an apical ocellus may or may not be present; in the holo- and allotypes it is present, consisting of a circular black spot ringed with pale ochreous and with a central white dot. The basal portion of secondaries within the irregular pale band is shaded with brown and appears much deeper in color than in the typical form; the marginal area is suffused with greenish gray and shows traces (at times quite distinct) of a diffuse brown marginal band; the pale median banding is quite prominent and much as in *inornata*, varying considerably in individuals.

"Female. Deeper ochre-brown in color than *inornata* and almost the same color as rather pale males of the typical form. Maculation otherwise as in male. Expanse 30 mm."

RANGE: Northern New Brunswick.

BIONOMICS: Nothing is known of the immature stages of *nipisiquit*. The insect may prove to be difficult to raise in the laboratory unless a variety of salt-marsh grasses is available. The very late emergence date and the fact that the habitat is flooded at spring tides by salt water suggest that the life history will be found to differ from that of the other *tullia* in North America. It may be found that the insect over-winters as an egg. This might account for the late date of emergence. Another possibility is that the young larvae burrow into grass or sedge stems to evade the ill effects of salt water.

ECOLOGY AND HABITS: "The habitat of *nipisiquit* is a typical east coast salt marsh, cut by muddy tidal creeks. During the spring tides most of the marshland must be completely submerged, and it is remarkable that the hibernating early stages come through alive, since salt water has a very toxic effect on most plants and other forms of life not especially adapted to withstand it. *Nipisiquit* does not confine itself to the edges of the marsh, but flies, often most commonly, in some of the lowest, wettest situations. It has a special liking for the spots where a species of low, brown colored marsh grass grows. . . . Unfortunately I cannot give you the name of this grass, but it is doubtful anyway if there is any real biological association here. It could be that the butterflies just like to hover about these open places where the grass is short, perhaps where the influence of the sun on the dark grass or bare ground makes it feel warmer and more pleasant to them.

" . . . In my experience *nipisiquit* is not generally distributed all over these marshes, but like many butterflies, tends to be localized to certain spots well within the limits of those areas, where, to all appearances, it ought to be occurring everywhere" (Douglas C. Ferguson, *in litt.*, March 12, 1953).

"Dr. Brown . . . [who] collected the long type series of *nipisiquit* at Bathurst, N. B. in 1939 . . . offers the following information about this rather striking subspecies. It occurred in great numbers on a low marsh along the coast. The marsh is only slightly higher than extreme high water mark, but protected on the seaward side against inundation by a low sand ridge. That it is more or less saline is indicated by its preponderantly halophytic vegetation. He stresses the fact that the butterfly was strictly confined to this salt marsh and calls attention to its rather late period of flight, (1.viii)—7–9, VIII in 1939 and 29.vii—4.viii in 1943, in which year Dr. McDunnough collected a rather smaller number of specimens at the same locality" (Paul Bruggemann, *in litt.*, February 2, 1953).

Bathurst is situated on a small bay at about the mid point of the south shore of Chaleur Bay. The country that lies back of the Bay is hilly. It has been developed from

the foreland of old Appalachia. The terrain is rugged, heavily timbered glaciated land. Along the coast, and thus in the area where *nipisiquit* is found, the climate is much influenced by sea fogs. Thornthwaite's formula for the climate at Bathurst is ArC'c, the same as for the coastal parts of eastern Newfoundland. Thus the two maritime strains of *inornata* enjoy the wettest parts of the entire range of the moiety.

Vaino Auer, in his classic study of peat bogs in southeastern Canada, did not report on the Bathurst bogs, nor is it known whether or not he even examined them. The nearest bog upon which he did report, and then only in part, is situated at Shippigan on the southeast point of Chaleur Bay. The lowest levels of this bog are composed of undecayed *Carex* peat, not more than 3 feet deep at the most. This is topped by a 4-foot zone of decayed *Sphagnum* peat in the middle, above which there is up to 12 feet of raw *Sphagnum* peat. No profiles of pollens were published for this bog.

Some distance south of Shippigan on the coast at Escuminac, Auer studied two bogs, Escuminac and Eel. For these he did publish pollen profiles. Because the structure of the bog at Shippigan is very much like that at Escuminac it is possible that the pollen profiles of the two are so similar that it was not felt necessary to publish both.

At the Escuminac bog, tree stumps were found at the contact between the *Carex* peat at the bottom and the *Sphagnum* peat that composes the greater part of the bog. This stump-bearing horizon lies about 25 feet below the present surface. The horizon seems to represent a time when the climate so changed that *Pinus* became the dominant tree of the forest, replacing *Picea* that had previously dominated the forest. *Pinus* dominance continued to the 10-foot level when an apparent shift in climate caused these trees to decline and *Betula*, *Abies*, and *Picea* to increase. The situation at the half-meter level shows the more boreal types of trees still aggressive in the forest.

Halliday (1952, p. 37) described the present composition of the forest: "The prevailing character of the forest is softwood, and the trees are often reduced in size in the immediate vicinity of the coast. Black Spruce associations with cedar and tamarack and white and wire birch, are dominant, especially on the swampy lands, and extensive areas of jack pine are found on sand flats. Red spruce is well distributed, usually in admixture with such hardwood species as yellow birch, beech, and some sugar maple. Hemlock was formerly of considerable importance as pure stands or admixture with the above. Balsam fir is possibly not so general as in other parts of the region; white spruce is present to a limited extent. Hardwood associations are restricted to small areas on ridges, and are often of a poor quality beech."

The interpretation of pollen profiles has not yet been reduced to a precise science. In broad terms the story told by the Escuminac bog suggests that the upper 10 feet accumulated in a period during which the climate was essentially what it is today. The pollens found agree with the types of trees now found in the region. This cool humid period was preceded by a warmer and possibly drier period of longer duration during which the pines dominated the forest. The conditions in northeastern New Brunswick then may well have been like those now found on the northern part of the coast of Massachusetts. The change in character of the peat at the 25-foot level may or may not have been associated with a radical change in climate. The replacement of *Carex* by *Sphagnum* seems to be a normal movement towards a climax in the New Brunswick bogs of today. This change in substrata has a marked effect upon the trees that grow on the bog, as may be observed in bogs that are today making the change.

The area under discussion seems to me to occupy a zone of tension between the deciduous forest and what Livingston and Shreve call the Northern Mesophyllic Evergreen Forest. Halliday has pointed out that Clements was in error when he considered the region to lie in the Boreal Forest. Excellent and thorough work of various Canadian botanists shows that there is little or no boreal character to either the forest or the climate of the region.

All of this has a great deal to do with the history, past, present, and future, of *nipisiquit* and probably explains the isolated nature of the insect and its restricted distribution. I

TABLE 6

STATISTICS OF VARIATION OF *Coenonympha inornata nipisiquit*

(Figures in italics not significant at the 1 per cent level of confidence.)

Variable	Males	Females
Number studied	141	64
Size		
Radius of left forewing (mm.)	18.57 ±0.61	18.86 ±0.58
Coefficient of variation	3.3	3.1
Forewing		
Presence of ocellus or trace on upper side (%)	12.0 ±2.7	57.7 ±6.2
Presence of ocellus or trace on under side (%)	82.2 ±3.2	95.3 ±2.6
Ray ends at M_3 (%)	*0.7 ±0.5*	0.0
Ray ends at Cu_1 (%)	47.5 ±4.2	9.4 ±3.6
Ray reaches or exceeds Cu_2 (%)	51.8 ±4.2	90.6 ±3.6
Hind wing		
Ray complete (%)	6.4 ±2.1	14.1 ±4.4
Ray broken (%)	83.7 ±3.1	84.4 ±4.5
Ray ends at M_3 (%)	*4.2 ±1.7*	*1.6 ±1.6*
Ray fragmentary (%)	5.7 ±2.0	0.0
Dark chevrons present (%)	49.6 ±4.2	14.1 ±4.4
Light patches present (%)	20.6 ±3.4	28.2 ±5.6
Dark and light marks present (%)	11.3 ±2.7	*4.7 ±2.6*
Submarginal marks absent (%)	40.0 ±4.1	62.5 ±6.0
Ocelli present (%)	0.0	0.0

see no reason to believe that *nipisiquit* is different from *inornata* in its basic environmental requirements. That it is restricted to sea marshes is a reaction to life in an environment that contains few niches fulfilling the climatic needs of the insect. I believe that New Brunswick temperatures generally may be too high for the insect and certainly were in the not distant past. Thus in search of the coolest areas *nipisiquit* crowded into sea marshes where the cooling effect of the sea is most felt during the warm summer months. I do not doubt that in cooler times it ranged more widely in New Brunswick. A continuation of warming weather may raise the local temperature of the Bathurst area so far beyond the reproductive tolerance of the insect that even the ameliorating powers of the sea will not sufficiently cool the sea marshes to allow *nipisiquit* to reproduce in numbers sufficient to maintain itself. It would be interesting to learn if *nipisiquit* can be weaned of its salt-marsh habitat and thus spread inland in the advent of cooler climate.

DISTRIBUTION: Bathurst, Gloucester, New Brunswick, July 29 to August 8.

In the collections of the Los Angeles County Museum and of George Rawson there are specimens that bear the date June 8, which were collected by McDunnough and W. J. Brown. The date for each specimen should read August 8.

Mr. Douglas Ferguson of the Nova Scotia Museum of Science has searched unsuccessfully for this interesting insect in several of the salt marshes that fringe the south shore of Chaleur Bay. Recovery of the subspecies from other New Brunswick marshes is awaited with great interest. Those from Shippigan southward to at least Escuminac should be explored repeatedly from mid-July onward.

VARIATION

Little variation is to be expected among the series studied, because all have been taken in the same salt marshes. This constancy was noted by McDunnough in his original

description. The data presented below have considerable value in the general study of variation among *tullia*. The material studied, 141 males and 64 females, is sufficient for establishing reasonably sound parameters. As a unique colony has supplied all the specimens that are known, the data may stand for the minimum variation that can be expected in a natural population of this species.

Mr. Bruggemann measured the material in the Canadian National Collection and I accumulated the data on the material from the Nova Scotia Museum of Science and from short series in the collections of the United States National Museum, Cyril F. dos Passos, and F. M. Brown.

With a single locality involved it is possible to compress all the statistical data into a single table (table 6).

Variation in Size

Nipisiquit is a large insect for this species in America. It is the largest of the *inornata* moiety and is significantly larger than either of the adjacent subspecies, *inornata* and *mcisaaci*. The low coefficient of variation is expected because of the peculiarity of the sample noted above.

Variation in Color

As is stated above, *nipisiquit* and *mcisaaci* are the darkest subspecies of *inornata*. In neither of these subspecies is the color of the males so variable as it is in *inornata*. The sexes of *nipisiquit* are strikingly different in color, which is not true of *mcisaaci*. I have yet to see a female that is as dark as the lightest colored male. In all the other subspecies of *inornata* and of *tullia* from North America there is an overlap in the color range of the two sexes. Among some of the western forms there is no sex difference in color.

Variation in Ocelli on Forewing

There is a significant sex difference in the appearance of these marks on the upper side of the wings. At least traces of the ocellus are found on half of the females examined, while similar marks occur on only 10 per cent of the males. On the under side the difference is not marked but is of statistical significance at the 1 per cent level.

The differences found between *nipisiquit* and *mcisaaci* in respect to these marks is highly significant. Between *nipisiquit* and *inornata* from Quebec the differences are weaker but still are of some significance.

On *nipisiquit* the ocellus on the under side is well developed and often pupilled with white. Very occasionally a second one or trace is found posterior to M_3. Such supernumerary ocelli are very rare on *tullia inornata* but not uncommon on *tullia ochracea*.

Variation in Ray on Under Side of Forewing

The double streak of buff and pinkish scales that lies just outside the cell is well developed on *nipisiquit*. The sex differences are slight and of no significance. *Nipisiquit* differs sharply from *mcisaaci* and not at all from *inornata* from Quebec in this character.

Variation in Ray on Under Side of Hind Wing

There is no significance to the slight differences in frequencies for the various conditions of this mark between the sexes. In this character, too, the differences found between *nipisiquit* and *mcisaaci* are highly significant, while those between *nipisiquit* and *inornata* from Quebec are negligible.

Variation in Submarginal Area on Under Side of Hind Wing

Like *inornata* and *mcisaaci*, *nipisiquit* lacks submarginal ocelli on this surface. The presence of dark chevrons and light patches in the area is one of the secondary characteristics of *tullia inornata*. *Nipisiquit* shows these marks, which are more frequent on the males than on the females. This is certainly true of the dark chevrons. The light patches occur on the sexes with about equal frequency. There are differences among *nipisiquit*, *mcisaaci*, and *inornata* that, while statistically significant, seem to have little taxonomic value.

Variation in Basal Area of Under Side of Hind Wing

There is no evidence of light patches at the base of the hind wings of *nipisiquit*.

COENONYMPHA INORNATA INORNATA EDWARDS

Coenonympha inornata EDWARDS, 1861, Proc. Acad. Nat. Sci. Philadelphia, p. 163.

Coenonympha laidion BUCKELL (*nec* Kirby), 1895, Ent. Rec., vol. 7, p. 106.

Coenonympha inornata race *quebecensis* BARNES AND BENJAMIN, 1926, Bull. Southern California Acad. Sci., vol. 25, p. 89. Type locality: Chelsea, Ottawa County, Quebec. In the United States National Museum, Washington, D. C. "Upper side similar to *inornata*, the hind wing with a pale gray outer margin interrupted and partly bordered by a dark, disconcolorous, band. Underside similar to *ampelos*, paler and brighter than in typical *inornata*, ocellus of fore wing present or absent, when present reduced in size. Number and sexes of types: Holotype ♀, 1–7 June; 8 ♂ paratypes 1–7 and 7–15 June."

TYPE LOCALITY: [Probably the east shore of] Lake Winnipeg, Manitoba.

COLLECTOR OF TYPE: Robert W. Kennicott.

LOCATION OF TYPE: Carnegie Museum, Pittsburgh, Pennsylvania.

ORIGINAL DESCRIPTION: "Male. Upper side ochrey brown, lighter in the disk of all the wings; costal margin of primaries and abdominal margin of secondaries grayish; no spots above or below; fringe gray, crossed by a dark line.

"Under side; primaries same color as above from the base to beyond the middle; then a transverse sinuous ray of paler color, and beyond this to hind margin grayish; sometimes this ray disappears, the basal color extending nearly to the apex; secondaries gray with a slight greenish tinge, darker from base to middle, and this shade separated from the paler margin by a transverse, tortuous, interrupted ray, the course of which is parallel to the hind margin."

RANGE: The forested region of eastern and central Canada north of the St. Lawrence River and contiguous forested areas of the United States in the western Great Lakes region.

BIONOMICS: Thus far little has been done to study the life history of *inornata*. Davenport is the only person I know who has raised this insect. In 1935 he collected 15 eggs from a dozen battered females confined over lawn grass. The insects were taken at Lake Nominingue, County Labelle, Quebec. Only one of these reached maturity. His brief notes (1941, p. 264) are quoted below:

"*Egg.* The eggs are singly attached to grass stems or leaves or the cage. They are about one millimeter high, shaped and sculptured as those described by Edwards for *california* and *ampelos*, and greenish-yellow when laid, later to become yellowish, threaded and streaked with red-brown. Approximately eight days for this stage.

"*Larva* . . . The new-born larva is flesh colored with a brown head. After eating it soon becomes the typical grass green color characteristic throughout larval life, but retains a brownish dorsal line and head. After the first molt the head is emerald and the body grass-green with a dorsal dark green line and two lateral stripes of green over a whitish-yellow basal ridge. The two caudal tails are pink and covered with tubercles. As in the larvae of *ampelos* and *california* the body and head are covered with fine, light tubercles set with hairs and the head capsule is finely granulated.

"*Chrysalis* . . . No better description of this stage can be given than that of Edwards for the chrysalis of *ampelos*:

' . . . cylindrical, stout, the upper end truncated, the abdomen swollen, conical at extremity; head case narrow, ending in a sharp cross ridge which is a little arched, the sides slightly convex, followed by a shallow depression; color delicate green; marked by nine black stripes placed as in *galactinus*' (*california*) 'of these, one on dorsal edge of each wing case from base to inner angle of wing;' (backed, in *inornata*, with white) 'a curved stripe on middle of each wing reaching the hind margin; a short stripe on same margin on ventral side of the curved one; two short stripes on the antennae cases; beside these, there is a black mark on either side of 13;' (in *inornata* on the last three abdominal segments) 'top of head case whitish.'

"Edwards neglects to mention the yellowish brown spiracles and also the 'anal segment, which terminates in a knobbed cremaster, amply provided with a dense cluster of amber coloured hooks' mentioned by Frohawk (1924) on the chrysalis of *tullia polydama*.

"About one day before emergence the chrysalis becomes grayish and transparent so that the ochre wings and darker body parts are quite evident.

"egg	*8 days*	*about 1 mm.*
1st instar	11–19 days	4 mm.
2nd instar	14–27 days	6 mm.
3rd instar	19–26 days	8 mm.
4th instar	(hibernation, Sept.–April)	9 mm.
5th instar	9 days	20 mm.
chrysalis	12 days	9 mm."

Davenport stored his lone surviving larva in the laboratory cold room at 40° F. He removed the insect on April 20 and pupation took place on April 29. The imago emerged on May 11. This is somewhat earlier than the insect appears in nature, probably due to the early date of removal from the cold room.

This subspecies is essentially single brooded. Along its southern boundaries in propitious years there is a small, partial second brood. This second brood appears in early September or the last few days of August. Specimens from the southern portion of the range found from mid August onward should be examined critically for condition before being considered second brood. I question the ability of these second-brood specimens to produce viable offspring. It seems more likely that the larvae will not be advanced enough by the time killing frosts occur to adopt diapause. This question should be explored by means of breeding experiments.

The period of flight becomes progressively later as the latitude increases. The insect is on the wing during June along the southern boundary of its range. In the northernmost parts late July and August seem to be the times to find it, which suggests that in the northern areas the insect may take two years to mature, unless the longer duration of daylight at high latitudes allows it to produce an annual brood—a point well worth investigating.

ECOLOGY AND HABITS: In Quebec, at Lake Nominingue, "I found the insect fairly common drifting about in its characteristic skipping and erratic manner over the damp and grassy low places dotted with alder and over the larger open meadows" (Davenport, 1941, p. 263).

"In all of the localities [in Quebec] where I have taken *inornata* it has been found on open grass covered land where the forest is sparse and consisting of small scattered evergreens with lots of grassy areas between clumps of trees. In some areas there would be a few scattered maples, birches and poplars. I have also taken it on cleared land that has been neglected and allowed to become overrun with wild grasses, weeds, etc. The specimens taken at Shawbridge have been collected along the railway embankment, a favorite place. The habitat as far as is known to me is dry, sandy soil areas" (A. C. Sheppard, *in litt.*, January 31, 1953).

Dr. P. H. H. Grey reported to me that he captured a single specimen in Morgan Arboretum, Macdonald College, in similar country to that around Shawbridge. This is the stray from the farthest south in Quebec.

" . . . I have taken a small series in the Massassagi Forest Reserve area about 45 miles north of Thessalon, Ontario, Canada (July 6, 1935). The habitat was open grassy places (cut over timberland) . . . most of the northern parts of Michigan and southeastern Ontario represent cut over timberland and this may have very interesting ecological significance so far as many Nymphalids are concerned. I mean by this that open spaces, sometimes bushy, that were formerly heavy timber should by all rules offer an opportunity for the increase and spread of such things as *Oeneis*, *Coenonympha*, *Minois*, etc. *C. inornata* is a rather weak flier, settling quite frequently in grass or weeds. It apparently does not commence to fly much until dew or moisture has evaporated" (G. W. Rawson, *in litt.*, January 30, 1953).

Walter Krivda, an experienced collector living in The Pas, Manitoba, has written to me about his experience there with this species. "The species appears in late June–early July and persists from 2 to 3 weeks depending upon the weather to a large degree. This year . . . [the flight] was cut very short, following a storm and cold weather afterwards.

"The species flies in a tall grass area (knee high) that is damp and its more moist areas are covered with sedges and willows (many species but no *S. interior*). This particular spot is not more than 3 or 4 acres in extent and is without doubt one of the local breeding

grounds for the species. The area . . . is somewhat open and the willows still young—being an old pasture. The ♂ and ♀ appear at the same time. The species will 'play possum,' very much like *Erebia discoidalis* Kby. if suddenly frightened" (*in litt.*, August 29, 1954).

Mr. E. G. Voss, who perhaps is most familiar with *inornata* in Michigan writes me: "The species is evidently of rare occurrence in the region of the Straits of Mackinac—I have taken it in three different years, in three different counties. In 1947, a late season, a single male was taken flying low over more or less marshy ground in the vicinity of Cecil Bay, Emmet County, a few miles southwest of Mackinaw City. The following year several of the butterflies were flying low and jerkily on July 2 in Mackinac County. The habitat in this case was a small field of tall grass between woods and the highway south of St. Ignace business district. The insect would light low down in the grasses, where they were taken without difficulty. I did not see *Coenonympha* again until 1952; this time it was in Cheboygan County, on the long-defunct Mackinaw City golf course, just south of the town. Again the butterflies were in a field of tall grasses near woods. They flew low and lit near the ground among the grasses (June 19 two males and July 2 one female). On the basis of the Mackinac and Cheboygan experiences, I would picture the habitat as well-drained fields of tall grass near the aspen woods which are so characteristic of northern Michigan's cut and burned over areas" (*in litt.*, February 7, 1953).

The first Michigan specimens were taken by Sherman Moore who has described these captures for me: "I remember fairly well the first time I took the species, on August 2, 1917. This was on Scott Point on the north shore of Lake Michigan about twenty miles east of Manistique. The point rises abruptly about twenty feet above the lake, the top is level and bare, the sides along the lake fringed with low bushes, including willow and dogwood. There was some growth of grass on the top. *Inornata* was found resting on the grass and on the bushes. It seems to prefer open, fairly dry localities. In Emmet County it was taken on sandy ridges back of the shore. These are partly grown over with brush, and separated by low wet swamp" (*in litt.*, February 8, 1953). Later Moore wrote me this: "In my opinion, the species has worked into the Northern Peninsula from the northwest, as have quite a number of other species, and . . . the specimens taken south of the Straits are strays which were carried across by high northwesterly winds, which are rather frequent even in mid-summer. This is almost certainly true of the High Island specimen. It has not been found on Beaver Island where I collected for five seasons. The Lepidopterous fauna of Beaver Island has definite northern affinity" (*in litt.*, February 22, 1953).

"*Inornata* in Minnesota occurs in the same sort of habitat as its far western relatives. Typically it is found in grassy meadows in oak savannas. Also its flight is similar. It does not appear to occur in swampy meadows nor in damp and rich lowlands near larger rivers. It is somewhat local in my limited experience with it near St. Paul, Minnesota. Most of the records are from the grasslands of central to northwestern Minnesota, but it might be expected over much of the state except the extreme northeast" (R. W. Macy, *in litt.*, February 9, 1953).

The above quotations from variously located experienced field collectors may be summarized as follows: While *inornata* is an insect of the boreal evergreen forest its preferred areas are the grassy openings in the forest. It seems to prefer dry fields or slopes but is at times found in more moist localities. On the southwestern perimeter of its range it invades the savannas that are transitional from the evergreen forests to the prairies. In these areas the insect tends to show much admixture of *benjamini* characters.

The entire range of *inornata* falls within the region covered by the Wisconsin ice sheet. This means that it is relatively a newcomer to the territory it occupies. Carbon-14 dates from Minnesota and Wisconsin suggest that the area now occupied by *inornata* in the southwestern extremity of its range was inclement to the species as recently as 11,000 years ago. There also is a distinct possibility that a few thousand years ago the insects ranged farther north than they now do. Pollen profiles from northern bogs all seem to show about five thousand years ago a short period of warmer climate across the present

range of *inornata*. If the interpretation of these profiles is correct it is likely that *inornata* is now recapturing territory held during the warmer period.

When the range of *inornata* is compared with the distribution of forests in Canada and the northern Lakes area it is evident that the southern parts of the Boreal Forest and the northern parts of the St. Lawrence-Great Lakes Forest contain the habitat of the subspecies. From a study of the composition of the sections of the Boreal Forest from which I have seen *inornata*, these trees seem to be the "markers" for the occurrence of the insect: jack pine (*Pinus banksiana* Lambert), white spruce (*Picea glauca* Voss), aspen (*Populus tremuloides* Michaux), white birch [*Betula papyrifera* v. *occidentalis* (Hooker) Sargent]. In the more southern St. Lawrence-Great Lakes Forest the "markers" are the same, with white pine (*Pinus strobus* Linné) replacing the jack pine and the large-toothed aspen (*Populus grandidentata* Michaux) replacing quaking aspen.

The climatic conditions that prevail in the range of *inornata* are, according to Thornthwaite's system, BrC'c and BrD'c in the eastern part and CdC'c and CrD'd in the western part. This suggests that the indices for *inornata* are something like 35 to 100 for Precipitation Effectiveness (sub-humid to humid), with the lower indices in the west, and 16 to 60 for Temperature Efficiency (temperate to cool temperate), with at least 50 per cent of the efficient temperature occurring during the three summer months.

Geologically most of the land occupied by *inornata* is glaciated old land. Most of it lies on the Laurentian Shield. In fact better coincidence is seen between the range of the insect and the extent of the Laurentian Upland of Atwood than between the range and any of the more biologically based systems for dividing the continent into provinces, such as Dice's Biotic Provinces or Merriam's Life Zones.

Variation

The series selected for detailed study leave something to be desired. Two areas that seem to me to be critical are not included—the north shore of the St. Lawrence River, or rather the estuary, and the western part of the province of Ontario. There is no material available from the first area, and I have seen only scattered and very short series from Ontario. I would like to have a good series from Algoma or Thunder Bay counties for study.

Quebec

A total of 66 males and 10 females from several localities in the province were carefully measured. This material is in my own collection and was given to me by Mr. A. C. Sheppard of Montreal. It comes from four stations and well represents what Barnes and Benjamin called *quebecensis*.

Nominingue, Labelle, latitude 46° 23′ N., longitude 75° 02′ W., 835 feet above sea level, lies northeast of Ottawa in section 4 of the Great Lakes-St. Lawrence Forest, a mixed forest that was dominated by white pine, although this species is now found in reduced numbers. In most places balsam fir and white spruce are the dominant conifers mixed with many hard and soft deciduous trees. The area was glaciated and lies upon the Laurentian Shield of Archaic rocks. The mean annual temperature is about 38° F., and the mean annual precipitation is 33.9 inches. I have five males from here.

Lac Marois, Terrebonne, latitude 45° 51′ N., longitude 74° 08′ W., at about 1000 feet elevation, lies northwest of Montreal in section 4 of the Great Lakes-St. Lawrence Forest where there are numerous boreal species of trees mixed with the normal flora of this section (see Nominingue). The area was glaciated and lies upon the Laurentian Shield. There are no meteorological stations sufficiently close to this station to present firm data. The mean annual temperature probably lies between 36° F. and 40° F., and the mean annual precipitation between 33 and 35 inches. Four males and three females came from here.

Shawbridge, Terrebonne, latitude 45° 52′ N., longitude 74° 05′ W., at about 800 feet above sea level, is only a few miles from Lac Marois, and the conditions are much like those at that station. Shawbridge is probably a little warmer and there is less boreal character to the forest. I have 35 males and a female from this place.

Rawdon, Montcalm, latitude 46° 28′ N., longitude 73° 42′ W., altitude 404 feet, is

north of Montreal. The conditions are about the same as at Shawbridge. My series is composed of 19 males and six females.

Ontario

Ontario is the designation I have used for a series of specimens from the Parry Sound-Algonquin Park area. This is far from adequate material to represent the province. Short series from four localities that lie in essentially the same kind of country have been pooled for the data presented. The localities are:

	Latitude	Longitude	Elevation, in Feet
Algonquin Park	45° 33′ N.	78° 33′ W.	1350
Burke Falls	45° 37′ N.	79° 24′ W.	980
Kearney	45° 33′ N.	79° 13′ W.	1100
Sand Lake	45° 38′ N.	79° 10′ W.	about 1200

Algonquin Park is in Nippissing County; the other places are in Parry Sound County. All the stations lie in section 4 of the Great Lakes-St. Lawrence Forest. This is essentially a mixed forest with sugar maple, yellow birch, hemlock, and white pine the dominant trees. Halliday (1952, p. 31) neatly summarizes the geology of the region: " . . . the bedrock is part of the great Precambrian Shield of Canada, and consists largely of crystalline limestones (Grenville series), schists, and gneisses of the altered sedimentaries and granite intrusives. The topography is rough and irregular, and glacial deposits of varied character, chiefly of a somewhat light texture, cover the greater part." There are innumerable lakes throughout the region. Climatic data are available only for Algonquin Park. There the mean annual temperature is 38° F., and the annual precipitation about 31 inches. The vegetative season extends from May 2 to October 15, 166 days. The other stations probably are somewhat warmer and wetter, with a slightly longer vegetative season.

Manitoba

Behrens River, Springfield, latitude 52° 22′ N., longitude 97° 01′ W., 720 feet above sea level, is on the east shore of Lake Winnipeg a little north of the mid point in section 21 of the Boreal Forest, consisting of black spruce, white spruce, and some poplars and birches. The area was glaciated and lies on the Laurentian Shield. Twenty years of observation yield a mean annual temperaure of about 30° F. and 18.5 inches of precipitation. The vegetative season extends from April 29 to September 30, 154 days. Mr. Bruggemann measured a series of 34 males and 21 females for me which is in the Canadian National Collection. This is one of several possible type localities for Edwards' *inornata*.

Norway House, Nelson, latitude 53° 58′ N., longitude 97° 50′ W., 720 feet above sea level, is at the northeast end of Lake Winnipeg in section 21 of the Boreal Forest, which has fewer deciduous trees and more tamarack than at Behrens River. The area was glaciated and is on the Laurentian Shield. Forty years of observations yield an annual mean temperature of 29° F. and a mean annual precipitation of 15.6 inches. The vegetative season extends from May 12 to September 28, 138 days. A series of 12 males and one female in the Canadian National Collection was measured for me by Mr. Bruggemann. This is a likely place as the type locality of *inornata*.

The Pas, Nelson, latitude 53° 51′ N., longitude 101° 16′ W., 881 feet altitude, is on the Saskatchewan River in the lake and swamp area northwest of the head of Lake Winnipeg. It is in section B15 of the Boreal Forest, the Manitoba lowlands section. Around The Pas the dominant trees are black spruce, tamarack, and jack pines on the ridges. The soils are poorly developed from glacial tills and the sediments of old Lake Agassiz. The mean annual temperature is 31° F., and the mean annual precipitation is about 15.4 inches, based on 27 years of records. The vegetative season extends from about April 29 to October 3, 158 days. A series of 49 males and 15 females collected by Walter Krivda was studied. I received this material too late to include its statistics in the main tables; they will be found in table 21.

Northwest Territories

Most of the material that I have seen from this area is either *mixturata* or *mackenziei*. Two series, noted below, seem better considered *inornata*.

Fort Simpson, latitude 61° 52′ N., longitude 121° 13′ W., 572 feet altitude, is at the

TABLE 7

RADIUS OF LEFT FOREWING IN MILLIMETERS

Station	Males				Females			
	n	Mean	*S.D.*	*V*	*n*	Mean	*S.D.*	*V*
All Quebec	66	17.60	0.62	3.5	10	17.67	0.63	3.6
All Ontario	9	17.10	0.82	4.8	6	17.28	0.77	4.5
Behrens River, Man.	34	17.31	0.82	4.7	21	18.01	0.36	2.0
Norway House, Man.	12	16.86	0.75	4.4	1	18.30	—	—
Hay River, N.W.T.	15	17.23	0.76	4.4	1	17.50	—	—
Fort Simpson, N.W.T.	4	17.37	0.45	2.6	5	18.20	0.58	3.2

junction of the Liard and Mackenzie rivers. It is in section 23 of the Boreal Forest, primarily white spruce with some stands of various *Populus*. The area was glaciated. The mean annual temperature is 24° F., and the mean annual precipitation 13.0 inches, based upon 42 years of record. The vegetative season extends from May 20 to September 20, 123 days. A series of four males and five females in the Canadian National Collection was measured by Mr. Bruggemann.

Hay River, McKenzie, latitude 60° 51′ N., longitude 115° 46′ W., 529 feet above sea level, is situated on the south shore of Great Slave Lake in section 23 of the Boreal Forest (see Fort Simpson). The area was glaciated. Forty-five years of observation yield annual means of 24° F. and 11.8 inches of precipitation. The vegetative season extends from May 24 to September 21, 120 days. Fifteen males and one female in the Canadian National Collection were measured for me by Mr. Bruggemann.

VARIATION IN SIZE

When the variety of environments from which the series studied were drawn is considered *inornata* is unusually constant in size. The subspecies averages significantly smaller than *nipisiquit* and probably larger than *mcisaaci*. It does not differ materially from *benjamini*. (Table 7.)

VARIATION IN COLOR

There seems to be more variation in color in *inornata* than among the specimens of any other of the subspecies. This is understandable if color, as I am convinced, is a response more to humidity than to genetic combinations. *Inornata* is definitely lighter colored than either *mcisaaci* or *nipisiquit* and slightly darker than *benjamini*. There is, however, a broad zone of intergradation between *inornata* and *benjamini*. This is the prairie grove region, where the transition from one to the other takes place so subtly that no line of demarcation is evident. As is true throughout *tullia inornata*, the females are noticeably lighter than the males, although there is an overlapping of extremely light males and extremely dark females.

VARIATION IN OCELLUS ON UPPER SIDE OF FOREWING

Edwards' types are described with "no spots above or below" (see p. 377). Although such specimens are known from the Lake Winnipeg region, they definitely are in the minority. In fact Edwards' description now fits material from Quebec far better than it does the known series from the type region. It is possible that Kennicott happened upon a small immaculate colony. I think it more likely that recent series have been collected in cut or burned-over areas where the species is more or less common rather than in natural grassy glades in the spruce forest as was likely of Kennicott's collecting. I believe that this is an instance where modern material from the type locality may be misleading.

There is a very marked difference between my Quebec samples and samples from Manitoba. The difference is highly significant and the likelihood that it is due to sampling error is so small that it can be ignored. The less disturbed forests of the Northwest Territory harbor *inornata* that are not significantly different from the Quebec series in this char-

TABLE 8

PRESENCE OF BLACK POINTS OR TRACES OF OCELLI ON UPPER FOREWING

(Figures in italics not significant at the 1 per cent level of confidence.)

Station	Males			Females		
	n	%	*S.E.*	*n*	%	*S.E.*
All Quebec	66	*6.1*	*± 2.9*	11	63.7	±14.5
All Ontario	9	None		6	*50.0*	*±20.4*
Behrens River	34	55.8	± 8.5	21	81.0	± 8.6
Norway House	12	58.3	±14.3	1	None	
Hay River	15	*20.0*	*±10.3*	1	None	
Fort Simpson	4	75.0	±21.6	5	60.0	±21.8
Manitoba and N.W.T.	65	49.3	± 6.2	28	71.5	± 8.5

acter. The Hay River sample represents such a population. (Table 8.)

VARIATION IN OCELLUS ON UNDER SIDE OF FOREWING

Although the difference between the Quebec sample and samples from the western periphery of the range of *inornata* is not so marked on the under side as on the upper, it nevertheless is, or approaches being, significant. On this surface the marks are true ocelli in the majority of cases, whereas on the upper side they are merely traces—a small cluster of black scales. (Table 9.)

TABLE 9

PRESENCE OF OCELLUS OR TRACES ON UNDER FOREWING

Station	Males			Females		
	n	%	*S.E.*	*n*	%	*S.E.*
All Quebec	66	54.6	± 6.2	11	72.7	±13.5
All Ontario	9	44.4	±16.5	6	83.3	±15.2
Behrens River	34	88.2	± 5.5	21	85.6	± 7.7
Norway House	12	75.0	±12.4	1	None	
Hay River	15	86.5	± 9.1	1	None	
Fort Simpson	4	100.0		5	100.0	
Manitoba and N.W.T.	65	86.2	± 4.3	28	82.1	± 7.3

TABLE 10

LENGTH OF RAY ON UNDER SIDE OF FOREWING

(Figures in italics not significant at the 1 per cent level of confidence.)

Station	Males						Females			
	To M_3		To Cu_1		To Cu_2		To Cu_1		To Cu_2	
	%	*S.E.*	%	*S.E.*	%	*S.E.*	%	*S.E.*	%	*S.E.*
All Quebec	None		13.6	± 4.2	86.4	± 4.2	*20.0*	*±12.6*	80.0	±12.6
All Ontario	None		*11.1*	*±10.5*	88.9	±10.5	None		100.0	
Behrens River	None		70.6	± 7.8	29.4	± 7.8	90.5	± 6.4	*9.5*	*± 6.4*
Norway House	*8.3*	*±7.9*	83.4	±10.8	*8.3*	*± 7.9*	Yes		—	
Hay River	*6.7*	*±6.5*	53.3	±12.9	40.0	±12.7	—		Yes	
Fort Simpson	None		*50.0*	*±25.0*	*50.0*	*±25.0*	*20.0*	*±17.9*	80.0	±17.9

TABLE 11

CONDITION OF RAY ON UNDER SIDE OF HIND WING

(Figures in italics not significant at the 1 per cent level of confidence.)

Station	Complete[a] % S.E.	Broken[b] % S.E.	M_3[c] % S.E.	Fragmentary[d] % S.E.	Absent
MALES					
All Quebec	10.6± 3.8	63.6± 5.9	22.8± 5.2	*3.0± 2.1*	None
All Ontario	*11.1±10.5*	66.7±15.7	*11.1±10.5*	*11.1±10.5*	None
Behrens River	17.6± 6.5	61.8± 8.3	*11.8± 5.5*	*8.8± 4.9*	None
Norway House	*25.0±12.4*	58.3±14.3	*8.3± 7.9*	*8.3± 7.9*	None
Hay River	*26.6±11.4*	73.4±11.4	None	None	None
Fort Simpson	None	100.0	None	None	None
FEMALES					
All Quebec	60.0±15.0	40.0±15.0	None	None	None
All Ontario	None	100.0	None	None	None
Behrens River	*23.8± 9.3*	42.8±10.3	28.6± 9.8	*4.8± 4.7*	None
Norway House	No	Yes	No	No	No
Hay River	Yes	No	No	No	No
Fort Simpson	60.0±21.8	*40.0±21.8*	None	None	None

[a] A recognizable band of light scales from the costal to the inner margin of the wing.
[b] Those specimens on which the irregular band is complete anterior to the cell but interrupted posterior to it.
[c] Those specimens on which the band is complete anterior to the cell but absent posterior to it.
[d] Individuals on which the band is represented by a spot on the costa, another at the end of the cell, and a third at the inner margin.

VARIATION IN RAY ON UNDER SIDE OF FOREWING

This mark is well developed on *inornata* in contrast to its weak development on *mcisaaci*. Although all the mainland material seems to bear well-developed rays, there is a noticeable difference in the extent of the ray. Very few *inornata* and *nipisiquit* show "short" rays, that is, rays that do not extend beyond M_3. On the other hand the prairie subspecies, *benjamini*, often bears a short ray. In this character there is little difference between eastern and western *inornata*. There is a tendency for the eastern populations to bear rays that terminate at or near Cu_2, while the western insects more frequently have a ray that terminates near Cu_1.

In table 10 I have omitted the category "absent" from the tabulation of the males and "absent" and "M_3" from that of the females, because these categories were not represented in the material studied.

VARIATION IN RAY ON UNDER SIDE OF HIND WING

Edwards, in his original description described this as a "transverse, tortuous, interrupted ray." Such definition states the condition commonly found. The ray on *inornata* and on *nipisiquit* is much the same. On the other hand that found on *mcisaaci* is more like the one found on *benjamini* except that on the former subspecies it is less well defined. Very few males of *inornata* show a break in the ray anterior to M_3. I have seen two females with such a break, but my sample of this sex is small. What material I have seen tends to indicate that the ray is better developed and less frequently interrupted on the females than on the males throughout the species. (Table 11.)

VARIATION IN SUBMARGIN ON UNDER SIDE OF HIND WING

Edwards' types of *inornata* bore no ocelli in the submargin on the under side of the hind wings. This condition is almost universal among specimens collected in Quebec. Ocelli or traces of them are found on specimens from both Fort Alexander and Behrens River on the east shore of Lake Winnipeg but not on those from Norway House. West of Lake Winnipeg ocelli occur on specimens in every series seen. I believe this is evidence

TABLE 12

MARKINGS IN SUBMARGIN ON UNDER SIDE OF HIND WINGS

(Figures in italics not significant at the 1 per cent level of confidence.)

Station	Dark Chevron % S.E.	Light Patch % S.E.	Both % S.E.	None % S.E.	"Ocelli" % S.E.
MALES					
All Quebec	10.6± 3.8	40.9± 6.1	*1.5± 1.5*	48.5± 6.1	None
All Ontario	None	77.8±13.9	None	*22.2±13.9*	None
Behrens River	73.5± 7.6	61.8± 8.3	35.3± 7.6	None	26.4± 7.6
Norway House	41.6±14.2	91.6± 8.0	41.6±14.2	*8.4± 7.9*	None
Hay River	33.3±12.2	60.0±12.7	*20.0±10.3*	*26.6±11.4*	*13.3± 8.8*
Fort Simpson	*25.0±21.6*	None	None	75.0±21.6	*25.0±21.6*
FEMALES					
All Quebec	None	80.0±12.6	None	*20.0±12.6*	None
All Ontario	None	100.0	None	None	None
Behrens River	*19.0± 8.6*	81.0± 8.6	*14.3± 7.6*	*14.3± 7.6*	28.6± 9.8
Norway House	No	Yes	No	No	No
Hay River	No	Yes	No	No	No
Fort Simpson	*20.0±17.9*	*20.0±17.9*	No	60.0±21.8	No

that Rocky Mountain *tullia ochracea* mixes with *tullia inornata*. The subspecies *inornata benjamini* show this strongly.

The dark chevrons and light patches that are found in this zone are much more frequent on *inornata* and *nipisiquit* than on *mcisaaci* and *benjamini*. They seem to be a very definite part of the pattern of Manitoba specimens, much more so than of material from Quebec. Edwards made no mention of them in his description of *inornata*. They are very rare, often totally lacking, from series collected in the Rocky Mountains. (Table 12.)

VARIATION IN BASAL LIGHT PATCHES ON UNDER SIDE OF HIND WINGS

The two basal light patches at the base of the hind wing on the under side, so characteristic of *tullia ochracea*, are not mentioned by Edwards in his description of *inornata*. They are mentioned in his description of *ochracea* described at the same time from "Lake Winnipeg; Kansas; California." Only *inornata benjamini* shows traces of these patches and then only among series collected in the southern part of the range of the insect.

SUMMARY

Summing up what I have found about *inornata inornata*, the insect is fairly constant in the central portion of its range where specimens agree with Edwards' description. Towards the extreme east, a region from which I have seen far too few specimens, there seems to be integradation to the maritime subspecies *mcisaaci*. To the southwest *inornata* intergrades to *benjamini* so perfectly that no sharp line of demarcation can be drawn. In this region the spruce forests that grow upon the Laurentian Shield harbor *inornata inornata* so long as the virgin timber is undisturbed. In areas where there has been extensive cutting or fire, the prairie form, *benjamini*, tends to invade and intermingle with *inornata*, probably producing a hybrid population.

The material collected by Kennicott and described by Edwards came from the shores of Lake Winnipeg. At the time Kennicott collected, the route to Norway House was up the east shore. There is no evidence that Kennicott traveled from Fort Alexander to Winnipeg on this trip, but instead he moved up the east shore, possibly stopping at Behrens River. The material found today at Behrens River does not agree sufficiently with Edwards' description for that post to be designated as the type locality. What the conditions were in Kennicott's day I do not know with any degree of certainty. The re-

gion may have been inhabited by *inornata* of great purity. Today the region on the east shore of Lake Winnipeg from which material has come that compares very favorably with Edwards' description is Norway House. I propose that, until proved wrong, this be considered the type locality of Edwards' *Coenonympha inornata.*

The salient characteristics of *inornata inornata* are: males perceptibly darker than females, absence of ocelli on the under side of the hind wings, absence of basal light marks on the under side of the hind wings, ray on the under side of the forewing generally extending to Cu_1 or Cu_2, ray on the under side of the hind wing rarely broken anterior to M_3. It must be understood that these hold true only in the case of series. Individual specimens may differ materially from the average condition.

One of the series studied in detail is so different from all the others that it is worth commenting on in detail. This is the material collected by Krivda at The Pas, Manitoba. Although I include it in *inornata inornata*, the series contains specimens that individually are little different from three recognized entities: *inornata*, *benjamini* and *mackenziei* Davenport. The last-named I do not include in the *tullia inornata* complex; it is more likely a member of the *tullia ochracea* complex. I am sure that as the forested area across Canada north of the prairies is searched and collections are made in it, additional complex populations will be found.

The color of these insects tends to be about intermediate to that of *inornata* and *benjamini*. On the under side of the forewings are a surprising number of secondary ocelli in the cubital region. On 18.3 per cent of the males and 20.0 per cent of the females at least traces of one and sometimes of two cubital ocelli are found. Cubital ocelli are not uncommon on specimens of certain strains of *ochracea* and *mackenziei*, but they are very rare indeed among *inornata*. The rays on the under side of both wings are quite variable. On many specimens the ray on the forewing is very broad, like that found on *mackenziei*. On the hind wings the condition of the ray is about normal for *inornata* on the males, but on the females it is complete on 80 per cent, a condition more akin to that found among *ochracea*.

The most striking anomaly in the series studied is found in the light basal patches on the under side of the hind wings. These patches appear on 16.3 per cent of the males and 13.3 per cent of the females. Such a condition is strange to *tullia inornata*. Among hundreds of other Canadian specimens that have been studied critically, only two females from Transcona and four scattered males showed the slightest traces of these marks. On four of the males from The Pas these patches are like those found on *ochracea*, but they are obscured by dark scales. The two females with patches have them as in these males. The other four males that bear patches have them large and free of overscaling. On these the posterior patch is so large that it joins with the light irregular ray across the middle of the wing. This condition is typical of *mackenziei*.

COENONYMPHA INORNATA BENJAMINI MCDUNNOUGH

Coenonympha inornata benjamini McDUNNOUGH, 1928, Canadian Ent., vol. 60, p. 272.

TYPE LOCALITY: Waterton Lakes, Alberta.

COLLECTOR OF TYPE: J. McDunnough.

LOCATION OF TYPE: Canadian National Collection, Ottawa, Ontario, Canada.

ORIGINAL DESCRIPTION: "In the prairie region, extending from southern Manitoba to the foothills of the Rocky Mountains, we meet with a somewhat modified race which has very generally been mistaken for *inornata*. In contradistinction to the typical subspecies, however, this race has normally a well-developed ocellus on the underside of primaries apically, consisting of a round black spot with pale centre, surrounded by a ring of pale ochreous; specimens with reduced or even obsolete ocellus do occasionally occur but are distinctly the exception rather than the rule; other specimens show traces of a weak submarginal row of ocelli on the underside of secondaries and very rarely there is a second ocellus on the primaries. The underside of secondaries is somewhat deeper greenish and the basal half shows decidedly more brown tinges than in the type form whilst on the upper side the pale suffusion along the outer margin is practically absent. Skinner's figures of males from Minneapolis, Minn. (Trans. Am. Ent. Soc., XXVI, Pl. VII, figs. 10, 11) evidently represent this race, although in fig. 11 the ocellus is smaller than normal. It was also this race to which I erroneously (1916, Contr. Nat. Hist. Lep. III (2) 71) applied the name *inornata*, having no knowledge at the time of Eastern Canadian specimens, and Benjamin has evidently fallen into the same error.

"I propose the name *BENJAMINI* for this prairie race of *inornata*, with following types:

"*Holotype.*—♂, Waterton Lakes, Alta., June 28, (J. McDunnough), No. 2888 in the Canadian National Collection, Ottawa.

"*Allotype.*—♀, same locality, July 1.

"*Paratypes.*—6♂ 4♀, same locality and collector, June 28, 30, July, 1, 6, 8, 10."

RANGE: The prairie areas and adjacent aspen grove region of south central Canada and north central United States as far south as South Dakota.

BIONOMICS: So far as I know, no one has studied the life history of this subspecies. I suspect that it will be found to be identical with that of *inornata inornata*.

ECOLOGY AND HABITS: Mr. C. S. Quelch of Transcona, Manitoba, has written to me at some length about conditions at his collecting points for this subspecies. "Transcona is a town seven miles east of Winnipeg and on the border line between the prairies and the bush country and rock of the Canadian Shield. The latter begins about 50 miles east of us. Around Transcona is flat country with scattered bluffs of poplar and willow. I would say typical prairie country. Birds Hill, four miles east, is a gravel ridge covered with poplar, oak, willow and an odd spruce. Matlock Beach is on the southeast shore of Lake Winnipeg, 45 miles north of Winnipeg and in the beginning of the northern bush country. There is quite a sprinkling of spruce though it is not really in the spruce belt. Birtle is a town in the valley of the Birdtail River in typical prairie country 200 miles west of Winnipeg near the Saskatchewan border" (*in. litt.*, November 18, 1949).

Paul Bruggemann and Richard Fitch, who have collected extensively in the northern parts of Saskatchewan and Alberta near the boundary between the two provinces, from Lloydminster north to the Saskatchewan River, agree about the habitat of *benjamini* in their area. It flies in the dry grasslands that are associated with the prairie groves of aspen and scattered spruce.

Kenneth Bowman, the veteran collector of Alberta butterflies, wrote to me, "I have taken it (*benjamini*) all over the mountains and also in the prairies and after submitting my specimens to Dr. McDunnough, they all came back '*benjamini*'" (*in litt.*, January 26, 1950).

My own experience in the Calgary-Banff area was that *benjamini* flew in the grassy areas where there was sufficient moisture to support a stand of aspen but not out on the true grasslands. However, my collecting experience in this area was not sufficiently long to exclude the true grasslands as a habitat for the insect.

Julius Adler has collected the insects ex-

tensively at Grand Forks, North Dakota, where he finds them in the grasslands associated with gullies and the more moist patches. Neil Euting found the insect in eastern Montana in similar locations. In western Montana I collected the insect near St. Mary's Lake associated with the aspen grove in open fields. This country is like that from which McDunnough described the subspecies.

The southernmost colonies of *inornata* are those found in the Black Hills of South Dakota. In the vicinity of Custer I found the butterflies rather common in dry grassy glades among old stands of Ponderosa pine.

The above notes may be summarized: *benjamini* is associated with the dry grasslands of the prairie provinces and states, being most abundant where there is sufficient moisture to support local stands of *Populus* or, in the southwestern extreme of the range, *Pinus ponderosa*.

The region where *benjamini* is at home is the northern Great Plains. It is a much warmer and drier habitat than that of *inornata inornata*. By far the greatest area of it is true grasslands. Along the permanent streams that cross this vast land there are narrow gallery forests of willows and poplars. Around the periphery, except to the south, is a zone of prairie groves—clusters of deciduous trees that have found a soil that is a little more moist than the average. In this zone and in the gallery forests *benjamini* is most at home.

North and east of the Missouri River the land was covered by ice during the Wisconsin age. The continental ice sheet extended westward to, or almost to, the alpine glaciers that poured forth from the valleys of the Rocky Mountains. It is very doubtful that any of the territory now held by the subspecies was habitable by it during those cold millenia. It, like the more eastern subspecies, must have passed the glacial stage far to the south. I feel confident that the Wisconsin period was spent by *benjamini* south of the Platte River. There are clues to this in the variation of the easternmost colonies of *tullia ochracea* in Colorado.

On the long northward journey that followed the retreat of the ice sheet, *benjamini* left an isolated colony in the Black Hills of South Dakota. This is now cut off from other *inornata* colonies by a broad expanse of badlands in which the species is not found. It appears likely that other such colonies were established in propitious spots in South and North Dakota. There is no evidence of such colonies in Wyoming. If they ever were established there, they have been lost, pushed out of existence by eastward-moving masses of the Great Basin strain of *tullia ochracea*. These now populate the Laramie and the Bighorn Mountains.

Within the northern Great Plains are several low mountains or ranges. The Riding Mountains in Manitoba, Turtle Mountain on the border between North Dakota and Saskatchewan, and the small knots of mountains that are scattered through southeastern Montana are examples. The very few specimens of *benjamini* that I have seen from these uplifted areas are all rather poor examples. It would be rewarding to collect in these areas and to study the changes that appear to have occurred in *tullia inornata*.

VARIATION

The prairie subspecies of *inornata* is much more variable than either the woodland or maritime subspecies. There probably are two different reasons for this increased variation. First, the subspecies has been sampled over a much larger area than any of the other subspecies, and the climatic and geographic variation of the region thus sampled is much greater than that of the regions sampled for the other subspecies. Second, the western periphery of the range of *benjamini* abuts the range of *tullia ochracea*, and it seems likely that occasional viable hybrids are formed that introduce into the *inornata* subspecies genes from the Rocky Mountain moiety. In fact it is my belief that *benjamini* originated through such introduction of genes, for ocelli on the under side of the hind wings and the other less evident characters of the *ochracea* moiety that crop out in *benjamini* throughout its range.

The series selected for detailed study fairly well encircle the range of the insect. I had hoped to find a long series of both sexes from somewhere in south central Saskatchewan to form the hub of this series but was not successful. One hundred and seventy-eight males

and 55 females were measured by me, and 15 specimens were measured by Ralph Chermock.

Transcona, St. Boniface, Manitoba, latitude 49° 51′ N., longitude 97° 00′ W., 780 feet above sea level, is a few miles east of Winnipeg. It lies in section 16 of the Boreal Forest, where the forest meets the grasslands. There are scattered groves of aspen and oak, with a rare spruce here and there. The area has been glaciated. I have no climatological data for Transcona, but a 66-year record for Winnipeg yields means of 35° F. in temperature and 21.2 inches of precipitation. The vegetative season extends from April 26 to October 11, 168 days. Mr. C. S. Quelch very kindly supplied me with a series of 26 males and 13 females from this station.

Lloydminster, South Battleford, Saskatchewan, latitude 53° 17′ N., longitude 110° 00′ W., about 2100 feet above sea level, lies astride the Alberta-Saskatchewan boundary. It is situated in section 17 of the Boreal Forest where aspen groves are scattered through the grasslands. The area was glaciated. Meteorological records over 28 years yield a mean annual temperature of about 33° F. Precipitation records are available only from April through October. On the basis of these and complete data from neighboring stations I estimate that the annual precipitation averages about 10 inches. The vegetative season extends from April 29 to October 1, 126 days. Mr. R. J. Fitch supplied me with 41 males and 14 females from this general region.

Wimborne, Red Deer, Alberta, latitude 51° 53′ N., longitude 113° 36′ W., about 3100 feet above sea level, is located on a tributary of the Red River about 20 miles southeast of Innisfal. It is at the southern edge of section 17 of the Boreal Forest where there are a few aspen groves scattered through the grasslands. A series of 15 specimens in the collection of Ralph Chermock were reported to me by him.

The Alberta series studied in the Canadian National Collection is composed of short series from the entire province. None of these series is really long enough to stand alone, so I pooled the data for a single entry in the tables. The stations from which three or more specimens were examined in detail are noted here. Most of them lie in the grasslands. Edmonton is within the Boreal Forest in an island of section 17 surrounded by section 18. Waterton Lakes is at the grasslands edge of the Douglas fir and lodgepole pine division of the Montane Forest.

	North Latitude	West Longitude	Altitude, in Feet
Waterton Lakes	*ca.* 49° 05′	113° 50′	*ca.* 5000
Medicine Hat	49° 27′	110° 48′	2929
Lethbridge	49° 42′	112° 50′	2983
Orion	50° 02′	110° 42′	2181
Gleichen	50° 52′	113° 02′	2961
Calgary	51° 03′	114° 03′	3500
Edmonton	53° 33′	113° 30′	2150

The mean annual temperature for these stations ranges from about 38° F. to about 42° F., and the annual precipitation is from about 13 inches to 18 inches. As the temperature lowers, northward, the precipitation tends to increase. The vegetative season ranges from 164 to 191 days, the shortest occurring at Edmonton and the longest at Medicine Hat.

St. Mary's Lake, Glacier, Montana, latitude 48° 45′ N., longitude 113° 28′ W., about 4500 feet above sea level, is just outside Glacier National Park. The material was collected in open fields among aspen groves that had developed on cut-over land. The true boundary of the Montane Forest lies a short distance to the east. I found no specimens in the forest, section 5, where Douglas fir and lodgepole pine are dominant. The area does not appear to have been under the Pleistocene ice but very near to it. It is possible that early Pleistocene alpine glaciers did cover the ground but that the evidence has been washed away by Wisconsin fluvio-glacial floods. Meteorological data from St. Mary's Lake are scant, consisting of only a few broken records of precipitation from 1913 to 1918. A few miles to the north and in essentially similar country is Babs, from which there are better records. There the mean annual temperature is about 30° F. and the annual precipitation averages 19.5 inches. The fragmentary St. Mary's Lake record suggests that the precipitation is a little higher than at Babs, and the location sug-

gests that the temperature is a little lower. At Babs the vegetative season extends from May 4 to October 11, 160 days. My short series, 10 males and three females, were compared with the types of *benjamini* by Demorest Daveport who considered them to be as nearly identical as possible.[1]

Eastern Montana is the designation I have given to two short series I have pooled for the statistical data here presented. These series came from the following places:

Big Sandy, Chouteau, Montana, latitude 48° 11′ N., longitude 110° 07′ W., at about 2700 feet above sea level, is in the short-grass prairie. The area is near the limit of continental ice and probably was glaciated. The mean annual temperature is 42° F. (eight years' record) and the precipitation is 11.5 inches (10 years' broken record). The vegetative season extends from April 15 to October 11, 179 days. Five males and three females from this place were lent to me by Mr. Neil Euting.

Poplar, Roosevelt, Montana, latitude 48° 07′ N., longitude 105° 03′ W., about 2000 feet above sea level, is in country just about like that at Big Sandy. A 44-year meteorological record yields means of about 41° F. in temperature and 13.0 inches of precipitation. The vegetative season extends from April 14 to October 18, 187 days. Mr. Euting lent me a pair from here.

Grand Forks, Grand Forks, North Dakota, latitude 47° 57′ N., longitude 97° 04′ W., about 830 feet above sea level, lies in the deep-grass prairie on glaciated terrain where Julius Adler collected the insect in moist habitats. The mean annual temperature is 38° F., and the annual precipitation averages 19 inches. The vegetative season extends from April to October 14, 179 days. Mr. Adler lent me a series of 27 males and six females.

Custer, Custer, South Dakota, latitude 43° 46′ N., longitude 103° 36′ N., is about 5300 feet above sea level in the Black Hills. There I found the subspecies common in dry grassy glades in the open stands of old Ponderosa pines. The mean annual temperaure is about 42° F., and the mean annual precipitation 19 inches. The vegetative season extends from April 23 to October 13, 173 days. The temperature data were supplied by the United States Forst Service. I have 10 males and five females from Custer.

[1] The type locality for *benjamini* lies in essentially the same kind of country a few miles north of the United States-Canada border. McDunnough's description of the type locality is identical with the terrain in which I collected the St. Mary's Lake series.

Variation in Size

There is no real significance to the differences found in size among the series studied. The difference between the females from Transcona and those from Grand Forks approaches statistical significance at the 1 per cent level, but the series measured are so small that the data are not trustworthy. (Table 13.)

The greater variability of the males from Lloydminster and from Grand Forks and the females from Lloydminster may indicate hybridization with *inornata inornata*. The high degree of variability among the five females from Custer may be an illusion, or it may

TABLE 13

Radius of Left Forewing in Millimeters

Station	Males				Females			
	n	Mean	*S.D.*	*V*	*n*	Mean	*S.D.*	*V*
Transcona, Man.	26	17.20	0.67	3.8	13	17.07	0.56	3.3
Lloydminster, Sask.	41	17.25	0.88	5.1	14	17.64	0.88	5.0
All Alberta	58	17.49	0.77	4.4	10	17.87	0.77	4.3
St. Mary's Lake, Mont.	10	17.37	0.65	3.7	3	17.97	—	—
Eastern Montana	6	16.99	0.65	3.8	4	17.75	—	—
Grand Forks, N.D.	27	17.74	1.04	5.9	6	18.22	0.48	2.6
Custer, S.D.	10	18.07	0.64	3.5	5	17.78	1.09	6.1

TABLE 14

PRESENCE OF OCELLUS OR TRACES ON UPPER SIDE OF FOREWING

(Figures in italics not significant at the 1 per cent level of confidence.)

Station	Males			Females		
	n	%	*S.E.*	*n*	%	*S.E.*
Transcona, Man.	26	57.7	± 9.7	13	84.6	±10.0
Lloydminster, Sask.	41	65.7	± 7.5	14	78.6	±10.9
Wimborne, Alta.[a]	15	73.3	±11.4		—	
All Alberta	58	76.0	± 5.8	10	100.0	
St. Mary's Lake, Mont.	10	40.0	±15.5	3	*33.3*	*±27.2*
Eastern Montana	6	*33.3*	*±19.3*	4	*50.0*	*±50.0*
Grand Forks, N.D.	27	59.2	± 9.5	6	66.7	±19.3
Custer, S.D.	10	70.0	±14.5	5	*40.0*	*±21.9*

[a] The Wimborne series was not sexed, but probably the majority are males.

indicate hybridization with *tullia ochracea*. The normal variability of the males from this station contra-indicate the latter suggestion.

VARIATION IN COLOR

The characteristic sexual color difference normal to *tullia inornata* is present in *benjamini*. There is only a slight overlap of the darkest females and lightest males. The males of *benjamini* are consistently darker than the darkest males of *tullia ochracea*. The females compare well with the males of eastern strains of the latter. Both males and females of *benjamini* tend to be lighter in color than those of *inornata inornata*. This is particularly true of material that comes from the southern and central parts of the range of *benjamini*.

VARIATION IN OCELLUS ON UPPER SIDE OF FOREWING

McDunnough, in his description of this subspecies, stresses the occurrence of an apical ocellus on the under side of the forewings as a mark of distinction from *inornata inornata*. Equally distinctive is the frequency with which this ocellus is found on the upper side. In this respect *benjamini* resembles the *ochracea* moiety more than it does the *inornata*. This mark of *benjamini*, although frequently present, is often not a well-developed ocellus but merely a cluster of black scales. *Inornata inornata* from the western periphery of its range cannot be separated from *inornata benjamini* on the basis of the statistics of this spot. They can be separated by means of the size of the spot, it being larger on *benjamini*. (Table 14.)

VARIATION IN OCELLUS ON UNDER SIDE OF FOREWING

As is said above, this is one of the marks by which McDunnough proposed to separate *inornata inornata* from *inornata benjamini*. Table 9 in the section devoted to *inornata inornata* shows that the ocellus is present at least half of the time, even on Quebec specimens. McDunnough's subspecies does differ, however, in this respect: the ocellus is rarely absent on *benjamini*. I have seen only two such specimens among more than 200 that were carefully studied. These came from Grand Forks where I suspect there is hybridization between *inornata* and *benjamini*. For this station the frequency for the ocellus on the males is 92.5 ± 5.1 per cent, which is not significantly different from 100 per cent. In all other cases studied every specimen, male or female, bore this mark.

VARIATION IN RAY ON UNDER SIDE OF FOREWING

This mark is very much like that on *inornata inornata*. There is a definite difference between specimens from Quebec and those from Manitoba, whether they be called *inornata* or *benjamini*. The difference between western *inornata* and eastern *benjamini* is of no significance. While this ray was found on all *inornata inornata* examined critically it is

TABLE 15

LENGTH OF RAY ON UNDER SIDE OF FOREWING

(Figures in italics not significant at the 1 per cent level of confidence.)

Station	n	Absent %	Absent S.E.	M_3 %	M_3 S.E.	Cu_1 %	Cu_1 S.E.	Cu_2 %	Cu_2 S.E.
MALES									
Transcona, Man.	26	*3.8*	*3.7*	*15.4*	*7.1*	65.4	9.3	*15.4*	*7.1*
Lloydminster, Sask.	41	*12.2*	*5.1*	*19.2*	*6.2*	34.2	7.4	34.2	7.4
All Alberta	58	*1.8*	*1.8*	*3.7*	*2.6*	24.1	5.8	70.3	6.2
St. Mary's Lake, Mont.	10	*30.0*	*14.5*	*20.0*	*12.6*	50.0	15.8	None	
Eastern Montana	6	*16.7*	*15.2*	None		*16.7*	*15.2*	66.7	19.3
Grand Forks, N.D.	27	None		22.2	8.0	44.5	9.6	33.3	9.1
Custer, S.D.	10	None		*10.0*	*9.5*	40.0	15.8	50.0	15.8
MALES AND FEMALES									
Wimborne, Alta.	15	None		*26.7*	*11.4*	33.3	12.2	40.0	12.7
FEMALES									
Transcona, Man.	13	None		*7.8*	*7.4*	69.2	12.8	*23.1*	*11.4*
Lloydminster, Sask.	14	None		*7.2*	*6.9*	57.2	13.2	35.7	12.8
All Alberta	10	None		None		40.0	15.5	60.0	15.5
St. Mary's Lake, Mont.	3	None		*33.3*	*27.2*	*33.3*	*27.2*	*33.3*	*27.2*
Eastern Montana	4	None		None		*25.0*	*20.2*	75.0	20.2
Grand Forks, N.D.	6	None		None		66.7	19.3	*33.3*	*19.3*
Custer, S.D.	5	*20.0*	*17.9*	None		None		80.0	17.9

TABLE 16

CONDITION OF RAY ON UNDER SIDE OF HIND WING

(Figures in italics not significant at the 1 per cent level of confidence.)

Station	n	Complete[a] %	Complete[a] S.E.	Broken[b] %	Broken[b] S.E.	M_3[c] %	M_3[c] S.E.	Fragmentary[d] %	Fragmentary[d] S.E.	Absent %	Absent S.E.
MALES											
Transcona	26	30.8	9.0	*15.4*	*7.1*	30.8	9.0	*11.5*	*6.2*	*11.5*	*6.2*
Lloydminster	41	19.5	6.2	17.1	5.9	26.8	7.0	17.1	5.9	19.5	6.2
All Alberta	58	17.3	5.0	31.1	6.1	10.3	4.0	32.8	6.2	*8.6*	*3.7*
St. Mary's Lake	10	None		None		*20.0*	*12.6*	70.0	14.5	*10.0*	*9.5*
Eastern Montana	6	None		*16.7*	*15.2*	*33.3*	*19.3*	*50.0*	*20.4*	None	
Grand Forks	27	*7.4*	*5.1*	*18.5*	*7.5*	22.2	8.0	51.9	9.5	None	
Custer	10	*30.0*	*14.5*	*20.0*	*12.6*	*20.0*	*12.6*	*30.0*	*14.5*	None	
MALES AND FEMALES											
Wimborne	15	None		40.0	12.7	*6.7*	*6.5*	33.3	12.2	*20.0*	*10.3*
FEMALES											
Transcona	13	*23.1*	*11.4*	61.5	13.5	*15.4*	*10.0*	None		None	
Lloydminster	14	*21.4*	*10.9*	42.8	13.2	None		*28.6*	*12.1*	*7.2*	*6.9*
All Alberta	10	*30.0*	*14.5*	*30.0*	*14.5*	*10.0*	*9.5*	*30.0*	*14.5*	None	
St. Mary's Lake	3	None		67.7	27.2	33.3	27.2	None		None	
Eastern Montana	4	*50.0*	*50.0*	*50.0*	*50.0*	None		None		None	
Grand Forks	6	*16.7*	*15.2*	*33.3*	*19.3*	*16.7*	*15.2*	*33.3*	*19.3*	None	
Custer	5	*40.0*	*21.9*	None		*20.0*	*17.9*	*40.0*	*21.9*		

[a] A recognizable band of light scales from the costal to the inner margin of the wing.

[b] Those specimens on which the irregular band is complete anterior to the cell but interrupted posterior to it.

[c] Those specimens on which the band is complete anterior to the cell but absent posterior to it.

[d] Individuals on which the band is represented by a spot on the costa, another at the end of the cell, and a third at the inner margin.

TABLE 17

MARKINGS IN SUBMARGIN ON UNDER SIDE OF HIND WINGS

(Figures in italics not significant at the 1 per cent level of confidence.)

Station	*n*	Dark Chevron % *S.E.*	Light Patch % *S.E.*	None % *S.E.*	"Ocelli" % *S.E.*
MALES					
Transcona	26	30.8± 9.0	None	69.2± 9.0	*15.4± 7.1*
Lloydminster	41	19.5± 6.2	*2.4±2.4*	79.1± 6.3	36.6± 7.5
All Alberta	58	41.3± 6.4	None	58.7± 6.4	50.9± 6.6
St. Mary's Lake	10	None	None	100.0	40.0±15.5
Eastern Montana	6	66.7±19.3	None	*33.3±19.3*	*50.0±20.4*
Grand Forks	27	*14.8± 6.8*	None	85.2± 6.8	40.7± 9.5
Custer	10	None	None	100.0	50.0±1.58
MALES AND FEMALES					
Wimborne	15	—[a]	—[a]	—[a]	60.0±12.7
FEMALES					
Transcona	13	None	None	100.0	*7.8± 7.4*
Lloydminster	14	*7.2± 6.9*	None	92.8± 6.9	*28.6±12.1*
All Alberta	10	*30.0±14.5*	None	70.0±14.5	70.0±14.5
St. Mary's Lake	3	None	None	100.0	*33.3±27.2*
Eastern Montana	4	*25.0±20.2*	None	75.0±20.2	75.0±20.2
Grand Forks	6	None	None	100.0	66.7±19.3
Custer	5	None	None	100.0	60.0±21.9

[a] Not recorded.

absent on insignificant numbers of specimens in five of the series of *benjamini* examined in detail. (Table 15.)

VARIATION IN RAY ON UNDER SIDE OF HIND WINGS

There is a strong tendency for this irregular line to be more fragmentary on *inornata benjamini* than on *inornata inornata*. In this respect *benjamini* from the eastern portion of its range differs from adjacent *inornata*. Interruption anterior to the cell occurs very rarely among *inornata inornata*, whereas among *benjamini* it occurs frequently enough to be considered "significantly different from zero" among the males (Table 16).

VARIATION IN SUBMARGIN ON UNDER SIDE OF HIND WINGS

McDunnough pointed out in the original description of *benjamini* that some specimens show a weakly developed row of ocelli on the under side of the hind wings. This is strongly characteristic of the subspecies in the western part of its range. In the eastern part of the range ocelli are found on some specimens but they are the exception rather than the rule. In fact the Behrens River sample of *inornata* is more strongly ocellated than my Transcona sample of *benjamini*. Generally speaking the ocelli become more evident and better formed the farther west the station is located.

The dark chevrons near the margin show a reverse tendency. These are less common in the western part of the range of *benjamini* than in the eastern periphery. They seem to be much less significant on *benjamini* than they are on *inornata inornata*. The light patches so commonly found on the woodland subspecies are almost totally absent from the prairie insect. I have seen but a single male from Lloydminster with these spots well enough defined to be counted. No specimen that I have seen bears both chevrons and

TABLE 18

OCCURRENCE OF TRACES OF BASAL LIGHT PATCHES ON UNDER SIDE OF HIND WINGS

(Figures in italics not significant at the 1 per cent level of confidence.)

Station	Males			Females		
	n	%	*S.E.*	*n*	%	*S.E.*
Transcona, Man.	26	*7.7*	*± 5.2*	13	*15.4*	*±10.0*
Lloydminster, Sask.	41	*2.4*	*± 2.4*	14	None	
Wimborne, Alta.[a]	15	None		—	—	
All Alberta	58	None		10	None	
St. Mary's Lake, Mont.	10	None		3	None	
Eastern Montana	6	*16.7*	*±15.2*	4	None	
Grand Forks, N.D.	27	*3.7*	*± 3.6*	6	None	
Custer, S.D.	10	None		5	None	

[a] The Wimborne series was not sexed, but probably the majority are males.

patches, whereas this condition is rather common among *inornata inornata* in its western periphery. I suspect that the light patches may be incipient ocelli. That might account for their absence among the ocellated forms and presence among the non-ocellated forms where they come in contact with the former. (Table 17.)

VARIATION IN BASAL LIGHT PATCHES ON UNDER SIDE OF HIND WINGS

In conformity with the rest of the *inornata* moiety, *benjamini* lacks these marks except on rare occasions when traces of them are found. In this respect *benjamini* differs markedly from the adjacent *ochracea* moiety. Neither the woodland nor the maritime subspecies of *inornata* show the slightest trace of these marks. In no series of *benjamini* studied in detail is the frequency with which traces of these patches are found significant. (Table 18.)

To sum up, the intergradation between *inornata inornata* and *inornata benjamini* is so complete that it is difficult to justify retaining a separate name for the prairie strains of this insect. In fact I think that *mcisaaci*, *inornata*, and *benjamini* are nothing more than points in a series of clines that extend from the Atlantic to the Rocky Mountains. There seem to be better reasons for retaining *mcisaaci* than *benjamini*. My personal preference is to sink the names *mcisaaci* and *benjamini* as synonyms of *inornata* and call the material represented by them the maritime and prairie strains, respectively. Others will differ; some will retain the names, some will include *nipisiquit* as a synonym of *inornata*. If the problem be considered from a broader view than that of simple taxonomy, it may be best to retain all four names, as "tags" for material being studied biologically. Until the whole biology of these insects is understood these tags may be useful.[1]

[1] After the plates for the present paper were printed, it was found that the legends to figures 4 and 6 of plate 29 were inadvertently transposed.

SUMMARY OF FINDINGS

THE STATISTICAL INFORMATION that I have gathered supports the empirical decisions of taxonomists. It gives strength to the acceptance of *nipisiquit* and *mcisaaci* as forms of *inornata* different from each other and from the mainland insects. Although these data support recognition of *quebecensis*, *inornata*, and *benjamini* when they are studied from the type areas, the data suggest very strongly that each of these is a local expression of a single subspecies. The limited number of series that I have studied in detail supports a theory that each of the named entities is a way point on a series of east to west clines.

With regard to each of the eight areas of variation that were studied intensively, the following conclusions seem to be tenable:

SIZE

The mainland material shows no significant differences from sample to sample. I have pointed out elsewhere (Brown and Comstock, 1952, p. 3) that taxonomically significant differences generally have a *t* score of seven or more. This is exceeded only when *nipisiquit* is compared with adjacent *inornata* or *mcisaaci* and when *mcisaaci* is compared with *inornata* or *nipisiquit*. The coefficient of

TABLE 19

SUMMARY OF MEASUREMENTS ON MALES

(Figures in italics not significant at the 1 per cent level of confidence.)

Variable	Unit	B	N	Q	O	P	BR	T	L	A
Number		141	224	66	9	49	34	26	41	58
Size	Mm.	18.57	16.87	17.60	17.10	17.14	17.31	17.20	17.25	17.49
Color	No.	9.7	8.5	8.0	8.3	7.8	7.7	7.9	7.0	6.8
FW ocelli										
Upper side	%	12.0	3.1	*6.1*	0.0	79.6	55.8	57.7	65.7	76.0
Under side	%	82.2	12.1	54.6	44.4	93.9	88.2	100	100	96.2
FW ray										
Absent	%	0.0	*0.9*	0.0	0.0	0.0	0.0	*3.8*	*12.2*	*1.8*
To M_3	%	*0.7*	21.0	0.0	0.0	*4.1*	0.0	*15.4*	*19.2*	*3.7*
To Cu_1	%	47.5	62.5	13.6	*11.1*	14.3	70.6	65.4	34.2	24.1
To Cu_2	%	51.8	15.6	86.4	88.9	81.6	28.4	*15.4*	34.2	70.3
HW ray										
Absent	%	0.0	0.0	0.0	0.0	0.0	0.0	*11.5*	19.5	*8.6*
Fragmentary	%	5.7	48.3	*3.0*	*11.1*	14.3	*8.8*	*11.5*	*17.1*	32.8
M_3 and broken	%	87.9	49.1	86.4	77.8	44.9	73.6	46.2	43.9	41.4
Complete	%	6.4	*2.7*	10.6	*11.1*	38.8	17.6	30.8	19.5	17.3
HW submargin										
Ocelli	%	0.0	0.0	0.0	0.0	32.7	26.4	*15.4*	36.6	50.9
Dark chevrons	%	49.6	*1.1*	10.6	0.0	44.9	73.5	30.8	19.5	41.3
Light patches	%	20.6	14.7	40.9	77.8	20.4	61.8	0.0	*2.4*	0.0
HW basal patches	%	0.0	0.0	0.0	0.0	16.3	0.0	*7.7*	*2.4*	0.0
Dominant color under side		Green	Green	Green	Green	Green-brown	Green	Green-brown	Green-brown	Brown

B, Bathurst, New Brunswick; N, Newfoundland; Q, Quebec; O, Ontario; P, The Pas, Manitoba; BR, Behrens River, Manitoba; T, Transcona, Manitoba; L, Lloydminster, Saskatchewan; A, Alberta.

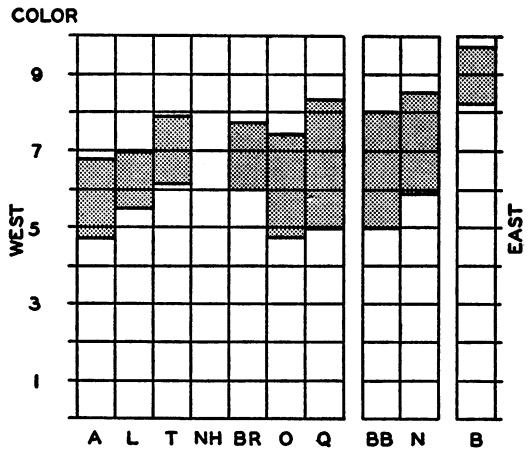


FIG. 1. Average color number for males and females of selected samples. Upper limit of stippled block is average male color; lower limit, average female color.

variation is small, around four. This is consistent with other satyrids that I have studied (1953a, 1953b) and smaller than I found in *Plebeius* (1951) and *Heliconius* (Brown and Comstock, 1952). The series studied were too few for any relationship between temperature and size to be demonstrated.

COLOR

There is a slight tendency for males of *inornata* to be darker in the eastern part of its range than in the western part. This seems to be related to humidity but may be due to

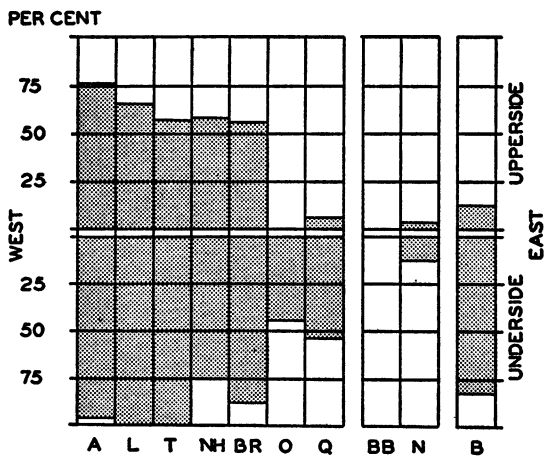


FIG. 2. Frequencies of at least traces of ocelli on forewings of males.

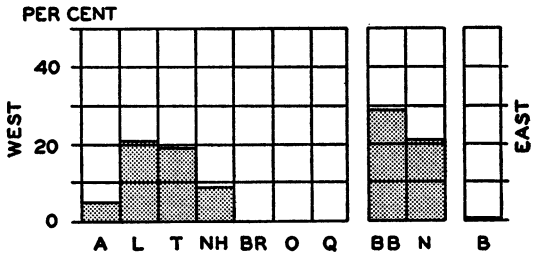


FIG. 3. Frequencies of "short ray" on under side of forewings of males.

infiltration of genes from the lighter-colored Rocky Mountain *ochracea*. There is greater divergence of color between the sexes in the east than in the west, except in the case of *nipisiquit*.

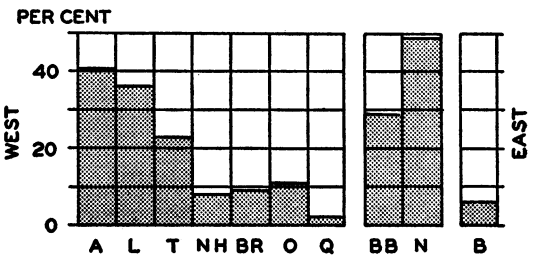


FIG. 4. Frequencies with which fragmentary rays or none are found on under side of hind wings of males.

A simple but rather crude regression formula for the relationship between color and relative humidity for males of *tullia inornata* is

$$C = \frac{RH+10}{9.5}$$

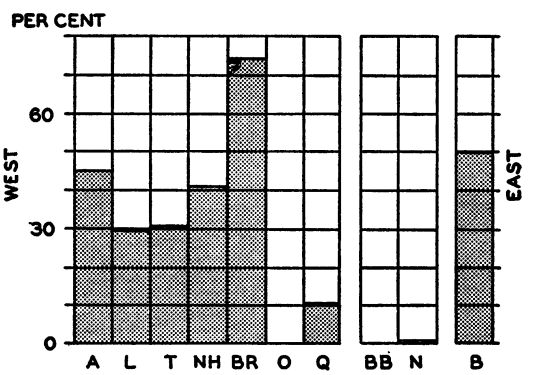


FIG. 5. Frequencies with which brown chevrons are found on under side of hind wings of males.

TABLE 20

SUMMARY OF MEASUREMENTS ON FEMALES

(Figures in italics not significant at the 1 per cent level of confidence.)

Variable	Unit	B	N	Q	O	P	BR	T	L	A
Number		64	35	10	6	15	21	13	14	10
Size	Mm.	18.86	17.14	17.67	17.28	17.49	18.01	17.07	17.64	17.87
Color	No.	8.2	4.5	5.4	4.7	5.5	6.0	6.1	5.5	4.7
FW ocelli										
Upper side	%	57.7	*7.7*	63.7	50.0	66.7	81.0	84.6	78.6	100
Under side	%	95.3	25.6	72.7	83.3	100	85.6	100	100	100
FW ray										
Absent	%	0.0	*2.5*	0.0	0.0	0.0	0.0	0.0	0.0	0.0
To M_3	%	0.0	0.0	0.0	0.0	0.0	0.0	*7.8*	*7.2*	0.0
To Cu_1	%	9.4	59.0	*20.0*	0.0	0.0	90.5	69.2	57.2	*40.0*
To Cu_2	%	90.6	38.5	80.0	100	100	*9.5*	23.1	35.7	60.0
HW ray										
Absent	%	0.0	0.0	0.0	0.0	0.0	0.0	0.0	*7.2*	0.0
Fragmentary	%	0.0	25.6	0.0	0.0	*6.7*	*4.8*	0.0	*28.6*	*30.0*
M_3 and broken	%	86.0	61.6	40.0	100	*13.3*	71.4	76.9	42.8	*40.0*
Complete	%	14.0	*12.8*	60.0	0.0	80.0	*23.8*	*23.1*	*21.4*	*30.0*
HW submargin										
Ocelli	%	0.0	0.0	0.0	0.0	40.0	28.6	*7.8*	28.6	70.0
Dark chevrons	%	14.1	0.0	0.0	0.0	36.7	*19.0*	0.0	*7.2*	*30.0*
Light patches	%	28.2	20.0	80.0	100	*20.0*	81.0	0.0	0.0	0.0
HW basal patches	%	0.0	0.0	0.0	0.0	*13.3*	0.0	*15.4*	0.0	0.0

B, Bathurst, New Brunswick; N, Newfoundland; Q, Quebec; O, Ontario; P, The Pas, Manitoba; T, Transcona, Manitoba; L, Lloydminster, Saskatchewan; A, Alberta.

in which C is the color tone on the scale used and RH is the relative humidity. The color of the females does not follow any such simple rule. In the semi-arid areas the rule holds for females if C-2 is substituted for C. In the humid eastern areas, the trend seems towards darker females with lowering humidity. A close approximation of the color number can be made with the use of this formula:

$$C = \frac{127 - RH}{1}$$

This poses an interesting problem. The regression lines for the males and the females in the humid east intersect around 50 per cent relative humidity. Under such conditions the males and females should have the same color number, about 6.5. It would be interesting to see if this occurs when several generations are bred in the laboratory under conditions that hold the relative humidity at 50 per cent. Among subspecies of *tullia* in southwestern United States where the relative humidity rarely averages 50 per cent, males and females are alike in color.

OCELLUS IN APEX OF FOREWING

This is rarely if ever well developed on the upper side. There it often is represented by a cluster of black scales. From Ontario eastward even these clusters of black scales are rare. From Lake Winnipeg westward at least half of the male specimens examined bear such spots. There is a sex difference in the frequency with which these marks occur. They are more frequent upon females than

TABLE 21

STATISTICS OF VARIATION FOR THE PAS STRAIN OF *Coenonympha inornata inornata* EDWARDS

(Figures in italics not significant at the 1 per cent level of confidence.)

Variable	Males	Females
Number studied	49	15
Size		
Radius of left forewing (mm.)	17.14 ±0.77	17.49 ± 0.66
Coefficient of variation	4.5	3.8
Forewing		
Presence of ocellus or traces on upper side (%)	79.6 ±5.8	66.7 ±12.2
Presence of ocellus or traces on under side (%)	93.9 ±3.6	100
Ray ends at M_3 (%)	*4.1 ±2.8*	0.0
Ray ends at Cu_1 (%)	14.3 ±5.0	0.0
Ray reaches or exceeds Cu_2 (%)	81.6 ±5.5	100
Hind wing		
Ray complete (%)	38.8 ±7.0	80.0 ±10.3
Ray broken (%)	46.9 ±7.1	*13.3 ± 8.7*
Ray fragmentary (%)	14.3 ±5.0	*6.7 ± 6.5*
Dark chevrons present (%)	44.9 ±7.1	36.7 ±12.4
Light patches present (%)	20.4 ±5.8	*20.0 ±10.3*
Both present (%)	*6.1 ±3.6*	0.0
Both absent (%)	40.8 ±7.0	45.3 ±12.8
Ocelli present (%)	32.7 ±6.7	40.0 ±12.6
Basal patches present (%)	16.3 ±5.3	*13.3 ± 8.7*

upon males. The existence of a cline is suggested by figure 9 based on the frequency with which the spot occurs on the under side of the males. *Nipisiquit* does not fit the cline, and I feel this fact is added evidence of the validity of recognizing the subspeces. The spots occur more frequently on the under side of both sexes. The sex difference is also present among the frequencies found on this surface, but it is not so marked as on the upper side.

RAY ON UNDER SIDE OF FOREWING

This tends to be longest on *inornata* and *quebecensis*. It becomes shorter east and west from Ontario. *Mcissacci* differs from the mainland material in the quality of the ray.

RAY ON UNDER SIDE OF HIND WING

This is least well developed on *mcisaaci*. I have reduced the data to a simple statistic by combining "absent" and "fragmentary" and opposing this to the sum of "M_3," "broken" and "complete." When this is done the area of maximum development is found to be around Lake Winnipeg, an area from which development declines eastward and westward. *Nipisiquit* is again out of line. Figure 10 demonstrates the data.

SUBMARGIN ON UNDER SIDE OF HIND WING

This bears a variety of markings on *tullia* —ocelli, brown chevrons, and light patches. These seem to vary independently, although there is a suggestion that ocelli and light patches may be related. Ocelli seem to be polygenic in character, and light patches may represent the outward expression of the presence of a minimum of the "ocelli" genes. Ocelli are absent throughout the east. They first appear in eastern Manitoba and from there westward are increasingly common. There are two ways of measuring the degree of ocellation. In tables 12, 17, 19, 20, and 21 the frequency with which ocellate specimens were found is recorded in per cent. A second method, originally developed when the ocel-

late western subspecies of *tullia* were studied, is to record the per cent of possible ocelli that are present.

The brown chevrons are least often found on eastern specimens, except *nipisiquit*. As yet I have found no apparent rhythm among the frequencies noted. The marks are quite common from Lake Winnipeg westward and among *nipisiquit*.

White patches seem to reach their peak frequency along the eastern shore of Lake Winnipeg, and the frequency declines eastward. To the west of the lake these marks are virtually never found.

Basal Light Patches

These patches, so evident on many subspecies of *tullia*, are absent from *tullia inornata*. Two individuals from Grand Forks, North Dakota, showed mere traces of them among the hundreds of specimens carefully analyzed.

The color of the under side of the hind wings tends to vary from east to west, but these data have not been recorded in a form that can be analyzed. Eastern specimens are definitely green hued; those from the west, brownish. If an adequate way is found to record these colors I believe it will show that this variation is clinal.

On the basis of these studies I am inclined to consider that only two subspecies of *inornata* are well defined: *inornata* and *nipisiquit*. Until the north shore of the St. Lawrence River is more thoroughly sampled for *inornata*, I am willing to add a third subspecies, *mcisaaci*. I believe that *mcisaaci* will be proved to be nothing more than the eastern terminus of the clines so evident in *inornata*.

ACKNOWLEDGEMENTS

This study could not have been made without the wholehearted cooperation of many men. Some have been acknowledged in the text through quotations from their letters. Another 50 or more members of the Lepidopterists' Society sent me data that have been used. I am particularly grateful for material lent or given to me by Mr. C. S. Quelch of Transcona, Manitoba; Mr. Julius Adler of Grand Forks, North Dakota; Mr. Neil Euting of Okauchee, Wisconsin; and Mr. A. C. Sheppard of Montreal, Quebec. Dr. T. N. Freeman and Mr. Paul Bruggemann at the Canadian National Collection in Ottawa gave unstintingly of their time and good advice and arranged loans of material in that collection. Dr. Ralph Chermock at the University of Alabama and Mr. Cyril dos Passos of Mendham, New Jersey, read early drafts of the study and greatly improved the final work through their constructive criticism. The final draft was read by Dr. T. N. Freeman, Mr. A. C. Sheppard, and Dr. P. H. H. Grey. To them I owe a special debt of gratitude.

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EXPLANATION OF TEXT FIGURES

On the histograms (figs. 1–5) the symbols across the bottom denote the series represented by each column. These symbols and their meanings are: A, Alberta series; L, Lloydminster, Saskatchewan, series; T, Transcona, Manitoba, series; BR, Behrens River, Manitoba, series; NH, Norway House, Manitoba, series; O, Ontario series; Q, Quebec series; BB, Bradore Bay, Quebec, series; N, Newfoundland series; B, Bathurst, New Brunswick, series.

Figures 6–14 have been designed to give at a glance the geographic distribution of certain qualities of *Coenonympha tullia inornata*. The numbered straight lines represent meridians and parallels that are spaced as close to scale as can be done without the use of curves. In these "geographs" all the meridians are west longitude and all the parallels north latitude.

The broken curved lines approximate the boundaries of the four taxonomic units that are here discussed. Where a statistically significant difference was found between adjacent areas a boundary was drawn as a heavy line. The stations from which collections were studied in detail are marked with symbols that are constant for taxonomic units: open circles for *mcisaaci;* solid circles for *nipisiquit;* open squares for *inornata;* open triangles for *benjamini*. The numbers opposite each station symbol are the means of the sample for the quality being demonstrated. When these numbers

are slanted they signify that the series studied was too short for a significant mean, or that the frequency is not significantly different from zero at the 1 per cent level of confidence. The unit of measurement for the numbers in each geograph is given in the accompanying legend.

DISTRIBUTIONAL DATA

Coenonympha inornata mcisaaci Dos Passos

Newfoundland: Bona Vista Bay Co.: Gander, June 12–July 5. Ferryland Co.: New Melbourne, July 20; Saint Johns, June 29–July 1. Foga Co.: Grand Falls, July 10; Lewisport, July, Aug.; Springdale, July 26; Saint Anthony, July 7–18. Saint George Bay Co.: Doyles Station, June 4–July 25; Harmon Field, June 24–July 1; Stephanville, no date. Not located: Cape Inornata, 1903, in Canadian National Coll. *Quebec:* Saguenay Co.: Bradore Bay, July 16–27.

Coenonympha inornata nipisiquit McDunnough

New Brunswick: Gloucester Co.: Bathurst, July 29–Aug. 8.

Coenonympha inornata inornata Edwards

Quebec: Argenteuil Co.: Lac Marois, June 24–30; Rivington, June 1–July 1. Berthier Co.: Lanoraie, July 1. Champlain Co.: Lac a la Tortue, July 21. Gatineau Co.: Aylmer, May 29–June 7; Chelsea, June 1–15; Gracefield, June 10–26; Kazabazua, June 5–28; Meach Lake, no date; Messines, July 10; Wright, June 29. Jacques Cartier Co.: Macdonald College, June 21, 1952, a stray (?). Labelle Co.: Bellerive, July 15; Lac Nominingue, June 11; Lacoste, June 6; Nominingue, May 2–July 1. Montcalm Co.: Rawdon, June 27–July 2. Montmorency Co.: Rivière aux Xawots, June 7. New Quebec Co.: Great Whale River, Aug. 2; Little Charlton Island, July; Port Harrison, July 7; Rupert House, July 18–27. Papineau Co.: Namur, June 19. Saint Maurice Co.: Shawinigan Falls, June 19–24. Terrebonne Co.: Saint Jovite, June 28–July 3; Shawbridge, June 11–Aug. 11. Not located: Chersey,[1] June (Kirkwood). *Ontario:* Algoma Co.: Amyot, July 5; Missisagi Forest Reserve, July 6–9; Thessalon, June 9; Sault Ste. Marie, July 2. Carleton Co.: Billings Bridge, June 9–14; Blackburn, May 28–June 13; Brittania, June 10; Mer Bleu, June 8; Ottawa, June 3–July 5; South March, June 2. Cochrane Co.: Big Piskwanish, July 21; Fort Albany, July 29; Hanna Bay on James Bay, July 4; Mishishikabe River, James Bay, July 17; Moosonee, July 17; Red Hook Point, James Bay, July 21. Hastings Co.: Bird's Creek, July 21. Leeds Co.: Lyn, June 26. Nipissing Co.: Algonquin Park, June 18–July 11; Lake Sasejewan, June 27; Smoky Falls, Mattagami River, July 27. Northumberland Co.:

[1] Possibly St. Théodore de Chertsey, Montcalm Co., suggested by A. C. Sheppard.

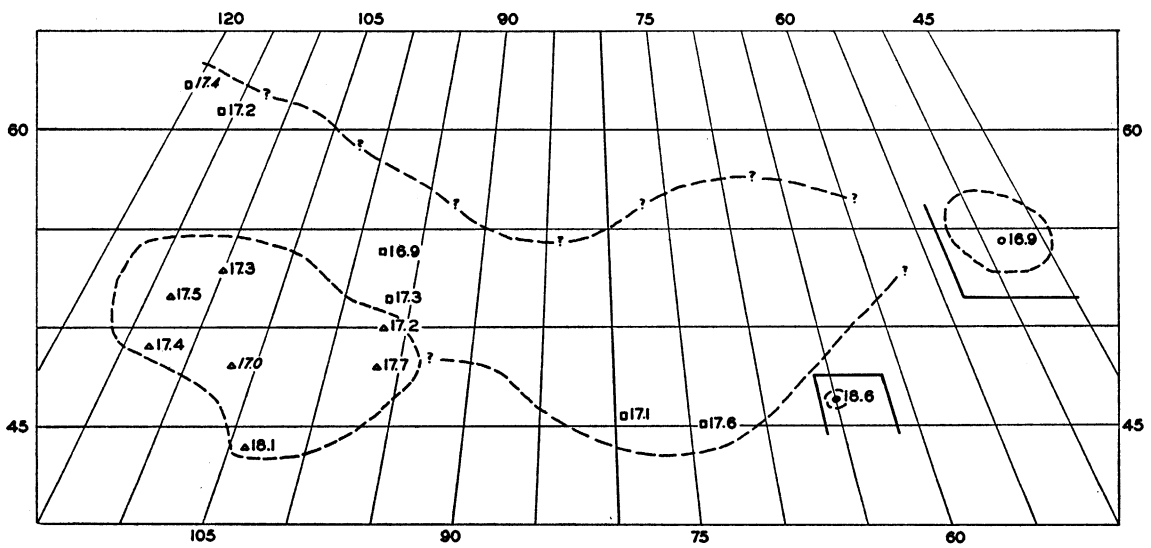

FIG. 6. Radius of left forewing of males measured in millimeters.

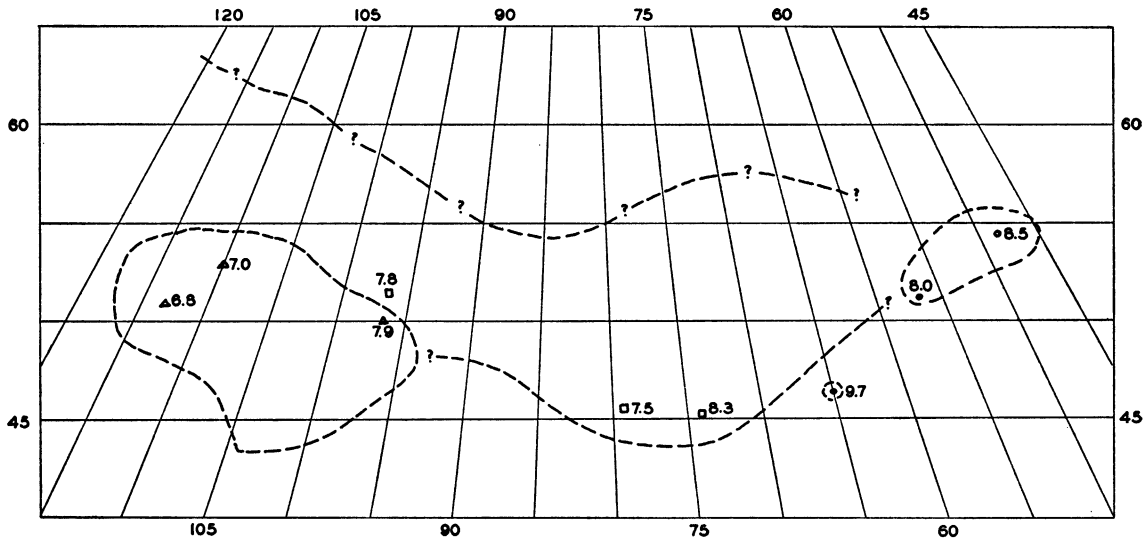

FIG. 7. Average color number for males. The numbers are synthetic, based on a series of specimens showing uniform increment of tint from lightest color found among *Coenonympha tullia california* (set at 0) to the darkest colored *Coenonympha tullia inornata* (set at 10).

Brighton, Sept. 10, second brood. Parry Sound Co.: Burke Falls, June 30; Kearney, June 26; Sand Lake, June 3–July 3. Renfrew Co.: Petawawa, June 26. Simcoe Co.: Thompsonville, Aug. 21, second brood (?). Timiskaming Co.: Low Bush, Lake Abitibi, July 15. New Co.: Eglington, July 13; Toronto, no date. *Manitoba:* Nelson Co.: Norway House, June 25–July 20; The Pas, June 30. Springfield Co.: Behrens River, July 2–10; Fort Alexander, July 4–30. *Northwest Territories:* Fort Simpson, July 10–29; Fort Smith, July; Hay River, July 15–28; Arcola, July 3.

Michigan: Alger Co.: Pictured Rocks, July 5; Charlevoix Co.: Beaver Island, July 17; High Island, July 17. Cheboygan Co.: near Mackinaw City, June 19–July 2. Chippewa Co.: Sault Ste.

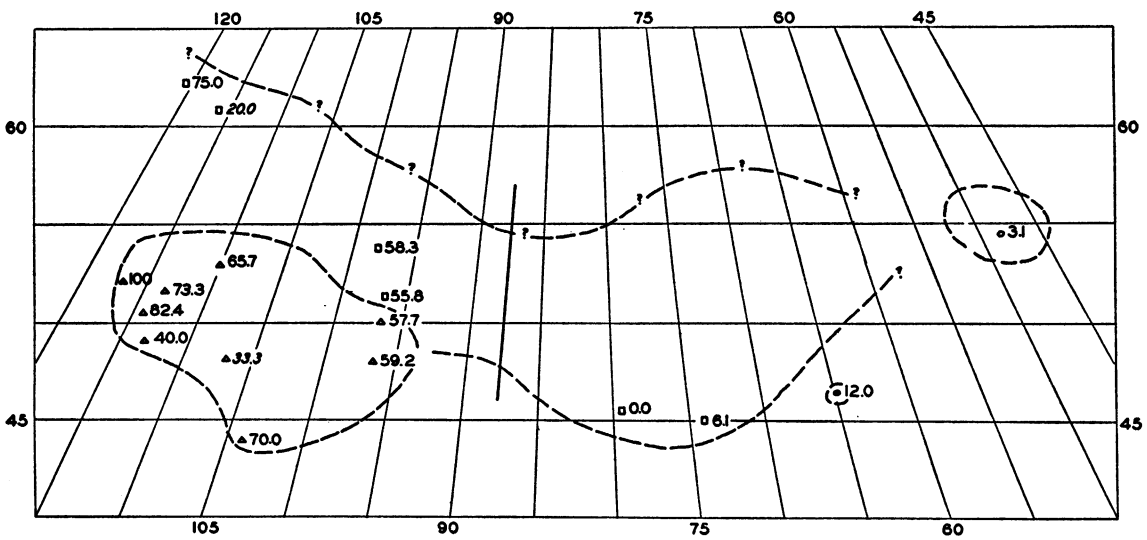

FIG. 8. Frequency with which at least traces of an apical ocellus occur on upper side of forewing of males. Numbers represent per cent.

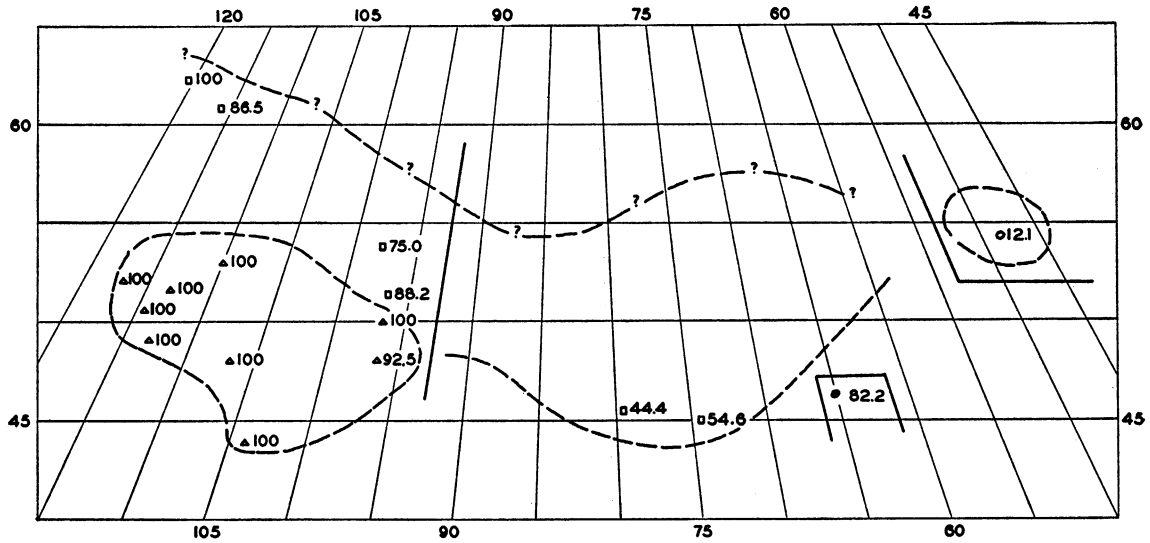

FIG. 9. Frequency with which at least traces of an apical ocellus occur on under side of forewing of males. Numbers represent per cent.

Marie, June 23–July 9. Emmet Co.: Mackinaw City, July 8. Mackinac Co.: Cecil Bay, June 18–Aug. 2; St. Ignace, July 2. Schoolcraft Co.: Blaney Park, June 26–July 7; Manistique, July 6; Scott Point, Aug. 2.

Coenonympha inornata benjamini McDunnough

Manitoba: Brandon Co.: Brandon, May 29–June 20; Reston, June 8. Lisgar Co.: Cartwright, June. MacDonald Co.: Aweme, June 9–July 15. Marquette Co.: Beulah, June 1–24; Birtle, May 5–July 20; Miniota, May 12–July 2. Neepawa Co.: Kelwood, July; McCreary, June 15–Aug. 16; Riding Mountains, July 9. Portage la Prairie Co.: Delta, July 5; Sand Ridge, June 14–24; Provancher Co.: Morris, June 26. St. Boniface Co.: Transcona, June 3–July 29. Selkirk Co.: Matlock Beach, June 3. Winnipeg Co.: Winnipeg, June 5–

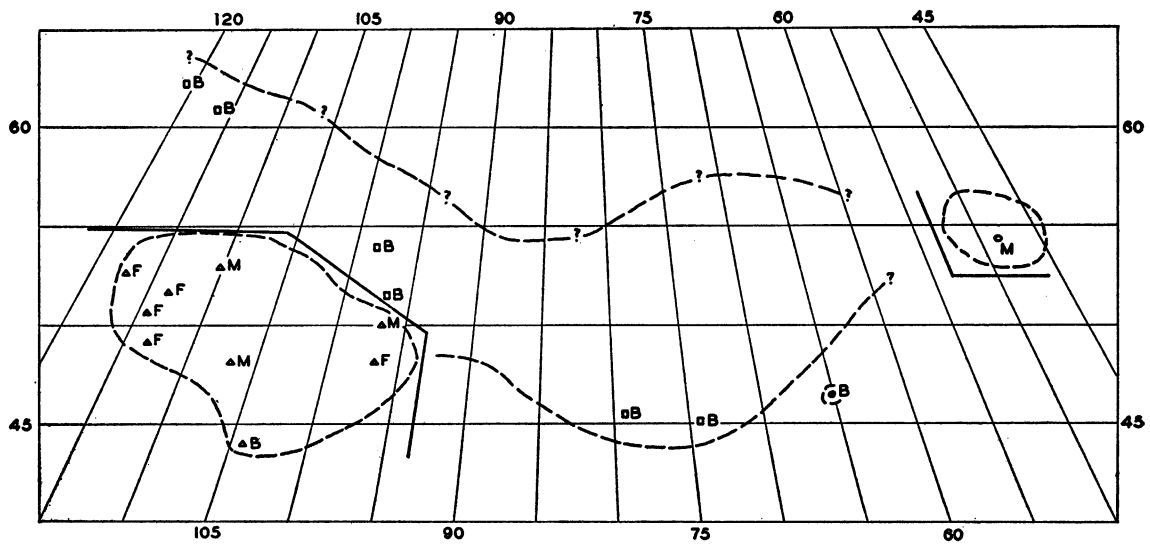

FIG. 10. Average condition of ray on under side of hind wings of males. *Abbreviations:* B, broken; F, fragmentary; M, entire anterior to median veins.

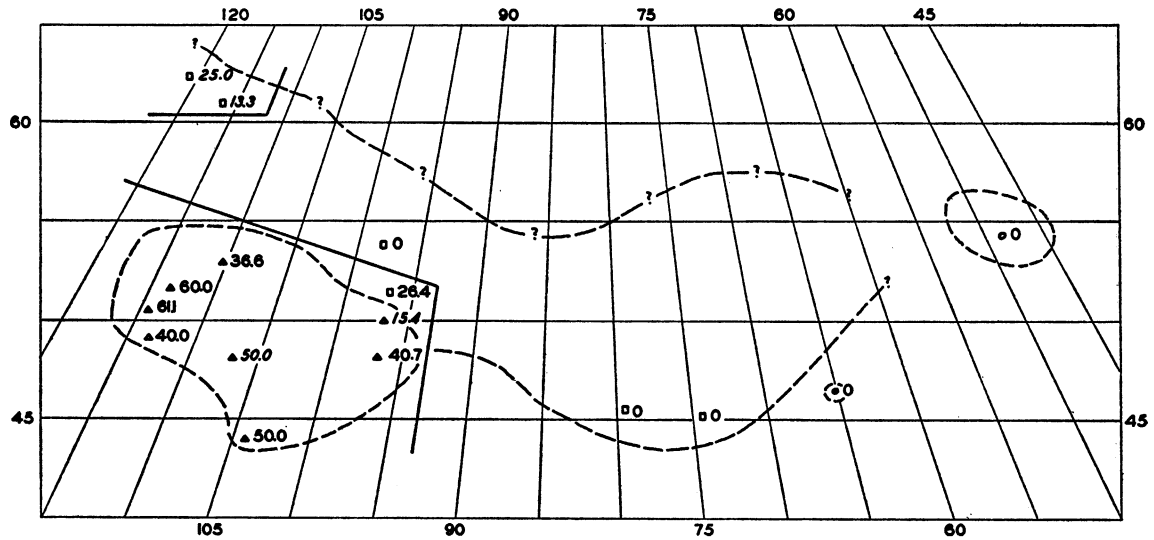

FIG. 11. Frequency with which ocelli occur in submargin on under side of hind wing of males. Numbers represent per cent.

19. *Saskatchewan:* Assiniboia Co.: Alameda, July 4; Arcola, July 1–3; Oxbow, July 5; Redvers, July 9; Roche Percee, July 4–6. Last Mountain Co.; Craven, June 22; Nokomis, June 28. Maple Creek Co.: Climax, June 10–12; Cypress Hills, May 28–June 3. Melville Co.: Ohlen, June 25. North Battleford Co.: Harlan, June 7–Aug. 11; Onion Lake, June 10. Prince Albert Co.: Duck Lake, July 22. Qu'Appelle Co.: Indian Head, June 3–July 1. Regina Co.: Regina, July 17. Saskatoon Co.: Saskatoon, June 3–9. South Battleford Co.: Atton's Lake near Cutknife, June 4–9; Lloydminster, May 15–July 23, Oct. 3, second brood. Not located: Christopher Lake, June 27–30 (A.R. Brooks), and Nieburn, June 24 (Fletcher). Both series in Canadian National Coll. *Alberta:* Acadia

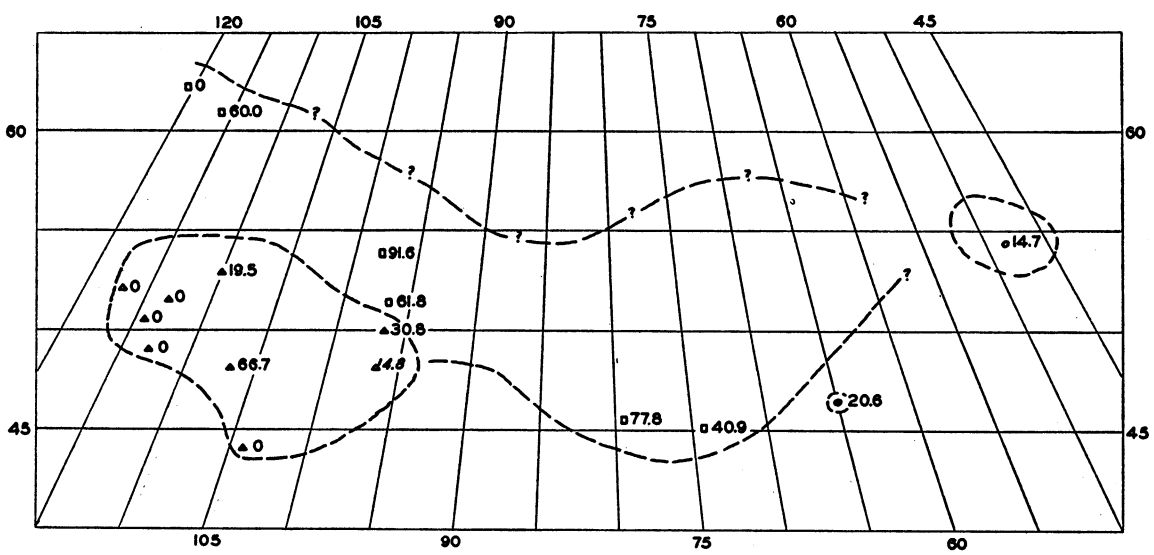

FIG. 12. Frequency with which light patches occur in submargin on under side of hind wing of males. Numbers represent per cent.

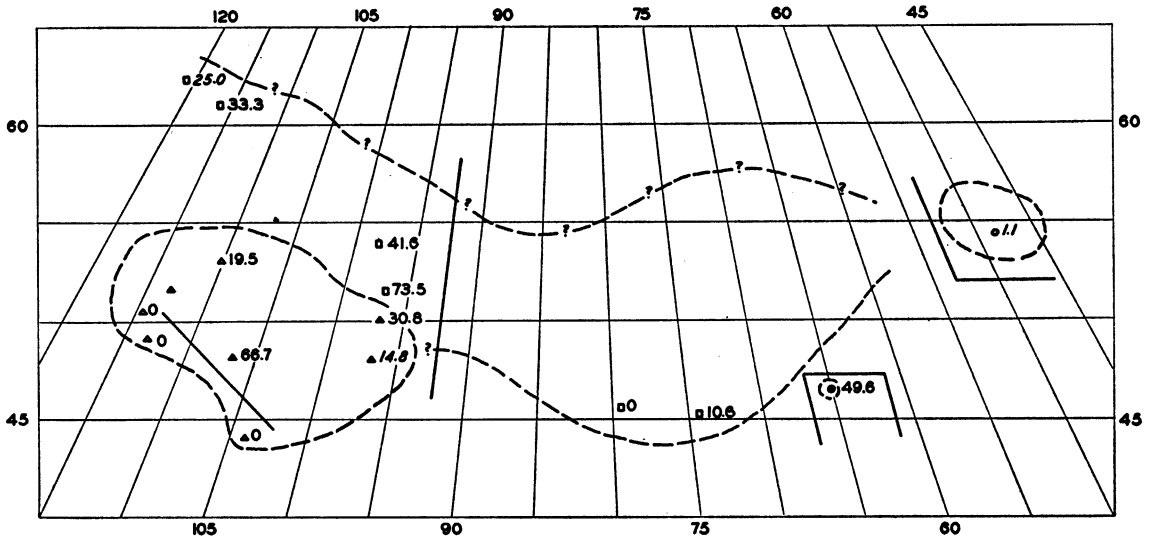

FIG. 13. Frequency with which dark chevrons occur in submargin on under side of hind wing of males. Numbers represent per cent.

Co.: Morrin, June 7. Battle River Co.: Lloydminster, see Saskatchewan. Bow River Co.: Gleichen, June 2–21; Calgary West Co.: Banff, June 1–July 31; Calgary, June 2–July 6; Canmore, July 6; Ghost River Park, July 6. Edmonton East Co.; Edmonton, June 10–July 12. Lethbridge Co.: Lethbridge, June 6–24; Waterton Lakes, June 28–Aug. 1. Macleod Co.: Hillcrest, June 24. Medicine Hat Co.: Medicine Hat, June 1–14; Orion, June 20; Suffield, June 1–10. Red Deer Co.: Didsbury, no date; Nordegg, July 23; Red Deer, June 11; Wimborne, July 14–16. Wetaskiwin Co.: Leduc, July 6. Not located: Waghorn, June 10, in Los Angeles County Museum, California. *British Columbia:* Cariboo Co.: Fort St. John, June 12; Rolla, July 1. Not located: Beau Lodge, June 29,

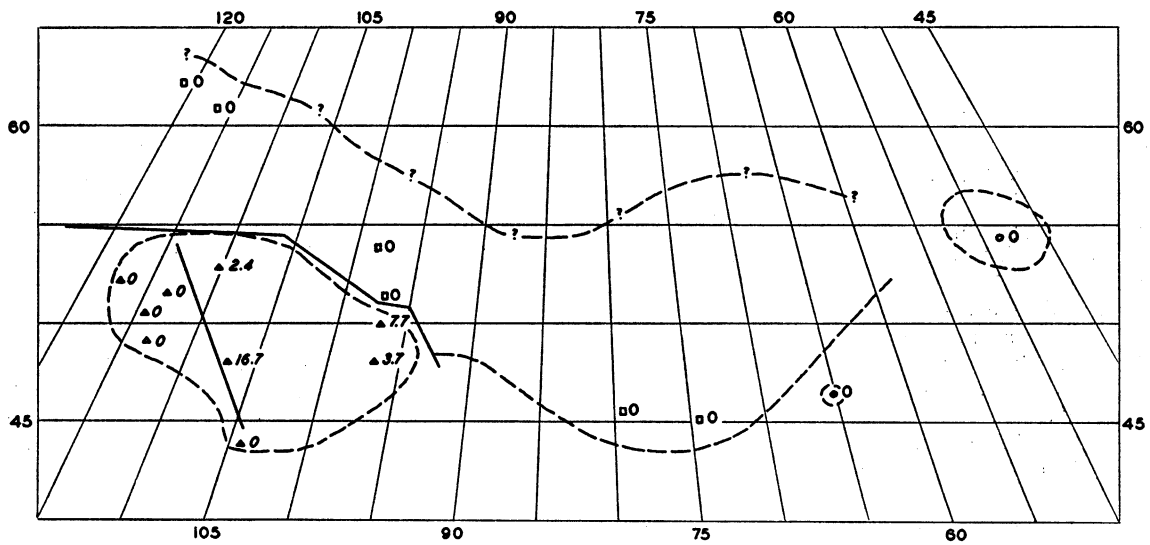

FIG. 14. Frequency with which basal light patches occur on under side of hind wing of males. Numbers represent per cent.

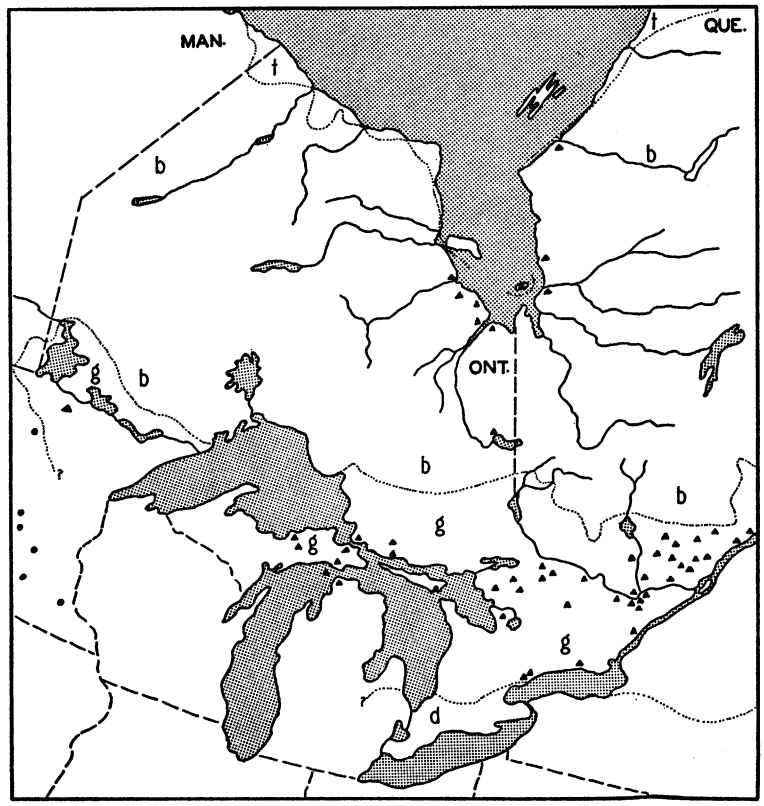

FIG. 15. Distribution of samples from Great Lakes-James Bay region. Stations for *inornata inornata* are marked with triangles; those for *inornata benjamini*, with dots. Dotted lines are approximate boundaries of forest areas: b, boreal spruce forest; d, deciduous forest; g, Great Lakes-St. Lawrence mixed forest; t, tundra.

1924, determined by and in collection of Dr. Ralph Chermock.

Montana: Beaver Head Co.: Polaris, May 2–8. Blaine Co.: Chinook, June 29. Cascade Co.: Monarch, June 8; Chouteau Co.: Big Sandy, June 6; Highwood, June 16–26. Custer Co.: Miles City, no date. Gallatin Co.: Bozeman, June 6. Glacier Co.: Anderson's Ranch, July 4; Glacier National Park, no date; Lake Sherbourne, July 17; St. Mary's, July 3–10; Upper St. Mary's Lake, July 3, 4. Granite Co.: New Chicago, no date. Lewis and Clark Co.: Helena, no date; Madison Co.: Elkhorn Ranch, July 25–29; Ruby Mountains, no date; Tobacco Root Mountains, no date. Roosevelt Co.: Poplar, June 8. Rosebud Co.: Forsythe, no date. Toole Co.: Sweetgrass, July 18. *North Dakota:* Grand Forks Co.: Grand Forks, June 6–July 4. McLean Co.: Turtle Mountain, no date. *Minnesota:* Anoka Co.: Johnsville, July 3; Beltrami Co.: Bemidji, no date; Black Duck, June 16; Red Lake, July 12. Carlton Co.: Barnum, July 5. Clearwater Co.: Itasca Park, July 1–15. Crow Wing Co.: Pelican Lake, June 19–Aug. 9. Douglas Co.: Camp Carlos, near Alexandria, June 22. Hennepin Co.: Lake Minnetonka, no date; Minneapolis, June 18–Aug. 1. Itasca Co.: Grand Rapids and Deer River, July 3. Kittson Co.: Orleans, June 26. Koochiching Co.: 40 miles south of International Falls, no date; Little Fork, July 3. Marshall Co.: Warren, June 19–July 6. Meeker Co.: Litchfield, June 16. Nicollett Co.: St. Peter, July 7. Polk Co.: locality not given, July 29. Pope Co.: Sedan, June 28–July 23. Red Lake Co.: Plummer, July 8–24. Not located: LaPorte, July 26 and Otto, no date, reported by Macy and Sheppard, 1941. *South Dakota:* Beadle Co.: Wolsey, May 30–June 2. Custer Co.: Custer, July 7–Aug. 4. Lawrence Co.: Spearfish Canyon, June 29.

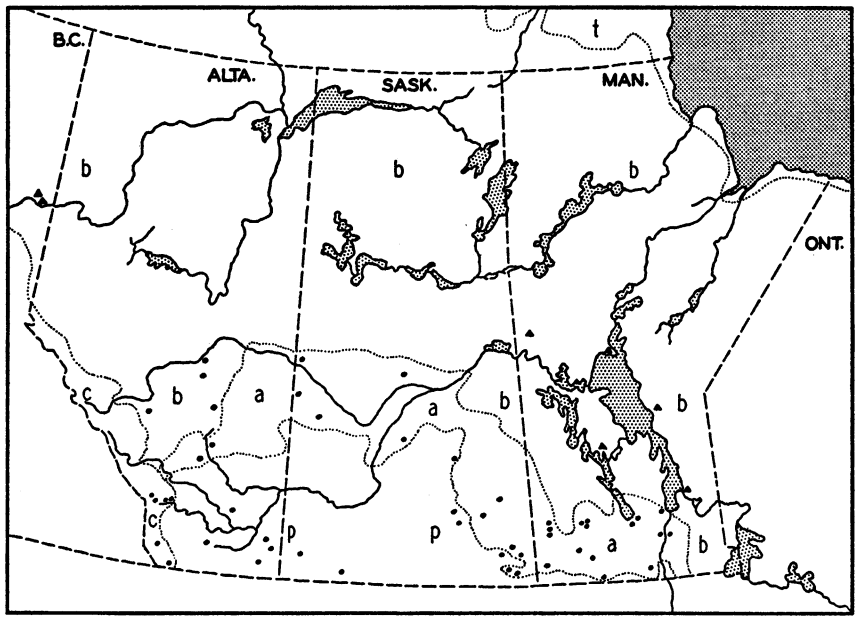

FIG. 16. Distribution of samples from prairie provinces of Canada. Symbols are the same as those for figure 15 with these additions: a, aspen groves; c, cordilleran forest; p, grasslands.

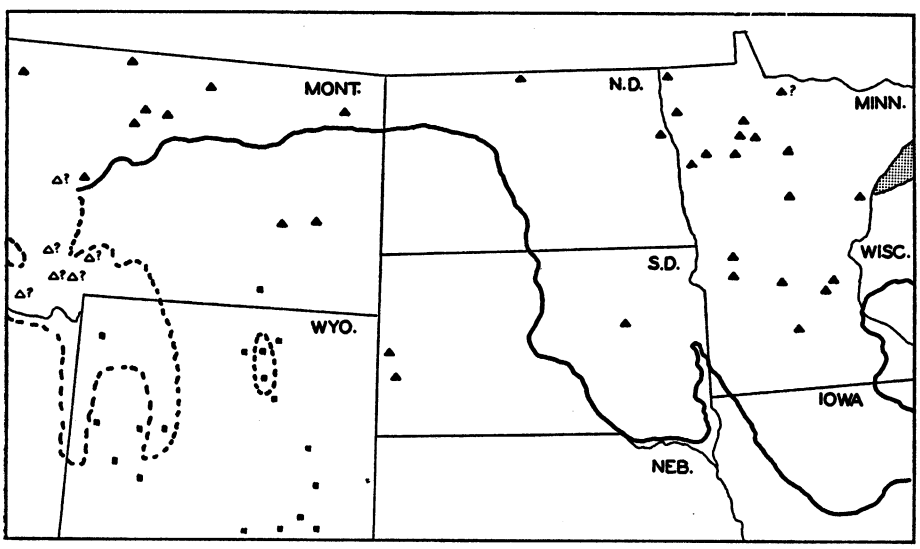

FIG. 17. Distribution of samples from prairie states of United States. Solid triangles indicate stations for *inornata benjamini;* open triangles with question mark, stations from which too few specimens have been seen for proper diagnosis. Solid squares indicate stations for *Coenonympha tullia ochracea*. Heavy line approximates southern boundary of ice at Wisconsin maximum. Broken portion of line relates to areas affected by alpine glaciation at the same time.

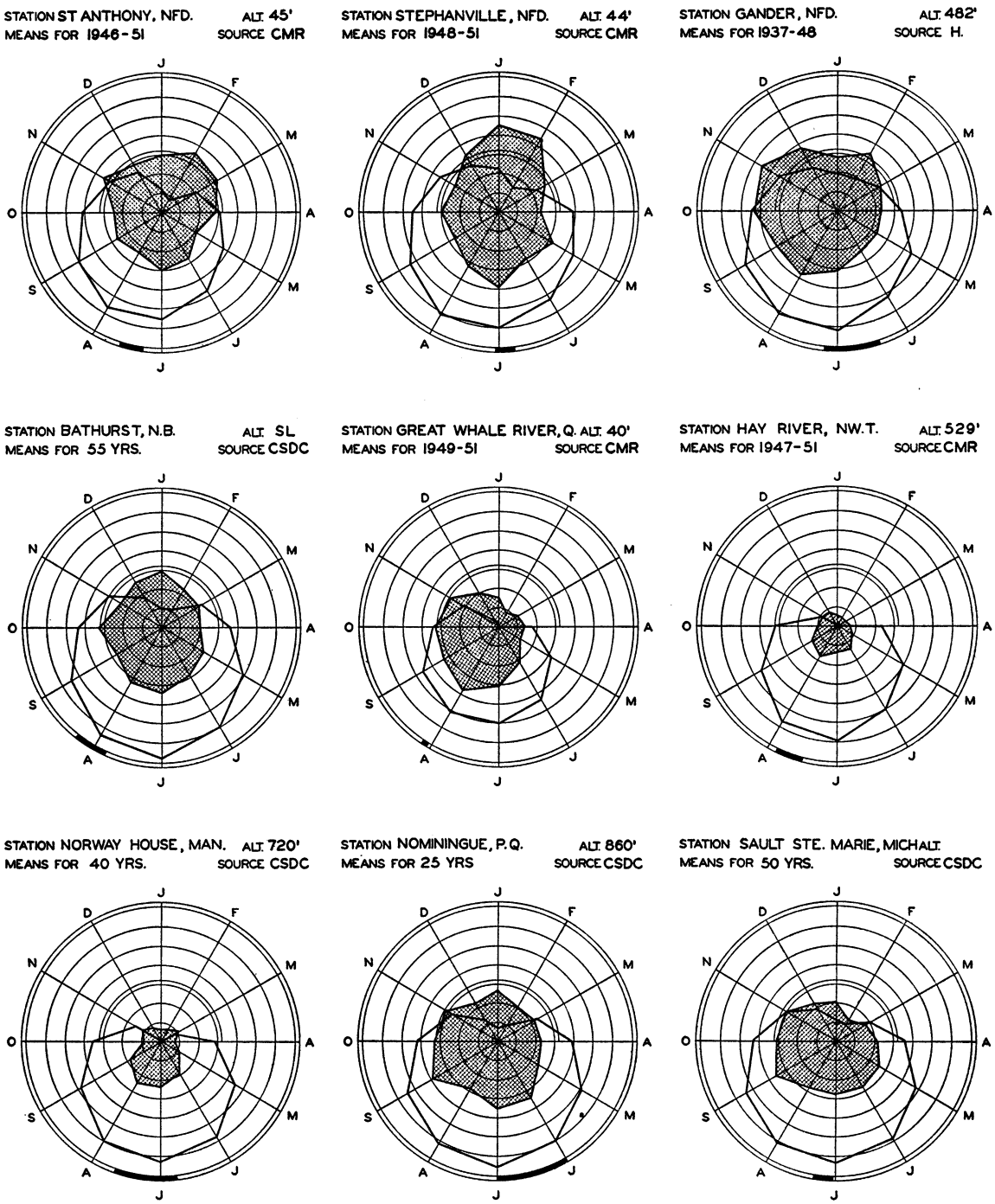

FIG. 18. Climatographs of selected stations for *Coenonympha inornata mcisaaci*, *C. i. nipisiquit*, and *C. i. inornata*. Precipitation polygon shaded; temperature polygon open. Concentric circles have values of 1 inch of precipitation or 10° F. Center is zero for both measures. Half circle through winter months represents 32° F. Heavy peripheral bar indicates known flight period of insect at station.

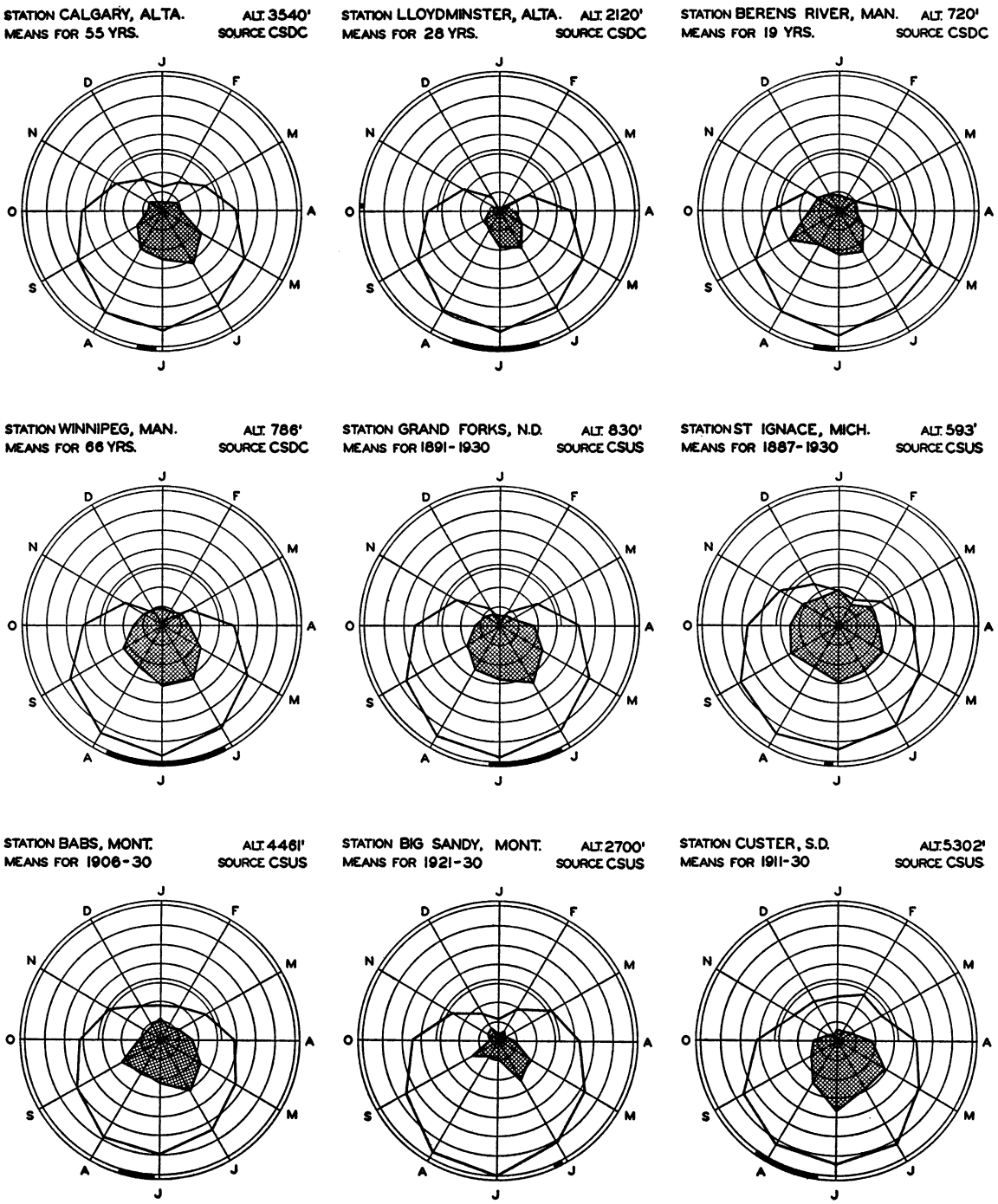

FIG. 19. Climatographs of selected stations for *Coenonympha inornata inornata* and *C. i. benjamini*. Sources for data are: CSUS, Climatic Summary of the United States, 1930; CSDC, Climatic Summary of the Dominion of Canada, vol. 1; CMR, Monthly Record, Canada; H, Hare (1952). The temperature data for Custer, South Dakota, are for one year, 1952, and were furnished by the Forest Service, United States Department of Agriculture (*in litt.*, January 8, 1954).