Introduction to the Insects of the Yukon

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This book is concerned with insects in the Yukon. But why the Yukon? Because, in the first place, less was known about the insect fauna of the Yukon than of any other major region of Canada. Some valuable collections existed, in Ottawa and in several provincial and university museums, but the content and significance of these collections had not in general been fully developed. It seemed, however, that systematic and faunistic entomologists across the country were prepared for a new, cooperative project of exploration and study, and this was timely because a parallel interest in the Yukon was developing not only among botanists but also among the earth scientists who were probing the late Tertiary, Pleistocene and Holocene history of the northern terrain. It was known furthermore that similar interests were developing in Alaska and also in northeastern Siberia, though by and large eastern and western workers had never met.

The special significance of the region is two-fold. The Yukon includes the Canadian part of Beringia, the area that extends from eastern Asia through Chukotka and Alaska to the western Yukon and that had remained ice-free during the Pleistocene glaciations. Secondly, it includes also the northernmost reach of the fauna that moved up from the south as the continental ice sheet dissipated, there to come into contact with the fauna released from Beringia. Knowledge of the content and character of the fauna of the Yukon would thus form a unique contribution to our knowledge of the fauna of Canada as a whole. The indispensable baseline, as in any faunistic study, would be a systematic inventory built up by exploratory collecting, and then, wherever possible, continuing into geographic and ecological studies and the attempt to understand the history and origins of the biota of the present day. A cooperative project with these aims was developed in the early discussions of the Scientific Committee of the Biological Survey of the Insects of Canada and interested workers were invited to take part. This volume represents a major part of what has been achieved to date.

The interest of entomologists was directed most actively to the significance of Beringia. Earlier collecting had suggested that as the Wisconsinan (last) glaciation ended, species from the Beringian Refugium would have spread mainly eastward, along and to the north of the present-day treeline, through the newly available high boreal and low arctic life zones, to which they were already climatically adapted, so as to form a main part of the present-day fauna of far northern Canada. This movement was complemented by another great movement from south of the continental ice sheets, a mainly boreal-adapted fauna moving generally northward to its climatic limit. A broad picture had been developed, but the important parameters were still, with few exceptions, unknown or ill-defined. How many species of Beringian insects are there, already recorded or waiting to be described and named or waiting to be discovered? What do we know of their present-day ranges, of their origins,

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of their history through Pleistocene times, and of their routes and rates of movement following deglaciation? And what of the species themselves, or their component races; how are they adapted to their northern, and frequently arctic, climate, and how did this originate? Are they young species or old ones? Of Holocene or late Pleistocene age?—or perhaps much older? And more generally, how is the history of Beringian insects related to the extensive and repeated changes of climate through late Tertiary, Pleistocene and Holocene times—climatic changes that continue, perhaps with increasing intensity, at the present day. The observed conditions and responses of this northern fauna could well provide clues to the oncoming climate changes that are now expected, the more so because in this far northwestern region the changes are expected to be maximal. The work proposed would provide the baseline.

The foregoing suggestions and questions were all formulated from a viewpoint in North America. But ice-free Beringia extended beyond the Yukon and Alaska across what is now the region of the Bering Strait and far into northeastern Asia. The two continents and their northern faunas formed a single whole alternating, during periods of deglaciation, with a separation into East Beringia and West Beringia, as they are now. The faunistic significance of such geographic changes cannot be understood without a knowledge of climate and chronology, as will be discussed in a later chapter. However, at the time this project was started, knowledge of the insects of West Beringia was minimal, at least among North American entomologists, and substantive discussion was not possible.

The generally mountainous but well dissected physiography of the Yukon offers a wide-ranging opportunity for the study of the mountain fauna as such, a study that has been somewhat neglected until quite recently. Almost inevitably the high-alpine fauna is related to that of the arctic and of Beringia, and organised findings would be very interesting. In the southwestern Yukon the St. Elias Mountains rise beyond the limit of macroscopic life, while northward the elevations diminish steadily and give way finally to a coastal plain of a full arctic character. Thus from south to north the alpine zone, above treeline, is reached at lower and lower altitudes until it merges, at sea level, with the arctic life-zone. So here again the Yukon presents a rewarding field of study—the nature of alpine and arctic fauna and habitats compared, as they approximate one another and ultimately merge. And such a study might provide a clue to the origin of truly arctic-adapted species, which perhaps originated before the onset of the ice-ages and then survived the Pleistocene in the Beringian Refugium.

There is an essential unity of the northern continents at the latitudes of Beringia, and the Bering Strait does not, as is often assumed, represent a separation of two regions, the Palaearctic and Nearctic. Within the confines of Beringia, Lafontaine and Wood have recently (1988) recorded some 245 species of noctuid moths. Of those that inhabit tundra areas, nearly two-thirds are more or less widely distributed on the tundra of both Palaearctic and Nearctic. Among the taiga species, however, only one fifth are common to Palaearctic and Nearctic, but more than half the remainder are members of closely related Palaearctic/Nearctic species pairs. The considerable uniformity of the tundra faunas indicates a significant freedom of movement in Holocene or Pleistocene times, whereas the taiga faunas of the New and the Old Worlds, adapted to warmer conditions that existed, at best, only marginally in the Beringian refugium, have been separated for a longer period of time; they indicate, in fact, the average time required for the development of daughter species in the subarctic (high boreal) life zone.

Not all the tundra fauna of Beringia have wide external ranges. If the noctuids of the dry tundra are considered separately no less than 20 of the 33 species are ‘Beringian endemics’, species that have not extended their range since deglaciation. They include a significant number of species with remarkable modifications, adaptive as noted earlier by Downes (1964). Not only do they show the ‘ellipsoid eye’ condition—a condition related to flight in broad daylight, an inevitable necessity for both arctic and alpine forms, for somewhat different reasons—but also species with non-flying females, usually with conspicuously reduced wings (brachypterous); species with translucent wings, the pigmentation and pattern reduced and wing-scales curling upward, not lying flat as usual; species with an abbreviated adult life span, the female releasing sex pheromones and the male assembling sometimes even before the female has emerged from the pupa; the eggs already mature on emergence and quickly laid, the adults non-dispersing, non-feeding, and probably short lived. Several of these species, inhabiting scree slopes and mountains, have been discovered only very recently.

Such restricted Beringian endemics, with their deep adaptations of structure and behaviour to life in the arctic, may be relatively old species, older than the Pleistocene ice-ages or even than the lowland arctic environment itself, formed some 3 million years ago. They may, in fact, be alpine rather than arctic in origin; as noted above, the habitable alpine environment converges to that of the arctic in northern latitudes.

These reflections are not entirely new; they derive also from the background of knowledge of arctic insects. Together they suggest that the insects of the Beringian Yukon provide questions and insights over many fields of interest: the basic tally of the species; their bionomics, life-cycles, niches, habitats and life-zones; evolutionary and geographic relationships; rates of evolution; subarctic, low arctic and high arctic environments; arctic and alpine adaptations to adversity; the geography and history of Beringian environments; subfossil and fossil insects; glacial and interglacial stages in Beringia; Holocene climates and habitats, and climatic change at the present day.

The insects of the Yukon represent also a second centre of interest in the much more diverse and numerous fauna of southerly type. Species of subarctic and boreal adaptation predominate extensively in the southern and southeastern Yukon. Most of them extend also far beyond the Yukon, into southern Alaska, British Columbia, the Mackenzie Valley, and the southern Northwest Territories; some are transcontinental or even Holarctic. This is the fauna that in glacial periods seems to have populated the lands to the south of the Laurentide and Cordilleran ice sheets, and that moved northward, towards the limit set by its boreal adaptation, to encounter the Beringian fauna more or less along the existing treeline. At the present time it dominates the southern Yukon and from there probes northward in the river valleys and lowlands, gradually restricted by the more severe climate, almost but not quite to the coast of the Arctic Ocean. Questions of the same type arise again: how many species, what are their external ranges, do all come from south of the ice sheet or were there smaller refugia elsewhere, and correspondingly, were there also some arctic-adapted species in that southern refugium? How were they affected by the complex course of deglaciation and the succeeding climatic changes; what routes were imposed on the faunal movement by climate or physiography or the pre-emptive settlement by pioneers; what of the inevitable mixing and hybridization, and of adaptation to regional climatic differences and to the continuing change in the light regime? And within the boreal zone in the Yukon there are isolated islands of a variety of very distinctive habitats, each with its own fauna and history—sandhills, the most northerly saline pools and flats, the most northerly cat-tail swamp, the most northerly hot springs, and so forth.

Species of the boreal forest that are common to both the Nearctic and Palaearctic regions may have established, or perhaps re-established, a range through Beringia only in recent times; it would be interesting to find them there also as fossils of interglacial age. But many boreal insects are represented in the Old World by a sister species, and the two stocks must surely have been distinct already at the onset of the Pleistocene glaciations and have not made contact since.

Nearly all of Canada and even the north-central States was ice-covered during the last (Wisconsinan) glaciation, except perhaps for a few limited and probably specialized coastal areas. Schwert and Ashworth (1988) have found treeline and arctic adapted species as subfossils immediately south of the continental ice sheet, followed successively by more definite zones of subarctic and then of merely cool-temperate species. The arctic-adapted species (in Iowa!) disappeared somewhat before the actual retreat of the ice front, apparently being overtaken by the climatic amelioration that first thinned the ice sheet before new habitable terrain was actually exposed; but the subarctic and boreal forms moved northward as the ice retreated to form in due course the main origin of the subarctic and boreal fauna of the present day.

To east and west, however, the north-south running mountains, the Appalachians and the Cordilleran complex, seem to have provided refugia in which populations could move to higher elevations as the general climate became warmer, and thus avoid extinction as the glaciation receded. Among the butterflies, for instance, species of *Boloria* and *Oeneis* persist on Mt. Washington, in the Gaspé and in southern Labrador and in the Rockies from Colorado northward, far to the south of their main present-day lowland ranges in the treeline and low arctic life zones. How can we distinguish these species (or populations) from those that 'wintered' in Beringia? Some species have perhaps been pushed southward and then spread north again in each successive glacial/interglacial phase; others may have lived as isolated endemics throughout the Pleistocene in southerly, mountainous regions; certainly *Gynaephora rossii* now has distinctive populations, unlike the lowland form at treeline, both on Mt. Washington and in the Rockies, and another, even more distinctive, in alpine areas in Hokkaido (northern Japan). Perhaps there is a general problem of the adaptive differences between alpine and arctic species, differences which, if they exist, must become progressively reduced northward. One must wonder how many interesting forms remain undiscovered at middle elevations in the Yukon, and what the Cordillera may represent as habitats or as routes of faunal movement; these are among the least studied aspects of the inland Northwest, with surprises yet to come.

The wide valleys of the southern and central Yukon are accessible from similar areas of British Columbia and probably from the middle Mackenzie. As would be expected, they have a mainly boreal fauna. Fully glaciated during Wisconsinan times, their fauna presumably represents the extended northward thrust of the boreal fauna from south of the continental ice sheet, even from south of 40°N. Continuing northward in narrowing galleries, it becomes a main element of the fauna of the Old Crow basin, at 68°N, the northern limit of the boreal fauna at this epoch. Some of its species have wide southern ranges, mainly western but others transcontinental and familiar to entomologists both from Edmonton and Ottawa.

This vast movement of subarctic and boreal insects from south of the ice-front towards their appropriate northern habitats and life-zones must have been extremely complex, but we know little about it. The process would not have been at random. The settlement of the Canadian landscape as we know it today, all within a few thousand years, would have been a subtle interaction of species and populations and habitats of considerable intricacy; probably, moreover, it is not an end result but rather a moment only in the development of equilibrium between the insects and the climate. The Richardson Mountains may have impeded the escape eastward from Beringia; and the Vancouveran fauna of the extreme west has been almost completely separated from the boreal-adapted fauna of the southern Yukon for over 500 km by the St. Elias mountains and icefields. In brief, the boreal and subarctic insects have provided the arena, mainly in the period 14 000–7000 B.P., for complex faunal changes involving mixing, adaptation, and evolution at the infraspecific level on an immense scale—for the boreal zone alone these movements would have involved an estimated 22 000 species (Danks and Foottit 1989). And it is in the Yukon also that the members of this southern fauna come most intimately in contact with species and populations of Beringian origin.

This book records a large part of the work of the 'Yukon Project' to date, but for the most part the study of the insect fauna of the Yukon—perhaps the most complex but least known natural area of Canada—lies ahead.

References

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