

ORIGINS OF THE NORTH AMERICAN INSECT FAUNA

INTRODUCTION AND COMMENTARY

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Background to the symposium

In 1929 and again in 1940, E.C. Van Dyke published interesting general discussions of the geographic relationships of the insects of North America, with special reference to the Coleoptera but considering also a number of other groups. These papers, perhaps more than any others, established a place for biogeographic studies of insects on this continent, and they have been succeeded by other valuable contributions including those by Ross (1951, 1953, 1967), Edmunds (1972, 1982), Halffter (1974, 1987), and Ball (1963, 1970).

When the Biological Survey of the Insects of Canada was organized in 1977, it was soon realized that continuing studies of the origins and history of the insect fauna were very desirable. One attempt to meet this need was the symposium held in Ottawa in 1978: *Temporal and Spatial Changes in the Canadian Insect Fauna*, published in *The Canadian Entomologist* 112, No. 11, 1980. That symposium was introduced by a paper by J.V. Matthews, Jr., a palaeontologist, who described the events that have shaped North America in terms both of plate tectonics and of the climatic changes, and drafted the account with the particular interests of entomologists in mind. Simultaneously, Matthews prepared a second, more extensive, paper on the same theme for *Canada and its Insect Fauna* (Memoirs of the Entomological Society of Canada 108, H.V. Danks (Ed.), 573 pp., 1979). The present group of papers continue the same themes, and were presented as a symposium at the joint meeting of the Entomological Society of America, the Entomological Society of Canada and the Entomological Society of Ontario in Toronto in 1982, under the title *Origins of the North American Insect Fauna*. The ambitious — or presumptuous — title is a statement only of the underlying aim, and the nine papers make up only a series of elements or views within the broad theme. Again Dr. Matthews provided an introductory statement, which recapitulated, for the audience, his earlier papers but was not intended for publication. The nine papers that followed take up the theme successively at the southern and at the North Atlantic portals, the Arctic, Beringia, and the West Coast; they range over many systematic groups and they include accounts of the long-term geographic history of an ancient family of mayflies and of two small orders that illustrate how the fauna of the present day may have originated in remarkably different ways depending on the history or mode of dispersal of the group, and other more detailed studies of the dispersal of particular groups of species in glacial and post-glacial times. Relatively slight attention is given to the inflow by southern and Caribbean routes. There exist, however, the very important papers on these areas by Halffter (1987), Ball (1970) and other entomologists, as well as the recent general survey of the Great American Biotic Exchange edited by Stehli and Webb (1985).

All the papers make use, more or less explicitly, of two major advances in recent decades, in the earth sciences and in biology respectively. On the geological side is the discovery of plate tectonics, the large-scale and continuing crustal movements that reshape the oceans and continents on a determinable time-scale. On the biological side there is

Hennig's new clarity of purpose and methodology in systematics, insisting that the foundational relationship of any two groups of organisms is their origin from a common ancestor at a particular period of time. These two historical processes, coordinated, delineate the evolutionary history of life on earth, the subject matter of biogeography.

It remains to note, and to apologize for, the considerable time that has elapsed since the papers were presented. All papers, however, have been seen and reconsidered by the authors at various times since the symposium took place (see dates of receipt of the final drafts), and, at their discretion, some have been considerably elaborated.

We acknowledge with thanks that H.V. Danks and J.R. Vockeroth read this introductory paper in draft and offered many useful comments.

Geographic history and life zones

Matthews (1979, 1980) consistently adopts an approach that brings together geographical facts and the characteristics of the life zones or climates. Both are essential in biogeographic interpretation. During the earlier part of the development of the North Atlantic Ocean there remained for a time the more or less complete land connections between Europe and North America known as the DeGeer Bridge, in the far north, the Greenland–Faeroes Bridge, and the Belle Isle–Rockall Bridge. The DeGeer Bridge existed in the Eocene and Oligocene periods, and spanned from Ellesmere Island through Spitsbergen to northern Europe. Deposits of fossil plants in these areas give evidence of warm temperate, or in some cases almost subtropical, climates. Almost without doubt the DeGeer Bridge was an important highway, uniting and serving for the exchange of the faunas of Europe and North America for a long period of time; but the fauna and flora it served have probably left no trace in those that exist in the same areas today. Rather, their descendants are to be found in warm temperate areas, in the Carolinas for instance, 5000 km or more to the south of Ellesmere Island. Similarly, Beringia, the land area encompassing eastern Siberia and northwestern North America, became cooler through the Tertiary period, apparently serving, step by step, as the habitat of progressively less warm-adapted biota. Thus Linsley (1963) has pointed out, using examples from the Cerambycidae, that vicariant groups of insects in eastern Eurasia and North America tend to become more distantly related to one another towards the south — vicariant species in cool temperate areas, British Columbia for instance, and vicariant genera in the warm temperate forests of central China and the southern Appalachians. As the temperature of the north decreased through Tertiary time, so the gradually evolving insects sought the life zone to which they were adapted in progressively more southerly areas. Today, Beringia has again become somewhat warmer than it was in full glacial times when it served as the refugium for tree-line and low arctic species. Many of these species are now dispersed across the tundra of northern North America; in its turn Beringia is receiving subarctic and cool temperate species from the south, some of which will probably pass over to Eurasia in the course of time (Lafontaine and Wood 1988).

The life zone concept, of which daily and seasonal temperature is perhaps the most important element, lies close in the background of many of the following papers. Life zones are not defined by sharp discontinuities such as a coastline or a range of mountains that evidently impede further dispersal, nor are they identical for all organisms. Indeed, each species has its own requirements of physical and biotic habitat, any feature of which may set a limit, usually somewhat gradually, to further dispersal. One of the lessons of recent Beringian studies (see Matthews 1980, p. 48) is that most species respond to changed conditions independently, not in "faunas" or "floras" as such. Nevertheless, the life zone can be described and identified as a phenomenon of the statistical type that sums up the geographic aspect of the habitat requirements of many species with differing but similar needs. The concept takes its place as the summary description of the wide environmental impedences to further establishment encountered over the land surface generally. Indeed,

the "barrier" presented by a mountain range is no more than a close-set series of such environmental effects, and according to its height it will be a barrier to warm-adapted species only, or also to boreal forms, or also to arctic ones. (A range running north and south, moreover, can serve as a pathway in either direction.) Again, a seacoast is a barrier only to insects restricted to a solid substrate. In the far north, where the snowfall is light, seasonally frozen channels such as those between the Canadian arctic islands are negligible as barriers, as plant fragments and soil and any associated insects are readily dislodged and blown across, safely frozen, by winter winds (Savile 1961). Insects adapted to fly in moderate winds, and so to be picked up by local rising air, may traverse hundreds of kilometres in a few hours and establish themselves across open seas (see Downes 1988). All geographic limitations, whether life zones or barriers, derive from the behaviour or ecology or physiology of the species. The poles of opinion in discussions of the relative importance of history and ecology in determining the presence or absence of a species (e.g. Danks 1979a, pp. 203–205; 1981, p. 362) can perhaps thus be brought closer together.

Neither the ranges of individual species nor the resulting life zones are adequately defined by the simple flowing lines shown on many maps. Especially when a species is being studied in detail, the limits of its range may be found to be quite complex, relating to changes of rainfall, exposure, soil type, vegetation and so forth. Thus a large fauna adapted to the Low Boreal or Canadian Zone has moved northward in post-glacial times and reaches, in the northwest, even beyond the arctic circle. At about the level of the southern Yukon (lat. 60°N), however, many of these species have become restricted to lower elevations, predominantly the wide and well-drained plains that fringe the larger rivers; whereas further north they become restricted to narrower tongues, and eventually to especially favourable and somewhat temporary patches of well-drained, well-insolated banks of riverside gravel loosely consolidated by herbaceous plants and small alder or poplar thickets. Danks (1979b, pp. 557–559) discussed this attenuation and fragmentation — and perhaps specialization — of populations at the "edge" of their range, not only at the northern limits but also as a general phenomenon. The edge of the range of a species is not a discrete boundary; rather the options for maintenance of a population are reduced gradually as the limit is approached. Such considerations, perhaps familiar to the ecologist, may be equally significant for the biogeographer. Clearly they make significant contact with concepts such as "filter-bridge" and "sweepstakes route".

The foregoing discussion assumes not only that a species is generally characteristic of a particular life zone or other area with a somewhat restricted range of climatic variation, but also that the genus or other higher taxon to which it belongs is similarly, if perhaps rather more broadly, restricted. This stability is also presumed to have been maintained, in general, over time on a geological scale. Thus the tulip tree, *Liriodendron*, is found as an Eocene fossil in what is interpreted on other grounds as a warm temperate (or even warmer) environment at lat. 75–80° N; and today it occurs in warm temperate North America and eastern Asia, some 40° to the south. Even more remarkably, the Plecoptera seem to have remained a very predominately cool temperate group, in both hemispheres, ever since the division of Pangaea (Hynes 1988). In the present symposium this strong tendency to stability of climatic adaptation is assumed and used very frequently, yet few authors refer to it explicitly, or attempt to define its limits.

The importance of habitat suitability for successful colonization is illustrated further by the mayflies of the West Indies (Peters 1988). The fauna is Neotropical in origin, but is characteristic mainly of mountain streams. None of these species, widespread in the Antilles, have been found in Florida (or elsewhere in the United States) apparently because of the lack of appropriate habitat throughout that long, low-lying peninsula. This contrasts strongly with the intimate faunal connection between the West Indies and Florida in many other groups, for instance the coastal mosquitoes and biting midges.

Ancient groups: the complexity of faunal origins

The history of the older groups of insects in North America has been influenced by the division of Pangaea and subsequently by the different, and in each case complex, geological and climatic developments of the southern and northern land masses. Not surprisingly, these older groups show a great complexity of faunal origins, differing widely from one instance to the next. They are represented in this symposium chiefly by the Leptophlebiidae, one of the most ancient, widespread and diverse families of mayflies (Peters 1988) and by two small and archaic orders, the Mecoptera (Byers 1988) and the Plecoptera (Hynes 1988).

The Leptophlebiidae are probably pre-Cretaceous in origin. The two main subfamilies, as currently understood, seem to date from the mid-Cretaceous; one of them, the Leptophlebiinae, has remained a northern, Laurasian group, and the other, the Atalophlebiinae, is less restricted but very predominantly southern (Gondwanian). With the opening of the North Atlantic, the Euramerican fauna of leptophlebiines would have been divided, and evidence of trans-Atlantic vicariance among existing forms is forthcoming; and in later Tertiary times, others reached western North America by way of Beringia, probably on more than one occasion. In the south, part of the Gondwanian diversity (Atalophlebiinae) reached tropical and subtropical South America, whence more recently three genera have spread into North America, in each case through Mexico rather than the Caribbean. One of these genera probably reached North America in mid-Tertiary times, the other two much later, after the final development of the Isthmus of Panama. Thus the relatively small North American fauna has developed by a variety of routes over a long period of time.

The Mecoptera are an ancient order of endopterygotes now reduced to a number of rather distantly related relict groups. The relationships of the various families are gradually being clarified, but without firm knowledge of when or where they originated. Three families — Panorpidae, Panorpodidae, Boreidae — are purely Laurasian in range; four others are purely Gondwanian; one, Bittacidae, is now worldwide in temperate and tropical areas but with an evident centre of diversity in Gondwanaland; and one, Meropeidae, consists of two relict genera only, one in eastern North America and one in western Australia. Most of the genera, throughout the order, appear to be rather old, and each genus (or sometimes species group) has its own distinctive range and probable history. In *Boreus*, a northern-adapted genus, several species groups have crossed Beringia independently, and there may be a tenuous connection at the present day. This relatively simple statement about *Boreus*, however, must not be taken as applicable to the family as a whole. The recently described genus *Caurinus*, found in Oregon and placed in a new subfamily, is so distinct that the possibility must be entertained that its occurrence within the main range (and habitat) of *Boreus* is merely coincidental. In *Panorpa*, and in the small endemic genus *Brachypanorpa* (Panorpodidae), the trans-Beringian movements would probably have been earlier than in *Boreus*, and the distinctiveness of the North American subgroups is greater. *Panorpa* in North America is essentially eastern, and it must be assumed that earlier western populations failed to contend with the changing climates and the resulting reduction of the deciduous forest; *Brachypanorpa*, however, survives both on the Pacific coast and in the Appalachians. There are no indications of trans-Atlantic movements in any of these groups.

The probable history of *Bittacus* contrasts strongly with that of these northern Laurasian groups. It seems to be an old and complex genus, originating in the south and spreading through tropical Gondwanaland before the separation of Africa and South America, and reaching North America mainly through Mexico.

The Plecoptera have followed their own distinctive course. With a basic adaptation to the cold stream habitat, the order was divided by the separation of Laurasia and Gondwanaland and its bipolar structure remains almost intact to the present day. (There is one

exception to this; certain members of the Perlidae established themselves in tropical regions, and one of them, the genus *Anacroneuria*, later reached North America through Mexico.) In the North American fauna there are pre-North Atlantic elements that are shared with Europe. Then, as the Cordilleras developed and provided extensive suitable habitats, an inflow from eastern Asia took place and is now represented by numerous and successful endemic western genera. In recent times, several mainly boreal genera and species entered North America through Beringia as the Pleistocene glaciation dispersed, and a corresponding westward movement took place from North America towards Beringia. Overall, the large number of small endemic groups, both at the generic level and, much more recently, at the specific level, has become a significant feature of the order in North America.

North-south vicariance

The north-south vicariance that is so striking a feature of the cool temperate adapted Plecoptera implies a movement across the equatorial region by cool-adapted forms. This process has rarely been explored in detail, but is not, however, a very rare phenomenon in old groups of insects. Crowson (1980) has pointed out that there is a similar temperate or cool temperate vicariance in a number of families of beetles, although in these cases it is usually at about the tribal level. He correlates this, tentatively, with a significant decrease in the temperature of equatorial seas in the last epoch of the Cretaceous period (see Stanley 1984). It is interesting to note that there are also a number of families of primitive Diptera, well represented in North America, which show this same north-south vicariance, at a similar level. Examples include the Thaumaleidae, Tanyderidae, Dixidae, Simuliidae, and Chironomidae (Podonominae and Diamesinae). The Simuliidae are especially interesting because the most advanced forms (*Simulium* and allies), which make up a considerable majority of existing species, have very successfully recolonized, in their later evolution, the warm temperate and tropical regions of the world.

North Atlantic vicariance

The sea-floor spreading, extending from the south northward, that gave rise to the North Atlantic Ocean, established a system of vicariance throughout the area; from then on the fauna was divided and the vicariants evolved independently. Up to the Late Cretaceous western Europe and eastern North America had been contiguous, forming a continent, Euramerica, bounded in the west by the Mid-continental Seaway and in the east by the Turgai Straits. From that time on, however, the fauna was divided, and the vicariants evolved independently. The effect of this division has already been noted in the Leptophlebiinae and in the northern Plecoptera, but in general the effects of North Atlantic vicariance have been little explored, and the work is difficult because of uncertainties both in the geographic history and the phylogenetic reconstructions. Noonan (1988), however, is able to draw together cases from six different orders of insects in which vicariance can be demonstrated on the two sides of the Atlantic Ocean, with the eastern American and European vicariants more closely related to one another than to the forms occurring in the American west. They include the interesting case of the aphids of the tribe Callaphidini, which are associated with deciduous forest trees. They had been studied in some detail by Richards (1965) who had proposed, before the ideas of plate tectonics had been clearly developed, that these aphids, and their host trees, were in contact in far northern temperate climates up to mid-Tertiary times, across the DeGeer Bridge. Through the continued cooling at high latitudes they have since been forced southward and today are to be found, still associated, in the widely separated temperate forest areas of North America and middle Europe.

The North Atlantic islands: recent long distance dispersal

The land bridges of the early Tertiary North Atlantic have long disappeared and at the present time at around 60°N latitude there are three islands of significant size — southern Greenland, Iceland, and the Faeroes — separated from adjacent continents and from one another by wide expanses of sea. These islands each have a substantial insect fauna that is nevertheless, by continental standards, small and disharmonic. There are no endemic species; all are found also in boreal (non-arctic) Europe or to a lesser extent in boreal North America. During the Pleistocene, however, these areas and large related areas of the North Atlantic were covered with ice.

The interpretation of these findings (Downes 1988) appears to be that earlier faunas, across the North Atlantic, were essentially eliminated by the Pleistocene glaciation, and that the faunas now established are post-glacial and thus very young. They originated, in the main, by aerial transport, chiefly from northwestern Europe but also from eastern North America. In effect, all these areas have been recolonized as though they were oceanic islands of post-glacial age. A few species appear to have crossed from continent to continent via the islands, which function at the present time as a weak route of intercontinental dispersal, of the "sweepstakes" class. A more general aspect of the study is that a fauna totalling more than 2000 species has been able to establish itself over one or more sea passages, varying from 200 to 800 km in minimum width, in the very short period, in terms of geographic change and probable life of species, of about 10 000 years. This extensive dispersion resulting in recolonization of the islands has established, *ipso facto*, a series of vicariant populations almost isolated from their continental origins, populations therefore that given enough time may generate a series of vicariant species.

Post-glacial recolonization of northern North America

The Pleistocene ice sheets covered almost all of the northern half of the North American continent; they extended up to 4500 km from north to south and almost as far between east and west and covered an area of about 10 000 000 km². The dispersal of the ice and the recolonization of the formerly ice-covered land has taken place very rapidly, beginning some 16 000 years ago and mainly completed by 7000 years ago. The paths followed, the adaptive problems encountered, and the resultant mixing of populations of different origins offer a wide field for ecological, behavioural, and genetic research.

At the height of the Pleistocene glaciation, specifically during the Late Wisconsinan period, a truly arctic fauna existed in a narrow zone along the southern margin of the ice front. Schwert and Ashworth (1988), in their study of the carabid beetles of this fauna in the mid-western United States, have shown that as the ice began to recede these arctic-adapted beetles disappeared almost at once; only the succeeding boreal (northern cool temperate) fauna followed the receding ice northward to become the main source of the boreal fauna up to its climatic limits at the northern tree-line of today. The authors consider that the dispersal of ice was delayed because of its great thickness and that the position of the southern margin of the ice sheet was not altered until the ambient climate had become distinctly subarctic or boreal; in these conditions arctic-adapted species rapidly became extinct. A related phenomenon can indeed be readily observed today, for instance in the western Cordillera, where glaciers flow down from mountain icefields into the boreal forest below, there to be succeeded, within a few hundred metres, by the biota of boreal forest or other decidedly non-arctic ecosystem.

In a generally mountainous region, however, arctic-adapted species would probably not be affected so drastically as they were in the plains. When the climate ameliorated, many of them might have survived by moving to higher elevations, and would thus be able to move northward and contribute eventually to the fauna of the arctic life zone. Other populations would remain to become the high elevation relicts that exist today in the western Cordillera and in the Appalachians. Examples include the moth *Gynaephora rossii*

(Curtis) with alpine relicts both in the east and in the west, and the blackfly *Simulium baffinense* Twinn at high altitudes in the Rockies as far south as Utah and Colorado.

Thus Schwert and Ashworth (1988) consider that although the subarctic and boreal fauna have moved northward from the south, the tree-line and arctic fauna of the present day must have come largely from Beringia, and from there spread eastward, in the same climatic zones, on its release from the refugium.

From a different standpoint, Lafontaine and Wood (1988) have come to similar conclusions. They studied the more than 200 species of noctuid moths that now inhabit the area in Alaska and the Yukon that during the Pleistocene glaciation(s) formed the eastern section of the unglaciated Beringian Refugium. The species in that area that live in taiga, boreal forest or grassland are mainly widespread in cool temperate North America and evidently have entered post-glacial Beringia from the south. The tundra species, on the other hand, are found typically both in East and West Beringia, i.e. in both the American and Asiatic areas of the Refugium. Some of them are restricted to Beringia and not found elsewhere, especially those that are characteristic of bare and exposed rocky habitats (scree, hilltops); but others have spread eastward along and north of the tree-line to varying extents, in some cases reaching even to Greenland. The existence of Beringian endemics, and especially the fact that some of them are highly modified species with brachypterous and flightless females, distinctly suggests a long-term stability of climate and habitat in that area.

Several authors (e.g. Freeman 1958; Vockeroth 1958) have noted that the arctic/subarctic line is the most clearly marked of all transitions between life zones, and that the arctic fauna is, at least to a significant degree, specifically distinct from its subarctic or cool temperate congeners. The observation suggests that arctic-adapted populations are not of Recent origin, but rather that they antedate the Pleistocene and may in some cases go back to the earliest widespread arctic fauna in the Miocene period. Much later, with species-level changes now well established, these arctic-adapted species have by the accidents of ice-age history been released from Beringia eastward onto the newly deglaciated tree-line and low arctic life zones where, very shortly thereafter, they were met by boreal-adapted species from the south. The evidence for these processes relates mainly to the last deglaciation only, but the suggestion implies that deglaciation (from the biological point of view) took a somewhat similar course in each of the several interstadial periods of the Pleistocene, a suggestion that is consistent with the complementary hypothesis that the climate of ice-age Beringia remained relatively stable. There is no suggestion here that the species of the North American arctic have evolved in Recent times from boreal counterparts, as the latter reached the arctic life zone from the south.

In the far West, at the present time, there is a distinctive coastal fauna, the Vancouverian fauna of Van Dyke (1940), lying beyond the main ranges of the Cordillera and strongly influenced by the moist air and moderate temperatures of the Pacific; it extends from south of San Francisco to western Alaska. During the Pleistocene this coastal area, from about 50° northward, had been largely overrun by the Cordilleran ice sheet, with the retreat of the glaciation taking place more or less contemporaneously with that of the Laurentide. The paper by Kavanaugh (1988) discusses the patterns of dispersal that have reestablished a fauna in the post-glacial period.

In earlier work, Kavanaugh had made detailed studies of the phylogenetic relationships of the species of *Nebria*, a genus of carabid beetles represented by many species in western North America and Eurasia. The information is used here to determine the patterns of geographic vicariance among sister taxa, whether of specific or infra-specific rank. It is shown that the main source of the coastal fauna of today was, in fact, the coastal region to the south, with the addition of a smaller number of species from further inland. These inland species, as the ice withdrew, reached the coast through a series of geographic gaps such as the Fraser River Valley in southern British Columbia. In the north, however, the

large ice-free Beringian refugium appears to have contributed little to the present coastal fauna and the few species of Beringian origin have remained restricted to northernmost coastal areas only.

It seems likely that a few small ice-free refugia existed on the extreme coast, or on offshore islands such as the Queen Charlottes (Foster 1965), Kodiak (Ball 1969; Lindroth 1969) and some of the Aleutians (Lindroth 1963). In several cases these isolated populations represent distinguishable species or subspecies which, however, have rarely succeeded in expanding their ranges since deglaciation, but have remained closely restricted to the refugial area. Kavanaugh (1988) suggests that during their enclosure in these small and isolated refugia the insects may have become closely adapted to the rather special conditions, and thus unable to compete successfully with more broadly adapted mainland forms. This suggestion can perhaps be extended also to the much larger Beringian Refugium; a significant minority not only of the Coleoptera but also of the Lepidoptera and Diptera have likewise remained more or less restricted to the area in post-glacial times.

Ancient western relicts

Kavanaugh's paper addresses mainly a Pleistocene and Recent aspect of the development of the western fauna. There is also, however, an entirely different and ancient aspect. In coastal and near coastal temperate forest areas, several isolated and rather archaic genera are to be found, separated by a great distance from the nearest known occurrence of their sister groups which in several cases is cool temperate montane Chile or other regions of austral Gondwanaland. The newly discovered genus of Bittacidae, *Orobittacus*, most closely related to the Australian *Tythobittacus* and the austral Chilean *Anabittacus*, is a case in point (see Byers 1988); another is the ceratopogonid midge *Paradasyhelea* (Wirth 1969) from the Olympic Peninsula and then again in austral Argentina and Chile, New Zealand and Australia; and another, more familiar, example is the trichocerid fly *Paracladura* that occurs in moist forest from California to British Columbia and is found also in austral South America and other sections of Gondwanaland. Another such instance is found in the Tettigoniidae (Rentz and Gurney 1985), in which three newly described genera from central Chile find their closest relatives in certain Australian genera and in the genus *Neduba* of western North America. Kavanaugh (1988) notes also the carabid genus *Promecognathus* found in California, whose sister group is found in southern Africa.

These cases have not been closely studied or precisely explained. Recent geological investigations of western North America have shown, however, that the coastal area of the Pacific Northwest has received substantial accretions of several small plates, which have extended the land surface beyond the Cordilleran region *sensu stricto*. It is tempting to associate the occurrences of these unexpected genera far beyond their "normal" range with this newly developing knowledge of the geological history. However, it is still unclear to what extent these plates, known also as "terranes", may have supported terrestrial or freshwater organisms prior to accretion with western North America, or may have been entirely submerged.

Age of present-day species

Coope (1970, 1979) and Matthews (1979, 1980), working on subfossil beetles in Britain and in Alaska, respectively, found that the species of the present day were usually unexpectedly old, clearly antedating the Pleistocene and some were identifiable even in the late Miocene, 5.7 million years ago. The repeated changes of climate from glacial to interstadial conditions throughout the Wisconsinan glaciation and the earlier changes throughout the Pleistocene caused very great displacements of populations and related changes in the composition of local species assemblages. These changes, however, were not accompanied by any detectable differences in form in the various species, still less by any differences that would be regarded, by the standards of the systematics of living insects,

as signifying the development of new species. Lafontaine and Wood (1988) have come to the same conclusion for the noctuid moths; the arctic species have for the most part trans-Beringian and even circumpolar ranges, and it is only in the taiga and boreal forest, which have been separated from their Old World counterparts probably since the Late Miocene, that numerous American/Eurasian sister-species pairs have developed. Again, Downes (1988) points out that there is no indication of speciation in Greenland, Iceland, or the Faeroes, during the Recent period, but at most only the development of island races in a number of cases, as has happened also in Shetland and Orkney, islands that were in contact with the British mainland during much of Pleistocene and Recent times.

In contrast to these conclusions, Kavanaugh (1988) in his study of the movements of beetles of the genus *Nebria* (Carabidae), Byers (1988) in his comments on the recent history of *Panorpa* (Mecoptera), and Hynes (1988) in his account of the Plecoptera, envisage the generation of distinctive subspecies or closely related species during the glacial and post-glacial (Recent) periods. Byers suggests that a chain of four species of the *subfurcata* group of *Panorpa* may have been generated, in the Appalachian region, as populations moved northward in post-glacial times. Thus, evidence presented in different parts of this symposium, as elsewhere, suggests very different ages of differentiation for extant species. Evidence for the ages of species presently inhabiting northern, lowland areas suggests Late Tertiary differentiation (e.g. Schwert and Ashworth [1988], Lafontaine and Wood [1988]), whereas evidence for the ages of southern forms isolated in montane habitats suggests differentiation in glacial or even post-glacial time (Byers [1988]; Hynes [1988]; and Kavanaugh [1988]). Perhaps rates of speciation have differed markedly in different habitats, life zones, and geographical areas through Cenozoic time. Clearly what is needed are more facts about a greater number of organisms, carefully collected and analysed.

The impact of man

Many of the faunal changes in progress at the present day are on a very different time-scale to those already discussed and are due predominantly to the influence of a single species — our own. Warwick (1980) showed that Nearctic man, settling as long as 2500 years ago in small villages by the shore of Lake Ontario, sufficiently affected the biota so that the changes in the shoreline fauna of chironomids can still be determined by studying the head capsules of the larvae preserved in the dateable silt. With the arrival of Palaearctic man from Europe less than 400 years ago, the more complex social organization and technology produced an almost immediate increase in such effects. From then on the rate of change increased continuously by transmission of useful discoveries by tradition and education, until at the present time new developments that radically alter the ecological valency of the human species take place within a single lifetime and indeed from one year to the next. The main process of change in ecological valency has shifted from the genetic mode — genes transmitted from one generation to the next, available for selection — to the social and electronic, words and signals transmitted among individuals, quasi-instantly.

Spence and Spence (1988) make a very interesting study of the spread of introduced carabid beetles and their effect on the surrounding fauna in areas now being settled by man in British Columbia. They find that at least 20 species of carabids have been introduced recently from western Europe (probably either in the ballast of sailing ships or in imported nursery stock), that these species represent a random sample of the fauna of the source area (at least in body size and taxonomic group representation), but that all are similar in that they characteristically occupy disturbed habitats in the source area, especially those habitats associated with human habitation and modification. In British Columbia, these species have remained strictly synanthropic, and their dispersal and colonization does not follow the patterns of range of the native biota but rather the changing patterns of the activity of man. The authors find little evidence that introduced forms have displaced native

species, except in cities and towns; rather, the effect of these introductions to date has been an increase in the faunal diversity of the region.

In conclusion, the papers presented in this symposium document a complex history and diverse origins for the North American insect fauna — a fauna developed, through both vicariance and dispersal, in response to global and regional geologic events and processes, to dramatically changing climate, and to interactions with other organisms in an evolving biota. New information and insights presented here help to clarify this faunal history, but our understanding of it is still embryonic. An expanded effort is needed to complete our inventory of species represented in North America and of the geographical and habitat distributions of these species. Also critically needed are analyses of the phylogenetic relationships of many more of the taxa represented. These analyses are necessary for the more meaningful interpretation of the zoogeographic patterns and relationships observed, both regionally, within the fauna, and globally, between the North American insect fauna and the faunas of other continents.

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