INSECTS OF WESTERN CANADA, WITH SPECIAL REFERENCE TO CERTAIN CARABIDAE (COLEOPTERA): PRESENT DISTRIBUTION PATTERNS AND THEIR ORIGINS

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Abstract

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Munroe (1956) summarized knowledge of the distribution patterns and history of the Canadian insect fauna; and a general synthesis beyond his conclusions is not yet possible. Results of studies on Nearctic *Nebria* taxa illustrate present distribution patterns and provide clues to the history of the montane fauna of western Canada. *Nebria* species and subspecies diversity is greatest in the Coast/Cascade Mountains just south of Canada and decreases northward. Major centers of endemism are located south of Canada, in the Coast/Cascade and southern Rocky Mountain systems, with minor centers found in western Alberta and the Queen Charlotte Islands. Species and subspecies vicariance patterns link Coast/Cascade and Rocky Mountain systems across the Okanagan lowland; and subspecies vicariance patterns link (1) Coast and Cascade mountains across Puget lowland/Georgia Strait and (2) central Canadian Rocky Mountains and Rocky Mountains of western Wyoming. These and other data presented on *Nebria* distribution patterns and faunal similarities among different mountain ranges and systems suggest that the present montane fauna of western Canada is derived from two source areas—one in the Coast/Cascade Mountain region, one in the Rocky Mountain region, each just south of the Canadian/U.S. border—which were separate and distinct during and after Wisconsinan time. Northern (e.g. Beringian) Wisconsinan refugia apparently did not contribute significantly to the present montane fauna.

The purpose of this paper is to provide a brief overview of present knowledge of distribution patterns among western Canadian insects and origins of these patterns. Because my own field and research experience has been chiefly with montane insects, specifically with montane carabid beetles, much of what I present below reflects this bias and is, in fact, based on some of my own studies. I limit my discussion of the origins of present distributional patterns to immediate antecedents of the latter, that is, to the late- and post-Glacial history of the fauna. I do so because, at least for most of western Canada, present patterns reflect reoccupation of the area from peripheral refugia with recession of Wisconsinan ice sheets. Earlier history is both poorly interpreted at present and of secondary importance in relation to late- and post-Glacial events.

Below, I briefly review previous distributional studies and patterns described from same. I then present results of my own work with species of genus *Nebria* Latreille (Carabidae) as one example of the kind of studies now in progress on the montane fauna of western Canada. I illustrate distributional patterns apparent and discuss inferences that can be drawn from these findings as they pertain to late- and post-Glacial history and, therfore, to origins of the fauna.

History of Distributional Studies on Western Canadian Insects

Although faunistic and taxonomic study of the insect fauna of western North America has proceeded almost continuously since the 1820's, when Russian entomologists first sampled its diversity, relatively few studies have examined extant *patterns* of distribution. In general, such studies require sophisticated and detailed knowledge of a fauna and, therefore, tend to appear only "late" among studies on a particular geographical area.

Composition of the western Canadian insect fauna and distributions of many of its members are not yet adequately known. However, a few remarkable papers have appeared sporadically and provided isolated, but important, generalizations about the fauna. First among these were studies by Van Dyke (1919, 1926, 1940), mainly (but not exclusively) on the Coleoptera of western North America. In these papers, he discussed relationships between this fauna and those of Eurasia and other regions. He also described faunal subdivisions for western North America based on coincident individual distribution patterns of insect species, and coined the term "Vancouverian" fauna for that of the Pacific Coast from central California to southeastern Alaska—an area rich in endemic and taxonomically isolated taxa.

Van Dyke's and other previous studies were summarized in a landmark paper entitled "Canada as an environment for insect life" by Munroe (1956). In it he described generalized distribution patterns of Canadian insects and discussed hypotheses concerning historical development of these patterns. His discussions were necessarily general and, in part, vague; but they remain as relevant today as when they appeared over 20 years ago. He recognized at least 30 patterns and grouped them as follows [numbers in parentheses denote number of different patterns in each group]: "eastern ranges" (5); "northeastern ranges" (2); "central ranges" (4); "western ranges" (5); "northwestern ranges" (4); "boreal ranges" (no divisions); "subarctic ranges" (2); "arctic ranges" (5); and "combined ranges" (3 or more). Distributional range patterns in all but the first two of these groups embrace western Canada, at least in part (see Munroe (1956: 450-459 and figs. 50-61)).

Because the patterns Munroe described represent generalizations based on study of the distributions of numerous taxa, few single taxa should be expected to reflect all the geographical limits of a pattern precisely. Nonetheless, the amount of information embodied in these generalizations is tremendous; and they clearly represent a plateau in our knowledge of the insect fauna. Extensions of our understanding of the present fauna and its origins beyond this level, however, have been and will continue to be slow and difficult. I suggest four prerequisites as essential for significant progress in this direction; namely: (1) continued advance in our knowledge of past climates and biotas through the kinds of studies presented elsewhere in this symposium (see papers by J. V. Matthews, Jr. and Alan and Anne Morgan); (2) more complete and detailed data on present geographical distributions of and geographical variation patterns in individual taxa; (3) accumulation of habitat preference and other natural history data on taxa to facilitate interpretation of present distributions and inference concerning past distributions; and (4) reconstructed cladograms for groups studied, because it is only in a context of cladistic relationships that distributional relationships among taxa can be meaningfully interpreted. A trend among several recent studies is most encouraging because they provide new data which satisfy one or more of these prerequisites. Among such treatments are those for limnephilid and rhyacophilid Trichoptera (Nimmo 1971), alpine butterflies of the Canadian Rocky Mountains (Pike 1978), coccinellid beetles of western Canada and Alaska (Belicek 1976), dytiscid beetles of Alberta and British Columbia (Larson 1975), and for carabid beetles of the *Cicindela maritima* species group (Cicindelini) (Freitag 1965), subgenus *Cryobius* (Pterostichini) (Ball 1963, 1966), and genus *Elaphrus* (Elaphrini) (Goulet 1977). Each of these studies was based to some degree on integrated distributional, natural history, and cladistic data; and each has provided certain generalizations about distribution patterns within and origins of the faunas concerned. Unfortunately, the first four studies noted were broad faunistic treatments of one or more families of insects, each of which appeared in the absence of suitable hypotheses of cladistic relationships among included taxa. Biogeographic implications of results of these studies are therefore more difficult to evaluate than analogous implications from studies with a cladistic perspective because of inherent uncertainty about the nature of taxa considered in the former (see Platnick and Nelson (1978) and Rosen (1978)). These studies serve, nonetheless, as distinct advances in our understanding of the inadequately-known western fauna; but because they are yet so few in number and so different in geographic, habitat, and taxonomic scope, their results are difficult to compare; and a new, general synthesis beyond that provided by Munroe (1956) is not yet possible.

Montane Fauna of Western Canada

Several studies listed above, especially those by Nimmo (1971) and Pike (1978), have dealt, chiefly or in part, with the montane fauna of western Canada. Although relatively little is yet known about this component of the western fauna, I suggest that studies on montane groups will ultimately contribute more to an understanding of the whole fauna than studies of lowland components. My reasoning is as follows. Because geographical and habitat ranges of montane taxa are relatively easily related to present physiographic features, potential routes of dispersal and barriers to same are often more readily apparent for montane than for lowland taxa. Both recognition of present distribution patterns and generation of hypotheses concerning past distributions are therefore relatively simpler for montane groups than for lowland groups.

An understanding of present relationships between montane and lowland faunal components can then be used to generate hypotheses about past relationships of both these components provided that the history of one component (namely the montane) can be inferred. For this and other reasons, I have concentrated my studies on montane groups.

There are several montane insect groups in western Canada which could be profitably studied to elucidate general patterns and facilitate inference on faunal history in general. Among those which come immediately to mind are alpine butterflies, caddisflies, and grylloblattids. However, my own studies have been with carabid beetles of genus *Nebria* Latreille, a Holarctic group of cool- or cold-adapted beetles represented in North America by 42 native species (three of which have Holarctic distributions) and 26 subspecies. Most species are restricted to montane regions, some to the margins of glaciers and permanent snowfields. A large percentage of these species, especially those represented only in alpine and dense forest areas, have members which have reduced hindwings and are, therefore, incapable of flight. Geographical and habitat distributions of species and subspecies are, with few exceptions, known in detail; and a hypothetical phylogeny for the Nearctic species has been proposed (Kavanaugh 1978). The above characteristics make *Nebria* an ideal group for zoogeographic studies in general and particularly for the inquiry at hand.

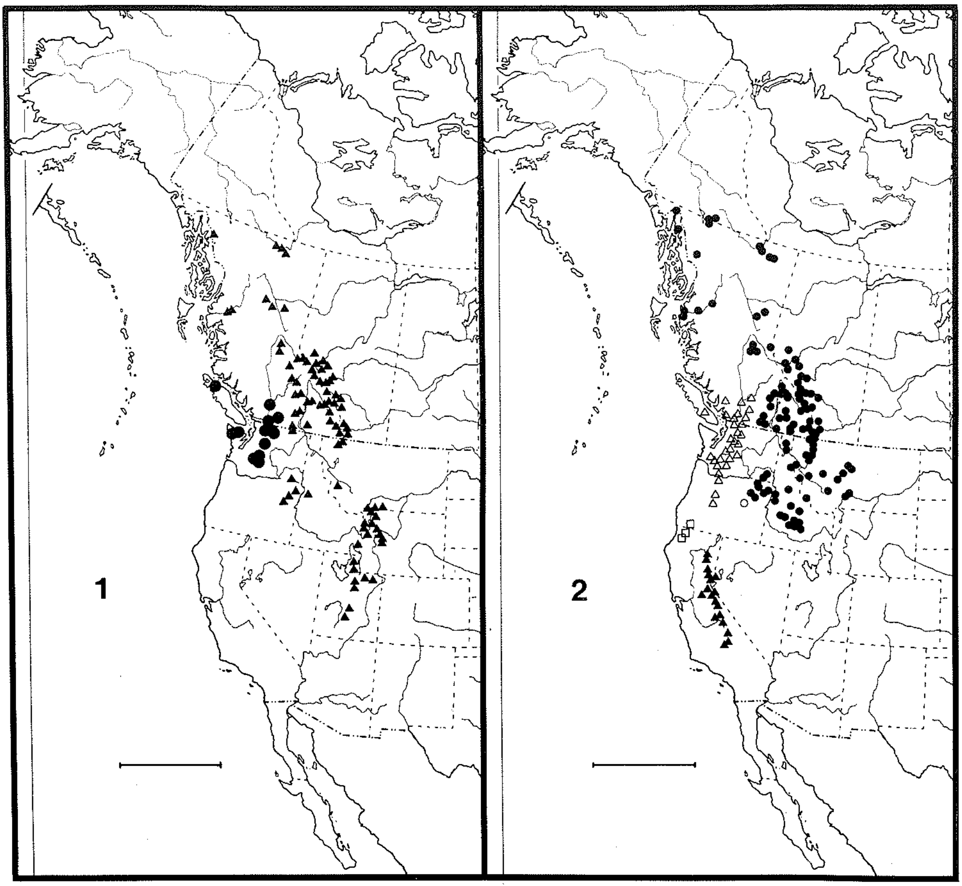
Geographical Distributions of Individual Taxa

Distributions of individual taxa are the data from which patterns can be recognized. Geographical distributions of several *Nebria* species demonstrate certain patterns which may, following future studies of other montane groups, prove to be general patterns of historical significance. In the geographical distributions of both *Nebria crassicornis* Van Dyke (Fig. 1) and *Nebria gebleri* Dejean (Fig. 2), a "vicariance" (or substitution) relationship is evident between respective subspecies in the Coastal/Cascade and the Rocky Mountain systems, separated by the Okanagan lowland (biotically a northern extension of the Great Basin). Of particular interest is the westward extension of the ranges of Rocky Mountain subspecies of both species to the Pacific Coast at and north of the area around Terrace, British Columbia. Spatial relationships of respective coastal and interior subspecies are clear in the Okanagan region (narrowly, but distinctly allopatric) but uncertain in the northwest because of a complete lack of representative sampling from the area between Terrace and Vancouver, B.C. In my opinion, this area is the most important region left to study in western Canada, followed by portions of Yukon Territory, Queen Charlotte Islands, and southeastern Alaska.

The geographical distribution of *Nebria meanyi* Van Dyke subspecies (Fig. 3) demonstrates vicariance between Cascade and Coastal ranges. Members of populations on opposite sides of the Strait of Juan de Fuca (i.e. on the Olympic Peninsula and on Vancouver Island) are more similar to each other (and are therefore treated as members of a single subspecies) than to members from populations across Georgia Strait and/or the Puget lowland. Similar vicariance is evident for subspecies of *Nebria acuta* Lindroth (Fig.4), except that the coastal vicar has not yet been recorded from Vancouver Island. In contrast, the subspecies of *Nebria kincaidi* Schwarz (Fig. 5) demonstrate a conflicting pattern: namely, vicariance of subspecies across the Puget lowland but not across Georgia Strait. This finding is most unexpected because, of the three species discussed, only *N. kincaidi* has members with reduced hindwings. Differential dispersal capabilities cannot, therefore, account for the distributional differences observed.

A north/south vicariance relationship is demonstrated by the subspecies of *Nebria schwarzi* Van Dyke (Fig. 6). This is an atypical pattern for *Nebria* in that ranges of most subspecies of the northern Rocky Mountain region (e.g. see distribution of *Nebria gyllenhali* Schönherr subspecies, Fig. 7) extend south to either northern or southern Wyoming; and related subspecies are restricted to montane areas in Colorado and New Mexico.

Relatively few taxa, species or subspecies, are endemic to western Canada (i.e. to the area north of the U.S. border). This finding could be predicted from what is known about the extent of ice sheets in the region in Wisconsinan time. *Nebria charlottae* Lindroth (Fig. 8) is restricted to this area, where it apparently occurs only on the Queen Charlotte Islands. Its sister species, *Nebria gregaria* Fischer von Waldheim (Fig. 8), is also endemic to a portion of the northeastern Pacific rim (i.e. the Aleutian Islands, Alaska). One subspecies



FIGS. 1-2. Geographical distribution maps. 1, *Nebria crassicornis* Van Dyke. 2, *Nebria gebleri* Dejean. Different symbols denote populations of different subspecies. Scale lines = 500 km.

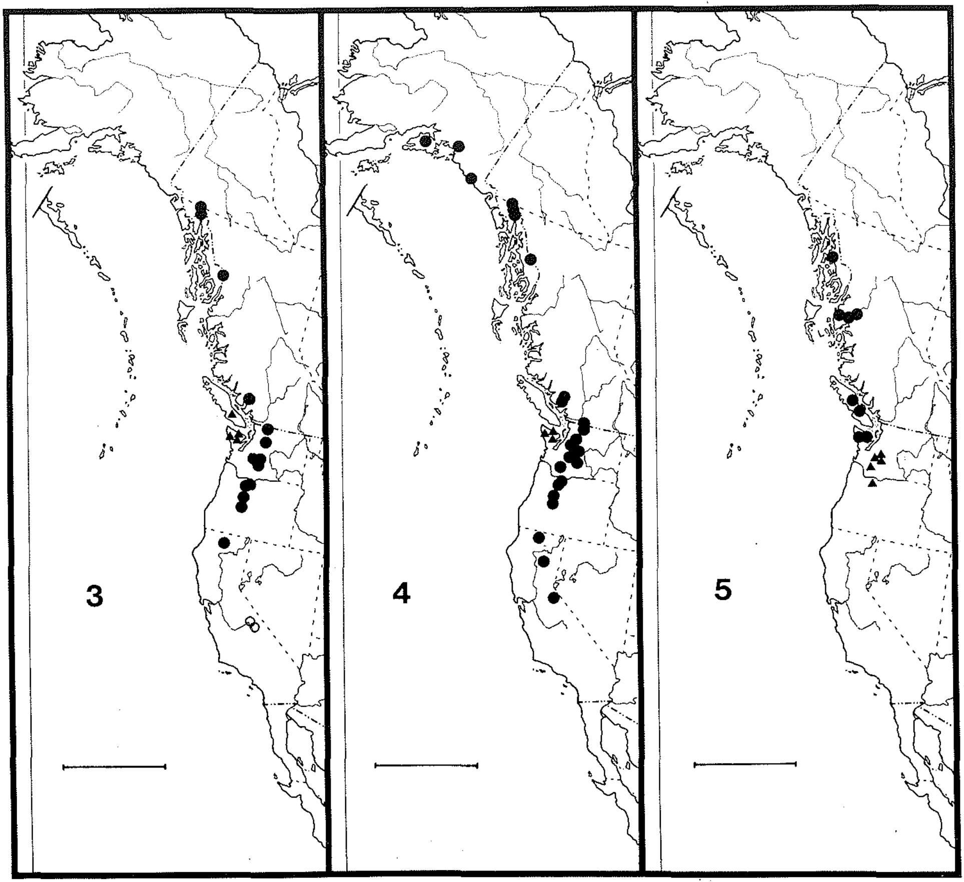
of *Nebria schwarzi* is restricted to the Rocky Mountain region of western Alberta and eastern British Columbia.

Pattern of Diversity

The above examples serve to illustrate the kinds of raw data needed for subsequent analyses of the present fauna and its history. From information on distributions of individual taxa, I have been able to describe the *Nebria* fauna as a whole and derive certain generalizations about it, which, I hope, will be tested by future workers using different groups of organisms. North American *Nebria* species and subspecies diversity is summarized in Fig. 9. Numbers refer to number of different taxa present within a five degree longitude and latitude grid unit. Highest diversity is centered in western Washington, northwestern Oregon, and southwestern British Columbia. Other areas of high diversity include the southern Sierra Nevada (California), central and southern Rocky Mountains, and west-central British Columbia. High diversity in the last-mentioned area is related to overlap of coastal and Rocky Mountain faunas in that area. Diversity decreases steadily, in a classic subtraction pattern, northward and abruptly southwestward and eastward from the Cordilleran region. The fauna of eastern North America is depauperate, even in montane areas.

Centers of Endemism

Centers of endemism are evident where ranges of restricted taxa overlap. To demonstrate the location of these centers, the midpoint of the geographical range of each taxon with maximum linear extent of its range less than 2500 km was plotted. Circles were then drawn

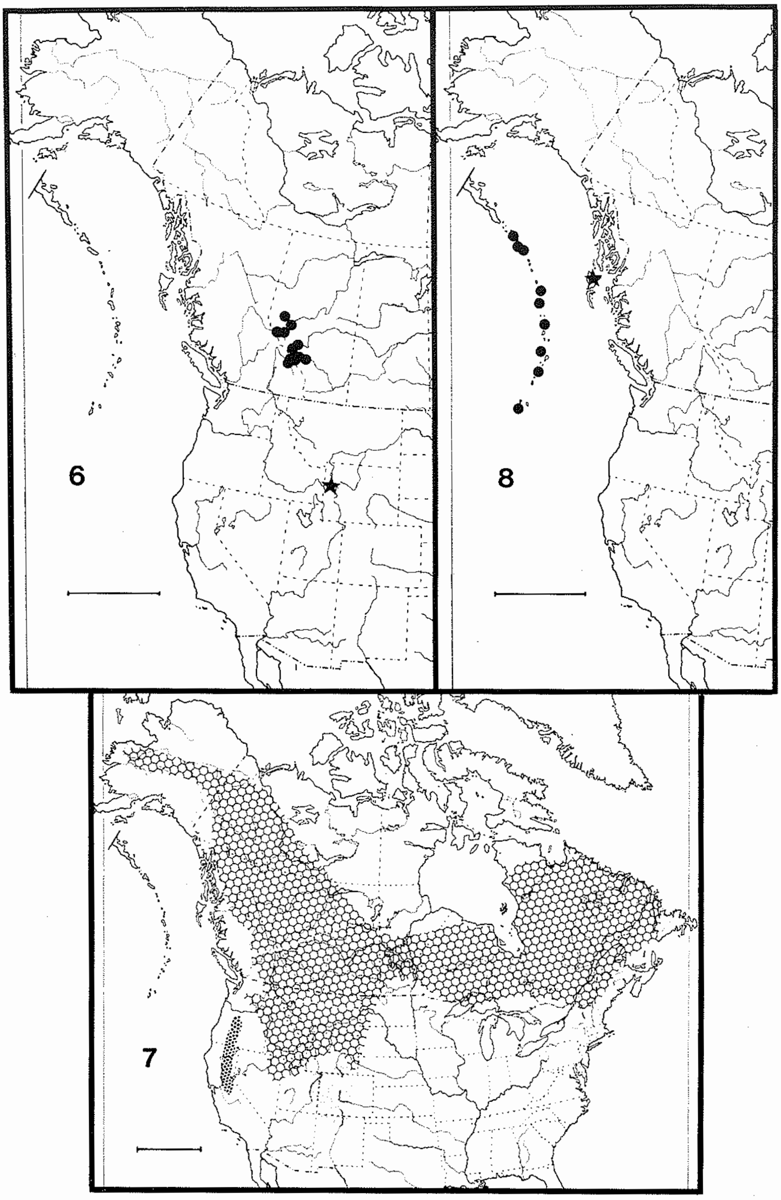


FIGS. 3–5. Geographical distribution maps. 3, *Nebria meanyi* Van Dyke. 4, *Nebria acuta* Lindroth. 5, *Nebria kincaidi* Schwarz. Different symbols denote populations of different subspecies. Scale lines = 500 km.

around these points at radii approximating extent of range, but only up to a 250 km maximum. Centers of endemism visualized through this procedure are illustrated in Fig. 10. Such centers are mainly south of Canada, in the Coast/Cascade and southern Rocky Mountain systems. The center apparent northwest of Vancouver is an artifact of the plotting method, while those in the Aleutian and Queen Charlotte Islands, western Alberta, and northeastern Canada are certainly valid (but each based on a single endemic taxon).

Similarities among Montane Faunas

In order to examine similarities among *Nebria* faunas of different mountain ranges or systems, I found it necessary to classify and code the latter. The code is illustrated, but not described, in Fig. 11. Numbers and letters refer to montane regions and mountain ranges (represented by dark lines), respectively. Systems and ranges thus coded were then compared with one another using two different statistical measures of faunal similarity; namely, (1) Simpson coefficients (Simpson 1960) and (2) Jaccard coefficients (Braun-Blanquet 1932). The Simpson coefficient is equal to the percentage of taxa shared by two faunas divided by the number of taxa in the smaller fauna. If, for example, two faunas have 3 and 10 species, respectively, and all three species in the smaller are shared with the larger, the coefficient equals 100. The Jaccard coefficient, however, is equal to the percentage of taxa shared divided by the number of taxa in the larger fauna. Thus, for the above example, the Jaccard



FIGS. 6–8. Geographical distribution maps. 6, *Nebria schwarzi* Van Dyke; different symbols denote different subspecies. 7, *Nebria gyllenhali* Schönherr; areas shaded differently denote ranges of different subspecies. 8, *Nebria charlottae* Lindroth (star) and *Nebria gregaria* Fischer von Waldheim (solid dots).

coefficient equals 30. When faunas compared are of equal size, the two coefficients are equal. Otherwise, Simpson coefficients tend to emphasize similarity and are useful in relating small, peripheral faunas (such as that on a small island) to diverse faunas (such as in adjacent mainland areas); and Jaccard coefficients tend to emphasize faunal distinctiveness and barriers (see also Murphy, 1976).

Figures 12 and 13 diagrammatically depict the montane regions coded in Fig. 11 and similarities among them based on Simpson and Jaccard coefficients, respectively. In both figures, regions linked by single lines have a coefficient of similarity equal to or greater than

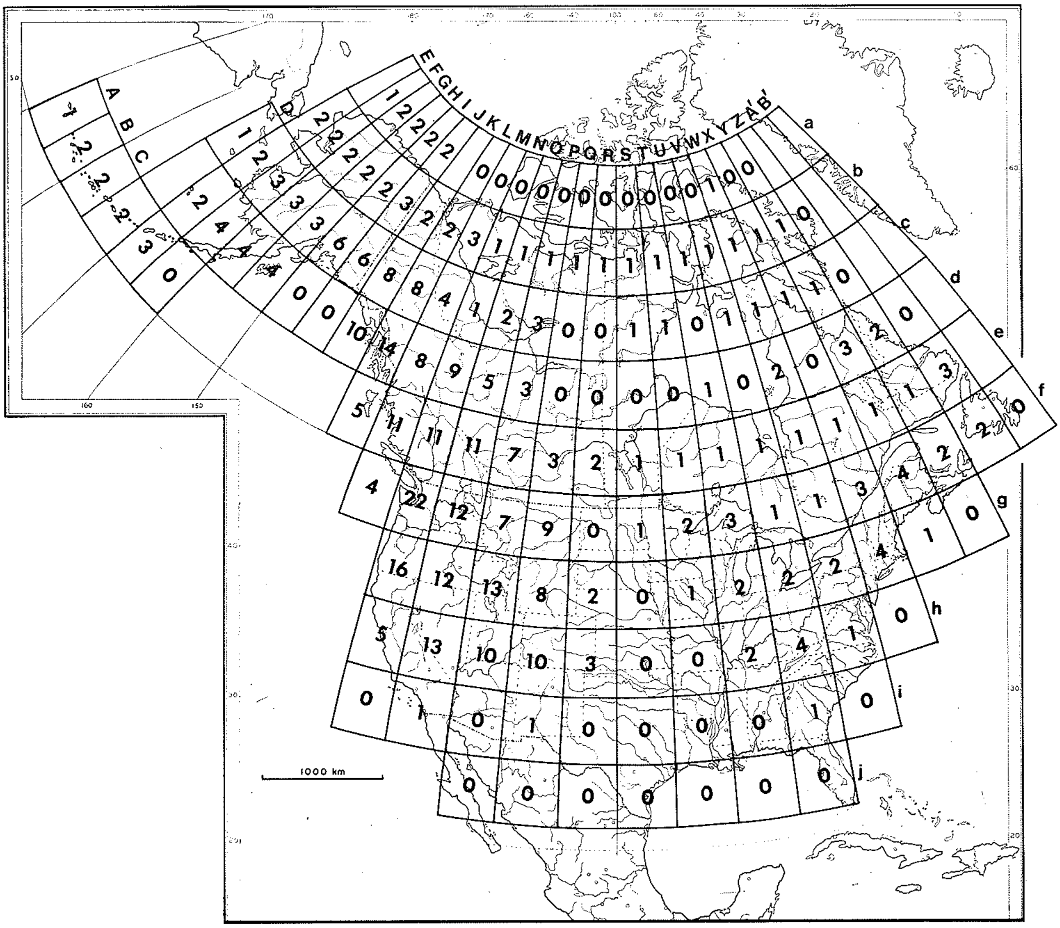


FIG. 9. Numbers of *Nebria* species and subspecies represented in 5° latitude and longitude intervals; capital and lower case letters refer to different intervals.

50; double lines denote coefficients equal to or greater than 75. Simpson coefficients (Fig. 12) demonstrate a relationship between relatively depauperate northern montane faunas and Rocky Mountain montane faunas south of Canada, and to south coastal faunas as well. Jaccard coefficients (Fig. 13) also support strong Rocky Mountain affinities, but these appear related, more precisely, to areas immediately south of Canada and not to the southern Rockies of Wyoming, Colorado, and so on. Affinities with south coastal faunas are also clarified in Fig. 13; that is, they are related to faunas just south of the Canadian/U.S. border and not as closely to those further south. Of interest is the fact that no clear affinities are apparent with the fauna of the extreme northwest (i.e. the Beringian region).

Patterns of Geographical Vicariance

Vicariance relationships among subspecies of certain species were described above. If all such relationships among *Nebria* subspecies are represented on a single map the results are as illustrated in Fig. 14. Dots connected by solid lines represent most proximate localities of respective subspecies pair members of a single species. Lines therefore traverse intervening gaps between subspecies and can be equated with "individual tracks" (see Croizat *et al.*, 1974). This illustrative technique provides no clue to the geographical ranges of taxa, but focuses on gaps between ranges. From Fig. 14, it is apparent that (1) three individual tracks link subspecies across the Great Basin/Plateau Region (including the Okanagan lowland),

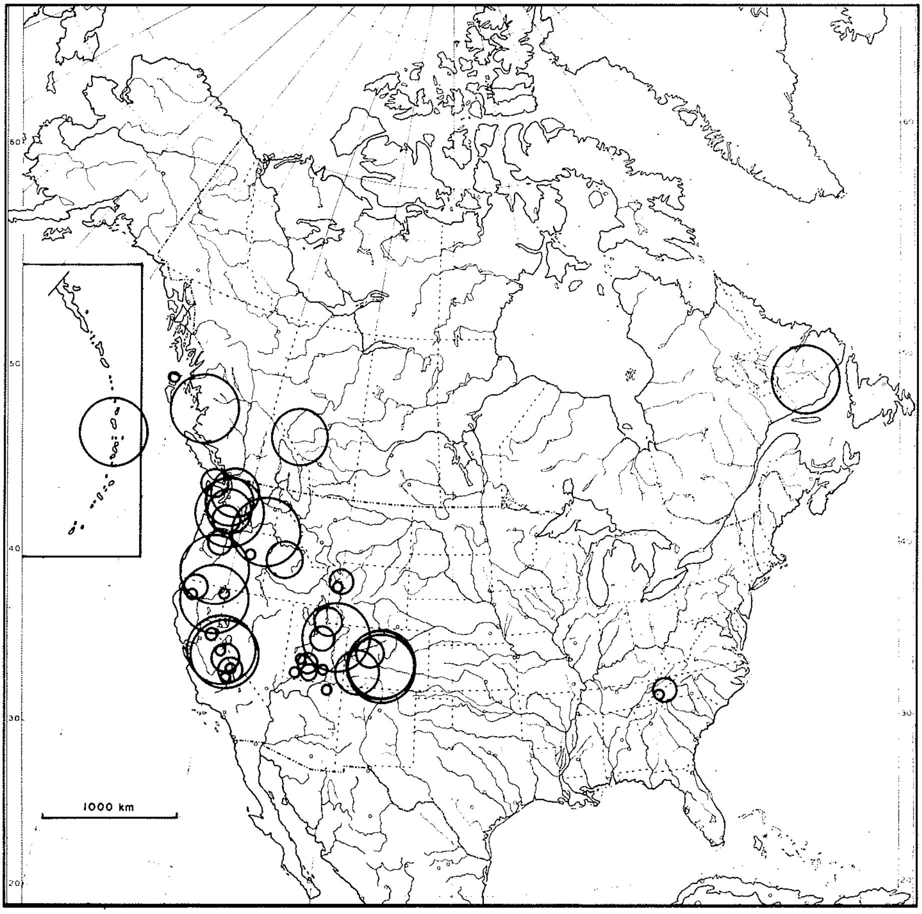


FIG. 10. Centers of endemism among Nearctic species and subspecies of *Nebria*. Circles are placed around centers of distribution of all taxa for which maximum linear extent of geographical range (= m.e.r.) is 1600 km or less. Radii of circles reflect respective range sizes, except that maximum radius plotted is 250 km (i.e. for all taxa with m.e.r. = 250 km or more, up to 1600 km) and minimum radius plotted is about 50 km (i.e. for all taxa with m.e.r. less than or equal to 100 km).

(2) three link subspecies across the Puget lowland, and (3) one links subspecies in eastern Alberta and western Wyoming. Equivalent vicariance relationships among sister species are illustrated in Fig. 15. Two individual tracks link sister species across the Great Basin/Plateau Region, one links sister species in the Aleutian and Queen Charlotte Islands, and one links sister species in eastern and western North America across the Lake Winnipeg region. Coincidence of individual tracks indicates the location of a "generalized track" (Croizat *et al.* 1974). Recognition of the latter is of particular interest because they may denote areas where historical (e.g. geological, climatic, etc.) events affected parts of or entire biotas. The only prominent generalized track in western Canada indicated by vicariance patterns among Nearctic *Nebria* is that across the Okanagan lowland (based on three subspecies and two sister species individual tracks).

Patterns of Geographical Distribution

Based on coincidence in geographical ranges of *Nebria* taxa, several distribution patterns can be recognized. These represent less general, more detailed counterparts of patterns described by Munroe (1956). I have classified these patterns into four groups, namely, (1)

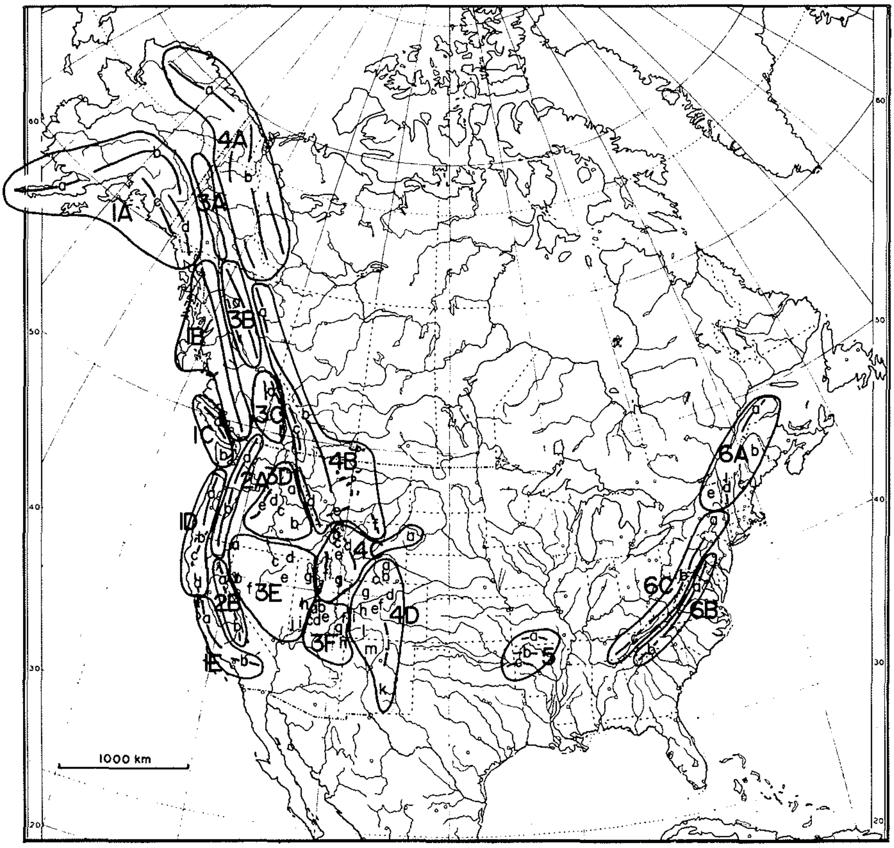


FIG. 11. Alphanumeric code for mountain systems and ranges of North America (here illustrated but not explained).

Northern, (2) Transamerican, (3) Rocky Mountain, and (4) Pacific Coastal patterns. Two Northern ("20" and "21") and two Transamerican ("22" and "23") patterns are illustrated in Fig. 16. Pattern "22" is disjunct, with eastern and western isolates. It is significant, I think, that both Transamerican patterns extend into the Cordilleran region, but neither Northern pattern does so (except in Alaska and Yukon Territory).

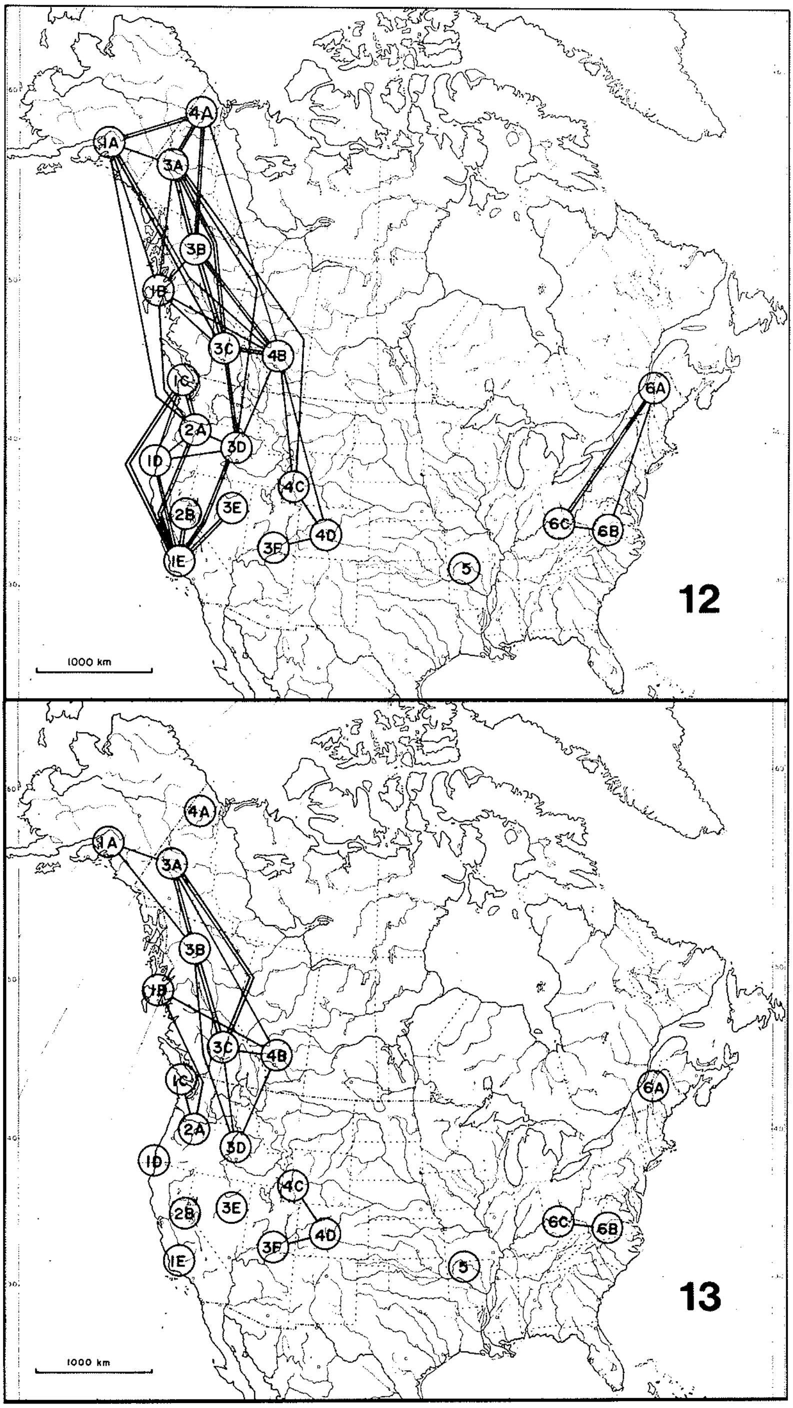
Rocky Mountain patterns are illustrated in Fig. 17. These patterns in general form concentric rings, variously extended north and west, about that portion of the Rocky Mountain system just south of the Canadian/U.S. border. As noted above, all the Canadian portions of these patterns extend to the Pacific Coast at a latitude near that of Terrace, British Columbia, thence north from that point.

Figure 18 illustrates Pacific Coastal patterns which, again, form roughly concentric rings, variously extended north, east, and/or northeast, about that portion of the Coast/Cascade Mountain systems just south of the Canadian/U.S. border.

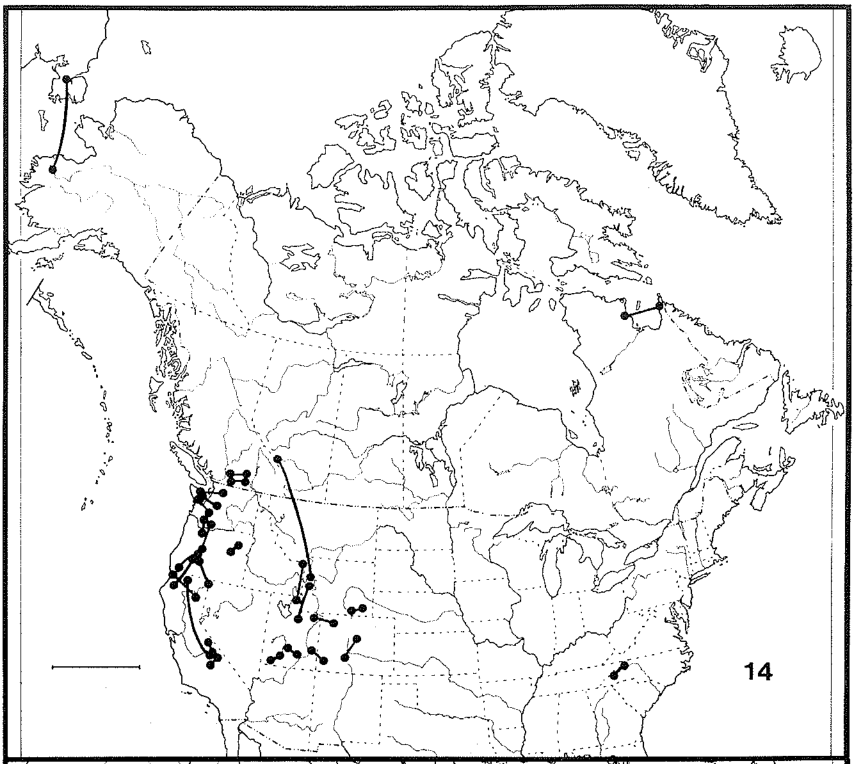
Synthesis and Summary

The kinds of distributional data and analyses presented above can serve as a basis for generation of hypotheses concerning at least the late- and post-Glacial history of the western montane *Nebria* fauna and of the fauna as a whole. Subsequent studies with other montane as well as lowland groups will provide tests of these hypotheses which will either support or require modification of them.

Diversity measures, centers of endemism, faunal similarity measures, vicariance patterns, and generalized distribution patterns outlined above all suggest that affinities of the western



FIGS. 12-13. Diagrammatic representation of *Nebria* faunal similarities, based on different coefficients of similarity, among major montane regions (physiographic units) (see Fig. 11 for illustration of alphanumeric code used for montane regions); single lines link those areas between which coefficients of similarity are greater than, or equal to, 50; double lines indicate similarity values greater than, or equal to, 75 between areas linked. 12, Simpson coefficients (Simpson 1960). 13, Jaccard coefficients (Braun-Blanquet 1932).



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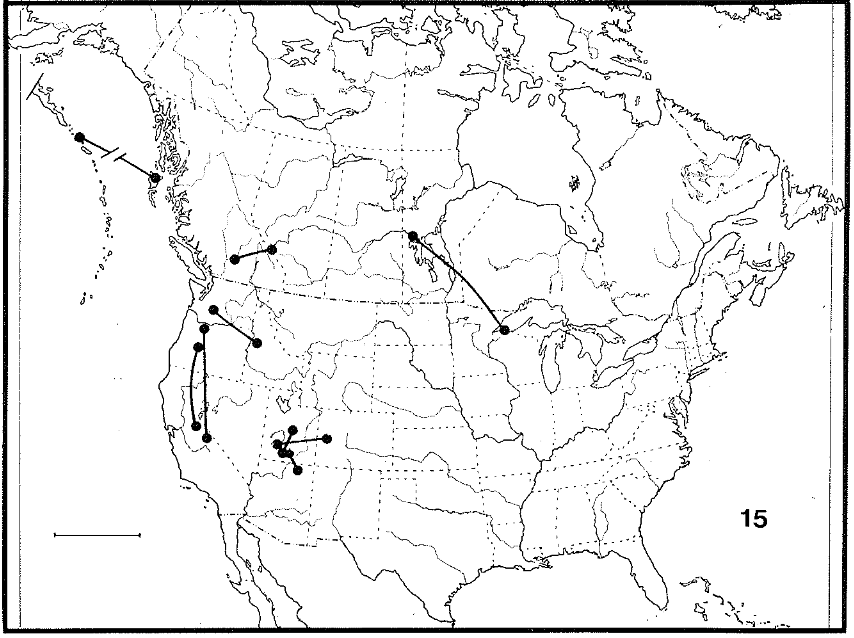

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FIGS. 14–15. Patterns of vicariance. In the following figures, lines connect points which define the shortest distance between respective ranges of vicars (i.e. sister taxa). 14, diagrammatic representation of vicariance patterns among Nearctic *Nebria* subspecies. 15, diagrammatic representation of vicariance patterns among sister species.

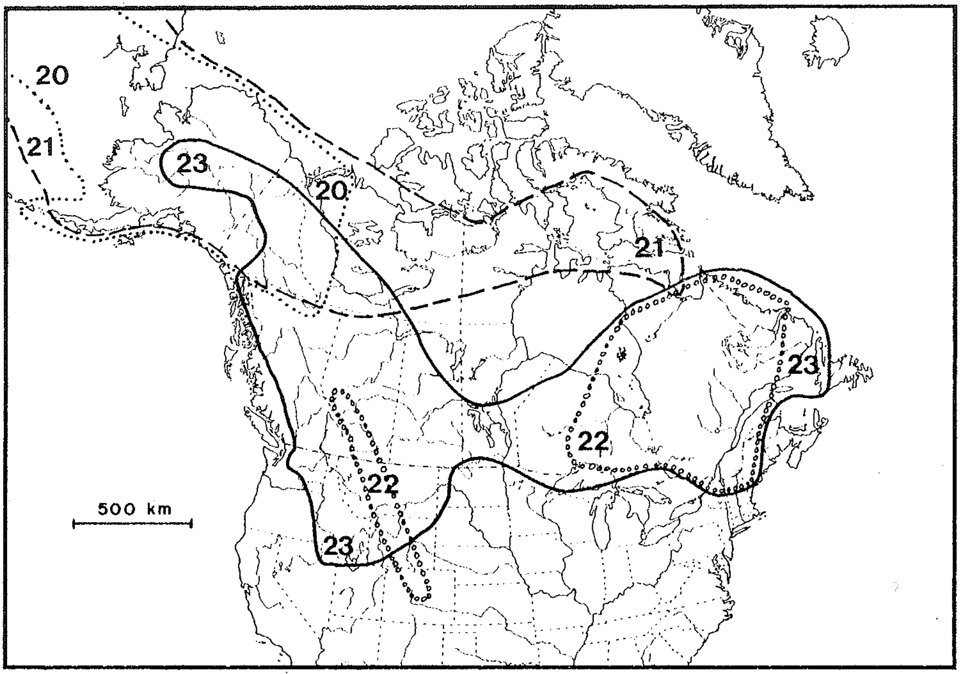


FIG. 16. Northern and transamerican geographical range patterns; pattern 20 = dotted line; pattern 21 = broken (dashed) line; pattern 22 = line of small open circles; pattern 23 = solid line.

montane *Nebria* fauna of Canada are with two, or perhaps three, separate areas south of the Canadian/U.S. border—one in the Rocky Mountains and one in the Coast/Cascade Mountains (Fig. 19). The latter area may actually include two distinct centers, separated by the Puget lowland/Georgia Strait, but present evidence for this is not conclusive. Analyses suggest that the two areas demonstrated served as separate source areas for reoccupation of the mountains of western Canada following the last deglaciation, and, further, that these areas and the respective *Nebria* faunas they contained have remained isolated from each other at least in late- and post-Glacial time. Subspecies vicariance patterns across the Great Basin/Plateau Region could possibly be explained as a product of development of an intervening barrier (i.e. a warm, dry, climatic zone) in post-Glacial time. On this basis alone, the montane fauna south of Laurentide and Cordilleran ice sheets could have been continuous across the area of present vicariance in Wisconsinan time. However, a post-Glacial origin for *species* vicariance patterns across the same region is more difficult to accept. Speciation rates for carabid beetles in general have been much slower than previously supposed (e.g. see Coope 1970; Matthews 1974, 1976). Although differentiation and speciation rates may be significantly faster for montane than for lowland organisms (upon which most previous rate data have been based) (see Kavanaugh 1979), I see no reason to suggest post-Glacial speciation for the *Nebria* sister species pairs considered here. Unless there have been, in post-Glacial time, both wholesale and highly selective extinctions of populations of taxa possibly exchanged (during the Wisconsinan) between the two areas, it is most likely that *Nebria* faunas of the respective areas have been isolated throughout and since that period. Continuity between these Rocky Mountain and Pacific Coast montane faunas apparently was not achieved during the last glacial episode, even in areas just south of the ice sheets.

Other major areas which, according to various authors, could have served as source areas for reoccupation of western Canada after retreat of the Wisconsinan ice sheets are outlined in Fig. 20. All these potential refugia embrace lowland rather than montane areas. Evidence presented above suggests that (1) *Nebria* populations survived (and may have differentiated) in coastal refugia in the Queen Charlotte and Aleutian islands, but these areas have not

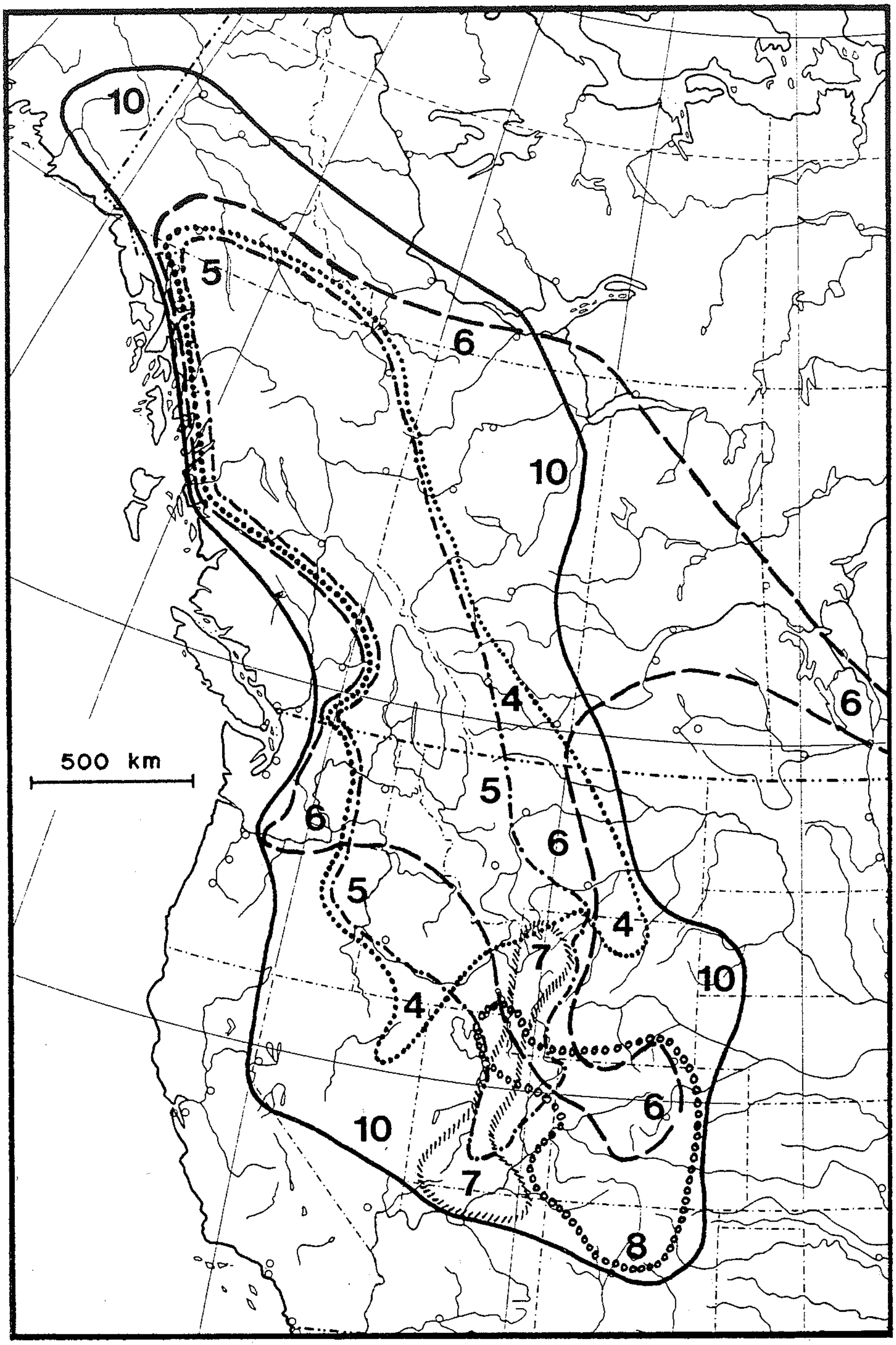


FIG. 17. Rocky Mountain geographical range patterns; pattern 4 = dotted line; pattern 5 = line alternating a single dot with a single dash; pattern 6 = broken (dashed) line; pattern 7 = line of oblique slash marks; pattern 8 = line of small open circles; pattern 9 is not illustrated; pattern 10 = solid line.

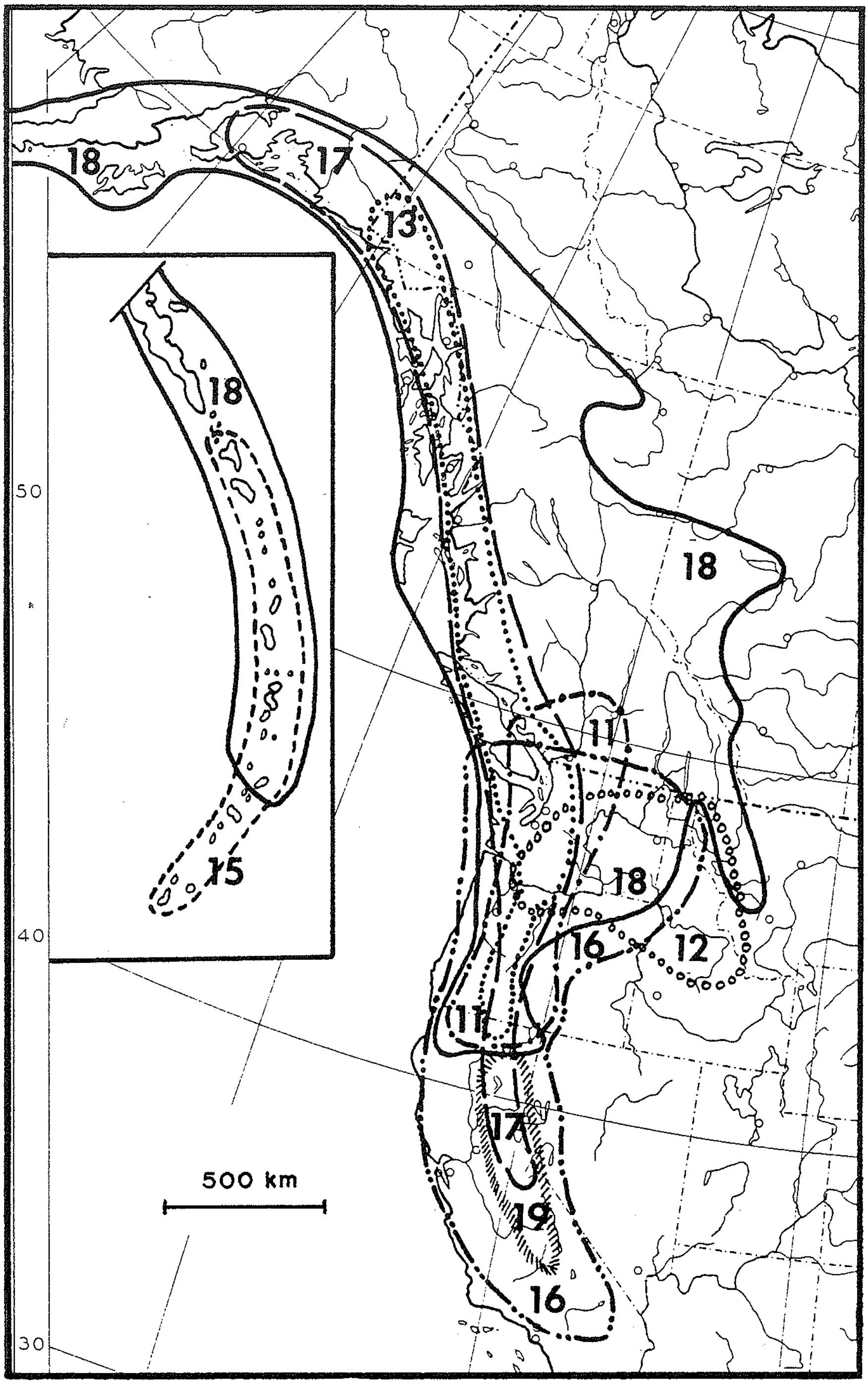
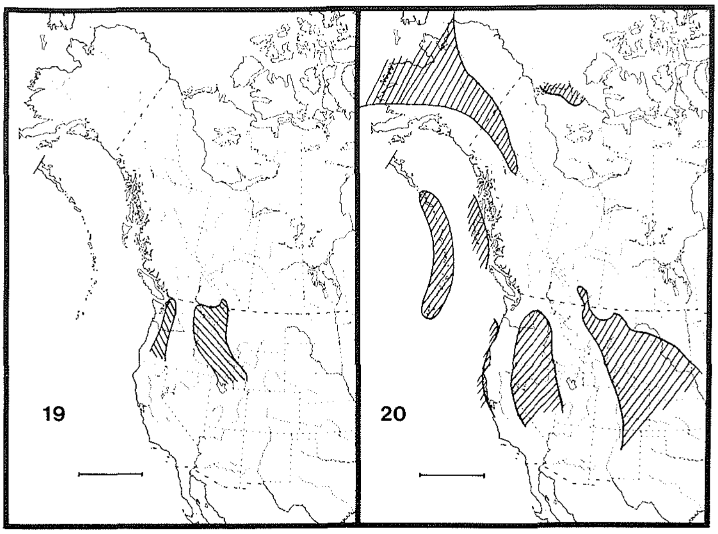


FIG. 18. Pacific coastal geographical range patterns; pattern 11 = line alternating a single dot with a single dash; pattern 12 = line of small open circles; pattern 13 = dotted line; pattern 14 is not illustrated; pattern 15 = broken line of short dashes; pattern 16 = line alternating two dots with a single dash; pattern 17 = broken line of long dashes; pattern 18 = solid line; pattern 19 = line of oblique slash marks.



FIGS. 19–20. Major areas (cross-hatched) which may have served as refugia during Wisconsin time. 19, Montane refugia. 20, lowland refugia.

contributed elements to the present mainland montane fauna; and (2) northern refugia, most notably the large unglaciated region of interior Alaska and Yukon Territory, have not contributed elements to the montane *Nebria* fauna of western Canada. These findings agree with those of Belicek (1976), Larson (1975), Nimmo (1971), and Pike (1978) for respective groups studied. Contributions of lowland refugia south of the ice sheets are difficult to assess; but these areas have apparently contributed little to the truly montane component of the present Canadian fauna. Present montane and lowland faunas of western Canada may well have had adjacent, but distinct, Wisconsinan refugia. These same faunas may be thought of as adjacent at present also. Perhaps this relationship of complementarity will prove useful in interpretation of histories of both faunal components in light of future studies.

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