THE INSECT FAUNA OF THE PACIFIC NORTHWEST COAST OF NORTH AMERICA: PRESENT PATTERNS AND AFFINITIES AND THEIR ORIGINS[1]

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Abstract

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The insect fauna of the Pacific Northwest Coast is diverse and rich in endemic forms. Nine different elements are recognized in the fauna, including (1) restricted coastal, (2) coast-centred, (3) Great Basin, (4) Rocky Mountain, (5) trans-American, (6) Holarctic, (7) trans-Beringian, (8) Alaskan, and (9) introduced elements. Elements (6), (7), and (8) are generally restricted to the northwestern portion of the coast; and representation of Rocky Mountain elements (4) increases in three major steps from south to north along the coast—at the Puget Lowland/Fraser River valley, the Prince Rupert area, and the Kenai Peninsula, respectively. Patterns of vicariance among sister taxa in the carabid beetle genus *Nebria* demonstrate relationships which, together with analyses of other faunal elements, show that the fauna of glaciated portions of the Coastal region has greatest affinity with faunas of southern coastal areas, less affinity with those of southern interior areas, and least affinity with faunas of northern areas. Areas of local endemism within the region include the Aleutian Archipelago, the southeastern Alaskan Panhandle, the Queen Charlotte Archipelago, the Olympic Peninsula/Vancouver Island, the northern Cascade Range, the Klamath Mountains system, and the Sierra Nevada. The extant coastal insect fauna has evolved from a widespread northern Tertiary fauna, elements of which were isolated in several separate refugia during Pleistocene glaciations. The northern two-thirds of the region has been recolonized in postglacial time from both coastal and interior refugia south of the Cordilleran and Laurentide ice sheets. Local endemism in the region reflects survival and differentiation of a few forms in small coastal refugia; but survivors from these refugia, as well as those from the Yukon/Beringian refugium, have generally been unable to extend their ranges to other parts of the Coastal region following deglaciation.

Résumé

La faune entomologique de la Côte de l'Ouest de l'Amérique du nord est diverse et riche en formes endémiques. On reconnaît neuf éléments zoogéographiques dans cette faune: (1) strictement côtier, (2) centré sur la côte, (3) du Grand Bassin, (4) des Montagnes Rocheuses, (5) trans-Américain, (6) holarctique, (7) trans-Béringien, (8) Alaskan, et (9) introduit. Les éléments (6), (7) et (8) sont généralement limités à la partie nord-ouest de la Côte; et la représentation de l'élément (4) des Montagnes Rocheuses passe par trois paliers du sud vers le nord le long de la Côte: l'ensemble des basses terres du Puget/vallée du fleuve Fraser, la région de Prince Rupert, et la Péninsule de Kenai. Des cas de vicariance entre taxons jumeaux du genre carabique *Nebria* révèlent des relations qui lorsque considérées en parallèle avec l'analyse d'autres éléments fauniques, montrent que la faune des parties glaciées de la Côte est très apparentée avec celle des régions côtières du sud, peu apparentée avec celle des régions intérieures du sud, et le moins apparentée avec celle des régions nordiques. Les endroits à caractère endémique de la région sont l'Archipel des Aléoutiennes, la région de l'extrême sud de l'Alaska, l'Archipel des Iles de la Reine Charlotte, l'ensemble Péninsule Olympique/Ile de Vancouver, le nord de la Chaîne des Cascades, les Montagnes de Klamath et de la Sierra Nevada. La faune entomologique côtière actuelle a évolué à partir d'une faune Tertiaire dispersée, dont certains éléments ont été isolés dans divers refuges séparés au cours des glaciations du Pléistocène. Les deux-tiers nord de la région ont été recolonisés à l'époque post-glaciaire à partir de refuges côtiers et intérieurs situés au sud des calottes Laurentide et Cordillérienne. L'endémisme local de la région indique la survie et la différenciation de quelques formes dans de petits refuges côtiers;

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mais en général, les survivants de ces refuges ainsi que ceux du refuge Yukonien/Béringien n'ont pas atteint les autres parties de la Côte après la déglaciation.

In a previous paper (Kavanaugh 1980), I presented an overview of extant distribution patterns among western Canadian insects, discussed origins of these patterns and of the regional fauna in general, and provided a review of the literature on these topics. In this paper, I focus on the fauna of the Pacific Northwest Coast, here defined as the area along the coast from the Aleutian Islands, Alaska, south to Monterey County, California (just south of San Francisco), and east to include the western slopes of the Sierra Nevada and Cascade Range (in the contiguous United States) and of the Coast Ranges of British Columbia and southeastern Alaska. This region is rich in physiographic and habitat diversity, and its synoptic climate is maritime. Summers are cool and moist, with early morning and afternoon fog and light rain common. Winters are relatively mild compared with adjacent regions, but heavy snowfall and snow accumulation are characteristic of montane and northern portions of the area.

The fauna of this region is highly distinctive, with many endemic and taxonomically isolated taxa represented. For example, Lindroth (1971) compared the carabid beetle faunas of different parts of Alaska and found that the Coastal region had the smallest percentage of Holarctic species represented (less than 50% of the fauna). This percentage is much less if the Aleutian Islands and Alaskan Peninsula are excluded from the Coastal region because those areas have proportionately greater Holarctic representation than more eastern and southern portions of the coast. The distinctive nature of the coastal fauna led Van Dyke (1919) to recognize this as the "Vancouverian" faunal region. Close affinities (particularly at the generic level) between this fauna and those of both the southeastern United States and southeastern Asia (especially southern China and Japan) have long been recognized (Van Dyke 1919, 1926, 1940).

Why is the fauna of this area of particular interest? As just noted, it is highly distinctive while showing clear taxonomic affinities with faunas of other, in some cases quite disjunct, areas. But further, the fauna has a large endemic component, even in northern parts of the region which are assumed to have been fully or largely glaciated in Pleistocene time (last as recently as 10 000 years ago). There are few, if any, other areas that are known to have been heavily glaciated and yet have such a distinctive fauna with a significant endemic component.

In the following discussion, I first present some typical generalized distribution patterns for elements of the fauna. I then illustrate specific distributions and vicariance patterns, areas of endemism, and apparent faunal barriers, based largely on my own research with the carabid beetle genus *Nebria*. Finally, I discuss faunal affinities in phylogenetic (evolutionary) perspective and conclude with comments on the origins of the fauna as a whole.

General patterns of distribution

The database for studies of general patterns of distribution in any fauna consists of the set of known distributions of individual species (and/or subspecies) represented in that fauna. To facilitate recognition of such general patterns among Pacific Northwest Coast insects, I have reexamined my own taxonomic work and surveyed the literature, looking specifically for distribution maps and descriptions of geographical distributions in recent taxonomic works. Sources of useful information about distributions of coastal species include revisionary work with Trichoptera (Nimmo 1971), Lepidoptera (Lafontaine 1982; Pike 1980), and Coleoptera (Belicek 1976; Bright 1969; Kavanaugh 1986; Larson 1975), especially Staphylinidae (Campbell 1973, 1978, 1979; Smetana 1971, 1982) and Carabidae (Ball 1969; Erwin and Kavanaugh 1981; Goulet 1983; Kavanaugh 1979*a*, 1979*c*, 1980, 1981, 1984; Lindroth 1957, 1961–69, 1963, 1969, 1970, 1979). General patterns of distribution among coastal insects were discussed by Munroe (1956), Scudder (1979), and Van Dyke (1919, 1926, 1940) and reviewed by Kavanaugh (1981) in papers dealing with larger geographical areas.

Insects represented in the fauna of the Pacific Coast are widely varied in their overall geographical distributions; yet certain general patterns are apparent. Congruence or at least extensive overlap in the ranges of different species, including species of many different groups, makes it possible to distinguish different elements in the coastal fauna based on their distributions both within and outside the Coastal region. Several such elements and examples of their general patterns of distribution can be distinguished.

1. RESTRICTED COASTAL ELEMENTS

These elements include species that are restricted to the Coastal region. These endemic species are varied in the extent of their respective geographical ranges (Fig. 1), with some broadly distributed and others moderately or highly restricted in distribution; and it is clear (see below) that, together, they form an assemblage that has a diversified history and multiple origins. Several different restricted coastal elements are recognized and discussed. Distinction can also be made between species that are widely distributed within the Coastal region and those restricted to extreme coastal areas, to coastal mountains and/or intermontane valleys, or to the western slope and crest of the Sierra Nevada/Cascade Range on the eastern edge of the region.

2. COAST-CENTRED ELEMENTS

The geographical ranges of some coastal species are mainly confined to that region but also extend eastward into the continental interior in particular areas (Fig. 2). Three such elements are those with range incursions into (1) the Columbia Plateau and Columbia River drainage basin, (2) the lower Fraser River valley, and (3) northern British Columbia and southern Yukon Territory.

3. GREAT BASIN ELEMENTS

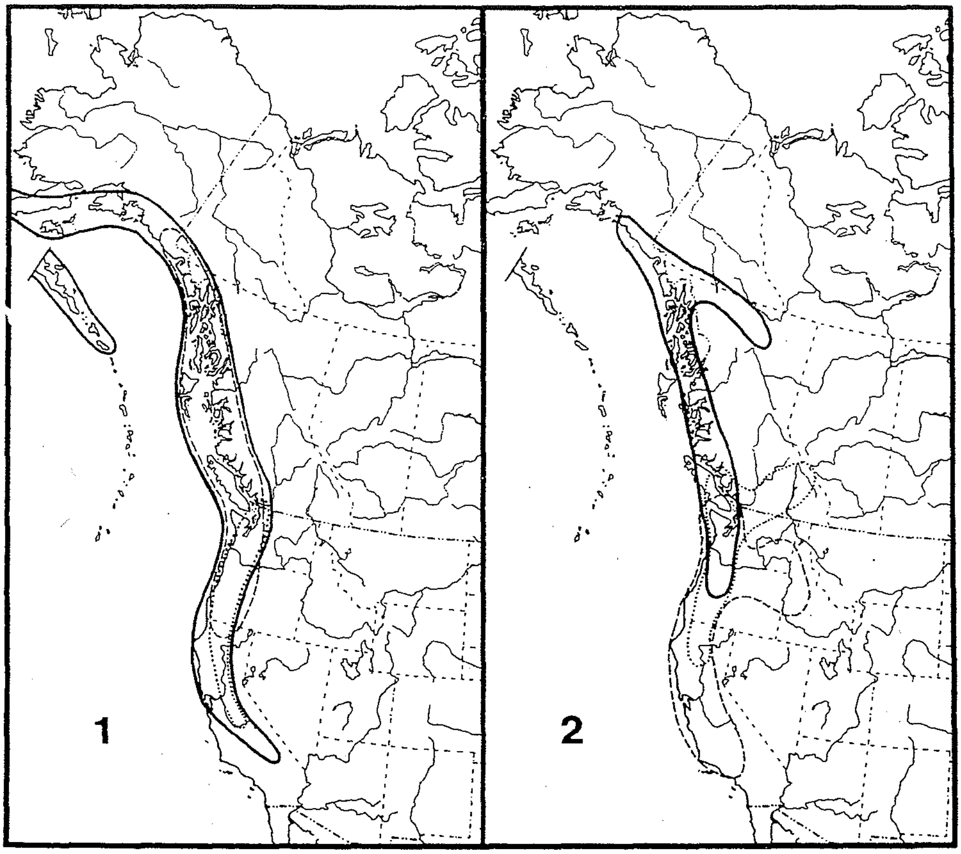
Geographical ranges of several species are centred in the Great Basin but extend into the Coastal region (Fig. 3). In general, this element is restricted to the extreme southern part of the region.

3. ROCKY MOUNTAIN ELEMENTS

Many species broadly distributed in the Rocky Mountain region are also represented in the coastal fauna (Figs. 4 and 5). Ranges of some of these species extend widely along the coast but others are restricted to southern or northern parts only. Three particular general patterns are apparent. In the first (Fig. 4), continuity between coastal and interior parts of the range occurs across the Columbia Plateau region (from southern British Columbia south to central Oregon), with the north/south extent of range in the Coastal region varied among species. The second pattern is one in which the distributional range extends much further south in the interior than in the coastal area (Fig. 5). In one variant of this pattern, coastal distribution extends as far south as the Puget Sound area, whereas in another the southern coastal limit is near Prince Rupert, British Columbia. In the third pattern, ranges of interior species reach the coast only in the north, at and/or west of the Kenai Peninsula, Alaska (Fig. 4, dotted–dashed line).

5. TRANS-AMERICAN ELEMENTS

The ranges of many Pacific Coast species extend eastward across North America, some even to the Atlantic Coast region. Ranges of some species are trans-American only at southern latitudes (Fig. 3) with limited Pacific Coast extent. Other ranges are latitudinally broader (Fig. 6) or restricted to more northern areas (Fig. 7), and extent of distribution along the Pacific Coast is also varied.



FIGS. 1, 2. General distribution patterns (solid, dashed, and dotted lines represent examples of variation on basic patterns): 1, restricted coastal elements; 2, coast-centred elements.

6. HOLARCTIC ELEMENTS

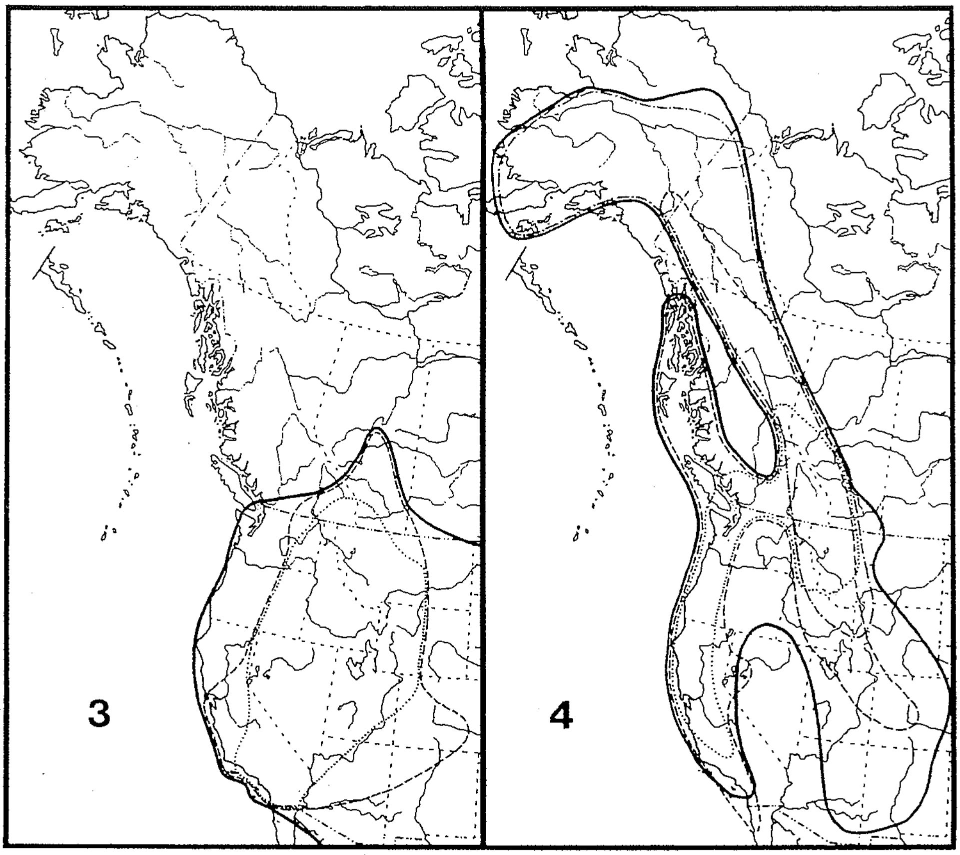
A number of species represented in the coastal fauna are Holarctic in distribution, ranging widely across North America and Eurasia (Fig. 8). Ranges of some of these Holarctic species are circumpolar but restricted to northern latitudes whereas others also extend south along interior and coastal mountain chains. In general, however, a diverse Holarctic element occurs along the Pacific Coast only in the northwestern part of the region, at and/or west of the Kenai Peninsula.

7. TRANS-BERINGIAN ELEMENTS

The ranges of some species extend from northeasternmost Siberia, through the islands of the Bering Sea, and east to Yukon Territory, westernmost Northwest Territories, and extreme northeastern British Columbia. This trans-Beringian distribution pattern (Fig. 9) could be considered just a variant of a Holarctic pattern, but it is much more limited in both latitudinal and longitudinal extent than a typical example of the latter. As with the Holarctic element, however, a significant trans-Beringian element is represented only in the northwestern part of the Coastal region.

8. ALASKAN ELEMENT

The ranges of a few coastal species are confined to Alaska, the Yukon Territory, and northernmost British Columbia (Fig. 7). In general, this element has the same limited coastal distribution as the Holarctic and trans-Beringian elements.



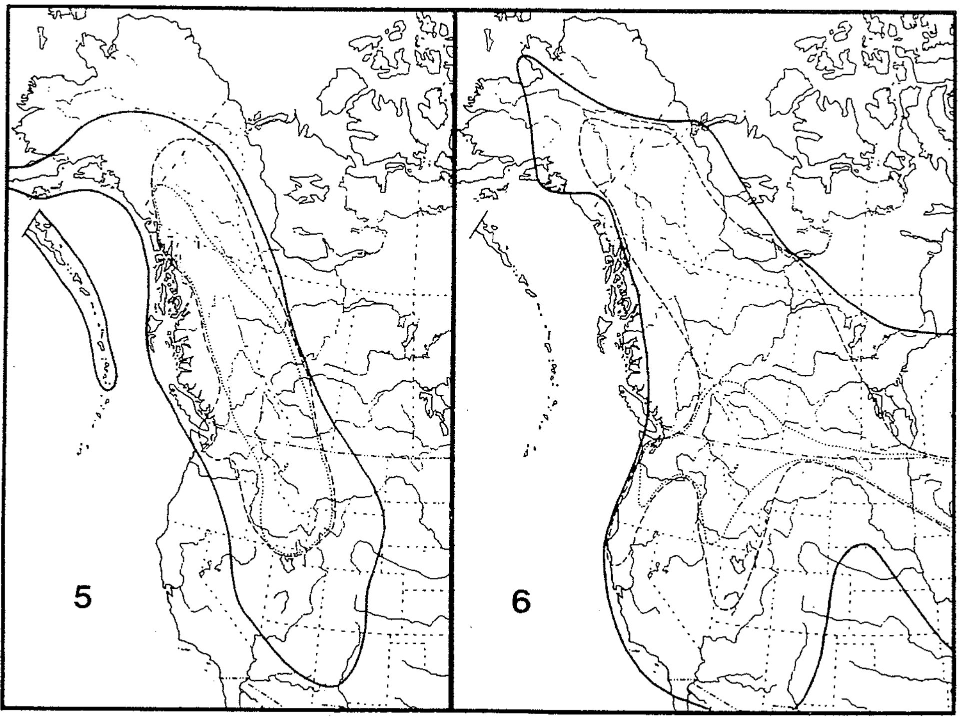
FIGS. 3, 4. General distribution patterns: 3, Great Basin (dashed and dotted lines) and trans-American (solid line) elements; 4, Rocky Mountain elements, patterns 1 and 3 (solid, dashed, dotted, and dotted-dashed lines represent examples of variation on basic patterns).

9. INTRODUCED ELEMENT

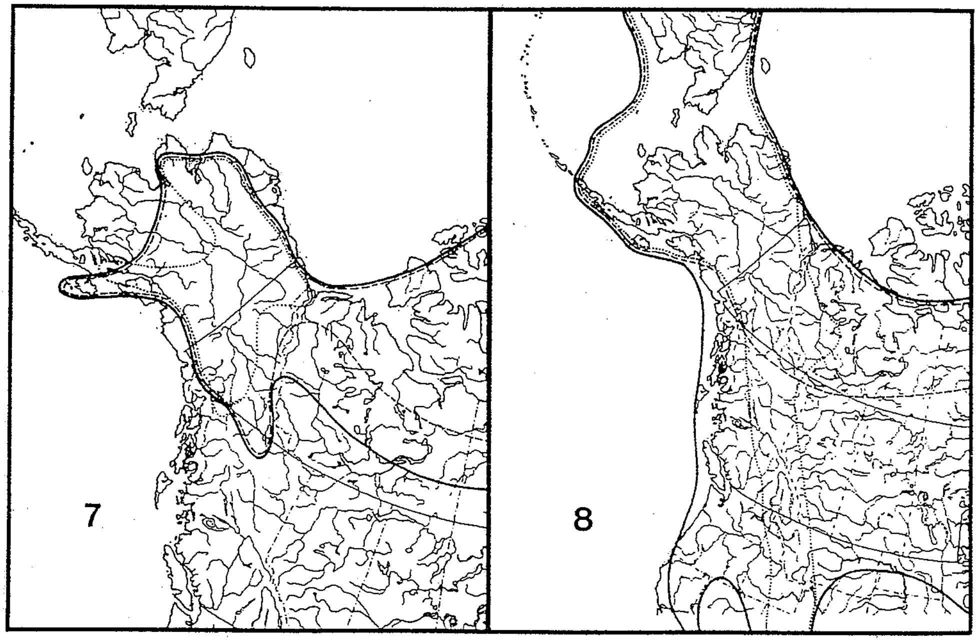
The Coastal region is rich in species that have been introduced from other continents, particularly from western Europe and eastern Asia. This introduced element is best represented in areas surrounding major ports (e.g. Vancouver, Seattle, Portland, and San Francisco). However, many introduced species have become well established and continue to expand their ranges from the primary introduction sites (Lindroth 1957; Spence and Spence 1988).

Brundin (1966), Croizat *et al.* (1974), Nelson and Platnick (1981), and numerous other biogeographers have justifiably stressed the importance of recognizing general patterns of distribution and the usefulness of these generalizations in historical biogeography. Prerequisite for appropriate biogeographic analysis of a fauna, however, are hypotheses of phylogenetic (cladistic) relationships among the organisms represented in that fauna. By relating phylogenetic to distributional data, vicariance relationships may become evident; and when congruence is found among distribution patterns of different groups, general vicariance patterns can then be recognized. General patterns of vicariance serve as strong evidence of faunal affinity and, when related to known events in Earth history, provide clues to faunal histories and origins.

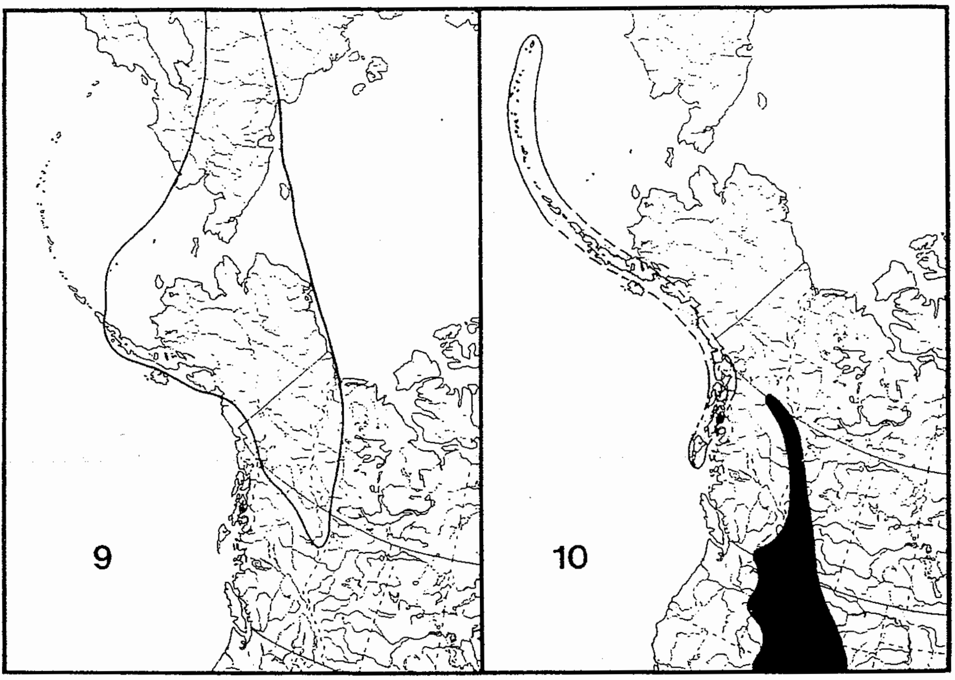
At least for most North American insect groups studied to date (and for which hypotheses of phylogenetic relationships have been proposed) general patterns such as



FIGS. 5, 6. General distribution patterns (solid, dashed, and dotted lines represent examples of variation on basic patterns): 5, Rocky Mountain elements, pattern 2; 6, trans-American elements.



FIGS. 7, 8. General distribution patterns: 7, trans-American (solid and dashed lines) and Alaskan (dotted line) elements; 8, Holarctic elements (solid, dashed, and dotted lines represent examples of variation on basic patterns).



FIGS. 9, 10. 9, general distribution pattern, trans-Beringian element; 10, geographical distribution of the *gregaria* (lighter stippled) and *arkansana* (darker stippled) species subgroups of *Nebria*; broken line segments indicate areas of apparent distributional gaps.

those described above are based on the congruent distributions of species with moderate or great powers of dispersal. Such species tend also to be sympatric with their nearest relatives (i.e. sister species and other congeners) rather than allopatric (vicariant). Consequently, these general patterns are unsatisfactory for demonstrating zoogeographic affinities in all but the most general way. An absence of evident patterns of vicariance among sister groups makes it difficult to interpret broad, generalized distribution patterns and their origins. Patterns derived from sympatric congeners may be used to describe the present fauna, but they are of little use in historical biogeography.

Distributions of species with restricted dispersal capabilities have seldom been used by biogeographers in the recognition of general patterns of distribution, perhaps because they are more easily overlooked and often unique (i.e. incongruent with distributions of other species). Such organisms tend to occupy smaller continuous geographical ranges than more vagile forms, and their ranges are also more easily fragmented, through development of various kinds of barriers to distribution, resulting in isolation of populations (Kavanaugh 1979*b*). Among possible evolutionary consequences of isolation on allopatric populations is differentiation which may lead to speciation or subspeciation. Isolation and differentiation of allopatric populations of relatively non-vagile organisms may therefore result in development of vicariance patterns that are useful in historical biogeographic analysis and interpretation but seldom found among more vagile forms. By reference to vicariance patterns seen among even a few of these species and to congruence, however slight, between these individual and more general patterns, it may be possible to analyse and interpret even the general patterns in a more useful manner.

Specific patterns of distribution

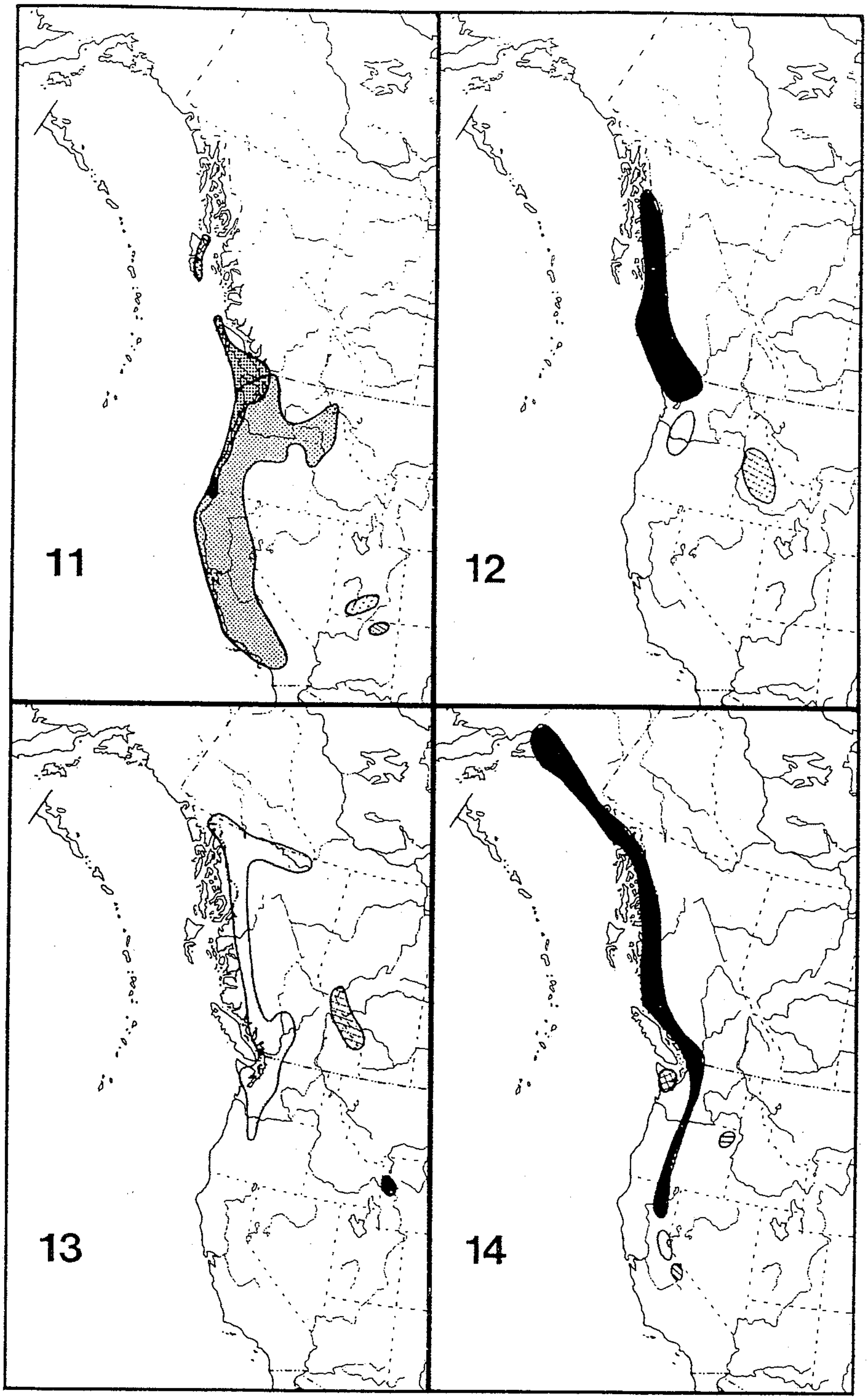
At present, the Nearctic fauna includes 55 species in the genus *Nebria* Latreille, a group I have studied for many years. Of these, 37 species are monotypic, the remainder are di- or poly-typic (i.e. represented by two or more subspecies; see Kavanaugh [1979*a*] for discussion of subspecies concept). All but six species are restricted to western North America, with only three restricted to the eastern half of the continent. Dispersal capabilities of these beetles are relatively limited. Members of many species have atrophied flight wings and therefore are incapable of flight. Even among species with full-winged adults, there has been only one record of flight to date.

This genus is an ideal indicator group for faunal and other biogeographic analyses. Species and subspecies diversity is high, and vagility of members is low. Geographical and habitat distributions of included taxa are relatively well known. A hypothesis of phylogenetic relationships among the species has been proposed (Kavanaugh 1978, and unpubl. data). But the most important characteristic of the group is that subspecies and most related ("sister") species, in pairs and also in more inclusive taxa (e.g. three- and four-species taxa), are allopatric (vicariant). Hence, individual vicariance patterns are abundant and clearly evident, and several of these patterns are repeated with only minor variation, thereby adding to their significance. Distributions of some *Nebria* species, subspecies, and species groups and subgroups are illustrated in Figures 10–26; but for discussion purposes, these are grouped according to vicariance relationships demonstrated so that patterns are easily identified.

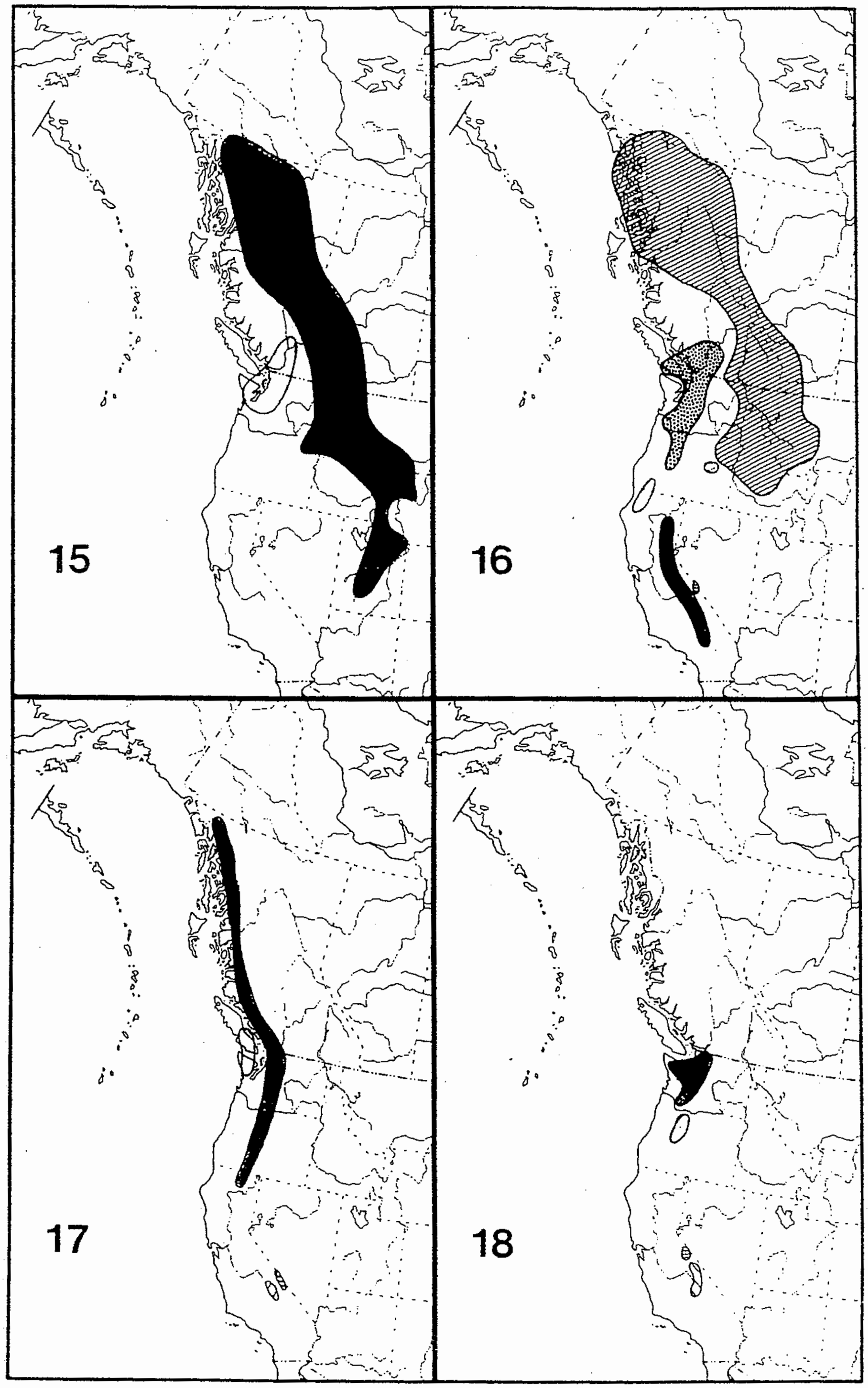
At least 11 *Nebria* taxon pairs demonstrate east/west vicariance patterns in which one or both vicars are found in the Pacific Northwest Coast region. These include six subspecies pairs, three species pairs, one four-species taxon, and one pair of species subgroups. The *gregaria* and *arkansana* species subgroups are vicariant sister taxa (Fig. 10), again with the former restricted to the Coastal region, the latter to interior western North America. The *eschscholtzii* species subgroup (Fig. 11) includes four species. *Nebria diversa* LeConte and *Nebria eschscholtzii* Menetries are broadly sympatric sister species, the former restricted to sea beaches in the central Coastal region, the latter with a coast-centred distribution. *Nebria desolata* Kavanaugh and *Nebria navajo* Kavanaugh are vicariant sister species, both restricted to small areas on the Colorado Plateau, and together these two species are the sister group and eastern vicar of *N. eschscholtzii* and *N. diversa.*

Three species pairs (*Nebria kincaidi* Schwarz/*Nebria carri* Kavanaugh [Fig. 12], *Nebria piperi* Van Dyke/*Nebria schwarzi* Van Dyke [Fig. 13], and *Nebria acuta* Lindroth/*Nebria wallowae* Kavanaugh [Fig. 14]) and two subspecies pairs (*Nebria crassicornis crassicornis* Van Dyke/*N. c. intermedia* Van Dyke [Fig. 15] and *Nebria gebleri cascadensis* Kavanaugh/*N. g. gebleri* Dejean [Fig. 16]) demonstrate vicariance between the Coastal region and at least some part of the Rocky Mountain region. Vicariance between mountains on the Olympic Peninsula (and Vancouver Island) and those on the adjacent mainland is shown by two subspecies pairs (*N. acuta quileute* Kavanaugh/*N. a. acuta* Lindroth [Fig. 14]) and *N. meanyi sylvatica* Kavanaugh/*N. m. meanyi* Van Dyke [Fig. 17]).

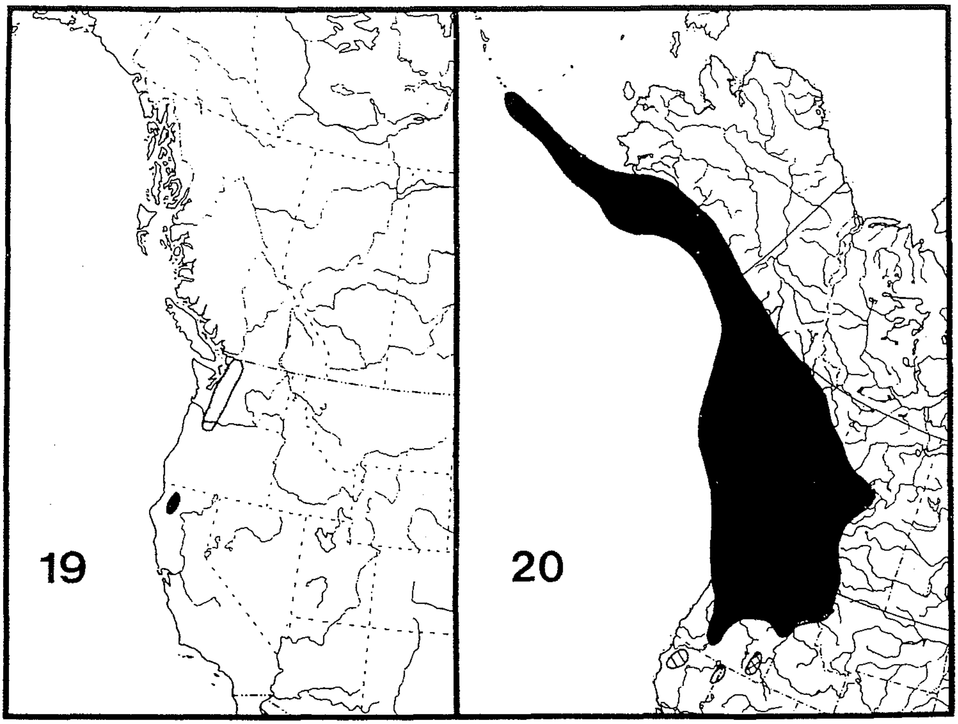
At least 16 *Nebria* taxon pairs (10 subspecies pairs, five species pairs, and one three-taxon unit) demonstrate north/south vicariance patterns, with one or both vicars found in the Northwest Coastal region. A variety of vicariance patterns is apparent between the Cascade Range and other areas to the north or south. One species pair (*Nebria vandykei* Bänninger/*Nebria ingens* Horn [Fig. 18]) and two subspecies pairs (*Nebria gebleri cascadensis*/*N. g. rathvoni* LeConte [Fig. 16] and *Nebria acuta acuta*/*N. a. sonorae* Kavanaugh [Fig. 14]) demonstrate vicariance between the Cascade Range and the Sierra Nevada. Vicariance between the Cascade Range and the Klamath Mountain system is shown by one species pair (*Nebria paradisi* Van Dyke/*Nebria turmaduodecima* Kavanaugh [Fig. 19])



FIGS. 11–14. Geographical distributions of *Nebria* taxa: 11, the *eschscholtzii* species subgroup: *Nebria diversa* LeConte (darker stippled), *Nebria eschscholtzii* Menetries (lighter stippled), *Nebria desolata* Kavanaugh (cross-hatched), *Nebria navajo* Kavanaugh (oblique-hatched); 12, *Nebria kincaidi* Schwarz (*N. k. kincaidi*, darker stippled; *N. k. balli* Kavanaugh, lighter stippled) and *N. carri* Kavanaugh (cross-hatched); 13, *Nebria piperi* Van Dyke (lighter stippled) and *N. schwarzi* Van Dyke (*N. s. schwarzi*, cross-hatched; *N. s. beverlianna* Kavanaugh, darker stippled); 14, the *acuta* species subgroup: *Nebria acuta acuta* Lindroth (darker stippled), *N. a. sonorae* Kavanaugh (lighter stippled), *N. a. quileute* Kavanaugh and/or *Nebria danmanni* Kavanaugh (cross-hatched), *Nebria lyelli* Van Dyke (oblique-hatched), *Nebria wallowae* Kavanaugh (transverse-hatched).



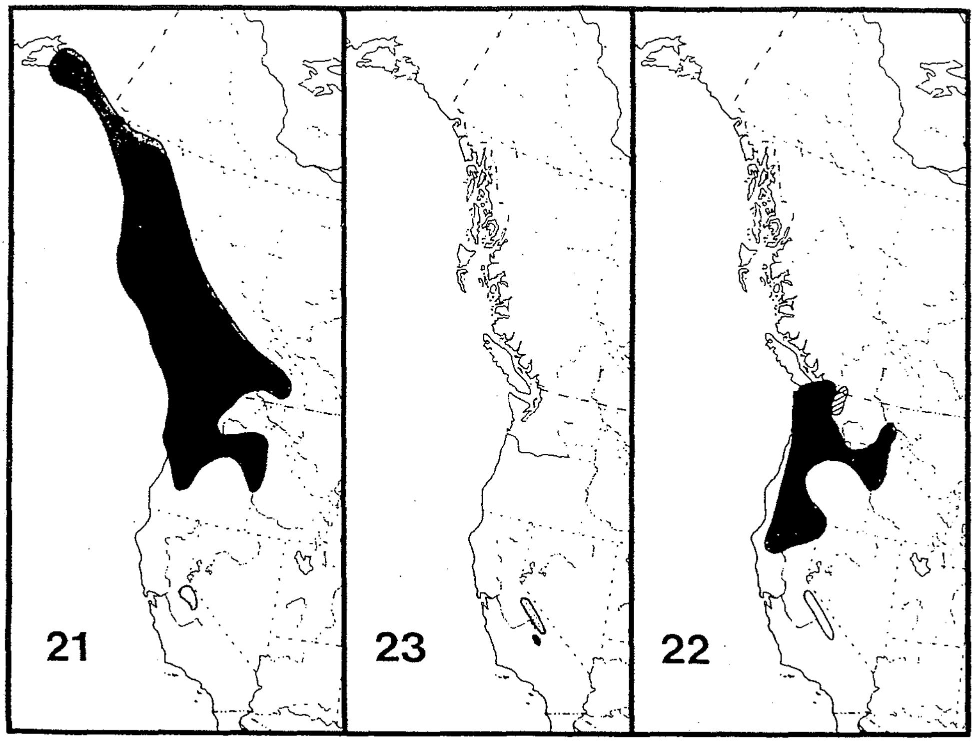
Figs. 15–18. Geographical distributions of *Nebria* taxa: 15, *Nebria crassicornis* Van Dyke: *N. c. crassicornis* (lighter stippled), *N. c. intermedia* Van Dyke (darker stippled); 16, *Nebria gebleri* Dejean: *N. g. gebleri* (oblique-hatched), *N. g. cascadensis* Kavanaugh (boldly stippled), *N. g. siskiyouensis* Kavanaugh (lighter finely stippled), *N. g. rathvoni* LeConte (darker finely stippled), *N. g. albimontis* Kavanaugh (transverse-hatched); 17, *Nebria meanyi* Van Dyke: *N. m. meanyi* (darker stippled), *N. m. sylvatica* Kavanaugh (lighter stippled), *N. m. lamarckensis* Kavanaugh (oblique-hatched), *N. m. giulianii* Kavanaugh (transverse-hatched); 18, *Nebria vandykei* Bänninger (*N. v. vandykei*, darker stippled; *N. v. wyeast* Kavanaugh, lighter stippled) and *Nebria ingens* Horn (*N. i. ingens*, oblique-hatched; *N. i. riversi* Van Dyke, transverse-hatched).



FIGS. 19, 20. Geographical distributions of *Nebria* taxa: 19, *Nebria paradisi* Darlington (lighter stippled) and *N. turmaduodecima* Kavanaugh (darker stippled); 20, *Nebria sahlbergii* Fischer (*N. s. sahlbergii* darker stippled; *N. s. modoc* Kavanaugh, lighter stippled; *N. s. triad* Kavanaugh, oblique-hatched) and *N. jeffreyi* Kavanaugh (cross-hatched).

and two subspecies pairs (*Nebria gebleri cascadensis*/*N. g. siskiyouensis* Kavanaugh [Fig. 16] and *Nebria sahlbergii sahlbergii* Fischer/*N. s. triad* Kavanaugh [Fig. 20]). A vicariance link between the Cascades and the Warner Mountains is shown by the subspecies pair, *N. s. sahlbergii*/*N. s. modoc* Kavanaugh (Fig. 20). Vicariance between different areas within the Cascade Range is shown by three taxon pairs. *Nebria campbelli* Kavanaugh is restricted to the extreme northern part of the Cascades but its sister taxon, the species pair *N. virescens* Horn/*Nebria altisierrae* Kavanaugh, is broadly distributed in more southern parts of the Coastal region (Fig. 22), including the Cascade Range itself. *Nebria kincaidi balli* Kavanaugh is restricted to the central portion of the Cascade Range whereas its sister subspecies, *N. k. kincaidi* Schwarz, is widely distributed in the northern Coastal region, including coastal parts of southeastern Alaska and British Columbia, on Vancouver Island and the Olympic Peninsula, and in the northern Cascades (Fig. 12). The two subspecies of *Nebria vandykei* (*N. v. vandykei* and *N. v. wyeast* Kavanaugh) show vicariance between portions of the Cascade Range north and south (respectively) of the Columbia River gap (Fig. 18).

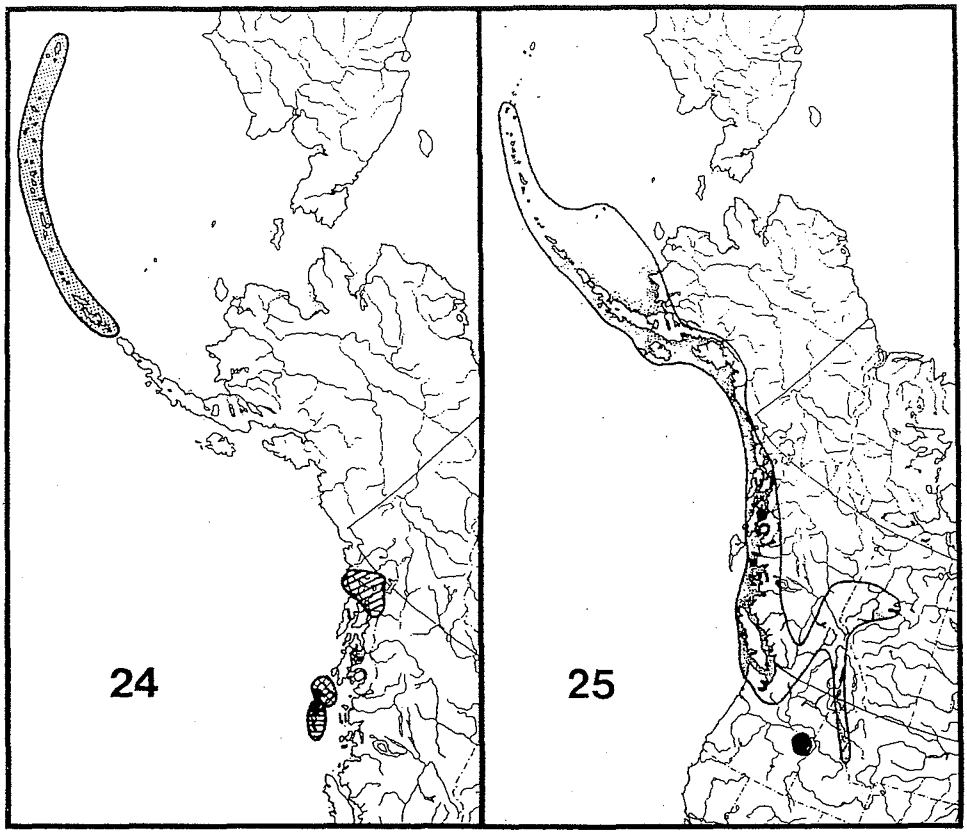
In addition to the links with the Cascade Range noted above, several vicariance patterns involve the Sierra Nevada and other areas. Two species pairs (*Nebria mannerheimii* Fischer/*Nebria darlingtoni* Kavanaugh [Fig. 21] and *Nebria virescens*/*Nebria altisierrae* [Fig. 22]) and one subspecies pair (*Nebria meanyi meanyi* Van Dyke/*N. m. lamarckensis* Kavanaugh [Fig. 17]) show vicariance between the Sierra Nevada and north and central Coastal regions (including both Coast and Cascade ranges). A vicariance link between the Sierra Nevada and the Olympic Peninsula is shown by the species pair *Nebria lyelli* Van



FIGS. 21–23. Geographical distributions of *Nebria* taxa: 21, *Nebria mannerheimii* Fischer (darker stippled) and *N. darlingtoni* Kavanaugh (lighter stippled); 22, the *virescens* species group: *Nebria virescens* Horn (darker stippled), *Nebria altisierrae* Kavanaugh (lighter stippled), *Nebria campbelli* Kavanaugh (oblique-hatched); 23, *Nebria spatulata* Van Dyke: *N. s. spatulata* (light stippled), *N. s. sierrae* Kavanaugh (solid).

Dyke/*Nebria danmanni* Kavanaugh. Two subspecies pairs (*N. ingens ingens* Horn/*N. i. riversi* Van Dyke [Fig. 18] and *Nebria spatulata spatulata* Van Dyke/*N. s. sierrae* Kavanaugh [Fig. 23]) demonstrate north/south vicariance between different portions of the Sierra Nevada itself.

Several other patterns of varied geographical axis and complexity are apparent among other *Nebria* taxon pairs. The species pair *Nebria gregaria* Fischer/*Nebria louiseae* Kavanaugh demonstrates vicariance between the Aleutian Islands and the southern islands of the Queen Charlotte Archipelago. The sister taxon of this species pair is *Nebria charlottae* Lindroth, a species restricted to Graham Island, the large, northern island of the latter archipelago (Fig. 24). The implication of these respective present distributions is a vicariance relationship between the northern portion of the Queen Charlotte Archipelago and an area including at least the southern part of that island group and the Aleutian Islands, and perhaps also the intervening coastal mainland, at least at some time in the past. The latter suggestion (i.e. a vicariance link between the Queen Charlotte Archipelago and the mainland to the north) is illustrated by the species pair *Nebria haida* Kavanaugh/*Nebria lituyae* Kavanaugh (Fig. 24). Two other species pairs, *Nebria sahlbergii* Fischer/*Nebria jeffreyi* Kavanaugh (Fig. 20) and *Nebria metallica* Fischer/*Nebria labontei* Kavanaugh (Fig. 25), show vicariance relationships between large portions of the Northwest Coastal region and single, isolated mountain ranges of the continental interior. *Nebria jeffreyi* is apparently restricted to the Steens Mountains of southeastern Oregon, and *N. labontei* is known only from the Wallowa Mountains of northeastern Oregon.



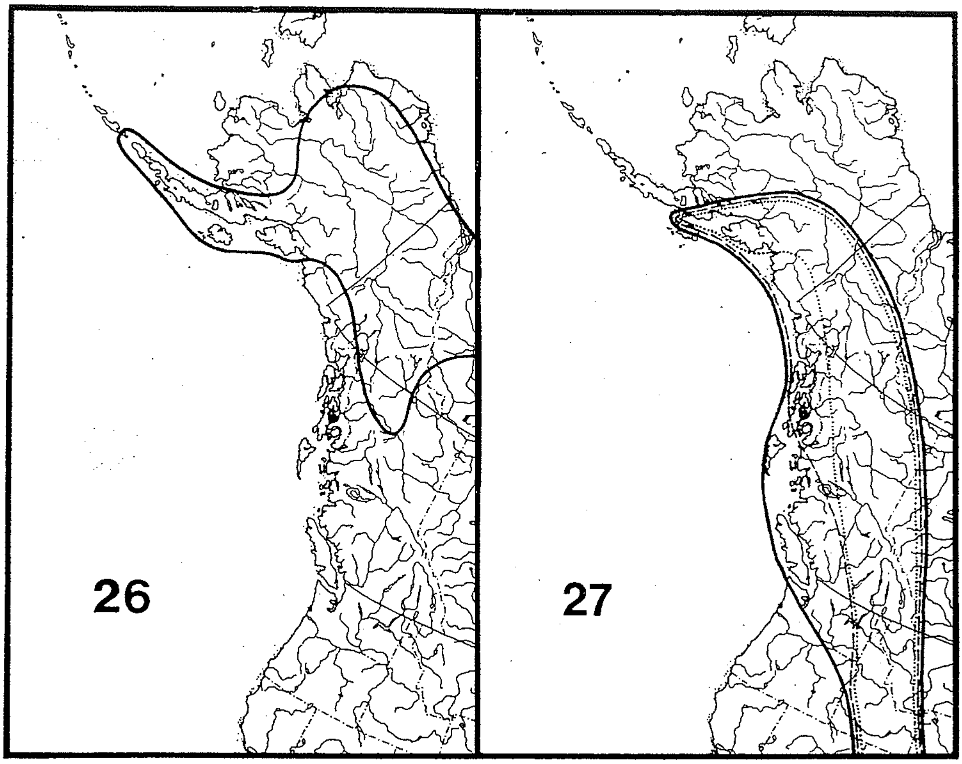
FIGS. 24, 25. Geographical distributions of *Nebria* taxa: 24, the *gregaria* species group: *Nebria gregaria* Fischer (light stippled), *Nebria lituyae* Kavanaugh (oblique-hatched), *Nebria haida* Kavanaugh (solid area in Queen Charlotte Islands), *Nebria charlottae* Lindroth (cross-hatched), *Nebria louisea* Kavanaugh (transverse-hatched); 25, *Nebria metallica* Fischer (lighter stippled) and *N. labontei* Kavanaugh (darker stippled).

The various vicariance patterns described above demonstrate three important facts: (1) that the coastal *Nebria* fauna is both distinct from and related to that of more eastern parts of North America, particularly the Rocky Mountain region; (2) that the former fauna itself includes distinct eastern and western vicariant components, one centred on the Olympic Peninsula (and Vancouver Island), the other on the coastal mainland (including the Sierra Nevada and Cascade Range); and (3) that there are distinct (but closely related) northern and southern components within the northwest coastal *Nebria* fauna, even within the faunas of single mountain systems.

Faunal zonation

As noted in the discussion of "General patterns of distribution", the geographical ranges of species representing particular faunal elements in the Coastal region form a pattern that requires further description and discussion. Some faunal elements occupy the entire region or at least range broadly in it, but the distributions of some other faunal elements are so characteristically limited that they permit us to recognize two distinctive zones within the region.

The first of these zones is what I call the "Northern/Interior Faunal Incursion Zone". As noted above, the area in which northern and interior elements (i.e. Holarctic, trans-Beringian, and Alaskan elements) are well represented in the Coastal region is quite limited



FIGS. 26, 27. Faunal incursion zones in the Pacific Northwest Coast region: 26, Northern/Interior Faunal Incursion Zone; 27, Rocky Mountain Faunal Incursion Zone (solid, dashed, and dotted lines represent examples of variation on basic pattern as discussed in text).

and extends from the Kenai Peninsula westward out into the Aleutian Islands (Fig. 26). Present geographical limits of the coastal distribution of these elements probably reflect present climatic barriers (see Karlstrom 1969, fig. 2.1 in particular). For example, there is an abrupt increase in precipitation in the Coastal region east and south of the Kenai Peninsula, and northern and interior elements are typically adapted to a drier and colder climate. However, historical factors have no doubt also affected the overall distribution of these elements in the Coastal region.

At least a few Rocky Mountain elements are found throughout the Coastal region, even in southern coastal areas (Figs. 5 and 6), but their numbers increase in three main steps along a south to north gradient (Fig. 27): first, at the latitude of the Puget Lowland area; second, in the vicinity of Prince Rupert, British Columbia; and third, in the Kenai Peninsula area. Of these step increases, the second is most abrupt, and the coastal area from Prince Rupert north and west to the Kenai Peninsula has a much more diverse Rocky Mountain element than the area further south. I therefore call this second stage area the "Rocky Mountain Faunal Incursion Zone" to emphasize the contribution of Rocky Mountain elements to the fauna of the Coastal region. Several factors probably contribute to the present stepwise pattern of faunal addition; but among these, physiographic rather than climatic features of the area may be most important determinants of geographical distributions. Each of the three areas of step increase corresponds to a relatively low-altitude break in the eastern montane boundary of the Coast region. These breaks include the Columbia and Fraser River valleys through the Cascade/Coast ranges, the Skeena River valley through northern Coast Ranges, and the Copper River and Matanuska River valleys between the northern end of the Coast Ranges and the Alaska Range, respectively. In addition, northern edges of both the Columbia Plateau of Washington and southern British Columbia and the Central Plateau of central British Columbia are crossed by a series of separate, north/south-trending mountain ranges which, together, may serve as broken but effective zones of faunal continuity between the Rocky Mountain system itself and the Puget Lowland and Prince Rupert areas, respectively. Topographic distinction between the northern Rocky Mountains and the northern Coast Ranges is even less evident than that between separate ranges in the Plateau areas, and faunal continuity in the north is clearly evident. Therefore, a combination of east/west montane corridors between the Rocky Mountains and the Coast and lowland gaps in the Cascade and Coast ranges may account for each step of the observed sequence of increased representation by Rocky Mountain elements.

Representation of coastal elements in faunas of northern and interior areas is quite limited, in fact, restricted to particular parts of the continental interior, as described under ''Coast-centred elements'' above (Fig. 2). Of these areas, the Columbia Plateau region (including lower and middle parts of the Columbia River drainage system east to central Idaho) has the most diverse coastal element in its fauna. Coastal species are such a conspicuous part of this fauna that I refer to the area as the ''Columbia Plateau Maritime Faunal Incursion Zone''. For many of the coastal species represented in this area, resident populations are part of a continuous or nearly continuous range. For other species, interior populations are disjunct, sometimes widely, from the main (i.e. coastal) range of the species. The occurrence of coastal forms in the Columbia Plateau region is at least partly due to present climate of the latter area, which is in some ways more like the coastal climate than that of other parts of the interior. For example, Kavanaugh (1979*c*) demonstrated correspondence between the geographical distribution of *Nebria eschscholtzii* (Fig. 11), a coast-centred species that is well represented in the Columbia Plateau region, and certain isotherms for January mean monthly minimum air temperature in western North America. That this climatic pattern is one of long standing (perhaps dating from pre-glacial or early glacial times, with or without interruption) is suggested by the occurrence of several vicariant pairs of sister taxa, each with one sister in the Coastal region and the other in western Idaho, at the eastern edge of the Plateau (e.g. *Nebria kincaidi* and *N. balli*, Fig. 12).

Endemism and barriers

The Pacific Northwest Coast region is rich in endemic taxa—at subspecies, species, generic, and even tribal and subfamilial levels. Some of these endemics are widely distributed within the region, but others are quite restricted, and foci of local endemism can be identified. Areas especially rich in endemic taxa are illustrated in Figure 28 and include: (*a*) the Aleutian Archipelago, (*b*) the Lituya Bay/Juneau region of the Alaskan Panhandle, (*c*) the Queen Charlotte Archipelago, (*d*) the Olympic Peninsula/Vancouver Island, (*e*) the northern Cascade Range, (*f*) the Klamath Mountain system, and (*g*) the Sierra Nevada. Most of the endemic taxa in a region of high endemism in central Idaho (eastern limit of the Columbia Plateau Maritime Faunal Incursion Zone, also noted in Fig. 28) have sister taxa in the Coastal region, and this component of its fauna is no doubt a derivative of the coastal fauna itself.

Observed limits to the geographical ranges of many of these endemic taxa, as well as some of the other faunal elements described above, are coincident with recognizable climatic and/or physiographic features of the region. I use this coincidence to infer that these features presently serve as barriers to dispersal and range extension. Apparent barriers can be classified as limiting either east/west or north/south dispersal and are illustrated in Figures 29 and 30, respectively. In these illustrations, inferred relative effectiveness of barriers is suggested by the relative thickness of lines drawn to represent them. At present,

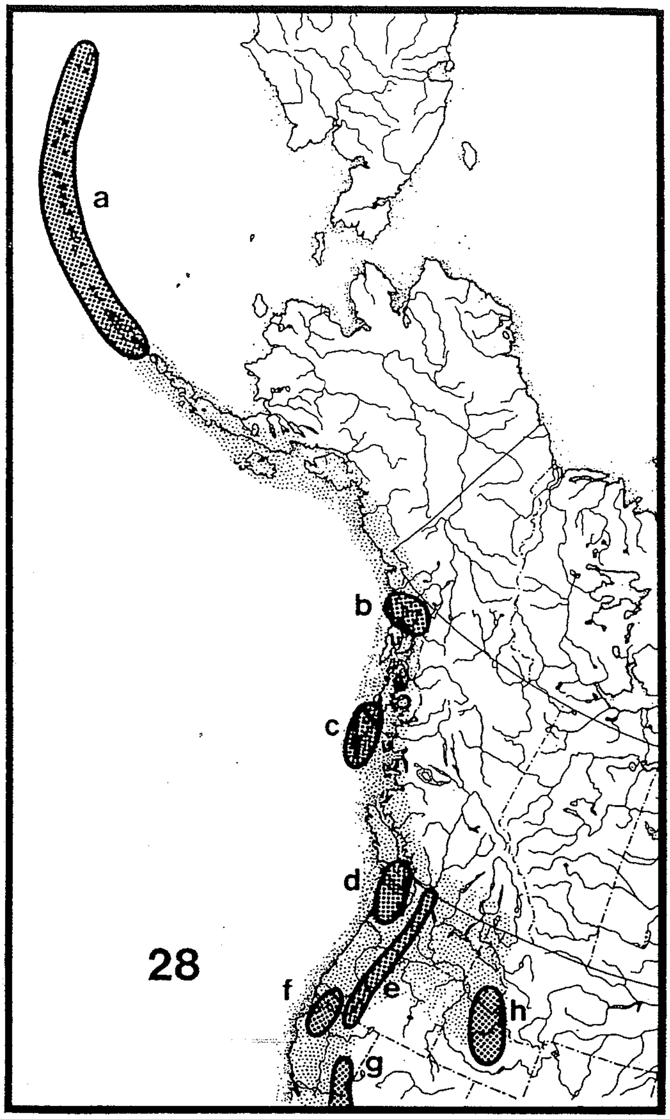
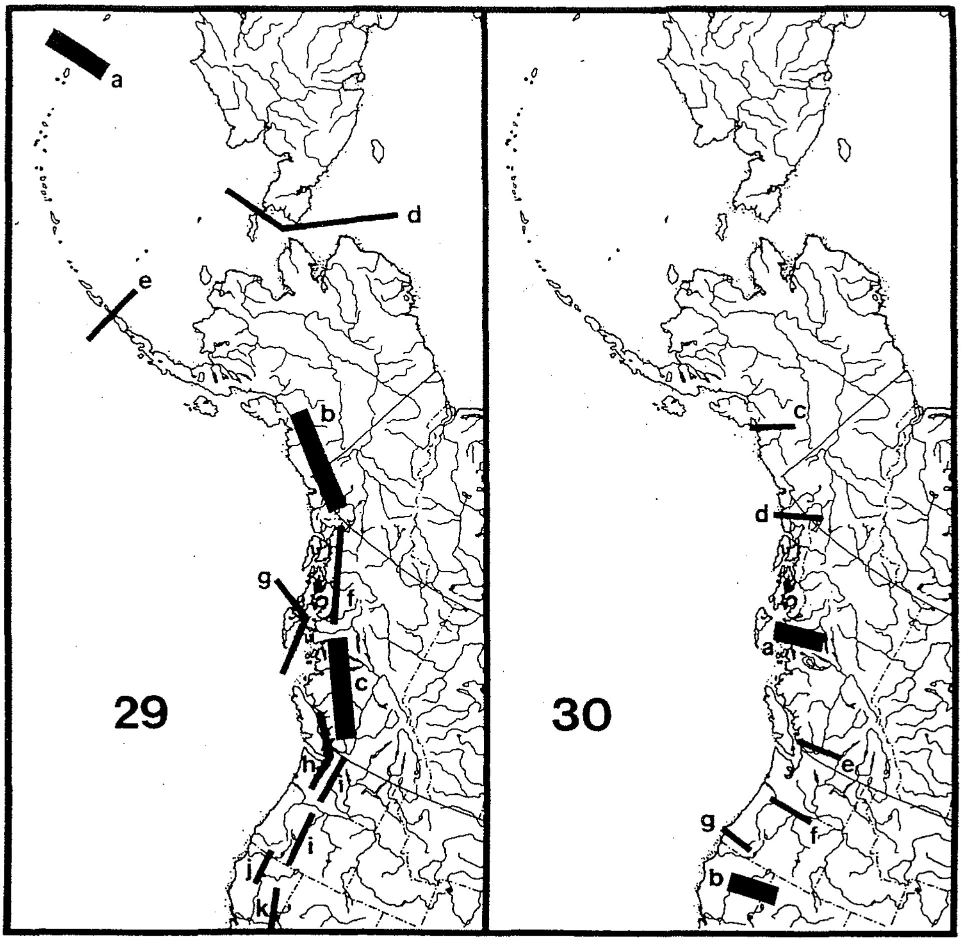


FIG. 28. Areas in the Pacific Northwest Coast region rich in endemic taxa: *a*, Aleutian Archipelago; *b*, Lituya Bay/Juneau region; *c*, Queen Charlotte Archipelago; *d*, Olympic Peninsula/Vancouver Island; *e*, northern Cascade Range; *f*, Klamath Mountain system; *g*, the Sierra Nevada; *h*, central Idaho (eastern limit of the Columbia Plateau Maritime Faunal Incursion Zone).

relative effectiveness is based only on my subjective impression of faunal dissimilarity across the barrier. I plan to test these "impressions" through a subsequent study using quantitative measures of similarity such as the association coefficient of Jaccard (Braun-Blanquet 1932) or the Simpson coefficient of faunal similarity (Simpson 1960).

Highly effective barriers to present east/west dispersal (Fig. 29) include (*a*) the strait between the Aleutian and Commander islands (Lindroth 1963), (*b*) the Chugach/Wrangell/St. Elias Mountain system, and (*c*) the Coast Ranges of the southern half of British Columbia. Other significant, but seemingly less effective, east/west barriers are (*d*) Bering Strait, (*e*) Unimak Pass (between Akun and Unimak islands in the Aleutian Archipelago),



FIGS. 29, 30. Inferred barriers to distribution and dispersal: 29, barriers to east/west dispersal; *a*, strait between Aleutian and Commander islands; *b*, Chugach/Wrangell/St. Elias Mountain system, *c*, Coast Ranges of southern British Columbia; *d*, Bering Strait; *e*, Unimak Pass; *f*, Coast Ranges of northern British Columbia; *g*, Dixon Entrance/Hecate Strait/Queen Charlotte Sound; *h*, Strait of Georgia/Puget Lowland; *i*, Cascade Range; *j*, lowlands east of Klamath Mountain system; *k*, Sierra Nevada; 30, barriers to north/south dispersal: *a*, Skeena River valley region; *b*, lowland gap between Cascade Range and Sierra Nevada; *c*, area of abrupt climatic shift near base of Kenai Peninsula; *d*, heavily glaciated upland just north of Glacier Bay; *e*, Fraser River valley; *f*, lower Columbia River valley; *g*, Rogue River valley.

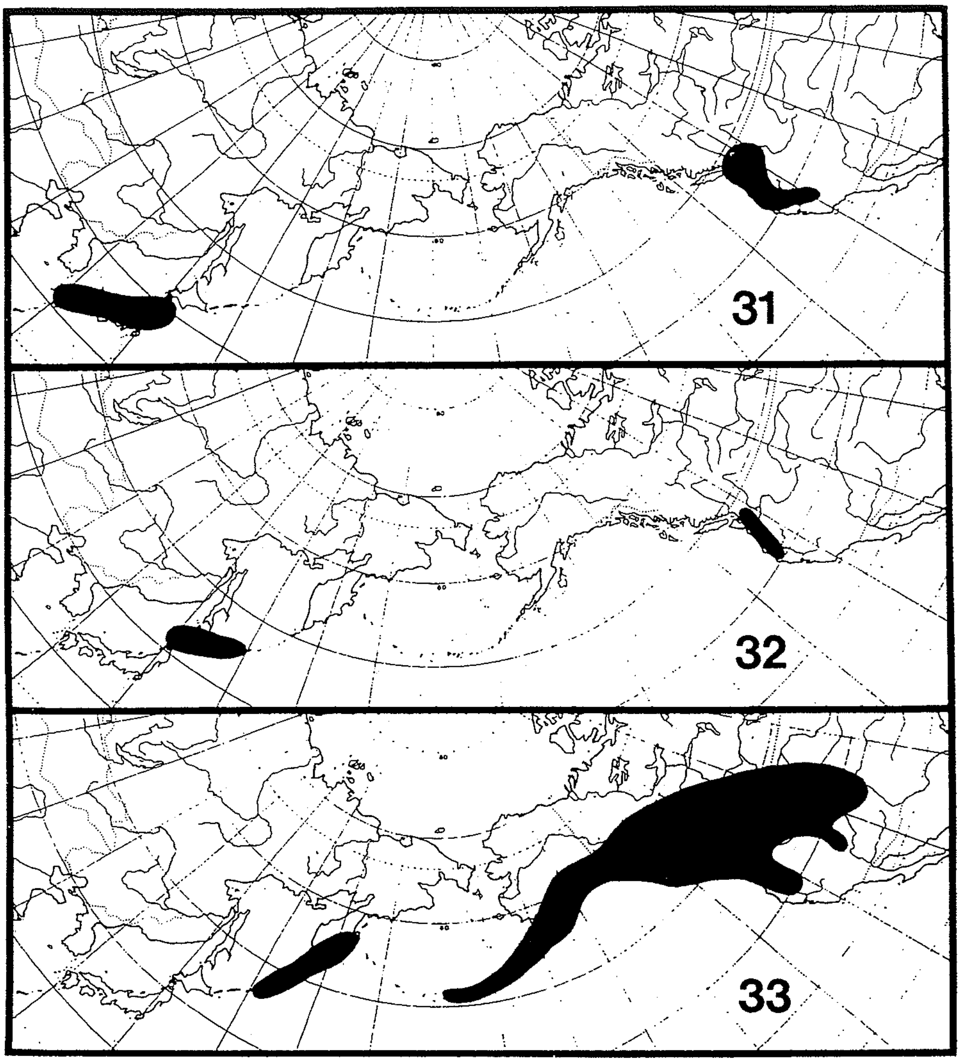
(*f*) the Coast Ranges of northern British Columbia, (*g*) Dixon Entrance/Hecate Strait/Queen Charlotte Sound (between the Queen Charlotte Archipelago and the mainland), (*h*) Strait of Georgia/Puget Lowland, (*i*) the Cascade Range, (*j*) lowlands north and east of the Klamath Mountain system, and (k) the Sierra Nevada. Most effective apparent barriers to present north/south dispersal (Fig. 30) include (*a*) the Skeena River valley region (which serves as the southern coastal range limit for many Rocky Mountain elements), and (*b*) the lowland gap between the Cascade Range and the Sierra Nevada in northeastern California. Other less effective, but significant, north/south barriers are (*c*) the area of abrupt climatic shift near the base of the Kenai Peninsula, (*d*) the heavily glaciated upland just north of Glacier Bay, and the (*e*) Fraser River, (*f*) lower Columbia River, and (*g*) Rogue River valleys. Again, these barriers are inferred from the known distributions of species present in or restricted to the region. Many of the *Nebria* species and subspecies pairs discussed above are separated by (i.e. are vicariant across) one or more of the barriers just mentioned, and degree of differentiation among respective isolates suggests that some of these barriers have functioned as such for thousands, if not millions, of years.

Faunal affinities

The affinity between any two faunas may have two components. First is *faunal similarity*, based on some measure relating the number of taxa shared by two faunas to the number of taxa in each fauna. Many such measures have been devised (e.g. Jaccard [Braun-Blanquet 1932] or Simpson [1960] coefficients of similarity) and are used routinely in faunal comparisons. At present, faunal inventories are still too incomplete for insects of the Coastal and other North American regions to permit meaningful quantitative comparisons among the faunas of these areas. However, analysis of faunal elements can provide a descriptive (qualitative) equivalent of the same kind of information about faunal affinity as statistical measures. Nine different faunal elements were described above, and six of these (restricted coastal, coast-centred, and introduced elements being excluded) indicate affinity with a particular North American fauna outside the Coastal region. The fauna of the south Coastal region shows affinities with Great Basin, central Rocky Mountain, and trans-American faunas; that of the central Coastal region with central and northern Rocky Mountain and trans-American faunas; and that of the northern Coastal region with northern Rocky Mountain, trans-American, Holarctic, trans-Beringian, and Alaskan interior faunas. The geographical distribution of elements representing each of these affinities within the Coastal region has already been described. Because this aspect of affinity is based on shared taxa, especially species and subspecies, it reflects present environmental conditions and relatively recent historical events.

The chief limitation of similarity analyses is that they depend on shared taxa. Potentially more useful information, especially for historical inference, can be gained from analyses of the second component of faunal affinity—namely, the *occurrence of vicariant sister taxa in faunas* compared. This aspect of affinity, which I explore briefly here, can only be effectively recognized and interpreted in relation to hypotheses of phylogenetic relationship for taxa represented. In the absence of detailed phylogenetic hypotheses for other groups represented in the area, I must again refer to my findings for *Nebria.* The east/west and north/south vicariance patterns described above under "Specific patterns of distribution" and illustrated in Figures 10–25 clearly demonstrate affinities both between the coastal fauna and other regional faunas and among different areas within the Coastal region itself. Because both vicariance patterns and analysis of faunal elements illustrate the same set of affinities between the coastal fauna and other North American regional faunas, only affinities found among different areas within the Coastal region need to be noted here. Most evident among these are affinities between the Olympic Peninsula/Vancouver Island fauna and that of the adjacent mainland (Figs. 14 and 17) and between faunas of the Cascade Range and the Sierra Nevada (Figs. 14, 16, and 18), the Cascade Range and Klamath Mountain system (Figs. 16, 19, and 20), and the Queen Charlotte Islands and the northern coastal area and Aleutian Islands (Fig. 24). None of these affinities are evident from an analysis of faunal similarity or of faunal elements; hence the vicariance patterns contribute unique information about affinity.

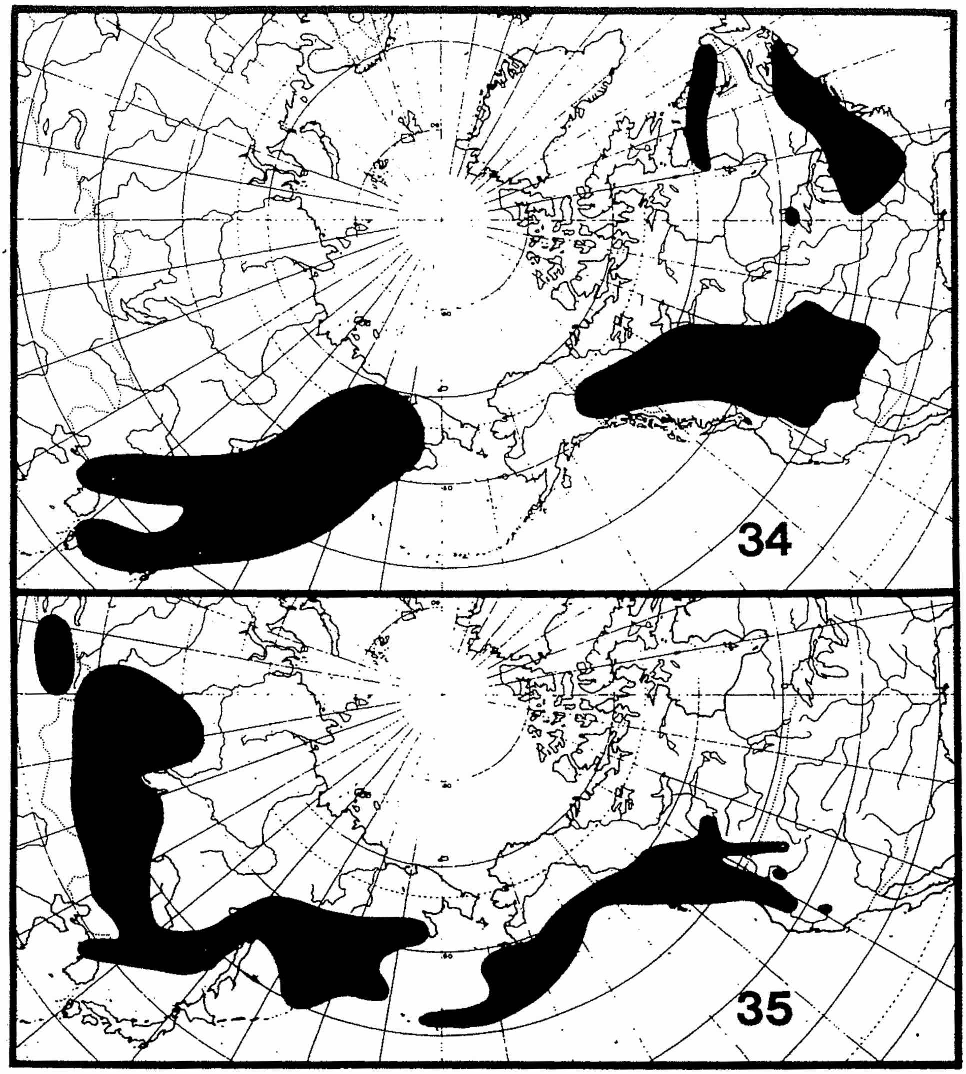
All vicariance patterns illustrated above, whether for subspecies or species pairs or even for pairs of species subgroups (Fig. 10), are restricted to areas within North America. However, the geographical distributions of several *Nebria* species groups, which are the informal taxonomic equivalents of subgenera, extend across the North Pacific to eastern Asia. Trans-Pacific vicariance relationships within species groups therefore provide the first evidence for faunal affinities between the Pacific Northwest Coast *Nebria* fauna and



FIGS. 31–33. Distributions of certain *Nebria* species groups: 31, the *virescens* group; 32, the *paradisi* group; 33, the *gregaria* group.

that of eastern Asia. Such affinities have been noted for many other insect groups (Van Dyke 1919, 1926, 1940).

The geographical ranges of five species groups, the *virescens, paradisi, gregaria, obliqua,* and *metallica* groups, are illustrated in Figures 31–35, respectively, and proposed phylogenetic relationships among them (Kavanaugh 1978) are as shown in Figure 36. Taken in the sequence presented, which also reflects the sequence of evolution of the groups, the pattern shown is one in which the geographical ranges of respective groups and their vicariance patterns across the North Pacific shift from more southern to more northern latitudes. The *virescens* group ranges latitudinally around 31–42°N in eastern Asia and 36–49°N in western North America, and its vicariant sister taxa are the most widely and southerly disjunct. Latitudinal range of the *paradisi* group on both continents is about 40–47°N, and disjunction between vicariant sister taxa is slightly narrower. The *gregaria, obliqua,* and *metallica* groups are successively more narrowly disjunct as their



FIGS. 34, 35. Distributions of certain *Nebria* species groups: 34, the *obliqua* group; 35, the *metallica* group.

ranges extend farther north on both sides of the Pacific. This pattern of vicariance and affinity is what one might predict based on overall Cenozoic climatic history of the North Pacific region and its probable effect on the *Nebria* fauna of that area. With the net cooling trend which began in mid-Tertiary time (Leopold and MacGinitie 1972; Wolfe 1969, 1978), the most warm-adapted elements would have had their ranges restricted to southernmost areas and been first to become isolated on opposite sides of the Pacific as their northern limits were forced southward. The least warm-adapted elements would have become isolated last, if at all. My interpretation of the evolution of genus *Nebria* is that there has been an overall trend for adaptation from temperate to successively colder climates, although stasis and/or reversals have occurred in the evolution of certain lineages. The distribution and vicariance patterns among sequentially evolved species groups appear to reflect this historical trend clearly. I suggest that this affinity pattern will be demonstrated repeatedly when phylogenetic relationships are better understood for other groups with

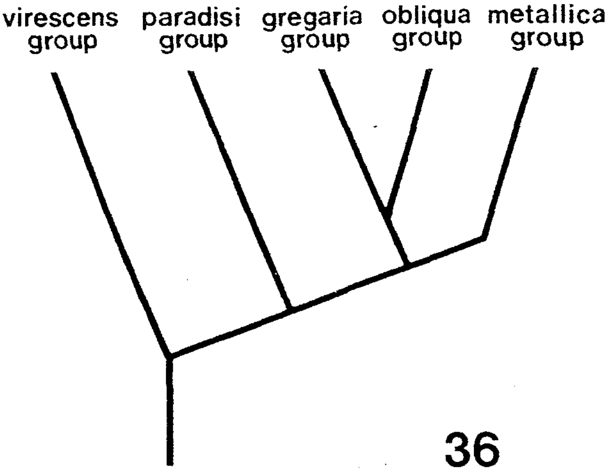


FIG. 36. Proposed phylogenetic relations among certain *Nebria* species groups.

faunal connections across the North Pacific region. Linsley's (1963) study of relationships among Cerambycidae across the North Pacific region appears to reflect this same pattern, but a detailed hypothesis of phylogenetic relationships among the groups involved has not yet been developed.

Origins of the extant fauna

The fauna of the Pacific Northwest Coast region is derived mainly from a widespread (Laurasian), northern, warm temperate Tertiary fauna that was fragmented as a result of the cooling trend initiated in mid-Tertiary time and reached its peak in the Pleistocene. Trans-Pacific affinities, such as those discussed for the carabid genus *Nebria* (see also Goulet 1983) demonstrate this quite clearly. Each descendant fragment of the ancestral fauna has subsequently evolved independently.

The coastal fauna also shows affinities of even greater antiquity with vicariant faunal remnants now restricted to continental fragments of Gondwanaland. For example, the sister group of the coastal endemic carabid genus *Promecognathus* is restricted to southern Africa. However, due to the diversity and complexity of these affinities and the absence of detailed information on phylogenetic relationships among the taxa involved, discussions of Gondwanian and other possible ancient affinities are both premature at this time and beyond the scope of this paper.

Although Tertiary and even older relationships and events provide background for development of the extant coastal fauna, the northern two-thirds of the region is occupied mainly by a fauna that represents recolonization of a formerly glaciated area in post-glacial time from a number of refugial sources. The locations of these proposed refugia can be inferred from data on faunal similarity, endemism, and vicariance presented above, and those that appear to have contributed to the coastal fauna are illustrated in Figure 37.

Five distinct refugia were located north or west of the Cordilleran ice sheet. The largest of these, the Yukon/Beringian refugium (Hopkins 1967; Lindroth 1979) appears to have contributed little to the coastal fauna. Remnants of the glacial fauna of the Aleutian Islands refugium (Lindroth 1963) survive in that region today, as endemic forms or differentiated populations of more widely distributed taxa; but contributions from that refugium to the present faunas of other parts of the Coastal region appear to have been minor. Similarly, proposed refugia on Kodiak Island (Lindroth 1969), in southeastern coastal Alaska (Mann and Kavanaugh unpubl. data), and the Queen Charlotte Islands (Foster 1965; Kavanaugh 1988) are inferred mainly from geologic evidence or the presence of endemic

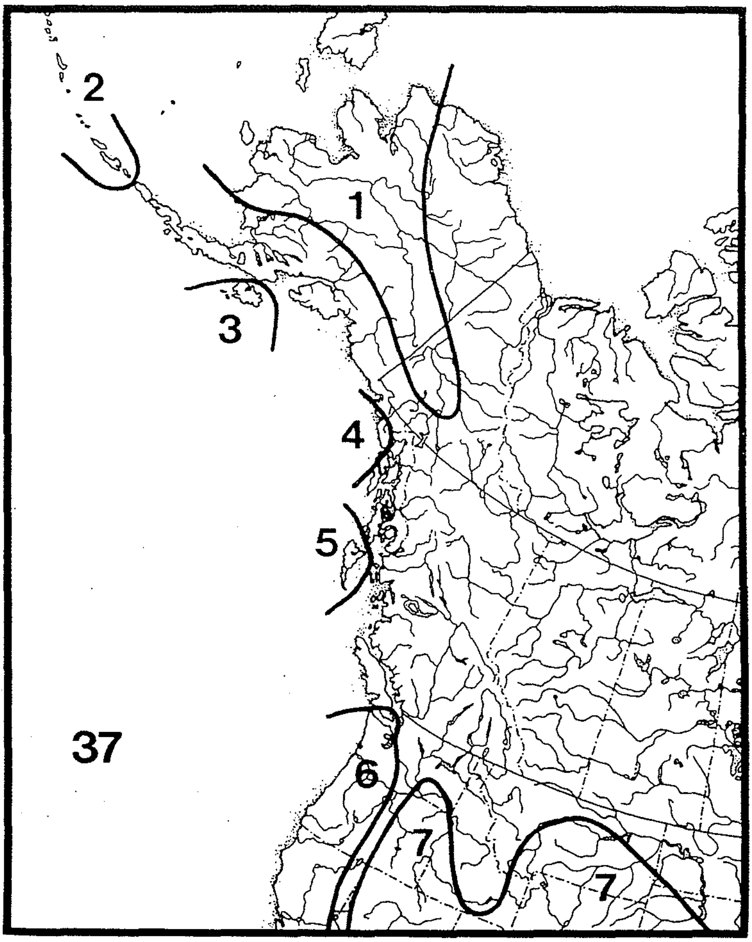


FIG. 37. Proposed glacial refugial areas for the fauna of the Pacific Northwest Coast region: 1, Yukon/Beringian refugium; 2, Aleutian Islands refugium; 3, Kodiak Island refugium; 4, southeastern Alaskan coastal refugium; 5, Queen Charlotte Islands refugium; 6, southern coastal refugium; 7, southern interior refugium.

forms in these areas. Few if any refugial forms appear to have colonized other parts of the Coastal region from these areas post-glacially. Restricted distributions of these forms suggest that the specializations that led to their survival in relative isolation left them unable to compete effectively for places in the more diverse continental faunas which, as more or less co-adapted units, recolonized the region post-glacially.

Clearly the most important source areas for recolonization of glaciated portions of the central and northern Coastal region were the two large glacial refugia south of the Cordilleran and Laurentide ice sheets, the southern coastal and southern interior refugia (Fig. 37). Of these, the southern coastal refugium was most important and complex. Endemism and vicariance relationships suggest that at least three different and geographically distinct faunal elements were present in this glacial refugium. These included: (1) a coastal montane element, former members of which now survive in mountains of the Olympic Peninsula and Vancouver Island; (2) a Cascade/Sierran montane element, which occupied unglaciated parts of the Cascade Range and Sierra Nevada and in which areas descendant populations still survive; and (3) a coastal lowland element, which occupied lowland and intermontane parts of the refugium. Forms representing each of these glacial elements are abundant in extant faunas of both central and northern parts of the Coastal region. Two distinct faunal elements, interior montane and interior lowland elements, appear to have been present in the southern interior glacial refugium. The contribution of this refugium to the coastal fauna is reflected by the occurrence of Rocky Mountain and some trans-American elements. As noted above, representation of these elements increases in stepwise fashion from south to north along the coast, and they are well represented mainly in the northern parts of the Coastal region. Of particular interest is the fact that, in formerly glaciated parts of the Coastal region, there is little or no evidence of local differentiation (or endemism) among elements derived from southern refugial source areas. In fact, these "undifferentiated" forms represent former southern endemics that have subsequently expanded their ranges greatly, whereas endemic forms in former northern and western refugial areas have not.

Conclusions

This study has shown that the origins of the Pacific Northwest Coast insect fauna are diverse, both geographically and temporally. The fauna has recruited elements liberally from several sources in post-glacial time, but Tertiary and Pleistocene events are nonetheless recorded in the phylogenetic and distributional relationships of at least some elements in the fauna. Many of the assertions made about the composition and development of the extant coastal fauna are based on studies of relatively few insect groups. I hope that interest in the fauna of this area will continue, and future studies will expand on present knowledge and permit tests of the conclusions presented here.

Acknowledgments

I thank G.C. Hunter and V.F. Lee for reviewing drafts of this manuscript and for their critical comments on its content. I also recognize the contributions of my many colleagues, past and present, whose taxonomic and faunistic studies of the insects of this region have contributed to present knowledge of the coastal fauna and served as part of the information base for this report.

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