The Ground-Beetle (Coleoptera: Carabidae) Fauna of the Queen Charlotte Islands. Its Composition, Affinities, and Origins

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Abstract

At present, 59 species of Carabidae are known to occur in the Queen Charlotte Islands. Two of these appear to have become extinct in historic times, and a 60th species is known only from fossil remains. Known habitat distribution, geographical range pattern, and development of hindwings are noted for each species. The fauna of the Archipelago is most similar to that of the adjacent coastal mainland, but more southerly affinities are also evident. Based on patterns among geographical ranges of species represented, six faunal elements are recognized (% of fauna in parentheses): 1) a Holarctic element (5%); 2) a transamerican element (19%); 3) a western North American element (27%); 4) a Pacific Coast North American element (42%); 5) an endemic element (5%); and, 6) an introduced element (1%). Of the three known endemic species, two (*Nebria charlottae* Lindroth and *Nebria louiseae* Kavanaugh) inhabit cobble-type upper sea beaches, while the third (*Nebria haida* Kavanaugh) is restricted to highest alpine areas. Composition of present and known fossil faunas suggest a composite origin for the former. A majority of species, including all but two of those represented in forested parts of the Archipelago, are probably post-glacial immigrants from one or two distinct southern refugia: 1) a coastal refugium (south of the Cordilleran Icesheet and west of the Cascade/Sierra Nevada divide); and, 2) an interior refugium (south of the Cordilleran and Laurentide Icesheets and east of the Cascade/Sierra Nevada divide). Presence and habitat distributions of endemic species suggest that alpine and upper sea beach habitats and organisms therein survived at least the last glacial period somewhere in the Archipelago and, hence, contributed to the present fauna. Northern glacial refugia appear to have made no contribution to the extant fauna.

Introduction

Carabid beetles, also known as "ground beetles", are a diverse group of insects with worldwide distribution. More than 20,000 species have already been described, but this may represent as little as half of the true number of extant species. Carabids are particularly well represented in cool- and cold-temperate areas, compared with other insect groups, with almost 800 species recorded from Canada and Alaska alone (Lindroth, 1961-69). Most carabids are nocturnal predators on insects and other invertebrates, but a few renegade groups have evolved for feeding on plants, particularly the seeds of grasses.

Carabids are a popular group among both amateur and professional entomologists, probably for several reasons. They are locally abundant, diverse, often conspicuous, and easy to collect, prepare, and study; and there are numerous professionals willing and able to make routine identifications, at least for European and North American carabid material. This combination of characteristics seems to stimulate general interest in the group. Biogeographers (*e.g.* Darlington, 1957, 1965, 1971; Lindroth, 1957, 1963, 1979a,b) have found carabids useful because these organisms tend to disperse relatively poorly, or at least slowly for insects, and

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hence are relatively good indicators of past biotic distribution, physiographic features, barriers, or climatic events—factors which have affected the development of present biotas. Students of Cenozoic history (*e.g.* Ashworth, 1979; Coope, 1979; Matthews, 1979a; Morgan & Morgan, 1980) have become keenly interested in carabids in recent decades because identifiable fragments of carabid beetles are often well preserved in peats and other deposits of late Tertiary and Quaternary age. Because much is known about the habitat requirements of extant representatives of these same species, much can be inferred about environmental conditions which prevailed when the fossils were alive.

An additional noteworthy characteristic of the group in general is the tendency for the evolution of brachyptery, or short-wingedness, among carabids for which flight capability is not advantageous (Darlington, 1936, 1943; Kavanaugh, 1985). In stable, enduring habitats, selection seems to strongly favor wing reduction, probably as a mechanism which permits reallocation of energy resources for more productive uses (such as reproduction). Brachyptery has evolved literally thousands of times independently among different carabid species and lineages. Lindroth (1979b) studied carabid beetle species which were dimorphic for wing length. He found that populations with brachypterous adults tend to predominate in areas of long-term occupation, such as refugia, while those with macropterous (long-winged) adults represent pioneer populations in newly occupied areas. For example, he used data on the distribution of such populations to distinguish between Scandinavian carabids which survived the last glacial period in refugia south of glacial ice from those which survived in northwest coastal refugia. Studies of this kind illustrate just one of many ways in which carabids have been used in biogeography.

Development of our present knowledge of the carabid beetle fauna of the Queen Charlotte Islands, has a rather simple history. Reverend J.H. Keen, a missionary to the Haida people during the late 1880s and early 1890s, provided the first account of the fauna (Keen, 1895). He recorded 24 species as present, although several of these were misidentified. The next published contribution was by Lindroth (1961-69), in which he corrected previous misidentifications and added six more species (including one new, endemic species) to the faunal list. During the past two decades, important additional carabid material has been collected by residents S. Douglas, N. Gessler, J. Miller, and T.E. Reimchen, and by visiting collectors J. Belicek, R.A. Cannings, R.W. Mathewes, M. Pitman, and B.G. Warner. I collected for two weeks in the Archipelago, with D.H. Mann during July 1981, exclusively on Graham and northern Moresby Islands. In July and August 1983, I spent an additional six weeks collecting with J.M. Campbell and M.D. Kavanaugh. During that period, we visited 15 different islands and collected at 80 different sites. As a result of these field efforts, 29 more species can now be added to the faunal list, including two additional new and (apparently) endemic species which I have described elsewhere (Kavanaugh, 1984).

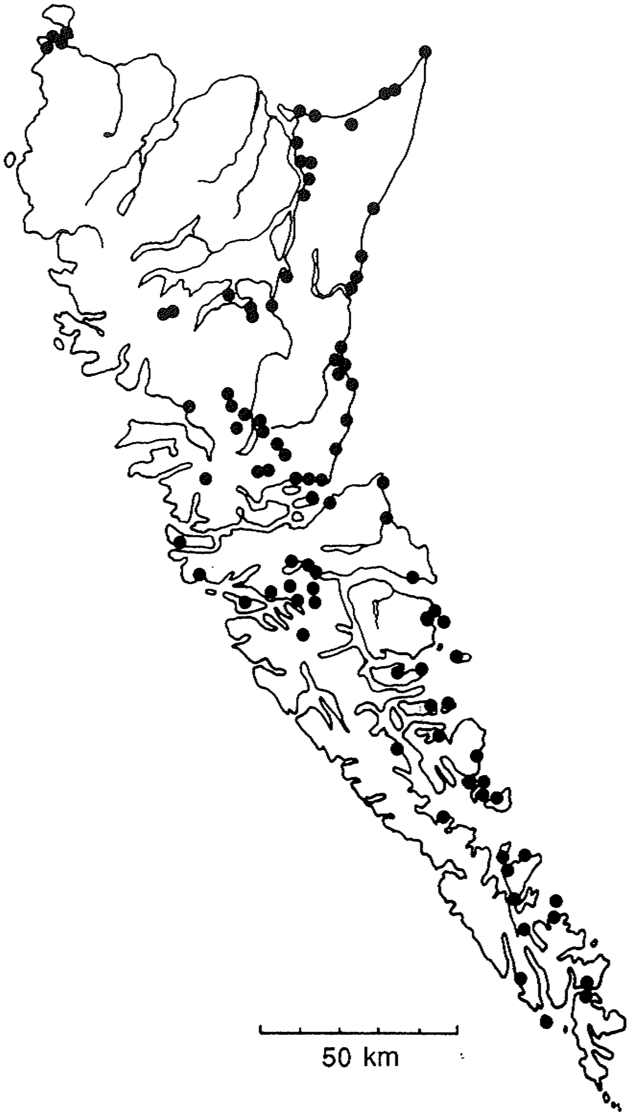

Fig. 1. Map illustrating all sites from which carabid beetles have been collected in the Queen Charlotte Islands, British Columbia.

My purpose here is to provide a brief report on: 1) our present knowledge of the carabid fauna of the Queen Charlotte Islands; 2) my preliminary analyses of this fauna and its affinities with faunas of other parts of the Pacific Northwest Coast; and, 3) the implications of these findings with regards to origins of the fauna in general and the question of glacial refugia in the Queen Charlotte Archipelago in particular. In a forthcoming paper I will provide more detailed information about each species represented in the fauna as well as a key for identification of adults.

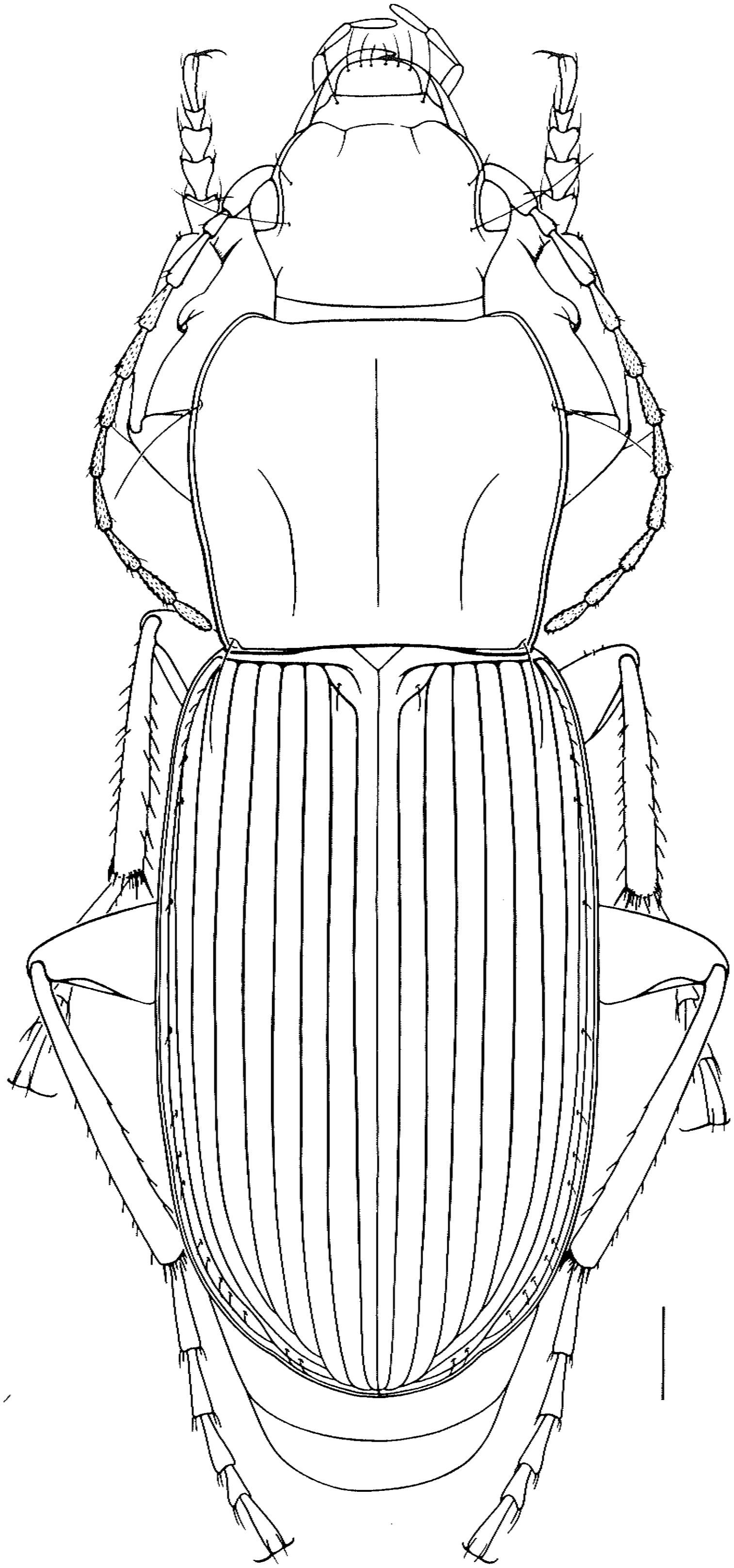

Fig. 2. *Pterostichus algidus* LeConte, adult male (from Peel Inlet at Moresby Camp Road, Moresby Island). Scale line = 1.0 mm. Illustration by Mary Ann Tenorio.

Materials

The material basis of this study includes about 7,000 carabid beetle specimens from the Queen Charlotte Islands. Most of these specimens were acquired during my expeditions in 1981 and 1983 and are deposited in the collection of the California Academy of Sciences. Other specimens were received for study on loan from collections in the following institutions: British Columbia Provincial Museum (BCPM), Victoria, British Columbia; Canadian National Collection of Insects (CNC), Biosystematics Research Institute, Ottawa, Ontario; Cornell University (CUIC), Ithaca, New York; Carnegie Museum (ICCM), Pittsburg, Pennsylvania; Museum of Comparative Zoology (MCZ), Harvard University, Cambridge, Massachussets; Oregon State University (OSUO), Corvallis, Oregon; Queen Charlotte Islands Museum (QCIM), Skidegate, British Columbia; University of Alberta, Strickland Museum (UASM), Edmonton, Alberta; University of British Columbia (UBC), Vancouver, British Columbia; United States National Museum of Natural History (USNM), Smithsonian Institution, Washington, D.C.; and Washington State University (WSU), Pullman, Washington.

The distribution of sites from which carabid beetles have been collected in the Queen Charlotte Islands is illustrated in Figure 1. As is apparent from this map, much of the Archipelago remains unsampled. Areas in special need of additional sampling include: western and central portions of Graham Island; western and southern Moresby Island; much of Louise, Lyell, Burnaby, and Kunghit Islands; and all islands not listed in Table 1. Such future sampling will probably show that a few additional species reside in the Archipelago, and data and analyses presented here must therefore be considered preliminary.

The Carabid Beetle Fauna

Present Faunal Diversity and Composition

At present, 59 species of carabid beetles are known to occur in the Queen Charlotte Islands (Table 4). Two of these species, *Carabus taedatus* Fabricius and *Scaphinotus angusticollis* Mannerheim, appear to have become extinct there in historic times (details to be provided in subsequent paper). A 60th species, *Nebria gyllenhali castanipes* Kirby, known in the Archipelago only from fossil remains, is probably also absent from the extant fauna. Fifty-six percent of known faunal diversity is accounted for by three carabid genera—*Bembidion* (20 sp.), *Pterostichus* (7 sp.), and *Nebria* (6 sp.)—although 22 genera are represented in the fauna.

To date, carabids have been collected on 23 islands (Table 1). The known fauna of Graham Island is most diverse, with 54 species represented, and faunas of Moresby and Lyell Islands include 32 and 13 species, respectively. Known faunas of eight islands include only a single species. Additional species will no doubt be found to occur on most if not all of these islands. Once faunas of the individual islands are better known, it should be possible to apply concepts of "equilibrium theory" (MacArthur & Wilson, 1967) to test for relationships between species diversity and island size, habitat diversity, and other parameters.

Table 1. Known carabid beetle diversity for each island sampled.

Island(s)	# of species represented on each island
Graham	54
Moresby	32
Lyell	13
Louise	10
Tanu	9
Kunga	8
Ramsay	7
Burnaby, Reef	6
Huxley, Talunkwan	5
Chaatl, Langara	4
Hotspring	3
Kunghit	2
Anthony, East Copper, Faraday, Harrison, Hibben, Maude, Murchison, West Skedans	1

Different carabid species appear to differ greatly in extent of their distributions in the Archipelago (Fig. 3). One species, *Pterostichus algidus* LeConte (Fig. 2), has been found on 20 of the 23 islands sampled. Adults of this species are also the most frequently encountered carabids on most islands, at least at low and middle elevations. Twenty-five species are known only from Graham Island at present, at least some of which are no doubt truly restricted to that island (due to unique microhabitats found there); three species are presently known only from Moresby Island.

Carabid species also differ in their environmental requirements and the range of habitats which they occupy in the Archipelago. In order to describe these habitat distributions, I use an arbitrary system of habitat classification which includes 13 general habitat types and two additional sub-types. These include: 1) upper sea beach, including sandy (1a) and cobble (1b) beach sub-types; 2) supra-tidal meadow; 3) lowland open ground (including synanthropic sites); 4) lowland marsh, bog, or mudflat; 5) lowland deciduous forest; 6) lowland coniferous forest; 7) lowland waterside habitat, including shore of large, open stream or lake (7a) and of small, shaded stream or seep (7b); 8) upland marsh, bog, or mudflat; 9) upland deciduous forest; 10) upland coniferous forest; 11) upland stream or lake shores; 12) subalpine (treeline) forest; and 13) alpine zone. The known habitat distributions of carabid species in the Archipelago are noted in Table 4. No such information is yet available for two species, *Scaphinotus angusticollis* and *Bembidion dyschirinum* LeConte.

Analyses of the Extant Fauna

Carabid species diversity in relation to habitat

Known species diversity for each habitat type is represented in Table 2. In most known carabid faunas (*e.g.* Armin, 1963; Darlington, 1943, 1971; Greenslade, 1968), species diversity is highest in lowland and/or lower montane habitats and decreases steadily with increased elevation. The Queen Charlotte Islands fauna is remarkable for its overall balance of diversity among different habitats and elevations. Highest diversity occurs in lowland waterside habitats. Seventeen species occur in each of these habitat sub-types, but only eight species (47%) are common to both. Although diversity is broadly distributed among different habitats, habitat specificity is nonetheless quite pronounced in the fauna (Table 3). About 63% of carabid species are restricted to only one or two habitat types, and only 16% of the species occupy five or more habitats.

Table 2. Carabid species diversity and habitat type.

Habitat	# of species	% of fauna
Upper sea beach, sand	6	11
Upper sea beach, cobble	7	12
Supra-tidal meadow	11	19
Lowland open ground (incl. synanthropic sites)	11	19
Lowland marshes or bogs	10	18
Lowland deciduous forest	15	26
Lowland coniferous forest	12	21
Lowland, large, open stream or lake shores	17	30
Lowland, small, shaded stream shores	17	30
Upland marshes or bogs	11	19
Upland deciduous forest	9	16
Upland coniferous forest	10	18
Upland stream or lake shores	6	11
Subalpine/mountain hemlock forest	5	9
Alpine zone	10	18

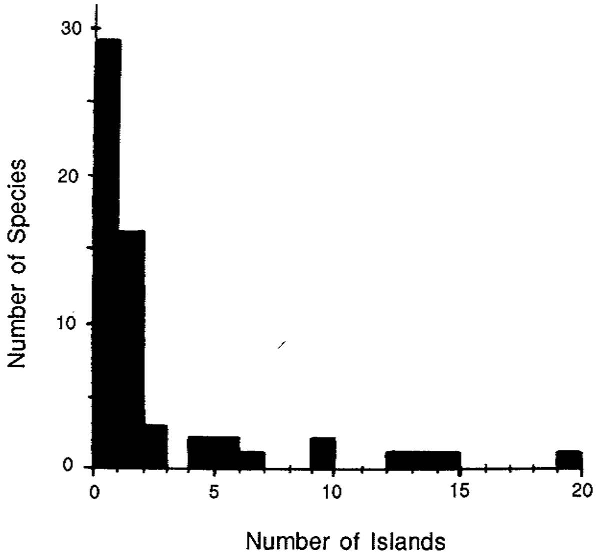

Fig. 3. Histogram illustrating frequency distribution for number of islands occupied by carabid species in the Queen Charlotte Islands, British Columbia.

Patterns among the ranges of species

The geographical ranges of carabid species represented in the Archipelago all appear to correspond, with some variation in detail, to one of six general distribution patterns (Fig. 4). 1) Holarctic (or at least trans-Beringian) pattern: geographical range includes at least northwestern North America and northeastern Eurasia, and may be circumpolar in some instances. 2) Transamerican pattern: geographical range is broad in North America, including at least part of the eastern half of the continent. 3) Western North American pattern: geographical range is restricted to the western part of the continent, from the Rocky Mountain region westward, broadly distributed in the west or absent from the southern Coastal region. 4) West Coast pattern: range is restricted to all or some part of the Pacific Coast region, including coastal lowlands, Coast Ranges, inter-

Table 3. Carabid beetle species and habitat specificity.

# of habitats occupied	# of species	% of fauna
1	21	37
2	15	26
3	8	14
4	4	7
5 or more	9	16

Table 4. A list of Carabidae known from the Queen Charlotte Islands, British Columbia, with habitat and geographical distributions and development of hindwings.

Taxon	Habitat†															Range‡	Wings§
	1a	1b	2	3	4	5	6	7a	7b	8	9	10	11	12	13		
Carabus taedatus Fabricius	–	–	–	–	–	–	–	–	–	–	–	–	–	–	x	WNA	B
C. nemoralis Muller	–	–	–	x	–	x	–	–	–	–	–	–	–	–	–	I	B
C. tuberculatus Harris	–	–	–	–	–	x	x	–	–	–	–	–	–	–	–	WC *	B
Scaphinotus marginatus Fischer	–	–	x	x	–	x	x	–	–	–	x	x	–	x	x	WNA	B
S. angusticollis Mannerheim	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	WC	B
Cicindela oregona guttifera LeConte	–	–	–	–	–	–	–	x	–	–	–	–	–	–	–	WNA	M
Leistus ferruginosus Mannerheim	–	–	–	–	–	x	–	–	–	–	–	–	–	–	–	WNA	M
Nebria gyllenhali castanipes Kirby	known only from fossil remains															TA	M
N. diversa LeConte	x	–	–	–	–	–	–	–	–	–	–	–	–	–	–	WC *	B
N. mannerheimii Fischer	x	x	x	x	–	–	–	x	–	–	–	–	–	–	–	WC	M
N. sahlbergii sahlbergii Fischer	–	–	–	–	–	–	–	x	x	–	–	–	x	–	–	WC	M
N. haida Kavanaugh	–	–	–	–	–	–	–	–	–	–	–	–	–	–	x	E	B
N. charlottae Lindroth	–	x	–	–	–	–	–	–	–	–	–	–	–	–	–	E	B
N. louiseae Kavanaugh	–	x	–	–	–	–	–	–	–	–	–	–	–	–	–	E	B
Notiophilus sylvaticus Eschscholtz	–	–	–	–	–	x	x	–	–	–	x	x	–	x	–	WC	B
Loricera decimpunctata Eschscholtz	–	–	–	x	x	x	–	x	x	x	–	–	x	–	–	WC	M
Elaphrus americanus sylvanus Goulet	–	–	–	–	x	–	–	x	–	x	–	–	–	–	–	WNA	M
E. clairvillei Kirby	–	–	–	–	x	–	–	–	–	x	–	–	–	–	–	TA	M
Broscodera insignis Mannerheim	–	–	–	–	–	x	x	–	x	–	x	x	x	x	x	WC	M
Dyschirius pacificus Lindroth	x	–	–	–	–	–	–	–	–	–	–	–	–	–	–	WC	B
Trechus ovipennis Motschulsky	x	x	–	–	–	–	–	x	x	–	–	–	–	–	–	WC	B
T. chalybeus Dejean	–	–	x	x	–	x	x	–	x	x	x	x	x	x	–	WNA	B
Bembidion zephyrum Fall	x	–	–	–	–	–	–	–	–	–	–	–	–	–	–	WC	M
B. inaequale opaciceps Casey	–	–	–	–	–	–	–	x	–	–	–	–	–	–	–	WNA	M
B. dyschirinum LeConte	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	WNA	M
B. castum Casey	–	–	–	–	–	x	–	–	x	–	–	–	–	–	–	WC	M
B. iridescens LeConte	–	–	–	–	–	–	–	x	x	–	–	–	–	–	–	WNA	M
B. incertum Motschulsky	–	–	–	–	–	–	–	–	x	–	–	–	–	–	x	WNA	M
B. quadrifoveolatum Mannerheim	–	–	–	–	–	–	–	x	x	–	–	–	x	–	–	WNA	M
B. farrarae Hatch	–	–	–	–	–	–	–	x	–	–	–	–	x	–	x	WNA	M
B. viator Casey	–	–	–	–	x	–	–	–	x	–	–	–	–	–	–	WC *	M
B. complanulum Mannerheim	–	–	–	–	–	–	–	–	–	–	–	–	–	–	x	WNA	M
B. planiusculum Mannerheim	–	–	–	–	–	–	–	x	x	–	–	–	–	–	–	WC	M
B. sejunctum Casey	x	–	–	–	–	–	–	–	–	–	–	–	–	–	–	TA *	M
B. transversale Dejean	–	–	–	–	–	–	–	x	–	–	–	–	–	–	–	TA *	M
B. incrematum LeConte	–	–	–	–	x	–	–	x	–	x	–	–	–	–	–	TA *	M
B. indistinctum Dejean	–	–	–	–	x	–	–	–	–	–	–	–	–	–	–	WC	M
B. versicolor LeConte	–	–	–	–	x	–	–	x	–	x	–	–	–	–	–	TA	M
B. fortestriatum Motschulsky	–	–	–	–	x	–	–	–	–	x	–	–	–	–	–	TA	M
B. spectabile Mannerheim	–	–	–	–	–	x	x	–	–	–	x	x	–	x	x	WC	M
B. oblonguloides Lindroth	–	–	–	–	–	x	x	–	x	–	–	–	–	–	–	WC	B
B. oblongulum Mannerheim	–	–	–	–	–	–	–	–	–	–	–	x	–	–	–	WC	B
Diplous aterrimus Dejean	–	–	–	–	–	–	–	x	x	–	–	–	–	–	–	WNA	M
Nomius pygmaeus Dejean	–	–	–	–	–	–	x	–	–	–	–	–	–	–	–	HA	M
Agonum belleri Hatch	–	–	–	–	x	–	–	–	–	x	–	–	–	–	–	WC *	B
A. metallescens LeConte	–	–	–	–	–	–	–	–	–	x	–	–	–	–	–	TA *	M
A. brevicolle Dejean	–	–	–	–	x	–	–	–	–	x	–	–	–	–	–	WC *	M
Pterostichus lama Ménétriés	–	–	–	–	–	–	x	–	–	–	–	–	–	–	–	WC *	B
P. crenicollis LeConte	–	x	x	x	–	x	x	–	x	–	x	x	–	–	–	WC *	B
P. amethystinus Mannerheim	–	–	–	–	–	x	x	–	–	–	x	x	–	–	–	WC	B
P. algidus LeConte	–	x	x	x	–	x	x	x	x	–	x	x	–	–	–	WC	B
P. castaneus Dejean	–	–	–	–	–	x	x	–	–	–	x	x	–	–	–	WNA	B
P. adstrictus Eschscholtz	–	x	x	x	–	–	–	x	–	–	–	–	–	–	–	HA	M
P. riparius Dejean	–	–	–	–	–	–	–	–	x	–	–	–	–	–	–	WNA	B
Amara sinuosa Casey	–	–	–	–	–	–	–	–	–	–	–	–	–	–	x	TA	M
A. ellipsis Casey	–	–	x	–	–	–	–	–	–	–	–	–	–	–	–	TA *	M
A. littoralis Mannerheim	–	–	x	x	–	–	–	–	–	–	–	–	–	–	–	TA	M
Harpalus sommulentus Dejean	–	–	x	x	–	–	–	–	–	–	–	–	–	–	–	WC	M
Trichocellus cognatus Gyllenhal	–	–	x	x	–	–	–	–	–	–	–	–	–	–	–	HA	M
Bradycellus nigrinus Dejean	–	–	x	–	–	–	–	–	x	x	–	–	–	–	–	TA	M

Footnotes →

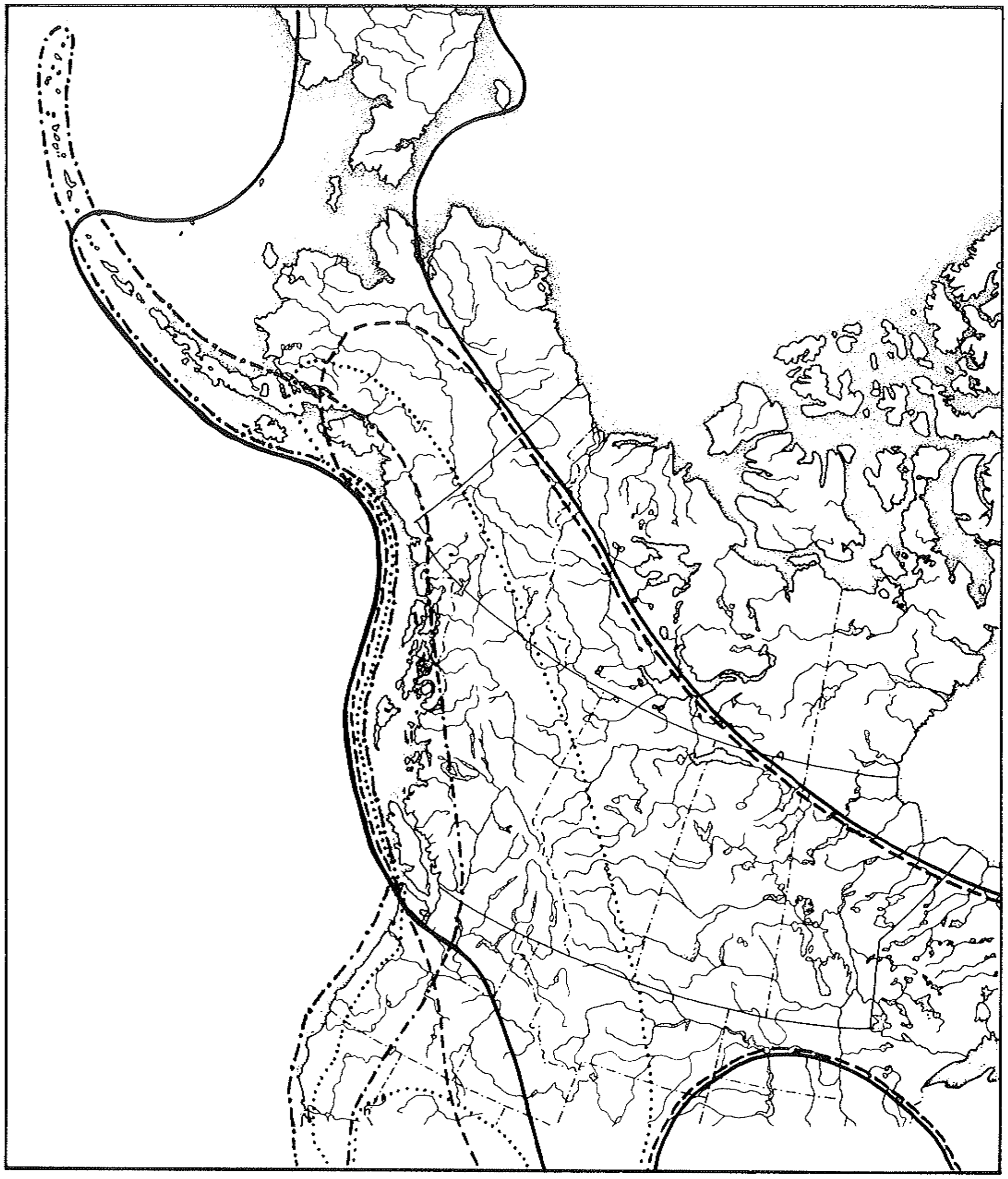

Fig. 4. Map illustrating general pattern of geographical distribution for Queen Charlotte Islands carabids: —— = Holarctic; ---- = Transamerican; ••••• = Western North America; -•-•- = West Coast.

Table 4. (Continued)

† Habitats: 1a) upper sea beach, sand; 1b) upper sea beach, cobble; 2) supra-tidal meadow; 3) lowland open ground (including synanthropic sites); 4) lowland marshes or bogs; 5) lowland deciduous forest; 6) lowland coniferous forest; 7a) large, open stream or lake shores; 7b) small, shaded stream shores; 8) upland marshes or bogs; 9) upland deciduous forest; 10) upland coniferous forest; 11) upland stream or lake shores; 12) subalpine/mountain hemlock forest; 13) alpine zone; x) recorded from this habitat; –) not recorded from this habitat; ?) habitat distribution unknown.

‡ Geographical range pattern: E) Endemic to Queen Charlotte Islands; HA) Holarctic, or at least trans-Beringian; I) Introduced to North America; WC) West Coast only (including Cascade Range and Sierra Nevada or not); WNA) Western North American (Rocky Mountains and points further west; TA) Transamerican; *) northern limit of known range at Queen Charlotte Islands.

§ Development of hindwings: B) Brachypterous adults; M) Macropterous adults.

montane valleys, east to the crest of the Sierra Nevada and Cascade Ranges in the contiguous United States and of the Coast Range in British Columbia, south to central California, and northwest to the outer Aleutian Islands. 5) Endemic pattern: range is restricted to the Queen Charlotte Islands Archipelago. 6) Introduced pattern: original distribution is Palearctic, with occurrence in the Archipelago a secondary result of introduction to the North American mainland (see Lindroth, 1957).

The range patterns to which the known geographical distributions of Queen Charlotte Islands carabids correspond are noted in Table 4, and findings are summarized in Table 5. Only 5% of the fauna (3 sp.) represent Holarctic forms; the same number of species are apparently endemic. The fauna comprises mainly species restricted to western North America, particularly the West Coast; 10 species (17% of the fauna) reach their northern range limit in the Archipelago. Relative proportions of Holarctic and restricted western North American elements in the carabid fauna of the Archipelago differ markedly with analogous elements in the flora (see other papers in this volume), which has much greater Holarctic representation.

Relationship between geographical and habitat ranges for carabid species is illustrated in Table 6. Two or more West Coast species occur in each habitat type, and Western North American (WNA) forms are absent only from sea beach habitats. Holarctic forms are absent from upland areas, except in the marsh, bog, and mudflat habitat. The three endemic species are restricted to one of only two habitats types, alpine summits or cobble sea beaches; and the introduced species is restricted to

Table 5. Geographical distributions of Queen Charlotte Islands carabids in relation to generalized range patterns

Range pattern	# of species	% of fauna
Holarctic	3	5
Transamerican	11	19
Western North American[a]	16	27
West Coast only[b]	25	42
Endemic to Queen Charlotte Islands	3	5
Introduced to North America	1	1
Northern limit of known range at Queen Charlotte Islands	10	17

a Rocky Mountains & points further west.
b Including Cascade Range and Sierra Nevada or not.

Table 6. Relationship between geographical range and habitat for Queen Charlotte Islands carabids. Values refer to number of species for each combination of habitat type and geographical range pattern.

	Range Pattern					
Habitat	Holarctic[a]	Transamerican	WNA[b]	West Coast[c]	Endemic[d]	Introduced[e]
Upper sea beach, sand	–	1	–	5	–	–
Upper sea beach, cobble	1	–	–	4	2	–
Supra-tidal meadow	3	2	2	4	–	–
Lowland open ground[f]	2	1	2	5	–	1
Lowland marshes or bogs	–	4	1	6	–	1
Lowland deciduous forest	–	–	4	10	–	1
Lowland coniferous forest	1	–	3	8	–	–
Lowland, large, open stream or lake shores	1	3	7	5	–	–
Lowland, small, shaded stream shores	1	–	6	9	–	–
Upland marshes or bogs	1	5	2	3	–	–
Upland deciduous forest	–	–	3	6	–	–
Upland coniferous forest	–	–	3	7	–	–
Upland stream or lake shores	–	–	3	2	–	–
Subalpine/mountain hemlock forest	–	–	2	3	–	–
Alpine zone	–	1	5	2	1	–

a Or at least trans-Beringian.
b Western North American (Rocky Mountains and points further west).
c West Coast only (including Cascade Range and Sierra Nevada or not).
d Endemic to Queen Charlotte Islands.
e Introduced to North America.
f Including synanthropic sites.

Table 7. Relationship between geographical range pattern and hindwing length for Queen Charlotte Islands carabids

Range Pattern	Total # species	# species brachypterous	% species brachypterous
Holarctic, or at least trans-Beringian	3	0	0
Transamerican	11	0	0
Western North American (Rocky Mountains & points further west)	16	6	38
West Coast only (incl. Cascade Range & Sierra Nevada or not)	25	13	52
Endemic to Queen Charlotte Islands	3	3	100
Introduced to North America	1	1	100
Total	59	22	37

lowland habitats, closely associated with human habitation and/or disturbance.

Table 7 illustrates the relationship between hindwing development and geographical range pattern for species in the carabid fauna. None of the Holarctic or Transamerican species in the Archipelago are represented by brachypterous adults. This is in sharp contrast to findings for carabid faunas of arctic and subarctic regions, for example, which include numerous Holarctic (or at least trans-Beringian) elements, many of which are brachypterous (Lindroth, 1969). More than 50% of the restricted West Coast species are represented by brachypterous adults, as are all three endemic species and the single introduced form. The relationship apparent in this fauna between habitat and brachyptery is generally similar to that found in other faunas studied (Erwin, 1979). The highest incidence of brachyptery (38-47% of species represented) is in forest habitats, both upland and lowland (coniferous and deciduous), with lowest incidence (6-23%) in riparian and lacustrine habitats, both upland and lowland (marsh, bog, mudflat and waterside habitats). Perhaps unexpected is the high incidence of brachyptery (42%) among species represented on cobble upper sea beaches.

Faunal Affinities

Comparison with known faunas of other Pacific Northwest Coastal (PNC) Areas

Inventory of the carabid beetle fauna of the Coastal region is far from complete. To date, faunas of only three areas have been intensively studied—namely, Kodiak Island (Lindroth, 1969), the Lituya Bay region of southeastern Alaska (unpubl. data), and the Queen Charlotte Islands (present report); and minor additions to even these faunal lists can be expected in the future. Known faunas of other areas no doubt represent some unknown fraction of species actually represented in each. Nonetheless, I have made comparisons between known faunas of several areas and that of the Queen Charlotte Islands (Table 8.) Faunal lists used in these comparisons were compiled from data provided by

Table 8. Comparisons among selected carabid beetle faunas of the Pacific Northwest Coastal region.

	Area[a]									
	AI	AP	KI	KP	LB	QCI	PR	V	VI	Total
Total number of species	30	54	51	68	29	59	48	156	166	273
Number shared with QCI	9	10	16	18	18	–	33	43	45	56
Percentage QCI fauna shared	15	17	27	31	31	–	56	73	76	
Simpson Coefficient[b]	30.0	18.5	31.4	30.5	30.5	–	68.8	72.9	76.3	
Jaccard Coefficient[b]	15.3	16.9	27.1	26.5	30.5	–	55.9	27.6	27.1	
Number of species brachypterous	11	15	18	13	9	21	13	22	29	55
Percentage of species brachypterous	37	28	35	19	31	36	28	14	17	20

[a] Faunal areas: AI) Aleutian Islands; AP) Alaskan Peninsula; KI) Kodiak Island; KP) Kenai Peninsula; LB) Lituya Bay; QCI) Queen Charlotte Islands; PR) Prince Rupert; V) Vancouver (British Columbia); VI) Vancouver Island.

[b] See text (**Faunal Affinities**) for discussion of Simpson and Jaccard Coefficients of faunal similarity.

Lindroth (1961-69), with modifications based on subsequent revisionary studies by other workers and supplemented with my own collecting records.

The known carabid fauna of the Queen Charlotte Islands includes more species (59 sp.) than that of the Prince Rupert area (48 sp.) on the adjacent mainland. The fauna of the latter area has not yet been as intensively sampled as that of the former area, and future additions to the faunal list for the Prince Rupert area can be expected. Nonetheless, this comparison clearly demonstrates that the carabid fauna of the Queen Charlotte Islands is unexpectedly diverse in relation to the fauna of the adjacent mainland compared with other areas (see Darlington, 1971; MacArthur &Wilson, 1967).

All carabid species represented in the Queen Charlotte Archipelago, except for the three endemic forms, are shared with one or more of the other faunas compared. In order to assess similarities between each of these faunas and that of the Archipelago, percentages of species shared and two similarity measures were calculated. The latter include the Simpson (Simpson, 1960) and Jaccard (Braun-Blanquet, 1932) Coefficients of faunal similarity. If faunas compared are about equal in diversity, then these two measures are equal in value and use; but if diversities are unequal, then the measures have different uses. Simpson Coefficients (S = 100 times the number of taxa shared divided by the number of taxa in the smaller fauna) emphasize similarity and are useful for inferring possible source areas for small, peripheral or depauperate faunas. Jaccard Coefficients (J = 100 times the number of taxa shared divided by the number of taxa in the larger fauna) provide a tougher test of similarity by accentuating differences.

Comparisons of both percentages of species shared and Simpson Coefficients demonstrate greatest similarities between the Queen Charlotte Islands carabid fauna (QCI) and faunas of areas to the south, including Vancouver Island (VI) and the mainland of southern British Columbia (V). These same measures show that the fauna of the adjacent mainland (PR) is much more similar to that of the Archipelago (QCI) than are any of the faunas to the north, but not as similar as more southern Coastal faunas. However, if Jaccard Coefficients are compared, the QCI fauna is found to be much more similar to the PR fauna than to any other. In all comparisons, similarities between QCI and all northern Coastal faunas are low.

The incidence of brachyptery is highest among island carabid faunas, including those of the Aleutian Islands (38%), Kodiak Island (35%), and the Queen Charlotte Archipelago (36%), but not the Vancouver Island fauna (17%). Faunas of the Alaskan Peninsula and Prince Rupert area, adjacent to the Aleutian and Queen Charlotte Archipelagos, respectively, also show relatively high incidence of brachyptery (28%) as does the Lituya Bay area fauna (31%).

Faunal Origins

Data and analyses presented above concerning geographical and habitat distributions of individual species, patterns among geographical and habitat ranges, and affinities of the Queen Charlotte Islands carabid fauna with other selected faunas of the Pacific Northwest Coastal region, provide the evidence needed to infer origins of the extant fauna of the Archipelago. Such inference must take into account the known environmental history of the region. Although much is yet to be learned about details of the Quaternary environmental history of the Queen Charlotte Archipelago and the Pacific Northwest Coast mainland, the major features of this history are clear (Matthews, 1979b). Most of the region was heavily and repeatedly glaciated in Pleistocene time, last as recently as 10,000 to 13,000 years ago or less. Several areas have been proposed as likely sources (refugia) from which post-glacial occupation of the region may have occurred. These include both extrinsic (peripheral) and intrinsic (within the region) refugia (Fig. 5). Abundant geologic and paleoenvironmental evidence attests to the existence of exten-

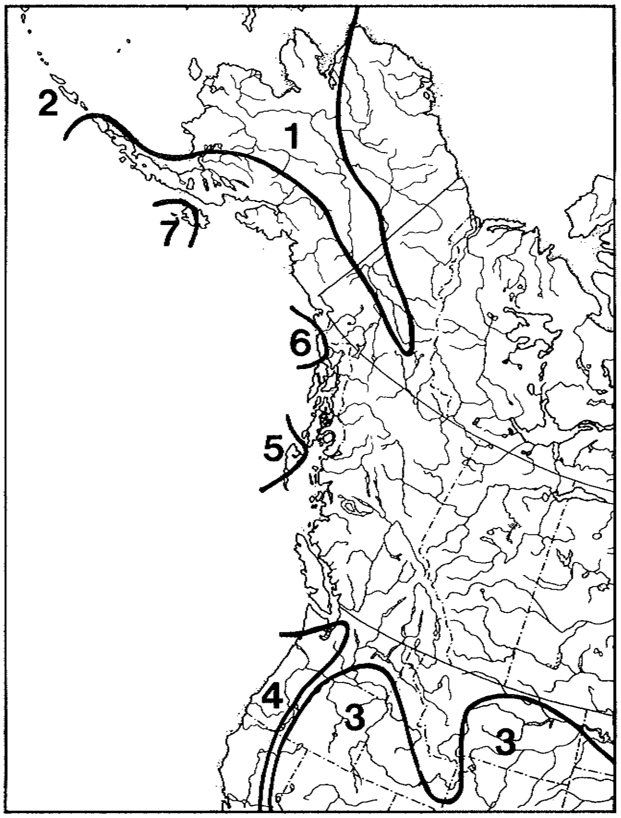

Fig. 5. Map illustrating areas which may have served as proposed glacial refugia for the fauna of the Pacific Northwest Coastal region. 1) Yukon/Beringian refugium; 2) Aleutian Islands refugium; 3) southern interior refugium; 4) southern coast refugium; 5) Queen Charlotte Islands refugium; 6) southeastern Alaska coastal refugium; 7) Kodiak Island refugium.

sive glacial refugia both south of the Cordilleran and Laurentide Icesheets (Scudder, 1979), east and west of the Sierra Nevada/Cascade crest, and northwest in the Yukon River Valley/Beringian region (Lindroth, 1979a; Matthews, 1979b). Another extrinsic refugial area was in the Aleutian Islands Archipelago (Lindroth, 1963). Some evidence also supports several local (intrinsic) glacial refugia in the Coastal region, including Kodiak Island (Lindroth, 1969), southeastern coastal Alaska (Mann & Kavanaugh, in prep.), and the Queen Charlotte Islands Archipelago (Foster, 1965). Available evidence suggests that several of these refugial areas have contributed to the extant carabid fauna of the Queen Charlotte Islands.

Clear affinities with Coastal faunas to the south, rather than the north, suggest a south Coastal origin for much of the fauna (Fig. 6). There is no evidence to suggest post-glacial immigration of elements from the Yukon/ Beringian refugium or any other proposed refugium north of the Archipelago, except perhaps from the Aleutian area.

Several carabid species in the Queen Charlotte Islands fauna are broadly distributed in western North America but not in the southern Coastal region. That these interior (Rocky Mountain area) forms, rather than closely related, southern Coastal species, occur in the Archipelago suggests: 1) a separate, southern interior origin for at least part of the fauna; and 2) that early post-glacial climate of at least parts of the Archipelago and adjacent coastal mainland may have been drier and colder than at present, thus favoring forms adapted to the southern interior rather than the southern Coastal region. This interpretation is supported by paleobotanical (R.W. Mathewes, pers. comm.) and carabid fossil evidence. I have recently studied a fragmentary fossil of *Nebria gyllenhali castanipes* Kirby, discovered by J.V. Matthews, Jr., in a sample collected by R.W. Mathewes and B.G. Warner at Cape Ball, Graham Island, from a deposit dated at 11,100 ± 90 yr B.P. This species is not known to occur in the Archipelago at present, nor anywhere west of interior British Columbia, although its present range extends from Yukon Territory and British Columbia east to Labrador and Newfoundland and south to Wyoming and Nevada. *Carabus taedatus* Fabricius, known in the Archipelago from a single fragmentary specimen which I collected under a huge boulder on the summit of a high peak on Moresby Island, may also have disappeared from the Archipelago in post-glacial time. Like *N. gyllenhali castanipes, C. taedatus* is not known to occur on the adjacent Coastal mainland at present; these two forms are frequently found together in subalpine and upper montane habitats in the Rocky Mountains, often associated with aspen (*Populus tremuloides*) and subalpine fir (*Abies lasiocarpa*).

The presence of endemic (precinctive) plants and animals in the Queen Charlotte Islands has been cited as evidence in support of one or more proposed glacial refugia in the Archipelago (Calder & Taylor, 1968; Foster, 1965), which could have served as an additional (*in situ*) source area for the extant fauna. Three alternative hypotheses that could account for the occurrence of these endemics seem plausible.

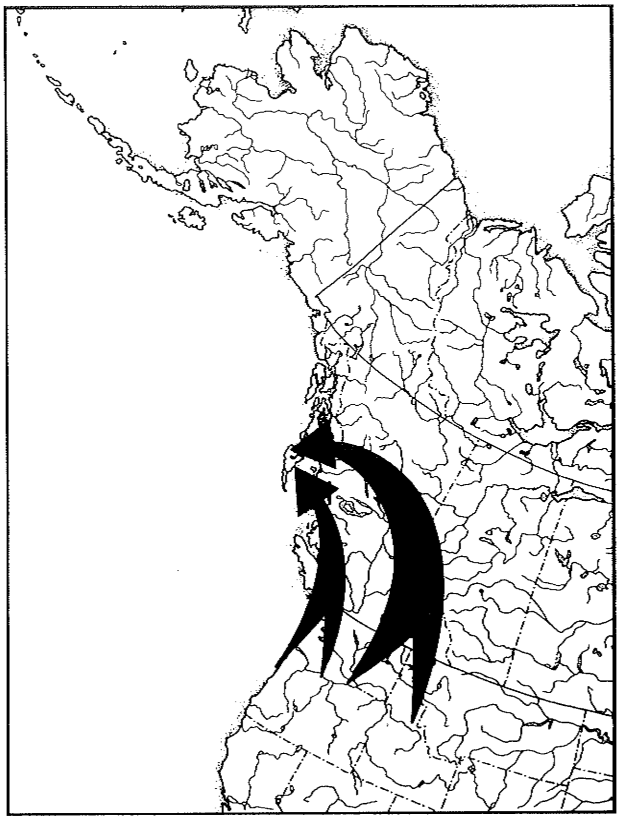

Fig. 6. Schematic representation of southern coastal and interior immigration routes for post-glacial colonization of the Queen Charlotte Archipelago.

Species thought to be endemic to the Archipelago may actually be more widely distributed (hence not precinctive). This has proven to be true for most (but not all) of the vascular plant taxa which previously were thought to be restricted to the Archipelago (Calder & Taylor, 1968), but which now are known to occur also on northern Vancouver Island (Ogilvie, this volume). Sampling along the adjacent Coastal mainland is still so incomplete that this possibility cannot yet be dismissed for the supposed endemic insects, including three carabid species, all members of genus *Nebria*, and one cercopid bug (Homoptera), *Aphrophora regina* Hamilton (1982: 1189). Nonetheless, this hypothesis does not account for all endemic forms, particularly some of the proposed endemic birds and mammals (Foster, 1965; Foster, this volume); and I predict that the carabid species will be shown to be precinctive in spite of future sampling on the Coastal mainland. Furthermore, glacial survival of an organism in the Archipelago is not necessarily precluded by its present occurrence on the

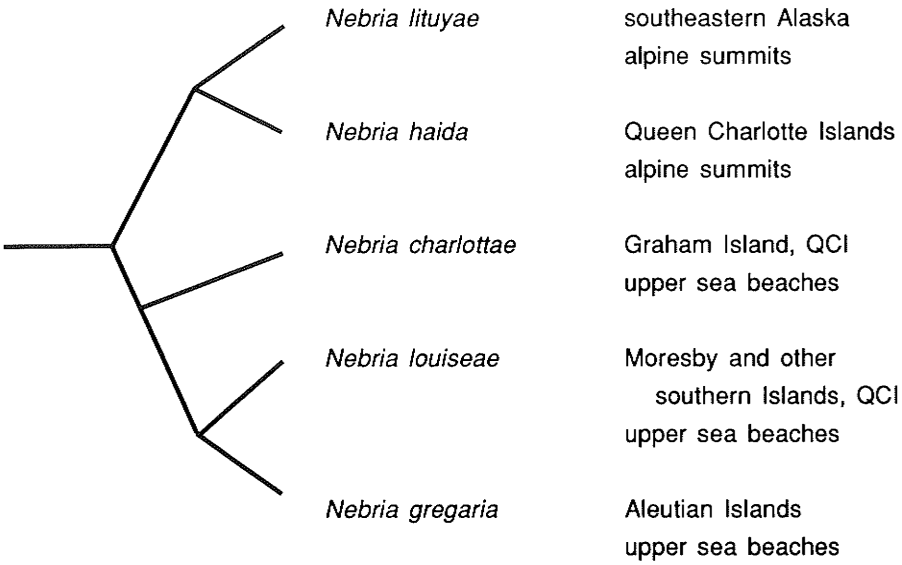

Fig. 7. Proposed phylogenetic relationships among species of *gregaria* infragroup of genus *Nebria*; geographical distribution and habitat noted for each species.

adjacent mainland. Post-glacial colonization of the mainland from a refugium in the Archipelago is no less plausible than the reverse colonization pathway. In fact, the distributions of two other carabid species illustrate this possibility. *Bembidion viator* Casey and *B. oblonguloides* Lindroth are known only from the Queen Charlotte Islands and the mainland immediately adjacent to the Archipelago (*i.e.* the Prince Rupert area). A glacial refugium in the Archipelago would certainly have been the most proximate source area for the mainland populations of these species.

A second hypothesis is that endemic organisms extant in the Archipelago survived glacial periods outside of the area, immigrated in post-glacial times, and subsequently became extinct elsewhere. This possibility cannot be dismissed; but I know of no paleontological evidence to support this hypothesis for any of the supposed endemic animal species.

A third hypothesis is that the endemic forms differentiated in post-glacial time *in situ* from ancestors that reached the Archipelago following deglaciation. Discovery of fossil specimens representing the endemic forms in deposits of glacial age from some site(s) in the Archipelago would refute this hypothesis. However, presence of respective sister species of the endemic forms on the adjacent mainland could be interpreted as supporting this hypothesis, although not conclusively. Such findings might suggest that the common ancestor of the sister species pair once occupied both island and mainland areas and that subsequent isolation permitted differentiation. But this isolation need not have occurred in post-glacial time. It could have been completed earlier, during either a glacial or interglacial period. Occurrence of the sister species on the adjacent mainland might represent simply a reoccupation of that area following deglaciation.

Unfortunately, phylogenetic relationships of most of the endemic plants and animals in the Archipelago have not yet been considered in detail; hence, information on the distributions of sister taxa is not generally available. However, a hypothesis of relationship among *Nebria* species, including the Queen Charlotte Islands endemics, has been developed (Kavanaugh, in prep.) and can be used to test the third hypothesis presented above. All three endemic forms are members of a single subgroup (the *gregaria* infragroup) of the *gregaria* species group of *Nebria*. Hypothesized phylogenetic relationships among species of this infragroup, based on cladistic analysis of characters of adult form and structure, are as illustrated in Fig. 7.

Nebria haida Kavanaugh (1984: 162) is restricted to treeless alpine summits and ridges of the high peaks on Graham and Moresby Islands. Its sister species, *Nebria lituyae* Kavanaugh (1979a: 100), which occurs in a similar habitat, is known only from the summits of coastal hills in the Lituya Bay and Juneau areas of southeastern Alaska. *Nebria louiseae* Kavanaugh (1984: 162) is restricted to cobble-type upper sea beaches on Moresby Island and other islands of the Queen Charlotte Archipelago south of Skidegate Channel. Its sister species, *Nebria gregaria* Fischer, is apparently restricted to the Aleutian Archipelago (although there are unsubstantiated records of its occurrence on the coastal mainland of Alaska) and inhabits upper sea beaches. *Nebria charlottae* Lindroth, known only from Graham Island, where adults are found in the same habitat as

N. louiseae adults, is the sister group of the species pair *N. louiseae*/*N. gregaria* of the *gregaria* infragroup. The sister group of the five species of the *gregaria* intergroup is the *arkansana* infragroup. The latter, which includes three species, is restricted to the interior of western North America, specifically to the Rocky Mountain region, where its members inhabit the margins of cool mountain streams.

If this set of relationships is correct, then origin of the endemic *Nebria* species in the Archipelago must have been complex. Simple fragmentation of the geographical range of a single common ancestral form cannot account for the geographical distribution and vicariance relationships of sister taxa among the five species. History of the group must have included at least one dispersal event, and probably as many as three, in addition to several vicariance events. Both geographical and habitat distributions suggest that the common ancestor of the *gregaria* infragroup became isolated in the Pacific Northwest Coastal region in pre-glacial or early glacial time. Montane streamside habitats, the presumed ancestral habitat type for the infragroup and present habitat for its sister group, would have become extremely limited, unstable areas in the Coastal region during glacial periods. This may account for apparent habitat specialization, early in the history of the infragroup, away from streamside habitats in two different directions—namely, onto alpine summits (which may have been available as nunataks during glacial periods) and sea beaches (which would have persisted and, perhaps, expanded during glacial periods). This "vicariance" in habitat is congruent with the first dichotomy in the dendrogram illustrated in Fig. 7, but I know of no evidence at present that can be used to establish the geographical relationships of these proposed sister taxa.

Differentiation of *N. haida* and *N. lituyae* from their common ancestor could have occurred in any one of several ways. Ancestors of *N. haida* could have reached the Archipelago through long-range dispersal from the mainland across the sea gap and differentiated subsequently, and this could have occurred either post-glacially or at some earlier time. Alternatively, the geographical range of the ancestral form could have initially included alpine areas both on the mainland and in the Archipelago, with differentiation resulting from subsequent fragmentation of the ancestral range, isolation, and resultant vicariance. Such a vicariance event could also have occurred post-glacially (second or third hypothesis above) or during a previous glacial or interglacial episode (either of which would require that *N. haida* survived at least the last glacial period in a refugium in the Archipelago).

Long-range dispersal of the ancestor of *N. haida* was unlikely for two reasons. All members of the gregaria infragroup are flightless, so it is appropriate to propose that the *haida*/*lituyae* common ancestor was also flightless. This would exclude long-range aerial transport. Both *N. haida* and *N. lituyae* are restricted to alpine regions, habitats presently most removed from the seashores and least likely to afford an opportunity for oversea transport. If the common ancestral form was restricted to the mainland and to the same habitat as its descendants, then it could only have had access to the Archipelago when alpine environmental conditions occurred at or near sea level. Such conditions could have occurred during glacial periods or, more likely, immediately before or after a glacial episode. However, because sea level was as much as 100 m lower than at present during full glacial times, at least parts of the Archipelago were probably connected to the mainland by dry land; and there would be no need to propose long-range dispersal over water at that time.

If the common ancestor of *N. haida* and *N. lituyae* colonized the Coastal region from a northern or southern glacial refugium in post-glacial time and the complete geographical ranges of these two species are as presently known, the ancestral form must have become extinct throughout much of the Coastal region, and its descendant species represent post-glacially differentiated relicts. While this interpretation may be correct, it makes little sense. At present, apparently suitable alpine habitat can be found at many locations along the Coast, and it is unclear why neither *N. haida* nor *N. lituyae* occurs in these areas if both differentiation and present distributions of these species are simply the result of post-glacial events. If, however, present distributions reflect differentiation and survival of respective forms in separate glacial refugia and only limited post-glacial dispersal from these refugia, then present distribution patterns seem appropriate. Unfortunately, sampling of alpine areas along the Coast is not yet complete, and we cannot be sure that the full geographical ranges of both species are known.

The geographical and evolutionary histories of the group including *N. charlottae*, *N. louiseae*, and *N. gregaria* and their common ancestor were no doubt influenced by some of the same climatic and geologic events as those discussed above for *N. haida* and *N lituyae* and their common ancestor. However, histories of the two groups may be different in at least two significant ways. First, members of the former group live on upper sea beaches rather than alpine summits and, hence, have easy access to the sea. Long-range transport on the sea surface may well have played a role in the distributional history of this group. Second, two endemic species of the former group (*N. charlottae* and *N. louiseae*) occur in the Archipelago and occupy seemingly identical habitats. Although these forms are allopatric in distribution, they are not sister species and, hence, are not true vicars. *Nebria charlottae*, as the sister group of the species pair *louiseae*/*gregaria*, must have differentiated from the common ancestor of *N. louiseae* and *N. gregaria* before they differentiated from each other.

If we assume that the occurrence of both *N. charlottae* and *N. louiseae* in the Archipelago is the result of post-glacial immigration (with or without subsequent differentiation), what refugial areas may have served as their source(s)? There is no evidence to suggest that the geographical range of this group of species or its common ancestor ever included areas south of the Archipelago, even on the mainland, so there is no reason to propose survival in southern glacial refugia. The Aleutian Islands appear to have served as a refugium during glacial episodes (Lindroth, 1963), and the common ancestor of *N. gregaria* and *N. louiseae* may have survived there, as is suggested by the present distribution of *N. gregaria*. Post-glacial southward range extension (or dispersal) of this ancestral form, either progressively along the Coast or directly over water, may eventually have resulted in occupation of the Queen Charlotte Archipelago and subsequent differentiation of *N louiseae*. But this southward expansion would have been a unique event, against the main flow of faunal movement, because the carabid fauna as a whole shows no other northern affinities. It therefore seems less complex to propose that *N. louiseae* survived and differentiated during the last glacial period in a refugium in the Queen Charlotte Archipelago. Several unsubstantiated records for *N. gregaria* from coastal mainland Alaska, however, may represent, 1) simply mislabelled material or, 2) a more extensive present distribution of *N. gregaria* than is presently recognized. If the latter, then this distribution may reflect either, a) limited post-glacial expansion of the range of *N. gregaria* itself out of the Aleutian refugial area or, b) post-glacial expansion of the *louiseae/gregaria* common ancestor. If (b) is correct, then the case for the post-glacial origin of *N. louiseae* from survivors of the Aleutian glacial refugium is strengthened.

Where did *N. charlottae* survive the last glacial period? The least complex hypothesis is that it survived in a refugium somewhere in the Archipelago, probably on Graham Island, to which it is now restricted. Its history could be similar to that proposed for *N. louiseae,* which reached the Archipelago from a northern source area, but in some earlier period than the latter. Alternatively, it could represent relict descendant of a widespread, early Pleistocene ancestral form, that occurred on both the mainland and on islands, populations of which became isolated and differentiated in the Queen Charlotte Archipelago during some glacial period prior to the last.

Evidence for Glacial Refugia in the Queen Charlotte Islands

To date, there is no evidence from the fossil record that conclusively demonstrates presence of the endemic *Nebria* species in the Archipelago during that time, but several lines of evidence are suggestive of refugial survival for them as well as for other organisms.

The endemic *Nebria* are restricted to only two habitats—namely, alpine summits and ridges and cobble-type sea beaches. Of all habitat types present in the Archipelago, these are the ones most likely to have survived a glacial episode. Alpine summits and ridges would have remained largely ice-free, as nunataks poking out above and between local glaciers and icecaps. Heusser (1954) has shown that surprisingly diverse biotas can survive under such conditions in heavily glaciated areas at present. Cobble sea beaches would also have persisted, at least at the bases of headlands between valley glaciers, providing the kind of sea-level refugium which *N. louiseae* would have needed to survive as its members live today. Lowered sea levels during glacial episodes would probably have provided an even greater total sea beach area than is available at present.

A second line of evidence is provided by the behavior of these beetles in their respective habitats. Adults of most *Nebria* species in montane parts of North America are most frequently found in close association with streams, seeps, snowfields, or glaciers; many forage on the surfaces of snowfields and glaciers at night for food. In marked contrast, *N. haida* adults are least frequently found near water or snow, have not been observed foraging on snowfields at night, and, generally, are found in the driest sites available in the alpine zone. This avoidance of water, snow, and ice represents an unusual behavioral pattern for members of the genus, but one that would appear to be of selected advantage in a nunatak area. Individuals venturing out on expanses of snow might not find their way back 'home' and be lost to their population; and wet areas would probably freeze quickly each night, even in summer, possibly trapping beetles in ice before they could move to safer sites. *Nebria louiseae* adults live in cobble-type upper sea beaches, almost always associated with freshwater seeps running through the cobble. Such seeps would probably have been abundant throughout the Archipelago on beaches and sea-level moraines beyond the margins of glaciers and snowfields at low elevations.

For the North American *Nebria* fauna in general, rates of taxonomically significant differentiation appear to vary, depending (at least in part) on habitat (Kavanaugh, 1979b). Among the *Nebria* taxa that seem to differentiate most slowly are those found at lowest and highest elevations (*e.g.* sea beach and alpine areas)—the former because they tend to disperse easily and maintain larger ranges, the latter perhaps because selective pressures are so severe in such habitats that little variation exists or can be tolerated in the population. If the three endemic *Nebria* species in the Queen Charlotte Islands have differentiated in post-glacial time, then they do not fit this pattern for the genus. In fact, individual populations of all three species tend to be well isolated from other conspecific populations. *Nebria haida* populations are found on separate mountain tops, even on different islands, and interpopulational exchange of individuals is highly improbable if not impossible. Populations of *N. louiseae* occur on different islands (although over-sea dispersal between islands is clearly possible), and those of *N. charlottae* in different parts of Graham Island are separated by wide stretches of unsuitable habitat. Yet for each of these species, intra- and interpopulational variation is surprisingly low. For each, a well-integrated, homogenous genome is inferred—one which could have resulted from intense selection on small populations under refugial conditions.

Finally, but perhaps most significantly, there is a growing body of paleoenvironmental evidence which confirms the existence of ice-free areas in the Queen Charlotte Islands at the height of the Late Wisconsinan glaciation, at least as much as 16,000 years ago (Clague *et al.*, 1982; Warner *et al.*, 1982). Available data indicate that a diverse tundra-like flora flourished, at least in the lowlands of northeastern Graham Island, at a time when the southern British Columbia mainland was experiencing maximum glaciation.

Based on evidence presently available, all three endemic *Nebria* species may well have survived at least the last glacial period in refugia within the Archipelago, and *N. charlottae* may have survived there for more than one glacial episode. Present habitat distributions of these possible refugial forms suggest that both alpine and sea beach habitats were available during at least the last glacial period, in upland (nunatak) and lowland refugia, respectively. At least two separate lowland refugia are indicated—one somewhere on Graham Island or adjacent exposed seafloor, in which *N. charlottae* survived; and one somewhere in the southern part of the Archipelago, in which *N. louiseae* survived. Two other carabid species, *Bembidion viator* and *B. oblonguloides*, may also have survived in refugia within the Archipelago but subsequently expanded their ranges to include the adjacent mainland in post-glacial time. If so, this would suggest that lowland marshes and at least some small forested areas were also present in some part of the Archipelago during the last glacial episode.

Perhaps future paleobotanical and paleontological studies in the Archipelago will uncover more conclusive evidence in support of this refugium hypothesis. In the meantime, a continued field effort is needed to increase our understanding of the present carabid fauna of the Archipelago and its affinities and origins. This must include additional collecting both within the area, especially in western Graham Island and the islands south of Skidegate Channel, and on the mainland. Few areas along the entire coastline between Vancouver and the Alaskan Peninsula have been intensively sampled. Additional sampling is essential for a proper inventory of the Pacific Northwest Coastal fauna, and such an inventory is necessary if we are to properly interpret the endemism found in the carabid fauna of the Queen Charlotte Islands.

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