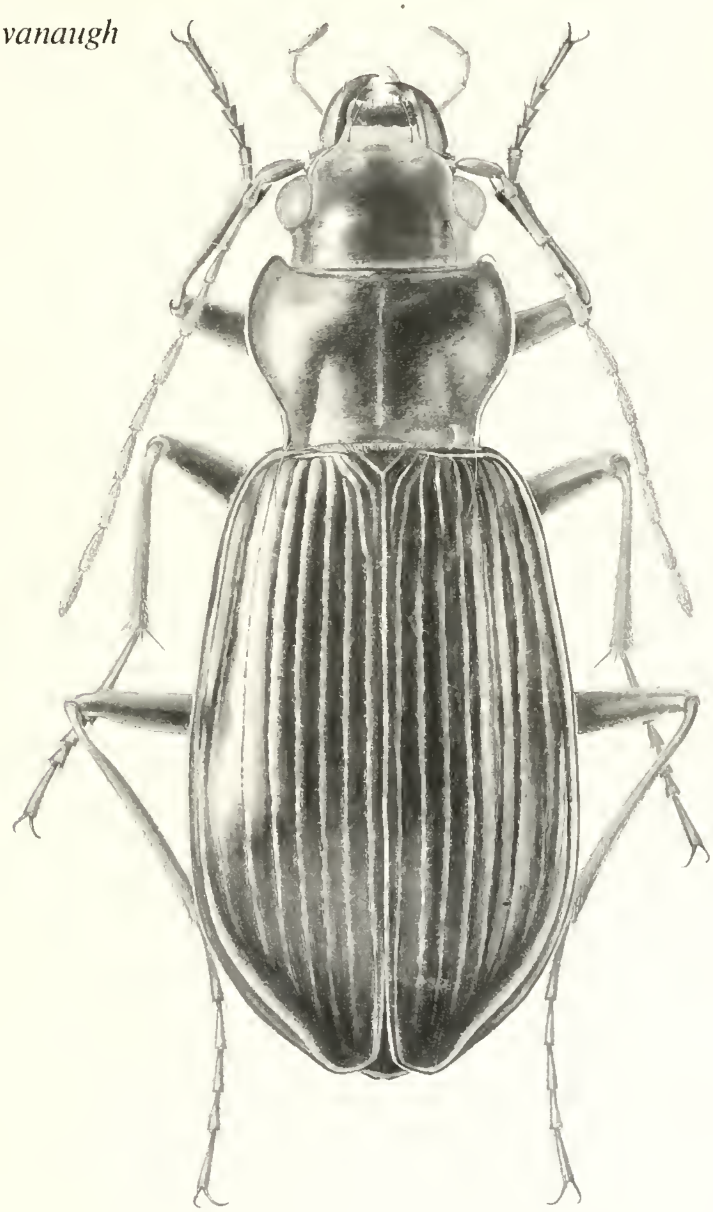
Carabid Beetles (Insecta: Coleoptera: Carabidae) of the Queen Charlotte Islands, British Columbia

By David H. Kavanaugh



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Abstract: This report about the carabid beetle fauna of the Queen Charlotte Islands is based on review of the literature, extensive fieldwork in the region, and study of more than 8,300 specimens. The archipelago itself is briefly described, and a historical outline of past geologic and biological research in the region is provided. History of the study of carabid beetles in the region is also reviewed. Information is provided about carabid beetles in general, their usefulness in biogeographic and paleoenvironmental studies, the equipment, materials, and techniques for their collection and preservation, and logistics for fieldwork in the archipelago. To date, carabid beetles have been sampled from 137 sites on 23 different islands. Fifteen different habitat types are recognized for carabids in the archipelago, and each is described and illustrated with photographs. The known fauna includes 62 species, representing 22 genera and 17 tribes; and two additional species are known only from fossil remains. Synonyms (if any), diagnostic combination, general description, geographical distribution within and outside the archipelago, habitat distribution, and discussion of dispersal potential are provided for each species. An illustrated key, designed for use by non-specialists, is included for identification of adult specimens. No nomenclatural changes are proposed, but the type locality of *Nebria charlottae* Lindroth is restricted to Masset, Graham Island. Comparisons among the geographical ranges of species reveal six different patterns (or elements) represented in the fauna (% of the fauna in parentheses): a Holarctic Pattern (5%), a Transamerican Pattern (20%), a Western North American Pattern (29%), a West Coastal Pattern (40%), an Endemic Pattern (3%), and an Introduced Pattern (3%). Within the archipelago, 24 species are known from only one island, the remainder are more widely distributed. Sixty-five percent of the species are restricted to only one or two habitats, and less than 12% occupy more than four habitats. The endemic species, *Nebria charlottae* Lindroth and *Nebria louiseae* Kavanaugh, are restricted to the cobble upper sea beach habitat. Relationship between geographical and habitat distributions and hindwing development is discussed. The present fauna is most similar to faunas of the adjacent mainland and areas to the south, along the British Columbia coast, and much less similar to faunas to the north. Data and analyses presented for the extant carabid fauna, along with accumulated data from paleoenvironmental studies for the archipelago and coastal region, form the basis for discussions of Quaternary history of the region, origins of the fauna, and the controversy concerning glacial refugia in the archipelago. Five carabid species appear to have survived at least the glacial period in refugia in or near the archipelago, and three of these have subsequently colonized the adjacent mainland. Two species are western European in origin, secondarily introduced from the British Columbia mainland within the last decade or two. The remaining species are post-glacial immigrants—many from one or more south coastal refugia (south of the Cordilleran Icesheet and west of the Cascade/Sierra Nevada divide) and at least a few from one or more southern interior refugia (south of the Cordilleran and Laurentide icesheets and east of the Cascade/Sierra Nevada divide)—that probably reached the archipelago between 10,500 and 13,000 years ago across a dry land bridge. Northern glacial refugia do not appear to have contributed to the extant fauna. Except for one instance of inter-island intraspecific variation, there is no indication of any incipient radiation of carabid beetles in the archipelago nor of any differentiation with respect to conspecific mainland populations of the species represented. The potential for use of the carabid fauna of the archipelago in continued testing of the "equilibrium theory" of island biogeography is discussed, as are other worthwhile opportunities for continued research on the fauna.

Resumé: Cet exposé sur la faune des coléoptères carabiques des Iles de la Reine Charlotte est basé sur une revue de la littérature, sur la recherche intensive sur le terrain, dans la région, ainsi que sur l'étude de plus de 8.300 specimens. Il offre une description brève de cet archipel et un synopsis historique des recherches passées sur sa géologie et sa biologie. L'histoire de l'étude des coléoptères carabiques de la région y est passée en revue. On trouvera également des données générales sur les coléoptères carabiques, leur utilité en ce qui concerne la recherche biogéographique et paléogeographique, ainsi que des renseignements sur l'équipement, les matériaux et techniques que nécessitent leur prélèvement et préservation et les demandes logistiques de la recherche sur le terrain dans cet archipel. Jusqu'ici les coléoptères carabiques ont été prélevés à 137 locations sur 23 îles. On reconnait quinze types d'habitats différents pour les carabides de l'archipel, chacun étant décrit et représenté photographiquement. La faune connue comprend un total de 62 espèces qui représentent 22 genres et 17 tribus, et deux espèces connue seulement à l'état fossile. Cet exposé offre les synonymes, s'il y a lieu, la combinaison diagnostique, une description générale, la distribution géographique dans l'archipel et en dehors de celui-ci, la distribution de l'habitat et enfin une discussion sur le potentiel de dispersion. Aucun change de nomenclature est proposé, mais le localité type de *Nebria charlottae* Lindroth est retreind à Masset, île Graham. Une clé illustrée permet aux non-specialistes d'identifier des spécimens adultes. En comparant les aires d'occupation géographique des différentes espèces, on découvre six éléments differents représentant la faune (% de la faune entre parenthèses): un élément holarctique (5%), un élément trans-Americain (20%), un élément représentant l'Ouest de l'Amérique du Nord (29%), un élément Côte-Ouest (40%), un élément endémique (3%) et un élément d'introduction (3%). A l'intérieur de l'archipel 24 espèces sont connues comme habitant une seule île, alors que les autres espèces sont dispersées plus largement. Soixante-cinq-pour-cent des espèces se limitent à un ou deux habitats et moins de 12% occupent plus de quatre habitats. L'habitat des espèces endemiques *Nebria charlattae* Lindroth et *Nebria louiseae* Kavanaugh se limite aux zônes élévées de plages marines de galets. Le rapport entre distributions géographiques et habitats et le développement des ailes postérieures est discuté. La faune présente ressemble le plus à celle du continent adjacent et à celle des territoires vers le sud, le long de la côte de Columbie Britanique, et le moins aux faunes s'etendant vers le nord. Les donnees et analyses presentees ici sur la faune courante des carabiques, ainsi que l'accumulation de données provenant d'études paleo-environnementales sur l'archipel et la region côtière, forment la base des discussions sur l'histoire Quaternaire de la région, sur les origines de la faune et sur la controverse relative aux refuges glaciaires de l'archipel. Cinq espèces de carabides semblent avoir surveeu au moins la dernière periode glaciaire dans des refuges de l'archipel ou de sa proximité et parmi celles-ci trois ont ultérieurement colonisé le continent adjacent. Deux espèces originaires de l'Europe Occidentale ont ete introduites secondairement de la Columbie Britanique dans les derniers dix ou vingt ans. Le reste sont des espèces immigrantes post-glaciaires dont un grand nombre provient d'un ou de plusieurs refuges côtiers (au sud de la calotte glaciaire de la Cordillère et à l'ouest de la ligne de partage des eaux Cascade/Sierra Nevada) plus quelques unes provenant d'un minimum d'un ou de plusieurs refuges de l'interieur sud (au sud de la calotte glaciaire de la Cordillère et de la calotte glaciaire laurentidienne et à l'est de la ligne de partage des eaux Cascade/Sierra Nevada)—ayant probablement penetré l'archipel il y a de 10.000 à 13.000 ans par une langue de terre. Les refuges glaciaires du nord ne semblent pas avoir contribue à la faune subsistante. Mis-a part un cas de variation intra-specifique inter-île discute plus haut, il n'existe aucune indication de radiation naissante chez les coléoptères carabiques dans l'archipel, non plus que de differenciation en ce qui concerne les populations du continent representées ici. L'utilisation potentielle de la faune carabique de l'archipel comme teste de "la théorie de l'equilibrium" de la biogéographie insulaire est discutée ainsi que d'autres possibilités qui justifient la continuation des recherches sur cette faune.

INTRODUCTION

The Queen Charlotte Islands are an archipelago of about 150 islands lying off the west coast of British Columbia (Fig. 1) in the area extending from approximately 52° to 54° north latitude and from 131° to 133° west longitude. The archipelago itself is about 260 km in length and about 90 km at its greatest width (across Graham Island). Distances of about 60 and 80 km, respectively, separate the archipelago from the nearest inshore islands and from mainland British Columbia. These closest approaches across Hecate Strait are opposite the northern end of the archipelago, on Graham Island. The nearest islands of the Alexander Archipelago in southeastern Alaska are about 50 km to the north, across Dixon Entrance, and the northern tip of Vancouver Island is about 240 km southeast of the southern tip of the archipelago, at Cape St. James, St. James Island.

Total land area of the archipelago is about 10,000 km^2. The areas of individual islands range from a few square meters (several small islands that are little more than protruding rocks) to just under 6,500 km^2 (Graham Island); but two islands (i.e., Graham and Moresby [2,640.5 km^2]) account for more than 90% of the total area. There is also great variation in topographic relief among the islands, with elevations ranging from a few meters (again, on the smallest islands) to about 1,160 meters (at the summit of Mount Moresby, Moresby Island, the highest point in the archipelago).

Sutherland Brown (1960; see his fig. 1) recognized three physiographic units in the Queen Charlotte Islands: the Queen Charlotte Ranges, which form the mountainous backbone of the archipelago, extending from southwestern Graham Island southward to the southern tip of the archipelago; the Skidegate Plateau, a dissected tableland that slopes toward the northeast from the eastern edge of the Queen Charlotte Ranges, extending from northwestern Graham Island to northeastern Moresby and Louise islands; and the Queen Charlotte Lowlands, a vast area of low, boggy land occupying most of the northeastern half of Graham Island and the northeastern tip of Moresby Island. Comprehensive discussion of the physiography and geology of the archipelago was provided by Sutherland Brown (1960, 1968; Sutherland Brown and Yorath 1989).

Williams (1968) presented a detailed review of the climate of the archipelago. Open to the vast Pacific Ocean on the west and isolated from the continental interior on the east by high mountains on the coastal mainland, the Queen Charlotte Islands enjoy a maritime climate that is cool in summer and mild in winter. Average annual precipitation exceeds 100 cm in all but the most sheltered parts of the archipelago and 750 cm in some sites on the western slope of the Queen Charlotte Ranges. Rainfall is distributed over most of the year, but is heaviest in the late fall and early winter and lightest in mid-summer. Significant snowfall occurs only in the mountains, where deepest snow accumulations may persist into late summer at highest elevations.

Home to the Haida people and their ancestors for at least the last 8,000 years (Fladmark 1979, 1989), the Queen Charlotte Islands were claimed for Spain by Juan Perez in July 1774. From this first contact, reports of incredibly abundant natural resources—the pelts of sea otters in particular—spread rapidly through the commercial world and quickly led to lively trade between the Haida and the ships of many nations. Among the traders who followed was British Captain George Dixon, who visited the islands in 1787 (Dixon 1789) and named them after his ship, the *Queen Charlotte*. It was almost another century, however, before interest in the biotic resources of the region extended beyond their commercial exploitation. In just the last three or four decades, the Queen Charlotte Islands have begun to serve as a focus of interest for scientists. One indication of the strength and diversity of current interest was an international symposium concerning the Queen Charlotte Islands that convened in August 1984, in Vancouver, British Columbia (Scudder and Gessler 1989). It brought together geologists, zoologists, botanists, anthropologists, historians, and conservationists, all engaged in ongoing studies in the archipelago, to review the current status of knowledge about the area in each of these fields.

There are several reasons for this increasing level of attention, particularly among biologists and geologists. The archipelago is an area of exceptional beauty and, hence, has natural appeal on this basis alone. It is a land of startling contrasts—quiet bays and wave-lashed headlands; vast lowlands of bog or marsh and mountains that rise more than 1,000 m, seemingly straight out of the sea; slopes with cool, dark, and trackless rainforests and hillsides so devastated by logging or mining that they look like the surface of an alien planet. Scientists attracted to the region, perhaps largely for aesthetic reasons, have found fertile ground for a diversity of studies.

Studies of the biotas of island archipelagoes have contributed greatly to modern biology, especially to our understanding of evolution, beginning with both Charles Darwin (in the Galapagos Islands) and Alfred Russel Wallace (in the Indo-Australian Archipelago). Although less widely known than the Galapagos or Hawaiian Island archipelagoes, the Queen Charlotte Islands, which have been called "the Canadian Galapagos" (Foster 1984), nonetheless offer biologists the same kind of opportunity to study the effects of varied degrees of isolation, island area, habitat diversity, and other factors on biotic diversity and evolution.

Even the earliest inventories (as discussed below) for several plant and animal groups in the Islands included some species and subspecies that were not known outside the archipelago (Foster 1965). The existence of such *endemic* forms in the Queen Charlotte Islands, an area thought to have been covered almost completely by glacial ice (Sutherland Brown and Nasmith 1962) during the last glacial period (i.e., perhaps as recently as 10,000–12,000 years ago), is problematic. What are the origins of these endemic forms? Are they truly endemic, or do they occur elsewhere as well, perhaps on the adjacent mainland, in areas not yet properly sampled? One popular explanation for the occurrence of endemic forms is that they survived at least the last glacial period somewhere in the archipelago, in a so-called "glacial refugium" (Foster 1965; Calder and Taylor 1968; Kavanaugh 1988, 1989). Did one or more such refugia exist, and, if so, did the present endemic forms survive or differentiate there? The quest for answers to these and other, related questions attracts increasing numbers of scientists to the archipelago each year.

Perhaps the most compelling explanation for increased interest in the region is a growing awareness of the rate at which its biotic resources are being exploited and depleted and its habitats destroyed or at least altered. The uniqueness and importance of the archipelago as a national and international treas-

FIGURE 1 Location of the Queen Charlotte Islands (area outlined on map) in relation to the rest of North America and in detail (inset expanded view; scale line = 50 km).

ure—a unique biotic, cultural, and historic resource—has been recognized through designation of a UNESCO World Heritage site (in 1981) on Anthony Island (Ninstints village site) and, most recently (July 1988), an extensive, new Canadian national park in the southern part of the archipelago, known as South Moresby/Gwaii Haanas National Park Reserve. Although such designations provide protection from many kinds of destructive exploitation and alteration, they may also result in new, potentially negative impacts, such as increased numbers of visitors requiring access to and services in the areas. Clearly, detailed knowledge of the biotic and other resources of the area is prerequisite to appropriate conservation and management of these resources; and an increase in this knowledge base is urgently needed.

Brief History of Geologic and Biotic Studies in the Archipelago

Geologic and biotic study of the Queen Charlotte Islands began with the report of George M. Dawson, who spent two and one-half months in the northern and eastern parts of the islands during the summer of 1878. His observations (Dawson 1880) of geographic and geologic features included the first evidence of extensive glaciation in the archipelago. The first vascular plant specimens from the islands were collected during this visit, and they served as the basis for the first list of plants for the archipelago (Dawson 1880). Based on reports obtained from the Haida, Dawson was the first nonnative to learn of the small caribou, later described as Dawson's Caribou (*Rangifer tarandus dawsoni* Seton-Thompson 1900) in his honor. Subsequent efforts by zoologists to obtain specimens of this unexpected animal (now apparently extinct) no doubt provided an initial stimulus for study of the fauna in general.

During the past century, published studies have dealt with bedrock geology and geologic history of both the islands (MacKenzie 1916; Holland and Nasmith 1958; Sutherland Brown and Nasmith 1962; Sutherland Brown 1968; Sutherland Brown and Yorath 1989) and the adjacent seafloors (Yorath and Hyndman 1982; Barrie and Bornhold 1989) in an effort to understand the origins and composition of the archipelago. Special attention has been given to Quaternary geology of the islands (Clague 1989), specifically to the extent of glaciation in the archipelago and the geologic evidence against or in support of glacial refugia in the area. Sutherland Brown and Nasmith (1962) concluded that the archipelago was heavily and almost completely glaciated during the last glacial period, except perhaps for the summits of the highest peaks, where microclimatic conditions were also extremely severe. Failure of the first paleoecological studies (Heusser 1955) to find dated pollen profiles older than early post-glacial time supported this view (Sutherland Brown and Nasmith 1962). However, Clague et al. (1982) found geologic evidence of only weak Late Wisconsinan glaciation in the coastal lowlands of eastern Graham Island, and recent paleoecological studies (Warner et al. 1982; Mathewes and Clague 1982; Mathewes et al. 1985) identified ice-free areas in the archipelago thousands of years before deglaciation occurred on the adjacent mainland. Pollen profiles from these sites revealed a surprisingly diverse flora at about 16,000 years before present (BP). Warner et al. (1984) studied organic deposits from a site in east-central Graham Island that date from a non-glacial interval of the mid-Wisconsinan (45,700 ± 970–27,500 ± 400 years BP) and indicate extensive forests and open wetlands in the area at that time. Recent work at Mary Point on northwestern Graham Island has produced evidence of upland vegetation between 30,000 and about 21,000 years BP (Blaise et al., in press). However, no organic deposits of full glacial age (about 21,000 to 16,000 years BP) have been found in the archipelago to date to support conclusively the presence of at least one refugium in the area.

Calder and Taylor (1968) reviewed the history of study of the present flora of the archipelago in detail. Reports by Persson (1958) and Schofield (1965, 1966a, b, 1969, 1976) provided a preliminary inventory of the bryophytes of the region and record the presence of both endemic and markedly disjunct taxa. In their treatment of the vascular plants of the archipelago, Calder and Taylor (1968) recorded 593 species and infraspecific taxa from the area. Of these, 472 were considered indigenous and 11 endemic to the Queen Charlotte Islands. Randhawa and Beamish (1972) surveyed chromosome numbers in *Saxifraga ferrugines* Graham and suggested refugial survival of diploids in the Queen Charlotte Islands. Mathewes (1989a) summarized the known paleobotanical history of the archipelago.

Inventory of the animals of the archipelago is predictably incomplete. All of the major groups adequately studied to date are vertebrates, including mammals (Osgood 1901; McCabe and Cowan 1945; Foster 1965; Cowan 1989), birds (Osgood 1901; Fleming 1916; Cowan 1989), and freshwater fishes (Carl et al. 1959; Moodie and Reimchen 1976a, b; Reimchen et al. 1985; Northcote et al. 1989). In each of these groups, several endemic infraspecific forms have been recognized. No reptiles have been recorded from the archipelago, and among amphibians, apparently only the boreal toad, *Bufo boreas boreas* Baird, occurs there (Logier and Toner 1961) as a native (although the Pacific tree frog, *Hyla regilla* Baird and Girard, has been introduced and is now established; see Foster 1989).

Among terrestrial and freshwater invertebrates of the archipelago, only arthropods have been studied to any significant extent. The present inventory even for this group consists mainly of isolated distributional records (e.g., for *Epidemia mariposa charlottensis* [Holland], the northern copper butterfly [Tilden and Smith 1986] and descriptions of new, including supposed endemic, species (e.g., the freshwater amphipod, *Paramoera carlottensis* Bousfield [1958:64], the spittlebug species, *Aphrophora regina* Hamilton [1982:1189], or the geometrid moth, *Xanthorhoe clarkeata* Ferguson [1987:98]). Walker and Mathewes (1988) recorded the occurrence of chironomids of the genus *Corynocera*, all known members of which are brachypterous (short-winged), in Late-Quaternary deposits from Hippa Lake and suggested that a species of this genus may have survived the last glacial period in a refugium in the archipelago.

The first important faunal listing for any invertebrate group in the archipelago was that for beetles (Coleoptera) by Keen (1895), who recorded 246 species in the Masset (northern Graham Island) area. (See below for additional comments concerning Carabidae.) For about the next 80 years, little additional faunal work was done in the region. In the past few decades, however, a number of important contributions have appeared and an encouraging trend in faunistic studies is evident. In their treatment of the dragonflies of the Brooks Peninsula of Vancouver Island, Cannings and Cannings (1983) reported that 13 species had been recorded for the Queen Charlotte Islands but did not list them. Currie and Adler (1986) presented a preliminary report on the black fly (Diptera: Simuliidae) fauna of the archipelago. A total of 16 species, representing three genera, have been recorded to date. Most recently, Anderson (1988) studied the weevil (Coleoptera: Curculionidae) fauna of the islands and found 19 species represented. Additional studies now in progress, especially those by J. M. Campbell for rove beetles (Coleoptera: Staphylinidae), G. G. E. Scudder for seed bugs (Heteroptera: Lygaeidae), and I. M. Smith for water mites (Acarina: Hydrachnida), should provide important new information on the invertebrate fauna of the archipelago.

Carabid Beetles and Their Usefulness in Biogeography and Paleoecology

Beetles of the family Carabidae, commonly known as "ground beetles" or simply "carabids," form a diverse group with worldwide geographical distribution. More than 25,000 species have been described, but the actual number of species is probably much greater. Carabids occupy a broad range of habitats, and in comparison with other insect groups, are especially well represented in cool and cold-temperate areas. For example, about 800 carabid species have been recorded from Canada and Alaska alone (Lindroth 1961–69), a level of diversity equaled by few other families of organisms. Most carabids are nocturnal predators of insects and other invertebrates, but many also scavenge for food and a few are specialized plant feeders (mainly or exclusively feeding on the seeds of grasses).

Carabids are an interesting and enjoyable group for study. Individuals are often abundant and easy to find and collect, and the diversity of species in a particular locality may be surprisingly high. For example, more than 300 species are represented at many localities in eastern North America, and I have collected adults of more than 50 species in just the 0.02 hectare area around my home (in northern California). Once collected, the preparation and study of carabids is also relatively simple. No special care need be taken in handling adults because their robust bodies are less susceptible to damage than those of most other insects. Systematic research on carabids is one of the most active areas in all of systematic biology, involving both professionals and individuals with avocational interest in the group. As a result, there are numerous specialists willing and able to help with routine identifications of specimens and provide information and encouragement for anyone interested in beginning his or her own studies.

Biogeographers (e.g., Darlington 1957, 1965, 1971; Lindroth 1957, 1963, 1979a, b; Kavanaugh 1980, 1988, 1989; Noonan 1988) have found carabids to be extremely useful organisms for study. Carabid species appear to disperse relatively slowly for insects. In part, this general characteristic of the group is explained by a tendency for the evolution of brachyptery, or short-wingedness, among carabids for which flight capability is not distinctly advantageous (Darlington 1936, 1943; Kavanaugh 1985). Brachyptery appears to have evolved thousands of times independently among different species and lineages of carabids. In a variety of stable habitats, strong selection seems to favor wing reduction, which perhaps permits reallocation of energy resources to more productive uses (e.g., reproduction). Lindroth (1979b) studied carabid species that were dimorphic for wing length (i.e., the species includes both full-winged, macropterous, and short-winged individuals). He found that populations with brachypterous adults tend to predominate in areas of long-term occupation by the species, such as in areas that served as glacial refugia, whereas populations with macropterous adults occupy more recently colonized areas. He used this tendency, for example, to distinguish between Scandinavian carabid species that survived the last glacial period in refugia south of glacial ice (where populations of brachypterous adults predominate today) from those that survived in northwest Scandinavian coastal refugia, north of the ice. Studies of this kind illustrate just one of the ways that carabids may serve as relatively good indicators of the past distributions of biotas in general and of distributional barriers and other physiographic features.

Another important characteristic of carabid beetles is that they appear to change their environmental (habitat) requirements very slowly, even on a geological timescale (Coope 1979). Quaternary geologists and paleoecologists (Ashworth 1979; Coope 1979; Matthews 1979a; Morgan and Morgan 1980) have come to rely heavily on carabid beetles in their studies. Identifiable fragments of carabids are often well preserved in organic deposits of late Tertiary and Quaternary age; and most, if not all, of the species represented in these samples are found also in the extant fauna. Mainly through detailed studies by Lindroth (1945–49, 1961–69), the habitat requirements of members of most species living today in cool- and cold-temperate, subarctic, and arctic regions of the Northern Hemisphere are reasonably well known. Assuming (as appears justified) that habitat requirements of these species have changed little if at all in Quaternary time, much can be inferred about the environmental conditions that prevailed when the fossil specimens of these same species were alive. Hence, at least under certain circumstances, carabid beetles can contribute significantly to our understanding of regional climatic history.

History of Study of the Carabidae of the Archipelago: A Context for the Present Report

Development of our present knowledge of the carabid beetle fauna of the Queen Charlotte Islands began with the Reverend J. H. Keen, Anglican missionary to the Haida people at Masset during the late 1880s and early 1890s. Keen (1895) provided the first list of beetles, including 24 carabids, for the islands, based solely on his own collections, all made "within a circle of five miles' radius from Massett." He did not identify the material himself, but solicited the help of his friend, James Fletcher, in Ottawa. In a note presented in Keen's paper (Keen 1895), Fletcher acknowledged the assistance of several "specialists," including J. Hamilton, G. H. Horn, T. L. Casey, and H. F. Wickham—the leading coleopterists in North America at that time—in confirming identifications.

In his treatment of the beetles of the Pacific Northwest, Hatch (1953) simply referred to Keen (1895) in his accounts for species recorded in the original Keen list. Hatch referred to the Queen Charlotte Islands specifically only in his discussion of *Scaphinotus marginatus* Fischer. The next significant advance was provided by Lindroth (1961–69), who corrected previous misidentifications and added six more species to the faunal list, including three new species (one of which, *Nebria charlottae* Lindroth, is endemic to the archipelago). Lindroth did not collect in the Queen Charlotte Islands but worked exclusively with material obtained from museums. During the past two and one-half decades, important additional carabid specimens were collected by local residents S. Douglas, N. Gessler, J. Miller, M. Morris, and T. E. Reimchen, and by visiting collectors J. S. Ashe, J. Belicek, R. A. Cannings, G. Mallick, R. W. Mathewes, M. Pitman, and B. G. Warner. This material added substantially to the geographical and seasonal sampling of the carabid fauna of the archipelago and served as an important resource for the present study.

My interest in the Queen Charlotte Islands, like that of so many other researchers, was kindled by the presence of supposed endemic species in the archipelago. In my study of the carabid genus *Nebria* Latreille for North America (Kavanaugh 1978), I found that only two forms are apparently endemic to Canada—*Nebria schwarzi schwarzi* Van Dyke, from the northern Rocky Mountains of Alberta and British Columbia, and *Nebria charlottae* Lindroth, from the Queen Charlotte Islands—and I was eager to develop hypotheses to account for the present occurrence of each in areas thought to have been glaciated during the last glacial period. *Nebria charlottae* was described from a single specimen collected by Keen, probably in the late 1880s. However, this specimen (part of the Keen collection, now deposited in the Canadian National Collection in Ottawa) was not recognized as something unique until Lindroth described it in 1961. Even then, Lindroth (1961–69:67) was reluctant to describe a new species based on what might have been just an aberrant individual of a previously described species (Lindroth, pers. comm.), perhaps *Nebria gregaria* Fischer, known from the Aleutian Islands.

I first visited the archipelago in July 1981, accompanied by D. H. Mann. Our purpose was to obtain additional specimens of *Nebria charlottae* so that its occurrence there and identity as a distinct species could be confirmed and its habitat defined. We discovered and sampled a large population of *N. charlottae* on the upper cobble sea beach at Tow Hill, on northeastern Graham Island. During the same visit, Mann and I collected a large series of specimens of another, unknown species of *Nebria*, which I later described as *Nebria haida* (Kavanaugh 1984), from an extensive alpine area in southeastern Graham Island, in honor of the native people of the archipelago. Later that same year, I examined a series of six specimens, collected by R. Cannings at Skedans village site on Louise Island, which represented yet another new, and apparently endemic, species, *Nebria louiseae* Kavanaugh (1984:162). These discoveries of what appeared to be two additional endemic carabid species in the archipelago prompted me to begin a more comprehensive study of carabid fauna of the region. Toward this end, I spent six weeks during July and August 1983, collecting with J. M. Campbell and M. D. Kavanaugh on 15 different islands and at 80 different sites in the archipelago. Results of studies through 1984 were presented at the Queen Charlotte Islands International Symposium in August 1984, as a preliminary report on and analysis of the carabid fauna of the archipelago (Kavanaugh 1989). In July and August 1986, J. L. Kavanaugh and I participated in a multidisciplinary expedition for biological inventory along the British Columbia coastal mainland and islands. Important new geographical and habitat distributional records for carabids in the archipelago and on the adjacent mainland were obtained on this trip, including discovery of a population of *Nebria haida*, a supposed Queen Charlotte endemic, in an isolated alpine area on the mainland north of Prince Rupert.

The purpose of this report is twofold: (1) to provide a comprehensive account of the carabid beetle fauna of the Queen Charlotte Islands; and (2) to stimulate others to expand on this and past studies in the archipelago. In support of the first objective, I present annotated accounts for all species represented in the fauna, analyses of present faunal diversity, discussions of faunal origins and evolution, and a review of the glacial refugium controversy in light of the present study. Much of the information presented previously (Kavanaugh 1989) is here updated and/or revised as needed. As an aid to anyone interested in working with carabid beetles, I provide an extensive, illustrated discussion of habitats, a review of collection and preservation techniques for carabids, an illustrated key for identification of adult carabid specimens, and a brief listing of future research opportunities in the archipelago.

Materials and Methods

This study is based on examination of about 8,350 carabid beetle specimens from the Queen Charlotte Islands. Most of these were obtained through my fieldwork in 1981, 1983, and 1986, and the remainder were borrowed from the collections of several North American institutions and one individual. The following acronyms are used in the text to refer to these collections (names of curators or their assistants who sent specimens are also included): AMor (Alan V. Morgan, University of Waterloo, Waterloo, Ontario N2L 3G1), BCPM (British Columbia Provincial Museum, Victoria, British Columbia V8V 1X4; R. A. Cannings), CAS (California Academy of Sciences, San Francisco, California 94118), CNC (Canadian National Collection of Insects, Biosystematics Research Institute, Ottawa, Ontario K1A 0C6; A. Smetana), CUIC (Cornell University, Ithaca, New York 14850; L. L. Pechuman), FMNH (Field Museum of Natural History, Chicago, Illinois 60605; J. S. Ashe), ICCM (Carnegie Museum, Pittsburg, Pennsylvania 15213; G. E. Wallace), MCZ (Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 02138; A. F. Newton, Jr.), OSUO (Oregon State University, Corvallis, Oregon 97331; J. D. Lattin and G. L. Peters), QCIM (Queen Charlotte Islands Museum, Skidegate, British Columbia V0T 1S0; N. Gessler and T. Gessler), UASM (University of Alberta, Strickland Museum, Edmonton, Alberta T6G 2E3; G. E. Ball), UBC (University of British Columbia, Spencer Museum, Vancouver, British Columbia V6T 1W5; G. G. E. Scudder and S. G. Cannings), USNM (United States National Museum, Smithsonian Institution, Washington, D.C. 20560; T. L. Erwin), WSU (Washington State University, Pullman, Washington 99163; W. J. Turner).

Collection and Preservation of Specimens

Carabid beetles are found in a wide variety of habitats in the Queen Charlotte Islands, from sea level to the summits of the highest mountains. For discussion of the known habitat distribution of any species in the archipelago, refer to the descriptive account for that species.

Collecting Sites and Techniques

During the day, carabids are most often found hiding under rocks, logs, or other debris on the ground, under the loose bark of fallen trees, in leaf litter, and in or under carpets or clumps of moss on the ground or on fallen or standing tree trunks. Adults of several species are day-active and are found and collected as they run on the ground, particularly on the moist banks of streams, lake shores, or at the edges of marshes. Members of some carabid species live only in marshes or bogs, and they are most easily collected by simply trampling the vegetation and/or spongy organic substrate down into the water, a technique known as treading. Treading is productive both at the edges of marshy or boggy areas and out in deeper water, wherever emergent or floating vegetation occurs. Carabids, especially small ones (e.g., *Bembidion* species), that hide under rocks, in coarse gravel, or buried in sand at the margins of streams or standing water bodies are flushed from their hiding places by simply splashing water over the shore area. This splashing technique drives the beetles out into the open, where they are easily seen and collected. Sifting through leaf litter, clumps of moss, markedly decayed wood, or even accumulations of animal feces (e.g., the large piles of black bear scat that are frequently encountered in the archipelago) yields excellent results, especially for the smaller beetles.

Because most carabids are active only or mainly at night, many are most easily found and best observed during that time. In the Queen Charlotte Islands, unlike many other parts of the world, very few carabids are attracted to lights. Nonetheless, searching for them with a flashlight or a headlamp (which leaves both hands free for collecting) is both informative and highly productive. Adults of several species, especially those that burrow in soil or deep in leaf litter, are seldom seen even in hiding during the day but are easily spotted on the surface at night. In areas where repeated sampling is possible or desirable, nocturnal carabids are collected in greatest numbers through the use of pitfall traps (see below).

Collecting Equipment

Most carabid beetles are fast runners and quick in their movements when disturbed. Because of their speed, they may be difficult for the beginner to catch. With practice and experience in reacting to their escape efforts, collecting these beetles by hand can become routine. All specimens can be handled quite safely; only members of *Pterostichus* species, because of their large size, pose even a slight threat of biting if given an opportunity. Most specimens used in this study were collected by hand.

The smallest carabids (e.g., members of *Bembidion* or *Trechus* species) are both more difficult to pick up by hand and more easily damaged than larger ones, so a gentle suction device (aspirator) is often used to capture them. A simple wire mesh sifting device (mesh width about 5 mm) is a great aid in separating small beetles from the leaf litter, mossy clumps, etc., in which they hide. Often the number of beetles captured in an area is greatly increased through the use of pitfall traps, especially in areas with dense vegetation or abundant litter or debris on the ground. Any smooth, vertical-sided container with a narrow edge that has been sunken into the ground so that its rim is flush with the surface can serve as a passive trap. Plastic drinking cups, which are both inexpensive and widely available, were used successfully for this purpose in this study. Beetles walking on the surface at night simply fall into the traps and cannot escape. When traps are left dry and checked daily, beetles are captured alive and then either preserved or kept alive for rearing purposes. When less frequent checking is possible, dilute ethanol is used in the traps to kill and preserve specimens. Live beetles left too long together in a trap will kill and eat or at least damage each other.

Few chemicals are needed for collecting and processing carabid beetles. Ethyl acetate (EtAc) is the killing agent of choice for carabid adults. Specimens killed and stored in EtAc fumes remain flexible longer and are easier to handle in subsequent processing (preparation and dissection) than those killed and stored in 70% ethanol (EtOH) or any of the other commonly used killing agents (e.g., potassium cyanide). If EtAc is unavailable, then adults can be killed by exposure overnight in a freezer and processed normally after thawing. All adult specimens collected for this study were killed with EtAc. Larval specimens (which are not discussed in this report) were collected and stored in 70% EtOH.

Preservation of Specimens

Carabid beetles are normally preserved as pinned and dried specimens. For this study, no special preservation techniques were required, but care was taken to protect specimens, during both processing and storage, from the high humidity present throughout the Queen Charlotte Islands. Moisture can foster the growth of fungi that will rapidly destroy specimens.

The scientific value of specimens collected and preserved largely depends on the quality of collection data associated with them. In the Queen Charlotte archipelago, where there are so many islands and such great topographic diversity but relatively few place names, adequate documentation of collection sites is often difficult. Nonetheless, in this study collection data recorded and preserved with the specimens included (a) island, (b) specific locality, including geographical coordintes if the locality was otherwise difficult to designate with precision, (c) elevation, (d) date of collection, and (e) name of collector. Associated field notes recorded the habitats in which beetles were collected (see Classification of habitats, below).

Logistics

Because of their number, climate, and extreme topographic relief, the Queen Charlotte Islands pose serious logistical problems for biotic inventory. Fieldwork in the areas covered by this report required diverse means of transport for personnel and equipment.

The network of roads in the archipelago, including the few paved public roads and numerous graveled and interconnected logging roads (access to which is sometimes controlled), is essentially restricted to the eastern half of Graham Island (except for the logging road to Rennell Sound on the southwest coast) and northeastern Moresby Island. Fieldwork in these areas was facilitated by the use of rented and borrowed trucks and automobiles. Other areas on these two islands and all other islands can be reached only by air or water transport or on foot.

Access to collecting sites in extreme northwestern Graham Island (the area around Taku, Kiusta, and Lepas Bay) and southern Langara Island was by chartered airplane from Masset. Access to sites above treeline on southwestern Graham Island (near Mount Needham), Morseby Island (Mount Moresby and Takakia Lake areas), and Lyell Island (Mount Kermode) was by helicopter chartered from Sandspit. Only the alpine areas on Slatechuck Mountain (southern Graham Island) and Carabus Peak (provisional name, northern Moresby Island) were reached on foot from low-elevation access roads. Access to sites on the northwest and east coasts of Moresby Island and on all other islands sampled was by inflatable rubber boat, equipped with an outboard motor, rented in Skidegate. Sampling in the southern part of the archipelago was limited greatly by availability of both fuel (few sources of fuel in the area and modest carrying capacity of the boat) and time for travel between sites.

The availability of other facilities and services in the Queen Charlotte Islands is generally limited, and long-term fieldwork in the area is made extremely difficult by the frequent rainy conditions. Success achieved in completing fieldwork and processing of specimens for this project is largely due to the generous, voluntary support of local residents, who contributed transportation, lodging, and other assistance that otherwise could not have been obtained. Suitable dry space in which to process materials collected was unavailable, except through the courtesy of one resident, and appropriate lodging facilities were restricted to Masset, Queen Charlotte City, and Sandspit. Lodging for fieldwork in all but these urban areas was in rainproof tents.

Geographical and Habitat Coverage

Islands Sampled

To date, beetles have been collected on 23 (about 16%) of the approximately 150 islands in the Queen Charlotte archipelago. Seventeen of these islands were sampled during this study, nine of them for the first time. Table 1 lists the islands sampled, their area, and maximum topographic relief.

Carabid beetles probably occur on every island in the archipelago. Inventories of the species for the individual islands sampled to date vary greatly in their completeness. Some of the larger and more remote islands (e.g., Kunghit Island) have been very poorly sampled in relation to their size, topography, and habitat diversity; and the faunal lists for most, if not all, islands will certainly be extended by additional, detailed sampling. Only Graham Island and the northern portion of Moresby Island have been surveyed extensively enough to properly reflect their faunal diversity. Based on my collecting experience in these areas, I suggest that the species lists for Graham and Moresby islands are, respectively, at least 90% and 75% complete; and the list for the archipelago, as a whole, is probably about 90% complete.

Locality Information

Localities in the archipelago from which carabid beetles have been collected to date are shown in Figure 2. One of the major problems with fieldwork in the area is that many physiographic features, especially in areas remote from urban centers, are still unnamed. As a result, many collection sites often have been recorded simply as distances from one or another of the few, scattered towns. All localities in Figure 2 and cited in respective sections on distribution for each species in the fauna (see below) are listed in Table 2. For ease in relating records for each species to the map in Figure 2, all localities are arranged in alphabetical order by island. To facilitate present and future discussions of distribution within the archipelago, names are provided for two mountains, four lakes, one stream, and two *Sphagnum* bog areas that were previously unnamed. These names are unofficial at present, but I intend to petition the Ministry of Crown Lands, Province of British Columbia, for their recognition.

Table 1. List of islands sampled for carabid beetles in the Queen Charlotte Islands.

Island	Area (km^2)	Maximum elevation (m)
Anthony	1.5	60
Burnaby	66.0	580
Chaall	37.5	730
East Copper	0.4	60
Faraday	3.1	180
Graham	6,480.4	1,070
Harrison	2.0	90
Hibben	33.2	730
Hotspring	0.3	30
Huxley	6.5	370
Kunga	4.8	430
Kunghit	130.4	520
Langara	31.8	150
Louise	275.8	1,040
Lyell	174.5	610
Maude	14.1	150
Moresby	2,640.5	1,160
Murchison	4.4	150
Ramsay	16.4	400
Reef	2.5	120
Talunkwan	44.9	640
Tanu	22.9	610
West Skedans	0.1	15

Coverage and Classification of Habitats

One of the primary objectives of this study has been to define the habitat distributions of carabid species found in the Queen Charlotte Islands. The major plant communities of the archipelago were described and classified by Calder and Taylor (1968); and during my fieldwork, effort was made to sample the carabid beetles in each of these described areas or communities. It was clear early on in the fieldwork that carabid species differed in both the particular habitats they occupy and in the ranges (diversity) of habitats in which they occur. However, these habitat distributions, with a few exceptions, suggested that a much less complex classification of habitats than that provided for plant communities by Calder and Taylor was both feasible and sufficiently accurate for carabid beetles. Consequently, the following classification of 15 different major habitats is used in both species accounts and faunal analyses.

Lowland Habitats. All areas at elevations less than or equal to 150 meters are here considered as lowland sites. Nine different lowland habitats are recognized for carabid beetles:

(1) Cobble Sea Beach.—As applied in this report, cobble sea beaches include all the communities described by Calder and Taylor (1968) as "shingle beaches" and represent the most common beach type in the archipelago. Substrates on the beaches include fine gravels mixed with sand, coarse gravels, small to large stones, and even boulders. The beaches vary not only

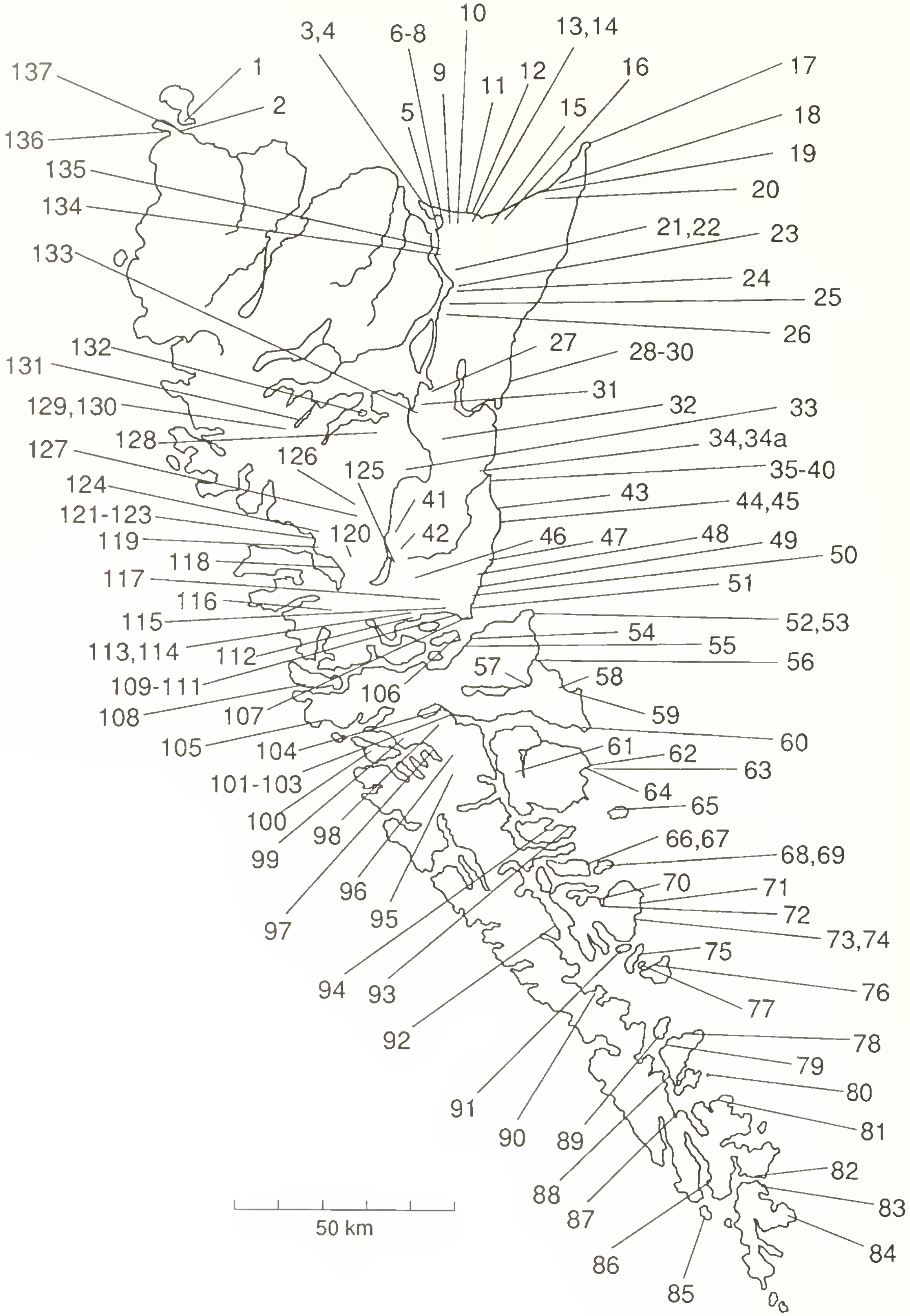


FIGURE 2. Map of the Queen Charlotte archipelago, illustrating the major islands and all localities from which carabid beetles have been collected. Refer to Table 2 for explanation of the locality number code.

TABLE 2. LIST OF COLLECTION LOCALITIES FOR CARABID BEETLES IN THE QUEEN CHARLOTTE ISLANDS.[1]

ANTHONY ISLAND: Ninstints—85.
BURNABY ISLAND: bay [unnamed] on north shore (SE of Alder Island)—78. Burnaby Narrows (at cabin)—88. Section Cove—79.
CHAATL ISLAND: Chaatl village site—108.
EAST COPPER ISLAND: no specific locality—80.
FARADAY ISLAND: no specific locality—91.
GRAHAM ISLAND: Agonum Bog (the name that I here apply to a large, previously unnamed *Sphagnum* bog, located 11.1 km NW of Queen Charlotte City on the northwest side of MacMillan–Bloedel Main Road, at about 53°20′N, 132°11′W, elevation 150 m. This name was chosen as a reference to ground-beetles of the little-known species *Agonum belleri* Hatch, members of which were collected in this bog)—46. Awun Lake (west shore)—131. Awun Lake (0.8 to 3.2 km W of)—129. Awun Lake (ridges W of)—130. Bonanza Creek (0.5 km W of Rennell Sound)—124. Cape Ball—28. Cape Ball River (at mouth)—29. Cape Ball River (1 km N of mouth)—30. Chinukundl Creek (at Highway 16)—50. Chown Brook (at Tow Hill Road)—13. Cinola Mine—33. Deep Creek Beach—134. Drizzel Lake—21. Drizzel Lake (2 km SW of)—22. Elaphrus Bog (the name that I here apply to a small, previously unnamed *Sphagnum* bog, located 19.5 km NW of Queen Charlotte City on the north side of MacMillan–Bloedel Main Road, at 53°21′26″N, 132°15′14″W, elevation 150 m). This name was chosen as a reference to the ground-beetle genus *Elaphrus*, two species of which are represented at the bog—42. Ghost Creek (4.7 km NW of Rennell Sound Road)—127. Ghost Creek drainage [i.e., an unnamed tributary of Ghost Creek] (7.3 km NW of Rennell Sound Road)—126. Gregory Creek (0.3 km E of Rennell Sound)—119. Highway 16 (1.9 km N of Chinukundl Creek)—49. Highway 16 (5.8 km N of Chinukundl Creek)—48. Highway 16 (12.8 km S of Tlell River bridge)—43. Honna Point—111. Jungle Beach—47. Kiusta village site (0.3 km E of)—2. Lawn Point—45. Lepas Bay (northeast shore)—136. Mamin River (1.0 km SE of Juskatla)—128. Masset—6. Masset (southeast shore of Delkatla Inlet)—7. Masset (southwest shore of Delkatla Inlet)—8. Masset (0.6 km NE on Tow Hill Road)—9. Masset (7 km E of)—10. Masset (14 km E of)—15. Masset (1.4 km S on east shore of Masset Inlet)—5. Masset (12 km S of)—135. Masset (16 km S of)—23. Masset Inlet (at Estrado Lagoon)—4. McAuley's Quarry—121. McIntyre Bay (Entry Point to Estrado Lagoon)—3. McIntyre Bay (North Beach at mouth of Chown Brook)—12. McIntyre Bay (0.7 km W of Yakan Point on North Beach)—19. Naikoon Provincial Park (at headquarters)—34. Naikoon Provincial Park (Misty Meadows Campground)—34a. Nebria Peak (the name that I here apply to a previously unnamed peak, the summit of which is at 53°15′40″N, 132°26′27″W). Three small, previously unnamed lakes on the northeast slope of Nebria Peak are here referred to as Lower Nebria Lake (at 53°15′54″N, 132°25′27″W, elevation 620 m), Middle Nebria Lake (at 53°15′50″N, 132°26′03″W, elevation 760 m), and Upper Nebria Lake (at 53°15′45″N, 132°26′08″W, elevation 810 m), respectively. This name was chosen as a reference to ground beetles of the species *Nebria haida* Kavanaugh, which were first found on the upper ridges of this mountain—116. Nipple Mountain (at base 10 km W of Queen Charlotte City)—112. Port Clements (0.1 km W of Highway 16)—27. Port Clements (8 km S of)—32. Pure Lake Provincial Park—24. Queen Charlotte City—109. Queen Charlotte City (1.5 km W of)—110. Queen Charlotte City (3 km NW)—115. Queen Charlotte City (24 km NW of)—41. Rennell Sound (at mouth of Bonanza Creek)—122. Rennell Sound (0.5 km NW of mouth of Bonanza Creek)—123. Rennell Sound Road (10 km E of Rennell Sound)—120. Rose Point—17. Shields Bay—118. Skidegate (Second Beach)—107. Skidegate (3.2 km NE of)—51. Skonum Point (8 km E of Masset)—11. Skowkona Creek (7.9 km NW of Queen Charlotte City)—117. Slatechuck Mountain—114. Tarundl Creek (east slope of Slatechuck Mountain)—113. Tlell (1 km S of Tlell River mouth)—35. Tlell (at Richardson Ranch)—36. Tlell (Wiggins Road)—37. Tlell (16 km S of)—44. Tlell (40 km N of)—26. Tlell (42 km N of)—25. Tlell River (at mouth)—38. Tlell River (1.2 km N of Highway 16 bridge)—39. Tlell River (at end of Richardson Road)—40. Tow Hill Park—18. Tow Hill Road (0.5 km E of Chown Brook bridge)—14. Tow Hill Road (5.3 km SW of Tow Hill Park)—20. Tow Hill Road (19 km E of Massett)—16. Yakoun Lake (Etheline Bay at outlet of Yakoun River)—125. Yakoun River (5.5 km S of Port Clements)—31. Yakoun River (at Port Clements–Juskatla Road)—133. Yaku village site (0.2 km SE of)—137.
HARRISON ISLAND: no specific locality—132.
HIBBEN ISLAND: no specific locality—100.
HOTSPRING ISLAND: north shore—77.
HUSLEY ISLAND: southeast shore—89.
KUNGA ISLAND: north shore (S of Titul Island)—68. west shore (on Klue Passage)—69.

TABLE 2. CONTINUED

KUNGHIT ISLAND: eastern uplands—84. Rose Harbour—83.
LANGARA ISLAND: Henslung Cove—1.
LOUISE ISLAND: Mount Kermode (south slope)—61. Skedans village site—62. Skedans village site (1.5 km W of)—64.
LYELL ISLAND: Gate Creek (at mouth of)—73. Gate Creek (1.0 km W of mouth)—74. Powrivco Bay (at Powrivco Creek)—72. Powrivco Point (0.5 km SW of)—70. Windy Bay—71.
MAUDE ISLAND: Renner Pass Farm—106.
MORESBY ISLAND: Alliford Bay—54. Carabus Peak (the name that I here apply to a previously unnamed peak, the summit of which is at 52°58′58″N, 132°04′22″W). This name was chosen as a reference to ground-beetles of the species *Carabus taedatus* Fabricius, a single fragmentary specimen of which was found on the summit of this mountain—96. Copper Bay—56. Copper Creek (6 km S of Copper Bay)—57. Cumshewa village site—60. Darwin Sound (at Hoya Passage)—92. Gray Bay—59. Gray Bay Road (3 km W of Gray Bay)—58. Haswell Bay (1.5 km SW of Hoskins Point)—90. High Goose Creek (the name that I here apply to a previously unnamed stream that flows from High Goose Lake [see below under Mount Moresby] WSW to the mouth of Peel Inlet at 52°59′51″N, 132°8′3″W)—99. Houston Stewart Channel (E of Raspberry Point)—82. Jedway (bay [unnamed] 3 km NE of)—81. Kaisun village site—105. Louscoone Inlet (E of Etches Point)—86. Moresby Camp (1 to 3 km S on road to Peel Inlet)—101. Mosquito Lake (east shore)—104. Mount Moresby (A beautiful and previously unnamed lake on the west slope of Mount Moresby [at 53°00′51″N, 132°05′25″W, elevation 620 m] is here referred to as High Goose Lake. This name was chosen as a reference to the Canada geese that were frequently seen and heard at the lake—98. Pallant Creek (at Moresby Camp)—102. Pallant Creek (0.2 km W of Moresby Camp)—103. Peel Inlet (at road to Moresby Camp)—97. Sandspit—52. Sandspit (1 km S of airstrip)—53. Skincuttle Inlet (0.8 km SW of Huston Point)—87. Takakia Lake—95. Whiteaves Bay—55.
MURCHISON ISLAND: no specific locality—75.
RAMSAY ISLAND: north shore (1.5 km E of west end)—76.
REEF ISLAND: north shore (0.6 km E of west end)—65.
SKEDANS ISLANDS: east shore of west island—63.
TALUNKWAN ISLAND: Heming Head (1 km NW of)—93. Thurston Harbour—94.
TANU ISLAND: Tanu village site—66. Tanu village site (stream NW of)—67.

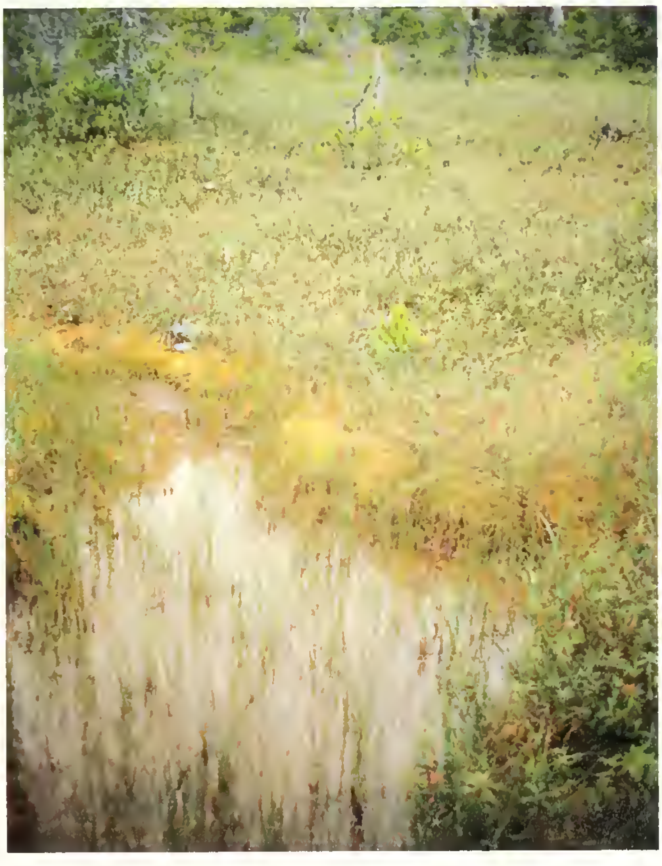
[1] Reference to the number at the end of each entry will permit location of that locality on the map in Figure 2.

in substrate characteristics but also in four other important features that appear to influence carabid abundance and diversity. (a) The degree to which beaches are subjected to wave and tidal action varies markedly. For example, the cobble beach just west of Tow Hill (Fig. 3), on the northeast shore of Graham Island, is pounded by heavy waves during parts of the year, while the beach at Kaisun (Fig. 4), in a more protected bay on the northwest coast of Moresby Island, receives more limited direct wave action. In general, carabids are more abundant (greater numbers of individuals present) and diverse (greater numbers of species represented) on more protected beaches. (b) The amount of driftwood present on the upper beach also varies markedly from beach to beach. Those beaches with abundant driftwood harbor carabids in greater diversity and abundance than those with little or no driftwood. The beetles and their potential prey can hide under driftwood during the day, which may explain the observed pattern. (c) The presence of freshwater seeping through the cobble beach from adjacent inland habitats (e.g., bogs or moist forest), a common occurrence on beaches in the archipelago, can also positively influence carabid diversity and abundance. In fact, several species occur only on beaches with such seepage. (d) The degree of exposure of the upper beach is also an important variable. Several species are found only on cobble beaches shaded by the adjacent forest edge. Other species occur only on open, exposed upper beaches.

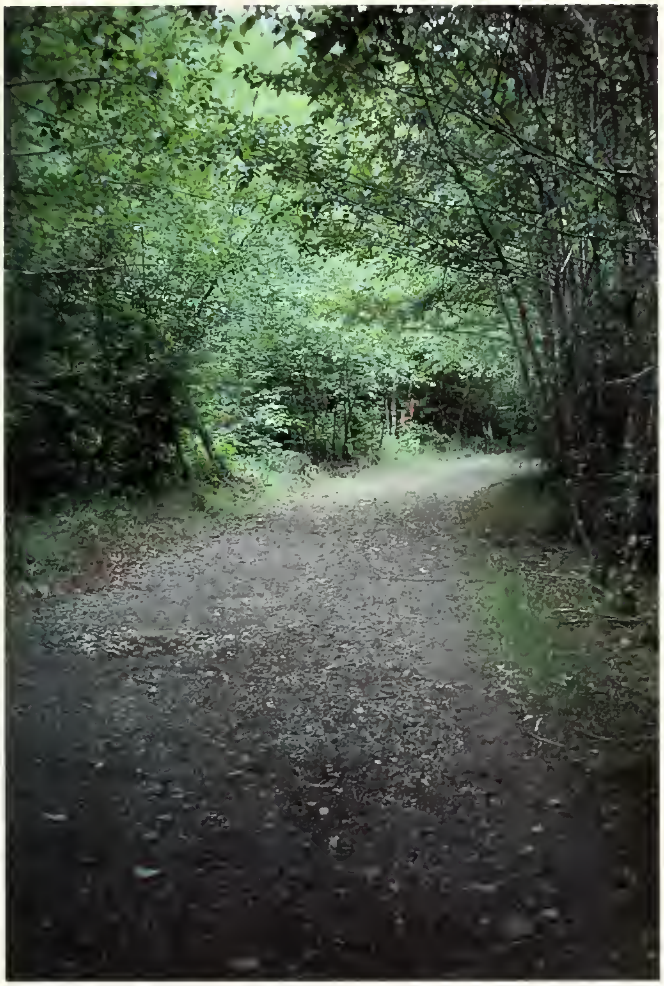
FIGURES 3–4. Cobble sea beach habitat. FIGURE 3. (top) View looking west from the base of Tow Hill, north shore of Graham Island. Carabid beetles, adults of *Nebria charlottae* in particular, are found in the cobble and under drift logs on the upper beach, just outside the forest edge, especially in places where freshwater seeps through the cobble from the forest interior. FIGURE 4. (bottom) View looking east along the beach at Kaisun village site, northwestern Moresby Island. Adults of *Nebria louiseae* and other carabid beetles were found at the upper edge of this beach in the cobble and under drift logs.

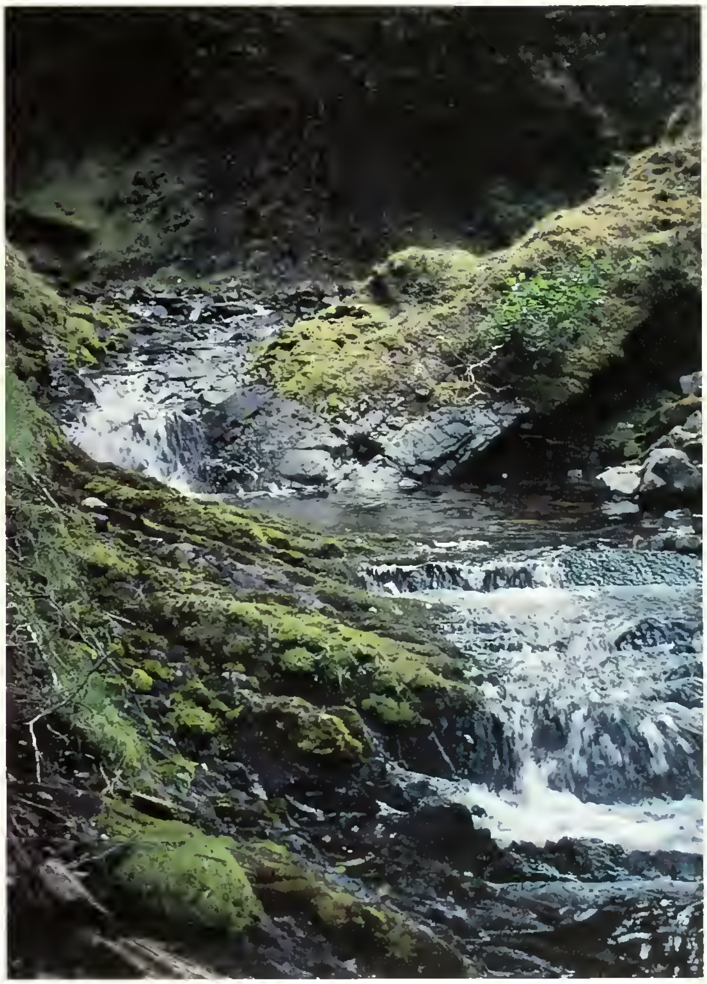
FIGURES 5–6. FIGURE 5. (top) Sandy sea beach habitat. View looking west along North Beach on the northwest shore of Graham Island. This continuous type of sandy beach is backed by a wide band of low dunes and is littered with driftwood, at least at its upper edge. Three carabid beetle species, *Nebria diversa*, *Dyschirius pacificus*, and *Bembidion sejunctum semiaureum*, occur only in this habitat. FIGURE 6. (bottom) Supra-tidal meadow habitat. View looking southwest from the eastern shore of Shields Bay in Rennell Sound, western Graham Island. This meadow of grasses and forbs occupies a flat terrace area, just a few meters above the highest tide line, between the beach and forest habitats. Adults of *Pterostichus adstrictus* and *Amara littoralis* are abundant in this habitat, and *Amara ellipsis* occurs only in such sites.

FIGURE 7. Open ground/synanthropic site habitat. View looking southeast along the north shore of Skidegate Inlet from just east of Queen Charlotte City, southern Graham Island. In the foreground is land cleared beside a main road; in the distant left, home sites and cultivated areas; and in the distant center and right, across Skidegate Inlet, clear-cut logged areas on northern Moresby Island. Carabid species abundant in such sites include *Pterostichus algidus*, *Pterostichus adstrictus*, *Amara littoralis*, and *Harpalus somnulentus*.

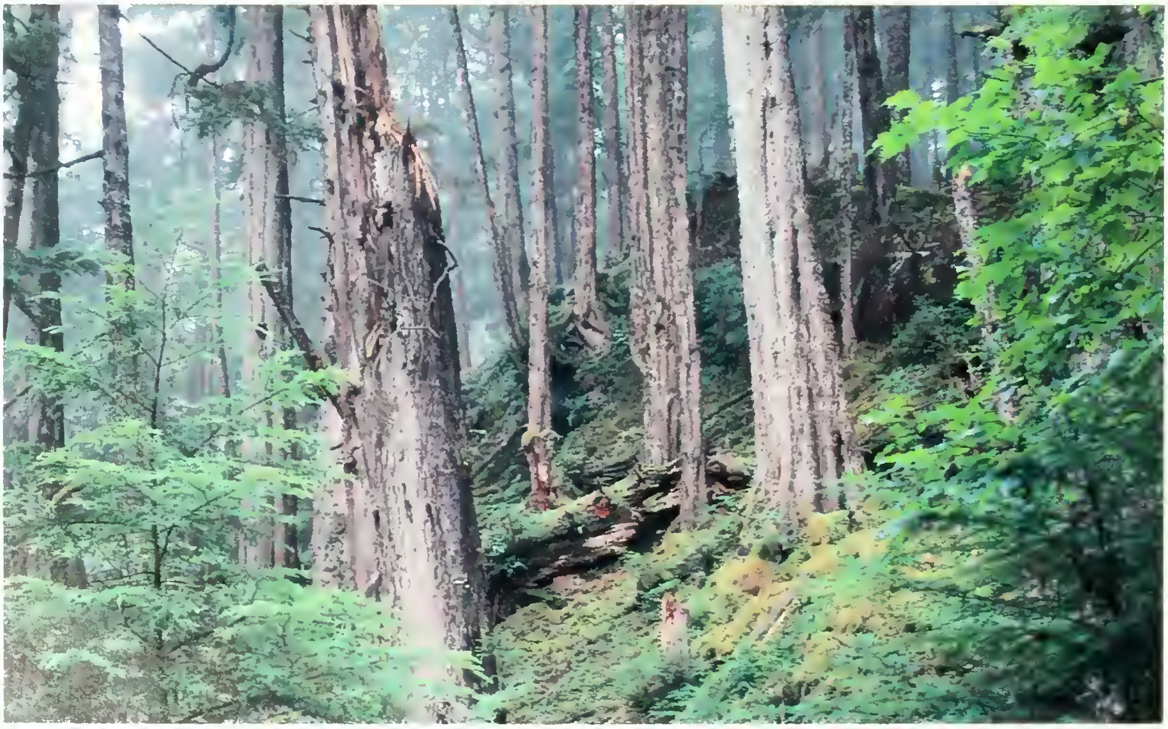


FIGURES 8–9. Lowland marsh or bog habitat. FIGURE 8. (top) Aerial view of extensive bog, muskeg, areas, west of Naden Harbour on northern Graham Island. Stretches of open water alternate with areas of dense *Sphagnum* moss blankets, shrubby vegetation, and moist forest patches. FIGURE 9. (bottom) Agonum Bog, southern Graham Island. Moist boggy areas such as this are home to several carabid species, including *Bembidion fortestriatum* and *Agonum belleri*.





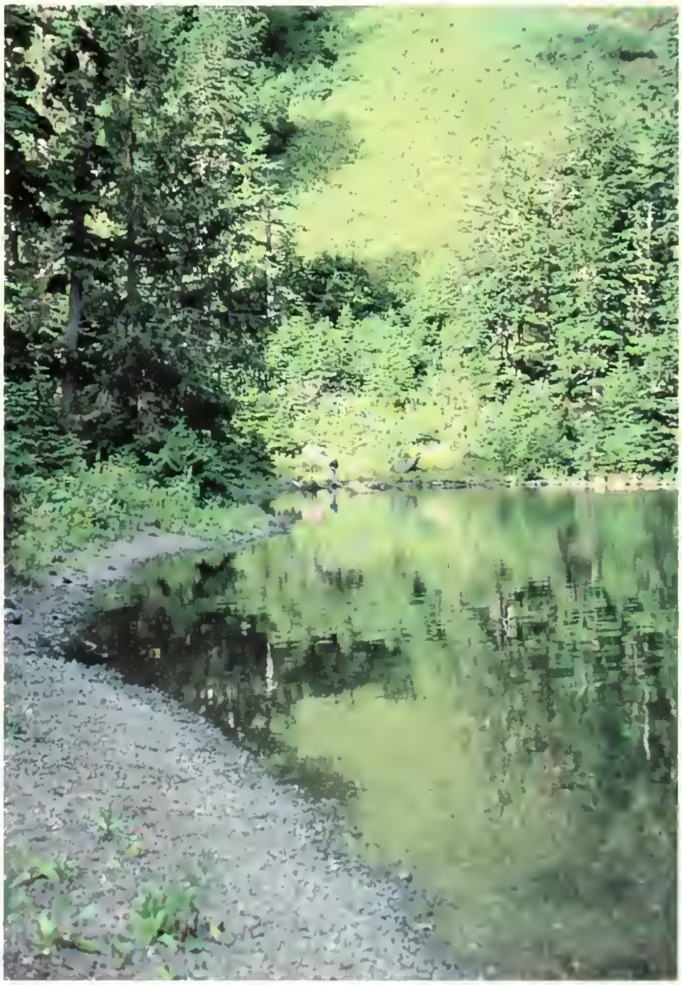
FIGURES 10–13. FIGURES 10–11. Lowland marsh or bog habitat, Elaphrus Bog, southern Graham Island. FIGURE 10. (top at left) The boggy and marshy margins of lowland ponds such as this teem with carabid beetles. FIGURE 11. (bottom at left) Carabid beetles are most readily collected in marshy areas by treading vegetation and organic litter down into the water or wet organic substrate. Beetles then float or climb to the surface, where they are easily seen and captured. Abundant in such sites are *Elaphrus americanus sylvanus*, *Loricera decempunctata*, *Bembidion incrematum*, *Bembidion versicolor*, *Agonum metallescens*, and *Agonum brevicolle*. FIGURE 12. (above left) Lowland deciduous forest habitat. Road to Peel Inlet, southeast of Camp Moresby, Moresby Island. Dense stands of red alder develop in disturbed lowland sites, often at the edges of logging road. Carabid species that are abundant in such stands include *Cychrus tuberculatus*, *Leistus ferruginosus*, *Trechus chalybeus*, *Pterostichus algidus*, and *Pterostichus crenicollis*. FIGURE 13. (above right) Lowland small, shaded stream shore habitat. Unnamed stream on the south shore of Skincuttle Inlet, 3 km northeast of Jedway, Moresby Island. The shaded rock and gravel banks of such small, but beautiful, streams are home to several species of carabid beetles, especially *Nebria sahlbergii sahlbergii*, *Bembidion quadrifoveolatum*, and *Bembidion planiusculum*.



FIGURES 14–17. FIGURES 14–15. Lowland coniferous forest habitat. FIGURE 14. (above top) Along road between Masset and Tow Hill, on the north coast of Graham Island. This coastal sand dune forest, essentially a pure stand of Sitka spruce, has developed on old, stabilized sand dunes. A thick carpet of mosses covers the forest floor and, in some spots, extends up tree trunks and out into the canopy. This habitat is home to many carabid species, including *Scaphinotus marginatus*, *Bembidion oblongulum*, *Pterostichus lama*, *Pterostichus amethystinus*, and *Pterostichus castaneus*. FIGURE 15. (above bottom) Kiusta village site, northwestern Graham Island. An example of the closed forest community, this is the most widely distributed forest type in the lowlands. Canopy cover is nearly complete and understory vegetation is poorly developed. The carabid beetle species, *Zacotus matthewsi*, apparently occurs only in this type of forest, which it shares with 12 other carabid species. FIGURES 16–17. Lowland open lake or large stream shore habitat. FIGURE 16. (top at right) Unnamed stream draining west into Lepas Bay, on the northwest coast of Graham Island. The sandy banks of this stream are exposed to direct sunlight during at least part of the day, and few carabids are found here, except where rocks, drift logs, or other debris provide cover. FIGURE 17. (bottom at right) View looking southwest toward Mosquito Mountain from the east shore of Mosquito Lake, Moresby Island. The exposed cobble and gravel beach in the foreground is home to several species of carabid beetles, particularly *Bembidion transversale*.

FIGURES 18–19. Upland marsh or bog habitat. FIGURE 18. (top) Southern slope of Mount Moresby, Moresby Island. Adults of *Trechus chalybeus* were found in large numbers in the soggy banks of this small, shaded pond at 650 m elevation. FIGURE 19. (bottom) Southeastern slope of Nebria Peak, southwestern Graham Island. Adults of *Bembidion versicolor* were found by treading vegetation at the edge of this exposed boggy site at 620 m elevation

FIGURES 20–21. FIGURE 20. (top) Upland deciduous forest habitat. Eastern slope of Nebria Peak, southwestern Graham Island. This forest type is represented by small clumps of Sitka alder, seen here at the edge of a subalpine meadow at 620 m elevation. There are no carabid beetle species unique to this habitat, but members of some species found in all adjacent habitats occur here as well. In the foreground, the lush meadow vegetation of grasses and herbaceous plants (false hellebore, *Veratrum eschscholtzii*, in particular) is also seen. FIGURE 21. (bottom) Upland coniferous forest habitat. Southern slope of Mount Moresby, near High Goose Lake, Moresby Island. A dense carpet of mosses covers the floor of this closed-canopied, mountain hemlock forest at 600 m elevation. Among the carabid beetle species that live in this habitat are *Scaphinotus marginatus*, *Notiophilus sylvaticus*, *Bembidion spectabile*, *Bembidion oblonguloides*, and *Pterostichus amethystinus*.



FIGURES 22–25. Upland stream or lake shore habitat. FIGURE 22. (above left) Nebria Creek, just above Lower Nebria Lake on eastern slope of Nebria Peak, southwestern Graham Island. The rock and gravel banks of cold, clear streams such as this, both in upland forested areas and above treeline, are home to several species of carabid beetles, including *Nebria sahlbergii sahlbergii*, *Broscodera insignis*, *Bembidion incertum*, *Bembidion quadrifoveolatum*, and *Bembidion farrarae*. FIGURE 23. (above right) High Goose Lake, southern slope of Mount Moresby. The small carabid beetles, such as adults of *Bembidion quadrifoveolatum*, that inhabit the rock and gravel shores of this lake at 620 m elevation, are most easily found and collected by simply splashing the shores with lake water. FIGURES 24–25. (top at right) Subalpine forest habitat. View looking southwest from the ridge northeast of Takakia Lake, Moresby Island. The discontinuous nature of this stunted forest of mountain hemlock is clearly seen here as a transition zone between upland coniferous forest (upper left of photograph) and alpine (foreground of photograph) habitats. At least some of the carabid beetle species found in each of these adjacent habitats occur in the subalpine forest as well, but no species appears to be restricted to this habitat type. FIGURE 25. (bottom at right) Alpine zone habitat. View looking northwest to Peel Inlet (in distant left of center of photograph) from ridge northeast of Takakia Lake, Moresby Island. Extensive areas of alpine heath community cover the lower and flatter ridges and slopes of the alpine zone.

FIGURES 26–27. Alpine zone habitat. FIGURE 26. (top) Ridge northeast of Takakia Lake, Moresby Island, at 900 m elevation. Loose rocks at the surface in this area of heath community offer ideal daytime hiding places for nocturnal carabid beetles. Adults of *Nebria haida*, *Bembidion incertum*, *Bembidion farrarae*, and *Bembidion complanulum* are abundant in such sites. FIGURE 27. (bottom) View looking east from the head of a glacial cirque on the northeastern slope of Mount Moresby, Moresby Island. Talus slopes abound below cliffs and the headwalls of cirques at highest elevations. In north-facing cirques and slopes, snowfields persist late into summer months, if not all year. These barren rocky areas are home to several carabid species, including *Nebria haida*, *Bembidion incertum*, *Bembidion complanulum*, and *Amara sinuosa*.

FIGURES 28–29. Alpine zone habitat. FIGURE 28. (top) Ridge just southeast of summit, Nebria Peak, southwestern Graham Island. Exposed, heavily weathered bedrock is found on the summits and upper ridges of the highest peaks. Alpine vegetation covers little of the surface in such sites, but carabid beetles, particularly adults of *Nebria haida* and *Bembidion complanulum*, abound. FIGURE 29. (bottom) View looking south from southern slope of Nebria Peak to the summits of other, unnamed peaks of the Queen Charlotte Ranges, southern Graham Island. Persistent snowfields occupy cirques and areas at the bases of cliffs in protected, north-facing sites.

Although the entire area between the mean high tide line and the highest extent of wave action in winter storms is included in this habitat, carabid beetles are generally found hiding only in the upper reaches of this zone during the day (but they may forage over much more of the upper beach at night). No intertidal carabids have been recorded from the archipelago.

(2) SANDY SEA BEACH.—Calder and Taylor (1968) distinguished two types of sandy sea beaches: (a) "crescent beaches," which are confined to the heads of open bays and limited in their extent by rocky bluffs or headlands at their ends; and (b) "continuous beaches," which form long strands (Fig. 5) that extend for many kilometers, uninterrupted by headlands or rocky outcrops. Continuous beaches are found on the northeast coast of Moresby Island, from Sandspit southward for a few kilometers, and the north and east coasts of Graham Island, where they extend with only minor interruption from the Tlell area north to Rose Spit and then west to Masset Spit. Crescent beaches are few, and most are found on the west coast of Graham and Moresby islands.

Like cobble beaches, both types of sandy sea beaches differ in several features that appear to influence carabid beetle diversity and abundance. In general, continuous beaches have more diverse carabid faunas than crescent beaches. All sandy beaches sampled had at least some driftwood present; and again, beaches with little driftwood have fewer carabid individuals than those with abundant drift. Again, too, the presence of freshwater seepage through the sand from inland habitats is associated with increased carabid diversity and abundance. Perhaps most important, however, is the relationship between development and extent of dunes at the upper beach margin and composition and diversity of the carabid fauna. All crescent beaches sampled had either a narrow dune fringe or none at all, whereas dune systems associated with the continuous beaches (Fig. 5) are extensive in most areas, up to 100 meters in width in some sites. Several carabid species appear to be restricted to sandy beaches with well-developed fringing dunes.

(3) SUPRA-TIDAL MEADOW.—At some coastal sites in the archipelago, there are narrow, slightly raised beach terraces that form a more or less well-defined "transition zone" (Calder and Taylor 1968) of low vegetation, mainly grasses and forbs, between the upper limit of sea beach and the forest edge (Fig. 6). This zone is rarely more than a few meters in width and usually between three and five meters in elevation (i.e., above mean high tide). The surface substrate may be of sand or gravel or of various combinations of these materials, often mixed also with small stones (cobble). Storm-tossed driftwood and other flotsam are also present in some places. These meadows vary in the density of their vegetative cover, but all are open (i.e., exposed to full sun) and relatively well drained. Hence, they are among the driest sites in the archipelago. Although both native and introduced grasses and forbs are present, these meadows certainly are naturally occurring and probably were much more widespread historically than at present. Naturally free of trees, they are easily occupied and modified by man. Historic and recent alteration of these terrace meadow areas, from their natural state to one that falls into the following habitat type, may account for their limited distribution at present. Carabid beetles are found throughout these meadows, usually under cover of stones or debris during the day.

(4) OPEN GROUND/SYNANTHROPIC SITE.—There are relatively few open (more or less barren) ground areas occurring naturally at low elevations in the archipelago. These include temporary, disturbed sites, such as areas cleared by landslides, flooding, fire, etc., and more enduring sites, such as rocky outcrops, cliff faces, and the bases of windswept headlands. However, this type of habitat (Fig. 7) is rapidly expanding due to man's activities. Clearing of the native forest for building and work sites, for roads, and through extensive logging and mining operations, has created extensive open ground habitat. Although adjacent deciduous and coniferous forest can quickly recolonize cleared land if allowed to do so, several kinds of sites are maintained in the cleared state. These include the areas around homes and other buildings, work yards, quarries, wide swaths along roads and beneath power lines, and pastures, maintained mainly for cattle and horses.

Due to high insolation and sparse, low vegetative cover, these open sites are usually very dry and warm during the day. Because they have relatively few places to hide, carabid beetles are easily found in these sites, where any debris on the ground can serve as cover for them. Some species are most abundant in this habitat, and others, including two introduced forms, occur only in areas disturbed and/or maintained by man (i.e., *synanthropic* sites).

(5) LOWLAND MARSH OR BOG.—Wet lowland sites are abundant throughout the archipelago but reach their greatest extent and diversity in northern and eastern Graham Island and northeastern Moresby Island. This is the most difficult of habitat types to characterize, because so many different combinations of wetland conditions are found in the Islands. Calder and Taylor (1968) recognized and described eight different plant communities in such sites: "wet" and "dry swamps," "mires," "raised" and "blanket bogs," "springs," "rills," and "flushes." Carabid beetles are found associated with all of these communities, as well as in "salt marshes of low salinity" (Calder and Taylor 1968). For the purposes of my report, all wetland sites that are neither lake nor stream shores, as defined below (see habitat types 8 and 9), are considered lowland marsh or bog, without regard to their size or extent. They may have either standing or flowing, fresh or slightly brackish water. Most sites are open to direct sunlight for most of the day, but wetlands at forest edges may be partly or fully shaded. The feature common to all these sites, but not to the excluded habitats, is the organic substrate at their margins. Included are several types of organic materials, such as peat, mud, decomposing plant material, or living vegetative mats (e.g., algae, mosses, or other aquatic or emergent aquatic plants). In general, the nature of the substrate is a more important determinant for composition of the carabid fauna than size or extent of the water body. Most carabid species occurring in this habitat type are found in most or all of the different kinds of included wetland sites. Only one species (i.e., *Agonum belleri* [Hatch]) appears to be restricted to a single type of wetland site (*Sphagnum* bogs) in the archipelago.

The most extensive wetland habitats in the archipelago are bogs (Fig. 8), and carabid beetles can be found most easily in these sites by treading (see collecting techniques above) the mossy vegetation, especially at the edges of open water areas (Fig. 9). The marshy edges of ponds in forest clearings (Fig. 10) are also excellent sites for carabid beetles. Again, treading the fringing vegetation or open, muddy flats adjacent to the ponds (Fig. 11) is the best way to find members of several carabid species in this habitat. Different species favor slightly different areas within these wet sites. Some species are found only on barren mud flats, others occupy only the sparse or dense vegetation at the water's edge, and others are found mainly in deeper water, where they hide in the leaves of floating or emergent vegetation. Carabid beetles occur in both open and shaded sites but are more abundant and diverse in the more open wet areas.

(6) Lowland Deciduous Forest.—More or less pure stands of deciduous forest (Fig. 12), chiefly of red alder (*Alnus rubra* Bong.), develop rapidly in disturbed lowland areas as a successional stage in natural reforestation in the archipelago. Disturbance may be from naturally occurring events (e.g., landslides, flooding, or fires) or from human activity (e.g., clear-cut logging and road cuts). In just a few years, lowland species of conifers become established in these stands and begin to replace the alders. Somewhat more stable stands of alders occur along river flood plains, perhaps in response to repeated disturbance.

In this habitat, carabid beetles are diverse and abundant. The dense alder stands provide cool, moist, and dark conditions that are ideal for many species. Beetles are found hiding in and under rotten logs and leaf litter on the ground. Sifting through damp alder leaf litter can be especially productive.

(7) Lowland Coniferous Forest.—Calder and Taylor (1968) recognized three different lowland forest communities, which differ in dominant tree species, density of the canopy, and development of the understory. (a) The "coastal sand-dune forest community" (Fig. 14) is found on old sandy beach ridges extending inland from present beaches, especially along the northern and eastern coast of Graham Island between Tlell and Masset. Sitka spruce (*Picea sitchensis* [Bong.] Carr.) is the dominant (if not the only) conifer; the canopy is dense and more or less complete, the understory has few or no shrubs or herbs, and the forest floor is covered by carpets of mosses. (b) The "meadow forest community" is found on flats and terraces of lowland streams. Sitka spruce is also dominant in this community, but western hemlock (*Tsuga heterophylla* [Raf.] Sarg.) and western red cedar (*Thuja plicata* D. Don.) occur sporadically; the canopy is partially open, and a dense herbaceous and shrubby understory is present. (c) The "closed forest community" (Fig. 15) is the most widely distributed coniferous forest type in the lowlands. Western hemlock is the dominant conifer, with Sitka spruce and western red cedar scattered throughout the forest; the canopy is dense and open only along streams and, temporarily, where trees have fallen; the understory is absent or very poorly developed; and the ground and lower portions of standing trees are covered with a thick layer of mosses and lichens. Because the same carabid species generally occur in all three of these communities, a single habitat type is recognized in this report.

Carabid beetles are found everywhere under cover in this habitat—under rocks of all sizes, in and under rotting logs and stumps, under the loose bark of rotting logs and stumps, in accumulations of leaf litter and within the needle duff layer, and in the layer of mosses and lichens. Some species are widespread in the habitat, others occur mainly in one or two of these specific microhabitats. Use of pitfall traps and sifting of leaf litter and clumps of moss are especially effective collecting aids in this habitat.

(8) Lowland Lake or Large, Open Stream Shore.—Sites included in this habitat type share two important features: (a) inorganic substrate, and (b) exposure to full sunlight during a substantial part of the day. Relatively few sites within the archipelago offer both conditions. Because the distance between mountain summits and the sea is usually quite short, most streams traverse steep gradients and drain small areas. As a result, there are very few large streams in the archipelago. In addition, dense forest closes in on most stream beds, creating shaded, rather than open, conditions. Only the widest streams have significant open shore areas that occur naturally (Fig. 16). Stream areas that have been disturbed by human activity (e.g., logging or stream-channel modification) may also provide the conditions typical of this habitat. Although several streams on Graham and Moresby islands offer some lowland sites representing this habitat, the only extensive areas of this type occur along the Yakoun River in eastern Graham Island. Most other streams in the eastern lowlands of Graham Island drain bog areas and have poorly defined banks for most of their length and/or shores of organic substrate and so are included in the lowland marsh or bog habitat in this report.

Lowland lake shores that are open to sunlight and have inorganic substrate are also limited. The shores of most lakes are marshy with organic substrate. In general, inorganic shores are restricted to areas subject to wind-driven wave action, usually only on the larger lakes (such as Mosquito Lake [Fig. 17] on Moresby Island), or where inflowing streams have deposited inorganic sediments.

The substrate on either lake or stream shores may be of silt, sand, fine to coarse gravel, cobble (stones), or various combinations of these materials. Some carabid species are associated with only one or two of these substrate types, others are found on all of them. Just as in other habitats, there is a clear relationship between carabid abundance and diversity on these shores and the nature and availability of cover for hiding during daylight hours. Rocky bars are especially good sites for collecting beetles, as are shores of any inorganic type that have stream-drifted wood or other debris or accumulations of loose stones under which beetles can hide. Use of the splashing technique and an aspirator is especially helpful in collecting the many small, fast carabids found in this habitat.

(9) Lowland Small, Shaded Stream Shore.—Small streams (Fig. 13) with well-shaded shores of silt, sand, gravel, cobble, bedrock, or mixed inorganic substrate are found throughout the archipelago, except in the flat lowlands of northeastern Graham Island and on many of the smaller islands. They range in size from mere trickles to plunging cascades, and most are subject to rapid and/or seasonal changes in flow. Sites in this habitat type are among the coolest in the lowlands, and some carabid species that are more widely distributed at higher elevations are generally restricted to this habitat in the lowlands. Collecting sites and techniques noted for the preceding habitat apply for this one as well.

Upland Habitats. All areas at elevations above 150 meters are here considered "upland" sites. Six different upland habitats are recognized for carabid beetles:

(10) Upland Marsh or Bog.—Like its lowland equivalent, this habitat type includes a variety of wetland sites that have, as a shared trait, organic substrate at their margins. Ponds (Fig. 18) and wet meadows abound in the mountains, both in small clearings in the forested areas and at treeline and above. Upland bogs (Fig. 19)—"blanket bogs" of Calder and Taylor (1968)—

are common at and above treeline. They also extend down into the forest zone, even into the lowlands in some areas, especially on the western slopes of the Queen Charlotte Ranges and Skidegate Plateau. In these wet sites, the typical hemlock/spruce/cedar forest is replaced by *Sphagnum* bog with scattered, scrublike lodgepole pine (*Pinus contorta* Dougl. ex Loud.), also known as shore pine. Wetlands above treeline are exposed to direct sunlight, whereas sites at lower elevations provide a range of exposures, from full sunlight to full shade.

Carabid beetles are less abundant and less diverse in upland wetlands than in equivalent lowland sites. Nonetheless, they occur in all the different kinds of upland sites and can be collected using the same techniques as were discussed for the lowlands.

(11) Upland Deciduous Forest.—This habitat type is represented in the archipelago only by small stands of Sitka alder (*Alnus crispa* [Ait.] Pursh ssp. *sinuata* [Regel] Hult.) that are found at the margins of some subalpine meadows and lakes (Fig. 20). It occupies a total area in the archipelago much smaller than that for any other habitat distinguished in this report. Because of its very limited extent, and because there are no carabid species restricted to or most abundant in this habitat, upland deciduous forest appears to be of little or no importance for the carabid fauna of the archipelago. This situation contrasts markedly with the importance of quaking aspen (*Populus tremuloides* Michx.) forest, an analogous habitat in montane regions of the interior of the continental mainland that is both widely distributed and home to diverse carabid assemblages, including several species apparently restricted to this habitat.

Carabid beetles found in Sitka alder stands occur also in adjacent coniferous forest and/or subalpine meadow habitats. Collecting techniques used in lowland deciduous forest work equally well in upland sites.

(12) Upland Coniferous Forest.—Forests of lower and mid-elevation montane areas in the archipelago are predominantly or exclusively stands of western hemlock. They represent a vertical continuation of the lowland "closed forest community" of Calder and Taylor (1968). At higher elevations, mountain hemlock (*Tsuga mertensiana* [Bong.] Sarg.) and, in wetter sites, yellow cedar (*Chamaecyparis nootkatensis* [Lamb.] Spach) occur with western hemlock; and in the highest forested areas, mountain hemlock is dominant. In these forests (Fig. 21), canopy cover is generally dense, understory shrubs and herbs are scattered or absent, and the ground and bases of standing trees are covered with a dense layer of bryophytes.

Most of the carabid species in this habitat are the same as those in lowland forest sites. Only one species (i.e., *Bembidion oblongulum* Mannerheim) appears to be restricted to the upper montane coniferous forest.

(13) Upland Stream or Lake Shore.—This habitat type is the upland equivalent of the two lowland lake and/or stream shore habitats (types 8 and 9 above) combined. All sites included in this habitat, like those in the two lowland types, have inorganic substrate (sand, gravel, cobble, bedrock, or some mixture of these materials). However, this upland habitat type includes the shores of both large and small lakes or streams, without regard to the degree to which they are exposed to sunlight (i.e., sites ranging from fully shaded to fully exposed are all included). In the archipelago, upland streams (Fig. 22) are common, both above treeline and in the forested zone. Most of these are small and shallow—few are more than two or three meters in width and 20 or 30 cm in mid-stream depth, except in pools. Most streams descend steep gradients and, therefore, are swift flowing with many cascades and falls. Upland lakes (Fig. 23) vary in size from just a few square meters to a few hundred hectares. Many of the larger lakes are concentrated at elevations between 500 and 750 m, just below treeline, at the transition between upland coniferous and subalpine forest. In many parts of the Queen Charlotte Ranges, slope gradients increase dramatically just below this level, and outlet streams from many of these lakes drop precipitously as spectacular waterfalls, some approaching 100 m in height. Perched in shallow basins above steep slopes, these lakes are devoid of fish.

The carabid fauna of all these waterside sites, whether lake or stream shore, shaded or exposed, or above or below treeline, is remarkably uniform. Collecting beetles in this habitat is more laborious than in lowland sites because many of them are less responsive to splashing than their lowland counterparts. Hence, the collector must turn stones or move gravel by hand to find them. Most of the carabids in this habitat are small and fast, so use of an aspirator aids collecting.

(14) Subalpine Forest.—In the Queen Charlotte Islands, treeline, the elevation above which trees do not grow, is generally between 750 and 1,000 m, depending on exposure, although individuals of tree species occur, in sheltered sites, at even higher elevations as dwarfed, shrublike plants. In some areas, particularly on the western slopes of the Queen Charlotte Ranges, relatively treeless areas extend down almost to sea level. These sites are not included in this habitat type because, unlike the true treeline, which is determined chiefly by temperature and seasonal climatic factors, these lower treeless areas reflect the distributions of certain soil and moisture conditions, wind exposure, and other factors that retard or preclude tree growth and/or survival.

The subalpine forest (Fig. 24) is basically a discontinuous band of mountain hemlock forest at treeline. This habitat is characteristically more open than other forest types, with more or less discrete forest stands separated (to varied degrees) by wet subalpine meadows, rocky ridges and outcrops, and/or talus slopes. Its carabid fauna is essentially transitional between faunas of the upland forest and true alpine areas, with several of its species shared with each of these habitats and no species restricted to it. Collecting techniques described above for both forested and open sites must all be used to guarantee an adequate sample of this fauna. Pitfall traps placed in both forest stands and intervening meadows can be highly productive.

(15) Alpine Zone.—For the purposes of this report, all sites above treeline, except for the shores of streams and lakes and the upland marsh and bog sites, as previously discussed, are included in a single, alpine, habitat type. In the archipelago, alpine habitat exists as a highly dissected, discontinuous series of "habitat islands" on the summits of the highest peaks and ridges in the Queen Charlotte Ranges, surrounded by a "sea" of forest and intervening lowlands. Significant alpine areas are found only on Graham, Moresby, and Louise islands. Calder and Taylor (1968) recognized four different kinds of "montane [i.e., alpine] communities" for plants, and a fifth type is also important for carabid beetles. This habitat is really an intricate

mosaic of all these communities, which intergrade with and/or replace one another with changing conditions of slope pitch and exposure, substrate, soil depth, and moisture.

(a) Meadow communities of lush, dense, herbaceous vegetation, sometimes approaching a meter in height, occur on flats and gentle slopes in alpine valley bottoms at or just above treeline (Figs. 20 and 24), where accumulations of soil are deepest and moisture is abundant. In fact, most meadows are so wet that they represent the marsh and bog habitat type. Only the drier edges of these meadows have a true alpine carabid fauna, which they share with other alpine sites. The total area in the archipelago occupied by drier meadow sites is small, certainly less than 10% of the area above treeline.

(b) Heath communities of low, dense, shrubby (mainly ericaceous) ground cover occupy ridges, gentle upper slopes, and steeper lower slopes, where drainage is better and soil thinner. These are clearly the most widespread communities in alpine areas (Fig. 25), perhaps occupying 60–70% of the total area above treeline. Heath cover is disrupted to a varied extent by rock cliffs, outcrops, and other barren areas, as discussed below, which together occupy 20–30% of the total area above treeline. Carabid beetles are most easily collected here by turning rocks and rubble by hand (Fig. 26). The use of pitfall traps, especially in the denser heath areas, is highly productive, but traps are often difficult or impossible to place properly in the rocky substrate. Aided by flashlight or headlamp, collecting and/or observing at night, while the beetles are active on the surface, is a productive alternative that results in minimal disturbance to this fragile environment.

(c) Talus slopes (Fig. 27) of loose rock rubble and boulders, which interrupt heath and meadow cover, develop below crumbling bedrock source areas on cliffs and summits. Few plants besides lichens occupy these unstable sites. While the surfaces of talus slopes provide some of the hottest and driest conditions anywhere in the archipelago, their interiors offer some of the coolest dry conditions available. Carabid beetles are abundant in these accumulations but difficult to find and collect. When disturbed, they quickly and easily drop deeper into the talus and out of reach.

(d) Cliff, runnel, and other rock outcrop communities are other types of barren alpine sites (Fig. 28) that offer either scattered or no vegetative cover and relatively dry conditions, but greater stability than talus slopes. Carabids are both abundant and diverse in these areas, wherever there are crevices and/or loose rocks in or under which they can hide. Again, collecting at night is highly productive in these sites.

(e) Small snowfields persist, in several high alpine areas of the archipelago, well into late summer in most years and year-round in some years. These sites are generally restricted to north-facing slopes (Figs. 27 and 29), usually at the bases of cliffs or headwalls of glacial cirques. As snowfields melt back to small, core sites during the summer, perinival sites (barren ground areas at the edges of persistent snowfields) are exposed. Right at the snowfield margin, conditions are very cold and moist. At greater distances from the margin, daytime temperatures grade higher and substrate moisture and humidity grade lower. Adults of several carabid species are most abundant in these perinival sites and apparently differ in their particular temperature and moisture preferences. This is suggested by the fact that they are most often found under cover at different distances from the snowfield margin. As the snow margins retreat through melting, the beetles change their hiding places, maintaining their same relative distances from the margin, thereby, presumably, tracking their preferred microclimate. Members of several alpine species are frequently found at night on the snowfields, walking, feeding on other small invertebrates, both dead and alive, or mating. It is clear that carabids in this habitat are well adapted, metabolically, for activity at temperatures at or below freezing.

Table 3 records the known and/or likely occurrence of each of the 15 habitat types on the 23 islands sampled to date.

Formats for Taxonomic Accounts

For tribes and genera, I provide only a diagnostic combination and brief discussion of diversity, distribution, and biology. These diagnoses are useful for distinguishing the supraspecific taxa in relation to each other only within the archipelago and not necessarily elsewhere.

Information about each species is presented in the following sequence: synonymy, with pertinent literature references; taxonomic notes (as needed); diagnostic combination; general description; dispersal potential; habitat distribution; geographical distribution; distribution in the archipelago; geographical variation (as needed); additional comments (as needed); and material examined.

Synonymy.—The list of synonyms provided for each species includes only those names used in the literature for beetles in the Queen Charlotte Islands and, hence, is not exhaustive for the species. Type locality is cited for each name, except for names incorrectly applied (i.e., misidentifications)

Diagnostic Combination.—The diagnosis is the minimum combination of character states needed to distinguish adults of the species from those of all other species in the fauna. Because character states listed in tribal and generic diagnoses are not repeated in specific diagnoses, all three levels of diagnoses must be used in concert.

General Description.—Descriptions under this heading are brief and intended simply to augment the diagnoses with other characteristics, such as body size and color, that may help to confirm identification.

The only measurement used in this study is body length, which is measured along the midline of the body, from the apical margin of the labrum to the apex of the longer elytron (see Fig. 30A, "bl"). Ranges in body length cited in the descriptions were established by visual selection and subsequent measurement of the smallest and largest specimens. These ranges refer only to specimens from the archipelago and are not necessarily accurate for the species throughout its geographical range.

Both the key and species descriptions are designed for use by individuals with little knowledge of or experience with carabid beetles. Illustrations are therefore provided for all characteristics that may be unfamiliar. Figure 30 (A–I) illustrates the basic structure of carabid beetles and identifies all body parts that are mentioned in the text.

One useful character that may be particularly difficult for the non-specialist to interpret is microsculpture on the elytra. In many carabid species, the surface of the elytra (as well as other body parts) is etched with a particular pattern of very fine lines

TABLE 3. HABITATS AVAILABLE ON ISLANDS SAMPLED FOR CARABID BEETLES.

Island	Habitat type[1,2]															No. hab.	No. spp.
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15		
Anthony	(x)	–	(–)	x	–	(x)	x	–	(–)	–	–	–	–	–	–	4	1
Burnaby	x	–	(–)	x	–	x	x	–	x	–	–	x	–	–	–	6	6
Chaatl	x	–	–	x	–	x	x	–	x	–	x	x	–	–	–	7	4
East Copper	x	–	–	(–)	–	(–)	x	–	–	–	–	–	–	–	–	2	1
Faraday	(–)	–	(–)	(–)	–	x	x	–	–	–	–	–	–	–	–	2	1
Graham	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	15	57
Harrison	x	–	–	x	–	x	x	–	–	–	–	–	–	–	–	4	1
Hibben	(x)	–	–	–	–	x	x	–	x	–	–	x	–	x	–	6	1
Hotspring	x	–	x	x	–	x	x	–	–	–	–	–	–	–	–	5	3
Huxley	x	–	–	(–)	–	(–)	x	–	–	–	–	–	–	–	–	2	5
Kunga	x	–	–	–	–	x	x	–	–	–	–	–	–	–	–	3	8
Kunghit	x	–	x	x	(x)	x	x	–	x	–	(–)	x	–	–	–	8	4
Langara	x	(–)	x	x	x	x	x	–	(x)	–	–	–	–	–	–	7	4
Louise	x	–	x	x	x	x	x	–	x	–	x	x	–	x	x	11	16
Lyell	x	–	x	x	x	x	x	–	x	–	x	x	–	–	–	9	14
Maude	x	–	x	x	–	x	x	–	–	–	–	–	–	–	–	5	1
Moresby	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	15	40
Murchison	(–)	–	(–)	(–)	–	x	x	–	–	–	–	–	–	–	–	2	1
Ramsay	x	–	–	–	–	x	x	–	(–)	–	–	–	–	–	–	3	6
Reef	x	–	–	–	–	(–)	x	–	–	–	–	–	–	–	–	2	6
Talunkwan	x	–	–	x	–	x	x	–	x	–	–	x	–	–	–	6	6
Tanu	x	–	–	x	–	x	x	–	x	–	(–)	x	–	–	–	6	10
West Skedans	x	–	–	x	–	(–)	x	–	–	–	–	–	–	–	–	3	1
Totals	21	2	8	15	6	19	23	2	11	2	5	10	2	4	3		

[1] Habitat types: 1 = Cobble upper sea beach; 2 = Sandy upper sea beach, 3 = Supra-tidal meadow, 4 = Lowland open/synanthropic; 5 = Lowland marsh or bog; 6 = Lowland deciduous forest; 7 = Lowland coniferous forest, 8 = Lowland open lake or large stream shore; 9 = Lowland small, shaded stream shore; 10 = Upland marsh or bog, 11 = Upland deciduous forest, 12 = Upland coniferous forest; 13 = Upland lake or stream shore, 14 = Subalpine forest; 15 = Alpine zone.

[2] Occurrence of habitat: x = habitat known to occur on island, – = habitat known not to occur on island, (x) = habitat not known but likely to occur on island; (–) = habitat neither known nor likely to occur on island.

known as microsculpture (see Fig. 59). To examine this pattern properly, a dissecting microscope with magnification of at least 50× (preferably at least 80×) is required. Proper lighting is also important. Light should be filtered through a thin piece of polypropylene or through translucent (matte finish) drafting film to reduce the reflective glare that can otherwise obscure detail of the line pattern. The elytral area examined for comparison of patterns should also be consistent. A preferred area for this purpose is on the third elytral interval, at a point approximately one-third of the elytral length from the base (Fig. 30A, "mics"). The pattern is often modified or distorted in the elytral striae, so comparisons should be made only in the middle of an interval.

The only character used in descriptions and the key that requires dissection or at least manipulation of specimens is the size of the hindwings. This feature can be examined easily in specimens that have not yet dried, or in dried specimens that have been softened in warm water for a few minutes, by simply lifting one elytron (preferably the left elytron in pinned specimens) with forceps. A full-sized wing (Fig. 40C), in the folded position, still has its reflexed apex visible. Shorter wings lack the reflexed apex (Figs. 40A and 40B).

DISPERSAL POTENTIAL.—The means by which members of a species may disperse at present and may have dispersed in the past are limited by (1) their locomotory capabilities and (2) the range of opportunities presented to them in their particular habitat(s). Both of these aspects of dispersal potential are briefly addressed, as appropriate, in this section. In particular, flight capabilities, as suggested by the size of hindwings, are assessed for each species.

HABITAT DISTRIBUTION.—For each species, the known range of habitats occupied by its members in the archipelago is described, based on the habitat classification previously discussed. Ranges reported here may not reflect the full habitat range of the species throughout its entire geographical range (i.e., outside the archipelago). More detailed description of microhabitat is provided for those species for which such data are available.

GEOGRAPHICAL DISTRIBUTION.—The known geographical range for each species is described. As discussed in the section on faunal analyses, the ranges of different species can be classified as representative of one of six different generalized distributional patterns, namely: Holarctic, Transamerican, Western North American, West Coastal, Endemic, or Introduced European Patterns. The range pattern to which the distribution of the species can be referred is also noted under this heading.

DISTRIBUTION IN THE ARCHIPELAGO.—Under this heading, I list only the islands from which each species has been recorded. Additional data, including specific locality, elevation, month(s) of collection, and depository(-ies) of specimens, are provided in Appendix A.

GEOGRAPHICAL VARIATION.—Morphological variation within the archipelago was recognized for only one species, *Scaphinotus marginatus* (Fischer). Discussion of the observed geographical variation is provided for that species.

ADDITIONAL COMMENTS.—Taxonomic notes and other comments or discussions that are inappropriate for any of the other descriptive sections are presented, as needed, under this heading.

MATERIAL EXAMINED.—For each species, the number of male and female specimens examined in this study is provided.

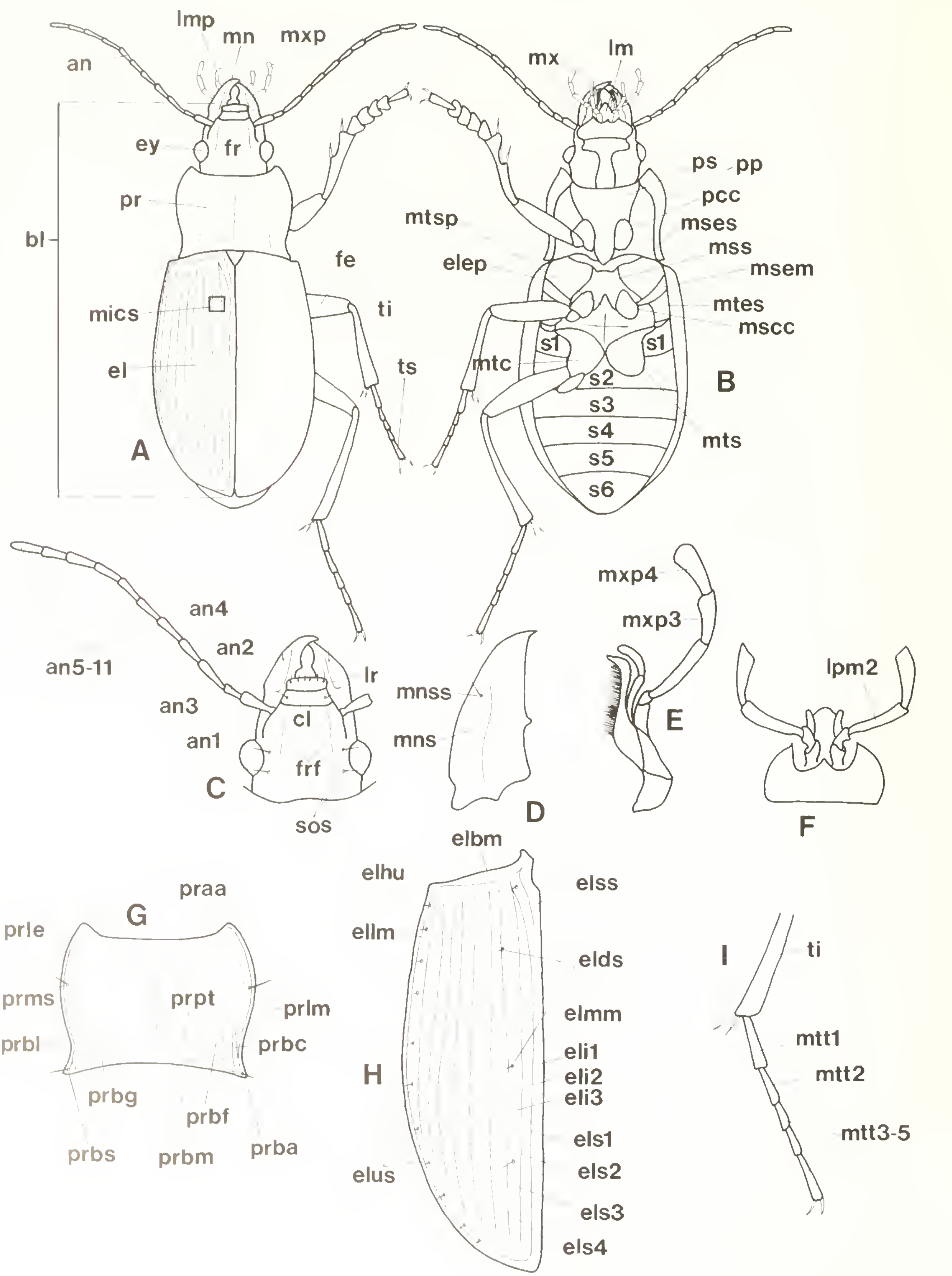
CARABIDAE OF THE QUEEN CHARLOTTE ISLANDS

The following combination of character states is diagnostic for adult ground-beetles (Carabidae) in western North America and can be used to recognize all members of this family found in the Queen Charlotte archipelago: first (anterior-most) visible abdominal sternum completely divided by the metacoxae into two lateral, triangular sclerites (Fig. 30B); metacoxae not expanded posteriorly to cover anterior three abdominal sterna; legs without long fringe setae (so-called swimming hairs); body and appendages not streamlined for aquatic life.

A KEY FOR IDENTIFICATION OF ADULT CARABIDAE FROM THE QUEEN CHARLOTTE ISLANDS

This key is based mainly on Ball's (1960) keys to tribes and genera and Lindroth's (1961–69) keys to species, but with additions to and modifications of couplets as needed.

1. Antennae inserted on frons between eyes, dorsal to and closer together than bases of mandibles (Fig. 31A) . . . (tribe Cicindelini) — 1. *Cicindela oregona* LeConte
1′. Antennae inserted at sides of head, between eyes and bases of mandibles (Fig. 31B) — 2
2(1). Lateral wall of mesocoxal cavity formed by mesosternum, mesepimeron, and metasternum (Fig. 32A) — 3
2′. Lateral wall of mesocoxal cavity formed entirely by mesosternum and metasternum, mesepimeron excluded (Fig. 32B) — 18
3(2). Procoxal cavity open behind, not enclosed by propleuron posteriorly (Fig. 33A) — 4
3′. Procoxal cavity entirely enclosed by propleuron posteriorly (Fig. 33B) — 15
4(3). Mandible without a setiferous puncture in scrobe (Fig. 34A) — 5
4′. Mandible with a setiferous puncture in scrobe (Fig. 34B) . . . (tribe Nebriini) — 9
5(4). Metacoxae contiguous in ventral middle of body (Fig. 35A) . . . (tribe Carabini) — 6
5′. Metacoxae separated in ventral middle of body (Fig. 35B) . . . (tribe Cychrini) — 7
6(5). Upper surface of elytron and pronotum with faint or marked brassy, copperish, or blue metallic reflection — 5. *Carabus nemoralis* Müller
6′. Upper surface of elytron and pronotum without metallic reflection, black or rufous brown — 6. *Carabus taedatus* Fabricius
7(5′). Labrum with four setae on anterior margin (Fig. 36A); elytron dull black, with contrasting large, shiny tubercles — 4. *Cychrus tuberculatus* Harris
7′. Labrum with six setae on anterior margin (Fig. 36B); elytron rufous-brown or black, without contrasting tubercles — 8
8(7′). Elytron rufous-brown, without metallic reflection, with 18 regular, punctate striae — 2. *Scaphinotus angusticollis* (Mannerheim)
8′. Elytron black, with faint or marked metallic violet or green reflection, with 16 or fewer striae (irregular and difficult to count, especially laterally, in some specimens) — 3. *Scaphinotus marginatus* (Fischer)
9(4′). Lateroventral margin of maxilla with several long, finger-like processes, each with a long, stout seta inserted apically (Fig. 37A) — 7. *Leistus ferruginosus* Mannerheim
9′. Lateroventral margin of maxilla without finger-like processes, setae inserted directly on ventral maxillary surface (Fig. 37B) — 10
10(9′). Pronotum (Fig. 38A) with basal angles obtuse (slightly denticulate in some individuals) AND lateral explanation narrow, at least at middle, basal sinuation of lateral margin shallow or absent; hindwings full-sized — 12. *Nebria mannerheimii* Fischer
10′. Pronotum (Fig. 38B–F) with basal angles rectangular or slightly acute, lateral explanation narrow or broad at middle, basal sinuation of lateral margin shallow or deep; hindwing full-sized or short (truncate distal to stigma or also narrowed) — 11
11(10′). Body pale yellow or tan; pronotum (Fig. 38B) very broad, markedly narrowed basally (posteriorly), lateral explanation narrow at middle; elytral silhouette (Fig. 39A) markedly ovoid, markedly narrowed basally (anteriorly); hindwing short and narrowed (Fig. 40A) — 13. *Nebria diversa* LeConte
11′. Body dark rufopiceous or black; pronotum (Fig. 38C–F) narrower, less markedly narrowed basally (posteriorly), lateral explanation broad, even at middle; elytral silhouette (Fig. 39B–E) rectangular, subrectangular, or subovoid, not or moderately narrowed basally (anteriorly); hindwing full-sized (Fig. 40C) or short (truncate distal to stigma) (Fig. 40B) — 12
12(11′). Head (Fig. 38C) moderate in relative size and width; pronotum (Fig. 38C) shorter, relatively narrow anteriorly and broad basally; elytral silhouette (Fig. 39B) subrectangular, only slightly narrowed basally, elytral striae deeply punctate; hindwing full-sized (Fig. 40C) — 11. *Nebria sahlbergii sahlbergii* Fischer
12′. Head (Fig. 38D) relatively large and wide; pronotum (Fig. 38D–F) longer, broader anteriorly and narrowed basally; elytral silhouette (Fig. 39C–E) subovoid, distinctly narrowed basally, elytral striae faintly punctate; hindwing short, truncate distal to stigma (Fig. 40B) — 13
13(12′). Pronotum (Fig. 38F) short, wide, basal sinuation of lateral margin short, very deep; elytra (Fig. 39D) with silhouette relatively short and broad, intervals flat; legs relatively short — 8. *Nebria charlottae* Lindroth
13′. Pronotum (Fig. 38D and 38E) longer, more slender, basal sinuation of lateral margin longer, moderately deep; elytra (Fig. 39C and 39E) with silhouette longer and more slender, intervals slightly or markedly convex; legs longer, more slender — 14



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14(13′). Pronotum (Fig. 38D) with apical angles short, relatively broad and slightly rounded; elytral silhouette (Fig. 39C) very narrow; femora and tibiae piceous or black; habitat above treeline in alpine zone 10. *Nebria haida* Kavanaugh

14′. Pronotum (Fig. 38E) with apical angles longer, relatively narrow and pointed; elytral silhouette (Fig. 39E) less narrowed; femora piceous, tibiae rufous or rufopiceous; habitat upper sea beach area 9. *Nebria louiseae* Kavanaugh

15(3′). Mandible with a setiferous puncture in scrobe (Fig. 41A); elytron with three rows of large, dull, ocellate foveae . . . (tribe Elaphrini) 16

15′. Mandible without a setiferous puncture in scrobe (Fig. 41B); elytron without large, dull, ocellate foveae (or if suggested, then foveae shiny) 17

16(15). Frons with a deep, finely and densely punctate pit in midline between eyes, pit surrounded by a shiny raised area with very sparse punctures (punctures separated by gaps of more than twice their diameter) 15. *Elaphrus clairvillei* Kirby

16′. Frons without a pit in midline between eyes (or, if faintly present, then pit surrounded by a flat or only slightly raised area with dense punctures (punctures, on average, about one diameter apart) 16. *Elaphrus americanus sylvanus* Goulet

17(15′). Body cylindrical, pedunculate (markedly constricted between pronotum and elytra); antennomeres 2–4 without long, erect setae (Fig. 42A) . . . (tribe Scaritini) 18. *Dyschirius pacificus* Lindroth

17′. Body dorsoventrally flattened, not pedunculate (not markedly constricted between pronotum and elytra); antennomeres 2–4 with several very long, erect setae (Fig. 42B) . . . (tribe Loricerini) 7. *Loricera decempunctata* Eschscholtz

18(2′). Head with one supraorbital setiferous puncture dorsomedial to each eye (Fig. 43A) 19

18′. Head with two supraorbital setiferous punctures dorsomedial to each eye (Fig. 43B) 24

19(18). Procoxal cavity open behind, not enclosed by propleuron posteriorly (Fig. 44A); eyes very large; frons with several parallel, longitudinal carinae between eyes . . . (tribe Notiophilini) 14. *Notiophilus sylvaticus* Eschscholtz

19′. Procoxal cavity (Fig. 44B) entirely enclosed by propleuron posteriorly; eyes small, moderate, or large in size; frons without distinct carinae between eyes (or, if present, then carinae convergent anteriorly) 20

20(19′). Mandible with a setiferous puncture in scrobe (Fig. 45A) (OR if scrobal seta absent, then body with distinct metallic purple reflection); antennomeres 5–11 covered with short, dense setae, antennomere 3 (Fig. 46A) glabrous except for long setae at distal apex, antennomere 4 with short, dense setae restricted to distal one-half or absent; pronotum narrowed basally, body therefore slightly pedunculate in shape . . . (tribe Broscini) 21

20′. Mandible without a setiferous puncture in scrobe (Fig. 47B) (and body without distinct metallic purple reflection); antennomeres 4–11 covered with short, dense setae, antennomere 3 (Fig. 46B) also with short dense setae, at least on distal one-third; pronotum not or only slightly narrowed basally, body not pedunculate in shape . . . (tribe Harpalini) 22

21(20). Body length 12.0 mm or more; body with distinct (brilliant in some individuals) metallic purple reflection (some individuals with brassy and/or copper highlights) 20. *Zacotus matthewsi* LeConte

21′. Body length less than 10.5 mm; body without metallic reflection 19. *Broscodera insignis* (Mannerheim)

22(20′). Pronotum (Fig. 47A) with basolateral setae present; elytron with numerous short, scattered setae laterally (on eighth and ninth intervals) and apically 61. *Trichocellus cognatus* (Gyllenhal)

22′. Pronotum (Fig. 47B) with basolateral setae absent; elytron without short, scattered setae laterally or apically (eighth and ninth intervals bare except for umbilicate series of setae in eighth stria and on ninth interval) 23

23(22′). Penultimate labial palpomere bisetose anteriorly (Fig. 48A); scutellar striole absent or very short (Fig. 49A) 62. *Bradycellus nigrinus* (Dejean)

23′. Penultimate labial palpomere plurisetose anteriorly (Fig. 49B); scutellar striole present, relatively long, clearly delineated (Fig. 49B) 60. *Harpalus somnulentus* Dejean

24(18′). Terminal maxillary palpomere small, narrow and less than one-half the length of the penultimate palpomere (Fig. 50A) . . . (tribe Bembidiini) 25

←

FIGURE 30. General structure of a carabid beetle (Coleoptera: Carabidae). A, general appearance, dorsal view. B, general appearance, ventral view; C, head, dorsal view; D, left mandible, dorsal view; E, left maxilla, ventral view. F, labium, ventral view; G, pronotum, dorsal view; H, left elytron, dorsal view; I, right metathoracic (hind) leg, dorsal view. Abbreviations: an = antenna, an1 = scape (first antennomere); an2 = pedicel (second antennomere); an3–an11 = third through eleventh antennomeres; bl = body length; cl = clypeus; el = elytron; elbm = basal margin of elytron; elds = discal setae of elytron; elep = epipleuron of elytron; elhu = humerus of elytron; eli1, eli2, etc. = first and subsequent intervals of elytron; ellm = lateral margination of elytron; elmm = medial margin of elytron; elss = scutellar striole of elytron; els1, els2, etc. = first and subsequent striae of elytron; elus = umbilicate setae of elytron, ey = compound eye; fe = femur; fr = frons; frf = frontal furrows; lm = labium; lmp = labial palpus; lmp2 = penultimate palpomere of labial palpus; lr = labrum; mics = preferred area for comparisons of elytral microsculpture; mn = mandible; mns = scrobe of mandible; mnss = seta in scrobe of mandible; mscc = mesocoxal cavity (i.e., cavity into which mesocoxa is inserted); msem = mesepimeron; mses = mesepisternum; mss = mesosternum; mtc = metacoxa; mtes = metepisternum; mts = metasternum; mtsp = metasternal intercoxal process, mt1–mt5 = first through fifth metatarsomeres; mx = maxilla; mxp = maxillary palpus; mxp3 = penultimate palpomere of maxillary palpus; mxp4 = terminal palpomere of maxillary palpus; pcc = procoxal cavity (i.e., cavity into which procoxa is inserted); pp = propleuron; pr = pronotum; praa = apical angle of pronotum; prba = basal angle of pronotum; prbc = basolateral carina of pronotum; prbf = basal fovea of pronotum; prbg = basal margination of pronotum; prbl = basal sinuation of lateral margin of pronotum, prbm = basal margin of pronotum; prbs = basolateral seta of pronotum; prle = lateral explanation of pronotum; prlm = lateral margin of pronotum; prms = midlateral seta of pronotum; prpt = posterior transverse impression of pronotum; ps = prosternum, sos = supraorbital setae; S1–S6 = first through sixth visible abdominal sterna; ti = tibia; ts = tarsus.

24′. Terminal maxillary palpomere subequal in length and width to penultimate palpomere (Fig. 50B) 44

25(24). Third elytral interval unevenly microsculptured, with each dorsal setiferous puncture inserted in the anterior part of a dull, coarsely microsculptured, slightly depressed field extended fully across the interval, areas between such fields shinier, less coarsely microsculptured, and flat or slightly convex 26

25′. Third elytral interval evenly microsculptured throughout, without contrasting dull and depressed fields of coarser microsculpture associated with dorsal setiferous punctures 27

26(25). Pronotum (Fig. 51A) narrow, apical angles short, not or only slightly flattened; elytra with posterior-most outer copperish shiny spot (on sixth and seventh intervals just posterior to middle of elytron) distinctly separate from medial shiny area (fifth interval dull, coarsely microsculptured in posterior one-half of elytron)
26. *Bembidion inaequale opaciceps* Casey

26′. Pronotum (Fig. 51B) broad, apical angles long, projected anteriorly, distinctly flattened; elytra with posterior-most outer copperish shiny spot continuous with medial shiny area as an obliquely transverse shiny band (shiny area extended across fifth interval at or near middle of elytron
25. *Bembidion zephyrum* Fall

27(25′). Eyes small (Figs. 52A and 52B); terminal maxillary palpomere long and slender, length equal to or greater than one-third length of penultimate palpomere (Fig. 53A); mandible very long and slender (Figs. 52A and 52B); body piceous, brown or rufous, without metallic reflection or pattern of pale maculae on elytra; legs, antennae, and mouthparts rufous or pale brown 28

27′. Eyes large or moderate in size (Fig. 52C); terminal maxillary palpomere shorter, length less than one-third length of penultimate palpomere (Fig. 53B); mandible shorter and/or broader (Fig. 52C); color of body and appendages varied 30

28(27). Body length more than 6.0 mm; hindwing full-sized, with reflexed apex distal to stigma (Fig. 53A)
42. *Bembidion spectabile* (Mannerheim)

28′. Body length less than 6.0 mm; hindwing short, reduced to a small scale-like vestige (Fig. 54B) 29

29(28′). Pronotum (Fig. 55A) longer, with basal sinuation of lateral margin longer, less abrupt; eyes moderately reduced in diameter and convexity (Fig. 52A)
43. *Bembidion oblonguloides* Lindroth

29′. Pronotum (Fig. 55B) shorter, lateral margin more convex, rounded, basal sinuation of lateral margin shorter, more abrupt; eyes markedly reduced in diameter and convexity (Fig. 52B)
44. *Bembidion oblongulum* (Mannerheim)

30(27′). Elytron with lateral margination prolonged medial to humerus, posteriorly divergent with respect to elytral margin (Fig. 56A) 31

30′. Elytron with lateral margination terminated at humerus (Fig. 56B) or slightly prolonged medially parallel to basal elytral margin (Fig. 56C) 37

31(30). Elytron with only sutural (first) stria evident to apex (Fig. 57A); pronotum narrow, cordiform, with basolateral carina long; tibiae pale rufous throughout
27. *Bembidion dyschirinum* LeConte

31′. Elytron with two or more striae evident to apex (Figs. 57B and 57C) 32

32(31′). Legs and antennal scape pale rufous or yellow; elytra markedly iridescent
29. *Bembidion iridescens* (LeConte)

32′. Legs and antennal scape darker, piceous to black; luster of elytra varied 33

33(32′). Dorsal body surface with distinct brassy metallic reflection (few individuals with faint blue metallic reflection or rufous dorsally); elytral intervals flat 34

33′. Dorsal body surface without or with faint blue or green metallic reflection; elytral intervals slightly or moderately convex 35

34(33). Pronotum (Fig. 58A) short, very broad; meshes of elytral microsculpture isodiametric or slightly or moderately transverse (Fig. 59A), elytra shiny but not iridescent
30. *Bembidion incertum* (Motschulsky)

34′. Pronotum (Fig. 58B) slightly longer and narrower; meshes of elytral microsculpture markedly transverse (Fig. 59B), elytra faintly iridescent
33. *Bembidion viator* Casey

35(33′). Meshes of elytral microsculpture (Fig. 59C) isodiametric or only slightly transverse (average width of meshes less than 1.5 times their length); habitat above treeline in alpine zone
34. *Bembidion complanulum* (Mannerheim)

35′. Meshes of elytral microsculpture (Fig. 59D) transverse (average width of meshes equal to or greater than 1.5 times their length); habitat varied 36

36(35′). Pronotum (Fig. 58C) longer, shape moderately cordate; elytron with dorsal setiferous punctures moderately foveate, width of depressions around punctures subequal to width of second interval
32. *Bembidion farrarae* Hatch

36′. Pronotum (Fig. 58D) shorter, shape more quadrate; elytron with dorsal setiferous punctures markedly foveate, width of depressions around punctures subequal to combined width of second and third intervals 31. *Bembidion quadrifoveolatum* Mannerheim

37(30′). Elytron with reduced number of striae (Fig. 57B), only medial three striae or fewer distinctly impressed (outer striae indistinct, represented only by rows of minute, faintly impressed punctures); meshes of elytral microsculpture distinctly transverse in both sexes 28. *Bembidion castum* Casey

37′. Elytron with five or more distinctly impressed striae (Fig. 57C), at least in basal one-half; meshes of elytral microsculpture varied in shape 38

38(37′). Metasternal intercoxal process (between mesocoxae) without margination (Fig. 60A) or with margination laterally only (Fig. 60B) 39

38′. Metasternal intercoxal process with margination anteriorly and laterally (Fig. 60C) 41

39(38). Head with frontal furrows convergent anteriorly and

extended anteriorly onto clypeus (Fig. 61A); body color shiny black, with a single rufous spot subapically on each elytron
41. *Bembidion fortestriatum* (Motschulsky)

39′. Head with frontal furrows parallel, or nearly so, not distinctly extended onto clypeus (Fig. 61B); body color not as above 40

40(39′). Elytron uniformly dark, piceous, black, or brown, without pale maculae; elytral striae smooth or with very faintly impressed punctulae; head and pronotum with faint blue metallic reflection; meshes of elytral microsculpture (Fig. 61E) moderately transverse and distinctly impressed
35. *Bembidion planiusculum* Mannerheim

40′. Elytron with extensive pale maculae, including an irregular transverse pale band subapically and more or less expanded humeral maculae; elytral striae with large, deeply impressed punctures; head and pronotum with marked brassy or copperish metallic reflection (very few individuals with blue metallic reflection on pronotum only); meshes of elytral microsculpture (Fig. 59F) markedly transverse, narrow, indistinctly impressed
38. *Bembidion incrematum* LeConte

41(38′). Body length less than 4.0 mm; head with frontal furrows slightly convergent and extended anteriorly onto clypeus (Fig. 61C) in most individuals
40. *Bembidion versicolor* (LeConte)

41′. Body length greater than 4.0 mm; head with frontal furrows parallel or nearly so, not extended onto clypeus (Fig. 61B) 42

42(41′). Body length less than 5.2 mm; elytral color pattern as in Fig. 62A 39. *Bembidion indistinctum* Dejean

42′. Body length greater than 5.5 mm; elytral color pattern as in Figures 62B or 62C 43

43(42′). Antennal scape pale rufous, antennomeres 2–11 markedly contrasting in color, piceous or black; elytral color pattern as in Figure 62C
37. *Bembidion transversale* Dejean

43′. Antennae with all antennomeres uniformly pale rufous or antennomeres 2–11 only slightly contrasting in color, rufopiceous; elytral color pattern as in Figure 62B 36. *Bembidion sejunctum semiaureum* Fall

44(24′). Mandible with a setiferous puncture in scrobe (Fig. 63A) 45

44′. Mandible without a setiferous puncture in scrobe (Fig. 63B) 49

45(44). Body length greater than 6.0 mm; head with a transverse sulcus posterior to eyes, frontal furrows extended posteriorly only to level of anterior supraorbital setiferous puncture (Fig. 64A) 46

45′. Body length less than 5.0 mm; head without a transverse sulcus posterior to eyes, frontal furrows extended in an arc posteriorly beyond level of posterior margin of eye (Fig. 64B) . . . (tribe Trechini) 47

46(45). Antennae short, antennomeres 4–11 each only slightly longer than wide; pronotum (Fig. 65A) with one or more setiferous punctures on lateral margin near apical angle, posterior transverse impression narrow and very deep . . . (tribe Psydrini)
45. *Nomius pygmaeus* (Dejean)

46′. Antennae long, antennomeres 4–11 each more than twice as long as wide; pronotum (Fig. 65B) without setiferous punctures on lateral margin near apical angle, posterior transverse impression broad, shallow . . . (tribe Patrobini)
21. *Diplous aterrimus* (Dejean)

47(45′). Elytron with anterior preapical setiferous puncture inserted closer to recurrent sulcus than to medial margin (Fig. 66A); pronotum (Fig. 67A) distinctly narrowed basally, basal sinuation of lateral margin deep 23. *Trechus ovipennis* Motschulsky

47′. Elytron with anterior preapical setiferous puncture inserted at least as close to medial margin as to recurrent sulcus (Fig. 66B); pronotum (Figs. 67B and 67C) broader basally, basal sinuation of lateral margin shallow or absent 48

48(47′). Pronotum (Fig. 67B) with basal angles distinctly obtuse, basal margin oblique medial to basal angles, basal margination complete, even in midline
22. *Trechus obtusus* Erichson

48′. Pronotum (Fig. 67C) with basal angles rectangular or slightly obtuse, basal margin straighter, basal margination interrupted broadly in midline
24. *Trechus chalybeus* Dejean

49(44′). Elytron with epipleuron not interrupted by an internal plica (Fig. 68A) . . . (tribe Platynini) 50

49′. Elytron with epipleuron crossed by an internal plica near apical portion of lateral margin (Fig. 68B) 53

50(49). Antenna (Fig. 69A) with distal one-half of third antennomere covered with short, dense setae; elytron with numerous coarse, setiferous punctures on first, third, fifth, and seventh intervals
54. *Agonum belleri* (Hatch)

50′. Antenna (Fig. 69B) with third antennomere glabrous except for ring of long setae at distal apex; elytron with first, fifth, and seventh intervals without setiferous punctures, only the usual setiferous punctures on third interval 51

51(50′). Pronotum (Fig. 70A) long and narrow, distinctly narrowed basally, widest well anterior to middle
53. *Agonum ferruginosum* (Dejean)

51′. Pronotum (Figs. 70B and 70C) broader, at least as broad basally as apically, widest at or near middle 52

52(51′). Elytron with second setiferous puncture (counted from base) of third interval (Fig. 71A) inserted in second stria or at least closer to second stria than to third; pronotum (Fig. 70B) with basal foveae broad and flat, without or with only a trace of convexity at middle; elytron without or with only faint brassy metallic reflection 56. *Agonum brevicolle* Dejean

52′. Elytron with second setiferous puncture of third interval (Fig. 71B) inserted in third stria, closer to third stria than to second, or midway between third and second striae; pronotum (Fig. 70C) with a distinct convexity in middle of basal foveae; elytron with distinct brassy metallic reflection
55. *Agonum metallescens* (LeConte)

53(49′). Penultimate labial palpomere with two setae anteriorly (Fig. 72A) . . . (tribe Pterostichini) 54
53′. Penultimate labial palpomere with three or more setae anteriorly (Fig. 72B) . . . (tribe Zabrini) 60
54(53). Elytron without discal setiferous punctures on third interval 55
54′. Elytron with two or more discal setiferous punctures on third interval 59
55(54). Body length greater than or equal to 20.0 mm; basal tarsomere of metatarsus without (or with only a faintly suggested) longitudinal ridge laterally (Fig. 73A) 46. *Pterostichus lama* (Ménétriés)
55′. Body length less than or equal to 19.5 mm; basal tarsomere of metatarsus with a distinct longitudinal ridge laterally (Fig. 73B) 56
56(55′). Distal (fifth) tarsomere of metatarsus with two or more pairs of stout setae on ventral surface (Fig. 74A) 48. *Pterostichus algidus* LeConte
56′. Distal (fifth) tarsomere of metatarsus glabrous ventrally (Fig. 74B) 57
57(56′). Pronotum (Fig. 75A) with lateral margin crenulate throughout 47. *Pterostichus crenicollis* LeConte
57′. Pronotum (Fig. 75B) with lateral margin smooth or nearly so throughout 58
58(57′). Elytra with distinct violet metallic reflection, distinctly flattened in cross-section, elytral silhouette (Fig. 76A) elongate, with lateral margins subparallel, elytral intervals flat or only slightly convex; male with last visible abdominal sternum flat medially 49. *Pterostichus amethystinus* Mannerheim
58′. Elytra without metallic reflection, distinctly convex in cross-section, elytral silhouette (Fig. 76B) shorter, subovoid, with lateral margins evenly arcuate, elytral intervals moderately convex; male with a bluntly pointed tubercle medially on last visible sternum 50. *Pterostichus castaneus* (Dejean)
59(54′). Body length less than 8.7 mm; setiferous punctures of third elytral interval not or only slightly foveate, foveal depressions not extended onto adjacent intervals; hindwings short, reduced to a small, scale-like lobe; pronotum (Fig. 77A) relatively long and slender, basal sinuation of lateral margin long, distinct 52. *Pterostichus riparius* (Dejean)
59′. Body length 8.9 mm or more; setiferous punctures of third elytral interval distinctly foveate, foveal depressions extended onto adjacent (second or fourth) intervals; hindwings full-sized, with reflexed apex distal to stigma; pronotum (Fig. 77B) shorter, broader, basal sinuation of lateral margin absent or short and very shallow 51. *Pterostichus adstrictus* Eschscholtz
60(53′). Antennae and legs entirely pale rufous; pronotum (Fig. 78A) relatively narrow 57. *Amara sinuosa* (Casey)
60′. Antennomeres 5–11 piceous, legs with at least femora piceous; pronotum (Figs. 78B and 78C) broader 61
61(60′). Antennae with only antennomeres 1 and 2 pale rufous, tibiae piceous; pronotum (Fig. 78B) with basal angles slightly rounded 58. *Amara ellipsis* (Casey)
61′. Antennae with antennomeres 1–3 and basal one-half of 4 pale rufous, tibiae rufous; pronotum (Fig. 78C) with basal angles rectangular, not or only slightly rounded 59. *Amara littoralis* Mannerheim

Systematic Accounts for Tribes, Genera, and Species

Arrangement of Taxa

Except for placement of the Psydrini and recognition of the Platynini as a tribe distinct from Pterostichini, the sequence used here to present tribes, genera, and accounts for species and subspecies represented in the fauna of the archipelago follows Lindroth's (1961–69) arrangement. This has been done both for ease of reference to information provided in that work and because this arrangement adequately reflects present classification of and knowledge of phylogenetic relationships among included taxa.

TRIBE CICINDELINI

Diagnostic Combination.—Antennae inserted on frons between eyes, dorsal to and closer together than bases of mandibles (Fig. 31A).

This tribe is worldwide in distribution, with four genera and more than 125 species represented in North America. Almost all North American species are ground-dwelling predators whose larvae live in and ambush prey from burrows that they construct in the soil. Several genera in tropical regions include adults that are arboreal predators.

Genus *Cicindela* Linnaeus

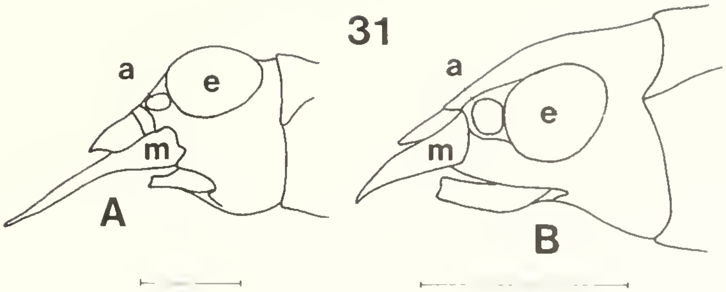
Diagnostic Combination.—Eyes very large; elytra flat, with a distinct pattern of pale spots. This is the only cicindeline genus known to occur in the archipelago. The only other genus that may occur there is *Omus* Eschscholtz, members of which have eyes that are moderate in size and elytra that are convex and black, without a pale elytral pattern.

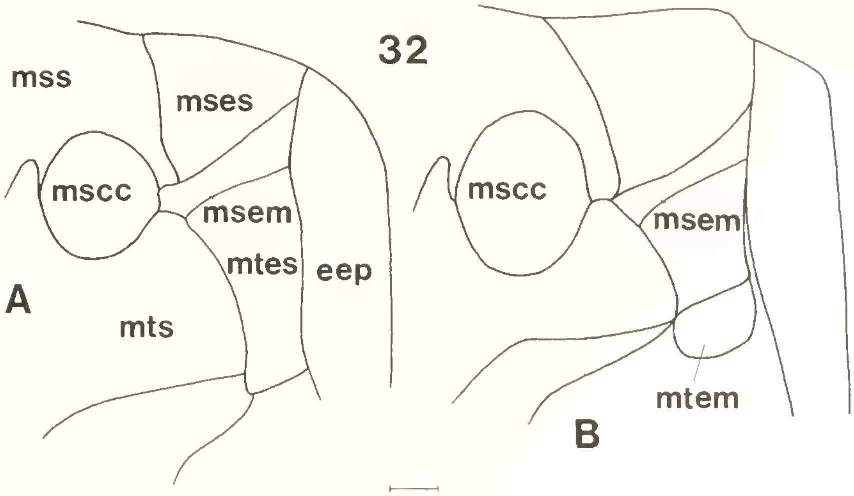
This genus is worldwide in distribution, but some of the numerous subgenera recognized are considered distinct genera by some authors. About 100 species occur in North America. Adults of most species are aggressive, diurnal predators in open, sparsely vegetated habitats, although a few species occur in forests. These beetles are difficult to observe or catch because they run and take flight rapidly when approached.

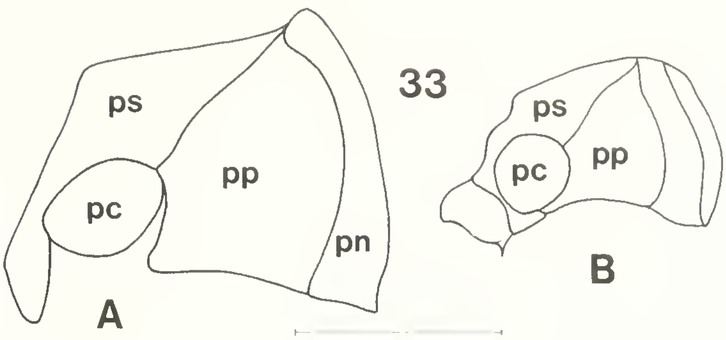
1. **Cicindela oregona** LeConte
(Figure 31A)

Cicindela oregona LeConte, 1857:41 (type area: "Oregon Territory and northern California as far as San Francisco").
Cicindela oregona guttifera LeConte—Freitag 1965:137.

Taxonomic Notes.—Freitag (1965) considered populations of *C. oregona* in the Queen Charlotte Islands as representative of the subspecies *Cicindela oregona guttifera* LeConte (1857: 42). However, when specimens collected in the course of this study were compared with specimens of both *C. o. guttifera* and *Cicindela oregona oregona* LeConte identified by Freitag, they were found to be more similar to the latter, based on characters





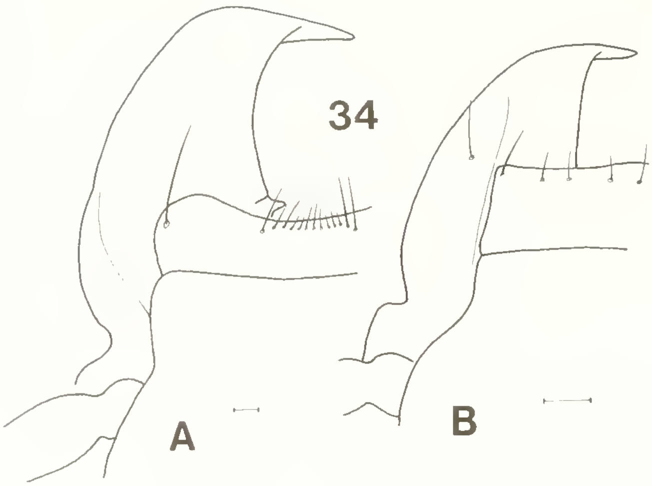


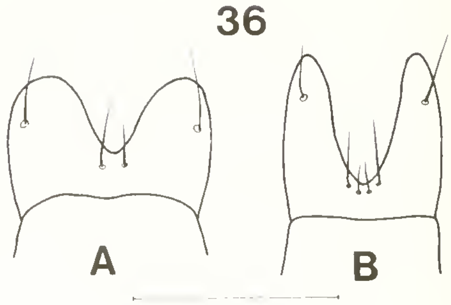
FIGURES 31–33. FIGURE 31. Head, left lateral view. A, *Cicindela oregona*; B, *Nebria mannerheimii*. a = insertion point for antenna, e = compound eye; m = mandible. Scale = 1.0 mm FIGURE 32. Pterothorax, left oblique lateroventral view. A, *Nebria mannerheimii*; B, *Pterostichus algidus*. eep = elytral epipleuron; mscc = mesocoxal cavity; msem = mesepimeron; mses = mesepisternum; mss = mesosternum; mtem = metepimeron; mtes = metepisternum. Scale = 0.1 mm. FIGURE 33. Prothoracic venter, left oblique lateroventral view. A, *Nebria mannerheimii*; B, *Elaphrus americanus sylvanus* pc = procoxal cavity; pn = proepipleuron of pronotum; pp = propleuron; ps = prosternum. Scale = 1.0 mm.

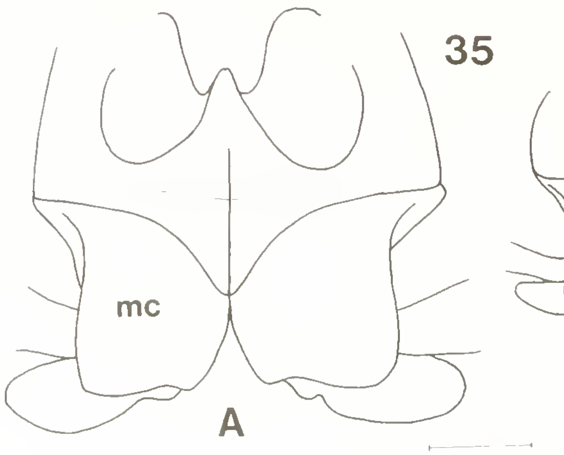
cited by Freitag (1965:125). Because of this discrepancy, I have included no subspecific designation here, but, instead, recommend further study of these problematic populations.

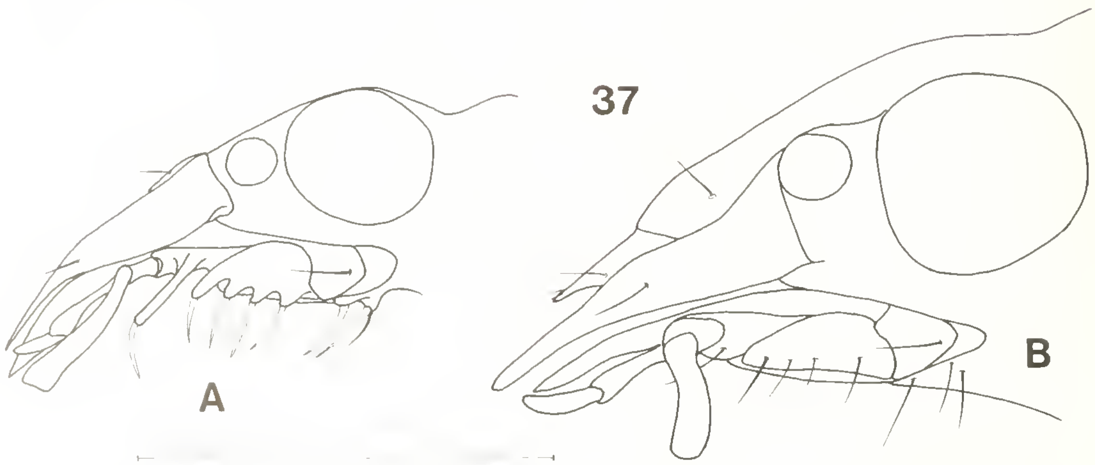
DIAGNOSTIC COMBINATION.—The only species of *Cicindela* known or likely to occur in the Archipelago.

GENERAL DESCRIPTION.—Size medium, body length 12.4–13.7 mm; head, pronotum, and elytra piceous or black, most individuals with very distinct brassy green metallic reflection and bright metallic blue, green, and copperish highlights in surface depressions, labrum and bases of mandibles pale yellow, first through fourth antennomeres and dorsal surfaces of all tibiae with vivid copperish reflection, elytra with humeral lunules (pale yellow maculations) represented by separate humeral and subhumeral spots, middle lunules markedly constricted or slightly interrupted anterior to expanded posteromedial spot, apical lunules represented by separate apical and subapical spots, venter









FIGURES 34–37. FIGURE 34. Left mandible, dorsal view. A, *Carabus nemoralis*; B, *Nebria mannerheimii*. Scale = 0.1 mm. FIGURE 35. Pterothoracic venter, ventral view. A, *Carabus nemoralis*; B, *Scaphinotus marginatus*. mc = metacoxa. Scale = 1.0 mm. FIGURE 36. Labrum, dorsal view. A, *Cychrus tuberculatus*; B, *Scaphinotus marginatus*. Scale = 1.0 mm. FIGURE 37. Head, left lateral view. A, *Leistus ferrugineosus*; B, *Nebria mannerheimii*. Scale = 1.0 mm.

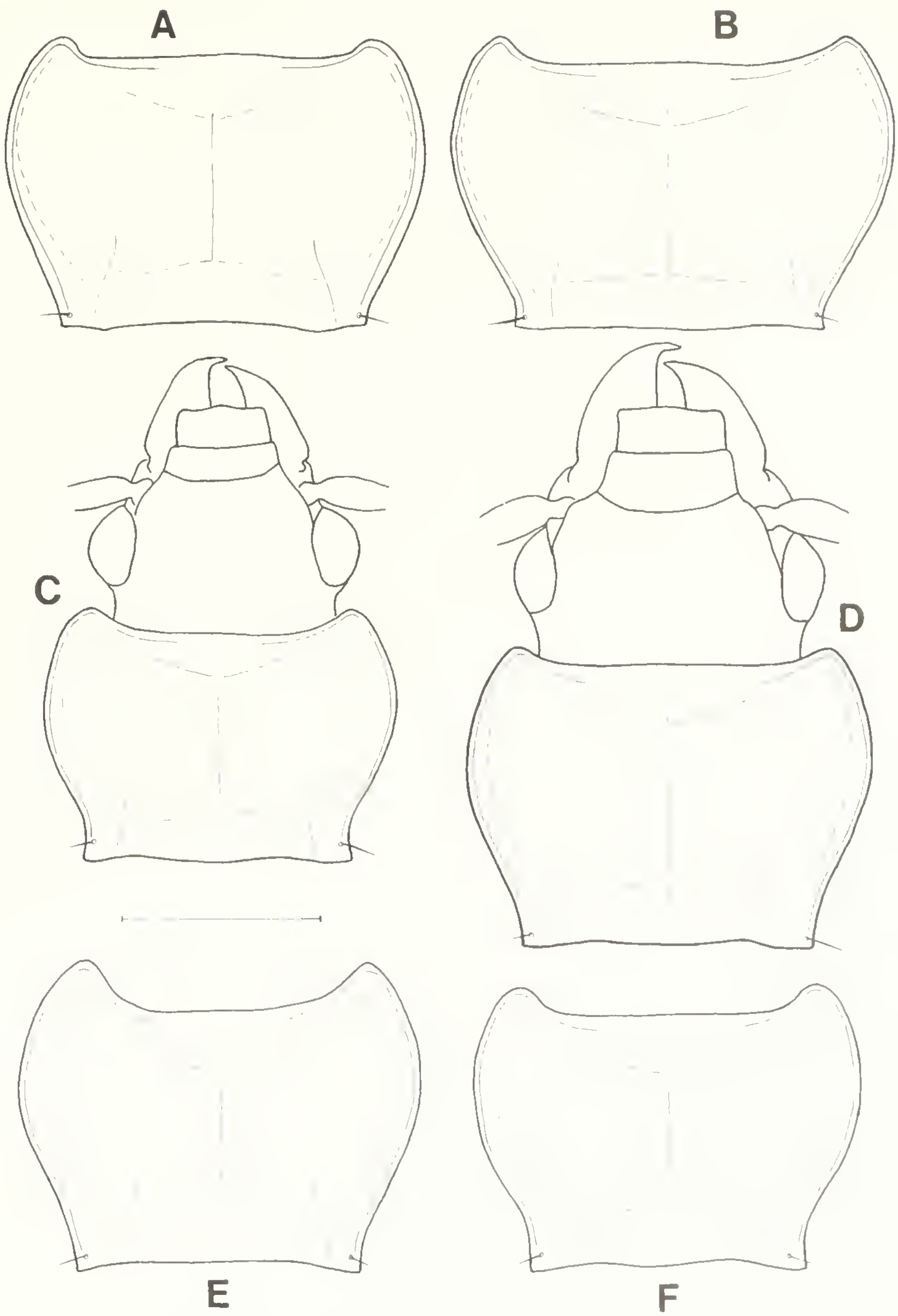


FIGURE 38. Pronotum, dorsal view. A, *Nebria mannerheimii*; B, *Nebria diversa*; C, with head, *Nebria sahlbergii sahlbergii*; D, with head, *Nebria haida*; E, *Nebria louiseae*; F, *Nebria charlottae*. Scale = 1.0 mm.

with vivid metallic green reflection, thoracic venter with brilliant copperish highlights laterally.

DISPERSAL POTENTIAL.—Adults are active fliers by day, capable of at least short-range aerial as well as ambulatory dispersal.

HABITAT DISTRIBUTION.—This species is restricted to open, gently sloping banks of large lowland rivers and lagoons, in areas of brackish water subject to tidal fluctuations. Adults are active by day on inorganic substrate of sand or coarse sand mixed with small cobble gravel in areas with very sparse vegetation.

GEOGRAPHICAL DISTRIBUTION.—Western North American, north to Valdez and Fort Yukon, Alaska, south to southern California and extreme northwestern Baja California along the coast, northeast to western Northwest Territories, western Alberta, Wyoming, and Colorado, and southeast to southern New Mexico.

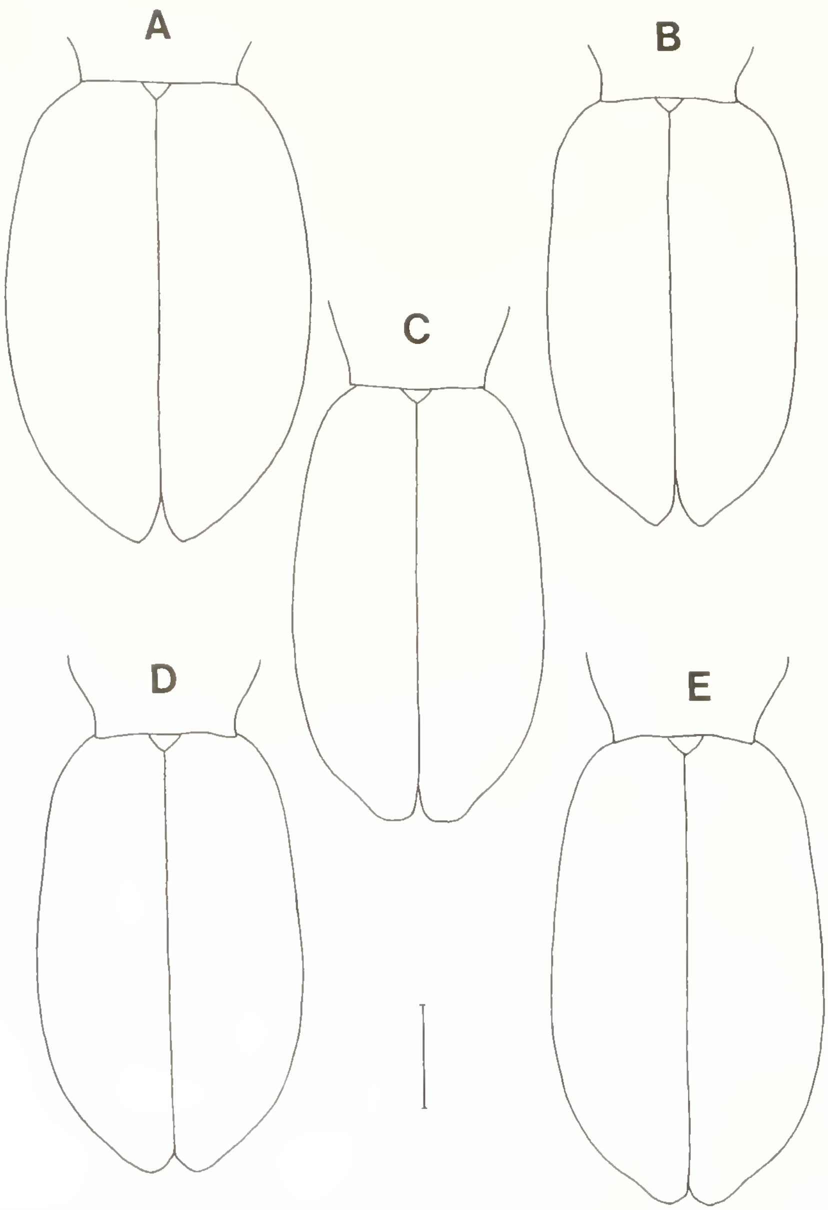


FIGURE 39. Elytral silhouette. A, *Nebria diversa*, B, *Nebria sahlbergii sahlbergii*; C, *Nebria haida*, D, *Nebria charlottae*; E, *Nebria louiseae*. Scale = 1.0 mm.

DISTRIBUTION IN THE ARCHIPELAGO.—At present, known only from northern Graham Island (see Appendix A for localities).

MATERIAL EXAMINED.—14 males, 8 females.

TRIBE CYCHRINI

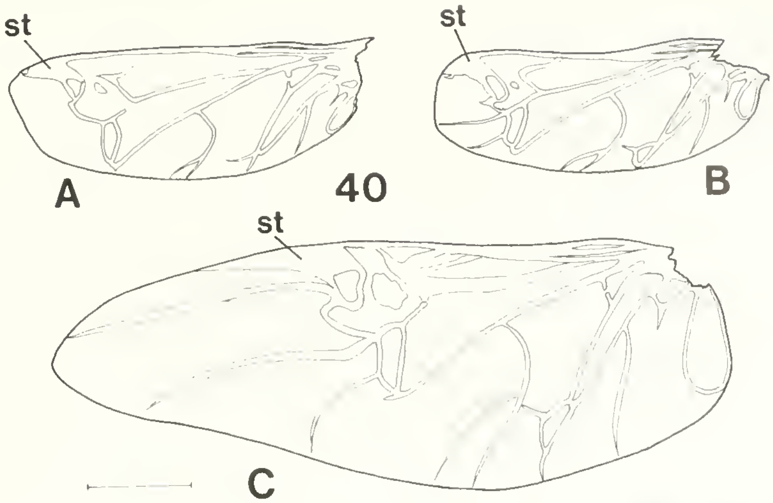
DIAGNOSTIC COMBINATION.—Antennae inserted at sides of head, between eyes and bases of mandibles (Fig. 31B); mandible without a setiferous puncture in scrobe (Fig. 34A); procoxal cavity open behind, not enclosed by propleuron posteriorly (Fig. 33A); lateral wall of mesocoxal cavity formed by mesosternum, mesepimeron, and metasternum (Fig. 32A); metacoxae separated in ventral middle of body (Fig. 35B). The cychrine body form is distinctive, with the head and mouthparts long and slender, elytra very broad, and the terminary palpomeres of both maxillae and labium expanded, spoon-like.

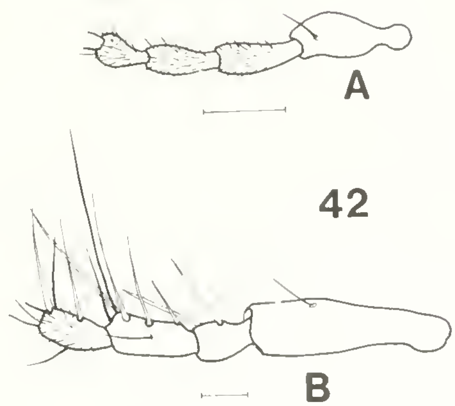
This tribe is Holarctic in distribution, with three genera and about 70 species represented in North America. Members of all species are structurally specialized predators on snails and slugs, although both adults and larvae also use a variety of other available food sources.

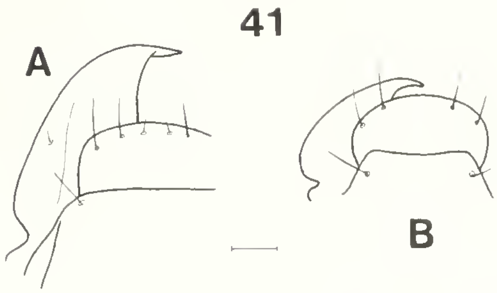
GENUS *SCAPHINOTUS* LATREILLE

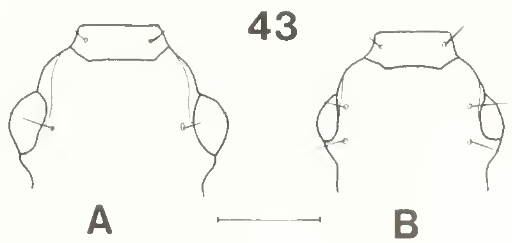
DIAGNOSTIC COMBINATION.—A cychrine with six setae on anterior margin of labrum (Fig. 36B).

This genus is restricted to the Nearctic Region, from Alaska to northern Mexico. About 60 species have been described, two of which have been recorded from the archipelago.









FIGURES 40–43. FIGURE 40. Left hindwing, dorsal view, extended. A, *Nebria diversa*; B, *Nebria louiseae*; C, *Nebria sahlbergii sahlbergii*. st = stigma. Scale = 1.0 mm. FIGURE 41. Left mandible, dorsal view. A, *Elaphrus americanus sylvanus*; B, *Loricera decimpunctata*. Scale = 0.1 mm. FIGURE 42. Left antenna, basal four antennomeres, dorsal view. A, *Dyschirius pacificus*; B, *Loricera decimpunctata*. Scale = 0.1 mm. FIGURE 43. Head, dorsal view. A, *Zacotus matthewsi*; B, *Pterostichus algidus*. Scale = 1.0 mm.

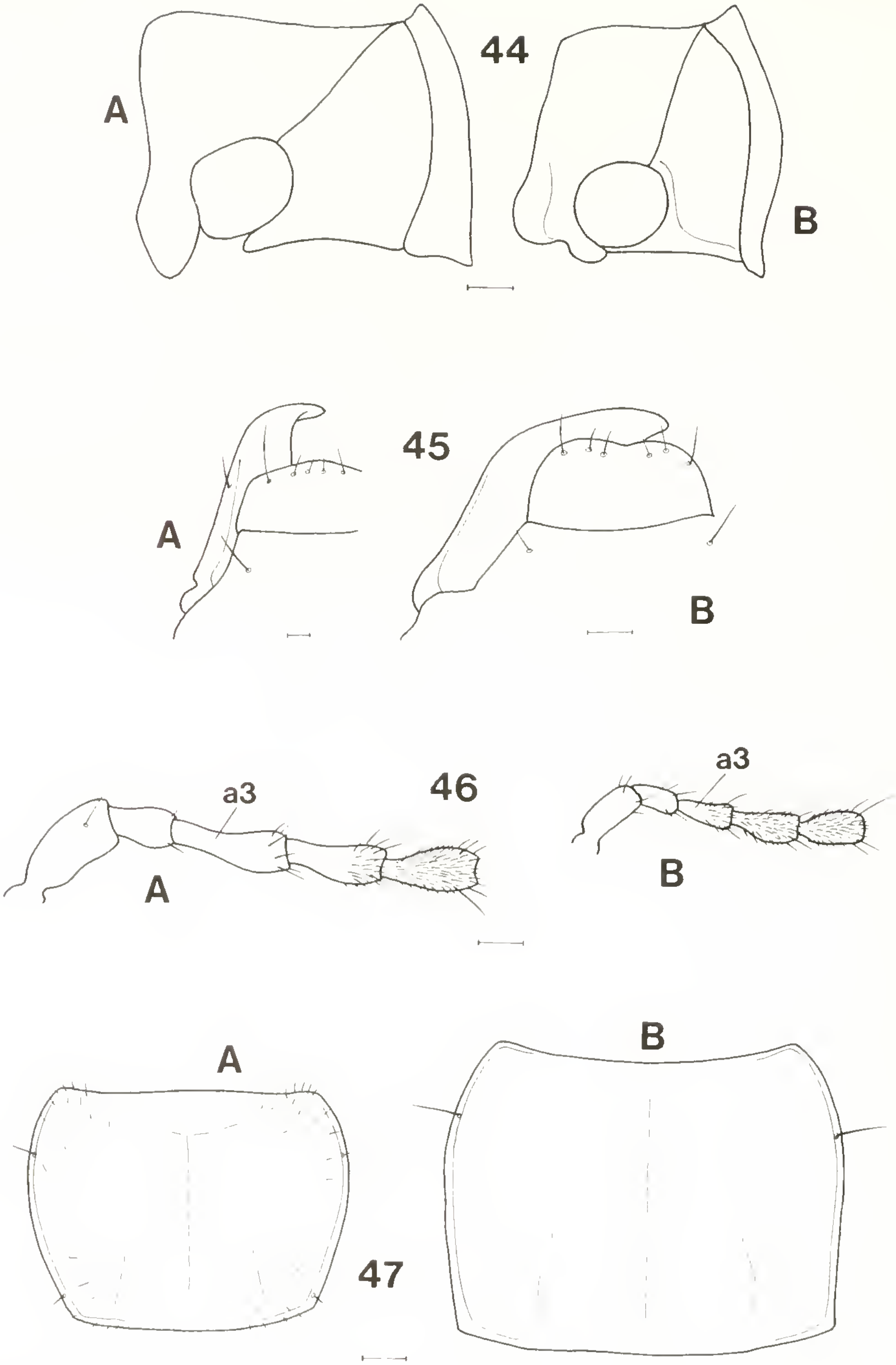
2. **Scaphinotus angusticollis** (Mannerheim)

Cychrus angusticollis Mannerheim, 1824:46 (type loc.: Sitka, Baranof Island, Alaska, as emended by Lindroth 1961:21).
Scaphinotus angusticollis (Mannerheim).—Gidaspow 1973:68.—Lindroth 1961: 21.

DIAGNOSTIC COMBINATION.—A *Scaphinotus* with rufous-brown elytron with 18 regular, punctate striae.

GENERAL DESCRIPTION.—Size large, body length 18.4–21.3 mm; head and pronotum piceous or black, with faint metallic brassy green reflection, especially near lateral margins of pronotum, elytra rufous brown, with faint metallic brassy green reflection laterally only, appendages black, venter rufopiceous.

DISPERSAL POTENTIAL.—Adults are markedly brachypterous, incapable of flight; association with logs on the forest floor along streams or just above sea beaches may provide a mechanism

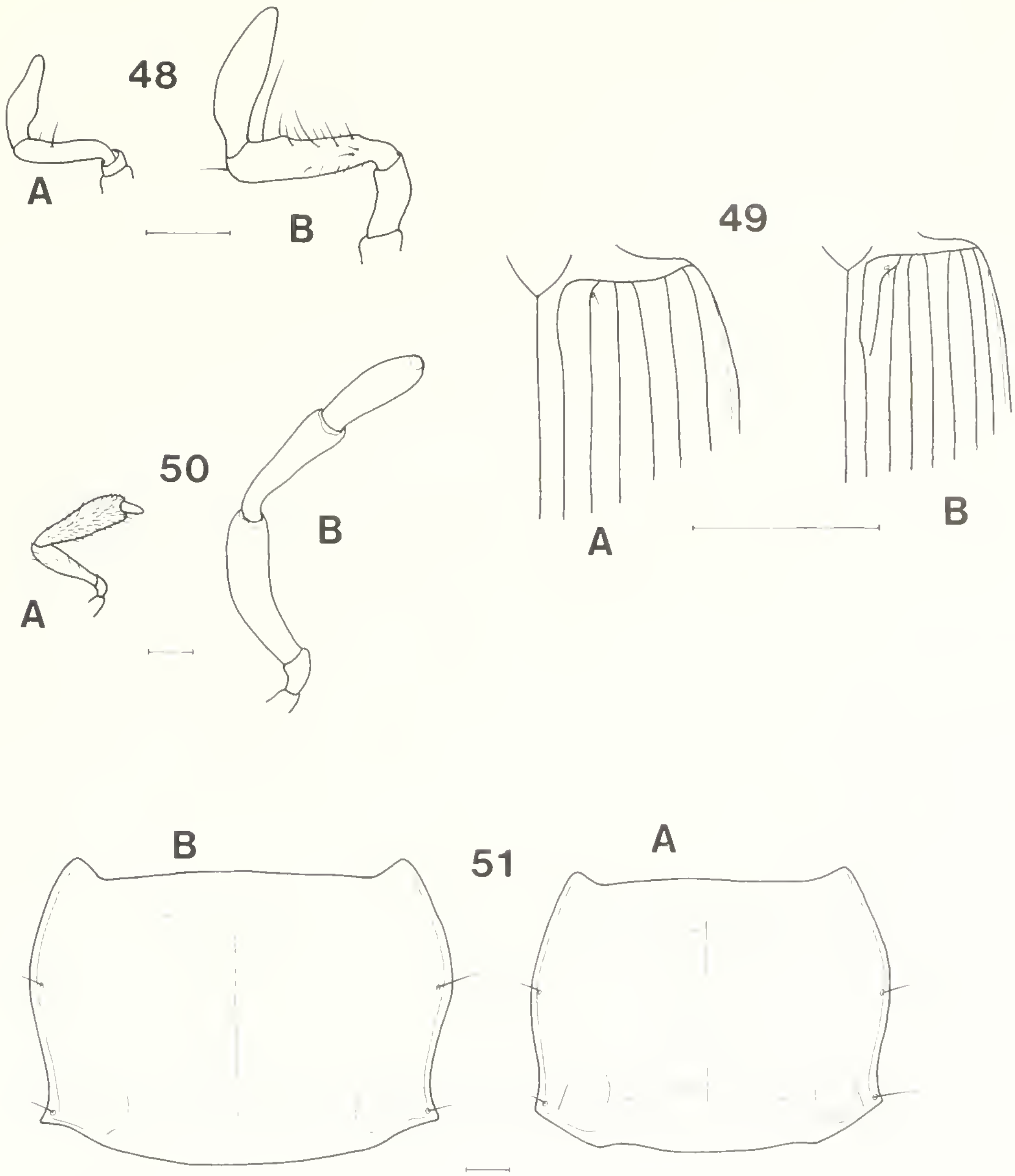


FIGURES 44–47. FIGURE 44. Prothorax, left oblique lateroventral view. A, *Notiophilus sylvaticus*; B, *Zacotus matthewsi*. FIGURE 45. Left mandible, dorsal view. A, *Zacotus matthewsi*; B, *Harpalus somnulentus*. FIGURE 46. Right antenna, basal five antennomeres, dorsal view. A, *Broscodera insignis*; B, *Bradycellus nigrinus*. a3 = third antennomere. FIGURE 47. Pronotum, dorsal view. A, *Trichocellus cognatus*; B, *Bradycellus nigrinus*. All scales = 0.1 mm.

for oversea dispersal in log rafts, otherwise limited to ambulatory dispersal.

HABITAT DISTRIBUTION.—Habitat preference in the archipelago is unknown; but on the mainland, the species is restricted generally to forested areas, from sea level to treeline, with dispersing adults found also on sea beaches and slightly above treeline.

GEOGRAPHICAL DISTRIBUTION.—Mainly West Coastal, northwest to Kodiak Island and the Kenai Peninsula, Alaska, south to northwestern California (Gidaspow 1973:68), east of the Coast



FIGURES 48–51. FIGURE 48. Right labial palpus, ventral view. A, *Bradycellus nigrinus*; B, *Harpalus somnulentus*. Scale = 0.1 mm. FIGURE 49. Base of right elytron, dorsal view. A, *Bradycellus nigrinus*; B, *Harpalus somnulentus*. Scale = 1.0 mm. FIGURE 50. Right maxillary palpus, ventral view. A, *Bembidion zephyrum*; B, *Pterostichus algidus*. Scale = 0.1 mm. FIGURE 51. Pronotum, dorsal view. A, *Bembidion inaequale opaciceps*; B, *Bembidion zephyrum*. Scale = 0.1 mm.

Ranges only in southern British Columbia (east to Revelstoke area) and to the eastern slope of the Cascade Range of Washington and Oregon.

DISTRIBUTION IN THE ARCHIPELAGO.—At present, known only from northern Graham Island (see Appendix A for locality data).

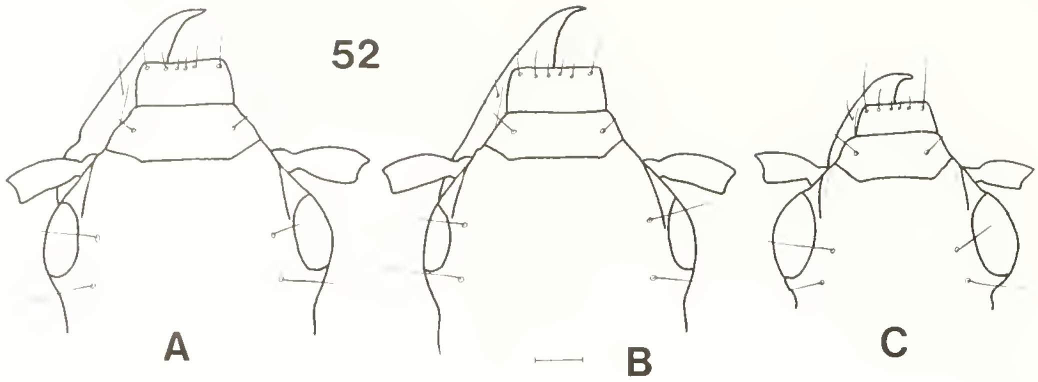
ADDITIONAL COMMENTS.—The two specimens on which the record for the Queen Charlotte Islands is based were collected by Rev. Keen in the 1890s and no other specimens have been collected since then. Extensive collecting efforts during the past five years, using hand-collecting and pitfall- and barrier-trapping techniques in suitable areas, have failed to produce a single individual of this species from the archipelago. However, wherever this species occurs on the mainland or on Vancouver Island, adults are easily found and collected, often in great numbers, using both hand-collecting and pitfall-trapping techniques. Therefore I suggest that this species is no longer extant in the archipelago, although it appears to have occurred there as recently as 90 years ago.

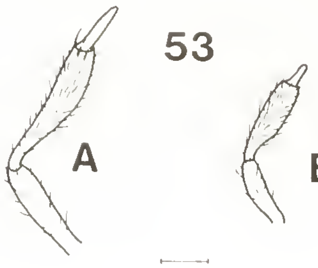
MATERIAL EXAMINED.—1 male, 1 female.

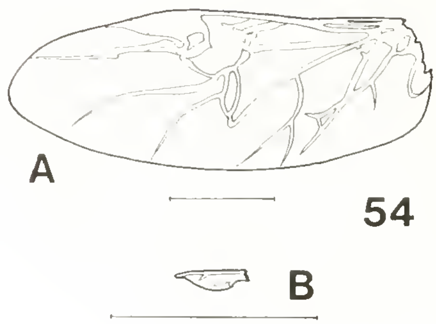
3. **Scaphinotus marginatus** (Fischer)

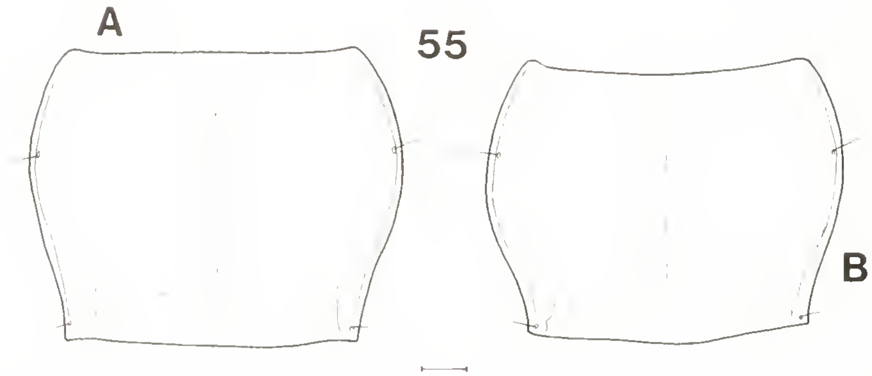
(Figures 35B, 36B)

Cychrus marginatus Fischer, 1822:79 (type loc.: Unalaska, Alaska).—Keen 1895: 166.









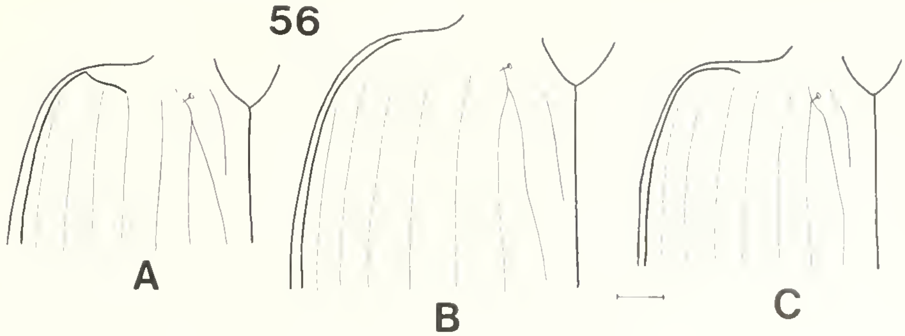
FIGURES 52–55. FIGURE 52. Head, dorsal view. A, *Bembidion oblonguloides*; B, *Bembidion oblongulum*; C, *Bembidion iridescens*. Scale = 0.1 mm. FIGURE 53. Right maxillary palpus, ventral view. A, *Bembidion spectabile*; B, *Bembidion iridescens*. Scale = 0.1 mm. FIGURE 54. Left hindwing, dorsal view, extended. A, *Bembidion spectabile*; B, *Bembidion oblongulum*. Scale = 1.0 mm. FIGURE 55. Pronotum, dorsal view. A, *Bembidion oblonguloides*; B, *Bembidion oblongulum*. Scale = 0.1 mm.

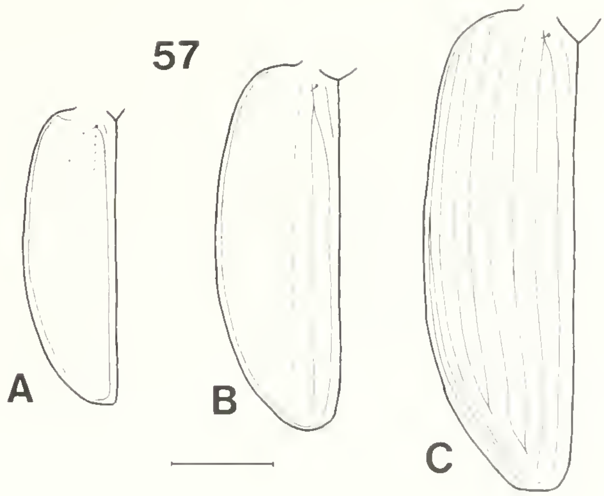
Cychrus marginatus var. *fulleri* Horn.—Keen 1895:166.
Scaphinotus insularis Casey, 1897:334 (type area: Queen Charlotte Islands).—Lindroth 1961:21.
Scaphinotus marginatus (Fischer).—Gidaspow 1968:151.—Lindroth 1961:21.

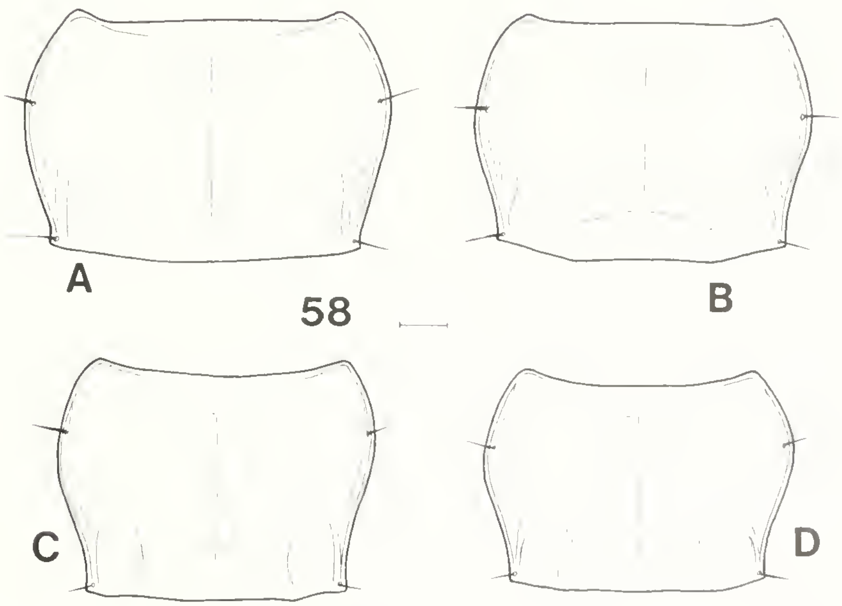
DIAGNOSTIC COMBINATION.—A *Scaphinotus* with black elytron with faint or marked metallic violet or green reflection and with 16 or fewer striae (irregular and difficult to count, especially laterally, in some specimens).

GENERAL DESCRIPTION.—Size medium, body length 11.6–19.9 mm; body and appendages black, head and pronotum with or without faint metallic green or violet reflection, elytra with faint or vivid metallic green or violet reflection and with brilliant green, copperish, or golden highlights in lateral grooves.

DISPERSAL POTENTIAL.—Adults are marked brachypterous, incapable of flight; association with logs on the forest floor along streams or just above sea beaches may provide a mechanism







FIGURES 56–58. FIGURE 56. Base of left elytron, dorsal view. A, *Bembidion incertum*; B, *Bembidion incrematum*; C, *Bembidion planiusculum*. Scale = 0.1 mm. FIGURE 57. Left elytron, dorsal view. A, *Bembidion dyschirinum*; B, *Bembidion castum*; C, *Bembidion incrematum*. Scale = 1.0 mm. FIGURE 58. Pronotum, dorsal view. A, *Bembidion incertum*; B, *Bembidion viator*; C, *Bembidion farrarae*; D, *Bembidion quadrifoveolatum*. Scale = 0.1 mm.

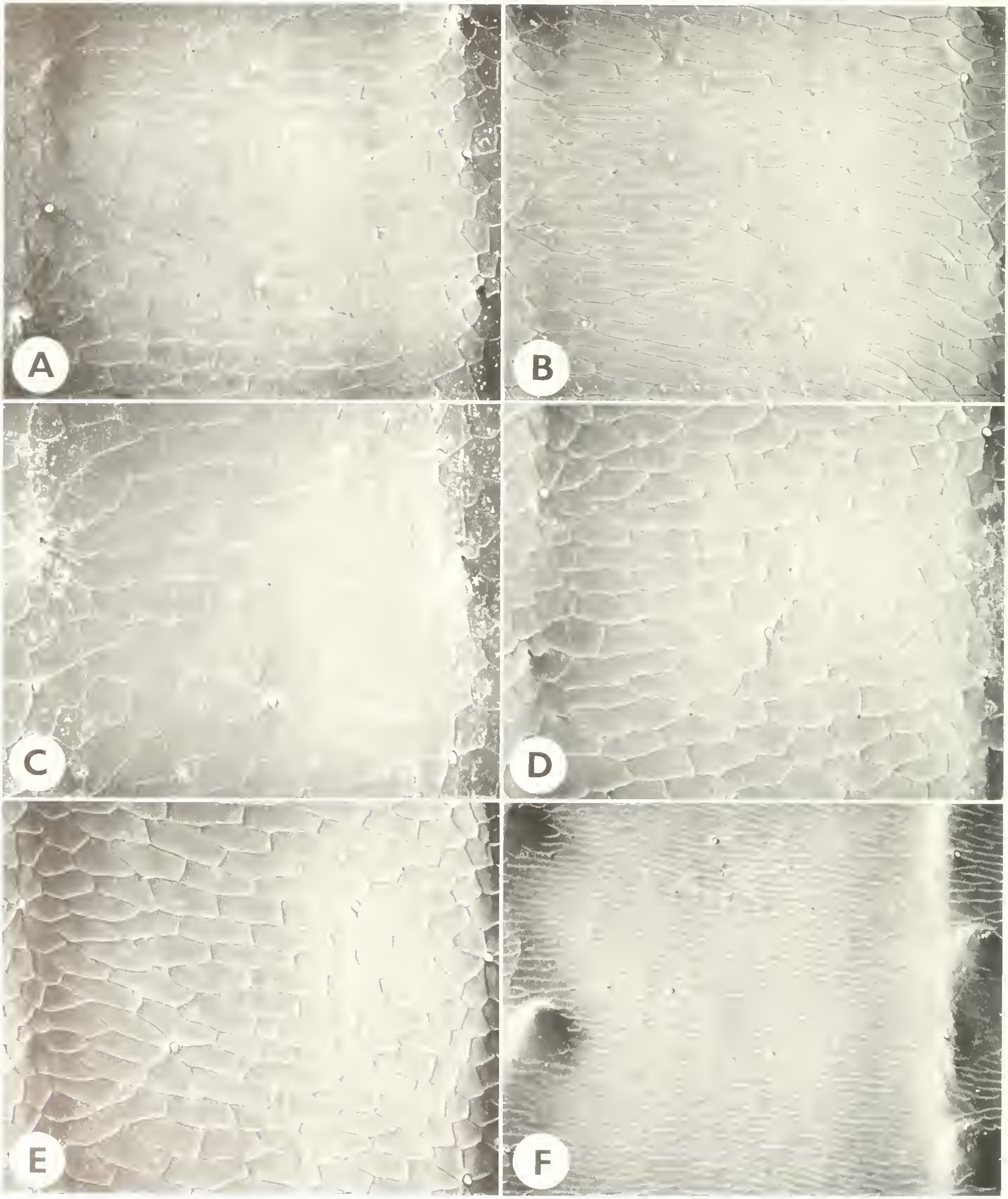
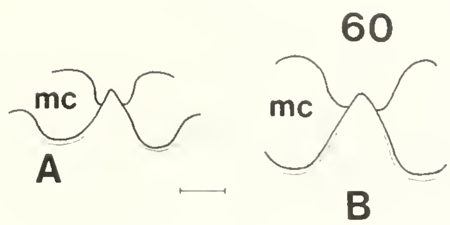
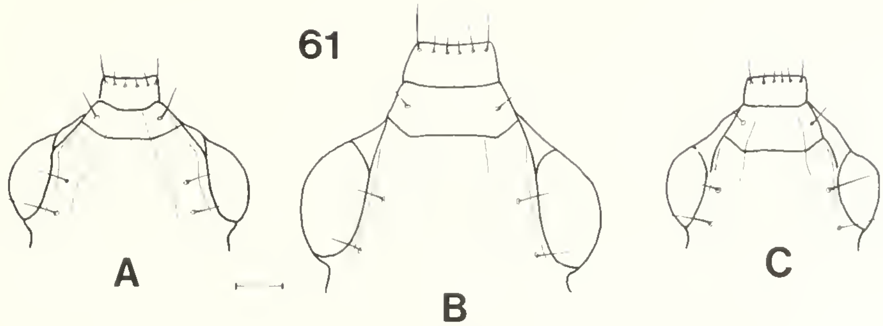
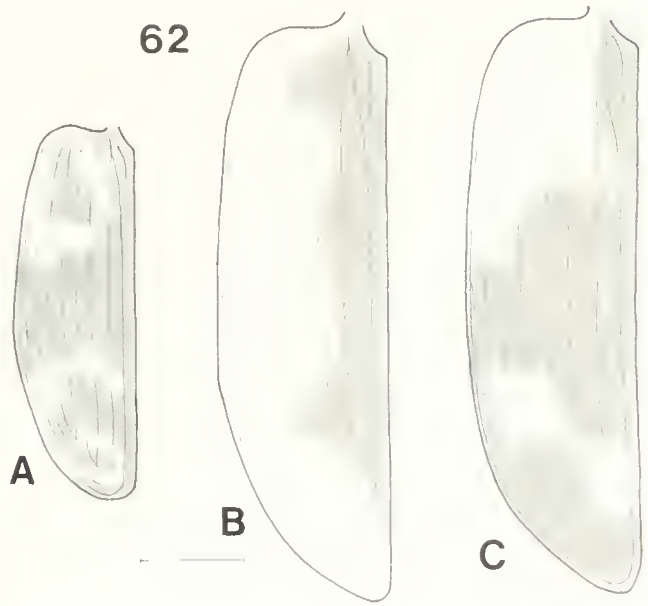


FIGURE 59. Elytral microsculpture, observed on third elytral interval, location noted in Figure 30A. A, *Bembidion incertum*, ×920; B, *Bembidion viator*, ×930; C, *Bembidion complanulum*, ×1,160; D, *Bembidion farrarae*, ×1,000; E, *Bembidion planiusculum*, ×980; F, *Bembidion incrematum*, ×700.







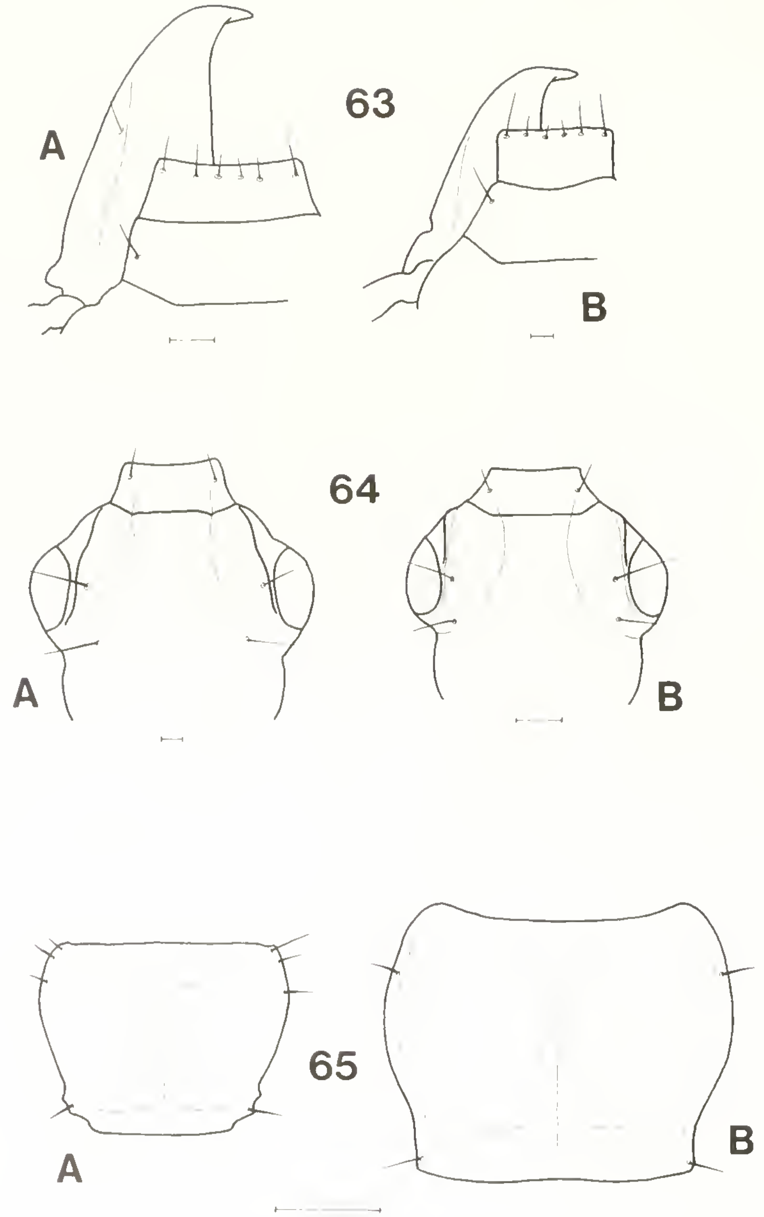
FIGURES 60–62. FIGURE 60. Metasternal intercoxal process, ventral view. A, *Bembidion fortestriatum*; B, *Bembidion incrematum*; C, *Bembidion indistinctum*. Scale = 0.1 mm. FIGURE 61. Head, dorsal view. A, *Bembidion fortestriatum*; B, *Bembidion incertum*; C, *Bembidion versicolor*. Scale = 0.1 mm. FIGURE 62. Left elytron, dorsal view. A, *Bembidion indistinctum*; B, *Bembidion sejunctum semiaureum*; C, *Bembidion transversale*. Scale = 1.0 mm.

for oversea dispersal in log rafts, otherwise limited to ambulatory dispersal.

HABITAT DISTRIBUTION.—This species is widespread, with adults found in supratidal meadows (Fig. 6), on open ground under cover, in disturbed areas (including synathropic sites), in all areas of deciduous (Fig. 12) and coniferous (Figs. 14, 15, and 21) forest from sea level to timberline; also in subalpine and alpine areas under stones; absent only from waterside areas.

GEOGRAPHICAL DISTRIBUTION.—Western North American, northwest to the outer Aleutian Islands and Alaskan Peninsula, south to northwestern California (Gidaspow 1968:152), east to Alberta, Montana, and Wyoming.

DISTRIBUTION IN THE ARCHIPELAGO.—At present, known from the following islands: Burnaby, Graham, Hibben, Huxley, Kunga, Kunghit, Louise, Lyell, Moresby, Ramsay, Reef, Talunkwan, and Tanu (see Appendix A for locality data).



FIGURES 63–65. FIGURE 63. Left mandible, dorsal view. A, *Diplous aterrimus*; B, *Pterostichus algidus*. Scale = 0.1 mm. FIGURE 64. Head, dorsal view. A, *Diplous aterrimus*; B, *Trechus chalybeus*. Scale = 0.1 mm. FIGURE 65. Pronotum, dorsal view. A, *Nomius pygmaeus*; B, *Diplous aterrimus*. Scale = 1.0 mm.

GEOGRAPHICAL VARIATION.—The population on isolated Reef Island differs from those of other islands and the mainland in the proportion of individuals with metallic green elytra and in the average size of individuals. Of the 30 specimens from Reef Island examined to date, 28 (93%) have green elytra. In contrast, less than 10% of all individuals examined from other islands have green elytra; and in all other samples, individuals with green elytra are either absent or clearly outnumbered by those with purple elytra. Beetles from Reef Island are slightly larger, on average, than those from other islands or the mainland, although large individuals are found throughout the range of the species.

MATERIAL EXAMINED.—170 males, 131 females.

GENUS *CYCHRUS* FABRICIUS

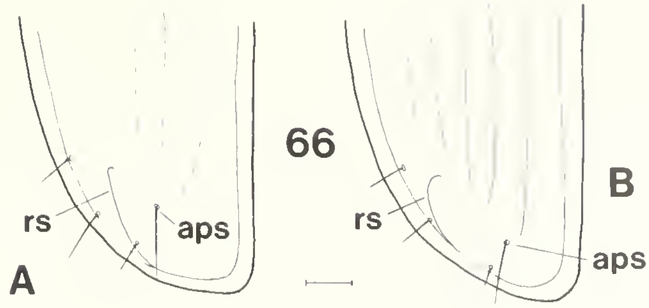
DIAGNOSTIC COMBINATION.—A cychrine with four setae on anterior margin of labrum (Fig. 36A).

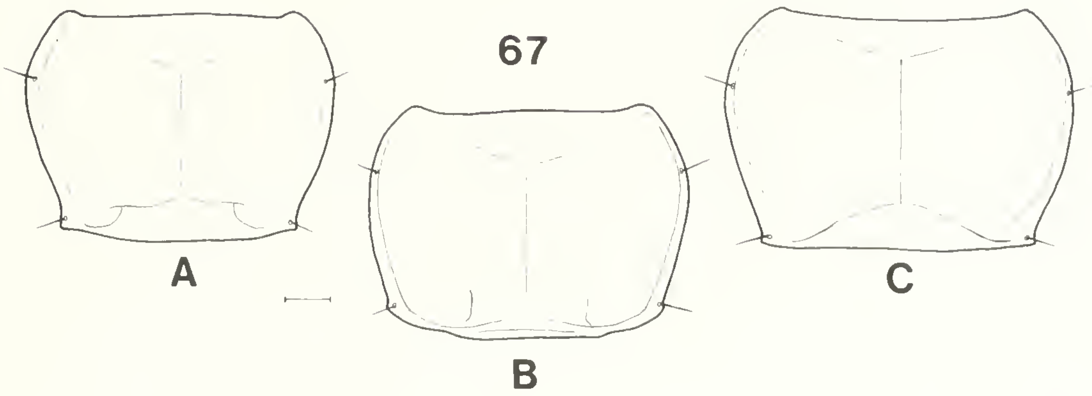
This genus is Holarctic in distribution, with only two species represented in North America, one along the Pacific coast, the other in the Central Rocky Mountains.

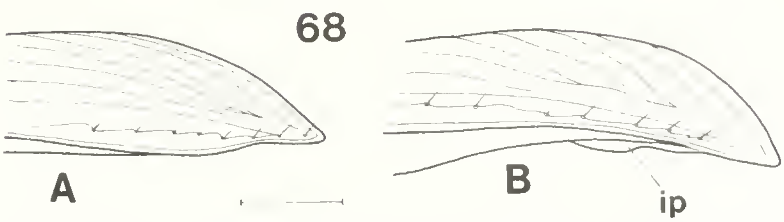
4. **Cychrus tuberculatus** Harris

(Figure 36A)

Cychrus tuberculatus Harris, 1839:200 (type loc.: Portland, Oregon, as restricted by Lindroth 1961:25).—Gidaspow 1973:94.—Keen 1895:166.—Lindroth 1961:25.







FIGURES 66–68. FIGURE 66. Apex of left elytron. A, *Trechus ovipennis*; B, *Trechus obtusus*. aps = anterior preapical setiferous puncture; rs = recurrent sulcus. Scale = 0.1 mm. FIGURE 67. Pronotum, dorsal view. A, *Trechus ovipennis*; B, *Trechus obtusus*; C, *Trechus chalybeus*. Scale = 0.1 mm. FIGURE 68. Apex of left elytron, lateral view. A, *Agonum brevicolle*; B, *Pterostichus algidus*. ip = internal plica of elytron. Scale = 1.0 mm.

DIAGNOSTIC COMBINATION.—The only species of *Cychrus* known or likely to occur in the archipelago.

GENERAL DESCRIPTION.—Size very large, body length 21.0–25.3 mm; body and appendages dull black; surface of head and pronotum with numerous shiny, raised, irregularly shaped, interconnecting ridges, elytra covered with shiny tubercles of varied size, with the largest tubercles arranged in three or four longitudinal rows.

DISPERSAL POTENTIAL.—Adults are markedly brachypterous, incapable of flight; association with logs on the forest floor along streams or just above sea beaches may provide a mechanism for oversea dispersal in log rafts, otherwise limited to ambulatory dispersal.

HABITAT DISTRIBUTION.—This species apparently is restricted to lowland areas of deciduous (Fig. 12) and coniferous (Figs. 14, 15) forest, where adults occur in leaf litter and under logs on the forest floor.

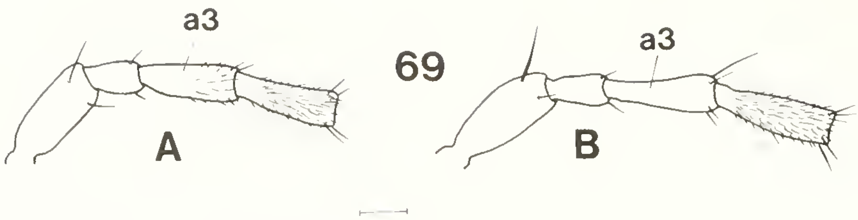
GEOGRAPHICAL DISTRIBUTION.—West Coastal, north to the Queen Charlotte Islands, south to northwestern California (Lindroth, 1961:25), east only to the Cascade Range.

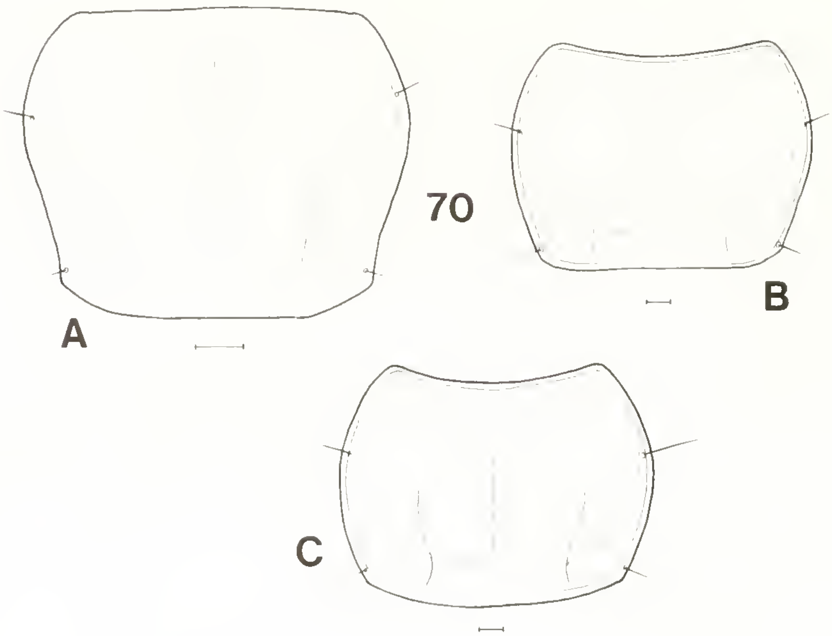
DISTRIBUTION IN THE ARCHIPELAGO.—At present, known only from Graham and Moresby Islands (see Appendix A for locality data).

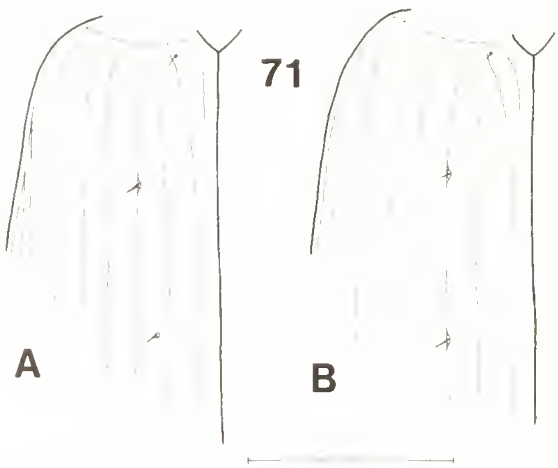
MATERIAL EXAMINED.—10 males, 8 females.

TRIBE CARABINI

DIAGNOSTIC COMBINATION.—Antennae inserted at sides of head, between eyes and bases of mandibles (Fig. 31B); mandible without a setiferous puncture in scrobe (Fig. 34A); procoxal cavity



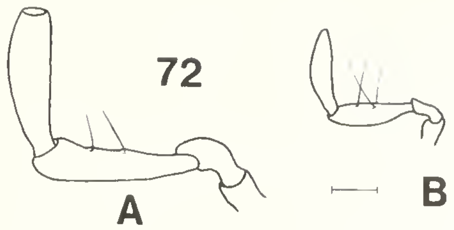


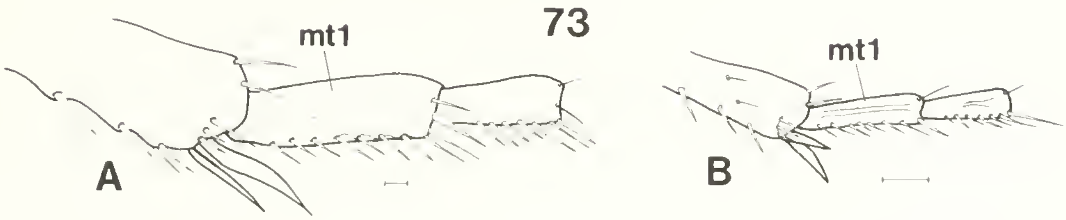


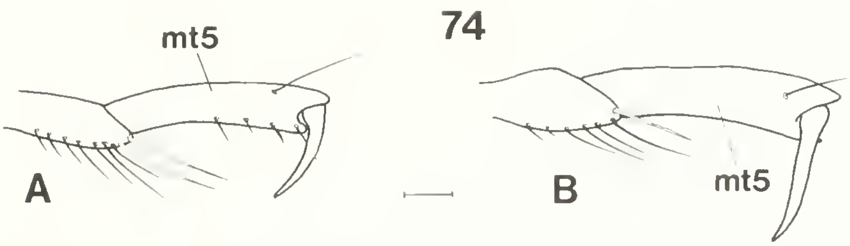
Figures 69–71. Figure 69. Right antenna, basal four antennomeres, dorsal view. A, *Agonum belleri*, B, *Agonum brevicolle*. a3 = third antennomere. Scale = 0.1 mm. Figure 70. Pronotum, dorsal view. A, *Agonum ferruginosum*; B, *Agonum brevicolle*; C, *Agonum metallescens*. Scale = 0.1 mm. Figure 71. Base of left elytron, dorsal view. A, *Agonum brevicolle*, B, *Agonum metallescens*. Scale = 1.0 mm.

open behind, not enclosed by propleuron posteriorly (Fig. 33A); lateral wall of mesocoxal cavity formed by mesosternum, mesepimeron, and metasternum (Fig. 32A); metacoxae contiguous in ventral middle of body (Fig. 35A).

This tribe is worldwide in distribution, with two genera and about 80 species represented in North America. Adults and larvae are aggressive predators on other insects (especially caterpillars), earthworms, and snails and slugs.







FIGURES 72–74 FIGURE 72. Right labial palpus, ventral view. A, *Pterostichus algidus*; B, *Amara littoralis*. FIGURE 73. Left hindleg, apex of tibia and basal two tarsomeres, lateral view. A, *Pterostichus lama*; B, *Pterostichus algidus*. mt1 = first metatarsomere. FIGURE 74. Left metatarsus, apical two tarsomeres, lateral view. A, *Pterostichus algidus*; B, *Pterostichus amethystinus*. mt5 = fifth metatarsomere. All scales = 0.1 mm.

GENUS *CARABUS* LINNAEUS

DIAGNOSTIC COMBINATION.—The only carabine genus known or likely to occur in the archipelago.

This genus is Holarctic in distribution, with 13 species represented in North America, including three introduced from Europe. Two species have been recorded from the archipelago.

5. **Carabus nemoralis** Müller

(Figures 34A, 35A)

Carabus nemoralis Müller, 1764:21 (type loc.: Frederiksdal, Sjaelland, Denmark).

DIAGNOSTIC COMBINATION.—A *Carabus* with upper surface of elytra and pronotum with faint or marked metallic brassy, copperish or blue reflection.

GENERAL DESCRIPTION.—Size very large, body length 22.8–24.4 mm; body and appendages piceous or black, head without metallic reflection, color of pronotum and elytra as noted above, and with brilliant brassy, violet, or blue highlights laterally, especially near basal angles of pronotum; elytra with three rows of foveate setiferous punctures separated by slightly elevated, elongate tubercles.

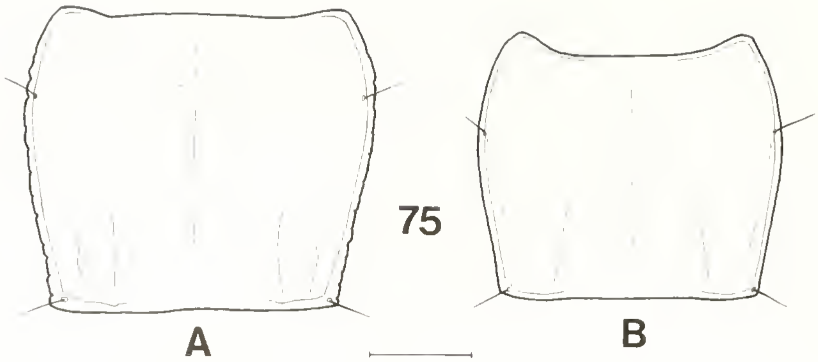
DISPERSAL POTENTIAL.—Adults are markedly brachypterous, incapable of flight; frequent association with human habitation (synanthropic sites) and objects (e.g., stacks of lumber, bales of hay, etc.) provides a mechanism for long- and short-range oversea transport with cargo; otherwise limited to ambulatory dispersal.

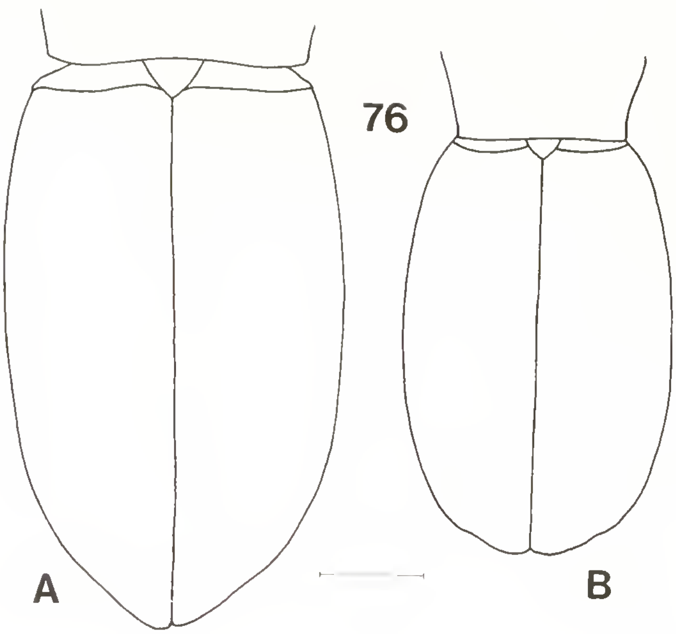
HABITAT DISTRIBUTION.—At present, this species is restricted to synanthropic sites, naturally disturbed areas, and adjacent deciduous forest areas at low elevation.

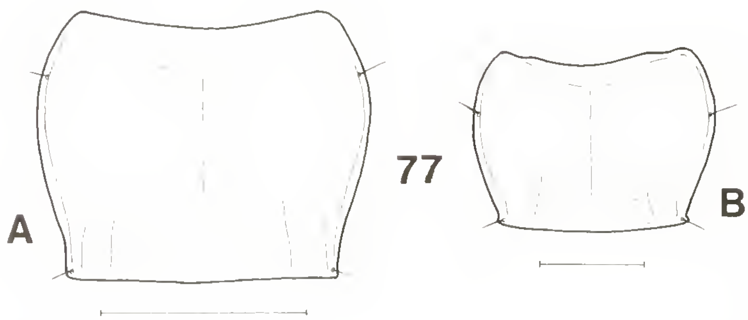
GEOGRAPHICAL DISTRIBUTION.—Introduced from Europe and presently expanding its range in North America from both coasts; in the west, northwest to the Queen Charlotte Islands, south to California and Nevada, east to Alberta, Montana, and Idaho.

DISTRIBUTION IN THE ARCHIPELAGO.—At present, known only from the Port Clements area of eastern Graham Island (see Appendix A for locality data).

MATERIAL EXAMINED.—12 males, 9 females.







FIGURES 75–77. FIGURE 75. Pronotum, dorsal view. A, *Pterostichus crenicollis*; B, *Pterostichus amethystinus*. FIGURE 76. Elytral silhouette. A, *Pterostichus amethystinus*; B, *Pterostichus castaneus*. FIGURE 77. Pronotum, dorsal view. A, *Pterostichus riparius* (Dejean); B, *Pterostichus adstrictus*. All scales = 1.0 mm.

6. **Carabus taedatus** Fabricius

Carabus taedatus Fabricius, 1787:196 (type loc.: Unalaska, Alaska, as restricted by Lindroth 1961:38).

TAXONOMIC NOTES.—Although Lindroth (1961:38) recognized two subspecies of *C. taedatus*, the pattern of geographical variation now known to occur in the range of this species is more complex than previously appreciated (G. Hunter Edelbrock, pers. comm.; manuscript in prep.). I therefore refrain from providing a subspecific designation here, pending completion of Hunter Edelbrock's study.

DIAGNOSTIC COMBINATION.—A *Carabus* with upper surface

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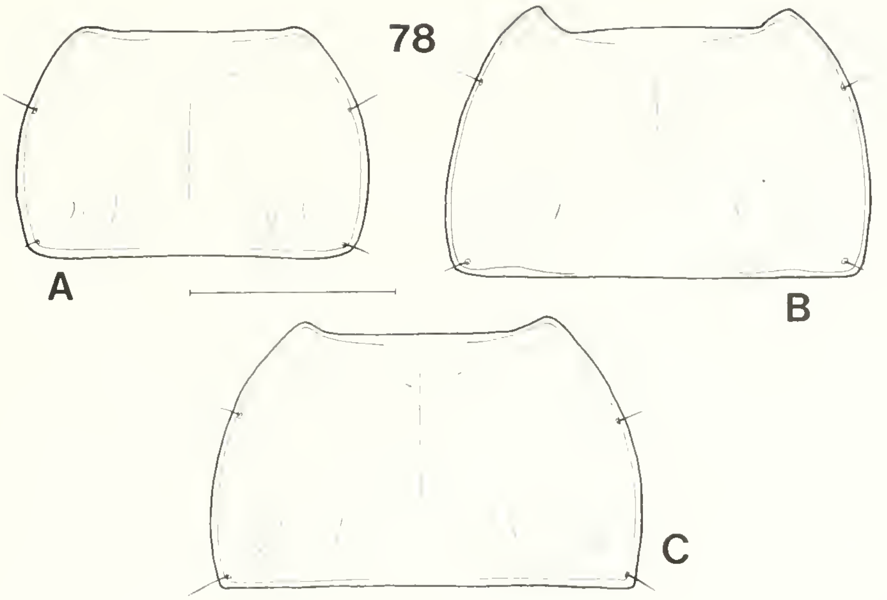


FIGURE 78. Pronotum, dorsal view. A, *Amara sinuosa* (Casey). B, *Amara ellipsis* (Casey). C, *Amara littoralis* Mannerheim. Scale line = 1.0 mm.

of elytra and pronotum without metallic reflection, black, or rufous brown.

GENERAL DESCRIPTION.—Size large or very large (range in body length unknown for the archipelago; but according to Lindroth [1961:38], range for the species is 16–26 mm); head and pronotum piceous or black, elytral color as noted above; elytra with seven rows of markedly foveate setiferous punctures separated by slightly or markedly elevated, elongate tubercles.

DISPERSAL POTENTIAL.—Adults are markedly brachypterous, incapable of flight, and limited to ambulatory dispersal.

HABITAT DISTRIBUTION.—I collected the only known specimen from the archipelago in the alpine zone, under a large, deeply embedded stone surrounded by sparse (tundra) heath vegetation, near the summit of a small, barren peak. On the mainland, habitat distribution is quite complex for this species. In some areas (e.g., Colorado and Washington), adults are found in both lowland and upland forested areas as well as above treeline; in other areas (e.g., Oregon and California), adults occur in forested areas but have not been found above treeline; and in the Aleutian Islands, they are found where no forests exist.

GEOGRAPHICAL DISTRIBUTION.—Mainly western North American, northwest to the inner Aleutian Islands and Alaskan Peninsula, north to southern Yukon Territory, Northwest Territories (Great Slave Lake), and northern Manitoba (Churchill), south to California and Arizona, east to Colorado and western Ontario (Nipigon, northwestern Lake Superior), with disjunct occurrence in northern Quebec (Great Whale River) and northwestern Newfoundland (Lindroth [1961:39]).

DISTRIBUTION IN THE ARCHIPELAGO.—At present, known only from the fragmentary specimen from northern Moresby Island (see Appendix A for locality data).

ADDITIONAL COMMENTS.—Extensive collecting efforts, using hand-collecting and pitfall- and barrier-trapping techniques in a variety of potentially suitable areas, failed to produce additional (live or dead) specimens of this species. I therefore suggest that this species is no longer extant in the Queen Charlotte archipelago and that the fragmentary specimen recovered is a fossil specimen (age not yet determined), which confirms occupation of the archipelago by this species at some earlier time.

MATERIAL EXAMINED.—1 (fragments only, sex undetermined).

TRIBE NEBRIINI

DIAGNOSTIC COMBINATION.—Antennae inserted at sides of head, between eyes and bases of mandibles (Fig. 31B); mandible with a setiferous puncture in scrobe (Fig. 34B); procoxal cavity open behind, not enclosed by propleuron posteriorly (Fig. 33A); lateral wall of mesocoxal cavity formed by mesosternum, mesepimeron, and metasternum (Fig. 32A).

This tribe is Holarctic in distribution, with three genera and about 60 species represented in North America.

GENUS *LEISTUS* FRÖHLICH

DIAGNOSTIC COMBINATION.—A nebriine with lateroventral margin of maxilla with several long, finger-like processes, each with a long, stout spine inserted apically (Fig. 37A). The form and arrangement of spines and cuticular extensions of the ventral aspect of the head and the mouthparts, which together form a basket-like enclosure known as a *collembola trap,* is distinctive for members of this genus.

This genus is Holarctic in distribution, with four species represented in North America, including one introduced from Europe. Springtails and other small insects and mites form the bulk of adult and larval diets.

7. **Leistus ferruginosus** Mannerheim
(Figure 38A)

Leistus ferruginosus Mannerheim, 1843:187 (type loc.: Sitka, Baranof Island, Alaska).—Keen 1895:166.—Lindroth 1961:57.

DIAGNOSTIC COMBINATION.—The only species of *Leistus* known or likely to occur in the archipelago.

GENERAL DESCRIPTION.—Size small, body length 8.2–8.5 mm; body and appendages brown or rufopiceous, mandibles and antennae slightly paler; mandibles markedly broad and explanate basally; head constricted behind prominent, convex eyes; pronotum markedly and abruptly narrowed basally.

DISPERSAL POTENTIAL.—Adults are macropterous and probably capable of at least short-range aerial as well as ambulatory dispersal.

HABITAT DISTRIBUTION.—This species apparently is restricted to lowland areas of deciduous forest (Fig. 12), where adults are found in red alder leaf litter. On the mainland, specimens have been collected also from the foliage of several *Vaccinium* species in the understory vegetation in lowland "meadow forest" (sensu Calder and Taylor 1968).

GEOGRAPHICAL DISTRIBUTION.—Western North American, northwest to the Kenai Peninsula, Alaska, south to southern Oregon, east to western Alberta.

DISTRIBUTION IN THE ARCHIPELAGO.—At present, known only from Graham and Moresby islands (see Appendix A for locality data).

MATERIAL EXAMINED.—4 males, 1 female.

GENUS *NEBRIA* LATREILLE

DIAGNOSTIC COMBINATION.—A nebriine without lateroventral processes on maxilla, setae inserted directly on ventral maxillary surface (Fig. 37B).

This genus is Holarctic in distribution, with 55 species represented in North America. Six species, including two endemics, occur in the archipelago.

8. **Nebria charlottae** Lindroth

(Figures 38F, 39D, 79)

Nebria charlottae Lindroth, 1961:67 (type loc.: Queen Charlotte Islands, British Columbia, here restricted to Masset, Graham Island).

DIAGNOSTIC COMBINATION.—A *Nebria* with body dark refopiceous or black; head relatively large and wide (Fig. 38D); pronotum (Fig. 38F) relatively short, wide, broad apically and narrowed basally, with basal angles distinctly rectangular, basal sinuation of lateral margin short, very deep; elytral silhouette (Fig. 39D) subovoid, relatively short and broad, distinctly narrowed basally, elytron with striae faintly punctate and intervals flat; legs relatively short, femora piceous, tibiae rufous; hindwing (Fig. 40B) short, truncate just distal to stigma.

GENERAL DESCRIPTION.—Form as in Figure 79, size medium, body length 9.9–12.1 mm; head and pronotum without metallic reflection, elytra with faint green metallic reflection (very few individuals with faint violet reflection).

DISPERSAL POTENTIAL.—Adults are brachypterous, incapable of flight; association with driftwood logs on sea beaches may provide a mechanism for oversea dispersal; otherwise limited to ambulatory dispersal.

HABITAT DISTRIBUTION.—This species apparently is restricted to north-facing, cobble-type upper sea beaches (Fig. 3) that are at least partially shaded by the adjacent forest edge. These beetles have only been found where the cobble is piled at least six inches deep and freshwater seeps through the sand/gravel substrate below. Some beaches on which this species occurs are strewn with driftwood logs, and adults are found in great numbers running, feeding, and copulating on these logs at night.

GEOGRAPHICAL DISTRIBUTION.—Known only from the Queen Charlotte archipelago.

DISTRIBUTION IN THE ARCHIPELAGO.—At present, known only from northern and western Graham Island (see Appendix A for locality data).

MATERIAL EXAMINED.—300 males, 354 females.

9. **Nebria louiseae** Kavanaugh

(Figures 38E, 39E, 40B)

Nebria louiseae Kavanaugh, 1984:162 (type loc.: Skedans, Louise Island, British Columbia).

DIAGNOSTIC COMBINATION.—A *Nebria* with body dark rufopiceous or black; head relatively large and wide (Fig. 38D); pronotum (Fig. 38E) relatively longer and more slender, broad apically and narrowed basally, with basal angles distinctly rectangular and apical angles long, relatively narrow and pointed, basal sinuation of lateral margin longer, moderately deep; elytral silhouette (Fig. 39E) subovoid, long and slender, distinctly narrowed basally, elytron with striae faintly punctate, intervals slightly or markedly convex; legs relatively long and slender, femora piceous, tibiae rufous; hindwing (Fig. 40B) short, truncate just distal to stigma; specimen from upper sea beach.

GENERAL DESCRIPTION.—Size medium, body length 10.0–11.9 mm; head and pronotum without metallic reflection, elytra with faint green or violet metallic reflection.

DISPERSAL POTENTIAL.—Adults are brachypterous, incapable of flight; association with driftwood logs on sea beaches may provide a mechanism for oversea dispersal; otherwise limited to ambulatory dispersal.

HABITAT DISTRIBUTION.—This species apparently is restricted to cobble-type upper sea beaches (Fig. 4) that are at least partially shaded by the adjacent forest edge during warmest periods of the day. As for *N. charlottae,* these beetles have only been found where the cobble is piled at least six inches deep and freshwater seeps through the sand/gravel substrate below. Some beaches on which this species occurs are strewn with driftwood logs, and adults are found in great numbers running, feeding, and copulating on these logs at night.

GEOGRAPHICAL DISTRIBUTION.—Known only from the Queen Charlotte archipelago.

DISTRIBUTION IN THE ARCHIPELAGO.—At present, known from the following islands: Burnaby, Hotspring, Lyell, Louise, Moresby, Ramsay, Reef, Talunkwan, Tanu, and West Skedans (see Appendix A for locality data).

MATERIAL EXAMINED.—486 males, 461 females.

←

FIGURE 79. *Nebria charlottae*, adult female, dorsal view. Illustration by Mary Ann Tenorio. Scale = 1.0 mm.

10. **Nebria haida** Kavanaugh
(Figures 38D, 39C)

Nebria haida Kavanaugh, 1984:162 (type loc.: Nebria Peak, Graham Island, British Columbia, here emended [see below]).

Taxonomic Notes.—Locality labels on the holotype and most paratypes of *N. haida* indicate that these specimens were collected "1.8 km N of Mt. Needham, 700–780 m," and this site was noted as type-locality in the original description of the species (Kavanaugh 1984:162). However, the peak located 1.8 km south of the collecting site was misidentified and, in fact, is unnamed. Mount Needham is located 20.5 km east of the collecting site. The site itself includes the summit and surrounding slopes of a distinct, previously unnamed peak, which is here referred to as Nebria Peak (see Table 2), the emended type-locality.

Diagnostic Combination.—A *Nebria* with body dark rufopiceous or black; head (Fig. 38D) relatively large and wide; pronotum (Fig. 38D) relatively longer and more slender, broad apically and narrowed basally, with basal angles distinctly rectangular and apical angles short, relatively broad and rounded, basal sinuation of lateral margin longer, moderately deep; elytral silhouette (Fig. 39C) subovoid, long and slender, distinctly narrowed basally, elytron with striae faintly punctate, intervals slightly or markedly convex; legs relatively long and slender, femora and tibiae piceous; hindwing (Fig. 40B) short, truncate just distal to stigma; specimen from above treeline in alpine zone.

General Description.—Size medium, body length 9.5–12.6 mm; head and pronotum without metallic reflection, elytra with faint violet reflection (very few individuals with faint green reflection).

Dispersal Potential.—Adults are brachypterous, incapable of flight, and limited to ambulatory dispersal.

Habitat Distribution.—Restricted to the alpine zone (Figs. 25–29), where adults and larvae are found under stones on ridges and summits above treeline, especially in areas of sparse vegetation (Figs. 26–30). Specimens collected at High Goose Lake (640 m) were found under stones on the lake shore at the inlet of a small stream and were no doubt washed down from the ridge above during a rainstorm (members of this species are not permanent residents at such a low elevation). Unlike members of most alpine *Nebria* species, these beetles appear to avoid waterside areas and the edges of snowfields and are instead most abundant in the driest sites available. My observations at night suggest that these beetles make little or no use of snowfields in their nocturnal foraging for food, whereas adults of many other *Nebria* species in other alpine areas forage extensively on snow-cover.

Geographical Distribution.—West Coastal, known only from the Queen Charlotte archipelago and adjacent mainland (Mount McNeil [about 35 km N of Prince Rupert]).

Distribution in the Archipelago.—At present, known only from Graham and Moresby islands (see Appendix A for locality data).

Material Examined.—446 males, 342 females.

11. **Nebria sahlbergii sahlbergii** Fischer
(Figures 38C, 39B, 40C)

Nebria sahlbergii Fischer, 1828:254 (type loc.: Sitka, Alaska).

Diagnostic Combination.—A *Nebria* with body dark rufopiceous or black; head (Fig. 38C) moderate in relative size and width; pronotum (Fig. 38C) shorter, relatively narrow apically and broad basally; with basal angles distinctly rectangular or acute; elytral silhouette (Fig. 39B) subrectangular, only slightly narrowed basally, elytron with striae deeply punctate; hindwing (Fig. 40C) full-sized.

General Description.—Size medium, body length 9.0–10.5 mm; head and pronotum without metallic reflection, elytra with faint green or violet metallic reflection.

Dispersal Potential.—Adults are macropterous, probably capable of at least short-range aerial as well as ambulatory dispersal.

Habitat Distribution.—This species is restricted to the rocky banks of small- to medium-sized streams at low elevation (Fig. 13) and of small-sized streams and lakes up to, but not above, treeline (Figs. 22, 23). Adults are found under stones in these waterside areas during daytime, especially in deeply shaded areas.

Geographical Distribution.—Western North American, northwest to the inner Aleutian Islands and Alaskan Peninsula, south to southern Oregon, east to western Alberta and eastern Washington and Oregon.

Distribution in the Archipelago.—At present, known from the following islands: Burnaby, Graham, Lyell, Moresby, and Tanu (see Appendix A for locality data).

Material Examined.—264 males, 130 females.

12. **Nebria mannerheimii** Fischer
(Figures 31B, 32A, 33A, 34B, 37B, 38A)

Nebria mannerheimii Fischer, 1828:253 (type loc.: Sitka, Alaska).
Nebria sahlbergi; Keen 1895:166.
Nebria mannerheimi; Lindroth 1961:75.

Diagnostic Combination.—A *Nebria* with pronotum (Fig. 38A) with basal angles obtuse, basal sinuation of lateral margin shallow or absent; hindwing (Fig. 40C) full-sized.

General Description.—Size medium, body length 9.8–12.5 mm; body and appendages rufopiceous or black, head and pronotum without metallic reflection, elytra with or without very faint green metallic reflection.

Dispersal Potential.—Adults are macropterous, probably capable of at least short-range aerial as well as ambulatory dispersal.

Habitat Distribution.—This species is widespread in open areas at low elevation; on upper sea beaches, where substrate may be sand, fine, or coarse gravel, or cobble, in supratidal meadows, on open ground under cover (e.g., in naturally disturbed areas or synanthropic sites such as quarries), and under stones on open, exposed inorganic shores of the larger lowland streams.

Geographical Distribution.—Mainly West Coastal, north to the Kenai Peninsula, Alaska, south to central Oregon, east of the Coast and Cascade ranges only along major river valleys (the Stikine, Skeena, Thompson, and Fraser rivers of British Columbia, the Columbia and lower Snake rivers of Oregon and Washington).

Distribution in the Archipelago.—At present, known only from Graham Island (see Appendix A for locality data).

Material Examined.—393 males, 239 females.

13. **Nebria diversa** LeConte
(Figures 38B, 39A, 40A)

Nebria diversa LeConte, 1863:2 (type loc.: Cape Flattery, Washington).—Keen 1895:166.—Lindroth 1961:75.

Diagnostic Combination.—A *Nebria* with body pale yellow or tan; pronotum (Fig. 38B) very broad, markedly narrowed basally, with basal angles distinctly rectangular or acute, basal sinuation of lateral margin deep; elytral silhouette (Fig. 39A) markedly ovoid, markedly narrowed basally; hindwing (Fig. 40A) short and narrowed.

General Description.—Size medium, body length 10.3–12.1 mm; meshes of microsculpture isodiametric on head, irregular (mixed isodiametric and slightly transverse) on pronotum and elytra, more deeply impressed in females than males.

Dispersal Potential.—Adults are brachypterous, incapable of flight; association with driftwood logs on sea beaches may provide a mechanism for oversea dispersal; otherwise limited to ambulatory dispersal.

Habitat Distribution.—This species is restricted to open sandy sea beaches, where adults and larvae are found under driftwood and other debris above the highest tide line, especially in areas where sand dunes have developed above the beaches (Fig. 5).

Geographical Distribution.—West Coastal, north to the Queen Charlotte Islands, south to northwestern California, restricted to coastal localities.

Distribution in the Archipelago.—At present, known only from Graham and Moresby islands (see Appendix A for locality data).

Material Examined.—327 males, 288 females.

TRIBE NOTIOPHILINI

Diagnostic Combination.—Head with one supraorbital setiferous puncture dorsomedial to each eye (Fig. 43A); frons with several parallel, longitudinal carinae between eyes; eyes very large; antennae inserted at sides of head, between eyes and bases of mandibles (Fig. 31B); procoxal cavity open behind, not enclosed by propleuron posteriorly (Fig. 44A); lateral wall of mesocoxal cavity formed entirely by mesosternum and metasternum (Fig. 32B). The relatively large eyes and short, parallel-sided body are distinctive for notiophilines.

This tribe occurs in the Nearctic, Neotropical, Palaearctic, and Oriental faunal regions, with all species included in a single genus. Adults and larvae are active, daytime predators, chiefly of springtails and mites.

Genus *Notiophilus* Dumeril

Diagnostic Combination.—The only notiophiline genus.

Eighteen species of this genus occur in North America, including two species introduced from Europe.

14. **Notiophilus sylvaticus** Eschscholtz
(Figure 44A)

Notiophilus sylvaticus Eschscholtz, 1833:24 (type loc.: Norfolk Strait (=Sitka Sound), Baranof Island, Alaska).—Keen 1895:166.—Lindroth 1961:100.

Diagnostic Combination.—The only species of *Notiophilus* known or likely to occur in the archipelago.

General Description.—Size small, body length 4.9–5.7 mm; head and pronotum black, elytra pale yellow but with epipleura and first and second elytral intervals (except near apex in some individuals) black, legs black but with tibiae pale yellow or rufous, basal three or four antennomeres yellow, rufous, or rufopiceous, more distal antennomeres black, dorsal body surface (least so on elytra) with moderate or brilliant brassy, copper, violet, or blue metallic reflection; second elytral interval as wide as third, fourth, and fifth intervals combined.

Dispersal Potential.—Lindroth (1961:100) noted that some populations of this species include both macropterous and brachypterous individuals; however, all specimens from the archipelago examined to date are brachypterous and limited to ambulatory dispersal.

Habitat Distribution.—This species is widespread in forested areas at all elevations, from near sea level to above treeline on the mountain peaks. Adults are found under the loose bark of fallen trees or in leaf litter, under stones or logs on the ground, or in the deep moss layer that covers much of the forest floor throughout the archipelago (Figs. 14, 15). Above treeline, beetles occur in the driest sites with very low, scattered vegetation, and are especially active in sunlight.

Geographical Distribution.—West Coastal, northwest to Kodiak Island and the Kenai Peninsula, Alaska, south to northwestern California, east only to the Coast Ranges.

Distribution in the Archipelago.—At present, known from the following islands: Graham, Kunga, Louise, Lyell, Moresby, and Tanu (see Appendix A for locality data).

Material Examined.—44 males, 36 females.

TRIBE ELAPHRINI

Diagnostic Combination.—Antennae inserted at sides of head, between eyes and bases of mandibles (Fig. 31B); mandible with a setiferous puncture in scrobe (Fig. 41A); procoxal cavity entirely enclosed by propleuron posteriorly (Fig. 33B); lateral wall of mesocoxal cavity formed by mesosternum, mesepimeron, and metasternum (Fig. 32A).

This tribe is Holarctic in distribution, with three genera and 27 species represented in North America.

Genus *Elaphrus* Fabricius

Diagnostic Combination.—Eyes large; pronotum with midlateral setiferous puncture absent; elytron with striae absent or faintly suggested basally only, setiferous punctures present on third, fifth, seventh, and ninth intervals. Members of this genus look like small tiger beetles (cicindelines), from which they can be distinguished by the point of insertion of antennae on the head. This is the only elaphrine genus known to occur in the archipelago. Adults of *Blethisa* Bonelli, the only other genus likely to occur there, have midlateral pronotal setiferous punctures and distinct elytral striae.

This genus is Holarctic in distribution, with 19 species in North America, two of which occur in the archipelago.

15. **Elaphrus clairvillei** Kirby

Elaphrus clairvillei Kirby, 1837:61 (type loc.: Lake Nipigon, Ontario, as restricted by Lindroth 1961:112).

Diagnostic Combination.—An *Elaphrus* with frons with a deep, finely and densely punctate pit in midline between eyes, surrounded by a shiny, raised area with very sparse punctures.

General Description.—Size small, body length 8.5–9.6 mm; body piceous or black, tibiae piceous, dorsal surface with faint or moderate green or dark copper metallic reflection and very sparse punctation (punctures separated by gaps of more than twice their diameter), areas within ocellate dorsal elytral foveae with marked metallic violet reflection, legs with femora, tarsi, and tibial apices with faint or moderate green metallic reflection; eyes very large, hemispheric.

Dispersal Potential.—Adults are macropterous and probably capable of at least short-range aerial as well as ambulatory dispersal.

Habitat Distribution.—This species is apparently restricted to the margins of freshwater bogs (Fig. 10), marshes, and seeps at low to middle elevations, where adults are active by day on open or partly shaded organic mudflats between patches of vegetation (Fig. 11).

Geographical Distribution.—Transamerican, from Alaska to Newfoundland; in the west, northwest to Anchorage and Circle, Alaska, south to northern California, northern Arizona, and Colorado.

Distribution in the Archipelago.—At present, known only from Graham Island (see Appendix A for locality data).

Material Examined.—4 males.

16. **Elaphrus americanus sylvanus** Goulet

(Figures 33B, 41B)

Elaphrus americanus sylvanus Goulet, *in* Goulet and Baum 1981:2271 (type loc.: 16 miles N of Powers, Coos County, Oregon).

Diagnostic Combination.—An *Elaphrus* with frons without a pit in midline between eyes (or if faintly present, then pit surrounded by a flat or only slightly raised area with dense punctures).

General Description.—Size small, body length 6.9–8.3 mm; body piceous or black, tibiae rufous (at least at middle), dorsal surface with moderate or marked green or dark copper metallic reflection and dense punctation (punctures, on average, about one diameter apart), areas within ocellate dorsal elytral foveae with marked metallic violet reflection, legs with femora, tarsi and tibial apices with marked green or copper metallic reflection; eyes very large, hemispheric.

Dispersal Potential.—Adults are macropterous and probably capable of at least short-range aerial as well as ambulatory dispersal.

Habitat Distribution.—This species is apparently restricted to the margins of freshwater streams, ponds, bogs (Fig. 10), marshes, and seeps at low to middle elevations, where adults are active by day on open, exposed organic mudflats between patches of vegetation (Fig. 11).

Geographical Distribution.—Western North American, north to northwestern British Columbia, south to southern Oregon, central Idaho, and central Colorado, east to southwestern Alberta.

Distribution in the Archipelago.—At present, known only from Graham and Moresby islands (see Appendix A for locality data).

Material Examined.—88 males, 62 females.

TRIBE LORICERINI

Diagnostic Combination.—Body slightly flattened dorsoventrally, not pedunculate (not markedly constricted between pronotum and elytra); antennae inserted at sides of head, between eyes and bases of mandibles (Fig. 31B); antennomeres 2–4 with several very long, erect setae (Fig. 42B); mandible without a setiferous puncture in scrobe (Fig. 41B); procoxal cavity entirely enclosed by propleuron posteriorly (Fig. 33B); lateral wall of mesocoxal cavity formed by mesosternum, mesepimeron, and metasternum (Fig. 32A); elytron with setiferous punctures slightly or moderately foveate, but foveae not large and dull (i.e., microsculpture of foveae not markedly contrasting with that of remainder of elytral surface). The pattern of setae on antennomeres 2–4 is distinctive for loricerines in the fauna of the archipelago.

This tribe is Holarctic in distribution (except for two montane forms in the northern Neotropical Region), with all species included in a single genus.

Genus *Loricera* Latreille

Diagnostic Combination.—The only loricerine genus.

Three species of this genus occur in North America north of Mexico.

17. **Loricera decempunctata** Eschscholtz

(Figures 41B, 42B)

Loricera decempunctata Eschscholtz, 1833:25 (type loc.: Sitka, Baranof Island, Alaska).—Keen 1895:166.—Lindroth 1961:122.

Diagnostic Combination.—The only species of *Loricera* known or likely to occur in the archipelago.

General Description.—Size small, body length 7.2–8.1 mm; body and appendages piceous or black, with mandibles, tibiae, and tarsi slightly paler in some individuals, head and pronotum without metallic reflection, elytra without or with very faint green or brassy metallic reflection, dorsal surface moderately shiny; head abruptly constricted posterior to eyes; antennal scape elongate, almost as long as combined lengths of antennomeres 2–4.

Dispersal Potential.—Adults are macropterous and probably capable of at least short-range aerial as well as ambulatory dispersal.

Habitat Distribution.—This species is widespread in moist areas from near sea level to just below treeline on mountain peaks, where adults and larvae live at the margins of streams, lakes, ponds, bogs, and marshes or of small seeps in either exposed or deeply shaded areas, on moist, organic substrate.

Geographical Distribution.—Mainly West Coastal, north to Kodiak Island and the Kenai Peninsula, south to northwestern California, east of the coast region only in southern British Columbia (to Revelstoke area).

Distribution in the Archipelago.—At present, known only from Graham and Moresby islands (see Appendix A for locality data).

Material Examined.—31 males, 33 females.

TRIBE SCARITINI

Diagnostic Combination.—Body elongate, pedunculate (markedly constricted between pronotum and elytra); antennae inserted at sides of head, between eyes and bases of mandibles (Fig. 31B); antennomeres 2–4 without long, erect setae (Fig. 42A); mandible without a setiferous puncture in scrobe (Fig. 41B); procoxal cavity entirely enclosed by propleuron posteriorly (Fig. 33B); lateral wall of mesocoxal cavity formed by mesosternum, mesepimeron, and metasternum (Fig. 32A); elytron without large, dull, ocellate foveae. Among tribes represented in the archipelago, scaritines are likely to be confused only with broscines, from which they can be distinguished by their lack of a setiferous puncture on the mandible and the inclusion of the mesepimeron in the lateral wall of the mesocoxal cavity.

This tribe is worldwide in distribution, with eight genera and more than 130 species represented in North America.

Genus *Dyschirius* Panzer

Diagnostic Combination.—A small scaritine with body cylindrical in cross-section; the only genus known or likely to occur in the archipelago.

This genus is worldwide in distribution, with about 60 species represented in North America. Adults and larvae are mainly subterranean, living in burrows that they construct in sand or clay substrates, usually near water. They are frequently found in association with staphylinid beetles of genus *Bledius* Leach or with variegated mud-loving beetles (Heteroceridae).

18. **Dyschirius pacificus** Lindroth

(Figure 42A)

Dyschirius tridentatus; Keen 1895:166.—Lindroth 1961:144.
Dyschirius pacificus Lindroth, 1961:144 (type loc.: Tofino, Vancouver Island, British Columbia).

Diagnostic Combination.—The only species of *Dyschirius* known or likely to occur in the archipelago.

General Description.—Size small (range in body length unknown for archipelago, single known specimen 5.0 mm; but according to Lindroth (1961:144), range for species is 4.6–5.0 mm); body piceous or black, legs, mouthparts, and scape and pedicel of antennae rufopiceous; head with frontal furrows deeply impressed, with surfaces between furrows and eyes convex, almost carinate, eyes large, almost hemispheric; pronotum globose with base narrow and distinctly margined, basal angles obliterated; anterior tibia markedly extended dorso-apically as a stout, tooth-like projection.

Dispersal Potential.—Adults are brachypterous, incapable of flight, and limited to ambulatory dispersal.

Habitat Distribution.—Keen (1895:166) noted that adults of this species (listed as "Dyschirius 3-dentatus, LeC.") were "numerous on gravelly beach at highwater mark in June"; but according to Lindroth (1961:145), they are restricted to sandy sea beaches in other parts of the range of this species. I found neither adults nor larvae of this species in either of these habitats during my fieldwork in the archipelago (during July and August); however, their occurrence as adults may be seasonal, perhaps limited to late spring and early summer.

Geographical Distribution.—West Coastal, north to the Queen Charlotte Islands, south to the central Oregon coast; restricted to coastal localities.

Distribution in the Archipelago.—Unknown; single known specimen labeled simply "Q.C.I.," but probably collected by Keen in the Masset area, Graham Island.

Material Examined.—1 female.

Tribe Broscini

Diagnostic Combination.—Body slightly pedunculate in shape (with pronotum narrowed basally); head with one supraorbital setiferous puncture dorsomedial to each eye (Fig. 43A); frons without distinct, parallel carinae between eyes; eyes small, moderate, or large in size; antennae inserted at sides of head, between eyes and bases of mandibles (Fig. 31B); antennomeres 5–11 covered with short dense setae, antennomere 3 glabrous except for long setae at distal apex, antennomere 4 with short, dense setae restricted to distal one-half or absent; mandible with a setiferous puncture in scrobe (Fig. 45A) (or, if absent, then body with distinct metallic reflection); procoxal cavity entirely enclosed by propleuron posteriorly (Fig. 44B); lateral wall of mesocoxal cavity formed entirely by mesosternum and metasternum (Fig. 32B). Among tribes represented in the archipelago, broscines are likely to be confused only with scaritines, from which they can be distinguished by the setiferous puncture present on the mandible (except in some *Zacotus* individuals) and the exclusion of the mesepimeron from the lateral wall of the mesocoxal cavity.

This tribe occurs in the Nearctic, Palaearctic, southern Neotropical, northern Oriental, and Australian faunal regions, with three genera, each including a single species, represented in North America.

Genus *Broscodera* Lindroth

Diagnostic Combination.—Body length less than 10.5 mm, surface without metallic reflection; eyes small in size.

This genus is restricted to the northwest coastal region of North America.

19. **Broscodera insignis** (Mannerheim)

Miscodera insignis Mannerheim, 1852:296 (type loc.: Sitka, Baranof Island, Alaska).

Diagnostic Combination.—The only known species of *Broscodera.*

General Description.—Size small to medium, body length 8.2–10.1 mm; body and appendages rufous or rufopiceous; head with frontal furrows shallow and surfaces between furrows and eyes only slightly convex, eyes flattened; pronotum elongate, with lateral margins markedly sinuate posteriorly, basal angles distinct, rectangular; anterior tibia truncate apically.

Dispersal Potential.—Adults are macropterous and probably capable of at least short-range aerial as well as ambulatory dispersal.

Habitat Distribution.—This species is widespread, from near sea level to above treeline on mountain peaks. Adults occur in greatest numbers at the margins of small streams (Fig. 22) in areas where fine rocky talus has slid to the stream edge or where bedrock is highly fractured and loose just at or above waterline. By day, the beetles hide deep in the loose rocky substrate, especially where it is very moist. A few adults are found away from streams, especially above treeline, under stones on barren slopes, or at the edges of snowfields.

Geographical Distribution.—West Coastal, north to just northwest of Glacier Bay, Alaska, south to northern Oregon, east to the Cascade Range in Washington and Oregon.

Distribution in the Archipelago.—At present, known only from Graham and Moresby islands (see Appendix A for locality data).

Material Examined.—29 males, 12 females.

Genus *Zacotus* LeConte

Diagnostic Combination.—Body length 12.0 mm or more, surface with distinct purple metallic reflection (brilliant, with green, brassy, or copper highlights in some individuals); eyes moderate in size.

This genus is restricted to western North America.

20. **Zacotus matthewsi** LeConte

(Figures 43A, 44B)

Zacotus matthewsi LeConte, 1869:373 (type loc.: Vancouver Island, British Columbia).

Taxonomic Notes.—From his study of genus *Zacotus*, Ball (1956) concluded that all specimens examined represented a single species, *Z. matthewsi* LeConte. His analysis of geographical variation in dorsal body color, luster, and macrosculpture led him to recognize two forms—a "western race," to which the name *Zacotus matthewsi matthewsi* LeConte can be applied, and an "eastern race," for which the name *Zacotus matthewsi subopacus* Hopping is available. He did not formally recognize these as subspecies and noted that additional specimens from "many localities" were needed before patterns of geographical variation could be properly interpreted and spacial relationships of forms be defined. Although available material from the archipelago (one specimen) clearly represents Ball's "western race" (*Z. m. matthewsi*), I include no subspecific designation here, pending further study.

Diagnostic Combination.—The only known species of *Zacotus*.

General Description.—Size medium, body length 12.0–18.0 mm; body form markedly convex, almost cylindrical; body and appendages rufopiceous to piceous; head with frontal furrows broad and moderately deep, surfaces between furrows and eyes moderately convex, frons, and vertex rugulose, vertex with a shallow to deep median fovea, eyes moderately convex; pronotum elongate, with lateral margins markedly sinuate posteriorly, basal angles distinct, rectangular; anterior tibiae truncate apically.

Dispersal Potential.—Adults are markedly brachypterous, incapable of flight; association with logs on the forest floor along streams or just above sea beaches may provide a mechanism for oversea dispersal in log rafts; otherwise limited to ambulatory dispersal.

Habitat Distribution.—The single known specimen was found alive in a deep pit (archaeological excavation) on sand/gravel substrate in second growth conifer forest, about 60 meters inland from the seashore (N. Gessler, pers. comm.). Elsewhere in their known range, members of this species occur in dense coniferous forest, where they are found under logs and deep in the needle duff layer during the day. At night, they are active on the surface, particularly in areas where needle duff is very deep and free of low plant cover (understory).

Geographical Distribution.—Western North American, north to southeastern Alaska (at least to the Ketchikan area), south to northern California, and east to southeastern British Columbia, northern Idaho, and northwestern Montana.

Distribution in the Archipelago.—At present, known only from northwestern Graham Island (see Appendix A for locality data).

Material Examined.—1 female.

TRIBE PATROBINI

Diagnostic Combination.—Body length greater than 6.0 mm; head with two supraorbital setiferous punctures dorsomedial to each eye (Fig. 43B), with a transverse sulcus posterior to eyes, frontal furrows extended posteriorly only to level of anterior supraorbital setiferous puncture (Fig. 64A); antennae long, inserted at sides of head, between eyes and bases of mandibles (Fig. 31B), antennomeres 4–11 each more than twice as long as wide; mandible with a setiferous puncture in scrobe (Fig. 63A) (a few individuals with setiferous puncture absent from one or both mandibles); terminal maxillary palpomere about equal in length and width to penultimate palpomere (Fig. 50B); pronotum (Fig. 65B) without setiferous punctures on lateral margin near apical angle, posterior transverse impression broad and shallow; lateral wall of mesocoxal cavity formed entirely by mesosternum and metasternum (Fig. 32B).

This tribe is Holarctic in distribution, with four genera and 12 species represented in North America.

Genus *Diplous* Motschulsky

Diagnostic Combination.—Body flattened in cross-section; pronotum (Fig. 65B) without basolateral carinae, median longitudinal impression not extended to basal margin. This is the only patrobine genus known to occur in the archipelago. In adults of *Patrobus* Dejean, the only other genus likely to occur there, basolateral carinae are present on the pronotum and the median longitudinal impression is extended to the basal pronotal margin.

This genus is Holarctic in distribution, with four species represented in North America.

21. **Diplous aterrimus** (Dejean)

(Figures 64A, 65B)

Patrobus aterrimus Dejean, 1828:32 (type loc.: "Norfolk Strait" [=Sitka Sound], Baranof Island, Alaska).

Diagnostic Combination.—The only species of *Diplous* known or likely to occur in the archipelago.

General Description.—Size small or medium, body length 8.7–11.0 mm; body and appendages black or piceous, except tarsi (and tibiae in a few individuals) piceous or rufopiceous, dorsal surfaces dull, without metallic reflection; body, especially elytra, moderately flattened dorsoventrally; elytral silhouette elongate, parallel-sided; hind trochanters slightly elongate, pointed apically.

Dispersal Potential.—Adults are macropterous and probably capable of at least short-range aerial as well as ambulatory dispersal.

Habitat Distribution.—This species is restricted to the rocky, inorganic banks of small- (Fig. 13) to large-sized streams at low elevations, where adults occur under stones in both exposed and shaded waterside areas.

GEOGRAPHICAL DISTRIBUTION.—Western North American, northwest to Sitka, Alaska, north to southern Yukon Territory, south to northeastern Oregon, east to Alberta and Colorado.

DISTRIBUTION IN THE ARCHIPELAGO.—At present, known only from Graham, Lyell, and Moresby islands (see Appendix A for locality data).

MATERIAL EXAMINED.—116 males, 122 females.

TRIBE TRECHINI

DIAGNOSTIC COMBINATION.—Body length less than 5.0 mm; head with two supraorbital setiferous punctures dorsomedial to each eye (Fig. 43B), without a transverse sulcus posterior to eyes, frontal furrows extended in an arc posteriorly beyond level of posterior margin of eye (Fig. 64B); antennae inserted at sides of head, between eyes and bases of mandibles (Fig. 31B); mandible with a setiferous puncture in scrobe (Fig. 63A); terminal maxillary palpomere about equal in length and width to penultimate palpomere (Fig. 50B); lateral wall of mesocoxal cavity formed entirely by mesosternum and metasternum (Fig. 32B). The posterolateral extension of the frontal furrows behind the eyes is distinctive for trechines among the small carabids of the archipelago. They are further distinguished from bembidiines by the form of the terminal labial palpomere and from small harpalines by the presence of two pairs of supraorbital setiferous punctures.

This tribe is worldwide in distribution, with nine genera and about 140 species represented in North America. Included are species that inhabit leaf litter, soil, and various subterranean habitats, including caves. Many of the cave-dwelling forms are structurally specialized for cave life (i.e., they are eyeless, flightless, depigmented forms with long legs, antennae, and tactile setae).

GENUS *TRECHUS* CLAIRVILLE

DIAGNOSTIC COMBINATION.—The only trechine genus known or likely to occur in the archipelago.

This genus is Holarctic in distribution, with about 40 species represented in North America, including three species introduced from Europe. Three species occur in the archipelago.

22. **Trechus obtusus** Erichson

(Figures 66B, 67B)

Trechus obtusus Erichson, 1837:122 (type loc.: Brandenburg, separate portions of which are presently part of Germany and Poland).

DIAGNOSTIC COMBINATION.—A *Trechus* with pronotum (Fig. 67B) broad basally, basal sinuation of lateral margin shallow or absent, basal angles distinctly obtuse, basal margin oblique medial to basal angles, basal margination complete, even at midline; elytron with anterior preapical setiferous puncture inserted at least as close to medial margin as to recurrent sulcus (Fig. 66B).

GENERAL DESCRIPTION.—Size very small, body length 3.5–3.6 mm; body brown or slightly piceous, legs, palpi, and antennal scape pale testaceous, second through eleventh antennomeres slightly darker, elytra with faint iridescent reflection; head with medial area between frontal furrows narrower than lateral area between furrow and eye; elytral silhouette subovoid.

DISPERSAL POTENTIAL.—Both macropetereous and brachypterous adults occur in the archipelago. The former probably are capable of at least short-range aerial dispersal. Association with human habitation and, specifically, with gardens and commercial nurseries (Kavanaugh and Erwin 1985) may provide a mechanism for long- and short-range oversea transport with nursery stock and/or other cargo; but adults are otherwise limited to ambulatory dispersal.

HABITAT DISTRIBUTION.—At present, this species is restricted to the lowlands in disturbed, synanthropic sites. Adults occur in shaded leaf litter on fine sandy/silty substrate in patches of red alder forest (Fig. 12) adjacent to cleared areas and under rocks on the exposed, sandy shore of a disturbed, slightly brackish-water slough.

GEOGRAPHICAL DISTRIBUTION.—Introduced from Europe, presently expanding its range on the western coast of North America (Kavanaugh and Erwin 1985), north to the Queen Charlotte Islands and Prince Rupert area, south to central California, restricted to areas west of the Cascade Range (Washington and Oregon) and Sierra Nevada (California).

DISTRIBUTION IN THE ARCHIPELAGO.—At present, known only from northern Graham Island (see Appendix A for locality data).

MATERIAL EXAMINED.—7 males, 15 females.

23. **Trechus ovipennis** Motschulsky

(Figures 66A, 67A)

Trechus ovipennis Motschulsky, 1845:348 (type loc.: Sitka, Baranof Island, Alaska, as emended by Lindroth 1961:195).—Keen 1895:167.—Lindroth 1961:196.

DIAGNOSTIC COMBINATION.—A *Trechus* with pronotum (Fig. 67A) distinctly narrowed basally, basal sinuation of lateral margin deep; elytron with anterior preapical setiferous puncture inserted closer to recurrent sulcus than to medial margin (Fig. 66A).

GENERAL DESCRIPTION.—Size very small, body length 3.5–4.1 mm; body brown or piceous, legs, palpi, and antennae pale testaceous or light brown; elytra with faint or moderate iridescent reflection; head with medial area between frontal furrows narrower than lateral area between furrow and eye; elytral silhouette distinctly ovoid.

DISPERSAL POTENTIAL.—Adults are brachypterous, incapable of flight, and limited to ambulatory dispersal.

HABITAT DISTRIBUTION.—This species is widespread at low elevations, on or near sea beaches or along the margins of streams inland for a short distance. Adults occur on sandy sea beaches under driftwood and in masses of buried wrack (i.e., eelgrass, kelp, and other seaweed that washes up on shore and is buried by shifting sand). These beetles have also been found under stones and in loose gravel at the shaded margins of small- to medium-sized streams inland (but always within 1.0 km of beach areas).

GEOGRAPHICAL DISTRIBUTION.—West Coastal, north to Sitka, Alaska, south to northern California, east only to localities in the Coast Ranges.

DISTRIBUTION IN THE ARCHIPELAGO.—At present, known from the following islands: Graham, Kunga, Louise, Moresby, Ramsay, and Talunkwan (see Appendix A for locality data).

MATERIAL EXAMINED.—69 males, 122 females.

24. **Trechus chalybeus** Dejean

(Figures 64B, 67C)

Trechus chalybeus Dejean, 1831:17 (type loc.: Unalaska, Unalaska Island, Alaska).

Diagnostic Combination.—A *Trechus* with pronotum (Fig. 67C) broad basally, basal sinuation of lateral margin shallow or absent, basal angles rectangular or slightly obtuse, basal margin relatively straight, basal margination interrupted broadly in midline; elytron with anterior preapical setiferous puncture inserted at least as close to medial margin as to recurrent sulcus (Fig. 66B).

General Description.—Size very small, body length 3.8–4.4 mm; body dark brown or piceous, legs, palpi, and antennal scape pale testaceous or rufous, second through eleventh antennomeres slightly darker (rufous or rufopiceous); elytra with faint to marked iridescent reflection; head with medial area between frontal furrows as wide as lateral area between furrow and eye; elytral silhouette subovoid.

Dispersal Potential.—Adults are brachypterous, incapable of flight, and limited to ambulatory dispersal.

Habitat Distribution.—This species is widespread in forested areas from near sea level to just above treeline on the mountain peaks. Adults are found under stones and in dense carpets of mosses in areas of coniferous forest (Figs. 14, 15, and 21), especially in moist seep areas or at the edges of forest ponds (Fig. 18), in leaf litter in areas of deciduous forest (Fig. 12), and under stones surrounded by low vegetation in exposed areas at or above treeline.

Geographical Distribution.—Western North American, north to inner Aleutian Islands and Alaskan Peninsula, Alaska, south to northern California, east to western Alberta and Montana.

Distribution in the Archipelago.—At present, known only from Graham and Moresby islands (see Appendix A for locality data).

Material Examined.—121 males, 79 females.

TRIBE BEMBIDIINI

Diagnostic Combination.—Head with two supraorbital setiferous punctures dorsomedial to each eye (Fig. 43B); antennae inserted at sides of head, between eyes and bases of mandibles (Fig. 31B); terminal maxillary palpomere small, narrow and less than one-half the length of penultimate palpomere (Fig. 50A); lateral wall of mesocoxal activity formed entirely by mesosternum and metasternum (Fig. 32B). Among tribes represented in the archipelago, bembidiines are likely to be confused only with trechines, from which they can be distinguished by the form of the terminal labial palpomere, or with small harpalines, which have only one pair of supraorbital setiferous punctures.

This tribe is worldwide in distribution, with about 20 genera (arranged in several subtribes) and 500 species represented in North America.

Genus *Bembidion* Latreille

Diagnostic Combination.—Eyes present; elytron with first stria straight, not recurved apically, scutellar striole present, intervals impunctate (except for fixed discal and umbilicate setiferous punctures). This is the only bembidiine genus known to occur in the archipelago. The only other genus likely to occur there is *Tachyta* Kirby, members of which have elytra with the first stria recurved and the scutellar striole absent.

This genus is worldwide in distribution, but with highest species diversity centered in temperate regions. More than 300 species are represented in North America, twenty of which have been recorded from the archipelago.

25. **Bembidion zephyrum** Fall

(Figures 50A, 51B)

Bembidion zephyrum Fall, 1910:96 (type loc.: Humboldt County, California).—Lindroth 1963:233.

Diagnostic Combination.—A *Bembidion* with pronotum (Fig. 51B) broad, apical angles long, projected anteriorly, distinctly flattened; elytra with a distinct transverse depression about midway between base and anterior setiferous puncture on third interval, third interval unevenly microsculptured, with each dorsal setiferous puncture inserted in the anterior part of a dull, coarsely microsculptured, slightly depressed field extended fully across the interval, areas between such fields shinier, less coarsely microsculptured, flat or slightly convex; elytra with posterior-most outer copperish shiny spot (on sixth to eighth intervals just posterior to middle of elytron) continuous with medial shiny area as an obliquely transverse shiny band (shiny area extended across fifth interval at or near middle of elytron).

General Description.—Size small, body length 4.9–6.0 mm; body and appendages black or piceous, except femora pale testaceous basally, dorsal surface without or with faint to marked green or brassy metallic reflection, elytra with contrasting pattern of dull fields and shiny, moderately brilliant copper areas as noted above.

Dispersal Potential.—Adults are macropterous and probably capable of at least short-range aerial as well as ambulatory dispersal.

Habitat Distribution.—This species apparently is restricted to open, sandy sea beaches. Adults are active by day on moist sandflats, above the hightide line, especially where freshwater streams enter and fan out on the beach.

Geographical Distribution.—West Coastal, north to the Queen Charlotte Islands, south to northern California.

Distribution in the Archipelago.—At present known only from extreme northwestern Graham Island (see Appendix A for locality data).

Material Examined.—90 males, 54 females.

26. **Bembidion inaequale opaciceps** Casey

(Figure 51A)

Bembidion opaciceps Casey, 1918:8 (type area: California).

Diagnostic Combination.—A *Bembidion* with pronotum (Fig. 51A) narrow, apical angles short, not or only slightly flattened; elytra without or with only a slight transverse depression near base, third interval unevenly microsculptured, with each dorsal setiferous puncture inserted in the anterior part of a dull, coarsely microsculptured, slightly depressed field extended fully across the interval, areas between such fields shinier, less coarsely microsculptured, flat or slightly convex; posterior-most outer copperish shiny spot (on sixth to eighth intervals just posterior to middle of elytron) distinctly separate from medial shiny area (fifth interval dull, coarsely microsculptured in posterior two-thirds of elytron).

General Description.—Size small, body length 4.9–5.0 mm; body and appendages black or piceous, at least hind femora also black or piceous basally, dorsal surface with marked green or brassy metallic reflection, elytra with pattern of contrasting dull fields and shiny, brilliant copper areas as noted above.

Dispersal Potential.—Adults are macropterous and probably capable of at least short-range aerial as well as ambulatory dispersal.

Habitat Distribution.—This species apparently is restricted to the margins of large, lowland streams, where adults are found active by day on moist, exposed, inorganic banks with scattered small stones or gravel, fine sandy or silty substrate, and no or only scattered vegetation.

Geographical Distribution.—Western North American, northwest to the Lower Yukon River valley, Alaska, south to California, east to Saskatchewan.

Distribution in the Archipelago.—At present, known only from Graham Island (see Appendix A for locality data).

Material Examined.—2 males, 3 females.

27. **Bembidion dyschirinum** LeConte
(Figure 57A)

Bembidium dyschirinum LeConte, 1861:340 (type loc.: E of Fort Colville, Stevens County, Washington).
Bembidion dyschirinum LeConte.—Lindroth 1963:256.

Diagnostic Combination.—A *Bembidion* with eyes moderate in size (Fig. 52C); mandible moderate in length and width (Fig. 52C); terminal maxillary palpomere very small, length less than one-third the length of penultimate palpomere (Fig. 53B); pronotum narrow, cordiform, with basolateral carina long; elytron with lateral margination prolonged medial to humerus (Fig. 56A), angulate with respect to basal margin, only sutural (first) stria evident to apex (Fig. 57A), third interval evenly microsculptured, without contrasting dull, depressed fields of coarse microsculpture associated with dorsal setiferous punctures; tibiae pale rufous throughout.

General Description.—Size very small (range in body length unknown for archipelago; but according to Lindroth (1963:255), range for species is 2.9–3.8 mm); body black or piceous, appendages rufous or rufopiceous, dorsal surface shiny, elytra without or with very faint brassy metallic reflection; third through seventh elytral striae represented only by rows of small punctures.

Dispersal Potential.—Unknown; but Lindroth (1963:256) reported both macropterous and brachypterous individuals for the species, with the former relatively rare and the latter limited to ambulatory dispersal.

Habitat Distribution.—Habitat range of this species in the archipelago is unknown; but elsewhere, according to Lindroth (1963:256), members of this species are restricted to highlands, where they occur in scattered leaf litter (e.g., of *Alnus* spp.) on sandy substrate at the edges of mixed forests.

Geographical Distribution.—Western North American, north to southeastern Alaska and southern Yukon Territory, south to Oregon and Colorado, east to Alberta and Montana.

Distribution in the Archipelago.—At present, known only from a record cited by Lindroth (1963) from northern Graham Island.

Additional Comments.—Inclusion of *B. dyschirinum* in this treatment is based on Lindroth's (1963:256) record of a specimen then in the collection of G. Stace Smith, from Masset (Graham Island). To date, I have been unable to locate this specimen or any other representing this species from a locality in the Queen Charlotte archipelago.

Material Examined.—none.

28. **Bembidion castum** Casey
(Figure 57B)

Bembidion erasum; Keen 1895:166.
Bembidion castum Casey, 1918:20 (type loc.: Santa Cruz Mountains, California).

Diagnostic Combination.—A *Bembidion* with eyes moderate in size (Fig. 52C); mandible moderate in length and width (Fig. 52C); terminal maxillary palpomere very small, length less than one-third the length of penultimate palpomere (Fig. 53B); elytron with meshes of microsculpture distinctly transverse in both sexes, lateral margination (Fig. 56B) terminated at humerus, number of striae reduced (Fig. 57B), only medial three or fewer striae distinctly impressed (outer striae indistinct, represented only by rows of minute, faintly impressed punctures), third interval evenly microsculptured, without contrasting dull, depressed fields of coarse microsculpture associated with dorsal setiferous punctures.

General Description.—Size very small, body length 3.6–4.2 mm; body, antennae, and palpi piceous, legs pale or dark rufous, dorsal surface moderately or very shiny, with head, pronotum, and elytra without or with faint to marked brassy metallic reflection (pronota of very few individuals with violet metallic reflection); males with elytral microsculpture effaced or only faintly impressed, elytral microsculpture of females distinctly impressed, with meshes transverse, twice as wide as long.

Dispersal Potential.—Lindroth (1963:262) noted that this species includes both macropterous and brachypterous individuals; but all specimens examined to date from the archipelago are macropterous and probably capable of at least short-range aerial as well as ambulatory dispersal.

Habitat Distribution.—This species apparently is restricted to low and middle elevations, where adults are found in scattered leaf litter (e.g., of *Alnus rubra*) on well-shaded, dry (or only slightly moist), silty substrate at the edges of mixed or strictly deciduous forests (Fig. 12), particularly on secondary floodplains of lowland streams.

Geographical Distribution.—West Coastal, north to Ketchikan, Alaska, south to central California, east only into the Coast Ranges in California and to the west slope of the Cascade Range in Washington and Oregon.

Distribution in the Archipelago.—At present, known from the following islands: Graham, Kunghit, Louise, and Moresby (see Appendix A for locality data).

Material Examined.—22 males, 22 females.

29. **Bembidion iridescens** (LeConte)
(Figures 52C, 53B)

Ochthedromus iridescens LeConte, 1851:191 (type loc.: San Jose, Santa Clara County, California).
Bembidion iridescens (LeConte).—Lindroth 1963:267.

Diagnostic Combination.—A *Bembidion* with legs and antennal scape pale rufous or yellow; eyes moderate in size (Fig. 52C); mandible moderate in length and width (Fig. 52C); terminal maxillary palpomere very small, length less than one-third the length of penultimate palpomere (Fig. 53B); elytron markedly iridescent, with lateral margination (Fig. 56A) prolonged for a short distance medial to humerus, arcuate with respect to basal margin, more than two striae evident to apex (Fig. 57C), third interval evenly microsculptured, without contrasting dull, depressed fields of coarse microsculpture associated with dorsal setiferous punctures.

General Description.—Size very small, body length 3.9–4.6 mm; body piceous, except elytral apex and apical one-third laterally distinctly paler, antennal scape, palpi (except penultimate maxillary palpomere), and legs pale testaceous; elytral microsculpture comprised of very thin, markedly transverse lines, not divided longitudinally to form distinct meshes.

Dispersal Potential.—Adults are macropterous and probably capable of at least short-range aerial as well as ambulatory dispersal.

Habitat Distribution.—This species apparently is restricted to the margins of lowland streams, where adults occur well back from the water under stones, drift debris, or leaf litter on well-shaded, moist, silty, or organic substrate, particularly in secondary floodplain areas. Near Skedans village site (Louise Island), however, adults of this species were found in outwash gravels near the mouth of a small, shaded stream.

Geographical Distribution.—Western North American, north to the Queen Charlotte Islands, south to central California, east to Alberta and eastern Washington.

Distribution in the Archipelago.—At present, known only from Graham, Louise, and Moresby islands (see Appendix A for locality data).

Material Examined.—25 males, 24 females.

30. **Bembidion incertum** (Motschulsky)

(Figures 56A, 58A, 59A, 61B)

Notaphus incertus Motschulsky, 1845:350 (type loc.: Sitka, Baranof Island, Alaska).

Diagnostic Combination.—A *Bembidion* with legs and antennal scape dark, piceous or black; dorsal body surface with distinct brassy metallic reflection (few individuals with faint blue metallic reflection or rufous dorsally); eyes moderate in size (Fig. 52C); mandible moderate in length and width (Fig. 52C); terminal maxillary palpomere very small, length less than one-third the length of penultimate palpomere (Fig. 53B); pronotum (Fig. 58A) short, very broad; elytron shiny but not iridescent, meshes of microsculpture isodiametric or slightly or moderately transverse (Fig. 59A), lateral margination (Fig. 56A) prolonged medial to humerus, arcuate with respect to basal margin, more than two striae evident to apex (Fig. 57C), intervals flat, third interval evenly microsculptured, without contrasting dull, depressed fields of coarse microsculpture associated with dorsal setiferous punctures.

General Description.—Size very small, body length 3.8–4.5 mm; body black; elytra with intervals flat, dorsal setiferous punctures on third interval slightly or moderately foveate.

Dispersal Potential.—Adults are macropterous and probably capable of at least short-range aerial as well as ambulatory dispersal.

Habitat Distribution.—Adults of this species are abundant on mountain peaks and ridges above treeline (Figs. 25–29), where they occur under stones in exposed areas of scattered tundra vegetation and also at the margins of snowfields. Members of this species also occur, although in fewer numbers, below treeline (lowest known elevation is 120 m), at the margins of lakes and very small streams, where they hide by day under stones on both shaded and exposed inorganic shores.

Geographical Distribution.—Western North American, northwest to the inner Aleutian Islands and Alaskan Peninsula, Alaska, south to California, east to Alberta and Colorado.

Distribution in the Archipelago.—At present, known from the following islands: Graham, Kunghit, Louise, and Moresby (see Appendix A for locality data).

Material Examined.—91 males, 102 females.

31. **Bembidion quadrifoveolatum** Mannerheim

(Figure 58D)

Bembidium quadrifoveolatum Mannerheim, 1843:218 (type loc.: Sitka, Baranof Island, Alaska).

Diagnostic Combination.—A *Bembidion* with legs and antennal scape dark, piceous or black; dorsal body surface without or with only faint blue or green metallic reflection; eyes moderate in size (Fig. 52C); mandible moderate in length and width (Fig. 52C); terminal maxillary palpomere very small, length less than one-third the length of penultimate palpomere (Fig. 53B); pronotum (Fig. 58D) small, shape moderately quadrate; elytron not iridescent, meshes of microsculpture (Fig. 59D) distinctly transverse (average width of meshes equal to or greater than 1.5 times their length), lateral margination (Fig. 56A) prolonged medial to humerus, arcuate with respect to basal margin, more than two striae evident to apex (Fig. 57C), intervals slightly or moderately convex, third interval evenly microsculptured, without contrasting dull, depressed fields of coarse microsculpture associated with dorsal setiferous punctures, dorsal setiferous punctures markedly foveate, width of depressions around punctures subequal to combined width of second and third intervals.

General Description.—Size very small, body length 3.4–4.4 mm; elytral intervals slightly to moderately convex.

Dispersal Potential.—Adults are macropterous and probably capable of at least short-range aerial as well as ambulatory dispersal.

Habitat Distribution.—This species is widespread, from near sea level to well above treeline on mountain peaks, where adults are found under stones or in gravel at the margins of small to large streams (Figs. 13, 22), ponds, or lakes (Fig. 23), on moist, exposed or shaded, sand/gravel substrate.

Geographical Distribution.—Western North American, northwest to inner Aleutian Islands and Alaskan Peninsula, Alaska, south to Oregon, east to southwestern Alberta.

Distribution in the Archipelago.—At present, known from the following islands: Graham, Louise, Lyell, Morseby, and Tanu (see Appendix A for locality data).

Material Examined.—362 males, 362 females.

32. **Bembidion farrarae** Hatch

(Figures 58C, 59D)

Bembidion farrarae Hatch, 1950:99 (type loc.: Mount Rainier, Washington).

Diagnostic Combination.—A *Bembidion* with body length 4.0 mm or more; legs and antennal scape dark, piceous or black; dorsal body surface without or with only faint blue or green metallic reflection; eyes moderate in size (Fig. 52C); mandible moderate in length and width (Fig. 52C); terminal maxillary palpomere very small, length less than one-third the length of penultimate palpomere (Fig. 53B); pronotum (Fig. 58C) slightly elongate, shape moderately cordate; elytron not iridescent, meshes of microsculpture (Fig. 59D) distinctly transverse (average width of meshes equal to or greater than 1.5 times their length), lateral margination (Fig. 56A) prolonged medial to humerus, arcuate with respect to basal margin, more than two striae evident to apex (Fig. 57C), intervals slightly or moderately convex, third interval evenly microsculptured, without contrasting dull, depressed fields of coarse microsculpture associated with dorsal setiferous punctures, dorsal setiferous punctures moderately foveate, width of depressions around punctures subequal to width of second interval.

General Description.—Size very small, body length 4.0–4.6 mm; body black.

Dispersal Potential.—Adults are macropterous and probably capable of at least short-range aerial as well as ambulatory dispersal.

Habitat Distribution.—Adults of this species are abundant on mountain peaks and ridges above treeline (Figs. 25–29), where they are found under stones in exposed areas of sparse tundra vegetation, most of them at the margins of snowfields. Members of this species also occur, although in very low numbers, below treeline to near sea level, at the margins of lakes (Fig. 23) and small or medium-sized streams (Fig. 22), where they hide by day under stones on shaded, inorganic banks.

Geographical Distribution.—Western North American, north to Valdez area, Alaska, south to Oregon, also reported from Colorado (Lindroth, 1963:278).

Distribution in the Archipelago.—At present, known only from Graham, Louise, and Moresby islands (see Appendix A for locality data).

Material Examined.—44 males, 45 females.

33. **Bembidion viator** Casey

(Figures 58B, 59B)

Bembidion viator Casey, 1918:31 (type loc.: Masset, Graham Island, British Columbia).—Lindroth 1963:279.

Diagnostic Combination.—A *Bembidion* with legs and antennal scape dark, piceous or black; dorsal body surface with distinct brassy metallic reflection (few individuals with faint blue metallic reflection or rufous dorsally); eyes moderate in size (Fig. 52C); mandible moderate in length and width (Fig. 52C); terminal maxillary palpomere very small, length less than one-third the length of penultimate palpomere (Fig. 53B); pronotum (Fig. 58B) slightly elongate, narrow; elytron faintly iridescent, meshes of microsculpture (Fig. 59B) markedly transverse, lateral margination (Fig. 56A) prolonged medial to humerus, arcuate with respect to basal margin, more than two striae evident to apex (Fig. 57C), intervals flat, third interval evenly microsculptured, without contrasting dull, depressed fields of coarse microsculpture associated with dorsal setiferous punctures.

General Description.—Size very small, body length 3.8–4.3 mm; body black; elytral silhouette subovoid, widest posterior to middle.

Dispersal Potential.—Adults are macropterous and probably capable of at least short-range aerial as well as ambulatory dispersal.

Habitat Distribution.—This species apparently is restricted to the shores of marshes at low and middle elevations, where adults have been collected by treading vegetation (e.g., *Carex* sp.) at the water's edge.

Geographical Distribution.—West Coastal, known only from the Queen Charlotte archipelago and the adjacent mainland (on the coast at Prince Rupert and inland at Smithers, British Columbia).

Distribution in the Archipelago.—At present, known only from Graham and Moresby islands (see Appendix A for locality data).

Material Examined.—4 females.

34. **Bembidion complanulum** (Mannerheim)

(Figure 59C)

Peryphus complanulus Mannerheim, 1853:152 (type loc.: Kodiak, Kodiak Island, Alaska).

Diagnostic Combination.—A *Bembidion* with legs and antennal scape dark, piceous or black; dorsal body surface without or with only faint blue or green metallic reflection; eyes moderate in size (Fig. 52C); mandible moderate in length and width (Fig. 52C); terminal maxillary palpomere very small, length less than one-third the length of penultimate palpomere (Fig. 53B); elytron not iridescent, meshes of microsculpture (Fig. 59C) isodiametric or only slightly transverse (average width of meshes less than 1.5 times their length), lateral margination (Fig. 56A) prolonged medial to humerus, arcuate with respect to basal margin, more than two striae evident to apex (Fig. 57C), intervals slightly or moderately convex, third interval evenly microsculptured, without contrasting dull, depressed fields of coarse microsculpture associated with dorsal setiferous punctures; specimen from above treeline in alpine zone.

General Description.—Size very small, body length 3.0–3.8 mm; body black or piceous; elytral silhouette with lateral margins almost parallel at middle, third elytral interval with setiferous punctures small, not or only slightly foveate.

Dispersal Potential.—Adults are macropterous and probably capable of at least short-range aerial as well as ambulatory dispersal.

Habitat Distribution.—This species is restricted to montane summits and ridges above treeline (Figs. 25–29), where adults occur in exposed areas of dense to sparse tundra vegetation, under stones in both moist and dry sites, particularly near the margins of snowfields.

Geographical Distribution.—Western North American, northwest to inner Aleutian Islands and Alaskan Peninsula, Alaska, south to northern Oregon, east to southwestern Alberta.

Distribution in the Archipelago.—At present, known only from Graham, Louise, and Moresby islands (see Appendix A for locality data).

Material Examined.—120 males, 111 females.

35. **Bembidion planiusculum** Mannerheim

(Figures 56C, 59E)

Bembidium planiusculum Mannerheim, 1843:216 (type loc.: Sitka, Baranof Island, Alaska).

Diagnostic Combination.—A *Bembidion* with head and pronotum with faint blue metallic reflection; head with frontal furrows parallel, or nearly so, not distinctly extended anteriorly onto clypeus (Fig. 61B); eyes moderate in size (Fig. 52C); mandible moderate in length and width (Fig. 52C); terminal maxillary palpomere very small, length less than one-third the length of penultimate palpomere (Fig. 53B); metasternal intercoxal process (between mesocoxae) with margination (Fig. 60B) laterally only; elytron uniformly dark, piceous, black, or brown, without pale maculae, meshes of microsculpture moderately transverse and distinctly impressed (Fig. 59E), lateral margination (Fig. 56C) prolonged medial to humerus and parallel to basal margin, five or more striae distinctly impressed (Fig. 57C), at least in basal one-half, striae smooth or with very faintly impressed punctulae, third interval evenly microsculptured, without contrasting dull, depressed fields of coarse microsculpture associated with dorsal setiferous punctures.

General Description.—Size very small, body length 3.6–4.7 mm; body and appendages piceous, elytra piceous or rufopiceous; elytral silhouette narrow, elongate, lateral margins almost parallel at middle, elytra apices narrow, sixth and seventh elytral intervals merged and distinctly carinate subapically.

Dispersal Potential.—Adults are macropterous, active fliers when disturbed on warm, sunny days, and probably capable of at least short-range aerial as well as ambulatory dispersal.

Habitat Distribution.—This species apparently is restricted to the margins of lowland streams (Fig. 13), where adults occur under stones on both exposed and well-shaded banks, on silt, sand, or gravel substrate.

Geographical Distribution.—West Coastal, northwest to Kenai Peninsula, Alaska, southern limit unknown, east to eastern slope of Coast Ranges in interior British Columbia.

Distribution in the Archipelago.—At present, known only from Graham, Lyell, and Moresby islands (see Appendix A for locality data).

Material Examined.—224 males, 229 females.

36. **Bembidion sejunctum semiaureum** Fall

(Figure 62B)

Bembidion semiaureum Fall, 1922:171 (type loc.: Humboldt County, California).

Diagnostic Combination.—A *Bembidion* with body length more than 5.4 mm; head with frontal furrows parallel or nearly so, not extended anteriorly onto clypeus (Fig. 61B); eyes moderate in size (Fig. 52C); antennae with all antennomeres uniformly pale rufous in color; mandible moderate in length and width (Fig. 52C); terminal maxillary palpomere very small, length less than one-third the length of penultimate palpomere (Fig. 53B); metasternal intercoxal process (between mesocoxae) with margination (Fig. 60C) anteriorly and laterally; elytron with lateral margination (Fig. 56C) prolonged medial to humerus and parallel to basal margin, medial four striae much more deeply impressed than other (lateral) striae, third interval evenly microsculptured, without contrasting dull, depressed fields of coarse microsculpture associated with dorsal setiferous punctures, color pattern as in Figure 62B.

General Description.—Size small, body length 5.9–6.5 mm; head and pronotum piceous or black, elytra (Fig. 62B) pale testaceous except first interval throughout and medial area in middle one-third of elytron darker (brown or piceous), appendages rufous, pronotum with faint brassy metallic reflection.

Dispersal Potential.—Adults are macropterous and probably capable of at least short-range aerial as well as ambulatory dispersal.

Habitat Distribution.—This species apparently is restricted to open, sandy sea beaches with dunes (Fig. 5), where adults are found under driftwood or other debris above the high tide line.

Geographical Distribution.—West Coastal, north to the Queen Charlotte Islands, south to northwestern California, restricted to coastal localities.

Distribution in the Archipelago.—At present known only from Graham Island (see Appendix A for locality data).

Material Examined.—7 males, 3 females.

37. **Bembidion transversale** Dejean

(Figure 62C)

Bembidion transversale Dejean, 1831:110 (type loc.: Nipigon, Lake Superior, Ontario, as restricted by Lindroth 1963:341).

Diagnostic Combination.—A *Bembidion* with body length greater than 5.5 mm; head with frontal furrows parallel or nearly so, not extended anteriorly onto clypeus (Fig. 61B); eyes moderate in size (Fig. 52C); antennae with scape pale rufous, antennomeres 2–11 contrasting piceous in color; mandible moderate in length and width (Fig. 52C); terminal maxillary palpomere very small, length less than one-third the length of penultimate palpomere (Fig. 53B); metasternal intercoxal process (between mesocoxae) with margination (Fig. 60C) anteriorly and laterally; elytron with lateral margination (Fig. 56C) prolonged medial to humerus and parallel to basal margin, five or more striae distinctly impressed (Fig. 57C), at least in basal one-half, third interval evenly microsculptured, without contrasting dull, depressed fields of coarse microsculpture associated with dorsal setiferous punctures, color patterns as in Figure 62C.

General Description.—Size small, body length 5.7–6.6 mm; head and pronotum black or piceous, elytra (Fig. 62C) piceous with large humeral pale spots (extended over laterobasal one-third to one-half of elytron), with or without subapical pale spots (present at least laterally in most individuals, extended medially to second elytral interval in a few individuals), legs rufous or rufopiceous, pronotum with faint metallic brassy reflection, elytra with faint brassy, green, or (in very few individuals) blue metallic reflection.

Dispersal Potential.—Adults are macropterous and probably capable of at least short-range aerial as well as ambulatory dispersal.

Habitat Distribution.—This species apparently is restricted to the margins of large streams and lakeshores (Fig. 17) at low elevation, where adults occur under stones or other cover on exposed or partially shaded banks, on moist silt, sand, or gravel substrate.

Geographical Distribution.—Transamerican, from coastal British Columbia to Newfoundland; in the west, north to southern Yukon Territory, south to California, Arizona, and New Mexico; on the coastal West Coast, north to the Queen Charlotte Islands.

Distribution in the Archipelago.—At present, known only from Graham and Morseby islands (see Appendix A for locality data).

Material Examined.—44 males, 41 females.

38. **Bembidion incrematum** LeConte

(Figures 56B, 57C, 59F, 60B)

Bembidium incrematum LeConte, 1860:316 (type loc.: Sitka, Baranof Island, Alaska).

Diagnostic Combination.—A *Bembidion* with head and pronotum with marked brassy or copperish metallic reflection (very few individuals with blue metallic reflection on pronotum only); head with frontal furrows parallel, or nearly so, not distinctly extended anteriorly onto clypeus (Fig. 61C); eyes moderate in size (Fig. 52C); mandible moderate in length and width (Fig. 52C); terminal maxillary palpomere very small, length less than one-third the length of penultimate palpomere (Fig. 53B); metasternal intercoxal process (between mesocoxae) with margination laterally only (Fig. 60B); elytron (Fig. 57C) with extensive pale maculae, including irregular transverse pale band subapically and more or less expanded humeral maculae, meshes of microsculpture (Fig. 59F) markedly transverse, narrow, indistinctly impressed, lateral margination (Fig. 56B) terminated at humerus, five or more distinctly impressed (at least in basal one-half) striae with large, deeply impressed punctures, third interval evenly microsculptured, without contrasting dull, depressed fields of coarse microsculpture associated with dorsal setiferous punctures.

General Description.—Size small or very small, body length 4.5–5.8 mm; head and pronotum black, elytra brown or piceous with pattern of pale spots as noted above, antennal scape piceous dorsally otherwise rufous, second through 11th antennomeres piceous, legs rufous or rufopiceous; elytra shiny, faintly iridescent, intervals flat.

Dispersal Potential.—Adults are macropterous and probably capable of at least short-range aerial as well as ambulatory dispersal.

Habitat Distribution.—This species apparently is restricted to the margins of small or medium-sized streams, ponds, bogs (Fig. 10), or marshes at low or middle elevations, where adults occur under debris or are active by day on exposed, moist or wet organic substrate, in areas with sparse vegetation (Fig. 11).

Geographical Distribution.—Transamerican, from coastal British Columbia to Newfoundland; in the west, northwest to Kenai Peninsula and lower Yukon River valley, north to Circle, Alaska, south to California.

Distribution in the Archipelago.—At present, known only from Graham and Moresby islands (see Appendix A for locality data).

Material Examined.—64 males, 62 females.

39. **Bembidion indistinctum** Dejean

(Figures 60C, 62A)

Bembidion indistinctum Dejean, 1831:67 (type loc.: San Diego, California, as restricted by Lindroth 1963:361).—Keen 1895:166.—Lindroth 1963:362.

Diagnostic Combination.—A *Bembidion* with body length 4.1–5.2 mm; head with frontal furrows parallel or nearly so, not extended anteriorly onto clypeus (Fig. 61B); eyes moderate in size (Fig. 52C); antennae with all antennomeres uniformly pale rufous in color or scape rufous (at least ventrally) and antennomeres 2–11 rufopiceous; mandible moderate in length and width (Fig. 52C); terminal maxillary palpomere very small, length less than one-third the length of penultimate palpomere (Fig. 53B); metasternal intercoxal process (between mesocoxae) with margination (Fig. 60C) anteriorly and laterally; elytron with lateral margination (Fig. 56C) prolonged medial to humerus and parallel to basal margin, all (or at least medial five or more) striae deeply impressed (Fig. 57C), lateral striae not greatly contrasting with medial striae in depth of impression, third interval evenly microsculptured, without contrasting dull, depressed fields of coarse microsculpture associated with dorsal setiferous punctures, color pattern as in Figure 62A.

General Description.—Size very small, body length 4.1–5.1 mm; head and pronotum black, elytra brown or piceous with extensive pattern (Fig. 62A) of pale spots (base pale except for first and second intervals, third interval with a separate short, longitudinal pale spot sub-basally, humeral pale spot extended posterolaterally to near mid-length and medially onto fourth interval sub-basally, large apical and subapical spots extended medially onto second interval, legs rufous, dorsal body surface with faint brassy or green metallic reflection.

Dispersal Potential.—Adults are macropterous and probably capable of at least short-range aerial as well as ambulatory dispersal.

Habitat Distribution.—As noted by Keen (1895:166) and Lindroth (1963:362), adults are abundant on moist, exposed clay or fine sand flats adjacent to brackish water bodies, such as seaside lagoons and the lower reaches of lowland streams. At Gray Bay, Moresby Island, individuals were found on the clay banks of drying ponds (elevation 4 m) 100 m inland from the upper sea beach and behind a fringe of coniferous forest above the beach. Nonetheless, this area may have been subject to periodic inundation by saltwater at highest tides or during storms through flooding of a nearby tidal stream.

Geographical Distribution.—West Coastal, north to Totem Bay, Kupreanof Island, Alaska, south to southern California, restricted to coastal localities.

Distribution in the Archipelago.—At present, known only from Graham and Moresby islands (see Appendix A for locality data).

Material Examined.—99 males, 74 females.

40. **Bembidion versicolor** (LeConte)

(Figure 61C)

Ochthedromus versicolor LeConte, 1848:462 (type loc.: Nipigon, Lake Superior, Ontario, as restricted by Lindroth 1963:377).

Bembidion versicolor (LeConte).—Lindroth 1963:378.

Diagnostic Combination.—A *Bembidion* with body length less than 4.0 mm; head with frontal furrows slightly convergent and extended anteriorly onto clypeus (Fig. 61C) in most individuals; eyes moderate in size (Fig. 52C); mandible moderate in length and width (Fig. 52C); terminal maxillary palpomere very small, length less than one-third the length of penultimate palpomere (Fig. 53B); metasternal intercoxal process (between mesocoxae) with margination (Fig. 60C) anteriorly and laterally; elytron with lateral margination (Fig. 56C) prolonged medial to humerus and parallel to basal margin, five or more striae distinctly impressed (Fig. 57C), at least in basal one-half, third interval evenly microsculptured, without contrasting dull, depressed fields of coarse microsculpture associated with dorsal setiferous punctures.

General Description.—Size very small, body length 3.0–3.5 mm; head and pronotum black, elytra piceous with pale areas extensive but varied in size (in most individuals, humeral pale areas large, extended posterolaterally to elytral mid-length, medially onto second or third interval, subapical pale spots large, V-shaped, extended medially onto second or third interval, apical pale spot present or not; in very few individuals, elytra almost entirely pale, except setiferous punctures and punctulae of elytral striae piceous), legs rufous, antennal scape rufous and antennomeres 2–11 piceous, dorsal surface of head and pronotum with faint to marked brassy metallic reflection (reflection green or violet in very few individuals).

Dispersal Potential.—Adults are macropterous, active fliers when disturbed on warm, sunny days, and probably capable of at least short-range aerial as well as ambulatory dispersal.

Habitat Distribution.—This species apparently is restricted to the margins of streams, ponds, bogs (Fig. 10), or marshes from near sea level to just below treeline (Fig. 19) on mountain peaks, where adults are active by day on exposed or partially shaded, moist or wet organic substrate. Beetles can be collected also by treading vegetation at the water's edge (Fig. 11) in all of these habitats.

Geographical Distribution.—Transamerican, from coastal British Columbia to Newfoundland; in the west, north to Circle, Alaska, southern limit unknown; on West Coast, north to Wrangell, Alaska.

Distribution in the Archipelago.—At present, known only from Graham and Moresby islands (see Appendix A for locality data).

Material Examined.—81 males, 129 females.

41. **Bembidion fortestriatum** (Motschulsky)

(Figures 60A, 61A)

Omala fortestriata Motschulsky, 1845:352 (type loc.: Sitka, Baranof Island, Alaska).
Bembidion peregrinum Casey, 1918:159 (type loc.: Queen Charlotte Islands, British Columbia).—Lindroth 1963:397.
Bembidion fortestriatum (Motschulsky).—Lindroth 1963:397.

Diagnostic Combination.—A *Bembidion* with body shiny black, a single rufous spot subapically on each elytron; head with frontal furrows distinctly convergent anteriorly and extended anteriorly onto clypeus (Fig. 61A); eyes moderate in size (Fig. 52C); mandible moderate in length and width (Fig. 52C); terminal maxillary palpomere very small, length less than one-third the length of penultimate palpomere (Fig. 53B); metasternal intercoxal process (between mesocoxae) without margination (Fig. 60A); elytron with lateral margination (Fig. 56B) terminated at humerus, five or more striae distinctly impressed (Fig. 57C), at least in basal one-half, third interval evenly microsculptured, without contrasting dull, depressed fields of coarse microsculpture associated with dorsal setiferous punctures.

General Description.—Size very small, body length 3.3–3.9 mm; antennae piceous, legs piceous or rufopiceous, elytral apices of some individuals with diffuse pale areas in addition to distinct lateral subapical spot noted above; pronotum with lateral margin markedly sinuate anterior to rectangular basal angle; elytral striae markedly punctate.

Dispersal Potential.—Adults are macropterous and probably capable of at least short-range aerial as well as ambulatory dispersal.

Habitat Distribution.—This species apparently is restricted to the margins of streams, ponds, bogs (Fig. 10), or marshes from near sea level to middle elevations (up to 250 m), where adults are active by day on exposed or partially shaded, moist, or wet organic substrate. Beetles can also be collected by treading vegetation at the water's edge (Fig. 11) in these habitats.

Geographical Distribution.—Transamerican, coastal British Columbia to Newfoundland; in the west, north to Fairbanks, south to Oregon; on the West Coast, north to Anchorage area.

Distribution in the Archipelago.—At present, known only from Graham and Moresby islands (see Appendix A for locality data).

Material Examined.—178 males, 195 females.

42. **Bembidion spectabile** (Mannerheim)

(Figures 53A, 54A)

Trechus spectabilis Mannerheim, 1852:298 (type loc.: Sitka, Baranof Island, Alaska).
Bembidion spectabile (Mannerheim).—Keen 1895:167.

Diagnostic Combination.—A *Bembidion* with body color piceous or rufopiceous, without metallic reflection or pattern of pale elytral maculae, legs, antennae and mouthparts rufous or pale brown; eyes small (Fig. 52A), moderately reduced in convexity; mandible very long and slender (Fig. 52A); terminal maxillary palpomere small, but long and slender, length equal to or greater than one-third the length of penultimate palpomere (Fig. 53A); elytron with third interval evenly microsculptured, without contrasting dull, depressed fields of coarse microsculpture associated with dorsal setiferous punctures; hindwing (Fig. 54A) full-sized, with reflexed apex distal to stigma. Adults of this species are similar to *Trechus* adults in general appearance but are easily distinguished from the latter by the form of the terminal maxillary palpomere.

General Description.—Size small, body length 6.3–6.6 mm; elytra faintly iridescent, elytral microsculpture comprised of very thin, markedly transverse meshes; pronotum very broad; elytral silhouette subovoid, broad, humeral carinae markedly developed.

Dispersal Potential.—Adults are macropterous and probably capable of at least short-range aerial as well as ambulatory dispsersal.

Habitat Distribution.—Adults of this species are widespread, but uncommon, from near sea level to above treeline. They occur under loose bark of fallen trees, under logs or stones, or in leaf litter on the forest floor in both coniferous (Figs. 14, 15) and mixed forest areas, or under stones above treeline.

Geographical Distribution.—West Coastal, north to Sitka area, Alaska, south to California, east to the Cascade Range in Washington and Oregon and Sierra Nevada in California.

Distribution in the Archipelago.—At present, known from the following islands: Graham, Huxley, Kunga, Lyell, and Moresby (see Appendix A for locality data).

MATERIAL EXAMINED.—2 males, 6 females.

43. **Bembidion oblonguloides** Lindroth

(Figures 52A, 55A)

Bembidion oblongulum; Keen 1895:167.

Bembidion oblonguloides Lindroth, 1963:404 (type loc.: Prince Rupert, British Columbia).

DIAGNOSTIC COMBINATION.—A *Bembidion* with body rufopiceous or rufous, without metallic reflection or pattern of pale elytral maculae, legs, antennae and mouthparts rufous; eyes small (Fig. 52A), moderately reduced in convexity; mandible very long and slender (Fig. 52A); terminal maxillary palpomere small, but long and slender, length equal to or greater than one-third the length of penultimate palpomere (Fig. 53A); pronotum (Fig. 55A) long, with basal sinuation of lateral margin longer, less abrupt; elytron with third interval evenly microsculptured, without contrasting dull, depressed fields of coarse microsculpture associated with dorsal setiferous punctures; hindwing (Fig. 54B) short, reduced to a small, scale-like lobe. Adults of this species are similar to *Trechus* adults in general appearance but are easily distinguished from the latter by the form of the terminal maxillary palpomere.

GENERAL DESCRIPTION.—Size small or very small, body length 4.6–5.7 mm; elytra faintly iridescent, elytral microsculpture very faintly impressed or effaced (if present, then comprised of very thin, markedly transverse meshes); pronotum narrowed; elytral silhouette subovoid, narrow and elongate, humeral carinae present but only moderately developed.

DISPERSAL POTENTIAL.—Adults are brachypterous, incapable of flight, and limited to ambulatory dispersal.

HABITAT DISTRIBUTION.—This species apparently is restricted to coniferous (Figs. 14, 15) or mixed forest areas at low or middle elevations (up to 500 m). Adults have been collected under stones and logs and from leaf litter on the deeply shaded forest floor on moist organic substrate, under stones at the margins of shaded seeps and very small streams, and by sifting clumps of moist mosses taken from the forest floor and the margins of seeps.

GEOGRAPHICAL DISTRIBUTION.—West Coastal, known only from the Queen Charlotte archipelago and adjacent mainland (Prince Rupert and Metlakatla, British Columbia).

DISTRIBUTION IN THE ARCHIPELAGO.—At present, known only from Graham Island (see Appendix A for locality data).

MATERIAL EXAMINED.—19 males, 19 females.

44. **Bembidion oblongulum** (Mannerheim)

(Figures 52B, 54B, 55B)

Trechus oblongulum Mannerheim, 1852:299 (type loc.: Sitka, Baranof Island, Alaska).

DIAGNOSTIC COMBINATION.—A *Bembidion* with body brown or rufous, without metallic reflection or pattern of pale elytral maculae, legs, antennae and mouthparts rufous or pale brown; eyes very small (Fig. 52B), markedly reduced in convexity; mandible very long and slender (Fig. 52B); terminal maxillary palpomere small, but long and slender, length equal to or greater than one-third the length of penultimate palpomere (Fig. 53A); pronotum (Fig. 55B) short, with basal sinuation of lateral margin short and abrupt; elytron with third interval evenly microsculptured, without contrasting dull, depressed fields of coarse microsculpture associated with dorsal setiferous punctures; hindwing (Fig. 54B) short, reduced to a small, scale-like lobe. Adults of this species are similar to *Trechus* adults in general appearance but are easily distinguished from the latter by the form of the terminal maxillary palpomere.

GENERAL DESCRIPTION.—Size very small, body length 4.6–4.9 mm; elytra not or very faintly iridescent, elytral microsculpture very faintly impressed or effaced (if present, then comprised of very thin, markedly transverse meshes); pronotum narrowed; elytral silhouette subovoid, narrow, slightly narrowed basally and widest posterior to mid-length, humeral carina present but only moderately developed.

DISPERSAL POTENTIAL.—Adults are brachypterous, incapable of flight, and limited to ambulatory dispersal.

HABITAT DISTRIBUTION.—This species apparently is restricted to coniferous forest areas just below treeline (Fig. 21), where adults have been found under deeply embedded stones on densely shaded forest floor, in dark, organic (but finely particulate) substrate.

GEOGRAPHICAL DISTRIBUTION.—West Coastal, north to the Kenai Peninsula, Alaska, southern limit unknown, apparently restricted to the region west of the crest of the Coast Ranges in British Columbia and southeastern Alaska.

DISTRIBUTION IN THE ARCHIPELAGO.—At present known only from Moresby Island (see Appendix A for locality data).

MATERIAL EXAMINED.—2 males, 1 female.

TRIBE PSYDRINI

DIAGNOSTIC COMBINATION.—Body length greater than 6.0 mm; head with two supraorbital setiferous punctures dorsomedial to each eye (Fig. 43B), with a transverse sulcus posterior to eyes; frontal furrows extended posteriorly only to level of anterior supraorbital setiferous puncture (Fig. 64A); antennae short, inserted at sides of head, between eyes and bases of mandibles (Fig. 31B), antennomeres 4–11 each only slightly longer than wide; mandible with a setiferous puncture in scrobe (Fig. 63A); terminal maxillary palpomere about equal in length and width to penultimate palpomere (Fig. 50B); pronotum (Fig. 65A) with one or more setiferous punctures on lateral margin near apical angle, posterior transverse impression narrow and very deeply impressed; lateral wall of mesocoxal cavity formed entirely by mesosternum and metasternum (Fig. 32B).

This tribe is worldwide in distribution, with only two genera represented in North America (each by a single species).

GENUS *NOMIUS* LAPORTE

DIAGNOSTIC COMBINATION.—Antennae with scape and pedicel (i.e., antennomeres 1 and 2) glabrous (except for single subapical seta on scape), antennomeres 4–11 with dense pubescence; elytron without discal setiferous punctures on third interval. This is the only psydrine genus recorded from the archipelago; but *Psydrus* LeConte may also occur there. Adults of *Psydrus piceus* LeConte have antennae with all antennomeres (including the scape and pedicel) densely pubescent and elytra with one or two discal setiferous punctures on the third interval.

This genus is Holarctic in distribution.

45. **Nomius pygmaeus** (Dejean)

(Figure 65A)

Morio pygmaeus Dejean, 1831:512 (type loc.. Eagle River, Lake Superior, Michigan).
Nomius pygmaeus (Dejean).—Lindroth 1961:175.

DIAGNOSTIC COMBINATION.—The only known species of *Nomius*.

GENERAL DESCRIPTION.—Size small (range in body length unknown for archipelago, single known specimen 7.0 mm, but according to Lindroth [1961:175], range for species is 6.0–7.7 mm); body and appendages rufous or rufopiceous, dorsal surface shiny, without metallic reflection; elytral microsculpture effaced; elytral silhouette subrectangular, elongate, lateral margins parallel at mid-length, striae moderately or markedly punctate.

DISPERSAL POTENTIAL.—Adults are macropterous and probably capable of at least short-range aerial as well as ambulatory dispersal.

HABITAT DISTRIBUTION.—Habitat preference in the archipelago for this species is unknown; but according to Lindroth (1961: 175), members of this species occur under loose bark of fallen trees in forested areas.

GEOGRAPHICAL DISTRIBUTION.—Holarctic, but apparently broadly disjunct (Lindroth, 1961:175); in the Palearctic Region, apparently restricted to southern Europe, northern Africa, and western Asia; in North America, Transamerican, from coastal British Columbia to Quebec; in the west, north to the Queen Charlotte Islands, Terrace, and Prince George, British Columbia, south to California.

DISTRIBUTION IN THE ARCHIPELAGO.—At present, known only from Talunkwan Island (see Appendix A for locality data).

MATERIAL EXAMINED.—1 female.

TRIBE PTEROSTICHINI

DIAGNOSTIC COMBINATION.—Head with two supraorbital setiferous punctures dorsomedial to each eye (Fig. 43B); antennae inserted at sides of head, between eyes and bases of mandibles (Fig. 31B); mandible without a setiferous puncture in scrobe (Fig. 63B); terminal maxillary palpomere about equal in length and width to penultimate palpomere (Fig. 50B); penultimate labial palpomere with two setae anteriorly (Fig. 72A); lateral wall of mesocoxal cavity formed entirely by mesosternum and metasternum (Fig. 32B); elytron with epipleuron crossed by an internal plica near apical portion of lateral margin (Fig. 68B).

This tribe is worldwide in distribution, with eight genera and more than 300 species represented in North America.

GENUS *PTEROSTICHUS* BONELLI

DIAGNOSTIC COMBINATION.—The only pterostichine genus known or likely to occur in the archipelago.

This genus is Holarctic in distribution, with more than 200 species (arranged in more than 25 subgenera) represented in North America. Seven species occur in the archipelago, several of which are abundant in disturbed areas. As a result, the relatively large, black adults of these species are the carabids most frequently encountered by the casual observer.

46. **Pterostichus lama** (Ménétriés)

(Figure 73A)

Feronia lama Ménétriés, 1844:60 (type area: California).
Pterostichus lama (Ménétriés).—Lindroth 1966:459.

DIAGNOSTIC COMBINATION.—A *Pterostichus* with body length greater than 20.0 mm; elytron without discal setiferous punctures on third interval; basal tarsomere of metatarsus without (or with only a faintly suggested) longitudinal ridge laterally (Fig. 73A).

GENERAL DESCRIPTION.—Size very large, body length 23.6–27.4 mm; body and appendages black, except distal antennomeres slightly paler (piceous or rufopiceous) in some individuals, head and pronotum moderately shiny, elytra dull; sixth visible abdominal sternum of male with distinct longitudinal carina in midline, female with only faintly or moderately distinct longitudinal tubercle (not a carina) in midline.

DISPERSAL POTENTIAL.—Adults are markedly brachypterous, incapable of flight; association with logs on the forest floor along streams or just above sea beaches may provide a mechanism for oversea dispersal in log rafts; otherwise limited to ambulatory dispersal.

HABITAT DISTRIBUTION.—Adults of this species are widespread, but uncommon, in lowland areas of coniferous forest (Figs. 14, 15), where they occur under loose bark of fallen trees or under or in rotting logs on the forest floor.

GEOGRAPHICAL DISTRIBUTION.—West Coastal, north to the Queen Charlotte Islands, south to southern California.

DISTRIBUTION IN THE ARCHIPELAGO.—At present, known from the following islands: Graham, Kunga, Louise, Lyell, Morseby, Reef, and Tanu (see Appendix A for locality data).

MATERIAL EXAMINED.—5 males, 12 females.

47. **Pterostichus crenicollis** LeConte

(Figure 75A)

Pterostichus crenicollis LeConte, 1873:311 (type area: Washington).—Keen 1895: 167.—Lindroth 1966:460.

DIAGNOSTIC COMBINATION.—A *Pterostichus* with body length less than or equal to 19.5 mm; pronotum (Fig. 75A) with lateral margin crenulate throughout; elytron without discal setiferous punctures on third interval; metatarsus with basal tarsomere with a distinct longitudinal ridge laterally (Fig. 73B), distal tarsomere glabrous ventrally (Fig. 74B).

GENERAL DESCRIPTION.—Size medium or large, body length 16.0–19.5 mm; body and appendages black, except distal antennomeres and tarsi slightly paler (piceous or rufopiceous) in some individuals, head and pronotum markedly shiny, elytra slightly shiny in male, dull in female, elytra of male without or with faint violet metallic reflection, female without metallic reflection; male and female without longitudinal carina or tubercle in midline on sixth visible abdominal sternum.

DISPERSAL POTENTIAL.—Adults are markedly brachypterous, incapable of flight; association with logs on the forest floor along streams or just above sea beaches may provide a mechanism for oversea dispersal in log rafts; otherwise limited to ambulatory dispersal.

HABITAT DISTRIBUTION.—Adults of this species are widespread and abundant at low and middle elevations (up to 800 m), where they occur under stones and logs and in leaf litter in areas of deciduous (Fig. 12) or coniferous (Figs. 14, 15) forest. They also occur on shaded cobble-type upper sea beaches (Fig. 3) above the hightide line, under stones along margins of small, shaded streams (Fig. 13), and under debris in open areas (synanthropic sites).

GEOGRAPHICAL DISTRIBUTION.—West Coastal, north to Skagway, Alaska, south to Oregon.

DISTRIBUTION IN THE ARCHIPELAGO.—At present, known from the following islands: Burnaby, Chaatl, Graham, Huxley, Langara, Louise, Lyell, Moresby, Ramsay, Reef, Talunkwan, and Tanu (see Appendix A for locality data).

MATERIAL EXAMINED.—136 males, 99 females.

48. **Pterostichus algidus** LeConte

(Figures 32B, 43B, 50B, 63B, 68B, 72A, 73B, 74A, 80)

Feronia valida Dejean, 1828:325 (type loc.: Norfolk Strait [=Sitka Sound, Baranof Island, Alaska]) (preoccupied by *Feronia valida* Dejean, 1828:294).—Keen 1895: 167.—Lindroth 1966:460.

Pterostichus algidus LeConte, 1852:238 (type area: Oregon).—Lindroth 1966:462.

DIAGNOSTIC COMBINATION.—A *Pterostichus* with body length less than 19.5 mm; elytron without discal setiferous punctures on third interval; metatarsus with basal tarsomere with a distinct longitudinal ridge laterally (Fig. 73B), distal tarsomere with two or more pairs of stout setae on ventral surface (Fig. 74A).

GENERAL DESCRIPTION.—Form as in Figure 80, size medium, body length 12.1–14.8 mm; body and femora and tibiae of legs black, tarsi, antennae, and palpi rufous, rufopiceous, or piceous, head and pronotum moderately shiny, elytra slightly dull in both male and female, elytra without metallic reflection; male and female without longitudinal carina or tubercle in midline on sixth visible abdominal sternum.

DISPERSAL POTENTIAL.—Adults are markedly brachypterous, incapable of flight; association with logs on the forest floor along streams or just above sea beaches may provide a mechanism for oversea dispersal in log rafts; otherwise limited to ambulatory dispersal.

HABITAT DISTRIBUTION.—Adults of this species are widespread, very abundant, almost ubiquitous at low and middle elevations (up to 250 m), where they occur under cover in all habitats except sandy sea beaches and bogs and marshes.

GEOGRAPHICAL DISTRIBUTION.—West Coastal, northwest to Kodiak Island, Alaska, south to Oregon.

DISTRIBUTION IN THE ARCHIPELAGO.—At present, known from the following islands: Anthony, Burnaby, Chaatl, East Copper, Faraday, Graham, Hotspring, Huxley, Kunga, Kunghit, Langara, Louise, Lyell, Maude, Moresby, Murchison, Ramsay, Reef, Talunkwan, and Tanu (see Appendix A for locality data).

MATERIAL EXAMINED.—446 males, 419 females.

49. **Pterostichus amethystinus** Mannerheim

(Figures 74B, 75B, 76A)

Pterostichus amethystinus Mannerheim, 1843:201 (type loc.: Sitka, Baranof Island, Alaska).—Keen 1895:167.—Lindroth 1966:465.

DIAGNOSTIC COMBINATION.—A *Pterostichus* with body length less than 19.5 mm; pronotum (Fig. 75B) with lateral margin smooth or nearly so throughout; elytron with distinct violet metallic reflection, distinctly flattened in cross-sectional aspect, silhouette (Fig. 76A) elongate, with lateral margins subparallel, intervals flat or only slightly convex, without discal setiferous punctures on third interval; metatarsus with basal tarsomere with a distinct longitudinal ridge laterally (Fig. 73B), distal tarsomere glabrous ventrally (Fig. 74B); male with last visible abdominal sternum flat medially.

GENERAL DESCRIPTION.—Size medium, body length 10.8–15.3 mm; body piceous or black, antennae and legs piceous or rufopiceous, palpi rufous or rufopiceous, head and pronotum moderately shiny, elytra slightly dull in both male and female; male and female without longitudinal carina or tubercle in midline on sixth visible abdominal sternum.

DISPERSAL POTENTIAL.—Adults are markedly brachypterous, incapable of flight; association with logs on the forest floor along streams or just above sea beaches may provide a mechanism for oversea dispersal in log rafts; otherwise limited to ambulatory dispersal.

HABITAT DISTRIBUTION.—This species is widespread, in areas of coniferous forest (Figs. 14, 15, 21), from near sea level to treeline on mountain peaks. Adults occur under loose bark of fallen trees or under logs on the forest floor.

GEOGRAPHICAL DISTRIBUTION.—West Coastal, north to Skagway, Alaska, south to northern California.

DISTRIBUTION IN THE ARCHIPELAGO.—At present, known from the following islands: Burnaby, Chaatl, Graham, Harrison, Hotspring, Huxley, Kunga, Langara, Louise, Lyell, Moresby, Ramsay, Reef, and Tanu (see Appendix A for locality data).

MATERIAL EXAMINED.—91 males, 87 females.

50. **Pterostichus castaneus** (Dejean)

(Figure 76B)

Feronia castanea Dejean, 1828:326 (type loc.: Norfolk Strait [=Sitka Sound], Baranof Island, Alaska).

Pterostichus castaneus (Dejean).—Keen 1895:167.—Lindroth 1966:466.

DIAGNOSTIC COMBINATION.—A *Pterostichus* with body length less than 19.5 mm; pronotum (Fig. 75B) with lateral margin smooth or nearly so throughout; elytron without metallic reflection, distinctly convex in cross-sectional aspect, silhouette (Fig. 76B) shorter, subovoid, with lateral margins evenly arcuate, intervals moderately convex, without discal setiferous punctures on third interval; metatarsus with basal tarsomere with a distinct longitudinal ridge laterally (Fig. 73B), distal tarsomere glabrous ventrally (Fig. 74B); male with a bluntly pointed tubercle in midline on last visible abdominal sternum.

GENERAL DESCRIPTION.—Size medium, body length 10.8–11.8 mm; body and femora piceous, rufopiceous, or brown, tibiae, tarsi, and antennae rufous or rufopiceous, palpi rufous, head, pronotum and elytra slightly or moderately shiny, dorsal surface without metallic reflection; female without carina or tubercle in midline on sixth visible abdominal sternum.

DISPERSAL POTENTIAL.—Adults are markedly brachypterous, incapable of flight; association with logs on the forest floor along streams or just above sea beaches may provide a mechanism for oversea dispersal in log rafts; otherwise limited to ambulatory dispersal.

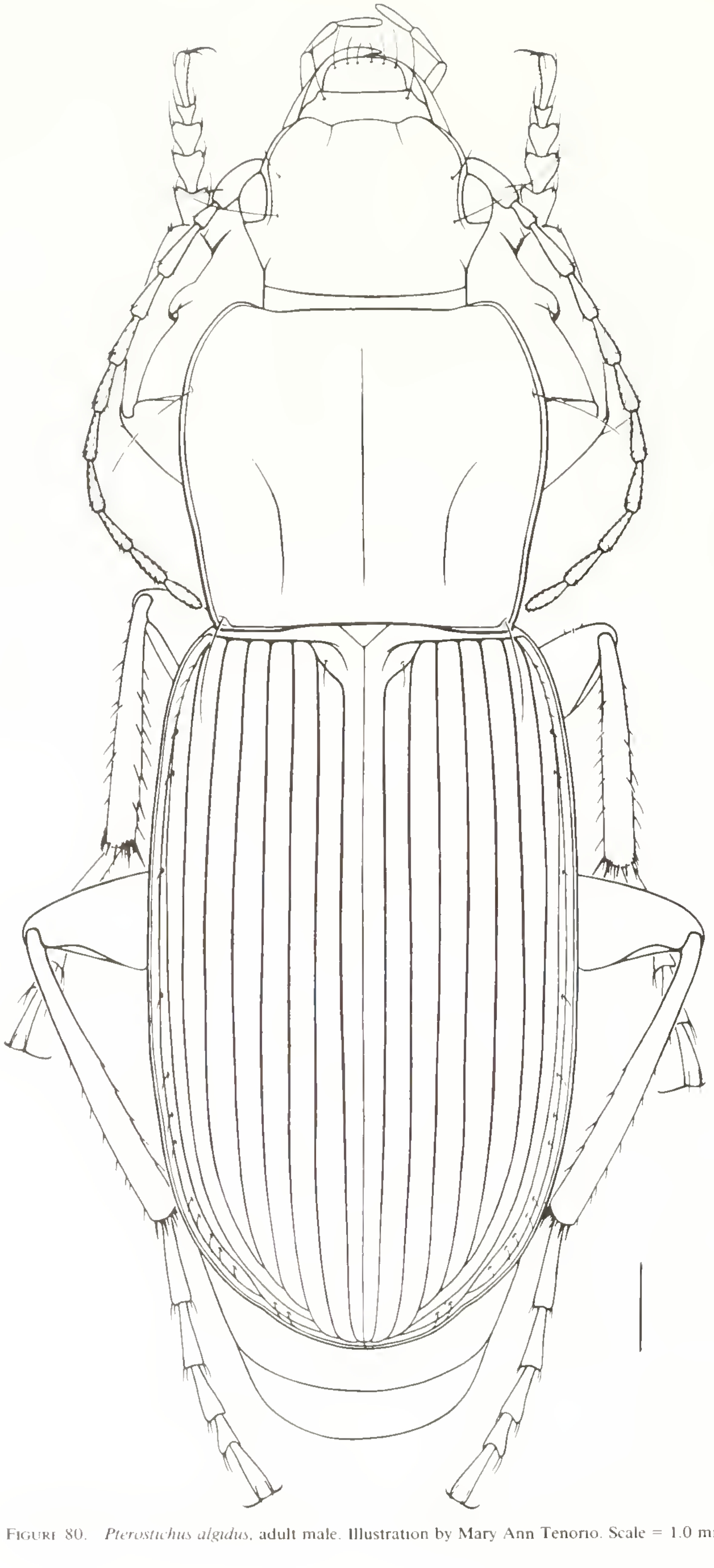


FIGURE 80. *Pterostichus algidus*, adult male. Illustration by Mary Ann Tenorio. Scale = 1.0 mm.

HABITAT DISTRIBUTION.—This species is widespread, in areas of coniferous forest (Figs. 14, 15, 21), from near sea level to just below treeline on mountain peaks. Most adults are found under loose bark or mats of mosses on fallen tree trunks and a few occur under logs on the forest floor.

GEOGRAPHICAL DISTRIBUTION.—Western North American, north to Skagway, Alaska, south to Oregon, east to eastern British Columbia (Revelstoke area).

DISTRIBUTION IN THE ARCHIPELAGO.—At present, known from the following islands: Chaatl, Graham, Kunga, Langara, Louise, Lyell, Moresby, and Tanu (see Appendix A for locality data).

MATERIAL EXAMINED.—62 males, 53 females.

51. **Pterostichus adstrictus** Eschscholtz

(Figure 77B)

Pterostichus adstrictus Eschscholtz, 1823:103 (type loc.: Unalaska, Unalaska Island, Alaska).
Pterostichus luczotii (Dejean).—Keen 1895:167.

DIAGNOSTIC COMBINATION.—A *Pterostichus* with body length 8.9 mm or more; pronotum (Fig. 77B) short, broad, basal sinuation of lateral margin short and very shallow; elytron with two or more discal setiferous punctures on third intervals; hindwing full-sized, with reflexed apex distal to stigma.

GENERAL DESCRIPTION.—Size medium, body length 8.9–12.6 mm; body and appendages black, except distal antennomeres, palpi, tibiae, and/or tarsi slightly paler (piceous or rufopiceous) in some individuals, head and pronotum moderately shiny, elytra moderately shiny in male, dull in female, elytra of male without or with faint brassy metallic reflection, female without metallic reflection; elytra with setiferous punctures of third interval distinctly foveate; male and female without longitudinal carina or tubercle in midline on sixth visible abdominal sternum.

DISPERSAL POTENTIAL.—Adults are macropterous and probably capable of at least short-range aerial as well as ambulatory dispersal.

HABITAT DISTRIBUTION.—This species is widespread at low elevations, where adults occur under stones on cobble-type upper sea beaches (Figs. 3, 4), under debris in supra-tidal meadow areas (Fig. 6), under cover on open ground (e.g., in synanthropic sites), and under drift debris (e.g., logs, boards, stone, etc.) on the banks of large, lowland streams.

GEOGRAPHICAL DISTRIBUTION.—Holarctic, circumpolar; in North America, Transamerican, from coastal British Columbia to Newfoundland; in the west, north to Circle, Alaska, south to California, Arizona, and Colorado; on the West Coast, northwest to the outer Aleutian Islands, Alaska.

DISTRIBUTION IN THE ARCHIPELAGO.—At present, known only from Graham and Moresby islands (see Appendix A for locality data).

MATERIAL EXAMINED.—119 males, 54 females.

52. **Pterostichus riparius** (Dejean)

(Figure 77A)

Feronia riparia Dejean, 1828:332 (type loc.: Norfolk Strait [=Sitka Sound], Baranof Island, Alaska).

DIAGNOSTIC COMBINATION.—A *Pterostichus* with body length less than 8.7 mm; pronotum (Fig. 77A) relatively long and slender, basal sinuation of lateral margin long, distinct; elytron with two or more discal setiferous punctures on third intervals; hindwing short, reduced to a small, scale-like vestige.

GENERAL DESCRIPTION.—Size medium, body length 8.1–8.6 mm; body black or piceous, femora and antennae rufopiceous (antennal scape and antennomeres 2–3 rufous in some individuals), palpi, tibiae, and tarsi rufous, dorsal body surface moderately shiny, elytra with faint brassy metallic reflection and faint iridescence; male and female without longitudinal carina or tubercle in midline on sixth visible abdominal sternum.

DISPERSAL POTENTIAL.—Adults are brachypterous, incapable of flight, and limited to ambulatory dispersal.

HABITAT DISTRIBUTION.—This species apparently is restricted to the margins of medium-sized, shaded streams at lower middle elevations, where adults have been found in piles of small stream drift debris (e.g., twigs and wood chips) on sandy substrate and in shaded gravel overlying sand in primary floodplain areas.

GEOGRAPHICAL DISTRIBUTION.—Western North American, northwest to the Alaskan Peninsula (Cold Bay), south to Oregon, east to Alberta and Montana, apparently absent from coastal localities south of the Queen Charlotte Islands.

DISTRIBUTION IN THE ARCHIPELAGO.—At present, known only from Graham Island (see Appendix A for locality data).

MATERIAL EXAMINED.—5 males, 1 female.

TRIBE PLATYNINI

DIAGNOSTIC COMBINATION.—Head with two supraorbital setiferous punctures dorsomedial to each eye (Fig. 43B); antennae inserted at sides of head, between eyes and bases of mandibles (Fig. 31B); mandible without a setiferous puncture in scrobe (Fig. 63B); terminal maxillary palpomere about equal in length and width to penultimate palpomere (Fig. 50B); lateral wall of mesocoxal cavity formed entirely by mesosternum and metasternum (Fig. 32B); elytron with epipleuron not interrupted by an internal plica (Fig. 68A).

This tribe is worldwide in distribution, but with very few species in the Australian Region. Sixteen genera and more than 400 species are represented in North America, including the Nearctic (i.e., northern montane) portion of Mexico.

GENUS *AGONUM* BONELLI

DIAGNOSTIC COMBINATION.—Head without a transverse impression on dorsum posterior to eyes; tarsal claws smooth, not serrate or pectinate. This is the only platynine genus known to occur in the archipelago. The only other genera likely to occur there are *Calathus* Bonelli, adults of which have pectinate tarsal claws, and *Platynus* Bonelli, adults of which have a shallow, but distinct, transverse impression dorsally on the head posterior to the eyes.

This genus is mainly Holarctic in distribution, apparently also with a few species isolated in South America. About 85 species are represented in North America, including four that occur in the archipelago. Most species occur near water, at the margins of streams or lakes, in marshes, or in bogs.

53. **Agonum ferruginosum** (Dejean)

(Figure 70A)

Anchomenus ferruginosus Dejean, 1828:128 (type area: California).

Diagnostic Combination.—An *Agonum* with antennae with third antennomere (Fig. 69B) glabrous except for ring of long setae at distal apex; pronotum (Fig. 70A) long and narrow, distinctly narrowed basally, widest well anterior to middle; elytron with first, fifth, and seventh intervals without setiferous punctures, only the usual discal setiferous punctures on third interval.

General Description.—Size small, body length 5.6–6.3 mm; body, antennae, and femora black, palpi, tibiae, and tarsi piceous or rufopiceous, elytra with very faint brassy metallic reflection.

Dispersal Potential.—Both macropterous and brachypterous adults occur in the archipelago, the former probably capable of at least short-range aerial dispersal, the latter limited to ambulatory dispersal.

Habitat Distribution.—This species apparently is restricted to open or partially shaded marshes and bogs at low elevation, where adults are collected by treading shoreline vegetation.

Geographical Distribution.—Western North American, north to Farragut Bay, Alaska, south to California, east to Saskatchewan and Colorado.

Distribution in the Archipelago.—At present, known only from northern Graham Island (see Appendix A for locality data).

Material Examined.—2 males, 2 females.

54. **Agonum belleri** (Hatch)

(Figure 69A)

Platynus belleri Hatch, 1933:120 (type loc.: Chase Lake, Snohomish County, Washington).

Diagnostic Combination.—An *Agonum* with antennae with distal one-half of third antennomere (Fig. 69A) covered with short, dense setae; elytron with numerous coarse, setiferous punctures on first, third, fifth, and seventh intervals.

General Description.—Size small, body length 5.7–7.3 mm; body and appendages black, head, pronotum, and elytra without or with faint to marked green, blue, violet, brassy, or copperish metallic reflection (color of reflection varied among body parts in some individuals).

Dispersal Potential.—Adults are brachypterous, incapable of flight, and limited to ambulatory dispersal.

Habitat Distribution.—This species apparently is restricted to wet *Sphagnum* bogs (Figs. 8, 9) at low and lower middle elevations (up to about 150 m), where adults are collected by treading shoreline and floating vegetation.

Geographical Distribution.—West Coastal, north to the Queen Charlotte Islands, south to western Washington.

Distribution in the Archipelago.—At present, known only from Graham Island (see Appendix A for locality data).

Material Examined.—7 males, 3 females.

55. **Agonum metallescens** (LeConte)

(Figures 70C, 71B)

Platynus metallescens LeConte, 1854:48 (type loc.: Sault Ste. Marie, Lake Superior, Ontario).

Diagnostic Combination.—An *Agonum* with antennae with third antennomere (Fig. 69B) glabrous except for ring of long setae at distal apex; pronotum (Fig. 70C) broad, at least as broad basally as apically, widest at or near middle, basal foveae with a distinct convexity at middle; elytron with distinct metallic brassy reflection, first, fifth, and seventh intervals without setiferous punctures, only the usual discal setiferous punctures on third interval, with second setiferous puncture of third interval (Fig. 71B) inserted in third stria, closer to third stria than to second, or midway between second and third striae.

General Description.—Size small, body length 7.6–8.7 mm; body and appendages black. Adults of this and the following species, *A. brevicolle*, are difficult to distinguish, except by reference to the male genitalia, which differ markedly. Intensity of elytral metallic reflection and position of the second setiferous puncture on the third elytral interval are characters for which slight, but apparently consistent, differences exist between members of these two species.

Dispersal Potential.—Adults are macropterous and probably capable of at least short-range aerial as well as ambulatory dispersal.

Habitat Distribution.—This species apparently is restricted to marshes and bogs (Fig. 10) at lower middle elevations (about 150 m), where adults are collected by treading shoreline and floating vegetation.

Geographical Distribution.—Transamerican, from British Columbia to Newfoundland; in the west, north to Terrace, British Columbia, southern limit unknown; on the coast apparently only in the Queen Charlotte Islands.

Distribution in the Archipelago.—At present, known only from Graham Island (see Appendix A for locality data).

Material Examined.—6 males, 8 females.

56. **Agonum brevicolle** Dejean

(Figures 68A, 69B, 70B, 71A)

Agonum brevicolle Dejean, 1828:159 (type area: California).

Diagnostic Combination.—An *Agonum* with antennae with third antennomere (Fig. 69B) glabrous except for ring of long setae at distal apex; pronotum (Fig. 70B) broad, at least as broad basally as apically, widest at or near middle, with basal foveae broad and flat, without or with only a trace of convexity at middle; elytron without or with only faint metallic brassy reflection, first, fifth, and seventh intervals without setiferous punctures, only the usual discal setiferous punctures on third interval, with second setiferous puncture of third interval (Fig. 71A) inserted closer to second stria than to third or in second stria.

General Description.—Size small, body length 7.8–8.7 mm; body and appendages black. See preceding species for additional comments.

Dispersal Potential.—Adults are macropterous and probably capable of at least short-range aerial as well as ambulatory dispersal.

Habitat Distribution.—This species apparently is restricted to marshes and bogs (Fig. 10) at low and middle elevations (up to 250 m), where adults are collected by treading shoreline and floating vegetation.

Geographical Distribution.—West Coastal, north to Queen Charlotte Islands, south to California.

Distribution in the Archipelago.—At present, known only from Graham and Moresby Islands (see Appendix A for locality data).

Material Examined.—42 males, 34 females.

TRIBE ZABRINI

Diagnostic Combination.—Head with two supraorbital setiferous punctures dorsomedial to each eye (Fig. 43B); antennae inserted at sides of head, between eyes and bases of mandibles (Fig. 31B); mandible without a setiferous puncture in scrobe (Fig. 63B); terminal maxillary palpomere about equal in length and width to penultimate palpomere (Fig. 50B); penultimate labial palpomere with three or more setae anteriorly (Fig. 72B); lateral wall of mesocoxal cavity formed entirely by mesosternum and metasternum (Fig. 32B); elytron with epipleuron crossed by an internal plica near apical portion of lateral margin (Fig. 68B). Among the tribes represented in the fauna of the archipelago, zabrines can be confused only with pterostichines, which have only two setae anteriorly on the penultimate labial palpomere, or with harpalines, which have only one pair of supraorbital setiferous punctures (Fig. 72A) and elytra with the epipleuron not interrupted by an internal plica (Fig. 68A). The zabrine body form, in which the base of the pronotum is as broad as (and closely conforming in outline with) the base of the elytra, is also distinctive.

This tribe is mainly Holarctic in distribution, with two genera and just a few species represented in northern portions of the Neotropical, Oriental, and Afrotropical faunal regions. Two genera and more than 100 species occur in North America. Although many zabrine larvae are carnivorous, adults are mainly vegetarian, feeding chiefly on seeds and flowers. Among carabids, zabrines are unusual in being most diverse in drier habitats (such as in open, grassy fields with sparse vegetation).

Genus *Amara* Bonelli

Diagnostic Combination.—The only genus known or likely to occur in the archipelago.

The distribution of this genus is the same as the tribe, Zabrini, except that the former does not occur in the Afrotropical Region. More than 100 species are represented in North America, with three recorded from the archipelago.

57. **Amara sinuosa** (Casey)
(Figure 78A)

Celia sinuosa Casey, 1918:277 (type loc.: Aldermere, British Columbia).

Diagnostic Combination.—An *Amara* with antennae and legs entirely pale rufous in color; pronotum (Fig. 78A) relatively narrow.

General Description.—Size small, body length 5.7–6.5 mm; body piceous, raised lateral margination of pronotum rufous; dorsal body surface moderately shiny, elytral microsculpture effaced in males, moderately impressed in females, with meshes irregular in shape, isodiametric or slightly or moderately transverse.

Dispersal Potential.—Adults are macropterous and probably capable of at least short-range aerial as well as ambulatory dispersal.

Habitat Distribution.—This species apparently is restricted to montane summits and ridges above treeline (Fig. 27), where adults occur on dry or slightly moist, organic substrate under small stones in open, gravelled areas.

Geographical Distribution.—Transamerican, from coastal British Columbia to Newfoundland; in the west, northwest to the Kenai Peninsula, Alaska, south to Oregon, Idaho, and Colorado.

Distribution in the Archipelago.—At present, known only from Moresby Island (see Appendix A for locality data).

Material Examined.—3 males, 2 females.

58. **Amara ellipsis** (Casey)
(Figure 78B)

Celia ellipsis Casey, 1918:252 (type area: Kansas).
Amara ellipsis (Casey).—Lindroth 1968:718.

Diagnostic Combination.—An *Amara* with antennae with only first and second antennomeres pale rufous, femora and tibiae piceous; pronotum (Fig. 78B) relatively broad, basal angles slightly rounded.

General Description.—Size small, body length 7.5–8.3 mm; body black or piceous, dorsal body surface with faint to marked brassy (blue in a few individuals) metallic reflection; elytra shiny in males, dull in females, elytral microsculpture with isodiametric meshes, faintly but distinctly impressed in males, deeply impressed in females.

Dispersal Potential.—Adults are macropterous and probably capable of at least short-range aerial as well as ambulatory dispersal.

Habitat Distribution.—This species apparently is restricted to rather open supra-tidal meadow areas (Fig. 6), where adults occurred under debris (e.g., driftwood) on sandy substrate.

Geographical Distribution.—Transamerican, from coastal British Columbia to Quebec; in the west, north to Queen Charlotte Islands and Prince George, British Columbia, southern limit unknown.

Distribution in the Archipelago.—At present, known only from eastern Graham Island (see Appendix A for locality data).

Material Examined.—1 male, 3 females.

59. **Amara littoralis** Mannerheim
(Figures 72B, 78C)

Amara littoralis Mannerheim, 1843:207 (type loc.: Sitka, Baranof Island, Alaska).—Lindroth 1968:731.
Amara impuncticollis; Keen 1895:167.

Diagnostic Combination.—An *Amara* with antennae with first, second, third, and basal one-half of fourth antennomeres pale rufous, femora piceous, tibiae rufous; pronotum (Fig. 78C) relatively broad, basal angles rectangular, not or only slightly rounded.

General Description.—Size small, body length 7.4–8.4 mm; body black or piceous, dorsal body surface with faint to marked brassy (blue or green in a few individuals) metallic reflection; elytra dull in both males and females (slightly duller in the latter), elytral microsculpture with distinctly isodiametric meshes in both sexes, more deeply impressed in females.

Dispersal Potential.—Adults are macropterous and probably capable of at least short-range aerial as well as ambulatory dispersal.

Habitat Distribution.—This species is restricted to supratidal meadows (Fig. 6) and other open areas (Fig. 7) at low and lower middle elevations. Adults occur under debris (e.g., driftwood, boards) or are active by day in driest sites with low, sparse vegetation. They are especially abundant in synanthropic sites.

Geographical Distribution.—Transamerican, from coastal British Columbia to Newfoundland; in the west, northwest to Kodiak Island and the Kenai Peninsula, Alaska, south to California and Kansas.

Distribution in the Archipelago.—At present, known only from Graham, Lyell, and Moresby islands (see Appendix A for locality data).

Material Examined.—9 males, 24 females.

TRIBE HARPALINI

Diagnostic Combination.—Body not pedunculate in shape (pronotum not or only slightly narrowed basally); head with one supraorbital setiferous puncture dorsomedial to each eye (Fig. 43A); frons without distinct, parallel carinae between eyes; eyes moderate in size; antennae inserted at sides of head, between eyes and bases of mandibles (Fig. 31B), antennomeres 4–11 covered with short, dense setae, antennomere 3 (Fig. 46B) also with short, dense setae, at least on distal one-third; mandible without a setiferous puncture in scrobe (Fig. 45B); pronotum (Figs. 48A, 48B, 79C) not or only slightly narrowed basally; procoxal cavity (Fig. 44B) entirely enclosed by propleuron posteriorly; lateral wall of mesocoxal cavity formed entirely by mesosternum and metasternum (Fig. 32B). Among tribes represented in the fauna of the archipelago, harpalines can be confused only with trechines (smaller species) or pterostichines, platynines, or zabrines (larger species). Harpaline adults can be distinguished easily from those of all these other groups by the presence of only one pair of supraorbital setiferous punctures on the head (Fig. 43A) rather than two.

This tribe is worldwide in distribution and about 25 genera and more than 300 species occur in North America. Species representing three harpaline genera have been recorded from the archipelago. Like zabrines, many harpalines are primarily or partially phytophagous, at least as adults. As a group, they occupy a broad habitat range, from xeric habitats in desert regions to mesic habitats in both temperate and tropical regions.

Genus *Harpalus* Latreille

Diagnostic Combination.—Penultimate labial palpomere plurisetose anteriorly (Fig. 48B); pronotum with basolateral setae absent (Fig. 47B); elytron without short, scattered setae laterally or apically (eighth and ninth intervals bare except for umbilicate series of setae in eighth stria and on ninth interval), scutellar striole present, relatively long, clearly delineated (Fig. 49B); metatarsus with length of tarsomere 1 distinctly shorter than combined lengths of tarsomeres 2 and 3. The only other harpaline genus with adults that might be confused with those of *Harpalus* species is *Anisodactylus* Dejean. Adults of all *Anisodactylus* species likely to occur in the area have metatarsi with tarsomere 1 distinctly longer than the combined lengths of tarsomeres 2 and 3.

This genus is represented in the Palearctic, Nearctic, northern Oriental, and eastern Afrotropical faunal regions, with 55 species occurring in North America north of Mexico.

60. **Harpalus somnulentus** Dejean

(Figures 45B, 48B, 49B)

Harpalus somnulentus Dejean, 1829:333 (type loc.: Norfolk Strait [=Sitka Sound], Baranof Island, Alaska).—Lindroth 1968:789.

Diagnostic Combination.—The only species of *Harpalus* known or likely to occur in the archipelago.

General Description.—Size small or medium, body length 8.1–9.1 mm; body dark brown or piceous, lateral margination of pronotum slightly paler, femora piceous or rufopiceous, tibiae rufous proximally, piceous or rufous distally, antennae, palpi, and tarsi pale testaceous or rufous; elytra shiny in males, dull in females.

Dispersal Potential.—Adults are macropterous and probably capable of at least short-range aerial as well as ambulatory dispersal.

Habitat Distribution.—Adults of this species are uncommon, restricted to supra-tidal meadows (Fig. 6) and other open areas (Fig. 7) at low elevation, where they occur under debris (e.g., stones, boards, etc.) in driest areas with sparse vegetation, especially in synanthropic sites.

Geographical Distribution.—Transamerican, from coastal Alaska and British Columbia east to Newfoundland, and from central Alaska and the Northwest Territories south to Arizona, New Mexico, Texas, and Alabama in the south (G. R. Noonan, pers. comm.).

Distribution in the Archipelago.—At present, known only from Graham and Moresby islands (see Appendix A for locality data).

Material Examined.—3 males, 3 females.

Genus *Trichocellus* Ganglbauer

Diagnostic Combination.—Penultimate labial palpomere bisetose anteriorly (Fig. 48A); mentum with a distinct tooth on anterior margin medially; pronotum with basolateral setae present (Fig. 47A); elytron with numerous short, scattered setae laterally (on eighth and ninth intervals) and apically, scutellar striole absent or very short (Fig. 49A), the eight posterior-most umbilicate setae on ninth interval not distinctly divided into two separate groups of four setae. The only other harpaline genus with adults likely to be confused with those of *Trichocellus* species is *Stenolophus* Stephens, members of which are not known to occur in the archipelago. Adults of all *Stenolophus* species likely to occur in the area lack a distinct tooth anteromedially on the mentum and have the eight posterior-most umbilicate setae of the ninth elytral interval distinctly divided into two groups of four setae.

This genus is Holarctic in distribution, with two species represented in North America.

61. **Trichocellus cognatus** (Gyllenhal)
(Figure 49A)

Harpalus cognatus Gyllenhal, 1827:455 (type loc.: Höberg, Västergötland, Sweden, as restricted by Lindroth 1968:875).
Trichocellus cognatus (Gyllenhal).—Lindroth 1968:876.

DIAGNOSTIC COMBINATION.—The only species of *Trichocellus* known or likely to occur in the archipelago.

GENERAL DESCRIPTION.—Size very small, body length 4.2–4.9 mm; body and appendages piceous or dark brown, except head with diffusely paler areas posterodorsal to eyes, pronotum with apical, basal, and lateral margins diffusely paler, elytra with first interval pale and basal one-sixth to one-half diffusely paler at least laterally, epipleura pale distally, antennae with scape pale, legs with at least bases of tibiae pale.

DISPERSAL POTENTIAL.—Adults are macropterous and probably capable of at least short-range aerial as well as ambulatory dispersal.

HABITAT DISTRIBUTION.—This species apparently is restricted to lowland areas of deciduous forest (Fig. 12) or adjacent supratidal meadow (Fig. 6) or areas of open ground. Adults occur in leaf litter or under debris on the ground and are especially abundant in some disturbed (synanthropic) sites.

GEOGRAPHICAL DISTRIBUTION.—Holarctic, circumpolar; in the Palearctic Region, trans-Eurasian, from Greenland and Iceland to the eastern Asian Pacific Coast; in North American, Transamerican, from the Aleutian Islands, Alaska, to Newfoundland; in the west, northwest to outer Aleutian Islands and Alaskan Peninsula, Alaska, south to southern California, Nevada, and New Mexico.

DISTRIBUTION IN THE ARCHIPELAGO.—At present, known only from Graham Island (see Appendix A for locality data).

MATERIAL EXAMINED.—61 males, 11 females.

GENUS *BRADYCELLUS* ERICHSON

DIAGNOSTIC COMBINATION.—Penultiumate labial palpomere bisetose anteriorly (Fig. 48A); mentum with a distinct tooth on anterior margin medially; pronotum with basolateral setae absent (Fig. 47B); elytron without short, scattered setae laterally or apically (eighth and ninth intervals bare except for umbilicate series of setae in eighth stria and on ninth interval), scutellar striole absent or very short (Fig. 49A), the eight posterior-most umbilicate setae on ninth interval not distinctly divided into two separate groups of four setae. The only other harpaline genus with adults likely to be confused with those of *Bradycellus* species is *Stenolophus* Stephens, members of which are not known to occur in the archipelago. Adults of all *Stenolophus* species likely to occur in the area lack a distinct tooth anteromedially on the mentum and have the eight posterior-most umbilicate setae of the ninth elytral interval distinctly divided into two groups of four setae.

This genus is mainly Holarctic in distribution, with a few species in the northern portion of the Neotropical Region. More than 30 species are represented in North America.

62. **Bradycellus nigrinus** (Dejean)
(Figures 46B, 47B, 48A, 49A)

Harpalus nigrinus Dejean, 1829:399 (type loc.: Norfolk Strait [=Sitka Sound], Baranof Island, Alaska).
Tachycellus nigrinus (Dejean).—Keen 1895:167.
Bradycellus nigrinus (Dejean).—Lindroth 1968:896.

DIAGNOSTIC COMBINATION.—The only species of *Bradycellus* known or likely to occur in the archipelago.

GENERAL DESCRIPTION.—Size small, body length 5.2–5.7 mm; body and appendages piceous or black, except antennal scape rufous or rufopiceous, bases of tibiae rufous or rufopiceous; elytra without or with very faint iridescence, elytral microsculpture with meshes markedly transverse.

DISPERSAL POTENTIAL.—Adults are macropterous and probably capable of at least short-range aerial as well as ambulatory dispersal.

HABITAT DISTRIBUTION.—This species apparently is restricted to low and middle elevations, where adults occur in synanthropic sites on moist substrate, under stones at the margins of small shaded streams (Fig. 13) on moist silty substrate, and in upland marshes (collected by treading shoreline vegetation).

GEOGRAPHICAL DISTRIBUTION.—Transamerican, from coastal British Columbia to Newfoundland; in the west, northwest to Kodiak Island, Alaska, south to California and New Mexico.

DISTRIBUTION IN THE ARCHIPELAGO.—At present, known only from Graham and Moresby islands (see Appendix A for locality data).

MATERIAL EXAMINED.—18 males, 21 females.

ANALYSES OF THE CARABID BEETLE FAUNA

PRESENT FAUNAL DIVERSITY, COMPOSITION, AND AFFINITIES

Present Carabid Diversity

To date, 62 species of carabid beetles (three more than reported by Kavanaugh 1989), representing 22 genera and 17 different tribes, have been recorded from the Queen Charlotte Islands. Two of the included species, *Carabus taedatus* Fabricius and *Scaphinotus angusticollis* Mannerheim, appear to have become extinct in the archipelago, the latter, at least, in historic times (see discussions in respective species accounts). Two additional species, *Nebria gyllenhali castanipes* Kirby and an *Elaphrus* species, known in the archipelago only from fossil material, are probably absent from the present fauna.

Twenty-one of the 24 species originally recorded by Keen (1895) are included in the present faunal list. Of these, 15 were correctly identified, two were given names now considered junior synonyms, and four were misidentified (but easily referable to species known to occur in the archipelago). The occurrence of the three remaining species cited by Keen (*Amara scitula* Zimmerman, *Amara interstitialis* Dejean, and *Tachycellus badiipennis* Haldeman) in the archipelago remains unsubstantiated. No specimens either referable to or misidentified as belonging to these species have been found in Keen's collection (in CNC) or in any other collection studied.

Fifty-three percent of the known carabid faunal diversity is accounted for by just three genera—*Bembidion* (20 species), *Pterostichus* (7 species), and *Nebria* (6 species). Of the remaining 19 genera, 13 are represented by a single species in the archipelago. Several genera or subgenera that contribute one or more species to the fauna of the adjacent mainland and inshore islands apparently are not represented in the fauna. These include

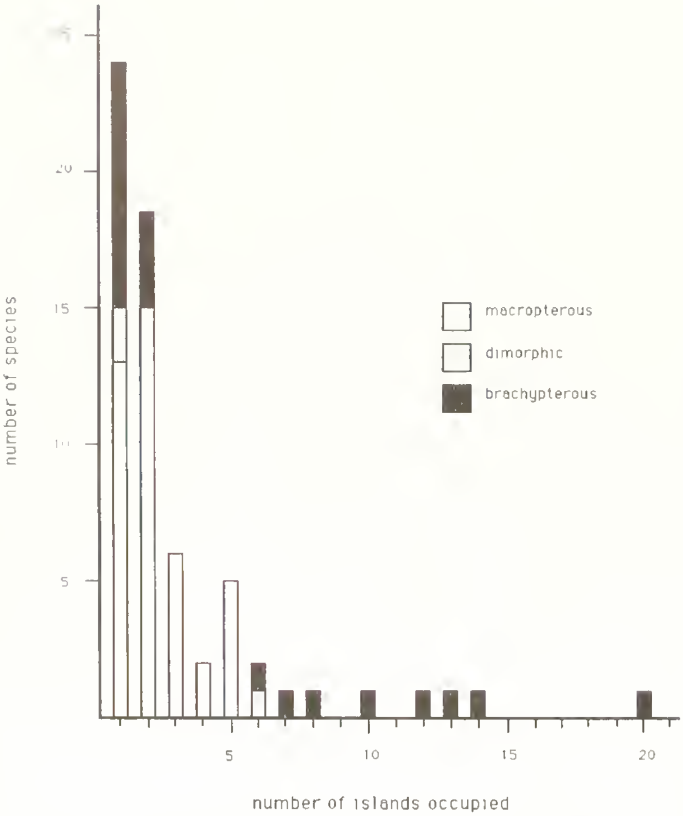


FIGURE 81. Graph illustrating the frequency distribution for number of islands known to be occupied by carabid species and the condition of flight wings for members of each species, in the Queen Charlotte Islands.

Trachypachus, *Patrobus*, subgenus *Tachyta* (the *nanus* group of Lindroth, 1961–69) of genus *Tachys*, *Psydrus*, and subgenus *Europhilus* (the *sordens* group of Lindroth, 1961–69) of genus *Agonum*. Additional sampling in the Queen Charlotte Islands may reveal the occurrence of species of one or more of these groups in the fauna.

Geographical Distributions of Carabids Within the Archipelago

The known occurrence of carabid species among the 23 islands that have been at least partially sampled to date (Table 1) is itemized in Table 4. Clearly, the species appear to differ greatly in their respective distributions within the archipelago. The most widespread species, *Pterostichus algidus*, has been found on 20 of the islands. Adults of this species are also the most frequently encountered carabids on most islands, at least at low and middle elevations. At the opposite end of the distributional spectrum, 24 species (including *Scaphinotus angusticollis* and *Carabus taedatus*, the two species that may have gone extinct in historic times) are known from a single island at present. Of these, 20 are apparently restricted to Graham Island, three (*Carabus taedatus*, *Bembidion oblongulum*, and *Amara sinuosa*) to Moresby Island, and one (*Nomius pygmaeus*) to Talunkwan Island. Figure 81 illustrates the frequency distribution for number of islands known to be occupied by carabid species in the archipelago. Additional sampling within the archipelago, both on previously sampled and as yet unsampled islands, certainly will extend the ranges of many species. However, at least some of the species restricted to Graham Island are unlikely to occur elsewhere because significant areas of the habitats they require apparently occur nowhere else in the archipelago (see below under Habitat Distributions).

Patterns Among the Geographical Ranges of Species

The geographical ranges of all the carabid species represented in the fauna of the archipelago can be classified as belonging to one of six general distribution patterns (Figs. 82–87). Included in each of the patterns are species with more or less extensive distributions, but all species classified in a single pattern share the essential distributional characteristics of that pattern, which are as follows:

1. Holarctic Pattern.—Figure 82. Geographical range includes at least northwestern North America and northeastern Eurasia, but may be much more extensive or fully circumpolar.
2. Transamerican Pattern.—Figure 83. Geographical range includes at least parts of both the eastern and western halves of North America, but may be much more extensive, restricted or not to certain latitudes.
3. Western North American Pattern.—Figure 84. Geographical range includes at least part of the western interior of North America (i.e., east of the crest of Sierra Nevada, Cascade, and Coast ranges) as well as western coastal areas, but may be widely distributed throughout western North America.
4. West Coastal Pattern.—Figure 85. Geographical range is restricted to the Pacific Coast region, east only as far as the crest of the Sierra Nevada, Cascade, and Coast ranges, more or less extensively distributed along the coast; in some species, slight eastward extensions beyond the coastal region, as here defined, up the largest river valleys (i.e., the Columbia, Fraser, and Skeena rivers).
5. Endemic Pattern.—Figure 86. Geographical range is restricted to one or more islands of the Queen Charlotte archipelago.
6. Introduced European Pattern.—Figure 87. Geographical range includes western Eurasia, with occurrence in the Queen Charlotte Islands a secondary result of introduction, in historic times, to the North American mainland (see Lindroth 1957).

Table 4 gives the pattern to which the known geographical distribution of each carabid species in the Queen Charlotte Islands corresponds. Relative representation of the different patterns in the fauna is summarized in Table 5 and illustrated in Figure 88. The fauna comprises mainly species restricted to western North America (72% of the fauna, 45 species), especially to the Pacific Coast region (43% of the fauna, 25 species, including the two species endemic to the archipelago). Eleven species (18% of the fauna) reach their northern geographical range limits in the archipelago, and all of these are either Transamerican or West Coastal in distribution. Only 5% of the fauna (three species) represent Holarctic forms.

The relative proportions of different elements (i.e., groups of species sharing particular geographical range patterns) in the carabid fauna of the archipelago differ markedly from those of analogous elements in the flora and in some other groups in the insect fauna studied to date. Relative proportions of these elements for vascular plants (Calder and Taylor 1968), dragonflies (Canning and Cannings 1983), blackflies (Currie and Adler 1986),

FIGURE 82. Geographical distributions. Holarctic Range Pattern.

TABLE 4. GEOGRAPHICAL DISTRIBUTIONS OF CARABID SPECIES IN THE QUEEN CHARLOTTE ISLANDS.

Taxon	Island[1,2]																							#1[3]	RP[4]	Wings[5]
	KT	AN	MO	EC	BU	HU	RA	HS	MR	FA	LY	KU	TN	TL	RF	LO	SK	HI	CH	MD	GR	HA	LG			
Cicindela oregona LeConte	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	x	–	–	1	3	m
Scaphinotus angusticollis Mannerheim	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	(x)	–	–	1	4	b
Scaphinotus marginatus Fischer	x	–	x	–	x	x	x	–	–	–	x	x	x	x	x	x	–	x	–	–	x	–	–	13	3	b
Cychrus tuberculatus Harris	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	x	–	–	–	–	x	–	–	2	4*	b
Carabus nemoralis Müller	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	x	–	–	1	6	b
Carabus taedatus Fabricius	–	–	(x)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	2	b
Leistus ferruginosus Mannerheim	–	–	x	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	x	–	–	2	3	m
Nebria charlottae Lindroth	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	x	–	–	1	5	b
Nebria louiseae Kavanaugh	–	–	x	–	x	–	x	x	–	–	x	–	x	x	x	x	x	–	–	–	–	–	–	10	5	b
Nebria haida Kavanaugh	–	–	x	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	x	–	–	2	4**	b
Nebria sahlbergii sahlbergii Fischer	–	–	x	–	x	–	–	–	–	–	x	–	x	–	–	–	–	–	–	–	x	–	–	5	3	m
Nebria mannerheimii Fischer	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	x	–	–	1	4	m
Nebris diversa LeConte	–	–	x	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	x	–	–	2	4*	m
Notiophilus sylvaticus Eschscholtz	–	–	x	–	–	–	–	–	–	–	x	x	x	–	–	x	–	–	–	–	x	–	–	6	4	b
Elaphrus americanus sylvanus Goulet	–	–	x	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	x	–	–	2	3	m
Elaphrus clairvillei Kirby	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	x	–	–	1	2	m
Loricera decempunctata Eschscholtz	–	–	x	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	x	–	–	2	4	m
Dyschirius pacificus Lindroth	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	x	–	–	1	4	b
Broscodera insignis Mannerheim	–	–	x	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	x	–	–	2	4	m
Zacotus matthewsi LeConte	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	x	–	–	1	3	b
Diplous aterrimus Dejean	–	–	x	–	–	–	–	–	–	–	x	–	–	–	–	–	–	–	–	–	x	–	–	3	3	m
Trechus obtusus Erichson	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	x	–	–	1	6	d
Trechus ovipennis Motschulsky	–	–	x	–	–	–	x	–	–	–	–	x	–	x	–	x	–	–	–	–	x	–	–	6	4	b
Trechus chalybeus Dejean	–	–	x	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	x	–	–	2	3	b
Bembidion zephyrum Fall	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	x	–	–	1	4	m
Bembidion inaequale opaciceps Casey	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	x	–	–	1	3	m
Bembidion dyschirinum LeConte	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	x	–	–	1	3	m
Bembidion castum Casey	x	–	x	–	–	–	–	–	–	–	–	–	–	–	–	x	–	–	–	–	x	–	–	4	4	m
Bembidion iridescens LeConte	–	–	x	–	–	–	–	–	–	–	–	–	–	–	–	x	–	–	–	–	x	–	–	3	3	m
Bembidion incertum Motschulsky	x	–	x	–	–	–	–	–	–	–	–	–	–	–	–	x	–	–	–	–	x	–	–	4	3	m
Bembidion quadrifoveolatum Mannerheim	–	–	x	–	–	–	–	–	–	–	x	–	x	–	–	x	–	–	–	–	x	–	–	5	3	m

TABLE 4. CONTINUED.

Taxon	Island[1,2]																							#I[3]	RP[4]	Wings[5]
	KT	AN	MO	EC	BU	HU	RA	HS	MR	FA	LY	KU	TN	TL	RF	LO	SK	HI	CH	MD	GR	HA	LG			
Bembidion farrarae Hatch	–	–	x	–	–	–	–	–	–	–	–	–	–	–	–	x	–	–	–	–	x	–	–	3	3	m
Bembidion viator Casey	–	–	x	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	x	–	–	2	4**	m
Bembidion complanulum Mannerheim	–	–	x	–	–	–	–	–	–	–	–	–	–	–	–	x	–	–	–	–	x	–	–	3	3	m
Bembidion planiusculum Mannerheim	–	–	x	–	–	–	–	–	–	–	x	–	–	–	–	–	–	–	–	–	x	–	–	3	4	m
Bembidion sejunctum semiaureum Fall	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	x	–	–	1	4*	m
Bembidion transversale Dejean	–	–	x	–	–	–•	–	–	–	–	–	–	–	–	–	–	–	–	–	–	x	–	–	2	2*	m
Bembidion incrematum LeConte	–	–	x	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	x	–	–	2	2*	m
Bembidion indistinctum Dejean	–	–	x	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	x	–	–	2	4	m
Bembidion versicolor LeConte	–	–	x	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	x	–	–	2	2	m
Bembidion fortestriatum Motschulsky	–	–	x	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	x	–	–	2	2	m
Bembidion spectabile Mannerheim	–	–	x	–	–	x	–	–	–	–	x	x	–	–	–	–	–	–	–	–	x	–	–	5	4	m
Bembidion oblonguloides Lindroth	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	x	–	–	1	4**	b
Bembidion oblongulum Mannerheim	–	–	x	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	4	b
Nomius pygmaeus Dejean	–	–	–	–	–	–	–	–	–	–	–	–	–	x	–	–	–	–	–	–	–	–	–	1	1	m
Pterostichus lama Ménétriés	–	–	x	–	–	–	–	–	–	–	x	x	x	–	x	x	–	–	–	–	x	–	–	7	4*	b
Pterostichus crenicollis LeConte	–	–	x	–	x	x	x	–	–	–	x	–	x	x	x	x	–	–	x	–	x	–	x	12	4*	b
Pterostichus algidus LeConte	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	–	–	x	x	x	–	x	20	4	b
Pterostichus amethystinus Mannerheim	–	–	x	–	x	x	x	x	–	–	x	x	x	–	x	x	–	–	x	–	x	x	x	14	4	b
Pterostichus castaneus Dejean	–	–	x	–	–	–	–	–	–	–	x	x	x	–	–	x	–	–	x	–	x	–	x	8	3	b
Pterostichus adstrictus Eschscholtz	–	–	x	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	x	–	–	2	1	m
Pterostichus riparius Dejean	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	x	–	–	1	3	b
Agonum ferruginosum Dejean	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	x	–	–	1	3	d
Agonum belleri Hatch	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	x	–	–	1	4*	b
Agonum metallescens LeConte	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	x	–	–	1	2*	m
Agonum brevicolle Dejean	–	–	x	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	x	–	–	2	4*	m
Amara sinuosa Casey	–	–	x	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	2	m
Amara ellipsis Casey	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	x	–	–	1	2*	m

TABLE 4. CONTINUED.

Taxon	Island[1,2]																									
	KT	AN	MO	EC	BU	HU	RA	HS	MR	FA	LY	KU	TN	TL	RF	LO	SK	HI	CH	MD	GR	HA	LG	#I[3]	RP[4]	Wings[5]
Amara littoralis																										
Mannerheim	–	–	x	–	–	–	–	–	–	–	x	–	–	–	–	–	–	–	–	–	x	–	–	3	2	m
Harpalus somnulentus																										
Dejean	–	–	x	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	x	–	–	2	2	m
Trichocellus cognatus																										
Gyllenhal	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	x	–	–	1	1	m
Bradycellus nigrinus																										
Dejean	–	–	x	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	x	–	–	2	2	m
Totals per island	4	1	40	1	6	5	6	3	1	1	14	8	10	6	6	16	1	1	4	1	57	1	4			

[1] Islands: AN = Anthony, BU = Burnaby, CH = Chaatl, EC = East Copper, FA = Faraday, GR = Graham, HA = Harrison, HI = Hibben, HS = Hotspring, HU = Huxley, KT = Kunghit, KU = Kunga, LG = Langara, LO = Louise, LY = Lyell, MD = Maude, MO = Moresby, MR = Murchison, RA = Ramsay, RF = Reef, SK = West Skedans, TL = Talunkwan, TN = Tanu.

[2] Distribution in the archipelago: x = known to occur on island; – = not known to occur on island; (x) = known from specimens collected on island, but species probably now extinct in the archipelago.

[3] #I = number of islands from which the species has been recorded.

[4] RP = geographical range pattern for the species: 1 = Holarctic; 2 = Transmerican; 3 = Western North American; 4 = West Coastal; 5 = Endemic; 6 = Introduced to North America; * = northern limit of known geographical range at the Queen Charlotte Islands; ** = range outside the archipelago restricted to the adjacent mainland coast.

[5] Wings = condition of the hindwings: m = macropterous, full-sized wings; b = brachypterous, shortened and/or narrowed wings, d = dimorphic, both macropterous and brachypterous individuals found in the archipelago.

weevils (Anderson 1988), and carabids are illustrated in Figure 89. The vascular plant flora and dragonfly fauna include a large Holarctic component (38% and 23% of the flora and fauna, respectively), whereas the blackfly, weevil, and carabid faunas have only a minor Holarctic representation (only 5 or 6% each). Among dragonflies, the Transamerican element is dominant (70% of the fauna), the Western North American element small (only 7%), and more restricted coastal elements absent. Both blackfly and carabid faunas include diverse Transamerican elements (31% and 19% of the faunas, respectively) but vascular plants and weevils do not (9% and 5%, respectively). The dominant element (44% of the species) in the blackfly fauna is the Western North American component, which is also very well represented in the carabid and weevil faunas (29% and 21% of the species, respectively). The latter two faunas are also similar in having the West Coastal element dominant (58% of the weevil and 40% of the carabid faunas). Among the groups compared here, only the vascular plant flora and carabid fauna include an endemic element at the species level (one and two species, 0.02% of the flora and 3% of the fauna, respectively), although endemic subspecies of mammals, birds, and plants also have been described. The vascular plant flora also includes a diverse (about 20% of the flora) Introduced element. This element is also represented, by two species each, in the weevil and carabid faunas.

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

Range pattern	No. spp.	NL[1]
Holarctic	3	0
Transamerican	12	4
Western North American	18	0
West Coastal	25	7
Endemic	2	n/a
Introduced	2	0

[1] NL = number of species that reach their northern distributional limit at the Queen Charlotte Islands.

Habitat Distributions of Carabids Within the Archipelago

Table 6 lists the known habitat distributions of carabid species in the Queen Charlotte Islands. Differences between data presented by Kavanaugh (1989, Table 2) and those provided here reflect both additional sampling and slight changes in the habitat classification itself (see Methods and Materials section for discussion of habitat types). Habitat distributions for two of the 62 carabid species in the fauna of the archipelago, *Scaphinotus angusticollis* and *Bembidion dyschirinum*, remain unknown. As noted above in the species account and elsewhere, *S. angusticollis* has probably become extinct in the archipelago. Additional sampling in all habitats, particularly in the Masset area, may yet produce specimens of *B. dyschirinum* and help to identify the habitat requirements of members of that species in the archipelago.

Carabid species diversity in relation to habitat type is summarized in Table 7 and illustrated in Figure 90. The fauna of the Queen Charlotte Islands is notable for its overall balance in diversity among the 15 habitat types recognized. Habitats with the highest diversity of carabid species are the lowland deciduous forest and lowland, small, shaded stream shore types (15 species each), followed closely by lowland marsh or bog, lowland coniferous forest, and lowland open/synanthropic habitats (with 14, 13, and 13 species each, respectively). The least diverse habitats are the upland lake or stream shore and subalpine forest types (with five species each), followed by the two upper sea beach habitats (with six species each). If the basic habitat types are grouped into beach, open ground, forest, wetland, and alpine habitat complexes (Table 7), then high species diversity in wetland (a total of 35 species, 58.3% of the fauna) and forest (20 species, 33.3% of the fauna) habitats is more readily apparent. In the carabid beetle faunas of most areas studied to date, species diversity is highest in lowland and/or lower montane habitats and decreases steadily with increased elevation (e.g., see Armin 1963; Darlington 1943, 1971; Greenslade 1968). This seems to be true also for the fauna of the Queen Charlotte Islands. If the basic habitat types are regrouped as either lowland or upland habitat complexes, then higher diversity of the lowland is obvious. Fifty-four species (90.0% of the fauna) occur in one or more lowland habitats, while 29 species (48.3% of the fauna) live in at least one upland habitat.

Although species diversity is distributed broadly among the different habitat types, carabid species nonetheless exhibit marked habitat specificity in the archipelago (Fig. 91). Twenty-four species (40.0% of the fauna) are apparently restricted to a single habitat type, and 65% of the species occur in only one or two habitats. Less than 12% of the species occupy more than four of the 15 habitat types recognized. At present, much less is known about the habitat distributions of most of the 60 non-endemic carabid species outside of the archipelago than within it. This is indeed unfortunate because equivalent knowledge of the habitat distributions of these same species on the mainland could provide data needed for meaningful tests of such concepts as "competitive release" (MacArthur 1972) in island populations, or conversely, competitive restriction in mainland populations. Diamond's (1970) study of the habitat distributions of birds on Karkar Island in relation to their distributions on 'mainland' New Guinea provides a classic example of such a test. The only carabid species for which such data are now available for populations both on the adjacent mainland and in the archipelago are the four non-endemic *Nebria* species. For each of these four species (*Nebria haida*, *N. sahlbergii sahlbergii*, *N. diversa*, and *N. mannerheimii*) habitat distributions of mainland and islandic populations are identical, even though mainland populations coexist with populations of at least six other congeneric species (*Nebria crassicornis* Van Dyke, *Nebria acuta* Lindroth, *Nebria gebleri* Dejean, *Nebria kincaidi* Schwarz, *Nebria meanyi* Van Dyke, and *Nebria piperi* Van Dyke), as well as with other potential competitors. These data suggest that (1) "competitive release" has not occurred for *Nebria* species in the archipelago, (2) habitat distributions of these same species on the mainland are not restricted by competition, or, most likely, (3) competition plays little or no role in restricting habitat distribution in either mainland or insular populations. To what extent competition affects the habitat distributions of other species in the archipelago remains unknown.

Table 8 illustrates relationships between geographical and habitat distributions and carabid diversity. Several patterns are readily apparent. The only faunal element represented in all habitat types is the West Coastal element, which is also the most diverse element in all but the lowland large lake or stream shore and upland lake or steam shore habitats. No one habitat type includes representatives of all six faunal elements. Holarctic and Introduced elements are restricted to lowland habitats, the latter to the immediate vicinity of human habitation or environmental disturbance. Transamerican elements are also restricted to lowland habitats, except for their occurrence (six species) in the upland marsh or bog habitat. The Endemic element is restricted to the cobble upper sea beach habitat type. Finally, the fauna of the sandy upper sea beach habitat type includes six species, all of which belong to the West Coastal faunal element.

Hindwing Development and Carabid Distributions

Table 4 records the degree of development of hindwings in adults of each of the 62 carabid species represented in the Queen Charlotte Islands, based on examination of all available specimens of each species. All adults of 38 species (61% of the fauna) have fully developed (i.e., *macropterous*) hindwings; 22 species (36%) have all adults with hindwings reduced in size (i.e., *brachypterous*); and 2 species (3%) are *dimorphic* in this regard (i.e., both macropterous and brachypterous adults occur in populations in the archipelago). Without exception, condition of the hindwings for members of each species in the archipelago is typical for that species throughout its geographical range. There is no evidence, for example, of the development of brachyptery within the archipelago for any species in which adults elsewhere are all macropterous; nor is there any indication that, in dimorphic species, either macropterous or brachypterous individuals are at any particular (selective) advantage in the archipelago.

Intuitively, one would expect that, all other factors being equal, organisms that can walk and fly should be able to disperse more efficiently and extensively than those that can only walk. Also, they should be able to cross at least some barriers, areas of unsuitable habitat (such as bodies of water), that walking individuals cannot cross. By extension, species that have individuals capable of flight should be able to establish and maintain larger geographical ranges, and perhaps also larger habitat ranges, than species with only flightless members. To the extent that such relationships between flight capability and distribution can be expected, what is observed is the carabid fauna of the Queen Charlotte Islands is in some ways surprising. For example, Figure 81 illustrates the relationship between hindwing development and the number of islands in the archipelago known to be occupied by a species. All members of the seven most wide-ranging species (i.e., all those that have been recorded from seven or more islands in the archipelago) are brachypterous, not macropterous. Hence there is no evidence to suggest brachyptery as a significant factor in limiting geographical distribution within the archipelago. However, the observed relationship between hindwing development and overall geographical distribution, as illustrated in Figure 92, is as predicted. Adults of those species with widest geographical distributions (i.e., all the Holarctic species, 92% of the Transamerican species, and 67% of the Western North American species) are macropterous, whereas 50% of the West Coastal and both of the Endemic species have brachypterous adults.

The relationship between hindwing development and habitat in the fauna of the archipelago is generally similar to that found in other faunas studied to date (Erwin 1979). The highest incidence of brachyptery is in forest habitats, whether lowland (67–85% of species represented in the habitat) or upland (88–91%), deciduous (67–88%) or coniferous (85–91%). The lowest incidence of brachyptery (and highest of macroptery) is in waterside habitats (0–27%), whether marsh or bog (7–18%) or lake or stream shore (0–27%). Whereas 33% of species in the sandy upper sea beach habitat have brachypterous members, 67% of those in the cobble sea beach habitat have short-winged adults. The relationship between habitat range and hindwing development, as seen in Figure 91, is similar to that for geographical range within the archipelago. The four species that occupy the broadest habitat ranges (more than seven habitats each) all have brachypterous adults. Hence, there is no evidence to suggest brachyptery as a factor limiting the habitat ranges of species in the archipelago.

It is clear that carabid species with only brachypterous adults nonetheless may be highly successful in establishing and, presumably, maintaining broad geographical and habitat ranges within the archipelago. In fact, some of these species actually appear to be more successful in this regard than those with macropterous adults. How can this be? What, if anything, is wrong with the initial predictions concerning relationships between hindwing development and distribution? Nelemans (1987) has shown that wing size alone may not be a reliable indicator of flight capability. He found that, at least in *Nebria brevicollis* Fabricius, all adults of which are macropterous, functional wing muscles develop only in adults that were well fed as larvae. While sufficient larval food could be provided under laboratory conditions to induce subsequent flight muscle development in most reared adults, few larvae appear to receive even the minimum requisite food in the wild to trigger development of muscles in the adult stage. The incidence of functional flight muscles among adults in the wild is very low. Darlington (1936, 1943) and Kavanaugh (1985) have discussed the suite of other structural adaptations, such as shortening of the metathorax and narrowing of the elytral base, that frequently accompany brachyptery per se among carabids. As a result of these associated structural modifications, brachypterous beetles are often far more efficient walking and running organisms than were their flying ancestors. If, in fact, flight muscles rarely if ever develop among macropterous carabids in the Queen Charlotte Islands, then these beetles may actually be poorer dispersers than their brachypterous equivalents. Clearly, studies of flight muscle development among the macropterous adults of species in the archipelago are needed to ascertain their true flight capability. If these beetles are functionally flightless, then their relatively restricted distributions do not, in fact, negate the original predictions.

Affinities of the Carabid Fauna

Inventory of the carabid species of the Pacific Northwest coastal region and of the distributions of these species within the region is far from complete. The only areas along the coast that have been intensively studied to date are Kodiak Island (Lindroth 1969), the Lituya Bay region of southeastern Alaska (D. H. Mann and Kavanaugh unpubl.), and the Queen Charlotte Islands (Kavanaugh 1989 and present report). The known faunas of other coastal areas from northwestern Washington to southwestern Alaska represent unknown fractions of the total number of species actually represented in each area. Nonetheless, enough

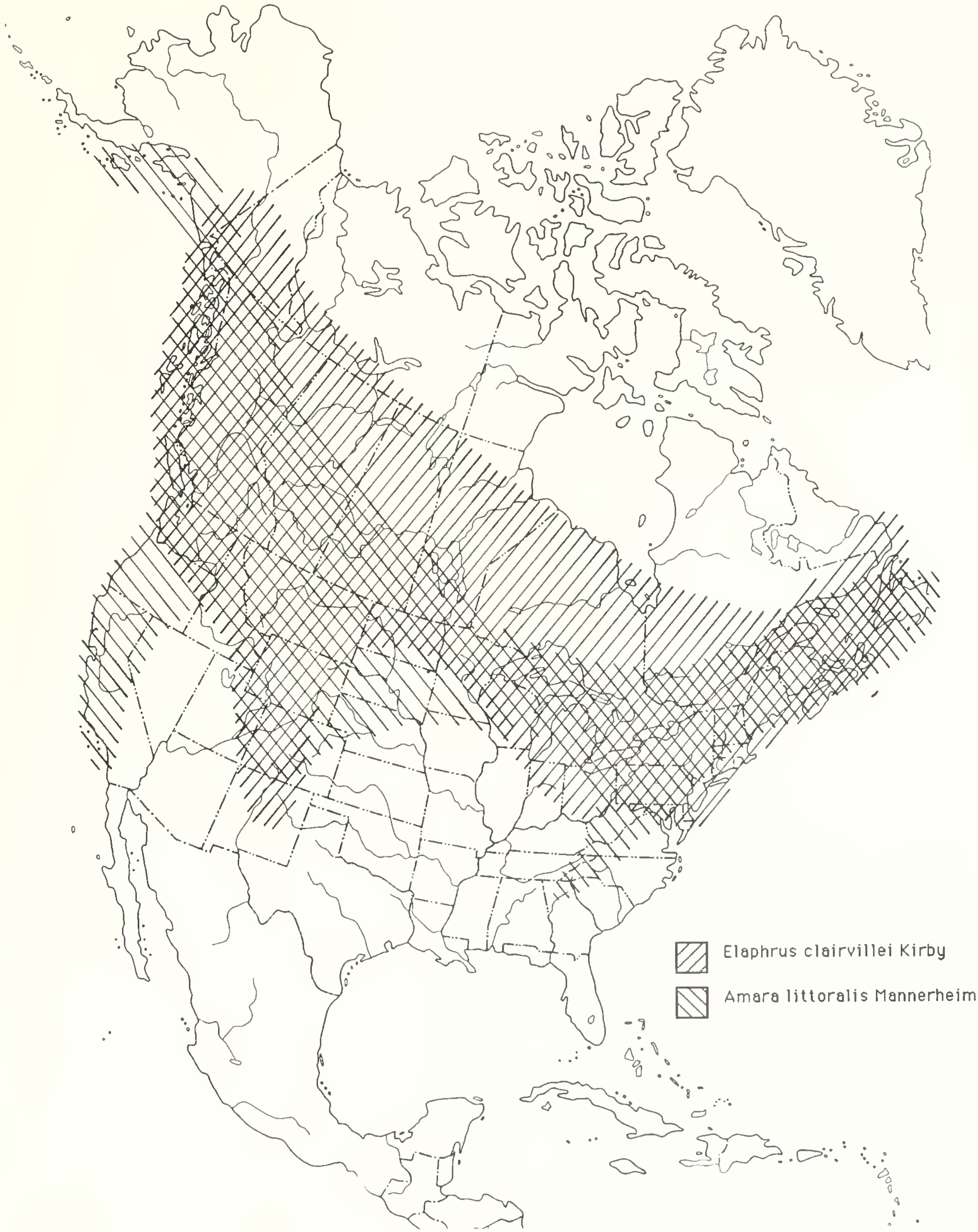
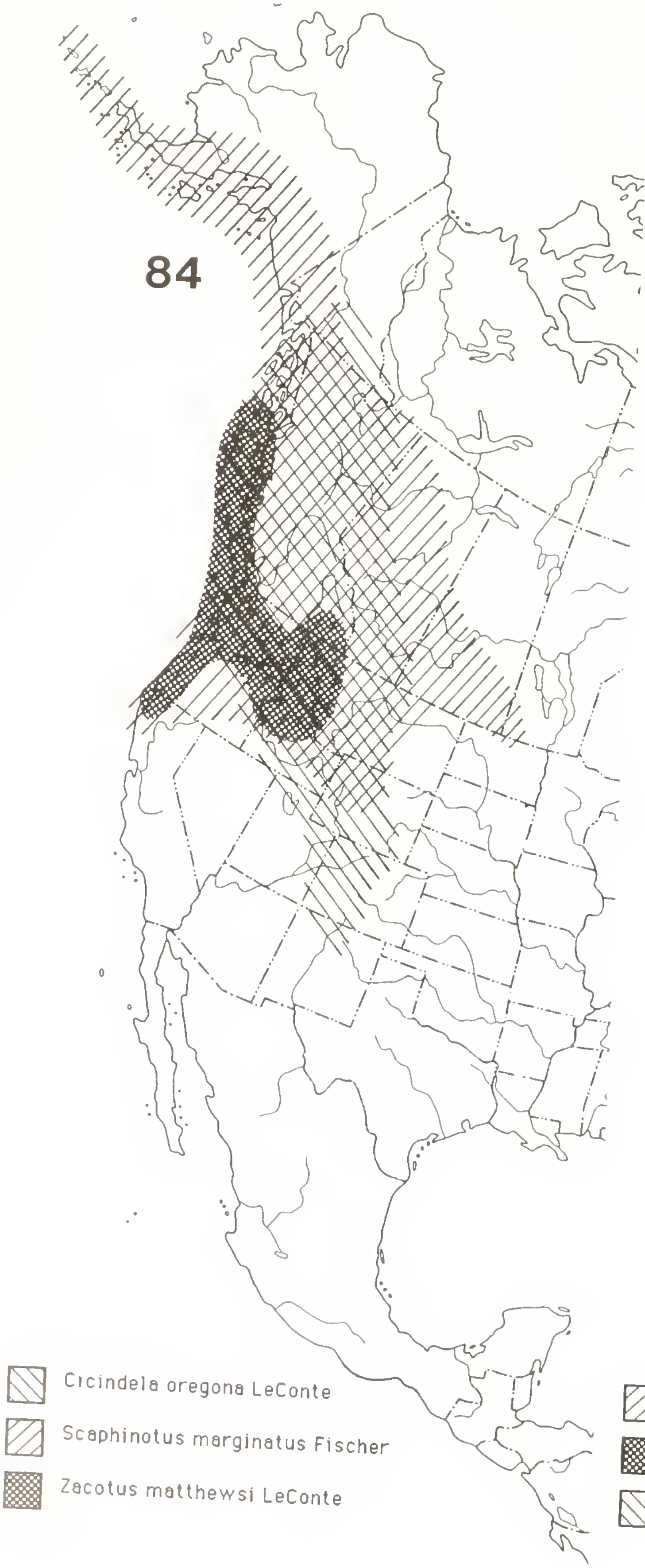


FIGURE 83. Geographical distributions. Transamerican Range Pattern.


84
Cicindela oregona LeConte
Scaphinotus marginatus Fischer
Zacotus matthewsi LeConte

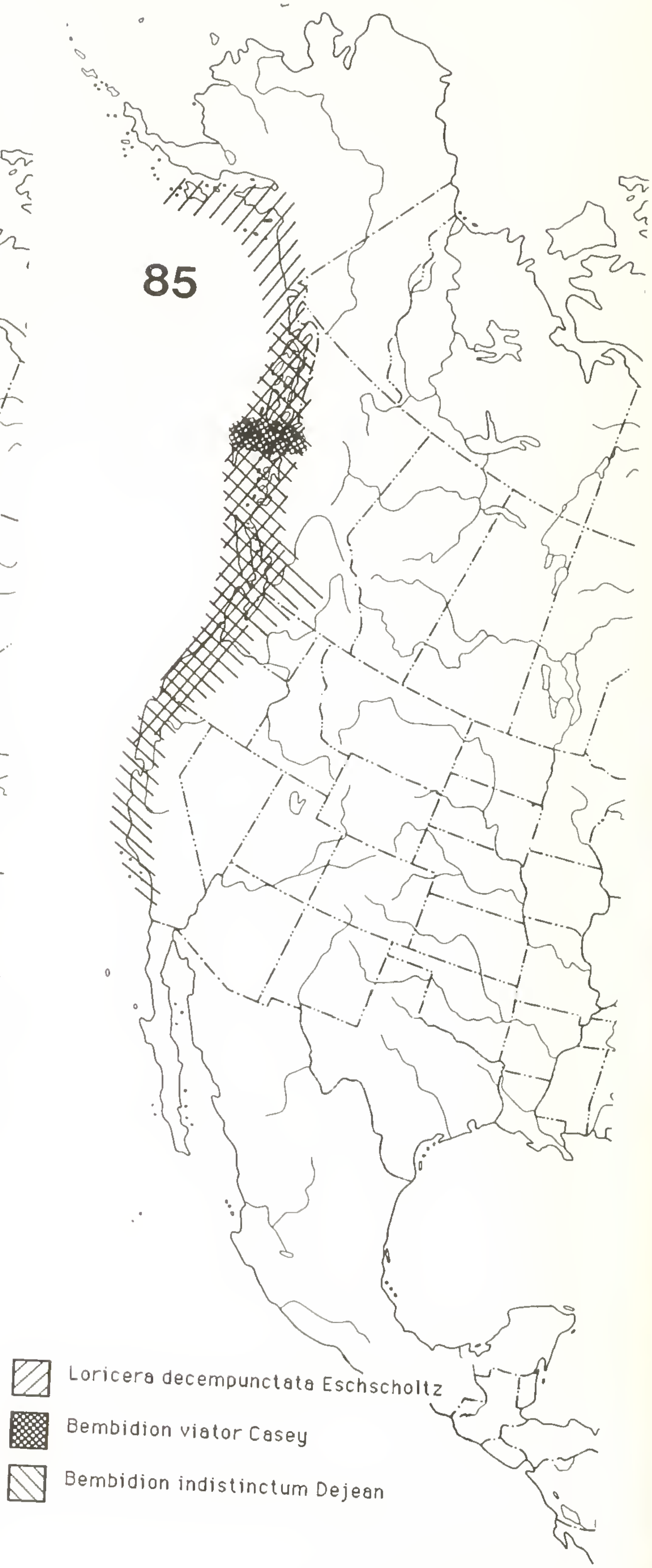

85
Loricera decempunctata Eschscholtz
Bembidion viator Casey
Bembidion indistinctum Dejean

Table 6. Habitat distributions of carabid beetles in the Queen Charlotte Islands.

Taxon	Habitat type[1,2]															No. habitats
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	
Cicindela oregona LeConte	–	–	–	–	–	–	–	x	–	–	–	–	–	–	–	1
Scaphinotus angusticollis Mannerheim	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Scaphinotus marginatus Fischer	–	–	x	x	–	x	x	–	–	–	x	x	–	x	x	8
Cychrus tuberculatus Harris	–	–	–	–	–	x	x	–	–	–	–	–	–	–	–	2
Carabus nemoralis Müller	–	–	–	x	–	x	–	–	–	–	–	–	–	–	–	2
Carabus taedatus Fabricius	–	–	–	–	–	–	–	–	–	–	–	–	–	–	x	1
Leistus ferruginosus Mannerheim	–	–	–	–	–	x	–	–	–	–	–	–	–	–	–	1
Nebris charlottae Lindroth	x	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
Nebria louiseae Kavanaugh	x	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
Nebria haida Kavanaugh	–	–	–	–	–	–	–	–	–	–	–	–	–	–	x	1
Nebria sahlbergii sahlbergii Fischer	–	–	–	–	–	–	–	x	x	–	–	–	x	–	–	3
Nebria mannerheimii Fischer	x	x	x	x	–	–	–	x	–	–	–	–	–	–	–	5
Nebria diversa LeConte	–	x	–	–	–	–	–	–	–	–	–	–	–	–	–	1
Notiophilus sylvaticus Eschscholtz	–	–	–	–	–	x	x	–	–	–	x	x	–	x	–	5
Elaphrus americanus sylvanus Goulet	–	–	–	–	x	–	–	–	–	x	–	–	–	–	–	2
Elaphrus clairville Kirby	–	–	–	–	x	–	–	–	–	x	–	–	–	–	–	2
Loricera decempunctata Eschscholtz	–	–	–	x	x	x	–	–	–	x	–	–	–	–	–	4
Dyschirius pacificus Lindroth	–	x	–	–	–	–	–	–	–	–	–	–	–	–	–	1
Broscodera insignis Mannerheim	–	–	–	–	–	–	–	–	x	–	–	–	x	x	x	4
Zacotus matthewsi LeConte	–	–	–	–	–	–	x	–	–	–	–	–	–	–	–	1
Diplous aterrimus Dejean	–	–	–	–	–	–	–	x	x	–	–	–	–	–	–	2
Trechus obtusus Erichson	–	–	–	x	x	x	–	–	–	–	–	–	–	–	–	3
Trechus ovipennis Motschulsky	–	x	–	–	–	–	–	–	x	–	–	–	–	–	–	2
Trechus chalybeus Dejean	–	–	x	x	–	x	x	–	–	x	x	x	–	x	x	9
Bembidion zephyrum Fall	–	x	–	–	–	–	–	–	–	–	–	–	–	–	–	1
Bembidion inaequale opaciceps Casey	–	–	–	–	–	–	–	x	–	–	–	–	–	–	–	1
Bembidion dyschirinum LeConte	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Bembidion castum Casey	–	–	–	–	–	x	–	–	x	–	–	–	–	–	–	2
Bembidion iridescens LeConte	–	–	–	–	x	–	–	x	x	–	–	–	–	–	–	3
Bembidion incertum Motschulsky	–	–	–	–	–	–	–	–	x	–	–	–	x	–	x	3
Bembidion quadrifoveolatum Mannerheim	–	–	–	–	–	–	–	x	x	–	–	–	x	–	–	3
Bembidion farrarae Hatch	–	–	–	–	–	–	–	–	x	–	–	–	x	–	x	3
Bembidion viator Casey	–	–	–	–	x	–	–	–	–	–	–	–	–	–	–	1
Bembidion complanulum Mannerheim	–	–	–	–	–	–	–	–	–	–	–	–	–	–	x	1

←

Figures 84–85. Geographical distributions. Figure 84. Western North American Range Pattern. Figure 85. West Coastal Range Pattern.

TABLE 6. CONTINUED.

Taxon	Habitat type[1,2] 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	No. habitats
Bembidion planiusculum Mannerheim	–	–	–	–	–	–	–	x	x	–	–	–	–	–	–	2
Bembidion sejunctum semiaureum Fall	–	x	–	–	–	–	–	–	–	–	–	–	–	–	–	1
Bembidion transversale Dejean	–	–	–	–	–	–	–	x	–	–	–	–	–	–	–	1
Bembidion incrematum LeConte	–	–	–	–	x	–	–	–	–	x	–	–	–	–	–	2
Bembidion indistinctum Dejean	–	–	–	–	x	–	–	–	–	–	–	–	–	–	–	1
Bembidion versicolor LeConte	–	–	–	–	x	–	–	–	–	x	–	–	–	–	–	2
Bembidion fortestriatum Motschulsky	–	–	–	–	x	–	–	–	–	x	–	–	–	–	–	2
Bembidion spectabile Mannerheim	–	–	–	–	–	x	x	–	–	–	x	x	–	x	x	6
Bembidion oblonguloides Lindroth	–	–	–	–	–	x	x	–	x	–	–	x	–	–	–	4
Bembidion oblongulum Mannerheim	–	–	–	–	–	–	–	–	–	–	–	x	–	–	–	1
Nomius pygmaeus Dejean	–	–	–	–	–	–	x	–	–	–	–	–	–	–	–	1
Pterostichus lama Ménétriés	–	–	–	–	–	–	x	–	–	–	–	–	–	–	–	1
Pterostichus crenicollis LeConte	x	–	x	x	–	x	x	–	x	–	x	x	–	–	–	8
Pterostichus algidus LeConte	x	–	x	x	–	x	x	x	x	–	x	x	–	–	–	9
Pterostichus amethystinus Mannerheim	–	–	–	–	–	x	x	–	–	–	x	x	–	–	–	4
Pterostichus castaneus Dejean	–	–	–	–	–	x	x	–	–	–	x	x	–	–	–	4
Pterostichus adstrictus Eschscholtz	x	–	x	x	–	–	–	x	–	–	–	–	–	–	–	4
Pterostichus riparius Dejean	–	–	–	–	–	–	–	–	x	–	–	–	–	–	–	1
Agonum ferruginosum Dejean	–	–	–	–	x	–	–	–	–	–	–	–	–	–	–	1
Agonum belleri Hatch	–	–	–	–	x	–	–	–	–	x	–	–	–	–	–	2
Agonum metallescens LeConte	–	–	–	–	–	–	–	–	–	x	–	–	–	–	–	1
Agonum brevicolle Dejean	–	–	–	–	x	–	–	–	–	x	–	–	–	–	–	2
Amara sinuosa Casey	–	–	–	–	–	–	–	–	–	–	–	–	–	–	x	1
Amara ellipsis Casey	–	–	x	–	–	–	–	–	–	–	–	–	–	–	–	1
Amara littoralis Mannerheim	–	–	x	x	–	–	–	–	–	–	–	–	–	–	–	2
Harpalus somnulentus Dejean	–	–	x	x	–	–	–	–	–	–	–	–	–	–	–	2
Trichocellus cognatus Gyllenhal	–	–	x	x	x	–	–	–	–	–	–	–	–	–	–	3
Bradycellus nigrinus Dejean	–	–	–	x	–	–	–	–	x	x	–	–	–	–	–	3
Totals per habitat	6	6	10	13	14	15	13	11	15	11	8	10	5	5	10	

[1] Habitat types: 1 = Cobble upper sea beach; 2 = Sandy upper sea beach; 3 = Supra-tidal meadow; 4 = Lowland open/synanthropic; 5 = Lowland marsh or bog; 6 = Lowland deciduous forest; 7 = Lowland coniferous forest; 8 = Lowland open lake or large stream shore; 9 = Lowland small, shaded stream shore; 10 = Upland marsh or bog; 11 = Upland deciduous forest; 12 = Upland coniferous forest; 13 = Upland lake or stream shore; 14 = Subalpine forest; 15 = Alpine zone.

[2] Habitat distributions: x = known to occur in habitat; – = not found in habitat, ? = habitat distribution unknown.

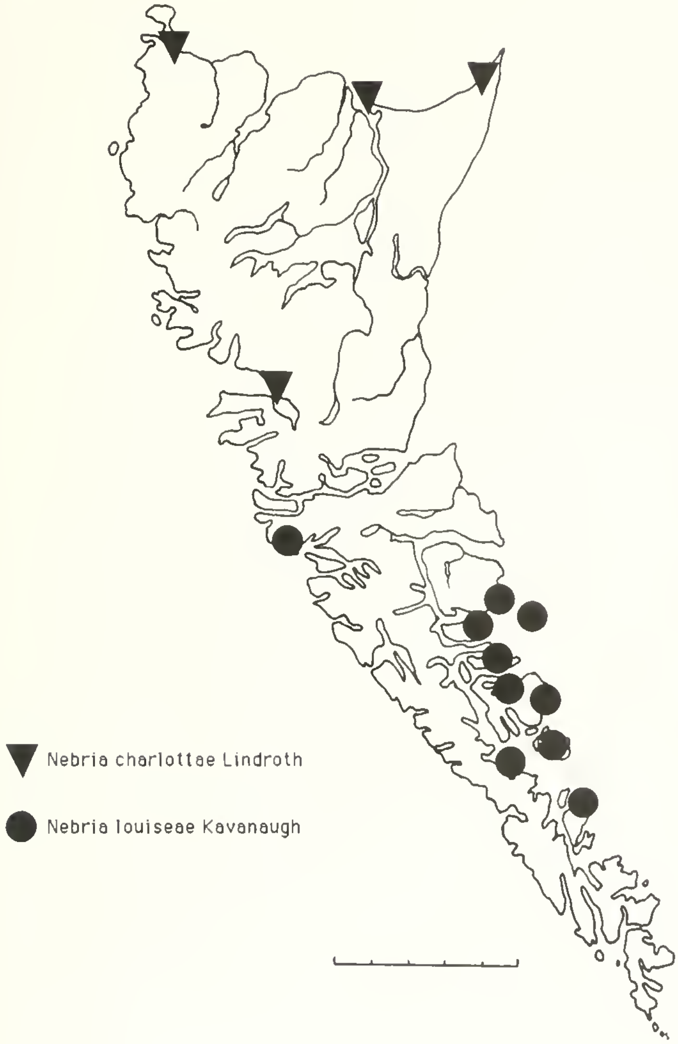


FIGURE 86. Geographical distributions. Endemic Range Pattern.

TABLE 7. DIVERSITY OF QUEEN CHARLOTTE ISLANDS CARABID SPECIES IN RELATION TO HABITAT.

Habitat type	No. spp.	% of fauna[1]
1. Cobble upper sea beach	6	10.0
2. Sandy upper sea beach	6	10.0
3. Supra-tidal meadow	10	16.7
4. Lowland open/synanthropic site	13	21.7
5. Lowland marsh or bog	14	23.3
6. Lowland deciduous forest	15	25.0
7. Lowland coniferous forest	13	21.7
8. Lowland open lake or large stream shore	11	18.3
9. Lowland small shaded stream shore	15	25.0
10. Upland marsh or bog	11	18.3
11. Upland deciduous forest	8	13.3
12. Upland coniferous forest	10	16.7
13. Upland lake or stream shore	5	8.3
14. Subalpine forest	5	8.3
15. Alpine zone	10	16.7
Grouped habitat complexes[2]		
Beaches (1 + 2)	11	18.3
Open areas (3 + 4)	14	23.3
Forests (6 + 7 + 11 + 12 + 14)	20	33.3
Wetlands (5 + 8 + 9 + 10 + 13)	35	58.3
Alpine zone (15)	10	16.7
Altitudinal habitat complexes[2]		
Lowland habitats (1 through 9)	54	90.0
Upland habitats (10 through 15)	29	48.3

[1] In this calculation, the total number of species in the fauna is 60, rather than 62, excluding the two species for which habitat distribution is still unknown.

[2] Number(s) listed after each habitat group correspond to the basic habitat types listed in the first part of the table.

is known about the fauna of the region as a whole to permit recognition of general trends in species diversity and patterns in the regional distributions of species.

Kavanaugh (1989) compared the carabid beetle fauna of the Queen Charlotte archipelago with the known faunas of eight other areas along the Pacific Northwest coast, using both Simpson (Simpson 1960) and Jaccard (Braun-Blanquet 1932) coefficients of faunal similarity. Areas compared included (1) the Aleutian Islands, (2) the Alaskan Peninsula, (3) Kodiak Island, (4) the Kenai Peninsula, (5) the Lituya Bay region, the (6) Prince Rupert and (7) Vancouver areas of mainland British Columbia, and (8) Vancouver Island. Although those comparisons were based only on data available by early 1984, inclusion of the many additional distributional records that have accumulated since that time does not significantly alter the original findings, which can be summarized as follows:

(a) The fauna of the Queen Charlotte Islands is unexpectedly diverse in relation to the adjacent mainland, when compared with other island areas worldwide (Darlington 1971; MacArthur and Wilson 1967). In general, insular faunas are either depauperate versions of adjacent mainland faunas (e.g., Iceland or the Faeroe Islands [Downes 1988] in relation to the northwestern coast of Europe) or highly distinctive faunas of moderate to low diversity in relation to comparable areas on mainlands (e.g., the Madeiran or Canary Islands in relations to coastal Europe or northern Africa). In fact, the fauna of the Queen Charlotte Islands (60 species, excluding the two species thought to have become extinct) is, at present, more diverse than the known fauna of the adjacent mainland coast (50 species). Although the latter area has not yet been intensively sampled and significant additions to its faunal list can be expected from future collecting efforts, the balance in diversity is, nonetheless, exceptional.

(b) The fauna of the Queen Charlotte archipelago is much more similar to faunas of the Prince Rupert area and all the included areas to the south than to those of any areas to the north, based on comparisons of both percentages of Queen Charlotte species shared and the coefficients of similarity examined (Kavanaugh 1989).

ORIGINS AND DEVELOPMENT OF THE FAUNA

Much of the evidence needed to infer the origins of the extant carabid fauna of the Queen Charlotte archipelago is provided by the data and analyses presented above, including the geographical and habitat distributions of individual species, patterns observed among these geographical and habitat ranges, and the relative affinities of the fauna with carabid faunas of other selected areas along the Pacific Northwest coast. This evidence must also be viewed in the context of the known en-

FIGURE 87. Geographical distributions. Introduced Range Pattern.

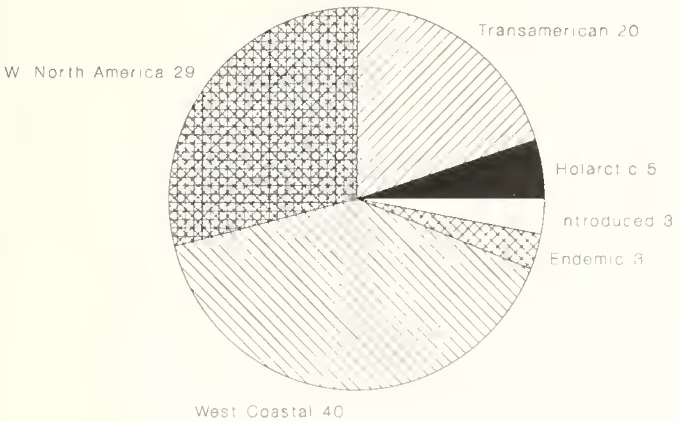


FIGURE 88. Diagram illustrating the relative representation of different faunal elements in the carabid beetle fauna of the Queen Charlotte Islands. Values = percentage of species (n = 62 species).

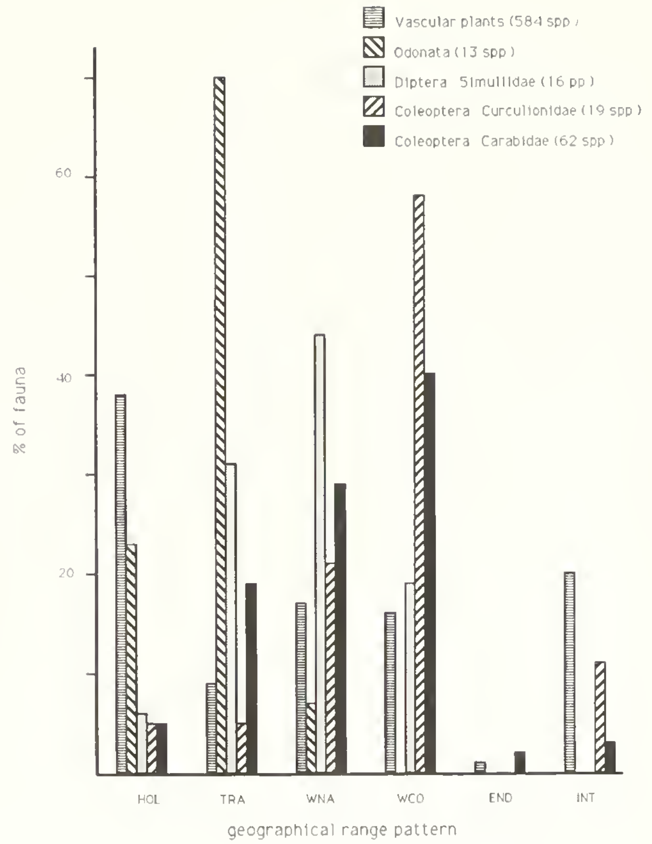


FIGURE 89. Graph illustrating the relative representation of different faunal elements (groups of species sharing a common geographical range pattern) for several different groups of organisms in the Queen Charlotte Islands. Geographical range patterns: HOL = Holarctic; TRA = Transamerican; WNA = Western North American; WCO = West Coastal; END = Endemic; and INT = Introduced.

vironmental history of the region. Although many details of this history for the Queen Charlotte Islands and for the coastal mainland are yet unknown, most of its major features are clear (Matthews 1979b).

Most of the Pacific Northwest coastal region was heavily and repeatedly glaciated during Pleistocene time, last as recently as 10,000–13,000 years ago (Sutherland Brown and Nasmith 1962; Clague 1989). However, several areas have been identified as likely sources (refugia) from which post-glacial dispersal into and within the region may have occurred (Heusser 1989; Kavanaugh 1989). Included among these sources are both extrinsic (peripheral) and intrinsic (within the region) refugia (Fig. 93). The existence of extensive glacial refugia, both northwest and south of the Cordilleran and Laurentide icesheets, is supported by abundant geologic and paleoenvironmental data (Hopkins 1967; Scudder 1979; Morgan and Morgan 1980). Biotic data suggest at least two distinct refugia south of the icesheets during glacial periods: one east and one west of the Sierra Nevada/Cascade crest (Kavanaugh 1988, 1989). In the northwest, the Yukon River Valley/Alaskan interior remained largely ice-free and continuous with northeastern Eurasia across the broadly exposed, unglaciated Bering Land Bridge (Hopkins 1967; Lindroth 1979a; Matthews 1979b). The Aleutian Islands remained separate from the land bridge during glacial periods and apparently served as another extrinsic refugial area (Lindroth 1963;

TABLE 8. DIVERSITY OF QUEEN CHARLOTTE ISLANDS CARABID SPECIES IN RELATION TO GEOGRAPHICAL RANGE PATTERN AND HABITAT TYPE.[1]

	Geographical range pattern					
Habitat type	Holarctic	Transamerican	W. No. Amer.	West Coastal	Endemic	Introduced
Cobble upper sea beach	1	–	–	3	2	–
Sandy upper sea beach	–	–	–	6	–	–
Supra-tidal meadow	2	3	1	4	–	–
Lowland open/synanthropic site	2	3	1	5	–	2
Lowland marsh or bog	1	4	3	5	–	1
Lowland deciduous forest	–	–	3	10	–	2
Lowland coniferous forest	1	–	3	9	–	–
Lowland open lake or large stream shore	1	1	6	3	–	–
Lowland small shaded stream shore	–	1	7	8	–	–
Upland marsh or bog	–	6	1	4	–	–
Upland deciduous forest	–	–	2	6	–	–
Upland coniferous forest	–	–	2	8	–	–
Upland lake or stream shore	–	–	4	1	–	–
Subalpine forest	–	–	1	4	–	–
Alpine zone	–	–	4	4	–	–

[1] Values refer to number of species for each combination of habitat type and geographical range pattern.

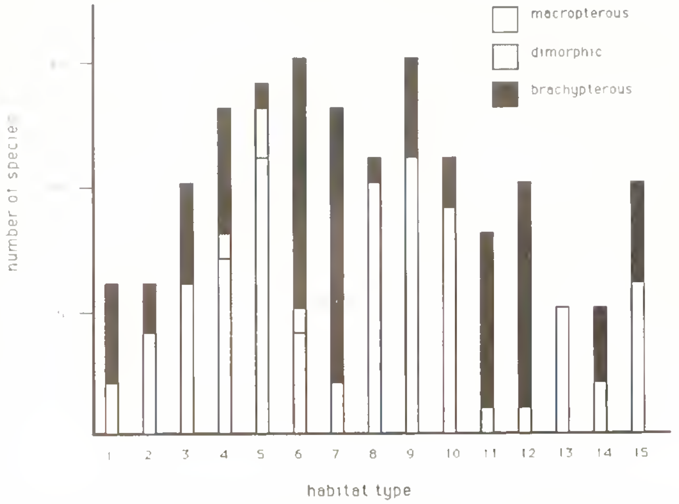


FIGURE 90. Graph illustrating the number of carabid species, and the condition of flight wings for members of each species, in different habitat types in the Queen Charlotte Islands. Habitat types: 1 = Cobble upper sea beach; 2 = Sandy upper sea beach, 3 = Supra-tidal meadow, 4 = Lowland open synanthropic; 5 = Lowland marsh or bog, 6 = Lowland deciduous forest, 7 = Lowland coniferous forest, 8 = Lowland open lake or large stream shore; 9 = Lowland small, shaded stream shore; 10 = Upland marsh or bog, 11 = Upland deciduous forest, 12 = Upland coniferous forest; 13 = Upland lake or stream shore; 14 = Subalpine forest, 15 = Alpine zone.

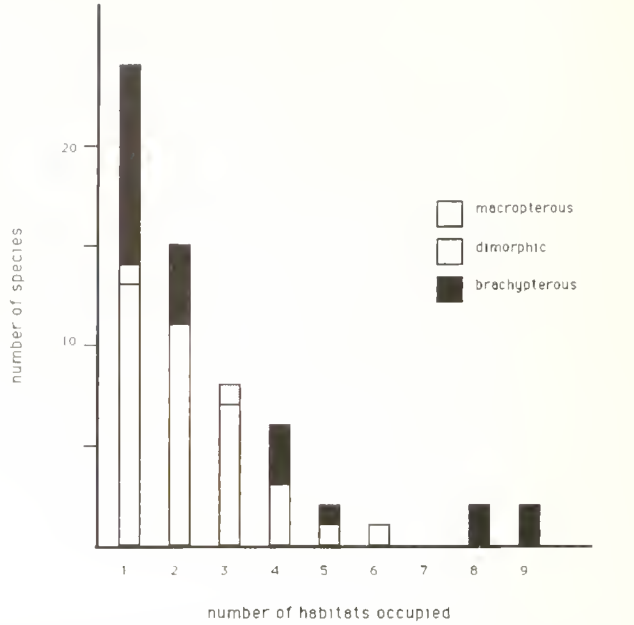


FIGURE 91. Graph illustrating the frequency distribution for number of habitats known to be occupied by carabid species and the condition of flight wings for members of each species, in the Queen Charlotte Islands.

Karlstrom 1969). Geologic, paleoenvironmental, and biotic evidence suggest that several areas within the Pacific Northwest coastal region, including parts of Kodiak Island (Lindroth 1969), southeastern coastal Alaska (Heusser 1960, 1989), the Queen Charlotte Islands (Foster 1965; Heusser 1989; Kavanaugh 1989), and Vancouver Island (Heusser 1960, 1989; Ogilvie 1989) served as intrinsic refugia, which were potential source areas for the present carabid fauna of the Queen Charlotte Islands.

Post-glacial Immigration From the South

Species that are restricted to the Pacific Coast region make up 40% of the carabid fauna of the Queen Charlotte Islands, the largest single component (25 species) in the fauna. Of these, 10 species reach the northern limit of their present distribution in the archipelago. Clear affinities with coastal faunas to the south, but not to the north, suggest a south coastal origin for most if not all of the species in this component of the fauna, probably through range extension northward along the coast (Fig. 94) following deglaciation. In fact, fossil remains of two of the West Coastal species (*Scaphinotus angusticollis* and *S. marginatus*) have been recovered from late glacial deposits in a coastal site just south of the Cordilleran ice margin (Morgan and Morgan 1980).

Together, species with Western North American (18 species), Transamerican (12 species), and Holarctic (three species) distributions represent 54% of the carabid fauna of the archipelago. Although they differ in the extent of their present distributions, these species all have one feature in common—they presently inhabit at least some area(s) south of the region that was covered by Cordilleran and/or Laurentide icesheet(s) in full-glacial times. Fossil remains of seven of these species (*Carabus taedatus*, *Elaphrus clairville*, *E. americanus*, *Bembidion incrematum*, *B. versicolor*, and *B. fortestriatum*) have been recovered from late glacial deposits in sites just south of the Laurentide Icesheet in

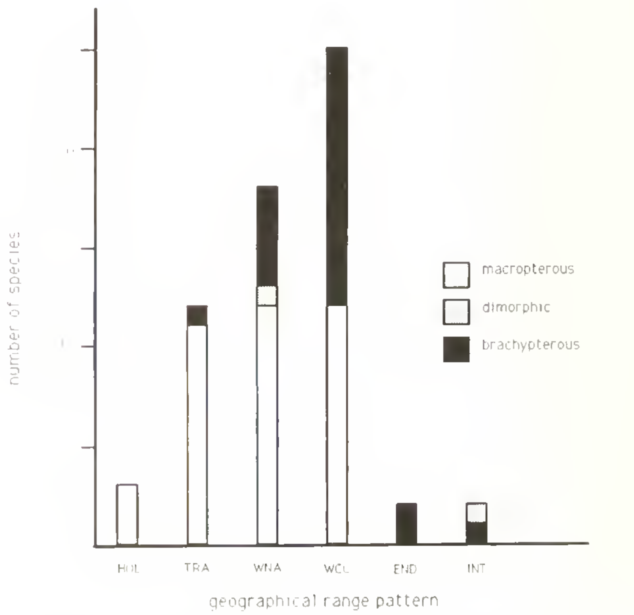


FIGURE 92. Graph illustrating the relationship between geographical range pattern and condition of the flight wings for members of carabid species, in the Queen Charlotte Islands. Geographical range patterns: HOL = Holarctic; TRA = Transamerican, WNA = Western North American; WCO = West Coastal, END = Endemic, and INT = Introduced.

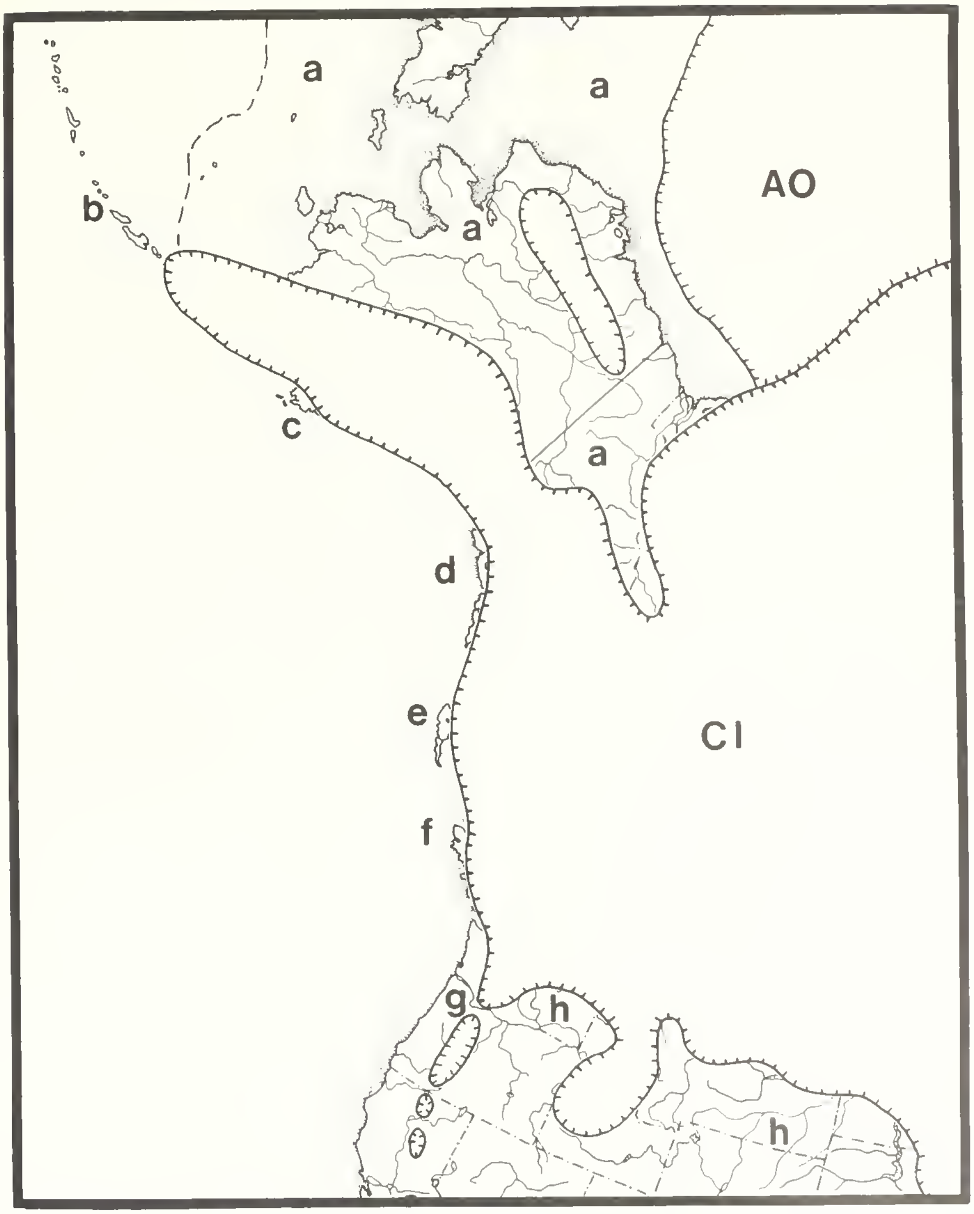


FIGURE 93. Map illustrating approximate extent of glacial icesheets, proportions of the Bering Land Bridge, and location of proposed refugia during the last glacial maximum (ca. 17,000 years ago) (adapted from Lafontaine and Wood [1988], Schwert and Ashworth [1988], and Kavanaugh [1989]): ticked solid line = boundaries of icesheets or major glaciers; dashed line = southern margin of the Bering Land Bridge; AO = Arctic Ocean (frozen, with polar icecap grounded on the Bering Land Bridge and broadly, but not completely, coalesced with the continental icesheet; CI = continental icesheet, including both Cordilleran and Laurentide Icesheets; a = Yukon/Beringian refugium; b = Aleutian Islands refugium, c = Kodiak Island refugium; d = southeastern Alaska coastal refugia; e = Queen Charlotte Islands refugia; f = Vancouver Island refugium; g = southern coastal refugium(-a); h = southern interior refugium(-a).

southeastern and southcentral Canada and the northcentral and northeastern United States (Morgan and Morgan 1980). Based on both present distributions and the fossil record (Ashworth 1979; Morgan and Morgan 1980; Schwert and Ashworth 1988), it seems likely that all of these species survived (or could have) in the continental refugium(-a) south of the ice. 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 (Kavanaugh 1989).

At least one of the carabid species in the extant fauna of the archipelago, *Diplous aterrimus*, is broadly distributed in western North America, but not in the southern coastal region. That such a southern interior form, rather than its closely related southern coastal counterpart, *Diplous filicornis* Casey, occurs in the archipelago suggests a separate, southern interior origin for at least part of the fauna. Just how many of the Western North American, Transamerican, and Holarctic species colonized the archipelago from the southern coastal refugium, from the southern interior refugium, or from both remains unclear at present. Why a southern interior form such as *Diplous aterrimus* should have colonized the northern coast while its southern coastal

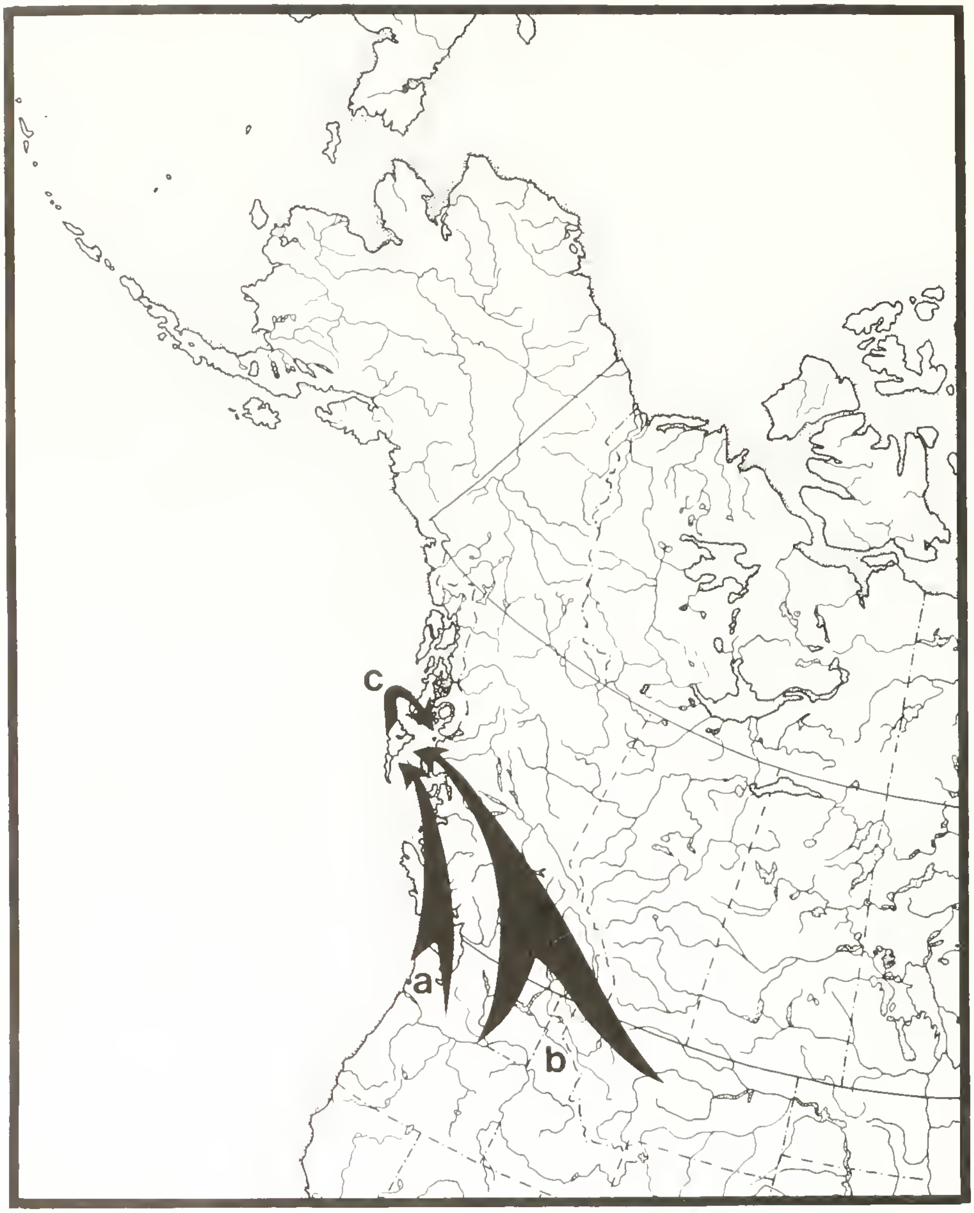


FIGURE 94. Schematic representation of proposed post-glacial immigrations into and emigration from the Queen Charlotte archipelago: a = immigration from southern coastal refugium(-a); b = immigration from southern interior refugium(-a), c = emigration from one or more refugia in the archipelago to the adjacent mainland.

counterpart apparently did not is an intriguing question. One possible explanation is that early post-glacial climate of at least parts of the archipelago and adjacent mainland coast was drier and colder than at present, conditions that would favor forms adapted to the southern interior rather than the southern coastal region. This interpretation is supported by some paleobotanical evidence (R. W. Mathewes 1989 and pers. comm.) and by the discovery of a fossil specimen of the carabid subspecies *Nebria gyllenhali castanipes* Kirby (by R. W. Mathewes and B. G. Warner) in deposits from Cape Ball, in eastern Graham Island, dated at 11,100 ± 90 years before present. This form, widely distributed over most of boreal North America, is not known to occur at present in the archipelago or anywhere else on the Pacific Coast west of interior British Columbia. In the Rocky Mountain region, this species is often represented in upper montane and subalpine habitats in association with aspen (*Populus tremuloides* Michx.), subalpine fir *Abies lasiocarpa* [Hook.] Nutt.), and the carabid species *Carabus taedatus*. As noted above, *C. taedatus* appears to have become extinct in the archipelago relatively recently. Clearly, the climate of the northwest coastal region did not become as maritime as it is today until after 11,000 years ago.

Survival in Refugia Within the Archipelago

The occurrence of plant and animal species that are apparently endemic to the Queen Charlotte Islands has been cited as evidence in support of the existence of one or more glacial refugia in the archipelago (Foster 1965; Calder and Taylor 1968; Kavanaugh 1989; Ogilvie 1989; Schofield 1989), which served as an additional, in situ source for the present fauna. However, as noted by Anderson (1988) and others, alternative hypotheses can account for the presence of these endemics. Each of these alternatives is considered here briefly.

First, species thought to be endemic to the archipelago may actually be more widely distributed. In fact, this has proven to be true for all but one of the 11 vascular plant taxa previously considered endemic (Calder and Taylor 1968). Ten of them are now known to occur also on northern Vancouver Island (Ogilvie 1989). The freshwater amphipod, *Paramoera carlottensis* Bousfield, described as an endemic, is now known to be widely distributed along the coast; and the supposed endemic carabid, *Nebria haida* (Kavanaugh 1984, 1989), recently has been found on the adjacent mainland, just north of Prince Rupert. Sampling along the adjacent coastal mainland and on other coastal islands remains so incomplete for insects that most or all of the remaining proposed endemic insects, including two carabids (*Nebria charlottae* and *Nebria louiseae*), one cercopid bug (*Aphrophora regina*), and one geometrid moth (*Xanthorhoe clarkeata* Ferguson) may also occur outside the archipelago.

Although discovery of populations of supposed endemic forms outside the archipelago weakens the hypothesis of endemism at present, it does not necessarily refute the hypothesis of glacial survival in refugia within the archipelago. Post-glacial colonization of the adjacent mainland or other islands from one or more refugia in the Queen Charlotte Islands is no less plausible than the reverse pathway (i.e., from mainland to islands). In fact the distributions of three non-endemic carabid species (which are included among those classified as West Coastal in distribution) suggest this possibility. *Nebria haida, Bembidion viator,* and *B. oblonguloides* are known only from the archipelago and the mainland immediately adjacent to it (i.e., the Prince Rupert area). A glacial refugium in the archipelago would have been the most proximate and likely source area for the mainland populations of these three species.

A second hypothesis to explain true endemism in the archipelago, to the extent that it occurs, is that these species survived glacial periods outside the area, immigrated in post-glacial time, and subsequently became extinct elsewhere. Although this possibility cannot be dismissed, I know of no paleontological evidence to support it for any of the supposed endemic plant or animal species.

A third hypothesis is that the endemic forms differentiated in post-glacial time within the archipelago, from populations of ancestral species that immigrated to the archipelago following deglaciation. This explanation has been invoked to account for the occurrence of several endemic vertebrates, particularly stickleback fishes (Moodie and Reimchen 1976a), in the archipelago. Presence on the adjacent mainland of the respective sister species of these supposed endemic forms would be strong, but not conclusive, evidence in support of this hypothesis. Discovery of such vicariance patterns would suggest that the common ancestors of the species pairs reached the archipelago from the mainland and that subsequent isolation permitted differentiation. However, this isolation need not have occurred in post-glacial time, but could have been completed earlier, during either a glacial or interglacial period. Present occurrence of the sister species on the adjacent mainland could represent reoccupation of that area following deglaciation. Unfortunately, knowledge of the phylogenetic relationships of plant and animal species in the archipelago is woefully lacking, hence the recognition of sister species and of their geographical and habitat distributions is generally not possible.

An important exception to this generalization, however, is the carabid genus *Nebria,* which includes the two endemic carabid species and the possible Glacial-age endemic, *Nebria haida,* and for which an hypothesis of phylogenetic relationships has been developed (Kavanaugh 1989). These three species are all members of the *gregaria* infragroup (Kavanaugh 1978), which presently includes five species. Evidence in support of (1) the taxonomic ranking of populations (and groups of populations) in this infragroup as distinct species and (2) the hypothesis of phylogenetic relationships among all those species discussed here will be presented separately in a revision of the Nearctic *Nebria* fauna (in prep.). The sister species of *N. haida* is *Nebria lituyae* Kavanaugh, known only from the Lituya Bay, White Pass, and Juneau areas of southern Alaska. Members of both of these species are restricted to treeless alpine summits and ridges in their respective areas. The sister species of *N. louiseae* is *Nebria gregaria* Fischer, which is apparently restricted to the Aleutian Islands. The sister taxon of *N. charlottae* is the species pair *N. louiseae* + *N. gregaria.* Members of all three species occur in cobble upper sea beaches, although adults and larvae of *N. gregaria* are also found under debris on supratidal flats of volcanic ash substrate. All five species in the *gregaria* infragroup occur in areas for which glacial refugia have been proposed on other biotic and/or geologic grounds. Kavanaugh (1989) reviewed various hypotheses to account for the present distributions of these species, the observed vicariance among species pairs, and the occurrence of both *N. louiseae* and *N. charlottae* in the archipelago (but with allopatric distributions). At present, the conclusions reached in that paper, and summarized here, best account for all available data: (1) *Nebria haida, N. louiseae, N. charlottae,* and perhaps also *Bembidion viator* and *B. oblonguloides* all probably survived at least the last glacial period in refugia within the archipelago; and (2) *Nebria charlottae* probably survived more than one glacial period in the archipelago, at least the last in a lowland refugium somewhere on Graham Island.

Unfortunately, no fossil specimens have yet been found to conclusively demonstrate the presence of the endemic *Nebria* or other carabid species in the archipelago during full glacial times; and until such specimens from that period are found, refugial survival of these carabids will remain in question. In fact, no organic deposits of any kind have been found that date from the crucial period between 21,000 and 16,000 years ago (Mathewes 1989a, and pers. comm.; Blaise et al., in press), so the hypothesis of glacial refugia in the archipelago remains unsupported by conclusive data at present. Nonetheless, what we know about the present habitat and geographical distributions of the proposed glacial survivors can provide clues as to the number, location, and nature of the refugia that they would have required.

During the last glacial period, populations of *Nebria haida* could have survived on the alpine summits, ridges, and headlands that remained ice-free, as nunataks, above and between small icecaps and the valley and piedmont glaciers that flowed off the Skidegate Plateau and out of the Queen Charlotte Ranges.

Such nunataks probably served as a network of small-scale refugia, on both Graham and Moresby islands, each with small populations of *N. haida* that were in genetic contact with each other through the dispersal of individuals. Heusser (1954) described the surprisingly diverse biotas that survive at present under similar conditions on nunataks in heavily glaciated regions, such as in the Juneau Icefield area of southeastern Alaska.

Survival of *Nebria charlottae* and *N. louiseae* would have required refugia that included cobble sea beaches, a habitat that would have persisted at least at the bases of headlands between valley glaciers on the west coast of Graham and Moresby islands. Suitable habitat may actually have been more extensive during full glacial times, when portions of the continental shelf were exposed due to lowered sea levels (Fairbridge 1960; Hopkins 1967; Warner, Mathewes, and Clague 1982). Separate lowland refugia are inferred for these two species—somewhere on Graham Island or the adjacent exposed continental shelf for *N. charlottae* and somewhere in the southern part of the archipelago for *N. louiseae*.

Luternauer et al. (1989) found and described Late Pleistocene terrestrial deposits on the continental shelf northwest of Vancouver Island, at a depth of 95 m below present sea level, which represents a site that was above sea level 10,500 years ago. This discovery suggests that the search for deposits of full glacial age, perhaps from areas that served as refugia, might best be redirected to areas of the submerged continental shelf. It is also important to note that a depression in sea level of 100 m would expose a broad, dry land connection between the eastern coast of the northern two-thirds of the archipelago and the mainland and inner islands in the Prince Rupert area. The findings of Luternauer et al. (1989) suggest that such a connection existed as recently as perhaps 10,500 years ago or later. It well may have served as the pathway for early post-glacial colonization of the archipelago by immigrants from the south and for colonization of the adjacent mainland by at least three carabid species from the archipelago.

If *Bembidion viator* and *B. oblonguloides* also survived in glacial refugia in the archipelago and, as suggested above, colonized the adjacent mainland in post-glacial time, then the refugium(-a) in which they survived should have included lowland marshes or bogs and at least some small patches of coniferous or deciduous forest. The paleobotanical record from northeastern Graham Island (Warner et al. 1982; Mathewes 1989a, b) confirms the presence of marshland vegetation and suggests the possibility of stunted spruce in the area as early as 16,000 years ago. Both *Bembidion* species are known only from Graham Island in the archipelago at present, but the probable location of a glacial refugium for their survival in the area cannot be determined using available data.

Introductions with Man

Spence and Spence (1988) identified 20 species introduced by humans into western Canada. Two species in the present fauna of the archipelago, *Carabus nemoralis* Müller, and *Trechus obtusus* Erichson, are native to western Europe, including the British Isles, and have been introduced into North America in historic times (Lindroth 1957). Both of these species are restricted to synanthropic sites in the archipelago, as well as elsewhere throughout their original and introduced ranges.

Specimens of *Carabus nemoralis* were first collected in the archipelago in August 1982, at Port Clements on Graham Island. All subsequent records have been from the same area. This species was first recorded from North America (New Brunswick) in 1870 (Lindroth 1957), from western North America (Washington) in 1909 (Hatch 1953), from Vancouver, British Columbia in 1925, and from Prince Rupert in 1958 (Lindroth 1961–69). In western Canada, it now occurs in scattered, apparently disjunct localities in the southern half of British Columbia and in Edmonton, Alberta. All adults of this species are brachypterous, hence flightless. Apparently, the species is extending its range in leaps, no doubt aided by humans, rather than by a gradual, progressive spread by means of its own dispersal (ambulatory) capabilities. Specimens of this species have been intercepted in shipments of nursery stock (in the bolus of soil around root balls) arriving in Vancouver (Spence and Spence 1988), and are known to have been transported in hay bales. Either of these means could have served as the mode of introduction to the archipelago as well. The restriction of *C. nemoralis* to one site on Graham Island suggests very recent introduction, probably during the late 1970s.

The first specimens of *Trechus obtusus* collected in the archipelago were found 1.4 km south of Masset, again on Graham Island, in August 1983. All subsequent records have been from Masset and its immediate vicinity. Hence, this species is probably also a very recent introduction. Kavanaugh and Erwin (1985) reviewed the history of this species in western North America and concluded that its primary introduction, as well as most of its subsequent spread, had been in nursery stock. *Trechus obtusus* has not yet been recorded from the Prince Rupert area, or anywhere else north of the greater Vancouver area. The latter is a most likely source area for the introduction of this species to the archipelago, whereas either the Vancouver or Prince Rupert areas could have served as sources for the introduction of *C. nemoralis*.

Dispersal To and Within the Archipelago

Clearly, all but a few of the species represented in the extant carabid fauna immigrated to the archipelago in post-glacial times; but when and how did they reach the islands? Was Hecate Strait a sea gap that had to be crossed, was it covered with glacial ice flowing west off of high peaks of the Coast Range of the mainland, or was it at least partly dry land, connecting the islands with the adjacent mainland? Evidence suggests that the area that is now Hecate Strait presented all of these aspects at one time or another since extensive lowland ice-free areas are first known to have occurred in the archipelago as early as 16,000 years ago (Warner et al. 1982; Clague 1989). Although sea level was probably low enough at this time to expose large parts of the floor of Hecate Strait, perhaps even providing a dry land link to the mainland, the adjacent mainland coast remained ice-covered until less than 13,000 years ago (Clague 1981). Hence, colonization directly from the mainland was probably not possible until after that time. If the magnitude of depression in sea level proposed by Luternauer et al. (1989) for the continental shelf northwest of Vancouver Island at 10,500 years ago occurred also in Hecate Strait at the same time, dry land would have connected the archipelago with the adjacent mainland. By 10,000 years ago, however, the archipelago was completely deglaciated and sea level had risen to its present level relative to land (Clague 1989). By about 8,000 years ago, sea level reached a post-glacial high about 15 m above present. It therefore appears that, to have reached the archipelago from the mainland across a land connection, post-glacial immigrants from the south must have done so between 13,000 and 10,000 years ago. It is possible that species extended their ranges northward at an earlier time on the exposed continental shelf to the west of the still glaciated mainland; but depressions more than 200 m below present sea level traverse the shelf in several areas along the route (Barrie and Bornhold 1989; Thomson 1989). It is therefore unlikely that a continuous dry land route has ever been available on the continental shelf in post-glacial time.

As noted above, in the discussion of species distributions within the archipelago in relation to brachyptery, there appears to be little or no barrier at present to the dispersal of some flightless carabid beetles between islands. It was noted, in fact, that some species with brachypterous adults occurred on more islands than those with macropterous individuals. It should be noted, however, that members of each of the broadly distributed species are associated with logs—either with rotting logs on the lowland forest floor (e.g., *Scaphinotus marginatus, Pterostichus algidus, P. amethystinus,* and *P. crenicollis*), or driftwood logs on sea beaches (e.g., *Nebria louiseae*). Inter-island dispersal by rafting in or on logs may account for the surprisingly wide distributions of these species in the archipelago. It may also have played a role in initial colonization of the archipelago for some of these same species, but no such mechanism for long-range dispersal across a water gap appears to be required. Although the distributions and relative abundances of various plant species in the archipelago have changed dramatically during the last 11,000 years (Mathewes 1989a), it seems clear that all 15 of the present habitat types were represented in the archipelago before 10,500 years ago, when dry land probably linked the archipelago to the mainland.

Summary

It appears that the extant fauna of the Queen Charlotte Islands includes: (1) two species that are western European in origin, recently and secondarily introduced to the archipelago from a source area on the mainland of British Columbia; (2) two–five species that survived at least the last glacial period in one or more refugia in the archipelago, at least three of which expanded their ranges in post-glacial times to include a limited area on the adjacent mainland; and (3) 55–58 species (including two that are probably now extinct in the archipelago) that survived the last glacial period in one or more refugia south of the Cordilleran and/or Laurentide icesheets and colonized the archipelago in post-glacial times. These immigrants probably reached the archipelago across a dry land connection with the mainland between 13,000 and 10,000 years ago.

Faunal Evolution

Although they have been called the "Canadian Galapagos" (Foster 1985), no adaptive radiations comparable to those we associate with the Galapagos Islands, the Hawaiian Islands, or even the West Indies are evident in the extant biota of the Queen Charlotte Islands, except perhaps among populations of three-spined stickleback fishes (Moodie and Reimchen 1976a, b; Reimchen et al. 1985; Gach and Reimchen 1989). The archipelago is remote, diverse in the number and form of its islands, and rich in habitat and species diversity. Yet the area was so recently and drastically affected by Pleistocene climatic changes and events that its biota is predominantly post-glacial in age.

In the extant carabid fauna, there is little indication that evolutionary change (divergence) has occurred among populations of individual species on different islands, or between mainland populations and their counterparts in the archipelago. Most surprisingly, there is apparently not a single instance of the development of brachyptery among carabids in the archipelago. Although many species represented have some or all adults brachypterous, members of respective populations of these species or their sister species on the mainland or elsewhere are also brachypterous, indicating a trait acquired before, not after, isolation in the archipelago.

The only known instance of inter-island differentiation noted to date in the carabid fauna of the archipelago is found in *Scaphinotus marginatus.* Adults of this species on Reef Island, the most isolated island that has been sampled, are larger on average than those from other islands or the mainland, although a few large individuals are found occasionally in populations throughout the range of the species. The Reef Island population also differs from all others sampled in the proportion of individuals that have a metallic green reflection on their elytra. On Reef Island, 28 out of 30 specimens (93%) studied had green elytral reflection. In all other known populations, individuals with green reflection are either absent or rare, and in no other sample do they represent as much as 10% of the population. In coastal areas, the elytra typically have a vivid, metallic violet reflection. The Reef Island population seems to represent a classic example of Mayr's (1942) founder principle. This population may be derived from a single large, green, gravid female ancestor that dispersed to the island and founded the population.

Carabid Species Diversity and Equilibrium Theory

Darlington (1943, 1957), initially through his study of carabids of the West Indies, was among the first to recognize a general relationship between the areas of islands and the diversity of species of a particular taxon that occurs on them. Expanding on these and other pioneer studies, including their own (e.g., Wilson 1961), MacArthur and Wilson (1963, 1967) developed a general theory of island biogeography, commonly referred to as the "Equilibrium Theory," to explain the faunal diversity on islands. According to this theory, species diversity reaches an equilibrium when the rate of extinction of species on an island equals the rate of immigration of new species to the island. For a given island, both time required to reach equilibrium and the number of species occurring at equilibrium may be influenced by factors such as its distance from source areas (e.g., mainland faunas) and its area, elevation, and habitat diversity.

During the past three decades, numerous studies have tested the general theory and explored the effects of various factors on species diversity on true islands (e.g., Diamond 1969; Wilson and Simberloff 1969) and islands of restricted habitat on continents (e.g., Brown 1971, 1978; Patterson and Atmar 1986; Davis et al. 1988; Dunn and Loehle 1988). Among these factors, the relationship between island area and species diversity has been studied most intensively. An approximation of this relationship is given by the equation $S = CA^z$ (MacArthur and Wilson 1967), where S is the number of species of a given taxon occurring on the island, C is a coefficient (or the intercept in the log-transformed linear equation), A is the area of the island, and z is an exponent of a power function (or the regression slope in the log-transformed linear equation). This equation can be used to describe the relationships between diversity and other factors as well.

The Queen Charlotte archipelago should be an ideal area for testing equilibrium theory and studying the effects of area and other factors on species diversity. There are about 150 different islands, varied in size from about 0.01 km^2 to more than 6,000 km^2, in altitude from less than 10 m to more than 1,150 m (Table 1), and in habitat diversity from one or two to 15 different major carabid habitat types (Table 3). The carabid fauna of the archipelago should be ideal for study as well. The fauna is diverse and species occur in all terrestrial habitats, from sea level to the summits of the highest peaks.

Unfortunately, the present state of our knowledge of the carabid fauna of the archipelago is such that its potential for study cannot yet be realized. To date, only 23 islands have been sampled at all, and none of these (except perhaps for Graham Island) sufficiently to establish the total number of species present. Although we know of two species that have recently colonized the islands (through human introduction) and perhaps as many as three species that occupied the archipelago in the past but do not now occur there, we lack (1) the baseline inventories of the archipelago as a whole, (2) the baseline inventories of individual islands in particular, and (3) the subsequent inventories that we need to calculate rates of immigration and extinction. Such calculations must await both adequate baseline (initial) and subsequent inventories for each island. All that can be done at present is to use available data for the 23 islands sampled to date (Tables 1, 3) to quantify, at least in a preliminary way, relationships between species diversity and island area, elevation, and habitat diversity in the archipelago. Figures 95–97 illustrate highly significant relationships apparent, through separate regression analyses, between carabid species diversity and each of these three factors, respectively.

The z value of 0.354, calculated for the species-area relationship, is somewhat higher than the expected 0.27 (MacArthur and Wilson 1967). This may be due to (a) an effect of increased habitat diversity on the largest islands (MacArthur and Wilson 1967), (b) incomplete sampling of carabid diversity on most of the islands (particularly on all but the largest islands), or (c) a combination of these and/or other, unknown factors. Z values of 0.706 and 1.260 for species-elevation and species-habitat diversity relationships, respectively, are difficult to interpret in the absence of comparative figures for other faunas and from other regions. However, with improved sample size and data, the interactions of these factors with area (as they affect species diversity), could be explored more appropriately using methods of principal component analysis.

MacArthur (1972) distinguished "oceanic islands" (islands, such as the Galagapos, that have never been connected by a land bridge to mainland areas) from "land bridge islands" (islands, such as Trinidad, that have been recently connected to mainland areas by a land bridge and whose colonists, at least some of them, need never have crossed a water gap). He noted that land bridge islands may contain more species than their equilibrium number (i.e., for their size, if they were oceanic islands) and that their diversity will decrease with time following isolation—rapidly on small islands, very slowly on larger land bridge islands. Clearly, the Queen Charlotte Islands, located on the continental shelf, are "land bridge islands," most if not all of which were connected to the mainland and/or each other perhaps as recently as 10,500 years ago. This may help to explain their relatively high diversity in relation to the adjacent mainland.

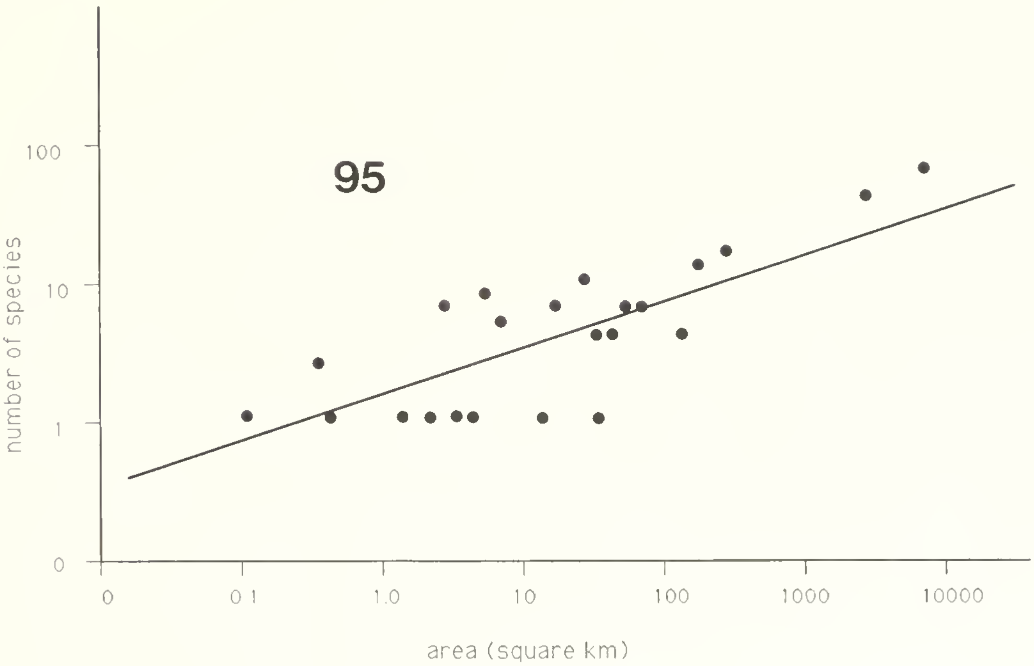
Opportunities for Future Research on Carabid Beetles in the Archipelago

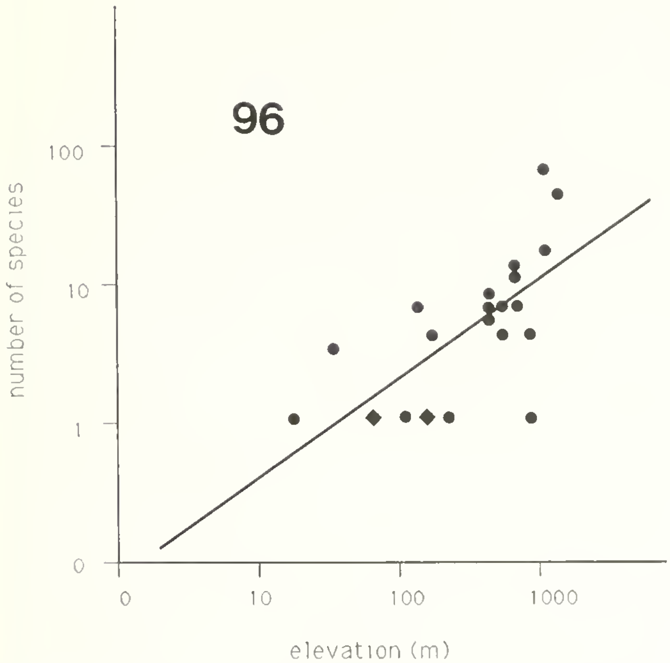
This report has reviewed the current status of our knowledge about the carabid beetle fauna of the Queen Charlotte Islands, its composition, affinities, and origins. Because the number of new species added to the faunal list from most recent collecting efforts has dropped significantly, and because all major habitat types in the archipelago have been sampled to some degree, it is unlikely that many more species presently occurring there remain unrecorded. Knowledge of the overall habitat and geographical distributions of the species represented in the fauna are reasonably well known, with a few exceptions; and these data, along with paleogeographic and paleoenvironmental findings, allow us to infer, with some confidence, the affinities and origins of most, if not all, of the fauna. Nonetheless, much remains to be learned about the carabid fauna and its history. The following is a brief, annotated list of projects on which future research could be most fruitful.

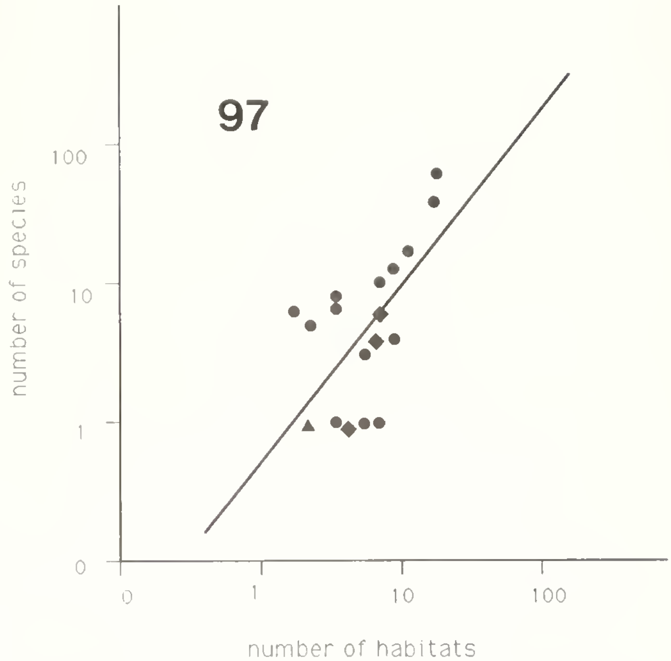
1. Distribution of species within the archipelago.—Many parts of the Queen Charlotte Islands remain inadequately sampled. These include: (a) the entire west coast of the archipelago, especially between Lepas Bay and Rennell Sound on Graham Island and almost the entire length of Moresby Island; (b) northern portions of the Skidegate Plateau on Graham Island; (c) Langara Island; (d) lowland marsh and bog areas of northwestern and northeastern Graham Island; (e) the entire San Cristoval Range of Moresby Island; (f) all islands not listed in Table 1—nothing is known about the faunas of these islands, so all records for carabid species occurring on them will represent new information; and (g) all islands listed in Table 1, except Graham and Moresby islands (but see items [a], [b], [d], and [e] above)—knowledge of the carabid faunas of these islands is still incomplete, for some, markedly so (e.g., only four species have been recorded from Kunghit Island, one from Maude Island). Collecting efforts in these areas will add greatly to our knowledge of the fauna, perhaps uncover unrecorded or undescribed species, expand our knowledge of the habitat and distributional ranges of the species, and permit better analyses of relationships between species diversity and island area and topographic and habitat diversity.

2. Monitoring of the faunas around townsites and in disturbed area.—Continued collecting in and at the margins of synanthropic sites will provide data needed to monitor the spread, if any, of the two known introduced species, *Carabus nemoralis* and *Trechus obtusus*, and any possible effects of such spread on the native fauna. Such a project would also be most likely to detect new introductions as they occur.

3. Sampling of the carabid faunas of the adjacent mainland and inshore islands.—Knowledge of the fauna of the adjacent







FIGURES 95–97. Relationships between carabid beetle species diversity and three variables for 23 islands in the Queen Charlotte archipelago. Solid dots = individual islands (data from Tables 1, 3), solid diamonds = two islands with equal values, solid triangle = three islands with equal values. FIGURE 95. Species diversity in relation to island area. The least-squares regression (solid line) is given by the equation log S (log number of species) = 0.174 + 0.354 log A (log area) [$t = 3.669$, $P \leq 0.01$]. FIGURE 96. Species diversity in relation to maximum island elevation. The least-squares regression (solid line) is given by the equation log S = −1.108 + 0.706 log A (log elevation) [$t = 3.370$, $P \leq 0.01$]. FIGURE 97. Species diversity in relation to habitat diversity. The least-squares regression (solid line) is given by the equation log S = −0.258 + 1.260 log A (log elevation) [$t = 3.353$, $P \leq 0.01$].

mainland remains inadequate. At present, more species have been recorded from the Queen Charlotte Islands than from the mainland west of the crest of the Coast Range, and it is unlikely that this relationship properly reflects relative diversities of the areas. Little is known about the faunas of the inshore islands along the British Columbia coast or the lower end of the Alexander Archipelago, just to the north of the Queen Charlotte Islands. Faunas of these areas should be intensively sampled, especially in the habitats known to harbor the apparent Queen Charlotte endemic species (i.e., cobble sea beaches) or proposed refugial survivors (i.e., alpine areas, lowland marshes or bogs, and deciduous and coniferous forests). Hypotheses developed in this report concerning the origins of the carabid fauna of the Queen Charlotte Islands, and the endemic species in particular, can be tested with faunal data from these areas.

4. Paleoenvironmental and paleontological studies.—Clearly, additional paleoenvironmental and paleontological data of appropriate age are needed if the existence of one or more glacial refugia in the archipelago is to be convincingly demonstrated. Although the present geographical and habitat distributions of organisms can be used to infer historical events, fossil specimens and associated paleoenvironmental data are required to corroborate these interpretations. The search for sites bearing organic deposits of full glacial age should certainly continue on land in the archipelago; but the prospects now seem brightest for the discovery of such sites on presently submerged portions of the continental shelf, particularly within the 100-meter isobath around the archipelago, and between it and the adjacent mainland.

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APPENDIX A

LOCALITY DATA FOR CARABIDAE IN THE QUEEN CHARLOTTE ISLANDS

Discussions of the geographical, altitudinal, and temporal distributions of carabid species within the archipelago, presented in the preceding text, are based on data from specimens listed here. For each species, distributional data are grouped first by island and then by specific locality. Altitudinal data, month(s) of collection, total number of specimens for each locality, and depositories for specimens are also provided.

1. *Cicindela oregona* LeConte

Graham Island: McIntyre Bay (Entry Point to Estrado Lagoon [2–5 m]) [Aug.] (16; CAS), Tlell River (1.2 km N of bridge on Highway 16 [1–3 m]) [July] (6; CAS).

Freitag (1965:137) cited additional records for this species from Juskatla and Queen Charlotte City (both on Graham Island), but I have not seen specimens from these areas.

2. *Scaphinotus angusticollis* (Mannerheim)

Graham Island: Masset (2; USNM).

3. *Scaphinotus marginatus* (Fischer)

Burnaby Island: bay on north shore (SE of Alder Island [10–20 m]) [Aug.] (3; CAS). **Graham Island:** Ghost Creek (4.7 km NW of Rennell Sound Road [210 m]) [July] (3; CAS), Ghost Creek drainage (7.3 km NW of Rennell Sound Road [240 m]) [July] (1; CAS), Honna Point [May] (2; AMor), Kiusta village site (0.3 km E of [3–5 m]) [Aug.] (1; CAS), Lepas Bay (northeast shore [5–15 m]) [Aug.] (1; CAS), Masset (and 12 km S of [55 m], 14 km E) [July–Aug.] (7; CAS, CNC), Nebria Peak (northeast slope [700–780 m], Lower Nebria Lake [640 m]) [July] (4; CAS), Naikoon Provincial Park (Misty Meadow Campground) [July] (3; FMNH), Port Clements [May, Aug.–Sep.] (8; CNC, QCIM), Slatechuck Mountain (east slope [370–790 m], north slope [760–980 m]) [July] (35; CAS, CNC, FMNH), Tlell River Park [July] (1; FMNH), Tow Hill Park ([5 m], W of headland) [May, July] (6; CAS, QCIM), Tow Hill Road (19 km E of Masset [10 m]) [July] (5; CAS). **Hibben Island:** [Aug.] (1; UBC). **Huxley Island:** southeast shore ([10–30 m]) [Aug.] (1; CAS). **Kunga Island:** north shore (S of Titul Island [6–25 m]) [Aug.] (3; CAS), west shore (on Klue Passage [5–50 m]) [Aug.] (3; CAS). **Kunghit Island:** Rose Harbour [Aug.] (1; UBC). **Louise Island:** Mount Kermode (south slope [885–1,080 m]) [Aug.] (1; CAS), Skedans village site ([3–30 m]) [Aug.] (12; CAS). **Lyell Island:** [July] (1; UBC), Gate Creek (at mouth of [3–10 m]) [Aug.] (12; CAS), Powrivco Point (0.5 km SW of [3–20 m]) [Aug.] (3; CAS), Windy Bay [June] (1; QCIM). **Moresby Island:** Cumshewa village site ([8–20 m]) [Aug.] (9; CAS, CNC), Darwin Sound (at Hoya Passage [8–30 m]) [Aug.] (1; CAS), Haswell Bay (1.5 km SW of Hoskins Point [5–30 m]) [Aug.] (6; CAS), Jedway (bay 3 km NE of [6–50 m]) [Aug.] (8; CAS), Kaisun village site ([5–50 m]) [Aug.] (2; CAS), Mount Moresby (south slope [460 m], west slope at High Goose Lake [640 m]) [July] (82; CAS), Pallant Creek (at Camp Moresby [10 m]) [July] (1; CAS), Skincuttle Inlet (0.8 km SW of Huston Point [5–10 m]) [Aug.] (4; CAS), Takakia Lake ([585 m], and slopes [590–670 m] and ridges [730–790 m] E of) [July] (27; CAS). **Ramsay Island:** north shore (1.5 km E of west end [3–4 m]) [Aug.] (1; CAS). **Reef Island:** north shore (0.6 km E of west end [20 m]) [Aug.] (30; CASA, QCIM). **Talunkwan Island:** Heming Head (1 km NW of [10–30 m]) [Aug.] (1; CAS). **Tanu Island:** Tanu village site ([5–50 m]) [Aug.] (9; CAS). **Island Unknown:** (1; CNC).

4. *Cychrus tuberculatus* Harris

Graham Island: Chown Brook [July] (1; CNC), Masset (7; CNC, USNM), Queen Charlotte City [July] (1; QCIM), Skowkona Creek (7.9 km NW of Queen Charlotte City [120 m]) [July–Aug.] (8; CAS). **Louise Island:** Skedans village site ([6–25 m]) [Aug.] (1; CAS).

5. *Carabus nemoralis* Müller

Graham Island: Port Clements (0.1 km W of Highway 16 [15 m]) [July–Nov.] (21; CAS, CNC, QCIM).

6. *Carabus taedatus* Fabricius

Moresby Island: Carabus Peak (north slope [850 m]) [July] (1; CAS).

7. *Leistus ferruginosus* Mannerheim

Graham Island: Kiusta village site (0.3 km E of [3–5 m]) [Aug.] (1; CAS), Skowkona Creek (7.9 km NW of Queen Charlotte City [120 m]) [July] (3; CAS). **Moresby Island:** Kaisun village site ([3–5 m]) [July] (1; CAS).

8. *Nebria charlottae* Lindroth

Graham Island: Bonanza Creek (0.5 km E of Rennell Sound [10 m]) [July] (1; CAS), Kiusta village site (0.3 km E of [3–5 m]) [July–Aug.] (90; CAS, CNC, QCIM), Masset (1; CNC), Masset Inlet (Estrado Lagoon [2–5 m]) [Aug.] (21; CAS), McIntyre Bay (Entry Point to Estrado Lagoon [2–5 m]) [Aug.] (1; CAS), Tow Hill Park (W of Tow Hill [1–3 m]) [July] (347; CAS, QCIM), Yaku Village site (0.2 km SE of [Aug.] (195; CAS, AMor).

9. *Nebria louiseae* Kavanaugh

Burnaby Island: bay on north shore (SE of Alder Island [3–5 m]) [Aug.] (40; CAS). **Hotspring Island:** north shore ([3–4 m]) [Aug.] (18; CAS). **Lyell Island:** Gate Creek (at mouth [3–6 m]) [Aug.] (120; CAS, CNC), Powrivco Point (0.5 km SW of [3–5 m]) [Aug.] (149; CAS). **Louise Island:** Skedans village site [June, Aug.] (6; BCPM, CAS, CNC). **Moresby Island:** Haswell Bay (1.5 km SW of Hoskins Point [5 m]) [Aug.] (2; CAS), Kaisun village site [July–Aug.] (315; CAS, CNC). **Ramsay Island:** north shore (1.5 km E of west end [3–4 m]) [Aug.] (11; CAS). **Reef Island:** north shore (0.6 km E of west end [5 m]) [Aug.] (68; CAS). **Skedans Islands:** east shore of west island ([5 m]) [Aug.] (6; CAS). **Talunkwan Island:** Heming Head (1 km NW of [3–5 m]) [Aug.] (89; CAS). **Tanu Island:** Tanu village site ([3–5 m]) [Aug.] (123; CAS, CNC).

10. *Nebria haida* Kavanaugh

Graham Island: Nebria Peak (northeast slope [700–780 m], above Middle Nebria Lake [790–910 m]) [July] (288; CAS, CNC). **Moresby Island:** Mount Moresby (northwest-facing cirque [910–1,070 m], east slope of south peak [910–940], northeast slope of south peak [940–1,080 m], west slope at High Goose Lake [640 m]) [July] (193; CAS, CNC), Takakia Lake (ridge E of [730–980 m]) [July] (304; CAS, CNC).

11. *Nebria sahlbergii sahlbergii* Fischer

Burnaby Island: bay on north shore (SE of Alder Island [3–20 m]) [Aug.] (18; CAS). **Graham Island** ([500 m]) [July] (2; FMNH): Awun Lake (0.8–1.2 km W of [35 m], 3.2 km W [50–60 m]) [Aug.] (18; CAS), Bonanza Creek (0.5 km E of Rennell Sound

[10–20 m]) [July–Aug.] (7; CAS), Chinukundl Creek (at Highway 16 [3 m]) [July] (6; CAS), Ghost Creek (4.3 km NW of Rennell Sound Road [210 m]) [July] (51; CAS, CNC), Ghost Creek drainage (7.3 km NW of Rennell Sound Road [240 m]) [July] (6; CAS, CNC), Gregory Creek (0.3 km E of Rennell Sound [5–10 m]) [Aug.] (26; CAS), Mamin River (1.0 km SE of Juskatla [915 m]) [July] (3; CAS), Nebria Peak (at Lower Nebria Lake [620 m]) [July] (7; CAS), Rennell Sound Road (10 km E of Rennell Sound [270 m]) [July] (17; CAS), Sheilds Bay [May] (7; AMor), Skowkona Creek (7.9 km NW of Queen Charlotte City [120 m]) [July] (4; CAS), Slatechuck Mountain (east slope at Tarundl Creek [300–370 m]) [July] (42; CAS), Tow Hill Park (W of Tow Hill) [May] (1; QCIM), Yakoun River (at Port Clements–Juskatla Road ([30 m]) [July] (1; CNC). **Lyell Island:** Gate Creek (at mouth [3–6 m] and 1.0 km W of mouth [15 m]) [Aug.] (26; CAS, CNC), Powrivco Bay (at Powrivco Creek [15 m]) [Aug.] (11; CAS). **Moresby Island:** Alliford Bay [May] (3; AMor), High Goose Creek (west base of Mount Moresby [3–90 m]) [July] (19; CAS), Jedway (bay 3 km NE [6–50 m]) [Aug.] (40; CAS), Mount Moresby (west slope at High Goose Lake [640 m]) [July] (19; CAS, CNC), Pallant Creek ([15 m]) [July] (29; CAS). **Tanu Island:** Tanu village site ([5–25 m]) [Aug.] (31; CAS, CNC).

12. *Nebria mannerheimi* Fischer

Graham Island: Bonanza Creek (0.5 km E of Rennell Sound [10 m]) [July–Aug.] (23; CAS), Cape Ball River (1 km N of mouth) [Aug.] (1; QCIM), Chinukundl Creek (at Highway 16 [3 m]) [July] (7; CAS), Deep Creek Beach [May] (1; QCIM), Drizzel Lake (2 km SW [60 m]) [July] (46; CAS), Ghost Creek (4.7 km NW of Rennell Sound Road [210 m]) [July] (3; CAS), Gregory Creek (0.3 km E of Rennell Sound [5–10 m]) [Aug.] (69; CAS), Lepas Bay (northeast shore [3–5 m]) [July, Aug.] (87; CAS, CNC, FMNH), Mamin River (1.0 km SE of Juskatla [15 m]) [July] (66; CAS, CNC), Masset (southeast shore of Delkatla Inlet, and 12 km S [55 m], 16 km S) [July–Sep.] (90; CAS, CUIC, ICCM, MCZ, OSUO, UASM, WSU), Port Clements (1.0 km W of Highway 16 [15 m] and 8 km S of) [July–Aug.] (41; CAS), Rennell Sound (at mouth of Bonanza Creek [3–5 m] and 0.5 km NW of Bonanza Creek [3 m]) [July] (3; CAS), Shields Bay [May] (7; AMor), Tow Hill Park ([1–3 m]) [July] (137; CAS), Yakoun River (at Port Clements–Juskatla Road [30 m]) [July–Aug.] (50; CAS).

13. *Nebria diversa* LeConte

Graham Island (3; CAS, ICCM): Masset (and 7 km E of) [May–Aug.] (80; BCPM, CAS, CNC, CUIC, FMNH, ICCM, MCZ, QCIM, UASM, UBC, UMMZ), McIntyre Bay (0.7 km W of Yakan Point at North Beach [2 m], at mouth of Chown Brook [2–5 m]) [May, July–Aug.] (131; CAS, CNC, QCIM), Rose Point [May] (2; OSUO, UBC), Tlell (and 42 km N, 16 km S, Richardson Ranch) [July–Aug., Nov.] (160; CAS, CNC, QCIM, UASM, UBC), Tlell River (at mouth [1–3 m] and 1 km S) [July] (36; CAS), Tow Hill Park ([1–3 m], at Tow Hill Road) [July–Aug.] (164; CAS, CNC, OSUO). **Moresby Island:** Sandspit (1 km S of airstrip [1–3 m]) [July] (17; CAS).

14. *Notiophilus sylvaticus* Eschscholtz

Graham Island: Bonanza Creek (0.5 km E of Rennell Sound [10 m]) [July] (1; CAS), Ghost Creek (4.7 km NW of Rennell Sound Road [210 m]) [July] (1; CNC), Ghost Creek drainage (7.3 km NW of Rennell Sound Road [240 m]) [July] (2; CAS), Kiusta village site (0.2 km E of [8 m]) [Aug.] (1; CAS), Nebria Peak (southeast slope [850 m], Lower Nebria Lake [620 m], northeast slope [700–780 m]) [July] (5; CAS, CNC), Port Clements (0.1 km W of Highway 16 [15 m]) [July] (1; CAS), Slatechuck Mountain (east slope [370–790 m], Tarundl Creek [370–580 m]) [July] (3; CAS, CNC), Tlell River (at end of Richardson Road [15 m]) [Aug.] (4; CNC), Tow Hill [July] (2; FMNH), Tow Hill Road (19 km E of Masset [10 m]) [July] (2; CAS). **Kunga Island:** north shore (S of Titul Island [6–25 m]) [Aug.] (7; CAS, CNC), west shore (on Klue Passage [5–50 m]) [Aug.] (2; CAS). **Louise Island:** Mount Kermode (south slope [885–1,080 m]) [Aug.] (1; CAS), Skedans village site ([6–30 m]) [Aug.] (13; CAS). **Lyell Island:** Gate Creek (at mouth [3–10 m]) [Aug.] (4; CAS, CNC), Powrvico Point (0.5 km SE of) [Aug.] (1; CNC). **Moresby Island:** Carabus Peak (north slope [850 m]) [July] (1; CAS), Darwin Sound (at Hoya Passage [8–30 m]) [Aug.] (1; CAS), Kaisun village site ([3–50 m]) [Aug.] (9; CAS, CNC), Mount Moresby (south slope [460 m], west slope at High Goose Lake [640 m]) [July] (14; CAS, CNC), Peel Inlet (at road to Moresby Camp [5 m]) [July] (1; CAS), Takakia Lake ([640 m], and ridges E of [730–790 m]) [July] (3; CAS, CNC). **Tanu Island:** Tanu village site (stream NW of [10–30 m]) [Aug.] (1; CAS).

15. *Elaphrus clairvillei* Kirby

Graham Island: Elaphrus Bog (19.5 km NW of Queen Charlotte City [150 m]) [July] (3; CAS), Ghost Creek drainage (7.3 km NW of Rennell Sound Road [240 m]) [July] (1; CAS).

16. *Elaphrus americanus sylvanus* Goulet

Graham Island: Bonanza Creek (0.5 km E of Rennell Sound [10 m]) [July] (1; CAS), Chinukundl Creek (5.8 km N on Highway 16 [2 m]) [July] (13; CAS), Elaphrus Bog (19.5 km NW of Queen Charlotte City [150 m]) [July] (32; CAS), Highway 16 (1.9 km N of Chinukundl Creek [10 m]) [Aug.] (4; CAS), Masset (southeast shore of Delkatla Inlet [2 m]) [Aug.] (94; CAS), Skowkona Creek (7.9 km NW of Queen Charlotte City [120 m]) [July] (2; CAS). **Moresby Island:** Mosquito Lake [July] (4; FMNH).

17. *Loricera decempunctata* Eschscholtz

Graham Island: Bonanza Creek (0.5 km E of Rennel Sound [10 m]) [July] (1; CAS), Chinukundl Creek (5.8 km N on Highway 16 [2 m]) [July] (2; CAS), Elaphrus Bog (19.5 km NW of Queen Charlotte City [150 m]) [July–Aug.] (3; CAS), Ghost Creek drainage (7.3 km NW of Rennell Sound Road [240 m]) [July] (1; CAS), Gregory Creek (0.3 km E of Rennell Sound [5–10 m]) [Aug.] (1; CAS), Highway 16 (1.9 km N of Chinukundl Creek [10 m]) [Aug.] (1; CAS), Kiusta village site [Aug.] (3; CNC), Lepas Bay (northeast shore [3–5 m]) [Aug.] (1; CAS), Mamin River (1 km SE of Juskatla) [July] (1; CNC), Masset (southeast shore of Delkatla Inlet [2 m] and 12 km S on Highway 16 [55 m]) [July–Aug.] (37; CAS), Port Clements (0.1 km W of Highway 16 [15 m]) [July–Aug.] (2; CAS), Tlell (40 km N of) [Aug.] (1; CAS), Tow Hill Park ([5 m]) [July] (4; CAS), Tow Hill Road (5.3 km SW of Tow Hill Park) [July] (1; CNC). **Moresby Island:** Pallant Creek (at Moresby Camp [3–10 m]) [July] (3; CAS); Peel Inlet (at road to Moresby Camp [5 m]) [July] (1; CAS), Takakia Lake ([585 m]) [July] (1; CAS).

18. *Dyschirius pacificus* Lindroth

Island Unknown: "Q.C.I." (1; CNC).

19. *Broscodera insignis* (Mannerheim)

Graham Island: Kiusta village site [Aug.] (1; CNC), Nebria Peak (Lower Nebria Lake [620–640 m]) [July] (2; CAS), Slatechuck Mountain ([910 m]) [July] (1; CNC), Yaku village site (0.2 km SE of [3–5 m]) [Aug.] (1; CAS). **Moresby Island:** Mount Moresby (northeast slope of south peak [940–1,080 m], west slope at High Goose Lake [640 m]) [July] (7; CAS), Takakia Lake ([585 m], and slopes [610–670 m] and ridges [730–940 m] E of) [July] (29; CAS, CNC).

20. *Zacotus matthewsi* LeConte

Graham Island: Kiusta village site [July] (1; QCIM).

21. *Diplous aterrimus* (Dejean)

Graham Island: Bonanza Creek (0.5 km E of Rennell Sound [10–20 m]) [July–Aug.] (40; CAS), Chinukundl Creek (at Highway 16 [3 m]) [July] (25; CAS), Ghost Creek (4.7 km NW of Rennell Sound Road [210 m]) [July] (14; CAS, CNC), Gregory Creek (0.3 km E of Rennell Sound [5–10 m]) [Aug.] (15; CAS), Mamin River (1.0 km SE of Juskatla [15 m]) [July] (3; CAS, CNC), Shields Bay [May] (4; AMor), Skowkona Creek (7.9 km NW of Queen Charlotte City [120 m]) [July] (11; CAS), Tlell River (at end of Richardson Road [15 m]) [July] (3; CAS), Yakoun Lake (Etheline Bay at outlet of Yakoun River [110 m]) [Aug.] (4; CAS), Yakoun River (at Port Clements–Juskatla Road [30 m]) [July] (2; CAS). **Lyell Island:** Gate Creek (1.0 km W of mouth [15 m]) [Aug.] (39; CAS). **Moresby Island:** Alliford Bay [May] (1; AMor), High Goose Creek (west base of Mount Moresby [3–90 m]) [July] (2; CAS), Pallant Creek (at Moresby Camp [3–10 m], 0.2 km W of Moresby Camp [20 m]) [July–Aug.] (56; CAS, CNC).

22. *Trechus obtusus* Erichson

Graham Island: Masset (southeast [2 m] and southwest [2–4 m] shores of Delkatla Inlet and 1.4 km S) [Aug.] (22; CAS, CNC).

23. *Trechus ovipennis* Motschulsky

Graham Island: Chinukundl Creek (5.8 km N on Highway 16 [2 m]) [July] (2; CAS), Masset (southeast shore of Delkatla Inlet [2 m] and 1.4 km S of) [July–Aug.] (6; CAS, CNC), Rennell Sound (at mouth of Bonanza Creek and 0.5 km NW of mouth [3–5 m]) [July–Aug.] (19; CAS), Tlell River (at end of Richardson Road [15 m]) [July] (1; CAS), Yaku village site (0.2 km SE of [3–5 m]) [Aug.] (2; CAS). **Kunga Island:** north shore (S of Titul Island [6–25 m]) [Aug.] (8; CAS, CNC). **Louise Island:** Skedans village site ([6–30 m] and 1.5 km W of [3–15 m]) [Aug.] (136; CAS, CNC). **Moresby Island:** Jedway (bay 3 km NE [6–50 m]) [Aug.] (2; CAS), Kaisun village site ([3–5 m]) [Aug.] (1; CAS), Pallant Creek (0.2 km W of Moresby Camp [20 m]) [Aug.] (11; CAS), Sandspit (1 km S of airstrip [2 m]) [July] (1; CAS). **Ramsay Island:** north shore (1.5 km E of west end [3–4 m]) [Aug.] (1; CAS). **Talunkwan Island:** Heming Head (1 km W of) [Aug.] (1; CNC).

24. *Trechus chalybeus* Dejean

Graham Island: Ghost Creek (4.7 km NW of Rennell Sound Road [210 m]) [July] (6; CAS), Highway 16 (5.8 km N of Chinukundl Creek [2 m]), CAS), 12.8 km S of Tlell River bridge) [July] (5; CAS, CNC), Nebria Peak (Lower Nebria Lake [620 m]) [July] (8; CAS), Skowkona Creek (7.9 km NW of Queen Charlotte City [120 m]) [July] (4; CAS), Slatechuck Mountain (north slope [760–980 m], east slope [430–670 m]) [July] (16; CAS, CNC), Tow Hill Road (19 km E of Masset [10 m]) [July] (46; CAS). **Moresby Island:** Carabus Peak (north slope [850 m]) [July] (1; CAS), Mount Moresby (west slope at High Goose Lake [640 m]) [July] (91; CAS, CNC), Takakia Lake (585–610 m] and ridges E of [610–670 m]) [July] (23; CAS, CNC).

25. *Bembidion zephyrum* Fall

Graham Island: Lepas Bay (northeast shore [3–5 m]) [Aug.] (144; CAS, CNC).

26. *Bembidion inaequale opaciceps* Casey

Graham Island: Yakoun River (5.5 km S of Port Clements [8 m] and at Port Clements–Juskatla Road [30 m]) [July–Aug.] (5; CAS).

27. *Bembidion dyschirinum* LeConte

No specimens seen.

28. *Bembidion castum* Casey

Graham Island ([500 m]) [July] (3; FMNH): Chinukundl Creek (at Highway 16 [3 m]) [July] (1; CAS), Cinola Mine [May] (3; AMor), Elaphrus Bog (19.5 km NW of Queen Charlotte City [150 m]) [Aug.] (1; CAS), Ghost Creek drainage (7.3 km NW of Rennell Sound Road [240 m]) [July] (1; CAS), Masset (and 1.4 km S and 14 km E) [July] (4; CNC, USNM), Queen Charlotte City ([15 m]) [July] (1; CAS), Skowkona Creek (7.9 km NW of Queen Charlotte City [120 m]) [Aug.] (1; CAS), Tow Hill Road (0.5 km E of Chown Brook bridge [10 m], 19 km E of Masset [10 m]) [July–Aug.] (25; CAS). **Kunghit Island:** ([490 m]) [July] (1; CAS). **Louise Island:** Mount Kermode (south slope [885–1,080 m]) [Aug.] (1; CAS). **Moresby Island:** Whiteaves Bay [May] (2; AMor).

29. *Bembidion iridescens* (LeConte)

Graham Island: Bonanza Creek (0.5 km E of Rennell Sound [20 m]) [Aug.] (1; CAS), Elaphrus Bog (19.5 km NW of Queen Charlotte City [150 m]) [Aug.] (1; CAS), Ghost Creek drainage (7.3 km NW of Rennell Sound Road [240 m]) [July] (2; CAS), Highway 16 (5.8 km N of Chinukundl Creek [2 m]) [July] (1; CAS), Port Clements [Aug.] (1; CAS), Queen Charlotte City ([30 m]) [July] (1; CAS), Skowkona Creek (7.9 km NW of Queen Charlotte City [120 m]) [July] (14; CAS), Yakoun River (5.5 km S of Port Clements [8 m], at Port Clements–Juskatla Road [30 m]) [July–Aug.] (3; CAS, CNC). **Louise Island:** Skedans village site (and 1.5 km W of [3–15 m]) [Aug.] (9; CAS, CNC). **Moresby Island:** Pallant Creek (at Moresby Camp [3–10 m]) [Mar., July] (16; CAS, QCIM).

30. *Bembidion incertum* (Motschulsky)

Graham Island: Ghost Creek (4.7 km NW of Rennell Sound Road [210 m]) [July] (2; CAS), Ghost Creek drainage (7.3 km NW of Rennell Sound Road [240 m]) [July] (5; CAS), Nebria Peak (northeast slope [700–850 m], Lower Nebria Lake [620–640 m], above Middle Nebria Lake [790–910 m]) [July] (96; CAS, CNC), Shields Bay [May] (1; AMor), Skowkona Creek (7.9 km NW of Queen Charlotte City [120 m]) [July] (2; CAS), Slatechuck Mountain (north slope [820–980 m], northeast slope [760–980 m], east slope at Tarundl Creek [300 m]) [July] (24; CAS, CNC, FMNH). **Kunghit Island:** ([490 m]) [July] (1; CAS). **Louise Island:** Mount Kermode (south slope [885–1,080 m]) [Aug.] (7; CAS). **Moresby Island:** Carabus Peak (north slope [850 m]) [July] (2; CAS), Mount Moresby (east slope of south peak [910–940 m], northeast slope of south peak [940–1,080 m], northwest-facing cirque [910–1,070 m], west slope at High Goose Lake [640 m]) [July] (14; CAS, CNC), Takakia Lake (590–610 m] and ridges E of [610–940 m]) [July] (39; CAS, CNC).

31. *Bembidion quadrifoveolatum* Mannerheim

Graham Island: Awun Lake (ridges W of [460–550 m]) [Aug.] (1; CAS), Bonanza Creek (0.5 km E [10–20 m]) [July] (107; CAS), Chinukundl Creek (at Highway 16 [3 m]) [July] (3; CAS), Drizzel Lake (2 km SW [60 m]) [July] (2; CAS), Elaphrus Bog (19.5 km NW of Queen Charlotte City [150 m]) [Aug.] (11; CAS), Ghost Creek (4.7 km NW of Rennell Sound Road [210 m]) [July] (83; CAS, CNC), Ghost Creek drainage (7.3 km NW of Rennell Sound Road [240 m]) [July] (19; CAS), Gregory Creek (0.3 km E of Rennell Sound [5–10 m]) [Aug.] (14; CAS), Highway 16 (5.8 km N on Highway 16 [2 m]) [July] (1; CAS), Mamin River (1.0 km SE of Juskatla [15 m]) [July] (7; CAS), Masset (southeast shore of Delkatla Inlet [2 m], 12 km S on Highway 16 [55 m]) [July–Aug.] (39; CAS), Naikoon Provincial Park (Misty Meadow Campground) [July] (10; FMNH), Port Clements (0.1 km W of Highway 16 [15 m]) [July] (9; CAS), Rennell Sound (0.5 km N of Bonanza Creek [2 m]) [July] (1; CAS), Rennell Sound Road (10 km E of Rennell Sound [270 m]) [July] (2; CAS), Shields Bay [May] (13; AMor), Skowkona Creek (7.9 km NW of Queen Charlotte City [120 m]) [July] (143; CAS), Slatechuck Mountain (northeast slope [760–980 m], east slope at Tarundl Creek [370 m]) [July] (8; CAS), Tlell River (at end of Richardson Road [15 m]) [July] (15; CAS), Yakoun River (5.5 km S of Port Clements [8 m], at Port Clements–Juskatla Road [30 m]) [July–Aug.] (41; CAS, CNC). **Louise Island:** Skedans village site (1.5 km W [3–15 m]) [Aug.] (29; CAS). **Lyell Island:** Gate Creek (1.0 km W of mouth [15 m]) [Aug.] (24; CAS, CNC), Powrivco Bay (at Lyell Island Logging Camp [15 m]) [Aug.] (9; CAS). **Moresby Island:** Alliford Bay [May] (3; AMor), Copper Creek (6 km S of Copper Bay [30 m]) [Aug.] (37; CAS), Gray Bay Road (3 km W of Gray Bay [15 m]) [Aug.] (2; CAS), Kaisun village site ([3–5 m]) [Aug.] (12; CAS), Pallant Creek (at Camp Moresby [10 m] and 0.2 km W [15–20 m]) [July–Aug.] (58; CAS, CNC), Takakia Lake ([585–610 m]) [July] (4; CAS), Whiteaves Bay [May] (1; AMor). **Tanu Island:** Tanu village site ([5–25 m]) [Aug.] (16; CAS).

32. *Bembidion farrarae* Hatch

Graham Island ([500 m]) [July] (1; FMNH): Bonanza Creek (0.5 km E of Rennell Sound [10 m]) [July] (1; CAS), Nebria Peak (northeast slope [700–850 m]) [July] (2; CAS), Slatechuck Mountain (northeast slope [760–980 m], east slope at Tarundl Creek [370 m]) [July] (4; CAS). **Louise Island:** Mount Kermode (south slope [885–1,080 m]) [Aug.] (1; CAS). **Moresby Island:** Mount Moresby (east slope of south peak [910–940 m]) [July] (78; CAS, CNC), Takakia Lake ([585 m] and ridges E of [980 m]) [July] (2; CAS, CNC).

33. *Bembidion viator* Casey

Graham Island: Awun Lake (ridges W of [460–550 m]) [Aug.] (1; CAS), Highway 16 (5.8 km N of Chinukundl Creek [2 m]) [July] (1; CAS), Tow Hill Park ([5 m]) [July] (1; CAS). **Moresby Island:** Mosquito Lake [July] (1; FMNH).

34. *Bembidion complanulum* (Mannerheim)

Graham Island: Nebria Peak (northeast slope [700–850 m], above Middle Nebria Lake [790–910 m]) [July] (25; CAS, CNC), Slatechuck Mountain [760–980 m]) [July] (3; CAS). **Louise Island:** Mount Kermode (south slope [885–1,080 m]) [Aug.] (13; CAS). **Moresby Island:** Mount Moresby (east slope of south peak [910–1,080 m], northwest-facing cirque [910–1,070 m]) [July] (114; CAS, CNC), Takakia Lake (ridges E of [730–940 m]) [July] (76; CAS, CNC).

35. *Bembidion planiusculum* Mannerheim

Graham Island: Bonanza Creek (0.5 km E of Rennell Sound [10–20 m]) [July–Aug.] (137; CAS), Chinukundl Creek (at Highway 16 [3 m]) [July] (2; CAS), Ghost Creek (4.7 km NW of Rennell Sound Road 210 m]) [July] (28; CAS, CNC), Gregory Creek (0.3 km E of Rennell Sound [5–10 m]) [Aug.] (82; CAS), Mamin River (1.0 km SE of Juskatla [15 m]) [July] (62; CAS, CNC), Shields Bay [May] (6; AMor), Tlell River (at end of Richardson Road [15 m]) [July] (3; CAS), Yakoun Lake (Etheline Bay at Yakoun River outlet [110 m]) [Aug.] (13; CAS), Yakoun River (5.5 km S of Port Clements [8 m], at Port Clements–Juskatla Road [30 m]) [July–Aug.] (13; CAS). **Lyell Island:** Gate Creek (1.0 km W of mouth [15 m]) [Aug.] (2; CAS). **Moresby Island:** High Goose Creek (west base of Mount Moresby [3–90 m]) [July] (4; CAS), Pallant Creek (at Moresby Camp [3–10 m] and 0.2 km W [15–20 m]) [July–Aug.] (101; CAS, CNC).

36. *Bembidion sejunctum semiaureum* Fall

Graham Island: Queen Charlotte City (10 km W at base of Nipple Mountain) [Aug.] (1; CAS), Tlell (1.0 km S of Tlell River mouth [2 m]) [July] (9; CAS, CNC).

37. *Bembidion transversale* Dejean

Graham Island: Awun Lake (west shore) [Aug.] (9; CAS), Highway 16 (1.9 km N of Chinukundl Creek [10 m]) [Aug.] (1; CAS), Mamin River (1.0 km SE of Juskatla [15 m]) [July] (3; CAS), Naikoon Provincial Park (misty Meadows Campground) [July] (16; FMNH), Tlell River (at end of Richardson Road [15 m]) [July] (13; CAS, CNC), Yakoun Lake (Etheline Bay at Yakoun River outlet [110 m]) [Aug.] (1; CAS), Yakoun River (5.5 km S of Port Clements [8 m], at Port Clements–Juskatla Road [30 m]) [July–Aug.] (7; CAS). **Moresby Island:** Copper Creek (6 km

S of Copper Bay [30 m]) [Aug.] (12; CAS), Mosquito Lake (east shore [80 m]) [July] (2; CAS), Pallant Creek (at Moresby Camp [3–10 m] and 0.2 km W of Moresby Camp [15–20 m]) [July–Aug.] (21; CAS).

38. *Bembidion incrematum* LeConte

Graham Island ([500 m]) [July] (5; FMNH): Bonanza Creek (0.5 km E of Rennell Sound [10 m]) [July] (12; CAS), Cinola Mine [May] (9; AMor), Elaphrus Bog (19.5 km NW of Queen Charlotte City [150 m]) [July] (12; CAS), Ghost Creek (4.7 km NW of Rennell Sound Road [210 m]) [July] (1; CAS), Highway 16 (1.9 km [10 m] and 5.8 km [2 m] N of Chinukundl Creek) [July–Aug.] (127; CAS), Masset (southwest shore of Delkatla Inlet [2–4 m]) [Aug.] (1; CAS), McAuley's Quarry [May] (1; AMor), Skowkona Creek (7.9 km NW of Queen Charlotte City [120 m]) [July] (32; CAS), Tlell River (at end of Richardson Road [15 m]) [July] (2; CAS), Tow Hill Road (19 km E of Masset [10 m]) [July] (2; CAS, CNC), Yakoun River (at Port Clements–Juskatla Road [30 m]) [July] (4; CAS, CNC). **Moresby Island:** Copper Creek (6 km S of Copper Bay [30 m]) [Aug.] (12; CAS).

39. *Bembidion indistinctum* Dejean

Graham Island: Chown Brook (at Tow Hill Road [5 m]) [Aug.] (14; CAS), Masset (southeast shore of Delkatla Inlet [2 m]) [Aug.] (2; CAS, CNC), Masset Inlet (Estrado Lagoon [2–5 m]) [Aug.] (135; CAS). **Moresby Island:** Gray Bay ([4 m]) [Aug.] (22; CAS).

40. *Bembidion versicolor* (LeConte)

Graham Island ([500 m]) [July] (2; FMNH): Bonanza Creek (0.5 km E of Rennell Sound [10 m]) [July] (3; CAS), Cinola Mine [May] (16; AMor), Elaphrus Bog (19.5 km NW of Queen Charlotte City [150 m]) [July–Aug.] (62; CAS, CNC), Highway 16 (1.9 km [10 m] and 5.8 km [2 m] N of Chinukundl Creek) [July–Aug.] (54; CAS), Masset (southeast shore of Delkatla Inlet [2 m] and 12 km S on Highway 16 [55 m]) [July–Aug.] (24; CAS, USNM), McAuley's Quarry [May] (23; AMor), Nebria Peak (above Middle Nebria Lake [790–910 m]) [July] (1; CAS), Skowkona Creek (7.9 km NW of Queen Charlotte City [120 m]) [July] (18; CAS), Tow Hill Road (19 km E of Masset [10 m]) [July] (3; CAS), Yakoun River (at Port Clements–Juskatla Road [30 m]) [July] (2; CAS). **Moresby Island:** Mosquito Lake [July] (2; FMNH).

41. *Bembidion fortestriatum* (Motschulsky)

Graham Island: Agonum Bog (11.1 km NW of Queen Charlotte City [150 m]) [July] (1; CAS), Elaphrus Bog (19.5 km NW of Queen Charlotte City [150 m]) [July] (254; CAS, CNC), Ghost Creek drainage (7.3 km NW of Rennell Sound Road [240] (2; CAS), Highway 16 (1.9 km [10 m] and 5.8 km [2 m] N of Chinukundl Creek) [July–Aug.] (87; CAS), Masset (southeast shore of Delkatla Inlet [2 m] and 14 km E) [July–Aug.] (7; CNC), McAuley's Quarry [May] (2; AMor), Port Clements (15 km N [60 m]) [July] (1; CAS), Skowkona Creek (7.9 km NW of Queen Charlotte City [120 m]) [July] (2; CAS), Tow Hill Park ([5 m]) [July] (2; CAS), Tow Hill Road (19 km E of Masset [10 m]) [July] (1; CAS). **Moresby Island:** Mosquito Lake [July] (24; FMNH).

42. *Bembidion spectabile* (Mannerheim)

Graham Island: Nebria Peak (northeast slope [700–780 m]) [July] (1; CAS), Port Clements [Apr.] (1; QCIM), Skowkona Creek (7.9 km NW of Queen Charlotte City [120 m]) [July] (1; CNC). **Huxley Island:** southwest shore ([10–30 m]) [Aug.] (1; CAS). **Kunga Island:** north shore (S of Titul Island [6–25 m]) [Aug.] (1; CAS). **Lyell Island:** Gate Creek (at mouth [3–10 m]) [Aug.] (1; CAS). **Moresby Island:** Takakia Lake ([590–610 m]) [July] (2; CAS).

43. *Bembidion oblonguloides* Lindroth

Graham Island ([500 m]) [July] (1; FMNH): Cinola Mine [May] (3; AMor), Ghost Creek drainage (7.3 km NW of Rennell Sound Road [240 m]) [July] (18; CAS, CNC), Masset (6; USNM), Port Clements (0.1 km W of Highway 16 [15 m]) [July–Aug.] (2; CAS, QCIM), Skowkona Creek (7.9 km NW of Queen Charlotte City [120 m]) [July] (2; CAS), Slatechuck Mountain (east slope [430 m]) [July] (5; CAS), Yaku village site (0.2 km SE [3–5 m]) [Aug.] (1; CAS).

44. *Bembidion oblongulum* (Mannerheim)

Moresby Island: Mount Moresby (west slope at High Goose Lake [640 m]) [July] (2; CAS), Takakia Lake ([610 m]) [July] (1; CAS).

45. *Nomius pygmaeus* (Dejean)

Talunkwan Island: Thurston Harbour [July] (1; CAS).

46. *Pterostichus lama* (Ménétriés)

Graham Island: Cape Ball [Aug.] (3; QCIM), Naikoon Provincial Park (at park headquarters [15 m]) [July] (2; CAS), Port Clements [Sep.] (1; QCIM), Queen Charlotte City [July] (1; CNC), Tlell River (1 km S of mouth [2 m]) [July] (1; CAS). **Kunga Island:** west shore (on Klue Passage [5–50 m]) [Aug.] (1; CAS). **Louise Island:** Skedans village site (1.5 km W [3–15 m]) [Aug.]) (1; CAS). **Lyell Island:** Gate Creek (at mouth [3–10 m]) [Aug.] (3; CAS). **Moresby Island:** Cumshewa village site ([8–20 m]) [Aug.] (2; CAS). **Reef Island:** north shore (1.0 km E of west end) [Aug.] (1; CNC). **Tanu Island:** Tanu village site [Sep.] (1; QCIM).

47. *Pterostichus crenicollis* LeConte

Burnaby Island: bay on north shore (SE of Alder Island [3–5 m]) [Aug.] (2; CAS). **Chaatl Island:** Chaatl village site ([10–30 m]) [Aug.] (1; CAS). **Graham Island:** Awun Lake (3.2 km W [50–60 m]) [Aug.] (1; CAS), Deep Creek Beach [May] (1; QCIM), Ghost Creek (4.7 km NW of Rennell Sound Road [210 m]) [July] (1; CAS), Ghost Creek drainage (7.3 km NW of Rennell Sound Road [240 m]) [July] (1; CAS), Highway 16 (1.9 km [10 m] and 5.8 km [2 m] N of Chinukundl Creek) [July–Aug.] (2; CAS), Kiusta village site (0.3 km E of [3–5 m]) [Aug.] (9; CAS, CNC), Lawn Point [May] (1; AMor), Lepas Bay (northeast shore [3–15 m]) [Aug.] (4; CAS), Mamin River (1.0 km SE of Juskatla [15 m]) [July] (6; CAS, CNC), Masset (southwest shore of Delkatla Inlet [2 m] and 1.4 km S on east shore of Masset Inlet [5 m] and 0.6 km NE on Tow Hill Road [10 m]) [July–Aug.] (7; CAS), Naikoon Provincial Park (at park headquarters [15 m])

[July] (1; CAS), Port Clements (0.1 km W of Highway 16 [15 m]) [July–Oct.] (15; CAS, QCIM), Queen Charlotte City (1.5 [15 m] and 24 km W) [July–Aug.] (5; CAS, FMNH), Rennell Sound Road (1.5 km N) [May] (1; AMor), Skowkona Creek (7.9 km NW of Queen Charlotte City [120 m]) [July–Aug.] (90; CAS, CNC), Slatechuck Mountain (east slope [370–790 m]) [July] (1; CAS), Tow Hill Park ([5 m] and W of headland) [May, July] (16; CAS, QCIM), Yakoun Lake (Etheline Bay at Yakoun River outlet [110 m]) [Aug.] (1; CAS), Yaku village site (0.2 km E of [3–15 m]) [Aug.] (3; CAS). **Huxley Island:** southeast shore ([10–30 m]) [Aug.] (1; CAS). **Langara Island:** Henslung Cove ([5–8 m]) [Aug.] (3; CAS). **Louise Island:** Skedans village site ([6–30 m] and 1.5 km W [3–15 m]) [Aug.] (15; CAS, CNC). **Lyell Island:** Gate Creek (at mouth [3–10 m] and 1.0 km W [15 m]) [Aug.] (7; CAS), Powrivco Creek (near mouth [15 m]) [Aug.] (1; CAS), Powrivco Point (0.5 km SW [3–5 m]) [Aug.] (4; CAS). **Moresby Island:** Copper Creek (6 km S of Copper Bay [30 m]) [Aug.] (6; CAS), Gray Bay ([3–10 m]) [Aug.] (2; CAS), Jedway (bay 3 km E [6–50 m]) [Aug.] (1; CAS), Kaisun village site ([5–50 m]) [Aug.] (3; CAS), Moresby Camp (3 km S on road to Peel Inlet [12–140 m]) [July] (1; CAS), Mosquito Lake [July] (1; FMNH), Pallant Creek (at Moresby Camp [3–10 m] and 0.2 km W [15 m]) [July] (3; CAS), Peel Inlet (at road to Moresby Camp [2 m]) [July] (2; CAS), Sandspit [May] (1; AMor), Skincuttle Inlet (0.8 km SW of Huston Point [5–10 m]) [Aug.] (1; CAS). **Ramsay Island:** north shore (1.5 km E of west end [3–30 m]) [Aug.] (2; CAS). **Reef Island:** north shore (0.6 km E of west end [5 m]) [Aug.] (3; CAS). **Talunkwan Island:** Heming Head (1 km NW [3–5 m]) [Aug.] (1; CAS). **Tanu Island:** Tanu village site ([5–50 m] and stream NW [10–20 m]) [Aug.–Sep.] (4; CAS, QCIM).

48. *Pterostichus algidus* LeConte

Anthony Island: Ninstints [June] (4; BCPM). **Burnaby Island:** [July] (1; UBC), bay on north shore (SE of Alder Island [3–5 m, 10–20 m]) [Aug.] (8; CAS), Burnaby Narrows (at cabin) [Sep.] (10; QCIM), Section Cove ([3–6 m]) [Aug.] (4; CAS). **Chaatl Island:** Chaatl village site ([10–30 m]) [Aug.] (2; CAS). **East Copper Island:** [Sep.] (8; QCIM). **Faraday Island:** [July] (1; UBC). **Graham Island:** Agonum Bog (11.1 km NW of Queen Charlotte City [150 m]) [July] (1; CAS), Cape Ball River (at mouth) [Aug.] (1; QCIM), Chown Brook (at Tow Hill Road [5 m]) [Aug.] (1; CAS), Deep Creek Beach [May] (4; QCIM), Elaphrus Bog (19.5 km NW of Queen Charlotte City [150 m]) [Aug.] (1; CAS), Ghost Creek (4.7 km NW of Rennell Sound Road [210 m]) [July] (7; CAS), Gregory Creek (0.3 km E of Rennell Sound [5–10 m]) [Aug.] (1; CAS), Honna Point [May] (6; AMor), Jungle Beach [July] (1; UBC), Kiusta village site (0.3 km E [3–10 m]) [Aug.] (10; CAS), Lawn Point [May] (8; AMor), Lepas Bay (northeast shore [3–15 m]) [Aug.] (3; CAS), Mamin River (1.0 km SE of Juskatla [15 m]) [July] (8; CAS), Masset (southeast [2 m] and southwest [2–4 m] shores of Delkatla Inlet and 0.6 km NE on Tow Hill Road [10 m], 1.4 km S on east shore of Masset Inlet [5 m]) [May, July–Aug.] (57; CAS, CNC), Masset Inlet (at Estrado Lagoon [2–5 m]) [Aug.] (2; CAS), McIntyre Bay (Entry Point to Estrado Lagoon [2–5 m], North Beach) [May, Aug.] (3; QCIM), Naikoon Provincial Park (Misty Meadows Campground) [July] (3; FMNH), Port Clements (0.1 km W of Highway 16 [15 m]) [May, July–Nov.] (76; CAS, CNC, QCIM, UBC), Queen Charlotte City (and 1.5 km [15 m] and 24 km W) [July–Sep.] (22; CAS, CNC, UBC), Rennell Sound (at mouth of Bonanza Creek [3–10 m]) [July–Aug.] (16; CAS), Shields Bay [May] (14; AMor), Skidegate (Second Beach, 3.2 km NE) [May, July–Aug., Oct.] (7; CAS, QCIM), Skonum Point [May] (6; AMor), Skowkona Creek (7.9 km NW of Queen Charlotte City [120 m]) [July–Aug.] (21; CAS, CNC), Tlell (Wiggins Road) [June–July, Sep.] (6; CNC, QCIM), Tlell River (at end of Richardson Road [15 m]), 12.8 km S of bridge on Highway 16, Tlell River Park) [July–Aug.] (10; CAS, CNC, FMNH), Tow Hill Park ([5 m], W of headland) [May, July] (18; AMor, CAS, QCIM), Tow Hill Road (0.5 km E of Chown Brook bridge [10 m], 19 km E of Masset [10 m]) [July–Aug.] (31; CAS), Yakoun Lake (Etheline Bay at Yakoun River outlet [110 m]) [Aug.] (5; CAS), Yakoun River (at Port Clements–Juskatla Road [30 m]) [July] (2; CAS), Yaku village site (0.2 km SE of [3–15 m]) [Aug.] (4; CAS). **Hotspring Island:** [June] (2; BCPM), north shore ([5–8 m]) [Aug.] (15; CAS). **Huxley Island:** southeast shore ([10–30 m]) [Aug.] (18; CAS). **Kunga Island:** north shore (S of Titul Island [6–25 m]) [Aug.] (4; CAS), west shore (on Klue Passage [5–50 m]) [Aug.] (8; CAS, CNC). **Kunghit Island:** Rose Harbour [Aug.] (1; UBC). **Langara Island:** Henslung Cove ([5–8 m]) [Aug.] (1; CAS). **Louise Island:** Skedans village site ([3–10 m] and 1.5 km W [3–15 m]) [July–Aug.] (57; CAS, CNC, UBC). **Lyell Island:** Gate Creek (at mouth [3–10 m] and 1.0 km W of [15 m]) [July–Aug.] (41; CAS, UBC), Powrivco Creek (near mouth [15 m]) [Aug.] (2; CAS), Powrivco Point (0.5 km SW of [3–5 m]) [Aug.] (12; CAS, CNC). **Maude Island:** Renner Pass Farm [June] (14; QCIM). **Moresby Island:** Alliford Bay ([10 m]) [July] (13; CAS), Copper Bay [June] (1; UBC), Cumshewa village site ([8–20 m]) [Aug.] (14; CAS, CNC), Darwin Sound (at Hoya Passage [8–30 m]) [Aug.] (1; CAS), Gray Bay ([3–10 m]) [Aug.] (11; CAS), Haswell Bay (1.5 km SW of Hoskins Point [5–30 m]) [Aug.] (1; CAS), Houston Stewart Channel (E of Raspberry Point) [June] (4; UBC), Jedway (bay 3 km NE of [6–50 m]) [Aug.] (21; CAS), Kaisun village site ([3–50 m]) [July–Aug.] (26; CAS, CNC), Louscoone Inlet (E of Etches Point) [June] (4; UBC), Moresby Camp (1–3 km S on road to Peel Inlet [12–140 m]) [July–Aug.] (23; CAS, CNC), Mosquito Lake [July] (1; FMNH), Pallant Creek (at Moresby Camp [3–10 m] and 0.2 km W of [15–20 m]) [July–Sep.] (18; CAS, QCIM), Peel Inlet (at road to Moresby Camp [2 m]) [July] (18; CAS), Sandspit (1 km S of airstrip) [May, July–Aug.] (19; AMor, CAS, QCIM), Skincuttle Inlet (0.8 km SW of Huston Point [5–10 m]) [Aug.] (15; CAS), Whiteaves Bay [May] (4; AMor). **Murchison Island:** [July] (1; UBC). **Ramsay Island:** north shore (1.5 km E of west end [3–30 m]) [Aug.] (5; CAS). **Reef Island:** north shore (1.0 km E of west end) [Aug.] (22; CNC, QCIM). **Talunkwan Island:** Heming Head (1 km SW of [3–5 m, 10–30 m]) [Aug.] (6; CAS, CNC). **Tanu Island:** Tanu village site ([3–50 m]) [July–Sep.] (69; CAS, CNC, QCIM, UBC).

49. *Pterostichus amethystinus* Mannerheim

Burnaby Island: bay on north shore (SE of Alder Island [10–20 m]) [Aug.] (1; CAS), Section Cove [Aug.] (1; CNC). **Chaatl Island:** Chaatl village site ([10–30 m]) [Aug.] (2; CAS). **Graham Island:** [May] (1; UBC), Ghost Creek (4.7 km NW of Rennell Sound Road [210 m]) [July] (5; CAS), Honna Point [May] (4; AMor), Kiusta village site (0.3 km E [5–10 m]) [Aug.] (3; CAS), Mamin River (1.0 km SE of Juskatla [15 m]) [July] (4; CAS), Masset ([10 m] and 0.6 km NE on Tow Hill Road [10 m]) [Aug.] (6; CAS), Naikoon Provincial Park (at park headquarters [15 m]) [July] (2; CAS), Nebria Peak (northeast slope [700–850 m]) [July] (1; CAS), Port Clements (0.1 km W of Highway 16 [15 m]) [July, Oct.] (19; CAS, QCIM), Pure Lake Provincial Park ([65 m]) [Aug.] (2; CAS), Queen Charlotte City (and 1.5 [15 m] and 24 km W) [July–Sep.] (9; CAS, CNC, UBC), Rennell Sound (at mouth of Bonanza Creek [3–10 m] [July, Aug.] (4; CAS, FMNH), Skidegate [Aug.] (1; UBC), Skidegate Inlet [Oct.] (1; UBC), Slatechuck Mountain (east slope [370–790 m] and at Tarundl Creek [300 m]) [July] (4; CAS), Tow Hill Park ([5 m]), beach W of headland [3–8 m]) [July] (3; CAS), Tow Hill Road (19 km E of Masset [10 m]) [July] (5; CAS), Yakoun Lake [Aug.] (1; CAS), Yaku village site (0.2 km E [5–15 m]) [Aug.] (2; CAS). **Harrison Island:** [June] (1; UBC). **Hotspring Island:** [July] (1; UBC). **Huxley Island:** southwest shore ([10–30 m]) [Aug.] (1; CAS). **Kunga Island:** north shore (S of Titul Island [6–25 m]) [Aug.] (2; CAS), west shore (on Klue Passage [5–50 m]) [Aug.] (3; CAS). **Langara Island:** [May, July] (3; UBC). **Louise Island:** Skedans village site ([6–30 m] and 1.5 km W [3–15 m]) [Aug.] (3; CAS). **Lyell Island:** Gate Creek (at mouth [3–10 m]) [Aug.] (8; CAS), Powrivco Point (0.5 km SW [5–20 m]) [Aug.] (1; CAS). **Morseby Island:** Alliford Bay ([10 m]) [July] (6; CAS), Cumshewa village site ([8–20 m]) [Aug.] (5; CAS), Haswell Bay (1.5 km SW of Hoskins Point [5–30 m]) [Aug.] (4; CAS, CNC), Kaisun village site ([3–50 m]) [July–Aug.] (5; CAS), Moresby Camp (3 km S on road to Peel Inlet [12–140 m]) [July] (1; CAS), Pallant Creek (at Moresby Camp [3–10 m] and 0.2 km W of Moresby Camp [15 m]) [July] (3; CAS), Peel Inlet (at road to Moresby Camp) [July] (1; CAS), Sandspit [May, July] (3; AMor, UBC), Skincuttle Inlet (0.8 km SW of Huston Point [5–10 m]) [Aug.] (4: CAS), Whiteaves Bay [May] (3; AMor). **Ramsay Island:** [July] (1; UBC), north shore (0.6 km E of west end [5–30 m]) [Aug.] (1; CAS). **Reef Island:** north shore (0.6 km E of west end [20 m]) [Aug.] (26; CAS, CNC, QCIM). **Tanu Island:** Tanu village site (5–50 m] and stream NW of [10–30 m]) [Aug.] (11; CAS, CNC).

50. *Pterostichus castaneus* (Dejean)

Chaatl Island: Chaatl village site ([10–30 m]) [Aug.] (1; CAS). **Graham Island:** Ghost Creek (4.7 km NW of Rennell Sound Road [210 m]) [July] (3; CAS), Queen Charlotte City (W of [500 m]) [July] (1; FMNH), Rennell Sound (at mouth of Bonanza Creek [5–10 m]) [Aug.] (1; CAS), Skowkona Creek (7.9 km NW of Queen Charlotte City [120 m]) [July] (1; CAS), Slatechuck Mountain (east slope [370–790 m]) [July] (18; CAS), Tlell River Park [July] (1; FMNH), Yaku village site (0.2 km SE [5–15 m]) [Aug.] (3: CAS). **Kunga Island:** west shore (on Klue Passage [5–50 m]) [Aug.] (5; CAS). **Langara Island:** Henslung Cove ([5–8 m]) [Aug.] (1; CAS). **Louise Island:** Skedans village site ([6–30 m]) [Aug.] (5; CAS). **Lyell Island:** Gate Creek (at mouth [3–10 m]) [Aug.] (11; CAS), Powrivco Point (0.5 km SW [5–20 m]) [Aug.] (1; CAS). **Moresby Island:** Cumshewa village site ([8–20 m]) [Aug.] (3; CAS, CNC), Haswell Bay (1.5 km SW of Hoskins Point [5–30 m]) [Aug.] (6; CAS), Mount Moresby (south slope [460 m], west slope at High Goose Lake [640 m]) [July] (19; CAS), Pallant Creek (at Moresby Camp [3–10 m] and 0.2 km W of Moresby Camp [15 m]) [July–Sep.] (16; CAS, CNC, QCIM), Skincuttle Inlet (0.8 km SW of Huston Point [5–10 m]) [Aug.] (3; CAS), Peel Inlet (at road to Moresby Camp [2 m]) [July] (1; CAS), Takakia Lake ([590–610 m]) [July] (8; CAS), Whiteaves Bay [May] (1; AMor). **Tanu Island:** Tanu village site ([5–50 m] and at stream SW of [10–30 m]) [Aug.–Sep.] (6; CAS, QCIM).

51. *Pterostichus adstrictus* Eschscholtz

Graham Island: Chown Brook (at Tow Hill Road [5 m]) [Aug.] (1; CAS), Deep Creek Beach [May] (4; QCIM), Elaphrus Bog (19.5 km NW of Queen Charlotte City [150 m]) [Aug.] (1; CAS), Ghost Creek (4.7 km NW of Rennell Sound Road [210 m]) [May, July] (4; AMor, CAS), Highway 16 (5.8 km N of Chinukundl Creek [2 m]) [July] (1; CAS), Kiusta village site (0.3 km E of [3–5 m]) [Aug.] (1; CAS), Lepas Bay (northeast shore [3–15 m]) [Aug.] (7; CAS), Mamin River (1.0 km SE of Juskatla [15 m]) [July] (1; CAS), Masset (southeast [2 m] and southwest [2–4 m] shores of Delkatla Inlet and 1.4 km S on east shore of Masset Inlet [5 m]) [July–Aug.] (7; CAS, CNC), Masset Inlet (at Estrado Lagoon [2–5 m]) [Aug.] (1; CAS), McAuley's Quarry [May] (3; AMor), McIntyre Bay (Entry Point to Estrado Lagoon [2–5 m]) [Aug.] (8; CAS), Naikoon Provincial Park (at park headquarters [15 m]) [July] (2; CAS), Port Clements (0.1 km W of Highway 16 [15 m]) [July–Sep.] (42; CAS, QCIM), Queen Charlotte City (and 1.5 [15 m] and 24 km W) [July–Aug.] (9; CAS), Shields Bay [May] (3; AMor), Skonum Point [May] (4; AMor), Tow Hill Road (0.5 km E of Chown Brook bridge [10 m]) [Aug.] (13; CAS), Yakoun River (at Port Clements–Juskatla Road [30 m]) [July] (45; CAS, CNC). **Moresby Island:** Gray Bay ([3–10 m]) [Aug.] (10; CAS), Mount Moresby (west slope at High Goose Lake [640 m]) [July] (1; CAS), Pallant Creek (0.2 km E of Moresby Camp [20 m]) [Aug.] (1; CAS), Sandspit (1.0 km S of airstrip [3–5 m]) [July] (4; CAS).

52. *Pterostichus riparius* (Dejean)

Graham Island: Ghost Creek (4.7 km NW of Rennell Sound Road [210 m]) [July] (6; CAS).

53. *Agonum ferruginosum* (Dejean)

Graham Island: Masset (southeast shore of Delkatla Inlet [2 m]) [Aug.] (2; CAS), Tow Hill Road (5.3 km SW of Tow Hill) [Aug.] (2; CAS, CNC).

54. *Agonum belleri* (Hatch)

Graham Island: Agonum Bog (11.1 km NW of Queen Charlotte City [150 m]) [July–Aug.] (8; CAS), Drizzel Lake ([55 m]) [July] (1; CAS), Elaphrus Bog (19.5 km NW of Queen Charlotte City [150 m]) [July] (1; CNC).

55. *Agonum metallescens* (LeConte)

Graham Island: Elaphrus Bog (19.5 km NW of Queen Charlotte City [150 m]) [July] (14; CAS).

56. *Agonum brevicolle* Dejean

Graham Island: Elaphrus Bog (19.5 km NW of Queen Charlotte City [150 m]) [July] (49; CAS, CNC), Ghost Creek drainage (7.3 km NW of Rennell Sound Road [240 m]) [July] (1; CAS), Rennell Sound Road (1.5 km N) [May] (2; AMor), Tow Hill Park ([5 m]) [July] (1; CAS), Tow Hill Road (5.3 km SW of Tow Hill, 19 km E of Masset [10 m]) [July–Aug.] (22; CAS, CNC). **Moresby Island:** Mosquito Lake [July] (1; FMNH).

57. *Amara sinuosa* (Casey)

Moresby Island: Mount Moresby (northeast slope of south peak [940–1,080 m]) [July] (5; CAS).

58. *Amara ellipsis* (Casey)

Graham Island: Tlell (1 km S of Tlell River mouth [3–5 m]) [July] (4; CAS).

59. *Amara littoralis* Mannerheim

Graham Island: Bonanza Creek (0.5 km E of Rennell Sound) [Aug.] (1; CNC), Chinukundl Creek (at Highway 16 [3 m]) [July] (1; CAS), Elaphrus Bog (19.5 km NW of Queen Charlotte City [150 m]) [July] (1; CNC), Highway 16 (5.8 km N of Chinukundl Creek [2 m]) [July] (2; CAS), Honna Point [May] (1; AMor), Masset (southeast shore of Delkatla Inlet [2 m] and 1.4 km S on east shore of Masset Inlet [5 m]) [July–Aug.] (2; CAS), Port Clements (0.1 km W of Highway 16 [15 m]) [July–Aug.] (2; CAS), Queen Charlotte City ([30 m] and 1.5 [15 m] and 24 km W) [July–Sep.] (12; CAS). **Lyell Island:** Gate Creek (at mouth [3–10 m]) [Aug.] (1; CAS). **Moresby Island:** Alliford Bay ([10 m]) [May, July] (3; CAS, CNC), Pallant Creek [Apr., June] (5; QCIM), Sandspit (1 km S of airstrip [2 m]) [July] (2; CAS).

60. *Harpalus somnulentus* Dejean

Graham Island: Masset (1.4 km S) [Aug.] (1; CNC), Queen Charlotte City ([30 m] and 1.5 [15 m] and 24 km W) [July–Aug.] (4; CAS). **Moresby Island:** Pallant Creek [June] (1; QCIM).

61. *Trichocellus cognatus* (Gyllenhal)

Graham Island: Masset (1.4 km S) [Aug.] (16; CAS, CNC), McIntyre Bay (Entry Point to Estrado Lagoon [2–5 m]) [Aug.] (1; CAS), Queen Charlotte City (24 km W) [Aug.] (1; CAS), Tow Hill Road (0.5 km E of Chown Brook bridge [10 m]) [Aug.] (54; CAS).

62. *Bradycellus nigrinus* (Dejean)

Graham Island: Bonanza Creek (0.5 km E of Rennell Sound [10 m]) [July] (1; CAS), Cinola Mine [May] (1; AMor), Elaphrus Bog (19.5 km NW of Queen Charlotte City [150 m]) [July] (13; CAS, CNC), McAuley's Quarry [May] (4; AMor), Port Clements (0.1 km W of Highway 16 [15 m]) [Apr., July] (2; CAS, QCIM). **Moresby Island:** Mosquito Lake [July] (11; FMNH), Pallant Creek [Mar.] (7; QCIM).

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