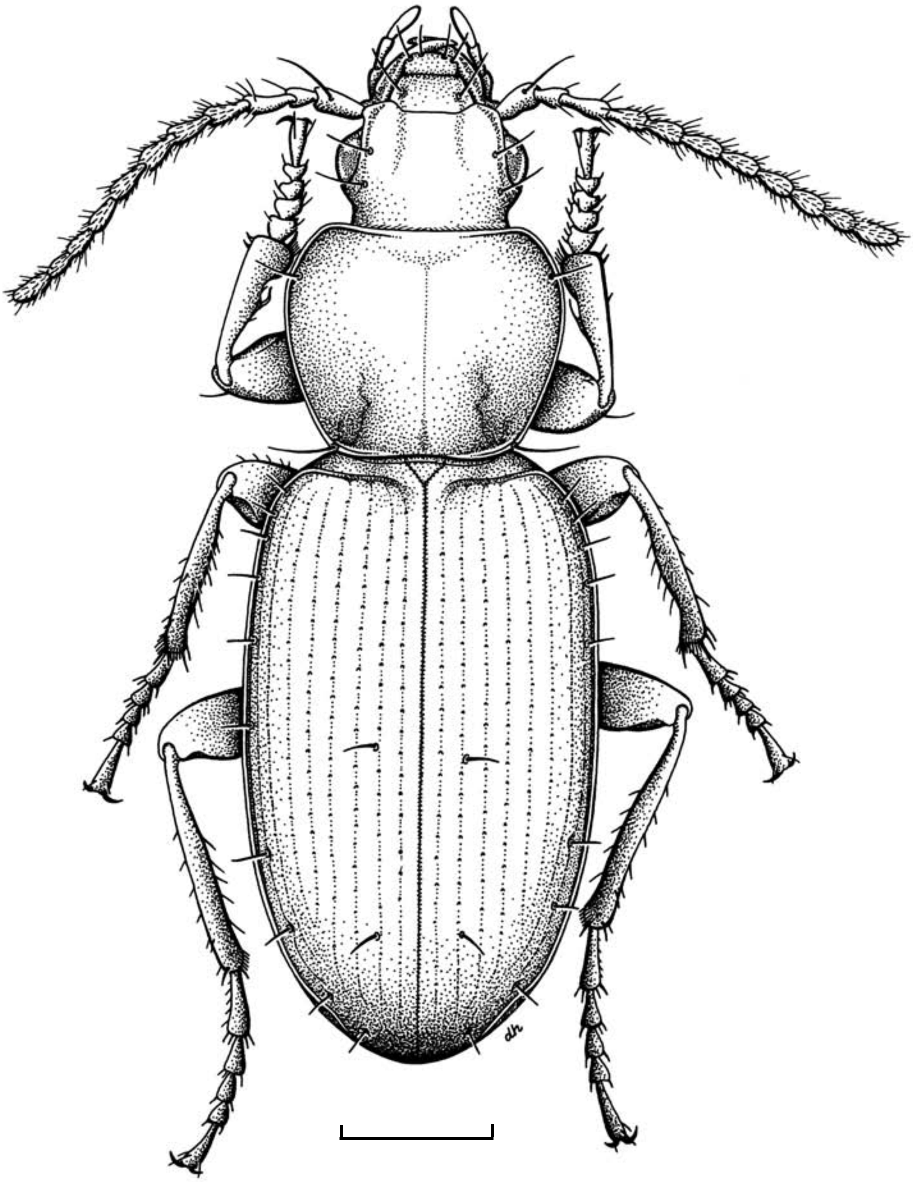

FRONTISPIECE. *Pterostichus (Cryobius) woodi* Ball and Currie, new species, known only from one locality in dry rocky tundra in the Yukon. [Dorsal aspect of male; Canada, Yukon, Dempster Highway km 155, up to 16 July 1982; pan trap; collector D.M. Wood; scale line 1 mm.]

# Ground Beetles (Coleoptera: Trachypachidae and Carabidae) of the Yukon: Geographical Distribution, Ecological Aspects, and Origin of the Extant Fauna

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**Abstract.** The Yukon ground-beetle fauna is analyzed in terms of species composition, geographical distribution, Wisconsinan and early Holocene fossils, habitat associations, and patterns of hindwing development. This analysis provides the basis for an interpretation about the development of the extant ground-beetle fauna of the Yukon Territory. In total, 209 species or subspecies of ground beetles are recorded from the Yukon Territory, of which at least 98, representing 46% of the extant ground-beetle fauna, are hypothesized to have been present in northwestern refugia during the Wisconsinan glaciation. This figure was derived from a combination of distributional and fossil evidence. The range of habitat associations exhibited by this autochthonous component suggests that the Beringian environment may have been more complex than suggested by the "mammoth steppe" or "polar desert" models. Our data are most consistent with the "mosaic model", in which a variety of habitats are hypothesized to have persisted within Beringia. The fauna associated with tundra, riparian zones, and marshes provides evidence that such habitats probably existed in Beringia during late Wisconsinan time, whereas the fauna associated with forest, grassy meadow, and other habitats shows only limited evidence of a long history in northwestern North America. This latter group is hypothesized to have been derived primarily from refugia south of Wisconsinan-age ice. The high degree of endemism in present-day tundra environments indicates long-term stability of that habitat. Analysis of the pattern of hindwing development indicates that brachyptery is most prevalent among the Beringian endemic component, whereas macroptery is dominant among the emigrant and immigrant components. This suggests the importance of flight in insect dispersal. The extensive ranges of the emigrant species provide evidence that Beringia was an important centre for repopulating the north following deglaciation. The corollary is that the number of species present in Beringia during Wisconsinan time may be underestimated if only restrictive distributional information is considered.

**Résumé.** *Les caraboïdes (Coleoptera: Trachypachidae et Carabidae) du Yukon: répartition géographique, aspects écologiques et origine de la faune actuelle.* On trouvera ici une analyse de la faune des caraboïdes du Yukon, composition en espèces, répartition géographique, fossiles du Wisconsinien et du début de l'Holocène, associations d'habitats, importance des ailes postérieures. Cette analyse permettra l'interprétation de l'évolution de la faune actuelle des carabes et trachypachides du Yukon. Au total, 209 espèces ou sous-espèces de ces coléoptères ont été trouvées au Yukon, dont au moins 98, soit 46% de la faune actuelle, sont présumées avoir survécu aux glaciations du Wisconsinien dans des refuges du nord-ouest, supposition basée sur la répartition des espèces actuelles et des espèces fossiles. L'étendue des associations d'habitats occupées par cette faune autochtone semble indiquer que le territoire béringien a sans doute été plus complexe que ne le proposent les modèles de la «steppe des mammouths» ou du «désert polaire». Nos données correspondent plutôt au modèle de «la mosaïque» qui suppose qu'une variété d'habitats prévaut depuis longtemps en Béringie. La faune associée à la toundra, aux zones ripariennes et aux zones marécageuses indique que ces habitats existaient probablement en Béringie à la fin du Wisconsinien, alors que la faune associée aux forêts, aux prairies herbeuses et à d'autres habitats ne permet pas de tirer de telles conclusions sur la présence de ces habitats dans le nord-ouest de l'Amérique du Nord. Il semble plutôt que ce groupe d'espèces ait été associé à des refuges situés au sud des glaciations du Wisconsinien. L'importance de l'endémisme dans les milieux actuels de toundra reflète la stabilité de cet habitat. L'examen des ailes postérieures indique que le

*pp. 445–489 in H.V. Danks and J.A. Downes (Eds.), Insects of the Yukon. Biological Survey of Canada (Terrestrial Arthropods), Ottawa. 1034 pp.* 

brachyptérisme prévaut chez les espèces endémiques béringiennes, alors que le macroptérisme est plutôt le fait des espèces émigrantes ou immigrantes. Il faut voir là une preuve de l'importance du vol dans la dispersion des insectes. La répartition étendue des espèces émigrantes semble démontrer que la Béringie représentait un important centre de repopulation du nord après les glaciations, le corollaire étant que le nombre d'espèces béringiennes présentes à l'époque du Wisconsinien peut être sous-estimé si l'on ne tient compte que de la répartition des espèces actuelles en Béringie.

## Introduction

"There are strange things done 'neath the midnight sun..."—so wrote Robert Service in the introductory lines of "The Cremation of Sam McGee", a poem that called forth a vision, shared far and wide by several generations of readers, of the Yukon Territory and life therein. In this poem and others, Mr. Service wrote perceptively about encounters by rather ordinary persons with rather peculiar circumstances, thereby adding immeasurably to the lore of an area made known by the discovery of gold, a noble metal to which inordinate value is attached, especially by those who do not have any. But Mr. Service's writings and observations proved to be of even greater value. One wonders what he might have written, could he have seen Robin Leech in 1962, on the upper reaches of the Canol Road, above treeline on the slopes of the Mackenzie Mountains, shooting pikas and collecting from their still quivering bodies their astounding flea fauna; or what might Service have written about Nigel Stork, had he seen him in 1981, treading long and hard on a cold rainy day, in a small bog in icy cold water beside the Porcupine River, near Old Crow, to force to the surface a few bedraggled ground beetles, near-frozen, but of burning hot interest to a small community of coleopterists and Quaternary geologists. Poets and lyricists rarely record such events, though the latter illustrate if not epitomize man's pioneering efforts to learn about the creatures with whom he shares space and other resources on this little-known planet.

With his bog-treading and similar activities in other habitats, Nigel Stork, then a member of the Department of Entomology of the Natural History Museum—or British Museum (Natural History) as it was known in the kinder, gentler era just past—was obtaining a bit of the ground-beetle material needed to understand this particular segment of the Yukon fauna. Indeed, knowledge of the Yukon ground beetles has accumulated rather slowly, about as slowly as the movements of the beetles that Dr. Stork's activities uncovered on the Old Crow Flats. At first not readily accessible to early biologist-explorers, and seemingly unprepossessing, the Yukon has not been an area of high priority for coleopterists intent on discovering and cataloguing the Nearctic beetle fauna. The Canadian Arctic Expedition (Hewitt 1920) visited the Yukon Territory at Demarcation Point in May 1914, and one specimen of *Pterostichus mandibularis* Kirby (= *P. brevicornis* Kirby) was collected there (Fall 1919: 15E). Two stops by Expedition biologists at Herschel Island in July 1914 and August 1916 evidently produced no ground beetles (Johansen 1921: 3K).

In 1924, Henry C. Fall, a gifted amateur coleopterist, spent June 21–30 at Whitehorse and Dawson, and recorded the names of the species he collected, including *Bembidion yukonum*, which he described with Dawson as type locality (Fall 1926). For the next quarter-century, which period embraced a world war that saw the Far East and Europe in flames, but left the New World virtually untouched, there was little coleopterological activity in the Yukon Territory; however, access by motor vehicle was made available by construction of the Alaska Highway, which passed through the southern part of the Yukon. Routine air transport made possible visits beyond the Alaska Highway and other roads.

Collectors sent into the field under the auspices of the Canada Department of Agriculture's Northern Insect Survey, taking advantage of the availability of ground and air transportation, visited and sampled various sites in the Yukon Territory (Danks 1981: 110). For example, in the late 1940's, parties of the Northern Insect Survey visited by ground transportation Burwash Landing, Haines Junction, and Whitehorse. The Firth River, near the Arctic Coast, was visited in 1956 by Robin E. Leech and Edward R. Cashman. In 1962, Leech and Peter Skitsko collected ground beetles along the Alaska Highway, the Canol Road, and the Dempster Highway that was being built then through the Ogilvie Mountains, and would be extended eventually northeastward, through the Richardson Mountains, and on to Inuvik, in the Northwest Territories, near the eastern shore of the Mackenzie River delta.

Carl H. Lindroth and George E. Ball collected ground beetles at sites in the Yukon along the Alaska Highway in 1958, the first time that intensive efforts were made to sample the ground beetles, per se, in the Territory.

In 1977, ground beetles were collected at Dawson and at sites along the Porcupine River, by John V. Matthews Jr. (Geological Survey of Canada) and Robert E. Roughley (Department of Entomology, University of Alberta).

During the late 1970's, important collections of ground beetles were obtained, especially along the Dempster Highway, through the efforts of Ales Smetana, J. Donald Lafontaine, and D. Monty Wood (Biosystematics Research Centre, Ottawa), Robert A. Cannings (Royal British Columbia Museum, Victoria), and Richard J. and Sydney G. Cannings (Department of Zoology, University of British Columbia). These collections were supplemented and enhanced by Ball, and David R. Maddison (Department of Entomology, University of Alberta), and Stork. Richard E. Morlan, Matthews, the Cannings brothers, and Ball, Maddison and Stork collected ground beetles also at Klo-Kut in the vicinity of Old Crow, along the Porcupine River, and on the adjacent mountains and tundra, in the late 1970's and early 1980's.

While systematists and others laboured to make known the extant ground-beetle species in the Yukon Territory, John V. Matthews Jr., a Quaternary geologist, and his colleagues interested in reconstructing northern palaeoenvironments, located and excavated Pleistocene age deposits that were rich in remains of ground beetles. The highly perceptive analyses of this material provided a valuable time dimension for these insect species, as well as the basis for synthesis that was exploited successfully by Scott Elias (1994).

Collectively, the efforts of these individuals produced several thousand ground-beetle adults, representing 209 species. This paper lists the species by name, and summarizes what is known about them in terms of their distribution in space and time, and in terms of the habitats that they occupy. This information is interpreted in an historical context to reconstruct the late Pleistocene environment of Beringia, of which the Yukon Territory is a part, and to reconstruct the populating of the Yukon and the north generally, in Holocene (i.e. postglacial) time.

## Materials and Methods

This study is based on examination of 4639 specimens, representing a total of 209 species or subspecies (Table 1). Material examined is housed in the Strickland Entomological Museum, University of Alberta (UASM), and in the institutions listed below. These latter were made available by the curators whose names follow the addresses of their respective institutions.

BMNH—Department of Entomology, The Natural History Museum, Cromwell Road, London, SW7 5BD, England; N.E. Stork.

TABLE 1. List of Yukon ground beetles indicating zoogeographic affinities, distributional patterns, wing form and habitat preferences for species and subspecies. Names followed by the symbol ‡ indicate distribution in both Palaearctic and Nearctic; unmarked names indicate Nearctic distribution. Abbreviations for distributional patterns: B, Beringian (East or East-West); P-B, Palaearctic-Beringian (East and West); N-B, Nearctic-Beringian (East or West); N, B–, Nearctic excluding Beringia; H, Circumpolar or nearly Circumpolar; U, uncertain; for further explanation, see text. Abbreviations for wings: m, macropterous; b, brachypterous; m/b, dimorphic. Abbreviations for habitats: A, arboreal; F, forest; M, marsh; Mg, grassy meadow; Msa, saline marsh; Mw, wet meadow; Ob, open bare ground; Os, open dry sand; Osw, open wet sand; R, riparian; S, shrub zone; T, tundra.

| Taxon | Distributional Pattern | | | | | | Wing | Habitat |
|---|---|---|---|---|---|---|---|---|
| | B | P-B | N-B | N, B– | H | U | | |
| **Trachypachidae** | | | | | | | | |
| Trachypachini | | | | | | | | |
| *Trachypachus* Motschulsky | | | | | | | | |
| *T. holmbergi* Mannerheim | | | | + | | | m | F |
| **Carabidae** | | | | | | | | |
| Carabini | | | | | | | | |
| *Carabus* Linnaeus | | | | | | | | |
| *C. chamissonis* Fischer[1] | | | + | | | | b | F |
| *C. maeander* Fischer‡ | | | | | + | | m/b | M |
| *C. taedatus* Fabricius ssp. *taedatus* | | | | + | | | b | R-T |
| *C. truncaticollis* Eschscholtz ssp. *truncaticollis* | + | | | | | | b | T |
| *C. vietinghoffi* Adams ssp. *vietinghoffi* ‡ | | + | | | | | b | R-T |
| Nebriini | | | | | | | | |
| *Pelophila* Dejean | | | | | | | | |
| *P. borealis* Paykull‡ | | | | | + | | m | M |
| *P. rudis* LeConte | | | + | | | | m | M |
| *Nebria* Latreille | | | | | | | | |
| *N. sahlbergi* Fischer ssp. *sahlbergi* | | | | + | | | m | R |
| *N. arkansana* Casey ssp. *edwardsi* Kavanaugh | | | | + | | | m | R |
| *N. acuta* Lindroth ssp. *acuta* | | | | + | | | m | R |
| *N. obliqua* LeConte (= *obtusa* LeConte) | | | | + | | | m | R |
| *N. gyllenhali* Schönherr ssp. *castanipes* Kirby | | | + | | | | m | F |
| *N. crassicornis* Van Dyke ssp. *intermedia* Van Dyke | | | + | | | | m | F |
| *N. frigida* R.F. Sahlberg‡ | + | | | | | | m | S |
| *N. nivalis* Paykull‡ | | | | | + | | m | R |
| *N. hudsonica* LeConte | | | | + | | | m | R |
| *N. gebleri* Dejean ssp. *gebleri* | | | | + | | | m | R |
| *N. meanyi* Van Dyke ssp. *meanyi* | | | | + | | | m | R |
| Opisthiini | | | | | | | | |
| *Opisthius* Kirby | | | | | | | | |
| *O. richardsoni* Kirby | | | + | | | | m | R |
| Notiophilini | | | | | | | | |
| *Notiophilus* Duméril | | | | | | | | |
| *N. semistriatus* Say | | | + | | | | m/b | Ob |
| *N. aquaticus* Linné‡ | | | | | + | | m/b | Ob |
| *N. borealis* Harris | | | + | | | | m/b | Ob |
| *N. sylvaticus* Eschscholtz | | | + | | | | m/b | T |
| Elaphrini | | | | | | | | |
| *Diacheila* Motschulsky | | | | | | | | |
| *D. polita* Falderman‡ | | + | | | | | b | T |
| *Blethisa* Bonelli | | | | | | | | |
| *B. quadricollis* Haldeman | | | | + | | | m | M |
| *B. multipunctata* Linné‡ | | | | | + | | m | M |
| *B. catenaria* Brown | | | + | | | | m | M |

TABLE 1. (*continued*)

| Taxon | Distributional Pattern | | | | | | Wing | Habitat |
|---|---|---|---|---|---|---|---|---|
| | B | P-B | N-B | N, B- | H | U | | |
| *Elaphrus* Fabricius | | | | | | | | |
| *E. lapponicus* Gyllenhal ssp. *lapponicus*‡ | | | | | + | | m | M |
| *E. clairvillei* Kirby | | | + | | | | m | M |
| *E. californicus* Mannerheim | | | + | | | | m | R |
| *E. americanus* Dejean ssp. *americanus* | | | + | | | | m | R |
| *E. tuberculatus* Mäklin | | + | | | | | m | R |
| *E. parviceps* Van Dyke‡ | | | + | | | | m | R |
| *E. purpurans* Hausen | | | + | | | | m | R |
| *E. angusticollis* R.F. Sahlberg ssp. *angusticollis*‡ | + | | | | | | m/b | R |
| Loricerini | | | | | | | | |
| *Loricera* Latreille | | | | | | | | |
| *L. pilicornis* Fabricius ssp. *pilicornis*‡ | | | | | + | | m | M-F |
| Scaritini | | | | | | | | |
| *Dyschiriodes* Jeannel | | | | | | | | |
| *D. politus* Dejean‡ | | | | | + | | m | R-M |
| *D. integer* LeConte | | | + | | | | m | R-M |
| *D. subarcticus* Lindroth | + | | | | | | m | R |
| *D. frigidus* Mannerheim | | | | + | | | m | R-M |
| *D. nigricornis* Motschulsky‡ | | | | | + | | b | M |
| *D. globulosus* Say | | | + | | | | m/b | Osw |
| Broscini | | | | | | | | |
| *Miscodera* Eschscholtz | | | | | | | | |
| *M. arctica* Paykull‡ | | | | | + | | m | F |
| Patrobini | | | | | | | | |
| *Patrobus* Dejean | | | | | | | | |
| *P. stygicus* Chaudoir | | | + | | | | m | M |
| *P. septentrionis* Dejean‡ | | | | | + | | m | M |
| *P. foveocollis* Eschscholtz‡ | | | + | | | | b | F |
| *Diplous* Motschulsky | | | | | | | | |
| *D. aterrimus* Dejean | | | + | | | | m | R |
| Trechini | | | | | | | | |
| *Trechus* Clairville | | | | | | | | |
| *T. chalybeus* Dejean | | | | + | | | b | S |
| *T. tenuiscapus* Lindroth | | | | + | | | b | F |
| *T. apicalis* Motschulsky‡ | | | + | | | | m/b | Mw-S-F |
| Gehringiini | | | | | | | | |
| *Gehringia* Darlington | | | | | | | | |
| *G. olympica* Darlington | | | + | | | | m | R |
| Bembidiini | | | | | | | | |
| *Asaphidion* Gozis | | | | | | | | |
| *A. alaskanum* Wickham | + | | | | | | m | R |
| *A. yukonense* Wickham | | | + | | | | m | R |
| *Bembidion* Latreille | | | | | | | | |
| *B. levettei* Casey | | | + | | | | m | R |
| *B. inaequale* Say ssp. *opaciceps* Casey | | | + | | | | m | R |
| *B. punctatostriatum* Say | | | | + | | | m | R |
| *B. carinula* Chaudoir | | | | + | | | m | R |
| *B. lapponicum* Zetterstedt‡ | | | | | + | | m | R |
| *B. foveum* Motschulsky‡ | | | | | + | | m | R |
| *B. nitidum* Kirby | | | | + | | | m | Ob |
| *B. interventor* Lindroth | | | + | | | | m/b | R |
| *B. dyschirinum* LeConte | | | + | | | | m/b | F |
| *B. kuprianovi* Mannerheim | | | + | | | | m | R |
| *B. incertum* Motschulsky | | | + | | | | m | R |

TABLE 1. (*continued*)

| Taxon | Distributional Pattern | | | | | | Wing | Habitat |
|---|---|---|---|---|---|---|---|---|
| | B | P-B | N-B | N, B- | H | U | | |
| *B. arcticum* Lindroth‡ | + | | | | | | m | R |
| *B. quadrifoveolatum* Mannerheim | | | | + | | | m | R |
| *B. compressum* Lindroth‡ | | | + | | | | m | R |
| *B. manningense* Lindroth | | | + | | | | m | R |
| *B. brachythorax* Lindroth‡ | | | + | | | | m | R |
| *B.* sp? (*Plataphodes*) | | | | | | + | ? | ? |
| *B. planatum* LeConte | | | + | | | | m | R |
| *B. rufinum* Lindroth | | | | + | | | m | R |
| *B. gratiosum* Casey | | | + | | | | m | R |
| *B. gebleri* Gebler ssp. *turbatum* Casey | | | + | | | | m | R |
| *B. rusticum* Casey ssp. *lenensoides* Lindroth | | | + | | | | m | R |
| *B. sulcipenne* J. Sahlberg ssp. *hyperboroides* Lindroth | + | | | | | | m | R |
| *B. flebile* Casey | | | + | | | | m | R |
| *B. hasti* C.R. Sahlberg‡ | | | | | + | | m | R |
| *B. quadrulum* LeConte | | | | + | | | m | R |
| *B. concolor* Kirby | | | + | | | | m | R |
| *B. mckinleyi* Fall ssp. *mckinleyi* | + | | | | | | m | R |
| ssp. *carneum* Lindroth | | | + | | | | m | R |
| *B. lenae* Csiki‡ | + | | | | | | m | R |
| *B. grapii* Gyllenhal‡ | | | | | + | | m/b | Ob |
| *B. yukonum* Fall‡ | | | | | + | | m/b | M-T |
| *B. dauricum* Motschulsky‡ | | | | | + | | m/b | T |
| *B. bimaculatum* Kirby | | | + | | | | m | R |
| *B. sordidum* Kirby | | | + | | | | m/b | R |
| *B. umiatense* Lindroth | + | | | | | | m/b | R |
| *B. petrosum* Gebler ssp. *petrosum*‡ | | | | | + | | m | R |
| *B. rupicola* Kirby | | | + | | | | m | Ob |
| *B. obscurellum* Motschulsky‡ | | | | | + | | m | R-Ob |
| *B. transversale* Dejean | | | | + | | | m | R |
| *B. scopulinum* Kirby‡ | | | | | + | | m/b | R |
| *B. incrematum* LeConte | | | + | | | | m | R |
| *B. scudderi* LeConte | | | | + | | | m | Msa |
| *B. obtusangulum* LeConte | | | | + | | | m | Msa |
| *B. coloradense* Hayward | | | | + | | | m | R |
| *B. intermedium* Kirby | | | + | | | | m | R |
| *B. semipunctatum* Donovan‡ | | | | | + | | m | R |
| *B. nigripes* Kirby‡ | | | | | + | | m | R |
| *B. versicolor* LeConte | | | + | | | | m | R |
| *B. timidum* LeConte | | | + | | | | m | R |
| *B. quadrimaculatum* Linné ssp. *dubitans* LeConte | | | + | | | | m | Ob |
| *B. mutatum* Gemminger and Harold | | | + | | | | m | Ob |
| *B. morulum* LeConte | | | + | | | | m/b | Ob |
| *B. convexulum* Hayward | | | + | | | | m/b | R |
| *B. roosvelti* Pic | | | | + | | | m/b | M |
| *B. transparens* Gebler‡ | | | | | + | | m/b | M |
| *B. concretum* Casey | | | + | | | | m | R |
| *B. fortestriatum* Motschulsky | | | + | | | | m | R |
| *Tachyta* Kirby | | | | | | | | |
| *T. angulata* Casey | | | + | | | | m | F-A |
| Pterostichini | | | | | | | | |
| *Pterostichus* Bonelli | | | | | | | | |
| *P. nearcticus* Lindroth | + | | | | | | b | T |
| *P. circulosus* Lindroth | + | | | | | | b | M |
| *P. adstrictus* Eschscholtz‡ | | | | | + | | m | Ob-Mg-S-F |

TABLE 1. (*continued*)

| Taxon | Distributional Pattern | | | | | | Wing | Habitat |
|---|---|---|---|---|---|---|---|---|
| | B | P-B | N-B | N, B- | H | U | | |
| *P. soperi* Ball *(Cryobius)* | + | | | | | | b | F-T |
| *P. arcticola* Chaudoir *(Cryobius)* | | | + | | | | b | T |
| *P. kotzebuei* Ball *(Cryobius)* | + | | | | | | b | F-T |
| *P. tareumiut* Ball‡ *(Cryobius)* | + | | | | | | b | T |
| *P. barryorum* Ball *(Cryobius)* | | | + | | | | b | T |
| *P. hudsonicus* LeConte *(Cryobius)* | | | + | | | | b | F |
| *P. similis* Mannerheim‡ *(Cryobius)* | + | | | | | | b | T |
| *P. parasimilis* Ball‡ *(Cryobius)* | + | | | | | | b | T |
| *P. bryanti* Van Dyke *(Cryobius)* | | | | | | | | |
| ssp. *bryanti* | + | | | | | | b | T |
| ssp. *bryantoides* Ball | + | | | | | | b | T |
| *P. pinguedineus* Eschscholtz‡ *(Cryobius)* | | | | | + | | b | R-T |
| *P. woodi* n. sp. *(Cryobius)* | + | | | | | | b | T |
| *P. riparius* Dejean *(Cryobius)* | | | + | | | | b | R |
| *P. ventricosus* Eschscholtz *(Cryobius)* | | | | | | | | |
| ssp. *ventricosus*‡ | + | | | | | | b | R-T |
| *P. caribou* Ball *(Cryobius)* | | | + | | | | b | T |
| *P. brevicornis* Kirby *(Cryobius)* | | | | | | | | |
| ssp. *brevicornis*‡ | | | | | + | | b | F-T |
| *P. empetricola* Dejean‡ *(Cryobius)* | | | + | | | | b | F-T |
| *P. mandibularoides* Ball *(Cryobius)* | | | + | | | | b | T |
| *P. nivalis* F. Sahlberg‡ *(Cryobius)* | + | | | | | | b | T |
| *P. punctatissimus* Randall | | | | + | | | b | F |
| *P. vermiculosus* Ménétries‡ | | | | | + | | b | T |
| *P. agonus* Horn‡ | + | | | | | | b | T |
| *P. costatus* Ménétries | + | | | | | | b | T |
| *P. sublaevis* J. Sahlberg | | | | | | | | |
| ssp. *rufofemoralis* Van Dyke | + | | | | | | b | T |
| *P. haematopus* Dejean‡ | | | | | + | | m/b | F-T |
| *P. rubripes* Motschulsky‡ | + | | | | | | b | T |
| *Calathus* Bonelli | | | | | | | | |
| *C. ingratus* Dejean | | | + | | | | m/b | F |
| *Sericoda* Kirby | | | | | | | | |
| *S. bogemani* Gyllenhal‡ | | | | | + | | m | F-A |
| *S. quadripunctata* De Geer‡ | | | | | + | | m | F-A |
| *S. bembidioides* Kirby | | | + | | | | m | F-A |
| *Agonum* Bonelli | | | | | | | | |
| *A. simile* Kirby | | | | + | | | m | M |
| *A. consimile* Gyllenhal‡ | | | | | + | | m | M |
| *A. exaratum* Mannerheim‡ | | | | | + | | m | M |
| *A. sordens* Kirby | | | | + | | | m | M |
| *A. gratiosum* Mannerheim | | | + | | | | m | M |
| *A. superioris* Lindroth | | | + | | | | m | M |
| *A. thoreyi* Dejean‡ | | | | | + | | m | M |
| *A. bicolor* Dejean‡ | | | | | + | | m | F |
| *A. piceolum* LeConte | | | | + | | | m/b | F |
| *A. anchomenoides* Randall | | | + | | | | m | F |
| *A. nigriceps* LeConte | | | + | | | | m/b | M |
| *A. quinquepunctatum* Motschulsky‡ | | | | | + | | m | M |
| *A. cupreum* Dejean | | | + | | | | m/b | Ob-Mg |
| *A. affine* Kirby | | | + | | | | m | M |
| *A. propinquum* Gemminger and Harold | | | + | | | | m | M |
| *Platynus* Bonelli | | | | | | | | |
| *P. mannerheimi* Dejean‡ | | | | | + | | b | M |
| Amarini | | | | | | | | |
| *Amara* Bonelli | | | | | | | | |
| *A. carinata* LeConte | | | | + | | | m | R-Mg |

TABLE 1. (*continued*)

| Taxon | Distributional Pattern | | | | | | Wing | Habitat |
|---|---|---|---|---|---|---|---|---|
| | B | P-B | N-B | N, B- | H | U | | |
| *A. lacustris* LeConte | | | + | | | | m | R-Mg |
| *A. torrida* Panzer‡ | | | | | + | | m | Ob-Mg |
| *A. alpina* Paykull‡ | | | | | + | | m/b | T |
| *A. bokori* Csiki‡ | | | | | + | | m | T |
| *A. hyperborea* Dejean‡ | | | | | + | | m | F-T |
| *A. schwarzi* Hayward | | | | + | | | m | F |
| *A. glacialis* Mannerheim‡ | | | | | + | | m | R |
| *A. browni* Lindroth | + | | | | | | m | R |
| *A. colvillensis* Lindroth | | | + | | | | m | R |
| *A. lindrothi* Hieke | | | | | | + | ? | ? |
| *A. obesa* Say | | | | + | | | m/b | Mg |
| *A. quenseli* Schönherr‡ | | | | | + | | m/b | Mg |
| *A. discors* Kirby | | | | + | | | m | Mg |
| *A. sinuosa* Casey | | | | + | | | m | Ob |
| *A. brunnea* Gyllenhal‡ | | + | | | | | m | S |
| *A. pseudobrunnea* Lindroth | | | + | | | | m | S |
| *A. farcta* LeConte | | | | + | | | m | Mg |
| *A. patruelis* Dejean | | | + | | | | m | Mg |
| *A. interstitialis* Dejean‡ | | + | | | | | m | Mg |
| *A. erratica* Duftschmid‡ | | | | | + | | m | Mg |
| *A. lunicollis* Schiödte‡ | | | | | + | | m | Mg |
| *A. aeneopolita* Casey | | | + | | | | m | Mg |
| *A. confusa* LeConte | | | + | | | | m | Mg |
| *A. littoralis* Mannerheim | | | + | | | | m | Mg |
| *A. cupreolata* Putzeys | | | | + | | | m | Mg |
| Harpalini | | | | | | | | |
| *Harpalobrachys* Tschitschérine | | | | | | | | |
| *H. leiroides* Motschulsky‡ | | | | | + | | m | Osd |
| *Harpalus* Latreille | | | | | | | | |
| *H. amputatus* ssp. *amputatus* Say[2] | | | + | | | | m | Mg |
| *H. laticeps* LeConte | | | + | | | | m | Mg-F |
| *H. quadripunctatus* Dejean‡ (= *egregius* Casey) | | | | | + | | m | Mg |
| *H. fulvilabris* Mannerheim | | | + | | | | m/b | F |
| *H. pleuriticus* Kirby | | | + | | | | m | Mg |
| *H. nigritarsis* C.R. Sahlberg‡ | | | | | + | | m | F |
| *H. fuliginosus* Duftschmid‡ | | | | | + | | m | F |
| *H. vittatus* Gebler ssp. *alaskensis* Lindroth‡[3] | + | | | | | | b | T |
| *H. opacipennis* Haldeman | | | | + | | | m | Mg |
| *H. fuscipalpis* Sturm‡ (= *basilaris* Kirby) | | | | | + | | m | Mg |
| *Trichocellus* Ganglbauer | | | | | | | | |
| *T. cognatus* Gyllenhal‡ | | | | | + | | m | F |
| *T. mannerheimi* R.F. Sahlberg‡ | | | | | + | | m/b | T |
| *Bradycellus* Erichson | | | | | | | | |
| *B. lecontei* Csiki | | | + | | | | m | M |
| *B. nigrinus* Dejean | | | + | | | | m | Mw-Mg |
| Chlaeniini | | | | | | | | |
| *Chlaenius* Bonelli | | | | | | | | |
| *C. niger* Randall | | | + | | | | m | M |
| Lebiini | | | | | | | | |
| *Lebia* Latreille | | | | | | | | |
| *L. viridis* Say | | | + | | | | m | S-A |
| *Syntomus* Hope | | | | | | | | |
| *S. americanus* Dejean | | | + | | | | m/b | Ob |

TABLE 1. (*continued*)

| Taxon | Distributional Pattern | | | | | | Wing | Habitat |
|---|---|---|---|---|---|---|---|---|
| | B | P-B | N-B | N, B- | H | U | | |
| *Cymindis* Latreille | | | | | | | | |
| *C. cribricollis* Dejean | | | | + | | | m/b | Osd |
| *C. unicolor* Kirby | | | + | | | | b | Ob-T |
| *C.* sp? | | | | | | + | ? | ? |

[1] *Carabus chamissonis* Fischer is presently known only from the Nearctic region; however, fossils of this species are known from Europe (Lindroth 1957).
[2] Species is Holarctic, but *H. a. amputatus* is Nearctic-Beringian.
[3] Species is Holarctic, but *H. v. alaskensis* is Beringian only.

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SMDV—Spencer Museum, Department of Zoology, University of British Columbia, Vancouver, British Columbia, Canada V6T 2A9; S.G. Cannings.

DEBU—Department of Environmental Biology, University of Guelph, Guelph, Ontario, Canada N1G 2W1; S.A. Marshall.

Additional locality records were obtained from the following publications: Lindroth 1961–1969; Ball 1966; Kavanaugh 1978; Goulet 1983; Bousquet 1987; and Maddison 1993. All records of Yukon ground beetles were plotted on maps to determine distributional patterns within the Yukon. Locality information and distribution maps for each species or subspecies are available from the Strickland Museum. Seven species are known from the Yukon Territory only as fossils of Pleistocene and early Holocene ages; however, present distributional patterns exhibited by these species indicate that extant representatives undoubtedly occur there, but have yet to be collected.

## The Yukon Ground-beetle Fauna

**Present Composition.** In total, 209 species or subspecies of ground beetles (tiger beetles excluded, and placed in their own family, the Cicindelidae) are currently recorded from the Yukon Territory (Table 1). These are arranged in 2 families, following the classification of Beutel and Roughley (1988). *Trachypachus holmbergi* Mannerheim is the only representative of the family Trachypachidae, whereas all other Yukon species belong to the family Carabidae. These latter are arranged among 17 tribes and 33 genera. Two species of Yukon ground beetles are not named or described. The 209 species or subspecies are comparable in diversity and composition to the 205 species recorded from Alaska (Lindroth 1971). This northwestern assemblage is rich compared to the 78 species of ground beetles listed from arctic North America (Danks 1981), but is depauperate compared to the approximately 850 species known from all of Canada. Only one species is endemic to the Yukon Territory: *Pterostichus* (*Cryobius*) *woodi* n. sp. (cf. Frontispiece).

The ground-beetle fauna of the Yukon Territory, and indeed of the adjacent parts of Beringia as well, is a typical northern assemblage. It is rich in the more primitive ground-beetle groups that are lacking from or scarce in the tropics (trachypachids, carabines, nebriines, notiophilines, opisthiines, and elaphrines), and has a standard array of the more derived groups (broscines, tachyines, bembidiines, patrobines, platynines, pterostichines,

TABLE 2. Numbers of species or subspecies in each of the geographical patterns exhibited by Yukon ground beetles.

| Geographical Pattern | No. of species | Percentage of fauna |
|---|---|---|
| Beringian (East or East-West) | 28 | 13 |
| Palaearctic-Beringian (East and West) | 5 | 2 |
| Circumpolar or nearly Circumpolar | 51 | 24 |
| Nearctic including Beringian | 85 | 41 |
| Nearctic excluding Beringia | 37 | 18 |
| Uncertain | 3 | 2 |
| Total | 209 | 100 |

and lebiines). The Scaritini, a primitive group that is worldwide in distribution, is represented by a few species of a single genus. Arboreal forms, which are well represented in tropical regions, are nearly absent from the boreal forest of northwestern North America.

In terms of diversity, the fauna is dominated by the principally riparian genus *Bembidion* (58 species or subspecies), the principally dry to mesic-adapted genus *Amara* (26 species), and the principally forest- and tundra-adapted *Pterostichus* s. lat. (29 species or subspecies). These 3 genera together comprise 55% of the Yukon ground-beetle fauna. A special feature of the Beringian ground-beetle assemblage is richness of 2 groups of brachypterous *Pterostichus*: the subgenus *Cryobius*, and the *Stereocerus*-*Lyperopherus* complex. Evidently, Beringia has been a centre of speciation for these groups. Their richness, in turn, indicates the lack of major environmental perturbations caused by the sequence of Pleistocene glaciations that deposited thick layers of ice over most of the northern lands to the east and south of the Yukon Territory.

**Geographical Patterns of the Extant Fauna.** Presented below are descriptions of 6 geographical patterns exhibited by Yukon ground beetles. Species are assigned to these categories based strictly on the distributional patterns exhibited by extant forms (i.e. without interpretations about postglacial dispersal, habitat associations or reference to the palaeontological literature). Table 1 lists species or subspecies assigned to each category; Table 2 shows the relative proportions of taxa assigned to each group.

***Beringian***. (Fig. 1) This category includes species that are distributed within the unglaciated areas of northwestern North America (East Beringia) and northeastern Siberia (West Beringia), or beyond these areas to only a limited extent. Thus, Yukon species satisfying these criteria are Beringian whether their distribution is Nearctic (i.e. East Beringia only) or Nearctic and Palaearctic (East plus West Beringia). The extent of ice-free Beringia during the Wisconsinan glacial maximum has been discussed thoroughly by Hughes (1971), Ager (1982), and Prest (1984). Lafontaine and Wood (1988) produced a map that summarized the results of these works. We take the Lena River as representing the western boundary of ice-free Beringia in the Palaearctic region, and the Richardson and Mackenzie Mountains (Northwest Territories) as the eastern limit in the Nearctic region. The southern limit of Beringia in the Nearctic region is rather irregular, and difficult to define in simple terms. In the Yukon Territory, virtually all the area south of 62°N was glaciated during the Wisconsinan advance. Glaciation north of this latitude was appreciable only in east-central Yukon, where a tongue-like extension of the Laurentide ice sheet reached approximately 64°N. In Alaska, Beringia is north of the southern coastal ranges. Because certain species in this category can be expected to occur at least marginally beyond the limit of ice-free Beringia, we accept records from as far south as northern British Columbia, and from as far east as the Mackenzie River Delta (Northwest Territories), providing their distribution is mainly

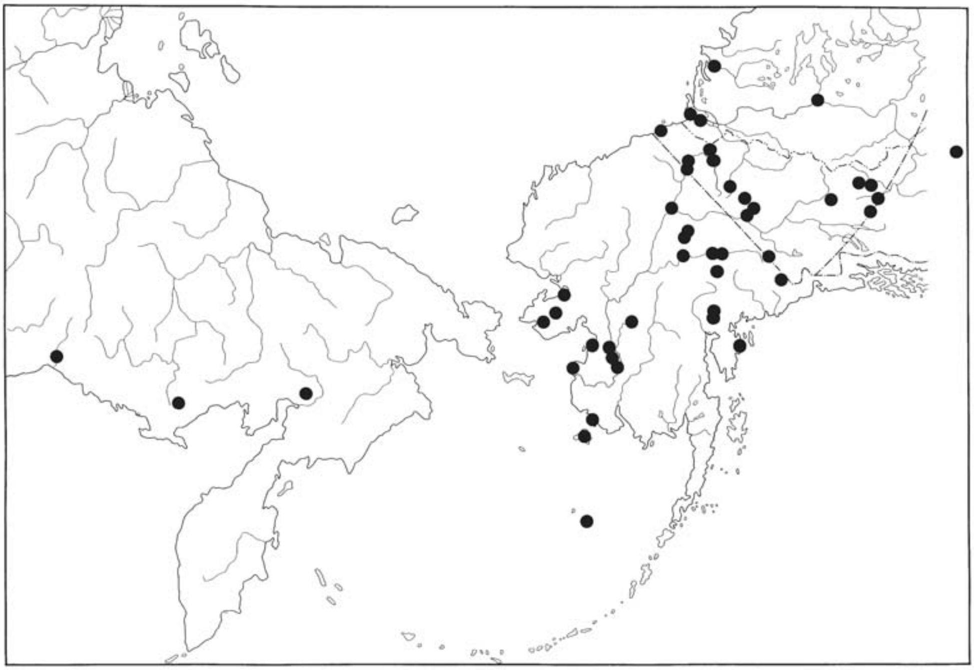

FIG. 1. Beringian distribution, as exemplified by *Nebria frigida* R.F. Sahlberg.

within Beringia as defined above. This provision is to avoid confusion with species that survived in adjacent areas, such as the Mackenzie River and Banks Island refugia.

Twenty-eight Yukon species or subspecies have a Beringian distribution, representing approximately 13% of the total ground-beetle fauna. Twelve taxa occur on both sides of the Bering Strait, whereas 16 occur only in the New World.

***Palaearctic-Beringian.*** Species so designated are distributed both in East Beringia and West Beringia, and beyond unglaciated areas only in the Palaearctic region. Five Yukon species belong here, representing about 2% of the total fauna.

***Nearctic-Beringian.*** (Fig. 2) Included in this category are species or subspecies that are distributed widely in the Nearctic region as well as in Beringia as defined above. Thus, Nearctic-Beringian taxa may have either a Nearctic or Nearctic-plus-West Beringian distribution. Although most ground beetles in this category are classified as Nearctic, probably some will prove to be West Beringian too when the fauna of West Beringia becomes better known. Taxa widely distributed in the Nearctic Region but not recorded from ice-free areas of the Yukon Territory are considered Nearctic-Beringian if they are known to occur in ice-free areas of Alaska.

Eighty-five species or subspecies belong here, representing 41% of the Yukon ground-beetle fauna. Seventy-nine taxa are known only from the Nearctic region. Six taxa are distributed widely in the Nearctic region, but occur also in unglaciated areas of the Palaearctic region.

***Nearctic excluding Beringia.*** (Fig. 3) Species or subspecies in this category are distributed widely in North America, but occur only marginally in the Yukon Territory. For conven-

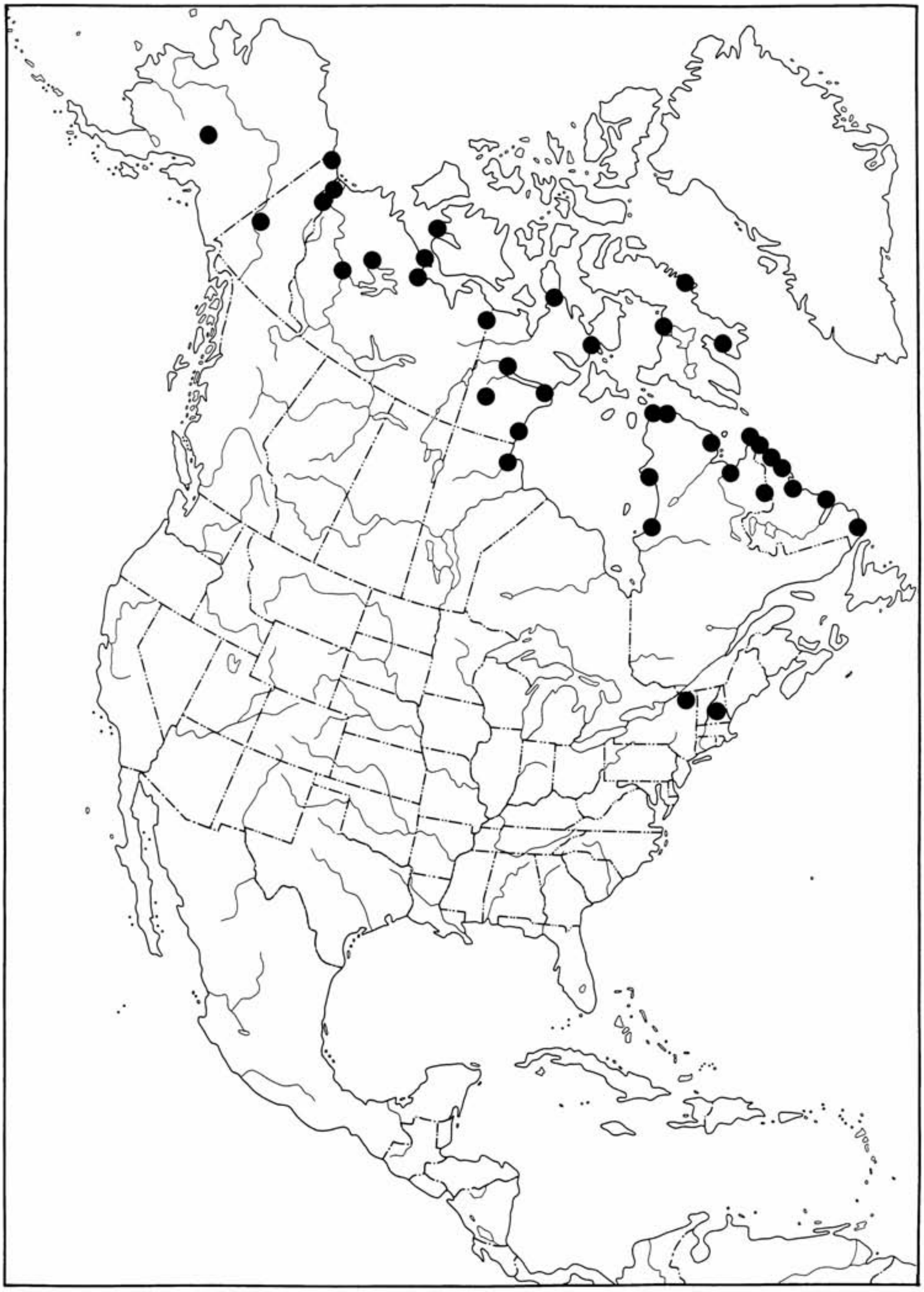

FIG. 2. Nearctic-Beringian distribution, as exemplified by *Pterostichus arcticola* Chaudoir.

ience, we take the Tintina Trench as the northern limit of species in this category. The Tintina Trench is a broad valley that is north of, and more or less parallel to, the Yukon River. Occupying one of the largest faults in the Yukon geological system, this trench is extended

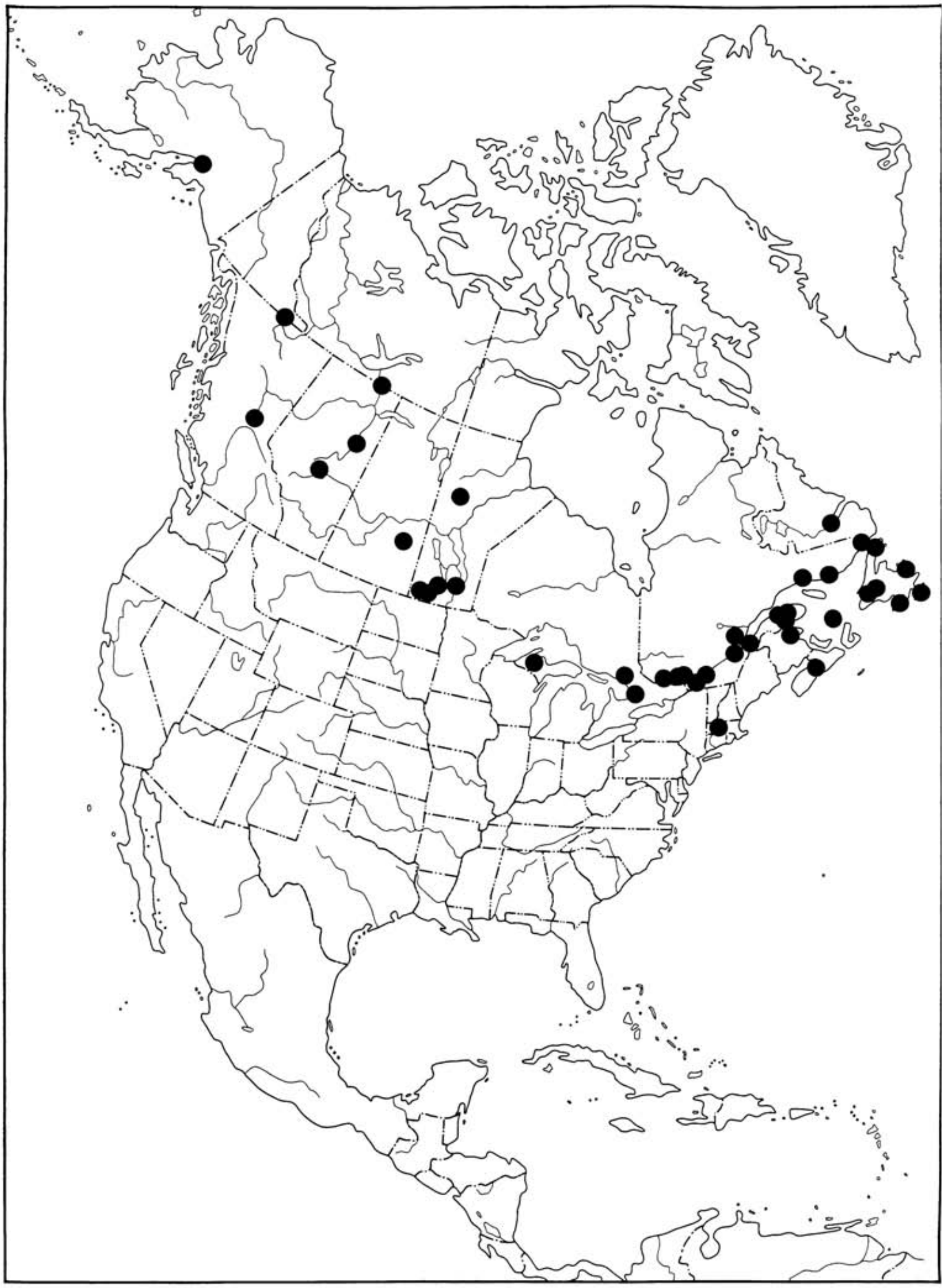

FIG. 3. Nearctic excluding Beringian distribution, as exemplified by *Blethisa quadricollis* Haldeman.

diagonally across the Yukon between Fortymile (northwest of Dawson City) and the headwaters of the Pelly River system (southeast of Ross River). Many Yukon ground beetles occur only within, or to the south of, the Tintina Trench, indicating that it may serve as an

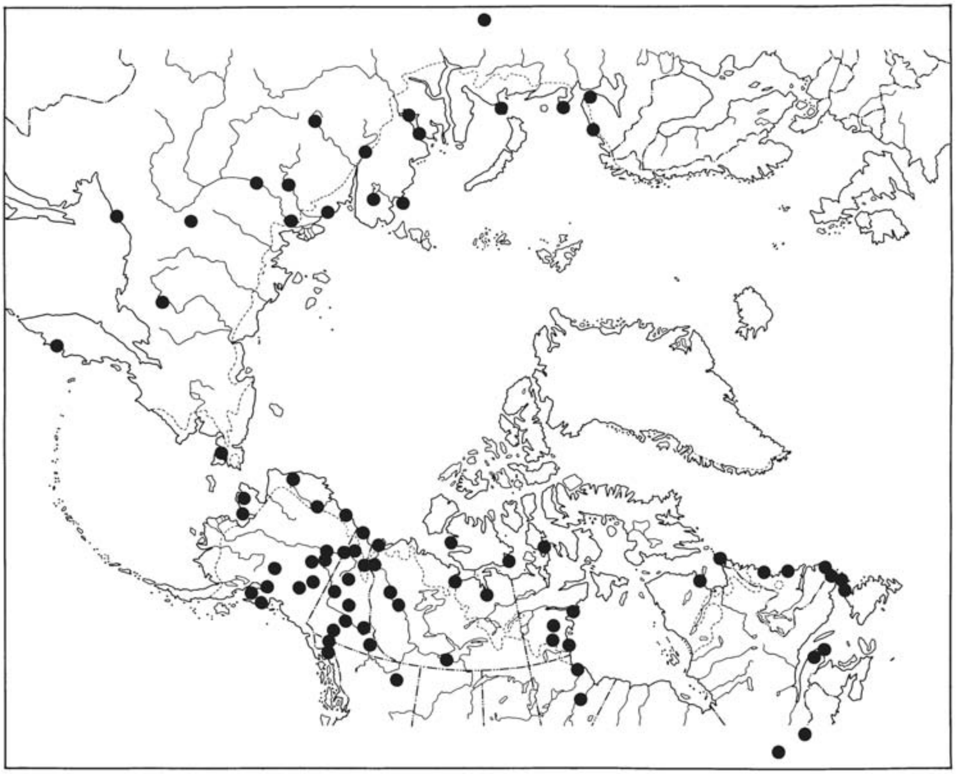

FIG. 4. Circumpolar or nearly Circumpolar distribution, as exemplified by *Pterostichus brevicornis* Kirby.

important geographical barrier to species advancing from the south. All species or subspecies designated as Nearctic excluding Beringia have a Nearctic distribution.

Thirty-seven taxa of Yukon ground beetles belong to this category, representing 18% of the total fauna.

***Circumpolar or nearly Circumpolar.*** (Fig. 4) This category includes species or subspecies that occur beyond the ice-free areas of Beringia in both the Nearctic and Palaearctic regions. All ground beetles so designated have an Holarctic distribution. Fifty-one Yukon taxa have a circumpolar or nearly circumpolar distribution, representing 24% of the total fauna.

***Uncertain.*** Included here are species that are known from only a single locality each, and thus cannot be assigned confidently to any of the distributional patterns described above. The 3 species assigned to this category have a Nearctic distribution, but only one, *Amara lindrothi* Hieke, has been described so far.

**Wisconsinan and Early Holocene Ground Beetles.** Ground-beetle remains are represented abundantly as fossils of Pleistocene and early Holocene ages (e.g. Matthews 1975*a*, *b*, 1976*a*, 1979; Ashworth 1979; Morgan and Morgan 1980; Morgan et al. 1983; Elias 1994). Such information is invaluable for elucidating distributional patterns of ground beetles, and provides the basis for insights about past climates and environments. Because most of Canada was glaciated as recently as 15 000 years ago, it is important to concentrate on areas that had a long ice-free history during Wisconsinan time. The 2 areas that served as major source areas (refugia) for the present-day Yukon fauna are in northwestern North America (including Beringia, parts of the Mackenzie and Anderson River valleys, and Banks Island), and southern Canada and the United States (areas at or beyond the southern limit of Wisconsinan ice) (Ashworth 1996: 128, fig. 3). Table 3 lists the species of Yukon Carabidae that are represented as Pleistocene and early Holocene fossils from these areas.

A survey of the palaeoecological literature reveals that 130 of the 209 species or subspecies of ground beetles recorded from the Yukon Territory are represented in Pleistocene and early Holocene deposits (Tables 3, 4). Ninety-five species are recorded as fossils from northwestern sites, of which 45 are known exclusively from those sites. Eighty-five species are recorded as fossils from sites south of Wisconsinan ice, of which 35 are known exclusively from the south. Fifty species are represented as fossils both north and south of Wisconsinan age ice.

**Habitats of Yukon Ground Beetles.** Although most ground beetles are capable of flight when disturbed, typically they remain closely associated with the habitat(s) for which they are adapted. Some ground beetles, such as members of *Pterostichus* subgenus *Cryobius*, are entirely flightless and incapable of dispersing far from their respective habitats. As a rule, the ranges of ground beetles are determined by climate and general features of the habitat rather than by specific types of food or particular assemblages of plants (Ball, in Campbell et al. 1979). Thus, present-day habitat patterns of ground beetles, when combined with distributional information, can be useful for formulating hypotheses about past distributions and histories of regional biota and climate (Kavanaugh 1979).

Ground beetles are, from a taxonomic perspective, among the most completely known groups of insects in northern North America, and something is known about the way of life for most species (e.g. Lindroth 1961–1969). Although most of the specimens examined for this study were collected by other workers (and have little in the way of specific habitat information), we can infer the habitat associations of most species by a combination of previous experience and locality information. In this endeavour, available ecoregion maps (e.g. Oswald and Senyk 1977; Ecological Stratification Working Group 1996) are of only limited use because they do not resolve specific habitat types within the broader categories recognized.

We recognize 6 major habitats of Yukon ground beetles as follows: riparian; open, wet ground; open, dry ground; shrub zone; forest; tundra; and ecological generalist. Four of these (open, wet ground; open, dry ground; shrub zone; and forest) are further subdivided to include more specific categories of habitat. The major habitats and their subdivisions are outlined in detail below. Habitat associations of each species or subspecies are summarized in Table 1. Total numbers of species and subspecies for each habitat type are presented in Table 5.

***Riparian.*** Representing the single most common habitat of Yukon ground beetles, the riparian zone is the terrain that occurs along the banks of streams and rivers. Often flooded and typically damp, river banks are an especially productive environment for ground beetles. Species are designated as riparian even if they occur periodically some distance from the stream bank, as is typical of many diurnal species that migrate to higher ground at night. This habitat is distributed throughout the Yukon wherever there is running water. Sixty-seven taxa of Yukon ground beetles live exclusively in the riparian zone, and another 9 taxa may occur there.

TABLE 3. The species of Yukon ground beetles represented as Pleistocene and Early Holocene fossils from selected sites in northwestern North America and southern Canada and the United States. Site numbers referred to in this table are explained in Table 4.

| | Northwestern sites | Southern sites |
|---|---|---|
| Carabini | | |
| *Carabus* Linnaeus | | |
| *C. chamissonis* Fischer | 16, 29, 32, 37, 39, 67 | 17, 41, 43 |
| *C. maeander* Fischer | 31 | 17, 60 |
| *C. taedatus* Fabricius | 31 | 51, 53, 54 |
| *C. truncaticollis* Eschscholtz | 1, 4, 6, 15, 16, 27, 29, 31, 32?, 35, 37, 39, 42, 50, 67, | |
| Nebriini | | |
| *Pelophila* Dejean | | |
| *P. borealis* Paykull | 1, 24, 36, 67 | 17, 43 |
| *P. rudis* LeConte | 29 | |
| *Nebria* Latreille | | |
| *N. nivalis* Paykull | 31 | |
| *N. gebleri* Dejean | 19 | |
| Opisthiini | | |
| *Opisthius* Kirby | | |
| *O. richardsoni* Kirby | | 41, 51 |
| Notiophilini | | |
| *Notiophilus* Duméril | | |
| *N. semistriatus* Say | 1?, 16, 39 | 47? |
| *N. aquaticus* Linné | | 43, 48, 49, 60, 62 |
| *N. borealis* Harris | 15?, 16, 19, 31, 67 | 43, 62 |
| *N. sylvaticus* Eschscholtz | 29 | |
| Elaphrini | | |
| *Diacheila* Motschulsky | | |
| *D. polita* Falderman | 1, 6, 7, 13, 15, 16, 19, 21, 22, 24, 29, 31, 37, 46, 50, 67, 68 | 17, 41, 43, 52 |
| *Blethisa* Bonelli | | |
| *B. quadricollis* Haldeman | | 23, 26 |
| *B. multipunctata* Linné | 22, 67 | 51 |
| *B. catenaria* Brown | 6, 27, 31, 67 | |
| *Elaphrus* Fabricius | | |
| *E. lapponicus* Gyllenhal | 1, 4, 5?, 13, 33, 46, 67 | 17, 25, 43, 59 |
| *E. clairvillei* Kirby | 67 | 9, 11, 17, 26, 48, 51, 54, 56, 62 |
| *E. californicus* Mannerheim | | 41, 51, 60, 62 |
| *E. americanus* Dejean | | 17 |
| *E. tuberculatus* Mäklin | 7 | |
| *E. parviceps* Van Dyke | 7, 36, 67 | 17?, 20, 30, 59 |
| Loricerini | | |
| *Loricera* Latreille | | |
| *L. pilicornis* Fabricius | 19 | 17, 40, 41, 48, 51 |
| Scaritini | | |
| *Dyschiriodes* Jeannel | | |
| *D. integer* LeConte | 46 | 48, 49, 65 |
| *D. subarcticus* Lindroth | 14 | |
| *D. frigidus* Mannerheim | 1, 15, 21?, 31 | |
| *D. nigricornis* Motschulsky | 1, 7, 16, 31 | 11, 43 |
| *D. globulosus* Say | | 48?, 62 |
| Broscini | | |
| *Miscodera* Eschscholtz | | |
| *M. arctica* Paykull | | 40, 43, 54, 59, 62 |
| Patrobini | | |
| *Patrobus* Dejean | | |
| *P. stygicus* Chaudoir | 46 | 65 |
| *P. septentrionis* Dejean | 22, 31, 46 | 41? |
| *P. foveocollis* Eschscholtz | 46 | |

TABLE 3. (*continued*)

| | Northwestern sites | Southern sites |
|---|---|---|
| Trechini | | |
| *Trechus* Clairville | | |
| *T. chalybeus* Dejean | 19 | 45? |
| *T. apicalis* Motschulsky | 7, 14, 29, 46 | 41, 53, 63 |
| Bembidiini | | |
| *Asaphidion* Gozis | | |
| *A. alaskanum* Wickham | 6?, 31, 32, 37 | |
| *A. yukonense* Wickham | | 53, 54, 55, 62 |
| *Bembidion* Latreille | | |
| *B. lapponicum* Zetterstedt | 36? | |
| *B. nitidum* Kirby | | 11, 62 |
| *B. interventor* Lindroth | | 51, 62 |
| *B. incertum* Motschulsky | 19 | |
| *B. arcticum* Lindroth | 16 | |
| *B. compressum* Lindroth | | 43 |
| *B. planatum* LeConte | | 45, 62, 63 |
| *B. gratiosum* Casey | 46 | |
| *B. sulcipenne* J. Sahlberg | | 30? |
| *B. flebile* Casey | | 45?, 51? |
| *B. hasti* C.R. Sahlberg | 36, 37? | 25, 59 |
| *B. concolor* Kirby | 22 | 26? |
| *B. mckinleyi* Fall | | 45, 59 |
| *B. grapii* Gyllenhal | 7, 22, 29, 39 | 40, 41, 43, 45, 48, 52, 53, 54 |
| *B. yukonum* Fall | | 51? |
| *B. dauricum* Motschulsky | 16, 24, 32, 38, 39 | 17, 28, 30, 43, 59? |
| *B. bimaculatum* Kirby | | 45 |
| *B. sordidum* Kirby | 22?, 27, 29, 36, 67 | 41, 43, 51, 52, 54, 59, 62 |
| *B. umiatense* Lindroth | 1, 4, 13, 29, 36, 37, 67 | |
| *B. obscurellum* Motschulsky | | 11 |
| *B. transversale* Dejean | | 63 |
| *B. scopulinum* Kirby | | 49, 51, 60, 62, 63 |
| *B. incrematum* LeConte | | 49? |
| *B. coloradense* Hayward | | 45 |
| *B. intermedium* Kirby | 22 | |
| *B. nigripes* Kirby | | 26?, 44, 49, 60, 63 |
| *B. versicolor* LeConte | | 26?, 45, 48?, 49, 60, 63, 66 |
| *B. timidum* LeConte | | 45? |
| *B. quadrimaculatum* Linné | 22 | 60 |
| *B. mutatum* Gemminger and Harold | | 48?, 49, 51, 53, 58, 60, 62 |
| *B. morulum* LeConte | 29, 37 | 43, 51, 54 |
| *B. convexulum* Hayward | 22 | |
| *B. transparens* Gebler | 22, 57 | 26, 45, 65 |
| *B. concretum* Casey | 7, 22, 46 | 11, 26, 45, 49, 51 |
| *B. fortestriatum* Motschulsky | 7 | 17?, 26, 45, 63, 64, 65 |
| Pterostichini | | |
| *Pterostichus* Bonelli | | |
| *P. nearcticus* Lindroth | 4, 13, 29, 32, 42, 50, 67 | |
| *P. circulosus* Lindroth | 7, 67 | |
| *P. adstrictus* Eschscholtz | 22, 31 | 10, 17, 40, 41, 48?, 51, 54, 63 |
| *P. soperi* Ball | 16, 33, 38, 39, 50 | |
| *P. arcticola* Chaudoir | 7, 31, 46 | 25 |
| *P. kotzebuei* Ball | 1, 2, 4?, 7, 16, 32, 33?, 38, 39, 46, 50 | |
| *P. tareumiut* Ball | 1, 3, 7, 15, 16, 19, 27, 31, 32, 33, 35, 37?, 38, 46, 67 | |

TABLE 3. (*continued*)

| | Northwestern sites | Southern sites |
|---|---|---|
| *P. barryorum* Ball | 31 | 43 |
| *P. hudsonicus* LeConte | 3, 29, 37? | |
| *P. similis* Mannerheim | 1, 7, 15, 16, 19, 27, 29, 46, 50 | |
| *P. parasimilis* Ball | 3, 8, 15, 16, 19, 27, 31, 32, 33, 35, 38, 46, 67 | |
| *P. bryanti* Van Dyke | 31 | |
| *P. pinguedineus* Eschscholtz | 1, 2, 3, 5, 7, 15, 16, 24, 27, 29, 31, 32, 35, 36, 38, 39, 42, 46, 50, 61, 67 | 25, 30 |
| *P. riparius* Dejean | | 34 |
| *P. ventricosus* Eschscholtz | 1, 3, 4, 5, 8, 12, 15, 16, 24, 27, 29, 32, 33, 37, 38, 39, 42, 50, 67 | 25?, 30, 43 |
| *P. caribou* Ball | 5, 7, 12, 27, 29, 31, 32, 36, 38, 42?, 46, 67 | 41, 43 |
| *P. brevicornis* Kirby | 1, 3, 4, 5, 7, 13, 14, 15, 16, 19, 21, 24, 27, 29, 31, 32, 33, 35, 36, 38, 39, 46, 50, 67, 68 | 11, 30, 54? |
| *P. empetricola* Dejean | 7, 19, 31 | |
| *P. mandibularoides* Ball | 1, 16?, 38?, 39? | |
| *P. nivalis* F. Sahlberg | 1, 3, 7, 15, 16, 19, 27, 31, 32, 33, 36, 38, 39, 46, 50, 67 | |
| *P. punctatissimus* Randall | 29? | 43, 51, 54, 65 |
| *P. vermiculosus* Ménétries | 1, 3, 5, 27, 29, 32, 37, 67 | 43 |
| *P. agonus* Horn | 5, 7, 8, 15, 19, 27, 31, 46, 67 | |
| *P. costatus* Ménétries | 1, 27, 33, 50, 67 | |
| *P. sublaevis* J. Sahlberg | 5, 6, 27, 29, 31, 32, 34, 42, 50, 67 | 43 |
| *P. haematopus* Dejean | 1, 3, 5, 6, 8, 15, 16, 21, 22, 27, 29, 31, 33, 35, 36, 38, 39, 46, 50, 67 | 11, 43, 59 |
| *P. rubripes* Motschulsky | 5? | |
| *Calathus* Bonelli | | |
| *C. ingratus* Dejean | | 49?, 51, 53 |
| *Sericoda* Kirby | | |
| *S. quadripunctata* De Geer | 67 | 63 |
| *Agonum* Bonelli | | |
| *A. consimile* Gyllenhal | 22 | 28 |
| *A. exaratum* Mannerheim | 1 | |
| *A. gratiosum* Mannerheim | 7, 31, 46, 57 | 48, 49, 51 |
| *A. thoreyi* Dejean | 31? | 63? |
| *A. quinquepunctatum* Motschulsky | 16, 24, 27, 29, 31, 67 | 43 |
| *A. cupreum* Dejean | | 40 |
| *Platynus* Bonelli | | |
| *P. mannerheimi* Dejean | | 10 |
| Amarini | | |
| *Amara* Bonelli | | |
| *A. torrida* Panzer | | 43 |
| *A. alpina* Paykull | 1, 2, 3, 4, 5, 6, 7, 8, 13, 15, 16, 21, 24, 27, 29, 31, 32, 33, 35, 36, 37, 38, 39, 42, 46, 50, 67, 68 | 25, 28, 41 |
| *A. bokori* Csiki | 1, 27, 29, 32, 33? 35, 50, 67 | |
| *A. hyperborea* Dejean | 1 | 63 |
| *A. glacialis* Mannerheim | 29, 32, 36, 42 | 59 |
| *A. browni* Lindroth | 50 | |
| *A. colvillensis* Lindroth | 32?, 37 | |
| *A. obesa* Say | | 51 |
| *A. quenseli* Schönherr | 29 | |
| *A. sinuosa* Casey | 7 | 63 |
| *A. erratica* Duftschmid | 27, 67 | |

TABLE 3. (*continued*)

| | Northwestern sites | Southern sites |
|---|---|---|
| Harpalini | | |
| *Harpalus* Latreille | | |
| *H. amputatus* ssp. *amputatus* Say | 16, 29, 32, 36, 38, 50, 67 | |
| *H. fulvilabris* Mannerheim | 67? | |
| *H. nigritarsis* C.R. Sahlberg | 50 | |
| *H. vittatus* Gebler ssp. *alaskensis* Lindroth | 32, 50? | |
| *Trichocellus* Ganglbauer | | |
| *T. cognatus* Gyllenhal | | 63 |
| *T. mannerheimi* R.F. Sahlberg | 4, 6?, 13, 22, 24, 29, 32, 36, 37, 46, 50, 61, 67 | 18 |
| *Bradycellus* Erichson | | |
| *B. lecontei* Csiki | 22 | |
| Chlaeniini | | |
| *Chlaenius* Bonelli | | |
| *C. niger* Randall | 29 | |
| Lebiini | | |
| *Syntomus* Hope | | |
| *S. americanus* Dejean | | 48, 56 |
| *Cymindis* Latreille | | |
| *C. cribricollis* Dejean | | 48?, 60 |
| *C. unicolor* Kirby | 39 | 43, 51, 54, 59 |

***Open, wet ground.*** Ground beetles living in this environment are hygrophilous or moderately hygrophilous, being confined to the vicinity of water. Four categories of open, wet ground are recognized as follows:

*Open wet sand.* Although not strictly riparian, this habitat occurs on the uppermost zone of river banks. It consists of moderately moist sand or sand mixed with clay, and typically is covered with sparse, depressed vegetation. Only one Yukon species, *Dyschiriodes globulosus* Say, is found predominantly in this habitat.

*Wet meadow.* This habitat consists of rather moist ground, and typically is associated with *Carex* and *Juncus* near the margins of marshes (see below). Neither of the 2 Yukon ground beetles that occur in wet meadows (*Trechus apicalis* Motschulsky and *Bradycellus nigrinus* Dejean) live exclusively there.

*Marsh.* A marsh is a mineral wetland or peatland that is periodically inundated by standing or slowly moving water. Rich in nutrients, this habitat is characterized by emergent vegetation such as reeds (*Phragmites*), rushes (*Typha*, *Scirpus*), or sedges (*Carex*, *Eriophorum*). Marsh-dwelling ground beetles inhabit the rich, soft, wet soil that is situated near the edge of the water. This habitat occurs on poorly drained soils throughout the Yukon Territory. Twenty-eight taxa live exclusively in marshy habitats, and another 5 taxa may occur there.

*Saline marsh.* Areas with poor drainage and high to very high salt content, and typically with marginal encrustations of white salt when dry. Ground beetles of saline marshes live some distance from the water, and are associated with halobiontic plants such as *Salicornia*, *Spergularia* and *Atriplex*. In the Yukon Territory, such areas occur mainly in the rain shadow east of the St. Elias and Alaska ranges. *Bembidion scudderi* LeConte and *B. obtusangulum* LeConte are the only 2 Yukon ground beetles associated with saline marshes.

TABLE 4. List of sites referred to in Table 3. This table is modified from Morgan and Morgan (1980).

| Site No. | Age (in years B.P.) | Name and location | Reference |
|---|---|---|---|
| 1 | Cromerian | Cape Deceit (A) Deering, Alaska | Matthews (1974*a*) |
| 2 | Kansan | Cape Deceit (B) Deering, Alaska | Matthews (1974*a*) |
| 3 | Yarmouthian | Cape Deceit (C) Deering, Alaska | Matthews (1974*a*) |
| 4 | ca. 730 000 | Morgans Bluff, Victoria Is., Northwest Territories | Matthews et al. (1986) |
| 5 | ca. 700 000 | Old Crow Basin (CRH-47), Yukon | Matthews and Telka (1997) |
| 6 | Unspecified interglacial | Kugruk River (Locality 1224), Alaska | Matthews (1977) |
| 7 | Pre-Wisconsinan | Southwestern Alaska | Elias (1992) |
| 8 | Sangamonian | Cape Deceit (D) Deering, Alaska | Matthews (1974*a*) |
| 9 | Sangamonian | Don Valley, Toronto, Ontario | Morgan and Morgan (1980) |
| 10 | Sangamonian | East Milford, Nova Scotia | Mott et al. (1982) |
| 11 | Early Wisconsinan | Gervais Formation, Minnesota | Ashworth (1980) |
| 12 | Early Wisconsinan | Hooper Island, Northwest Territories | Mackay and Matthews (1983) |
| 13 | Early Wisconsinan | Cape Collinson Formation, Banks and Victoria Is., Northwest Territories | Matthews et al. (1986) |
| 14 | Early Wisconsinan | Old Crow Basin, Yukon | Morlan and Matthews (1978) |
| 15 | Early Wisconsinan | Cape Deceit (E) Deering, Alaska | Matthews (1974*a*) |
| 16 | Early Wisconsinan | Fairbanks (Eva Creek A), Alaska | Matthews (1968) |
| 17 | Early Wisconsinan | Scarborough Bluffs, Toronto, Ontario | Morgan and Morgan (1980) |
| 18 | Early Wisconsinan | Woodbridge, Ontario | Morgan and Morgan (1980) |
| 19 | Early Wisconsinan | Southwestern Alaska | Elias (1992) |
| 20 | Early or Middle Wisconsinan | Beaver Valley, Collingwood, Ontario | Morgan and Morgan (1980) |
| 21 | Early to Late Wisconsinan | Prince of Wales Formation, Banks Island, Northwest Territories | Matthews et al. (1986) |
| 22 | ca. 125 000 | Ch'ijee's Bluff (interglacial), Yukon | Matthews and Telka (1997) |
| 23 | ca. 75 000 | St. Pierre, Quebec | Morgan et al. (1986) |
| 24 | >52 000 and <125 000 | Ch'ijee's Bluff (sample A) Yukon | Matthews and Telka (1997) |
| 25 | >54 000 | Chaudière Valley, Quebec | Matthews et al. (1987) |
| 26 | >50 000 | Innerkip, Ontario | Pilny and Morgan (1987) |
| 27 | 43 000 | Titaluk River, Alaska | Morgan et al. (1986) |
| 28 | 40 200 ± 430 | Mary Hill (A) Coquitlam, British Columbia | Armstrong and Clague (1977) |
| 29 | Middle Wisconsinan | Bonnet Plume Basin, Yukon | Hughes et al. (1981) |
| 30 | Middle Wisconsinan | Clarksburg, Ontario | Warner et al. (1988) |
| 31 | Middle Wisconsinan | Southwestern Alaska | Elias (1992) |
| 32 | ca. 36 000–37 000 | Upper Porcupine River, Yukon | Matthews and Telka (1997) |
| 33 | ca. 32 500 | Porcupine River (Bluefish Basin), Yukon | Matthews (1975*a*) |
| 34 | ca. 31 000 ± 640 | Old Crow Basin (CRH-32), Yukon | Matthews and Telka (1997) |
| 35 | ca. 30 000–31 000 | Titilak River, Alaska | Nelson 1982 in Matthews and Telka (1997) |
| 36 | 29 600 ± 300 | Mayo Indian Village (Unit 1), Yukon | Matthews et al. (1990) |
| 37 | ca. 25 000 | Rock River exposure (Bell Basin), Yukon | Matthews and Telka (1997) |
| 38 | >24 400 | Fairbanks (Eva Creek B), Alaska | Matthews (1968) |
| 39 | 24 400 ± 650 | Fairbanks (Eva Creek C), Alaska | Matthews (1968) |
| 40 | 23 313 ± 391 | Garfield Heights, Cleveland, Ohio | Coope (1968) |
| 41 | 21 460 ± 470 | Wedron, Illinois | Garry et al. (1990*a*) |
| 42 | 20 800 ± 200 | Bluefish exposure (REM 76-113), Yukon | Matthews and Telka (1997) |
| 43 | 18 090–16 710 | Conklin Quarry, Iowa | Baker et al. (1986) |
| 44 | 17 850 ± 550 | Lamb Spring, Colorado | Elias and Toolin (1990) |
| 45 | 13 000–11 000 | Rostock, Ontario | Pilny et al. (1987) |
| 46 | Late Wisconsinan to Holocene | Southwestern Alaska | Elias (1992) |
| 47 | ca. 13 000 to recent | Mertztown (Longswamp), Pennsylvania | Morgan and Morgan (1980) |
| 48 | 13 000–6900 | Gage St., Kitchener, Ontario | Schwert et al. (1985) |

TABLE 4. (*continued*)

| Site No. | Age (in years B.P.) | Name and location | Reference |
|---|---|---|---|
| 49 | 12 730 ± 220 | Winter Gulf, N. Collins, New York | Schwert and Morgan (1980) |
| 50 | 12 420 ± 180 | Cape Deceit (F) Deering, Alaska | Matthews (1974*a*) |
| 51 | 12 400 ± 60 | Norwood, Minnesota | Ashworth et al. (1981) |
| 52 | 12 080+ | Newton Site, Pennsylvania | Barnosky et al. (1988) |
| 53 | 11 860 ± 110 | Two Creeks, Wisconsin | Morgan and Morgan (1979) |
| 54 | ca. 11 700 | Kewaunee, Wisconsin | Garry et al. (1990*b*) |
| 55 | ca. 11 500 | Columbia Bridge, Vermont | Matthews (in Morgan and Morgan 1980) |
| 56 | ca. 11 500–9000 | Nichols Brook, New York | Fritz et al. (1987) |
| 57 | 11 500–9000 | Isabella Basin (B) Fairbanks, Alaska | Matthews (1974*b*) |
| 58 | 11 050 ± 420 | Parkhill Creek, Ontario | Morgan and Morgan (1980) |
| 59 | 11 050 ± 130 | St. Eugene, Quebec | Mott et al. (1981) |
| 60 | 10 920 ± 160 | Lockport Gulf, Lockport, New York | Miller and Morgan (1982) |
| 61 | 10 900 ± 80 | Clarence Lagoon, Yukon | Matthews (1975*b*) |
| 62 | 10 600 ± 160 | Eighteen Mile River, Kincardine, Ontario | Ashworth (1977) |
| 63 | 10 100 ± 150 | Mont St. Hilaire, Quebec | Mott et al. (1981) |
| 64 | 10 000 ± 130 | Baie Du Bassin, Amherst Is., Quebec | Prest et al. (1976) |
| 65 | 9940 ± 160 | Mosbeck, Minnesota | Ashworth et al. (1972) |
| 66 | 9750 ± 140 | Seibold, North Dakota | Ashworth and Brophy (1972) |
| 67 | 9700 | Ikpikpuk River, Alaska | Morgan et al. (1986) |
| 68 | 9150 ± 150 | Cape Deceit (G) Deering, Alaska | Matthews (1974*a*) |

***Open, dry ground.*** Ground beetles that live in this habitat are not confined to the vicinity of water and thus are classified as xerophilous or moderately xerophilous. Included are microhabitats as diverse as the upper zones of river banks, dunes, cultivated fields, gravel pits and moraines. The “southern steppe” and “dune” communities described by Lafontaine and Wood (1988) are included in this category. Three types of open, dry ground are recognized as follows:

*Open dry sand.* Roadside blowouts, dry sandy moraines and dunes occur irregularly throughout the Yukon Territory. The largest of these sandy habitats are represented by the dunes at Carcross and the wide glacial valleys of the St. Elias and Alaska ranges. *Cymindis cribricollis* Dejean and *Harpalobrachys leiroides* Motschulsky are the only 2 Yukon ground beetles that live on dry sand.

*Open bare ground.* This habitat consists of gravelly, well drained (often moraine) ground that may or may not be covered with short, sparse, vegetation. Such conditions occur locally throughout the Yukon Territory, and are associated with many disturbed sites. Eleven Yukon species live exclusively in this environment, and another 5 may occur there.

*Grassy meadow.* Consisting of varied assemblages of grasses and herbs, this community is characterized by denser growths of vegetation than the open bare-ground habitat described above. Grassy meadows occur throughout the Yukon Territory, including ditches along most highways. This habitat is not closely associated with water bodies, and thus is drier than the wet meadow habitat. Seventeen species of Yukon ground beetles live exclusively in this habitat, and another 7 species may occur there.

***Shrub Zone.*** The predominant vegetation here is low woody plants that produce numerous shoots or trunks from near the base. The shrub zone is typically an ecotone between the various types of open ground described above and the forest habitat (see below). *Salix* (willow), *Betula* (dwarf birch), and *Alnus* (alder) are the most common shrubs occurring in the Yukon Territory. Ground beetles assigned to this category live among dead leaves that

TABLE 5. Numbers of species or subspecies in each of the habitat types recognized for Yukon ground beetles.

| Habitat | No. of species/subspecies | Percent of fauna |
|---|---|---|
| Riparian | 67 | 32 |
| Open, wet ground | | |
| Open wet sand | 1 | <1 |
| Wet meadow | 0 | 0 |
| Marsh | 28 | 13 |
| Saline marsh | 2 | 1 |
| Open, dry ground | | |
| Open dry sand | 2 | 1 |
| Open bare ground | 11 | 5 |
| Grassy meadow | 17 | 8 |
| Shrub zone | | |
| Ground | 4 | 2 |
| Arboreal | 1 | <1 |
| Forest | | |
| Ground | 19 | 9 |
| Arboreal | 4 | 2 |
| Tundra | 25 | 12 |
| Ecological generalists | 25 | 12 |
| Unknown | 3 | 2 |
| Total | 209 | 100 |

accumulate on the ground beneath the bushes. Only 4 Yukon species are classified as inhabitants of the shrub zone, and another 3 may occur there.

*Shrub/Arboreal.* This is actually just a specialized subdivision of the shrub zone. Unlike most shrub-zone species which are strictly ground dwellers, shrub/arboreal species live upon the vegetation that rises vertically above the ground. Only one Yukon species, *Lebia viridis* Say, is assigned to this category. Specimens occur typically on the leaves of *Alnus* (alder), or on the flowers of *Solidago* (goldenrod).

***Forest.*** Boreal forest represents the single most extensive habitat in the Yukon Territory. *Picea* (white and black spruce), *Abies* (balsam fir), *Pinus* (jack and lodgepole pine), *Betula* (white birch), and *Populus* (trembling aspen and cottonwood) are principal tree species in the southern Yukon, whereas *Picea* and *Larix* (larch) dominate north of the Ogilvie Mountains (Rowe 1972; Ecological Stratification Working Group 1996). The northernmost forests consist of stunted and open-growing stands of trees. Such stands typically are separated by tracts of tundra-adapted vegetation. Forest-dwelling ground beetles exhibit no evident predilection toward coniferous or deciduous stands, and thus are relegated to a single, broad, category. Species in this environment occur typically among the living and dead vegetation that covers the forest floor. Nineteen Yukon species live exclusively in forested areas, and another 15 species may occur there.

*Forest/Arboreal.* Included in this category are forest-inhabiting ground beetles that live under the bark of logs on the ground. Only 4 Yukon species belong here: *Tachyta angulata* Casey, *Sericoda bembidioides* Kirby, *S. bogemani* Gyllenhal and *S. quadripunctata* De Geer. The latter 3 species are associated with burnt forest.

***Tundra.*** Representing the second most extensive habitat in the Yukon Territory, tundra includes all treeless vegetation types that are affected by continuous permafrost. Such environments are designated tundra whether occurring in the mountains (alpine tundra) or in the far north (arctic tundra). Alpine tundra is rather discontinuous, occurring on mountain tops throughout the Yukon. Extensive tracts are situated in the southwestern corner of the

Yukon (St. Elias and Alaska ranges), central Yukon (Ogilvie and Mackenzie Mountains), and northern Yukon (Richardson Mountains). The vegetation here is dominated by *Salix* (dwarf willow), *Betula* (dwarf birch), dwarf Ericaceae, *Dryas* (mountain avens), and crustose and fruticose lichens. True arctic tundra occurs only on northern coastal Yukon, where *Betula*, *Salix*, *Ledum* (northern labrador tea), *Dryas* and *Vaccinium* form a nearly continuous cover (Ecological Stratification Working Group 1996). Tundra vegetation also occurs among and between the open stands of black spruce that characterize the plateau (Porcupine Plateau, Eagle Plain) between the Ogilvie and Richardson Mountains. Ground beetles evidently do not exhibit preference for dry versus wet tundra, and so no distinction is made here. Most tundra species live among leaves under bushes. Twenty-five Yukon taxa live exclusively in tundra environments, and another 12 taxa may occur there.

***Ecological generalists.*** Species that occupy 2 or more of the habitats discussed above are termed ecological generalists. Fifteen different combinations of habitat associations are exhibited by the 25 species assigned to this category. Twenty-three species occur in 2 different habitats, one species occurs in 3 different habitats, and one species occurs in 4 different habitats. The most common combination of habitat associations among ecological generalists is Forest/Tundra, with a total of 7 species. Other habitat combinations with multiple species are: Riparian/Tundra (3 species), Riparian/Marsh (3 species), Open bare ground/Grassy meadow (2 species), and Riparian/Grassy meadow (2 species).

**Patterns of Hindwing Development.** Although flight is acknowledged generally to be one of the major factors in emergence of the Insecta as a dominant terrestrial taxon, development and maintenance of this process is a metabolic expense. Flight is important in dispersal, in enabling fliers to escape quickly from the effects of unfavourable environmental circumstances, to find suitable places for survival, and maintain breeding connections in populations. If, however, circumstances are such that the cost of such benefits exceeds their value, or if intrinsic value of brachyptery outweighs the value of macroptery (Kavanaugh 1985: 144; Liebherr 1988: 161; Wagner and Liebherr 1992), the flight mechanism, which is subject to the forces of natural selection, is reduced through restriction of flight to certain periods during the life cycle, restriction of flight to only some members of a population, or complete loss of the ability to fly.

Reduction of flight capability is achieved through reduction of wing size, reduction of the metathoracic wing muscles, or both. As Darlington (1936), Erwin (1970: 20) and Kavanaugh (1985: 412) have indicated, total reduction of the flight mechanism involves for beetles a series of stages, the end result of which is a species whose adults have the metathorax reduced in size, and without flight muscles; the wings reduced to small stubs; the elytra fused to one another along the suture; and the elytral humeri reduced so that they are sloped inward rather than being rectangular (Kavanaugh 1985: 422, fig. 2).

Erwin (1979: 549) noted that body form is modified, and in similar ways, in flightless adults of many species that are otherwise unrelated to each other. Liebherr (1988: 161) postulated that loss of flight allows for increase in body size, which itself has marked advantages in way of life of taxa.

Loss of flight is a common occurrence in ground-inhabiting hexapods, such as ground beetles and tenebrionids. Darlington (1936) and Den Boer et al. (1980) emphasized the importance of stable habitats in providing the conditions necessary for lack of selection in maintaining flight capability.

Lindroth (1971) discussed the pattern of wing development among Alaskan Carabidae in terms of Holarctic distribution patterns. He showed a positive correlation between

TABLE 6. Relationship between geographical distribution patterns and hindwing development among Yukon ground beetles.

| Distribution Pattern | Macropterous | | Dimorphic | | Brachypterous | | Total |
|---|---|---|---|---|---|---|---|
| | N | % | N | % | N | % | |
| Beringian (East or East-West) | 8 | 28.6 | 2 | 7.1 | 18 | 64.3 | 28 |
| Palaearctic-Beringian (East and West) | 3 | 60.0 | 0 | 0.0 | 2 | 40.0 | 5 |
| Circumpolar or nearly Circumpolar | 35 | 69.2 | 11 | 21.2 | 5 | 9.6 | 51 |
| Nearctic including Beringian | 60 | 70.2 | 15 | 17.9 | 10 | 11.9 | 85 |
| Nearctic excluding Beringia | 29 | 78.4 | 4 | 10.8 | 4 | 10.8 | 37 |
| Total | 135 | 65.6 | 32 | 15.5 | 39 | 18.9 | 206 |

macroptery (the normal, long-winged condition of adults) and range extent. For example, of 27 Alaskan endemics and species with ranges extended only from west of Hudson Bay to eastern Siberia, brachyptery (reduced wings) is the predominant condition. On the other hand, for 53 Holarctic species with wider ranges, macroptery predominates.

The Yukon fauna shows a similar pattern (Table 6). Sixty-four per cent of the Beringian ground-beetle component is brachypterous, whereas for the more widely distributed taxa, macroptery and dimorphism (i.e. some individuals of a species macropterous, others brachypterous) are predominant.

From an ecological perspective, brachyptery is predominant only in the tundra (Table 7). For forest habitats and among ecological generalists, wing reduction is exhibited by nearly half of the taxa. In the more open and unstable riparian habitats, wing reduction is less frequent, and brachyptery is exhibited by only one riparian species.

## Development of the Extant Ground-beetle Fauna of the Yukon Territory

An excellent general context for the following discussion is provided by Elias (1994: 175–190), beginning with “Late Tertiary origins of the tundra biome”. During the late Wisconsinan glacial maximum, when most of northern North America was covered by continental ice, the unglaciated parts of Alaska and the Yukon Territory were joined with eastern Russia via the Bering land bridge. As such, the northwestern corner of North America represented the easternmost extension of a vast territory (Beringia), that extended westward across Asia as an essentially treeless habitat. Biogeographers have long been interested in the flora and fauna of this region because it served as an important source area for organisms that repopulated North America following deglaciation. Because most insects are sparsely

TABLE 7. Relationship between hindwing development and habitat among Yukon ground beetles.

| Habitat | Macropterous | | Dimorphic | | Brachypterous | | Total |
|---|---|---|---|---|---|---|---|
| | N | % | N | % | N | % | |
| Riparian | 60 | 89.5 | 6 | 9.0 | 1 | 1.5 | 67 |
| Open, wet ground | 23 | 74.2 | 5 | 16.1 | 3 | 9.7 | 31 |
| Open, dry ground | 21 | 70.0 | 9 | 30.0 | 0 | 0.0 | 30 |
| Shrub zone | 4 | 80.0 | 0 | 0.0 | 1 | 20.0 | 5 |
| Forest | 14 | 60.9 | 4 | 17.4 | 5 | 21.7 | 23 |
| Tundra | 1 | 4.0 | 4 | 16.0 | 20 | 80.0 | 25 |
| Ecological generalists | 12 | 48.0 | 4 | 16.0 | 9 | 36.0 | 25 |
| Total | 135 | 65.5 | 32 | 15.5 | 39 | 19.0 | 206 |

represented in the fossil record, hypotheses about faunas present in Beringia during the Wisconsinan glacial maximum have depended mainly on distributional or ecological information. Ground beetles, in contrast, are abundantly represented as identifiable fossils of Pleistocene and early Holocene ages, and thus are excellent models for testing biogeographic assumptions based on distributional or ecological information.

Hypotheses based solely on distributional or ecological assumptions are limited in that they may not reflect accurately the full range of organisms that could have survived in the Beringian refugium. For example, endemic species are invariably included in the category of "Beringian centrants", species supposed to have been present in Beringia during the glaciation, whereas widespread species typically are excluded; however, fossil evidence suggests that many widespread species probably survived in Beringia during full-glacial conditions. These species differ from the endemic component mainly in their dispersal capability, which, in turn, is associated with development of the hindwings. Adherence to strict distributional criteria therefore may under-represent the actual number of Beringian centrant species. Similarly, hypotheses about environmental conditions are limited in that interpretations are based largely on the habitat associations exhibited by the endemic component. For example, because many Beringian endemic species are brachypterous forms associated with tundra (e.g. *Pterostichus* subgenus *Cryobius*), it is tempting to conclude that Beringia consisted primarily of tundra habitats during full-glacial conditions. However, fossil evidence suggests that many Beringian species were widespread macropterous taxa that were not closely associated with tundra. Evidently, the endemism criterion may be too restrictive when reconstructing the full range of habitats that might have existed during late Wisconsinan time.

To avoid problems associated with interpretations based on overly restrictive distributional or ecological criteria, we offer a list of probable Beringian centrants by using a combination of distributional and fossil evidence. Then we interpret the general nature of the Yukon ground-beetle fauna in view of this list.

**Beringian Centrants as Suggested by Distributional Evidence.** Most species or subspecies of Yukon ground beetles are distributed widely in North America, and thus do not provide decisive evidence about the origin of this fauna. Indeed, only the "Beringian endemic" pattern reasonably can be assigned to the Beringian centrant component. This distributional pattern accounts for only 28 species, or about 13% of the Yukon ground-beetle fauna.

Evidence is accumulating that many arctic and subarctic insects, although not strictly confined to unglaciated regions of Alaska and the Yukon Territory, probably originated from the Beringian refugium (e.g. Freeman 1958, 1964; Lafontaine and Wood 1988). In a synthesis of fossil and distributional evidence, Schwert and Ashworth (1988) proposed a model in which Beringia was the principal centre of origin for arctic and subarctic beetle faunas. Ashworth (1996) presents evidence derived from a study of mt-DNA that the Holarctic *Amara alpina* is a bicentric species, with vicars that survived in the Beringian refugium and to the south of the Laurentide ice sheet, and that the Beringian-based assemblage was the source of the extant populations that occupy northern North America from the Yukon Territory to northern Quebec and Baffin Island.

Table 8 lists the names of 38 species or subspecies that are distributed widely across the Canadian arctic-subarctic, but are not included in the Beringian category. Also included there are the 5 Yukon species that exhibit a Palaearctic-East Beringian distribution. If these 43 species are added to the Beringian centrant component as suggested by the endemism criterion, then the total number of species or subspecies hypothesized to have a Beringian origin is more than doubled to 71 species, representing 33% of the Yukon ground-beetle fauna.

**Beringian Centrants as Suggested by Wisconsinan and Early Holocene Fossils**. Fossils of Wisconsinan and Early Holocene ages provide direct evidence about the species or subspecies of ground beetles that may have survived in the Beringian refugium. Table 8 lists 74 species of ground beetles that are represented in middle and late Wisconsinan deposits from northwestern North America. Records of early Wisconsinan fossils are excluded from the analysis to reduce, as much as possible, contamination from species that may have occurred temporarily in northwestern sites (e.g. during interglacial periods), but which probably did not belong to the Beringian stock that repopulated much of northern North America following deglaciation. Twenty-seven of the 74 species represented as northwestern fossils were not included in this Beringian component based on distributional information. In contrast, 23 species included as Beringian centrants based on distributional data are not represented as middle or late Wisconsinan fossils. It is evident that neither of the 2 sources alone provides a complete estimate of species that likely survived in northwestern refugia during Wisconsinan time. The total number of hypothesized Beringian centrant species based on distributional and fossil evidence is 98, of which nearly half (47) are supported by both types of evidence (Table 8). We note that there is still much palaeoecological work to be done in northwestern North America, and the estimated number of Beringian centrant species is likely to increase over time. Accordingly, some of the species assigned to the Beringian component based solely on distributional information probably will be found eventually also as fossils. The estimated total of 98 species based on distributional and fossil evidence represents about 46% of the extant Yukon ground-beetle fauna.

Having established a list of species that probably were present in Beringia during late Wisconsinan time, we have now the basis for interpreting the general nature of the present-day ground-beetle fauna of the Yukon Territory.

**Development and General Features of the Extant Ground-beetle Fauna.** The general nature of the ground-beetle fauna of the Yukon Territory can be inferred, in part, on the basis of studies by others, using either northern ground beetles or other insect taxa. For example, Lindroth (1971) showed that Holarctic elements dominated the ground-beetle fauna of the arctic, and that brachypterous taxa were concentrated in northern Beringia. Similarly, in a remarkably clearly written and detailed analysis, Lafontaine and Wood (1988), working with moths of the family Noctuidae, emphasized the prominence of Holarctic elements in the Beringian fauna. They indicated that Beringia could have been the source area for postglacial colonization of regions to the west, in Siberia, and to the east in the North American arctic. Identifying ecological elements of the fauna, they recognized the following groups: wet-tundra species; dry-tundra species; dune species; southern-steppe species; taiga species; and boreomontane species. Each of these groups was reported to have a distinctive distribution pattern in the north. Of special interest was the dry tundra assemblage, for it was rich in Beringian endemics, and provided the basis for the hypothesis that these species had occupied Beringia for a long time, thus supporting a more general hypothesis that Beringia has been available for an uninterrupted long period of time for occupation by organisms (Hultén 1937).

If the noctuid fauna provided strong evidence for the presence in Beringia of tundra throughout the Pleistocene epoch, it did not provide evidence for the persistence there of forest and southern steppe. Thus, Lafontaine and Wood (1988) postulated that such habitats,

TABLE 8. List of Yukon species or subspecies of ground beetles hypothesized to have had a Beringian origin, with summary of evidence used. MW, Middle Wisconsinan fossils; LW, Late Wisconsinan fossils; B, Beringian distribution; N, northern or markedly northern distribution (including species with a Palaearctic-Beringian distribution).

| Taxon | Fossils | | Distribution | |
|---|---|---|---|---|
| | MW | LW | B | N |
| Carabini | | | | |
| *Carabus* Linnaeus | | | | |
| *C. chamissonis* Fischer | + | + | | + |
| *C. maeander* Fischer | + | | | |
| *C. taedatus* Fabricius | + | | | |
| *C. truncaticollis* Eschscholtz ssp. *truncaticollis* | + | + | + | |
| *C. vietinghoffi* Adams ssp. *vietinghoffi* | | | | + |
| Nebriini | | | | |
| *Pelophila* Dejean | | | | |
| *P. borealis* Paykull | + | + | | + |
| *P. rudis* LeConte | + | | | + |
| *Nebria* Latreille | | | | |
| *N. frigida* R.F. Sahlberg | | | + | |
| *N. nivalis* Paykull | | | | + |
| Notiophilini | | | | |
| *Notiophilus* Duméril | | | | |
| *N. semistriatus* Say | | + | | |
| *N. borealis* Harris | | + | | + |
| *N. sylvaticus* Eschscholtz | + | | | |
| Elaphrini | | | | |
| *Diacheila* Motschulsky | | | | |
| *D. polita* Falderman | + | + | | + |
| *Blethisa* Bonelli | | | | |
| *B. multipunctata* Linné | | + | | |
| *B. catenaria* Brown | + | + | | + |
| *Elaphrus* Fabricius | | | | |
| *E. lapponicus* Gyllenhal ssp. *lapponicus* | + | + | | + |
| *E. clairvillei* Kirby | | + | | |
| *E. tuberculatus* Maklin | | | | + |
| *E. parviceps* Van Dyke | + | + | | + |
| *E. angusticollis* R.F. Sahlberg ssp. *angusticollis* | | | + | |
| Scaritini | | | | |
| *Dyschiriodes* Jeannel | | | | |
| *D. integer* LeConte | | + | | |
| *D. subarcticus* Lindroth | | | + | |
| *D. frigidus* Mannerheim | + | | | |
| *D. nigricornis* Motschulsky | | | | + |
| Patrobini | | | | |
| *Patrobus* Dejean | | | | |
| *P. stygicus* Chaudoir | | + | | |
| *P. septentrionis* Dejean | + | + | | |
| *P. foveocollis* Eschscholtz | | + | | |
| Trechini | | | | |
| *Trechus* Clairville | | | | |
| *T. apicalis* Motschulsky | + | | | |
| Bembidiini | | | | |
| *Asaphidion* Gozis | | | | |
| *A. alaskanum* Wickham | + | | + | |
| *A. yukonense* Wickham | | | | + |
| *Bembidion* Latreille | | | | |
| *B. lapponicum* Zetterstedt | + | | | + |
| *B. arcticum* Lindroth | | | + | |
| *B. compressum* Lindroth | | | | + |
| *B. brachythorax* Lindroth | | | | + |
| *B. gratiosum* Casey | | + | | |
| *B. rusticum* Casey ssp. *lenensoides* Lindroth | | | | + |

TABLE 8. (*continued*)

| Taxon | Fossils | | Distribution | |
|---|---|---|---|---|
| | MW | LW | B | N |
| *B. sulcipenne* J. Sahlberg ssp. *hyperboroides* Lindroth | | | + | |
| *B. hasti* C.R. Sahlberg | + | | | + |
| *B. mckinleyi* Fall ssp. *mckinleyi* | | | + | |
| *B. lenae* Csiki | | | + | |
| *B. grapii* Gyllenhal | + | | | |
| *B. yukonum* Fall | | | | + |
| *B. dauricum* Motschulsky | + | | | + |
| *B. sordidum* Kirby | + | + | | |
| *B. umiatense* Lindroth | + | + | + | |
| *B. morulum* LeConte | + | | | + |
| *B. transparens* Gebler | | + | | |
| Pterostichini | | | | |
| *Pterostichus* Bonelli | | | | |
| *P. nearcticus* Lindroth | + | + | + | |
| *P. circulosus* Lindroth | | + | + | |
| *P. adstrictus* Eschscholtz | + | | | |
| *P. soperi* Ball | + | + | + | |
| *P. arcticola* Chaudoir | + | + | | + |
| *P. kotzebuei* Ball | + | + | + | |
| *P. tareumiut* Ball | + | + | + | |
| *P. barryorum* Ball | + | | | + |
| *P. hudsonicus* LeConte | + | | | + |
| *P. similis* Mannerheim | + | + | + | |
| *P. parasimilis* Ball | + | + | + | |
| *P. bryanti* Van Dyke ssp. *bryanti* | + | | + | |
| ssp. *bryantoides* Ball | | | + | |
| *P. pinguedineus* Eschscholtz | + | + | | + |
| *P. woodi* n. sp. | | | + | |
| *P. ventricosus* Eschscholtz ssp. *ventricosus* | + | + | + | |
| *P. caribou* Ball | + | + | | + |
| *P. brevicornis* Kirby ssp. *brevicornis* | + | + | | + |
| *P. empetricola* Dejean | + | | | + |
| *P. mandibularoides* Ball | + | | | + |
| *P. nivalis* F. Sahlberg | + | + | + | |
| *P. punctatissimus* Randall | + | | | |
| *P. vermiculosus* Ménétries | + | + | | + |
| *P. agonus* Horn | + | + | + | |
| *P. costatus* Ménétries | + | + | + | |
| *P. sublaevis* J. Sahlberg ssp. *rufofemoralis* Van Dyke | + | + | + | |
| *P. haematopus* Dejean | + | + | | + |
| *P. rubripes* Motschulsky | | | + | |
| *Sericoda* Kirby | | | | |
| *S. quadripunctata* De Geer | | + | | |
| *Agonum* Bonelli | | | | |
| *A. gratiosum* Mannerheim | | + | | |
| *A. thoreyi* Dejean | + | | | |
| *A. bicolor* Dejean | | | | + |
| *A. quinquepunctatum* Motschulsky | + | + | | + |
| Amarini | | | | |
| *Amara* Bonelli | | | | |
| *A. alpina* Paykull | + | + | | + |
| *A. bokori* Csiki | + | + | | + |
| *A. glacialis* Mannerheim | + | + | | + |
| *A. browni* Lindroth | | + | + | |
| *A. colvillensis* Lindroth | + | | | |
| *A. quenseli* Schönherr | + | | | |
| *A. brunnea* Gyllenhal | | | | + |
| *A. pseudobrunnea* Lindroth | | | | + |

TABLE 8. (*continued*)

| Taxon | Fossils | | Distribution | |
|---|---|---|---|---|
| | MW | LW | B | N |
| *A. interstitialis* Dejean | | | | + |
| *A. erratica* Duftschmid | + | + | | + |
| Harpalini | | | | |
| *Harpalobrachys* Tschitschérine | | | | |
| *H. leiroides* Motschulsky | | | | + |
| *Harpalus* Latreille | | | | |
| *H. amputatus* ssp. *amputatus* Say | + | + | | |
| *H. fulvilabris* Mannerheim | | + | | |
| *H. nigritarsis* C.R. Sahlberg | | + | | |
| *H. vittatus* Gebler ssp. *alaskensis* Lindroth | + | + | + | |
| *Trichocellus* Ganglbauer | | | | |
| *T. mannerheimi* R.F. Sahlberg | + | + | | + |
| Chlaeniini | | | | |
| *Chlaenius* Bonelli | | | | |
| *C. niger* Randall | + | | | |
| Lebiini | | | | |
| *Cymindis* Latreille | | | | |
| *C. unicolor* Kirby | + | | | + |

now widespread in Beringia, either have arrived there in postglacial time, or if they did persist, they must have been reduced markedly during the Wisconsinan glacial stage. Lafontaine and Wood concluded, therefore, that the extant Beringian biota is a combination of older endemic taxa that occupy tundra and sand dunes, and taxa that have arrived there in postglacial time, and that occupy forest and southern-steppe habitats.

The ground-beetle fauna of the Yukon Territory shows a similar pattern to that of the noctuids, and is composed of 3 distributionally defined elements: (1) Beringian residents (species that occupied the unglaciated portions of the Yukon during the Wisconsinan glacial stage, and probably earlier, and have not extended their ranges beyond or much beyond the limits of the areas that were ice-free during the Wisconsinan glacial stage); (2) postglacial emigrants (species that occupied Beringia during the Wisconsinan glacial stage, but dispersed in postglacial time substantially beyond the ice-free areas); and (3) postglacial immigrants (species with ranges that were south of the continental glaciers during Wisconsinan time, and have entered the Yukon Territory following glacial melt).

Table 8 lists the names of the 98 taxa that probably were present in ice-free parts of the Yukon Territory during the Wisconsinan glacial stage. The ranges of 28 species (about one-third of that group) still are, or are nearly, confined to Beringia, suggesting minimal postglacial dispersal. This group of species is the resident group (Table 9), which coincides with the Beringian endemic category. Half of the taxa are brachypterous, and 86% are confined to tundra and open wetland habitats. Fifty per cent of the resident species are more or less confined to the tundra, and are regarded as tundra specialists. None of these taxa is in dry-land situations, and only 2 species, listed as “ecological generalists”, are in forest habitats.

The emigrant species (Table 10) comprise about 71% of the Wisconsinan inhabitants of the Yukon portion of Beringia. About 76% of these species are macropterous or wing-dimorphic, and thus capable of dispersing by flight. All 6 ecological zones recognized are occupied by these species collectively, including tundra. More than half of the species

TABLE 9. Relationship between habitat and hindwing development for Yukon ground beetles classified as Beringian residents, still more-or-less confined to unglaciated areas.

| Habitat | Wing development and number of species | | | |
|---|---|---|---|---|
| | Macropterous | Dimorphic | Brachypterous | Total |
| Riparian | 7 | 2 | 0 | 9 |
| Open, wet ground | 0 | 0 | 1 | 1 |
| Open, dry ground | 0 | 0 | 0 | 0 |
| Shrub Zone | 1 | 0 | 0 | 1 |
| Forest | 0 | 0 | 0 | 0 |
| Tundra | 0 | 0 | 14 | 14 |
| Ecological generalists* | 0 | 0 | 3 | 3 |
| Total | 8 | 2 | 18 | 28 |

*Ecological generalists occur on tundra, and are either riparian or forest-inhabiting.

occupy the open tundra and wetland habitats, but only 11 species (16%) are tundra specialists.

The immigrant species (Table 11) number 108. About 96% of these taxa are macropterous or wing-dimorphic. Five ecological zones are occupied, with 56% of the group occurring in wet lands, and 42% being riparian specialists. The forest component is substantial, as is the dry-land component. No tundra-inhabiting ground beetles belong to the immigrant component.

Distribution patterns suggest that Beringia has been not only a northern region of survival, but also one of speciation of old Beringian stocks. Thus, this area has a number of endemic and closely related species of the pterostichine subgenus *Cryobius*, as shown by the following summary, based on Ball (1963, 1966).

*Cryobius* is a markedly diverse species-complex that probably is Asian in origin (Shilenkov 1992: 62). Probably species are numerous in the eastern Asian mountains. For example, Shilenkov (1992: 56) lists 5 endemic species from the high altitudes of South Siberia. Probably the early differentiation of *Cryobius* was associated with mid-Tertiary orogenic processes, and with the accompanying and subsequent climatic changes, resulting in fragmentation of initially widespread species' ranges. Details remain to be established. Currently, Beringia is occupied by 18 taxa ranked as species. An initial attempt to reconstruct the phylogenetic relationships of principally the Nearctic species of *Cryobius* was not very

TABLE 10. Relationship between habitat and hindwing development for Yukon ground beetles classified as Beringian emigrants, dispersing after deglaciation substantially beyond the ice-free areas.

| Habitat | Wing development and number of species | | | |
|---|---|---|---|---|
| | Macropterous | Dimorphic | Brachypterous | Total |
| Riparian | 12 | 1 | 0 | 13 |
| Open, wet ground | 12 | 2 | 1 | 15 |
| Open, dry ground | 4 | 5 | 0 | 9 |
| Shrub zone | 2 | 0 | 0 | 2 |
| Forest | 3 | 1 | 4 | 8 |
| Tundra | 1 | 4 | 6 | 11 |
| Ecological generalists* | 3 | 3 | 6 | 12 |
| Total | 37 | 16 | 17 | 70 |

* Ecological generalists are as follows: (1), in forest and tundra; (2), in the riparian zone and tundra; (3) in riparian and marsh (i.e. in wet ground habitats); (4) in marsh and tundra; (5) on open bare ground and tundra; and (6) in three or more habitats.

TABLE 11. Relationship between habitat and hindwing development for Yukon ground beetles classified as postglacial immigrants, entering the Yukon after deglaciation.

| Habitat | Wing development and number of species | | | |
|---|---|---|---|---|
| | Macropterous | Dimorphic | Brachypterous | Total |
| Riparian | 41 | 3 | 1 | 45 |
| Open, wet ground | 11 | 3 | 1 | 15 |
| Open, dry ground | 17 | 4 | 0 | 21 |
| Shrub zone | 3 | 0 | 1 | 4 |
| Forest | 11 | 3 | 1 | 15 |
| Tundra | 0 | 0 | 0 | 0 |
| Ecological generalists* | 7 | 1 | 0 | 8 |
| Total | 90 | 14 | 4 | 108 |

* Ecological generalists are as follows: (1), in grassy meadow and bare ground; (2), in grassy meadow and riparian; (3), in grassy meadow and wet meadow; (4), in riparian and bare ground; (5), in marsh and forest (i.e. wetland habitats); and (6) in forest and tundra.

successful (Ball 1966: 134–138, fig. 210), but the following points seem worth reiterating in the present context.

The distribution of 3 pairs of postulated adelphotaxa of the subgenus *Cryobius* suggest isolation and differentiation, with one isolate being confined to Beringia, and the other occurring principally elsewhere, the latter species being confined to tundra (Table 12). The distribution of 3 species complexes suggests isolation and differentiation within Beringia. Table 13 indicates differentiation patterns of such species, with each Stage 1 species being the adelphotaxon of those that differentiated later (Stage 2), and stage 3 taxa being the allopatric descendants of the stage 2 taxa, and being the most recent to differentiate from one another. See Appendix 1 for comments and descriptive material in support of the classification of *P. planus* and its relatives. *Pterostichus bryanti* exhibits marked geographical variation.

Summarizing in terms of major components, brachypterous tundra specialists dominate the Beringian faunal element. Among the Beringian emigrants, the macropterous riparian-wetland taxa are the most numerous. Among the immigrants, the macropterous riparian taxa are the most numerous. Excluding the shrub-zone component, the other ecological

TABLE 12. Beringian endemic species of *Pterostichus*, subgenus *Cryobius*, with vicars centered elsewhere geographically. Abbreviations: T, tundra; F, forest; R, riparian.

| Central-Western Palaearctic Region | Beringia | Nearctic Region, east of the Mackenzie River Delta |
|---|---|---|
| | *P. tareumiut* (T)[1] | *P. barryorum* (T)[2] |
| | *P. kotzebuei* (T-F) | *P. arcticola* (T) |
| *P. middendorffi* (T)[3] | *P. ventricosus* (R-F)[4] | *P. caribou* (T) |

[1] The range of *P. tareumiut* extends eastward to Cambridge Bay, Northwest Territories.
[2]The record of *P. barryorum* from McMurray, Alberta (in the boreal forest), based on a single specimen (Ball 1966: 49), is not accepted now, because no additional material of this species from so far south has been found.
[3] *P. middendorffi* Sahlberg is the postulated adelphotaxon of *P. ventricosus* + *P. caribou*.
[4] *P. ventricosus* exhibits substantial geographical variation in Beringia, with the subspecies *P. v. paludosus* confined to the Kolyma District of eastern Siberia, and that of *P. v. ventricosus* throughout most of Beringia, and exhibiting marked clinal variation.

TABLE 13. Species assemblages of *Pterostichus*, subgenus *Cryobius*, postulated to have originated and/or differentiated within Beringia. Abbreviations: T, tundra; F, forest.

| Stage 1 taxa | Stage 2 taxa | Stage 3 taxa |
|---|---|---|
| *P. gerstlensis* (F)[1] | *P. arcticola* and *kotzebuei* | |
| *P. planus* (T)[2] | P. auriga complex and *kaninensis* complex | *P. auriga* (T) and *woodi* (T) *kaninensis* and *bryanti* (T)[3] |
| *P. nivalis* (T)[4] | *P. brevicornis* complex [5] *P. ventricosus* | *P. brevicornis* (T-F)[6] and *b. delicatus* (T) *P. v. ventricosus* and *v. paludosus* |

[1] *P. gerstlensis* Ball is the postulated adelphotaxon of *P. arcticola* + *P. kotzebuei*.
[2] *P. planus* Sahlberg is the postulated adelphotaxon of the *P. auriga* and *P. kaninensis* complexes.
[3] *P. kaninensis* is Palaearctic, and is represented in Beringia only by the Siberian subspecies, *P. k. kurnakovi* Ball. *P. bryanti* Van Dyke is a Nearctic complex of subspecies, most of which are confined to Beringia.
[4] *P. nivalis* Sahlberg is the postulated adelphotaxon of the *P. brevicornis* complex.
[5] The *P. brevicornis* complex includes *P. brevicornis* (and subspecies *P. b. brevicornis* Kirby and *P. b. delicatus* Casey), *P. mandibularoides* Ball and *P. empetricola* Eschscholtz. Adelphotaxon relationships within this complex have not been postulated.
[6] Although the range of *P. b. brevicornis* extends far beyond Beringia, the range of *P. b. delicatus* is confined to the Beringian islands of the Bering Sea.

components and the ecological generalists are well represented also, especially by taxa with macropterous adults.

Of the 206 Yukon ground-beetle species whose ranges can be analyzed, probably 157 are unicentric (i.e. the extant populations are descended from ancestors that came from a single centre—either glacial age ones in Beringia, or ones that reached the Yukon Territory by dispersal from elsewhere in postglacial time). The remaining 49 species probably are bicentric, and may be represented in northern regions by both glacial-age stocks from Beringia, and descendants of dispersing stocks from elsewhere. Table 14 provides names and sources of evidence for hypothesizing a bicentric origin for these species. Whether these species are represented in the Yukon Territory only by stocks present during the glacial ages or by these and immigrant stocks remains to be determined. For *Bembidion mckinleyi*, it seems clear that the Yukon is populated by both a glacial-age, centrant, group (*B. m. mckinleyi*) and a more recently arrived more southern component, represented by *B. m. carneum*. For other bicentric species, molecular techniques (e.g. Bernatchez and Dodson 1991) may be required to establish the relative contribution of populations derived from northern versus southern refugial areas. According to the model of Schwert and Ashworth (1988) most cold-adapted species that persisted in southern refugia probably were exterminated during deglaciation; hence, Beringia is considered to be the principal refugium for arctic-subarctic beetles. In contrast, the fauna associated with boreal forest is presumed to have been derived primarily from southern populations.

Three conflicting hypotheses are current about the types of environments that may have existed in Beringia during the Wisconsinan glacial maximum. The mammoth-steppe concept contends that the landscape was dominated by a highly productive, arid, grassland vegetation during both glacial and interglacial periods (Guthrie 1982, 1990). This environment was evidently rich enough to support a great diversity of large mammals, many now extinct. An entirely different view, held mainly by palynologists, is that Beringia was an unproductive polar desert, similar to present-day arctic and alpine fell-fields (e.g. Cwynar and Ritchie 1980; Ritchie and Cwynar 1982; Ritchie 1984; Colinvaux and West 1984). This group

TABLE 14. List of names of Yukon species of ground beetles hypothesized to have both Beringian and southern source areas for extant populations.

| Taxon | Evidence | | |
|---|---|---|---|
| | Distributional pattern | Localities for fossil remains* | |
| | | Northern | Southern |
| *Carabus chamissonis* Fischer | | + | + |
| *Carabus maeander* Fischer | | + | + |
| *Carabus taedatus* Fabricius | | + | + |
| *Pelophila borealis* Paykull | | + | + |
| *Notiophilus semistriatus* Say | | + | + |
| *Notiophilus borealis* Harris | | + | + |
| *Diacheila polita* Falderman | | + | + |
| *Blethisa multipunctata* Linné | | + | + |
| *Elaphrus lapponicus* Gyllenhal | | + | + |
| *Elaphrus clairvillei* Kirby | | + | + |
| *Elaphrus parviceps* Van Dyke | | + | + |
| *Dyschiriodes integer* LeConte | | + | + |
| *Dyschiriodes nigricornis* Motschulsky | | + | + |
| *Patrobus stygicus* Chaudoir | | + | + |
| *Patrobus septentrionis* Dejean | | + | + |
| *Trechus apicalis* Motschulsky | | + | + |
| *Asaphidion yukonense* Wickham | + | | + |
| *Bembidion compressum* Lindroth | + | | + |
| *Bembidion sulcipenne* J. Sahlberg | + | | + |
| *Bembidion hasti* C.F. Sahlberg | | + | + |
| *Bembidion mckinleyi* Fall | + | | + |
| *Bembidion grapii* Gyllenhal | | + | + |
| *Bembidion yukonum* Fall | + | | + |
| *Bembidion dauricum* Motschulsky | | + | + |
| *Bembidion sordidum* Kirby | | + | + |
| *Bembidion morulum* LeConte | | + | + |
| *Bembidion transparens* Gebler | | + | + |
| *Bembidion concretum* Casey | | + | + |
| *Pterostichus adstrictus* Eschscholtz | | + | + |
| *Pterostichus barryorum* Ball | | + | + |
| *Pterostichus pinguedineus* Eschscholtz | | + | + |
| *Pterostichus ventricosus* Eschscholtz | | + | + |
| *Pterostichus caribou* Ball | | + | + |
| *Pterostichus brevicornis* Kirby | | + | + |
| *Pterostichus punctatissimus* Randall | | + | + |
| *Pterostichus vermiculosus* Ménétries | | + | + |
| *Pterostichus sublaevis* J. Sahlberg | | + | + |
| *Pterostichus haematopus* Dejean | | + | + |
| *Sericoda quadripunctata* De Geer | | + | + |
| *Agonum gratiosum* Mannerheim | | + | + |
| *Agonum thoreyi* Dejean | | + | + |
| *Agonum quinquepunctatum* Motschulsky | | + | + |
| *Amara alpina* Paykull | | + | + |
| *Amara glacialis* Mannerheim | | + | + |
| *Amara quenseli* Schönherr | + | + | |
| *Harpalus amputatus* Say | + | + | |
| *Harpalus nigritarsis* C.R. Sahlberg | + | + | |
| *Chlaenius niger* Randall | + | + | |
| *Cymindis unicolor* Kirby | | + | + |

*Based on Middle to Late Wisconsinan-age fossils.

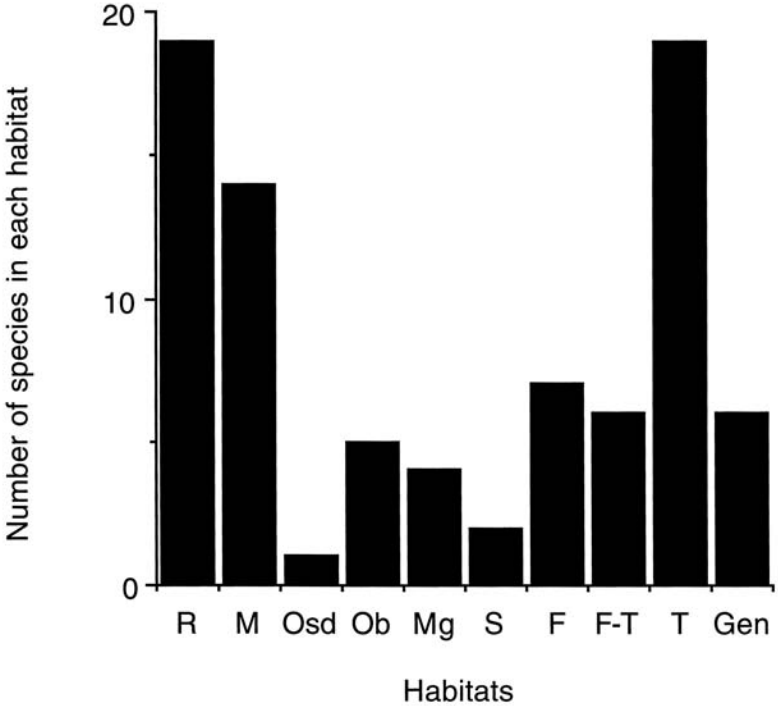


FIG. 5. Histogram illustrating the frequency distribution of habitat preferences exhibited by the 98 species or subspecies of Yukon ground beetles hypothesized to have a Beringian origin. Abbreviations for habitats: F, Forest; F-T, Forest-tundra; Gen, Ecological generalists; Ob, Open bare ground; Osd, Open dry sand; R, Riparian; S, Shrub zone; T, Tundra.

contends that it is unlikely that eastern Beringia could have supported a large and diverse assemblage of large mammals. A third view envisions an environment dominated by a mosaic of steppe-like and tundra-like biotopes, and thus is a hybrid of the first 2 mentioned groups (e.g. Schweger 1982; Anderson 1985). The mosaic concept entails an essentially treeless landscape with restricted shrublands and marshes, and predominance of steppe-tundra biotopes. These latter evidently were characterized by discontinuous herbaceous cover dominated by xeric vegetation.

What do habitat associations exhibited by Beringian centrant ground beetles suggest about conditions during Wisconsinan time? Fig. 5 summarizes the habitat associations of the 98 species or subspecies that probably were present in Beringia during Wisconsinan time. Sixty-three of these species or subspecies, representing 64% of the total, occupy one of 3 habitat types: tundra (25), riparian (22), and marsh (16). By application of the Principle of Uniformitarianism (i.e. that habitat associations remain constant over time), we postulate that both upland and lowland areas served as centres of high diversity for Beringian ground beetles.

The relatively high proportion of marsh-inhabiting centrant species does not conform to the hypothesis that such habitats were limited during glacial time. Indeed, a recent study of late Quaternary beetle faunas from southwestern Alaska provides evidence of a refugium for mesic and hydrophilous species (Elias 1992). Ground beetles associated with forest (7 species) and forest-tundra (5 species) account for about 12% of Beringian centrants. This

TABLE 15. Comparison of the extant ground beetle assemblage with that of the Wisconsinan glacial stage assemblage, of the Yukon Territory.

| Habitat | Assemblage and number of species | | | | | |
|---|---|---|---|---|---|---|
| | Wisconsinan | | Extant | | Change | |
| | N | % | N | % | N | % |
| Riparian | 22 | 22.4 | 67 | 32.5 | +45 | +10.3 |
| Open, wet ground | 16 | 16.3 | 31 | 15.0 | +15 | − 1.3 |
| Open, dry ground | 9 | 9.2 | 30 | 14.6 | +21 | + 5.5 |
| Shrub zone | 3 | 3.1 | 7 | 3.4 | + 4 | + 0.3 |
| Forest | 8 | 8.2 | 23 | 11.2 | +15 | + 3.0 |
| Tundra | 25 | 25.5 | 25 | 12.1 | 0 | –14.2 |
| Ecological generalists | 15 | 15.3 | 23 | 11.2 | + 8 | − 4.1 |
| Total | 98 | 100.0 | 206 | 100.0 | | |

at first seems surprising because Beringia is assumed to have been essentially treeless during the last ice age (Elias 1994:184). However, limited evidence suggests that cottonwood (*Populus balsamifera* Linn.), aspen (*Populus tremuloides* Michaux), alder (*Alnus*) and larch (*Larix*) (e.g. Hopkins et al. 1981; Anderson 1985) could have survived in northwestern refugia. Scattered groves of trees currently exist well beyond the northern limit of treeline, in isolated local sites such as deeply thawed ground along rivers, springs, and seepages. Perhaps such microhabitats persisted in Beringia, providing refuge for certain forest- and forest-tundra-adapted species.

The small proportion of ground beetles associated with open dry sand (one species), open bare ground (4 species), and grassy meadow (4 species) does not seem consistent with an environment dominated by highly productive, arid grassland. However, we note that most grassland ground beetles are adapted to rather warmer conditions than indicated for Beringia during full glacial conditions.

The habitat associations exhibited by Beringian centrant ground beetles do not favour strongly one particular model of full-glacial conditions in northwestern North America. Tundra, riparian and marsh habitats were evidently centres of high diversity during Wisconsinan time; however, presence of a forest or forest-tundra element, perhaps closely associated with the riparian habitat, is also indicated. It seems unlikely that an unproductive polar desert environment, as envisioned by palynologists, could account for the full range of habitat associations exhibited by the centrant ground-beetle component. Although tundra unquestionably was an important and enduring feature of the Beringian landscape (as suggested by high endemicity in the *Pterostichus* subgenus *Cryobius*), it seems clear that other types of environments also were present during late Wisconsinan time. Such habitats could have developed during interglacial periods, and then persisted in isolated microenvironments during full glacial conditions (ca. 15 000–30 000 yr B.P.). Vegetation capable of asexual reproduction can persist without producing pollen or fertile seeds, and thus may not have contributed perceptibly to the fossil record.

Our data suggest that lowlands were areas of high diversity for the Beringian centrant species. As such, evidently they contributed substantially to the fauna that repopulated much of North America following glaciation. Interestingly, few of these ground beetles exhibit habitat associations associated with dry steppe—a major component of the "mammoth steppe" model. This pattern underscores the possible role of microenvironments as refugia for ground beetles during full glacial conditions. The "mosaic" model probably best explains the diversity of habitat associations exhibited by the Beringian centrant ground-beetle fauna.

Table 15 summarizes the changes that have occurred in the ecological composition of the Yukon ground-beetle fauna in postglacial time. The more striking changes are the decrease in frequency of the tundra elements relative to the fauna as a whole, and the increase in frequency of the riparian elements. Similarly, relative frequency of brachyptery has decreased from 36% in the glacial-age fauna to 19% in the extant fauna.

Because we were not able to distinguish clearly between "wet" and "dry" tundra elements, we cannot make a direct comparison of the data about habitat occupation of ground beetles with those of noctuid moths presented by Lafontaine and Wood (1988). However, our data support the hypothesis that tundra persisted in the Yukon (and by extension, in Beringia) for an extended period. We did not identify a "southern steppe" assemblage as such, but the ground beetles of xeric to mesic open habitats probably fit into such a group. Their increase in postglacial time suggests a recent spread of this type of habitat in the Yukon Territory. Similarly, the increase in the ground beetles of the forest assemblage supports a postglacial spread of this habitat. The extensive ranges of the emigrant species provide ample evidence that Beringia served as a centre for repopulating the north in postglacial time. Thus, our observations support the conclusions of others about the nature and importance of the Beringian fauna in northern biogeography.

The marked increase in riparian taxa in the Yukon Territory during postglacial time suggests that such insects are good dispersers, but it suggests also a marked increase in this complex of habitats in the Yukon area.

The high frequency of brachyptery among the Beringian endemic species, and the high frequency of macroptery among the emigrant and immigrant groups is suggestive of the importance of flight in insect dispersal. However, in emphasizing this generality, we recognize that some taxa with brachypterous adults have become quite widespread, also.

In conclusion, we believe that the data we have assembled are interpreted appropriately in the context of the general theory of Beringia. The seminal conclusions of the late and great Swedish botanist and biogeographer Eric Hultén (1937) about the biogeographic significance of Beringia, supplemented and amplified by the work of others during the intervening years (e.g. Lindroth 1979), seem to be founded very well.

## Epilogue

This contribution marks an early stage in the study of the ground beetles of the Yukon Territory. Little is known about them, or indeed, about the northern ground-beetle fauna as a whole, though Danks (1981: 324) ranks them as "relatively well known". A phylogenetic analysis of the autochthonous ground-beetle species of Beringia is required to develop testable hypotheses about the evolution of these taxa (Wheeler 1990: 1036) and about their associations with the area in which they live and to which they are confined. Ball (1966) provided such an analysis for the species of *Cryobius*, but in retrospect, that treatment is inadequate, and must be revised. Ranges of species need to be mapped in detail, and much has to be discovered about habitats and their occupation. From the standpoint of taxonomic analysis, exploration of the dry, seemingly barren montane slopes that provided exciting material and inspiration for Lafontaine and Wood (1988) ought to be rewarding. For example, while searching for noctuid moths, Lafontaine and Wood found a new species of the subgenus *Cryobius* in, and apparently confined to, that habitat.

Palaeoecological studies continue to provide insights about the communities of ground beetles that populated Beringia and other glacial refugia during the Wisconsinan glaciation. This information is invaluable for testing hypotheses about the origins of faunas, based only on distributional or ecological data. The possible role of microenvironments as refugia for these communities is an area requiring further study.

Another area of interest is the bicentric taxa, i.e. those with populations that survived in the refugium, and also with populations that have re-invaded from the south: for some species, the formerly widely separated vicars are already distinguishable by external features; for others, analyses at the molecular level ought to provide evidence of differences that evolved when the 2 groups were isolated.

Study of the dimorphically winged species would extend Lindroth's (1971) pioneering observations, and would provide the basis for more detailed and precise interpretation of the histories of the Beringian taxa.

As Lindroth (1971: 7) noted, the opportunity that work in the north brings for cooperative ventures between Russian and North American scientists must not be overlooked. Certainly, such ventures have proven to be highly rewarding scientifically.

Thanks to the efforts of the hardy miners, like Service's fictional "Sam McGee", who came to the Yukon nearly a century ago, the goldfields that they discovered are exhausted or nearly so, or can be exploited further only by bulky, complex machinery that does incredible damage to the environment. In contrast, the goldfields of Yukon entomology hardly have been touched. Those who choose to study the biota of this region will be rewarded in abundance through the knowledge and insights that they acquire and make known to others.

## Acknowledgements

The authors are pleased to express their appreciation to the institutions and curators noted in the Materials and Methods section for loan of the specimens that contributed to the empirical base of this chapter. The efforts of the collectors noted in the text are much appreciated. In particular, the senior author is grateful to Nigel E. Stork and David R. Maddison, with whom he journeyed north in 1981, to Jacques Cinq-Mars, Richard Morlan, and John V. Matthews, in whose campsite at Old Crow we were made welcome, and to the late Carl H. Lindroth for the grand shared experiences on the trip made with him, in 1958.

The late Timothy G. Spanton compiled much of the published information that we had occasion to use, and made preliminary range maps of species distributions. Danny Shpeley contributed his expertise in identifying many of the ground beetles, particularly those in the genus *Bembidion*. Diane Hollingdale prepared the illustration that serves as the frontispiece of this chapter. We are grateful to these individuals.

A preliminary draft of the manuscript was reviewed by Antony Downes, and his comments were both useful and valuable in strengthening certain areas of the text. We thank the Editor, Hugh V. Danks, for his encouragement and critical comments.

Most aspects of this project were supported by funds from the Natural Sciences and Engineering Research Council of Canada through Grant A-1399, to the senior author. Preparation of the frontispiece was made possible through funding available to Hugh V. Danks.

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## Appendix 1. Taxonomic notes on the genus *Cryobius.*

We offer here some taxonomic notes in justification of our statements about the subgenus *Cryobius* in the text, above.

Ball (1966: 59) recognized the *P. planus* subgroup of *Cryobius*, including therein the Nearctic species *P. planus* Sahlberg, *bryantoides* Ball, *tiliaceoradix* Ball, *biocryus* Ball, *stantonensis* Ball, *cacumenis* Ball, and *bryanti* Van Dyke, and the Palaearctic species, *P. kaninensis* Poppius. Lindroth (1969: 1118) added the Nearctic species *P. haftorni*. Most of these species were based on very few specimens, and with the accumulation of additional material, it has become quite clear that many of these taxa are at best subspecies of a single species. Also, Ball (1966: 82) placed the species *P. auriga* Ball in a subgroup of its own. However, it is reasonably clear that this species is a member of the *planus* subgroup. Further, recent collecting in the Ogilvie Mountains has produced yet another species of the *planus* subgroup, which is described below. The following list summarizes our current views about the species of the *planus* subgroup.

*P. planus* Sahlberg
*P. kaninensis* (sensu lato)
  *P. k. kaninensis* Poppius
  *P. k. kurnakovi* Ball
*P. bryanti* (sensu lato)
  *P. b. biocryus* Ball
  *P. b. tiliaceoradix* Ball
  *P. b. cacumenis* Ball (= *haftorni* Lindroth)
  *P. b. bryantoides* Ball
  *P. b. bryanti* Van Dyke
  *P. b. stantonensis* Ball
*P. auriga* Ball
*P. woodi* Ball and Currie, **new species**

**The *P. planus* subgroup in the Yukon Territory.** Adults of the *planus* subgroup have been collected at various Yukon localities: along the Dempster Highway, at km 155, in the Ogilvie Mountains, and at George's Gap, in the Richardson Mountains; at "Erebia Creek", in the Richardson Mountains; and at "June Creek" and "Sunday Mountain", in the British Mountains. Also, a specimen was collected in Alaska, near Galbraith Lake, on the Prudhoe Bay Road, 68°24′N 129°25′W. All of these specimens are in the Canadian National Collection of Insects, in Ottawa, Ontario. These samples are compared with one another and with samples of other taxa of the *planus* subgroup acquired since Lindroth's work, published in 1969.

Samples of other taxa are as follows. The subspecies *P. b. stantonensis* Ball: specimens collected in 1974 and 1977, at Wood Bay, at the mouth of the Anderson River, near Stanton, the type locality. The specimens are in the Strickland Museum, Department of Zoology, University of Alberta. The subspecies *P. b. cacumenis* Ball (type locality Eagle Summit, Alaska): all specimens were collected in the Yukon-Tanana Highlands, Alaska, between Fairbanks to the south and the Yukon River, to the north. The Eagle Summit series is in the collections of the Department of Entomology, California Academy of Sciences, San Francisco, California. The other specimens belong to Dr. J.V. Matthews, Geological Survey of Canada, Ottawa, Ontario. The single male of *P. auriga* Ball (type locality, Cape Thompson, Alaska), also was collected in the Yukon-Tanana Highlands, at Boundary, Alaska, and is the property of J.V. Matthews.

Features compared are body size (Standardized Body Length [Ball 1966], and maximum width [of elytra]), and values for ratios that are more or less diagnostic: A10L/A10W (antennomere 10, length/width); LT/ED (length of temple/ eye diameter); PW/FL (maximum width of pronotum/ length of hind femur); and FL/FW (hind femur: length/ width). See Table 16 for details.

At km 155, 2 strikingly different samples of *Cryobius* were taken at the same time and in the same place. One is new, and is described below as *Pterostichus woodi*. The other is a distinctive form of *P. b. bryanti* Van Dyke. At George's Gap, a male and female were collected, which are small for *P. b. bryanti* (type area probably the Richardson Mountains), but otherwise seem to belong to that subspecies and are assigned accordingly. Additional samples of this subspecies were collected in the Richardson Mountains, British Mountains, and in Western Alaska, at localities noted above.

Both males and females of the 2 Ogilvie Mountains taxa differ from one another in body size, generally (females of the 2 overlap in width), with the *P. b. bryanti* samples having the larger means. For antennal proportions and leg length compared to pronotal and leg width, the differences are absolute, with the *P. b.bryanti* samples having the longer antennal articles (and thus longer antennae), longer hind femora and narrower pronota.

Although the *P. woodi* sample in body size is about the same as the George's Gap specimens of *P. b. bryanti*, the 2 groups differ clearly in body proportions, and in the same way as *P. woodi* differs from the sample of *P. b. bryanti* with which it is sympatric.

The samples of *P. b. bryanti* differ from one another in body size, and variously in the 4 diagnostic ratios.

*P. woodi* adults are small compared to the Boundary male of *P. auriga*, but in body proportions the 2 groups are very similar to one another.

Except for the km 155 (Ogilvie Mountains) sample, the specimens of *P. b. bryanti* are distinctly smaller than those of *P. b. stantonensis* and *P. b. cacumenis*. Males of *bryanti* and of *stantonensis* differ in all 4 proportions. Males of *bryanti* and *cacumenis* overlap in values for width, and for the ratio FL/FW. Females exhibit more extensive overlap, but the pattern is similar to that of the males.

In summary, analysis of the mensural data supports our contention about the taxonomic distinctness of the Yukon samples of the *P. planus* subgroup. Although the differences among the subspecies of *P. bryanti* are of similar magnitude to those between *P. b. bryanti* and *P. woodi* at km 155, the fact that the latter pair is sympatric must be taken as evidence of specific difference. Also, it seems likely that the range of the postulated adelphotaxon of *P. woodi, P. auriga*, overlaps the ranges of at least *P. b. cacumenis* and *P. b. biocryus*, which would support the specific distinction of *P. auriga*. In turn, if *P. auriga + woodi* is the adelphotaxon of *P. bryanti + kaninensis*, then there is evidence of several cycles of differentiation of this lineage in Beringia.

The following new species shares these character states, which, in combination, establish its membership in subgenus *Cryobius*, and in the *planus* subgroup. Form slender, elongate, body depressed.

*Chaetotaxy.* Head: vertex with 2 pairs of supraorbital setae; clypeus with single pair. Antenna: scape with single seta; antennomeres 2 and 3 each with apical ring of several setae; antennomeres 4–11 each with extensive vestiture of short setae. Labrum with 6 setae, anteriorly. Pronotum with 2 pairs of marginal setae. Each elytron with 2 discal setae in interval 3; without parascutellar seta, basally. Leg setae (fore, middle, hind): coxae (0-2-2); trochanters (1-1-1); femora (0-2-2), antero- or postero-ventrally; tarsomere 5 with one to several marginal setae ventrally. Abdominal sterna IV–VI each with single pair of setae; sternum VII with one pair of setae in males, 2 pairs in females.

*Thorax.* Pronotum with dorsal surface more or less deplanate. Metepisterna each slightly longer than width at base.

*Elytra.* Parallel-sided, depressed, apical declivity short, sloped rather gradually to apex; humeri narrowed somewhat, angles distinct though obtuse, without denticles. Plica not evident postero-laterally.

*Hindwings.* Short stubs, brachypterous.

*Male genitalia.* Median lobe with apical portion rather short, in lateral aspect straight; in ventral aspect with apex broadly rounded, not pointed. Internal sac with 2 sclerites. Parameres typical of *Pterostichus*.

*Ovipositor.* Stylomere 2 with apex broadly rounded, not pointed; ensiform setae 2 —one medial and one lateral.

## *Pterostichus (Cryobius) woodi*, new species

*Type material*. Fourteen males, 30 females. HOLOTYPE male, labelled: YUKON km. 155/ Dempster Hwy/ up to 16.VII.82/ D.M. Wood/ pan trap (CNCI). ALLOTYPE female and PARATYPES (12 males, 29 females), from same locality as holotype (CNCI). PARATYPE male, labelled: YT Km 185 Dempster/ Hwy 1500 m el/ 5.VII.1985 S.G. Cannings (SMDV).

*Specific epithet.* Latinized genitive form of the surname of Dr. D.M. Wood, Biological Resources Division, CLBRR, Agriculture Canada, who collected most of the specimens in the type series.

*Recognition.* Infuscated palpomeres, antennomeres, tibiae and tarsomeres distinguish adults of this species from the adults of those species with which it is known to be sympatric. In colour pattern and reduced elytral striation, *P. woodi* adults are like adults of *P. auriga*, but the 2 groups are distinctly different in pronotal form. Pronotal form (cordate, lateral margins not sinuate posteriorly—see Frontispiece) distinguishes adults of *P. woodi* from those Beringian species that exhibit dark appendages. Small size and shallow elytral interneurs distinguish adults of *P. woodi* from adults of *P. caribou*, both species exhibiting a similar pronotal form.

*Description.* Form as in Frontispiece. Character states as above, and as follows. Data about body size and diagnostic ratios as in Table 16.

*Colour.* Dorsal and ventral surfaces dark piceous to black. Antenna with scape more or less infuscated, antennomeres 2–11 black. Mouthparts: mandibles with basal portions rufo-piceous, distal part of terebral area and incisor rufous; palpomeres piceous, except rufous terminal portions of terminal palpomeres. Legs: coxae dark piceous; trochanters and femora rufous; tibiae and tarsi rufo-piceous to piceous.
*Microsculpture.* Head: dorsal surface (including clypeus) with microlines reduced, mesh pattern obscurely transverse. Labrum with microlines deeper, mesh pattern isodiametric to slightly transverse. Pronotum with microlines shallow, mesh pattern transverse. Elytra with microlines more distinct than on head and pronotum, mesh pattern transverse. Ventral surface with microlines shallow, mesh pattern distinct, transverse on most sclerites, but longitudinal on proepisterna.
*Lustre.* Dorsal surface generally shining; ventral surface iridescent.
*Head.* Frontal impressions pair of narrow grooves extended from epistomal suture posteriorly to about plane of anterior margins of eyes. Eyes convex, moderately prominent.
*Thorax.* Pronotum cordate, maximum width distinctly anterad middle; lateral margins rounded evenly, not sinuate posteriorly; basal and apical margins subequal in width; postero-lateral angles obtuse but not rounded. Median longitudinal impression shallow; postero-lateral impressions basin-like, with long narrow impression mediad and short indistinct impression postero-laterad.
*Elytra.* Interneurs (striae) punctate, shallow, obsolescent posteriorly on declivity; on disc, progressively less distinct from one to 7, and punctures smaller (5–7 each represented by row of shallow punctures), 8 deep; parascutellar interneur absent. Intervals flat, or nearly so.

*Habitat.* This species is known only from a locality in dry rocky tundra (see Lafontaine and Wood 1988: 114, fig. 5).

*Geographical distribution.* This species is known only from the Ogilvie Mountains, Yukon Territory.

*Chorological affinities.* This species is sympatric with *P. b. bryanti* and *P. soperi* Ball. It is allopatric in relation to the localities for its putative adelphotaxon, *P. auriga.*

*Phylogenetic relationships.* Adults of this species and of *P. auriga* are markedly similar in colour pattern and in elytral striation, and on this basis, the 2 species are regarded as adelphotaxa of one another.

TABLE 16. Data about variation in body size (mm) and in values for diagnostic ratios among selected species samples of the *P. (Cryobius) planus* complex. Abbreviations: SBL, Standard body length; A10L/A10W, antennomere 10 length/width; LT/ED, length of temple/eye diameter; PW/FL, maximum width of pronotum/hind femur; FL/FW, hind femur length/width.

| | N | SBL (mm) | | Width (mm) | | A10L/A10W | | LT/ED | | PW/FL | | FL/FW | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Range | Mean | Range | Mean | Range | Mean | Range | Mean | Range | Mean | Range | Mean |
| **Males** | | | | | | | | | | | | | |
| *P. b. stantonensis* Ball | | | | | | | | | | | | | |
| Wood Bay, NT | 11 | 6.34–7.30 | 6.84 | 2.46–2.88 | 2.75 | 1.45–1.73 | 1.59 | 0.20–0.26 | 0.21 | 1.05–1.10 | 1.07 | 3.80–4.28 | 4.06 |
| *P. b. cacumenis* Ball | | | | | | | | | | | | | |
| Eagle summit | 12 | 6.40–7.62 | 6.86 | 2.56–2.88 | 2.77 | 1.50–1.72 | 1.62 | 0.28–0.36 | 0.31 | 0.98–1.06 | 1.02 | 4.20–4.50 | 4.35 |
| Harrison Creek | 1 | 6.50 | | 2.62 | | 1.60 | | 0.30 | | 1.00 | | 4.42 | |
| Mount Prindle | 2 | 6.34–7.39 | 6.86 | 2.72–3.14 | 2.93 | 1.54 | | 0.32–0.38 | 0.35 | 1.00–1.04 | 1.02 | 4.13–4.38 | 4.26 |
| *P. b. bryanti* Van Dyke | | | | | | | | | | | | | |
| km 155 | 2 | 6.94–7.14 | 7.04 | 2.72 | | 2.10–2.44 | 2.27 | 0.56–0.62 | 0.59 | 0.78–0.80 | 0.79 | 5.42–5.47 | 5.44 |
| George's Gap | 1 | 5.54 | | 2.24 | | 1.88 | | 0.45 | | 0.94 | | 4.42 | |
| *P. woodi*, n. sp. | | | | | | | | | | | | | |
| km 155 | 14 | 5.34–6.11 | 5.48 | 2.05–2.37 | 2.21 | 1.44–1.75 | 1.65 | 0.32–0.44 | 0.37 | 1.06–1.14 | 1.10 | 3.57–4.54 | 4.00 |
| *P. auriga* Ball | | | | | | | | | | | | | |
| Boundary | 1 | 6.53 | | 2.56 | | — | | 0.38 | | 1.05 | | 4.62 | |
| **Females** | | | | | | | | | | | | | |
| *P. b. stantonensis* Ball | | | | | | | | | | | | | |
| Wood Bay, NT | 11 | 6.66–7.52 | 7.05 | 2.72–2.98 | 2.86 | 1.45–1.60 | 1.54 | 0.24–0.30 | 0.26 | 1.03–1.14 | 1.08 | 3.94–4.43 | 4.25 |
| *P. b. cacumenis* Ball | | | | | | | | | | | | | |
| Eagle summit | 6 | 6.56–7.23 | 7.03 | 2.75–3.04 | 2.90 | 1.36–1.60 | 1.48 | 0.29–0.41 | 0.34 | 1.00–1.02 | 1.01 | 4.47–4.92 | 4.64 |
| *P. b. bryanti* Van Dyke | | | | | | | | | | | | | |
| km 155 | 8 | 6.62–7.07 | 6.79 | 2.26–2.82 | 2.75 | 2.00–2.30 | 2.17 | 0.54–0.68 | 0.62 | 0.79–0.85 | 0.83 | 5.28–6.36 | 4.18 |
| George's Gap | 1 | 5.82 | | 2.14 | | 2.25 | | 0.66 | | 0.98 | | 4.73 | |
| Erebia Creek | 2 | 6.05–6.21 | 6.13 | 2.34–2.56 | 2.45 | 1.67–1.88 | 1.78 | 0.33–0.37 | 0.35 | 0.88–0.92 | 0.90 | 4.77–5.08 | 4.92 |
| British Mts. | 4 | 5.63–6.34 | 5.87 | 2.24–2.50 | 2.31 | 1.40–1.56 | 1.46 | 0.26–0.33 | 0.29 | 0.95–1.00 | 0.98 | 4.30–4.63 | 4.45 |
| Prudhoe Bay, AK | 1 | 5.73 | | 2.24 | | 1.56 | | 0.28 | | 0.96 | | 4.41 | |
| *P. woodi*, n. sp. | | | | | | | | | | | | | |
| km 155 | 11 | 5.31–5.92 | 5.66 | 2.08–2.40 | 2.27 | 1.33–1.86 | 1.49 | 0.33–0.47 | 0.38 | 1.10–1.19 | 1.12 | 3.85–4.42 | 4.18 |