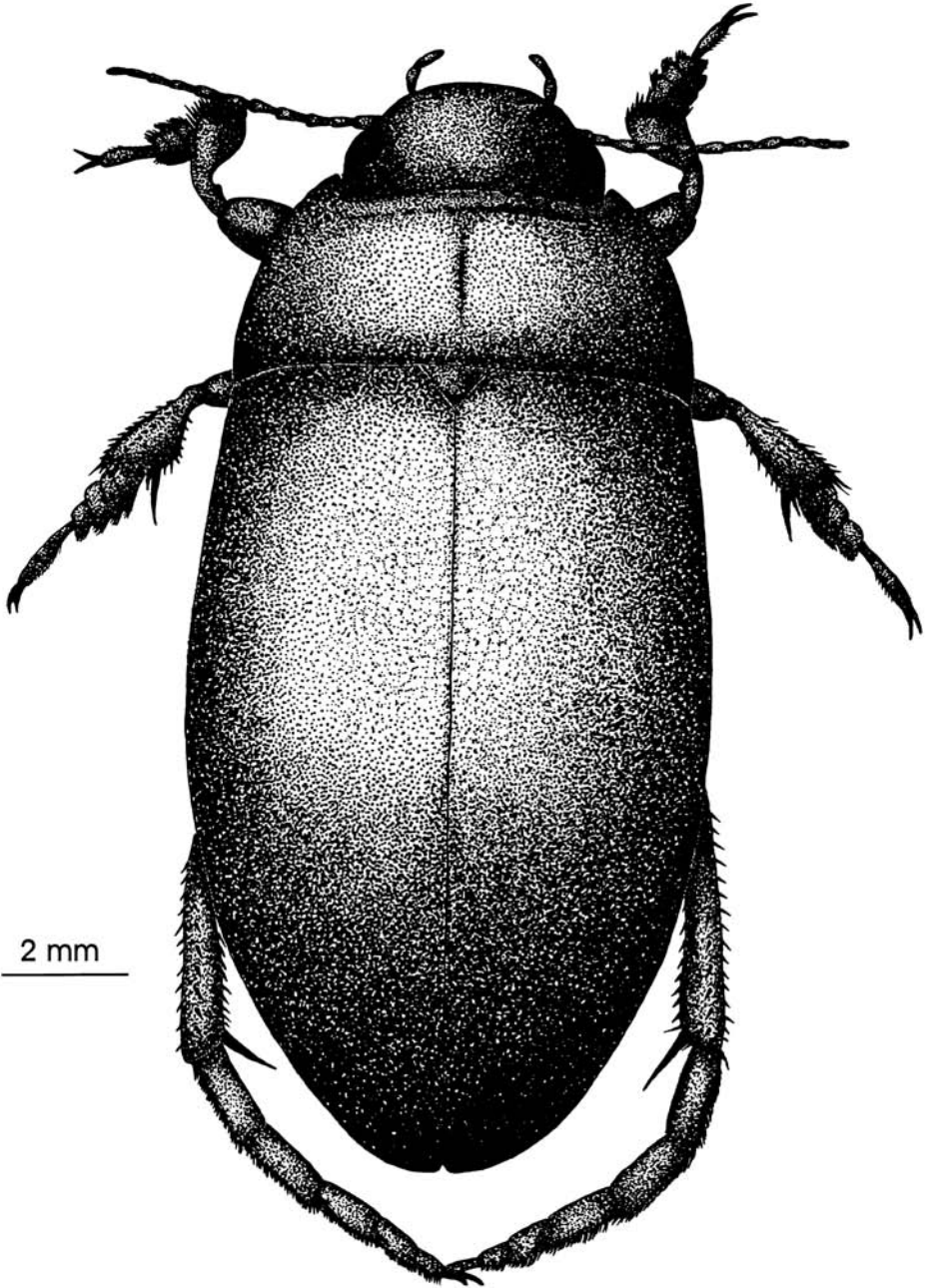


Dytiscid water beetles of the Yukon



FRONTISPIECE. *Neoscutopterus horni* (Crotch), a large, black species of dytiscid beetle that is common in sphagnum bog pools throughout the Yukon Territory.

Dytiscid Water Beetles (Coleoptera: Dytiscidae) of the Yukon

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Abstract. One hundred and thirteen species of Dytiscidae (Coleoptera) are recorded from the Yukon Territory. The Yukon distribution, total geographical range and habitat of each of these species is described and multi-species patterns are summarized in tabular form. Several different range patterns are recognized with most species being Holarctic or transcontinental Nearctic boreal (73%) in lentic habitats. Other major range patterns are Arctic (20 species) and Cordilleran (12 species), while a few species are considered to have Grassland (7), Deciduous forest (2) or Southern (5) distributions. Sixteen species have a Beringian and glaciated western Nearctic distribution, i.e. the only Nearctic Wisconsinian refugial area encompassed by their present range is the Alaskan/Central Yukon refugium; 5 of these species are closely confined to this area while 11 have wide ranges that extend in the arctic and/or boreal zones east to Hudson Bay.

Résumé. *Les dytiques (Coleoptera: Dytiscidae) du Yukon.* Cent treize espèces de dytiques (Coleoptera: Dytiscidae) sont connues au Yukon. Leur répartition au Yukon, leur répartition globale et leur habitat sont décrits et un tableau résume les regroupements d'espèces. La répartition permet de reconnaître plusieurs éléments: la majorité des espèces sont holarctiques ou transcontinentales-néarctiques-boréales (73%) dans des habitats léntiques. Vingt espèces sont arctiques, 12 sont cordillériennes, alors qu'un petit nombre sont de la prairie herbeuse (7), ou de la forêt décidue (2), ou sont australes (5). Seize espèces ont une répartition béringienne et viennent de la région englacée de l'ouest néarctique et le seul refuge néarctique du Wisconsinien couvert par leur répartition actuelle est le refuge Alaska/centre du Yukon; 5 des espèces sont restreintes à cette région alors que les 11 autres ont des répartitions qui s'étendent jusque dans l'Arctique et (ou) dans les zones boréales jusqu'à la Baie d'Hudson.

Introduction

The Yukon Territory is rich in habitat for water beetles. Streams, lakes, ponds and peatlands form extensive and conspicuous parts of landscapes. The varied topography as well as seasonal and inter-regional variation in water regimes contribute to habitat diversity. A feature common to the entire territory is a long, cold winter during which precipitation accumulates as snow. With spring melt, this stored water is released so that in even the driest areas basins are at least temporarily recharged and generally overfilled. The early part of the warm season is characterized by high water levels and high water tables flooding shorelines and poorly drained areas and producing vernal pools, the types of habitats in which the majority of dytiscid beetles exist.

The Yukon dytiscid fauna has not been intensively collected. Nevertheless, incidental collecting by many people and water-beetle collecting expeditions by Mr. and Mrs. J. L. Carr along the Alaska and Dempster Highways in 1979, and a joint collecting expedition by the J. Carr and D. Larson families in the southern and eastern parts of the Territory in 1987, probably have discovered a large proportion of the species. Although the Yukon species list is fairly close to being complete, the Yukon ranges of these species are known only sketchily, for broad geographical expanses separate the records, which are concentrated along the few roads. Virtually all work has been done on the adult stages, and there are few direct observational data on the life histories or larval habitats of species within the Yukon Territory.

Materials and Methods

Yukon records are based upon examination of specimens in several collections, the principal collections and their curators being:

BCPM—British Columbia Provincial Museum, Victoria, British Columbia: R. Cannings.

CARR—B. and J. Carr Collection, Calgary, Alberta.

CNCI—Canadian National Collection of Insects, Ottawa, Ontario: A. Smetana.

MUNC—Dept. of Biology, Memorial University of Newfoundland, St. John's, Newfoundland: D. Larson.

ROME—Royal Ontario Museum, Toronto, Ontario: G. Wiggins.

SMDV—Dept. of Zoology, University of British Columbia, Vancouver, British Columbia: S. Cannings.

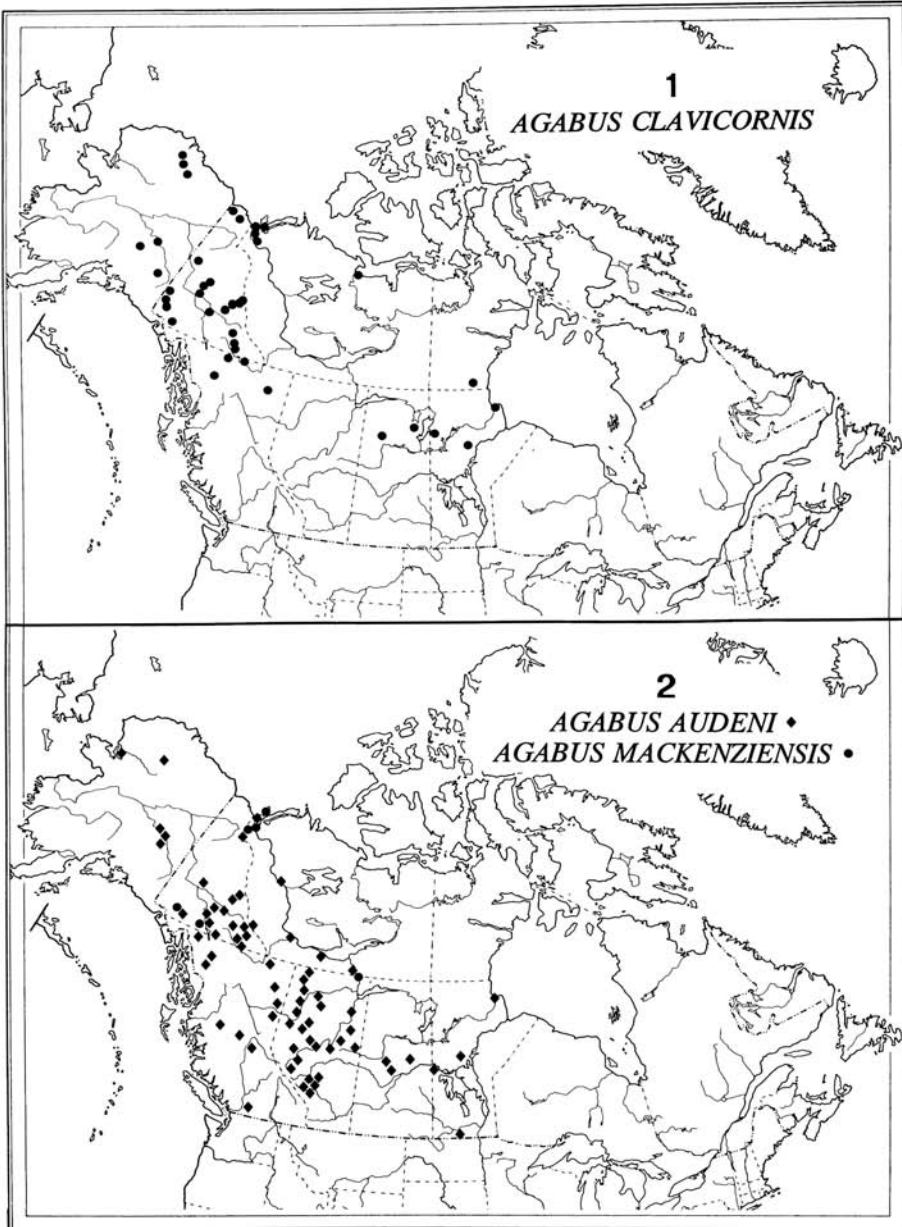
All records are based on specimens that have been examined by me unless otherwise indicated.

The distribution patterns recognized and their terminology generally follow Scudder (1979). The ranges of the various species are diverse but Scudder's patterns approximate the range types of most. However, some species have distributions that include 2 or more range types and therefore are tabulated under each range pattern so that the species total for all range patterns exceeds the total number of species in the fauna. The range patterns recognized are:

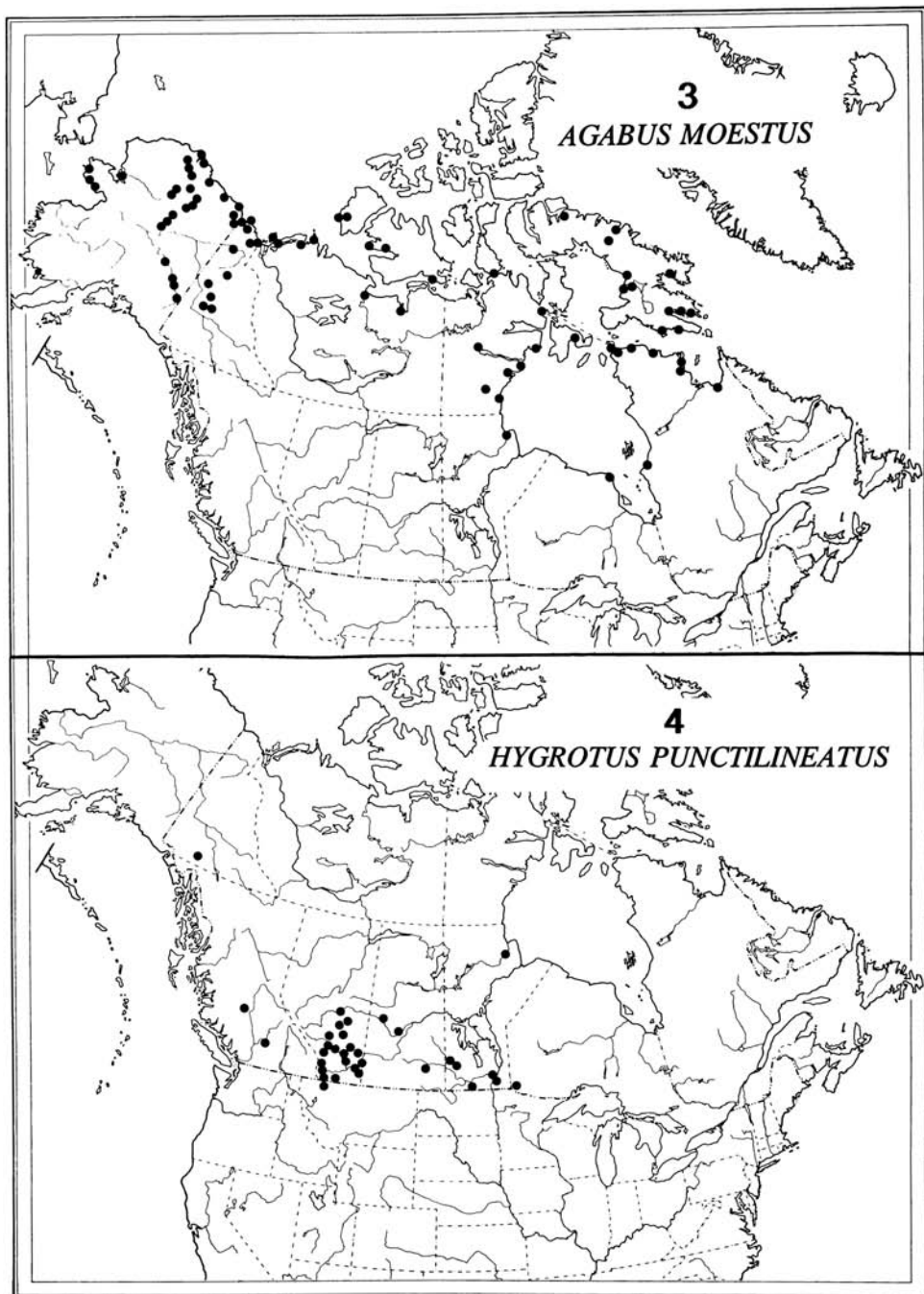
1. Holarctic. The species occur on both sides of the Bering Strait;
2. Transcontinental. The range extends across North America from the Atlantic to the Pacific Ocean;
3. Beringian and glaciated western Nearctic. The Nearctic range is west of Hudson Bay and includes Alaska and the Yukon Territory but otherwise is entirely within the area that was ice-covered during the Wisconsinan maximum (Figs. 1, 2). Some of these species also occur in the Palaearctic;
4. Arctic. The species occur primarily north of the tree line (Fig. 3);
5. Boreal. The distribution is within the boreal zone as defined by Danks and Footitt (1989) (Fig. 5);
6. Cordilleran. The range is within the mountain systems of western North America, extending south of the Canadian-U.S. border (Fig. 6);
7. Grassland. These species occur on the Great Plains with some also in intermontane valleys of the Cordilleran region (Fig. 4).
8. Southern. These species have ranges that are transcontinental south of the boreal zone (Fig. 7).
9. Deciduous. These species occur in the deciduous forest biome south of the Great Lakes as well as in the southern boreal zone, reaching their northwestern limit in the southern Yukon (Fig. 8).

In each species account, distribution within the Yukon is described generally and ecoregions (Scudder 1997) from which the species has been collected are listed.

Natural history information is based, for the most part, on observations made in the Yukon but augmented by experience elsewhere. Habitats are defined in accordance with Roughley and Larson (1991) and assignment of species to habitat type is based primarily on Larson (1985, figs. 5 and 6, appendix 1; 1987*b*) and Roughley and Larson (1991). The primary habitat division is between lotic and lentic habitats. Few dytiscids occur in swiftly flowing water, especially in erosional sites where current is strong enough to produce bottom



FIGS. 1–2. North American collection localities. 1, *Agabus clavicornis* Sharp (61), an Holarctic, Beringian and glaciated western Nearctic species; 2, *Agabus audeni* Wallis (56) (◆) and *A. mackenziensis* Larson (73) (●), Beringian and glaciated western Nearctic species.



FIGS. 3-4. North American collection localities. 3, *Agabus moestus* (Curtis) (74), an Holarctic, arctic species; 4, *Hygrotus punctilineatus* (Fall) (9), a grassland species.

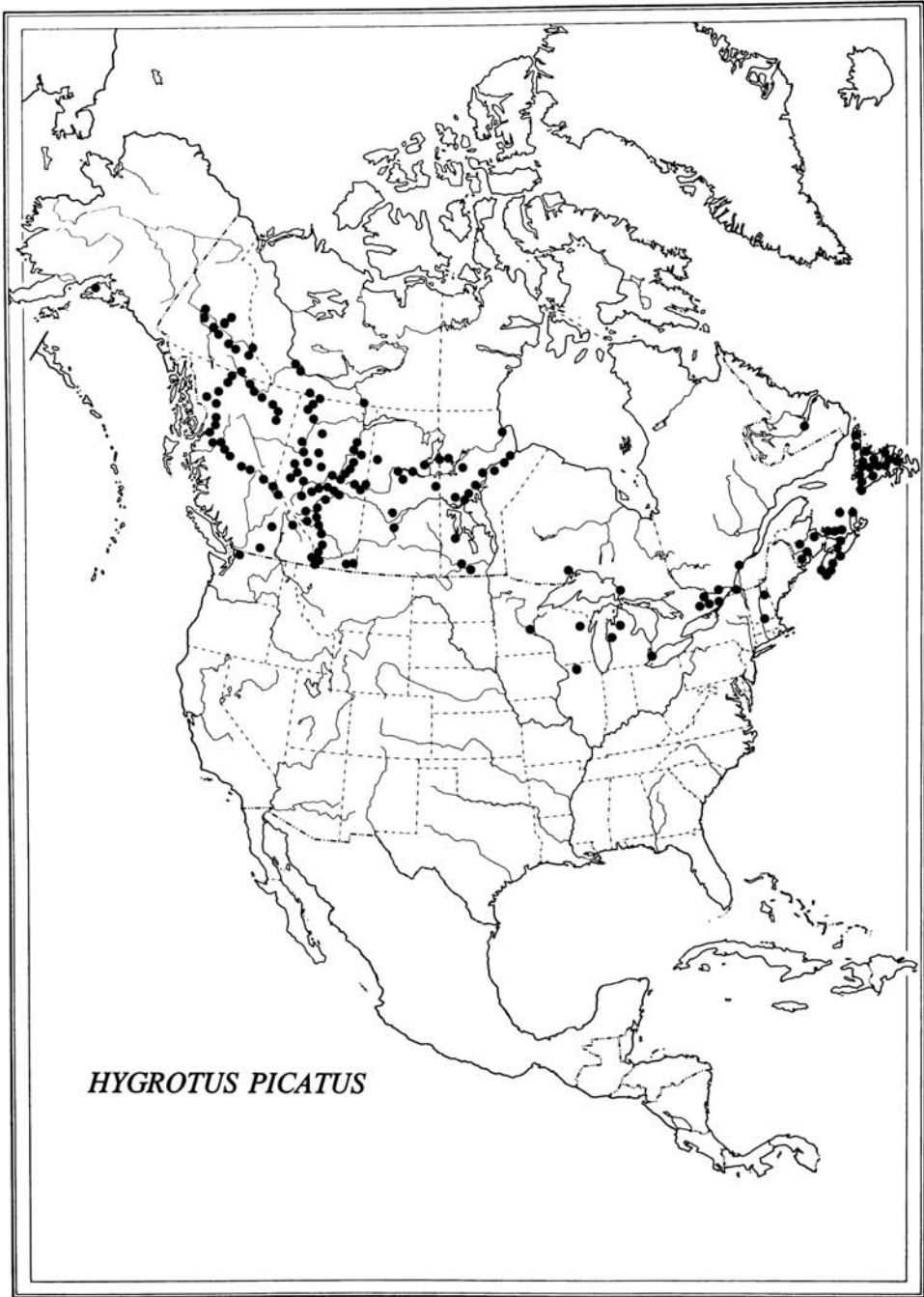


FIG. 5. Collection localities for *Hygrotus picatus* (Kirby) (8), a transcontinental boreal species.

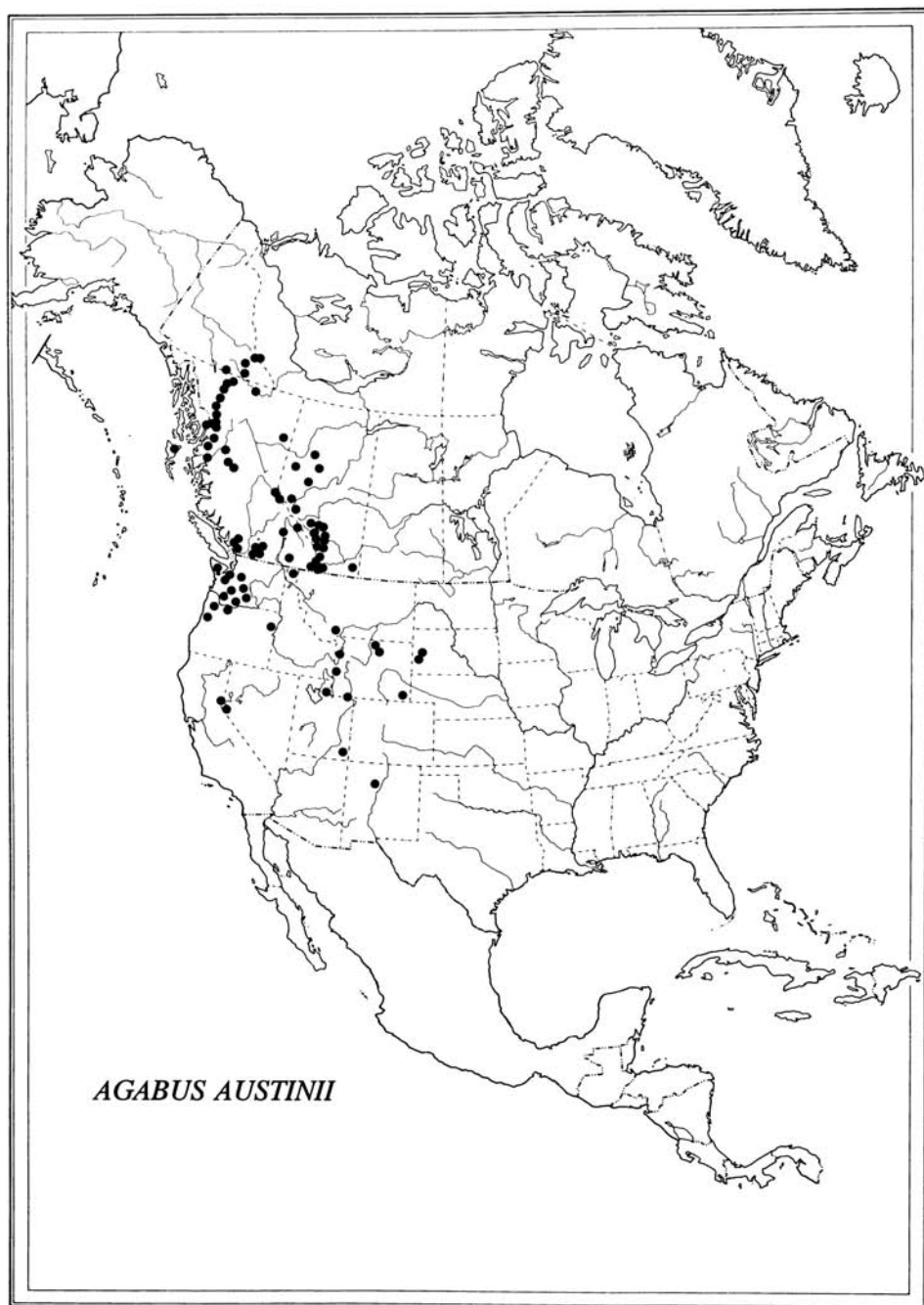


FIG. 6. Collection localities for *Agabus austinii* Sharp (57), a Cordilleran species.

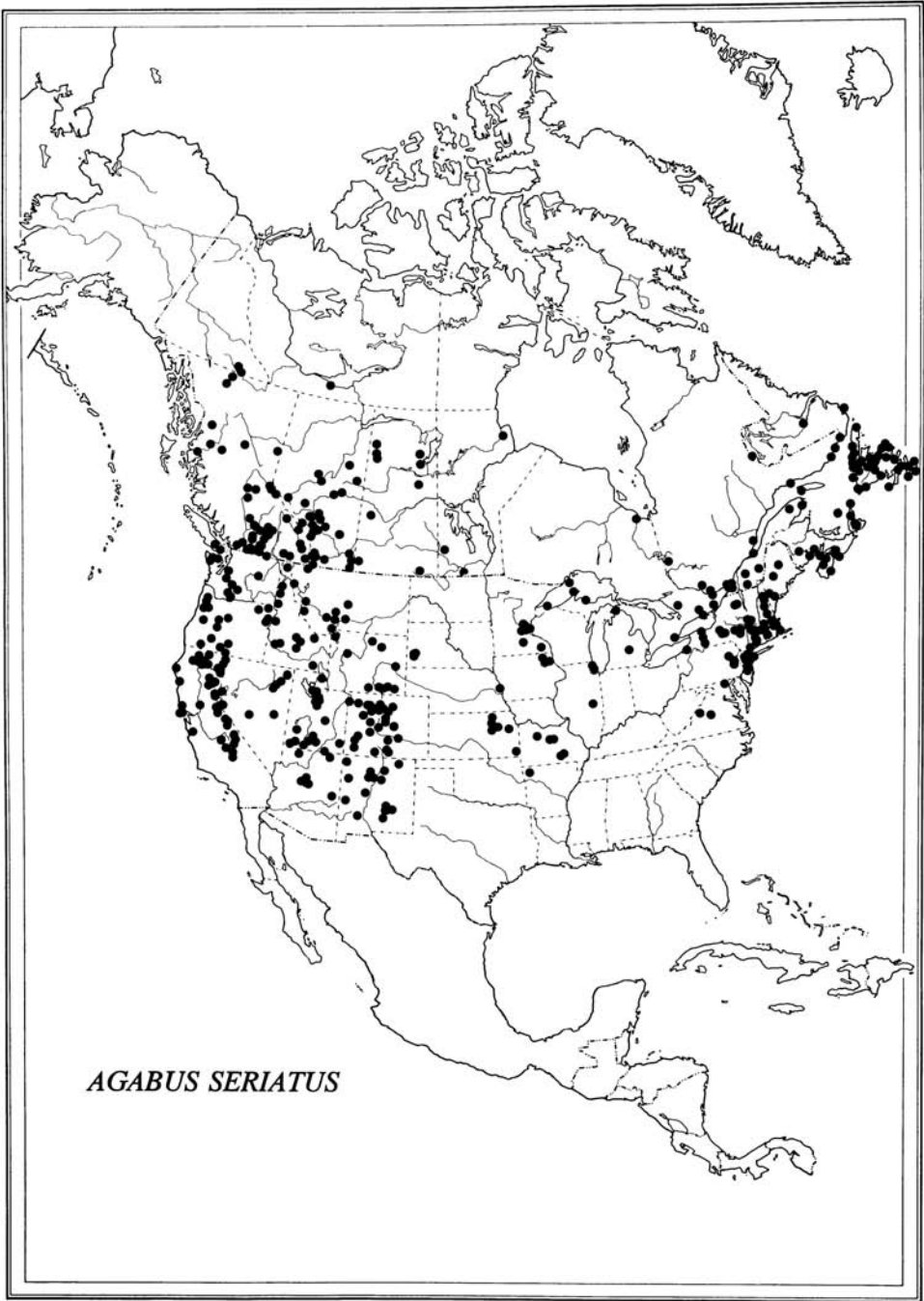


FIG. 7. Collection localities for *Agabus seriatus* (Say) (79), a transcontinental southern species.

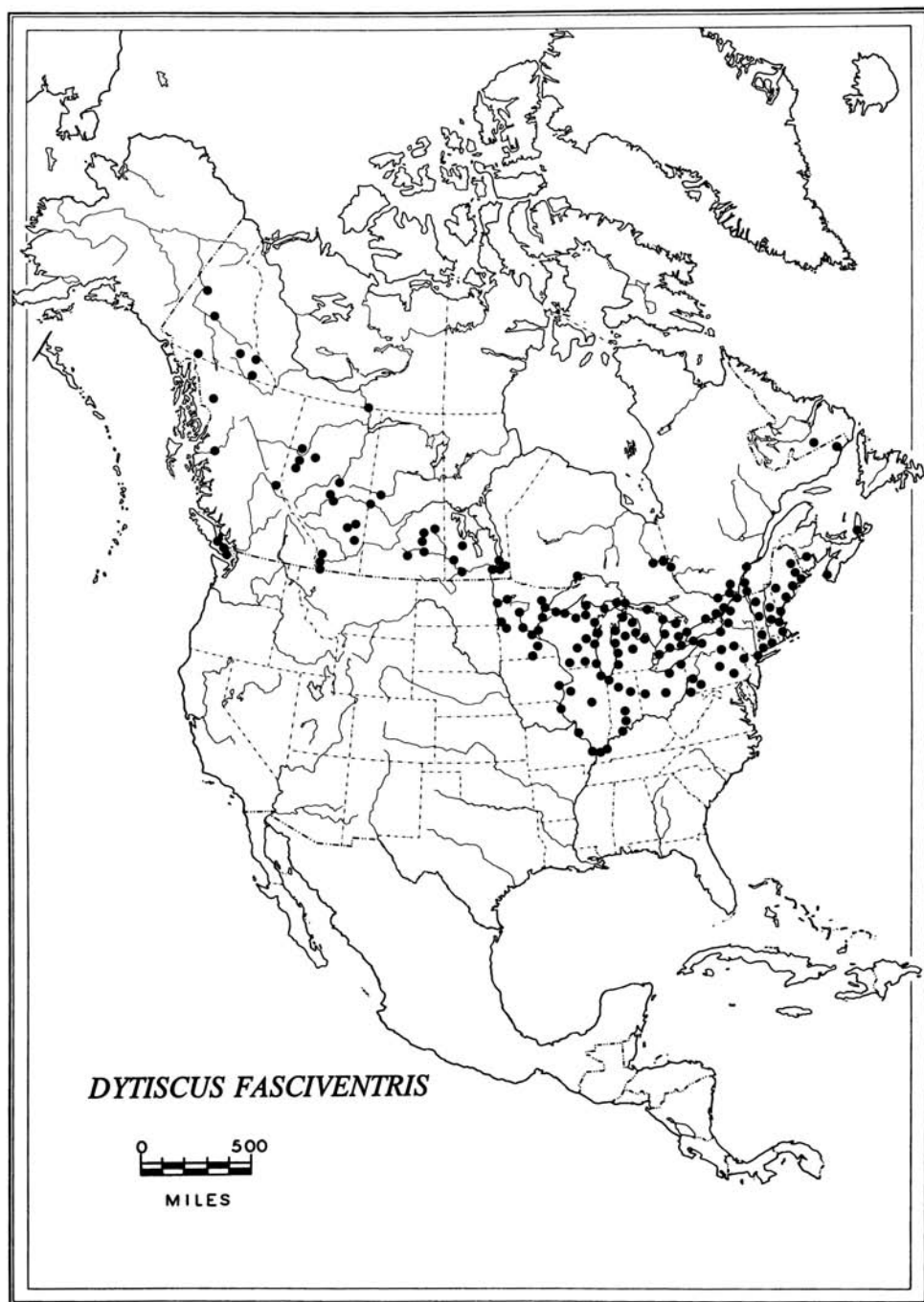


FIG. 8. Collection localities for *Dytiscus fasciventris* Say (108), a deciduous forest species (modified from Roughley 1990).

scouring. However, many species occur in depositional areas at the margins of small streams or in stream-fed pools. If these are the primary habitats of a species, the species is considered to be lotic. Important characteristics of lentic habitats are permanence, exposure, salinity, presence of mosses and peat accumulation (peatland), and the nature of the surrounding terrestrial vegetation.

The habitat requirements of most species are known only through collection of adult specimens; thus habitat assignment is based on correlation between adult occurrence and macroscopic site characteristics. Problems arise in habitat assignment because the habitat categories are not discrete but rather intergrade into one another in complex ways. For example, *Neoscutopterus angustus* is recorded from peatlands as well as streams, because the species is basically lotic, occurring among the emergent vegetation of slow, boggy streams in peatland areas. *Ilybius pleuriticus* occurs in ponds, many of which are situated within bogs or surrounded by boggy margins, and thus is recorded as both a peatland and a pond species. A species may occur in from one to several habitat types. Because of this mixing of species and overlap of habitat types, assignment of 2 species to a given habitat type does not imply their co-occurrence in a particular water body. They may not occur together regularly but the general features used to classify habitats are common to the sites occupied by both.

Annotated List of Yukon Species of Dytiscidae

The family Dytiscidae is the dominant group of aquatic beetles throughout northern portions of the Holarctic region. This pattern is maintained in the Yukon Territory where 112 described species and at least one undescribed species (*Hydroporus* sp.) have been collected to date. These species are listed below and for each information is given on total range, distribution within the Yukon and habitat. A second list shows another 22 species with ranges that suggest they will be discovered in the Yukon too.

Subfamily Laccophilinae

Members of this subfamily form an important part of the fauna of temperate and tropical regions of the world. A single species occurs in boreal North America.

1. *Laccophilus biguttatus* Kirby

Distribution: Holarctic, transcontinental, boreal, Alaska and British Columbia to Labrador and south along Cordillera to New Mexico (Zimmerman 1970; Roughley and Nilsson 1994).

Yukon records: Southern Yukon, collection records extend north to the Stewart River (10, 11, 13, 15).

Biological information: Lentic. Specimens occur in the emergent zone of marshes, more or less permanent ponds and lakes, generally those with broadly exposed shorelines or situated in grassland areas, seldom in peatland ponds.

Subfamily Hydroporinae

This subfamily contains small to minute water beetles. The tribe Bidessini, which contains the smallest dytiscids, is rich in species in lower latitudes but only one Nearctic species, *Liodessus affinis* Say, extends as far north as the southern boreal zone. The other genera found in the Yukon are dominant members of the fauna of alpine and higher-latitude regions of the Northern Hemisphere.

2. *Liodessus affinis* (Say)

Distribution: Nearctic, transcontinental, southern, widely distributed in North America south of the arctic zone.

Yukon records: Southern Yukon, north to Pelly River (10, 14, 19).

Biological information: Principally lentic in marshes and ponds, but also in lotic habitats such as springs and pools adjacent to streams, especially in the southern parts of the range. Yukon collections generally from artificial or disturbed pools and ponds, usually on clay or mineral substrates where there is sparse emergent vegetation and often filamentous algae.

3. *Hygrotus marklini* (Gyllenhal)

H. canadensis (Fall)

Distribution: Holarctic, transcontinental, boreal North America, Alaska and British Columbia to Newfoundland and south along Cordillera to northern New Mexico and Arizona (Anderson 1983).

Yukon records: Pelly and Yukon River valleys (10, 17).

Biological information: Lentic, marshes and both temporary and permanent ponds. Yukon collections are from the emergent zone of shallow but permanent, sun-warmed grassland ponds and lakes, these in more or less closed drainage basins and with apparently hard water.

4. *Hygrotus novemlineatus hudsonicus* Fall

Distribution: Holarctic, subspecies *H. n. hudsonicus* restricted to low arctic and northern boreal regions of North America, from Alaska to northern Quebec (Anderson 1983).

Yukon records: Arctic, all records from north of 68°N (2, 3).

Biological information: Habitat not recorded, probably lentic in the emergent-vegetation zone of ponds.

5. *Hygrotus impressopunctatus* (Schaller)

Distribution: Holarctic, transcontinental in boreal and mid-temperate North America, from Alaska to Newfoundland and south to Arizona, New Mexico, Kansas and New Jersey (Anderson 1983).

Yukon records: Collection records north to Dawson, probably throughout forested parts of the Territory (10, 11, 15, 17, 19).

Biological information: Lentic, in marshes and the emergent-vegetation zone of many types of ponds and lakes but generally rare or absent from peatland habitats. Newfoundland distribution correlated with mineral enrichment of water (Larson and Colbo 1983) but not a pronounced halophile elsewhere.

6. *Hygrotus infuscatus* (Sharp)

H. dentiger (Fall)

Distribution: Nearctic, grasslands of western North America, from southern Yukon and Northwest Territories to California and New Mexico and east to Manitoba (Anderson 1983).

Yukon records: Anderson (1967, fig. 2) indicates a collection record near Whitehorse (17).

Biological information: Lentic. In Alberta the species occurs in both temporary and permanent grassland ponds, in fresh to slightly saline water (Larson 1975).

7. *Hygrotus patruelis* (LeConte)

Distribution: Nearctic, transcontinental in boreal zone and northern prairies, Alaska to Newfoundland and south to New Mexico and Kansas (Anderson 1983).

Yukon records: Southeast, Liard River drainage (15).

Biological information: Lentic, in marshes and both temporary and permanent ponds. Specimens collected from Nahanni Range Road, km 66, were in a small but deep, barren borrow pit with a substrate of soft clay and gravel.

8. *Hygrotus picatus* (Kirby)

Distribution: Nearctic, transcontinental, boreal zone, Alaska and British Columbia to Newfoundland and New England (Anderson 1983; Fig. 5).

Yukon records: Common north to Pelly River, probably throughout forested regions (10, 11, 14, 15, 19).

Biological information: Lentic. A peatland species occurring among emergent vegetation at the edges of peatland ponds, marshy areas of fens and colder marshes.

9. *Hygrotus punctilineatus* (Fall)

Distribution: Nearctic, western grasslands from southern Yukon Territory and British Columbia to western Ontario (Anderson 1983; Fig. 4).

Yukon records: One collection record: Takhini, Alaska Hwy. km 1522 (BCPM) (17).

Biological information: Lentic. Yukon habitat not recorded, in Alberta usually in rather barren, slightly to distinctly saline ponds (Larson 1975).

10. *Hygrotus sayi* Balfour-Browne

Distribution: Nearctic, transcontinental, southern, Canada south of the arctic and most of the United States except the southeast and southcentral states (Anderson 1971).

Yukon records: Southern Yukon, north to Pelly River (10, 11, 14, 17, 19).

Biological information: Lentic, among emergent vegetation at the margins of permanent ponds and lakes.

11. *Hygrotus suturalis* (LeConte)

Distribution: Nearctic, transcontinental, boreal, Alaska and British Columbia to Newfoundland and south along Cordillera to Colorado (Anderson 1983).

Yukon records: Southern Yukon, north to Mayo (10, 11, 15).

Biological information: Lentic. Collected from among emergent vegetation at the margin of permanent ponds and small lakes, both in grassland and forested areas.

12. *Hygrotus turbidus* (LeConte)

Distribution: Nearctic, transcontinental, boreal, Alaska to Nova Scotia and south to northern California, Colorado, Indiana and New Jersey (Anderson 1976).

Yukon records: Central (10).

Biological information: Lentic, in marshes and the emergent zone of permanent ponds (Larson 1975).

13. *Hygrotus unguicularis* (Crotch)

Distribution: Nearctic, transcontinental, boreal, Alaska to Newfoundland and south to Utah and Colorado (Anderson 1983).

Yukon records: Southern Yukon, Yukon and Pelly River valleys (10, 17, 19).

Biological information: Lentic, in shallow, sun-warmed grassland ponds and lakes, generally where emergent vegetation is short or sparse, such ponds usually in closed drainage basins with water tending to be relatively hard.

14. *Hydroporus paugus* Fall (*Hydroporus oblitus* group)

Distribution: Nearctic, transcontinental, boreal, Alaska and British Columbia to Newfoundland.

Yukon records: Records from central Yukon, probably widely distributed in forested areas (11, 15).

Biological information: Lentic, peatlands, generally in cold water among mosses or peat, in peatland pools and in small springs and seeps, on peat substrates, among mosses and *Carex*.

15. *Hydroporus rubyae* Larson (*Hydroporus oblitus* group)

Distribution: Nearctic, transcontinental, boreal, Yukon Territory and British Columbia to Newfoundland.

Yukon records: Southeastern (9, 11, 19).

Biological information: Lentic, at the margin of peatland pools and among waterlogged mosses.

16. *Hydroporus appalachius* Sherman

Distribution: Nearctic, boreal and grassland, Yukon, Northwest Territories and Alberta to Quebec and New Hampshire.

Yukon records: Whitehorse (1 CNCI); Ogilvie R., km 230 Dempster Hwy. (SMDV) (8, 17).

Biological information: Lentic and lotic, occurs in various habitats including edges of clear, rocky lakes, in springs and in pools of intermittent streams.

Taxonomic notes: The status of this species is not clear. It and *H. occidentalis* form a complex with an aggregate range of much of northern North America. *Hydroporus occidentalis* is Cordilleran while *H. appalachius* occurs east of the Rocky Mountains. Within the general range of each species, and along the region of range contact, specimens of uncertain association exist. Colour pattern is useful for separating the 2 species along with subtle differences in shape (Larson 1975). In the Mackenzie Mountains specimens with expanded pale maculations exist but these generally have the habitus of *H. occidentalis* and so have been identified as that species. Northern Yukon specimens have both the colour pattern and habitus of *H. appalachius*. A single specimen from Whitehorse has been tentatively identified as *H. appalachius*.

17. *Hydroporus badiellus* Fall

Distribution: Nearctic, transcontinental, boreal, Alaska to Newfoundland.

Yukon records: Widespread in forested regions (9, 10, 11, 15, 19).

Biological information: Lentic, peatlands, occurs in saturated moss mats or in sphagnum moss at the margins of peatland pools and boggy lakes.

18. *Hydroporus columbianus* Fall

Distribution: Nearctic, transcontinental, boreal, Yukon Territory and British Columbia to New Brunswick.

Yukon records: Southeastern (19).

Biological information: Lentic. This species has been collected from eutrophic marshes.

19. *Hydroporus dentellus* Fall

Distribution: Nearctic, transcontinental, boreal, Alaska to Labrador and Nova Scotia.

Yukon records: In forested regions of the southern half (9, 10, 11, 14, 15, 19).

Biological information: Lentic. Specimens occur among dense emergent vegetation of marshes, fens and boggy lake shores.

20. *Hydroporus despectus* Sharp

Distribution: Nearctic, transcontinental, boreal, Alaska to Newfoundland.

Yukon records: Widespread (10, 11, 15, 19).

Biological information: Lentic, specimens occur in marshes and in small peatland pools.

Taxonomic notes: This species is imprecisely defined and its limits are uncertain. Specimens assigned to *H. despectus* are similar in size to *H. tenebrosus* but tend to be darker in colour and with male pro- and mesotarsomeres 3 smaller and more quadrate.

21. *Hydroporus fuscipennis* Schaum

Distribution: Holarctic, transcontinental, boreal and northern grasslands, Alaska to Newfoundland.

Yukon records: Throughout Yukon, north to Firth River (2, 4, 8, 9, 10, 11, 14, 15, 17).

Biological information: Lentic, in marshes and the emergent zone of pools and small ponds, usually on firm substrates and not associated with peat.

22. *Hydroporus lapponum* Gyllenhal

Distribution: Holarctic, low arctic and northern boreal, Nearctic range Alaska to Newfoundland.

Yukon records: Throughout Yukon, reaching southern limits of range in northern British Columbia (2, 3, 4, 8, 9, 10, 11, 14, 15, 19).

Biological information: Lentic, among flooded grasses, in marshes, and at the margins of small ponds. Occurs in forested as well as alpine and arctic areas but generally is absent from grassland ponds.

23. *Hydroporus larsoni* Nilsson

Distribution: Nearctic, transcontinental, boreal, Yukon Territory and British Columbia to Labrador.

Yukon records: Throughout Yukon, collection records extend from British Columbia border to Rampart House (4, 5, 8, 11, 19).

Biological information: Lentic, in emergent vegetation of marshes and at the margin of small pools and ponds.

24. *Hydroporus mannerheimi* Balfour-Browne

Distribution: Nearctic, Cordilleran, Alaska and Yukon Territory to Alberta and California.

Yukon records: Yukon records are from the Logan Mountains in the southeast. The species occurs along coastal Alaska and has been collected near Cassiar, British Columbia, so it is likely to have a broader distribution in southern and western Yukon (15).

Biological information: Lentic and lotic, occurs among emergent vegetation of permanent, usually spring- or stream-fed ponds, in depositional areas along slow streams and at the margins of cold, clear lakes.

25. *Hydroporus morio* Aubé

Distribution: Holarctic, arctic, alpine and boreal, Nearctic range from Alaska and British Columbia to Newfoundland and north to Ellesmere Island and Greenland.

Yukon records: Throughout Yukon, north at least to McDougall Pass (67°42'N) (5, 8, 9, 10, 11, 15, 17, 19).

Biological information: Lentic, in small, cold, peatland pools. Specimens occur in small, shaded pools in spruce forest as well as exposed pools in alpine and arctic regions.

26. *Hydroporus nigellus* Mannerheim

Distribution: Nearctic, boreal, transcontinental from Alaska to Labrador.

Yukon records: Southern half, probably throughout forested regions (9, 10, 11, 15, 19).

Biological information: Lentic, in cold marshes and peatlands.

Taxonomic notes: The limits of this species against *H. despectus* and *H. tartaricus* are not well understood. I have applied this name to specimens that are similar to *H. despectus* specimens but slightly smaller on average, shinier with less coarse punctation and males with narrower pro- and mesotarsi. Similar forms occur in the Palearctic and the species may be Holarctic.

27. *Hydroporus notabilis* LeConte

Distribution: Part of a complex with an Holarctic range (Angus 1985), Nearctic specimens belong to *H. n. notabilis* which has a transcontinental, low arctic and boreal range from Alaska and British Columbia to Newfoundland.

Yukon records: Throughout Yukon, collections from British Columbia border to Firth River (1, 2, 3, 8, 9, 10, 11, 12, 14, 15, 16, 17, 19).

Biological information: Lentic, in marshes and peatland pools, especially common in exposed, sun-warmed artificial habitats such as tire ruts or roadside pools on peaty soils.

28. *Hydroporus obscurus* Sturm

Distribution: Holarctic, boreal, transcontinental, Nearctic range from Alaska to Newfoundland.

Yukon records: Collections from the southeast, Watson Lake and along Nahanni Range Road, but probably widespread in forested regions (15, 19).

Biological information: Lentic, peatlands, occurs in the moss mat at the edge of pools as well as in saturated areas of moss carpets.

29. *Hydroporus occidentalis* Sharp

Distribution: Nearctic, Cordilleran, Yukon Territory south to Utah and Colorado.

Yukon records: Mackenzie Mountains north to Macmillan Pass and near Mayo, probably widespread in mountainous areas of the southern half (9, 10, 11, 15).

Biological information: Lentic and lotic, occurs in small silty spring or seepage-fed pools, often where the water is cold to the touch. A long series was collected from embayments along the shore of a lake where seeps of water emerged from the mossy banks.

Taxonomic notes: See discussion under *H. appalachius*.

30. *Hydroporus polaris* Fall

Distribution: Nearctic, arctic, transcontinental, Alaska to Quebec and north to Ellesmere Island.

Yukon records: Most southerly record, Dawson (CNCI), probably widely distributed in the arctic zone (1, 2, 3, 4, 10).

Biological information: Habitat not recorded, probably lentic at the margin of tundra pools and ponds.

31. *Hydroporus puberulus* LeConte

Distribution: Holarctic, boreal, transcontinental from Alaska to Newfoundland.

Yukon records: Southern Yukon, north to Mayo (9, 11, 14, 15, 17, 19).

Biological information: Lentic, among emergent vegetation in cold marshes and in peatland pools, often abundant in artificial pools on peaty soils.

32. *Hydroporus rectus* Fall

Distribution: Nearctic, boreal, transcontinental from Alaska to Newfoundland and New England.

Yukon records: North to Ogilvie River (8, 9, 11, 14, 15, 19).

Biological information: Lentic, occurs among moss and emergent *Carex* at the margin of peatland pools.

33. *Hydroporus rufinasus* Mannerheim

Distribution: Nearctic, boreal, transcontinental from Alaska to Nova Scotia.

Yukon records: North to Blackstone River, Dempster Highway (SMDV) (8, 10, 14, 15, 19).

Biological information: Occurs in peatlands, among emergent vegetation and mosses at the edge of ponds and lakes.

34. *Hydroporus sibericus* Sahlberg

Distribution: Holarctic, low arctic, Beringian and glaciated western Nearctic, eastern Palearctic, Alaska to Northwest Territories.

Yukon records: Mile 196 Dempster Hwy., probably widespread in arctic zone as it occurs in this zone in Alaska and Northwest Territories (8).

Biological information: Lentic, occurs in small, grassy tundra pools.

35. *Hydroporus signatus* Mannerheim

Distribution: Nearctic, subspecies *H. s. signatus* boreal, transcontinental from Alaska to Newfoundland and New England and south along the mountains to Colorado (Gordon 1981).

Yukon records: All collection records from southeast, probably widespread in forested areas (11, 15, 19).

Biological information: Lentic, habitat various including small, shallow peatland pools, barren clay or gravel bottomed pools such as borrow pits, spring-fed pools and the margins of cold lakes.

36. *Hydroporus striola* (Gyllenhal)

Distribution: Holarctic, boreal, Nearctic range from Alaska to Newfoundland.

Yukon records: Throughout Yukon, north to Firth River (2, 4, 8, 10, 17, 19).

Biological information: Lentic, among emergent vegetation or debris in marshes and at the margins of both permanent and seasonal pools, often on peat soil but not a sphagnum moss associate.

37. *Hydroporus tartaricus* LeConte

Distribution: Nearctic, boreal, transcontinental.

Yukon records: Southeast (11, 19).

Biological information: Lentic, in cold marshes and peatland pools.

Taxonomic notes: This species is very similar to *H. nigellus* and the limits between the two are not understood. Specimens assigned to *H. tartaricus* are smaller and less coarsely punctate than those assigned to *H. nigellus*.

38. *Hydroporus tenebrosus* LeConte

Distribution: Nearctic, boreal, transcontinental, Alaska to Newfoundland.

Yukon records: Southern Yukon, north to Pelly River (10, 14, 17, 19).

Biological information: Lentic, in marshes and the emergent zone of ponds, both temporary and permanent, usually in grassland or open areas.

39. *Hydroporus tristis* (Paykull)

Distribution: Holarctic, boreal, Nearctic range transcontinental from Alaska to Newfoundland.

Yukon records: Southern Yukon, north to Pelly River, probably throughout forested regions (9, 11, 15, 19).

Biological information: Lentic, emergent zone of marshes as well as peatland pools.

40. *Hydroporus* (s. str.) undescribed sp.

Distribution: Nearctic, boreal, Yukon and northern British Columbia to Churchill, Manitoba.

Yukon records: Yukon records from central and northern regions but probably throughout as there are several collections from adjacent British Columbia and Mackenzie Delta, Northwest Territories (2, 10, 11).

Biological information: Lentic, occurs in small embayments in sphagnum mosses at the margins of boggy ponds and lakes.

41. *Hydroporus* (*Sanfilippodytes*) sp.

Distribution: Not known, probably Cordilleran.

Yukon records: Southeast, Yukon/Northwest territories border near Cantung (15).

Biological information: Collected from small, rock-filled, spring-fed, alpine pools.

Taxonomic notes: At least one species of this subgenus occurs in the Yukon but at present it is not possible to name it. This subgenus is endemic to North America. Most species are Cordilleran but one or more are transcontinental boreal.

42. *Stictotarsus griseostriatus* (DeGeer)

Distribution: Holarctic, boreal and Cordilleran, Nearctic range from Alaska to Newfoundland south to California, Arizona and New Mexico (Zimmerman and A. Smith 1975).

Yukon records: Widely distributed in the southern half in both boreal and alpine zones (9, 11, 12, 15, 19).

Biological information: Lentic and lotic. This tends to be a colonizing species, found in newly formed habitats or habitats that have been physically disturbed by factors such as ice or water scour or water level fluctuation so that much of the substrate is bare and composed of mineral materials such as clay, sand or rock.

Taxonomic notes: This species has been placed previously in *Hydroporus*, *Deronectes* or *Potamonectes*. The current assignment to *Stictotarsus* is by Nilsson and Angus (1992) but I doubt that this is the last word on the classification of the species.

43. *Stictotarsus spenceri* (Leech)

Distribution: Nearctic, Cordilleran, Yukon Territory to Utah (Daussin 1989; Zimmerman and A. Smith 1975).

Yukon records: In the south, in the drier, warmer valleys (10, 19).

Biological information: Lentic. Yukon collections all from shallow, sun-warmed, sandy-bottomed lakes, these lakes generally with no evident outlet and therefore with some evaporative enrichment. Most specimens were collected in open *Scirpus* stands.

Taxonomic notes: See notes under species 42.

44. *Stictotarsus striatellus* (LeConte)

Distribution: Nearctic, Cordilleran and boreal, range extending from Yukon Territory to Manitoba and south to Mexico (Zimmerman and A. Smith 1975).

Yukon records: Collection records only from the southeast (19).

Biological information: Mainly lotic, occurring in eddies and depositional areas of small streams as well as pools and small ponds fed by cold streams. Specimens also occur along wave-washed shorelines of larger lakes and in barren alpine lakes.

Taxonomic notes: See notes under species 42.

45. *Oreodytes laevis* (Kirby)

Distribution: Nearctic, boreal, transcontinental, Alaska to Newfoundland.

Yukon records: Widespread, probably throughout Yukon (3, 10, 14, 15).

Biological information: Lentic and lotic. Yukon collections from bare, mineral substrates along wave-washed and ice-scoured shorelines of large lakes. Alberta and British Columbia specimens have also been collected from backwaters of cool, gravelly streams and pools adjacent to such streams.

46. *Oreodytes recticollis* Fall

O. leechi Zimmerman

Distribution: Nearctic, Beringian and glaciated western Nearctic, eastern Alaska and Yukon (Zimmerman 1985; Alarie 1993).

Yukon records: Southwestern Yukon (10, 13, 17).

Biological information: Habitat not known, Yukon paratypes were collected from a roadside pool. Most species of this genus are lotic or occur on mineral substrates in cold lakes; thus these are the probable habitats.

47. *Oreodytes obesus cordillerensis* Larson

Distribution: Nearctic, Cordilleran, subspecies *O. o. cordillerensis* from southern Yukon to eastern Washington and Colorado (Zimmerman 1985; Larson 1990).

Yukon records: Southern Yukon, north to Dawson (10, 11, 19).

Biological information: Primarily lotic, occurring over mineral substrates in eddies and slow moving sections of small to large streams and along barren, wave- and ice-scoured shorelines of large, cold lakes.

48. *Oreodytes sanmarkii* (Sahlberg)

Distribution: Holarctic, arctic and montane, Beringian and glaciated western Nearctic, in the Nearctic occurring in the Arctic west of Hudson Bay.

Yukon records: Recorded from Caribou Bar Creek near Old Crow, but a specimen of *O. obesus* from Dawson shows some *O. sanmarkii* characteristics (Larson 1990). *Oreodytes sanmarkii* probably replaces *O. obesus* in the arctic northern half of the Yukon (4).

Biological information: Lotic, occurring in eddies and quiet sections of streams, on mineral substrates.

49. *Laccornis conoideus* (LeConte)

Distribution: Nearctic, transcontinental in boreal zone, Yukon and northwestern British Columbia to Newfoundland (Wolfe and Roughley 1990).

Yukon records: Widespread in boreal and low arctic regions (4, 5, 8, 10, 11, 14, 15, 19).

Biological information: Lentic, in marshes and among emergent vegetation and debris at the margin of small pools and ponds, including those of peatlands.

Subfamily Colymbetinae

This subfamily of medium-sized water beetles is very diverse in colder regions of the Northern Hemisphere. Almost 50% of the North American species of the subfamily occur in the Yukon Territory.

50. *Agabus adpressus* Aubé

Distribution: Holarctic, arctic, Beringian and glaciated western Nearctic, Nearctic range extends from Alaska to the west side of Hudson Bay.

Yukon records: Widespread, mainly tundra (6, 8, 10, 16).

Biological information: Lotic, occurs under rocks and other cover along the margins of streams and exposed lake shores (Larson and Nilsson 1985).

51. *Agabus ajax* Fall

Distribution: Nearctic, boreal, Yukon to Labrador and south along Cordillera to Colorado (Larson 1994).

Yukon records: Collections from southeast, north to Selwyn Mountains and west to Ross River, probably more widely distributed in forested areas of the southern half (9, 10, 11, 15, 19, 20).

Biological information: Occurs in exposed, emergent zone of permanent ponds and lakes. Adults appear in late spring and early summer and apparently do not overwinter.

52. *Agabus ambiguus* (Say)

Distribution: Nearctic, in southern boreal and northern temperate regions most common east of Rocky Mountains, southern Yukon and British Columbia to Newfoundland and south to Colorado and North Carolina (Larson 1989).

Yukon records: Extreme southeast (19).

Biological information: Lotic, occurs in depositional areas of springs, small streams and in spring-fed ponds (Larson 1989).

53. *Agabus antennatus* Leech

Distribution: Nearctic, boreal and northern Great Plains, transcontinental, Alaska to Labrador and south to Colorado.

Yukon records: Many records north to Dawson, also from British Mountains (2, 10, 11, 15, 17, 19).

Biological information: Occurs among emergent vegetation along the margins of permanent ponds and protected lake shores, most frequently in exposed, sun-warmed sites but also in habitats where the water is shaded and cool.

54. *Agabus anthracinus* Mannerheim

Distribution: Nearctic, boreal, transcontinental from Alaska to Newfoundland and south along mountains to California, Colorado and West Virginia (Larson 1989).

Yukon records: Throughout the south, north to Old Crow (4, 8, 9, 10, 11, 12, 14, 15, 19).

Biological information: Lentic, occurs among dense emergent vegetation in more or less permanent water of fens, marshes and at the margins of ponds.

55. *Agabus arcticus* (Paykull)

Distribution: Holarctic, low arctic and boreal, Nearctic range from Alaska to Newfoundland (Larson 1989).

Yukon records: Widespread, probably throughout the Territory (4, 5, 6, 8, 9, 10, 11, 12, 15, 19).

Biological information: Occurs at the margin of permanent ponds and lakes, generally on firm, mineral substrates and among emergent sedges.

56. *Agabus audeni* Wallis

Distribution: Nearctic, boreal, northwestern, Alaska and British Columbia to Manitoba (Larson 1991; Fig. 2).

Yukon records: Yukon collection records north to Mayo but also occurring in the Mackenzie Delta (10, 11, 12, 15, 17, 19).

Biological information: Lentic. Among emergent *Carex* and grasses of fens and small, shallow, often seasonal pools.

57. *Agabus austinii* Sharp

Distribution: Nearctic, Cordilleran, southeastern Yukon to northern California and New Mexico (Fig. 6).

Yukon records: Southeastern Yukon (11, 15, 19).

Biological information: Lentic, in depositional areas of cold, clear springs and small streams, among emergent plants (Larson 1989).

58. *Agabus bicolor* (Kirby)

Distribution: Nearctic, boreal, Alaska to Nova Scotia (Larson 1991).

Yukon records: Southern Yukon, north to Mayo (9, 10, 11, 15, 19).

Biological information: Lentic, among emergent vegetation of small, shaded bog and fen pools.

59. *Agabus bifarius* (Kirby)

Distribution: Holarctic, boreal, in eastern Palaearctic, Nearctic range from Alaska to Labrador and New England.

Yukon records: Southern Yukon, north to Pelly River (10, 11, 17, 19).

Biological information: Lentic, in marshes and small pools with dense emergent vegetation, frequently found in temporary ponds.

60. *Agabus canadensis* Fall

Distribution: Nearctic, grasslands of Great Plains and intermontane valleys, southern Yukon and British Columbia to Manitoba and south to Washington and Colorado (Larson 1991).

Yukon records: All records are from the south-central region (10, 17).

Biological information: Lentic, in marshes and seasonal pools in grassland or parkland.

61. *Agabus clavicornis* Sharp

Distribution: Holarctic, low arctic and boreal, Beringian and glaciated western Nearctic, Alaska to west side of Hudson Bay, south to northern British Columbia, Saskatchewan and Manitoba (Fig. 1).

Yukon records: Throughout Yukon, from British Columbia border to Arctic Coast (1, 3, 8, 9, 10, 11, 12, 13, 19).

Biological information: Lentic, among emergent *Carex* in small, cold, permanent ponds of peatlands and marshes.

62. *Agabus clypealis* (Thomson)

Distribution: Holarctic, low arctic, Beringian and glaciated western Nearctic, Nearctic records only from northern Yukon and lower Mackenzie Valley (Larson 1991).

Yukon records: Arctic (5).

Biological information: Habitat not described, probably lentic, in small tundra pools.

63. *Agabus colymbus* Leech

Distribution: Nearctic, low arctic, Beringian and glaciated western Nearctic, Alaska to northern Manitoba.

Yukon records: Arctic, Yukon record from Dempster Hwy. km 87, South Fork Pass (8).

Biological information: Lentic, small, grassy tundra pools.

64. *Agabus confinis* (Gyllenhal)

Distribution: Holarctic, boreal, transcontinental in North America from Alaska to Newfoundland and south along Cordillera to Colorado (Larson 1991).

Yukon records: Throughout Yukon except arctic, north to Old Crow (4, 6, 8, 9, 10, 11, 12, 15, 19).

Biological information: Lentic, in marshes and peatlands, in small, cool pools where the water is shaded by *Carex* (Larson 1991).

65. *Agabus coxalis* Sharp

Distribution: Holarctic, boreal, Beringian and glaciated western Nearctic, eastern Palaearctic, Nearctic range from Alaska and northern British Columbia to western Northwest Territories (Larson 1994).

Yukon records: South-central Yukon (10, 11, 17).

Biological information: Lentic, in marshes and the emergent zone of shallow, sandy-bottomed, mineral-enriched grassland lakes. Like the related species, *A. ajax*, this species probably does not overwinter as an adult and therefore is found in habitats that retain water throughout the summer.

66. *Agabus discolor* (Harris)

Distribution: Nearctic, boreal, Alaska to Labrador and New England (Larson 1991).

Yukon records: Southeastern Yukon, north to Macmillan Pass, Selwyn Mountains (9, 10, 11, 15, 19).

Biological information: Lentic, marshes and peatlands, in small grassy or sedge-filled pools which are at least semipermanent, and often spring-fed (Larson 1991).

67. *Agabus elongatus* (Gyllenhal)

Distribution: Holarctic, arctic and northern boreal, Beringian and glaciated western Nearctic, Nearctic range from Alaska to Hudson Bay and south to central Alberta (Larson 1991).

Yukon records: Collection records extend from British Columbia border to arctic coast (1, 5, 8, 9, 11, 15, 19).

Biological information: Lentic, peatland pools. Occurs in small, cold, mossy pools in spruce forest as well as in tundra pools.

68. *Agabus erichsoni* Gemminger and von Harold

Distribution: Holarctic, boreal, Nearctic range transcontinental from Alaska to Newfoundland.

Yukon records: Widespread, north to Firth River and margin of arctic (3, 9, 10, 11, 12, 15, 16, 17, 19).

Biological information: Lentic, in the emergent zone of marshes and fen pools, often in seasonal habitat.

69. *Agabus fuscipennis* (Paykull)

Distribution: Holarctic, boreal, in western Nearctic from Alaska and British Columbia to Ontario (Larson 1994).

Yukon records: Southern Yukon (12, 19).

Biological information: Lentic, among emergent *Carex* and grasses of permanent marshes and fen pools.

70. *Agabus infuscatus* Aubé

Distribution: Holarctic, boreal and low arctic, Nearctic range from Alaska to Newfoundland (Larson 1994).

Yukon records: Widespread, north to Old Crow (6, 8, 9, 10, 12, 16, 17).

Biological information: Lentic, found in various habitats but most abundant in small, permanent pools and ponds with bare rock or rock and clay substrate.

71. *Agabus inscriptus* (Crotch)

Distribution: Nearctic, boreal, transcontinental from Alaska to Newfoundland (Larson 1991).

Yukon records: Throughout Yukon to margin of arctic (3, 5, 6, 8, 9, 10, 11, 15, 17, 19).

Biological information: Lentic, in various peatland habitats including the emergent zone of small cold pools and in cold, shaded mossy pools in spruce forest.

72. *Agabus leptapsis* LeConte

Distribution: Nearctic, boreal, southern Yukon and northern British Columbia (probably not reaching Pacific) to Newfoundland and New England (Larson 1989).

Yukon records: Collection records are from the extreme southeast only (19).

Biological information: Generally lotic, found among emergent sedges and grasses in depositional areas at the margin of slow, peatland streams.

73. *Agabus mackenziensis* Larson

Distribution: Nearctic, boreal, Beringian and glaciated western Nearctic, Yukon and western Northwest Territories (Fig. 2).

Yukon records: Yukon collection records are from the southwest (12, 17) but the species also occurs in the lower Mackenzie Valley, Northwest Territories, adjacent to the Yukon.

Biological information: Probably lentic, habitat not described.

74. *Agabus moestus* (Curtis)

Distribution: Holarctic, low and mid arctic, Nearctic range from Alaska to Quebec and lower tier of arctic islands (Larson 1991; Fig. 3).

Yukon records: An arctic and low-arctic species, occurring south to Dawson and Mayo (1, 2, 3, 6, 8, 10, 11).

Biological information: Lentic, at the edges of lakes and permanent ponds and in small, cold, spring-fed pools (Larson 1991).

75. *Agabus opacus* Aubé

Distribution: Holarctic, boreal, Nearctic range from Alaska to Newfoundland and New England.

Yukon records: Known only from the southeast corner but probably widespread in the southern half based on collection records from adjacent Alaska and Northwest Territories (19).

Biological information: Lentic, in small, usually seasonal peatland pools which are densely overgrown with sedges or grasses, frequently found in tire ruts of disused roads or along road allowances.

76. *Agabus phaeopterus* (Kirby)

Distribution: Nearctic, boreal, transcontinental, Alaska to Newfoundland and along Cordillera to Colorado (Larson 1991).

Yukon records: Southern half, north to Ogilvie Mountains (8, 9, 10, 11, 15, 17, 19).

Biological information: Lentic, in marshes and the emergent zone of small, often vernal ponds.

77. *Agabus punctulatus* Aubé

Distribution: Nearctic, southern in low boreal and mid-temperate zones, central Yukon to Nova Scotia, south in the west to Arizona and New Mexico.

Yukon records: Known from only the central region (10).

Biological information: Lentic, occurs in small, often temporary, pools in grassland or open shrub habitat.

78. *Agabus semipunctatus* (Kirby)

Distribution: Nearctic, boreal, transcontinental from Alaska to Newfoundland.

Yukon records: In southern half, north to Mayo (10, 11, 13, 17, 19).

Biological information: Lentic, in small peatland pools, usually among sphagnum mosses.

79. *Agabus seriatus* (Say)

Distribution: Nearctic, southern in southern boreal, mid-temperate and montane zones, transcontinental from southern Yukon and British Columbia to Newfoundland and south to California and New Mexico (Fig. 7).

Yukon records: Known only from southeastern corner (19).

Biological information: Lentic, usually in springs and small streams, occurs on both gravel and rubble substrates as well as among rooted plants.

80. *Agabus strigulosus* (Crotch)

Distribution: Nearctic, Cordilleran, Alaska and Yukon to Manitoba and south to California and New Mexico (Larson 1989).

Yukon records: Known only from the southeast (11, 15, 19).

Biological information: Lentic, among emergent vegetation in marshes and at the margin of small ponds, usually where there is some flushing from seeps or small streams (Larson 1989).

81. *Agabus thomsoni* (Sahlberg)

Distribution: Holarctic, low arctic, boreal and montane, transcontinental in Nearctic from Alaska to Newfoundland and south along Cordillera to Colorado (Larson 1991).

Yukon records: Widespread (1, 2, 3, 5, 6, 8, 9, 10, 11, 12, 13, 15, 16, 17, 19).

Biological information: Lentic, in the emergent zone of pools and ponds, spring-fed pools and in barren gravel or peat-bottomed ponds.

82. *Agabus tristis* Aubé

Distribution: Holarctic, low arctic, boreal and Cordilleran, in eastern Palaearctic, Nearctic range apparently disjunct, widespread in the west from Alaska to Northwest Territories and south to California and New Mexico, also with populations east of Hudson Bay from Baffin Island to New Hampshire (Larson 1989).

Yukon records: Yukon records from the southern half, north to Dawson (10, 11, 12, 15, 19), in adjacent Northwest Territories extending north to mouth of Mackenzie River.

Biological information: Lentic-lentic. At the margin of alpine ponds and lakes and among emergent sedges of depositional areas of springs, small streams and beaver ponds (Larson 1989).

83. *Agabus velox* Leech

Distribution: Nearctic, low arctic, Beringian and glaciated western Nearctic, Alaska to northern Manitoba.

Yukon records: Probably widespread in the Arctic and the northern boreal forest but collection records only from central area (8, 11).

Biological information: Lentic, emergent zone of small peatland pools.

84. *Agabus wasastjernae* (Sahlberg)

Distribution: Holarctic, boreal, transcontinental in Nearctic from Alaska to Newfoundland.

Yukon records: Collection records are from the southeast (11, 15, 17, 19).

Biological information: Lentic, in peatland pools.

85. *Agabus zaitzevi* Poppius

Distribution: Holarctic, low arctic, Beringian and glaciated western Nearctic, Alaska to northern Manitoba.

Yukon records: One collection record, from the north slope of the British Mountains (3).

Biological information: Lentic, in grassy tundra pools.

86. *Agabus zetterstedti* Thomson

Distribution: Holarctic, low arctic, Nearctic range from Alaska to northern Manitoba (Larson 1991).

Yukon records: In the arctic northern regions (1, 3, 8).

Biological information: Lentic, in small temporary pools with aquatic mosses (Nilsson 1985).

87. *Carrhydrus crassipes* Fall

Distribution: Nearctic, boreal, Beringian and glaciated western Nearctic, Yukon and British Columbia to western Ontario.

Yukon records: Eastern and central (10, 19).

Biological information: Lentic, in permanent pools with dense stands of emergent *Carex* and mats of decaying *Carex* stalks.

88. *Ilybius angustior* (Gyllenhal)

Distribution: Holarctic, boreal, Nearctic range from Alaska to Newfoundland and south along Cordillera to Colorado (Larson 1987a).

Yukon records: Throughout Yukon (2, 5, 8, 9, 10, 11, 12, 15, 17, 19).

Biological information: Lentic, marshes and peatlands, occurs among emergent vegetation of semipermanent to permanent pools, ponds and lakes.

89. *Ilybius discedens* Sharp

Distribution: Nearctic, boreal, transcontinental from Alaska to Newfoundland (Larson 1987a).

Yukon records: In forested regions, north to Mayo (9, 10, 11, 19).

Biological information: Lentic, occurs exclusively in peatlands, in small pools and among emergent vegetation at the margins of ponds.

90. *Ilybius picipes* (Kirby)

Distribution: Holarctic, boreal, Nearctic distribution transcontinental from Alaska to Newfoundland (Larson 1987a).

Yukon records: Southern Yukon, north to Macmillan Pass and Pelly River (9, 10, 11, 12, 14, 15, 19).

Biological information: Lentic, specimens occur in the emergent zone of peatland pools.

91. *Ilybius pleuriticus* (LeConte)

Distribution: Nearctic, boreal, northern British Columbia (but not reaching Pacific coast) and southern Yukon to Newfoundland (Larson 1987a).

Yukon records: Southeast (11, 15, 19).

Biological information: Lentic, peatlands. Most Yukon collections from the margins of ponds and small lakes surrounded by black spruce/sphagnum bog.

92. *Ilybius subaeneus* (Erichson)

Distribution: Holarctic, low arctic, boreal, northern grasslands and subalpine, Nearctic range transcontinental from Alaska to Newfoundland and south in Cordillera to Colorado (Larson 1987a).

Yukon records: Widespread (5, 7, 8, 9, 10, 11, 12, 13, 14, 15, 17, 19).

Biological information: Lentic. Beetles occur among emergent vegetation at the margin of semipermanent to permanent ponds and lakes, generally in sites that are exposed to the sun.

93. *Ilybius vittiger* (Gyllenhal)

Distribution: Holarctic, low arctic, Beringian and glaciated western Nearctic, Nearctic range from Alaska to northern Manitoba (Larson 1987a).

Yukon records: Collection records are from northern arctic regions but the range is probably throughout the Yukon (see Biological information) (5, 6).

Biological information: Lentic, in small peatland pools with emergent vegetation. Collection localities indicated by Larson (1987a) were mainly arctic but the species has since been found well into the boreal zone (Prophet River, Alaska Hwy., British Columbia, MUNC).

94. *Colymbetes dahuricus* Aubé

Distribution: Holarctic, boreal, Nearctic range from Alaska to Quebec (Zimmerman 1981).

Yukon records: In the south, north to Dawson (9, 10, 11, 14, 15, 19).

Biological information: Lentic, in cold marshes and peatlands, among dense emergent *Carex*.

95. *Colymbetes densus* LeConte

Distribution: Nearctic, Cordilleran, southern Yukon to California and Wyoming (Zimmerman 1981).

Yukon records: All collection records are from the southeastern corner but the species probably occurs across the southern part of the Territory as it is found in adjacent portions of British Columbia and Alaska (19).

Biological information: Lentic, in marshes and the emergent zone of ponds, often in spring or stream-fed ponds.

96. *Colymbetes dolobratus* (Paykull)

Distribution: Holarctic, low to mid arctic, Nearctic range includes Baffin Island and Greenland and on the mainland extends from Alaska to Newfoundland (Zimmerman 1981).

Yukon records: Widely distributed (2, 3, 4, 5, 8, 9, 15).

Biological information: Lentic, in marshes and the emergent zone of ponds and lakes.

Taxonomic notes: The relationship between *C. dolobratus* and *C. sculptilis* is unresolved (Zimmerman 1981). *Colymbetes dolobratus* is smaller, paler, has slenderer metafemora and occurs in the arctic while the more southerly *C. sculptilis* is larger, darker and with broader metafemora. However, specimens from intermediate localities are intermediate in characteristics (Zimmerman 1981). Because this variation has not been carefully studied in the Yukon, arctic and alpine specimens have been assigned to *C. dolobratus* and specimens from forested or grassland areas to *C. sculptilis*.

97. *Colymbetes paykulli* Erichson

Distribution: Holarctic, boreal, Nearctic range from southeastern Yukon and northwestern British Columbia to Newfoundland (Zimmerman 1981).

Yukon records: Collection records are from the southeast (14, 15, 19).

Biological information: Lentic, in cold marshes and the emergent zone of ponds and lakes, almost constantly in peatland habitats.

98. *Colymbetes sculptilis* Harris

Distribution: Nearctic, southern, boreal to mid-temperate, transcontinental from Alaska to Newfoundland and Atlantic coast (Zimmerman 1981).

Yukon records: Central and southern Yukon, in grassland and forested areas (10, 14).

Biological information: Lentic, occurs in marshes and among emergent vegetation at the edges of ponds and lakes, generally in exposed sites where the water is sun-warmed.

Taxonomic notes: See notes under species 96.

99. *Neoscutopterus angustus* (LeConte)

Distribution: Nearctic, boreal, Yukon and northern British Columbia to Newfoundland and Maine.

Yukon records: Known from one collection in the southeast: Hwy. 4 km 148, near Tuchtua (MUNC) (19).

Biological information: Lentic, occurs among moss and *Carex* at the margin of sluggish peatland streams.

100. *Neoscutopterus horni* (Crotch) (Frontispiece)

Distribution: Nearctic, boreal, transcontinental from Alaska to Labrador.

Yukon records: Forested areas of the south, north to Dawson (9, 10, 11, 14, 15, 19).

Biological information: Lentic, exclusively in peatlands, among mosses and *Carex* where the water is cold.

101. *Rhantus binotatus* (Harris)

Distribution: Nearctic, southern, boreal to mid-temperate and montane, range extends from Alaska to Newfoundland and south along the western mountains to California and New Mexico (Zimmerman and R. Smith 1975).

Yukon records: Collection records all from southern regions (17, 19).

Biological information: Lentic-lotic, found in pools and among emergent vegetation but generally in sites that are fed by springs or small streams and there is some flushing, albeit often very slight.

102. *Rhantus sericans* Sharp

R. frontalis (Marshall)

Distribution: Nearctic, southern Yukon. The range of *R. sericans* extends from Alaska to western Quebec and south to California, New Mexico and Missouri (Zimmerman and R. Smith 1975).

Yukon records: South-central, primarily in or adjacent to grassland areas (10, 17).

Biological information: Lentic, in warm, exposed marshes and the emergent zone of exposed ponds. Occurs in both seasonal and permanent habitats.

Taxonomic notes: Nearctic specimens have been considered conspecific with Palaearctic specimens and treated under the name *R. frontalis* (e.g. Zimmerman and R. Smith 1975). Balke (1990) separated the *R. frontalis* complex into 3 species, 2 in the Palaearctic and *R. sericans* in the Nearctic.

103. *Rhantus suturellus* (Harris)

Distribution: Nearctic, boreal, transcontinental from Alaska to Newfoundland (Zimmerman and R. Smith 1975).

Yukon records: Wide range throughout Yukon (1, 3, 4, 9, 10, 11, 15).

Biological information: Lentic, among emergent vegetation of peatlands.

104. *Rhantus wallisi* Hatch

Distribution: Nearctic, boreal, transcontinental from Alaska to Newfoundland (Zimmerman and R. Smith 1975).

Yukon records: Widely distributed in the southern half (10, 11, 14, 15, 17, 19).

Biological information: Lentic, in marshes and the emergent-vegetation zone of small pools, ponds and lake margins, less frequent in peatlands than *R. suturellus*.

Subfamily Dytiscinae

This is a group of medium to very large water beetles. The subfamily is widely distributed but very few species occur in arctic or alpine zones. However, there are a number of characteristic boreal or north temperate species.

105. *Dytiscus alaskanus* Balfour-Browne

Distribution: Nearctic, boreal, transcontinental from Alaska to Newfoundland, south in Cordillera to Colorado (Roughley 1990).

Yukon records: Widespread, probably throughout Yukon (4, 7, 9, 10, 11, 13, 15, 17, 19).

Biological information: Lentic, in the emergent zone of permanent ponds and lakes, often in small bog-ringed lakes.

106. *Dytiscus circumcinctus* Ahrens

Distribution: Holarctic, boreal to mid-temperate, Nearctic range from Alaska and British Columbia to Maine (Roughley 1990).

Yukon records: Widely distributed in the forested areas with a few records from possibly arctic regions (4, 10, 11, 12, 17, 19).

Biological information: Lentic, mainly in deeper marshes or in extensive emergent zone of lakes.

107. *Dytiscus dauricus* Gebler

Distribution: Holarctic, boreal and montane, Nearctic range from Alaska to Newfoundland and south in the west to California, Arizona and Colorado (Roughley 1990).

Yukon records: Throughout Yukon (4, 5, 6, 8, 9, 10, 11, 12, 15, 17, 19).

Biological information: Lentic, in marshes and the emergent zone of ponds and lakes.

108. *Dytiscus fasciventris* Say

Distribution: Nearctic, southern boreal to mid-temperate, transcontinental from Yukon and coastal British Columbia to Quebec and New England (Roughley 1990; Fig. 8).

Yukon records: In the southern half, north to Dawson (10, 11, 15, 17, 19).

Biological information: Lentic, in warm marshes and small forest ponds.

109. *Dytiscus harrisii* Kirby

Distribution: Nearctic, boreal, transcontinental from Alaska to Newfoundland (Roughley 1990).

Yukon records: Collection records only from central Yukon, probably widespread in forested zones (9, 10).

Biological information: Lentic, usually in peatland habitats such as the emergent zone of boggy lakes, in beaver ponds and in pools in sluggish peatland streams.

110. *Hydaticus aruspex* Clark

Distribution: Holarctic, boreal, Nearctic range transcontinental from Alaska to Newfoundland (Roughley and Pengelly 1982).

Yukon records: Known only from the central Yukon (10).

Biological information: Lentic, among dense emergent vegetation of marshes and margins of small ponds, sometimes found in peatlands in sites with cold water but also in sun-warmed sites.

111. *Acilius semisulcatus* Aubé

Distribution: Nearctic, boreal, transcontinental from Alaska to Newfoundland.

Yukon records: Widespread in southern half (8, 10, 11, 13, 14).

Biological information: Lentic, at the edge of the open water of ponds and lakes, often along the quaking banks of boggy lakes.

112. *Graphoderus occidentalis* Horn

Distribution: Nearctic, Yukon and British Columbia to Quebec.

Yukon records: Central, in grassland areas (10).

Biological information: Lentic, in the emergent zone of exposed ponds.

113. *Graphoderus perplexus* Sharp

Distribution: Nearctic, transcontinental, Alaska to Newfoundland.

Yukon records: Widespread in the southern half (10, 11, 14, 17, 19).

Biological information: Lentic, among emergent vegetation at the margins of ponds and small lakes, often in peatland lakes.

Additional Species Expected to Occur in the Yukon

The following list shows species not recorded from the Yukon Territory but likely to be discovered. These species occur in adjacent portions of Alaska, the Northwest Territories, British Columbia or northern Alberta and in habitats similar to those in the Yukon.

Subfamily Hydroporinae

114. *Desmopachria convexa* (Aubé). Northwest Territories, British Columbia, Alberta. Nearctic, boreal. Small pools in fen moss mats.

115. *Hygrotus compar* (Fall). Alaska, British Columbia, Alberta. Nearctic, boreal, grassland. Marshes and temporary ponds.

116. *Hygrotus lutescens* (LeConte). Alaska, British Columbia. Nearctic, Cordilleran. Marshes and small ponds.

117. *Hygrotus (Neoporus) superioris* Balfour-Browne. Northwest Territories, British Columbia, Alberta. Nearctic, boreal, grassland. Lake and pond margins and slow, warm streams.

118. *Hygrotus (Neoporus) undulatus* Say. Northwest Territories, British Columbia, Alberta. Nearctic, boreal. Boggy streams and beaver ponds.

119. *Hydroporus stagnalis* Gemminger and von Harold. Northwest Territories, Alberta. Nearctic, boreal. Peatland pools and moss mats.

120. *Hydroporus* (s. str.) *longiusculus* Gemminger and von Harold. Alaska, British Columbia. Nearctic, Pacific. Marshes and small ponds.
121. *Nebrioporus depressus* (Fab.). Northwest Territories, Alberta. Holarctic, boreal. Lakeshores and slow, warm streams.
122. *Oreodytes alaskanus* (Fall). British Columbia, Washington. Nearctic, Cordilleran. Streams and wave-washed lake shores.
123. *Oreodytes scitulus* (LeConte). Northwest Territories, British Columbia, Alberta. Nearctic, boreal and Cordilleran. Streams and wave-washed lake shores.
124. *Laccornis oblongus* (Stephens). Northwest Territories. Holarctic, arctic-boreal. Marshes.

Subfamily Colymbetinae

125. *Agabus hypomelas* Mannerheim. Alaska, British Columbia, Alberta. Nearctic, Cordilleran. Spring-fed peaty pools.
126. *Agabus inexpectatus* Nilsson. Alaska. Holarctic, arctic. Small tundra pools.
127. *Agabus vancouverensis* Leech. Alaska, British Columbia. Nearctic, Pacific. Alpine ponds and lakes.
128. *Ilybius churchillensis* Wallis. Alaska, Northwest Territories. Nearctic, arctic. Marshes and small ponds.
129. *Ilybius quadrimaculatus* Aubé. Alaska, British Columbia, Alberta. Nearctic, Cordilleran. Marshes.
130. *Rhantus sinuatus* (LeConte). Northwest Territories, British Columbia, Alberta. Nearctic, boreal. Eutrophic marshes.
131. *Rhantus consimilis* (Motschulsky). Northwest Territories, British Columbia, Alberta. Nearctic, Cordilleran, grassland. Marshes and small ponds.

Subfamily Dytiscinae

132. *Dytiscus cordieri* Aubé. Alaska, Northwest Territories, British Columbia, Alberta. Nearctic, boreal. Marshes and ponds.
133. *Acilius abbreviatus* Mannerheim. Alaska, British Columbia, Alberta. Nearctic, Cordilleran. Ponds.
134. *Acilius athabascaae* Larson. British Columbia, Alberta. Nearctic, boreal. Bog-ringed ponds and lakes.
135. *Graphoderus liberus* (Say). Northwest Territories, British Columbia, Alberta. Nearctic, boreal. Brownwater ponds and small lakes.

Zoogeographic Analysis

Distribution Patterns of Yukon Species. The proportions of Yukon species showing the various range patterns are indicated in Table 1. Generally, the range of each species has been inferred on the basis of a combination of sparse collection records, knowledge of the ecology of the beetle, and extrapolation on the basis of probable occurrence of suitable habitat. In Table 1 and the following discussion, the total number of species for all range patterns exceeds the number of species in the Yukon fauna (113 species) because some species have broad ranges and have been included in 2 or more categories and some range categories are geographic areas and others are basically life zones/ habitats so they are not mutually exclusive. Because of the interrelationship between distribution patterns and habitat, information on both is included in the above species list and summarized in Table 2 as the number of species of each range type in each habitat type.

The greater part of the Yukon fauna consists of widely distributed boreal species (83 species). These are predominantly inhabitants of marshes, peatlands and ponds but about 12% of these species (species no. 16, 35, 42, 45, 52, 72, 82, 99, 101) occur in lotic habitats. About 41% of this fauna is Holarctic (1, 3, 5, 21, 22, 25, 27, 28, 31, 36, 39, 42, 55, 59, 61, 64, 65, 67, 68, 69, 70, 75, 81, 82, 84, 88, 90, 92, 93, 94, 97, 106, 107, 110).

TABLE 1. Number (and percentage) of Yukon dytiscid species with various range patterns and percentage of these species that are also Holarctic. The total number of species for all range patterns exceeds the number of species in the Yukon fauna (113 species) because some species have ranges broader than a single pattern and have been included in two or more patterns.

Range pattern	Number of species (Percent of Yukon fauna)	Percent also Holarctic
Holarctic	43 (38%)	100
Transcontinental	75 (66%)	41
Beringian and glaciated western Nearctic	15 (13%)	67
Arctic	20 (18%)	85
Boreal	83 (73%)	41
Cordilleran	12 (11%)	8
Grassland	7 (6%)	0
Deciduous	2 (2%)	0
Southern	5 (4%)	0

TABLE 2. Range pattern and occurrence in major habitat types for Yukon dytiscid beetle species.

Range pattern (Number of species)	Habitat type Number (percentage) of species								
	Lentic	Lotic	Peat- land	Marsh	Pond	Lake	Stream	Spring	Saline
Holarctic 43	41 (95)	4 (9)	18 (42)	34 (79)	14 (33)	7 (16)	4 (9)	2 (5)	0 (0)
Transcontinental 75	72 (96)	9 (12)	36 (48)	48 (64)	30 (40)	10 (13)	8 (11)	9 (12)	0 (0)
Beringian and glaciated western Nearctic 15	12 (80)	3 (20)	4 (27)	10 (67)	2 (13)	3 (20)	3 (20)	0 (0)	0 (0)
Arctic 20	18 (90)	3 (15)	6 (30)	13 (65)	6 (30)	3 (15)	3 (15)	2 (10)	0 (0)
Boreal 83	82 (99)	9 (11)	43 (52)	53 (64)	31 (37)	12 (14)	8 (10)	8 (10)	0 (0)
Cordilleran 12	8 (67)	10 (83)	0 (0)	4 (33)	3 (25)	8 (67)	10 (83)	7 (58)	1 (8)
Grassland 7	7 (100)	1 (14)	0 (0)	4 (57)	3 (43)	1 (14)	1 (14)	1 (14)	1 (14)
Deciduous 2	2 (100)	0 (0)	0 (0)	2 (100)	1 (50)	0 (0)	0 (0)	0 (0)	0 (0)
Southern 5	5 (100)	3 (60)	0 (0)	3 (60)	3 (60)	1 (20)	3 (60)	3 (60)	0 (0)

The second major component of the fauna is a group of 20 arctic species (4, 25, 27, 30, 34, 48, 50, 55, 61, 62, 63, 67, 74, 81, 82, 83, 85, 86, 93, 96), of which at least 85% are Holarctic. These are mainly species of marshes, with a smaller proportion of them than among the boreal group of species occupying peatlands and ponds. Three species (48, 50, 82) (15%) occur in streams.

Eleven species (24, 29, 41, 43, 44, 46, 47, 57, 80, 82, 95) have a Cordilleran range overall or at least in part. Most of these species (9 spp., 82%) are lotic and together make up 45% of the lotic fauna of the Yukon. Many of these lotic species also occur in cold lakes. The lentic Cordilleran species occur principally in marshes and ponds with none considered a peatland inhabitant.

The 7 species (6, 9, 16, 53, 60, 77, 102) with grassland ranges are diverse in overall ranges. Some are widely distributed, occurring across the continent east of the Rocky Mountains (16, 77) or are transcontinental in open sites (53). Most species (6, 9, 60, 102) are primarily western, occurring on the Great Plains and in western mountain valleys, generally in regions of grassland or open xeric forest.

The deciduous forest range is similar to an eastern boreal range except that the species occur in the southern portions of the boreal zone and also have an extensive range in the deciduous forest biome of the eastern United States. Two lentic species (77, 108) have been assigned to this pattern. Southern species (2, 5, 10, 52, 79) are those that are essentially transcontinental in the southern boreal zone as well as in more southern zones and thus cross several geographical regions. Three of these species occur in lotic habitats. Species assigned to both of these groups make a small contribution to the fauna of the southern Yukon.

No species with a Pacific Coast distribution is known from the Yukon. The northern range limits of most Pacific species occur along the British Columbia coast well south of the Yukon Territory border. However, 3 of the expected additional species, *Hydroporus longiusculus*, *Agabus hypomelas* and *A. vancouverensis* (120, 125, 127), occur in both Alaska and British Columbia and thus may occur in the southwestern Yukon.

Fifteen species are considered Beringian and glaciated western Nearctic (34, 46, 48, 50, 61, 62, 63, 65, 67, 73, 83, 85, 86, 87, 93). These species have ranges that vary from being restricted to Alaska, Yukon and the extreme western Northwest Territories (34, 46, 62, 65, 73) to being much broader and extending throughout the low arctic and boreal regions west of Hudson Bay (48, 50, 61, 63, 67, 83, 85, 86, 87, 93). Ten (67%) of these species also occur in the Palaearctic: species 34, 61, 65 and 85 are restricted to the eastern Palaearctic whereas 48, 50, 62, 67, 86 and 93 occur across the northern Palaearctic into Europe. These species occur in both arctic and boreal zones where they are primarily inhabitants of marshes but 4 species (27%) occur primarily in peatlands. The 3 lotic species (20%) are also the 3 lotic species with arctic ranges.

Distribution Patterns Within the Yukon. Collecting is inadequate to allow detailed mapping of the Yukon distribution of dytiscids. However, a few broad patterns are apparent. The arctic fauna occupies the northern part of the Territory, extending south to about the latitude of Dawson and Mayo although there is a broad overlap of boreal and low arctic faunas in the Peel and Porcupine River drainages. Nine species (22, 25, 27, 55, 61, 67, 81, 82, 93) occur in both arctic and boreal zones and occur throughout the Yukon. For example, *Hydroporus morio* (25) is more or less ubiquitous. The primarily arctic *Hydroporus lapponum* (22) reaches its southern limit near the Yukon/British Columbia border whereas the mainly boreal species *H. notabilis* (27) reaches its northern limit at the Beaufort Sea. Water-beetle distributions generally correlate well with major distribution patterns of terrestrial vegetation (Larson 1975, 1985). However, it is not unreasonable that discrepancies occur, for usually there is no apparent causality between terrestrial vegetation type and nature of aquatic habitat; rather, both are products of common climatic conditions. Local features may make it possible for atypical habitat to exist beyond its normal range. Thus, an extensive interdigitation of boreal and arctic faunas occurs across much of the Yukon.

TABLE 3. Major associations or communities of dytiscid beetles identified by Larson (1985) in Alberta with the number of Alberta species comprising each community and the number and percentage of these species also occurring in the Yukon.

Community	No. of Alberta species	No. of species in the Yukon	Percent of Alberta species in the Yukon
Alpine lakes	10	6	60
Subalpine streams	12	7	58
Foothill streams	11	6	54
Warm foothill streams	35	24	68
Warm streams and lakes	19	13	68
Alpine and subalpine pools	53	42	79
Foothill marshes	39	28	72
Peatlands	57	55	96
Boreal marshes	79	68	86
Permanent ponds	79	60	76
Temporary ponds	44	32	73
Saline ponds	13	7	54

Interestingly, arctic species do not extend south along the alpine zone of mountain chains, for in the southern Mackenzie Mountains (sampled intensively along Nahanni Range Road and Canol Road) the fauna is boreal and Cordilleran. None of the species considered to have primarily arctic distributions was collected from alpine sites in these regions. The arctic species that occurred in these areas were those with arctic-boreal distributions. On the other hand, northernmost records were found for several Cordilleran species (24, 41, 44, 57, 80). Apparently, the Cordilleran species are more successful in penetrating north along the mountain ranges into this arctic-alpine ecotone than are arctic species in penetrating south. Possibly this is due to habitat differences, for uplands are characterized by flowing waters making more suitable habitat available for the lotic Cordilleran species than for the predominantly lentic arctic fauna.

Some boreal species are probably confined to, or are at least most abundant in, the broad valleys of the south and southeastern Yukon. For example, the infrequently collected species *Agabus leptapsis* (Larson 1989, fig. 6) and *Neoscutopterus angustus* (72, 99) are known only from the lower Liard Valley. *Hydroporus obscurus* and *H. rectus* (28, 32) have similar general ranges but extend farther north and west.

An unusual dytiscid fauna occurs in certain lentic habitats in the more xeric southern and central valleys. Shallow, sandy lakes (e.g. southeast of Ross River) contain several species that, while not obligate halophiles, are often associated with saline waters, namely *Hygrotus unguicularis*, *Stictotarsus spenceri* and *Agabus coxalis* (13, 43, 65), as well as several other *Hygrotus* and *Agabus* species often found in slightly saline waters.

Thus, the Yukon has received species from a variety of source areas, and these species are of varied ecology. Do these factors together produce a fauna of unusual richness for this latitude? Comparing the fauna of the Yukon Territory with neighbouring areas of similar latitude, species richness is about equivalent, with 92 species known from Alaska and 111 from the Northwest Territories. The smaller number of species recorded from Alaska is no doubt due to a lesser collecting effort there than in the Territories. The Yukon has only two-thirds of the number of species of British Columbia (167) or Alberta (153). Larson (1985) identified 12 major associations or communities of Dytiscidae in Alberta. Some of the species included in each of these communities occur in the Yukon but the relative proportion of Alberta species also present in the Yukon varies among communities (Table 3).

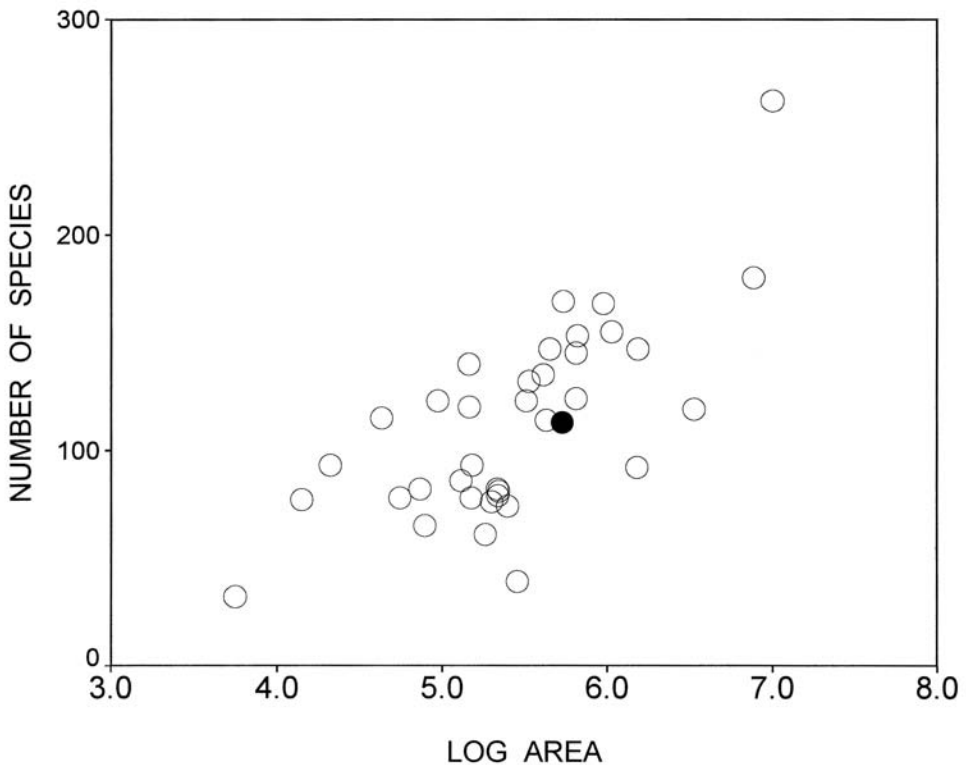


FIG. 9. Relationship between area ($\log_{10} \text{ km}^2$) and number of dytiscid species present. Closed circle represents Yukon Territory. Number of species = $-142 + 46.8 (\log_{10} \text{ km}^2)$; $r = 0.71$. Data are presented in Appendix 1.

The Alberta community that is most intact in the Yukon is the peatland community of which 96% of the Alberta species also occur in the Yukon. The boreal-marsh community is also well represented in the Yukon (86%) as is the permanent-pond community (76%). These communities together contain most of the lentic boreal species; thus this boreal fauna extends into at least the southern Yukon with little diminution. The alpine- and subalpine-pool fauna is similar between the 2 areas (79%). The greatest species reductions occur in the saline-pond, stream, and warm-lake communities (54 to 68%). The attenuation in the saline-pond fauna correlates with the scarcity of this habitat in the Yukon. However, reduction in the lotic fauna can not be explained in terms of a shortage of flowing-water habitat in the Yukon. Roughley and Larson (1991) noted a decrease from south to north in spring-inhabiting species and this seems to be a general pattern for the lotic fauna as the Yukon fauna is relatively poorer in lotic species than more southerly faunas.

For a region of its size and geographical setting, is the Yukon fauna of unusual diversity? This question was examined by surveying the literature for lists of dytiscid species from areas of various sizes. For each area, the following data were recorded: total number of dytiscid species; area in square kilometres; mean latitude (a single measurement of latitude based on the midpoint between north and south extremes); and elevational range (difference between lowest and highest point within the geographical area). Data were obtained for all Canadian provinces and territories and Canada as a whole (Bousquet 1991), ten states of the

United States (various state faunal surveys), England, Scotland and Ireland (Balfour-Browne 1940, 1950), France (Guignot 1933) and Australia (Watts 1978)—see Appendix 1.

In general, there was no significant correlation between species diversity and latitude or elevational range. However, diversity was significantly correlated with area (Fig. 9). Within this analysis, the Yukon was close to the calculated regression line, indicating that its fauna was of about average species richness for a land mass of its area. This differs from the pattern shown by most higher taxa where species richness is markedly reduced in higher latitudes. In all other major families of beetles, including the other large aquatic family, Hydrophilidae, the Yukon fauna is much less species rich than the faunas of British Columbia or Alberta (Bousquet 1991). The reason for the rich northern dytiscid fauna is apparently that many dytiscid species are adapted to shallow or marginal, vegetation rich, seasonal habitat. This habitat is abundant and diverse in the boreal zone of the Holarctic region. The northward extension of the boreal zone into comparatively high latitudes in the Yukon contains almost all the Holarctic boreal fauna and a large majority of the Nearctic boreal fauna. In addition, the presence of all of the Nearctic arctic dytiscid fauna and significant augmentation of the fauna by members of several more southerly-centred communities combine to produce a diverse fauna at a high latitude.

Acknowledgements

In the summer of 1987, I was accompanied on a collecting trip to the Yukon Territory by Bert and John Carr and my family, Margaret, Kate and Michael. I thank these excellent field companions for their enthusiasm, which made this a highly successful expedition. I am grateful to J.A. Downes and H.V. Danks for reviewing several drafts of this manuscript. This work was supported by a Natural Sciences and Engineering Research Council of Canada individual operating grant.

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Appendix 1. Geographical areas, and the number of dytiscid species, area, elevational range, and mid-latitude for each.

Region	Number of species	Area (km ²)	Elevation (m)	Latitude (°)	Reference
Alaska	92	1 518 800	6194	66	Bousquet 1991
Yukon Territory	113	536 324	5950	65	
Northwest Territories	119	3 379 683	2762	65	Bousquet 1991
British Columbia	168	948 596	3054	55	"
Alberta	153	661 185	3247	55	"
Saskatchewan	124	651 900	900	55	"
Manitoba	145	650 087	767	55	"
Ontario	155	1 068 582	700	54	"
Quebec	147	1 540 680	1268	54	"
New Brunswick	82	73 437	672	47	"
Nova Scotia	78	55 491	700	45	"
Prince Edward Island	32	5657	140	46	"
Labrador	74	250 000	1621	57	"
Newfoundland	78	150 000	806	49	"
Canada	262	9 976 139	5950	56	"
California	125	411 013	5000	39	Leech and Chandler 1956
Florida	84	151 670	100	28	Young 1954
Minnesota	79	217 735	500	46	Wallis 1973
Nevada	39	286 297	3500	37	LaRivers 1951
North Dakota	60	183 022	870	47	Gordon and Post 1965
Oregon and Washington	114	427 796	4300	46	Hatch 1953
Utah	81	219 931	2800	39	Anderson 1962
Wisconsin	140	145 438	400	44	Hilsenhoff 1975
England	86	130 359	913	52	Balfour-Browne 1940, 1950
Scotland	65	78 772	1309	57	"
France	169	543 998	4102	46	Guignot 1933
Australia	180	7 686 849	2000	19	Watts 1978