Frontispiece. Larva and case of Sphagnophylax meiops Wiggins and Winchester (Limnephilidae). This monotypic genus is a phylogenetic and geographic relict, known only from transient tundra pools in East Beringia. Length of mature larva 14 mm and of case 17 mm.
Caddisflies (Trichoptera) of the Yukon, with Analysis of the Beringian and Holarctic Species of North America

GLENN B. WIGGINS and CHARLES R. PARKER
Centre for Biodiversity and Conservation Biology (formerly Department of Entomology)
Royal Ontario Museum, 100 Queen’s Park, Toronto, Ontario, Canada M5S 2C6;
and Department of Zoology, University of Toronto
Current address of C.R. Parker:
U.S. Geological Survey Biological Resources Division, Great Smokies Field Station 1314 Cherokee Orchard Road, Gatlinburg, Tennessee 37738, U.S.A.

Abstract. The Trichoptera recorded from the Yukon Territory now number 145 species, constituting 11 per cent of the North American fauna north of Mexico. Present distribution known for each species in the Yukon is outlined, and biological information at familial and generic levels is briefly summarized. For biogeographic analysis, evidence bearing on the distribution of the species is considered under 4 categories. Members of category I are wholly Nearctic in distribution (98 species, 68 per cent of Yukon Trichoptera) and, in the absence of evidence to the contrary, are considered to have repopulated the Yukon and other northern areas from glacial refugia to the south of the Laurentide and Cordilleran ice sheets of Wisconsinan time.

Species of category II are Holarctic, and are now more or less widely distributed in Eurasia and northern North America (28 species, about 18 per cent of Yukon Trichoptera). These species could have passed the last glacial period in unglaciated Beringia, or to the south of the ice, or in both areas.

Category III is composed of Palearctic species which, from evidence available, are now confined in North America mainly to unglaciated Beringia or somewhat beyond (13 species, about 10 per cent of Yukon Trichoptera). Several represent a paradox of Beringian distribution—widely distributed Palearctic species, evidently successful colonizers when they entered North America but, with retreat of the ice, have not extended their Nearctic range. Geological and biological factors underlying this paradox are discussed. Two Palearctic species are recorded from North America for the first time: Rhyacophila mongolica Schmid, Arefina and Levanidova and Limnephilus diphyes McLachlan.

Category IV comprises 8 species (including 2 additional species expected from the Yukon), about 4 per cent of the fauna, known mainly from the Yukon or from adjacent areas of Alaska or the Northwest Territories; these species are considered to be Beringian endemics or glacial relicts. Finally, because almost all of the Holarctic Trichoptera now recognized in North America are reviewed in the foregoing groups, the remaining Holarctic species that do not occur in Beringia are considered briefly in a fifth category, although they have not been recorded from the Yukon and most do not appear to be species of far northern latitudes. The origin of the Trichoptera of Greenland is also discussed.

Ecological factors influencing the northern penetration of Yukon and Beringian Trichoptera are considered with an analysis of lotic and lentic-dwelling species through a latitudinal gradient of 49° to 70°N—from the southern border of British Columbia to the Arctic coastline of the Yukon. At latitude 60°N, the southern boundary of the Yukon, diversity has declined by almost 50 per cent from levels obtaining in British Columbia, 49° through 60°N. The main depletion occurs in the Spicipalpia and filter-feeding Annulipalpia; case-making caddisflies of the Integripalpia show less reduction. Similar trends are continued through the Yukon from 60° to 70°N, where species diversity in the Trichoptera declines by another 59 per cent. Although most North American Trichoptera occur in running waters, there is a marked reduction of species in these habitats with increasing latitude. Of 60 species recorded in the Yukon north of the Arctic Circle (67°–70°N), 81 per cent are Integripalpia with case-making larvae living mainly in lentic habitats. Factors underlying the decline of lotic species, and the proportional increase of lentic species at higher latitudes are considered. Trichoptera of lentic habitats were much more successful in crossing the Bering land bridge than were species dependent on lotic waters.

Taxonomic changes resulting from this study include suppression of Grammotaulius subborealis Schmid as a junior subjective synonym of G. alascensis Schmid. The status of Limnephilus famousus Banks is clarified as a species distinct from Limnephilus santanus Ross, and a lectotype is designated for L. famousus; L. isobela Nimmo is recognized as a junior subjective synonym of L. famousus Banks. Goera radissonica Harper and Méthot, described from northern Quebec, is recognized as a junior subjective synonym of Goera tungsenss Martynov, originally described from Siberia. A morphological variant of Ceraclea nigronervosa (Retzius) is described. The distributional

and taxonomic status of Mystacides interjectus (Banks) and M. sepulchralis (Walker) is reviewed and clarified. This study provides a taxonomic and conceptual framework for further investigation of the Holarctic Trichoptera.


Les espèces de la catégorie II sont holarctiques et sont maintenant généralement bien répandues en Eurasie et dans le nord de l’Amérique du Nord (28 espèces, environ 18% des trichoptères du Yukon). Ces espèces ont probablement passé la dernière période glaciaire dans la partie non englacée de la Béringie, ou alors au sud des glaces, ou ont occupé les deux endroits.


La catégorie IV comprend 8 espèces (dont 2 qui n’ont pas encore été trouvées au Yukon), soit environ 4% de la faune, connues surtout au Yukon ou dans les zones adjacentes en Alaska et dans les Territoires du Nord-Ouest; ces espèces sont considérées comme endémiques en Béringie ou comme des espèces relictues des glaciations. Enfin, comme la plupart des trichoptères holarctiques reconnus en Amérique du Nord appartiennent aux catégories précédentes, les autres espèces holarctiques qui n’ont jamais été trouvées en Béringie sont examinées brièvement et forment une cinquième catégorie d’espèces jamais rencontrées au Yukon et dont la plupart ne semblent pas être des espèces très nordiques. L’origine des trichoptères du Groenland est également examinée.

Les facteurs écologiques qui ont pu influencer la dispersion vers le nord des trichoptères du Yukon et de la Béringie sont étudiés et une analyse des espèces lotiques et lenticides présentes le long d’un gradient latitudinal du 49° au 70° parallèle, du sud de la Colombie-Britannique à la côte arctique du Yukon, donne un aperçu global de la situation. À la latitude 60°N, le long de la frontière australe du Yukon, la diversité est déjà réduite de près de 50% par rapport à la situation qui prévaut en Colombie-Britannique, soit entre les latitudes 49°N et 60°N, diminution qui affecte surtout les Spicipalpia et les Annulipalpia filtreurs; les Integripalpia constructeurs de fourreaux sont encore présents en assez grand nombre. La tendance se poursuit vers le nord, entre les parallèles 60 et 70, et la diversité est réduite d’un autre 59%. Bien que la plupart des trichoptères nord-américains soient des espèces d’eau courante, le nombre de ces espèces diminue à mesure que la latitude augmente. Des 60 espèces rencontrées au Yukon au nord du cercle arctique (67°–70°N), 81% sont des Integripalpia dont les larves vivent dans des fourreaux en milieu lenticide. Les facteurs susceptibles d’expliquer le déclin des espèces lotiques et l’augmentation proportionnelle des espèces lenticides aux latitudes plus élevées sont examinés. Les trichoptères des milieux lenticides semblent avoir réussi à traverser le pont continental de Bering plus facilement que les espèces des milieux lotiques.

Cette étude a donné lieu à certains remaniements taxonomiques: Grammotaulius subborealis Schmid est considéré comme un synonyme subjectif récent de G. alasensis Schmid. Le statut de Limnephilus fumosus Banks est réaffirmé et l’espèce est distincte de Limnephilus santanus Ross; un lectotype a été désigné pour représenter L. fumosus; L. isobela Nimmo est reconnu comme un synonyme subjectif récent de L. fumosus Banks. Goera radissonica Harper et Métrot, décrit du nord du Québec, est reconnu comme un synonyme subjectif récent de Goera tungusensis Martynov d’abord trouvé en Sibérie. Une variante morphologique de Ceraclea nigronervosa (Retzius) est décrite. La répartition et le statut taxonomique de Mystacides interjectus (Banks) et de M. sepulchralis (Walker) sont révisés et clarifiés. Ce travail a permis d’établir un nouveau cadre de recherche taxonomique et conceptuel pour l’étude des trichoptères holarctiques.

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Introduction

In this study we have undertaken to examine the Trichoptera of the Yukon Territory of northern Canada from a dynamic viewpoint. Several lines of biological investigation coincide to make the Yukon especially appropriate for such an analysis.

Repopulation of the Yukon following the last recession of Pleistocene glaciers is of unusual biogeographic interest because the western half of this area was part of the unglaciated Beringian refugium that extended westward through central Alaska, over the exposed continental shelf underlying Bering Strait and adjacent coastal areas, and incorporating a large part of northeastern Asia. While northern North America and extensive areas of Europe and Asia were covered by ice during the last glacial (Wisconsinan) advance, the unglaciated Beringian refugium harboured cold-adapted species, enabling some of them to move from one continent to the other across the Bering land bridge connecting North America and Asia. Evidence indicates that a number of the species in the present trichopteran fauna of the Yukon entered North America in this way and passed the Pleistocene glacial periods in the Beringian refugium, while most Nearctic species were confined to the south of the advancing front of the Laurentide continental and Cordilleran montane glaciers.

From an ecological viewpoint, an investigation of Yukon Trichoptera offers an opportunity to contrast the ecological success of a diverse group of aquatic insects at high latitudes with the success of the same group in more temperate parts of North America. The species advancing from southern refugia as the glacial ice receded had to contend with different habitat conditions at higher latitudes. For terrestrial insects, evidence on the ecological costs
imposed by these conditions is available from a number of groups; but for aquatic insects other than Chironomidae (e.g. Oliver 1968) there is little evidence or synthesis. To what extent did longer colder winters, shorter summers, and shorter photoperiods influence the success of a group of insects with wholly aquatic larvae? Trichoptera are especially appropriate for seeking answers to questions of this kind because of their relatively high diversification; apart from Chironomidae, there are more species of Trichoptera than of any other group of freshwater insects, and those species occupy an exceptionally wide range of aquatic habitats and ecological niches (Wiggins and Mackay 1978).

Combining both biogeographic and ecological viewpoints, investigation of the Yukon Trichoptera reveals results in nature when related species of Nearctic and Palaearctic origins come together to form aquatic communities. As an ecological testing ground for these natural experiments, the Yukon is well suited because of its high diversity of aquatic habitats. Mountain ranges divide the land into several major drainage systems, giving rise to small rapid streams, which in turn unite to form river systems of increasing order and potential biological diversity. Marshes, ponds, and lakes abound, providing rich resources for aquatic insects adapted for life in lentic waters. The treeline, southern margin of the arctic biome, passes through the northern Yukon at about latitude 67°N. To the north, arctic tundra extends to the Arctic Ocean; on the slopes of the mountains, biotic zones range through coniferous forests to alpine tundra and ice-fields. Although freshwater habitats are highly diverse within the Yukon, the success of insects in forming aquatic communities under climatic conditions of high latitudes is not well understood. Therefore, examination of these fundamental biological issues can add to our understanding of the biology of Trichoptera; the same issues underlie management of aquatic systems in the Yukon Territory.

The analysis begins, necessarily, with a survey of the species of Trichoptera known to occur in the Yukon. Systematic interpretation of the species has been aided by the advanced state of knowledge on the Trichoptera of Russia (e.g. Lepneva 1964, 1966; Martynov 1924a), and by the recent synthesis of aquatic insects of the Russian Far East by I.M. Levanidova (1982).

**Materials and Methods**

Most of the collections of Trichoptera studied were made by field parties from the Department of Entomology, Royal Ontario Museum (ROME), over a 4-year period from 1979 to 1982, and are deposited there. Collections from other institutions were also studied: Canadian National Collection of Insects, Ottawa (CNCI); Illinois Natural History Survey, Champaign, Illinois (INHS); Royal British Columbia Museum (BCPM); U.S. National Museum of Natural History (USNM); University of British Columbia Insect Collection, Vancouver (SMDV); Zoological Institute, Russian Academy of Sciences, St. Petersburg (ZMAS).

All species known from the Yukon Territory are listed, including species recorded in the scientific literature but not represented in the material we examined—principally records compiled by Nimmo and Wickstrom 1984 (henceforth NW 1984). Although we have many larval collections, these records are included only if larvae are the single source of evidence, as for *Allomyia*, or can be identified reliably to species as in some *Hydropsyche*. Distributional records are grouped by ecogeographic regions of the Yukon (Fig. 1); the detailed list of our records is too long for inclusion here, but is deposited in the library of the Royal Ontario Museum. At this early stage in understanding the distribution of Trichoptera in the Yukon, the records are highly correlated with the access roads; however, some general patterns seem to emerge. Biological and distributional characteristics of the higher taxa are
Fig. 1. Ecogeographic regions of the Yukon Territory (after Scudder 1997); collection records of Yukon Trichoptera are summarized in accordance with these numbered regions. 1. Arctic Coastal Plain; 2. British Mountains; 3. Arctic Plateau; 4. Porcupine Plain (including Old Crow Plain, Old Crow Mts., N. Porcupine Plateau); 5. Richardson Mountains; 6. Eagle Plain (including S. Porcupine Plateau); 7. Peel Plateau (including Bonnet Plume Basin); 8. Ogilvie Mountains (including N. and S. Ogilvie Mts.); 9. Wernecke/Selwyn Mountains; 10. Yukon/Tintina (including Lewes Plateau, part of Klondike Plateau, and Tintina Trench); 11. Eastern Plateaus (including Stewart, Macmillan, and Pelly Plateaus); 12. Shakwak Trench (including Wellesley Basin); 13. Western Ranges (including Ruby, Nisling, and Dawson Ranges, part of Klondike Plateau); 14. Pelly Mountains; 15. Logan Mountains; 16. Saint Elias/Coast Mountains; 17. Southern Lakes (including Aishihik Basin, Takhini Valley, Teslin Plateau, and Nisutlin Plateau); 18. Cassiar Mountains; 19. Liard Plain (including Dease Plateau); 20. Hyland/Liard Plateaus.
outlined briefly to provide a broader context for the Yukon species; distributional information for North America is based on the manuscript for an Annotated Catalogue of the Trichoptera of North America North of Mexico (Wiggins and Flint in prep.), and for Europe on Botoșâneanu and Malicky (1978). Extended comment required on the status of certain species is included under Taxonomic Notes. Families, genera, and species are listed alphabetically under the 3 suborders of Trichoptera proposed by Wiggins and Wichard (1989) and Frania and Wiggins (1997). The classification of families and genera follows Wiggins (1996). Roman numerals following the names indicate the category to which the species is assigned for biogeographic analysis. Arabic numbers associated with the species names provide a cross-reference to distributional and other data in the annotated species list. Dates for collections of adults are based on material examined and on published records.

**Annotated Species List of the Yukon Trichoptera**

This list records 145 species, mainly from specimens we examined, but also from literature records where no material was available. Additional species undoubtedly have yet to be found. Distributional records for the Yukon are grouped by ecogeographic regions as identified in Fig. 1.

**Suborder Spicipalpia**

These are the cocoon-making caddisflies, characterized by pupal cocoons of stout silk lacking openings of any kind for circulation of water over the pupa. They are for the most part inhabitants of cool running waters, although larvae of some genera of the Hydroptilidae are adapted to warmer lentic sites.

**Family Glossosomatidae**

Larvae occur on rocks in flowing waters where they graze on diatoms, other algae, and deposits of fine organic particles. The family is represented in most faunal regions of the world; 6 Nearctic genera are recognized, comprising approximately 75 species.

**Genus Glossosoma.** Species occur through the Nearctic, Palaearctic, and Oriental faunal regions; of 22 North American species now known, all but 3 are confined to the western mountains. Three species are recorded from the Yukon, representing 2 of the 3 Nearctic subgenera: G. (Ripaeoglossa) alascense; G. (Synafophora = Eomystra) intermedium and verdona.

1. **Glossosoma alascense** Banks (I) Nearctic, western montane
   Distribution: Yukon, Alaska, south to Utah.
   *Yukon records*: 8, 10, 12 (ROME); 16, 19 (NW 1984).
   Biological information: Adults have been collected in the Yukon 23 June – 9 August.

2. **Glossosoma intermedium** (Klapalek) (II) Holarctic, transcontinental
   Distribution: Yukon to Montana, Quebec, Tennessee; central Europe to Finland and the northern part of European Russia, eastward through Siberia to Chukotka and Kamchatka (Levanidova 1975, 1982).
   *Yukon records*: 5, 10, 12, 19 (ROME).
   Biological information: Adults have been collected in the Yukon 23 May – 9 August.

3. **Glossosoma verdona** Ross (I) Nearctic, western montane
   Distribution: Yukon, Alaska, south to California and Utah.
   *Yukon records*: 8, 17 (SMDV); 10 (ROME).
   Biological information: Adults have been collected in the Yukon 31 May – 28 June.

**Family Hydroptilidae**

Hydroptilidae are widely distributed throughout the world with genera characteristic of all types of fresh waters from cold springs to lakes. Larvae feed principally on algae,
especially filamentous forms. At least 5 of the 16 North American genera are represented in the Yukon, each by a single species.

**Genus Agraylea.** This is an Holarctic genus with 4 North American species; larvae live in standing waters of lakes, and areas of reduced current in streams.

4. *Agraylea cognatella* McLachlan (II)
   *Palaearctic-East Beringian*
   *Distribution:* Yukon; northern Europe (Botoşăneanu and Malicky 1978); Russian Far East (Levanidova 1975; Botoşăneanu and Levanidova 1988).
   *Yukon records:* 4, 5, 11 (ROME).
   *Biological information:* Adults have been collected in the Yukon 5–23 July.
   *Taxonomic notes:* North American specimens recorded as *A. multipunctata* Curtis (e.g. NW 1984, YT: 16, 17) will have to be re-examined because that species appears to be restricted to Europe and Asia (Vineyard and Wiggins in prep.).

**Genus Hydroptila.** Representatives of this genus occur through much of the world, including approximately 90 species in North America alone; larvae occur in lakes and in flowing waters.

5. *Hydroptila rono* Ross (I)
   *Nearctic, transcontinental*
   *Distribution:* Yukon to California, Quebec, and Pennsylvania.
   *Yukon records:* 17 (ROME).
   *Biological information:* Adults have been collected in the Yukon 11–26 July.

**Genus Ochrotrichia.** This genus is confined to the New World, where approximately 50 species are known in North America. Larvae occur in running-water habitats. An unidentified species was recorded from the Yukon.

6. *Ochrotrichia sp.*
   *Distribution:* Unknown.
   *Yukon records:* 16 (NW 1984).
   *Biological information:* Adults have been collected in the Yukon 26 July.

**Genus Oxyethira.** Occurring widely throughout the world, this genus includes approximately 40 North American species; larvae live in beds of aquatic plants in lakes and slow rivers.

7. *Oxyethira araya* Ross (I)
   *Nearctic, transcontinental*
   *Distribution:* Yukon, Minnesota to Maine; continued absence of records between Yukon and Minnesota raises the possibility that these populations are disjunct, perhaps reflecting their separation during glaciation.
   *Yukon records:* 4, 10, 12 (ROME).
   *Biological information:* Adults have been collected in the Yukon 20 June–12 July.

**Genus Stactobiella.** This is a small Holarctic genus with 6 North American species; larvae live in small, rapid streams.

8. *Stactobiella delira* (Ross) (I)
   *Nearctic, transcontinental*
   *Distribution:* Yukon to California, Maine, and Tennessee, most of North America, but not recorded from central or eastern Canada.
   *Yukon records:* 10 (ROME).
   *Biological information:* Adults have been collected in the Yukon 22–25 July.

**Family Rhyacophilidae**

Larvae are confined to cool, running waters, and for the most part are predacious on other insects. The family occurs in all continents of the northern hemisphere except Africa. Only 2 genera are recognized, and both occur in North America.
Genus Rhyacophila. This is a genus of at least 500 species, the largest in the Trichoptera. More than 100 species occur in North America, chiefly in the western mountains; 14 species have been recorded in the Yukon. Evidence shows that life cycles of *Rhyacophila* species at high latitudes tend to be longer than the single year in temperate latitudes (Irons 1988).

*Distribution:* Yukon, Alaska to New Mexico.
*Yukon records:* 17 (NW 1984).
*Biological information:* Adults have been collected in the Yukon 7 August.

10. *Rhyacophila angelita* Banks (I) Nearctic, disjunct
*Distribution:* Yukon to California, New Mexico; Minnesota, Quebec, New Hampshire. Distributional records indicate that the eastern and western populations of this species may be disjunct.
*Yukon records:* Nimo (1971).
*Biological information:* None available.

11. *Rhyacophila bifila* Banks (I) Nearctic, western montane
*Distribution:* Yukon to California.
*Yukon records:* 17 (NW 1984).
*Biological information:* Adults have been collected in the Yukon 9 August.

12. *Rhyacophila brunnea* Banks (I) Nearctic, transcontinental
*Distribution:* Yukon to northeastern North America, south to New Mexico and California.
*Yukon records:* 10, 16 (ROME); 12, 17, 19 (NW 1984).
*Biological information:* Adults have been collected in the Yukon 30 June–26 August.
*Taxonomic notes:* The present concept for this species (Smith and Manuel 1984) subsumes *R. acropedes* Banks, *R. ignorata* Schmid, and *R. acuminata* Fields.

*Distribution:* Yukon, Alaska to California and New Mexico.
*Yukon records:* 12, 17, 19 (NW 1984); 16 (ROME).
*Biological information:* Adults have been collected in the Yukon 23 June–8 August.

*Distribution:* Previously known only from Mongolia and the Russian Far East, this species is recorded from North America for the first time.
*Yukon records:* 4 (ROME).
*Biological information:* Adults have been collected in the Yukon 16 July.
*Taxonomic notes:* See Taxonomic Note 1.

15. *Rhyacophila narvae* Navas (II) Holartic, western montane
*Distribution:* Subsumes the western Nearctic *R. vepulsa* Milne (Schmid 1970), extending its distribution from the Russian Far East to California.
*Yukon records:* 17 (NW 1984).
*Biological information:* Adults have been collected in the Yukon 25 June.

16. *Rhyacophila pellisa* Ross (I) Nearctic, western montane
*Distribution:* Yukon to California and Utah.
*Yukon records:* 10, 16 (ROME); 19 (SMDV); 12 (NW 1984).
*Biological information:* Adults have been collected in the Yukon 24 March–28 August.

17. *Rhyacophila tucula* Ross (I) Nearctic, western montane
*Distribution:* Yukon, Alaska to Utah and Colorado.
*Yukon records:* 10 (ROME).
*Biological information:* Adults have been collected in the Yukon 10–12 August.

*Distribution:* Yukon, Alaska to Utah and Montana.
*Yukon records:* 17, 19 (NW 1984).
*Biological information:* Adults have been collected in the Yukon 23 July–8 August.

*Distribution:* Yukon, Alaska to California and New Mexico.

*Yukon records:* 11, 17 (SMDV).

*Biological information:* Adults have been collected in the Yukon 23 July–3 August.


*Distribution:* Yukon, Alaska to Oregon and Montana.

*Yukon records:* 12, 17 (NW 1984).

*Biological information:* Adults have been collected in the Yukon 23 June–27 July.


*Distribution:* Yukon to Montana and California.

*Yukon records:* 10 (CNCI); 16 (ROME); 17 (SMDV).

*Biological information:* Adults have been collected in the Yukon 9–27 July.


*Distribution:* Yukon, Alaska to Utah

*Yukon records:* 8 (ROME); 12, 16, 17, 19 (NW 1984).

*Biological information:* Adults have been collected in the Yukon 23 July–1 August.

**Suborder Annulipalpia**

These are the retreat-making or net-spinning caddisflies whose larvae are concealed in fixed tubular retreats or nets on rocks, logs, and plants. Most of the larvae live in running waters; some construct fine-meshed nets of silk to strain suspended food materials from the current, others graze fine organic particles or prey on insects. Pupation occurs in open perforate cells, with water circulating through the cell around the pupa.

**Family Hydropsychidae**

Hydropsychids are the dominant caddisflies of running waters over much of North America, both in species diversity and in biomass, but the family is markedly reduced in the Yukon. The family is widespread throughout the world; 11 genera with approximately 150 species are represented in North America, but only 4 genera are known in the Yukon. Larvae construct nets of silken meshes which filter suspended particles and insects from the current, the size of the mesh differing in most genera.

**Genus Arctopsyche.** Species of *Arctopsyche* occur through much of the Holarctic and Oriental regions; 4 are known in North America. Larvae construct coarse-meshed filter nets and are primarily insectivorous.

23. *Arctopsyche grandis* (Banks) (I) Nearctic, disjunct

*Distribution:* Yukon to California, with a disjunct occurrence in Quebec.

*Yukon records:* 10, 11, 19 (ROME).

*Biological information:* Adults have been collected in the Yukon 23 July–3 August.

24. *Arctopsyche ladogensis* (Kolenati) (II) Holarctic, transcontinental

*Distribution:* Yukon, Alaska to Newfoundland and New Hampshire; a record from Utah (Baumann and Unzicker 1981) leaves a large gap to the Yukon in the recorded distribution of this species in western North America; northern Europe and Asia through Siberia to Mongolia and Kamchatka (Lepneva 1964), but not recorded from Chukotka (Levanidova 1982).

*Yukon records:* 4, 12, 17 (ROME); 10 (NW 1984).

*Biological information:* Adults have been collected in the Yukon 26 June–14 August.

**Genus Cheumatopsyche.** Some 40 species of this genus are known in North America, and the group is widespread through most other faunal regions.
25. *Cheumatopsyche campyla* Ross (I)  
**Nearctic, transcontinental**  
*Distribution*: Yukon to California, Newfoundland, Alabama.  
*Yukon records*: 19 (ROME).  
*Biological information*: Adults have been collected in the Yukon 15–21 July.

26. *Cheumatopsyche* sp. female (not *C. campyla*)  
*Distribution*: Unknown.  
*Yukon records*: 10 (ROME).  
*Biological information*: Adults have been collected in the Yukon 23 July.

**Genus Hydropsyche**. This is the dominant North American genus of the family with more than 70 Nearctic species, but only 5 are represented in the Yukon.

27. *Hydropsyche alhedra* Ross (I)  
**Nearctic, transcontinental**  
*Distribution*: Yukon to Massachusetts and North Carolina.  
*Yukon records*: 10 (ROME).  
*Biological information*: Adults have been collected in the Yukon 14 June.

28. *Hydropsyche alternans* (Walker) (I)  
**Nearctic, transcontinental**  
*Distribution*: Yukon, Alaska and British Columbia to Newfoundland and Massachusetts.  
*Yukon records*: 4, 10 (NW 1984); 16, 17 (ROME).  
*Biological information*: Adults have been collected in the Yukon 1–20 July.

29. *Hydropsyche ambris* Ross (I)  
**Nearctic, western montane**  
*Distribution*: Yukon to Oregon.  
*Yukon records*: 17, 19 (ROME).  
*Biological information*: Adults have been collected in the Yukon 23 May–17 June.

30. *Hydropsyche cockerelli* Banks (I)  
**Nearctic, western montane**  
*Distribution*: Yukon to California.  
*Yukon records*: 17 (SMDV).  
*Biological information*: Adults have been collected in the Yukon 2–25 July.

31. *Hydropsyche oslari* Banks (I)  
**Nearctic, western montane**  
*Distribution*: Yukon to California.  
*Yukon records*: 10 (ROME, SMDV).  
*Biological information*: Adults have been collected in the Yukon 25 July–15 August.

**Genus Parapsyche**. Species of *Parapsyche* are widely distributed through the northern hemisphere; 7 species are known in North America, mainly in the western mountains. Larvae live in small, cold streams and, like *Arctopsyche*, construct filter nets of coarse meshes.

32. *Parapsyche elsis* Milne (I)  
**Nearctic, western montane**  
*Distribution*: Yukon, Alaska to California.  
*Yukon records*: 10, 12 (NW 1984); 16, 19 (ROME).  
*Biological information*: Adults have been collected in the Yukon 25 July–8 August.

**Family Philopotamidae**  
Larvae live in amorphous tubular silken nets of very small mesh which strain out fine particulate organic matter carried by the current. *Wormaldalia* is the only one of the 3 North American genera recorded from the Yukon, although *Dolophilodes* is known from Alaska (Nimmo 1986).

**Genus Wormaldalia**. This genus is widely distributed in both the northern and southern hemispheres. We have *Wormaldalia* larvae from the Yukon (10; ROME) and from the Northwest Territories.
33. *Wormaldia gabriella* (Banks) (I)  
*Distribution*: Yukon to California; Quebec. Records from the Hudson Bay drainage of northern Quebec (Roy and Harper 1979) indicate a major disjunction from the general western range of this species.  
*Yukon records*: A record for this species from the northern Yukon (NW 1984) was attributed to Schmid (1982); Yukon was not included among 9 provinces and states listed by Schmid but a Yukon record does appear on a distribution map. This species was recorded by Winchester (1984) from the area of Inuvik, Northwest Territories (68°31.2′N 135°54.2′W), close to the Arctic coast and adjacent to the Yukon.

**Family Polycentropodidae**  
This is an important cosmopolitan family of retreat-making caddisflies with 6 genera and more than 70 species in North America; 2 genera occur in the Yukon. Most larvae are predacious and construct a variety of silken retreats and capture-nets.

**Genus *Neureclipsis***. This is a small Holarctic genus with 6 North American species. Larvae live in slow currents, concealed in voluminous sack-like silken nets that filter suspended particles.

34. *Neureclipsis bimaculata* (Linnaeus) (II)  
*Distribution*: Yukon, Alaska to Newfoundland, Illinois; Europe through Siberia to Kamchatka.  
*Yukon records*: 12 (ROME).  
*Biological information*: Adults have been collected in the Yukon 26 July.

**Genus *Polycentropus***. This is the largest genus in the family, widely distributed through the world, and with more than 40 species in North America. Larvae of different species live in lotic and lentic habitats and also in bog ponds and temporary pools, confirming a broad ecological tolerance for the genus.

35. *Polycentropus aureolus* (Banks) (I)  
*Distribution*: Yukon to Newfoundland and Ohio.  
*Yukon records*: 4, 16 (NW 1984).  
*Biological information*: Adults have been collected in the Yukon 25–27 July.

36. *Polycentropus flavus* (Banks) (I)  
*Distribution*: Yukon, Alaska to Newfoundland, Illinois and California.  
*Yukon records*: 4, 5, 10, 12, 17 (ROME, SMDV); 11, 16 (NW 1984).  
*Biological information*: Adults have been collected in the Yukon 19 June–24 July.

37. *Polycentropus remotus* Banks (I)  
*Distribution*: Yukon, Alaska to Newfoundland and Kentucky.  
*Yukon records*: 4, 10, 12 (ROME, SMDV).  
*Biological information*: Adults have been collected in the Yukon 29 June–23 July.

38. *Polycentropus smithae* Denning (I)  
*Distribution*: Yukon, British Columbia, Quebec, New Hampshire.  
*Yukon records*: 4, 10, 12 (ROME, SMDV).  
*Biological information*: Adults have been collected in the Yukon 24 June–27 July.

39. *Polycentropus weedi* Blickle and Morse (I)  
*Distribution*: Yukon to Newfoundland, New Hampshire.  
*Yukon records*: 8 (ROME, SMDV).  
*Biological information*: Adults have been collected in the Yukon 29 June–6 August.

**Suborder Integripalpia**

These are the case-making caddisflies whose larvae construct portable tubular cases of plant or mineral materials fastened together with silk. In contrast to the Annulipalpia with fixed retreats, these larvae move with their cases in search of food. Larvae in most families
are detritivores, although some are algal grazers or predators. For pupation, the larval case is sealed with perforate silk at each end, allowing water to circulate directly over the pupa.

**Family Apataniidae**

Five North American genera are assigned to this family and 2 of them occur in the Yukon.

**Genus Allomyia.** Most of the species known in this genus are confined to cold mountain streams of western North America; a few are known also in the Far East of Russia. Larvae graze diatoms and fine organic particles from rocks.

40. *Allomyia* sp.

This record is based on one larval collection from the Yukon (10 ROME) which cannot be identified to species.

**Genus Apatania.** Seventeen species of *Apatania* are known in North America, and many others occur in the Palearctic and Oriental regions. Larvae live in cool waters, usually streams but also lakes at higher latitudes, where they scrape diatoms and other algae from rocks (e.g. Irons 1988).

41. *Apatania crymophila* McLachlan (II) Holarctic, northwestern and central

_Distribution_: Yukon, Alaska, Manitoba; northern Europe and Asia.

_Yukon records_: 4, 8, 10, 12, 16 (ROME, SMDV).

_Biological information_: Adults have been collected in the Yukon 26 May – 12 August.

42. *Apatania stigmatella* (Zetterstedt) (II) Holarctic, transcontinental

_Distribution_: Yukon, Alaska to Newfoundland; northern Europe through Siberia to Chukotka, Kamchatka and the Amur basin (Levanidova 1982).

_Yukon records_: 8, 10, 11, 12, 16, 17 (ROME, SMDV, CNCI).

_Biological information_: Adults have been collected in the Yukon 15 July – 28 August.

43. *Apatania zonella* (Zetterstedt) (II) Holarctic, transcontinental

_Distribution_: Ellesmere Is. (Northwest Territories), Yukon, Alaska, Quebec, Minnesota; Greenland; through northern Europe and Asia to the Amur basin (I.M. Levanidova, pers. comm.).

_Yukon records_: 4, 12, 16 (ROME).

_Biological information_: Adults have been collected in the Yukon 15 June – 6 August.

**Family Brachycentridae**

This is a small family of the northern hemisphere with 5 genera and about 30 species in North America; larvae live mainly in flowing water.

**Genus Brachycentrus.** Larvae of *Brachycentrus* species live in larger and, on the whole, warmer rivers and streams than do those of other genera in the family. Larvae feed on suspended particles from the current and graze periphytic algae.

44. *Brachycentrus americanus* (Banks) (II) Holarctic, transcontinental

_Distribution_: Yukon, Alaska to California, Quebec, Massachusetts; Siberia, Mongolia, Japan.

_Yukon records_: 4, 10, 12 (ROME, SMDV).

_Biological information_: Adults have been collected in the Yukon 22 June – 9 August.

**Genus Micrasema.** Larvae are confined to small cold streams, where they graze algae and moss from rocks.

45. *Micrasema gelidum* McLachlan (II) Holarctic, transcontinental

_Distribution_: Yukon, Alaska to Wisconsin and Quebec; northern Europe and Asia.

_Yukon records_: 1 (SMDV); 4, 8, 10 (ROME); 12 (NW 1984).

_Biological information_: Adults have been collected in the Yukon 30 June – 29 July.

_Taxonomic notes_: *M. kluane* Ross and Morse is a junior synonym (Botoșăneanu 1988).
46. *Micrasema bactro* Ross (I)  
**Distribution:** Yukon to Utah.  
**Yukon records:** 10, 12 (ROME).  
**Biological information:** Adults have been collected in the Yukon 23 June – 23 July.

**Family Goeridae**

This is a small family widely distributed in the northern hemisphere, but extended to tropical latitudes in Asia and even to southern Africa. There are 4 North American genera comprising about a dozen species. Larvae of most species live in cool running water, and some in the water-saturated muck of spring seepage.

**Genus Goera.** This is the largest genus in the family with 6 species in North America. Larvae that are known live in streams and graze diatoms and organic particles from rocks.

47. *Goera tungusensis* Martynov (II)  
**Distribution:** Northwest Territories, Quebec; Siberia.  
**Yukon records:** This species is included provisionally in the Yukon fauna on the basis of a single female collected in the Northwest Territories, very close to the Yukon border (Midway L., 67°14′N 135°26′W, 8 July 85, SMDV). This female is similar to, but not entirely identical with, the female of *G. tungusensis* from Siberia.  
**Taxonomic notes:** See Taxonomic Note 2.

**Family Lepidostomatidae**

This family is widely distributed in the northern hemisphere, with some 70 Nearctic species. Two genera are recognized in North America, *Thelliopsyche* and *Lepidostoma*, with most species assigned to the latter; 4 subgenera have been proposed for species in *Lepidostoma*, 3 of them represented in the Yukon fauna. No Holarctic species are known. Larvae of most species live in cool, running water, where they are important detritivores; some *Lepidostoma* larvae live in the littoral zone of lakes.

**Genus Lepidostoma.** This genus is widely represented in North America and Eurasia.

48. *Lepidostoma cascadense* (Milne) (I)  
**Distribution:** Yukon, Alaska to California.  
**Yukon records:** 17 (NW 1984).  
**Biological information:** Adults have been collected in the Yukon 28 June – 24 July.

49. *Lepidostoma cinereum* Banks (I)  
**Distribution:** Yukon, Alaska to California and Utah, to Newfoundland and Maine.  
**Yukon records:** 10, 14 (ROME); 11 (NW 1984).  
**Biological information:** Adults have been collected in the Yukon 5 July – 12 August.  
**Taxonomic notes:** *Lepidostoma strophe* Ross is a junior synonym.

50. *Lepidostoma pluviale* (Milne) (I)  
**Distribution:** Yukon to California.  
**Yukon records:** 10, 16, 19 (ROME).  
**Biological information:** Adults have been collected in the Yukon 27 July – 9 August.  
**Taxonomic notes:** *Lepidostoma veleda* Denning is a junior synonym.

51. *Lepidostoma roafi* (Milne) (I)  
**Distribution:** Yukon, Alaska to California.  
**Yukon records:** 17 (NW 1984).  
**Biological information:** Adults have been collected in the Yukon 28 June – 24 July.

52. *Lepidostoma stigma* Banks (I)  
**Distribution:** Yukon to Utah.  
**Yukon records:** 17 (NW 1984).  
**Biological information:** Adults have been collected in the Yukon 24 July.
53. *Lepidostoma unicolor* (Banks) (I) Nearctic, transcontinental, western montane

*Distribution:* Yukon to Quebec, California, and Arizona.

*Yukon records:* 10 (ROME, SMDV).

*Biological information:* Adults have been collected in the Yukon 4–9 August.

**Family Leptoceridae**

The Leptoceridae are a large family represented on all continents. In North America there are approximately 100 species assigned to 8 genera, 5 of which are represented in the Yukon fauna. Larvae live in lakes, marshes, and slow rivers, feeding on organic particles and aquatic plants, or on insects.

**Genus Ceraclea.** Of some 36 North American species in this genus, 4 are known in the Yukon. Larvae live in large rivers and the littoral zone of lakes where some species feed on colonies of freshwater sponges (Resh et al. 1976).

54. *Ceraclea annulicornis* (Stephens) (II) Holarctic, transcontinental

*Distribution:* Yukon, Alaska to California, Newfoundland and Kentucky; northern Europe and Asiatic Russia to the Amur region and Japan (Lepneva 1966).

*Yukon records:* 4 (SMDV).

*Biological information:* Adults have been collected in the Yukon 3 July.

55. *Ceraclea cancellata* (Betten) (I) Nearctic, transcontinental

*Distribution:* Yukon, Alaska to Newfoundland, south to Florida and Arizona.

*Yukon records:* 10, 12 (ROME).

*Biological information:* Adults have been collected in the Yukon 20 July–9 August.

56. *Ceraclea nigromervosa* (Retzius) (II) Holarctic

*Distribution:* Yukon, Alaska, British Columbia and Wyoming; northern Europe and Asia.

*Yukon records:* 4, 10, 12, 17 (ROME, SMDV).

*Biological information:* Adults have been collected in the Yukon 5 June–11 July.

**Taxonomic notes:** See Taxonomic Note 3.

57. *Ceraclea resurgens* (Walker) (I) Nearctic, transcontinental

*Distribution:* Yukon, Oregon to Maine and Louisiana.

*Yukon records:* 10, 12, 14, 15 (ROME, SMDV).

*Biological information:* Adults have been collected in the Yukon 17–28 July.

**Genus Mystacides.** This is an Holarctic and Oriental genus with 3 widely distributed North American species; larvae live in standing or slowly moving water, where they are mainly predacious.

58. *Mystacides alafimbriata* Hill-Griffin (I) Nearctic, western

*Distribution:* Yukon, Alaska to California and Mexico.

*Yukon records:* 10, 17 (ROME); 12 (NW 1984).

*Biological information:* Adults have been collected in the Yukon 2 July–5 August.

**Taxonomic notes:** See Taxonomic Note 4.

59. *Mystacides interjectus* (Banks) (I) Nearctic, transcontinental

*Distribution:* Yukon, Alaska to Quebec, Massachusetts and Ohio.

*Yukon records:* 4, 10, 12, 17, 19 (ROME, SMDV).

*Biological information:* Adults have been collected in the Yukon 24 June–5 August.

**Taxonomic notes:** See Taxonomic Note 5.

60. *Mystacides sepulchralis* (Walker) (I) Nearctic, transcontinental

*Distribution:* Yukon, Alaska to California, Newfoundland and Georgia.

*Yukon records:* 4, 5, 8, 10, 12, 14, 16, 17, 19 (ROME, SMDV).

*Biological information:* Adults have been collected in the Yukon 26 June–19 August.

**Taxonomic notes:** See Taxonomic Note 4.
Genus *Oecetis*. This is a genus of worldwide distribution, with approximately 20 Nearctic species; larvae are predacious and live in both lentic and lotic waters.

61. *Oecetis immobilis* (Hagen) (I)  
*Nearctic, transcontinental*  
*Distribution*: Yukon, Montana to Maine, Ohio.  
*Yukon records*: 4 (ROME, SMDV).  
*Biological information*: Adults have been collected in the Yukon 14–23 July.

62. *Oecetis inconspicua* (Walker) (I)  
*Nearctic, transcontinental; Neotropical*  
*Distribution*: Yukon, Alaska to California, Newfoundland, Florida, Texas; Mexico, Bahamas, Cuba, Venezuela.  
*Yukon records*: 4, 10, 12, 14, 15, 17, 19 (ROME, SMDV).  
*Biological information*: Adults have been collected in the Yukon 17 July–2 August.

63. *Oecetis ochracea* (Curtis) (II)  
*Holarctic, transcontinental*  
*Distribution*: Yukon to Alaska; central and northern Europe (Malicky 1988), through Siberia to Chukotka and Kamchatka, and Mongolia (Levanidova 1982).  
*Yukon records*: 4, 10, 12, 16 (ROME).  
*Biological information*: Adults have been collected in the Yukon 20–23 July.

Genus *Triaenodes*. This is a widely distributed genus with about 25 Nearctic species; larvae occur in lentic and lotic habitats, where they feed on plant materials.

64. *Triaenodes baris* (Ross) (I)  
*Nearctic, transcontinental*  
*Distribution*: Yukon to Wisconsin, Maine.  
*Yukon records*: 10 (ROME).  
*Biological information*: Adults have been collected in the Yukon 1 July.

65. *Triaenodes tardus* Milne (I)  
*Nearctic, transcontinental*  
*Distribution*: Yukon, Alaska to Arizona, Maine, Tennessee.  
*Yukon records*: 10 (ROME).  
*Biological information*: Adults have been collected in the Yukon 20–23 July.

Genus *Ylodes*. Some 15 species are now assigned to this Holarctic genus, most of them from northern Asia. All 4 species known in North America occur in the Yukon. Larvae live in lentic waters.

66. *Ylodes frontalis* (Banks) (I)  
*Nearctic, western and central*  
*Distribution*: Yukon, Alaska to California, Saskatchewan, South Dakota.  
*Yukon records*: 10, 12 (ROME).  
*Biological information*: Adults have been collected in the Yukon 26 June–8 August.

67. *Ylodes kaszabi* (Schmid) (III)  
*Palaearctic-East Beringian*  
*Distribution*: Yukon, Alaska, Northwest Territories; Mongolia (Schmid 1965b).  
*Yukon records*: 12 (ROME).  
*Biological information*: Adults have been collected in the Yukon 27 July.

68. *Ylodes reuteri* (McLachlan) (II)  
*Holarctic*  
*Distribution*: Yukon to Colorado and Manitoba; through much of Europe (Botoșăneanu and Malicky 1978), Caucasus (Martynov 1909), Egypt and Saudi Arabia (L. Botoșăneanu, pers. comm.), Siberia (I.M. Levanidova, pers. comm.) to Mongolia (Mey and Dulmaa 1985).  
*Yukon records*: 17 (SMDV).  
*Biological information*: Adults have been collected in the Yukon 27 July.  
*Taxonomic notes*: *Triaenodes griseus* Banks is a junior synonym (Manuel and Nimmo 1984).

69. *Ylodes schmidi* Manuel and Nimmo (IV)  
*East Beringian*  
*Distribution*: Known only from the Yukon.  
*Yukon records*: 17 (CNCI) (Manuel and Nimmo 1984).  
*Biological information*: Adults have been collected in the Yukon 24 July.
Family Limnephilidae

This is the largest family of Trichoptera in North America with some 230 species in 39 genera. Limnephilidae are the dominant and most diverse group in northern latitudes, and constitute more than half of the species of Trichoptera in the Yukon. Larvae occur in all types of aquatic habitats, and are largely detritivorous.

Genus Anabolia. This is an Holarctic genus with 5 North American species widely distributed over the northern part of the continent. Larvae are detritivores in slow streams, marshes, and temporary pools.

70. Anabolia bimaculata (Walker) (I) Nearctic, transcontinental
   Distribution: Yukon to Utah, Newfoundland, New Hampshire.
   Yukon records: 6, 10, 11, 12, 15, 16, 17 (ROME, SMDV).
   Biological information: Adults have been collected in the Yukon 12 July – 29 August.

Genus Arctopora. This is a small, Holarctic genus of 3 species (Fig. 19). Larvae of at least A. pulchella live in temporary pools, and probably marshy sites generally.

71. Arctopora pulchella (Banks) (I) Nearctic, transcontinental
   Distribution: Yukon, Alaska to Newfoundland and New Hampshire.
   Yukon records: 4, 8, 11, 12, 14, 16, 17 (ROME, SMDV); 10 (NW 1984).
   Biological information: Adults have been collected in the Yukon 23 June – 12 August.

72. Arctopora trimaculata (Zetterstedt) (III) Palaearctic-East Beringian
   Distribution: Yukon, Alaska; northern Europe (Botoșăneanu and Malicky 1978) and Asia from Scandinavia through Siberia to the Amur region and Sakhalin (Schmid 1952).
   Yukon records: 4, 5 (ROME, SMDV).
   Biological information: Adults have been collected in the Yukon 8 – 23 July.

Genus Asynarchus. Species of Asynarchus occur over the northern half of North America, and several of them also occur in Eurasia. Larvae live in streams, ponds, and temporary pools, and are probably detritivores.

73. Asynarchus aldinus (Ross) (I) Nearctic, western
   Distribution: Yukon to Utah.
   Yukon records: 10, 16, 17 (NW 1984).
   Biological information: Adults have been collected in the Yukon 23 July – 21 August.

74. Asynarchus iteratus McLachlan (II) Holarctic, northwestern and central
   Distribution: Yukon, Alaska to Manitoba (Churchill: Lehmkühl and Kerst 1979); northern Asia to Kamchatka (Lepneva 1966).
   Yukon records: 4 (CNCI); 5, 10 (ROME).
   Biological information: Adults have been collected in the Yukon 25 July – 6 August.

75. Asynarchus lapponicus (Zetterstedt) (II) Holarctic, transcontinental
   Distribution: Yukon to Newfoundland and Maine; northern and central Europe (Malicky 1988, fig. 11) through Siberia to Chukotka (Levanidova 1982).
   Yukon records: 1 (SMDV); 2 (CNCI); 8 (ROME).
   Biological information: Adults have been collected in the Yukon 21 July – 1 August.

76. Asynarchus montanus Banks (I) Nearctic, transcontinental
   Distribution: Yukon, Alaska to Newfoundland and Utah.
   Yukon records: 4, 6, 8, 10, 11, 12, 14, 16, 17, 19 (ROME, SMDV).
   Biological information: Adults have been collected in the Yukon 30 June – 29 August.

77. Asynarchus mutatus (Hagen) (I) Nearctic, transcontinental
   Distribution: Yukon to Newfoundland.
   Yukon records: 16 (ROME).
   Biological information: Adults have been collected in the Yukon 29 July – 6 August.
Genus *Chyranda*. The single species of *Chyranda* is widely distributed in small, cold streams in northern and western montane regions of North America. Larvae are detritivorous (e.g. Irons 1988).

78. *Chyranda centralis* (Banks) (I) Nearctic, transcontinental

- **Distribution**: Yukon, Alaska to California and Quebec.
- **Yukon records**: 8, 11, 14, 16, 17 (ROME, SMDV); 12 (NW 1984).
- **Biological information**: Adults have been collected in the Yukon 27 July–12 August.

Genus *Clistoronia*. *Clistoronia* are confined to western North America, where 4 species are known. Larvae live in small lakes and ponds, where they are detritivorous.

79. *Clistoronia magnifica* (Banks) (I) Nearctic, western montane

- **Distribution**: Yukon, Alaska to California.
- **Yukon records**: 11, 12, 16, 17 (CNCI, ROME, SMDV).
- **Biological information**: Adults have been collected in the Yukon 17 June–17 August.

Genus *Dicosmoecus*. Four species of *Dicosmoecus* inhabit running waters in western montane North America, and 2 others occur in eastern Asia (Wiggins and Richardson 1982). The 2 Yukon species feed mainly on vascular plant materials and insects.

80. *Dicosmoecus atripes* (Hagen) (I) Nearctic, western montane

- **Distribution**: Yukon, Alaska to California, New Mexico.
- **Yukon records**: 8, 10, 12, 14, 16 (ROME); 17, 19 (CNCI).
- **Biological information**: Adults have been collected in the Yukon 23 June–18 August. Dippers, or water ouzels, representing a small family of passeriform birds (Cinclidae) frequenting streams, feed on larvae of this species in Alaska (Ellis 1978b).

81. *Dicosmoecus obscuripennis* Banks (III) Palaearctic-East Beringian

- **Distribution**: Yukon, Alaska; Russian Far East (Nagayasu and Ito 1993).
- **Yukon records**: 4, 8, 10, 12 (ROME); 17 (CNCI).
- **Biological information**: Adults have been collected in the Yukon 26 July–7 August.

Genus *Ecclisomyia*. This is a small Holarctic genus confined to montane areas of western North America and eastern Asia; larvae live in small streams or rocky lake shores, and feed on diatoms and plant detritus (Irons 1988).

82. *Ecclisomyia conspersa* Banks (I) Nearctic, western montane

- **Distribution**: Yukon, Alaska to California.
- **Yukon records**: 8, 10, 12, 14, 16, 17 (CNCI, ROME, SMDV); 19 (NW 1984).
- **Biological information**: Adults have been collected in the Yukon 26 May–17 August.

Genus *Glyphopsyche*. This is a Nearctic genus of 2 species; larvae of *G. irrorata* live in accumulations of plant materials in slowly flowing waters and in marshes, where they are probably detritivorous.

83. *Glyphopsyche irrorata* (Fabricius) (I) Nearctic, transcontinental

- **Distribution**: Yukon, Alaska to California and Newfoundland.
- **Yukon records**: 12 (ROME).
- **Biological information**: Adults have been collected in the Yukon 26 May.

Genus *Grammotaulius*. This is a widespread Holarctic genus of northern and montane ponds and slow streams. Larvae are probably detritivorous.

84. *Grammotaulius alascensis* Schmid (IV) East Beringian

- **Distribution**: Yukon, Alaska, Northwest Territories.
- **Yukon records**: 2 (NW 1984); 4, 8, 10 (ROME, SMDV).
- **Biological information**: Adults have been collected in the Yukon 23–31 July.
- **Taxonomic notes**: *Grammotaulius subborealis* Schmid (1964) is a **new synonym**. See Taxonomic Note 6.
85. **Grammotaulius interrogationis** (Zetterstedt) (I) Nearctic, transcontinental
   
   **Distribution:** Yukon, Alaska to Newfoundland; Greenland.
   
   **Yukon records:** 8, 10, 11, 12, 14, 16, 17 (ROME, SMDV).
   
   **Biological information:** Adults have been collected in the Yukon 24 June–25 August.

86. **Grammotaulius signatipennis** McLachlan (III) Palaearctic-East Beringian
   
   **Distribution:** Yukon; northern Eurasia from Sweden and Poland to Kamchatka (Schmid 1950a; Levanidova 1982).
   
   **Yukon records:** 11 (CNCI).
   
   **Biological information:** Adults have been collected in the Yukon 4 September.
   
   **Taxonomic notes:** See Taxonomic Note 6.

**Genus Grensia.** A single circumpolar species is assigned to this genus; larvae live mainly in tundra lakes and ponds.

87. **Grensia praeterita** (Walker) (III) Holarctic, far northern
   
   **Distribution:** Yukon, Alaska, Northwest Territories; Greenland; far northern Eurasia.
   
   **Yukon records:** 8 (ROME).
   
   **Biological information:** Adults have been collected in the Yukon 18 June.

**Genus Hesperophylax.** Seven species are recognized in the Nearctic genus *Hesperophylax*, and they inhabit an unusually wide range of habitats from springs to rivers and lakes (Parker and Wiggins 1985). Larvae feed mainly on detritus.

88. **Hesperophylax designatus** (Walker) (I) Nearctic, transcontinental
   
   **Distribution:** Yukon to California, Newfoundland, and Illinois.
   
   **Yukon records:** 10, 11, 12, 17 (ROME, SMDV).
   
   **Biological information:** Adults have been collected in the Yukon 9 June–6 August.

**Genus Lenarchus.** This is a northern Holarctic genus in which 5 of the 9 Nearctic species have been recorded from the Yukon. Larvae live in lentic sites—small lakes, marshes, and temporary pools, especially at higher elevations and latitudes, and feed on organic debris.

89. **Lenarchus crassus** (Banks) (I) Nearctic, transcontinental, northern
   
   **Distribution:** Yukon to Newfoundland.
   
   **Yukon records:** 4, 8, 14 (ROME); 12 (CNCI).
   
   **Biological information:** Adults have been collected in the Yukon 8 July–12 August.

90. **Lenarchus expansus** Martynov (IV) Palaearctic-East Beringian
   
   **Distribution:** Yukon, Alaska; Siberia and the Russian Far East (I.M. Levanidova, pers. comm).
   
   **Yukon records:** 1, 8, 10 (CNCI); 4 (ROME).
   
   **Biological information:** Adults have been collected in the Yukon 29 June–27 July.

91. **Lenarchus fautini** (Denning) (I) Nearctic, western
   
   **Distribution:** Yukon to Utah.
   
   **Yukon records:** 8, 12 (ROME); 14, 15 (SMDV).
   
   **Biological information:** Adults have been collected in the Yukon 6–31 July.

92. **Lenarchus keratus** Ross (I) Nearctic, transcontinental
   
   **Distribution:** Yukon to Michigan, Quebec.
   
   **Yukon records:** 10 (ROME).
   
   **Biological information:** Adults have been collected in the Yukon 24 July.

93. **Lenarchus vastus** (Hagen) (I) Nearctic, western
   
   **Distribution:** Yukon to California.
   
   **Yukon records:** 8, 10, 11, 12, 14, 16, 17 (ROME).
   
   **Biological information:** Adults have been collected in the Yukon 11 June–2 September.

**Genus Limnephilus.** This is the dominant trichopteran genus of northern latitudes of the globe, and includes approximately 85 Nearctic species (Ruiter 1995); about 27 species are
known in the Yukon, constituting 20 per cent of the Trichoptera. Larvae range widely in habitat, although most live in standing waters where they are major detritivores.

94. **Limnephilus argenteus** Banks (I)  
*Nearctic, transcontinental*  
*Distribution:* Yukon, Alaska to Newfoundland.  
*Yukon records:* 4, 6, 8, 10, 17 (ROME); 11, 16 (SMDV).  
*Biological information:* Adults have been collected in the Yukon 3 June–18 July.

95. **Limnephilus canadensis** Banks (I)  
*Nearctic, transcontinental*  
*Distribution:* Yukon to Maine, Oregon.  
*Yukon records:* 10 (NW 1984).  
*Biological information:* Adults have been collected in the Yukon 6 August.

96. **Limnephilus diphyes** McLachlan (III)  
*Palaearctic-East Beringian*  
*Previously known from Scandinavia through northwestern Siberia (Botoşăneanu and Malicky 1978) to the Amur district and Kamchatka (I.M. Levanidova, pers. comm), this species is recorded from North America for the first time.*  
*Yukon records:* 5, 8, 10 (ROME); 11, 17 (SMDV).  
*Biological information:* Adults have been collected in the Yukon 10 June–26 July.  
*Taxonomic notes:* See Taxonomic Note 7.

97. **Limnephilus dispar** McLachlan (II)  
*Holarctic, transcontinental*  
*Distribution:* Yukon, Alaska to Colorado, Newfoundland; northern and central Europe (Malicky 1988, fig. 15), Siberia (Martynov 1914, 1924a), the Amur basin and Kamchatka (Levanidova 1982).  
*Yukon records:* 4, 8, 10, 16, 17 (ROME, SMDV).  
*Biological information:* Adults have been collected in the Yukon 31 May–18 July.  
*Taxonomic notes:* L. minusculus (Banks) is a junior synonym (Malicky 1979).

98. **Limnephilus externus** Hagen (II)  
*Holarctic, transcontinental*  
*Distribution:* Yukon to California, Newfoundland; northern Europe, Siberia, China (Fischer 1968).  
*Yukon records:* 4, 8, 10, 11, 12, 14 (ROME); 16, 17 (SMDV).  
*Biological information:* Adults have been collected in the Yukon 21 July–2 September.

99. **Limnephilus extractus** Walker (I)  
*Nearctic, transcontinental*  
*Distribution:* Yukon to Utah, Quebec.  
*Yukon records:* 4, 10, 16, 17 (ROME); 12 (SMDV).  
*Biological information:* Adults have been collected in the Yukon 14 June–29 July.

100. **Limnephilus femoralis** Kirby (II)  
*Holarctic, transcontinental*  
*Distribution:* Yukon to Washington and Maine; Greenland (Mosely 1929); northern Europe, Kamchatka (Ulmer 1927) but not Siberia.  
*Yukon records:* 4 (SMDV); 17 (ROME).  
*Biological information:* Adults have been collected in the Yukon 5 July–6 August.

101. **Limnephilus fenestratus** (Zetterstedt) (III)  
*Palaearctic-East Beringian*  
*Distribution:* Yukon, Alaska, Northwest Territories; northern Europe, Iceland (Gislason 1981), Mongolia (Mey and Dulmaa 1985), Bering Island (I.M. Levanidova, pers. comm.) (Fig. 21).  
*Yukon records:* 4, 8 (ROME); 12 (CNCI, SMDV).  
*Biological information:* Adults have been collected in the Yukon 21 July–2 September.

102. **Limnephilus fumosus** Banks (IV)  
*East Beringian*  
*Distribution:* Yukon, Alaska, Northwest Territories.  
*Yukon records:* 11 (SMDV); 12 (ROME).  
*Biological information:* Adults have been collected in the Yukon 12 June–22 July.  
*Taxonomic notes:* This species has been confused with L. santanus Ross; *Limnephilus isobelae* Nimmo (1991) is a new synonym. See Taxonomic Note 8.

103. **Limnephilus hageni** Banks (I)  
*Nearctic, transcontinental*  
*Distribution:* Yukon, British Columbia to Quebec.  
*Yukon records:* 4, 10, 11, 12, 14, 15, 19 (ROME); 16 (NW 1984).
104. **Limnephilus hyalinus** Hagen (I)  
**Nearctic, transcontinental**  
**Distribution:** Yukon, Alaska to Maine, Colorado.  
**Yukon records:** 10 (ROME, CNCI); 16 (NW 1984); 17 (SMDV).  
**Biological information:** Adults have been collected in the Yukon 18 July –12 August.

105. **Limnephilus infernalis** (Banks)  
**Nearctic, transcontinental**  
**Distribution:** Yukon to Colorado, Maine.  
**Yukon records:** 4, 10, 11, 17 (ROME, SMDV).  
**Biological information:** Adults have been collected in the Yukon 28 July –17 August.

106. **Limnephilus janus** Ross (I)  
**Nearctic, transcontinental**  
**Distribution:** Yukon to Colorado, Maine.  
**Yukon records:** 10 (ROME, SMDV).  
**Biological information:** Adults have been collected in the Yukon 21–27 July.

107. **Limnephilus kennicotti** Banks (I)  
**Nearctic, transcontinental**  
**Distribution:** Yukon, Oregon to Newfoundland; Greenland (Fig. 21).  
**Yukon records:** 2 (ROME); 10 (CNCI); 12 (NW 1984); 16, 19 (SMDV).  
**Biological information:** Adults have been collected in the Yukon 28 July –24 August.  
**Taxonomic notes:** See under *L. fenestratus* (category III).

108. **Limnephilus nigriceps** (Zetterstedt) (II)  
**Holartic, northern**  
**Distribution:** Yukon, Alaska to Manitoba; Europe and Siberia to Kamchatka (Lepneva 1966).  
**Yukon records:** 8 (SMDV); 10 (CNCI); 12, 16 (NW 1984).  
**Biological information:** Adults have been collected in the Yukon 27 July –21 August.

109. **Limnephilus pallens** Banks (IV)  
**Nearctic**  
**Distribution:** Yukon, Alaska, Northwest Territories, Michigan (Ruiter 1995).  
**Yukon records:** 1 (SMDV); 2 (CNCI); 16 (NW 1984).  
**Biological information:** Adults have been collected in the Yukon 14 July –18 August.

110. **Limnephilus partitus** Walker (I)  
**Nearctic, transcontinental**  
**Distribution:** Yukon, Alaska to Newfoundland.  
**Yukon records:** 4 (SMDV); 10, 12, 16 (ROME); 17 (CNCI).  
**Biological information:** Adults have been collected in the Yukon 14 July –9 August.

111. **Limnephilus parvulus** (Banks) (I)  
**Nearctic, transcontinental**  
**Distribution:** Yukon to Newfoundland, Maine.  
**Yukon records:** 11 (SMDV); 17 (ROME).  
**Biological information:** Adults have been collected in the Yukon 31 May –25 June.

112. **Limnephilus perpusillus** Walker (I)  
**Nearctic, transcontinental**  
**Distribution:** Yukon to Newfoundland, south to Colorado.  
**Yukon records:** 10 (SMDV); 12 (ROME).  
**Biological information:** Adults have been collected in the Yukon 16–27 July.

113. **Limnephilus picturatus** McLachlan (II)  
**Holartic, transcontinental**  
**Distribution:** Yukon, Alaska to Colorado, east to Quebec; Greenland; northern Europe, Iceland (Gislason 1981) through Siberia to Kamchatka, the Amur region, Sakhalin, and Chukotka (Levanidova 1982).  
**Yukon records:** 1, 16 (NW 1984); 2 (CNCI); 5, 6, 12 (ROME); 4, 8, 14, 19 (ROME, SMDV); 17 (SMDV).  
**Biological information:** Adults have been collected in the Yukon 9 July –20 August.

114. **Limnephilus rhombicus** (Linnaeus) (II)  
**Holartic, transcontinental**  
**Distribution:** Yukon, Alaska to Colorado, east to Newfoundland, West Virginia, Ohio; Greenland; Europe (Malicky 1988, fig. 18), through Turkestan (Schmid 1955), Siberia, Mongolia to Kamchatka (Lepneva 1966; Levanidova 1982).  
**Yukon records:** 4, 10, 12 (ROME); 17 (INHS).  
**Biological information:** Adults have been collected in the Yukon 16 June –30 July.
115. *Limnephilus sansoni* Banks (I)  
**Nearctic, western montane**  
*Distribution:* Yukon, Alaska to Colorado.  
*Yukon records:* 6, 8, 10, 11, 12 (ROME); 11, 16 (ROME, SMDV); 17 (CNCI).  
*Biological information:* Adults have been collected in the Yukon 14 July – 29 August.

116. *Limnephilus secludens* Banks (I)  
**Nearctic, transcontinental**  
*Distribution:* Yukon, Alaska to California, Quebec.  
*Yukon records:* 10, 12, 17 (CNCI, ROME, SMDV).  
*Biological information:* Adults have been collected in the Yukon 21 July – 2 September.

117. *Limnephilus sericeus* (Say) (II)  
**Holarctic, transcontinental**  
*Distribution:* Yukon, Alaska to Colorado, Newfoundland to Ohio; Europe (Malicky 1988, fig. 16), Siberia to Kamchatka, Japan (Lepneva 1966).  
*Yukon records:* 10, 14, 16 (ROME); 12, 17 (SMDV).  
*Biological information:* Adults have been collected in the Yukon 2 – 31 August.

118. *Limnephilus stigma* Curtis (III)  
**Palaearctic-East Beringian**  
*Distribution:* Yukon, Alaska to California, Colorado, Michigan, Newfoundland; eastern Siberia and Kamchatka to the Kurile Islands.  
*Yukon records:* 4, 10, 11, 12, 14, 16, 17, 19 (ROME, SMDV).  
*Biological information:* Adults have been collected in the Yukon 27 July.  
*Taxonomic notes:* *L. indivisus* (Figs. 26, 27), the similar sister species, has not been confirmed for the Yukon; see under *L. stigma* (III).

119. *Limnephilus sublunatus* Provancher (I)  
**Nearctic, transcontinental**  
*Distribution:* Yukon to Newfoundland, Colorado.  
*Yukon records:* 10, 11 (ROME).  
*Biological information:* Adults have been collected in the Yukon 3 – 10 August.

120. *Limnephilus tarsalis* (Banks) (I)  
**Nearctic, western**  
*Yukon records:* 10 (ROME).  
*Biological information:* Adults have been collected in the Yukon 27 July.  
*Taxonomic notes:* *L. alvatus* Denning is a junior synonym (Ruiter 1995).

**Genus Nemotaulius.** This is a small Holarctic genus with a single species in North America distributed across the northern part of the continent. Larvae live in lentic waters.

121. *Nemotaulius hostilis* (Hagen) (I)  
**Nearctic, transcontinental**  
*Distribution:* Yukon, Alaska to Newfoundland, West Virginia, Colorado.  
*Yukon records:* 4, 10, 12 (ROME, SMDV).  
*Biological information:* Adults have been collected in the Yukon 27 June – 27 July.

**Genus Onocosmoecus.** *Onocosmoecus unicolor* is a small Holarctic genus of 2 species (Wiggins and Richardson 1987); larvae live in cool waters of slow streams and lake margins where they are detritivores.

122. *Onocosmoecus unicolor* (Banks) (II)  
**Holarctic, transcontinental**  
*Distribution:* Yukon, Alaska to California, Colorado, Michigan, Newfoundland; eastern Siberia and Kamchatka to the Kurile Islands.  
*Yukon records:* 6, 8, 10, 11, 12, 14, 16, 17, 19 (ROME, SMDV).  
*Biological information:* Adults have been collected in the Yukon 24 July – 20 August.

**Genus Philartcus.** Several species of *Philartcus* occur in Asia but only one in North America, from Manitoba westward; larvae live in slow streams and small ponds where they are probably detritivores.

123. *Philartcus quaeris* (Milne) (I)  
**Nearctic, western and north-central**  
*Distribution:* Yukon, British Columbia to Manitoba, Colorado.  
*Yukon records:* 17 (ROME, SMDV).
Biological information: Adults have been collected in the Yukon 26 June – 3 August.

**Genus Psychoglypha.** This is an important Nearctic genus wholly confined to western montane areas except for one northern and transcontinental species, *P. subborealis*. Larvae are confined to cool running waters and are detritivorous.

124. *Psychoglypha alascensis* (Banks) (I) Nearctic, western montane
Distribution: Yukon, Alaska to California.
Yukon records: 10 (SMDV); 14 (ROME).
Biological information: Adults have been collected in the Yukon 15 June – 22 August.

125. *Psychoglypha subborealis* (Banks) (I) Nearctic, transcontinental
Distribution: Yukon, Alaska to California, New Hampshire, Newfoundland.
Yukon records: 12, 17 (ROME, SMDV).
Biological information: Adults have been collected in the Yukon 26 April – 24 July.

**Genus Sphagnophylax.** *Sphagnophylax* is a relict genus of arctic tundra in the Yukon and adjacent Northwest Territories (Wiggins and Winchester 1984). Larvae of the single species live in transient tundra pools and feed on plant materials.

126. *Sphagnophylax meiops* Wiggins and Winchester (IV) East Beringian
Distribution: Yukon, Northwest Territories.
Yukon records: 4 (ROME).
Biological information: Adults have been collected in the Yukon 23 July.

**Family Molannidae**

The Molannidae are a small family mainly confined to the northern hemisphere; larvae are omnivorous, living in lentic or slowly flowing waters.

**Genus Molanna.** This is an Holarctic and Oriental genus with 6 North American species. Only one, *M. flavicornis*, is transcontinental; the others are eastern.

127. *Molanna flavicornis* Banks (II) Holarctic, transcontinental
Distribution: Yukon to Nova Scotia, New York, disjunct populations in Colorado; Eurasia.
Yukon records: 4, 10 (ROME, SMDV).
Biological information: Adults have been collected in the Yukon 2 June – 26 July.
Taxonomic notes: Designation of this species as Holarctic hinges on the proposal by Fuller (1987) that it is conspecific with the Eurasian *M. albicans* Zett.

**Genus Molannodes.** *Molannodes* is an Holarctic genus with one species widely distributed across northern Europe and Asia, and highly localized in northern North America; a second species occurs in Japan.

128. *Molannodes tinctus* Zetterstedt (II) Holarctic
Distribution: Yukon, Alaska, Northwest Territories, Saskatchewan, Ontario; northern Europe, Asia.
Yukon records: 4, 12 (ROME, SMDV).
Biological information: Adults have been collected in the Yukon 23 June – 25 July.

**Family Phryganeidae**

The Phryganeidae are an Holarctic and Oriental family of 74 species, well represented throughout northern North America (Wiggins in press). Larvae live in lakes and marshes or in slow rivers and streams; they are omnivorous to largely predacious in feeding. The largest caddisflies belong to this family.

**Genus Agrypnia.** This is an Holarctic genus with 10 North American species, mainly transcontinental and northern; all but one of the 10 are known in the Yukon. Larvae occur in marshes, lakes and slow rivers, and are mainly predacious.
129. *Agrypnia colorata* Hagen (II)  
*Holarctic, transcontinental*  
*Distribution:* Yukon, Utah to Newfoundland; Siberia to Mongolia, Finland.  
*Yukon records:* 4, 6, 12 (ROME, SMDV).  
*Biological information:* Adults have been collected in the Yukon 25 June – 27 July.

130. *Agrypnia deflata* (Milne) (I)  
*Nearctic, transcontinental*  
*Distribution:* Yukon, Alaska to Colorado, Newfoundland.  
*Yukon records:* 4, 12 (ROME, SMDV); 6, 10, 16 (ROME); 17 (CNCI).  
*Biological information:* Adults have been collected in the Yukon 29 June – 8 August.

131. *Agrypnia glacialis* Hagen (I)  
*Nearctic, transcontinental*  
*Distribution:* Yukon, Alaska to California, North Dakota, Newfoundland; Greenland.  
*Yukon records:* 4, 11, 12, 17 (ROME, SMDV).  
*Biological information:* Adults have been collected in the Yukon 6 June – 15 July.

132. *Agrypnia improba* (Hagen) (I)  
*Nearctic, transcontinental*  
*Distribution:* Yukon, Oregon to Newfoundland, North Carolina.  
*Yukon records:* 10, 12, 15, 17 (ROME, SMDV); 19 (CNCI).  
*Biological information:* Adults have been collected in the Yukon 16 June – 30 July.

133. *Agrypnia mcdunnoughi* (Milne) (I)  
*Nearctic, transcontinental*  
*Distribution:* Yukon to Newfoundland.  
*Yukon records:* 10, 17 (ROME, SMDV); 19 (NW 1984).  
*Biological information:* Adults have been collected in the Yukon 17 June – 20 July.

134. *Agrypnia obsOLEta* (Hagen) (III)  
*Palaearctic-East Beringian*  
*Distribution:* Yukon and British Columbia; Europe and Asia.  
*Yukon records:* 2 (SMDV); 4 (ROME).  
*Biological information:* Adults have been collected in the Yukon 25 June – 23 July.

135. *Agrypnia pagetana* Curtis (II)  
*Holarctic*  
*Distribution:* Yukon, Alaska, British Columbia through the Northwest Territories to Manitoba; northern and central Europe to northern Italy, Bulgaria, Caucasus (Botoșăneanu and Malicky 1978).  
*Yukon records:* 2, 4, 10, 11, 12, 19 (ROME, SMDV).  
*Biological information:* Adults have been collected in the Yukon 6 June – 23 July.

136. *Agrypnia sahlbergi* (McLachlan) (III)  
*Palaearctic-East Beringian*  
*Distribution:* Yukon, Alaska, and British Columbia; northern Scandinavia, Asia.  
*Yukon records:* 5, 8, 12 (ROME, SMDV).  
*Biological information:* Adults have been collected in the Yukon 5 June – 30 July.

137. *Agrypnia straminea* Hagen (I)  
*Nearctic, transcontinental*  
*Distribution:* Yukon to Newfoundland and Colorado, Illinois, North Dakota.  
*Yukon records:* 8, 10, 11, 12, 15, 16, 17, 19 (ROME, SMDV).  
*Biological information:* Adults have been collected in the Yukon 10 June – 5 August.

**Genus Banksiola.** This is a Nearctic genus of 4 eastern species, and one common and widespread transcontinental species (Wiggins 1956). Larvae live in lentic waters.

138. *Banksiola crotchi* Banks (I)  
*Nearctic, transcontinental*  
*Distribution:* Yukon, Alaska to California, Newfoundland, Ohio.  
*Yukon records:* 4, 10 (ROME).  
*Biological information:* Adults have been collected in the Yukon 27 June – 27 July.

**Genus Oligotricha.** This is a small Eurasian genus with a single species extending into northwestern North America (Wiggins and Kuwayama 1971). Larvae live in standing waters.

139. *Oligotricha lapponica* (Hagen) (III)  
*Palaearctic-East Beringian*  
*Distribution:* Yukon, Alaska; northern Europe, Asia.  
*Yukon records:* 4, 12 (ROME, SMDV).  
*Biological information:* Adults have been collected in the Yukon 6 – 25 July.
Genus *Phryganea*. This is an Holarctic genus with 2 North American species living in lentic waters. One of them, *P. cinerea*, is common throughout northern and montane areas.

140. *Phryganea cinerea* Walker (I)  
**Nearctic, transcontinental**  
**Distribution:** Yukon, Alaska to Newfoundland and California, North Dakota, Ohio.  
**Yukon records:** 4, 10, 12, 17 (ROME); 17 (NW 1984).  
**Biological information:** Adults have been collected in the Yukon 15 June – 27 July.

Genus *Ptilostomis*. This Nearctic genus of 4 species includes 2 with transcontinental distributions; in addition to *P. semifasciata*, *P. ocellifera* (Walker) has been recorded from Alaska and British Columbia (Liard R. Hot Springs Prov. Pk., 59°26′N 126°04′W, 8.vi.80, ROME), and probably occurs in the Yukon. Larvae are predacious for the most part, and live in all types of aquatic habitats, including temporary pools.

141. *Ptilostomis semifasciata* (Say) (I)  
**Nearctic, transcontinental**  
**Distribution:** Yukon to Newfoundland, Virginia.  
**Yukon records:** 6, 12, 17 (ROME).  
**Biological information:** Adults have been collected in the Yukon 22 June – 13 July.

Family Uenoidae

This is a family of the northern hemisphere with 5 North American genera, all inhabiting rapid streams (Vineyard and Wiggins 1988). Two genera are recorded from the Yukon, and one other, *Neophylax*, is represented in Alaska. Larvae graze algae and fine organic particles on rocks.

Genus *Neothremma*. This genus is restricted to western montane North America where 7 species are known (Wiggins and Wisseman 1992). Larvae occur in rapid streams, and we have collected them at several Yukon sites.

142. *Neothremma didactyla* Ross (I)  
**Nearctic, western montane**  
**Distribution:** Yukon to Oregon.  
**Yukon records:** 15, 17 (ROME).  
**Biological information:** Adults have been collected in the Yukon 23 July.

Genus *Oligophlebodes*. This is a Nearctic genus of 7 western species; larvae are confined to turbulent mountain streams.

143. *Oligophlebodes ruthae* Ross (I)  
**Nearctic, western montane**  
**Distribution:** Yukon to Utah.  
**Yukon records:** 17 (SMDV).  
**Biological information:** Adults have been collected in the Yukon 23 July.

144. *Oligophlebodes sierra* Ross (I)  
**Nearctic, western montane**  
**Distribution:** Yukon, Alaska to California.  
**Yukon records:** 16 (ROME).  
**Biological information:** Adults have been collected in the Yukon 29 July.

145. *Oligophlebodes zelti* Nimmo (I)  
**Nearctic, western montane**  
**Distribution:** Yukon to Montana.  
**Yukon records:** 17, 19 (NW 1984).  
**Biological information:** Adults have been collected in the Yukon 23 – 24 July.

**Taxonomic Notes**

Note 1. *Rhyacophila mongolica* Schmid, Arefina and Levanidova (14)

Among a series of 5 pharate adults collected by a Royal Ontario Museum field party in the Yukon (30 mi W Old Crow, Sunaghun Cr., 16.vii. 1981, ROME #810565), one well developed male (Fig. 2) is considered conspecific with specimens of *R. mongolica* (Schmid
et al. 1993); our material has been compared with specimens provided by these authors from Russia. This is the first North American record for this species, otherwise widely distributed in the Russian Far East and Mongolia. The pharate male differs from its sister species *R. sibirica* McLachlan in details of segment X (cf. Figs. 2b, 3).

**Note 2.** *Goera tungusensis* Martynov (47)

*Goera radissonica* Harper and Méthot 1975, **new synonymy**

During this study, we found that *Goera radissonica* Harper and Méthot (1975) from northern Quebec is a junior subjective synonym of *Goera tungusensis* Martynov (1909) from Siberia, confirmed through comparison by W.K. Gall of the holotype male of *G. radissonica* with specimens of *G. tungusensis* obtained from the Zoological Institute, St. Petersburg.

**Note 3.** *Ceraclea nigromervosa* (Retzius) (56)

We found 2 forms of adults of this species in the Yukon and Beringian collections studied. In both forms the dark veins of the forewing contrast strongly against the membrane, but the wing membrane is reddish brown in one and gray to colourless in the other. The gray-winged form is inferred to be typical for the species, in accordance with McLachlan’s (1877) description which applies to specimens from northern and central Europe; we have similar material from Finland. However, the brown-winged form shows several distinctive characters in the male genitalia as described below.

Male genitalia (brown-winged form, Fig. 4). Segment IX in ventral view approximately twice as wide as long (width less than twice length in gray-winged form, Fig. 6); basal segment of inferior appendages extended into a prominent posteroventral process (little extended in gray-winged form). Segment X with superior appendages long and tapered apically (shorter and not tapered in gray-winged form); segment X with each ventrolateral lobe bearing short stout setae basally (stout setae lacking in gray-winged form). Phallus with apical membranous endotheca spherical in caudal view (less expanded in gray-winged form).

Female genitalia. The female genitalic structure is variable and no characters concordant with the males were found; characters illustrated for each form (Figs. 5, 7) can occur in both
Figs. 4–7. Ceraclea nigronervosa (Retzius) (56) (Leptoceridae). 4, Brown-winged form (YT: 810525d ROME), male genitalia: a, lateral; b, dorsal; c, caudal; d, ventral; e, phallos, lateral; 5, Brown-winged form (YT: 810525d ROME), female genitalia: a, lateral; b, dorsal; 6, Gray-winged form (YT: 810522b ROME), male genitalia: a, lateral; b, dorsal; c, caudal; d, ventral; e, phallos, lateral; 7, Gray-winged form (Russia: Tunguska, Yenisei R., ROME), female genitalia: a, lateral; b, dorsal.
brown- and gray-winged specimens. Thus females can be identified only by the brown membrane of the forewings and by association with males.

In North America material of the brown-winged form was examined from the Yukon (10, 12, 17; ROME, SMDV), Alaska, and British Columbia; the gray-winged form was collected only in the Yukon (4, 10, 12; ROME). Adult specimens were collected along lakes and streams and on the banks of the Yukon River. However, we received a series of the brown-winged form collected near St. Petersburg, Russia, by V.D. Ivanov; genitalic structure of males is entirely consistent with our Beringian variant (Fig. 4). Consequently, we infer that two morphs may occur sympatrically over much of the range attributed to *C. nigroneurovosa*, and perhaps the two differ in preferred habitat or life cycle. The issue has to be resolved by a worker with access to populations in Europe and Asia.

**Note 4. Mystacides sepulchralis** (Walker) (60)

Although this species is common and widely distributed over much of North America including the Yukon and Alaska (Yamamoto and Wiggins 1964), its status beyond North America requires clarification. Holarctic distribution was attributed to *M. sepulchralis* by Yamamoto and Ross (1966), even while recognizing as valid the Siberian species *M. bifidus* Martynov (1924b); supporting evidence was not given, and we know of none apart from a record from Siberia attributed initially to *M. sepulchralis* (Martynov 1910) but later assigned to *M. bifidus* (Martynov 1935).

There is considerable variation in genitalic characters of *M. sepulchralis*. Through the assistance of V.D. Ivanov, we have obtained information on genitalic characters of the holotype of *M. bifidus* in the Zoological Institute, St. Petersburg; and we have examined other specimens, indicating that there is at least some variation in this species, too. The two forms are very close, and clearly are sister taxa; but Martynov affirmed his view (Betten and Mosely 1940) that the Siberian *M. bifidus* Martynov and the North American *M. sepulchralis* (Walker) are separate species. We follow that interpretation here because small morphological differences in other species are used here as the basis for inferring separation during glacial periods. Detailed analysis of the variation in populations within each continent might reveal evidence of a Beringian interchange; whether such differences would confirm status as species or as intraspecific variants would emerge from the analysis. For the present, we interpret *M. sepulchralis* as a strictly North American species.

Larvae of *M. bifidus*, for which we have no information, could be relevant to this question. In recent years, distinctive larvae in some populations of *M. sepulchralis* from eastern North America have been found with head markings of discrete spots similar to those in *M. alafimbriata*, and quite unlike the largely black heads characteristic of most *sepulchralis* populations in North America (cf. figs. 3 and 4, Yamamoto and Wiggins 1964). Association of these larvae with adults confirms that they are *M. sepulchralis*. This larval dimorphism could have been established in populations isolated during the glacial period to the southeast of the continental ice mass, although it does not appear to be reflected in characters of the adults.

The sister species of *M. sepulchralis/bifidus* is *M. alafimbriata*, confined to western North America including the Yukon and Alaska (Yamamoto and Wiggins 1964). *Mystacides alafimbriata* and *sepulchralis* are only slightly different morphologically; and although there appears to be little overlap in their ranges, the two have been taken in the same collections in a few localities, all in the Yukon and Alaska. Possibly *M. alafimbriata* was derived from populations isolated to the south of the Cordilleran glacier in the mountains of western North America. Outlying montane glaciers along the Rocky and Cascade Mountain ranges served
to isolate refugia in the coniferous forest zone south of the continental ice sheet and in the southern coastal refugium (Kavanaugh 1988, fig. 37).

**Note 5. Mystacides interjectus** (Banks) (59)

This species is widely distributed across the northern half of North America (Yamamoto and Wiggins 1964, as *longicornis*), including the Yukon and Alaska. In distinguishing between the North American *M. interjectus* (Banks) and the Eurasian *M. longicornis* (Linnaeus), Yamamoto and Ross (1966) treated *M. sibiricus* Martynov (1935) as a junior synonym of *M. interjectus* (Banks 1914), thereby apparently extending the range of the North American form into Asia. This interpretation was followed by Mey and Dulmaa (1985) in identifying specimens from Mongolia as *M. interjectus*. However, illustrations of the male genitalia of *M. sibiricus* by Martynov (1935, figs. 28–30) show that this species belongs not to the *interjectus* lineage, but to the *longicornis* complex. Our interpretation is consistent with a male from Lake Baikal identified as *M. sibiricus* (Fig. 8) in the Zoological Institute, St. Petersburg; it is confirmed from examination of the syntype series of approximately 100 specimens in the Zoological Institute by V.D. Ivanov, who has designated a lectotype male of *Mystacides sibiricus* Martynov (Ivan Lake, 45 km NW of Chita City, 15.vii.1925, Vinogradov leg.). Whether *Mystacides sibiricus* Martynov and *longicornis* Linnaeus are distinct species will have to be determined by examination of specimens over a wide geographic range in Eurasia; currently, we know of no evidence to support the occurrence of *M. interjectus* in the Palaearctic region.

Distinction between *M. interjectus* and *longicornis* was based by Yamamoto and Ross (1966) on the structure of segment X; but we believe that the two are best distinguished by the structure of the male inferior appendages in caudal aspect. In *M. interjectus* (Fig. 9) the concave ventral face of the inferior appendage is conspicuously narrowed in caudal aspect; in *M. longicornis* and *M. sibiricus*, the concave ventral face is wide, and rather uniformly so throughout. Moreover, the phallotheca in *M. longicornis* and *M. sibiricus* terminates apically in a pair of stout sclerotized hooks; these hooks are scarcely developed in *M. interjectus*. Over the whole of its range in North America, *M. interjectus* is somewhat variable in genital morphology, but we find no indication of regional differences in the Yukon, Alaska, or elsewhere to indicate that populations were separated during glaciation.
The longicornis species group comprising *M. nigra*, *longicornis*, and *interjectus* (Yamamoto and Ross 1966) is apparently of Palaearctic origin. Separation between *M. longicornis* and *interjectus* was probably by vicariant speciation of a continuous circumboreal ancestral range brought about by separation of Asia and North America.

**Note 6. Grammotaulius alascensis** Schmid (84)

*Grammotaulius subborealis* Schmid 1964, **new synonymy**

These 2 taxa, together with *G. signatipennis* McLachlan, constitute a complex in which identification is rendered all the more difficult by the fact that no explicit diagnosis has been proposed to distinguish one from another. Because a series of Yukon specimens (Dempster Hwy. km 105, nr. Blackstone R., 30.vii.1979, ROME #791183, 19 males) shows characters intermediate between those illustrated for males of *G. alascensis* and *G. subborealis* (Schmid 1964, figs. 6–13), the latter name is placed here as a junior subjective synonym under *G. alascensis* which has page priority. In the characters illustrated by Schmid for the females, the pair of slender membranous lobes arising from the posterodorsal margin of segment IX + X was interpreted inconsistently (Schmid 1964, figs. 4, 5): in *G. alascensis* the slender lobe is shown as an appendage of a sclerotized rounded lobe at the base of the anal tube; in *G. subborealis* the slender lobe is shown correctly as a median structure separate from the sclerotized lobe. These paired membranous lobes are actually eversible, and appear in genital preparations of *Grammotaulius* and many other Limnephilidae in variable conditions of eversion; in Schmid’s figures of *G. signatipennis* (1950a, figs. 52–54) they do not appear at all, as is often the case, although the lobes are extended in other cleared specimens of this species.

In this emended sense, *G. alascensis* appears to be the North American sister species of *G. signatipennis*. Our material of *G. signatipennis* is not extensive, but the principal distinguishing character of the males is evidently the posteroventral edge of the superior appendages, which is very heavily sclerotized, darkened, and rather linear in *G. alascensis*, but more rounded and less sclerotized in *G. signatipennis*. In some specimens of the latter species, the posteroventral margin of the superior appendage is somewhat more heavily sclerotized than illustrated (Schmid 1950a, fig. 50). The intermediate appendages in our North American material show considerable variation, as was illustrated by Schmid. We have seen a specimen of *G. alascensis* from the Hudson Bay coastline of the Northwest Territories (Eskimo Point, 30.ix.1939, CNCI). From all of this, *G. alascensis* can be regarded as a highly variable North American species. We do not have sufficient material to assess variation for a consistent character separating females of these 2 species.

We are advised by O.S. Flint that the Alaskan specimens attributed to *G. signatipennis* McLachlan (Flint 1964: Nunivak Is., USNM) are in fact *G. alascensis* Schmid. However, *G. signatipennis* must remain as part of the North American fauna because we have found a single male from the Yukon (Dawson, Moose Cr., CNCI) in which the genitalic structure is typical for this species. The forewings show the typical markings only faintly, which we attribute to the rather teneral condition of the specimen.

**Note 7. Limnephilus diphyes** McLachlan (96)

This species is recorded here for the first time from North America; diagnostic characters in genitalic morphology are illustrated (Figs. 10, 11; and also by Malicky 1983, pp. 191 and 200). The original description by McLachlan (1880) provides a good account of the general morphology. *Limnephilus diphyes* appears to belong to the *sitchensis* group (Schmid 1955), and can be distinguished from the other species by the prominent notch in the superior appendages of the male.
Note 8. *Limnephilus fumosus* Banks (102)

*Limnephilus isobela* Nimmo 1991, new synonymy

Information available in the taxonomic literature is inadequate for the distinction of *L. fumosus* Banks from its very similar sister species *L. santanus* Ross. Banks (1900) based *L. fumosus* on a series of 3 male and 2 female specimens from Alaska; diagnostic characters for this species were not clearly described, and Banks’ assertion that *L. fumosus* also occurred in Washington probably stemmed from failure to distinguish between *L. fumosus* and the more southerly sister taxon later recognized as *L. santanus*. In the original description of *L. santanus* from Oregon, Ross (1949) gave an explicit diagnosis only for the female. To establish the identity of these 2 species, we studied the type material of *L. fumosus* in the U.S. National Museum of Natural History, and of *L. santanus* in the Illinois Natural History Survey; genitalic morphology of both sexes is illustrated here. We also designate *Limnephili-

Figs. 10–11. *Limnephilus diphyes* McLachlan (96) (Limnephilidae) (YT: ROME 800105a). 10, Male genitalia: a, lateral; b, ventral; c, phallus, lateral; 11, Female genitalia: a, lateral; b, ventral.
lus isobela Nimmo (1991) as a junior subjective synonym of *L. fumosus* Banks; the type locality given for *L. isobela* Nimmo is Isobel Pass (= Isabel or Isabell Pass) mi. 206, Richardson Highway, Yukon, but the Richardson Highway and Isabel Pass are within Alaska.

Males of the 2 species can be separated by the parameres, which are bifid apically in *L. fumosus* (Fig. 12) but undivided in *L. santanus* (Fig. 14). The females are distinguished by the structure of segment X; in *L. fumosus* segment X is produced as a pair of heavily sclerotized blade-like projections (Fig. 13), broad apically in ventral aspect with the posterior margin broadly U-shaped. In females of *L. santanus* (Fig. 15) segment X terminates in a pair of elongate slender processes, and in ventral aspect is narrowed apically. In addition to genitalic differences, *L. fumosus* and *L. santanus* differ in the colour of the forewings: *Limnephilus fumosus* is uniformly brown with conspicuous light areas, much as illustrated by Banks (1900, fig. 10), whereas *L. santanus* is brown with light speckling widely distributed over the wing, in addition to the large light areas along the chord and at the apex, as described by Ross (1949).
Ross (1949) stated that the type of *L. fumosus* is a female; however, a type has not been designated. Therefore, we select the following male from the type series as the lectotype of *Limnephilus fumosus* (Banks, 1900): LECTOTYPE male: Alaska, Berg Bay, June 10 ’99; Harriman Expedition ’99, T. Kincaid, collector; #192, USNM Paratype (*sensu cotype*) No. 5262.

Records confirmed for *Limnephilus fumosus* indicate that this species is known from Alaska, Yukon, and the Northwest Territories (NT: Midway L., 67°14’N 135°26’W, 8.vii.1985, SMDV). A series in the ROME identified as *L. santanus* was cited by Nimmo and Wickstrom (1984: YT. Mirror Creek, Alaska Hwy. mile 1209, 28.vi.1958, ROME); these specimens have been re-examined in light of the information now available for these 2 species, and they are *L. fumosus*. Nimmo’s list of Alaskan Trichoptera (1986) includes *L. fumosus* based on earlier records from the literature, and also *L. santanus* based on material

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**Figs. 14–15. Limnephilus santanus** Ross (Limnephilidae) (OR: INHS). 14, Holotype male, genitalia: a, lateral; b, dorsal; c, caudal; d, phallus, lateral; e, phallus, dorsal; 15, Allotype female, genitalia: a, lateral; b, ventral.
deposited in the CNCI; we have been unable to locate this recent material in the CNCI, but we suspect that it belongs to *L. fumosus*. Consequently, occurrence of *L. santanus* in Alaska remains subject to confirmation. Nimmo and Scudder (1983) record *L. santanus* from British Columbia; we have been unable to locate their material in the CNCI, but the record should be confirmed in light of this new information.

The morphological distinction between these 2 species is rather slight but seems consistent; as in a number of close congeneric species in the Limnephilidae, the structural distinction between them appears to have arisen in the parameres of the males and in small, presumably reciprocal, changes in the genitalic structure of the females.

**Biogeographic Analysis of the Yukon and Holarctic Trichoptera**

Here we seek some understanding of the sources from which Trichoptera have come to occupy the Yukon. The number of species of Trichoptera known in the Yukon Territory stands now at 145, constituting 11 per cent of the Nearctic Trichoptera known north of Mexico, and doubtless more have yet to be recorded. The history of the Yukon trichopteran fauna is analyzed under 4 categories of species; several other species from adjacent Alaska or the Northwest Territories, although not recorded from the Yukon, are relevant to this analysis and are included (designated by †). The remaining Holarctic species that have not been recorded in Beringia are brought together for comparison in a fifth category; and consequently all North American species of Trichoptera that also occur in Europe or Asia are treated here in some manner.

**Category I. Nearctic species widespread in North America**

**II. Holarctic species widespread in North America**

**III. Palaearctic-East Beringian species**

**IV. Beringian species**

**V. Holarctic species not in Beringia**

Relevant evidence is outlined for the species discussed, and although it is incomplete and often speculative in interpretation, a taxonomic and conceptual context is established from which more focussed questions can be identified. Phylogenetic analysis of the genera for the species concerned, although an important asset, is well beyond the scope of this study. In addition to the investigation of Yukon Trichoptera, our objective in this study is an initial outline of issues relating to the origin of Holarctic Trichoptera in North America. Particular attention has been given to intraspecific morphological variation in the Holarctic and amphitheringian species, in an attempt to detect differences in populations that could be indicative of geographic disjunction during glacial periods. The broad scope of this study has precluded special efforts to enlarge series of the variable species to statistically significant levels; our observations, based on the material available, are to be regarded as an indication of the potential for more exacting analysis of intraspecific variation in certain species. In the absence of evidence to the contrary, we have assumed that these differences have a genetic basis, but the possibility cannot be excluded that ecological factors could be involved (e.g. Danks 1981: 360).

**Geological and Climatic Context.** For much of the past 65 million years of the Cenozoic era, overland connections between the major continents at the northern end of the globe permitted interchange of animals and plants (Matthews 1979a, fig. 2.6), establishing the ancestry of the present biota. Continental crust connecting North America with Asia stood
above the sea for the first 40 million years of the Cenozoic era during the Palaeocene (65–58 million years B.P.), Eocene (58–37 ma B.P.), and Oligocene (37–24 ma B.P.) epochs, permitting open biotic interchange between the 2 continents (Stanley 1986). The effective barrier to biotic interchange through early Cenozoic epochs was the Turgai Strait and perhaps the Cherskiy Seaway subdividing Siberia on a north-south axis (Matthews 1979a, fig. 2.2). The Bering land bridge connecting North America and Asia was inundated by the sea at intervals during the last 25 million years of the Cenozoic, through the Miocene (24–5 ma B.P.) and Pliocene (5–1.8 ma B.P.) epochs (Stanley 1986); flooding during the mid-Pliocene some 3 ma B.P. closed the Bering land bridge until lowered sea level again exposed it during the major Pleistocene glacial advances.

Combined with these intercontinental connections, warm moist climatic conditions prevailed at arctic latitudes through the Palaeocene to the Eocene. Cooler and drier climates followed in late Eocene, probably caused by changes of geography, ocean currents, volcanism, and variations in Earth’s solar orbit. This cooling trend continued through the Oligocene, Miocene, and Pliocene until marked decline in temperature led to establishment of an arctic climate in the north, with glaciers forming about 2 ma B.P. (Stanley 1986). Exposure of the Bering land bridge (Fig. 16) resulted from declining sea levels as large volumes of water were bound up in the glacial ice that covered much of northern North America, Asia, and Europe. A number of major glacial advances followed in the Pleistocene, each advance receding to some extent during a subsequent interglacial period. The last major Pleistocene glacial advance in North America, the Wisconsinan, began approximately 100 000 years ago and reached its maximum about 18 000 years ago, before beginning the present period of glacial recession.

Land connections between northeastern North America and Europe had disappeared by mid-Miocene time, some 15 million years ago. Prior to that, in early Cenozoic epochs before sea-floor spreading between North America and Europe had separated the land masses, there were at least 2 principal overland connections (Matthews 1979a, fig. 2.3): the De Geer bridge interconnecting through northern Greenland; and the Greenland–Faeroes bridge bridge through Iceland.

Biological Aspects. As a result of this geological and climatic history, the present fauna of North America has been derived over millions of years when intercontinental movement across northern land connections was favoured by warm to mild climates. When ocean barriers arose between the continents, and northern climates cooled, the North American biota was isolated from that of Europe, followed intermittently by separation from Asia. The Pleistocene epoch of the past 1.8 million years provided an opportunity once again for biotic interchange between North America and Asia. This time, however, harsh climates prevailed, and the largely unglaciated Bering land bridge connecting Nearctic (East) and Palaeartic (West) Beringia permitted only cold-adapted species to pass from one continent to the other.

Formation of the glaciers was governed by the configuration of land, sea, and mountains—relationships that differ between Asia and North America. Over much of northeastern Asia glaciers were confined to higher mountains (Fig. 16), leaving most of that area unglaciated throughout the Pleistocene epoch. In North America, by contrast, the Laurentide continental glacier and the Cordilleran glacier of the western mountain ranges flowed together to the east and south of the Yukon (Fig. 16); and with each glacial advance the unglaciated Nearctic Beringian refugium was closed off as the advancing ice eliminated animals and plants in its path, reducing the levels of species-packing in Beringian communities. During periods of interglacial recession, contact may have been possible between the
Beringian refugium, and perhaps other glacial refugia, with the main body of the North American biota to the south of the glaciated areas. An ice-free corridor was opened between the Laurentide and Cordilleran glaciers during periods of interglacial recession, connecting Beringia with unglaciated areas to the south for extensive periods (e.g. Reeves 1973; Pielou 1991). This corridor would have held major freshwater drainage systems arising from glacial melting, but whether the climate sustained suitable habitats for aquatic insects such as Trichoptera is an open question. To provide food for aquatic insects, habitats must support plant materials of both allochthonous and autochthonous origin. However, at least one species of Trichoptera now exists in the rigorous climate of Ellesmere Island, indicating that the ice-free corridor may have supported some species during the Pleistocene. Should that have happened, Beringian species including those of Palaeartic origin could have passed to the south of the Laurentide and Cordilleran glaciers during Pleistocene interglacial periods. A Nahanni glacial refuge for freshwater organisms in the southeastern Yukon is supported by genetic analysis of lake whitefish stocks (Foote et al. 1992), adding support to the possibility of survival of aquatic insects in the corridor area during glaciation. But if the ice-free corridor did function as an interglacial passage for Trichoptera, it must have been a two-way corridor; and the ecological resistance of expanding Nearctic communities in the south to dispersing Palaeartic species could have been a constraint to the southbound movement of species from Beringia (e.g. Vermeij 1991).

Exposure of the Bering land bridge during Pleistocene glaciations connected quite different refugial areas in Nearctic and Palaeartic Beringia (Fig. 16). Palaeartic Beringia

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**Fig. 16.** Approximate boundaries of unglaciated Beringia during Wisconsinan glacial maximum: based on Ager (1982), Lafontaine and Wood (1988). Separation between Laurentide and Cordilleran glaciers indicates location of postulated intermittent ice-free corridor.
was much larger than Nearctic Beringia and also extended to lower latitudes; therefore, it would have supported more species of plants and animals, including Trichoptera (see under Ecological Considerations). By contrast, glaciation in North America isolated the Alaska–Yukon peninsula, largely if not entirely closing off exchange of species with lower latitudes (above). Consequently, the 2 species pools must have been imbalanced when the Bering land bridge was exposed. We infer that whatever dispersal followed the opening of the Bering land bridge would necessarily have been weighted in favour of a Palaeartic-to-Nearctic movement; in a group-to-group comparison, not only would there have been more species in Palaeartic Beringia, but also there probably would have been more vacant ecological niches in Nearctic Beringia because of extinctions caused by glaciation. For mammalian species, predominantly eastward dispersal across the Bering land bridge has been inferred from evidence for the Pleistocene, but movement at about the same level in each direction during the Pliocene (Vermeij 1991). These conclusions are consistent with the concept that dissimilar patterns of glaciation in North America and Asia are correlated with asymmetric interchange of species. Moreover, global analysis of past biotic interchanges leads to the general conclusion that the resistance of a biota to invasion is reduced by previous extinction of species in that biota (Vermeij 1991).

Superimposed upon these general factors influencing the interchange of animals and plants between North America and Asia are the special requirements of aquatic insects. Only the Odonata have the capacity for active dispersal over longer distances between the aquatic habitats of larvae. Adult Trichoptera are subject at best to passive dispersal by strong winds; even then, ovipositing females would have to be relocated in the vicinity of appropriate aquatic habitats. Dispersal by wind over the narrow sea barrier of the present-day Bering Strait seems at least as likely as dispersal across long distances overland; but there is little supporting evidence for successful dispersal across Bering Strait, nor is there evidence for post-Pleistocene intercontinental interchange of Trichoptera by way of the Aleutian Island chain (e.g. Karlstrom and Ball 1969). Even so, several species of Trichoptera evidently did reach Greenland by dispersal at high latitudes over sea barriers from distant glacial refugia (see category I, Greenland Trichoptera). Beringia during much of the Pleistocene is depicted as arid and steppe-like with the muskeg and wet tundra, now so typical, greatly diminished in extent (Schweger et al. 1982). Thus, Nearctic Beringia, the corridor between Asia and North America, would seem to have provided a different mix of habitats and probably more restricted habitats for aquatic insects than are now available. Moreover, the glacier-fed water courses were probably similar to glacial streams of today that support few aquatic insects because they carry heavy loads of suspended glacial debris which are deposited to form unstable and largely unproductive substrates, shifted by braided channels as the volume of meltwater fluctuates. Unglaciated upland parts of Beringia, however, probably had streams that were similar to present-day upland streams in tundra regions. These streams would have joined the lowland river systems that traversed the exposed coastal shelf (Fig. 16), forming a network of freshwater systems that is believed to have facilitated an exchange of fish species between Asia and North America (Lindsey and McPhail 1986). Because of the high biological diversity of Trichoptera, however, the availability of freshwater habitats across Beringia is only one aspect of the issue; another aspect is the extent to which these freshwater habitats coincided with the requirements of the species that had access to them. These issues are explored under Ecological Considerations.

We infer that the Bering land bridge of Pleistocene time would have been a difficult passage for many aquatic insects because the cold dry climate was not well suited to dispersal of the adult insects, and because freshwater habitats would have been localized, unsuitable,
or different in other ways from those of the present. More favourable conditions for the movement of aquatic insects between Asia and North America would seem to have been available during the millions of years that the 2 continents were connected in Pliocene time and earlier, before the land connection between the 2 continents was inundated in the mid-Pliocene, some 3 million years ago.

**Origin of the Beringian and Holarctic Trichoptera.** The origin of Beringian and Holarctic species can be interpreted in several ways. Some species could have had an Holarctic distribution pre-dating the separation of North America from Asia in Pliocene time some 3 ma B.P. Thus, some Holarctic species (category II) could have been confined to the south of the advancing ice in unglaciated parts of the continent, giving rise to intraspecific variants or even sibling species which now can be detected; disjunct populations of some of these species may have been isolated in unglaciated Nearctic Beringia by the converging Laurentide and Cordilleran ice masses. Palaearctic-East Beringian species (category III) may never have occurred much beyond their present range in North America, or, if they did, were overtaken by the advancing ice and confined as glacial relicts to the Beringian refugium where they remain. Some others could be Nearctic species that dispersed from Beringia to Asia during the past 1.8 million years of the Pleistocene. For most of the Beringian Holarctic species, the evidence now available is not sufficient to interpret clearly which of the possibilities seems most likely. However, a pattern of vicariant distribution of sister species in North America and Eurasia often emerges, dating perhaps from the Pliocene or earlier, and augmented in some cases by apparent later dispersal of the Palaearctic form to North America, presumably by way of the Bering land bridge during the Pleistocene.

The fundamental issues in piecing together the origin of the Beringian Trichoptera are the age of the species and their rate of structural change over time. This information is unknown, but clearly we are dealing with species that differ from their closest living relative (sister species) by a wide range of distinguishing characters, and thus could and probably do represent species of different ages. Some Beringian species pairs are virtually sibling species, e.g. *Limnephilus fenestratus* (101) and *L. kennicotti* (107). The small, but consistent, morphological distinctions between some pairs of sister species could have arisen in disjunct populations along the southern margin of the North American glaciers. Others are well differentiated although clearly sister species, e.g. *Agrypnia deflata* (130) and *A. obsoleta* (134), which probably had a vicariant origin arising from an earlier intercontinental subdivision of the range of a common circumboreal ancestor. Flooding of the land connection between Asia and North America in the mid-Pliocene, some 3 million years ago, or earlier, offers possible origins for dichotomies of this sort, although disjunctions between some conspecific North American and Asian populations could have been imposed by cold climate even before the land connection was overrun by the sea. At the far end of the scale for the age of trichopteran taxa inferred from morphological divergence is *Sphagnophylax meiops* (126) (Frontispiece, Fig. 28), known only from unglaciated Nearctic Beringia or marginally beyond, and which appears to have lost the power of flight. The monotypic genus *Sphagnophylax* is the only genus-level taxon known in Trichoptera that is confined to Beringia, and is clearly both a phylogenetic and a geographic relict (Wiggins and Winchester 1984).

Placing these speciation events in geological time with any assurance is not yet possible for Trichoptera. Inferring the relative times of origin of species from levels of morphological divergence achieves some consistency in interpreting the history of a number of species of disparate age, and is employed in this study because few other clues are available; but we
recognize that if correct for some species, this morphological guideline may be illusory for others. One indication that the species did not diverge at uniform rates is provided by members of category V; several of these are widespread Holarctic species that must have passed between Asia and North America at some time before the onset of harsh Pleistocene climates because there is little evidence that they are adapted now to far northern latitudes. Secondly, fossil evidence of known age is rarely available for species of Trichoptera, but in Coleoptera where it is available, extant species of the north were found to be unexpectedly old and clearly in existence well before Pleistocene time, with some identifiable in late Miocene 5.7 ma B.P. (e.g. Downes and Kavanaugh 1988). A very slow rate of evolutionary change in some Trichoptera is demonstrated by the small structural differences between a Baltic amber species of *Lype* (Psychomyiidae) and a Recent European species (Ross 1958, fig. 1); the age of the amber species is placed at upper Eocene—some 50 ma B.P. Perhaps this is an isolated and atypical example, but for insect species generally an age of 25 million years has been estimated (e.g. Briggs 1966). Comprehensive analysis of the fossil record reveals that insects show very low rates of extinction; among vertebrates, by contrast, few living species are more than a million years old (Labandeira and Sepkoski 1993). The age of species and the time required for their origin are different concepts; but inferences reflecting the rate of evolution for insect species must be tempered by the evidence that at least 760 species of Drosophilidae have evolved on the Hawaiian Islands since their origins 6 million to 500 000 years ago (Kaneshiro 1993).

Finally, there is the larger question of the age of the cold, far northern biomes themselves. Tundra develops in regions that are too cold for the growth of trees, and arctic tundra is believed to have arisen in the north as disjunct areas of ecological regression in late Miocene forests (Matthews 1979b; Danks 1981). The Seward Peninsula of Alaska, just below the Arctic Circle (67°N lat.), was forested up to about 5.7 million years ago in late Miocene time (Hopkins et al. 1971). Palaeobotanical evidence indicates that the forest-tundra ecotone probably lay just to the north of the Seward Peninsula at that time, suggesting that tundra probably covered most of the North American Arctic Archipelago by 6 ma B.P. (Matthews 1979b). Thus, tundra may be a relatively young biome in the north, and adaptation of tundra species a rather recent phenomenon. Some arctic tundra Trichoptera may have been derived from alpine tundra habitats, which in Beringia would have dated from the time that the high mountains of the western Cordillera and of northeastern Asia reached elevations which precluded the growth of trees. Evidence from fossil insects suggests, however, that species may have adapted to arctic tundra conditions from lineages occurring in the boreal forest (Matthews 1979a; Danks 1981). Because of their diversity and broad ecological penetration, Trichoptera could be an appropriate group for testing these hypotheses. Phylogenetic analysis in the highly diverse boreomontane genus *Limnephilus* would be a promising avenue of investigation to reveal the habitats of the phyletic ancestors of the present inhabitants of arctic and alpine tundra. However, a good deal more basic information about the biology, distribution, taxonomy, and phylogenetic relationships of the species of *Limnephilus* will be required. Trichoptera established in pre-Pleistocene arctic tundra might have found glacial refuge in alpine tundra of accessible mountain ranges, or in disjunct lowland tundra refugia along the southern margin of the continental glacier.

I. Nearctic Species Widespread in North America

This is the largest category of the Yukon Trichoptera—98 species comprising 68 per cent of the total fauna. None of these species is known from Europe or Asia, and their generally widespread occurrence now at more southerly latitudes in North America suggests
that they passed the last glaciation south of the ice or in other refugia under climatic conditions less severe than those in Beringia, and returned to northern latitudes as the glaciers receded. The possibility cannot be excluded that some of these species could have passed the last glacial period in East Beringia, failed to cross the Bering land bridge to Asia, and dispersed southward after recession of the glaciers. Most of these strictly Nearctic caddisfly species which now occur in the Yukon probably originated before the glaciation of the past 2 million years, although some may be the product of isolation in separate refugial areas to the south of the glaciers, e.g. the dichotomy between *Mystacides alafimbriata* and *M. sepulchralis*. Numbers in parentheses following the species names provide a cross-reference to distributional and other data in the Annotated List of Yukon Trichoptera.

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<td><em>Polycentropus weedi</em> Blickle and Morse (39)</td>
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G.B. Wiggins and C.R. Parker
These Nearctic Trichoptera from glacial refuges to the south are of 2 broad groups—western montane species and transcontinental species. The western montane species are mainly members of the Spicipalpia and Annulipalpia whose larvae live in lotic habitats characteristic of mountainous terrain. This group is particularly diverse southward through Oregon to California and Colorado, but markedly less successful to the north (Table 1 below): Glossosomatidae, Rhyacophilidae, Hydropsychidae, Philopotamidae, Polycentropodidae, Brachycentridae (Micrasema), Lepidostomatidae, Limnephilidae (Chyranda, Discosmoecus, Ecclisomyia, Psychoglypha), and Uenoidae. Figures for declining species diversity at higher latitudes (Table 1) indicate that the lotic species of the western montane Trichoptera have populated the glaciated terrain of the Yukon with limited success. Lentic species of western montane origin in a few genera of the Limnephilidae (Asynarchus, Clistoronia, Lenarchus, Limnephilus) and the Leptoceridae (Mystacides, Ylodes) have extended farther north in the Yukon than have the lotic species of montane origin.

Transcontinental species are inferred to have passed glaciation along a much wider ice front because overall they are now widely distributed in North America. They are, for the most part, species of lentic waters and slowly moving streams. These species are primarily case-makers of the Integripalpia; their diversity also declines with increasing latitude (Table 1), but not as much as in the Spicipalpia and Annulipalpia where most species live in lotic waters. Transcontinental Trichoptera occur to a large extent across the boreal forest biome but their lake and marsh habitats also extend through deciduous forests and grasslands. Larvae of these species, and of Trichoptera generally, have little or no specific relationship with vascular plants, and feed for the most part on the fungi colonizing plant detritus and on algae, or on other insects. In general, the effect of low temperature on aquatic habitats seems to be the major constraint to repopulation of the Yukon by species in both groups of Category I Trichoptera; this topic is explored further under Ecological Considerations.

There is an interesting recurrence in northern Quebec of disjunct populations of several species which otherwise appear to be confined to western or northwestern North America (Roy and Harper 1979; Harper 1989: Arctopsyche grandis (23) (Hydropsychidae), Wormaldia gabriella (33) (Philopotamidae), and Goera tungusensis (47) (Goeridae). The first 2 are Nearctic species (category I) which probably passed the Wisconsinan glaciation south of the ice, and now range broadly in western montane areas from the Yukon southward. Goera tungusensis is Holarctic (category II) and may also have passed the last glacial period.
along the southern margin of the ice, or it may have entered North America for the first time during the Pleistocene. This shared pattern of postglacial distribution might indicate that each of these species passed the Wisconsinan glaciation as disjunct eastern populations; larvae of each of them usually occur in cool lotic habitats.

**Greenland Trichoptera.** Species of Trichoptera occurring in both North America and Greenland pose relevant distributional questions arising from glaciation because most of them occur in the Yukon as well. Some are Holarctic species, and some are strictly Nearctic, but the fact that all of them occur in Greenland raises the possibility that they illustrate some general principles of high-latitude distribution. Since the insect fauna of Greenland includes few if any endemic species, and was derived to a large extent by postglacial dispersal from North America (Downes 1966), we infer that these Nearctic species of Trichoptera reached Greenland after recession of the glaciers. Occurrence of a Palaearctic species, *Limnephilus griseus* (Linnaeus), in Greenland (Fristrup 1942) raises a further possibility that some of the Holarctic species might have reached Greenland from Europe; records for a second Palaearctic limnephilid from Greenland, *Halesus radiatus* (Curt.), are believed to be in error (N.P. Kristensen, pers. comm.). Ice rafting from western Norway has been postulated as a sweepstakes route for the repopulation of Iceland and other North Atlantic islands by insects about 10,000 years ago (Buckland et al. 1986). Although adult Trichoptera are generally short-lived, an adult diapause in species of *Limnephilus* adapted to transient waters could prolong the life span, perhaps enabling these species to endure such a passage; their egg masses embedded in gelatinous matrix are resistant to desiccation (Wiggins 1973). All of the Greenland Trichoptera are case-making species of the Integripalpia whose larvae live in lentic waters or in slow currents of streams.

Common patterns in the far northern distribution of Lepidoptera and of several other groups of insects reveal 2 elements in the fauna of Greenland (Downes 1966). Species of the high arctic occurring on adjacent Ellesmere Island are very largely shared with northern Greenland. In the Trichoptera, only 2 species of the Greenland fauna can be considered high-arctic forms—*Apatania zonella* (43) and *Grensia praeterita* (87). The first occurs on Ellesmere Island (Corbet 1966) where it is the most northerly species of Trichoptera known in North America, although it is an Holarctic species and is recorded also from Yukon to Quebec; *Grensia praeterita* is a circumpolar species recorded mainly above treeline although not from Ellesmere Island. The high-arctic species are held to have reached Greenland by way of a far northern route across the Arctic Archipelago (Downes 1966), raising the possibility that they could have passed the Wisconsinan glaciation in a Peary Land refugium along the northern edge of Greenland (e.g. Danks 1981, fig. 5). The relatively small number of high-arctic Trichoptera indicates that these insects are not well adapted to the rigours of existence at high latitudes.

The second element in the Greenland insect fauna comprises species of more southerly distribution that are of low-arctic or boreal origin (Downes 1966). Most of the Greenland Trichoptera appear to be of this group because they range widely across the boreal forest and often farther to the south. These species are likely to be postglacial dispersants to Greenland, although probably by way of the Arctic Archipelago and Baffin Island. It appears that most of them moved into deglaciated North America from refuges in the central part of the continent, finally reaching Greenland.

Evidence relevant to category I species in Greenland is outlined below, and for other species under the category indicated; 2 of the Nearctic species known from Greenland have not been recorded from the Yukon (†).
Apataniidae
\textit{Apatania zonella} (Zetterstedt) (II, 43)

Limnephilidae
\textit{Grammotaulius interrogationis} (Zetterstedt) (I, 85)

The type locality of this transcontinental Nearctic species is in Greenland (Mosely 1929; Schmid 1950a). Genitalic structures of males showed marked variation both within and between populations, but we found no congruent pattern. Schmid (1950a) considered \textit{G. interrogationis} to be the sister species of 3 others (2 Palaearctic, 1 Nearctic).

\textit{Grensia praeterita} (Walker) (III, 87)

\textit{Limnephilus femoralis} Kirby (II, 100); \textit{L. picturatus} McLachlan (II, 113); \textit{L. rhombicus} (Linnaeus) (II, 114)

These 3 widely distributed Holarctic species could have reached Greenland from North America, or from Europe as did the Palaearctic species \textit{L. griseus}. In Yukon and other Nearctic material of \textit{L. rhombicus} there is substantial variation in both male and female genitalic structure, but we found no geographic correlation to indicate separation of populations by glacial barriers. Congruent variation found in \textit{L. picturatus} was analyzed (II).

\textit{Limnephilus kennicotti} Banks (I, 107)

This Nearctic species is discussed under \textit{L. fenestratus} (III), its very similar sister species.

\textit{Limnephilus moestus} Banks (†)

The range of this Nearctic species extends from the Northwest Territories to Colorado, east to Newfoundland and West Virginia, and to Greenland (Forsslund 1932). It has not been recorded from the Yukon or Alaska. The species was assigned to the \textit{sitchensis} group of 6 Nearctic species (Schmid 1955). Few species of Nearctic Trichoptera have the broad latitudinal range from West Virginia to Greenland shared by \textit{L. moestus} and the following species \textit{L. ornatus}.

\textit{Limnephilus ornatus} Banks (†)

This species is known from Alaska [Naknek (CNCI); Parks Hwy. (ROME 821118); Kodiak Is. (ROME); Popof Is. (Banks 1900)], and from Alberta and Montana to Newfoundland, south to West Virginia. Although recorded from Alaska, \textit{L. ornatus} is not known from the Yukon or from British Columbia (Nimmo and Scudder 1978, 1983), nor is it known elsewhere in the western montane states; this is a large gap for a conspicuous species and suggests a disjunct population in Alaska. The species has been recorded from Greenland (Mosely 1932), but not from northern Asia; a record from Japan (Ulmer 1907), never confirmed, was rejected by Schmid (1965a). If \textit{L. ornatus} passed the last glacial period in the Beringian refugium, there is no evidence that it spread to Asia. No close relatives of \textit{L. ornatus} were indicated in the classification by Schmid (1955).

Phryganeidae
\textit{Agrypnia glacialis} Hagen (I, 131)

This transcontinental Nearctic species is the sister of the Palaearctic \textit{A. picta} Kolenati, widely distributed through northern Europe and Asia to Kamchatka. There is no evidence that either species has moved across the Bering land bridge, in contrast to the congeneric species pair \textit{A. deflata} and \textit{obsoleta} (see category III). However, there are records for \textit{A. glacialis} from Greenland, and the Eurasian sister species \textit{A. picta} occurs as far west as
Britain and Iceland. We infer that this evidence indicates vicariant speciation from a circumboreal ancestor. Outlying records of *A. glacialis* in Idaho, Utah and California suggest relict montane populations from the time when the species occurred south of the Pleistocene glacial ice. In these populations, and also in the Greenland material, variations in male genitalic structure are more common than in the populations of northern North America (Wiggins in press).

II. Holarctic Species Widespread in North America

Each of these species is now widely distributed in both North America and Eurasia; 28 of them are known in the Yukon, constituting about 18 per cent of the Trichoptera. Many are now transcontinental, and these broad Nearctic ranges seem more likely to follow from glacial refuge along the southern margin of the ice. Thus, a number of these Holarctic species probably occurred in North America before the Pleistocene, and probably have been on this continent for at least the past 3 million years, before the connection between Asia and North America was overrun by the sea in mid-Pliocene time. However, southward movement of any of these species from Beringia through the ice-free corridor between the Laurentide and Cordilleran glaciers might have occurred during interglacial periods of the Pleistocene (see Biological Aspects), and is difficult to detect. For some category II species, sister relationships between Nearctic and Palaearctic species pairs suggest origin from common circumboreal ancestors, and perhaps arose from intercontinental vicariance in the Pliocene or earlier. Evidence indicates that for the most part species involved in recent dispersal moved from Asia to North America (see Biogeographic Analysis). A few species, e.g. *Brachycentrus americanus* and *Onocosmoecus unicolor*, appear to have originated in North America and dispersed to Asia across the Bering land bridge.

Evidence from intraspecific morphological variation suggests that some Nearctic species were divided, with populations confined to the south of the advancing glacial front while disjunct conspecific populations were restricted to Beringia: e.g. *Brachycentrus americanus* (44), *Micrasema gelidum* (45), *Oecetis ochracea* (63), *Ylodes reuteri* (68), *Linnephilus picturatus* (113), *Onocosmoecus unicolor* (122), and *Agrypnia colorata* (129). For the remaining species of category II, evidence available now is inadequate to support any inference about their origin and direction of dispersal.

Although several of these species now occur in arctic tundra habitats, most of them are also widely distributed in forest and grassland biomes at more temperate latitudes. Consequently, these species do not comply with the general pattern in some other groups that the arctic and treeline species were derived from Beringia, while the boreal and subarctic fauna moved northward from refugia below the glacial front. The most northerly species of category II are *Asynarchus iteratus* (74) and *Apatania zonella* (43).

Two species (†) known from Alaska or the Northwest Territories are also considered under this category; although not yet recorded from the Yukon, they probably occur there.

<table>
<thead>
<tr>
<th>Spicipalpia</th>
<th>Annulipalpia</th>
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<tr>
<td>Glossosomatidae</td>
<td>Hydropsychidae</td>
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<tr>
<td><em>Glossosoma intermedium</em> (Klapalek)</td>
<td><em>Arctopsyche ladogensis</em> (Kolenati)</td>
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<td>Polycentropodidae</td>
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<td><em>Oxyethira ecoruta</em> Morton (†)</td>
<td><em>Neureclipsis bimaculata</em> McLachlan</td>
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<td>Rhyacophilidae</td>
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<tr>
<td><em>Rhyacophila narvae</em> Navas</td>
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Glossosomatidae

**Glossosoma intermedium** (Klapalek) (2)

This is the only Holarctic species of *Glossosoma*, and the only transcontinental species in North America. According to Ross (1956, charts 31, 43), the sister species of *G. intermedium* is *G. verdona* Ross; he inferred that the two originated in North America and *intermedium* spread to Eurasia by way of the Bering land bridge. If this dispersal occurred during the Pleistocene, *G. intermedium* would be one of the few species that moved from North America to Asia. However, by this interpretation, some populations of *G. intermedium* probably would have been confined south of the ice, accounting for the present transcontinental distribution. This sister-group relationship opens a second possibility that *G. intermedium* is the Eurasian vicariant from a common Holarctic ancestor; this species might then have reached North America by way of the Bering land bridge. Occurrence of *G. intermedium* in the northern Yukon (Fig. 1, region 5) indicates its adaptation to far northern conditions; and if *G. intermedium* reached North America during the Pleistocene glaciation, its present transcontinental distribution would have been achieved after glacial recession. In any event, occurrence of the 2 sister species in the Yukon invites ecological comparison (e.g. Irons 1988), leading perhaps to some understanding of factors underlying the wide distribution of *G. intermedium*. Ross considered the subgenus *G. (Synafophora = Eomystra)*, to which *G. intermedium* belongs, to be the biological analogue of the *sibirica* group of *Rhyacocephila*—species of both groups tolerant of low gradient streams and sharing the dispersal capability of ecological generalists which enabled some to reach eastern North America.

Hydroptilidae

**Oxyethira ecornuta** Morton (†)

One of the few Holarctic species known in this family, *O. ecornuta* occurs through northern Europe (Botoșâneanu and Malicky 1978) to the Far East of Russia (Botoșâneanu and Levanidova 1988); our collections include specimens from Alaska, and although not yet recorded from the Yukon, this species probably occurs there. There is material from Ontario in the ROME collection, suggesting a disjunct distribution and the possibility that this species at least in part passed the last glaciation south of the continental glacier. The species was placed in the *flavicornis* group by Kelley (1984), and was believed to be the sister species of *O. flavicornis* (Pictet) from Europe; both are said to occur in lentic habitats.
**Rhyacophilidae**  
*Rhyacophila narvae* Navas (15)  
This species is a member of the *sibirica* group, and was proposed as the sister taxon of *R. transquilla* Tsuda from Japan (Ross 1956; Schmid 1970). Origin of *Rhyacophila narvae* in Asia was proposed by these authors. If dispersal to North America occurred during the Pleistocene, river systems of the Bering land bridge must have provided larval habitats of cool, fast-flowing water required by the larvae (Lepneva 1964). If dispersal of *R. narvae* to North America occurred before the Pliocene separation of the 2 continents, this Holarctic species has resisted the vicariant subdivision postulated for some others.

**Hydropsychidae**  
*Arctopsyche ladogensis* (Kolenati) (24)  
This is the only Holarctic species in the genus and, of 4 species of *Arctopsyche* in North America, it is the only one with a transcontinental distribution. It is the sister species of *A. amurensis* Martynov from the Amur region of Russia (Schmid 1968). If the 2 species originated in Asia, *A. ladogensis* could have reached North America during the Pleistocene or before by way of the Bering land bridge. However, vicariant speciation of a circumboreal ancestor following separation of North America and Asia, perhaps in the Pliocene, is also a possible explanation for the sister-group relationship. In this interpretation, *A. ladogensis* would be a Nearctic species confined at least in part to the Beringian refugium, and dispersing to Asia across the land bridge; a disjunct population in Utah (Baumann and Unzicker 1981) is consistent with Nearctic origin of *A. ladogensis* and its occurrence both north and south of the ice. We found no consistent morphological differences between Nearctic and Palaearctic representatives, but have not examined specimens from Utah. Larvae live in strong currents of rivers and larger streams (Lepneva 1964), and occurrence of this species in the far north of the Yukon (Fig. 1, region 4) indicates that it is suited for trans-Beringian dispersal.

**Polycentropodidae**  
*Neureclipsis bimaculata* (Linnaeus) (34)  
This is the only Holarctic species of *Neureclipsis*, and the only transcontinental species in North America. There are morphological differences between Nearctic and Palaearctic specimens which could reflect distinctions at the level of populations or even species, but the general background variation has yet to be assessed over broad geographic areas. These differences suggest the possibility of vicariant subdivision of a circumboreal ancestor when North America and Asia were separated during the Pliocene. Transcontinental distribution across central North America suggests that, at least in part, this species occurred to the south of the ice during glaciation.

**Apataniidae**  
*Apatania crymophila* McLachlan (41); A. *stigmatella* (Zetterstedt) (42); A. *zonella* (Zetterstedt) (43)  
These are the only Holarctic species known in *Apatania*, and all 3 could have passed the last glaciation in Beringia. However, transcontinental penetration of North America seems likely to have been achieved through postglacial dispersal from refugial areas south of the ice mass, implying that at least A. *stigmatella* and *zonella* occurred in North America before the Pleistocene, and thus probably before the Pliocene separation between North America and Asia. *Apatania crymophila* was proposed as the sister species of the European *A. wallengreni* McLachlan, and A. *stigmatella* the sister species of A. *shoshone* Banks in
western North America (Schmid 1954a). *Apatania zonella* shows rather distant relationship with other species (Schmid 1954a), and is parthenogenetic (Corbet 1966). Recorded from Ellesmere Island and Greenland, *A. zonella* is the most northerly of Nearctic Trichoptera.

**Brachycentridae**

*Brachycentrus americanus* Banks (44)

This species occurs through northern and western North America, and its range has been extended to include Siberia, Mongolia, and Japan with recognition of *Oligoplectrodes potanini* Martynov as a junior subjective synonym (Schmid 1983); it has been recorded also from Kamchatka, but not Chukotka (Levanidova 1982). This is the only Nearctic species assigned to the subgenus *B. (Oligoplectrodes)* (Flint 1984); 2 other species occur in Asia—*B. kozlovi* Martynov and *B. punctatus* Forsslund. From illustrations of the male genitalia of these species, it appears that the 2 Asian taxa are sister species, together constituting the sister lineage of *B. americanus*.

We have examined specimens from much of the range in North America [159 ♂, 220 ♀] and also material from Siberia, Mongolia, and Japan; a unique characteristic of *B. americanus* is the high variability of tibial spurs in North American populations. The typical and plesiomorphic tibial spur complement for all *Brachycentrus* species is 2,3,3; but in populations of *B. americanus* in Asia and Alaska tibial spurs are largely consistent at 2,2,3 (Fig. 17). Most Yukon specimens also have spur counts of 2,2,3; although approximately 20 per cent of those examined have 2,2,2, and occasionally the full complement of 2,3,3, with some spurs reduced in size. Regional variation representing all 3 spur conditions of *B. americanus* was found in varying proportions over much of North America to the south; in Manitoba, northern Ontario, and in Utah and Colorado the plesiomorphic 2,3,3 condition occurred in most specimens examined. Assuming genetic control for this variation, the parsimonious interpretation for the pattern of character distribution is that *B. americanus* arose in North America where the plesiomorphic spur count of 2,3,3 occurs. Uniformity in northeastern Asia for the reduced spur condition of 2,2,3 indicates a pervasive founder effect from an apomorphic ancestor that probably came from North America. In Nearctic Beringian populations isolated by encroaching glaciers, tibial spurs could have stabilized at 2,2,3, with colonizers from these populations entering Asia by way of rivers of the Bering land bridge. Occurrence of *B. americanus* in the northern Yukon (Fig. 1, region 4: Porcupine Plain) indicates that it is adapted to conditions that would have been available in trans-Beringian dispersal during the Pleistocene. The main Nearctic body of *B. americanus* south of the continental ice mass would have been characterized by plesiomorphic tibial spurs of 2,3,3 (Fig. 17). Distribution for *B. americanus* in North America (Flint 1984, fig. 23) suggests that disjunct populations occur in the northeast, in Wisconsin, Minnesota and Michigan, and in the western mountains. These disjunctions may be maintained now by the Great Lakes and by extensive areas where the cool streams required by larvae of this species are lacking. The disjunctions could be a consequence of separate refugia during glacial advances, restricting gene flow and enabling differing numbers of tibial spurs to become established in different areas. Following retreat of the ice, renewed contact between the Nearctic populations could have led to the mixture of spur counts against a strong background of the plesiomorphic 2,3,3 that now characterizes populations of *B. americanus* in North America (Fig. 17). The high incidence of the reduced 2,2,3 condition in western North America might also be a result of southward dispersal of Beringian populations. Based on life-history data from the interior of Alaska, a life cycle of 2 years was inferred (Irons 1988).
Fig. 17. Approximate distribution of character states for tibial spurs in *Brachycentrus americanus* (Banks) (44) (Brachycentridae).
An intensive taxonomic analysis of this species complex was carried out by Botoșăneanu (1988), who concluded from a study of male genitalic morphology that *M. gelidum* represents a polytypic superspecies of 6 prospecies, allopatrically distributed over a large part of northern Eurasia and North America. Three of the prospecies are represented in the Yukon and Alaska and in the Far East of Russia: *M. (gelidum) gentile* McLachlan (junior synonym *M. scissum* McLachlan, Kimmins and Denning 1951); *M. (gelidum) extremum* Botoșăneanu; and *M. (gelidum) gelidum* McLachlan which also extends across the whole of northern Eurasia to Norway (junior synonyms: *M. kluane* Ross and Morse 1973; *M. subscissum* Martynov; *M. sibiricum* Martynov). Because *M. gelidum* is a member of a Nearctic group comprising *M. bactro* Ross, *M. diteris* Ross, *M. onisca* Ross, and *M. sprulesi* Ross, its origin was believed to have been in western North America (Botoșăneanu 1988); and the mosaic of prospecies constituting *M. gelidum* was attributed to the isolation of populations during Pleistocene glacial periods and their recolonization following glacial retreat. Complexity within the superspecies *M. gelidum* was interpreted to indicate that glacial intervals preceding the last Wisconsinan period were effective in isolating populations for periods sufficient to effect morphological divergence. One form in the complex, *M. (gelidum) canusa* Botoșăneanu (1988), occurs in central North America, and probably was isolated along the southern margin of the glacial ice; but the more northerly Nearctic forms were inferred to have passed periods of glacial advance in the Beringian refugium. As with species of *Apatania*, larval habitats for members of the *gelidum* complex broaden with increasing latitude—those in the most southerly localities living in spring streams, but northward habitats include rivers and also lakes in the most northerly localities (Botoșăneanu 1988). Consequently larval habitat probably would not have been a deterrent to dispersal of the northern populations across the Bering land bridge during the Pleistocene, an inference further supported by occurrence of *M. gelidum* on the Arctic coastal plain (Fig. 1, region 1).

**Goeridae**

*Goera tungusensis* Martynov (47)

The range of this species known originally from Siberia must now be extended to northern Quebec, the Northwest Territories, and almost certainly the Yukon (see Taxonomic Note 2). We also have from Alaska a pharate male that may represent a morphological variant of this species, or perhaps an unnamed sister taxon. If Pleistocene dispersal of *G. tungusensis* across the Bering land bridge to North America is indicated, the species could have extended eastward in North America after withdrawal of the glaciers. However, the widely scattered North American records suggest the possibility of repopulation of deglaciated areas from south of the ice where a pre-Pliocene circumboreal ancestor took refuge, and from which a disjunct Alaskan population has begun to diverge.

**Leptoceridae**

*Ceraclea annulicornis* (Stephens) (54)

Phylogenetic analysis (Yang and Morse 1988) indicated that *C. annulicornis* is one of an unresolved group of 4 species—2 in China, and *C. rathae* (Flint) from eastern North America. Species that are now transcontinental in North America, such as *C. annulicornis*, probably passed the Pleistocene to the south of the ice mass and if so, would have occurred in North America before glaciation.
Ceraclea excisa (Morton) (∗)

Although not known from the Yukon, this species probably occurs there because it is recorded from Alaska (Milne 1934; Morse 1975), Wisconsin, and Michigan to Quebec and Massachusetts; and it extends through northern Europe and Siberia to the Amur region (Lepneva 1966). It is considered to be the sister taxon of the group of 4 species that includes C. annulicornis (Yang and Morse 1988); its widespread occurrence in North America leads to the same interpretation as for the preceding species.

Ceraclea nigronervosa (Retzius) (56)

Although most species of the nigronervosa group are confined to North America (Morse 1975), C. nigronervosa is the sole Holarctic species. Larvae live in large rivers, where they feed on colonies of freshwater sponge (Resh 1976; Solem and Resh 1981). In addition to typical nigronervosa specimens that are consistent with most others examined from Europe and Asia, our North American material reveals a brown-winged variant with distinctive male genitalic characters (Fig. 4) which is also represented in Europe (Taxonomic Note 3). Thus the 2 forms appear to be broadly sympatric and could have reached North America during the Pleistocene by way of unglaciated Beringia, and spread southward following glacial retreat. This interpretation would require that sponges, the food of the larvae, occurred in waters of the Bering land bridge; and this is feasible because C. nigronervosa now occurs in the far northern Yukon (Fig. 1, region 4). However, this species might have been in North America before the Pliocene separation from Asia because the range of C. nigronervosa now extends to Wyoming.

Oecetis ochracea (Curtis) (63)

This is the only Holarctic species in Oecetis, and no phylogenetic analysis of the genus has been made. The subspecies O. o. carri Milne (1934) was segregated to discriminate between North American and European populations by genitalic characters. We found no evidence to support this interpretation; variation in genitalic characters was evident, but showed no geographic correlation. However, specimens from northern Europe and the Yukon are darker brown in colour overall than those from other parts of North America. Although slight, this indication of genetic continuity in O. ochracea through Nearctic Beringia and Europe suggests that the light-coloured Nearctic populations were derived from ancestors forced to the south of the continental glacier; if so, this species probably was present in North America before the Pleistocene glaciation.

Ylodes reuteri (McLachlan) (68)

In discussing the Nearctic range of this species, Ross (1965, as Triaenodes griseus) alluded to morphological variants in the Rocky Mountains, the western part of the Northwest Territories, and the Hudson Bay area. Highly variable populations in southern Saskatchewan were interpreted as an intergrading blend from all 3 areas—an example of caddisfly species that passed the last glaciation in discrete areas in the Rocky Mountains, in eastern North America, and in Beringia. If so, Y. reuteri or its ancestor must have occupied North America early enough, before Asia and North America were separated in the Pliocene, to have become established to the south of the glaciers.

Limnephilidae

Asynarchus iteratus McLachlan (74)

This species was assigned to the lapponicus group (Schmid 1954b), and was considered to be so close to A. aldinus (Ross) from Alberta that the two could be geographic variants of the same species. The close similarity suggests that separation between them might have
been brought about by segregation of a portion of the Nearctic population of *A. iteratus* to the south of the advancing glaciers, giving rise to *A. aldinus*, while *A. iteratus* became confined to Beringia as a glacial relict. If that were so, *A. iteratus* or its ancestor probably reached North America from Asia before the land bridge between the 2 continents was overrun by the sea during the Pliocene.

*Asynarchus lapponicus* (Zetterstedt) (75)

Variation in the superior and intermediate appendages of the males showed no coherent pattern correlated with geographic distribution. Among the species assigned to the *lapponicus* group (Schmid 1954b), the sister species of *A. lapponicus* would be the northern North American species *A. montanus* Banks. Prominent morphological differences in the genitalia of the 2 species suggest that they have been separate for some time, perhaps through inter-continental vicariant speciation, with *A. lapponicus* dispersing from Asia to North America across the Bering land bridge during the Pleistocene. Disjunct distribution between northern and central populations of this species in Europe (Malicky 1988, fig. 11) suggests that it was widely distributed in Europe and Asia before the glacial advances of the Pleistocene. If *A. lapponicus* was confined to Beringia during Pleistocene glaciation, it has spread widely in North America following recession of the ice, in contrast to some other Nearctic Beringian species (see category III). The larval habitat for *A. lapponicus* is littoral areas of lakes, tundra pools, and slow streams (Winchester 1984), and the species is univoltine at the latitude of Tuktoyaktuk, Northwest Territories (69°29′N).

*Limnephilus dispar* McLachlan (97); *L. externus* Hagen (98); *L. femoralis* Kirby (100); *L. nigriceps* (Zetterstedt) (108); *L. picturatus* McLachlan (113); *L. rhombicus* (Linnaeus) (114); *L. sericeus* (Say) (117).

Phylogenetic relationships within the large genus *Limnephilus* have not been investigated in sufficient depth to support inferences about the geographic origin of the species. All of these species have a transcontinental distribution in North America, and probably occurred on this continent before glaciation in the Pleistocene. We found morphological variation in several of the species, but a congruent pattern was evident only in *L. picturatus*.

Comparison of specimens of *L. picturatus* from all parts of the range in North America [64 ♀, 85 ♂] with Eurasian material indicates genetic continuity between Nearctic Beringia and Eurasia, and restriction in gene flow between Beringian populations and those from other parts of North America. This argues for isolation of Nearctic populations of *L. picturatus* south of the glaciers while Palearctic immigrants of the species entered Beringia. Accordingly, *L. picturatus* probably would have occurred in North America before the Pleistocene, and its Holarctic distribution would pre-date the Pliocene separation between North America and Asia. On melting of the glaciers, the more southerly Nearctic populations appear to have been more successful in colonizing deglaciated territory than have the Beringian populations. Analysis of Greenland populations for these variable characters might shed light on their origin.

Thus, the patch of stout setae on the ventral surface of the hindwing R₂ in males is well developed in all Eurasian specimens examined and in about 95 per cent of Beringian specimens, but equally well developed in only about one third of other North American specimens. The pterostigma is light in colour in 90 per cent of Beringian and Palearctic specimens examined, but light in about 50 per cent of other North American specimens.

Inferior appendages in the male genitalia are triangular in dorsal aspect in about 86 per cent of Nearctic Beringian specimens; about 4% of specimens from other parts of North America are similar in this character, where the predominant condition is for parallel dorsal
margins on the inferior appendages. Eurasian specimens examined are, however, about evenly divided between these 2 conditions. In the parameres of the male genitalia of Nearctic Beringian specimens there are more than 10 long, very fine, setae on the dorsal preapical lobe and the setae on the mesal surface extend anterad of the dorsal process. In specimens from other parts of North America there are fewer than 10 setae on the dorsal lobe of the parameres and the setae are coarser, as they are also in Eurasian specimens examined; but the fine setae on the mesal surface in Eurasian material extend anterad of the dorsal lobe as in Beringian specimens.

In females, the dorsal margin of segment IX is truncate in 98 per cent of Nearctic Beringian specimens examined and also in Eurasian specimens, differing from the rounded condition found in 87 per cent of North American populations generally. Segment X in dorsal aspect is bifid in only about 17% of Nearctic Beringian females examined, but in 90% of specimens from elsewhere in North America; in most Nearctic Beringian specimens the apex of X is blunt or pointed rather than bifid.

This species is univoltine at Tuktoyaktuk, Northwest Territories, where larvae live in tundra ponds (Winchester 1984).

**Onocosmoecus unicolor** (Banks) (122)

It seems likely that *Onocosmoecus* is part of a complex of dicosmoecine genera that arose in North America (Wiggins and Flint in prep.). Marked variation in this species is confirmed by no fewer than 6 synonyms, but analysis of specimens from many localities revealed no congruent geographic pattern (Wiggins and Richardson 1987). We infer that some populations passed the Pleistocene glaciation south of the ice in North America because the only other species known in the genus, *O. sequoiae* Wiggins and Richardson, is confined to the Sierra Nevada Mountains of California and may have originated there as a glacial disjunct. Widespread occurrence of variable populations of *O. unicolor* in North America from British Columbia to Newfoundland indicates that other populations of this species extended across a broad front to the south of the glaciers, and that *O. unicolor* occurred in North America before Pleistocene glaciation began. This leads to the further possibility that other populations of *O. unicolor* in the Beringian refugium dispersed to eastern Asia across the Bering land bridge during the Pleistocene glaciation. Larvae of this species live in cool waters of slow streams and the littoral zone of lakes, habitats that would have been readily available on the Bering land bridge; larvae in streams in interior Alaska fed entirely on plant detritus (Irons 1988).

**Molannidae**

**Molanna flavicornis** Banks (127)

This is the only North American species of *Molanna* with a transcontinental distribution. It is very similar to and is perhaps identical with the Eurasian *Molanna albicans* Zett., resulting in a circumboreal range through northern Eurasia and North America (Fuller 1987). The *albicans* group of several species evidently arose in Eurasia and only this single Nearctic extension now exists. Montane populations in Colorado are interpreted as glacial relicts, indicating that this species ranged widely to the south of North American glaciers during the Pleistocene, and thus its Holarctic distribution would have been established before Asia and North America were separated in the Pliocene. Larvae live on the bottom of cool lakes.

**Molannodes tinctus** Zetterstedt (128)

Collections of this northern Eurasian species in Alaska and the Yukon have led to the entrenched view that it was a glacial relict confined to the Beringian refugium. In recent
years, however, isolated collections of the species have been made in Saskatchewan and northern Ontario (Fuller 1987). Based on the broad distribution of *M. tinctus* in northern Europe and Asia, and on phylogenetic evidence for the origin of *Molannodes* in Asia (Fuller 1987), an eastward dispersal by way of the Bering land bridge is inferred. Evidence is equivocal as to whether dispersal occurred in Pleistocene time or earlier.

**Phryganeidae**

*Agrypnia colorata* Hagen (129)

Material from Asia has been referred by most authors to *A. principalis* (Martynov), but this name is a junior subjective synonym of *A. colorata* Hagen (Wiggins in press). All Beringian specimens examined and all from the Palaearctic portion of the range are dark in colour on the thorax, legs, and wings; and all have fully developed tibial spurs of 2,4,4, typical for the family Phryganeidae (Fig. 18). The single exception in Palaearctic material that we examined is a light-coloured female from the Keriya River area of China (Sinkiang Prov.; ZMAS), although the tibial spurs were fully developed. In contrast, most North American specimens taken outside Beringia are light in colour on the thorax, legs, and wings, and have the tibial spurs reduced in some way. The pattern of reduction is variable—some spurs may be absent, others reduced to tiny knobs; and in any pair of spurs, one might be reduced or lacking and the other normal; opposite members of a pair of legs often have different spur conditions. Exceptions occur in series from Fort McPherson, Northwest Territories and Kamloops, British Columbia (ROME), in which specimens are dark as in Beringian and Palaearctic material, but the tibial spurs are variable as in most North American populations. No congruent variation was found in genitalic characters. [Specimens examined: N. Am.—58 ♀, 55 ♂]

The sister species of *A. colorata* is *A. legendrei* (Navas) known only from China. We interpret the light-coloured *A. colorata* to be a vicariant Nearctic form derived from dark ancestral stock with unmodified spurs following separation of Asia from North America, perhaps in Pliocene time. Nearctic populations would have been isolated to the south of the Pleistocene glaciers when light colour and unstable tibial spurs could have been established; disjunct montane populations of the light-coloured form in Wyoming and Utah are consistent with this interpretation (Wiggins in press). The plesiomorphic dark Palaearctic form with stable tibial spurs would have dispersed to Nearctic Beringia across the land bridge. Following retreat of the ice, contact between the 2 forms in North America could have given rise to intergrading populations such as those near Kamloops and Fort McPherson.

*Agrypnia pagetana* Curtis (135)

No close relative of this species is known (Wiggins in press). We infer that *A. pagetana* is a Eurasian species that reached North America across the Bering land bridge, perhaps during the Pleistocene, and dispersed through northern North America following recession of the glaciers. It has not been recorded east of Hudson Bay. Populations of *A. pagetana* in Europe range farther south to more temperate climates than in North America. Larvae of this species live in small tundra ponds and slow-flowing streams; they are univoltine at Tuktoyaktuk, Northwest Territories (lat. 69°29’N) (Winchester 1984).

**III. Palaearctic-East Beringian Species**

Because of their broad Eurasian range and restricted North American distribution, these species are inferred to be of Palaearctic origin. Dispersal to North America across the Bering land bridge during the Pleistocene seems the most likely route for a number of these species. The 13 species in category III constitute about 10 per cent of the Yukon fauna.
Failure of these East Beringian species to broaden their postglacial Nearctic range perhaps could be attributed to competition for resources from species advancing from the south which were better adapted to the freshwater habitats of the deglaciated terrain, or in any case from species that reached the new habitats first. As discussed previously, closure of Beringia by conjunction of the Laurentide and Cordilleran ice sheets probably would have caused some extinction in Nearctic Beringia; consequently a wider range of ecologically coordinate species from the much larger, and biologically more diverse, West Beringia would have encountered reduced competition when they dispersed to East Beringia. But this advantage of the Palaeartic species might well have been less effective in postglacial time when Nearctic species were reassembled in more tightly packed communities.
other reasons, most Palaeartic-East Beringian species of category III have functioned neither as aggressive colonists nor ecological generalists in North America; but quite clear is the contrast with Europe and Asia where most of them are widely distributed, and apparently are successful generalists. It is one of the striking paradoxes of Beringian distributions that wide-ranging, and evidently competitively successful, Eurasian species remain confined to their East Beringian outpost, evidently unable to disperse much beyond their former glacial refuge. This distributional paradox can be added to the productivity paradox (e.g. Hopkins et al. 1982) as significant questions about the biological history of Beringia. This issue focusses on species of category III because they may differ from category II essentially in lacking the competitive ecological edge required in new communities; Palaeartic species having that competitive edge now meet the distributional criterion of category II.

For several of them (Ylodes kaszabi, Arctopora trimaculata, Grammotaulius signatipennis, Limnephilus stigma, and Agrypnia obsoleta), sister-group relationships suggest intercontinental vicariance, perhaps during the Pliocene or earlier, followed later by dispersal of the Palaeartic form to East Beringia, probably across the Pleistocene land bridge.

In Agraylea cognatella and Limnephilus fenestratus, morphological similarity to their respective Nearctic sister species is so close that dichotomy during the Pleistocene could be reasonably inferred. Subdivision of the range by glacial ice seems likely, with the Nearctic sister species originating in isolation to the south of the glaciers.

### Hydroptilidae

**Agraylea cognatella** McLachlan (4)

The Palaeartic range of *A. cognatella* appears to be circumscribed by *A. multipunctata* Curtis which is widely distributed through Europe and western Asia (Botoşăneanu and Levanidova 1988); in North America, *A. cognatella* is evidently circumscribed to the south of Beringia, not by *A. multipunctata* as has been the traditional interpretation (e.g. Ross 1944), but by a sibling species *A. fraterna* Banks apparently now widely distributed on this continent (Vineyard and Wiggins in prep.). It seems reasonable to infer from present evidence that *A. cognatella* is a Palaeartic-East Beringian species now confined in North America to the refugium, and that *A. fraterna* passed the glacial period to the south of the ice where it may have arisen.

### Rhyacophilidae

**Rhyacophila mongolica** Schmid, Arefina and Levanidova (14)

Spicipalpia

- *Agraylea cognatella* McLachlan

Integripalpia

- *Ylodes kaszabi* Schmid

Hydroptilidae

- *Arctopora trimaculata* (Zetterstedt)
- *Dicosmoecus obscuripennis* Banks
- *Grammotaulius signatipennis* McLachlan
- *Grensia praeterita* (Walker)
- *Limnephilus diphyes* McLachlan
- *Limnephilus fenestratus* (Zetterstedt)
- *Limnephilus stigma* Curtis

Phryganeidae

- *Agrypnia obsoleta* (Hagen)
- *Agrypnia sahlbergi* (McLachlan)
- *Oligotricha laponica* (Hagen)
In phylogenetic analyses of *Rhyacophila*, some 25 species from eastern and western North America, Siberia, Japan, and Europe have been assigned to the *sibirica* species group (Ross 1956; Schmid 1970). This group forms the major component of *Rhyacophila* in Palaearctic Asia, and includes the only 2 Holarctic members of the genus known to date—*R. narvae* and *R. mongolica* (Taxonomic Note 1). *Rhyacophila mongolica* is considered the sister species of *R. sibirica* McLachlan (Schmid et al. 1993). Among 14 species of *Rhyacophila* occurring in the Yukon, *R. mongolica* (Fig. 2) is recorded much farther north than any of the others (Fig. 1, region 4), indicating that the species was ecologically adapted for dispersal to North America across the Bering land bridge during the Pleistocene.

**Leptoceridae**

*Ylodes kaszabi* (Schmid) (67)

The genus *Ylodes* appears to have originated in north-central Asia (Manuel and Nimmo 1984), and *Y. kaszabi* occurs in Mongolia. A sister-species relationship with the Nearctic *Y. schmidi* suggests the possibility of intercontinental vicariant origin during the Pliocene or perhaps earlier; thus *Y. kaszabi* is inferred to have been a Palaearctic species that later reached North America by way of the Bering land bridge during the Pleistocene.

**Limnephilidae**

*Arctopora trimaculata* (Zetterstedt) (72)
In addition to *A. trimaculata*, 2 North American sister species are recognized in *Arctopora*: *A. pulchella* (Banks) (71), transcontinental from Yukon and Alaska to Newfoundland and New Hampshire; and *A. salmon* (Smith) in Idaho (Fig. 19). The evidence suggests vicariant speciation from a circumboreal common ancestor, followed by derivation of the North American species pair from subdivision of the range, possibly by glacial ice. This interpretation leads further to Pleistocene dispersal of *A. trimaculata* from Asia to North America across the Bering bridge; but the species remained confined to East Beringia following deglaciation, perhaps because *A. pulchella* was better adapted for colonizing the new habitats. In any case, the 2 species are now geographically sympatric in East Beringia (Fig. 19).

*Dicosmoecus obscuripennis* Banks (81)

*Dicosmoecus obscuripennis* is the only member of the Palaearctic *palatus* species group recorded from North America (Wiggins and Richardson 1982). Study of additional collections provided by I.M. Levanidova (Vladivostok) revealed that this species is actually widespread in eastern Russia—a situation further investigated by Nagayasu and Ito (1993); Asian specimens examined are larger, the length of male forewings 20–25 mm, in contrast to 18–20 mm for North American specimens. If this species reached North America from Asia during the Pleistocene, passage over the Bering land bridge might not have been wholly dependent upon the clear running waters to which larvae of species of *Dicosmoecus* are usually confined because larvae of *D. obscuripennis* have been found along lake margins in the Russian Far East (I.M. Levanidova, pers. comm.). After retreat of the glaciers, *D. obscuripennis* appears not to have penetrated North American habitats much beyond its glacial-age Beringian range. Possibly a limiting factor in North America is the widespread occurrence of *D. atripes* (80), an ecologically vigorous species of the western montane region ranging from California to Yukon and Alaska, which appears to have reached Beringia from the south following glacial recession (Fig. 20).

*Grammotaulius signatipennis* McLachlan (86)

This is the sister species of *G. alascensis* Schmid recorded from northern North America (Taxonomic Note 6). From the evidence available, *G. signatipennis* is probably a Palaearctic species, extended in range to North America across the Bering land bridge during the Pleistocene.

*Grensia praeterita* (Walker) (87)

This is one of the very few truly arctic species of Trichoptera, and it probably occurred in Beringia, at least in part, during glacionation. In contrast to most of the other species assigned to category III, *G. praeterita* has extended its postglacial range considerably beyond Beringia. Evidently, the species does not occur on the mainland of North America east of Hudson Bay (Harper 1989), indicating that its dispersal to Greenland was probably by way of the Arctic Archipelago. Comparison of Yukon specimens with material from the Northwest Territories and Russia revealed no morphological differences, although the latter were slightly larger.

*Limnephilus diphyes* McLachlan (96)

This species is recorded from North America for the first time (Taxonomic Note 7). Its affinities are obscure, but since it has not been collected south of Alaska and the Yukon, the evidence suggests that *L. diphyes* is a Palaearctic species that reached North America during the Pleistocene and has not spread beyond East Beringia. Larvae of *L. diphyes* live in sphagnum bog pools (Johansson et al. 1991).
Fig. 20. Distribution of *Dicosmoecus atripes* (Hagen) (80) and *D. obscuripennis* Banks (81) (Limnephilidae); the latter is widely distributed in eastern Asia.
Limnephilus fenestratus (Zetterstedt) (101)

The very similar sister taxon of *L. fenestratus* is *L. kennicotti* (107) (category I), which occurs widely through northern North America and in Greenland (Fig. 21). We have identified both taxa in separate collections from the Yukon (Kluane and Firth River). The two are most readily separable by male genitalic structure: in *L. fenestratus* the intermediate appendages are relatively short and do not extend beyond the superior appendages in lateral aspect, but are longer in *L. kennicotti* and do extend beyond the superior appendages in lateral aspect. Diagnostic characters for males and females of both species were illustrated by Kimmins and Denning (1951, figs. 10, 11, as *L. miser* McLachlan which is a junior subjective synonym of *L. fenestratus* proposed by Schmid 1955; and figs. 12, 13, as *L. moselyi* Kimmins and Denning from Greenland which is a junior subjective synonym of *L. kennicotti* proposed by Ross and Merkley 1952).

We presume that records of *L. fenestratus* from Greenland by Fristrup (1942), repeated by Gislason (1981), were based on Mosely’s (1929) misidentification of *L. kennicotti* as *L. miser* (= *fenestratus*); a series of specimens we examined from Greenland (Zoologisk Museum, Copenhagen, per N.P. Kristensen) proved to be *L. kennicotti*. From the Yukon, Nimmo and Wickstrom (1984) do not record *L. fenestratus*, but provide several records for
L. kennicotti; we have confirmed that their material from Kluane National Park and Firth River is L. kennicotti, but that from Burwash Landing is really L. fenestratus. In the Yukon material examined, we found some indication that male genitalic characters intergrade between these 2 taxa. Moreover, putative distinction between females (Kimmins and Denning 1951) has proven unreliable because of variation in genital characters, culminating in our material in 2 females collected with a male of L. fenestratus (Yukon: Old Crow Flats, ROME 810587a); one female shows characters attributed to L. kennicotti, the other to L. fenestratus. Further evidence on variation is required before the status of these taxa can be confirmed. [North American specimens examined: L. fenestratus 26 ♂, 29 ♀; L. kennicotti 18 ♂, 32 ♀].

Whether or not these 2 forms are distinguished as species, their distributional relationships are informative in a Beringian context. If the very close morphological similarity between the 2 taxa is interpreted to indicate separation during the Pleistocene, L. kennicotti could have diverged as a disjunct population along the southern margin of the North American glaciers. By this interpretation, L. fenestratus would have been the Holarctic ancestor, and its present East Beringian population would be a glacial relict. As the ice receded, widespread recolonization by L. kennicotti over northern North America evidently led to its dispersal to Greenland, approaching the western limit of its ancestral stock represented by L. fenestratus in Iceland (Fig. 21). Judging from material we have examined, L. fenestratus has extended its Nearctic range little if at all beyond unglaciated Beringia; L. kennicotti has shown marked capacity for colonizing deglaciated habitats, evidently far into the northern Yukon where the 2 forms are now apparently sympatric. Some intergradation in the morphological characters distinguishing the two (see above) suggests that this postglacial sympatry has yet to reach some equilibrium.

Limnephilus stigma Curtis (118)

Records for the close sister species L. indivisus Walker, now widespread over much of North America, approach the Nearctic limit of L. stigma in the Northwest Territories (Fort Smith, CNCI) and northern British Columbia (Alaska Hwy. km 359, Prophet R. Prov. Park, ROME). Specimens from Kluane in the Yukon were identified as L. indivisus by Nimmo and Wickstrom (1984), but our examination of that same material indicates that they are L. stigma. In the continued absence of intermediates, we infer that the 2 species do not hybridize. It has long been recognized that L. stigma (Figs. 22–25) is very similar morphologically to the widespread North American species L. indivisus Walker (e.g. Betten and Mosely 1940). Males of L. indivisus are distinguished by the much longer intermediate appendages and by the ventral gap in the mesal dentation of the superior appendages (Fig. 26); females of L. indivisus are distinguished by the narrow and deeply incised apex of segment X, especially evident in ventral aspect (Fig. 27).

Material of L. stigma from Yukon and Alaska [26 ♂, 24 ♀] differs slightly in genital characters from specimens examined from Europe and northern Asia [18 ♂, 16 ♀]. In East Beringian males (Fig. 24b), the peripheral dentate ridge on the superior appendages bears a large point underlying the intermediate appendages which is lacking from European specimens (Fig. 22b). Males in our Nearctic material of L. stigma bear a prominent sclerotized point on each paramere (Fig. 24d); this sclerotized point is lacking in specimens we examined from Europe (Fig. 22c; and Malicky 1983, p. 188), but is present in specimens examined from Kamchatka. In East Beringian females (Fig. 25), the apex of segment X is more narrowly tapered than in Eurasian material (Fig. 23), especially in ventral aspect.
Figs. 22–25. *Limnephilus stigma* Curtis (111) (Limnephilidae). 22, Male genitalia of specimen from Europe: a, lateral; b, caudal; c, phallus, lateral; 23, Female genitalia of specimen from Europe: a, lateral; b, dorsal; c, ventral; 24, Male genitalia of specimen from Yukon: a, lateral; b, caudal; c, superior appendage, mesal; d, phallus, tip of paramere; 25, Female genitalia of specimen from Yukon: a, lateral; b, dorsal; c, ventral.
The sister species could have arisen through vicariant speciation of the circumboreal range of a common Pliocene ancestor, giving rise to *L. stigma* in Eurasia and *L. indivisus* in North America; during the last glacial advance, *L. indivisus* probably would have been restricted to the south of the ice, while *L. stigma* could have entered the East Beringian refugium but did not extend its range. Larvae of these species inhabit small marshy water bodies, including temporary pools (Wiggins 1973).

**Phryganeidae**

*Agrypnia obsoleta* (Hagen) (134)

We have material of this widely distributed Eurasian species from the northern Yukon. Its Nearctic sister species, *A. deflata* (Milne) (130), is common over much of northern and western montane North America; although designated as a subspecies *A. obsoleta deflata* by some authors (e.g. Milne 1934; Fischer 1964; Nimmo and Wickstrom 1984), the evidence does not support this interpretation (Wiggins in press). Specimens from British Columbia identified as *A. obsoleta* (Nimmo and Scudder 1983: Glacier Nat. Park, 1♂ 1♀) have been examined, and are *A. deflata*.

Two successive events seem to have been involved: vicariant subdivision of the circumboreal ancestor from which the sister species *A. obsoleta* and *deflata* were derived in Eurasia and North America respectively, perhaps during the Pliocene or earlier; and subsequent Pleistocene dispersal of *A. obsoleta* to East Beringia during a recent glacial advance, perhaps with *A. deflata* restricted to the south of the Laurentide and Cordilleran glaciers. Outlying montane populations of *A. deflata*, for example in Colorado (Wiggins in
press), can be interpreted as relicts from this time. With recession of the ice, *A. deflata* now occurs in northern and montane North America to the Yukon and Alaska, but evidently *A. obsoleta* has dispersed little beyond Beringia.

*Agrypnia sahlbergi* (McLachlan) (136)

This species is widespread from Scandinavia through northern and eastern Asia. It is recorded here from the Yukon and also from Alaska, and recently from British Columbia (Nimmo and Scudder 1978). We infer that it reached this continent by way of the Bering land bridge during the Pleistocene, and evidently has dispersed southward to a limited extent.

*Oligotricha lapponica* (Hagen) (139)

All 5 species of *Oligotricha* are Palaearctic (Wiggins and Kuwayama 1971), but only *O. lapponica* extends to North America where records are confined to the Yukon and Alaska. From this evidence, we infer a Eurasian origin for *O. lapponica*, and it probably reached North America across the Bering land bridge during the Pleistocene. The forewings usually bear reticulate dark markings on a lighter background (Wiggins and Kuwayama 1971), but in some populations from northern Lapland of Sweden and Finland the wings are uniform dark brown—*O. lapponica* var. *hyperborea* (Forsslund 1933). Some specimens we have seen from East Beringia also have uniform dark brown wings, others have normal reticulate wings. The brown-winged form of *O. lapponica* in Europe and in East Beringia probably arose from independent changes in the genotype. This condition suggests a parallel with melanic forms that occur in some butterflies, apparently as they approach their ecological limits (Downes 1966); but in one species of the genus, *O. striata* (Linnaeus) of Europe, the wings are consistently uniform dark brown (Wiggins and Kuwayama 1971).

This species is a good example of the Beringian distributional paradox—a widespread and successful species throughout Eurasia, but evidently still circumscribed in North America within the borders of unglaciated Beringia (cf. *Asynarchus lapponicus* (75), category II). Biotic factors responsible for this situation could include the closely related phryganeid *Banksiola crotchi* (Banks) (138)—a common and locally abundant transcontinental Nearctic species that is clearly aggressive ecologically (Wiggins 1956); *Oligotricha* and *Banksiola* are sister genera (Wiggins in press). Larvae of both genera live in shallow waters of lakes, marshes, and slow streams; consequently, suitable habitats that might otherwise accommodate *O. lapponica* in North America beyond Beringia are likely to have been pre-empted by *B. crotchi* or possibly by some other species in the Phryganeidae. Coupled with this is the probability of some genetic drift in the populations isolated in Nearctic Beringia, perhaps altering their competitive potential; some change in the genome can be inferred from reappearance of the uniform brown forewings.

IV. Beringian Species

These species share distributional and biological characteristics indicating that they were confined to Beringia during the Pleistocene glacial period. Five are Nearctic species recorded from the Yukon, Alaska, or the Northwest Territories. On present evidence these species appear to be East Beringian endemics or glacial relicts from a broader pre-Pleistocene range in North America. Two species, *Lenarchus expansus* and *Asynarchus innuitorum*, occur in both Nearctic and Palaearctic Beringia, but are not known elsewhere. Most of these species appear to be confined to arctic or alpine tundra, and are consistent with the general pattern in other groups in which the arctic species were derived from Beringia. One Nearctic species, *Limnephilus pallens*, is assigned provisionally to category IV because some records
are anomalous with the general pattern. Two species (†) not yet recorded from the Yukon may occur there.

Integripalpia
Leptoceridae
Ylodes schmidi Manuel and Nimmo
Apataniidae
Allomyia picoides (Ross) (†)
Limnephilidae
Asynarchus innuitorum (Nimmo) (†)
Grammotaulus alascensis Schmid

Leptoceridae
Ylodes schmidi Manuel and Nimmo (69)

This species is known only from the type locality in the Yukon, and was proposed as the sister species of Y. kaszabi (67) (Manuel and Nimmo 1984). Under that species (category III), it was suggested that Y. schmidi may have originated as the Nearctic vicariant from a common ancestor that occurred in both northwestern North America and eastern Asia.

Apataniidae
Allomyia picoides (Ross) (†)

This species has not been recorded outside of Alaska (Katmai; Ross 1950); although its range may or may not extend to the Yukon, it can be considered a Nearctic (East) Beringian endemic or relict.

Limnephilidae
Asynarchus innuitorum (Nimmo) (†)

Although this species has not been recorded yet from the Yukon, it was described from a tundra stream in the vicinity of Tuktoyaktuk, Northwest Territories, a short distance from the Yukon border (Fig. 1) (Winchester 1984: Limnephilus species A); and it has been found also across the Bering Strait in Chukotka (A.P. Nimmo, pers. comm.). Assigned originally to Limnephilus, this species was transferred to Asynarchus by Ruiter (1995:23-24). On the basis of existing information, we infer that A. innuitorum is a Beringian endemic, and probably also a glacial relict.

Grammotaulus alascensis Schmid (84)

This species appears to be the Nearctic sister species of the originally Palaearctic G. signatipennis (86) (category III). Present evidence suggests that G. alascensis passed glaciation in East Beringia, and dispersed eastward to Hudson Bay as the ice receded (See Taxonomic Note 6).

Lenarchus expansus Martynov (90)

Records for this species indicate that it is known only from the Beringian refugium in both Asia (Schmid 1952: Kolyma delta, Jana plains) and North America (Alaska, see also Nimmo 1986; Yukon, see above). In West Beringian specimens the forewings are light tan in colour with only faintly contrasting markings (Martynov 1914); but in all except one specimen (YT: Firth R.; CNCI) in the Nearctic material that we have seen, the dark markings of the forewing contrast strongly with the light base colour. Diversification in colour is probably a consequence of the isolation of the 2 populations. Since we found no morphological differences, the amphi-Beringian range could have been achieved by way of the
Pleistocene Bering land bridge. The species was assigned to the subgenus *L. (Lenarchus)* (Schmid 1952), the only Holarctic member of the group of 6 Nearctic and Palaearctic species. Although *L. expansus* is an amphi-Beringian species, its origin in either Asia or North America remains unresolved.

Larvae of most *Lenarchus* live in standing waters, but those of *L. expansus* have been found in water-saturated tundra sod (MacLean and Pitelka 1971). Under these conditions, restriction of this species to Beringia is noteworthy because, although wet tundra habitat seems scarcely limiting now, it is thought to have been rare in Pleistocene Beringia, when much drier conditions prevailed (Schweger et al. 1982). Consequently, wet tundra must have been available in Beringia throughout the Pleistocene, at least in localized patches. (See also *Sphagnophylax meiops*.)

**Limnephilus fumosus** Banks (102)

Present information on distribution of the two very similar North American sister species, *L. fumosus* and *L. santanus*, suggests that they may be the products of populations that became disjunct during the formation of glaciers. If *Limnephilus fumosus* is confined to northern latitudes, it probably passed the Pleistocene glacial period in Beringia, although there is no evidence for dispersal to Asia across the Bering land bridge. *Limnephilus santanus* is known from Oregon and probably occurs in Washington (Banks 1900). Oregon was not covered by ice, but lies at the southern edge of the maximum extent of glaciation; thus records from British Columbia are critical in interpreting the postglacial history of these 2 species (see Taxonomic Note 8). All of this indicates that *L. fumosus* is probably a glacial relict confined to East Beringia.

**Limnephilus pallens** Banks (109)

This species was assigned to the *asiaticus* group (Schmid 1955) with 3 other North American and 8 Eurasian species. Judging from the male genitalic morphology (Nimmo 1991), *L. pallens* appears to be more closely related to several of the Eurasian species, especially *L. tricalcaratus* Mosely (1936) from Tibet, than to North American species. Larvae of this species live in tundra ponds (Lehmkuhl and Kerst 1979), and thus its adaptation to far northern conditions during Pleistocene glaciation seems assured. If this species passed the glacial period in a northern refugium such as East Beringia, evidently it did not become established in West Beringia. If *L. pallens* is a Nearctic Beringian endemic species, it must have dispersed eastward to Hudson Bay (Lehmkuhl and Kerst 1979; Rankin Inlet) following glacial recession. However, a recent record for *L. pallens* from the Michigan shore of Lake Huron (Ruiter 1995) raises the possibility that this eastern extension could have been derived from the southern margin of the glaciers, as the ice retreated. Because of these discrepancies, assignment of *Limnephilus pallens* to category IV is provisional.

**Sphagnophylax meiops** Wiggins and Winchester (126)

This species (Frontispiece, Fig. 28) has been collected in the Yukon and in adjacent parts of the Northwest Territories (Aklavik, Tuktoyaktuk), but is otherwise unknown. *Sphagnophylax* is a monotypic genus, which on morphological grounds appears to represent an aberrant lineage in the limnephiline tribe Limnephilini (Winchester et al. 1993); and *Sphagnophylax* is the only trichopteran genus known that is confined to Beringia. Consequently, *S. meiops* would be both a phylogenetic and a geographic relict, apparently preserved from extinction only by the unglaciated Beringian refugium. The larval habitat of wet moss in transient tundra pools is significant because larvae of some other phylogenetically relict Trichoptera also occur in wet edaphic sites; a low incidence of competitors and
predators in these sites may be a factor in the survival of relict Trichoptera (Wiggins 1984). Occurrence of this species in wet tundra is also interesting because the Beringian refugium for at least part of the Pleistocene is inferred to have been a region of low precipitation throughout the year and a predominantly dry upland region with little muskeg where Sphagnum was absent (Schweger et al. 1982). Survival of S. meiops, and also of Lenarchus expansus (see above) which evidently lives under similar conditions, indicates that areas of wet tundra persisted in Beringia.

Reduced wings (Fig. 28) and anomalous venation suggest that this species has limited ability to fly and perhaps is even flightless; and the eyes are unusually small for adult Trichoptera. Similar modifications occur in a number of arctic Lepidoptera (Downes 1964).

V. Holarctic Species Not in Beringia

Because categories II, III and IV include almost all of the North American Trichoptera now recognized as occurring in Europe and Asia as well, it is useful for comparison to add here the few remaining Holarctic species. Six species are assigned to category V, and none has been recorded from the Yukon; most of them probably dispersed from one continent to the other under more equable conditions of climate some time before the separation of Asia and North America in the Pliocene. With Holarctic distribution established long ago, these species appear now to be disjunct relicts, still resistant to cladogenetic divergence.

Fig. 28. Adult of Sphagnophylax meiops Wiggins and Winchester (126) (Limnephilidae). Brachyptery and anomalous venation suggest that this species is probably flightless, and perhaps was preserved from extinction only by the unglaciated Beringian refugium. Forewing length 4 mm. (From Canadian Journal of Zoology)
Hydroptilidae

*Ithytrichia clavata* Morton

This species is widely distributed in North America from British Columbia to California, through Texas, Kansas, Oklahoma to Quebec and New Hampshire; it is widespread through northern and western Europe (L. Botoșăneanu, pers. comm.). It is not now a far northern species in either North America or Europe, and would seem unlikely to have dispersed across the Bering land bridge during a glacial climate regime. Moreover, the larvae live in running water, a habitat used by only very few successful Pleistocene dispersants. This evidence suggests that Holarctic distribution was achieved before the Quaternary glacial periods occurred, and perhaps the Nearctic and Palaearctic forms have diverged to some extent not yet recognized, as in the *Agraylea multipunctata* complex (Vineyard and Wiggins in prep.). In any event, the name *I. clavata* was based initially on populations in New York (Ithaca), and further taxonomic resolution is focussed on European populations.

*Oxyethira mirabilis* Morton

The range of this species in northern Europe has been extended to eastern Canada with recognition of *O. barnstoni* Harper as a junior subjective synonym (Kelley 1984). The pattern of distribution, if now adequately understood, suggests a north Atlantic dispersal. It is the only European representative in the *aeola* group of *O. (Oxytrichia)*, which is otherwise entirely confined to North and South America (Kelley 1984).

Polycentropodidae

*Polycentropus picicornis* Stephens

This species occurs through most of Europe (Botoșăneanu and Malicky 1978), Siberia and Mongolia to Kamchatka (Lepneva 1964; Mey and Dulmaa 1985). It is known locally in North America from the Northwest Territories to New Hampshire and may yet be recorded from the Yukon. Larvae live in small bodies of standing water and in slow currents of rivers (Lepneva 1964). This pattern of northern distribution suggests that *P. picicornis* could have passed between Asia and North America more recently than other species of category V, possibly during the Pleistocene.

Psychomyiidae

*Psychomyia flavida* Hagen

This species was described from North America where it is transcontinental and abundant in running waters. The Asian *P. composita* Martynov was proposed as a junior subjective synonym of *P. flavida* (Schmid 1965b); consequently, a wide distribution through Siberia, Mongolia, and North America now has to be attributed to *P. flavida*. In this context, the absence of records of any *Psychomyia* from the Russian Far East (e.g. Levandova 1982) is of interest. In North America, *P. flavida* has not been recorded in the extreme northwest, but only to the edge of treeline at Churchill, Manitoba (Lehmkuhl and Kerst 1979), and ranges from British Columbia to California and Nova Scotia to North Carolina. Thus, whatever its place of origin, dispersal of *P. flavida* across the Bering land connection between North America and Asia probably occurred in a climate more moderate than the Pleistocene glacial periods.

Limnephilidae

*Grammotaulius betteni* Hill-Griffin

Known originally from Oregon, this species has also been recorded from China (Schmid 1950a). Larvae live in slow streams and small marshy ponds (Hill-Griffin 1912), some of
which are probably temporary (Wiggins 1977); however, the species is not part of the northern Nearctic fauna.

_Hydatophylax variabilis_ Martynov

Widely distributed through northern Eurasia from Sweden to Kamchatka (Schmid 1950b) and Chukotka (Levanidova 1982) at the eastern extremity of Siberia, this species has also been collected at several localities in southeastern Alaska. It has not been recorded from the Yukon or elsewhere in North America. The species is part of an Asian complex (Schmid 1950b), and on present evidence represents dispersal across the land connection between North America and Asia—either in Pleistocene or Pliocene time. This is the only Holarctic trichopteran known to occur in the coastal extension of southeastern Alaska; several Nearctic species appear to have moved northward to this area after retreat of the glaciers, but are not known elsewhere in Alaska or in the Yukon. This pattern of distribution might reflect a coastal glacial refugium for aquatic insects (e.g. Kavanaugh 1988), but streams with ample organic detritus would be required for survival of the larvae (e.g. Irons 1988).

**Ecological Considerations**

Aquatic insects have major roles in the cycling of nutrients and energy which underlies the natural productivity of freshwater systems. At temperate latitudes, aquatic insect larvae are diverse and abundant; and in individual systems, Trichoptera are usually high in both diversity and abundance in relation to other aquatic insects (Wiggins and Mackay 1978). However, our analysis has shown that species diversity in Trichoptera shows a marked decline at higher latitudes. Because the fauna is now fairly well defined, the Yukon Trichoptera provide a promising focus for inquiry into the exploitation of aquatic habitats by caddisflies at higher latitudes and into the biological factors responsible for this latitudinal decline in diversity.

We examine these questions by contrasting patterns of geographic distribution and the use of resources in different behavioural and ecological groups of Yukon Trichoptera with the same groups at more temperate latitudes in North America. Considering first the generic level, approximately 150 genera are recognized in North American Trichoptera—case-makers, retreat-makers, and cocoon-making species combined (Wiggins 1996). Comparison between genera of running-water (lotic) and standing-water (lentic) forms in the North American Trichoptera yields a ratio for lotic genera to lentic genera of about 4:1. This is a valid biological comparison because the genus is an ecological as well as a morphological unit for Trichoptera (Wiggins and Mackay 1978); with few exceptions, habitats for species at this broad level of discrimination are consistent within genera of Trichoptera. A ratio of 4:1 demonstrates that in North America overall there are, by a substantial margin, more ecological niches accessible to Trichoptera in running waters than in standing waters.

A similar comparison between lotic and lentic genera for the 51 genera of Trichoptera recorded from the Yukon yields a ratio of approximately 1:1. The contrast between 4:1 for North America and 1:1 for the Yukon substantiates a marked decline in lotic-dwelling taxa with increasing latitude. This decline could be attributed either to reduction in the resources available to lotic Trichoptera, or to diminishing ability of Trichoptera to exploit lotic niches at higher latitudes; this issue is best approached at the species level.

To examine the decline in diversity of Trichoptera at the species level in the north, the Yukon fauna of 145 species can be contrasted with that of British Columbia immediately to the south, where 279 species have been recorded (Nimmo and Scudder 1978, 1983). In broad
terms, these figures demonstrate that from latitude 49°N on the southern border of British Columbia to 60°N at the southern border of the Yukon, the trichopteran fauna decreases by 134 species—approximately 50 per cent (Table 1). An adjunct to this database is available from a list of the Trichoptera of Alaska (Nimmo 1986). These 3 adjacent areas have similar montane topography and all have been affected by glaciation to some extent, either directly or indirectly.

To extend the analysis, the northern terminus of this latitudinal gradient in the Yukon can be represented by ecogeographic regions 1 through 5 (Fig. 1), from approximately latitude 67°N at the Arctic Circle to 70°N, extending through treeline and coastal tundra to the Arctic shoreline. Sixty species of Trichoptera are recorded within that area (Table 1), although others will likely still be found. Consequently, the Yukon Trichoptera fauna declines from 145 species to approximately 60 species, about 59 per cent, through the latitudinal gradient of 60° to 70°N.

Numbers of species in each family of Trichoptera compiled for these areas are summarized in Table 1. Through approximately the same latitudinal range, total numbers of species in the faunas of Yukon and Alaska are close, as are the figures for all 3 suborders. The trichopteran fauna of British Columbia is approximately twice that of either Yukon or Alaska; and within the overall latitudinal range of 49° to 70°N the fauna decreases from 279 species to 60—approximately 78 per cent overall. Changes in proportions of the 3 major groups of Trichoptera in these regional faunas are shown in Table 2; there is a general decline in proportions of species of the Spicipalpia and Annulipalpia, and an increase in the proportion of species of the case-making Integripalpia.

<table>
<thead>
<tr>
<th>Family</th>
<th>British Columbia lat. 49° to 60°N</th>
<th>Alaska lat. 60° to 70°N</th>
<th>Yukon lat. 67° to 70°N</th>
</tr>
</thead>
<tbody>
<tr>
<td>Spicipalpia</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Glossosomatidae</td>
<td>13</td>
<td>4</td>
<td>3</td>
</tr>
<tr>
<td>Hydroptilidae</td>
<td>14</td>
<td>4</td>
<td>5</td>
</tr>
<tr>
<td>Rhyacophilidae</td>
<td>43</td>
<td>15</td>
<td>14</td>
</tr>
<tr>
<td>Annulipalpia</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hydropsychidae</td>
<td>21</td>
<td>7</td>
<td>10</td>
</tr>
<tr>
<td>Philopotamidae</td>
<td>7</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Polycentropodidae</td>
<td>13</td>
<td>6</td>
<td>6</td>
</tr>
<tr>
<td>Integripalpia</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Apataniidae</td>
<td>7</td>
<td>5</td>
<td>4</td>
</tr>
<tr>
<td>Brachycentridae</td>
<td>5</td>
<td>4</td>
<td>3</td>
</tr>
<tr>
<td>Calamoceratidae</td>
<td>1</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Goeridae</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Lepidostomatidae</td>
<td>11</td>
<td>3</td>
<td>6</td>
</tr>
<tr>
<td>Leptoceridae</td>
<td>22</td>
<td>12</td>
<td>16</td>
</tr>
<tr>
<td>Limnephilidae</td>
<td>98</td>
<td>57</td>
<td>57</td>
</tr>
<tr>
<td>Molannidae</td>
<td>1</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>Phryganeidae</td>
<td>14</td>
<td>8</td>
<td>13</td>
</tr>
<tr>
<td>Rossianidae</td>
<td>1</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Uenoidae</td>
<td>8</td>
<td>3</td>
<td>4</td>
</tr>
<tr>
<td>Totals</td>
<td>279</td>
<td>132</td>
<td>145</td>
</tr>
</tbody>
</table>
In far northern parts of the Yukon from latitude 67° to 70°N (Table 2), the Spicipalpia decline substantially from their representation over the Yukon and Alaska as a whole, due mainly to a drastic reduction in the lotic and predatory Rhyacophilidae. The Annulipalpia maintain about the same proportion as for the Yukon generally, with a large decline in filter-feeding lotic Hydropsychidae, but a small reduction in the Polycentropodidae which are mainly predacious species tolerant of slow currents and lentic waters. Correspondingly, the proportion of case-making Integripalpia in the far northern trichopteran fauna increases somewhat to 81 per cent (Table 2). Species of the Limnephilidae decline from 57 in the Yukon generally to 26 in the far northern section (Table 1). The genus Limnephilus is represented in the Yukon overall by 27 species, but declines to 15 in the extreme northern part. Limnephilid species of the far northern part of the Yukon occur almost entirely in standing waters or slow currents in streams of low gradient; Dicosmoecus obscuripennis (81) is perhaps the sole exception, and occurs largely in lotic waters.

Reduction in species of the Spicipalpia and Annulipalpia in the Yukon and Alaska (Table 1) translates biologically into a decrease of Trichoptera in running-water habitats at these latitudes, consistent with the generic analysis. Each of the 3 Spicipalpian families represented is substantially reduced (Table 1); and to whatever extent trophic factors are responsible for the decline, they do differ for each family. Larvae in the Glossosomatidae are grazers of diatoms and fine organic particles. In the Hydroptilidae, larvae in almost all of the genera represented feed on filamentous algae. Larvae of most species in the Rhyacophilidae are believed to be predacious, although there is some evidence for specific restriction to certain prey groups, and a few feed on algae and vascular plant tissue; for this family a decline of prey organisms in lotic habitats at higher latitudes could have some influence on diversity.

In the Annulipalpia through the latitudinal gradient of 49° to 70°, species decrease by about 50 per cent in both the Hydropsychidae and Polycentropodidae. The Philopotamidae show a marked decline in species by about 85 per cent, and are rare in collections from the Yukon; larvae in this family are filter-feeders, but consume finer organic particulates than do other filter-feeding Trichoptera. The fine particulate organic matter consumed by filter-feeders and by Annulipalpia generally is largely produced by larvae of the shredder guild of aquatic insects, which includes most case-making Trichoptera (Integripalpia). Decline in filter-feeding Hydropsychidae could be caused by a decrease in fine particulate organic matter carried in suspension by the current; reduced populations of lotic insects

<table>
<thead>
<tr>
<th>Major group</th>
<th>British Columbia lat. 49° to 60°N</th>
<th>Alaska lat. 60° to 70°N</th>
<th>Yukon lat. 67° to 70°N</th>
</tr>
</thead>
<tbody>
<tr>
<td>Spicipalpia</td>
<td>25%</td>
<td>17%</td>
<td>15%</td>
</tr>
<tr>
<td>(mainly carnivores and algal feeders in lotic habitats)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Annulipalpia</td>
<td>15%</td>
<td>11%</td>
<td>10%</td>
</tr>
<tr>
<td>(fixed retreats in lotic habitats)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Integripalpia</td>
<td>60%</td>
<td>72%</td>
<td>75%</td>
</tr>
<tr>
<td>(portable cases, mainly in lentic habitats)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>100%</td>
<td>100%</td>
<td>100%</td>
</tr>
</tbody>
</table>

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generally could affect the supply. Part of the nutrient value of this resource is aquatic hyphomycete fungi growing on faecal particles of other aquatic invertebrates; the fungi are known to grow at low temperatures (Bärlocher and Kendrick 1973). However, studies by Irons et al. (1994) suggest that microbial populations are physiologically less able to maintain optimal metabolic rates at the cold temperatures of high latitudes. Other suspended materials including ultra-fine particulate matter may be involved, but the decline in filter-feeding Trichoptera raises the likelihood that nutritional resources from suspended particulates in general may be marginal for supporting Trichoptera. These factors suggest that filter-feeding species of the Hydropsychidae which are successful at higher latitudes may derive a larger proportion of their food from insect prey than do those at lower latitudes, and perhaps are preadapted through a tendency toward increased predation; the hydropsychid subfamily Arctopsychiinae (Arctopsyche, Parapsyche) is such a group, and is relatively well represented at higher latitudes. Filter-feeding larvae of the Polycentropodidae (Polycentropus, Neureclipsis) also derive a larger part of their food from insect prey than do Hydropsyche and Cheumatopsyche (e.g. Wiggins 1977, 1996). This difference could underlie the more northerly Yukon distribution for polycentropodids among Annulipalpia, and is another question to which more detailed study of Yukon Trichoptera might be directed.

Our analysis shows that within the latitudinal gradient of 49° to 70°N, there is a marked decline in lotic Trichoptera, chiefly Spicipalpia and Annulipalpia, in all of their niches of resource exploitation. Changing trophic resources in lotic habitats will be responsible for some of this decline, but physical changes in running-water habitats must be taken into account. The range of lotic habitats at higher latitudes does not differ significantly from that available to the south, and these habitats are highly diverse in the Yukon and Alaska; but colder temperatures influence winter survival of lotic Trichoptera in smaller streams that freeze to the bottom (e.g. Harper 1981), including the hyporheic zone. Larval Trichoptera do not overwinter in streams that freeze to the bottom in subarctic interior Alaska (Irons et al. 1993), but survive only in sections that do not freeze (Irons 1988). Surveys of Arctic slope streams show that communities of benthic invertebrates are more diverse and of higher density in spring streams than in tundra streams, which in turn are richer than mountain streams (Craig and McCart 1975). The differences were attributed largely to the perennial flow from groundwater in spring streams, contrasted with interrupted flow when the other streams are frozen to the bottom during the long winter period. Trichoptera occurred in 68 per cent of 59 spring streams sampled, but in only 21 per cent of 98 tundra streams, and 1 per cent of 137 mountain streams. Taxonomic refinement below the ordinal level was not provided, but would have been highly informative even at the family level; in any event, both Plecoptera and Ephemeroptera maintained relatively high occurrence of 95 to 63 per cent in all 3 stream types in the same survey. In the larger rivers, water would remain unfrozen beneath the ice. Consequently, the low extremes of temperature in rivers would not differ greatly from lotic waters at more southerly latitudes, although the longer duration of the ice cover might reduce the annual period suitable for growth. However, bottom substrates of large northern rivers tend to be mainly unstable shifting sediments (Barton 1986; Soluk 1985), and inappropriate for stationary, filter-feeding annulipalpian Trichoptera. For example, the low number of caddisflies colonizing streams following the Mt. St. Helens eruption in Washington was attributed by Anderson (1992) to shifting substrata and high mobility of the stream bed. In a glacier-fed river in Alaska, Trichoptera were one of the last insect orders to appear at the progression of sampling sites from the headwaters, downstream (Slack et al. 1979). Studying development of freshwater communities following rapid recession of a neoglacial ice sheet in Alaska, Milner (1987) found that Chironomidae, Ephemeroptera, and
Plecoptera colonized streams but Trichoptera had a minimal role in the formation of new communities. Marked decline in the proportion of Trichoptera in lotic systems of Alaska generally was found by Oswood (1989). Therefore, compared to their dominant role in lotic systems at temperate latitudes (Wiggins and Mackay 1978), Trichoptera are ill-suited to running waters at high latitudes, where larvae are exposed to encasement in ice, unstable substrates, and suspended flow.

However, larvae of several species of case-making Trichoptera (Integripalpia: Limnephilidae, Phryganeidae) in a slow arctic tundra stream near Tuktoyaktuk, Northwest Territories (lat. 69°N), remained frozen in the ice from October through May, when they resumed development to complete their univoltine life cycle (Winchester 1984). Tundra streams support lentic species for the most part. These observations suggest that certain lentic Trichoptera are physiologically capable of tolerating freezing of body fluids, even though some evidence indicates that avoiding freezing by supercooling is unlikely for most aquatic insects (Oswood et al. 1991). In Norway, Solem (1981) found larvae of *Agrypnia obsoleta* (Phryganeidae) to survive enclosure in solid ice for 6 months to −11°C; laboratory experiments confirmed freezing resistance for *A. obsoleta*, but larvae of *Phryganea bipunctata* were dead after several weeks in ice. Larvae of *Agrypnia obsoleta* (Phryganeidae), *Oecetis ochracea* (Leptoceridae), and 2 species of *Molanna* (Molannidae) which survived freezing in ice in a Swedish river had blocked the openings of their cases, although they were not in prepupal or pupal stages (Olsson 1981). These observations raise the critical question whether the portable integripalpian case confers some physiological advantage for overwintering trichopteran larvae embedded in ice? In Chironomidae, larvae constructing winter cocoons have a higher survival rate in frozen habitats than do larvae without cocoons (Danks 1971). Tolerance to the freezing of body fluids appears to be a requirement of Trichoptera living at high latitudes, but these observations further suggest that there may be behavioural as well as physiological components to that tolerance. Resistance to low levels of oxygen is another aspect of the survival of aquatic insects encased in ice (Moore and Lee 1991).

A wholly different approach to cold winter temperatures is shown in 2 species of the Limnephilidae, *Glyphopsyche irrorata* and *Psychoglypha subborealis* (83, 125). Adults of both species collected from October through May near Juneau, Alaska by Ellis (1978a) became sexually mature in spring. This unusual strategy for surviving cold winter conditions raises the question whether larvae of these species are tolerant of freezing; larvae of *G. irrorata* occur in lentic habitats, *P. subborealis* in lotic. Both species are assigned to category I, and are inferred to have reached the Yukon from more southerly areas following retreat of the glaciers.

Among the 3 suborders, there is a considerably smaller latitudinal decline in species of the case-making Integripalpia of about 40 per cent through 49° to 70°N (Table 1). Again, trophic characteristics in the families of Integripalpia are not uniform. Larvae of Apataniidae, Goeridae, Uenoidae, and Brachycentridae in part, feed mainly by grazing diatoms from rock surfaces; this is the same trophic guild to which the Glossosomatidae (Spicipalpia, see above) belong. All of these groups occur in lotic habitats, demonstrating that in running waters food resources for grazing larvae do support Trichoptera at latitudes of 60° to 70°N.

Other groups of Integripalpia in streams at high latitudes are detritivorous: Lepidostomatidae; and Limnephilidae (*Chyranda, Dicosmoeus, Hesperophylax, Onocosmoeus, Psychoglypha*). As members of the functional group of shredders, larvae of these species feed mainly on allochthonous plant debris supporting microbial growth. This food resource may be limiting; the supply of detritus in a subarctic Alaskan stream was meagre compared with that in temperate streams (Cowan and Oswood 1984), and was believed to influence
strategically the spatial and temporal patterns of detritivores. Moreover, microbial processing of plant detritus in high latitude streams was held to be impeded at low temperatures (Irons et al. 1994).

Although the success of case-making Trichoptera in subarctic running waters is constrained by ice and by low levels of allochthonous detritus, biological interactions in subarctic ponds and lakes appear to be rather different because it is in these lentic habitats that Trichoptera flourish at higher latitudes. Case-making Integripalpia constitute 75 per cent of the species of Yukon Trichoptera (Table 2), and more than half of these (56 per cent) live in lentic habitats. Since inputs of allochthonous detritus are relatively lower in ponds and lakes because the ratio of shoreline to water area is much lower than it is in streams, autochthonous plant matter seems to be the energy resource underlying the success of detritivorous Trichoptera in these habitats. A number of species of both submerged and emergent vascular aquatic plants occur in southern parts of the arctic tundra, and considerably more in the subarctic (e.g. Hobbie 1973; I.L. Wiggins and Thomas 1962).

Case-making larvae in the Phryganeidae, Molannidae, and Leptoceridae (Ceraclea, Mystacides, Oecetis) are predacious on insects and other invertebrates; overall, these groups decrease rather little at higher latitudes (Table 1).

The latitudinal gradient analyzed here reflects the scale of environmental constraints met by species of Trichoptera dispersing to the north in the wake of receding glacial ice. The gradient also reveals a pattern in their use of the resources of aquatic systems under conditions imposed by increasing latitude. However, the relatively smaller decline in case-making Integripalpia within this latitudinal gradient can also be interpreted as a reflection of the capacity of some species of the Limnephilidae and Phryganeidae to exploit lentic habitats at high latitudes. Both families appear to have originated in running waters, but most extant species have been derived subsequently in lentic habitats. Thus, some groups of Limnephilidae and Phryganeidae can be seen as preadapted through origin to low temperatures and northerly photoperiods. If a number of species in these families have the physiological capability to live under conditions of extreme cold, the failure of most other families to do so may reflect the warmer climatic conditions in which they originated. Consequently, although reduced resources in aquatic communities may account for some of the depletion in species diversity, most groups of Trichoptera may have evolved at more temperate latitudes and probably still lack the physiological capability to persist under relatively recent regimes of cold climates at high latitudes (see above, Origin of the Beringian and Holarctic Trichoptera).

Diptera are one of the most successful insect orders in the far north, particularly the family Chironomidae (e.g. Oliver 1968). Because most chironomid larvae are aquatic, and adults feed sparingly if at all, the success of this family in the far north has been attributed to their independence from plants and other insects (Downes 1962). Trichoptera, however, are biological analogues of Chironomidae but are represented in the far north by far fewer species, further indicating that intrinsic limitations of Trichoptera influence the penetration of these insects into far northern latitudes. Larvae of Chironomidae and of Empididae survive freezing in Alaskan subarctic streams (Irons et al. 1993).

Larval habitat and food must also have governed the success of Trichoptera in their passage across the Bering land bridge. Among the present Holarctic and Beringian Trichoptera are 43 lentic species but only 8 lotic species—a ratio of approximately 5 lentic : 1 lotic—indicating that caddisflies inhabiting standing waters have been far more successful as colonizers bridging the gaps between larval habitats, and in moving between Asia and North America. During glacial maxima, Beringian species dispersing across the land bridge
would have had to cross cold, dry land of low relief (Schweger et al. 1982). The clear, stable and well-oxygenated streams required by some species probably would have been sparse, although lakes and marshes would have occurred in low-lying areas.

A related aspect is that larvae in Apatania, Ecclisomyia, and Micrasema are mainly grazers confined to cool streams at lower latitudes, but in the far north also occur in lakes. If ice conditions at higher latitudes render stream habitats unsuitable for larvae in these genera (see the foregoing), their transfer to cold lakes would provide an ecological alternative, which in Apatania may underlie extension of A. zonella to Ellesmere Island (Lake Hazen 81°49′N; Corbet 1966)—the most northerly record for Trichoptera.

Because many Holarctic and Beringian species are colonizers, it is significant that 13 of the 51 species (25 per cent) belong to the single genus Limnephilus, a dominant group in standing waters through much of the northern hemisphere. Although the life histories of few Nearctic Limnephilus are known in detail, a good deal of the success of these species in standing waters is probably due to the specialized characteristics by which many of them successfully exploit temporary pools (Wiggins 1973): marked tendency to disperse as adults; eggs deposited not in water but on damp substrates in a gelatinous matrix resistant to desiccation; and rapid larval development. Moreover, 6 additional Beringian species belong to other northern limnephilid genera that also occur in transient waters—2 in Asynarchus, 2 in Grammotaulius, and 1 in each of Arctopora and Lenarchus. Species in these genera share most of the same developmental characteristics found in Limnephilus (e.g. Wiggins 1973), and in all they account for 37 per cent of the Holarctic Trichoptera in North America. Adaptations to transient waters are clearly apomorphic specializations in Trichoptera (Wiggins et al. 1980) and occur mainly in the family Limnephilidae; transient pools are a dominant aquatic biotope at high latitudes.

One characteristic of species of Limnephilidae in transient waters at temperate latitudes is deferral of oviposition through diapause until the height of the dry phase of the pool basins has passed (Wiggins 1973). Females of these species are inactive until sexual maturity is induced by decreasing photoperiod (Novak and Sehnal 1963); at higher elevations temperature was also found to be a factor in breaking diapause. At high latitudes, temperatures conducive to larval development are available for only a few months, and yet species of Limnephilidae appear to be univoltine in tundra streams and ponds near Tuktoyaktuk at latitude 69°29′N (e.g. Winchester 1984). These species appear to have no diapause during their life cycle, development proceeding until inhibited by low temperature. Development deferred by obligate diapause in the short growing season would be biologically costly for Trichoptera at high latitudes if a second year of larval growth was thereby required, suggesting that the ecological strategy in species of Trichoptera successful at high latitudes is uninterrupted larval development initiated from a low temperature threshold. At temperate latitudes, diapause in the life cycle of these species of Limnephilidae makes existence in transient pools possible by imposing a delay in development while the pool and its basin are dry; this delay can be accommodated because the annual growth period is still adequate for univoltine development. By contrast, life cycles with uninterrupted development have a selective advantage for rapid growth in transient waters at high latitudes, suggesting that the incidence of diapause in congeneric species of Limnephilidae must change between temperate and arctic latitudes.

At high latitudes within the zone of continuous permafrost, basins of transient surface pools probably do not become desiccated by exposure to the sun, as do basins of temporary pools at more southerly latitudes. Although exposed surface waters in transient tundra pools do evaporate during the brief summer (e.g. Winchester et al. 1993), a supply of water is
assured from melting permafrost, and the meltwater is shielded from evaporation by moss and other plant materials; underlying substrates are not likely to become desiccated because the frozen permafrost below prevents the water from draining away. These are the classic factors producing muskeg in the far north (e.g. Pielou 1991); and this rather paradoxical relationship between transient tundra pools, permafrost, and insolation could underlie a unique type of habitat for aquatic insect larvae adapted to an arctic climate. Among the Trichoptera, only case-making detritivorous species occur in transient tundra pools. Three species, all members of the Limnephilidae, are now known in these habitats: *Lenarchus expansus* and *Sphagnophylax meiops* (category IV), and *Asynarchus lapponicus* (II) (90, 126, 75); but to what extent do larvae of other species use water-saturated tundra habitats in the basins of transient tundra pools? Moreover, if because of the relatively recent origin of the arctic biome (see Biogeographic Analysis), time has been insufficient for the evolutionary potential of aquatic insects to fully exploit these tundra pools with their constant supply of water from permafrost, these habitats may provide an evolutionary plateau of the future. Perhaps it is not coincidental that *Sphagnophylax meiops* (Frontispiece, Fig. 28), a relict species on both geographic and phylogenetic grounds, and the sole trichopteran genus confined to Beringia, still persists only in just such an arctic tundra habitat.

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