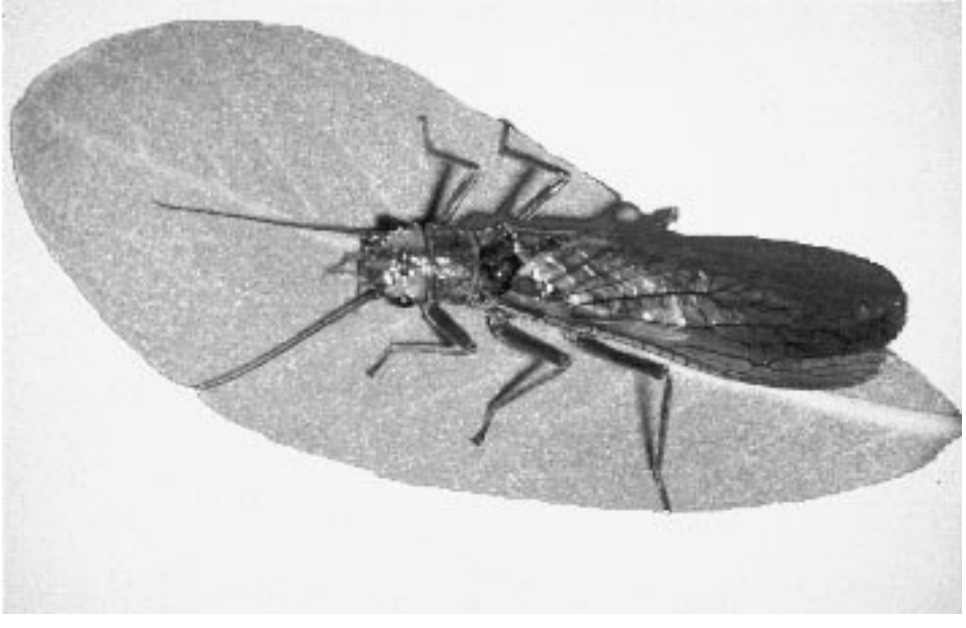

FRONTISPIECE. *Hesperoperla pacifica* (Banks), a large perlid stonefly (up to 3 cm in length) widespread in western North America including the Yukon. Photograph by John C. Abbott.

Stoneflies (Plecoptera) of the Yukon

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Abstract. Intensified collection efforts over the past two decades have increased the known Yukon stonefly fauna almost fourfold, from 19 to the current 71 species, representing 8 families and 33 genera. We have classified the extant fauna into 6 distributional elements: I, Western Nearctic (54 species); II, Northwestern Nearctic (7 species); III, Transberingian (4 species); IV, Holarctic (3 species); V, Transcontinental Nearctic (2 species); and VI, East Beringian endemic (1 species). Eighty-six percent of Yukon species are representative of stoneflies that are restricted to the western Nearctic (elements I, II), 10% are Transberingian or Holarctic, 3% are transcontinental and only one species, *Alaskaperla ovibovis* (Ricker), is a regional Nearctic endemic. Ancestors of all Yukon species appear to be of Asiamerican origin. Most of the dominant, widespread western Nearctic element (I; 76% of Yukon fauna) likely survived the Wisconsinan glaciation in the southwestern refugium of Ricker (1964) then moved back north into the Yukon in postglacial times; 8 of these species that are more northern in distribution, and all the rest of the elements that are comprised of cold-adapted species, probably survived the last glacial period in unglaciated refugia of Beringia, then spread back southward into the Yukon and farther in some cases as far south as latitudes roughly bounded by a northern California to Montana line.

The interchange of Nearctic and Palaearctic stonefly faunas across the Bering land bridge and Beringia have overwhelmingly influenced the extant western stonefly fauna, and particularly that of the Yukon. The substantially gilled families Peltoperlidae and Perlidae are absent from the cold lakes and streams of the far Northwest, that experience extended cold and/or frozen conditions. The most successful stoneflies in these habitats are species in the other families that are cold-adapted through combinations of: (1) nymphal development in unfrozen winter habitats such as the hyporheal, springs or other unfrozen water or substrates, (2) extended voltinism, coupled with winter diapause of eggs or nymphs, (3) timing of feeding to correspond with microorganism processing of alder and willow leaves, (4) capacity to exploit permanent tundra ponds, with their profuse supply of organic detritus for food or (5) capacity for adults to emerge, mate and oviposit during winter. The relatively low amount of Coarse Particulate Organic Matter (CPOM) in some arctic and subarctic streams probably limits the presence and abundance of large shredders such as *Pteronarcys* and *Pteronarcella*. The comparatively lower diversity and abundance of herbivorous forage insects could be limiting to large-gilled predators such as Perlidae, that also apparently have low cold-adaptive capacity in comparison with Perlodidae.

Résumé. *Les plécoptères (Plecoptera) du Yukon.* Les efforts de récolte au cours des deux dernières décennies ont fait passer de 19 à 71 le nombre d'espèces connues de plécoptères au Yukon, représentant 8 familles et 33 genres. La faune actuelle compte six éléments: I, espèces de l'ouest néarctique (54), II, espèces du nord-ouest néarctique (7), III, espèces transbéringiennes (4), IV, espèces holarctiques (3), V, espèces néarctiques transcontinentales (2) et VI, espèces endémiques de la Béringie orientale (1). Quatre-vingt-six pourcent des espèces du Yukon sont restreintes à l'ouest de la zone néarctique (éléments I et II), 10% sont transbéringiennes ou holarctiques, 3% sont transcontinentales et une seule espèce, *Alaskaperla ovibovis* (Ricker), est une espèce endémique. Les ancêtres de toutes les espèces du Yukon semblent être d'origine américano-asiatique. La plupart des espèces dominantes, de l'ouest néarctique (I, 76% de la faune du Yukon), ont probablement survécu aux glaciations du Wisconsinien dans le refuge sud-ouest de Ricker (1964), pour remonter ensuite vers le nord et coloniser le Yukon après les glaciations; 8 de ces espèces qui ont une répartition plus nordique et tous les autres éléments qui se composent d'espèces adaptées au froid ont probablement survécu à la dernière période glaciaire dans des refuges non englacés de la Béringie, puis se sont redispersées vers le sud dans le Yukon et plus loin, dans certains cas jusqu'à des latitudes aussi australes que le nord de la Californie et le Montana.

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Les allées et venues d'espèces néarctiques et paléarctiques par le pont continental de Bering et par la Béringie ont fortement influencé la faune actuelle de l'ouest, notamment celle du Yukon. Les familles Peltoperlidae et Perlidae, abondamment munies de branchies, sont absentes des lacs et ruisseaux froids de l'extrême nord-ouest qui subissent des périodes de froid et de gel prolongées. Les plécoptères les mieux établis dans ces habitats sont les espèces des autres familles qui se sont adaptées au froid grâce à diverses stratégies: (1) développement larvaire dans des habitats qui ne gèlent pas l'hiver, notamment l'étage hyporhéique, les sources ou autres eaux ou substrats qui ne gèlent pas, (2) voltinisme étendu combiné à une diapause des oeufs ou des larves en hiver, (3) synchronisme de l'alimentation des larves avec la période de dégradation des feuilles d'aulne et de saule par les microorganismes, (4) capacité d'exploiter les étangs permanents de la toundra, riches en détritus organiques ou (5) capacité des adultes d'émerger, de s'accoupler et de pondre au cours de l'hiver. La quantité relativement faible de grosses particules organiques (CPOM) dans certains ruisseaux arctiques et subarctiques crée une contrainte qui explique sans doute la faible abondance de déchiqueteurs tels *Pteronarcys* et *Pteronarcella*. La diversité et l'abondance relativement faibles d'insectes herbivores peuvent expliquer l'absence des prédateurs fortement munis de branchies, comme les Perlidae, qui sont en outre dotés d'une faible capacité d'adaptation au froid comparativement aux Perlodidae.

Introduction

Stoneflies have remained an inadequately known element of the Yukon insect fauna. Stark et al. (1986) and Stewart and Stark (1988) reported only 17 species from the Territory, assembled from the scattered literature records. The first listing of the Plecoptera from far northwestern North America was by Ricker (1944), and it included only two species, *Diura bicaudata* (Linnaeus) and *Isogenoides colubrinus* (Hagen) from the Yukon. Ricker (1964) plotted distributions of about 100 selected species of Canadian stoneflies known at that time (19 in the Yukon) and proposed their probable biogeographic origins, dispersals and affinities in relation to Pleistocene events.

Except for Ricker's studies in British Columbia (Ricker 1943; Ricker and Scudder 1975), there have been no concerted, systematic studies of the Plecoptera fauna of northwestern Canada and Alaska. Sporadic collecting continued in the region from the 1940's through 1970's, and much of this material was deposited in the Canadian National Collection and identified by W.E. Ricker, resulting in several species additions to the Yukon fauna that have not been reported previously. Interest in stoneflies of the far northwestern corner of the continent increased considerably in the 1980's, with extensive collections in the Yukon and British Columbia by S.G. and R.A. Cannings and others, and initiation of a long-term study of Plecoptera of Alaska and adjacent Canadian Territories by K.W. Stewart and M.W. Oswood. The latter investigators have a book manuscript in preparation that will provide a historical analysis, illustrated keys, biology and ecology and biogeography of the approximately 200 species now known to occur in Alaska, British Columbia, the Northwest Territories and the Yukon. The present report is therefore a subset of that work, and intended as the first major documentation and biogeographic analysis of the Yukon fauna. This contribution should be considered a preliminary analysis, because a thorough systematic survey of the Yukon stonefly fauna is yet to be achieved.

We have now documented 71 stonefly species representing 33 genera from the Yukon, 41 of which are being reported for the first time from the Territory. Recent collections have confirmed most of the early literature species records and provided valuable, yet in many cases rather small numbers of, locality records. The data reported here have come largely from our own limited collecting along the Alaska-Yukon border and recent examination of several hundred vials of stoneflies loaned by the Royal Ontario Museum (ROME), Spencer Entomological Museum of the University of British Columbia (SMDV), the Canadian National Collection (CNCI) and individuals. We thank G.B. Wiggins, S.G. Cannings, K.M. Needham, R. Hutchinson and P.T. Dang for arranging the extensive loans.

Stoneflies (Plecoptera) constitute an important order of aquatic insects that are found almost exclusively in lotic ecosystems. Nymphs of a few species, such as *Arcynopteryx compacta* (McLachlan), *Bolshecapnia spenceri* (Ricker) and *Nemoura arctica* Esben-Peterson, occur in alpine or arctic lakes where the combination of gravelly substrates and cold, waveswept shallows simulate flowing water conditions. Only one species, *Utacapnia tahoensis* (Nebeker and Gaufin) is known to live underwater in all life stages, in Lake Tahoe. The order is divided into two suborders: (1) Arctoperlaria, found, as the name implies, in the Northern Hemisphere, with the exception of the family Notonemouridae, and (2) Antarctoperlaria, found in the Southern Hemisphere. All North American, and therefore Yukon, species belong to the Arctoperlaria. They are further subdivided into the groups Euholognatha, whose nymphs and adults are largely herbivorous (shredders, scrapers, grazers, detritivores), and Systellognatha, whose nymphs have diverse food habits, but are largely insectivores (engulfers). The adults of most Systellognatha have reduced mouthparts and feed, if at all, only on pollen, nectar or fruit juices.

Most adult stoneflies have longitudinally pleated, macropterous wings that are folded over the abdomen when at rest. Males, and to a lesser extent females of a few species, particularly in the family Capniidae, exhibit varying degrees of brachyptery. Even macropterous species are considered to be relatively poor fliers with low vagility, which makes the group important from the standpoint of inferring past dispersals and colonizations from current distributions. Wing venation is generally primitive, with numerous crossveins. Male external genitalia are highly modified into paraprocts, epiprocts and other mechanical "devices" that help engage and hold the female subgenital plate during copulation. Adults also have paired tarsal claws, paired multisegmented cerci (except males in Leuctridae and some Taeniopterygidae with 1-segmented cerci), 10 abdominal segments and in some cases gill stubs on the thorax and/or abdomen.

Adult stoneflies have the most complex and advanced system of intersexual vibrational communication known in insects. Males and females produce species-specific vibrational signals by percussive drumming or rubbing with their abdomens, or tremulation (Stewart and Maketon 1991). After duet establishment, females become stationary and males search by triangulation or other pattern for the female (Abbott and Stewart 1993).

Stonefly nymphs are important, integral components of the food web in stream ecosystems. Species assemblages have segregated their life histories and partitioned their food and space resources, and play vital roles in the energy economy and secondary production of these systems. Nymphs lack gills, or possess gills of various shapes and number at various body locations (Shepard and Stewart 1983; Stewart and Stark 1988), and always have well-developed, paired, multisegmented cerci. A complete account of stonefly nymphal morphology is presented by Stewart and Stark (1988).

The known life cycles of North American stoneflies are either univoltine (1 year) or semivoltine (2 or more years). Both types may be either heterodynamic (having an egg or nymphal diapause) or homodynamic (having no regular period of dormancy). Development of species with heterodynamic cycles is referred to as fast; in this case, nymphs develop through their full 10–22 instars and cohort production interval in a 3–8 month period. Species with homodynamic development require a longer nymphal growth period, referred to as slow; in this case the nymph stage approximates the full required generation time. Recent studies have proven that every aspect of stonefly life histories and voltinism can have a high degree of plasticity, even within some species. A full account of the taxonomy and biology of North American stoneflies was presented by Stewart and Stark (1988).

As of August 1996, 102 genera and 608 species of stoneflies were known from North America. These are distributed among the 4 euholognathan families Capniidae, Leuctridae, Nemouridae and Taeniopterygidae and the 5 systellognathan families Chloroperlidae, Peltoperlidae, Perlidae, Perlodidae and Pteronarcyidae. Except for the few transcontinental and Holarctic northern-latitude species discussed in this chapter, there is a rather distinct separation of the extant North American fauna into eastern and western components. These components are largely separated by the grasslands and unforested cold or semi-arid central regions of the continent.

Checklist of Yukon Species, with Distributional Categories

The following categories are used in the checklist and annotated list; they are discussed in the section on Biogeography.

I. Western Nearctic species, widespread in the west.
II. Northwestern Nearctic species, restricted to northern latitudes in the west.
III. Transberingian species, occurring in West Beringia as well as in North America. Russian information is from Levanidova (1982).
IV. Holarctic species.
V. Transcontinental Nearctic species, found across North America.
VI. East Beringian endemic species, confined to the far northwest Nearctic region (Alaska, Yukon, Northwest Territories).

Taxa or species being reported for the first time in the Yukon Territory are marked *.

Group Euholognatha

Family Capniidae

1. *Capnia cheama* Ricker*. II.
2. *Capnia coloradensis* Claassen. I.
3. *Capnia confusa* Claassen. I.
4. *Capnia elongata* Claassen*. I.
5. *Capnia gracilaria* Claassen. I.
6. *Capnia nana* Claassen. I.
7. *Capnia nearctica* Banks. III.
8. *Capnia petila* Jewett. I.
9. *Capnia pileata* Jewett*. I.
10. *Eucapnopsis brevicauda* Claassen*. I.
11. *Isocapnia crinita* (Needham and Claassen)*. I.
12. *Isocapnia fraseri* Ricker*. II.
13. *Isocapnia grandis* (Banks)*. I.
14. *Isocapnia integra* Hanson*. II.
15. *Isocapnia vedderensis* (Ricker)*. I.
16. *Mesocapnia oenone* (Neave). II.
17. *Mesocapnia variabilis* (Klapálek)*. III.
18. *Utacapnia columbiana* (Claassen). I.

Family Leuctridae*

19. *Paraleuctra forcipata* (Frison)*. I.
20. *Paraleuctra occidentalis* (Banks)*. I.
21. *Paraleuctra purcellana* (Neave)*. I.
22. *Paraleuctra vershina* Gaufin and Ricker*. I.
23. *Perlomyia collaris* Banks*. I.

Family Nemouridae

24. *Amphinemura linda* (Ricker)*. V.
25. *Nemoura arctica* Esben-Petersen*. IV.
26. *Nemoura rickeri* Jewett*. II.
27. *Podmosta decepta* (Frison)*. I.
28. *Podmosta delicatula* (Claassen)*. I.
29. *Podmosta weberi* (Ricker). III.
30. *Prostoia besametsa* (Ricker)*. I.
31. *Zapada cinctipes* (Banks)*. I.
32. *Zapada columbiana* (Claassen)*. I.
33. *Zapada frigida* (Claassen)*. I.
34. *Zapada haysi* (Ricker)*. I.
35. *Zapada oregonensis* (Claassen). I.

Family Taeniopterygidae

36. *Taenionema kincaidi* (Hoppe). I.
37. *Taenionema pacificum* (Banks). I.
38. *Taenionema pallidum* (Banks). I.

Group Systellognatha

Family Chloroperlidae
39. *Alaskaperla ovibovis* (Ricker)*. VI.
40. *Alloperla medveda* Ricker. I.
41. *Alloperla serrata* Needham and Claassen. I.
42. *Alloperla severa* (Hagen). I.
43. *Kathroperla perdita* Banks*. I.
44. *Neaviperla forcipata* (Neave)*. II.
45. *Paraperla frontalis* (Banks). I.
46. *Paraperla wilsoni* Ricker. I.
47. *Plumiperla diversa* (Frison). III.
48. *Suwallia autumna* (Hoppe)*. I.
49. *Suwallia dubia* (Frison)*. I.
50. *Suwallia lineosa* (Banks)*. I.
51. *Suwallia pallidula* (Banks)*. I.
52. *Sweltsa borealis* (Banks). I.
53. *Sweltsa coloradensis* (Banks). I.
54. *Sweltsa fidelis* (Banks). I.
55. *Triznaka signata* (Banks)*. I.
56. *Utaperla sopladora* Ricker. I.

Family Perlidae*
57. *Hesperoperla pacifica* (Banks)*. I.

Family Perlodidae
58. *Arcynopteryx compacta* (McLachlan)*. IV.
59. *Cultus pilatus* (Frison)*. I.
60. *Diura bicaudata* (Linnaeus). IV.
61. *Diura knowltoni* (Frison). I.
62. *Isogenoides colubrinus* (Hagen). I.
63. *Isoperla decolorata* (Walker). II.
64. *Isoperla fusca* Needham and Claassen. I.
65. *Isoperla petersoni* Needham and Christenson. I.
66. *Isoperla sobria* (Hagen). I.
67. *Kogotus nonus* (Needham and Claassen)*. I.
68. *Megarcys signata* (Hagen)*. I.
69. *Skwala americana* (Klapálek)*. I.

Family Pteronarcyidae
70. *Pteronarcys californica* Newport*. I.
71. *Pteronarcys dorsata* (Say)*. V.

Annotated List of Genera and Species of Plecoptera from the Yukon

The accounts that follow are arranged phylogenetically by families after Stark et al. (1986); genera and their respective species are arranged alphabetically under each family. Distribution and biological notes are given for each genus, and general distribution and specific localities within the Yukon (by stream, town or other reference name and available elevation, latitude and longitude) are provided for each species. Biological notes are provided for species that have been studied in Alaska or the Yukon. The specific localities for each species are arranged alphabetically. Geographic distributions and biological notes have been compiled from Baumann et al. (1977), Stewart and Stark (1988), and subsequent literature.

Abbreviations used are as follows: Rd., road; Hwy., highway; Mt., mountain; L., lake; Lks., lakes; R., river; Cr., creek; km, kilometre; mi, mile (= 1.6 km); m, metre (indicates elevation above sea level).

Distances on major highways and roads are measured from their starting points, as follows:

Alaska Highway: starts at Dawson Creek, British Columbia; ends at Fairbanks, Alaska.

Klondike Highway: starts at Whitehorse, Yukon; ends at Dawson, Yukon, with an extension west into Alaska.

Dempster Highway: starts at Dawson, Yukon; ends at Inuvik, Northwest Territories.

Haines Road: starts at Haines, Alaska; ends at Haines Junction, Yukon.

Canol Road: starts at Johnson's Crossing, Yukon, through Ross River, Yukon, and ends on the Mackenzie River opposite Norman Wells, Northwest Territories.

Family Capniidae

Genus *Capnia*. Holarctic; 52 Nearctic species, distributed mostly in the West and Midwest. Adults small, black, under 12 mm. Winter and spring emergence from February–April in the southern Rocky Mountains to May–July in the Yukon and high elevations. Nymphs light to medium brown in mineral substrates of small and large streams. The few known life

histories suggest that most North American *Capnia* species probably have univoltine, fast life cycles with summer nymphal diapause. Nymphs are largely detritivores and many shred deciduous leaves in streams. The North American species in this genus were recently revised by Nelson and Baumann (1989).

1. ***Capnia cheama* Ricker** Northwestern Nearctic
Distribution: Yukon to Montana.
Yukon records: Porcupine R., Rampart House near Alaska border.

2. ***Capnia coloradensis* Claassen** Western Nearctic
Distribution: Yukon, Saskatchewan to New Mexico.
Yukon records: Boutellier Cr. at Kluane R., 960 m; Kluane, Christmas Cr.; Moose Cr. Campground, km 562 Klondike Hwy., 63°30′N 137°01′W; Ogilvie Mts., North Fork Pass, 1230 m; same, North Fork Crossing, mile 42 Dempster Hwy.; Vangorda Cr., 960 m, 62°18′N 133°15′W.

3. ***Capnia confusa* Claassen** Western Nearctic
Distribution: Alaska, Yukon, Saskatchewan to New Mexico.
Yukon records: Blackstone R., km 103 Dempster Hwy., 64°43′N 138°22′W and km 89.5, 64°36′N 138°22′W; Horseshoe Bay Campground, Alaska Hwy.; km 142 Dempster Hwy.; North Fork Pass, Tombstone Campground; Ogilvie Mts., North Fork Crossing, mi 42 Dempster Hwy., and North Fork Pass, 1230 m.

4. ***Capnia elongata* Claassen** Western Nearctic
Distribution: Yukon to California.
Yukon records: North Fork Pass, Tombstone Campground

5. ***Capnia gracilaria* Claassen** Western Nearctic
Distribution: Yukon, Saskatchewan to Nevada, New Mexico.
Yukon records: Christmas Camp; Kluane, Boutellier Cr. tributary, 960 m; same, Christmas and Boutellier Cr.; Moose Cr., km 562 Klondike Hwy., 63°30′N 137°01′W; North Klondike R., Tombstone Camp; Ogilvie Mts., North Fork Crossing, 1050 m, mi 42 Dempster Hwy.; Wolf Cr. Campground at Whitehorse.

6. ***Capnia nana* Claassen** Western Nearctic
Distribution: Alaska, Yukon to Colorado.
Yukon records: Boutellier Cr., tributary Kluane R., 960 m; Ogilvie Mts., North Fork Pass, 1230 m; Wolf Cr. at Whitehorse, 1140 m.

7. ***Capnia nearctica* Banks** Transberingian
Distribution: Alaska, Yukon to Baffin Island, and Ontario; Russian Far East (Levanidova 1982).
Yukon records: Alligator L., 1110 m; Horseshoe Bay Campground, km 1713 Alaska Hwy., 61°02′N 138°31′W; La Force L., 690 m, 62°41′N 132°20′W; Little Salmon L., 62°10′N 134°40′W; Ogilvie Mts., North Fork Crossing, mi 42 Dempster Hwy., 1050 m and North Fork Pass, 1230 m.

8. ***Capnia petila* Jewett** Western Nearctic
Distribution: Yukon to Oregon, Wyoming.
Yukon records: Kluane, Boutellier Cr.

9. ***Capnia pileata* Jewett** Western Nearctic
Distribution: Yukon to California.
Yukon records: Philip Cr., 68°52′N 138°47′W.

Genus *Eucapnopsis*. Japan and Western Nearctic; the single Nearctic species, *E. brevicauda*, occurs in the west from Alaska and Yukon south to California and New Mexico. The small black adults emerge February–July in the Rocky Mountains and Yukon, depending on elevation and latitude. Nymphs yellowish brown, 4–6 mm, in stream substrates. Univoltine, fast life cycle; small nymphs in diapause about 7 months from spring through summer, growing actively from autumn to emergence.

10. ***Eucapnopsis brevicauda*** **Claassen** Western Nearctic
Distribution: Alaska, Yukon to California, New Mexico.
Yukon records: Irwin Lks., 960 m, 62°13′N 133°W; Lapie R., km 175 South Canol Rd.; km 634 Klondike Hwy.; Mayo R. at Mayo; Moose Cr. Campground, km 562 Klondike Hwy. 63°30′N 137°01′W.

Genus *Isocapnia*. Eastern Palaearctic and Western Nearctic; 11 Nearctic species distributed in the west, from Alaska and Yukon south to California and New Mexico. Adults brown to black, some species as large as 15–20 mm; brachypterous dwarf male morphs occur in some large river species. Emergence February–June depending on elevation and latitude. Nymphs occur deep in hyporheic gravel under or adjacent to streams until just prior to emergence. Little detail is known of life histories, but nymphal size variation suggests that at least some species are semivoltine.

11. ***Isocapnia crinita*** (Needham and Claassen) Western Nearctic
Distribution: Yukon, Saskatchewan to Colorado.
Yukon records: Crooked Cr., Klondike Hwy., 63°16′N 136°46′W; Ogilvie R., mi 150 Dempster Hwy.

12. ***Isocapnia fraseri*** **Ricker** Northwestern Nearctic
Distribution: Yukon, British Columbia.
Yukon records: Ogilvie Mts., North Fork Pass, 1230 m.

13. ***Isocapnia grandis*** **(Banks)** Western Nearctic
Distribution: Alaska, Yukon to California, Colorado.
Yukon records: Cornwall Cr., Richardson Mts.; Ogilvie Mts., North Fork Crossing, mi 43 Dempster Hwy., 1050 m.

14. ***Isocapnia integra*** **Hanson** Northwestern Nearctic
Distribution: Yukon to Montana.
Yukon records: Alaska Hwy. between Watson L. and Whitehorse.

15. ***Isocapnia vedderensis*** **(Ricker)** Western Nearctic
Distribution: Yukon to New Mexico.
Yukon records: Alaska Hwy. between Watson L. and Whitehorse.

Genus *Mesocapnia*. Holarctic; 15 Nearctic species, distributed mostly in the west, from Alaska and Yukon south to Mexico. Adults small, black, usually under 10 mm. Emergence February–April in southern Rocky Mountains to mid-summer in Alaska and Yukon. Voltinism, life histories and food habits little known, probably generally similar to *Capnia*.

16. ***Mesocapnia oenone*** **(Neave)** Northwestern Nearctic
Distribution: Alaska, Yukon to Oregon, Montana.
Yukon records: Rancheria R., mi 721.6 Alaska Hwy.

17. ***Mesocapnia variabilis*** **(Klapálek)** Transberingian
Distribution: Yukon, British Columbia; Siberia and Russian Far East.
Yukon records: Blackstone R., km 103 Dempster Hwy., 64°43′N 138°22′W; same, km 420, 66°35′N 136°18′W; Engineer Cr., km 165 Dempster Hwy.; Richardson Mts., Arctic Circle Crossing, Dempster Hwy., km 409 Dempster Hwy., 66°37′N 136°20′W and km 458 Dempster Hwy., 66°58′N 136°14′W; Vittrekwa R., km 482 Dempster Hwy., 67°09′N 136°03′W.

Genus *Utacapnia*. Nearctic; the 11 species, except *U. labradora* (Ricker), are distributed in the west, from Alaska and Yukon south to California and New Mexico. Adults black, 7–11 mm. Emergence February–April in southern range to June–July at high elevation in Alaska and Yukon. There have been no published accounts of biology of any species in this genus.

18. ***Utacapnia columbiana* (Claassen)** Western Nearctic
Distribution: Alaska, Yukon to California, Montana.
Yukon records: La Force L., 690 m, 62°41′N 132°20′W; Ogilvie Mts., North Fork Pass, 1230 m; Porcupine R., Rampart House near Alaska border; Wolf Cr. Campground at Whitehorse; Yukon R. at Dawson.

Family Leuctridae

Genus *Paraleuctra*. Eastern Palaearctic, Nearctic and Oriental; 8 of the 9 Nearctic species are western, from Alaska and Yukon south to California and New Mexico. Adults are small, usually under 10 mm, and emerge in spring and summer months, depending on elevation and latitude. Nymphal biology and life histories are largely unknown.

19. ***Paraleuctra forcipata* (Frison)** Western Nearctic
Distribution: Alaska, Yukon to California, Montana.
Yukon records: Irwin Lks., 960 m, 62°13′N 133°W; Ogilvie Mts., North Fork Crossing, 1050 m, mi 42 Dempster Hwy. and North Fork Pass, 1230 m; Otter L., 1200 m, 62°30′N 130°25′W; Whitehorse, at Wolf Cr.

20. ***Paraleuctra occidentalis* (Banks)** Western Nearctic
Distribution: Alaska, Yukon to California, New Mexico.
Yukon records: Irwin Lks., 960 m, 62°13′N 133°W; North Fork Pass, Tombstone Campground; North Klondike R., Tombstone Camp, and km 64 and 73 Dempster Hwy.; Ogilvie Mts., North Fork Crossing, mi 42 and 43 Dempster Hwy., 1050 m and North Fork Pass, 1230 m; Vangorda Cr., 1140 m, 62°18′N 133°15′W.

21. ***Paraleuctra purcellana* (Neave)** Western Nearctic
Distribution: Yukon to Oregon, Wyoming.
Yukon records: Ogilvie Mts., North Fork Crossing, mi 42 Dempster Hwy., 1050 m.

22. ***Paraleuctra vershina* Gaufin and Ricker** Western Nearctic
Distribution: Alaska, Yukon to California, New Mexico.
Yukon records: Garin L., 960 m, 62°15′N 133°W.

Genus *Perlomyia*. Western Nearctic; 2 species distributed from Alaska and Yukon south to California and New Mexico. Adults dark, 7–12 mm, emerging March–June depending on elevation and latitude. Found primarily in springs or spring-fed small streams. Nymphal biology largely unknown.

23. ***Perlomyia collaris* Banks** Western Nearctic
Distribution: Yukon to California, Idaho.
Yukon records: Ogilvie Mts., North Fork Crossing, mi 42 Dempster Hwy.

Family Nemouridae

Genus *Amphinemura*. Holarctic and Oriental; 13 Nearctic species with only 2, *A. delosa* (Ricker) and *A. linda* (Ricker), widespread in the west. Adults small, dark, less than 10 mm. Emergence variable by species; western species emerge June–September. Nymphs occur only in permanent streams. Eastern species are detritivores and have univoltine life cycles; no definitive life-history or ecological studies have been reported for the 8 western species that occur mostly in the Southwest and Mexico.

24. ***Amphinemura linda* (Ricker)** Transcontinental Nearctic
Distribution: Alaska, Yukon, Colorado to Labrador, Ontario.
Yukon records: Richthofen Cr., 61°08′N 135°21′W; Takhini Hot Springs, 720 m.

Genus *Nemoura*. Holarctic and Oriental; 5 Nearctic species distributed in the west (*N. arctica* is transcontinental), except *N. trispinosa* in the east and midwest. Adults small, under 10 mm, dark. Emergence from spring to late summer, depending on elevation and

latitude. Nymphs are shredders-detritivores, and limited studies indicate that northern species have univoltine, slow life cycles.

25. ***Nemoura arctica* Esben-Petersen** Holarctic
Distribution: Alaska, Yukon to South Dakota, Quebec; Eurasia.
Yukon records: Blackstone R., km 139 Dempster Hwy.; same, km 144, 65°02′N 138°11′W; same, km 95, 64°39′N 138°23′W; same, km 148, 65°05′N 138°08′W; Blackstone R. Valley, km 141 Dempster Hwy.; Bluefish R., 67°08 N 140°49W; Cornwall Cr., km 439 Dempster Hwy.; Eagle R., Dempster Hwy.; Engineer Cr., km 159.5 Dempster Hwy., 65°05′N 138°28′W; Engineer Cr., km 173 Dempster Hwy.; La Force L., 690 m, 62°41′N 132°20′W; Little Atlin L.; Macmillan Pass; Milepost 737 Alaska Hwy.; Ogilvie R., km 214 Dempster Hwy.; Ogilvie Mts., North Fork Pass, 1230 m; Ogilvie R., km 218 Dempster Hwy.; Old Squaw L. near Kusaua L., 1500 m; Philip Cr., 68°58′N 138°35′W; Richardson Mts, 12 km N Arctic Circle, 66°40′N 136°20′W; Richardson Mts. West Slope, km 456 Dempster Hwy.; Otter L., 1200 m, 62°30′N 130°25′W; Whitehorse, 65°01′N 138°11′W.
Biological information: This species is widespread in the Yukon and Alaska, and adults emerge in June and July. The life cycle is semivoltine (Stewart et al. 1990).

26. ***Nemoura rickeri* Jewett** Northwestern Nearctic
Distribution: Alaska, Yukon to Manitoba, Saskatchewan.
Yukon records: Bluefish R., 67°08′N 140°49′W at Old Crow; Richardson Mts. West Slope, km 449 Dempster Hwy., 703 m.

Genus *Podmosta*. Eastern Palaearctic and Nearctic; 4 of the 5 Nearctic species found in the west, from Alaska and Yukon south to California and New Mexico. Small adults, less than 6 mm, emerge April–August throughout range. Nymphs occur in small streams at high elevations in western mountains and small subarctic streams. Anecdotal life-history data have suggested univoltine, fast life cycles for northern species.

27. ***Podmosta decepta* (Frison)** Western Nearctic
Distribution: Alaska, Yukon to Oregon, Colorado.
Yukon records: Lapie R. near Lapie Lks.; Moose Cr. Campground, Klondike Hwy., 63°30′N 137°01′W; Ogilvie Mts., North Fork Crossing, mi 43 Dempster Hwy., 1050 m.

28. ***Podmosta delicatula* (Claassen)** Western Nearctic
Distribution: Yukon to California, Colorado.
Yukon records: Christmas Cr., km 1688 Alaska Hwy., 61°10′N 138°14′W; Lapie R., km 175 South Canol R., 61°45′N 133°06′W; Moose Cr. Campground, km 562 Klondike Hwy., 63°30′N 137°01′W; Rose L. 61°35′N 133°5′W; same, 7 km E Rancheria, 60°04′N 130°29′W; Otter L., 1200 m, 62°30′N 130°25′W.

29. ***Podmosta weberi* (Ricker)** Transberingian (endemic)
Distribution: Alaska, Yukon; Chukotka and Kamchatka Peninsulas and northern Far East of Russia.
Yukon records: Watson L., Alaska Hwy.

Genus *Prostoia*. Nearctic; 3 of the 4 Nearctic species are found in the east, with only *P. besametsa* found widely distributed in the west, from Alaska and Yukon to California and New Mexico. Adults dark, 5–6 mm, emerging February–March in the Ozark Mountains to March–August at northern latitudes. The herbivorous/detritivorous nymphs are found mainly in coarse particulate organic matter in small streams, and species studied have univoltine, fast life cycles.

30. ***Prostoia besametsa* (Ricker)** Western Nearctic
Distribution: Yukon to California, New Mexico.
Yukon records: Rose L., 61°35′N 133°5′W.

Genus *Zapada*. Nearctic; 10 species, 8 of which are western, from Alaska and Yukon to California and New Mexico. Adults 5–10 mm, emerging mainly February–August, depending on elevation and latitude. Some combination of *Zapada* species is common in

most streams of western mountain ranges and high-latitude streams. Nymphs are shredders, found mainly in coarse particulate organic matter. Ubiquitous species generally have univoltine life cycles at southern latitudes and semivoltine cycles in Canada.

31. ***Zapada cinctipes* (Banks)** Western Nearctic
Distribution: Alaska, Yukon, Saskatchewan to California, New Mexico.
Yukon records: Bear Cr., Alaska Hwy., 60°37′N 137°39′W; W Haines Jct., 60°47′N 137°40′W; Dickson L., Mt. Mye, 1500 m, 62°21′N 133°8′W; Irwin Lks., 960 m, 62°13′N 133°W; Kluane, Christmas Cr. at Boutellier Cr.; Wolf Cr., Alaska Hwy., 60°36′N 134°36′W; Wolf Cr. Campground at Whitehorse.
Biological information: This species is univoltine in the central Rocky Mountains, but probably semivoltine in far northwestern streams (Stewart and Stark 1988). Adults are present along streams in the Yukon during June–August, depending on elevation.

32. ***Zapada columbiana* (Claassen)** Western Nearctic
Distribution: Alaska, Yukon to California, Wyoming.
Yukon records: Beaver Cr., km 10.5 South Canol Rd., 60°33′N 133°09′W; Ogilvie Mts., North Fork Crossing, mi 42 Dempster Hwy., 1050 m; Scout Car Cr., km 47 Dempster Hwy., 61°21′N 138°26′W.
Biological information: This species has a semivoltine life cycle in Alberta (Mutch and Pritchard 1984). The nymphs, like other species of *Zapada*, are shredders and adults are present in the Yukon during early summer.

33. ***Zapada frigida* (Claassen)** Western Nearctic
Distribution: Alaska, Yukon to California, New Mexico.
Yukon records: Small stream, km 175 Haines Rd., 60°12′N 136°58′W.

34. ***Zapada haysi* (Ricker)** Western Nearctic
Distribution: Alaska, Yukon to California, New Mexico.
Yukon records: Blackstone R., km 103 Dempster Hwy., 64°43′N 138°22′W; Dickson L., Mt. Mye, 1500 m, 62°21′N 133°8′W; Glacier Cr., Alaska Hwy., 61°32′N 139°19′W; North Klondike R., km 73 Dempster Hwy.; Nahanni Range Rd. Summit, 62°01′N 128°25′W; Ogilvie Mts., North Fork Crossing, mi 42 Dempster Hwy., 1050 m; same, North Fork Pass, 1230 m; S channel Blackstone R., km 147 Dempster Hwy., 65°03′N 138°10′W; Takhanne R., 60°07′N 136°56′W; Whitehorse; Willow Cr., km 468 Klondike Hwy., 62°51′N 136°35′W.
Biological information: Adults are present at varying elevations in Alaska and the Yukon from May–July (Stewart et al. 1990). Seasonal growth patterns of nymphs in far northwestern streams suggest a short-term hatching of eggs in late summer and a semivoltine life cycle requiring 2 or more years. Nymphs are shredders and thus are recruited heavily in September and October when regional leaf input is high.

35. ***Zapada oregonensis* (Claassen)** Western Nearctic
Distribution: Alaska, Yukon to California, Colorado.
Yukon records: Mile 106 Canol Rd.; North Fork Pass, Tombstone Campground; North Klondike R., km 73 Dempster Hwy.; Pine Cr., Alaska Hwy., 60°45′N 137°35′W; Watson L., Alaska Hwy.; Whitehorse; Wolf Cr. at Whitehorse.
Biological information: Adults are present in the Yukon from May–July. The life cycle and life history have not been studied in detail but are probably similar to those of its congeners in the Yukon.

Family Taeniopterygidae

Genus *Taenionema*. Eastern Palaearctic and Nearctic; 12 Nearctic species, all western except *T. atlanticum* Ricker and Ross, distributed from Alaska and Yukon to California and New Mexico. Adults brown to black, 6–12 mm, emerging early spring (March–April) at lower elevations and latitudes to June–July in Alaska and Yukon. Nymphs are detritivores in small streams and rivers, and the few life-history studies have indicated univoltine cycles. The genus was recently revised by Stanger and Baumann (1993).

36. ***Taenionema kincaidi* (Hoppe)** Western Nearctic
Distribution: Yukon to California, Nevada.

Yukon records: Swift River, almost on Yukon-British Columbia border at 60°N 133°W (USNM).

37. ***Taenionema pacificum* (Banks)** Western Nearctic
Distribution: Yukon to California, New Mexico.
Yukon records: Big Creek; Gosm L., 960 m, 62°15′N 133°W; Klondike R., Tombstone Camp; Marshall Cr., Alaska Hwy., 60°50′N 137°19′W; Ogilvie R., Elephant Rock, and km 220 Dempster Hwy., 61°31′N; Wolf Cr. at Wolf Cr. Campground, km 1458 Alaska Hwy., 60°37′N 134°58′W; Yukon R. at Dawson; Koidern R., Lake Cr. Campground, km 1853 Alaska Hwy., 61°50′N 140°07′W; Quill Cr., Haines Hwy.
Biological information: This is a relatively common, early-spring-emerging species (April–June) in the Yukon and Alaska. Nymphs grow steadily from July through the winter. The life cycle is univoltine, slow (Stewart et al. 1990).

38. ***Taenionema pallidum* (Banks)** Western Nearctic
Distribution: Yukon to California, New Mexico.
Yukon records: Andy Cr., km 1246 Alaska Hwy., 59°59′N 132°06′W; Whitehorse; Yukon R. at Dawson; Haines Rd., km 175, 60°12′N 136°58′W.

Family Chloroperlidae

Genus *Alaskaperla*. Endemic to Far Northwestern North America; monospecific, found only in Alaska, Northwest Territories and Yukon. Emergence June–July and univoltine slow life cycle suggested (Stewart et al. 1991). Like many Chloroperlidae, the nymphs occur in surface layers of stream substrates only just prior to emergence; probably insectivorous.

39. ***Alaskaperla ovibovis* (Ricker)** East Beringian endemic
Distribution: Alaska, Northwest Territories, Yukon.
Yukon records: Clear L., km 592 Klondike Hwy., 63°37′N 137°36′W; Old Crow, km 35 WSW, 67°30′N 140°43′W, 300 m; Sakiw Cr., milepost 1110 Alaska Hwy., 61°29′N 139°16′W.

Genus *Alloperla*. Eastern Palaearctic and Nearctic; 29 Nearctic species, only 7 of which are western, distributed from Kodiak Island, Alaska and Yukon to California and Wyoming. Adults yellow or light green, 6–12 mm. Summer emergers, April in Mississippi to June–August in Alaska and Yukon. No detailed accounts of nymphal development, trophic dynamics or habitat partitioning have been published.

40. ***Alloperla medveda* Ricker** Western Nearctic
Distribution: Yukon to Idaho, Wyoming.
Yukon records: Watson L., Alaska Hwy.

41. ***Alloperla serrata* Needham and Claassen** Western Nearctic
Distribution: Alaska, Yukon to Washington, Wyoming.
Yukon records: Burwash Flats, milepost 1105 Alaska Hwy.; Nahanni Range Rd. Summit, 62°01′N 128°25′W; Ogilvie Mts., North Fork Crossing, mi 42 Dempster Hwy.; Swift R.

42. ***Alloperla severa* (Hagen)** Western Nearctic
Distribution: Alaska, Yukon to California, Colorado.
Yukon records: Carmacks; Chilkat Pass (British Columbia-Yukon), 960 m; Christmas Cr., Kluane L.; Garin? L., 960 m, 62°15′N 133°W; Irwin Lks., 960 m, 62°13′N 133°W; Moose Cr. Campground, km 562 Klondike Hwy., 63°30′N 137°01′W; Ogilvie R. at Elephant Rock, Dempster Hwy.; Porcupine R., km 6 E Old Crow, 67°34′N 139°41′W; Porcupine R., Rampart House near Alaska border; Rose L., Rose R., 61°35′N 133°5′W; Snafu Cr.; Takhanne R., 60°07′N 136°56′W; Upper Liard R., 60°03′N 128°59′W; Yukon R., Dawson.

Genus *Kathroperla*. Western Nearctic; 2 species (Stark and Surdick 1987), Alaska, Yukon to California and Montana. Adults, 20–25 mm, emerge May–July, depending on elevation and latitude. There are no major published accounts of nymphal biology; nymphs, as in *Paraperla*, are hyporheal during development.

43. ***Kathroperla perdita* Banks** Western Nearctic
Distribution: Yukon to California, Montana.
Yukon records: Kluane National Park, Cottonwood Cr.

Genus *Neaviperla*. Western Nearctic (and possibly Siberia, Surdick 1985); monospecific, found Alaska and Yukon to Washington and Montana. Nymphs were indistinguishable from species of *Suwallia* prior to 1985, accounting for lack of published accounts on life history and ecology.

44. ***Neaviperla forcipata* (Neave)** Northwestern Nearctic
Distribution: Alaska, Yukon to Washington, Montana.
Yukon records: Blackstone R., km 141 Dempster Hwy.; E Dawson 14 mi, 390 m; E Rancheria, km 7, 60°04′N 130°29′W; Rose R., km 154 South Canol Rd., 61°34′N 133°05′W; Rose R. at Rose L., 61°35′N 133°5′W; Takhanne R.

Genus *Paraperla*. Western Nearctic; the 2 species occur from the Yukon to California and New Mexico. Adults are brown, 16–20 mm. They emerge March–August, depending on elevation and latitude. Nymphs occur in the hyporheal beneath and beside larger streams, and are collected in surface layers only just prior to emergence. Nymph sizes before and after emergence suggest 2–3-year, semivoltine life cycles.

45. ***Paraperla frontalis* (Banks)** Western Nearctic
Distribution: Alaska, Yukon to California, New Mexico.
Yukon records: Ogilvie Mts., North Fork Crossing, mi 42 Dempster Hwy.; Ten Mile Cr., km 1308 Alaska Hwy., 60°14′N 132°54′W; Yukon R. at McQuesten; Yukon R. at Dawson.

46. ***Paraperla wilsoni* Ricker** Western Nearctic
Distribution: Yukon to California, Montana.
Yukon records: Ogilvie Mts., North Fork Crossing, mi 43 Dempster Hwy., 1050 m; Vangorda Cr., 1140 m, 62°18′N 133°15′W.

Genus *Plumiperla*. Transberingian; *P. spinosa* is endemic to California; *P. diversa* is widespread from Alaska and Yukon to California and New Mexico, and occurs in streams of Kamchatka Peninsula (Levanidova 1982). Adults are light yellow with no head markings, 6–8 mm. They emerge from May in the southern Rocky Mountains to as late as September in Alaska (Stewart et al. 1990) and Yukon. Nymphs occur in springs and streams of all sizes, and the life cycle in northern latitudes appears to be univoltine, fast.

47. ***Plumiperla diversa* (Frison)** Transberingian
Distribution: Alaska, Yukon to California, New Mexico; Kamchatka Peninsula (Levanidova 1982).
Yukon records: Big Creek; Blackstone R. Valley, km 141; Chilkat Pass (British Columbia-Yukon), 960 m; Christmas Cr., Alaska Hwy., 61°00′N 138°14′W; Fish Cr., Alaska Hwy. at Fish L. Rd., 60°39′N 135°15′W; Kluane, Jarvis Cr., Alaska Hwy., 60°55′N 137°53′W; Lower Rancheria R., km 1107 Alaska Hwy., 60°12′N 130°03′W; Moose Cr., km 22 on South Canol Rd., 60°33′N 133°09′W; Morley R., Alaska Hwy., 60°00′N 132°08′W; North Klondike R., km 68 Dempster Hwy., 64°28′N 138°12′W; Nahanni Range Rd. Summit, 62°01′N 128°25′W; Ogilvie R., km 220 Dempster Hwy., 65°31′N 138°15′W; same, mi 150 Dempster Hwy.; Ogilvie Mts., North Fork Crossing, mi 43 Dempster Hwy., 1050 m; same, mi 42 Dempster Hwy.; same, North Fork Pass, 1230 m; Partridge Cr., Milepost 737 Alaska Hwy.; Philip Cr., 68°58′N 138°35′W; Scout Car Cr., km 47 Dempster Hwy., 64°21′N 138°26′W; Streams crossing Alaska Hwy. between Watson Lake and Whitehorse; Takhanne R.; Ten Mile Cr., km 1308 Alaska Hwy., 60°14′N 132°54′W; "White River"; Willow Cr. crossing Klondike Hwy., ca. 15 mi N Pelly Crossing, 62°59′N 136°29′W; Willow Cr., km 468 Klondike Hwy., 62°51′N 136°35′W; Yukon R. at Dawson.
Biological information: P. diversa is widespread in springs and clearwater streams of the Far Northwest. Peak emergence is in July, and the species has a univoltine, slow life cycle in regional streams (Stewart et al. 1990).

Genus *Suwallia*. Nearctic and eastern Palaearctic; 6 Nearctic species. *S. marginata* (Banks) is eastern and 5 western species occur from Alaska and Yukon to California and New Mexico. Adults are yellow, 6–10 mm. They emerge in summer and early fall. Nymphs occur deep in stream substrates until just prior to emergence. No definitive studies of life cycles have been published.

48. ***Suwallia autumna* (Hoppe)** Western Nearctic
Distribution: Yukon to Oregon, Colorado.
Yukon records: Blackstone R., km 103 Dempster Hwy., 64°43′N 138°22′W.

49. ***Suwallia dubia* (Frison)** Western Nearctic
Distribution: Alaska, Yukon to Oregon, Colorado.
Yukon record: Groundhog Cr., Lapie Pass.

50. ***Suwallia lineosa* (Banks)** Western Nearctic
Distribution: Yukon, Saskatchewan to Oregon, Colorado.
Yukon records: Nahanni Range Rd. Summit, 62°01′N 128°25′W; Rancheria R., mi 721.6 Alaska Hwy.

51. ***Suwallia pallidula* (Banks)** Western Nearctic
Distribution: Alaska, Yukon to California, New Mexico.
Yukon records: Blackstone R., km 141 Dempster Hwy.; campground at Mayo; Carmacks; Magundy R., km 448 Campbell Hwy., 62°11′N 133°46′W; Porcupine R., 6 km E at Old Crow, 67°34′N 139°41′W; 14 mi E Dawson, 390 m; Rancheria R., mi 721.6 Alaska Hwy.; Rose L., Rose R. 61°35′N 133°5′W.

Genus *Sweltsa*. Nearctic and eastern Palaearctic; 27 Nearctic species of which 20 are western, distributed generally from Alaska and Yukon to California and New Mexico. Adults are tan to yellow, 8–18 mm. They are late spring to autumn emergers, depending on species, elevation and latitude. Some species like *S. borealis* and *S. coloradensis* are found in streams of all sizes. No definitive life-history studies of western species have been reported. The eastern *S. mediana* (Banks) and *S. onkos* (Ricker) have 2-year, semivoltine cycles (Harper 1973).

52. ***Sweltsa borealis* (Banks)** Western Nearctic
Distribution: Alaska, Yukon to California, New Mexico.
Yukon records: Chilkat Pass (British Columbia-Yukon), 960 m; Whitehorse.

53. ***Sweltsa coloradensis* (Banks)** Western Nearctic
Distribution: Yukon to California, New Mexico.
Yukon records: Carmacks; Garin L., 960 m; Irwin Lks., 960 m, 62°13′N 133°W; Ogilvie R., km 220 Dempster Hwy.; same, at Ogilvie; McQuesten; Ogilvie R., mi 150 Dempster Hwy.; Partridge Cr., Milepost 737, Alaska Hwy.; Pine Cr., Alaska Hwy., 60°45′N 137°35′W; Yukon R. at Dawson.

54. ***Sweltsa fidelis* (Banks)** Western Nearctic
Distribution: Alaska, Yukon to California, Colorado.
Yukon records: Evelyn Cr., 60°45′N 133°05′W; La Force L., 690 m, 62°41′N 132°20′W; Nahanni Range Rd. Summit, 62°01′N 128°25′W; Whitehorse; Ogilvie Mts., North Fork Crossing, mi 43 Dempster Hwy., 1050 m; Otter L., 1200 m, 62°30′N 30°25′W; Watson L., Alaska Hwy. near British Columbia.

Genus *Triznaka*. Western Nearctic; 2 species, generally distributed from Alaska and Yukon to California and New Mexico. Adults are yellow to brown, 7–9 mm. They are summer emergers, to August in the Yukon. Nymphs are rare in collections, reflecting their hyporheal occurrence during development. Life histories remain unreported.

55. ***Triznaka signata* (Banks)** Western Nearctic
Distribution: Alaska, Yukon to Oregon, New Mexico.
Yukon records: Carmacks; Porcupine R., Rampart House near Alaska border.

Genus *Utaperla*. Nearctic; 2 species, *U. gaspesiana* Harper and Roy is eastern and the western *U. sopladora* is found from Alaska and Yukon to Nevada and Wyoming. Adults are black, 7–10 mm. They emerge in summer, to late July in the Yukon. There are no published accounts of life histories of either species.

56. ***Utaperla sopladora* Ricker** Western Nearctic
Distribution: Alaska, Yukon, British Columbia to Utah.
Yukon records: Cornwall Cr., Richardson Mts., Dempster Hwy.; La Force L., 690 m, 62°41′N 132°20′W; Moose Cr. Campground, km 562 Klondike Hwy., 63°30′N 137°01′W; North Fork Pass, km 72 Dempster Hwy., 64°30′N 138°13′W; Ogilvie Mts., North Fork Crossing, mi 43 Dempster Hwy., 1050 m; Ogilvie R. at Ogilvie; same, km 220 Dempster Hwy., 65°31N 138°15′W; same, km 206 Dempster Hwy., 65°25′N 138°14′W; same, mi 150 Dempster Hwy.; Ogilvie R. tributary, km 208 Dempster Hwy., 65°25′N 138°11′W; Rose L., 61°35′N 133°5′W; Small pond, km 215.5 Dempster Hwy., 56°27′N 138°12′W; Tombstone Campground, km 72 Dempster Hwy., 64°31′N 138°28′W; Otter L., 1200 m, 62°30′N 130°25′W; Yukon R. at Dawson.

Family Perlidae

Genus *Hesperoperla*. Western Nearctic; 2 species, *H. hoguei* Baumann and Stark endemic to California and *H. pacifica* ubiquitous, from Alaska and Yukon to California and New Mexico. Adults brown or yellow, variable body length to 30 mm. Emergence from April at low elevations in its southern range to September–October in the north. Nymphs are insectivorous and found in a wide variety of habitats from spring seeps to large rivers. Detailed life-history studies have not been reported, but nymphal size variations in numerous western streams suggest 2–3-year, semivoltine cycles (Stewart and Stark 1988).

57. ***Hesperoperla pacifica* (Banks)** (Frontispiece) Western Nearctic
Distribution: Alaska, Yukon to California, New Mexico.
Yukon records: Big Cr.; Stream crossing Alaska Hwy. between Watson L. and Whitehorse; Tatchun Cr. at campground, km 384 Klondike Hwy., 62°17′N 136°16′W.

Family Perlodidae

Genus *Arcynopteryx*. Holarctic; *A. compacta* is the only one of 5 species that occurs in both Old and New Worlds. In North America, *A. compacta* is distributed from Alaska, Yukon and Saskatchewan south to high elevations in Colorado, and eastward to Maine and New Hampshire. Adults emerge from March in the southern Rocky Mountains to August in the Brooks Range of Alaska. The insectivorous nymphs inhabit cold streams and high-elevation and high-latitude lakes having stony shorelines, and are univoltine.

58. ***Arcynopteryx compacta* (McLachlan)** Holarctic
Distribution: Alaska, Yukon, Colorado to Maine, New Hampshire; Eurasia.
Yukon records: Alligator L., 1110 m; Big Cr.; Blackstone R., km 141 Dempster Hwy.; Bluefish Caves, 67°08′N 140°48′W; Cornwall Cr. km 439 Dempster Hwy.; Faster R.; Fish Cr. at Fish L. Rd., Alaska Hwy., 60°39′N 135°15′W; Ogilvie Mts., North Fork Pass, 1230 m.
Biological information: This species is found in both high-elevation lakes and in clearwater streams. Peak emergence of adults is in May–June and nymphs grow fast to maturity in October; the life cycle is univoltine, fast (Stewart et al. 1990; Lillehammer 1985).

Genus *Cultus*. Nearctic; 6 species, half of which are western occurring from the Yukon to California and New Mexico. Size of adults variable, from 8–14 mm depending on species; males smaller than females. They emerge April to August, depending on elevation and latitude. Biology of the genus is poorly known; nymphs are insectivorous and the eastern *C. decisus* is univoltine.

59. ***Cultus pilatus* (Frison)** Western Nearctic
Distribution: Yukon to California, Montana.

Yukon records: Eagle R., Dempster Hwy.

Genus *Diura*. Holarctic; 3 Nearctic species, 2 western and *D. nanseni* (Kempny) recorded from New Hampshire and Quebec. Adults of *D. bicaudata* and *D. knowltoni* emerge in Alaska and Yukon in June and July. Nymphs and adults are rare in collections. Nymphs are insectivorous. *D. bicaudata* has a univoltine life cycle in Sweden and Norway, but there are no reports on the biology of either species in North America (Stewart and Stark 1988).

60. ***Diura bicaudata* (Linnaeus)** Holarctic
Distribution: Alaska, Yukon to Manitoba, Saskatchewan; Eurasia.
Yukon records: Fortymile (Fort Cudahy).

61. ***Diura knowltoni* (Frison)** Western Nearctic
Distribution: Yukon to California, New Mexico.
Yukon records: Yukon R. at Dawson.

Genus *Isogenoides*. Nearctic; 9 species, 3 of which are western, occurring from Alaska and the Yukon southward to Arizona, California and New Mexico. Biology of western species is inadequately known. Adults emerge from May in southern parts of their range to late June–July in Alaska and the Yukon. Nymphs are insectivorous, and *I. frontalis* is univoltine in Saskatchewan (Dosdall and Lemkuhl 1979).

62. ***Isogenoides colubrinus* (Hagen)** Western Nearctic
Distribution: Alaska, Yukon to California, Colorado.
Yukon records: Carmacks; Porcupine R., Rampart House near Alaska border; same, Old Crow; Whitehorse; Dawson.

Genus *Isoperla*. Holarctic; 58 Nearctic species of which 27 are western (4 widely distributed over the continent or in the west and midwest). Adults of various species emerge from April in the Southwest to July–August in Alaska and the Yukon. Food habits of nymphs are highly variable according to species; most are insectivorous, but some are herbivorous or have ontogenic shifts from detritivory to insectivory (Stewart and Stark 1988). Life cycles of the few studied species are univoltine. Western species of the genus were revised by Szczytko and Stewart (1979).

63. ***Isoperla decolorata* (Walker)** Northwestern Nearctic
Distribution: Alaska, Yukon to British Columbia, Saskatchewan.
Yukon records: Bluefish Caves, 67°08′N 140°48′W, 600 m; Carmacks; Kluane, UV light; Old Crow; Porcupine R. at Dave Lord Cr., 67°33′N 139°8′W; Porcupine R., Rampart House near Alaska border; same, E Old Crow, 67°34′N 139°41′W; 14 mi E Dawson.

64. ***Isoperla fusca* Needham and Claassen** Western Nearctic
Distribution: Yukon to Oregon, Wyoming.
Yukon records: Evelyn Cr., 4 km, 60°45′N 133°65′W; Watson L., Alaska Hwy. near British Columbia; Whitehorse.

65. ***Isoperla petersoni* Needham and Christenson** Western Nearctic
Distribution: Alaska, Yukon to British Columbia, Wyoming.
Yukon records: Blackstone R., km 141 Dempster Hwy., 65°01′N 138°12′W; Blackstone R. side channel km 142 Dempster Hwy., 65°03′N 138°10′W; Dawson, 14 mi E; McCabe Cr., Klondike Hwy. 5 mi S Minto Landing, 62°32′N 136°45′W; Nahanni Range Rd. Summit, 62°01′N 128°25′W; Ogilvie R., km 200 Dempster Hwy., 65°52′N 138°18′W; Rancheria 7 km E, 60°04′N 130°29′W; Streams crossing Alaska Hwy. between Watson L. and Whitehorse.
Biological information: This species is common and abundant in many clearwater streams of the Yukon and Alaska. It emerges from June–August, and its flexible life cycle, being largely univoltine

with late summer recruits possibly requiring 2 years to complete growth, was first reported by Stewart et al. (1990).

66. ***Isoperla sobria* (Hagen)** Western Nearctic
Distribution: Alaska, Yukon to California, New Mexico.
Yukon records: Wolf Cr.; Watson L., Alaska Hwy.

Genus *Kogotus*. Western Nearctic; 2 species distributed from Alaska and the Yukon southward to California, Colorado and New Mexico. Adults emerge in Alaska and the Yukon in August, and both species are probably univoltine. Nymphs are insectivorous.

67. ***Kogotus nonus* (Needham and Claassen)** Western Nearctic
Distribution: Yukon to California, Wyoming.
Yukon records: Moose Cr. at campground, km 562 Klondike Hwy., 63°31′N 137°01′W; Rancheria, 7 km E Rancheria R., 60°04′N 130°29′W.

Genus *Megarcys*. Eastern Palaearctic, Western Nearctic; 5 Nearctic species occurring from Alaska and Yukon southward to California, Colorado and New Mexico. Adults emerge in the Yukon in June–July. *M. signata* is univoltine in the Central Rocky Mountains; early instars appear in July–October and the largely insectivorous nymphs grow rapidly during warmer months (Stewart and Stark 1988).

68. ***Megarcys signata* (Hagen)** Western Nearctic
Distribution: Alaska, Yukon to British Columbia, Colorado.
Yukon records: Koidern R., Alaska Hwy., 61°52′N 140°08′W; Ogilvie Mts., North Fork Crossing, mi 42 Dempster Hwy., 1050 m; Rancheria R., km 1107 Alaska Hwy., 60°12′N 130°03′W; Streams crossing Alaska Hwy. between Watson L. and Whitehorse.

Genus *Skwala*. Eastern Palaearctic, Western Nearctic; 2 Nearctic species distributed from the Yukon southward to California, Colorado and New Mexico. Both species are univoltine in the Central Rocky Mountains, and their nymphs are insectivorous. Adults emerge in the Far Northwest in June.

69. ***Skwala americana* (Klapálek)** Western Nearctic
Distribution: Yukon to California, New Mexico.
Yukon records: Mayo R. at Mayo.

Family Pteronarcyidae

Genus *Pteronarcys*. Eastern Palaearctic, Nearctic; 8 Nearctic species, of which 2 (*P. californica* and *P. princeps*) are western and one (*P. dorsata*) is transcontinental. The western species, and eastern species at northern latitudes, are semivoltine, requiring 2–3 years to complete a generation. Nymphs are shredders of coarse particulate organic matter in streams.

70. ***Pteronarcys californica* Newport** Western Nearctic
Distribution: Alaska, Yukon to California, New Mexico.
Yukon records: Klusha Cr., km 296 Klondike Hwy.

71. ***Pteronarcys dorsata* (Say)** Transcontinental Nearctic
Distribution: Alaska, Yukon, British Columbia, Kansas to Labrador, Florida, Louisiana.
Yukon records: Whitehorse.

Biogeography

Stoneflies are important and often dominant food-web components of most temperate stream ecosystems (Stewart and Stark 1988). Their densities in Yukon streams remain largely undocumented, but they undoubtedly play vital roles in the trophic dynamics and energetics of these systems. In light of the inadequate fossil record of Plecoptera (Hynes

1988; Zwick 1973, 1980), our reconstruction of historical events leading to stonefly colonization and subsequent dispersals in far northwestern North America is largely based on the rather limited knowledge of current distributions of the regional species and on previous interpretations for the continent (Hynes 1988; Stewart and Stark 1988) and for Canada (Ricker 1964; Dosdall and Lehmkuhl 1979).

The approximately 2000 world Plecoptera species have descended from ancestors probably originating near Permian times, about 250 million years ago somewhere in Pangaea (Illies 1965). The division of Pangaea about 120 million years later into southern Gonwanaland and northern Laurasia was possibly the basis for the largely amphipolar current distribution of the order into the 2 distinctive suborders Antarctoperlaria and Arctoperlaria (Zwick 1980; Hynes 1988).

We can dismiss the Antarctoperlaria and one particular section of the Neotropical Arctoperlaria from our discussion of the Yukon fauna, because no representatives of the former are known to have moved northward into North America, and only 2 species of the large neotropical genus *Anacroneuria* (Arctoperlaria, family Perlidae) have invaded northward as far as Arizona and Texas (Baumann and Olson 1984; Stark and Baumann 1987).

The pre-Pleistocene origin of the extant Yukon Plecoptera fauna is highly speculative, but thought to be entirely Asiamerican (Stewart and Stark 1988). This corresponds to the non-endemic stonefly grouping of Hynes (1988: 34) of western genera, shared with the Far East or Japan. The approximately 68 endemic North American genera and their large number of species apparently have evolved over a long period of time from ancient invaders of the continent. Readers are referred to Illies (1965), Ricker (1964), Hynes (1988) and Stewart and Stark (1988) for a more detailed discussion of possible pre-Pleistocene Plecoptera invasions of North America.

The 71 known Yukon stonefly species are representative of 6 distributional elements:

I. Western Nearctic (54 species; 76.1%).
II. Northwestern Nearctic (7 species; 9.9%).
III. Transberingian (4 species; 5.6%).
IV. Holarctic (3 species; 4.2%).
V. Transcontinental Nearctic (2 species; 2.8%).
VI. East Beringian endemic (Alaska, Yukon, Northwest Territories) (1 species; 1.4%).

Yukon faunal elements for the 2 aquatic insect orders Ephemeroptera and Trichoptera were identified and discussed, respectively, by Harper and Harper (1997) and Wiggins and Parker (1997). Those elements and their relative importance (number of species per category) correspond only partially to those listed above for stoneflies. For example, within the largest category of caddisflies, species that are wholly Nearctic in distribution (representing 68% of Yukon Trichoptera), have approximately 62% that are transcontinental and 38% restricted to western North America. These proportions contrast to the 86% of the Yukon stonefly fauna (Categories I and II above) that are restricted to the western Nearctic and only 3% that are transcontinental (Category V). Distributionally related mayfly elements correspond fairly closely with those of stoneflies, except for the absence of Transberingian and East Beringian endemic species. The currently known mayfly fauna, like that of stoneflies, is dominated by western Nearctic species.

By far the largest distributional element represented by the Yukon stonefly fauna is the group of species widespread in the western Nearctic (Category I; 54 species or 76.4% of Yukon fauna). The most common and widespread species of this group in the Yukon are *Capnia coloradensis* (2), *Capnia confusa* (3), *Capnia gracilaria* (5), *Eucapnopsis brevicauda* (10), *Utacapnia columbiana* (18), *Zapada cinctipes* (31), *Zapada haysi* (34),

Taenionema pacificum (37), *Alloperla severa* (42), *Suwallia pallidula* (51) and *Isoperla petersoni* (65). The remaining 43 species are less common and more restricted, at least in their known Yukon and regional distribution. We consider the ancestors of species of this group to be Asiamerican in origin. Their current widespread and sometimes disjunct occurrence at more southerly latitudes suggests that most of them survived the Wisconsinan glaciation in the "southwestern" refugium of Ricker (1964), then in postglacial times moved back north into the Yukon. One widespread species of this group that has yet to be documented for the Yukon, but is fairly common in Alaska, is *Pteronarcella badia* (Hagen).

Some species of Category I, however, particularly *Capnia elongata* (4), *C. petila* (8), *C. pileata* (9), *Utacapnia columbiana* (18), *Paraleuctra forcipata* (19), *Perlomyia collaris* (23), *Paraperla wilsoni* (46) and *Cultus pilatus* (59), that extend southward only to latitudes bounded roughly by a northern California to Montana line, could have survived Pleistocene glaciations in the northwestern (Beringian) refugium, then spread back southward in postglacial times. Our distinction of these 8 species from the 7 Yukon species of Category II, that are currently also distributed southward roughly only as far as British Columbia-Washington to Montana, may be due to the limited knowledge of current distributions and lack of definitive information on their differential dispersal capabilities or exact age. The 7 Category II species are: *Capnia cheama* (1), *Isocapnia fraseri* (12), *Isocapnia integra* (14), *Mesocapnia oenone* (16), *Nemoura rickeri* (26), *Neaviperla forcipata* (44) and *Isoperla decolorata* (63). These northwestern forms apparently are cold-adapted Nearctic species whose ancestors were of Asiamerican origin. They, and the 8 other cold-adapted species of Categories III–VI, probably passed the last glacial period in the unglaciated parts of Beringia; however, we are not able to explain why they are not found in northeastern Asia (West Beringia).

Three Holarctic species are represented in the Yukon stonefly fauna, *Nemoura arctica* (25), *Arcynopteryx compacta* (58) and *Diura bicaudata* (60); all 3 are common on both sides of the Bering strait (Levanidova 1982). *N. arctica* and *D. bicaudata* are common arctic tundra species; their absence in alpine zones of mountain ranges south of Canada suggests that they survived Pleistocene glaciations in unglaciated Beringia, then reinvaded eastward across the Yukon after glacial recession. Populations of *Arcynopteryx compacta*, found as far south as Colorado in the west and Maine and New Hampshire in the east, indicate that this species could have survived glacial maxima in a broad continental band south of the ice (southeastern and southwestern refugia of Ricker 1964) as well as in unglaciated Beringia.

Postglacial invaders from the northwestern refugium undoubtedly also included the Nearctic-West Beringian species *Capnia nearctica* (7), transcontinental Nearctic *Amphinemura linda* (24), East-West Beringian *Mesocapnia variabilis* (17), *Podmosta weberi* (29) and *Plumiperla diversa* (47), and East Beringian endemic *Alaskaperla ovibovis* (39). The widespread western Nearctic and North Slope Alaska distribution of *Plumiperla diversa* suggests that it may have survived glaciation in both the southwestern and northwestern refugia.

There is no indication of movement into the Yukon or other far northwestern areas of North America by the "old" eastern stonefly fauna (Hynes 1988), of Euramerican origin. The current transcontinental distribution of *Pteronarcys dorsata* (71) across northern latitudes from Alaska to Maine and Labrador, and its predominance in the East down to Florida, Mississippi and Louisiana might seem to suggest an east to west invasion; however, the eastern Palaearctic-Nearctic distribution of the genus indicates an Asiamerican origin for North American species.

The presence of *P. dorsata* and *P. californica* (70) in the Yukon is based on scanty, but dependable material (1 ♀ *P. dorsata* from Whitehorse in SMDV collection determined by W.E. Ricker; a good 1980 series of 3 ♂, 1 ♀, 2 ♂ exuviae of *P. californica* from Klusha Creek on the Klondike Hwy., determined by K.W. Stewart). These few specimens, in light of the recently intensified collecting in the region and large size of these species would suggest that they are not widely distributed or very successful in far northwestern stream ecosystems, possibly in part because of the relatively low amounts of coarse particulate organic matter in many streams available to them as shredders. It is likely, then, that *P. dorsata* was distributed across North America in pre-Pleistocene times and survived the recent glaciations in the Beringian and southeastern refugia, then spread back into its current northwestern range primarily from the Beringian refuge and into the Northeast from the Southeastern refugium as the ice retreated. We consider it a less feasible possibility that *P. dorsata* spread back north, then westward into the Yukon from the Southeastern refugium, using the large plains river systems, where it is not prevalent, as dispersal corridors. *P. dorsata* and *P. californica* have never been found to inhabit the same section of any stream. Apparently, *P. dorsata* is unable to compete with *P. californica* in western mountain streams, particularly at high elevations, and the western *P. californica* has not been able to move across low-elevation river corridors and become competitive with *P. dorsata* in the east.

The Bering land bridge and Beringia have been of immense importance to the interchange of Nearctic and Palaearctic stonefly faunas at various times during and prior to the Pleistocene epoch. The extant western stonefly fauna has been overwhelmingly influenced by this intermittent exchange, with no detectable influence from early faunal exchanges between North America and Europe or from the Neotropics. Yukon stoneflies survived the ice age south of ice margins, primarily in the region west of the Continental Divide ("Cascadia", "southwestern refugium") or in the unglaciated areas adjacent to the Yukon Valley, along the arctic coastal plain from the Bering Strait east to beyond the Mackenzie River and in the western arctic islands. These are the same refugia from which fishes reinvaded the Yukon and Mackenzie Basins (Lindsey and McPhail 1986).

The arctic and subarctic climate and differential cold-adaptive capability of various stonefly groups have undoubtedly greatly influenced their relatively low diversity in the Yukon and northern latitudes in general. The substantially gilled families Peltoperlidae and Perlidae are absent from cold alpine and tundra lakes and northern latitude streams that freeze solid or remain cold over an extended time in winter. Peltoperlidae appear to be absent from Beringia, and the only perlid that has successfully invaded a few streams in Alaska and the Yukon is *Hesperoperla pacifica* (57). Oswood et al. (1991) recently reviewed the overwintering adaptations of freshwater benthic macroinvertebrates, particularly at high elevations and latitudes. They proposed that the scarcity of Ephemeroptera and Plecoptera (referring to nymphs) in frozen substrates of both lentic and lotic habitats would seem to indicate that these taxa either remain in habitats that do not freeze or seasonally migrate horizontally or vertically to unfrozen water or substrates. Species in families with known hyporheal nymphal development such as Capniidae, Leuctridae and Chloroperlidae seem to be the most successful stoneflies in streams that experience extended cold and frozen conditions.

Stewart et al. (1990) found that successful species in Alaska, such as *Zapada haysi* (34), *Nemoura arctica* (25), *Plumiperla diversa* (47), *Taenionema pacificum* (37), *Isoperla petersoni* (65) and *Arcynopteryx compacta* (58) have adapted to the adverse effects of freezing and extreme cold by combinations of: (1) living in springs or unfrozen water or substrates of streams or lakes, and (2) extended voltinism (extension of life cycle over several years), with short periods of summer nymphal growth coupled with nymphal (and possibly

egg) diapause during winter. Particular species such as *Nemoura arctica* not only live in streams, but have also exploited and become very successful in tundra lakes and ponds that provide permanent, reliable muskeg habitat with profuse amounts of organic detritus for food. The winter-emerging stoneflies, particularly of the families Capniidae and Taeniopterygidae, and some others such as *Zapada columbiana* (32) (Downes 1965) are obviously cold-adapted, since they are able to emerge from the crevices of an ice-covered stream or on floating ice in alpine lakes, then successfully mate there or on surrounding snow and the females oviposit back into the cold water.

An ecological factor that may be limiting to some herbivorous stoneflies in arctic and subarctic streams is the relatively low amount and quality of coarse particulate organic matter (CPOM) present. The supply of detritus and CPOM is generally meagre in these streams compared to canopied lower latitude temperate streams (Cowan and Oswood 1983); this could be particularly limiting to larger shredders such as Pteronarcyidae and Peltoperlidae, and it seems plausible that some species may not have been able to adapt the timing of their nymphal food requirements to the presence of microbial "peanut butter" associated with willow and alder processing in cold streams.

The lower insect diversity and abundance in these streams may limit large predators such as perlids, that already apparently have low cold-adaptive capacity and would have to compete for resources with more cold-adapted, large perlodids. Movement of large perlid predators may also be limited by ice during seasonal periods when they must feed actively.

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