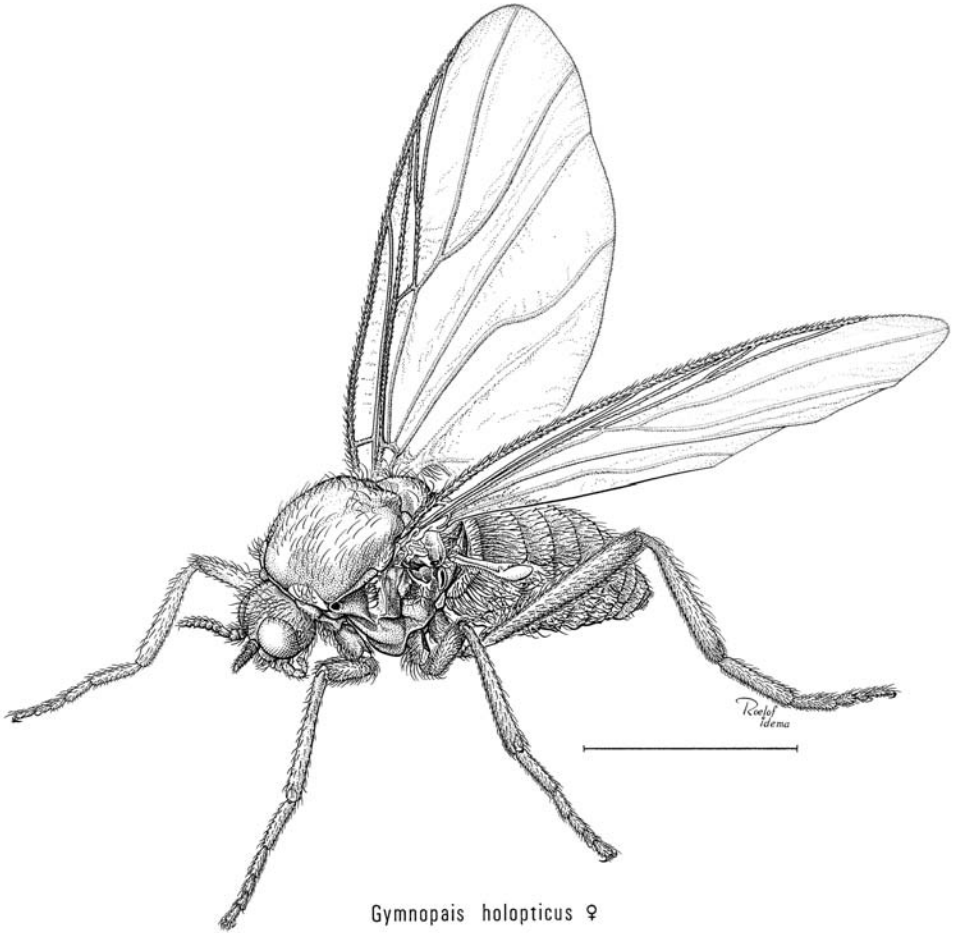


Black flies of the Yukon



FRONTISPIECE. Female of *Gymnopsis holopticus* Stone, a black fly confined to the Yukon and Alaska; the mouthparts are slightly developed and incapable of piercing skin. The larvae lack head fans and live in the headwaters of mountain streams. Scale line 1 mm.

Black Flies (Diptera: Simuliidae) of the Yukon, with Reference to the Black-fly Fauna of Northwestern North America

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Abstract. The black flies of Yukon, Alaska, and the westernmost Northwest Territories are analyzed in terms of species composition, geographical distribution, and feeding habits of adult females. Seventy-six species are recorded from the region, distributed among 9 of 13 Nearctic genera. Fifty-five of these species are known from the Yukon, and many of the remaining 21 are likely to occur there. Fifty-eight species are already formally described and named; the other 18 species are either undescribed morphospecies or cytologically recognized sibling species. Comparison of this northwestern assemblage with black flies from the northern Palaearctic Region reveals that the Old World and New World faunas are more similar than previously recognized; as many as 39% of northwestern black flies also occur in the Palaearctic Region. In terms of distributional patterns, northwestern black flies are classified as follows: 16% Holarctic (= circumpolar or circumboreal), 12% Palaearctic-East Beringian, 5% Palaearctic-Cordilleran, 4% Nearctic-West Beringian, 1% Holarctic excluding Beringia, 11% Widespread Nearctic, 9% Northern Nearctic, 1% Nearctic Disjunct, 1% Western Nearctic, 33% Cordilleran, and 7% East Beringian. The incidence of autogeny (25%) is much higher than reported for most other regions of North America. Among anautogenous black flies, 40% are mammalophilic and 34% are ornithophilic. It is hypothesized that 41% of northwestern black flies survived in the Beringian refugium during the Wisconsinan glacial maximum. More than half of this assemblage (53%) are arctic- or mountain-adapted species with reduced mouthparts, indicating that tundra must have been well represented in the Beringian landscape. A lowland anautogenous component is also indicated, suggesting the possibility that black flies fed upon Beringian mammals and birds throughout the Wisconsinan glacial maximum.

Résumé. Les mouches noires (Diptera: Simuliidae) du Yukon dans le cadre d'une étude de la faune du nord-ouest nord-américain. La composition en espèces, la répartition géographique et les habitudes alimentaires des femelles adultes sont examinées dans le cadre d'une étude des mouches noires du Yukon, de l'Alaska et de la partie occidentale des Territoires du Nord-Ouest. Soixante-seize espèces appartenant à 9 des 13 genres néarctiques ont été répertoriées dans la région. Cinquante-cinq de ces espèces ont été effectivement trouvées au Yukon et les 21 autres sont susceptibles d'y être rencontrées. Cinquante-huit des espèces sont déjà décrites et nommées et les 18 autres sont des espèces morphologiques encore inédites ou des espèces soeurs qui se distinguent cytologiquement. La comparaison de ce regroupement du nord-ouest avec les mouches noires du nord paléarctique a révélé que les faunes néarctique et paléarctique sont plus semblables qu'il n'apparaissait au départ; 39% des espèces du nord-ouest nord-américain se retrouvent aussi dans la région paléarctique. La faune des mouches noires du nord-ouest se répartit de la façon suivante: 16% des espèces sont holarctiques (= circumpolaires ou circumboréales), 12% se retrouvent dans la zone paléarctique et en Bérिंगie orientale, 5% dans la zone paléarctique et dans la Cordillère, 4% sont de la zone néarctique et de la Bérिंगie occidentale, 1% sont holarctiques à l'exclusion de la Bérिंगie, 11% sont répandues dans toute la zone néarctique, 9% sont confinées au nord de la zone néarctique, 1% ont une répartition néarctique discontinue, 1% sont des espèces néarctiques de l'ouest, 33% sont de la Cordillère et 7% sont de la Bérिंगie orientale. L'autogénie est beaucoup plus commune (25%) que dans la plupart des autres régions de l'Amérique du Nord. Parmi les espèces non autogènes, 40% sont mammalophiles et 34% sont ornithophiles. L'hypothèse retenue veut que 41% des mouches noires du nord-ouest aient survécu dans le refuge bérिंगien durant la période du Wisconsinien où les glaces étaient le plus étendues. Plus de la moitié de ces espèces (53%) sont des espèces arctiques ou alpines à pièces buccales réduites, ce qui semble indiquer que la toundra était bien représentée dans le paysage bérिंगien. Une composante anautogène des terres basses semble aussi avoir prévalu, ce qui indique la possibilité que les mouches noires aient vécu du sang des mammifères et des oiseaux de Bérिंगie pendant toute la période où les glaciations du Wisconsinien ont été à leur apogée.

Introduction

Few groups of insects are as closely associated with the north as are black flies. The bloodsucking habit of females is legendary in northern latitudes, rendering unprotected activities all-but-impossible during vernal infestations. It is therefore ironic that the north remains among the least known areas in North America in terms of its simuliid fauna. Relatively few northern species are anthropophilic, most blood-feeding upon either other mammals or birds. But up to a quarter of northern species do not require blood at all, with females using protein acquired during the larval stage to produce eggs. Such innocuous species are less likely to draw the attention (or ire) of the collector. An even greater impediment to documenting the northern fauna is the existence of sibling species. Studies of the polytene chromosomes of larval black flies reveal that many nominal species recognized by morphotaxonomists actually consist of 2 or more reproductively isolated populations. Unfortunately, very few northern collections have received cytological scrutiny to date. All these factors, combined with the inherent difficulties of transportation and fieldwork, have frustrated efforts to document the northern simuliid fauna.

The only comprehensive accounts of northwestern simuliids are long out of date, having been published during the 1950's. The objectives of this chapter are to summarize present knowledge about the species occurring in northwestern North America, and to analyze these species in terms of their composition, geographical distribution, and feeding habits of adult females. The geographical terms of reference are intentionally more inclusive than just the Yukon Territory. Collections from Alaska and westernmost Northwest Territories provide records of many species that eventually may be found in the Yukon. Inclusion of Alaska and the westernmost Northwest Territories also more closely approximates the historical limits of Beringia, providing a sounder basis from which to interpret geographical patterns.

Materials and Methods

This study is based on black flies examined or reported from Alaska, Yukon, and the Northwest Territories west of the Mackenzie River. Most of the material examined is housed in the entomological collection of the Royal Ontario Museum (ROME). Other sources of material are listed below, followed by the name of the curator responsible for the simuliid collection:

CNCI: Biological Resources Division, Eastern Cereal and Oilseed Research Centre, Agriculture and Agri-Food Canada, Ottawa, Ontario, Canada K1A 0C6; J.M. Cumming.

CUCC: Department of Entomology Collection, Clemson University, Clemson, South Carolina 29631, USA; P.H. Adler.

USNM: United States National Entomological Collection, Department of Entomology, U.S. National Museum of Natural History, Washington, D.C. 20560, USA; A.L. Norrbom.

The checklist of northwestern black flies (Table 1) was generated mainly from material examined. Records of cytologically recognized sibling species were obtained primarily from literature sources. Such references are indicated, as appropriate, in the annotated list. Unpublished cytological data were provided by P.H. Adler (Clemson University) and F.F. Hunter (Brock University). Chromosomally recognized sibling species are listed under the appropriate species complex, with the same informal designations (letters or numbers) employed in the cytological literature. Long-established synonymies are not included (cf. Crosskey 1988 for most of the relevant synonymies); however, references to possible new synonymies are included in the annotated list. Formal synonymy is deferred pending

TABLE 1. List of black-fly species from northwestern North America, with distributional patterns and feeding habits. Abbreviations for distributional patterns: H, Holarctic; P-EB, Palaearctic-East Beringian; P-C, Palaearctic-Cordilleran; N-WB, Nearctic-West Beringian; H, B-, Holarctic excluding Beringia; N, Nearctic; NN, Northern Nearctic; ND, Nearctic disjunct; WN, Western Nearctic; C, Cordilleran; EB, East Beringian. Abbreviations for feeding habits: A, autogenous; O, ornithophilic; M, mammalophilic.

| Taxon | Species no. in lists | Distributional pattern | Feeding habit |
|---|-------------------------|---------------------------|------------------|
| Subfamily Simuliinae Newman, 1834 | | | |
| Tribe Prosimuliini Enderlein, 1921 | | | |
| <i>Gymnopsis</i> Stone, 1949 | | | |
| <i>G. dichopticooides</i> Wood, 1978 | 1 | C | A |
| <i>G. dichopticus</i> Stone, 1949 | 2 | EB | A |
| <i>G. fimbriatus</i> Wood, 1978 | 3 | EB | A |
| <i>G. holopticooides</i> Wood, 1978 | 4 | NN | A |
| <i>G. holopticus</i> Stone, 1949 | 5 | EB | A |
| <i>Helodon</i> Enderlein, 1921 | | | |
| Subgenus <i>Distosimulium</i> Peterson, 1970 | | | |
| <i>H. pleuralis</i> (Malloch, 1914) | 6 | ND | O |
| Subgenus <i>Helodon</i> s. str. | | | |
| <i>H. alpestris</i> (D. R. and V., 1935) | 7 | P-EB | A |
| <i>H. clavatus</i> (Peterson, 1970) | 8 | N-WB? | A |
| <i>H. onychodactylus</i> (D. and S., 1927) complex | | | |
| Cytospecies 2a | 9 | C | O |
| Cytospecies 2b | 10 | C | O |
| Cytospecies 4a/4b | 56 | C | O |
| Cytospecies 10 | 11 | C | O |
| Form 9 | 12 | C | O |
| <i>H. perspicuus</i> (Sommerman, 1958) | 13 | P-EB? | A |
| Subgenus <i>Parahelodon</i> Peterson, 1970 | | | |
| <i>H. decemarticulatus</i> (Twinn, 1936) | 14 | NN | O |
| <i>Prosimulium</i> Roubaud, 1906 | | | |
| <i>hirtipes</i> species group | | | |
| <i>P. doveri</i> Sommerman, 1962 | 57 | C | M |
| <i>P. esselbaughi</i> Sommerman, 1964 | 15 | C | M |
| <i>P. formosum</i> Shewell, 1959 | 16 | C | M |
| <i>P. frohnei</i> Sommerman, 1958 | 17 | C | M |
| <i>P. fulvum</i> (Coquillett, 1902) complex | 18 | C | M |
| <i>P. travisi</i> Stone, 1952 | 19 | C | M |
| <i>macropyga</i> species group | | | |
| <i>P. neomacropyga</i> Peterson, 1970 | 20 | P-EB? | A |
| <i>P. ursinum</i> (Edwards, 1935) | 21 | H | A |
| <i>magnum</i> species group | | | |
| <i>P. dicum</i> Dyar and Shannon, 1927 | 58 | C | M |
| Tribe Simuliini Newman, 1921 | | | |
| <i>Cnephia</i> Enderlein, 1921 | | | |
| <i>C. eremites</i> Shewell, 1952 | 59 | H? | A |
| <i>Greniera</i> Doby and David, 1959 | | | |
| <i>G. denaria</i> (D., P. and W., 1962) | 22 | NN | O |
| <i>Mayacnephia</i> Wygodzinsky and Coscarón, 1973 | | | |
| <i>M.</i> "Species X", Currie, 1986 | 23 | C | O |
| <i>Metacnephia</i> Crosskey, 1969 | | | |
| <i>M. borealis</i> (Malloch, 1919) | | | |
| <i>arctocanadensis</i> Yankovsky, 1996 | 60 | N-WB | A |
| <i>M. saileri</i> (Stone, 1952) | 24 | P-EB? | O |
| <i>M. saskatchewanana</i> (Shewell and Fredeen, 1958) | 25 | NN | O |
| <i>M. sommermanae</i> (Stone, 1952) | 26 | P-EB | A |
| <i>M. villosa</i> (DeFoliart and Peterson, 1960) | 27 | C | O |
| <i>Stegopterna</i> Enderlein, 1930 | | | |
| <i>St. decafilis</i> Rubtsov, 1971 | 28 | P-EB | A |
| <i>St. emergens</i> (Stone, 1956) | 29 | H? | A |
| <i>St. permutata</i> (Dyar and Shannon, 1927) | 61 | C | M |
| <i>Simulium</i> Latreille, 1802 | | | |
| Subgenus <i>Byssodon</i> Enderlein, 1925 | | | |

TABLE 1. (continued)

| Taxon | Species no. in lists | Distributional pattern | Feeding habit |
|---|-------------------------|---------------------------|------------------|
| <i>S. maculatum</i> (Meigen, 1804) | 62 | P-EB | O |
| Subgenus <i>Eusimulium</i> Roubaud, 1906 | | | |
| <i>aureum</i> species group | | | |
| <i>S. aureum</i> Fries, 1824 complex | 30 | | |
| Cytospecies C | 63 | NN | O |
| Cytospecies D | 64 | NN | O |
| <i>S. bracteatum</i> Coquillett, 1898 | 65 | N | O |
| <i>annulum</i> species group | | | |
| <i>S. canonicolum</i> (D. and S., 1927) complex | 31 | C | O |
| <i>S. n. sp. near canonicolum</i> | 32 | C | O |
| <i>pusillum</i> species group* | | | |
| <i>S. furculatum</i> (Shewell, 1952) | 33 | H, B- | A |
| <i>S. n. sp. near giganteum</i> | 66 | EB | A |
| <i>S. subpusillum</i> Rubtsov, 1940 | 67 | H | M |
| <i>vernum</i> species group | | | |
| <i>S. bicorne</i> D., R. and V., 1935 | 34 | P-C | O |
| <i>S. croxtoni</i> Nicholson and Mickel, 1950 | 35 | NN | O |
| <i>S. decolletum</i> Adler and Currie, 1986 | 36 | P-C | O |
| <i>S. dendrofilum</i> (Patrusheva, 1962) | 68 | P-EB | A |
| <i>S. pugetense</i> (D. and S., 1927) complex | | | |
| Cytospecies A | 37 | N | O |
| Cytospecies B | 69 | C | O |
| Cytospecies E | 70 | C | O |
| <i>S. silvestre</i> (Rubtsov, 1956) | 38 | P-C | O |
| Subgenus <i>Hellichiella</i> Rivosecchi and Cardinali, 1975 | | | |
| <i>S. baffinense</i> Twinn, 1936 | 39 | H | A |
| <i>S. nebulosum</i> Currie and Adler, 1986 | 71 | C | O |
| <i>S. sp. (gouldingi</i> of authors, not Stone) | 72 | EB | ? |
| Subgenus <i>Psilozia</i> Enderlein, 1936 | | | |
| <i>S. vittatum</i> Zetterstedt, 1838 complex | | | |
| Cytospecies IS-7 | 40 | N | M |
| Cytospecies ILL-1 | 73 | N | M |
| Subgenus <i>Simulium</i> s. str. | | | |
| <i>malyschevi</i> species group | | | |
| <i>S. arcticum</i> Malloch, 1914 complex | | | |
| Cytospecies ILL-st | 74 | C | M |
| Cytospecies ILL-1 | 75 | WN | M |
| Cytospecies ILL-2 | 41 | C | M |
| Cytospecies IL-3.4 | 42 | C | M |
| <i>S. corbis</i> Twinn, 1936 | 43 | H | M |
| <i>S. malyschevi</i> D., R. and V., 1935 | 44 | H | M |
| <i>S. nigricoxum</i> Stone, 1952 | 45 | N-WB | M |
| <i>hunteri</i> species group | | | |
| <i>S. hunteri</i> Malloch, 1914 | 46 | C | M |
| <i>noelleri</i> species group | | | |
| <i>S. decorum</i> Walker, 1848 | 47 | N | M |
| <i>S. noelleri</i> Friederichs, 1920 | 48 | H | M |
| <i>slossonae</i> species group | | | |
| <i>S. transiens</i> Rubtsov, 1940 | 49 | H | M |
| <i>S. rugglesi</i> Nicholson and Mickel, 1950 | 76 | N | M |
| <i>tuberosum</i> species group | | | |
| <i>S. tuberosum</i> (Lundström, 1911) complex | | | |
| Cytospecies FG | 50 | N | M |
| <i>S. tuberosum</i> s. str. | 51 | H | M |
| <i>S. vulgare</i> D., R. and V., 1935 | 52 | P-C | M |
| <i>venustum</i> species group | | | |
| <i>S. rostratum</i> (Lundström, 1911) | 53 | H | M |
| <i>S. rubtsovi</i> Smart, 1945 | 54 | P-EB | M |
| <i>S. truncatum</i> (Lundström, 1911) | 77 | H | M |
| <i>S. venustum</i> Say, 1823 complex | 55 | N | M |

TABLE 1. (continued)

* The nominal taxon *Schoenbaueria* Enderlein applies to species here included in the *pusillum*-group when ranked at the generic or subgeneric levels. The *pusillum*-group is recognized only for convenience because it may be paraphyletic with respect to the *vernum*-group, as here defined. Included are all the species listed by Crosskey (1988) under *Schoenbaueria* (as a subgenus of *Simulium* s. lat.), as well as *S. giganteum* Rubtsov, 1940, *S. tsharae* (Yankovsky, 1982), and *S. ussovae* (Bodrova, 1990). The latter three species have been referred to *Hemicnetha* Enderlein by certain specialists in accordance with the views of Petrova et al. (1971). However, there is no close relationship between these Palearctic species and *Hemicnetha*, a strictly New World (mainly Neotropical) lineage.

examination of type material and acquisition of topotypical specimens for cytological analysis. The suprageneric classification is that of Currie (1988).

History

The first written accounts of black flies from northwestern North America can be found in the diaries of early explorers. Captain John Franklin, the first European to set foot in the Yukon Territory, encountered black flies during his second expedition to the “shores of the polar sea”. His diary for August 30, 1825, reads as follows: *Favoured by a N.W. gale, we made great progress on the 30th. The temperature of the air varied in the course of the day from 62° to 41°. The brûlot and sand-flies were very teasing wherever we landed; but these, unlike the mosquitoes [sic.], disappear with the sun.* (Franklin 1928)¹

This encounter took place near the confluence of the Mackenzie and Great Bear Rivers, just east of the present-day border between the Yukon and Northwest Territories. The behaviour of ceasing blood-feeding after sunset is characteristic of mammalophilic black flies. Later, near the confluence of the Mackenzie and Peel Rivers, Franklin entered the following for September 4, 1826: *The temperature varied during the day from 29° to 55°, and, in the evening, the sand flies were troublesome.*

There can be little doubt that black flies added to the hardships endured by aboriginal peoples and early European explorers. The species to which Franklin referred was probably *Simulium nigricoxum* Stone, a late season anthropophilic species that breeds in medium- to large-sized streams and rivers.

The earliest scientific account of northwestern black flies was based on collections made at the end of the 19th century. Edward H. Harriman was a wealthy New Yorker who, with the cooperation of the Washington Academy of Sciences, commissioned an expeditionary force of some 25 scientists to north-coastal British Columbia and Alaska during the summer of 1899. Entomologist Trevor Kincaid collected thousands of insects during the course of the expedition, including a small number of black flies. An account about the 4 species collected was published by Coquillett (1900).

The end of World War II heralded the first serious attempts to document the black flies of northwestern North America. Construction of the Alaska Highway facilitated access to areas previously accessible only by foot, horseback, boat, or float plane. Under the direction of B.V. Travis, the “Alaskan Insect Project” conducted intensive fieldwork from April to November of 1948. Numerous scientific publications resulted from the project, including

¹Brûlot is a French Canadian term for gnat or midge. Derived from the word brûler, it refers to the burning sensation elicited by females of biting midges (Ceratopogonidae). The term “sand fly”, which generally is reserved for phlebotomine flies (Psychodidae), was often applied to simuliids by British explorers. Captain James Cook used the term sand fly during his exploration of New Zealand, where the name is still applied to black flies.

important taxonomic treatments by Stone (1952: keys to adults and pupae of 36 species) and Sommerman (1953: key to larvae of 30 species). These latter remain the only identification guides to the Simuliidae of northwestern North America. The legacy of the Alaskan Insect Project can be measured by the number of patronyms honouring participating scientists, including L.H. Dover, C.O. Esselbaugh, W.C. Frohne, R.I. Sailer, K.M. Sommerman and B.V. Travis.

The Canadian “Northern Insect Survey”, also initiated in 1947, provided material from 58 arctic and subarctic localities across Canada and Alaska. Nearly 7000 pinned adult black flies, and more than 1200 vials of larvae and pupae, were collected during a 7-year period (Shewell 1957). Material collected from Alaska, Yukon, and the western Northwest Territories remains a valuable part of the simuliid collection housed in the Canadian National Collection of Insects.

An enormous contribution towards the knowledge of northwestern black flies was provided by D.M. Wood, who undertook several collecting trips to the Yukon and Alaska during the 1960s, 1970s and 1980s. He amassed an impressive collection of all life-history stages of the family including the first collections of northwestern black flies into Carnoy’s solution. Larvae thus collected provided K. Rothfels (University of Toronto) and students valuable material for cytological study. The resulting publications revealed much about the nature of sibling speciation in general, and species composition in northwestern North America in particular. Peterson’s (1970) publication on the *Prosimulium* of Canada and Alaska benefitted greatly from collections made during the 1963 expedition, as did Wood’s (1978) revision of the Nearctic species of *Twinnia* and *Gymnopais*.

Few accounts about northwestern black flies have appeared during the last 30 years. Most have been cytological studies of more widely distributed sibling complexes (e.g. Allison and Shields 1989; Shields and Procnier 1982). Corkum and Currie (1987) provided distributional information at the morphospecies level for more than 30 sites in Yukon and Alaska; Hiltner and Hershey (1992) and Hershey et al. (1995) studied various aspects of black-fly ecology on the north slope of Alaska; and Hunter et al. (1997) reported on black-fly induced mortality of great horned owls in southwestern Yukon.

Annotated List of Yukon Black Flies

Included here are species or species complexes with one or more confirmed Yukon records. Ecological information and species associations are drawn from northwestern North America as a whole, and not strictly from the Yukon Territory. Detailed locality information is not provided except for rarely collected species or first territorial records. Specific records are available, upon request, from the author. Taxa are arranged alphabetically by tribe, genus and subgenus.

Tribe Prosimuliini Enderlein, 1921

Genus *Gymnopais* Stone, 1949

1. *G. dichopticoides* Wood, 1978

Cordilleran

Distribution: Alaska and Yukon south along the Rocky Mountains to southwestern Alberta.

Yukon records: Richardson, Ogilvie, St. Elias and Logan Mountains; Kluane Ranges.

Biological information: *Gymnopais* larvae, along with those of the closely related genera *Twinnia* Stone and *Jamnback* and *Levitinia* Chubareva and Petrova, are distinguished from most other black flies in lacking the typical labral fans that serve in filter feeding. They instead rely on their specially modified mandibles and hypostoma to scrape algae and associated matter from the stones on which they live (Wood 1978; Currie and Craig 1988). The immature stages of *Gymnopais* are most often

found in the uppermost reaches of cold, clear, mountain streams. *G. dichopticoidea* is not as closely tied to the mountains as are the other Nearctic species of *Gymnopaia*, with populations also occurring in lowland streams associated with areas of permafrost, such as *Sphagnum* bogs. There is one generation per year with overwintering in the egg stage. Eggs begin hatching at ice break-up in early to mid June. Depending on species and stream temperature larvae may persist well into September. Pupation begins in late July and continues until ice cover in late September and October. For parthenogenetic species such as *G. dichopticoidea*, it is possible that ice-trapped adults could still shed viable eggs once they have perished and their abdominal walls have disintegrated. A similar phenomenon has been described for the parthenogenetic species *P. ursinum* (Carlsson 1962) (see 21). Several species of *Gymnopaia* may often be found coexisting in the same stream; other associated species include *H. alpestris*, *P. neomacropyga*, *P. ursinum*, *P. frohnei*, *St. decapilis*, *M. sommermanae*, *S. bicorne*, and *S. decolletum*. The adult emergence period is from mid August to mid September in northwestern North America. Although fully winged, the adult of *G. dichopticoidea* exhibits no inclination to fly. All species of *Gymnopaia* are obligately autogenous.

Taxonomic notes: *G. dichopticoidea* (Type locality: south end of Kluane Lake, mile 1057 Alaska Highway) is an allotriploid parthenogenetic species (HDD) that is derived through hybridization between the diploid sexual species *G. dichopticus* (D) and *G. holopticus* (H) (Wood 1978; Rothfels 1979).

2. *Gymnopaia dichopticus* Stone, 1949

East Beringian

Distribution: Yukon and Alaska.

Yukon records: Ogilvie Mountains.

Biological information: Aspects of the ecology of *G. dichopticus* are similar to those described for *G. dichopticoidea* (see 1 above) except that the immature stages are restricted to mountain streams. In this sexual species, the male has markedly reduced eyes and the head is scarcely distinguishable from that of the female. Males emerge slightly earlier than females at the same site. Neither sex seems capable of sustained flight, although they can skim just above the surface of the ground for short distances when disturbed. Mating takes place on the ground along the stream margin. Timed observations (n = 5 at ambient temperature) of reared adults from the Ogilvie Mountains reveals that coupling is maintained for between 27.5 and 46 (average 40) min.

Taxonomic notes: *G. dichopticus* is the genotype of *Gymnopaia* Stone, 1949 (Type locality: Alaska, Steese Highway mile 19.1 from Fairbanks). Along with *G. fimbriatus* (see 3), *G. dichopticus* exhibits the most restricted distribution among Nearctic *Gymnopaia* species.

3. *Gymnopaia fimbriatus* Wood, 1978

East Beringian

Distribution: Yukon and Alaska.

Yukon records: Richardson and Ogilvie Mountains.

Biological information: Ecological aspects are similar to those described above (see 1 and 2). *G. fimbriatus* is a bisexual species in which males have markedly reduced eyes. Mating behaviour is similar to that described for *G. dichopticus* except that coupling is maintained for between 64 and 119 min. (average 84 min.; n = 4 observations at ambient temperature). Males have been observed walking on the surface of water in pools and slowly moving channels; they attempt coupling with any conspecific individual encountered, including other males. In several instances 3 or more males were observed "grappling" on the water surface.

Taxonomic notes: Populations of *G. fimbriatus* (Type locality: Ogilvie Mountains, Dempster Highway mile 47.5) are almost entirely confined to the Yukon Territory. There is only one Alaskan record of this species, slightly west of the Yukon border [Mt. Fairplay Summit, Taylor Hwy. mi 33 north of Tetlin Junction, 25.viii.1982, D.C. Currie]. Populations in the Richardson and northern Ogilvie Mountains have individuals that differ from the typical form in having 2 (as opposed to 3) pupal gill filaments (cf. fig. 52 in Wood 1978). In these populations the lateral-most gill filament is markedly reduced or absent.

4. *Gymnopaia holopticoidea* Wood, 1978

Northern Nearctic

Distribution: Alaska and Banks Island east to Baffin Island and Labrador.

Yukon records: Richardson, Ogilvie, and St. Elias Mountains.

Biological information: Aspects of the ecology of *G. holopticoidea* are similar to those of other *Gymnopaia* species (see 1).

Taxonomic notes: This allotriploid parthenogenetic species (HHD) is derived through hybridization between the diploid sexual species *G. dichopticus* (D) and *G. holopticus* (H) (Wood 1978; Rothfels 1979). Specimens from the Canadian Arctic Archipelago, Quebec and Labrador are similar in form, suggesting that they were derived from the same ancestral stock that populated the north following deglaciation (Wood 1978). Specimens from Alaska and the Yukon, on the other hand, are rather varied, suggesting that the *G. holopticoideis* was derived through multiple hybridization events. The type locality of this species (Northwest Territories, Victoria Island, Kuujjua River Valley, 71°17'N 114°00'W) is among the northernmost records for black flies in North America.

5. *Gymnopsis holopticus* Stone, 1949 (Frontispiece) East Beringian

Distribution: Yukon and Alaska (Fig. 6).

Yukon records: British, Richardson, and Ogilvie Mountains; Tintina Trench.

Biological information: Ecological aspects similar to those described for *G. dichopticoideis* (see 1). Males of this sexual species are distinguished from all others in the genus in having normal (i.e. holoptic) eyes. Both sexes are capable of flight, contrasting with the flightless condition in all other *Gymnopsis* species. Observations of mating reveal that coupling is maintained for a markedly shorter interval than for either *G. dichopticus* or *G. fimbriatus*, ranging from 10 to 17.5 min. (average 12.5 min.; n = 8 observations at ambient temperature).

Taxonomic notes: The type locality of *G. holopticus* is in Alaska (Steese Highway, mile 16.2 from Fairbanks).

Genus *Helodon* Enderlein, 1921

Subgenus *Distosimulium* Peterson, 1970

6. *Helodon pleuralis* (Malloch, 1914) Nearctic Disjunct

Distribution: Western populations from Alaska and Yukon south to southern British Columbia and Alberta, eastern populations from northern Quebec, Labrador and Newfoundland (Fig. 3).

Yukon records: Tintina Trench south to British Columbia border.

Biological information: The immature stages occur in medium- to large-sized streams and rivers. There is one generation per year with overwintering in the larval stage (Sommerman et al. 1955). Females are anautogenous on birds, with great horned owls (*Bubo virginianus*) indicated as hosts in the southern Yukon (Hunter et al. 1997).

Taxonomic notes: Two cytological forms of *H. pleuralis* (Type locality: Kaslo, British Columbia) are known; one from western North America, and one from northern Quebec and Newfoundland. Whether these isolated cytotypes represent mere geographic variants, or are valid species, cannot be determined at present (Rothfels 1979). However, the vicariant east-west distribution of cytologically distinct forms suggests different geographical histories. Palaearctic species referable to the subgenus *Distosimulium* include *H. daisetsense* (Uemoto, Okazawa and Onishi, 1976) from Japan (Hokkaido), and possibly *H. mesenevi* (Patrusheva, 1975a) from Siberia (Taimyr). Published descriptions and illustrations indicate that these Palaearctic species are distinct from *H. pleuralis*.

Subgenus *Helodon* s. str.

7. *Helodon alpestris* (Dorogostaisky, Rubtsov and Vlasenko, 1935) Palaearctic-East Beringian

Distribution: Alaska, Yukon and northern British Columbia; Siberia (incl. Commander Island).

Yukon records: Richardson and Ogilvie Mountains.

Biological information: The immature stages of *H. alpestris* live in cool, small- to large-sized, mountain streams. Commonly associated species include *P. neomacropyga*, *M. sommermanae*, *M. saileri*, *S. decolletum*, *S. nigricoxum*, *S. corbis*, and *S. vulgare*. There is one generation per year with overwintering in the egg stage; adults appear from mid-August to mid-September (Sommerman et al. 1955). Females have slightly developed mouthparts and are incapable of bloodsucking.

Taxonomic notes: Four nominal subspecies have been recognized in *H. alpestris*: *alpestris* s. str. (Type locality: Lake Baikal, Slyudanka River), *altaicum* Rubtsov, 1956 (Type locality: Altai, Katonka River), *relense* Rubtsov, 1956 (Type locality: Lake Baikal, Rel' River), and *komandorensis* Rubtsov, 1971b (Type locality: Commander Islands). It is not known which, if any, of these names apply to Nearctic populations.

8. *Helodon clavatus* (Peterson, 1970) Nearctic-West Beringian?

Distribution: Yukon and British Columbia; Russian Far East?

Yukon records: Southern Yukon.

Biological information: The single Yukon locality (Wolf Cr.) is a rapidly flowing, 6 metre wide, salmonid stream. Larvae were found exclusively on trailing vegetation, along with members of the *H. onychodactylus* complex, *S. arcticum* complex, *S. tuberosum* complex, and *S. venustum* complex. Little else is known about the biology of this species, although Peterson (1970) suggests that it is univoltine. The reduced mouthparts of females indicate that *H. clavatus* is obligately autogenous.

Taxonomic notes: *H. rhizomorphus* (Rubtsov, 1971a) was described from a single collection of larvae and pupae from Kolyma (Type locality: Klyuch Pyatiletki, Ust-Srednikan). Although Rubtsov considered this species to be closely related to *Prosimulium rhizophorum* Stone and Jamnback, 1955 (Type locality: Bear Creek Township, Luzerne Co., Pennsylvania), illustrations of the hypostoma and pupal gill reveal that it is more closely related to, and perhaps conspecific with, *H. clavatus* (Type locality: Wolf Creek, Yukon). The relationship of *H. clavatus* with the structurally similar *H. albertensis* (Peterson and Depner 1972) (Type locality: Crowsnest Pass, Alberta) needs clarification.

9. *Helodon onychodactylus* (Dyar and Shannon, 1927) complex, Cytospecies 2a Cordilleran

Distribution: Alaska and Yukon south to Colorado.

Yukon records: Ogilvie Mountains, Southern Yukon.

Biological information: The immature stages live in rapidly-flowing medium- to large-sized streams and rivers. Larvae are found almost exclusively on trailing vegetation; pupae typically are buried beneath the substrate and are difficult to find. Associated species include *H. onychodactylus* 2b, *S. pugetense* A, *S. corbis*, and members of the *S. arcticum* complex. Although specific host records are not known for individual cytospecies, females of the *H. onychodactylus* complex have bifid claws and are assumed to be ornithophilic.

Taxonomic notes: Cytological and distributional information is from Newman (1983), Henderson (1986) and P.H. Adler (pers. comm.). The cytospecies to which the name *onychodactylus* (Type locality: Long's Peak, Colorado) applies has not been established.

10. *Helodon onychodactylus* (Dyar and Shannon, 1927) complex, Cytospecies 2b Cordilleran

Distribution: Yukon south to Wyoming.

Yukon records: Southern Yukon.

Biological information: The single Yukon record [Wolf Cr., Alaska Hwy. km 1459, 30.vii.1994, D.C. Currie and D.M. Wood] is from a cool (13°C), 6 metre wide, salmonid stream. Mature larvae were collected from trailing twigs and grasses, along with *H. clavatus*, *S. arcticum* complex, *S. tuberosum* complex, and *S. venustum* complex. Adult females are assumed to be ornithophilic.

Taxonomic notes: As for 9 above.

11. *Helodon onychodactylus* (Dyar and Shannon, 1927) complex, Cytospecies 10 Cordilleran

Distribution: Alaska and Yukon south to Colorado.

Yukon records: Southern Yukon.

Biological information: The immature stages of this species have been collected from rapidly flowing, small-sized (0.2–4 m wide) streams in northwestern North America. Larvae attach themselves exclusively to trailing vegetation, especially submerged branches. Associated species include *P. travisi*, *P. doveri*, *M. saileri*, *S. bicorne*, *S. silvestre*, *S. pugetense* A, *S. tuberosum* FG, and *S. venustum* CC complex. Aspects of the biology of this species are probably similar to that described for other members of the *H. onychodactylus* complex (see 9).

Taxonomic notes: Distributional and cytological information is from Henderson (1986) and P.H. Adler (pers. comm.).

12. *Helodon onychodactylus* (Dyar and Shannon, 1927) complex, Form 9 Cordilleran

Distribution: Yukon.

Yukon records: Southern Yukon.

Biological information: This cytological form is known from only a single locality, about 30 kilometres west of Haines Junction [Marshall Cr., 30.v.1983, G. Shields] (Henderson 1986). The collection contained mature larvae, suggesting that Form 9 emerges earlier than other Yukon species in the

H. onychodactylus complex. Nothing is known about way of life. For the purposes of the present study adult females are assumed to be ornithophilic.

Taxonomic notes: The distribution of *H. onychodactylus* Form 9 is provisionally given as Cordilleran because the record is from the southern Yukon, suggesting that its range may extend southward. Moreover, Henderson (1986) leaves open the possibility that Form 9 is just a geographic variant of Newman's (1983) Cytospecies 2 from Washington and Oregon. Early-season collections are needed to establish the species-status and distribution of this cytological form more firmly. See also comments under 9 above.

13. *Helodon perspicuus* (Sommerman, 1958)

Palaeartic-East Beringian?

Distribution: Alaska, Yukon, Banks Island; Siberia?

Yukon records: Ogilvie Mountains, Kluane Ranges.

Biological information: This univoltine species overwinters in the egg stage (Sommerman 1958). The immature stages live in medium- to large-sized rivers in association with *H. alpestris*, *M. saileri*, *S. corbis*, *S. malyschevi*, *S. vulgare*, and *S. tuberosum* s. str. Adults emerge in late August and early September, and can be found resting on streamside vegetation. Mating probably occurs on the ground (Sommerman 1958). Females are obligately autogenous.

Taxonomic notes: *H. perspicuus* (Type locality: Eagle River, Alaska) is almost certainly conspecific with one of 2 Palaeartic species: *H. buturlini* (Rubtsov, 1956) (Type locality: Tolstaya-Mayachnaya, Russian Far East); and *H. irkutensis* (Rubtsov, 1956) (Type locality: Irkut River, Eastern Siberia). The identity of the latter species is problematic because the original description was based on larvae. Although pupae and females referred to *H. irkutensis* were subsequently described by Rubtsov (1971b), the association is questionable because it was not based on topotypical material. The name *H. perspicuus* is retained for Nearctic populations pending further study. Hiltner and Hershey's (1992) record of *H. martini* (Peterson 1970) from Alaska refers to *H. perspicuus*. Whether *H. martini* (Type locality: Clyde Inlet, Baffin Island) is specifically distinct from *H. perspicuus*, or is merely the product of east/west clinal variation, needs clarification.

Subgenus *Parahelodon* Peterson, 1970

14. *Helodon decemarticulatus* (Twinn, 1936) complex

Northern Nearctic

Distribution: Alaska and Yukon east to Newfoundland, south to Wisconsin and New Hampshire.

Yukon records: Old Crow Range, Southern Yukon.

Biological information: The immature stages live in small-sized lowland streams. There is one generation per year with overwintering in the egg stage. Females are anautogenous on woodland birds (Bennett 1960). Specimens have been collected from great horned owls (*Bubo virginianus*) near Kluane Lake, Yukon (Hunter et al. 1997).

Taxonomic notes: According to Rothfels (1979) there are at least 2 sibling species under the name *H. decemarticulatus* (Type locality: Carleton Place, Ontario). Unfortunately, no information was provided about the geographical distribution of the 2 siblings. The distribution given here includes the range of all populations referable to the name.

Genus *Prosimulium* Roubaud, 1906

hirtipes species group

15. *Prosimulium esselbaughi* Sommerman, 1964

Cordilleran

Distribution: Alaska and Yukon, south to California.

Yukon records: Ogilvie Mountains, Kluane Ranges.

Biological information: This univoltine species overwinters in the larval stage, and therefore emerges earlier than most other *Prosimulium* species. The immature stages live in cool, clear, small- to medium-sized streams. Associated species include *P. doveri*, *P. travisi*, and *S. bicornis*. Larvae and pupae are typically found attached to stony substrata. Females are mammalophilic, with humans indicated as hosts (Sommerman 1964).

Taxonomic notes: *P. esselbaughi* (Type locality: Fort Richardson, Alaska) was misidentified as *P. hirtipes* in early publications on northwestern black flies. The chromosomes were described (as *P. hirtipes* 2) by Basur (1962).

16. *Prosimulium formosum* Shewell, 1959

Cordilleran

Distribution: Alaska and Yukon, south to California.

Yukon records: Southern Yukon.

Biological information: A univoltine species with overwintering eggs. The immature stages are typically found in slow-flowing woodland- and muskeg streams. Larvae can be found in large numbers at the outflows of beaver dams. Females are anautogenous on mammals.

Taxonomic notes: There are very few records of *P. formosum* (Type locality: Bowser, Vancouver Island, British Columbia) from northwestern North America, with only 2 records from the southern Yukon [Watson Lake and Whitehorse]. Chromosomal features were described by Basrur (1962).

17. *Prosimulium frohnei* Sommerman, 1958

Cordilleran

Distribution: Alaska and Yukon south to Colorado.

Yukon records: Ogilvie Mountains, Kluane Ranges.

Biological information: This univoltine upland species overwinters in the egg stage. The immature stages are confined to the headwaters of mountain streams, often in association with *Gymnopais* spp., *P. ursinum* complex and *P. neomacropyga*. Other aspects of the ecology of *P. frohnei* are provided by Sommerman (1958). Females have well-developed biting mouthparts but hosts are unknown. Mammalophilily is assumed based on the simple claw of females.

Taxonomic notes: The type locality of *P. frohnei* is in Alaska (Eklutna Lake, 40 miles northeast of Anchorage). Basrur (1962) described the chromosomes of this species.

18. *Prosimulium fulvum* (Coquillett, 1902) complex

Cordilleran

Distribution: Alaska and Yukon, south to California.

Yukon records: Ogilvie Mountains, Kluane Ranges.

Biological information: The immature stages live in cold, small-sized, mountain streams. Alaskan populations are univoltine with overwintering in the larval stage (Sommerman et al. 1955). Horses and other large mammals are preferred hosts (Hearle 1932). Females are attracted to humans but seldom bite (pers. obs.).

Taxonomic notes: Several sibling species are included under the name *P. fulvum* (Type locality: Bear Paw Mountain, Montana) (P.H. Adler, pers. comm.). The chromosomes of northwestern populations have been described by Basrur (1962). Adults are distinguished from those of all other northwestern species by their orange colour.

19. *Prosimulium travisi* Stone, 1952

Cordilleran

Distribution: Alaska and Yukon, south to California and Arizona (Fig. 5).

Yukon records: Ogilvie Mountains, Southern Yukon.

Biological information: The immature stages of *P. travisi* live in small, cold, spring-fed streams. Associated species include *P. doveri*, *P. esselbaughi*, *S. bicorne*, *S. pugetense* A, and *S. silvestre*. Overwintering is in the egg stage, with one generation per year (Currie 1986). Host preferences are not known, but females are assumed to be mammalophilic based on their simple tarsal claws.

Taxonomic notes: The chromosomes of *P. travisi* (Type locality: Anchorage, Alaska) were described by Basrur (1962).

macropyga species group

20. *Prosimulium neomacropyga* Peterson, 1970

Palaeartic-East Beringian?

Distribution: Alaska, Yukon; Russian Far East?

Yukon records: Richardson and Ogilvie Mountains.

Biological information: The immature stages of *P. neomacropyga* live in the headwaters of cold, clear, tundra streams, typically in association with *Gymnopais* spp., *H. alpestris*, *M. saileri*, *M. sommermanae*, and *S. decolletum*. Larvae and pupae are usually found attached to the undersurfaces of stones. There is one generation per year with overwintering in the egg stage. Females are obligately autogenous.

Taxonomic notes: *P. neomacropyga* is closely related to the *P. macropyga* (Lundström, 1911) complex of the Palaeartic Region, which consists of the typical form ("Lmur. Litsa", Murmanskaya Oblast?) plus 4 nominal subspecies: *ventosum* Rubtsov, 1956 (Spuskovaya River, Eastern Siberia); *zaitzevi* Rubtsov, 1956 (Pemal, Western Siberia); *arcticum* Rubtsov and Carlsson, 1965 (Dudinke District, north-central Siberia); and *korshunovi* Patrusheva, 1975b (Kharp, Polar Urals). Although the name "*P. macropyga*" has been applied to specimens from Chukotka (Bodrova 1977), the close geographical proximity of this peninsula to the type locality of *P. neomacropyga* (Cape Thompson, Alaska) suggests that the latter name may apply to populations from the Russian Far East. The relationships of the

various nominal subspecies of *P. macropyga* to each other, and to *P. neomacropyga*, need further study. See also Taxonomic notes for *P. ursinum* (21).

21. *Prosimulium ursinum* (Edwards, 1935)

Holarctic

Distribution: Alaska and Yukon east to Baffin Island and Labrador; Greenland and Iceland; Scandinavia, Bear Island.

Yukon records: Ogilvie Mountains, Kluane Range, Southern Yukon.

Biological information: A truly arctic black fly, *P. ursinum* exhibits many specializations for life in the far north. Cytological studies reveal that populations referable to this species consist only of triploid, parthenogenetic females (Madahar 1967, 1973). Females are autogenous and carry mature eggs at the time of emergence. The eggs are relatively large, with only 31 to 91 produced per female (Davies 1954). The abdominal walls of females are subject to rupture, ensuring that the eggs are shed if unfavourable conditions prevent oviposition. Carlsson (1962) suggested that eggs could be liberated even if the pharate female was unable to emerge. In northwestern North America the immature stages are confined to small, cold, upland streams. Associated species include *Gymnopais* spp., *H. alpestris*, *M. saileri*, *M. sommermanae*, *St. decafilis*, *S. decolletum*, *S. bicorne*, and *S. aureum* C. Suspended food is so scarce in such environments that *P. ursinum* larvae may resort to predation to satisfy their nutritional requirements (Currie and Craig 1988). There is one generation per year with overwintering in the egg stage.

Taxonomic notes: Nearctic populations referable to *P. ursinum* were formed through a reciprocal cross between *P. neomacropyga* and an unknown diploid species (Rothfels 1979), possibly a nominal Palaearctic species in the *macropyga*-group. Few populations have been studied chromosomally so it is not known how many hybridization events might have taken place in the Holarctic Region. The specific epithet *ursinum* Edwards (Type locality: Bear Island) is retained for all triploid populations, pending further study. It is conceivable that this species also occurs in the Russian Far East, although perhaps misidentified as one of the nominal subspecies of *P. macropyga* (see Taxonomic notes for 20).

Tribe Simuliini Newman, 1921

Genus *Greniera* Doby and David, 1959

22. *Greniera denaria* (Davies, Peterson and Wood, 1962)

Northern Nearctic

Distribution: Yukon to Maine.

Yukon records: Ogilvie Mountains.

Biological information: Very little is known about the biology of this species. The immature stages are typically found in small, shallow, seasonal, drainage streams. Larvae attach themselves to trailing vegetation, whereas pupae are usually found attached to the undersurfaces of stones. This is an early season black fly at southern latitudes, with one generation per year and overwintering eggs. Females are anautogenous on birds (Davies et al. 1962).

Taxonomic notes: This is the first record of *Greniera* from northwestern North America [Yukon, Ogilvie Mts., Dempster Hwy. km 66, 28–29.vii.1994, D.C. Currie and D.M. Wood, malaise trap, ROME].

Genus *Mayacnephia* Wygodzinsky and Coscarón, 1973

23. *Mayacnephia* “Species X”, Currie, 1986

Cordilleran

Distribution: Yukon south to Washington.

Yukon records: Southwestern Yukon, Kluane Ranges.

Biological information: This little collected species has previously been reported only from southwestern Alberta (Currie 1986). Larvae and pupae live in small, shallow, upland streams. There is one generation per year with overwintering eggs. The bifid claws of adult females suggest that *Mayacnephia* “Species X” is ornithophilic.

Taxonomic notes: This is the first record of *Mayacnephia* from northwestern North America [Whitehorse, 24.vi.1950, W.R. Richards, CNCI; Alaska Hwy. km 1683, 60°58'N 139°07'W, 7.vi.1979, R. Jaagumagi, ROME]. This is a mainly Mesoamerican genus, with Nearctic representatives previously known only from as far north as southern British Columbia and Alberta. The Yukon records represent a range extension of approximately 1500 kilometres. It is not known whether these populations are truly disjunct, or whether the distributional gap is the product of insufficient collecting (see also Taxonomic notes for 27).

Genus *Metacnephia* Crosskey, 1969**24. *Metacnephia saileri* (Stone, 1952)**

Palaeartic-East Beringian?

Distribution: Alaska, Yukon, northern British Columbia; northern Eurasia.*Yukon records:* Ogilvie Mountains, Southern Yukon.*Biological information:* The immature stages live in clear, fast-flowing, medium- to large-sized streams and rivers. Commonly associated species include *H. alpestris*, *H. perspicuus*, *S. decolletum*, *S. corbis*, *S. malyschevi*, and *S. vulgare*. There are one or 2 generations per year in Alaska, depending on elevation (Sommerman et al. 1955). Overwintering is probably in the egg stage. The markedly developed biting mouthparts and bifid claws suggest that females are anautogenous on birds.*Taxonomic notes:* The concept of *Metacnephia saileri* (Stone, 1952) (Type locality: Lower Fire Lake, Alaska) has undergone several changes during the last decade. Originally applied to populations throughout western and northern North America, the validity of the name was called into question when Alaskan material was found to conform cytologically to specimens of *M. pallipes* (Fries, 1824) from Norway (Procnier 1982a; Currie 1986). Based on this information, Currie (1986) considered *M. saileri* to be a junior synonym of *M. pallipes*. Crosskey (1988) also recognized *pallipes* as an Holarctic species-complex, but retained the name *M. saileri* for populations from northern North America. Recent examination of the type series reveals that *M. pallipes* Fries has been misinterpreted ever since Rubtsov's (1940) redescription based on Russian material (Zwick 1995). This species actually belongs to *Cnephia* Enderlein, rather than to *Metacnephia*, and *pallipes* is now established as the senior synonym of *laponica* Enderlein and *heymonsi* Enderlein (Zwick 1995). The name *M. saileri* is therefore available and valid for *M. pallipes* in the sense of Rubtsov. Procnier (1982a) established that there are at least 3 chromosomally distinct species in the *M. saileri* complex: one from northwestern North America and Norway (to which the name *saileri* applies), one from northern Alberta, and one from northern Quebec. Populations referable to the *M. saileri* complex (as *M. pallipes*) have long been recognized from the Russian Far East (Bodrova 1977). Chromosomal analysis of a single larva from the Magadan Region (X₀ X₁) [Kolyma Hwy. km 282, North Omchuk R., 29.vi.1995, D.C. Currie and P.H. Adler, ROME] confirms that these Far East populations belong to *M. saileri* s. str. (P.H. Adler, pers. comm.). Further collections are needed to establish whether *M. saileri* exhibits a strictly East Beringian distribution in North America.**25. *Metacnephia saskatchewanana* (Shewell and Fredeen, 1958)** Northern Nearctic*Distribution:* Yukon to northern Quebec.*Yukon record:* Tintina Trench.*Biological information:* Larvae and pupae of this univoltine species occur in large-sized streams and rivers. Adults emerge only 4 to 6 weeks after ice break-up, suggesting that larvae overwinter (Fredeen 1981). Females have been collected from immature domestic geese in Quebec [False R. near Fort Chimo, 6.vii–5.viii.1959, CNCI]. Adult males have been taken from the flowers of *Saxifraga tricuspidata* in the Northwest Territories [McConnell R., 21–22.vii.1968, K. MacInnes, CNCI].*Taxonomic notes:* This is the first record of *M. saskatchewanana* (Type locality: Prince Albert, Saskatchewan) from the Yukon Territory [Klondike Hwy. km 562, Moose Cr. Campground, malaise trap, 63°30'N 137°01'W, 18–20.vi.1979, ROME]. The chromosomes have been described by Procnier (1982a).**26. *Metacnephia sommermanae* (Stone, 1952)**

Palaeartic-East Beringian

Distribution: Alaska, Yukon; Siberia, Russian Far East.*Yukon records:* Ogilvie Mountains.*Biological information:* This infrequently collected species is closely associated with tundra in northwestern North America. The immature stages are restricted to small, cold, shallow, upland streams. *M. sommermanae* has been collected in association with *G. holopticus*, *H. alpestris*, *P. neo-macropyga*, *P. ursinum*, *St. decafilis*, *S. decolletum* and *S. nigricoxum*. There is one generation per year with overwintering eggs (Sommerman et al. 1955). Females are obligately autogenous.*Taxonomic notes:* The name *M. crassifistula* (Rubtsov, 1956) (Type locality: Altai State Reserve, Altai) is applied to a distinctive species that occurs throughout Siberia and the Russian Far East. The original description and figures suggest that it is very close to, and perhaps conspecific with, *M. sommermanae* (Type locality: Steese Highway, Alaska). However, the extensive range of *M. crassifistula*, and variation in the form of the pupal gill, is suggestive of a species complex. Bodrova (1980, cf. fig. 6) contrasted the gill of typical *crassifistula* (fig. 6a) with that of a form from the Russian Far East (fig. 6b). The inflated gill of this latter agrees well with that of typical *sommermanae*, and so the

name can reasonably be applied to Far Eastern populations. Procnier (1982a) described the chromosomes of this species.

27. *Metacnephia villosa* (DeFoliart and Peterson, 1960) Cordilleran

Distribution: Yukon south to Utah and Colorado.

Yukon records: Southern Yukon.

Biological information: Very little is known about the biology of this species. Larvae and pupae inhabit small, cool, streams in Alberta (Currie 1986). There is evidently one generation per year with overwintering in the egg stage. The bifid claws and markedly developed mouthparts suggest that females of *M. villosa* are anautogenous on birds.

Taxonomic notes: This is the first record of *M. villosa* (Type locality: Sublette County, Wyoming) from the Yukon Territory [Watson Lake, 21–26.vi.1948, Mason and Hughes, CNCI; Whitehorse, 13.vi.1950, W.R. Richards, CNCI]. These southern Yukon records are at least 1100 km north of the nearest population in south-central British Columbia. Whether this is a collecting artifact, or is indicative of a disjunct distribution, needs further study. A similar distributional pattern is exhibited by *Mayacnephia* “Species X” (see Taxonomic notes for 23).

Genus *Stegopterna* Enderlein, 1930

28. *Stegopterna decafilis* Rubtsov, 1971a

Palaeartic-East Beringian

Distribution: Alaska, Yukon; Eastern Siberia.

Yukon records: Ogilvie Mountains, Southern Yukon.

Biological information: The immature stages of *St. decafilis* live in small, cold, mountain streams, in association with *G. holopticus*, *H. alpestris*, *M. sommermanae*, and *S. decolletum*. Eggs hatch shortly after ice break-up in early June, with pupation beginning in mid July. The slightly developed mouthparts of females indicate that *St. decafilis* is not capable of blood feeding.

Taxonomic notes: Larvae and pupae referable to *St. decafilis* (Type locality: Kular, Eastern Siberia) are known from 3 Yukon localities and 2 Alaskan localities: Yukon, Glacier Cr., Dempster Hwy. km 24.5, 25.vii.–17.ix.1981, D.C. Currie, ROME; Yukon, Dempster Hwy. km 18, 18.vii.1982, D.M. Wood, CNCI; Yukon, Whitehorse, Fish L. Rd., vii.1982, D.M. Wood, CNCI; Alaska, mi 43 Taylor Hwy., Logging Cabin Cr., 63°49'N 142°14'W, 12.viii.1980, D.C. Currie; Alaska, mi 78 Steese Hwy., McMannus Cr., 25.vii.1994, D.C. Currie and D.M. Wood. This is the first record of this species from the Nearctic Region.

29. *Stegopterna emergens* (Stone, 1952)

Holarctic?

Distribution: Alaska and Yukon east to Baffin Island and Labrador, south to Alberta and Wisconsin; northern Eurasia?

Yukon records: British Mountains.

Biological information: The immature stages of this univoltine species occur in shallow, small-order streams. Overwintering is probably in the egg stage. Hatching in Alaska is from late May to late June, depending on elevation (Sommerman et al. 1955). Emergence of adults occurs between mid June and mid August. Females are obligately autogenous.

Taxonomic notes: Bodrova (1977) tentatively applied the name *St. richteri* [= *freyi* Enderlein] *dentata* Rubtsov and Carlsson, 1965 (Type locality: Sverdlovsk, Western Russia) to a population from Chukotka. The branching pattern of the pupal gill (1+2) (2+2) (1+2+2), and the non-biting mouthparts of the adult female, indicate that this Far Eastern population is actually *St. emergens* Stone (Type locality: Fairbanks, Alaska). The relationship of this species to *St. freyi dentata* and *St. tshukotensis* Rubtsov, 1971a (Type locality: Chaun, Russian Far East) needs further study. The suggestion that *St. emergens* is actually a circumpolar species (Shewell 1958) seems well founded.

Genus *Simulium* Latreille, 1802

Subgenus *Eusimulium* Roubaud, 1906

aureum species group

30. *Simulium aureum* Fries, 1824 complex

Holarctic

Distribution: Alaska to Newfoundland, south to Guatemala; Eurasia.

Yukon records: Kluane Range.

Biological information: Cytological studies indicate that there are at least 12 cytological forms in the *S. aureum* complex (Leonhardt 1985). The immature stages are usually found in slow-flowing, small- to medium-sized streams. Although host preferences are not known for most cytospecies, females are

believed to be ornithophilic based on the structure of the tarsal claw. Adults referable to the *S. aureum* complex were collected from great horned owl in southwestern Yukon (Hunter et al. 1997).

Taxonomic notes: The name *S. aureum* Fries, 1824 (Type locality: Esperöd and Björnstrop, Skania, Sweden) does not apply to North American populations because none of the recognized cytospecies exhibits an Holarctic distribution. The *S. aureum* complex has not been studied chromosomally in the Yukon Territory; however, collections from Alaska and the adjoining Northwest Territories suggests that as many as 3 species may occur there (see species accounts 63–65).

annulum species group

31. *Simulium canonicolum* s. str. (Dyar and Shannon, 1927) Cordilleran

Distribution: Yukon to Wyoming.

Yukon records: Southern Yukon.

Biological information: Most of the publications on *S. canonicolum* are unreliable because at least 5 species (3 undescribed) are referable to the *S. canonicolum* complex in North America (P.H. Adler, pers. comm.). Members of the complex typically occur in rapidly flowing, medium- to large-sized salmonid streams and rivers. There is one generation per year with overwintering in the egg stage. Adult females are anautogenous on birds. Members of the *S. canonicolum* complex (see 32 below) have been collected from great horned owls (*Bubo virginianus*) in southwestern Yukon.

Taxonomic notes: *S. canonicolum* (Type locality: Yellowstone Canyon, Wyoming) is recorded for the first time in northwestern North America, based on a single collection from southern Yukon [Klondike Hwy. km 228.5, Fox Cr., 61°11'N 135°24'W, 16.vi.1982, R. Jaagumagi and E. Fuller, ROME]. The chromosomes of *S. canonicolum* were described by Golini and Rothfels (1984).

32. *Simulium* n. sp. near *canonicolum* (Dyar and Shannon, 1927) Cordilleran

Distribution: Yukon south to California.

Yukon records: Kluane Range.

Biological information: Aspects of the biology of this species are similar to that described for *S. canonicolum*. The immature stages are found on trailing vegetation in rapidly flowing streams and rivers. Collection data indicated that there is one generation per year with overwintering in the egg stage. Emergence of adults is probably completed by the end of July. Birds are probable hosts of females. Females of the *S. canonicolum* complex were taken from corpses of great horned owls in southwestern Yukon (Hunter et al. 1997).

Taxonomic notes: The pupa is readily distinguished from those of all other species in North America. The gill, branching 2+2, has markedly elongate petioles that are up to half the gill length. The single Yukon record is from the Kluane Range [Alaska Hwy. at Bear Cr., west of Haines Junction, 60°24'N 137°40'W, 25.vi.1980, ROME].

pusillum species group

33. *Simulium furculatum* (Shewell, 1952) Holarctic excluding Beringia?

Distribution: Yukon east to Labrador and Newfoundland, south to New Hampshire (Fig. 2); Siberia?

Yukon records: Southern Yukon (Lewes River).

Biological information: This species breeds in medium- to large-sized streams and rivers. It is relatively rare west of the Mackenzie River, but develops in enormous numbers on the sparsely-treed taiga of central Northwest Territories and northern Quebec (Shewell 1958). There is one generation per year with overwintering in the egg stage. Members of this species group are distinguished from all others in *S. (Eusimulium)* in lacking an accessory tooth near the base of the female tarsal claw. The presence of simple claws suggests that females of the *S. pusillum*-group do not blood-feed upon birds, as is typical of *S. (Eusimulium)*. Unfortunately, host records are completely lacking for this species group. Offers of mammalian and avian hosts under experimental conditions failed to attract females of *S. furculatum* in northern Manitoba (Hocking and Pickering 1954). These same authors observed both males and females feeding on the nectar of flowers from *Salix cordifolia* Pursh, *Rubus acaulis* Michx., and *Achillea millefolium* L. Laboratory-reared females fed only on sucrose and water had up to several hundred well developed eggs in their ovaries. This raises the possibility that, although equipped with markedly developed biting mouthparts, females of *S. furculatum* can lay eggs without a blood meal. Chutter (1970) established that this species is facultatively autogenous in the first gonotrophic cycle; however, no evidence has been adduced that *S. furculatum* has multiple gonotrophic cycles. In the

absence of blood-feeding records, this species is classified as autogenous for the purposes of the present study.

Taxonomic notes: *S. furculatum* (Type locality: Churchill, Manitoba) is widely distributed in forested regions in North America. Stone (1952) and Sommerman et al. (1955) reported this species from Alaska based on collections made near Summit Lake, Richardson Highway; however, it is possible that these specimens actually belong to *Simulium* n. sp. near *giganteum*, which was collected from the same vicinity (see Taxonomic notes for species 66). The occurrence of *S. furculatum* in Alaska needs confirmation. Chromosomal analysis indicates that Nearctic populations all belong to a single species, although northwestern populations (Norman Wells, Northwest Territories) possess one frequent and 3 less frequent unique inversions (Hunter 1989). *S. furculatum* is very similar structurally to 2 nominal species from the Palaearctic Region: viz. *S. pusillum* Fries, 1824 (Type locality: Turtola and Kardis, northern Finland) and *S. tsharae* (Yankovsky, 1982) (Type locality: Ingur, Chitinskaya Oblast). These 3 species differ from all others in the *pusillum*-group by a combination of the form of the pupal gill (branching 2+3+3; dorsal, lateral, ventral) and absence of a subbasal tooth on the female claw. *S. pusillum* and *S. furculatum* can be distinguished readily from each other by the form and number of parameral spines, and by the relative length of the primary gill trunks (these markedly longer in *S. furculatum* than in *S. pusillum*). Accordingly, the name *S. furculatum* is retained for Nearctic populations. The status of *S. tsharae* is less clear. Illustrations of the larva, pupa, and female (cf. Yankovsky 1982) are entirely consistent with *S. furculatum*. However, the male is needed to fully assess the status of *S. tsharae*. The identity of *S. pusillum* sensu Bodrova (1977) from Chukotka is uncertain.

vernum species group

34. *Simulium bicorne* Dorogostaisky, Rubtsov and Vlasenko, 1935

Palaearctic-Cordilleran

Distribution: Alaska and Yukon, south to Utah; eastern Siberia.

Yukon records: Ogilvie Mountains, Kluane Range, Southern Yukon.

Biological information: The immature stages of this little-known species live in small-order (usually 0.2–1 m wide) upland streams. Larvae and pupae prefer trailing vegetation, where they are often collected with *S. baffinense* and *S. silvestre*. Other associated species include *P. travisi*, *P. esselbaughi*, *P. doveri*, and *St. decafilis*. According to Sommerman et al. (1955), Alaskan populations are univoltine with overwintering eggs. Hatching begins in late May and June, with the emergence period from mid June until mid August. There are no confirmed blood-feeding records for this species; however, the toothed mouthparts and bifid claws suggest that females of *S. bicorne* are ornithophilic.

Taxonomic notes: The name *S. bicorne* D., R. and V., 1935 (Type locality: Lake Baikal) has long been applied to a North American species whose pupal cocoon bears a bifid anteromedian projection. In typical *S. bicorne* (Dorogostaisky et al. 1935; p. 179, fig. 4) the pupal projection is divided almost to the base. No Nearctic population has the projection so deeply cleft; and the degree of bifurcation is varied even within a single population. Whether such variation reflects intra- or interspecific differences needs clarification. Brockhouse described the chromosomes of populations from Alaska and the Yukon. Yankovsky (1979), based on a study of pharate adults, described 2 closely related species: *S. corniferum* (type locality: Murmansk, Western Russia) and *S. paracorniferum* (type locality: Khabarovsk, Russian Far East). Although Yankovsky (1979) suggests that the name *S. corniferum* might apply to Alaskan populations, it is difficult to assess the characters of teneral adults. The name *S. bicorne* is retained for North American populations pending further study.

35. *Simulium croxtoni* Nicholson and Mickel, 1950

Northern Nearctic

Distribution: Yukon east to Newfoundland, south to Minnesota.

Yukon records: Central Yukon.

Biological information: Western populations of *S. croxtoni* breed in small, shallow, low-gradient, streams. The immature stages are found on trailing vegetation, and are particularly abundant at the outflows of impounded water such as beaver ponds. Females are reported as blood feeders upon wild and domestic birds (Bennett 1960).

Taxonomic notes: *Simulium croxtoni* (Type locality: west of International Falls, Minnesota) is here recorded for the first time in northwestern North America [Yukon, 0.5 km N. Klondike R. Bridge, Dempster Hwy., 21.vi.1982, D.M. and G.C. Wood, CNCI]. Adults of this species are morphologically similar to *S. fionae* Adler, 1990, and an undescribed species near *S. fionae*. Accordingly, published distributional and ecological information must be interpreted with caution, particularly in eastern North

America where all 3 species occur together. Chromosomal and distributional information is from Hunter and Connolly (1986) and McCreadie et al. (1995).

36. *Simulium decolletum* Adler and Currie, 1986 Palaeartic-Cordilleran

Distribution: Alaska and Yukon, south to Alberta; Siberia.

Yukon records: Ogilvie Mountains.

Biological information: Larvae and pupae are most often collected in cold, small- to medium-sized, upland streams. Associated species include *H. alpestris*, *M. saileri*, *M. sommermanae*, *S. silvestre*, and *S. vulgare*. Hershey et al. (1995) recorded this species from lake outflows and higher-order streams in northern Alaska. Overwintering is probably in the egg stage. Adult females probably blood-feed upon birds.

Taxonomic notes: This species was long confused with members of the *S. pugetense* complex in northwestern North America. Sommerman et al. (1955), for example, commented on populations of larval "*S. pugetense*" that had compound (as opposed to simple) anal papillae. These populations almost certainly belong to the morphologically similar *S. decolletum*. Most accounts about the biology of this species have been published under the name *S. pugetense*. Rubtsov (1956) recognized a distinctive form of *S. longipile* (Zhilishche spring, Lake Baikal; fig. 201) that differed from the typical form (Mol'ka River, Eastern Siberia; fig. 200) in details of vestiture and male terminalia. The Baikal form was later subsumed in *S. pugetense* (Dyar and Shannon, 1927) (Type locality: Seattle, Washington), based on perceived similarities with *pugetense* sensu Stone (1964) (Rubtsov 1965). *S. pugetense* is a Nearctic species complex (see 37 below) whose members can be distinguished readily from most other *vernum*-group taxa by details of the male ventral plate and female genital fork. Published illustrations of the Baikal form clearly indicate that it does not belong to any member of the *S. pugetense* complex. Rather, these specimens appear entirely consistent with *S. decolletum* Adler and Currie, 1986 (Type locality: Obed, Alberta), a species that is distributed in North America from Alaska and the Yukon Territory south to Alberta. The Lake Baikal form of *S. longipile* (Rubtsov 1956: 463, in part, fig. 201) is here considered conspecific with *S. decolletum*. The relationship of *S. decolletum* to *S. fontinale* Radzivilovskaya, 1948 (Type locality: Kabanii spring, Russian Far East) is more problematic. According to Rubtsov (1956), *S. fontinale* is closely related to *S. longipile* s. lat. But it is not certain that Rubtsov's concept of *S. fontinale* is based on typical specimens, or indeed if such material still exists (cf. Rubtsov 1956, pp. 464–465, "Taxonomic remarks"). The chromosomes of *S. decolletum* were described (as *Eusimulium* "Yukon") by Brockhouse (1985).

37. *Simulium pugetense* (Dyar and Shannon, 1927) complex, Nearctic

Cytospecies A

Distribution: Alaska east to Quebec, south to California.

Yukon records: Southern Yukon.

Biological information: The only known Yukon collection was taken from a 10 m wide outflow from a beaver pond [vicinity Whitehorse, McIntyre Cr. at Fish L. Rd. crossing, 15.vii.1994, D.C. Currie and D.M. Wood, ROME]. Larvae were collected from trailing vegetation along with *S. silvestre*, *S. vittatum* IS-7, *S. decorum*, *S. tuberosum* s. str., and *S. tuberosum* FG. Although not frequently collected, this species is locally abundant in medium- to large-sized streams in northern British Columbia and southern Alaska. *S. pugetense* A is an early-developing species, with mature larvae present as early as April in Alaska (Allison and Shields 1989). Published information on "*S. pugetense*" from Alaska (Sommerman et al. 1955) probably applies to a combination of Cytospecies A, Cytospecies B (see 70) and the morphologically similar *S. decolletum* Adler and Currie (see 36 above).

Taxonomic notes: Two species are referable to the *S. pugetense* complex in northwestern North America, with only Cytotype A known from the Yukon Territory (Hunter and Connolly 1986; Allison and Shields 1989; P.H. Adler, pers. comm.). The name *S. pugetense* Dyar and Shannon (Type locality: Seattle, Washington) probably does not apply to either northwestern cytospecies based on present information. Reports of this species from the Palaeartic Region are evidently based on Rubtsov's (1965) synonymy of the Lake Baikal form of *S. longipile* Rubtsov, 1956, with *S. pugetense* sensu Stone (1964). However, as indicated under 36 above, it is more likely that the name *S. decolletum* Adler and Currie applies to the Lake Baikal form. There is no convincing evidence that any member of the *S. pugetense* complex occurs in the Palaeartic Region.

38. *Simulium silvestre* (Rubtsov, 1956) Palaeartic-Cordilleran

Distribution: Alaska and Yukon, south to Vancouver Island; Eurasia.

Yukon records: Ogilvie Mountains, Southern Yukon.

Biological information: The immature stages of this species occur in small- to medium-sized upland and lowland streams. Larvae are most frequently found on trailing vegetation in association with *S. baffinense*, *S. aureum* C and *S. bicorne*. Populations living at the outflows of tundra ponds and beaver ponds are found in association with outlet specialists such as *S. rostratum*, *S. vittatum* IS-7, *S. decorum* and *S. noelleri*. Larvae and pupae were found together in mid July in Alaska and Yukon, but little else is known about their phenology. Aspects of the biology of *S. silvestre* are discussed under "*S. latipes*" (= *S. vernum* s. lat.) by Sommerman et al. (1955); however, several species probably were included under that name. In the Palaearctic Region, overwintering is in the egg stage (Rubtsov 1956). Although Rubtsov (1956) indicates that females occasionally attack humans, it is more likely that they are blood-feeders upon birds.

Taxonomic notes: *S. silvestre* (Rubtsov, 1956) (Type locality: Pashka, Irkutsk Region) is here recorded for the first time in North America. This species has long been confused with structurally similar representatives of the *S. vernum* complex. The occurrence of *S. silvestre* in northwestern North America was established through chromosomal and morphological comparisons with cytologically verified material from the Palaearctic Region (P.H. Adler, pers. comm.).

Subgenus *Hellichella* Rivosecchi and Cardinali, 1975

39. *Simulium baffinense* Twinn, 1936

Holarctic

Distribution: Alaska east to Baffin Island and northern Quebec, south along the Rocky Mountains to Utah; northern Eurasia.

Yukon records: Ogilvie Mountains.

Biological information: The immature stages of this species inhabit small-sized, low gradient, streams. Larvae and pupae are often found on trailing vegetation in association with *S. bicorne* and *S. silvestre*. Other associated species include *S. aureum* A and C, *S. tuberosum* complex, and *S. venustum* complex. There is one generation per year with winter passed in the egg stage (Sommerman et al. 1955). The emergence period is from late July through August. Females are obligately autogenous (Peterson 1959; Davies et al. 1962). Shewell (1958) classified *S. baffinense* as an Arctic and Hudsonian species.

Taxonomic notes: *S. baffinense* (Type locality: Lake Harbour, Baffin Island) exhibits a circumpolar distribution. Populations occur at high latitudes in northern North America, and at high elevations in the Cordillera. In the Palaearctic Region, *S. baffinense* is known from northern Sweden and Chukotka (Carlsson 1962; Bodrova 1977).

Subgenus *Psilozia* Enderlein, 1936

40. *Simulium vittatum* Zetterstedt, 1838 complex,

Nearctic

Cytospecies IS-7

Distribution: Alaska east to Quebec, south to Arizona and Virginia (Fig. 1).

Yukon records: Ogilvie Mountains, Kluane Ranges, Southern Yukon.

Biological information: This is one of the most common and widely distributed black flies in North America. Aspects of the biology of Cytospecies IS-7 are given by Adler and Kim (1984). In northwestern North America the immature stages are most frequently encountered in the outflows of impounded water, such as beaver ponds and tundra pools. Larvae attach themselves to stones and trailing vegetation, although the latter seems to be preferred. Associated species include *S. decorum*, *S. noelleri*, *S. rostratum*, *S. venustum* complex, and *S. tuberosum* complex. There are 2 or 3 generations per year, depending on the type of stream (Sommerman et al. 1955). Overwintering is either in the egg stage or larval stage. Females of the *S. vittatum* complex are facultatively autogenous in the first gonotrophic cycle, and are anaautogenous on mammals in subsequent gonotrophic cycles (Davies and Györkökös 1990). They are occasionally annoying to humans due to their swarming about the head and probing the skin. However, there are few blood-feeding records on humans.

Taxonomic notes: *S. vittatum* IS-7 is one of 2 widely distributed cytospecies in the *S. vittatum* complex (Rothfels and Featherston 1981). The other, Cytospecies IIIIL-1, is known from Alaska but not from the Yukon (see 73). Cytospecies IS-7 is much more abundant in the northwest than is IIIIL-1, so most of the regional literature on "*S. vittatum*" applies to the former species. It is not known which of the 2 cytospecies, if either, carries the name *vittatum* Zetterstedt, 1838 (Type country: Greenland). Populations of the *S. vittatum* complex are also known from Iceland and the Faeroe Islands (Peterson 1977; Pederson 1971). There are no reliable means to distinguish the 2 cytospecies morphologically.

Subgenus *Simulium* s. str.*malyschevi* species group41. *Simulium arcticum* Malloch, 1914 complex, Cordilleran
Cytospecies III-2

Distribution: Alaska and Yukon south to the Queen Charlotte Islands and west-central Alberta.

Yukon records: Southern Yukon.

Biological information: This cytospecies is known from a single Yukon locality [Whitehorse, Klondike Hwy. km 3.7, Takhini R., 30.vii.1994, D.C. Currie and D.M. Wood, ROME]. Larvae were collected from trailing branches along the margin of this large (ca. 100 m wide), deep, rapidly flowing, river. The immature stages of Cytospecies III-2 occur most often in medium- to large-sized lowland rivers, and occasionally in fast-flowing medium-sized (5 m wide) streams. They have been found in association with other river-inhabiting species including *H. onychodactylus* 10, *S. transiens*, *S. tuberosum* s. str., *S. malyschevi*, and *S. arcticum* IL-3.4. Little is known about the biology of this species. Published accounts of “*S. arcticum*” from northwestern North America probably refer to a composite of 4 different cytospecies. Both larvae and eggs have been reported as the overwintering stage in Alaska (Sommerman et al. 1955); however, this may reflect differences in phenology among cytotypes. Shields and Procnier (1982) suggest that Cytospecies III-2 may have at least 2 generations per year in Alaska, based on the presence of mature larvae approximately 6 weeks apart in the same stream. Adult females are anautogenous on mammals.

Taxonomic notes: Cytological and distributional information is from Shields and Procnier (1982), Procnier and Shemanchuk (1982), Procnier (1984), Currie and Adler (1986) and P.H. Adler (pers. comm.). The name *arcticum* Malloch, 1914 (Type locality: Kaslo, British Columbia) probably does not apply to any northwestern cytotype based on distributional information. No species referable to the *S. arcticum* complex are known from the Palearctic Region.

42. *Simulium arcticum* Malloch, 1914 complex, Cordilleran
Cytospecies IL-3.4

Distribution: Alaska south to west-central Alberta.

Yukon records: Southern Yukon.

Biological information: Larvae were collected from trailing branches and trailing vegetation along the margins of large (100–400 m wide), deep, piedmont rivers. Associated species included *S. transiens*, *S. tuberosum* s. str. and *S. arcticum* III-2. *S. corbis* is often associated with Cytospecies IL-3.4 in Alaska (Shields and Procnier 1982). These authors suggest that Cytospecies IL-3.4 may have at least 2 generations per year. Other aspects of the biology of this species are discussed under 41 above.

Taxonomic notes: *S. arcticum* IL-3.4 is known from 3 Yukon localities [Carmacks, Yukon R., 30.vii.1994, D.C. Currie and D.M. Wood, ROME; Takhini R. at Alaska Hwy. crossing, 15.vii.1994, D.C. Currie and D.M. Wood, ROME; Whitehorse, Klondike Hwy. km 3.7, Takhini R., 30.vii.1994, D.C. Currie and D.M. Wood, ROME]. This is the first record of this species from the Yukon Territory. The southernmost record for this species is the North Saskatchewan River in west-central Alberta (Procnier 1984). See also Taxonomic notes for 41.

43. *Simulium corbis* Twinn, 1936 Holarctic

Distribution: Alaska east to Labrador and Newfoundland, south to central British Columbia and Maine; northern Eurasia.

Yukon records: Richardson Mountains, Ogilvie Mountains, Southern Yukon.

Biological information: The immature stages of *S. corbis* occur in medium- to large-sized streams and rivers. Associated species in northwestern North America include *H. alpestris*, *H. perspicuus*, *H. onychodactylus* 2a, *M. saileri*, *S. arcticum* complex, *S. nigricoxum*, *S. malyschevi*, *S. tuberosum* s. str., and *S. vulgare*. Overwintering is in the egg stage, with eggs hatching after ice break-up. One generation per year is indicated over most of this species range (e.g. Anderson and Dicke 1960; Currie 1986). The report of a second generation in Alaska (Sommerman et al. 1955) may have resulted from confusion with the later developing *S. nigricoxum*. Adult females are anautogenous on mammals, with snowshoe hares (*Lepus americanus* Erxleben) and caribou (*Rangifer tarandus* (L.)) indicated as hosts in Newfoundland (McCreadie et al. 1994).

Taxonomic notes: *S. corbis* (Type locality: Blanche River, Quebec) exhibits a circumpolar distribution. Published accounts about the ecology of this species in northwestern North America may refer, in part, to *S. nigricoxum*, which is morphologically similar in the immature stages.

44. *Simulium malyschevi* Dorogostaisky, Rubtsov and Vlasenko, 1935 Holarctic

Distribution: Alaska east to west-central Manitoba; Siberia, northern China, Korea, Japan.

Yukon records: Ogilvie Mountains.

Biological information: This little-collected species breeds in watercourses that range in width from 5–150 metres. The water is typically cool, clear, and rapidly flowing, supporting abundant populations of Arctic Grayling (*Thymallus arcticus* (Pallas)) and Dolly Varden (*Salvelinus malma* (Walbaum)). The immature stages are most often collected from trailing substrata. Associated black flies include *H. alpestris*, *H. perspicuus*, *M. saileri*, *S. arcticum* IIL-2 and IL-3.4, *S. corbis*, and *S. vulgare*. Larvae and pupae of *S. malyschevi* have been collected between July and early September in Alaska (Sommerman et al. 1955). Adult females are probably anautogenous on mammals. Humans are indicated as hosts in Eastern Siberia (Rubtsov 1962).

Taxonomic notes: The name *malyschevi* D., R. and V. (Type locality: Ushakovka River, Trans-Baikal, Russia) has long been applied to populations of this distinctive species in North America. In addition to the typical form, 2 nominal subspecies are recognized in the Palaearctic Region: *albipes* Rubtsov, 1956 (Type area: “Trans-Baikal and Primorsk Territory”) and *lucidum* Rubtsov, 1956 (Angara River, Eastern Siberia). At least 3 other closely related nominal species are known from the eastern Palaearctic Region: *bidentatum* Shiraki, 1935 (type country: Japan), *daisense* Takahashi, 1950 (type country: Japan) and *tumminum* Bodrova, 1990 (Type locality: Tumin, Russian Far East). It is uncertain which, if any, of these names apply to populations from the Nearctic Region. The name *S. malyschevi* is retained for Nearctic populations, pending further study.

45. *Simulium nigricoxum* Stone, 1952 Nearctic-West Beringian?

Distribution: Alaska east to Hudson Bay (Fig. 4); Siberia?

Yukon records: Ogilvie Mountains, Kluane Ranges.

Biological information: The immature stages of *S. nigricoxum* live in medium- to large-sized (15–30 m wide) upland streams. They apparently do not occur in large piedmont rivers, as do members of the *S. arcticum* complex. Larvae typically attach themselves to the sides and undersurfaces of stones in the fastest regions of flow. However, they may also be found on trailing vegetation along the margins of streams. Associated black flies include *H. alpestris*, *H. perspicuus*, *M. saileri*, *S. decolletum*, *S. silvestre*, *S. corbis*, *S. tuberosum* s. str., and *S. vulgare*. There is probably only one generation per year with overwintering in the egg stage. Emergence begins in mid July, with adults on the wing through August and into September. Females are attracted to, and blood-feed upon, humans. Although there are no other host records from North America, females probably attack other mammals as well.

Taxonomic notes: *S. nigricoxum* (Type locality: Hood River, Arctic Sound, Northwest Territories) is a distinctive species that exhibits a markedly northern distribution in western North America. This species is very closely related to, and perhaps is conspecific with, *S. decimatum* D., R. and V., 1935 from the Palaearctic region (Type locality: Irkut River, Trans-Baikal, Russia). Populations referable to the latter species are distributed at northern latitudes across Eurasia, but also occur in Mongolia and China (Crosskey et al. 1996). Further studies are needed to determine whether these widely distributed populations belong to a single species. Comparison of typical *S. nigricoxum* with “*S. decimatum*” from northern Sweden reveals that they belong to different species; however, the relationship of these 2 populations to nominotypical *S. decimatum* remains unclear. The name *nigricoxum* is retained for Nearctic populations pending further study. *S. nigricoxum* is recorded tentatively from Chukotka because Far Eastern populations (cf. Bodrova 1977) are almost certainly more closely related to *S. nigricoxum* from Alaska than they are to typical *S. decimatum*.

hunteri species group

46. *Simulium hunteri* Malloch, 1914 Cordilleran

Distribution: Southern Alaska and Yukon, south to Mexico.

Yukon records: Southern Yukon.

Biological information: The immature stages of *S. hunteri* can be found in watercourses ranging from tiny roadside trickles to large-sized (25 m wide) streams. However, they are most often collected in smaller-sized (ca. 1 m wide) streams. There are few records of this species in northwestern North America. Sommerman et al. (1955) found larvae of *S. hunteri* in association with *M. saileri* and *S. tuberosum* complex in Alaska; in northern British Columbia larvae were collected with *S. pugetense* A, *S. tuberosum* FG, and *S. venustum* complex [Cassiar, Cassiar Hwy. km 612, 31. vii. 1994, D.C. Currie and D.M. Wood]. A biting female was collected from the author’s arm near Whitehorse, Yukon

[Wolf Cr., Alaska Hwy. km 1459, 30.vii.1994, D.C. Currie and D.M. Wood]. Females were taken from cows in Colorado (Malloch 1914).

Taxonomic notes: The only representative of the *S. hunteri*-group in northwestern North America, this species reaches its northern limit in southern Yukon and Alaska. Members of the *hunteri*-group are distributed mainly in Central America, with only 6 species represented in North America (Crosskey 1988). *S. hunteri* has not been studied chromosomally, but the wide range of habitat associations exhibited by the immature stages is suggestive of a species complex (Currie and Adler 1986). The type locality is Virgin Dale, Colorado.

noelleri species group

47. *Simulium decorum* Walker, 1848

Nearctic

Distribution: Alaska to Newfoundland, south to Oregon, Colorado and Florida.

Yukon records: Ogilvie Mountains, Southern Yukon.

Biological information: Larvae of this species occur almost exclusively at the outflows of impounded water. In northwestern North America they are most often collected from the outlets of beaver ponds, but may also be found downstream of tundra pools. Larvae and pupae occur in large numbers on submerged twigs and trailing vegetation. Associated species include *S. aureum* A and C, *S. silvestre*, *S. vittatum* IS-7, *S. noelleri*, and *S. rostratum*. Sommerman et al. (1955) reported from 2 to 4 generations in Alaska, depending on latitude. Winter is probably passed in the egg stage. Females are facultatively autogenous in the first gonotrophic cycle, but most nulliparous and parous females are capable of bloodsucking (Chutter 1970; Simmons and Edman 1981; Davies and Györkös 1990). Although females occasionally are collected from birds, more typically they are associated with mammalian hosts, including horses, deer, moose, cattle, and humans (Davies and Peterson 1956; Davies et al. 1962; Fredeen 1973; Pledger et al. 1980).

Taxonomic notes: *S. decorum* Walker, 1848 (Type locality: St. Martin's Falls, Ontario) has long been the only name applied to representatives of the *noelleri*-group in North America. Cytological studies reveal that there are at least 2 species in the Nearctic Region: one widely distributed (to which the name *decorum* applies); and one with a markedly northern distribution. This latter species is sufficiently similar to Palaearctic *S. noelleri* Friederichs, 1920 (Type locality: Paulinzella/Thuringia, Germany) to invite comparison. In all North American populations, IL lacks the heavy basal band and serves as the sex arm; however, the inversions characterizing the Y chromosome differ, being basal and complex at Churchill, Manitoba (Rothfels 1981), but simple and between the "neck" and "heavy" markers in populations from Alaska and the Yukon. Populations of *S. noelleri* from the Palaearctic Region have several sex-chromosome systems (Rothfels 1981), all different from those of Nearctic populations. The various sex-chromosome systems suggest that *S. noelleri* is a species complex. But until more evidence supporting this proposition is adduced, and until populations of morphologically similar species from the Palaearctic Region (e.g. *nikkoense* Shiraki, 1935; *palustre* Rubtsov, 1956; *vershininae* Yankovsky, 1982) can be studied chromosomally, all such entities, including the northern Nearctic cytospecies, are considered conspecific. Chromosomes of 21 larvae from a mixed population of *S. decorum* and *S. noelleri* in Alaska [Isabel Pass, Richardson Hwy. mi 206, 16.vii.1994, D.C. Currie and D.M. Wood, ROME and CUCC] were as follows: 6 larvae (2 females, 4 males) were classical *S. decorum*, whereas 14 (11 females, 3 males) were typical of *S. noelleri*. One female larva was heterozygous for the heavy band in the base of IL, suggesting that hybridization between the 2 species sometimes occurs (P.H. Adler, pers. comm.).

48. *Simulium noelleri* Friederichs, 1920

Holarctic

Distribution: Alaska east to Hudson Bay; Eurasia.

Yukon records: Ogilvie Mountains.

Biological information: There are only 3 records of *S. noelleri* in northwestern North America, associated with the outflows of upland ponds [Yukon, Ogilvie Mts., vicinity North Fork Pass, Dempster Hwy. km 84, 29.vii.1994, D.C. Currie and D.M. Wood, ROME and CUCC; Alaska, Isabel Pass, Richardson Hwy. mi 206, 16.vii.1994, D.C. Currie and D.M. Wood, ROME and CUCC; see also Hershey et al. 1995]. The Yukon site was the outlet of a tundra pool; the Isabel Pass site was the outlet of a subalpine beaver pond. Larvae and pupae were present at both localities. Associated species include *S. baffinense*, *S. silvestre*, *S. aureum* A and C, *S. vittatum* IS-7, *S. decorum*, *S. rostratum*, and *S. vulgare*. Little else is known about this species in North America. Aspects of the biology of *S. noelleri* probably are included under the name *S. decorum* in Sommerman et al. (1955).

Taxonomic notes: *S. noelleri* is here recognized for the first time in the Nearctic Region. Stone (1964b) foreshadowed the possibility when he proposed synonymy of *S. decorum* with *S. argyreatum* (which Rubtsov wrongly considered a senior synonym of *S. noelleri*). However, he retained the name *decorum* in his checklist of North American simuliids (Stone 1965), and the name has been applied to all New World populations of the complex ever since. Populations of “*Simulium* n.sp. nr. *decorum*” from the Mackenzie River Delta east to Hudson Bay (Shewell 1957) probably belong to *S. noelleri*. The chromosomes have been described by Rothfels (1981). See also Taxonomic notes for *S. decorum* (44).

slossonae species group

49. *Simulium transiens* Rubtsov, 1940

Holarctic

Distribution: Alaska and Yukon south to British Columbia, east to west-central Manitoba; Siberia, Mongolia, China.

Yukon records: Southern Yukon.

Biological information: The immature stages of *S. transiens* occur in medium- to large-sized piedmont rivers, where typically they are found attached to trailing substrata. Associated species include *S. tuberosum* s. str. and *S. arcticum* IIL-2 and IL-3.4. Little is known about the biology of this infrequently collected species. The immature stages have been collected from late May to mid August in Alberta (Currie 1986), suggesting that there may be more than one generation per year in that province. There are 2 generations per year with overwintering eggs in eastern Siberia; adult females are reported to be biters of humans (Rubtsov 1956, 1962).

Taxonomic notes: Rubtsov (1964) proposed the genus *Parabyssodon* for *S. transiens* Rubtsov, 1940 [Type locality: eastern Siberia, Belaya River]. Crosskey (1988) recognized *Parabyssodon* as a subgenus of *Simulium* s. lat., and included the closely related species *S. rugglesi* Nicholson and Mickel and *S. slossonae* Dyar and Shannon. However, present evidence suggests that *Parabyssodon* is paraphyletic with respect to *Simulium* s. str. *Parabyssodon* is here subsumed in *Simulium* s. str., and the informal name *slossonae*-group is used for the 3 included species.

tuberosum species group

50. *Simulium tuberosum* (Lundström, 1911) complex,

Nearctic

Cytospecies FG

Distribution: Alaska and Yukon east to Labrador, south to California and Tennessee.

Yukon records: Southern Yukon

Biological information: This species inhabits small- to medium-sized (0.5–10 m wide) streams. Commonly associated species include *H. onychodactylus* 10, *S. pugetense* A, *S. vittatum* IS-7, and *S. arcticum* complex. Little is known about the biology of this sibling in Northwestern North America; it is multivoltine in Alberta and Pennsylvania, with overwintering in either the larval or egg stages (Adler 1986; Adler and Kim 1986). Nothing is known about host preferences, but females are assumed to be anautogenous on mammals.

Taxonomic notes: Cytological and distributional information from Mason (1982) and Adler and Kim (1986). The larva of this species is distinguished from those of *S. tuberosum* s. str. and *S. vulgare* by details of the postgenal cleft and colouration (Adler 1986; Adler and Kuusela 1994).

51. *Simulium tuberosum* (Lundström, 1911) s. str.

Holarctic

Distribution: Alaska and Yukon east to Newfoundland, south to British Columbia and Virginia; Eurasia.

Yukon records: Western and Southern Yukon.

Biological information: The immature stages of this Holarctic species occur in a wide variety of lowland streams, ranging in width from 3.0 to more than 500 m. Northwestern populations are most frequently encountered in medium- to large-sized rivers. Associated species include *M. saileri*, *S. transiens*, *S. decorum*, *S. rubtsovi*, *S. vulgare*, and *S. arcticum* IL-3.4 and IIL-2. Larvae and pupae of *S. tuberosum* typically attach themselves to trailing substrata. Probably there is more than one generation per year. Females are inferred to be anautogenous on mammals.

Taxonomic notes: The name *S. tuberosum* Lundström (Type locality: Enontekis, Finnish Lapland) has been associated with *tuberosum*-group sibling “AB” (Adler and Kuusela 1994). Cytological epithets and distributional information are from Mason (1982), Adler and Kim (1986) and Adler and Kuusela (1994). See also Taxonomic notes for 50.

52. *Simulium vulgare* Dorogostaisky, Rubtsov and Vlasenko, 1935

Palaeartic-Cordilleran

Distribution: Alaska and Yukon, south to west-central Alberta; northern Eurasia.

Yukon records: Northern Yukon, Ogilvie Mountains.

Biological information: This Holarctic species has been collected in watercourses that range in width from 0.5 to more than 100 m; however, they are most often encountered in larger-sized streams and rivers. The immature stages are attached to stones and trailing vegetation, often in association with *H. alpestris*, *H. perspicuus*, *M. saileri*, *S. malyschevi*, *S. corbis*, *S. nigricoxum*, and members of the *S. arcticum* complex. Virtually nothing is known about the biology of *S. vulgare* in North America. There is one generation per year in Chukotka (Bodrova 1977). Like other members of the *S. tuberosum* group, females of *S. vulgare* are assumed to be blood-feeders upon mammals.

Taxonomic notes: Adler and Kuusela (1994) established that the name *S. vulgare* D., R. and V. applies to *tuberosum*-group sibling "FGI". Cytological and distributional information is from Mason (1982), Adler (1986), and Adler and Kuusela (1994). Larvae are distinguished from those of other northwestern *tuberosum*-group species by the form of the postgenal cleft and absence of pigment on the suboesophageal ganglion (Adler and Kuusela 1994).

venustum species group

53. *Simulium rostratum* (Lundström, 1911)

Holarctic

Distribution: Alaska and Yukon east to Newfoundland, south to Oregon; Eurasia.

Yukon records: Ogilvie Mountains.

Biological information: This species was long confused with members of the *S. venustum* complex, and little is known about its biology in northwestern North America. The immature stages are most often collected from low-gradient streams, particularly those enriched with organic matter. Outflows of lakes and beaver ponds, and streams originating from lowland bogs and marshes, are especially suitable as breeding sites. The immature stages attach themselves to stones and trailing vegetation, although the latter seems to be the preferred substratum. Collection sites in Alaska and the Yukon during mid July (n = 9) ranged from 0.5 to 6.0 metres in width; and from 12° to 18°C in temperature (average 14.5°C). *S. rostratum* is most often collected in association with *S. vittatum* IS-7, *S. decorum*, *S. vulgare* and *S. venustum* complex. A biting female of *S. rostratum* was collected from the shoulder of a human in the Yukon [Ogilvie Mts., Dempster Hwy. km 66, 13.viii.1982, D.C. Currie, ROME]. There are no other reliable host records from northwestern North America; however, females of the *S. rostratum/verecundum* complex are known to blood-feed upon lynx (*Lynx canadensis* Kerr), fox (*Vulpes vulpes* (L.)), and caribou (*Rangifer tarandus* (L.)) in Newfoundland (McCreadie et al. 1994).

Taxonomic notes: The name *S. rostratum* Lundström (Type area: Finnish Lapland) applies to sibling "ACD" of the *Simulium verecundum* complex (Rothfels et al. 1978; Crosskey 1988). This species occurs widely in northern Europe, Greenland, and North America. Published references to *verecundum* Stone and Jamnback, 1955 (Type locality: Monroe Co., Pennsylvania) in northwestern North America refer to *S. rostratum*. Most published accounts of "*S. rostratum*" from the Old World actually refer to *S. corbis*, the former name having been misinterpreted by Rubtsov (Zwick 1987). Biological information from the Palaeartic region is published under the names *S. verecundum* of authors (not Stone and Jamnback; misidentification) and *S. sublacustre* Davies, 1966 (Type country: England). This latter name is now considered a junior synonym of *S. rostratum* s. str. (Zwick 1987).

54. *Simulium rubtzovi* Smart, 1945

Palaeartic-East Beringian

Distribution: Alaska, Yukon, westernmost Northwest Territories; Siberia.

Yukon records: Western Yukon.

Biological information: This species is here recorded for the first time from the Yukon Territory [vicinity Snag, Dry Cr. #2 at Alaska Hwy. crossing, km 1904.5, 16.vii.1994, D.C. Currie and D.M. Wood, ROME]. The site was a low gradient, 6 m wide, brownwater stream. Larvae were collected from trailing vegetation in association with *S. venustum* complex, *S. decorum* complex, *S. tuberosum* s. str. and *S. vulgare*. Very little is known about the biology of *S. rubtzovi* in the Nearctic Region, with only 3 previous records from Alaska (Stone 1952; Sommerman et al. 1955). According to Rubtsov (1956) this species has 2 generations per year in Russia. Females are assumed to be anautogenous on mammals.

Taxonomic notes: *S. rubtzovi* Smart is a replacement name for *S. simile* Rubtsov, 1940 [Type locality: Trans-Baikal, tributaries of Uda River], the latter name being preoccupied by *S. simile* Silva Figueroa, 1917 and *S. simile* Malloch, 1919.

55. *Simulium venustum* Say, 1823 complex

Nearctic

Distribution: Alaska and Yukon east to Newfoundland, south to California and Louisiana.*Yukon records:* Southern Yukon.

Biological information: This complex of 10 or more sibling species includes some of the most notorious blood-sucking pests of humans and other mammals in North America. The immature stages typically occur in small- to medium-sized streams up to 6 m in width (and occasionally in streams up to 15 m in width). Trailing vegetation is the preferred substrate. Associated species included *H. onychodactylus* 10, *M. saileri*, *S. vittatum* IS-7, *S. arcticum* IIL-St, *S. tuberosum* complex, and *S. rostratum*. Probably there is only one generation per year in northwestern North America, with overwintering in the egg stage. Females of this sibling complex are known to blood-feed upon a wide variety of mammalian hosts including snowshoe hares (*Lepus americanus* Erxleben), mink (*Mustela vison* Schreber), racoon (*Procyon lotor* (L.)), fox (*Vulpes vulpes* (L.)), lynx (*Lynx canadensis* Kerr) and caribou (*Rangifer tarandus* (L.)) (Hunter 1990; McCreddie et al. 1994).

Taxonomic notes: The *S. venustum* complex contains at least 10 species (Rothfels et al. 1978; Rothfels 1981; Adler 1986). Few Yukon populations have been studied chromosomally; however, at least 2 species are expected based on collections from Alaska, northern British Columbia and western Northwest Territories: Cytospecies CC3, and *S. truncatum* (see 77 below) (Rothfels et al. 1978; P.H. Adler, pers. comm.). Rothfels et al. (1978) suggest that the name *venustum* Say, 1823, applies to *venustum*-group sibling CC. The type series, from “Shippingsport, falls of the Ohio” (= present-day Louisville, Kentucky), is lost. Published records of “*S. venustum*” from the Palaeartic Region probably apply to the structurally similar *S. truncatum* (see 77).

Annotated List of Northwestern Black Flies Not Recorded from the Yukon Territory

Included here are species that have been recorded from Alaska, northern British Columbia and the westernmost Northwest Territories. Many of these species may eventually be found in the Yukon Territory.

Tribe Prosimuliini Enderlein, 1921

Genus *Helodon* Enderlein, 1921Subgenus *Helodon* s. str.**56. *Helodon onychodactylus* (Dyar and Shannon, 1927)
complex, Cytospecies 4a/4b**

Cordilleran

Distribution: Alaska south to California.

Biological information: Aspects of the ecology of this species are probably similar to those described for other species in the *H. onychodactylus* complex (see species accounts 9–12).

Taxonomic notes: Cytological and distributional information is from Newman (1983), Henderson (1986), and P.H. Adler (pers. comm.). This species is known from only one site in northwestern North America [Alaska, Monument Cr., 27.v.1983, G. Shields] (Henderson 1986).

Genus *Prosimulium* Roubaud, 1906*hirtipes* species group**57. *Prosimulium doveri* Sommerman, 1962**

Cordilleran

Distribution: Alaska, British Columbia?

Biological information: *P. doveri* is a univoltine species that overwinters in the egg stage. Larvae and pupae are confined to small (0.2–1 m wide), cold, often intermittent streams. Associated species include *P. travisi*, *P. esselbaughi*, *H. onychodactylus* 10, *S. bicornis*, *S. silvestre*, and *S. pugetense* A. Females, which are anautogenous on mammals, have been described as “one of the most vicious human biters” in the vicinity of Anchorage (Sommerman 1962). Adults are on the wing between late July and mid August. Aspects of the biology of this species are given under the name *P. travisi* by Sommerman et al. (1955); more detailed information is provided by Sommerman (1962).

Taxonomic notes: This species (Type locality: Eklutna Lake) is definitely known only from the Anchorage area and Kenai Peninsula of Alaska. Although adults referable to *P. doveri* have been reported from the Queen Charlotte Islands (Currie and Adler 1986), it is possible that this record actually applies to an undescribed species in the *P. doveri* complex. Rothfels (1979) recognized

3 cytological entities in North America: one from Alaska (to which the name *doveri* Sommerman applies); one from British Columbia; and one from Utah and Colorado. Unfortunately, specific locality information was not provided. Whether the Queen Charlotte Islands population conforms to typical *P. doveri*, or in fact belongs to the British Columbian cytotype, requires further study. But given the markedly southern distribution of *P. doveri* s. str. in Alaska, it seems possible that this species is more widely distributed along the Alaskan panhandle. The chromosomes of *P. doveri* were described (under the name *P. hirtipes* E) by Basrur (1962).

magnum species group

58. *Prosimulium dicum* Dyar and Shannon, 1927 Cordilleran

Distribution: Alaskan panhandle south to California, east to Alberta and New Mexico.

Biological information: The immature stages of *P. dicum* occur in rapidly flowing, medium- to large-sized streams. Adults from the Alaskan panhandle and north-coastal British Columbia are on the wing from early June to early August (Dyar and Shannon 1927; Currie and Adler 1986). Overwintering is in the egg stage. Females are equipped with markedly developed biting mouthparts, but host records are lacking. Large mammals are probable hosts (Currie and Adler 1986).

Taxonomic notes: The record of *P. dicum* (Type locality: Hoodspout, Washington) from Alaska is based on a collection of 9 paratypical females from Ketchikan (Dyar and Shannon 1927; Stone 1952). Although Peterson (1970) considered this to be a questionable record, the occurrence of *P. dicum* in north-coastal British Columbia and the Queen Charlotte Islands (Currie and Adler 1986) suggests that it may also occur on the Alaskan panhandle.

Tribe Simuliini Newman, 1921

Genus *Cnephia* Enderlein, 1921

59. *Cnephia eremites* Shewell, 1952 Holarctic?

Distribution: Alaska and Victoria Island, east to Southampton Island; Eastern Siberia to Russian Far East?

Biological information: Little is known about the biology of this infrequently-collected species. The immature stages have been collected from lake outlets and higher-order streams in northern Alaska (Hershey et al. 1995). Shewell (1952) found large numbers in the outflow of a large, shallow lake on Southampton Island. Pupae cluster so closely together that their cocoons appear matted together (Shewell 1952). Depending on location adults may emerge from June to August. Females of *C. eremites* are autogenous with reduced mouthparts (Davies and Peterson 1956; Davies and Györkös 1990). Shewell (1957) considered *C. eremites* to be an arctic-adapted species.

Taxonomic notes: *Cnephia eremites* (Type locality: Coral Harbour, Southampton Island, Northwest Territories) is distributed at high latitudes in North America. This species probably also occurs in the Yukon, but suitable streams in the northern part of the Territory remain inadequately surveyed. Published illustrations of typical *C. arborescens* Rubtsov from Taimyr (Rubtsov 1971a) and Chukotka (Bodrova 1977) agree in all respects to *C. eremites*. It seems almost certain that the 2 species are conspecific. The chromosomes of *C. eremites* were described by Procnier (1982b).

Genus *Metacnephia* Crosskey, 1969

60. *Metacnephia borealis* (Malloch, 1919) Nearctic-West Beringian

arctocanadensis Yankovsky, 1996 unjustified replacement name.

Distribution: Banks Island and the Mackenzie River Delta east to Baffin Island and Labrador; Russian Far East.

Biological information: Virtually nothing is known about the biology of this arctic-adapted species. Davies (1989) reported that one in 1319 specimens collected from Baker Lake, Northwest Territories, were gynandromorphs. Females have slightly developed mouthparts and are incapable of piercing the skin.

Taxonomic notes: Although there are no records of *M. borealis* (Type locality: Woolaston Peninsula, Victoria Island) from Alaska or the Yukon Territory, suitable habitats (i.e. large-sized northern streams and rivers) have not been adequately surveyed. Populations identified as *M. tredecimata* (Edwards, 1920) (Type Country: England) from the Far East almost certainly belong to *M. borealis* as judged by the form of the pupal gill (cf. Bodrova 1980, fig. 2b). The chromosomes of *M. borealis* and *M. tredecimata* have been described by Procnier (1982a). Yankovsky (1996) wrongly considered *Metacnephia borealis* (Malloch, 1919) to be a junior homonym of *Prosimulium boreale* (Zetterstedt, 1842) [= *P. ferrugineum* (Wahlberg, 1884)], giving the replacement name *M. arctocanadensis* to the

former species. No modern specialist considers the 2 species to be congeneric, and therefore the replacement name for *M. borealis* Malloch is unjustified.

Genus *Stegopterna* Enderlein, 1930

61. *Stegopterna permutata* (Dyar and Shannon, 1927) Cordilleran

Distribution: Alaska south to California.

Biological information: There is no information about the biology of this species in northwestern North America. In British Columbia, *St. permutata* occurs in small, shallow, often temporary streams, such as roadside ditches. Larvae can be found attached to a variety of stony and trailing substrata; pupae are typically buried beneath the substrate and are difficult to find. There is one generation per year with overwintering in the egg stage. *St. permutata* is an early-season species, the period of adult emergence extending from March through June. Seasonality is dependent on elevation, latitude, and proximity to the Pacific Ocean. Adult females are anautogenous on mammals. They are attracted to humans and can be annoying due to their swarming about the head and probing the skin.

Taxonomic notes: There are 6 cytological forms in the *Stegopterna mutata* complex in North America: 2 eastern and 4 western (Basrur and Rothfels 1959; Madahar 1969). The name *S. mutata* Malloch, 1914 (Type locality: Glassboro, New Jersey) probably does not apply to any western population. Although the complex has not been studied cytologically in Alaska and the Yukon Territory, it seems likely that the name *S. permutata* Dyar and Shannon, 1927 (Type locality Prince Rupert, British Columbia), long considered a synonym of *St. mutata*, applies to populations from south-coastal Alaska. Cytologically scored material from Prince Rupert and environs (F.F. Hunter and P.H. Adler, pers. comm.) suggests that the name *permutata* applies to cytospecies "X" of Madahar (1969). Most northwestern records of this species (as *St. mutata*) are from south-coastal Alaska; the inland record from College, Alaska, might apply to this species (Stone 1952).

Genus *Simulium* Latreille, 1802

Subgenus *Byssodon* Enderlein, 1925

62. *Simulium maculatum* (Meigen, 1804) Palaeartic-East Beringian

Distribution: Western Alaska; Eurasia.

Biological information: Nothing is known about the biology of this species in North America. In the Palaeartic Region larvae and pupae develop in large rivers (Rubtsov 1956). Other aspects of the biology of *S. maculatum* are discussed by Yankovsky (1978). Females have been described as nefarious bloodsuckers of humans and livestock in the northern Palaeartic region. However, the presence of bifid claws suggests that females of *S. maculatum* may also blood-feed upon birds, as do females of the closely related Nearctic species *S. meridionale* Riley (the "turkey gnat").

Taxonomic notes: The name *S. meridionale* Riley, 1887 has long been applied to members of the genus-group taxon *Byssodon* Enderlein throughout the Nearctic Region. Although *Byssodon* has not been studied cytologically in North America, the extensive range and ecological diversity of its members is suggestive of a species complex (Stone and Snoddy 1969). There are only 3 records of "*S. meridionale*" from northwestern North America, all from the vicinity of the lower Yukon River in western Alaska (Stone 1952). The next closest Nearctic record is in north-central Alberta (Currie 1986), more than 2300 kilometres to the southeast. The apparently disjunct Alaskan population is almost certainly more closely related to populations of *maculatum* Meigen, 1804 (Type locality: Stolberg area?, Germany) from eastern Siberia than they are to typical *S. meridionale* (Long View, Mississippi). Similarly, none of the currently recognized synonyms of *S. meridionale* (viz. *occidentale* Townsend, 1891; *tamaulipense* Townsend, 1897; and *forbesi* Malloch, 1914) can reasonably be ascribed to this northwestern population on geographical grounds. Examination of adult females from Alaska indicates that they agree well with those of *S. maculatum* s. lat. as redescribed by Yankovsky (1978). Five nominal subspecies of *S. maculatum* are currently recognized from the Palaeartic Region (Crosskey 1988); however, differences among them are not sufficiently marked to assign a subspecific name to Alaskan populations. The type locality of *S. maculatum lenae* (Rubtsov, 1956) (Lena basin, Eastern Siberia) is much closer geographically to Alaska than that of any other nominal subspecies. The only other species of *S. (Byssodon)* from the eastern Palaeartic Region, *S. pseudonearcticum* Rubtsov, 1940, can be distinguished from *S. maculatum* based on differences in the female terminalia (Yankovsky 1978).

Subgenus *Eusimulium* Roubaud, 1906*aureum* species group63. *Simulium aureum* Fries, 1824 complex,
Cytospecies C

Northern Nearctic

Distribution: Alaska east to Newfoundland, south to Vancouver Island.*Biological information:* The immature stages of *S. aureum* C are found most often in the outflows of beaver ponds and small, sedge-lined ditches. Associated species include *S. baffinense*, *S. bracteatum*, *S. silvestre*, *S. vittatum* IS-7, *S. decorum*, *S. noelleri*, *S. rostratum*, *S. venustum* complex, and *S. tuberosum* FG. Published accounts about the biology of “*S. aureum*” in northwestern North America probably apply, in part, to Cytospecies C (cf. Sommerman et al. 1955). Adult females are anautogenous on birds.*Taxonomic notes:* This species exhibits a principally northern distribution in North America. The single record of *S. aureum* C from Vancouver Island [west of Courtnay, Forbidden Plateau, 5.vi.1991, D.C. Currie, ROME] represents a southern range extension of some 1850 km. Further collections from intervening areas are needed to determine whether or not this represents an isolated population. Cytological and distributional information is from Leonhardt (1985) and P.H. Adler (pers. comm.). See also Taxonomic notes for 30.64. *Simulium aureum* Fries, 1824 complex,
Cytospecies D

Northern Nearctic

Distribution: Western Northwest Territories east to Newfoundland.*Biological information:* Aspects of the biology of this species are probably similar to that described for other *aureum*-complex species (see 30 and 63).*Taxonomic notes:* The only northwestern record for Cytospecies D is Norman Wells, Northwest Territories (Leonhardt 1985).65. *Simulium bracteatum* Coquillett, 1898

Nearctic

Distribution: Alaska south to British Columbia, east to Quebec and Pennsylvania.*Biological information:* This member of the *S. aureum* species-group is found almost exclusively at the outflows of beaver ponds in northwestern North America. Larvae and pupae are most often found attached to trailing vegetation, in association with other outlet species: *S. aureum* C, *S. silvestre*, *S. baffinense*, *S. vittatum* IS-7, *S. rostratum*, *S. decorum*, and *S. noelleri*. Other aspects of the biology of *S. bracteatum* are probably similar to those described for other members of the *S. aureum* complex (see species accounts 30 and 63).*Taxonomic notes:* Crosskey (1988) suggested that the name *S. bracteatum* Coquillett, 1898 (Type locality: Cambridge, Massachusetts) applies to cytospecies A of the *S. aureum* complex. This interpretation is followed here. Cytological and distributional information is from Leonhardt (1985) and Adler and Kim (1986).*pusillum* species group66. *Simulium n. sp. near giganteum* (Rubtsov, 1940)

East Beringian

Distribution: Alaska.*Biological information:* The only specimen examined, an adult female, was collected from a subalpine meadow in the Alaska Range. Character states of the head (small eyes, non-biting mouthparts) suggest that this species is arctic-adapted. Little else can be inferred about its way of life.*Taxonomic notes:* This record is based on a single female swept from grass in east-central Alaska [Isabel Pass, Richardson Hwy. mi 206, 16.vii.1987, D.M. Wood, CNCI]. The exceptionally broad frons and details of the terminalia indicate that the specimen belongs to an undescribed species. Reports of “*S. furculatum*” from the vicinity of Summit Lake, Alaska—only a few kilometres south of Isabel Pass—probably refer to the same species (see Stone 1952; Sommerman et al. 1955). Sommerman et al. (1955) collected 2 reared adults, 4 pupae, and one larva from a 60 ft wide, 1.5 ft deep stream (probably Gulkana Creek, the outflow of Summit Lake). The pupal gill is described as having 8 filaments; 4 simple, 2 bifurcate. This differs from typical *S. furculatum* (Type locality: Churchill, Manitoba) in which the gill branches 2+3+3 (dorsal, lateral, ventral).67. *Simulium subpusillum* Rubtsov, 1940

Holarctic

Distribution: Alaska to Hudson Bay; northern Eurasia.

Biological information: The only Nearctic records for this species—as *Simulium* (*Schoenbaueria*) sp.—are from tundra streams on the North Slope of Alaska (Hershey et al. 1995). The immature stages were collected from first-order and higher-order streams. Nothing else is known about the biology of this species in northwestern North America. In Chukotka, larvae and pupae of *S. subpusillum* were collected from tundra streams that varied from 0.5–2.5 m in width, and 10–30 cm in depth (Bodrova 1977). There is one generation per year with pupation beginning in July. Adults are on the wing at the beginning of August (Bodrova 1977). Females are described as bloodsuckers but specific host records are lacking (Rubtsov 1956). Mammalophily is assumed based on the simple tarsal claws of females.

Taxonomic notes: This is the first record of *S. subpusillum* (Type area: Luga Region, western Russia) from North America [Alaska, North Slope Borough, outlet E-1 Lake, Toolik Field Station, 4.vii.1992, R.W. Merritt, CUCC].

vernum species group

68. *Simulium dendrofilum* (Patrusheva, 1962)

Palaeartic-East Beringian

Distribution: Alaska; western Siberia to Chukotka.

Biological information: The only North American record for this species is from the outflow of an arctic lake in northern Alaska (see Hershey et al. 1995 for description of site). This is similar to the habitat described for *S. dendrofilum* in the Russian Far East (Bodrova 1977). Trailing sedges are reported to be the preferred substrate for larvae. There is one generation per year with emergence completed by early August (Bodrova 1977). The slightly developed mouthparts of the female (dissected from the pupa) suggests that this species is incapable of taking blood.

Taxonomic notes: *S. dendrofilum* (Patrusheva, 1962) (Type locality: Tomsk, Siberia) is tentatively recorded for the first time in North America based on a paratype adult female and a pupal exuviae [Alaska, North Slope Borough, outlet E-1 Lake, Toolik Field Station, 25.vi.1993, J. Wheeler, CNCI]. The branching pattern of the gill, 2+3+3 (dorsal, lateral, ventral), is similar to that of certain species in the *S. vernum* and *S. subpusillum* groups. However, the markedly elongate dorsal and ventral primary trunks of *S. dendrofilum* distinguish that species from all others in North America. *S. dendrofilum* has been referred to *Eusimulium*, *Montisimulium* and *Schoenbaueria* by previous authors (Patrusheva 1962; Bodrova 1977; Crosskey 1988). Correct placement must await discovery of the male. *S. dendrofilum* is assigned to the *vernum* group of subgenus *Eusimulium* for the purposes of the present study.

69. *Simulium pugetense* (Dyar and Shannon, 1927) complex, Cordilleran
Cytospecies B

Distribution: Alaska south to Vancouver Island.

Biological information: The presence of *S. pugetense* B in northwestern North America is based on collections from 4 Alaskan sites (Allison and Shields 1989). Larvae appear in April, with pupation occurring from May until August, depending on latitude. According to Allison and Shields (1989) development of Cytospecies B is about one month behind that of Cytospecies A from the same vicinity. There may be 2 generations per year at some sites. Like other members of the *S. pugetense* complex, females of Cytospecies B are assumed to be anautogenous on birds.

Taxonomic notes: Distributional and cytological information from Hunter and Connolly (1986) and Allison and Shields (1989). See also Taxonomic notes for 37.

70. *Simulium pugetense* (Dyar and Shannon, 1927) complex, Cordilleran
Cytospecies E

Distribution: Alaskan panhandle to south-coastal British Columbia.

Biological information: This little-collected species is known only from the west coast of Canada and the Alaskan panhandle. The single Alaskan record is based on a small collection of larvae from Revillagigedo Island [Spike Creek, 13.xi.1996, M. Wipfli, CUCC]. The immature stages occur in small-sized (0.25–5 m wide) woodland streams. Eggs evidently hatch from late fall to early spring, with larvae present from November until July. The timing and duration of development is probably influenced by proximity of breeding sites to the ocean. Commonly associated species included *P. formosum*, *P. esselbaughi*, *St. permutata*, *S. nebulosum*, *S. aureum* B, *S. hunteri*, and *S. venustum* complex. Females of *S. pugetense* E are assumed to be ornithophilic.

Taxonomic notes: Distributional and cytological information is from Hunter and Connolly (1986) and P.H. Adler (pers. comm.). See also Taxonomic notes for 37.

Subgenus *Hellichiella* Rivosecchi and Cardinali, 197571. *Simulium nebulosum* Currie and Adler, 1986 Cordilleran

Distribution: Alaskan panhandle south to California.

Biological information: The immature stages of *S. nebulosum* occur abundantly in small-sized (0.25–4 m wide) woodland streams. In breeding sites near the Pacific Ocean, larvae are present from mid November until mid July suggesting multiple generations. Associated species include *P. formosum*, *Twinnia nova*, *S. pugetense* E, *S. caledonense*, *S. craigi*, *S. aureum* B, *S. hunteri* and *S. tuberosum* FG. The only northwestern record of *S. nebulosum* is a single immature larva from the Alaskan Panhandle [Revillagigedo Island, Spike Creek, 13.xi.1996, M. Wipfli, CUCC]. The bifid claws and well-developed mouthparts of females suggest that this species is ornithophilic.

Taxonomic notes: The type locality of *S. nebulosum* is Kaslo, British Columbia.

72. *Simulium (Hellichiella)* sp. East Beringian
gouldingi of authors, not Stone, 1952 (misidentification)

Distribution: Alaska.

Biological information: The only known locality for this species is a small, warm, sluggishly flowing, lake outflow near Fairbanks, Alaska (Sommerman et al. 1955). Maturing larvae were collected in late May, and pupae in early June.

Taxonomic notes: *S. gouldingi* Stone (Type locality: Wilkes Barre, Pennsylvania) was reported from Alaska on the basis of 8 larvae and 3 paratypical pupae from the vicinity of Fairbanks (Stone 1952; Sommerman et al. 1955). Re-examination of the pupae in concert with the illustration of the larval head capsule by Sommerman (1953) reveals that they belong to an undescribed species in the subgenus *Hellichiella* (P.H. Adler, pers. comm.). Sommerman's (1953) illustration presumably was based on larvae collected from the same locality as the pupae (cf. Sommerman et al. 1955). Larvae evidently are extremely small (3.5 mm in length). It is doubtful that the name *gouldingi* Stone applies to any black fly from western North America.

Subgenus *Psilozia* Enderlein, 193673. *Simulium vittatum* Zetterstedt, 1838 complex, Nearctic
Cytospecies III-L-1

Distribution: Alaska east to Quebec, south to California and Georgia.

Biological information: Aspects of the biology of Cytospecies III-L-1 in northwestern North America are probably similar to that described for Cytospecies IS-7 (see 40). The only northwestern record [Gunsight Mt., Alaska] consisted of larvae collected in sympatry with Cytospecies IS-7 (Rothfels and Featherston 1981). Biological information elsewhere in North America is provided by Adler and Kim (1984) and Adler (1986).

Taxonomic notes: Cytological and distributional information is from Rothfels and Featherston (1981) and Adler and Kim (1986). The single northwestern record of Cytospecies III-L-1 is more than 2000 km from the next closest population in Uranium City, Saskatchewan (Ciborowski and Adler 1990). See also Taxonomic notes for Cytospecies IS-7 (40).

Subgenus *Simulium* s. str.*malyschevi* species group74. *Simulium arcticum* Malloch, 1914 complex, Cordilleran
Cytospecies III-st

Distribution: Alaska south to west-central Alberta.

Biological information: Published records (Shields and Procnier 1982) indicate that *S. arcticum* III-st is an early developing species, with mature larvae present in late April. Larvae and pupae are typically found attached to trailing vegetation in medium-sized (5–15 m) streams. Although *S. arcticum* III-st is reported to be univoltine (Shields and Procnier 1982), the presence of larvae in late July suggests that populations may be multivoltine at some sites. Associated species include *S. vittatum* IS-7, *S. malyschevi*, *S. tuberosum* FG, and *S. venustum* complex. Adult females, like those of other members of the *S. arcticum* complex, are assumed to be blood-feeders upon mammals.

Taxonomic notes: Cytological and distributional information is from Shields and Procnier (1982) and Procnier (1984). Northwestern populations of *S. arcticum* III-st have been collected only from Anchorage and environs in southern Alaska. See also Taxonomic notes for entry 41.

75. *Simulium arcticum* Malloch, 1914 complex, Western Nearctic
Cytospecies III-1

Distribution: Alaska east to Manitoba, south to west-central Alberta.

Biological information: This multivoltine species develops approximately one month later than sympatric populations of *S. arcticum* III-st (Shields and Procnunier 1982). Mature larvae are present in suitable streams from late May to late September. Little else is known about the biology of this species in northwestern North America. Adult females are assumed to be anautogenous on mammals.

Taxonomic notes: Cytological and distributional information is from Shields and Procnunier (1982) and Procnunier (1984). *S. arcticum* III-1 is more widely distributed in Alaska than is *S. arcticum* III-st, its range extended northward at least to the vicinity of Fairbanks (see also Taxonomic notes for 41 and 74).

slossonae species group

76. *Simulium rugglesi* Nicholson and Mickel, 1950 Nearctic

Distribution: Alaska east to Labrador and Newfoundland, south to Utah, Minnesota and Vermont.

Biological information: There is no information about the biology of *S. rugglesi* in northwestern North America. The immature stages live in large-sized streams and rivers in Alberta and Saskatchewan (Fredeen 1981; Currie 1986). Overwintering is in the egg stage, with one generation per year indicated for most regions (Anderson and Dicke 1960; Davies et al. 1962; Currie 1986). Larvae have been collected in September in Saskatchewan, suggesting that there may be a second generation in that province (Fredeen 1981). Females of *S. rugglesi* blood-feed primarily upon waterfowl and occasionally on other birds. They are vectors of the blood parasite *Leucocytozoon simondi* (Shewell 1955).

Taxonomic notes: The only northwestern record of *S. rugglesi* Nicholson and Mickel, 1950 (Type locality: Todd County, Minnesota) is from mi 139 on the Steese Hwy., Alaska (Stone 1952, 1965; Sommerman et al. 1955). I have not seen northwestern specimens, nor have I found further references to this species in Alaska or the Yukon Territory. If authentic, the single record indicates that *S. rugglesi* is a rare species.

venustum species group

77. *Simulium truncatum* (Lundström, 1911) Holarctic

Distribution: Alaska east to Newfoundland, south to British Columbia and New York; Eurasia.

Biological information: The single northwestern record of this species is from northern Alaska, where larvae were collected from a first-order tundra stream and a lake outlet (Hershey et al. 1995). The occurrence of *S. truncatum* at a lake outlet is consistent with observations elsewhere in North America (Hunter 1990). *S. truncatum* is univoltine with overwintering in the egg stage throughout its range. Adult females, along with those of the morphologically similar *S. venustum* complex, are among the most noxious bloodsucking pests of humans and other mammals in northern North America. Aspects of the biology of *S. truncatum* are similar to that described for members of the *S. venustum* complex (see 55).

Taxonomic notes: The name *S. truncatum* Lundström (Type area: Finnish Lapland) applies validly to sibling "EFG/C" of the *S. venustum* complex (Rothfels et al. 1978; Rothfels 1979). *S. truncatum* has only recently been recognized in North America, where it has long been confused with *S. venustum* Say. The occurrence of *S. truncatum* in northwestern North America is based on cytologically determined material from the North Slope of Alaska (Hershey et al. 1995). See also Taxonomic notes for 55.

Composition of the Northwestern Black-Fly Fauna

Seventy-six species of black flies are known from northwestern North America, of which 55 are formally described and named. (Note that 77 entries appear in the Annotated List because of uncertainty about which cytospecies of *S. aureum* occurs in the Yukon; cf. entry 30.) The remaining 21 species are either undescribed morphospecies (those distinguishable on the basis of external structural characters), or are cytologically recognized sibling species. The number of species from northwestern North America represents about 25 percent of the approximately 265 species known from North America. Although the geographical area is large, the northwestern fauna is surprisingly rich compared with other well-surveyed regions in temperate North America, for example Alberta (63 species) and

TABLE 2. Number of species in northwestern genera of black flies, and the percentage of the North American fauna represented by these species.

| Genus | No. of species | Percentage of North American fauna |
|-----------------------------|----------------|------------------------------------|
| Parasimuliinae | | |
| <i>Parasimulium</i> s. lat. | 0 | 0 |
| Simuliinae | | |
| Prosimuliini | | |
| <i>Gymnopais</i> | 5 | 100 |
| <i>Helodon</i> s. lat. | 10 | 59 |
| <i>Prosimulium</i> | 9 | 23 |
| <i>Twinnia</i> | 0 | 0 |
| Simuliini | | |
| <i>Cnephia</i> | 1 | 25 |
| <i>Ectemnia</i> | 0 | 0 |
| <i>Gigantodax</i> | 0 | 0 |
| <i>Greniera</i> | 1 | 20 |
| <i>Mayacnephia</i> | 1 | 17 |
| <i>Metacnephia</i> | 5 | 63 |
| <i>Stegopterna</i> | 3 | 43 |
| <i>Simulium</i> s. lat. | 41 | 25 |
| Total | 76 | |

Ontario (63 species). In contrast, the northwestern assemblage is depauperate relative to the 55–60 species known from a single county (Mono) in California (Adler in Hershey et al. 1995). More species will be recognized from the northwest as additional material is studied chromosomally. It should also be noted that only areas accessible by road have been adequately surveyed to date. Further collections from the far north and westernmost part of Alaska should yield additional records. Similarly, virtually no collections exist from the early spring. Early emerging simuliids (e.g. *Stegopterna*, *Greniera*, *S. (Hellichella)*, and *S. vernum*-group) probably are under-represented in the present study.

The 76 northwestern species are distributed among 9 of the 13 genera recognized in North America (Table 2). This number is comparable to the 11 genera recorded from the Canadian prairie provinces (Currie 1986; Fredeen 1985; Crosskey 1994) and the 8 genera recorded from the northeastern United States (Cupp and Gordon 1983). Only *Parasimulium* Malloch (south-coastal British Columbia, Washington, Oregon, and California), *Twinnia* Stone and Jamnback (British Columbia and Alberta, south to California), *Ectemnia* Enderlein (Alberta to Quebec, south to Georgia) and *Gigantodax* (Arizona and New Mexico) are absent from northwestern North America. In contrast, the region is especially rich in species of *Gymnopais*, *Helodon*, and *Metacnephia*, with 64% of all Nearctic species referable to those genera.

As in other regions of North America, the northwestern fauna is dominated numerically by species of *Simulium* s. lat., which constitute 53% of all black flies known from the region (Table 2). This figure is low compared to the North American fauna, in which *Simulium* s. lat. constitutes approximately 60% of all species. The proportionally smaller *Simulium* component can be attributed to high species richness in *Metacnephia* and the prosimuliine genera.

Five of 7 North American subgenera of *Simulium* are present in the northwest, with only *Hemicnetha* Enderlein² and *Psilopelmia* Enderlein not represented (Table 3). These

²*Hemicnetha* Enderlein, 1934, as here defined subsumes the genus-group taxa *Shewellomyia* Peterson, 1975, and *Hearlea* Vargas, Martínez Palacios and Díaz Nájera, 1946.

TABLE 3. Number of species among northwestern subgenera of *Simulium* s. lat., and the percentage of the North American fauna represented by these species.

| Subgenus | No. of species | Percentage of North American fauna |
|-------------------------|----------------|------------------------------------|
| <i>Byssodon</i> | 1 | 50 |
| <i>Eusimulium</i> | 17 | 43 |
| <i>Hellichella</i> | 2 | 17 |
| <i>Hemicnetha</i> | 0 | 0 |
| <i>Psilopelmia</i> | 0 | 0 |
| <i>Psilozia</i> | 2 | 33 |
| <i>Simulium</i> s. str. | 19 | 27 |
| Total | 41 | |

2 subgenera attain their greatest richness in the Neotropical Region, with species reaching their northernmost limit in southern Canada. Nearly all the species of *Simulium* s. lat. (87%) are distributed among 2 subgenera: *Eusimulium* (15 species) and *Simulium* s. str. (19 species). The proportion of *Eusimulium* to *Simulium* s. str. is higher (0.79) than found in most other regions in North America, which taken as a whole is approximately 0.55. In Alberta the proportion is 0.67, whereas in Pennsylvania it is only 0.40. In general, the incidence of *Eusimulium* increases from east to west across the continent.

Nearctic versus Holarctic Species

Old World and New World simuliid specialists have traditionally worked in isolation from each other. This is true particularly of Russian and North American workers, who struggled with both language and political barriers during a period when most nominal taxa were described from those regions. But with translations of seminal Russian works now readily available (e.g. Rubtsov 1956), and with the break-up of the former Soviet Union, the opportunity exists to re-examine relationships between the Old World and New World faunas.

In the most recent checklist of world species (Crosskey 1988), only 20% of northwestern species are recognized as Holarctic in the traditional sense (i.e. species occurring in both the Palaearctic and Nearctic Regions regardless of distributional pattern within each region). Re-examination of the available literature on a species-by-species basis, and recent acquisitions of cytologically fixed material from northern Europe and the Russian Far East, indicate that the Holarctic component could be as high as 29 species, representing 38% of the northwestern fauna (see annotated list for summary of evidence).

Unfortunately, many nominal species from the eastern Palaearctic are inadequately described, or have been re-described from dubiously associated material. Zwick (1995) remarks on some problems associated with misassociated names. Furthermore, the practice of describing material from only the immature stages, or from pharate adults dissected from pupal exuviae, renders the identity of such taxa difficult or impossible to evaluate. Even examination of type specimens, if designated, would shed little light on the question of conspecificity between Palaearctic and Nearctic species. The problem is compounded because many nominal species consist of 2 or more isomorphic sibling species. Type localities must be revisited for collections of all life-history stages, as well as for larvae suitable for chromosomal study. This approach has already proved successful for resolution of long-standing species-identity problems in the *Simulium tuberosum* complex (Adler and

Kuusela 1994). But given present progress, it will be decades before outstanding species-identity problems can be satisfactorily resolved. Further descriptions based on inadequate material should be discouraged.

Geographical Patterns of Northwestern Black Flies

Presented below are descriptions of 11 particular patterns exhibited by northwestern black flies. In certain instances, an undescribed species may be known from only one or several northwestern localities (*Simulium* n. sp. near *giganteum* (66), *S. (Hellichiella)* sp. (72)). In the absence of evidence to the contrary, such species are assigned to the "East Beringian" category as described below. It is possible that these little-known species may eventually be found to be more widely distributed as the north becomes more completely surveyed. Not all species could be assigned confidently to a particular pattern because of collecting gaps and species-identity problems in the eastern Palaearctic Region. Table 1 lists species assigned to each distributional category, with a question mark following provisional designations. Because there are few reliable records of northwestern species in the Palaearctic Region, only examples of Nearctic distributional patterns are illustrated (Figs. 1–6).

Holarctic. This category includes species that are widespread in both the Nearctic and Palaearctic regions. Most of the species assigned here have a circumpolar or circumboreal distribution (e.g. *P. ursinum* (21), *S. rostratum* (53)); but also included are species whose distributions are extended well beyond the ice-free margins of both East Beringia and West Beringia (e.g. *S. malyschevi* (44), *S. transiens* (49)). Twelve species are assigned here, 9 of which belong to *Simulium* s. lat.: *Eusimulium* (67), *Hellichiella* (39), and *Simulium* s. str. (7 species: 43, 44, 48, 49, 51, 53, 77). Holarctic species comprise 16% of northwestern black flies.

Palaearctic-East Beringian. Included here are species that are widely distributed in the Palaearctic Region, but occur in the Nearctic Region only in Beringia. A total of 9 species in 5 genera belong to this category: *Helodon* (7, 13), *Prosimulium* (20), *Stegopterna* (28), *Metacnephia* (24, 26), and *Simulium* s. lat. (3 species: 54, 62, 69). Palaearctic-East Beringian species account for 12% of northwestern black flies. The Nearctic distribution of Palaearctic-East Beringian species is exemplified by Fig. 6 below.

Palaearctic-Cordilleran. Species assigned here are widely distributed in the Palaearctic Region, but occur in the Nearctic Region only in the Cordillera. This category differs from the Palaearctic-East Beringian pattern in that the southern range is extended southward beyond the margin of Wisconsinan ice. As such the Nearctic distribution of Palaearctic-Cordilleran species is similar to that described for Cordilleran species (Fig. 5 below). Four species are included in the Palaearctic-Cordilleran category, representing 5% of the northwestern simuliid fauna: *S. bicornis* (34), *S. decolletum* (36), *S. silvestre* (38), and *S. vulgare* (52).

Nearctic-West Beringian. Species thus classified occur beyond the ice-free margin of Beringia in the Nearctic Region, but occur only in Beringia in the Palaearctic Region. Included here are 4% of northwestern black flies, as follows: *H. clavatus* (8), *M. borealis* (60), and *S. nigricoxum* (45).

Holarctic excluding Beringia. The distributional area for this category includes only glaciated territory in both the Old World and the New World. One species, *S. furculatum*

(33), is tentatively assigned to this category. The occurrence of *S. furculatum* in the Palaearctic Region has not been firmly established (see Taxonomic notes for entry 33 in annotated list).

Nearctic. (Fig. 1) This category includes species that are widely distributed in North America. Most are transcontinental, with the southern part of their ranges extended beyond the southern limit of Wisconsinan ice. Eight species are assigned here, all belonging to *Simulium* s. lat.: *Eusimulium* (2 species: 37, 65), *Psilozia* (2 species: 40, 73) and *Simulium* s. str. (4 species: 47, 50, 55, 76). This category includes some of the most common and widely recognized black flies in North America, including the notorious bloodsucking pest of humans, *Simulium venustum*. Together, species exhibiting a Nearctic distribution account for 11% of the northwestern simuliid fauna.

Northern Nearctic. (Fig. 2) Included here are species distributed widely across northern North America. Most are transcontinental, with their eastern range only in glaciated North America. Seven species belong in this category, representing 9% of the northwestern simuliid fauna: *Gymnopais* (4), *Helodon* (*Parahelodon*) (14), *Greniera* (22), *Metacnephia* (25), and *Simulium* (*Eusimulium*) (3 species: 35, 63, 64).

Nearctic Disjunct. (Fig. 3) Species so designated exhibit a disjunct east/west distribution. The only simuliid in this category is *Helodon* (*Distosimulium*) *pleuralis* (6). Western populations are distributed from Alaska and the Yukon south to Idaho and Montana; eastern populations are confined to eastern Quebec, Labrador, and Newfoundland.

Western Nearctic. (Fig. 4) This category includes species that occur west of Hudson Bay, but does not include those with a strictly Cordilleran distribution (see below). Only one species, *S. arcticum* Cytospecies IIL-1, is assigned here. Five other species exhibit a similar distributional pattern in the Nearctic Region, but their ranges also extend into the Palaearctic Region: *S. malyschevi* (44), *S. nigricoxum* (45), *S. noelleri* (48), *S. transiens* (49) and *S. subpusillum* (67).

Cordilleran. (Fig. 5) This category includes species that exhibit a narrowly western range, from the Rocky Mountains west to the Pacific Ocean. Twenty-five species belong here as follows: *Gymnopais* (1), *Helodon* s. str. (5 species: 9–12, 56), *Prosimulium* (7 species: 15–19, 57, 58), *Mayacnephia* (23), *Metacnephia* (27), *Stegopterna* (61), *Simulium* (*Eusimulium*) (5 species: 31, 32, 69, 70, 71), and *Simulium* s. str. (4 species: 41, 42, 46, 74). More than half of the species assigned to this category are prosimuliines. Collectively, the 25 species represent 33% of the northwestern simuliid fauna.

East Beringian. (Fig. 6) Included here are species that are known only from Beringia, and thus can be termed Beringian endemics. In total, 5 species are assigned to the East Beringian category, representing approximately 7% of the northwestern simuliid fauna: *G. dichopticus* (2), *G. fimbriatus* (3), *G. holocticus* (5), *Simulium* sp. near *giganteum* (66), and *Simulium* (*Hellichella*) sp. (72).

The Cordilleran category is by far the most common distributional pattern exhibited by northwestern simuliids, with nearly a third of the species thus classified. This underscores the high species richness and endemism typically associated with mountain faunas. Adler (in Hershey et al. 1995), for example, found between 55 and 60 species of black flies occurring in the mosaic of stream habitats in Mono County, California. Mountains have a

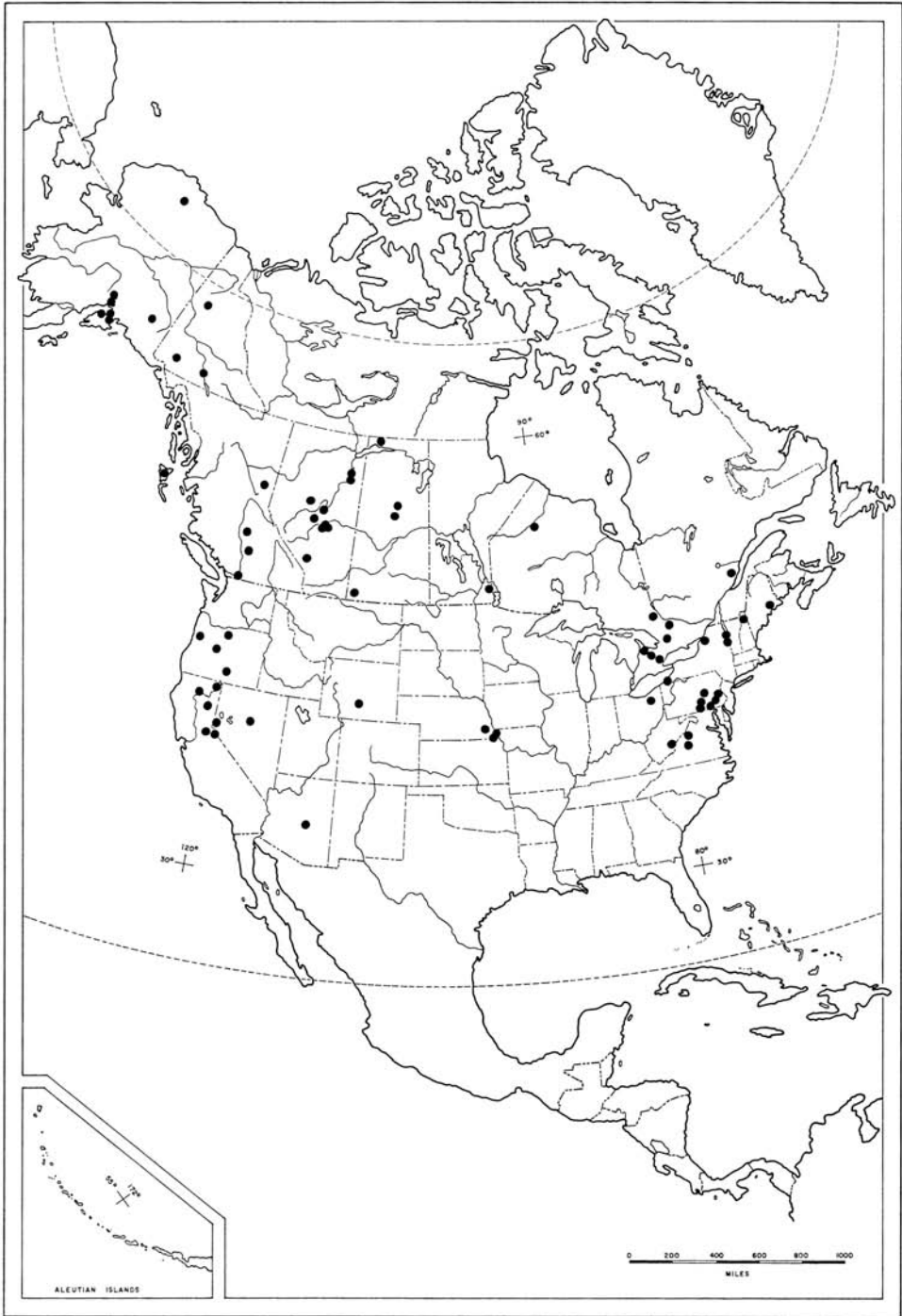


FIG. 1. Nearctic distributional pattern as exemplified by *Simulium vittatum* Zetterstedt (40).

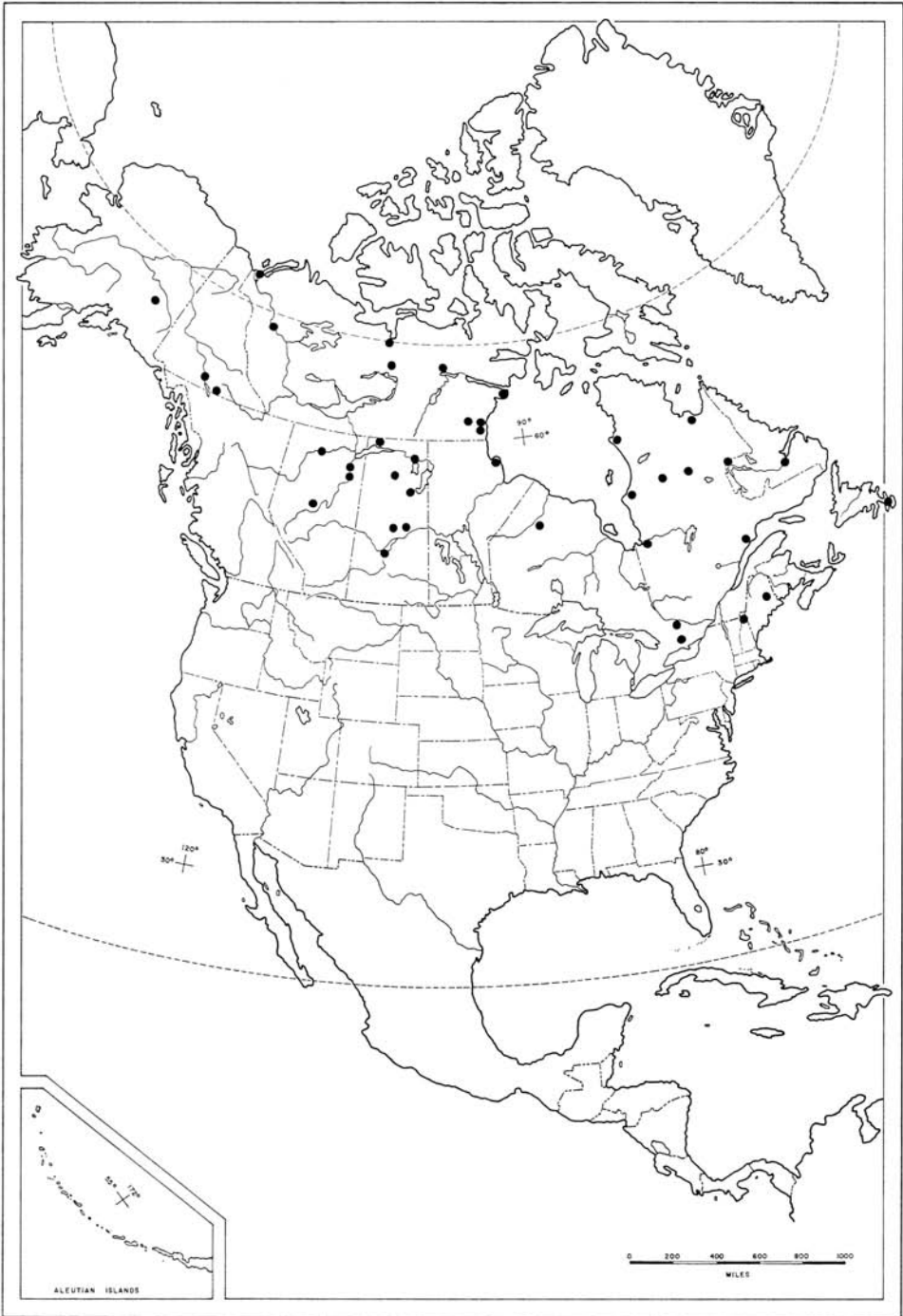


FIG. 2. Northern Nearctic distributional pattern as exemplified by *Simulium furculatum* (Shewell) (33).

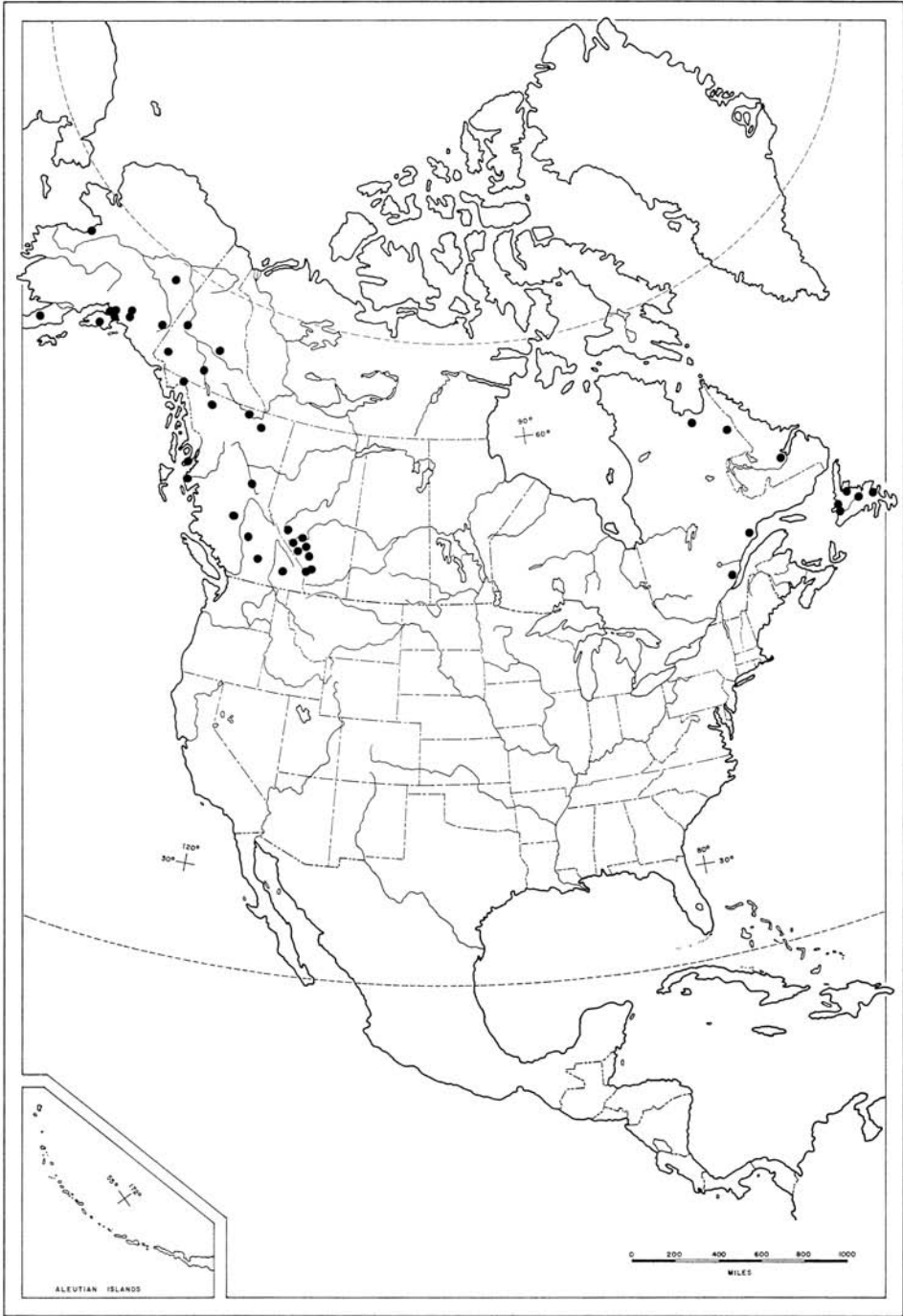


FIG. 3. Nearctic Disjunct distributional pattern as exemplified by *Helodon pleuralis* (Malloch) (6).

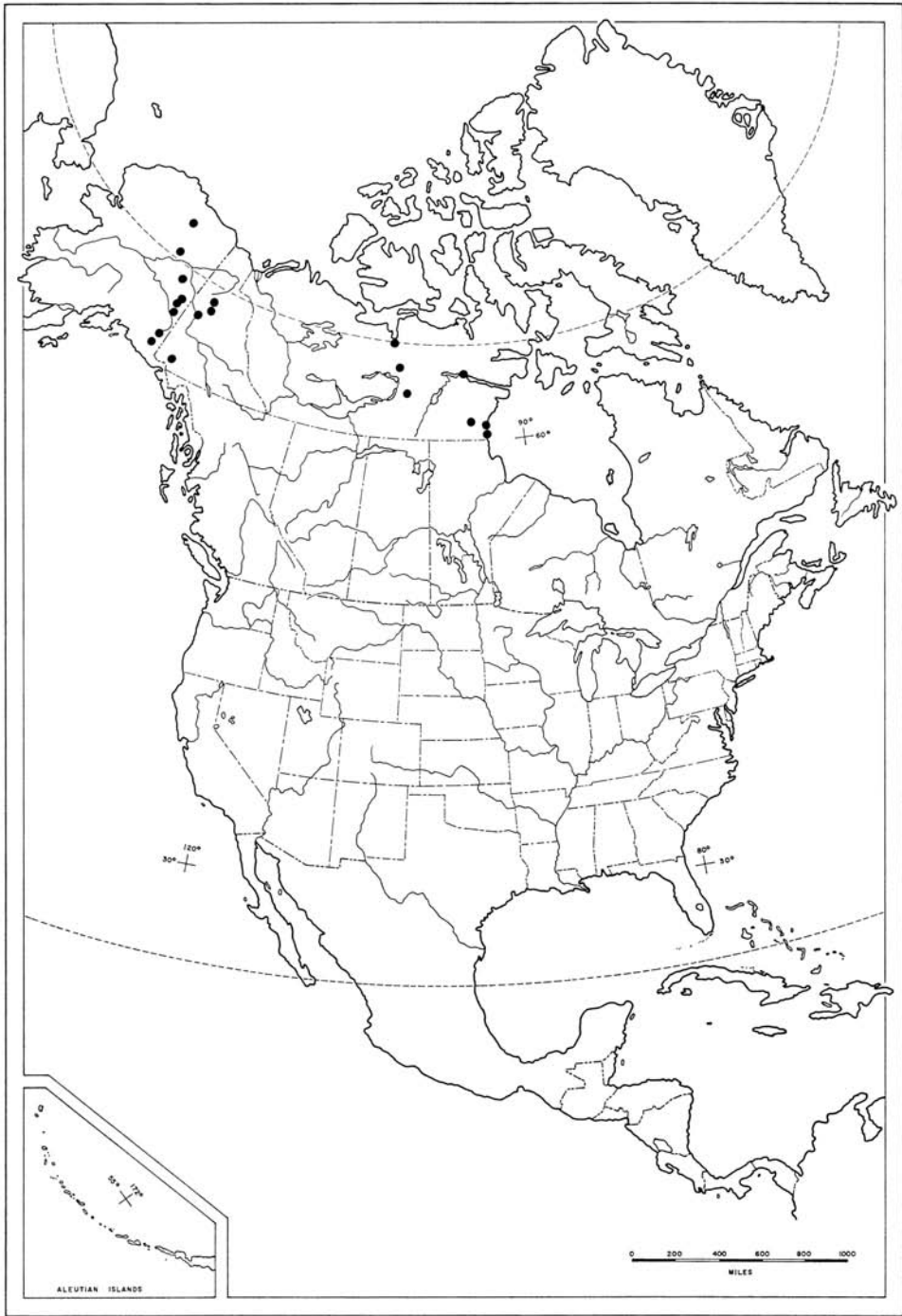


FIG. 4. Western Nearctic distributional pattern as exemplified by *Simulium nigricoxum* Stone (45).

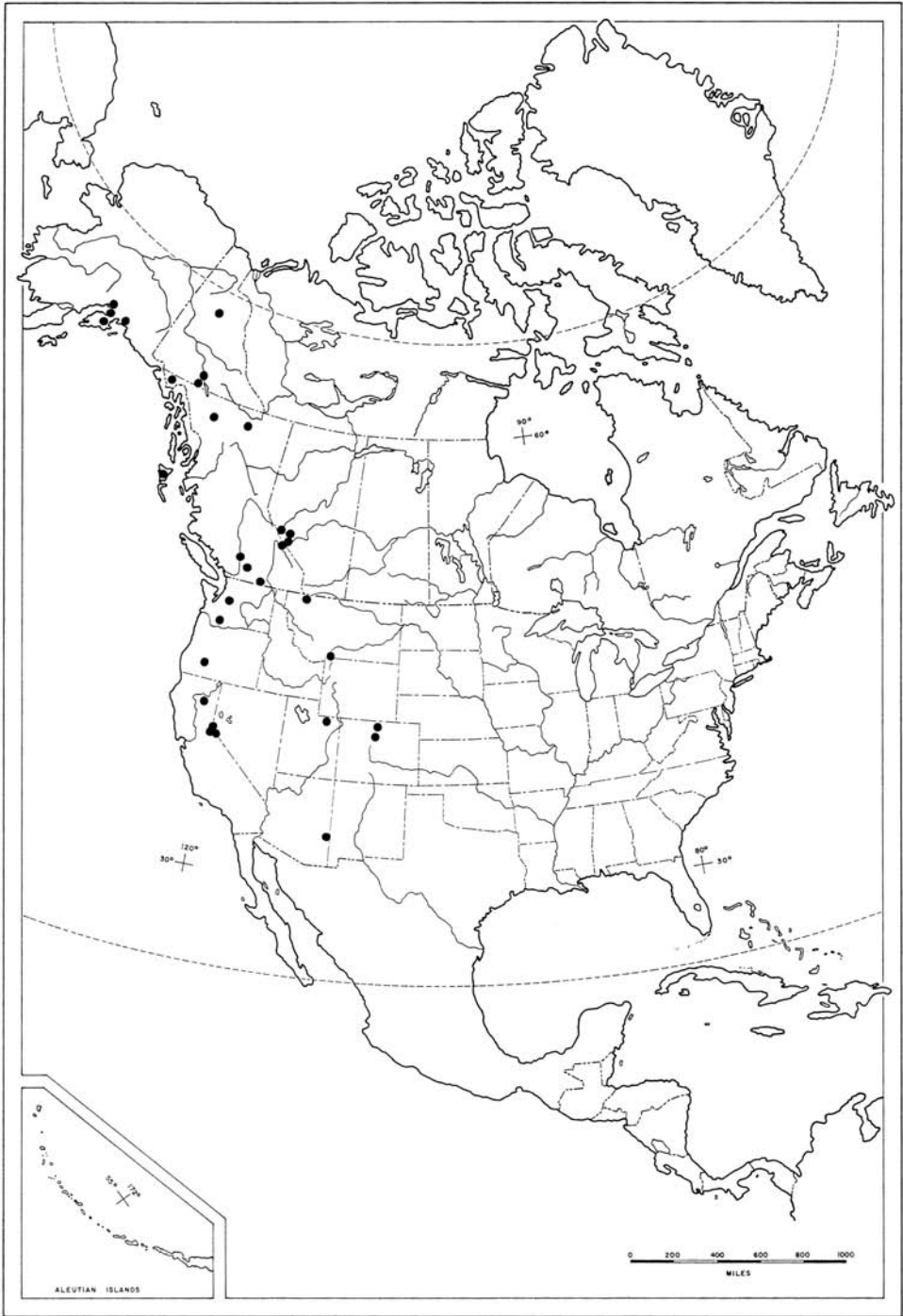


FIG. 5. Cordilleran distributional pattern as exemplified by *Prosimulium travisi* Stone (19).



FIG. 6. East Beringian distributional pattern as exemplified by *Gymnopsis holopticus* Stone (5).

greater heterogeneity of stream habitats than non-mountainous terrain, which in turn is positively correlated with species richness in black flies.

Species with ranges extending into the Palaearctic Region (including the Holarctic, Palaearctic-East Beringian, Palaearctic-Cordilleran, Nearctic-West Beringian, and Holarctic excluding Beringia categories) account for nearly 40% of the northwestern fauna. The association between the Old World and New World faunas is clearly much closer in northwestern North America than previously supposed. Interestingly, no species were found to have an amphiberian distribution (i.e. occurring in both East and West Beringia, but not in glaciated areas); however, 7% were found to occur only in East Beringia. Among Beringian endemics, the 3 species of *Gymnopsais* are closely associated with mountains in which they live and presumably evolved in situ. Being flightless or capable of flight for only short distances, they were evidently unable to colonize the mountains of West Beringia. Whether the 2 undescribed species of East Beringian *Simulium* are truly endemic needs further study.

The Palaearctic-Cordilleran category warrants special mention. This distributional pattern is similar to the Palaearctic-East Beringian category except that the southern range is extended well beyond the margin of Wisconsinan ice in the Nearctic Region. Given the high vagility of most black flies it is perhaps not surprising that certain species could disperse south following deglaciation. Further, high elevation streams in the southern Cordillera are ecologically similar to those in East Beringia, and in fact have many lotic taxa in common. Three of the 4 species exhibiting a Palaearctic-Cordilleran distribution are ornithophilic, raising the possibility that the southern extension of their range may have been aided by transportation on birds.

The relatively small number of species in the Northern Nearctic category (7) does not reflect accurately the relative contribution of northern-adapted species to the fauna. Among the 12 species classified as Holarctic, at least 7 exhibit a Northern Nearctic distribution in the New World. Including species in the Palaearctic-East Beringian, Nearctic-West Beringian, and East Beringian categories, nearly half of the northwestern simuliid fauna can be characterized as northern or arctic-adapted. In contrast, only 9 northwestern species (12%) are widely distributed in North America, with ranges extending far beyond the southern limit of Wisconsinan ice.

Feeding Habits of Northwestern Black Flies

Although female black flies are well-known bloodsuckers of warm-blooded vertebrates, very little is known about the host preferences of individual species. Feeding habits can nonetheless be inferred from the structure of the mouthparts and form of the tarsal claw.

Anautogenous (bloodsucking) species have their mandibles and laciniae armed with serrations and teeth, respectively. Such armature is lacking from the mouthparts of obligate autogenous (non-bloodsucking) species. For the purposes of the present study, species with armed mouthparts are classified as anautogenous even if they are facultatively autogenous. For example, neither *S. decorum* nor members of the *S. vittatum* complex blood-feed during the first gonotrophic cycle (Davies and Györkös 1990); yet both require blood for development of subsequent egg batches.

Anautogenous species are classified as ornithophilic or mammalophilic based on the form of the female tarsal claw (Shewell 1955). Ornithophilic species have a variously-sized accessory tooth near the base of the claw, which presumably aids in grasping the feathers. The claw of mammalophilic species is typically in the form of a simple talon, without a

TABLE 4. Incidence of autogeny, ornithophily and mammalophily among black flies from northwestern North America, Alberta and Pennsylvania.

| Feeding habit | Region | | |
|---------------|-----------|----------|--------------|
| | Northwest | Alberta | Pennsylvania |
| Autogenous | 19 (25%) | 6 (10%) | 2 (4%) |
| Ornithophilic | 26 (34%) | 29 (46%) | 9 (20%) |
| Mammalophilic | 30 (40%) | 28 (44%) | 34 (76%) |
| Unknown | 1 (1%) | | |
| All | 76 | 63 | 45 |

subbasal tooth. Unfortunately, the distinction between the 2 feeding groups is not clear in all instances, with certain species blood-feeding on mammals and birds regardless of claw structure. Simple-clawed females of *S. venustum*, for example, are known to blood-feed on various species of birds (though their numbers were low relative to well-established ornithophilic species with bifid claws) (Bennett 1960). In field experiments offering both avian and mammalian hosts, females of *S. venustum* overwhelmingly attacked the latter (Hunter 1990). In the absence of well-established host records, the relationship between claw structure and feeding habit is sufficiently robust to make generalizations for most taxa.

Nineteen northwestern black flies (25%) have slightly developed mouthparts and thus are classified as obligate autogenous species (Table 1). The percentage of autogenous species is high compared to other regions of North America, for example Alberta (10%) and Pennsylvania (4%) (Table 4). At the world level only about 2.4% of black flies are ascribed to this category (Crosskey 1990).

Autogeny is clearly correlated with latitude and elevation, the phenomenon being especially pronounced at northern latitudes. Because black flies descended from a blood-sucking ancestor (Wood and Borkent 1989), autogeny must have evolved independently numerous times within the family. Seven of 9 genera have autogenous representatives in northwestern North America. The incidence is highest in *Gymnopsis*, in which all species are autogenous.

Among anautogenous black flies, 30 species (40%) are mammalophilic and 26 species (34%) are ornithophilic. The ratio of mammalophily to ornithophily is about 1.2:1, which is similar to the figure from Alberta (1:1). However, the ratio is much lower than for the North American fauna as a whole (ca. 3:1). Mammalophily predominates in the east (e.g. 3.8:1 in Pennsylvania), with a trend towards increasing ornithophily in the west (Table 4). The high incidence of ornithophily in northwestern North America is due principally to high species richness in the bird-feeding lineages *Helodon* and *S. (Eusimulium)*.

Development of the Extant Black-fly Fauna in Northwestern North America

During the Wisconsinan glacial maximum, the northwestern corner of North America represented the easternmost extension of a vast treeless territory (Beringia) that extended westward in Asia. Whether the Beringian terrain was dominated by arctic tundra or arid steppe, or consisted of a mosaic of these habitats, is a matter of continuing debate (Guthrie 1990). Nonetheless, Beringia supported a rich biota when much of the rest of North America was covered by thick layers of continental ice. Mammoths (*Mammuthus*), woolly rhinoceros (*Coelodonta*), lion (*Felis*), bison (*Bison*), musk-oxen (*Ovibos*), bonnet-horned musk-oxen

(*Symbolos*), camel (*Camelops*), sheep (*Ovis*), caribou (*Rangifer*), and horse (*Equus*) are but a few of the mammals that lived in Beringia during the Wisconsinan glacial maximum (14–25 ka B.P.) (Matthews 1982; Dixon 1984; Guthrie 1990). Birds also flourished in the Beringian landscape, though not as richly represented in the fossil record. The evidence strongly suggests that a variety of warm-blooded hosts must have been available to black flies during the Wisconsinan glacial maximum.

In the absence of a simuliid fossil record, the development of the extant northwestern fauna has to be inferred from distributional data. For the purposes of the present study I will use a similar approach to that described by Ball and Currie (1997). Black flies currently living in the northwest either were derived autochthonously (Beringian centrants), or were migrants that invaded the region following deglaciation (Beringian immigrants). Within the centrant group, species are further classified as Beringian residents (their distribution largely or entirely within the ice-free area), or Beringian emigrants (their distribution extending south and east beyond the margin of Wisconsinan ice).

The 5 species exhibiting an East Beringian distribution can reasonably be assigned to the Beringian resident category, as can the 9 species exhibiting a Palaeartic-East Beringian distribution (Table 5). All these species are either endemic to the northwest, or are Palaeartic with a restricted (northwestern) distribution in North America. Evidence is growing that Beringia was an important source area for organisms that re-invaded the north following deglaciation (e.g. Schwert and Ashworth 1988; Ashworth 1996).

Species that exhibit a markedly northern distribution beyond the ice-free margins of Beringia, regardless of the particular geographical pattern, can be designated as Beringian emigrants (12 species). Although exhibiting a Cordilleran distribution, it is likely that *Gymnopsais dichopticoidea* also belongs to the Beringian-emigrant category. Cytological information reveals that *G. dichopticoidea* is an allotriploid parthenogenetic species, formed through hybridization between the female of *G. dichopticus* and male of *G. holopticus* (Wood 1978; Rothfels 1979). Given that the latter 2 sexual species are endemic to Beringia, and that the southern range of the flightless *G. dichopticoidea* is extended only into Alberta, it is included in the Beringian emigrant category for the purposes of the present study. Similarly, the 4 species assigned to the Palaeartic-Cordilleran pattern are classified as Beringian emigrants, as discussed in the section on geographical patterns. In summary, 14 species are Beringian residents and 17 species are Beringian emigrants (Table 5); all other northwestern black flies (45 species) are hypothesized to be Beringian immigrants.

It is currently not possible to determine whether any northwestern species has a bicentric origin (i.e. species that survived as vicars in Beringia and south of Wisconsinan ice). For example, based on distributional information, many species in the Cordilleran category could just as parsimoniously originate from Beringia as from south of Wisconsinan ice. Currie and Walker (1992) reported "*P. esselbaughi/travisi*" from late Pleistocene deposits in south-coastal British Columbia. Although the fragmentary nature of the specimens rendered species-level identification impossible, both species occur widely in westernmost North America from Alaska and the Yukon south to California (Fig. 5). The occurrence of 10.5 ka B.P. fossils from southern British Columbia strongly suggests a southern origin for this species; however, similar collections from the Yukon and Alaska might reveal that it also survived in Beringia. Hypotheses about the origins of widespread taxa are tenuous in the absence of fossil information from all possible source areas. Given existing problems with the recovery and identification of fossil black flies, perhaps other sources of information could be exploited more profitably. Study of mitochondrial DNA, for example, has provided convincing evidence about the North American origins of lake whitefish (*Coregonus*

TABLE 5. List of black flies hypothesized to have a Beringian origin (= Beringian centrants), with indication of distributional patterns, postglacial dispersal category, and feeding habits. See text for explanation. Abbreviations for distributional patterns: H, Holarctic; P-EB, Palaearctic-East Beringian; P-C, Palaearctic-Cordilleran; N-WB, Nearctic-West Beringian; NN, Northern Nearctic; C, Cordilleran; EB, East Beringian. Abbreviations for feeding habits: A, autogenous; O, ornithophilic; M, mammalophilic.

| Taxon | Species no. in lists | Distribu- tional pattern | Dispersal category | Feeding habit |
|---|-------------------------|-----------------------------|-----------------------|------------------|
| Subfamily Simuliinae Newman, 1834 | | | | |
| Tribe Prosimuliini Enderlein, 1921 | | | | |
| <i>Gymnopais</i> Stone, 1949 | | | | |
| <i>G. dichopticooides</i> Wood, 1978 | 1 | C | Emigrant | A |
| <i>G. dichopticus</i> Stone, 1949 | 2 | EB | Resident | A |
| <i>G. fimbriatus</i> Wood, 1978 | 3 | EB | Resident | A |
| <i>G. holopticooides</i> Wood, 1978 | 4 | NN | Emigrant | A |
| <i>G. holopticus</i> Stone, 1949 | 5 | EB | Resident | A |
| <i>Helodon</i> Enderlein, 1921 | | | | |
| Subgenus <i>Helodon</i> s. str. | | | | |
| <i>H. alpestris</i> (D., R. and V., 1935) | 7 | P-EB | Resident | A |
| <i>H. perspicuus</i> (Sommerman, 1958) | 13 | P-EB? | Resident | A |
| <i>Prosimulium</i> Roubaud, 1906 | | | | |
| <i>macropyga</i> species group | | | | |
| <i>P. neomacropyga</i> Peterson, 1970 | 20 | P-EB? | Resident | A |
| <i>P. ursinum</i> (Edwards, 1935) complex | 21 | H | Emigrant | A |
| Tribe Simuliini Newman, 1921 | | | | |
| <i>Cnephia</i> Enderlein, 1921 | | | | |
| <i>C. eremites</i> Shewell, 1952 | 59 | H? | Emigrant | A |
| <i>Metacnephia</i> Crosskey, 1969 | | | | |
| <i>M. borealis</i> (Malloch, 1919) | 60 | N-WB | Emigrant | A |
| <i>M. saileri</i> (Stone, 1952) | 24 | P-EB? | Resident | O |
| <i>M. sommermanae</i> (Stone, 1952) | 26 | P-EB | Resident | A |
| <i>Stegopterna</i> Enderlein, 1930 | | | | |
| <i>St. decafilis</i> Rubtsov, 1971 | 28 | P-EB | Resident | A |
| <i>St. emergens</i> (Stone, 1956) | 29 | H? | Emigrant | A |
| <i>Simulium</i> Latreille, 1802 | | | | |
| Subgenus <i>Byssodon</i> Enderlein, 1925 | | | | |
| <i>S. maculatum</i> (Meigen, 1804) | 62 | P-EB | Resident | O |
| Subgenus <i>Eusimulium</i> Roubaud, 1906 | | | | |
| <i>aureum</i> species group | | | | |
| <i>S. aureum</i> Fries, 1824 complex | | | | |
| Cytospecies C | 63 | NN | Emigrant | O |
| <i>pusillum</i> species group | | | | |
| <i>S. n. sp. near giganteum</i> | 66 | EB | Resident | A |
| <i>S. subpusillum</i> Rubtsov, 1940 | 67 | H | Emigrant | M |
| <i>vernum</i> species group | | | | |
| <i>S. bicorne</i> D., R. and V., 1935 complex | 34 | P-C | Emigrant | O |
| <i>S. decolletum</i> Adler and Currie, 1986 | 36 | P-C | Emigrant | O |
| <i>S. ?dendrofilum</i> (Patrusheva, 1962) | 69 | P-EB | Resident | A |
| <i>S. silvestre</i> (Rubtsov, 1956) | 38 | P-C | Emigrant | O |
| Subgenus <i>Hellichiella</i> Rivosecchi and Cardinali, 1975 | | | | |
| <i>S. baffinense</i> Twinn, 1936 | 39 | H | Emigrant | A |
| <i>S. sp. (gouldingi of authors)</i> | 72 | EB | Resident | ? |
| Subgenus <i>Simulium</i> s. str. | | | | |
| <i>malyschevi</i> species group | | | | |
| <i>S. malyschevi</i> D., R. and V., 1935 | 44 | H | Emigrant | M |
| <i>S. nigricoxum</i> Stone, 1952 | 45 | N-WB | Emigrant | M |
| <i>noelleri</i> species group | | | | |
| <i>S. noelleri</i> Friederichs, 1920 | 48 | H | Emigrant | M |
| <i>slossonae</i> species group | | | | |
| <i>S. transiens</i> Rubtsov, 1940 | 49 | H | Emigrant | M |
| <i>tuberosum</i> species group | | | | |
| <i>S. vulgare</i> D., R. and V., 1935 | 52 | P-C | Emigrant | M |
| <i>venustum</i> species group | | | | |
| <i>S. rubtzovi</i> Smart, 1945 | 54 | P-EB | Resident | M |

clupeiformis) and carabid beetles (*Amara alpina*) (Bernatchez and Dodson 1991; Ashworth 1996).

These reservations notwithstanding, a conservative estimate of Beringian centrants can be made by combining the resident and emigrant components. A total of 31 species, representing 41% of the northwestern fauna, probably had a Beringian origin based on distributional information. This agrees well with the percentage of ground beetles classified as Beringian centrants (Ball and Currie 1997). One of the most striking features of this assemblage is the high incidence of autogeny: about 53% of centrant black flies have reduced mouthparts. All black flies in this group are mountain- or arctic-adapted species, suggesting that tundra environments were well represented in Beringia. Most autogenous species typically breed in small- to medium-sized upland streams (e.g. *Gymnopais* spp.), indicating that such watercourses must have existed throughout Wisconsinan time.

A lowland anautogenous component is also represented (Table 5). Members of the *S. malyschevi* species-group, for example, breed in medium- to large-sized piedmont streams and rivers. Females of this group contain among the most aggressive bloodsuckers in northwestern North America (e.g. *S. nigricoxum*). The 7 centrant mammalophilic species must have blood-fed throughout the Wisconsinan glaciation, suggesting that suitable hosts were available. Although there is no a priori reason to believe that representatives of the extinct Pleistocene fauna were immune to attack (e.g. mammoths, woolly rhinoceros, lions, camels), it is difficult to speculate on which, if any, of the extant simuliid species might have fed on these hosts. In the absence of a fossil record, it is impossible to know whether any late Wisconsinan simuliids became extinct with their mammalian hosts. The frozen corpses of extinct mammals offer the possibility (albeit unlikely) that simuliids of Pleistocene age could yet be discovered. Ornithophilic species account for 22% of Beringian centrants. This suggests that avian hosts must also have been available during late Wisconsinan time.

One group that warrants special mention is *Gymnopais*. Perhaps no other group of black flies is as closely associated with Beringia as are members of this group. The larvae are remarkable in that they lack the characteristic pair of labral fans that serve in filter feeding (Currie and Craig 1988). The fanless condition, which is shared with larvae of the closely related genera *Twinnia* Stone and Jamnback and *Levitinia* Chubareva and Petrova, sparked a controversy over the phylogenetic position of these black flies. Larvae are unable to filter-feed in the typical simuliid fashion, and instead must scrape algae and associated material from the stones on which they live. Wood (1978) convincingly argued that *Gymnopais* and its relatives were derived from a fanned ancestor, and that the fanless condition is a secondary adaptation to life in the headwaters of streams (which are least suitable for filter-feeding). *Gymnopais* was hypothesized to have been derived from a *Twinnia*-like ancestor that adapted to colder and colder streams as arctic conditions developed in the north during the Tertiary. This ancestor gave rise to the various species of *Gymnopais*, which probably have lived continuously in Beringia since then. All 5 Nearctic species of *Gymnopais* live in northwestern North America. The 3 sexually reproducing species (*G. dichopticus*, *G. holopticus*, and *G. fimbriatus*) exhibit an East Beringian distribution, whereas the 2 parthenogenetic species (*G. dichopticoidea* and *G. holopticoidea*) have ranges that extend well beyond the margin of Wisconsinan ice. The wider distribution of the latter 2 species may stem from their emancipation from mate finding.

The adults of *Gymnopais* share a number of features with arctic-adapted insects. They are slight of body and have a vestiture of sparse, short, erect hairs (Frontispiece). Females are autogenous and carry just a few (18–50) relatively large eggs. Most fully gravid simuliid females carry between 200 and 800 eggs. Although the wings are fully formed in all species,

only adults of *G. holopticus* exhibit any inclination to fly. The flight muscles of the remaining species are markedly reduced, with eggs often projecting anteriorly into the thorax of females (pers. obs.). Flightless species can often be found resting under streamside stones, or walking about on long, slender legs. They are so atypical in proportions and habits that they may not even be recognized as simuliids by the casual observer.

Concluding Remarks

The Beringian refugium has served as a focus for northern biogeographers ever since its existence was proposed by Hultén (1937). Distributional evidence suggests that 42% of northwestern black flies survived in Beringia during the Wisconsinan glacial maximum, providing an important source for populations now living across northern Canada.

It has been nearly a century since Coquillett's (1900) first scientific account of black flies from northwestern North America. Despite the scattered and sporadic nature of studies from the region, a substantial body of work has begun to accumulate, especially in recent years. Nonetheless, this account has highlighted several areas for further research. Species-identity problems and collecting gaps are serious impediments to the types of analyses attempted here. Considerably more collections are needed—especially those suitable for cytological study—before these issues can be addressed. Given the similarity between the Palaearctic and Nearctic fauna at northern latitudes, comparative material is needed from both sides of the Bering Sea.

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