

Trichoptera of Canada

Cory S. Sheffield¹, Jeremy R. deWaard², John C. Morse³, Andrew K. Rasmussen⁴

1 Royal Saskatchewan Museum, 2340 Albert Street, Regina, Saskatchewan, S4P 2V7, Canada **2** Centre for Biodiversity Genomics, University of Guelph, Guelph, Ontario, N1G 2W1, Canada **3** Department of Plant & Environmental Sciences, Clemson University, E-143 Poole Agricultural Center, Clemson, South Carolina 29634-0310, USA **4** Center for Water Resources, College of Agriculture and Food Sciences, Florida A&M University, 113 South Perry-Paige Bldg., Tallahassee, Florida 32307-4100, USA

Corresponding author: Cory S. Sheffield (Cory.Sheffield@gov.sk.ca)

Academic editor: D. Langor | Received 3 November 2018 | Accepted 9 December 2018 | Published 24 January 2019

<http://zoobank.org/C106DC12-3BF8-4892-A0F6-6A84180C2164>

Citation: Sheffield CS, deWaard J, Morse JC, Rasmussen AK (2019) Trichoptera of Canada. In: Langor DW, Sheffield CS (Eds) The Biota of Canada – A Biodiversity Assessment. Part 1: The Terrestrial Arthropods. ZooKeys 819: 507–520. <https://doi.org/10.3897/zookeys.819.31140>

Abstract

Trichoptera, or caddisflies, are common members of freshwater ecosystems as larvae and are important indicators of aquatic system health. As such, the species are relatively well studied, with keys available for larvae and adults of many of the taxa occurring in Canada. The number of species recorded from Canada since 1979 (Wiggins 1979) has increased from 546 to 636, an increase of 16.4%. Of those species newly recorded, 17 represent newly described taxa since 1979. Taking into consideration the species likely to be subsequently found in Canada based on records in adjacent parts of the United States and results from DNA barcoding, an estimated 129–181 species remain to be documented in Canada.

Keywords

biodiversity assessment, Biota of Canada, caddisflies, Trichoptera

Trichoptera, or caddisflies, is a species-rich group of holometabolous insects with more than 16,000 extant species worldwide (Morse 2018 and see <http://entweb.sites.clemson.edu/database/trichopt/>), the seventh largest order of insects (Adler and Foottit 2017). The order originated approximately 234 Mya (Malm et al. 2013), and is considered the sister group to Lepidoptera (butterflies and moths) (Morse 1997, Wiggins

1998, Misof et al. 2014). Trichoptera have larvae and pupae that are almost exclusively aquatic (Morse 2017); *Philocasca demita* Ross (Limnephilidae) and *Manophylax* (*Madeophylax*) spp. are some exceptions (Schmid 1998, Chuluunbat et al. 2010). Mackay and Wiggins (1979) suggest that the high trichopteran diversity was driven by the larval secretion of silk, which provided opportunities to exploit different ecological niches. Wiggins (1998) further speculated that the diversification of Trichoptera has taken place entirely within aquatic habitats, due to larvae being able to exploit food resources in new ways thanks to their diverse case/retreat/filter-net construction. The legs of pupal Trichoptera are modified for the water to land transition, allowing pharate adults to swim to the water surface and sometimes to land, with specialized claws used for crawling on stones or plants (Friedrich and Kubiak 2018).

Caddisfly larvae are well known for their underwater architecture, with some taxa constructing elaborate cases out of a range of materials. The behaviours, type of materials used, and the shape of the case often being diagnostic for trichopteran identification (Weaver and Morse 1986, Wiggins 1996, 2004). Some workers (Wiggins and Wichard 1989, Frania and Wiggins 1997, Wiggins 1998, Kjer et al. 2001, Holzenthal et al. 2007, Malm et al. 2013) have recognized three suborders of Trichoptera corresponding to larval construction behaviours (and see Morse 1997, 2017). Annulipalpia (or “fixed-retreat-makers”) attach themselves to substrates using silk which often also acts to gather food items from the passing water currents. Integripalpia contain species with “portable-case-making” larvae, constructing tubular cases of various materials (e.g., leaves, wood, small pebbles) held together with silk. “Spicipalpia”, consist of larvae that construct closed, semi permeable cocoons for pupation, but which exhibit a wide range of larval behaviours, including some free-living predatory larvae and herbivorous forms that build portable enclosures to provide shelter while they graze, but do not build traditional tube cases or filtering nets like the majority of caddisfly taxa (Malm et al. 2013). Morse (1997, 2017) provided more specific details on the taxa historically included within “Spicipalpia” (i.e., Rhyacophiloidea, Glossosomatoidea, Hydroptiloidea), but the most recent phylogenies (e.g., Kjer et al. 2016, Morse et al. in preparation) consider these families to be basal lineages of Integripalpia. For this faunistic summary, we structure Table 1 to reflect the recent summary of trichopteran higher classification provided by Holzenthal et al. (2011), modified for taxa found in Canada.

Trichoptera continue to be the subjects of much taxonomic work largely because this insect order is among the most important and diverse of all aquatic taxa (Holzenthal et al. 2007), exceeded in number in freshwater habitats only by Coleoptera (16,000+ species) and Diptera (51,000+ species) (Morse 2017), and are key elements of freshwater ecosystems for biological assessment and water quality monitoring. Especially because of their importance in freshwater biomonitoring, Trichoptera is one of the few insect orders in which keys exist for both the larvae (e.g., Wiggins 1996, 1998, Morse and Holzenthal 2008) and adults (e.g., Cooper and Morse 1998, Schmid 1998, Wiggins and Currie 2008), though Wiggins (1979) and Morse (2017) indicated that there is a major deficiency in our ability to identify the immature stages.

Trichoptera taxonomy has a rich history in Canada, with workers such Glenn B. Wiggins, Andrew P. Nimmo, and Fernand Schmid laying a solid foundation for ongoing

and future work. Many other North America workers continue to contribute to knowledge of the Canadian trichopteran fauna (see Table 1). Since Wiggins' (1979) summary of the Canadian fauna, Morse (1993) published a checklist of 1653 North American species, which included the fauna of Mexico and Greenland, but did not partition these by country. Schmid (1998) published keys to the genera occurring in Canada and the adjacent United States, which included estimates of numbers of species in each. Unfortunately, precise numbers for species richness in Canada were not provided, though he did provide estimates for Canada and adjacent areas. Most of the data supporting the current assessment (Table 1) are based on an online list of Nearctic Trichoptera (Rasmussen and Morse 2018). Since the time of Wiggins' (1979) summary, the number of Trichoptera species recorded from Canada has increased from 546 to 636, representing an increase of 16.4%. Of the newly recorded species, 17 were described since 1979.

In his overview of Canadian caddisflies, Wiggins (1979) recognized 18 families of Trichoptera within three superfamilies: Rhyacophiloidea (four families), Hydropsychoidea (three families), and Limnephiloidea (11 families), these corresponding to the suborders 'Spicipalpia', Annulipalpia, and Intergripalpia, respectively, and tallied 546 species (Table 1). Since that time, different higher level classification schemes based on phylogenetic analyses have been applied to Trichoptera, both in North America (e.g., Wiggins 1996, Schmid 1998) and globally (Holzenthal et al. 2007, 2011).

The Canadian fauna includes ten superfamilies and 25 families (Table 1; after Holzenthal et al. 2011). Rhyacophiloidea (= Spicipalpia of other authors), as recognized by Wiggins (1979), is now partitioned into three superfamilies: Glossosomatoidae (Glossosomatidae); Hydroptiloidea (Hydroptilidae, Ptilocolepidae [= Hydroptilidae, subfamily Ptilocolepinae of Schmid (1998) and likely Wiggins 1979, so not included in the 1979 work]); and Rhyacophiloidea (Rhyacophilidae). By contrast, Hydropsychoidea is currently applied in a much narrower sense than by Wiggins (1979); it is now represented by a single family, Hydropsychidae, which includes Arctopsychidae of Schmid (1998). Of the other three families included in Hydropsychoidea in Wiggins (1979), Philopotamidae has been placed in Philopotamoidea and Psychomyiidae and Polycentropodidae are now in Psychomyioidea. One additional family within Psychomyioidea is newly recorded in Canada since 1979, Dipseudopsidae [treated as Hyalopsychidae by Schmid (1998)]. An additional five families have been newly recorded from Canada (Wiggins 1996, Schmid 1998, Rasmussen and Morse 2018) based on changes in classification, all within superfamily Limnephiloidea: Apataniidae, Goeridae, Thremmatidae, Uenoidae, and Rossianidae. The latter three families were considered part of Limnephilidae by Wiggins (1979), and Rossianidae was previously recognized as the subfamily Dicosmoecinae of Limnephilidae by Schmid (1998), and likely also by Wiggins (1979). Of the eleven families placed in the Limnephiloidea by Wiggins (1989), ten now reside in different superfamilies: Brachycentridae, Lepidostomatidae, and Phryganeidae have been placed in Phryganeoidea; Calamoceratidae, Molannidae, Leptoceridae, and Odontoceridae placed in Leptoceroidea; and Beraeidae, Helicopsychidae, and Sericostomatidae placed in Sericostomatoidea. These additions and reclassifications account for ca. 40 of the additional species within Canada (Table 1).

Table I. Census of Trichoptera in Canada¹.

Taxon ¹	No. species reported by Wiggin (1979)	No. species currently known from Canada ²	No. BINs ³ available for Canadian species	Est. no. undescribed or unrecorded species in Canada ⁴	General distribution by ecozone ⁵	Information sources ⁶
Suborder Annulipalpia						
Superfamily Philopotamoidea						
Philopotamidae	13	14	20	1–13	most ecozones	Schmid 1982, Armitage 1991
Superfamily Psychomyioidea						
Dipscopidae ⁷	0	3	4	1–2	Atlantic Maritime, Mixedwood Plains, Prairies	Schmid 1983, Schuster and Hamilton 1984, Sturkie and Morse 1998
Polycentropodidae	36	37	32	6	most ecozones	Nimmo 1986, Armitage and Hamilton 1990, Neboiss 1993, Chamorro and Holzenthal 2010
Psychomyiidae	2	4	2	1–4	Atlantic Maritime, Mixedwood Plains, Prairies	Schmid 1983, Armitage and Hamilton 1990
Superfamily Hydropsychoidea						
Hydropsychidae ⁸	48	56	62	10–15	most ecozones	Schmid 1968, Gordon 1974, Nimmo 1987, Geraci et al. 2010, Burington 2011
Suborder Integripalpia – “Spicipalpia”						
Superfamily Glossosomatoidae						
Glossosomatidae	21	26	22	8–15	most ecozones	Ross 1956, Nimmo 1974, 1977, Schmid 1982, Wijmer and Morse 2000, Erni et al. 2010, Robertson and Holzenthal 2013, Genco and Morse 2017
Superfamily Hydroptiloidea						
Hydroptilidae	52	75	78	10	most ecozones	Kingsolver and Ross 1961, Denning and Bickle 1972, Ito et al. 2014, Harris and Flint 2016
Prilocolepidae ⁹	?	2	1	0	Pacific Maritime, Newfoundland Boreal; possibly Mixedwood Plains, Boreal Shield, Atlantic Maritime	Ito et al. 2014
Superfamily Rhyacophiloidea						
Rhyacophilidae	57	65	36	15	most ecozones	Schmid 1966, 1970, 1981, Nimmo 1971, Prather and Morse 2001
Suborder Integripalpia – Brevitentatoria						
Superfamily Leptoceroidea						
Calamoceratidae	2	2	1	0	Pacific Maritime, Western Interior Basin, Montane Cordillera, Mixedwood Plains	Bowles and Flint 1997, Schmid 1998
Melannidae ¹⁰	7	6	3	0	most ecozones, except Arctic Maritime and Arctic	Roy and Harper 1980, Schmid 1983, 1998
Leproceridae	56	68	118	30–50	most ecozones	Yamamoto and Wiggins 1964, Holzenthal 1982, Floyd 1995, Glover 1996, Manuel 2010

Taxon ¹	No. species reported by Wiggins (1979)	No. species currently known from Canada ²	No. BINs ³ available for Canadian species	No. undescribed or unrecorded species in Canada ⁴	General distribution by ecozone ⁵	Information sources ⁶
Odontoceridae						
Superfamily Sericostomatoidae	4	5	3	0	Mixedwood Plains, Atlantic Maritime	Schmid 1983, Parker and Wiggins 1987
Beraeidae	1	1	0	1	Mixedwood Plains	Wiggins 1954, Schmid 1998
Helicopsychidae	1	1	5	3	most ecozones	Moulton and Stewart 1996, Johanson 2002
Sericostomatidae	2	2	2	2	Mixedwood Plains	Ross and Wallace 1974, Schmid 1998, Keth and Harris 2008
Suborder Integripalpia – Plenitentatoria						
Superfamily Limnephiloidea						
Apataniidae	?	16	8	0	most ecozones, except Atlantic Maritime	Schmid 1953, Chen 1992, Flint 2007
Groteridae	?	5	4	2	Atlantic Maritime, Mixedwood Plains, Montane Cordillera, Western Interior Basin, Pacific Maritime	Schmid 1983, 1998
Limnephilidae	179	157	128	30	most ecozones	Parker and Wiggins 1985, Ruitter 1995
Rossianidae	?	1	0	0	Montane Cordillera, Western Interior Basin, Pacific Maritime	Schmid 1998
Thremmatidae	?	16	9	3	Newfoundland Boreal and south of boreal on mainland	Vineyard et al. 2005, Hoensens et al. 2015
Uenoidae	?	2	1	0	widespread in Canada	Wiggins et al. 1985
Superfamily Phryganeoidea						
Brachycentridae	15	16	16	2	most ecozones	Wiggins 1965, Schmid 1983, Flint 1984
Lepidostomatidae	26	30	27	2–3	most ecozones	Weaver 1984, 1988
Phryganeidae	24	26	28	2–5	most ecozones	Wiggins 1956, 1960, 1998
Total	546	637	611	129–181		

¹Modified from Holzenthal et al. (2011) and Ito et al. (2014). ²Data extracted from Rasmussen and Morse (2018). ³Barcode Index Numbers (BINs), as defined by Ratnasingham and Hebert (2013). Estimates based on data in Schmid (1998) and Rasmussen and Morse (2018) and from BINs. ⁴See Figure 1 in Langor (2019) for a map of ecozones. ⁵See Figure 1 in Langor (2019) for a map of ecozones. ⁶The references cited do not necessarily represent a comprehensive list for each family but rather some of the most significant contributions. See Schmid (1998) for major taxonomic works for Canada to that time and, more importantly, Rasmussen and Morse (2018) provide the most complete species level account of relevant literature with distributional data. BOLD refers to DNA barcode data from the Barcode of Life Data System (www.boldsystems.org). ⁷Dipseudopsidae = Hyalopsychidae of Schmid (1998). ⁸Includes Arctopsychidae of Nimmo (1987) and Schmid (1998). Records of this family outside of the Pacific Maritime and Newfoundland Boreal are based on single specimen accounts from the literature with no collection information (Ito et al. 2014). ⁹The decrease of one species since 1979 is due to the fact that *Molanna cinerea* Hagen, 1861 is now considered nomen dubium.

DNA barcoding (*sensu* Hebert et al. 2003) has been applied extensively to the Trichoptera fauna of Canada, especially in northern areas (Zhou et al. 2009, Ruiter et al. 2013) and elsewhere, with a comprehensive global library containing more than 16,000 unique haplotypes already well established (Zhou et al. 2016). The 610 Barcode Index Numbers (BINs; Ratnasingham and Hebert 2013) assigned to the Canadian Trichoptera in the Barcode of Life Data System (BOLD; Ratnasingham and Hebert 2007), seemingly represent 96% of the number of described species known from Canada (Table 1). However, many BINs are not yet associated with described species and, in several cases, the ratio of species to BINs is low. For instance, the families Hydropsychidae, Philopotamidae, Hydroptilidae, Phryganeidae, Helicopsychidae, and especially Leptoceridae all have more BINs than known Canadian species suggesting that there are many additional species in Canada remaining to be documented and highlighting that there is still much opportunity for research on Trichoptera in Canada. However, this may also mean that there is enough variation in the barcode region of COI of some Canadian Trichoptera that multiple BINs exist for an individual species, as has been demonstrated in other insect groups (Gibbs 2018). As stressed by Zhou et al. (2016), BINs are not synonymous with species (although there is typically high congruence) and should not be treated as such.

Estimates of the number of undocumented (undescribed or unreported) species in Canada were made by first considering species that are known from adjacent parts of the USA but not yet recorded from Canada. Such species are likely to occur there based on habitat and climate. Furthermore, we took into consideration the number of BINs reported for each family and the likelihood that some of these represent undocumented species. We conservatively estimate that 129–181 additional species will eventually be found in Canada, meaning that the total Canadian fauna could be >800 species (Table 1). The families with the highest numbers of undocumented species are expected to be Leptoceridae (30–50 species) and Limnephilidae (30).

Almost all Canadian jurisdictions (except Prince Edward Island and Labrador) have checklists or at least some faunistics work. Examples include: Yukon (Nimmo and Wickstrom 1984, Wiggins and Parker 1997), Northwest Territories/Nunavut (Nimmo 1984, Winchester 1984, Cordero et al. 2017), British Columbia (Nimmo and Scudder 1978, 1983, Cannings and Roberts 2007, Cannings 2007, Erasmus et al. 2018), Alberta (Nimmo 2001, Hinchliffe 2010), Saskatchewan (Smith 1975, 1984, Hoemsen et al. 2015), Manitoba (Zhou et al 2009, Ruiter et al. 2013), Quebec (Nimmo 1966, Roy and Harper 1979, 1981), New Brunswick and Nova Scotia (Banks 1930, Peterson and van Eeckhaute 1990, 1992), and the island of Newfoundland (Banks 1908, Marshall and Larson 1982). In addition, an up-to-date online global species list (Morse 2018) is available as is an online Endnote-based literature database with more than 12,000 records (Holzenthal et al. 2012), both highly valuable for study of Trichoptera in Canada. Despite the very good taxonomic foundation and state of knowledge concerning faunal composition, there is still plentiful effort needed in Canada before the fauna is fully known. In particular, there are still major challenges to identify the

immature stages of Trichoptera (Wiggins 1979), and DNA barcoding offers a means of associating identifiable adults (male and female) to unidentifiable immature stages (Zhou et al. 2007). Barcode data will also help with understanding phylogenetic relationships (Frandsen et al 2016). There are many areas of Canada that need additional caddisfly sampling, particularly northern areas and remote areas in the south. Increased sampling in areas close to the southern border with the USA is also likely to add new Canadian records. With a comprehensive DNA barcode library for Trichoptera well underway (Zhou et al. 2016), the future for Trichoptera studies globally, and within Canada, looks promising.

Acknowledgements

We thank the Biodiversity Institute of Ontario, Guelph, Ontario for access to Trichoptera DNA barcode sequences for summary purposes, and David Langor and two anonymous reviewers for helpful comments on the manuscript.

References

- Adler PH, Foottit RG (2017) Introduction. In: Foottit RG, Adler PH (Eds) Insect Biodiversity: Science and Society. Wiley-Blackwell, Oxford, United Kingdom, 1–7. <https://doi.org/10.1002/9781118945568.ch1>
- Armitage BJ (1991) Diagnostic atlas of the North American caddisfly adults. I. Philopotamidae. 2nd edition. The Caddis Press, Athens, Alabama, 131 pp.
- Armitage BJ, Hamilton SW (1990) Diagnostic atlas of the North American caddisfly adults. II. Ecnomidae, Polycentropodidae, Psychomyiidae, and Xiphocentronidae. The Caddis Press, Athens, Alabama, 270 pp.
- Banks N (1908) Some Trichoptera and allied insects from Newfoundland. *Psyche* 15: 61–67. <https://doi.org/10.1155/1908/78191>
- Banks N (1930) Trichoptera from Cape Breton, Nova Scotia. *Bulletin of the Brooklyn Entomological Society* 25: 127–132.
- Bowles DE, Flint JR OS (1997) A review of the genus *Phylloicus* Müller (Trichoptera: Calamoceratidae) in the United States with a redescription of *Phylloicus ornatus* (Banks). In: Holzenthal RW, Flint Jr OS (Eds) Proceedings of the Eighth International Symposium on Trichoptera. Ohio Biological Survey, Columbus, Ohio, 53–58.
- Burlington ZL (2011) Larval taxonomy, phylogeny and historical biogeography of the genus *Cheumatopsyche* (Trichoptera: Hydropsychidae) in North America. MSc Thesis, Clemson University, Clemson.
- Cannings RA (2007) Checklist list of the Trichoptera (Caddisflies) of British Columbia (2007). BC Efauna. <http://ibis.geog.ubc.ca/biodiversity/efauna/documents/TrichopteraofBC2007.pdf>
- Cannings RA, Roberts G (2007) The caddisfly family Helicopsychidae (Insecta: Trichoptera) new to British Columbia. *Journal of the Entomological Society of British Columbia* 104: 89–90.

- Chamorro ML, Holzenthal RW (2010) Taxonomy and phylogeny of New World *Polyplectropus* Ulmer, 1905 (Trichoptera, Psychomyioidea, Polycentropodidae) with the description of 39 new species. Zootaxa 2582: 1–252.
- Chen YE (1992) The larva and pupa of *Apatania praevolans* Morse (Trichoptera: Limnephilidae), with a key to described larvae of North American species of *Apatania*. Aquatic Insecta 14: 49–55. <https://doi.org/10.1080/01650429209361461>
- Chuluunbat S, Morse JC, Lessard JAL, Benbow ME, Wesener MD, Hudson J (2010) Evolution of terrestrial habitat in *Manophylax* species (Trichoptera: Apataniidae), with a new species from Alaska. Journal of the North American Benthological Society 29: 413–430. <https://doi.org/10.1899/09-106.1>
- Cooper HJ, Morse JC (1998) Females of *Chimarra* (Trichoptera: Philopotamidae) from eastern North America. Journal of the New York Entomological Society 106: 185–198.
- Cordero RD, Sánchez-Ramírez S, Currie DC (2017) DNA barcoding of aquatic insects reveals unforeseen diversity and recurrent population divergence patterns through broad-scale sampling in northern Canada. Polar Biology 40: 1687–1695. <https://doi.org/10.1007/s00300-016-2062-3>
- Denning DG, Bickle RL (1972) A review of the genus *Ochrotrichia* (Trichoptera: Hydroptilidae). Annals of the Entomological Society of America 65: 141–151. <https://doi.org/10.1093/esa/65.1.141>
- Erasmus DJ, Yurkowski EA, Huber DPW (2018) DNA barcode-based survey of Trichoptera in the Crooked River reveals three new species records for British Columbia. PeerJ 6:e4221 <https://doi.org/10.7717/peerj.4221>
- Etnier DA, Parker CR, Baxter Jr JT, Long TM (2010) A review of the genus *Agapetus* Curtis (Trichoptera: Glossosomatidae) in eastern and central North America, with description of 12 new species. Insecta Mundi 149: 1–77.
- Flint Jr OS (1984) The genus *Brachycentrus* in North America, with a proposed phylogeny of the genera of Brachycentridae (Trichoptera). Smithsonian Contributions to Zoology 398: 1–58. <https://doi.org/10.5479/si.00810282.398>
- Flint Jr OS (2007) Synonymy of some eastern North American species of *Apatania* (Trichoptera: Apataniidae). Proceedings of the Entomological Society of Washington 109: 739–740.
- Floyd MA (1995) Larvae of the caddisfly genus *Oecetis* (Trichoptera: Leptoceridae) in North America. Bulletin of the Ohio Biological Survey 10(3): 1–85.
- Frandsen PB, Zhou X, Flint Jr OS, Kjer KM (2016) Using DNA barcode data to add leaves to the Trichoptera tree of life. Zoosymposia 10: 193–199.
- Frania HR, Wiggins GB (1997) Analysis of morphological and behavioural evidence for the phylogeny and higher classification of Trichoptera (Insecta). Royal Ontario Museum Life Sciences Contributions 160: 1–67. <https://doi.org/10.5962/bhl.title.53487>
- Friedrich F, Kubiak M (2018) Comparative anatomy of pupal tarsi in caddisflies (Insecta: Trichoptera) with focus on the claw system. Zoomorphology 137(2): 305–314. <https://doi.org/10.1007/s00435-018-0398-7>
- Genco MS, Morse JC (2017) Pupae of North American Glossosomatidae (Trichoptera). Freshwater Science 36(4): 816–822. <https://doi.org/10.1086/694336>

- Geraci CJ, Zhou X, Morse JC, Kjer KM (2010) Defining the genus *Hydropsyche* (Trichoptera : Hydropsychidae) based on DNA and morphological evidence. Journal of the North American Benthological Society 29: 918–933. <https://doi.org/10.1899/09-031.1>
- Gibbs J (2018) DNA barcoding a nightmare taxon: assessing barcode index numbers and barcode gaps for sweat bees. Genome 61: 21–31. <https://doi.org/10.1139/gen-2017-0096>
- Glover JB (1996) Larvae of the caddisfly genera *Triaenodes* and *Ylodes* (Trichoptera: Leptoceridae) in North America. Ohio Biological Survey, Columbus, Ohio, 89 pp.
- Gordon AE (1974) A synopsis and phylogenetic outline of the Nearctic members of *Cheumatopsyche*. Proceedings of the Academy of Natural Sciences of Philadelphia 126: 117–160.
- Harris SC, Flint Jr OS (2016) New species of microcaddisflies (Trichoptera: Hydroptilidae) from the western United States, Canada, Mexico and Belize. Insecta Mundi 499: 1–22.
- Hebert PDN, Cywinski A, Ball SL, deWaard JR (2003) Biological identifications through DNA barcodes. Proceedings of the Royal Society B, Biological Sciences 270: 313–321. <https://doi.org/10.1098/rspb.2002.2218>
- Hinchliffe RP (2010) First record of *Ithytrichia* (Trichoptera: Hydroptilidae) in Alberta, Canada. Entomological News 121: 466–486. <https://doi.org/10.3157/021.121.0508>
- Hoemsen BM, Phillips ID, Parker DW, Bell AJ, Bergsveinson JA, Armstrong JS, Chivers DP (2015) Extended family: a caddisfly new to Saskatchewan, Canada with notes on the life history of *Neophylax splendens* (Trichoptera: Thremmatidae). The Canadian Entomologist 147: 425–431. <https://doi.org/10.4039/tce.2014.46>
- Holzenthal RW (1982) The caddisfly genus *Setodes* in North America (Trichoptera: Leptoceridae). Journal of the Kansas Entomological Society 55: 253–271.
- Holzenthal RW, Blahnik RJ, Prather AL, Kjer KM (2007) Order Trichoptera Kirby, 1813 (Insecta), Caddisflies. In: Zhang Z, Shear WA (Eds) Linnaeus Tercentenary: Progress in Invertebrate Taxonomy. Zootaxa 1668, 639–698.
- Holzenthal RW, Mendez PK, Steiner JWH, Huisman J (2012) Trichoptera Literature Database: a collaborative bibliographic resource for world caddisfly research. <http://www.trichopterlit.umn.edu/>
- Holzenthal RW, Morse JC, Kjer KM (2011) Order Trichoptera Kirby, 1813. In: Zhang Z (Ed.) Animal biodiversity: An outline of higher-level classification and survey of taxonomic richness. Zootaxa 3148: 209–211.
- Ito T, Wisseman RW, Morse JC, Colbo MH, Weaver JS (2014) The genus *Palaeagapetus* Ulmer (Trichoptera, Hydroptilidae, Ptilocolepinae) in North America. Zootaxa 3794(2): 201–221. <https://doi.org/10.11646/zootaxa.3794.2.1>
- Johanson KA (2002) Systematic revision of the American *Helicopsyche* of the subgenus *Feropsyche* (Trichoptera, Helicopsychidae). Insect Systematics & Evolution 60: 1–147.
- Keth AC, Harris SC (2008) The North American Genus *Agarodes* Banks (Trichoptera: Sericostomatidae). The Caddis Press, Columbus, Ohio, 33 pp.
- Kingsolver JM, Ross HH (1961) New species of Nearctic *Orthotrichia* (Hydroptilidae, Trichoptera). Illinois State Academy of Science Transactions 54: 28–33.
- Kjer KM, Blahnik RJ, Holzenthal RW (2001) Phylogeny of Trichoptera (caddisflies): characterization of signal and noise within multiple datasets. Systematic Biology 50(6): 781–816. <https://doi.org/10.1080/106351501753462812>

- Kjer KM, Thomas JA, Zhou X, Frandsen PB, Prendini E, Holzenthal RW (2016) Progress on the phylogeny of caddisflies (Trichoptera). *Zoosymposia* 10: 248–256. <http://doi.org/10.11646/zoosymposia.10.1.23>
- Langor DW (2019) The diversity of terrestrial arthropods in Canada. In: Langor DW, Sheffield CS (Eds) *The Biota of Canada – A Biodiversity Assessment. Part 1: The Terrestrial Arthropods.* *ZooKeys* 819: 9–40. <https://doi.org/10.3897/zookeys.819.31947>
- Mackay RJ, Wiggins GB (1979) Ecological diversity in Trichoptera. *Annual Review of Entomology* 24: 185–208. <https://doi.org/10.1146/annurev.en.24.010179.001153>
- Malm T, Johanson KA, Wahlberg N (2013) The evolutionary history of Trichoptera (Insecta): a case of successful adaptation to life in freshwater. *Systematic Entomology* 38(3): 459–473. <https://doi.org/10.1111/syen.12016>
- Manuel KL (2010) *The longhorn caddisfly genus Triaenodes* (Trichoptera: Leptoceridae). The Caddis Press, Columbus, Ohio, 109 pp.
- Marshall JS, Larson DJ (1982) The adult caddisflies (Insecta: Trichoptera) of insular Newfoundland. *Memorial University of Newfoundland Occasional Papers in Biology* 6: 1–85.
- Misof B, Liu S, Meusemann K, Peters RS, Donath A, Mayer C, Frandsen PB, Ware J, Flouri T, Beutel RG, Niehuis O, Petersen M, Izquierdo-Carrasco F, Wappler T, Rust J, Aberer AJ, Aspöck U, Aspöck H, Barret D, Blanke A, Berger S, Böhm A, Buckley TR, Calcott B, Chen J, Friedrich F, Fukui M, Fujita M, Greve C, Grobe P, Gu S, Huang Y, Jermiin LS, Kawahara AY, Krogmann L, Kubiak M, Lanfear R, Letsch H, Li Y, Li Z, Li J, Lu H, Machida R, Mashimo Y, Kapli P, McKenna DD, Meng G, Nakagaki Y, Navarrete-Heredia JL, Ott M, Ou Y, Pass G, Podsiadlowski L, Pohl H, von Reumont BM, Schütte K, Sekiya K, Shimizu S, Slipinski A, Stamatakis A, Song W, Su X, Szucsich NU, Tan M, Tan X, Tang M, Tang J, Timelthaler G, Tomizuka S, Trautwein M, Tong X, Uchifune T, Walzl MG, Wiegmann BM, Wilbrandt J, Wipfler B, Wong TK, Wu Q, Wu G, Xie Y, Yang S, Yang Q, Yeates DK, Yoshizawa K, Zhang Q, Zhang R, Zhang W, Zhang Y, Zhao J, Zhou C, Zhou L, Ziesmann T, Zou S, Li Y, Xu X, Zhang Y, Yang H, Wang J, Wang J, Kjer KM, Zhou X (2014) Phylogenomics resolves the timing and pattern of insect evolution. *Science* 346(6210): 763–767. <https://doi.org/10.1126/science.1257570>
- Morse JC (1993) A checklist of the Trichoptera of North America, including Greenland and Mexico. *Transactions of the American Entomological Society* 119: 47–93.
- Morse JC (1997) Phylogeny of Trichoptera. *Annual Review of Entomology* 42: 427–450. <https://doi.org/10.1146/annurev.ento.42.1.427>
- Morse JC (2017) Biodiversity of aquatic insects. In: Foottit RG, Adler PH (Eds) *Insect Biodiversity: Science and Society*, vol 1, 2nd Ed. John Wiley & Sons Ltd., New Jersey, 205–227. <https://doi.org/10.1002/9781118945568.ch8>
- Morse JC (Ed.) (2018) *Trichoptera World Checklist.* <http://entweb.clemson.edu/database/trichopt/index.htm>
- Morse JC, Holzenthal RW (2008) *Trichoptera Genera.* In: Merritt RW, Cummins KW, Berg MB (Eds) *An Introduction to the Aquatic Insects of North America*, 4th Ed. Kendall/Hunt Publishing Co. Dubuque, Iowa, 481–552.
- Moulton SR, Stewart KW (1996) Caddisflies (Trichoptera) of the Interior Highlands of North America. *Memoirs of the American Entomological Institute* 56: 1–315.

- Neboiss A (1993) Revised definitions of the genera *Nyctiophylax* Brauer and *Paranyctiophylax* Tsuda (Trichoptera: Polycentropodidae). In: Otto C (Ed.) Proceedings of the Seventh International Symposium on Trichoptera, Umeå, Sweden, 3–8 August 1992. Backhuys Publishers, Leiden, The Netherlands, 107–111.
- Nimmo AP (1966) A list of Trichoptera taken in Montreal and Chambly, Quebec, with descriptions of three new species. *The Canadian Entomologist* 98: 688–693. <https://doi.org/10.4039/Ent98688-7>
- Nimmo AP (1971) The adult Rhyacophilidae and Limnephilidae (Trichoptera) of Alberta and eastern British Columbia and their post glacial origin. *Quaestiones Entomologicae* 7: 3–234.
- Nimmo AP (1974) The adult Trichoptera (Insecta) of Alberta and eastern British Columbia and their post-glacial origins. II. The families Glossosomatidae and Philopotamidae. *Quaestiones Entomologicae* 10: 315–349.
- Nimmo AP (1977) The adult Trichoptera (Insecta) of Alberta and eastern British Columbia, and their post glacial origins. II. The families Glossosomatidae and Philopotamidae, supplement 1. *Quaestiones Entomologicae* 13: 69–71.
- Nimmo AP (1984) Preliminary annotated checklist of the Trichoptera (Insecta) of the North West Territories, Canada. *The Musk-ox* 34: 95–100.
- Nimmo AP (1986) The adult Polycentropodidae of Canada and adjacent United States. *Quaestiones Entomologicae* 22: 143–252.
- Nimmo AP (1987) The adult Arctopsychidae and Hydropsychidae (Trichoptera) of Canada and adjacent United States. *Quaestiones Entomologicae* 23: 1–189.
- Nimmo AP (2001) Checklist of Alberta Trichoptera. <http://www.biology.ualberta.ca/facilities/strickland/trichoptera.htm>
- Nimmo AP, Scudder GGE (1978) An annotated checklist of the Trichoptera (Insecta) of British Columbia. *Sysis* 11: 117–133.
- Nimmo AP, Scudder GGE (1983) Supplement to an annotated checklist of the Trichoptera (Insecta) of British Columbia. *Sysis* 16: 71–83.
- Nimmo AP, Wickstrom R (1984) Preliminary annotated checklist of the Trichoptera (Insecta) of the Yukon. *Sysis* 17: 3–9.
- Parker CR, Wiggins GB (1985) The Nearctic caddisfly genus *Hesperophylax* Banks (Trichoptera: Limnephilidae). *Canadian Journal of Zoology* 63: 2443–2472. <https://doi.org/10.1139/z85-361>
- Parker CR, Wiggins GB (1987) Revision of the caddisfly genus *Psilotreta*. *Life Sciences Contributions of the Royal Ontario Museum, Toronto* 144: 1–55.
- Peterson RH, van Eeckhaute L (1990) Distributions of stonefly (Plecoptera) and caddisfly (Trichoptera) species in three stream systems in New Brunswick and Nova Scotia, Canada, with reference to stream acidity. *Canadian Technical Report of Fisheries and Aquatic Sciences* 1720: 1–42.
- Peterson RH, van Eeckhaute L (1992) Distributions of Ephemeroptera, Plecoptera, and Trichoptera of three maritime catchments differing in pH. *Freshwater Biology* 27: 65–78. <https://doi.org/10.1111/j.1365-2427.1992.tb00523.x>

- Prather AL, Morse JC (2001) Eastern Nearctic *Rhyacophila* species, with revision of the *Rhyacophila invaria* group (Trichoptera: Rhyacophilidae). *Transactions of the American Entomological Society* 127: 85–166.
- Rasmussen AK, Morse JC (2018) Distributional checklist of Nearctic Trichoptera (August 2018 Revision). Unpublished, Florida A&M University, Tallahassee, Florida, 506 pp. <http://www.Trichoptera.org>
- Ratnasingham S, Hebert PDN (2007) BOLD: the Barcode of Life Data System [<http://www.barcodinglife.org>]. *Molecular Ecology Notes* 7: 355–364. <https://doi.org/10.1111/j.1471-8286.2007.01678.x>
- Ratnasingham S, Hebert PDN (2013) A DNA-based registry for all animal species: the Barcode Index Number (BIN) System. *PLOS ONE* 8(7): e66213. <https://doi.org/10.1371/journal.pone.0066213>
- Robertson DR, Holzenthal RW (2013) Revision and phylogeny of the caddisfly subfamily Protoptilinae (Trichoptera: Glossosomatidae) inferred from adult morphology and mitochondrial DNA. *Zootaxa* 3723: 1–99. <https://doi.org/10.11646/zootaxa.3723.1.1>
- Ross HH (1956) Evolution and classification of the mountain caddisflies. University of Illinois Press, Urbana, Illinois, 213 pp.
- Ross HH, Wallace JB (1974) The North American genera of the family Sericostomatidae. *Journal of the Georgia Entomological Society* 9: 42–48.
- Roy D, Harper PP (1979) Liste préliminaire des Trichoptères du Québec. *Annales de la Société entomologique du Québec* 24: 148–171.
- Roy D, Harper PP (1980) Females of the Nearctic *Molanna* (Trichoptera: Molannidae). *Proceedings of the Entomological Society of Washington* 82(2): 229–236.
- Roy D, Harper PP (1981) An analysis of an adult Trichoptera community in the Laurentian highlands of Quebec. *Ecography* 4: 102–115. <https://doi.org/10.1111/j.1600-0587.1981.tb00986.x>
- Ruiter DE (1995) The genus *Limnephilus* Leach (Trichoptera: Limnephilidae) of the new world. *Bulletin of the Ohio Biological Survey* 11: 1–200.
- Ruiter DE, Boyle EE, Zhou X (2013) DNA barcoding facilitates associations and diagnoses for Trichoptera larvae of the Churchill (Manitoba, Canada) area. *BMC Ecology* 13: 5. <https://doi.org/10.1186/1472-6785-13-5>
- Schmid F (1953) Contribution à l'étude de la sous-famille des Apataniinae (Trichoptera, Limnophilidae). I. *Tijdschrift voor Entomologie* 96: 109–167.
- Schmid F (1966) Le genre *Himalopsyche* Banks (Trichoptera: Rhyacophilidae). *Annales de la Société entomologique du Québec* 11: 123–176.
- Schmid F (1968) La famille des arctopsychides (Trichoptera). *Mémoires de la Société Entomologique du Québec* 1: 1–84.
- Schmid F (1970) Le genre *Rhyacophila* et la famille des Rhyacophilidae (Trichoptera). *Memoirs of the Entomological Society of Canada* 102(S66): 5–334. <https://doi.org/10.4039/entm10266fv>
- Schmid F (1981) Revision des Trichoptères canadiens, I. La famille des Rhyacophilidae (An-nulipalpia). *Memoirs of the Entomological Society of Canada* 113(S116): 1–83. <https://doi.org/10.4039/entm113116fv>

- Schmid F (1982) Revision des Trichoptères Canadiens: II. Les Glossosomatidae et Philopotamidae (Annulipalpia). *Memoirs of the Entomological Society of Canada* 114: 1–76. <https://doi.org/10.4039/entm114122fv>
- Schmid F (1983) Revision des trichoptères canadiens III. Les Hyalopsychidae, Psychomyiidae, Goeridae, Brachycentridae, Sericostomatidae, Helicopsychidae, Beraeidae, Odontoceridae, Calamoceratidae et Molannidae. *Mémoires de la Société Entomologique du Canada* 125: 1–109. <https://doi.org/10.4039/entm115125fv>
- Schmid F (1998) Genera of the Trichoptera of Canada and adjoining or adjacent United States. The Insects and Arachnids of Canada, Part 7. NRC Research Press, Ottawa, Ontario, 319 pp.
- Schuster GA, Hamilton SW (1984) The genus *Phylocentropus* in North America (Trichoptera: Polycentropodidae). In: Morse JC (Ed.) *Proceedings of the 4th International Symposium on Trichoptera*, Clemson, South Carolina, 11–16 July 1983. W Junk Publishers, The Hague, Series Entomologica 30: 347–362.
- Smith DH (1975) The taxonomy of the Trichoptera (Caddisflies) of the Saskatchewan River System in Saskatchewan. MSc Thesis, University of Saskatchewan, Saskatoon, 273 pp.
- Smith DH (1984) Systematics of Saskatchewan Trichoptera larvae with emphasis on species from the boreal streams. PhD Thesis, University of Saskatchewan, Saskatoon, 1302 pp.
- Sturkie SK, Morse JC (1998) Larvae of the three common North American species of *Phylocentropus* (Trichoptera: Dipseudopsidae). *Insecta Mundi* 12(3–4): 175–179.
- Vineyard RN, Wiggins GB, Frania HE, Scheftner PW (2005) The caddisfly genus *Neophylax* (Trichoptera, Uenoidae). Royal Ontario Museum Contributions in Science 2: 1–148.
- Weaver JS (1984) The evolution and classification of Trichoptera, with a revision of the Lepidostomatidae and a North American synopsis of this family. PhD Thesis, Clemson University, Clemson, 411 pp.
- Weaver JS (1988) A synopsis of the North American Lepidostomatidae (Trichoptera). Contributions of the American Entomological Institute 24(2): 1–141.
- Weaver JS, Morse JC (1986) Evolution of feeding and case-making behavior in Trichoptera. *Journal of the North American Benthological Society* 5(2): 150–158. <https://doi.org/10.2307/1467869>
- Wiggins GB (1954) The caddisfly genus *Beraea* in North America. *Life Sciences Contributions of the Royal Ontario Museum* 39: 1–18.
- Wiggins GB (1956) A revision of the North American caddisfly genus *Banksiola* (Trichoptera: Phryganeidae). *Contributions of the Royal Ontario Museum Division of Zoology and Paleontology* 43: 1–12. <https://doi.org/10.5962/bhl.title.52191>
- Wiggins GB (1960) A preliminary systematic study of the North American larvae of the caddisfly family Phryganeidae (Trichoptera). *Canadian Journal of Zoology* 38: 1153–1170. <https://doi.org/10.1139/z60-120>
- Wiggins GB (1965) Additions and revisions to the genera of North American caddisflies of the family Brachycentridae with special reference to the larval stages (Trichoptera). *The Canadian Entomologist* 97: 1089–1106. <https://doi.org/10.4039/Ent971089-10>
- Wiggins GB (1979) Trichoptera. In: Danks HV (Ed.) *Canada and its insect fauna. Memoirs of the Entomological Society of Canada No. 108*, 482–484. <https://doi.org/10.4039/entm111108482-1>

- Wiggins GB (1996) Larvae of the North American Caddisfly Genera (Trichoptera). Second Edition (2005 reprint). University of Toronto Press, Toronto, Ontario, 457 pp.
- Wiggins GB (1998) The caddisfly family Phryganeidae (Trichoptera). University of Toronto Press, Toronto, Ontario, 306 pp.
- Wiggins GB (2004) Caddisflies: The Underwater Architects. University of Toronto Press, Toronto, Ontario, 292 pp. <https://doi.org/10.3138/9781442623590>
- Wiggins GB, Currie DC (2008) Trichoptera Families. In: Merritt RW, Cummins KW, Berg MB (Eds) An Introduction to the Aquatic Insects of North America. 4th Edition. Kendall/Hunt Publishing Co. Dubuque, Iowa, 439–480.
- Wiggins GB, Parker CR (1997) Caddisflies (Trichoptera) of the Yukon, with analysis of the Beringian and Holarctic species of North America In: Danks HV, Downes JA (Eds) Insects of the Yukon. Biological Survey of Canada (Terrestrial Arthropods), Ottawa, Ontario, 787–866.
- Wiggins GB, Weaver JS, Unzicker JD (1985) Revision of the caddisfly family Uenoidae (Trichoptera). The Canadian Entomologist 117: 763–800. <https://doi:10.4039/Ent117763-6>
- Wiggins GB, Wichard W (1989) Phylogeny of pupation in Trichoptera, with proposals on the origin and higher classification of the order. Journal of the North American Benthological Society 8(3): 260–276. <https://doi.org/10.2307/1467330>
- Winchester NN (1984) Life histories and post-glacial origins of tundra caddisflies (Trichoptera) from the Tuktoyaktuk Peninsula. MSc thesis, University of Victoria, Victoria, BC, 502 pp.
- Wymer DA, Morse JC (2000) Larva, pupa, and adults of *Glossosoma nigrior* (Trichoptera: Glos-sosomatidae) with a review of the eastern North American species of *Glossosoma*. Entomological News 111: 149–158.
- Yamamoto T, Wiggins GB (1964) A comparative study of the North American species of the caddisfly genus *Mystacides*. Canadian Journal of Zoology 42: 1105–1126. <https://doi.org/10.1139/z64-108>
- Zhou X, Adamowicz SJ, Jacobus LM, DeWalt RE, Hebert PDN (2009) Towards a comprehensive barcode library for arctic life – Ephemeroptera, Plecoptera, and Trichoptera of Churchill, Manitoba, Canada. Frontiers in Zoology 6: 1–30. <https://doi.org/10.1186/1742-9994-6-30>
- Zhou X, Frandsen PB, Holzenthal R, Beet CR, Bennett KR, Blahnik RJ, Bonada N, Cartwright D, Chuluunbat S, Cocks GV, Collins GE, deWaard J, Dean J, Flint Jr OS, Hausmann A, Hendrich L, Hess M, Hogg ID, Kondratieff BC, Malicky H, Milton MA, Morinière J, Morse JC, Mwangi FN, Pauls SU, Gonzalez MR, Rinne A, Robinson JL, Salokannel J, Shackleton M, Smith B, Stamatakis A, St Clair R, Thomas JA, Zamora-Muñoz C, Ziesmann T, Kjer KM (2016) The Trichoptera barcode initiative: a strategy for generating a species-level Tree of Life. Philosophical Transactions of the Royal Society B, Biological Sciences 371: 20160025. <https://doi.org/10.1098/rstb.2016.0025>
- Zhou X, Kjer KM, Morse JC (2007) Associating larvae and adults of Chinese Hydropsychidae caddisflies (Insecta: Trichoptera) using DNA sequences. Journal of the North American Benthological Society 26: 719–742. <https://doi.org/10.1899/06-089.1>