Zoosymposia 18: 118–126 (2020)
https://www.mapress.com/j/zs

ISSN 1178-9905 (print edition)
ZOOSYMPOSIA
ISSN 1178-9913 (online edition)

https://doi.org/10.11646/zoosymposia.18.1.15
http://zoobank.org/urn:lsid:zoobank.org:pub:326990D8-9701-4E3D-A01A-35B268A4A464

Origin of the Trichoptera species in Iceland

GÍSLI MÁR GÍSLASON & SNAEBJÖRN PÁLSSON
Institute of Life and Environmental Sciences, Askja-Natural Science Building, University of Iceland, Askja, IS-101 Reykjavik, Iceland.
snaebj@hi.is, https://orcid.org/0000-0002-4297-3500
Corresponding author: gmg@hi.is, https://orcid.org/0000-0001-8507-1796

Abstract

This paper focuses on the origin of Trichoptera species in Iceland in light of the island biogeography of caddisflies in the North-Atlantic islands, i.e., Greenland, Svalbard, Iceland, Faroe Islands, Shetland, and Orkney, and adjacent larger regions, Norway and Britain. Three of the 12 recorded species have circumpolar distribution, the other nine are Palaearctic. The number of species declines with the distance from the mainland of Europe and is independent of the island sizes. However, the occurrence of species is stochastic, with only a few species common to the more remote islands—e.g., Iceland has 12 species and the Faroe Islands 20, but only 4 species are common to both islands. Studies on phylogeographic patterns of two species, *Potamophylax cingulatus* and *Apatania zonella*, show different history based on genetic markers. *Potamophylax cingulatus* in Iceland is from a western European lineage, distinct from two eastern and southern European lineages that may have diverged in southern refugia during the glacial periods of the latest Ice Age. The ancestors of the Icelandic population have migrated from the Iberian Peninsula up the west cost of Europe to the Faroe Islands and Iceland. The parthenogenetic *A. zonella* in Iceland originated near the Bering Strait, and has migrated along two routes, one westward through northern Eurasia and the other eastward through North America and Greenland to Iceland, where the two populations meet. Preliminary phylogeographic studies on two other circumpolar species, *Limnephilus fenestratus* and *L. picturatus* indicate possible interchanges between North America and Europe, but due to a low number of samples, it is difficult to state where the Icelandic population came from.

Key words: Ice-age, aquatic insects, colonisation, Atlantic islands

Introduction

The North Atlantic islands have few aquatic invertebrate species, almost no aquatic endemics, but their faunas are closely related. With the exception of the high arctic island of Svalbard, Iceland presently has the fewest number of insect species. Sixteen hundred and six species have been recorded (1240 in the last published species list, Olafsson 1991, Olafsson pers. comm.) compared with the twenty thousand species in Norway and in Britain, the largest regions nearest Iceland. This raises the biogeographical question as to when and how the colonisation of Iceland and the other North Atlantic Islands took place.

The Tertiary climate was warm with relatively small latitudinal gradients and moist climate, and a tropical to subtropical flora and fauna flourished in Europe, reaching as far north as Svalbard and Ellesmere Islands (Downes 1988). Towards the end of the Eocene (34 Ma), a cooling trend became evident, first at high latitudes. The climate warmed again during the Miocene but then progressive cooling set in, culminating in the onset of the Quaternary 'Ice Age' some 2.6 Ma. During the last glacial maximum (22 Ka), ice covered almost all of Greenland, the present evidence indicating that only isolated nunataks and possibly fragments along coastal shelves remained ice-free (Brochmann *et al.* 2003). The late Weichselian ice sheet similarly covered virtually all of Svalbard, Iceland, Scandinavia, Scotland, and the Scottish isles, extending as far as southern Ireland and southern England (Brochmann *et al.* 2003, CLIMAP 1976), but in the Antarctic only the South Island (Te Waipounamu) of New Zealand and the small islands further south, were affected.

Some northern areas were, however, ice-free during the last cold period of the Weichselian period, due to low precipitation, and were refugial areas for migration into northern Europe. These were areas on both sides of the Bering Strait (Brochman *et al.* 2003) and southern Europe—i.e., Iberian Peninsula, Italy, Hungary, Romania, Bulgaria, the Balkans, and most of France (Hewitt 2000).

Submitted: 27 May 2019; Accepted by Pongsak Laudee: 7 Jan. 2020; published: 12 Jun. 2020

A recent review (Buckland & Panagiotakopulu, 2010), with special emphasis on the Faroe Islands, indicated that most or all insects colonised the North Atlantic Islands after the latest Ice Age.

Aquatic insects—a review of previous and present studies

The islands of the North Atlantic vary both in distance from the mainland of Europe (Table 1) and in size (Table 2). The distance from mainland North America is generally of less importance because Greenland, being a high Arctic environment, is a large barrier for the colonisation from the west (Downes 1988). Organisms had to travel a considerable distance from the mainland of Europe when colonising North Atlantic islands. Studies on invertebrates in Iceland, with emphasis on their origin, have focused on aquatic insects and crustaceans (Gíslason 2005) and have revealed mostly a European origin.

TABLE 1. Distances (km) between North Atlantic islands.

	Svalbard	Greenland	Iceland	Faroes	Norway	Shetland	Orkney
Svalbard							
Greenland	400						
Iceland	1548	290					
Faroes	1790	1025	435				
Norway	823	1441	971	582			
Shetland	1876	1411	770	284	289		
Orkney	2055	1492	850	316	419	78	
Britain	2120	1500	823	320	479	166	12

TABLE 2. Extent (x 1000 km^2) of ice free areas on North Atlantic islands, Norway, and Britain.

Norway	Shetland	Orkney	Britain	Faroe Islands	Svalbard	Iceland	Greenland
322.6	1.4	1.0	242.6	1.4	24.1	94.3	340.0

Aquatic insect groups, such as Ephemeroptera and Plecoptera, are non-existent on Svalbard and the Faroes and only a single ephemeropteran taxon is found in Greenland. Iceland has a single species for each group (Table 3), but islands close to Britain, such as Orkney and Shetland have 6–15 species. Of the Simuliidae (Diptera) only 2–5 species are found on the islands, whereas Chironomidae are much better represented, with 30–117 species recorded on the islands, compared to the 439 and 505 species recorded in Britain and Norway, respectively.

TABLE 3. Number of species of aquatic insects on islands in the North Atlantic and Norway (Andersen & Wiberg-Larsen 1987; Andrew 2014; Barry 1985; Crosskey 1965; Edington & Hildrew 1995; Elven & Andersen 2019; Hrafnsdóttir 2005; King 1890; Naturhistoriska Riksmusset 2018; Nilsson 1996, 1997; Peterson 1977; Pinder 1978; Pennington 2018a, 2018b; Wallace *et al.* 1990).

	Ephemeroptera	Plecoptera	Trichoptera	Simuliidae	Chironomidae
Svalbard	0	0	1	0	58
Greenland	1	0	7	5	117
Iceland	1	1	12	4	80
Faroes	0	0	20	2	72
Shetland	6	2	37	2	30
Orkney	15	13	73	2	?
Britain	47	34	198	34	439
Norway	46	35	195	45	505

The number of Trichoptera species varied from 7 to 73 species on all the islands except Svalbard (1 species) and Britain (198 species) (Gíslason 2005, Barnard and Ross 2012, Andrew 2014) (Table 3). All of the twelve Icelandic species are found in Scandinavia but only nine in Britain, with none of the three circumpolar species found in Iceland occurring in the British Isles (Fig. 1). Four of the species are shared with the Faroes, which in turn has 20 species (Fig. 1). Greenland has a few species in common with the other islands and with Norway (Fig. 1). All 20 Faroese species are also found in Britain, but only twelve in Norway. The species common to Greenland and Svalbard and found on the other islands and Norway have a circumpolar distribution. Other species found in Greenland are related to the North American fauna. The number of island species decreases significantly with distance from Britain (b = - 0.19 per 100 km, $P < 0.002$, $R2 = 0.975$) (Fig. 2)). Trichoptera species number does not increase significantly with increasing size of islands (Pearson's $r = 0.441$, $n = 8$, $p = 0.28$ NS), but the size of the islands may not reflect the number of suitable freshwater habitats. However, precise information of the area of lakes and rivers on the islands is not available, but seem to vary between 3% (Iceland) and 0.8% (the Faroe Islands). This does not include small waterbodies.

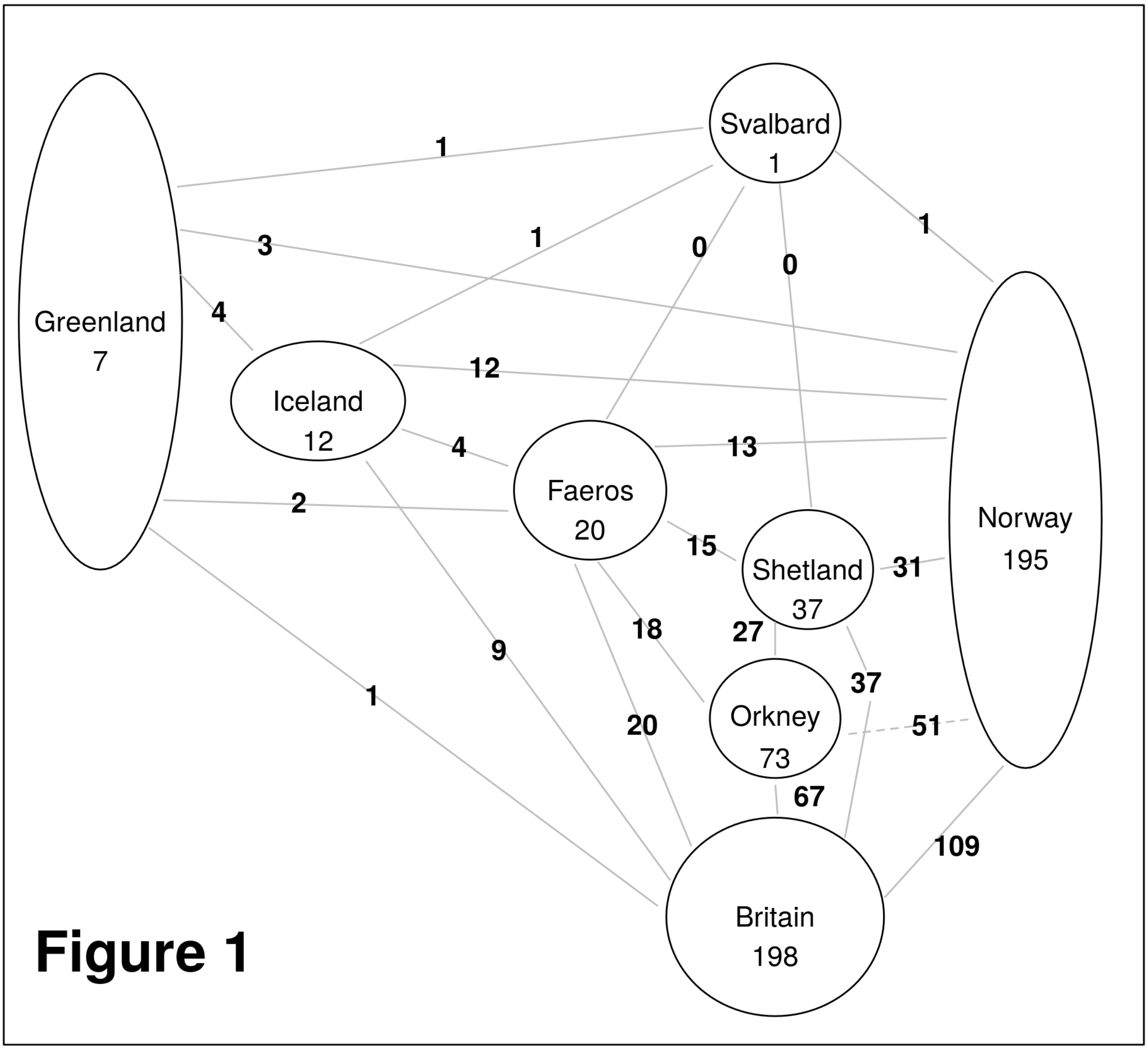

FIGURE 1. Numbers of Trichoptera species on the North Atlantic islands and the numbers of species they have in common.

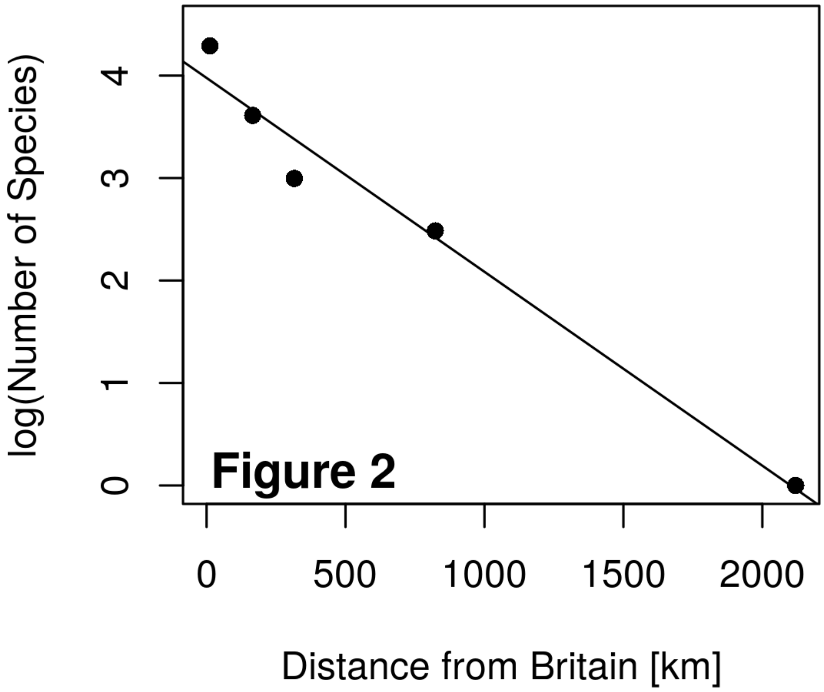

FIGURE 2. Number of Trichoptera species (ln) on the North Atlantic islands versus distance from the mainland of Britain (Greenland excluded).

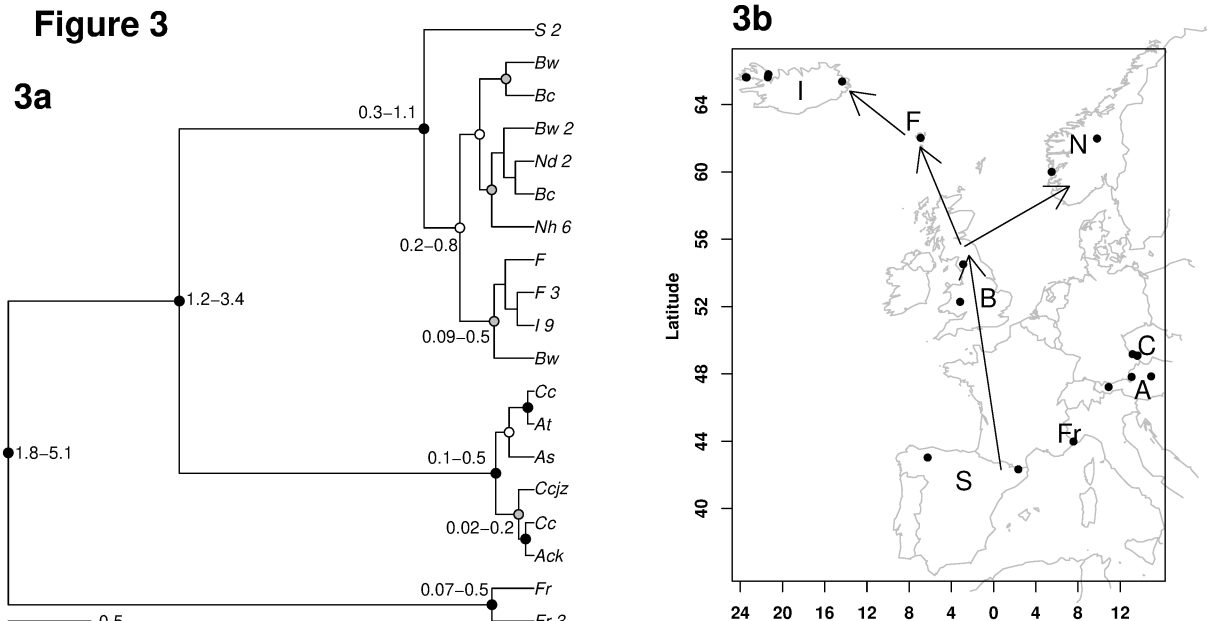

FIGURE 3. Phylogeography of *Potamophylax cingulatus* (Stephens 1837). 3a) Bayesian phylogeny based on the COI mtDNA haplotypes (barcode region) for *Potamophylax cingulatus*. Tip labels refer to geographical origin of unique haplotypes. Number at tip labels refer to the frequencies of haplotypes. Numbers at nodes refer to 95% confidence interval to the time of common ancestor in million years (Ma). Shadings at nodes refer to support or posterior probabilities P: black = $P > 0.95$, grey = $0.7 < P \leq 0.95$, white = $P \leq 0.7$. 3b) Estimated route of migration. I = Iceland, F = Faroe Islands, N = Norway, B = Britain, S = Spain, Fr = France, A = Austria, and C = Czech Republic (small letters after capital letters refer to different sampling locations within the countries) (from Gíslason *et al.* 2015).

In a study of the caddisfly *Apatania zonella* (Zetterstedt 1840), an arctic circumpolar, mainly parthenogenetic species with only 1–2% males (Corbet 1966; Gislason 1977; Raastad & Solem 1989), specimens were obtained from different parts of Iceland, Norway, Alaska, northern USA, Canada, and Greenland. The *A. zonella* specimens from Iceland, characterised by high genetic variation, originated from more than one colonisation event, with at least one from North America through Greenland and another from Scandinavia (Pálsson *et al.* 2016). The specimens in NW Iceland were generally more related to Scandinavian specimens, whereas specimens in SW and S Iceland were more similar to Greenlandic specimens. However, some admixture or interbreeding of the two lineages has occurred in Iceland (Pálsson *et al.* 2016). Another Palaearctic trichopteran species, *Potamophylax cingulatus* (Stephens 1837) colonised Iceland in the 20th century and was distributed in lowlands of East and Northeast Iceland until 1978 (Gíslason 1981; Gíslason *et al.* 2015). The species is now found in all lowland areas in Iceland (Gíslason *et al.* 2015). The species has diverged into at least three mtDNA lineages in Europe which may correspond to previously described subspecies, one in middle Europe (Austria, Czech Republic), a second in southeastern France, and one on the Iberian peninsula. Individuals from the Iberian population colonised Western Europe along the coast to the British Isles where one group dispersed to the Faroe Islands and Iceland and another to Scandinavia (Gíslason *et al.* 2015). The Icelandic specimens are, thus, more closely related to the Faroes and British specimens than to those from Scandinavia (Gíslason *et al.* 2015). A preliminary study on the genetic relationship of the two other circumpolar Trichoptera species, *Limnephilus fenestratus* (Zetterstedt 1840) and *L. picturatus* McLachlan 1875 indicates that some interbreeding occurred between European and North American populations (Figs. 5. and 6), but more samples are needed for conclusive results.

Discussion

There is no evidence of land bridges between the islands during the last 20 million years (see e.g., Heezen & Tharp 1963). The pre-Pleistocene fauna was similar to the present day fauna of North America (Friedrich *et al.* 1972), while the contemporary fauna is mainly of Palaearctic origin. As Iceland and the other islands in the North Atlantic discussed here were covered by glaciers during the last glacial maximum, the patterns in species composition of the different islands are due to dispersal and colonisation after the latest glaciation event 10–15 thousand years ago. Thus, the present day caddis fauna of Iceland has only a single Arctic species, *Apatania zonella* (Fig. 1) (Gislason 1981).

The maximum extent of the ice sheet during the Late Weichselian limited ice-free areas and these were likely to have been on Andøya in Lofoten and on SW Coast of Norway, with some in the Faroes and on the Outer Hebrides and NW Scotland. Southern England and Ireland were also ice-free. Iceland and Svalbard were most likely entirely covered by ice, while according to Brochmann *et al.* (2003) some nunataks in Greenland might have been ice-free. The Trichoptera fauna on the North Atlantic islands has a boreal distribution (Fig. 1), related to the present fauna of continental Norway and northern Britain. Thus, it is neither related to the pre-Ice Age fauna, nor are there arctic species to any extent, except in the present high Arctic (Svalbard and N-Greenland), which would be expected if some species had survived the Ice Age.

The number of species of Trichoptera declines with distance from continental Europe (Fig. 2), but not with island area. Insects, like Trichoptera, do not have life stages that can be transported by birds and usually disperse on the wing. It is also possible that at the end of the Ice Age, when pack ice covered the Arctic Ocean as far south as Iceland, a number of insect species were transported by floating ice from Norway and the British Isles to the North Atlantic islands (Buckland *et al.* 1986). The isolated position of Iceland explains why the Trichoptera fauna is poorly represented here, making up only 6% of the total Trichoptera fauna of Norway and Britain. Further, the Trichoptera fauna has also been isolated in relation to colonisation from Greenland, having an almost entirely Nearctic origin (Böcher 2002).The importance of relatively recent colonisation is also supported by the fact that almost all invertebrate species in Iceland (> 95%) have a boreal distribution in the Palaearctic region, with only a few species with a circumpolar distribution. Only the high arctic species would have survived the harsh arctic environment. Geological evidence (Geirsdóttir *et al.* 2009, 2013) strongly suggests that ice-free areas hardly existed in Iceland during the coldest period of the Ice-age, making it impossible for terrestrial invertebrates, or invertebrates with a terrestrial life stage to survive.

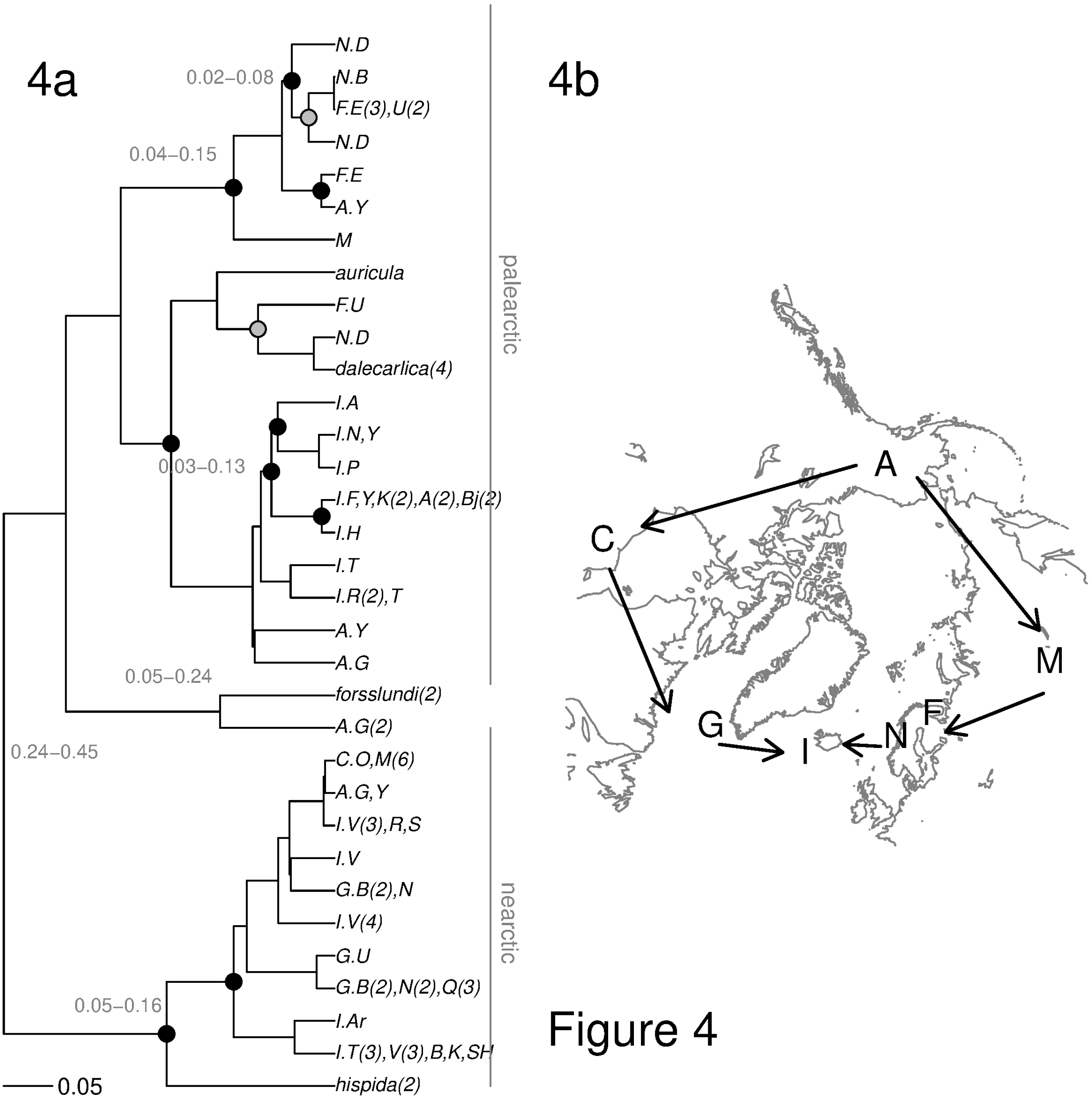

FIGURE 4. Phylogeography of *Apatania* spp. 4a) A Bayesian genealogy of cytochrome c oxidase subunit I barcode region (COIa) sequences within *Apatania zonella* (Zetterstedt 1840) and 4 other *Apatania* species (*Apatania auricula* Forsslund 1930*, A. dalecarlica* Forsslund 1942 (in Forsslund & Tjeder 1942)*, A. forsslundi* W. Tobias 1981*,* and *A. hispida* (Forsslund 1930)). The tree was rooted with a sequence from *Limnephilus centralis* Curtis 1834 and included *A. muliebris* McLachlan 1866, *A. wallengreni* McLachlan 1871, and *A. stigmatella* (Zetterstedt 1840) (not shown). The divergence time of *A. muliebris, A. wallengreni*, and *A. stigmatella* from the specimens shown in the tree was in the same order of magnitude (1.6, 3.6, and 3.9 Ma). Posterior probabilities (P > 0.95) are shown at the nodes. Intervals represent 95% confidence intervals for the time to common ancestor. The unit of the scale bar is Ma. 4b) Estimated route of migration A = Alaska, Yukon, C = Canada, G = Greenland, I = Iceland, N = Norway, F = Finland, and M = Mongolia (small letters after capital letters refer to different sampling locations) (from Pálsson *et al.* 2016).

Figure 5

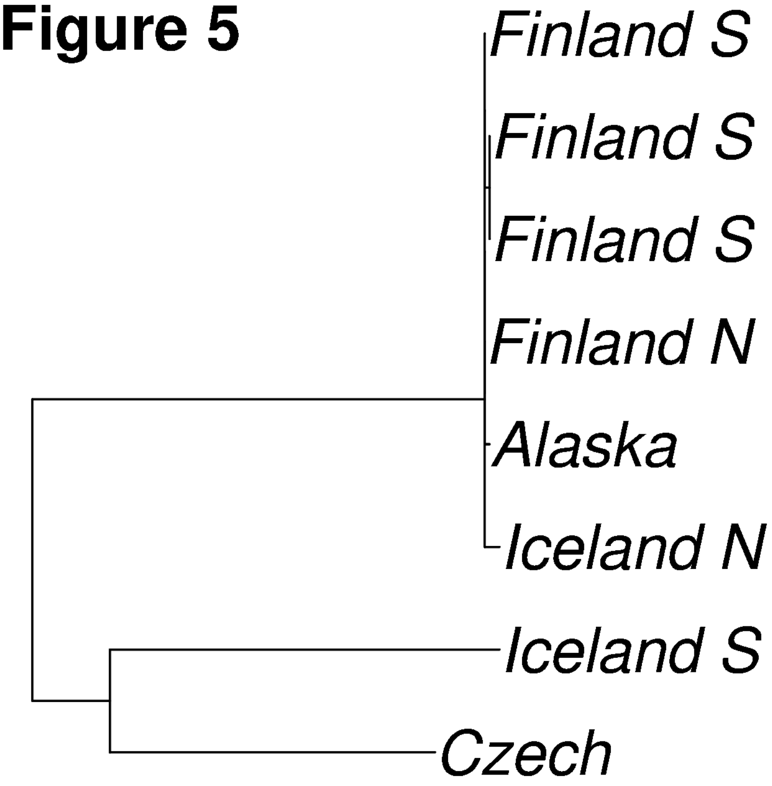

FIGURE 5. A Bayesian genealogy of cytochrome c oxidase subunit I barcode region (COIa) sequences within *Limnephilus fenestratus* (Zetterstedt 1840). Only two samples from Iceland were available. (Unpublished records from the BOLD database).

Figure 6

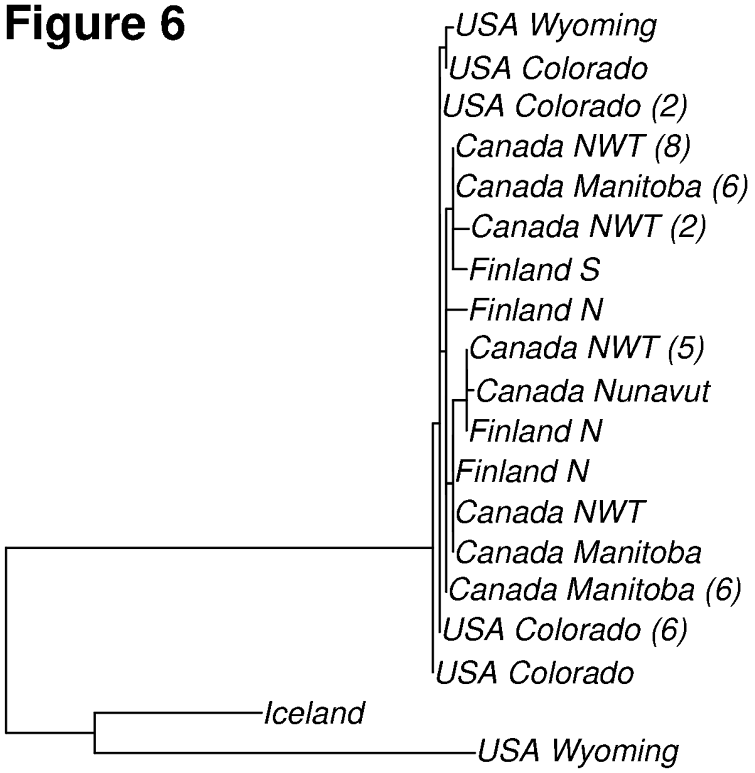

FIGURE 6. A Bayesian genealogy of cytochrome c oxidase subunit I barcode region (COIa) sequences within *Limnephilus picturatus* McLachlan 1875. Only one sample from Iceland was available. (Unpublished records from the BOLD database)).

This analysis, with the exception of the endemism found amongst crustaceans (Kornobis *et al.* 2010) in subterranean groundwater systems, seems to fit well with a Holocene origin of higher plants in Iceland and on the other North Atlantic islands (Aegisdóttir & Thórhallsdóttir 2004).

Acknowledgement

Thanks are due to Ms Elísabet R. Hannesdóttir for Trichoptera collection in 1996, Ms Laurène Alicia Lecaudey and Ms Sonia S. Munoz for their genetic analysis of *Apatania zonella* and *Potamophylax cingulatus,* respectively, and Dr. Karl Kjer for information obtained from the BOLD database. We thank the caddisfly experts Dr. Peter Wiberg-Larsen and Trond Andersen Cand. scient. for their critical review of the manuscript.

References

Aegisdóttir, H.H. & Thorhallsdóttir, T.E. (2004) Theories on migration and history of the North-Atlantic flora: Areview. *Jökull*, 54, 1–16.

Andersen, T. & Wilberg-Larsen, P. (1987) Revised check-list of NW European Trichoptera. *Entomologica scandinavica*, 18, 165–184.

Andrew, R.H. (2014) Orkney caddis (Trichoptera) species list with ecological notes: Part 1. *Orkney Field Club Bulletin*, 2014, 43–52

Barnard, P. & Ross, E. (2012) The adult Trichoptera (caddisflies) of Britain and Ireland. *Handbooks for the Identification of British Insects*, 1. Part 17, 192 pp.

Barry, J.R. (1985) *The natural history of Orkney*. Collins, London, 300 pp.

Böcher, J. (2002) *Insekter og andre smådyr—I Grønlands fjeld og ferskvand*. Forlaget Atuagkat, Nuuk, 302 pp.

Brochmann, N.C., Gabrielsen, T.M., Nordal, I., Landvik, J.Y. & Elven, R. (2003) Glacial survival or tabula rasa? The history of North Atlantic biota revisited. *Taxon*, 52, 417–450.
https://doi.org/10.2307/3647444

Buckland, P.C. & Panagiotakoulu, E. (2010) Reflections on North Atlantic Island Biogeography: a Quaternary entomological view. *Annales Societatis Scientiarum Færoensis Supplimentum*, 52, 181–209.

Buckland, P.C., Perry, D.W., Gíslason, G.M. & Dugmore, A.J. (1986) The pre-Landnám fauna of Iceland: A palaeoontological contribution. *Boreas*, 15, 173–184.
https://doi.org/10.1111/j.1502-3885.1986.tb00081.x

CLIMAP (1976) The surface of the ice age earth. *Science*, 191, 1131–1144.
https://doi.org/10.1126/science.191.4232.1131

Corbet, P.S. (1966) Parthenogenesis in caddisflies (Trichoptera). *Canadian Journal of Zoology*, 44, 981–982.
https://doi.org/10.1139/z66-100

Crosskey, R.W. (1965) A new species of *Simulium* (*Eusimulium*) from St. Helena Island, South Atlantic (Diptera: Simuliidae). *Proceedings of the Royal Entomological Society of London B*, 34, 33–37.
https://doi.org/10.1111/j.1365-3113.1965.tb01646.x

Curtis, J. (1834) Description of some hitherto nondescript British species of mayflies of anglers. *The London and Edinburgh Philosophical Magazine and Journal of Science*, 3 (4), 120–125, 212–218.
https://doi.org/10.1080/14786443408648304

Downes, J.A. (1988) The post-glacial colonization of the North Atlantic islands. *Memoirs of the Entomological Society of Canada*, 144, 55–92.
https://doi.org/10.4039/entm120144055-1

Edington, J.M. & Hildrew, A.G. (1995) *A Revised Key to the Caseless Caddis Larvae of the British Isles*: *A Key with Ecological Notes*. Freshwater Biological Association, Ambleside, Scientific Publication No. 53, 134 pp.

Elven, H. & Andersen, T. (2019). Nøkkel til vårfluefamilier. Artsbanken. Available from: https://www.artsdatabanken.no/Pages/262183?Key=1518696646 (accessed 4 March 2019)

Forsslund, K.H. (1930) Zwei neue *Apatelia*-Arten (Trichoptera, Limnophiliden). *Entomologisk Tidskrift*, 51, 216–218.

Forsslund, K.H. & Tjeder, B. (1942) Catalogus insectorum Sueciae. II. Trichoptera. *Opuscula Entomologica*, 7, 93–106.

Friedrich, W.L., Símonarson, L.A. & Heie, O.E. (1972) Steingervingar í millilögum í Mókollsdal (English summary: Tertiary fossils from Mókollsdalur, NW-Iceland). *Náttúrufræðingurinn*, 42, 4–17.

Geirsdóttir, Á., Miller, G.H., Axford, Y. & Ólafsdóttir, S. (2009) Holocene and latest Pleistocene climate and glacier flutctuations in Iceland. *Quaternary Science Reviews*, 28, 2107–2118.
https://doi.org/10.1016/j.quascirev.2009.03.013

Geirsdóttir, Á., Miller, G.H., Larsen, D.J. & Ólafsdóttir, S. (2013) Abrupt Holocene climate transitions in the northern North Atlantic region recorded by synchronized laustrine records in Iceland. *Quaternary Science Reviews*, 71, 48–62.

https://doi.org/10.1016/j.quascirev.2013.03.010

Gíslason, G.M. (1977) Aspects of the biology of Icelandic Trichoptera, with comparative studies on selected species from Northumberland, England. Ph.D. Dissertation, Department of Zoology, University of Newcastle upon Tyne, 412 pp.

Gíslason, G.M. (1981) Distribution and habitat preferences of Icelandic Trichoptera. *In*: Moretti, G.P. (Ed.), *Proceedings of the 3rd International Symposium on Trichoptera*. Dr. W. Junk Publishers, The Hague, Series Entomologia. 20, pp. 99–109. https://doi.org/10.1007/978-94-009-8641-1_14

Gíslason, G.M. (2005) The origin of the freshwater fauna of the North-Atlantic Islands. Present distribution in relation to climate and possible migration routes. *Verhandlungen der Internationale Vereinigung für Theoretische und Angewandte Limnologie*, 29, 198–203. https://doi.org/10.1080/03680770.2005.11901995

Gíslason, G.M., Hannesdóttir, E.R., Munoz, S.S. & Pálsson, S. (2015) Origin and dispersal of *Potamophylax cingulatus* (Steph.) (Trichoptera: Limnephilidae) in Iceland. *Freshwater Biology*, 60, 387–394. https://doi.org/10.1111/fwb.12501

Heezen, B.C. & Tharp, M. (1963) The Atlantic floor. *In*: Löve, A. & Löve, D. (Eds.), *North Atlantic Biota and Their History*. Pergamon Press, Oxford, pp. 21–27.

Hewitt, G. (2000) The genetic legacy of the Quaternary ice ages. *Nature*, 405, 907–913. https://doi.org/10.1038/35016000

Hrafnsdóttir, Th. (2005) Diptera 2 (Chionomidae). *Zoology of Iceland*, 3 (48), 1–169.

King, J.J.F.X. (1890) Neuroptera from the island of Unst. *Entomologist's Monthly Magazine* (2), 1 (26), 176–180.

Kornobis, E., Pálsson, S., Kristjánsson, B.K. & Svavarsson, J. (2010) Molecular evidence of the survival of subterranean amphipods (Arthropoda) during Ice Age underneath glaciers in Iceland. *Molecular Ecology*, 19, 2516–2530. https://doi.org/10.1111/j.1365-294X.2010.04663.x

McLachlan, R. (1866) Note respecting a species of *Apatania*. *Entomologist's Monthly Magazine*, 3, 113.

McLachlan, R. (1871) Notes on the Trichoptera of Zetterstedt's "Insecta Lapponica," in connection with the nomenclature of British species. *Entomologist's Monthly Magazine*, 7, 281–282.

McLachlan, R. (1875) *A monographic revision and synopsis of the Trichoptera of the European fauna*, *Part 2*. John van Voorst, London, pp. 47–108. https://doi.org/10.5962/bhl.title.28556

Naturhistoriska Riksmusset (2018) Check-list of Norwegian Trichoptera. Available from: http://www2.nrm.se/en/trichopteranorway.html (accessed 8 May 2018)

Nilsson, A. (Ed.) (1996) *Aquatic Insects of North Europe*. A Taxonomic Handbook. Apollo Book, Stenstrup, Denmark.

Nilsson, A. (Ed.) (1997) *Aquatic Insects of North Europe 2*. A Taxonomic Handbook. Apollo Book, Stenstrup, Denmark.

Ólafsson, E. (1991) *Íslenskt skordýratal.* (*A checklist of Icelandic insects*). Icelandic Institute of Natural History report no. 17, 69 pp. [In Icelandic, English summary]

Pálsson, S., Lecaudey, L.A. & Gíslason, G.M. (2016) Phylogeographic origin of *Apatania zonella* (Trichoptera) in Iceland. *Freshwater Science*, 35, 65–79. https://doi.org/10.1086/684850

Pennington, M. (2018a) Trichoptera. Available from: http://www.nature-shetland.co.uk/entomology/caddis.htm (accessed 8 May 2018)

Pennington, M. (2018b) Diptera. Available from: http://www.nature-shetland.co.uk/entomology/diptera.htm (accessed 8 May 2018)

Peterson, B.V. (1977) The black flies of Iceland (Diptera: Simuliidae). *Canadian Entomologist*, 109, 449–472. https://doi.org/10.4039/Ent109449-3

Pinder, L.C.V. (1978) *A Key to Adult Males of British Chironomidae.Vol. 1–2*. Freshwater Biological Association, Ambleside, Scientific Publication No. 37, 169 pp.

Raastad, J.E. & Solem, J.O. (1989) Autogeny as successful reproductive strategy in high altitude blackflies (Diptera, Simuliidae). *Annales de Limnologie*, 25, 243–249. https://doi.org/10.1051/limn/1989026

Stephens, J. (1836–1837) *Illustrations of British Entomology*; *or a Synopsis of Indigenous Insects*: *Containing their Generic and Specific Distinctions*; *with an Account of their Metamorphoses*, *Times of Appearance*, *Localities*, *Food*, *and Economy*, *as far as Practicable*. *Mandibulata*. *Vol. VI*. Baldwin and Cradock, London.

Tobias, W. (1981) Eine neue *Apatania*-Art aus Norwegen (Trichoptera: Limnephilidae). *Entomologische Zeitschrift*, 91, 62–65.

Wallace, I.D., Wallace, B. & Philipson, G.N. (1990) *A Key to the Case-bearing Caddis Larvae of Britain and Ireland*. Freshwater Biological Association, Ambleside, Scientific Publication No. 51, 237 pp.

Zetterstedt, J.W. (1840) *Fauna Insectorum Lapponica*. *Vol. 5*. Leipzig. https://doi.org/10.5962/bhl.title.8242