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RESEARCH

The distribution of *Smittia brevipennis* (Diptera, Chironomidae, Orthocladiinae) in the Russian high-Arctic assessed using molecular analyses

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Abstract
Smittia brevipennis (Diptera, Chironomidae) has sporadic distribution across the circumpolar Arctic with only two localities known from the Russian Arctic. Here we report two new localities for this species from the Russian high-Arctic: the Franz Josef Land Archipelago and the Vize Island. Morphological descriptions of larvae and female imago are given, and cytochrome c oxidase I (COI) gene sequences are obtained and compared within available COI sequences for the genus *Smittia* worldwide. The COI sequences of *S. brevipennis* showed no variability across its circumpolar range including Canada, Alaska, Svalbard, Franz Josef Land and Vize Island. It is unique for the chironomids inhabiting such an extensive range and may not only indicate relatively recent and rapid colonization of the high-Arctic areas by *S. brevipennis,* but also can be explained by small sample size or the COI gene may be not an appropriate sequence for some *Smittia* species including *S. brevipennis*. Possible ways and means of historical dispersal across the circumpolar range of this brachypterous parthenogenetic orthoclad chironomids are discussed. The most likely way of *S. brevipennis* dispersal is rafting by drift ice or driftwood.

Keywords Arctic · Vize Island · Franz Josef Land · Cytochrome c oxidase I (COI) · Dispersal · Nonbiting midges · Brachyptery

Introduction

Smittia brevipennis (Boheman 1856) is a brachypterous parthenogenetic (Saether 2004) species of orthoclad chironomids (Chironomidae, Orthocladiinae) with peculiar ecology and sporadic distribution across the circumpolar Arctic including Norway (Svalbard), Russia, USA (Alaska), and Canada. It is the type species of the genus *Smittia* Holmgren 1869, described from Svalbard (Holmgren 1869; Stur and Ekrem 2020; Coulson et al. 2024).

The only two locations in the north-western Taimyr and the New Siberian Islands, both east of 90^0 E, were known from the Russian Arctic (Saether 2004) after the samples collected by A. A. Birula during the First Russian Polar Expedition of the Academy of Sciences led by Baron von Toll (1900–1903) and from the samples collected by M. I. Brussnew during the subsequent rescue expedition led by lieutenant A. Kolchak (1903); both collections were delivered to the collection of C. Lundström (1915). During our research, adult females and larvae were found in two new areas: the Franz Josef Land Archipelago, northern Barents Sea, and the Vize Island, northern Kara Sea, Russian high-Arctic.

Ways of colonization of the remote islands and adaptations to establishing and survival under harsh Arctic conditions are the two questions to be addressed in the ecology of little-studied sporadically distributed high-Arctic species, *S. brevipennis*.

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In some biological features, *S. brevipennis* is similar to the brachypterous parthenogenetic Antarctic orthoclad chironomids *Eretmoptera murphyi* Schaeffer, 1914. Larvae of both species are terrestrial (Cranston 1985; orig.), and no males have been observed to date. However, the population genetic structure of the two species differs.

Amongst chironomids, parthenogenesis is a relatively rare phenomenon found in 21 species of Chironominae, 36 Orthocladiinae and 4 Telmatogetoninae (Lindeberg 1971; Armitage et al. 1995; Gokhman and Kuznetsova 2017; Lackmann et al. 2020; Sperling and Glover 2023).

Parthenogenesis is an adaptation of chironomids to survive in harsh environments (Lackmann et al. 2020). Parthenogenetic populations are usually small in size, and females are theoretically capable of producing offspring themselves, reducing the risk associated with finding a mate and allowing for rapid population and productivity growth (Lackmann et al. 2020). In the Northern Hemisphere, isolated parthenogenetic populations within bisexual species are more often found at high latitudes and altitudes (for example, on barren tundra of Arctic islands) under unstable conditions. Asexual populations at the margin of a species range can lead to geographic isolation of bisexual and unisexual populations (geographic parthenogenesis; Vandel 1928). Chironomids inhabiting high latitudes and surviving harsh environmental conditions usually have sexual populations at the warmer edge of their range, e.g., *Paratanytarsus laccophilus* species group (Lackmann et al. 2020), *P. grimmii* (Carew et al. 2013), and *Tanytarsus heliomesonyctios* (Orel and Semenchenko 2019; Stur and Ekrem 2020). At the same time, in Antarctica this phenomenon is not observed (Allegrucci et al. 2012).

The question of colonization of the remote islands of the Arctic Ocean by terrestrial invertebrates and plants is widely discussed. There are two major hypotheses to explain the formation of insular faunas after the Last Glacial Maximum (LGM): the tabula rasa hypothesis (no LGM survival followed by immigration) and the nunatak hypothesis (LGM survival on mountains protruding through the ice sheet) (Birks 1993, 1994; Coulson et al. 2014). According to Birks (1993), no statistically significant evidence exists to support the hypothesis that nonglaciated areas and nunataks are able to explain the current distribution of alpine plants in Norway. Moreover, recent findings of plant macrofossils beyond the margins of the last ice sheet have further reduced the position of the nunatak hypothesis (Birks 1994; Johansen and Hytteborn 2001).

There are several possible means of colonization of remote Arctic islands: wind, oceanic currents including rafting (drift ice and driftwood), birds, mammals, and human (McAlpine 1965; Coulson et al. 2002). Many invertebrate taxa reach remote locations by active flight. Despite the lack of wings in many arthropods, their likelihood of being effectively wind-dispersed is high, owing to their small size or adaptive dispersal strategies (Thomas and Jepson 1999; Coulson et al. 2003).

Birds can carry small arthropods both in their feathers and along with nesting material (Lebedeva and Krivolutsky 2003). Chironomid larval head capsules in nesting material of birds have been recorded in Svalbard (Pilskog et al. 2014; Stur and Ekrem 2020).

Large mammals may occasionally transport mites, spiders, springtails, and insects from one island to another. Both their immature stages and adults may frequently become caught in the hair, particularly when the animals lie down, and conceivably they could be transported long distances when they move on (McAlpine 1965).

Fewer researches have considered the possibility of long-distance dispersal of biota with drifting ice and driftwood in the northern hemisphere (i.e., Johansen and Hytteborn 2001), however already Darwin (1859) assumed icebergs loaded with soil and stones to be occasional dispersal agents in the Arctic.

All the above-mentioned colonization processes differ from each other in their speed. Molecular-genetic methods can be used to estimate the colonization rate and to address the question on the probable dispersal ways of *S. brevipennis*. We performed genetic analysis and compared the gene COI sequences of the specimens obtained in our study with those available from other parts of the species' range. Based on the low genetic diversity revealed in our study, a hypothesis has been put forward regarding the historical dispersal of *S. brevipennis* across the islands and mainland coast of the Arctic Ocean. Below, we discuss the results of genetic analysis and provide a description of the morphology of the female imago and larvae from new localities in the Russia high-Arctic.

Materials and methods

In the Franz Josef Land Archipelago, adult females (approx. $n = 10$) were collected in 2012, 2013, 2016, and 2021 from plants by Hand and fixed with 70% ethanol; larvae were collected in 2016 from soil by Hand and fixed with 70% ethanol. On the Vize Island, four 50 × 50 cm freshwater benthic samples and a single soil sample were taken for larval examination in 2022. All the samples were washed with water through 300 µm mesh, fixed in situ with a strong solution of table salt and stored at ambient temperature. Larvae were extracted in the laboratory. Permanent preparations in sandarac medium without chloral hydrate were made from the individual specimens (Krasheninnikov 2011). Additionally, we checked close-up in situ photos of flowering plants from both localities in search of insects.

The morphological terminology, measurements and abbreviations followed Sæther (1980). Measurements and lab photos were taken using a Zeiss Axio Imager. A series of images taken at different focal planes were stacked using Helicon Focus software.

Total genomic DNA was extracted from the thorax of one imago specimens and whole body of four larvae using a DNeasy Blood and Tissue Kit (Qiagen, Hilden, Germany) or an Evrogen Extract DNA Blood & Cells following the manufacturer's instructions. The standard barcode region of the mitochondrial gene cytochrome c oxidase I (COI) was amplified using the primers LCO1490 and HCO2198 (Folmer et al. 1994). The PCRs involved a heating step at 95 °C for 30 s, followed by 35 cycles of denaturation at 95 °C for 30 s, annealing at 48 °C for 30 s and elongation at 72 °C for 1 min, with a final extension phase of 72 °C for 5 min. PCR was performed in a 10 µl reaction volume using 5 µl of Go Taq Green Master Mix (Promega Corp., Madison, WI, USA), 0.5 µM of each primer, 3 µl of nuclease-free water, and 1.5 µl of genomic DNA. The PCR products were confirmed by electrophoresis on a 1.5% agarose gel. Four out of five specimens had positive PCR products. Amplification products were purified by exonuclease I (ExoI) and alkaline phosphatase (FastAP) (Thermo Fisher Scientific, Inc., USA) and bidirectionally sequenced by an ABI 3130 × sequencer (Applied Biosystems) using the BigDye Terminator v3.1 cycle kit. Inter- and intraspecific genetic distances were also calculated based on the observed p-distances using MEGA7.

In addition to our own data COI barcodes from the Barcode of Life Data System (http://www.boldsystems.org/, accessed on 10 January 2025) of each unique barcode index number (BIN) corresponding to defined to the species level *Smittia* species were added to the dataset. Moreover, *S. stercoraria, S. aterrima, S. leucopogon, S. edwardsi, S. pratorum* belonged to several BINs, whilst *S. pratorum* and *S. nudipennis* belonged to one BIN (Fig. 1). We also used one sequence of *S. brevipennis* collected from each unique locality (Table 1, Fig. 1).

Phylogenetic analysis was performed using Bayesian inference (BI) in the software MrBayes ver. 3.2.7 (Ronquist et al. 2012). PartitionFinder 2.1.1 (Lanfear et al. 2012) was used to select the best-fit partitioning scheme and models separately for each codon position of protein-coding genes using the greedy algorithm with linked branch lengths for the corrected Bayesian information criterion as the optimality criterion for model selection. The best models for the first, second and third codon positions of COI were GTR + I (Tavare 1986), F81 + I (Felsenstein 1981) and HKY + G (Hasegawa et al. 1985), respectively. Four Markov chains (three heated chains, one cold) were run for 5 million generations, with the first 25% of the sampled trees discarded as burn-in. Ttrace files from BI analysis were visually inspected in Tracer 1.7 (Rambaut et al. 2018), and the tree was subsequently visualized in FigTree v. 1.4.4. The obtained sequences have been deposited in GenBank under numbers OR922272–OR922275.

Results

Distribution and habitats

During our study *S. brevipennis* was found in two new localities from the Western Russian high-Arctic, including remote Franz Josef Land Archipelago (N 81.2013°, E 55.559°) and offshore Vize Island (N 79.4872°, E 76.9948°).

All adult females in the Franz Josef Land were observed in terrestrial habitats with tundra vegetation. In addition to the collected specimens, imagoes were observed on yellow-coloured flowers of sulphur buttercup *Ranunculus sulphureus* (Sol., 1774) and the polar poppy *Papaver radicatum* subsp. *polare* (Tolm., 1923) (Fig. 2). No adults were found on the Vize Island despite reasonable efforts applied in 2020.

On the Vize Island, *S. brevipennis* larvae ($n = 8$) were collected in the only habitat under the small colony of kittiwakes *Rissa tridactyla* (Stephens 1826). The larval abundance was 32 ind./m^2, and the biomass was estimated to be 16 mg/m^2. The substrate consisted of slightly wet ornithogenic soil containing lots of bird guano, feathers, nesting materials (including fragments of seaweed) and bird food remains.

A single larva from Franz Josef Land was collected from wet soil near a small stream on a low marine terrace in Tikhaya Bay, Hooker Island.

Morphology of female imago and larvae

Detailed descriptions of *S. brevipennis* are given for the specimens collected in the Russian high-Arctic for the first time.

Smittia brevipennis (Boheman 1856)

Chironomus brevipennis Boheman 1856: 575.

Smittia brevipennis Boheman sensu Lundström (1915: 20).

Metriocnemus sibiricus (Lundström 1915) misidentification in Krasheninnikov and Gavrilo 2013: 160; Krasheninnikov and Gavrilo 2014: 3

Figures 3 and 4

Material examined

Altogether, 7 female imagoes and 9 larvae were examined.

The Franz Josef Land Archipelago includes the following: 1 adult female; 1 larva, Jackson Island, Nansen and Johansen wintering site; 11.VIII.2016, N 81.20134° E 55.55901°; A.B., Krasheninnikov; 1 adult female, Hayes Island, nearby

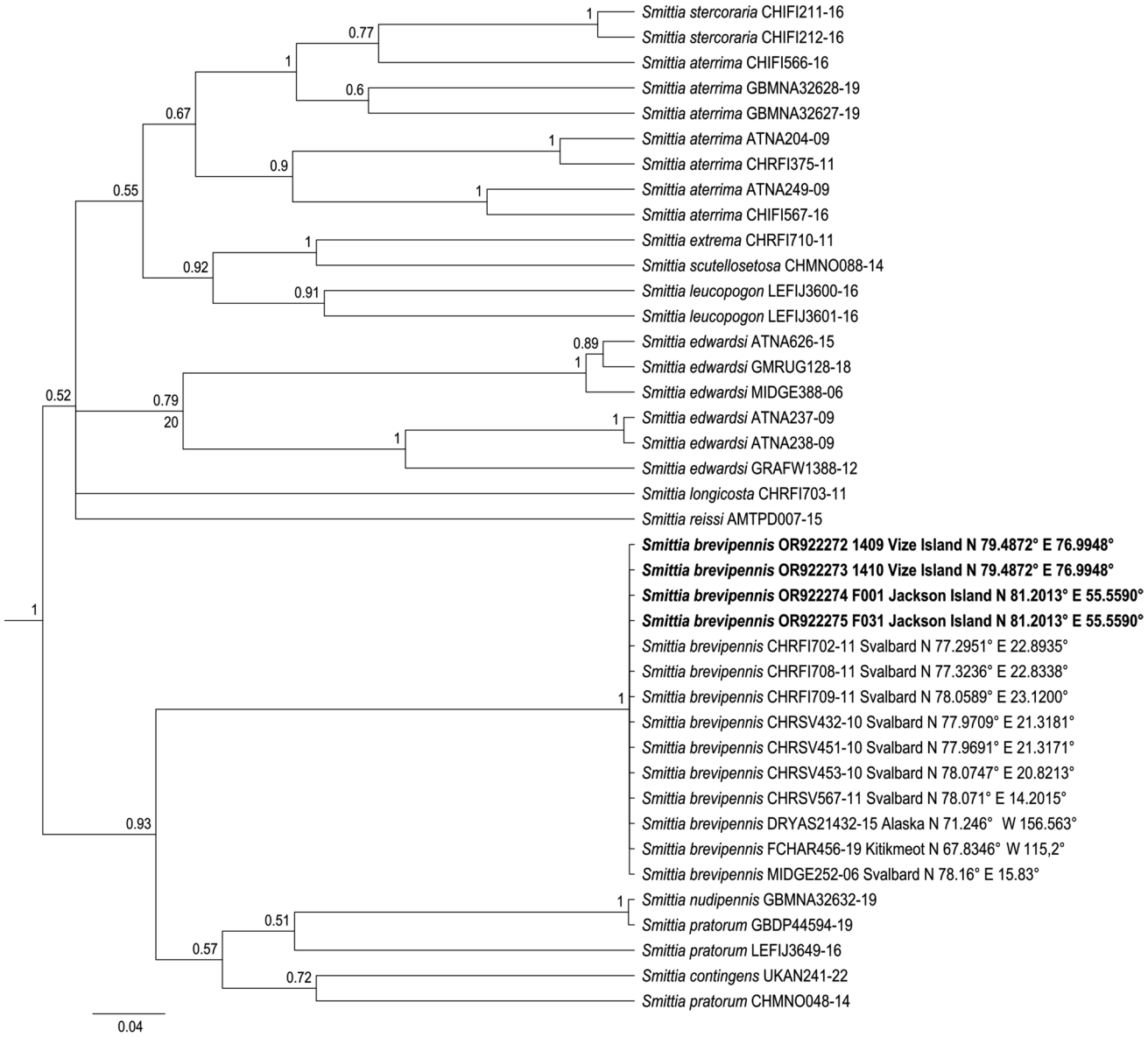

Fig. 1 Bayesian inference (BI) trees based on the cytochrome c oxidase I probabilities (higher than 0.7) are given above the tree nodes. Specimens obtained in this study are in bold

Krenkel weather station; 09.VIII.2012, N 80.631019° E 58.12812°; M.V., Gavrilo; 1 adult female, George Land, south coast between Niel and Krauter capes 13.VIII.2012, N 80.2522° E 46.90636°; M.V., Gavrilo; 1 adult female, Hooker Island, Rubini Rock, 02.VIII.2013, N 80.317417° E 52.85125°, M.V., Gavrilo; 3 adult females, West Northbrook Island, Cape Flora, 21.VII.2021, N 79.94992° E 50.11263°, M.V., Gavrilo.

The Vize Island: 8 larvae, top layer of ornithogenic soil under a kittiwake colony, 28.VIII.2022, N 79.487190° E 76.994830°, M.V. Gavrilo, V.G. Pchelinzev, A.V. Bezrukov.

FEMALE IMAGO ($n = 3$).

Figure 3

The total length was 2.66–2.89 mm. Wing length 0.72–0.76 mm, reduced. The total length/wing length was 3.55–4.02. The colouration was blackish brown.

Head. Eye pubescent, reniform. AR 0.42–0.44. The lengths of the flagellomeres (in μm) are 67–78, 47–51, 47–55, 55, and 98. Antenna apex with strong subapical seta. Temporal setae 7–8, consisting of 2–3 inner verticals, 3–4 outer verticals, and 2 postorbitals. Clypeus with 10–12 setae. Palpomere lengths (in μm): 31, 31–35, 63–71, 59–67, 71–82. Head width 360–390 μm.

Thorax. Antepronotum with 3–6 lateral setae. Acrostichals 3–8 (starting near antepronotum); dorsocentrals

Table 1 Data on *Smittia brevipennis* specimens used for molecular genetic analysis ($n = 32$)

Process IDs	*N*	Life stage/sex	Country/State	Region/Exact Site	Coordinates
FCHAR450-19 FCHAR454-19 FCHAR451-19 FCHAR452-19 FCHAR456-19	5	Larvae	Canada, Nunavut	Kitikmeot, Two Mile Creek, 4.5 km West of Kugluktuk	N 67.7346° W 115.2°
DRYAS21432-15 DRYAS21685-15	2	Larvae	USA, Alaska	North Slope Borough, Barrow	N 71.246° W 156.563°
CHRFI701-11 CHRFI704-11 CHRFI706-11 CHRFI707-11 CHRFI702-11	5	Larvae	Norway, Svalbard	Edgeoya	N 77.2951° E 22.8935°
CHRFI708-11	1	Larva	Norway, Svalbard	Edgeoya	N 77.3236° E 22.8338°
CHRSV451-10	1	Larva	Norway, Svalbard	Edgeoya	N 77.9691° E 21.3171°
CHRSV432-10	1	Larva	Norway, Svalbard	Edgeoya	N 77.9709° E 21.3181°
CHRFI709-11	1	Larva	Norway, Svalbard	Edgeoya	N 78.0589° E 23.12°
CHRFI708-11 CHRSV451-10 CHRSV432-10 CHRFI709-11 CHRSV557-11 CHRSV560-11 CHRSV562-11 CHRSV564-11 CHRSV567-11 CHRSV568-11 CHRSV569-11 CHRSV559-11	8	Larvae	Norway, Svalbard	Spitsbergen, cowshed	N 78.071° E 14.2015°
CHRSV453-10	1	Larva	Norway, Svalbard	Edgeoya	N 78.0747° E 20.8213°
MIDGE250-06	1	Imago/female	Norway, Svalbard	Spitsbergen, Adventdalen valley, Fallfelle	N 78.16° E 15.75°
MIDGE251-06 MIDGE252-06	2	Imago/female	Norway, Svalbard	Spitsbergen, Adventdalen valley, Fallfelle	N 78.16° E 15.83°
GBAAW72732-24 GBAAW72734-24	2	Larva	Russia, Krasnoyarsk Krai	The Vize Island, top layer of soil under a bird colony	N 79.4872° E 76.9948°
GBAAW72733-24 GBAAW72735-24	2	Imago/female, larvae	Russia, Arkhangelsk region	The Franz Josef Land archipelago, Jackson Island, Nansen site	N 81.2013° E 55.559°

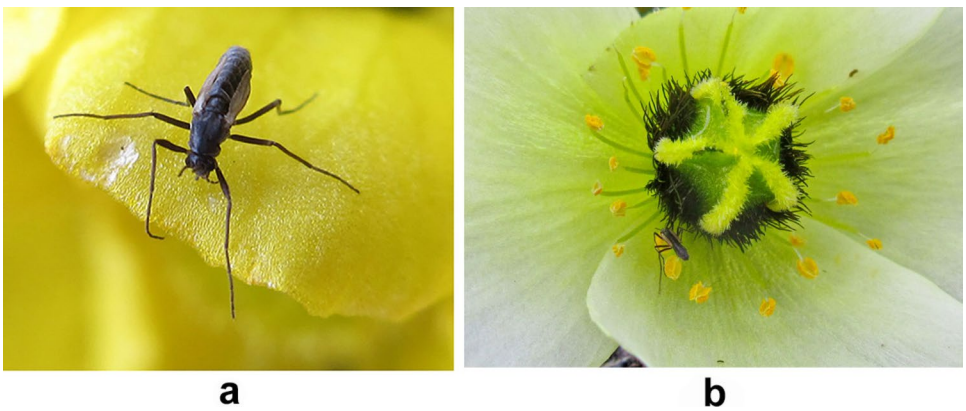

Fig. 2 *Smittia brevipennis* (Boheman). Female imago. **a** Female on *Ranunculus sulphureus* flower on Tikhaya Bay, Hooker Island, Franz Josef Land archipelago; **b** female on *Papaver radicatum* subsp. *polare* flower on Cape Flora, West Northbrook Island, Franz Josef Land archipelago

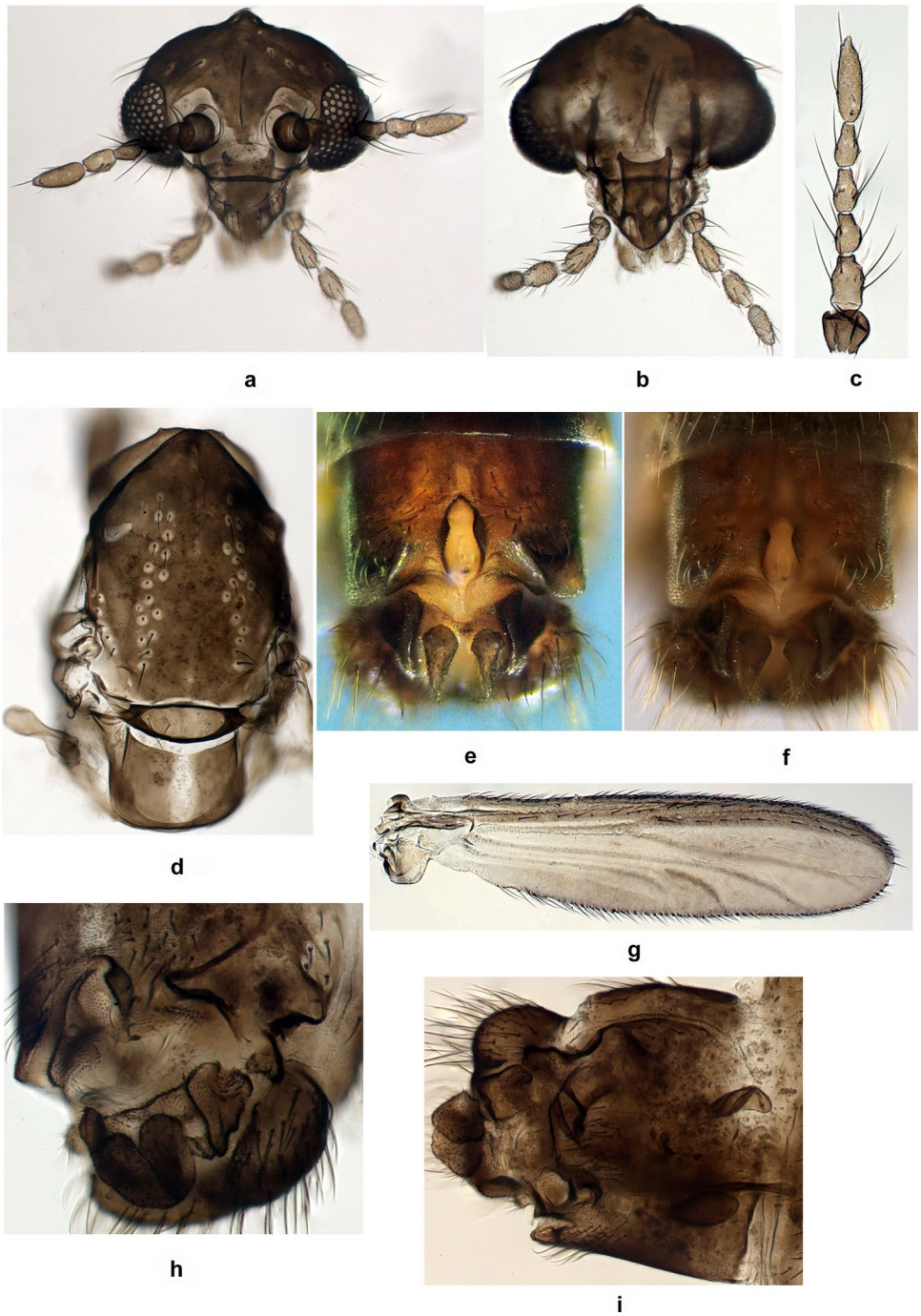

Fig. 3 *Smittia brevipennis* (Boheman). Female imago. **a** Head, front view; **b** head, back view; **c** antenna; **d** thorax, dorsal view; **e** female genitalia, ventral view; **f** female genitalia, ventral view; **g** wing; **h** female genitalia, ventral view; **i** female genitalia, lateral view

13–17; prealars 5–6. Scutellum with 4–5 setae. There is a large, light site in the humeral region.

Wing. Costal extension 62–78 µm long. Brachiolum with 1–4 setae, R with 9–12, R_1 with 2–4, R_{4+5} with 13–15, and coastal extension with 4 nonmarginal setae. The squama is bare.

Legs. The spur of the front tibia was 35 µm long, the spurs of the mid tibia were 27–31 µm and 16–20 µm long, and the spurs of the hind tibia were 47–51 µm and 24 µm long. Comb of 12 setae. The lengths (in µm) and proportions of legs are shown in Table 2.

Abdomen. Tergite VIII with about 68 setae. Sternite VIII with about 44 median setae and 6–7 setae to each side.

Genitalia. Tergite IX undivided but with caudal concavity, with about 80 setae. Gonocoxite with 5–10 setae. Cercus 94–110 µm long. Seminal capsule elongate ovoid, 94–110 µm long, 47 µm wide. Spermathecal ducts with long loops. Gonapophysis VIII divided, with a large ventrolateral

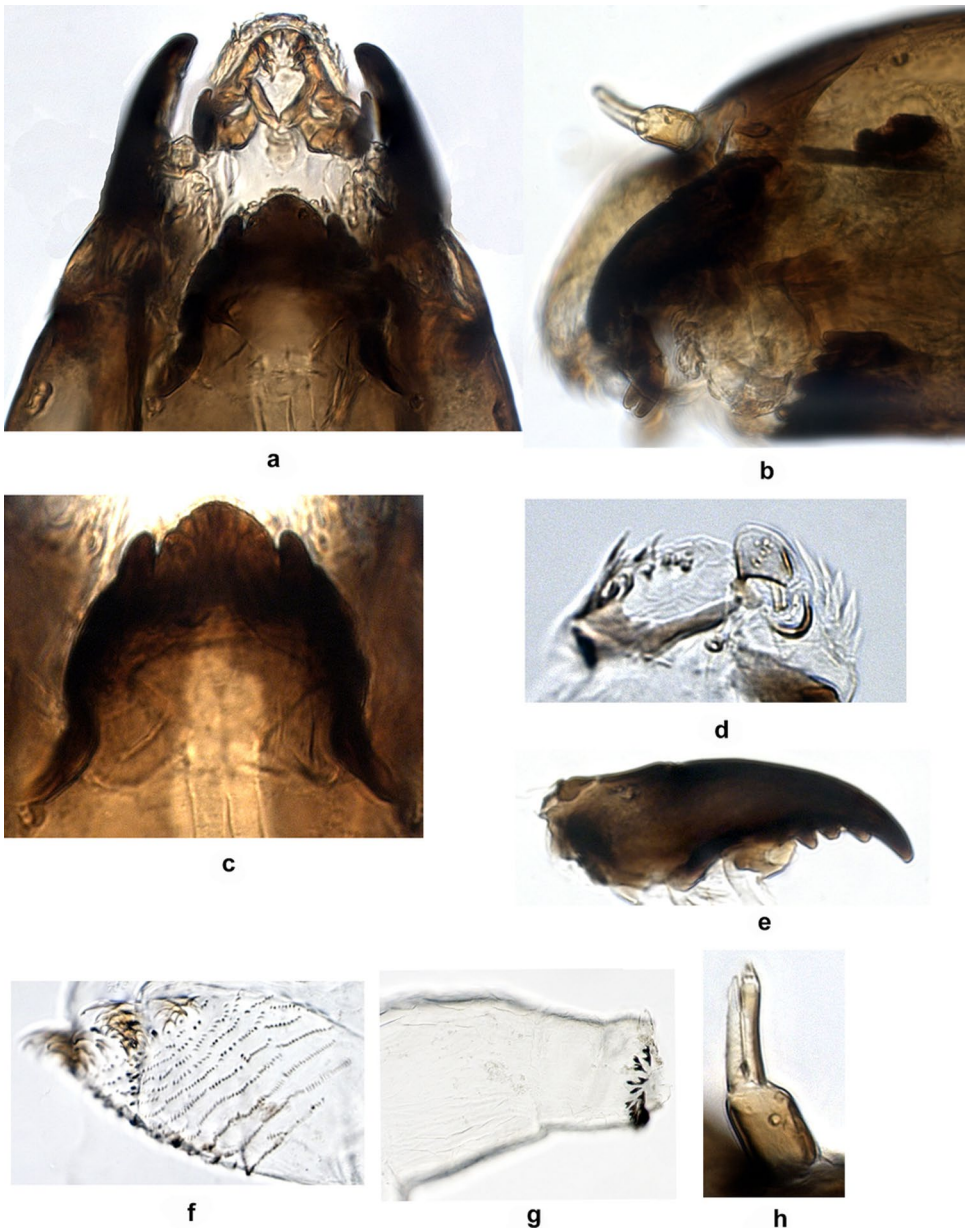

Fig. 4 *Smittia brevipennis* (Boheman). Larva. **a** Head, ventral view; **b** head, lateral view; **c** mentum; **d** maxilla; **e** mandible; **f** anterior parapods; **g** posterior parapods; **h** antenna

Table 2 Lengths (in µm) and proportions of leg segments of *Smittia brevipennis* (Boheman) from Franz Josef Land archipelago, female ($n=3$)

	f	t	ta_1	ta_2	ta_3	ta_4	ta_5	LR	BV	SV	BR
P_1	546–577	577–624	281–312	187–203	125–140	94	94	0.48–0.52	2.79–2.87	3.75–4.00	1.22–1.29
P_2	593–624	577–655	250–265	140–156	109–125	78	94	0.40–0.43	3.25–3.54	4.69–4.93	1.22–1.25
P_3	624–702	686–749	374–421	172–328	17	78–94	94	0.55–0.57	2.61–3.33	3.42–3.50	1.38–1.44

lobe and a relatively narrow dorsomesal lobe. Notum 265–328 µm long.

LARVA ($n=3$).

Figure 4

The total length was 4.9–5.4 mm. The head capsule was 156 µm long and 94 µm wide.

Antenna. The antennae were longer than 1/2 the length of the mandible and 4 were segmented; segment 2 was as long as first; and terminal segments were reduced. Blade well developed, the same length as flagellum. Weak Lauterborn organs present.

Labrum. S I plumose, each branch strongly incised; remaining S setae simple; S III weak. Labral lamellae absent. Premandible with 2 apical teeth; brush absent.

Mandible. An apical tooth shorter than the combined width of 3 inner teeth. Seta subdentalis was present but small. Seta interna with some terminally serrated branches.

Mentum. A single median tooth domed; 5 pairs of lateral teeth were present, the outer four of which could be covered by the mentum plane. The ventromental plate was weak, without setae beneath.

Maxilla. The sensilla on the palp and galea were reduced. Palp partially divided into 2 parts.

Body. The anterior parapods were basally fused, with numerous fine spines on the basal part and several simple claws at the divided apex. Posterior parapods were reduced but separated and had simple claws. Procercus absent; no anal setae present. Anal tubules were reduced.

DNA barcoding

Forty sequences from 13 species of the genus *Smittia* were used for Bayesian analysis, including four DNA barcodes of *S. brevipennis* (658 bp) obtained in this study and 10 sequences of this species from Svalbard (Norway), Kitikmeot (Canada) and Alaska (USA) obtained from BOLD (Fig. 1). No stop codons, deletions, or insertions were observed. The mean nucleotide frequency distributions of the analysed sequences were A, 0.28; C, 0.17; T, 0.38; and G, 0.17. All 14 DNA barcodes of *S. brevipennis* belonged to the same haplotype, so the intraspecific distances were zero (K2P = 0). The mean distance between *S. brevipennis* and other species of the genus *Smittia* (Fig. 1) was 16.2%. The species closest to *S. brevipennis* were *S. contingens* (BOLD:ADV8914) and *S. nudipennis* (BOLD:ACY4849). The interspecific distances of the entire dataset varied between 1.01% and 18.31% (13.4% on average).

Bayesian inference revealed two primary clades (Fig. 1). The first moderately supported clade (Bayesian posterior probability, BPP = 0.93) included *S. brevipennis, S. contingens*, *S. pratorum* and conspecific *S. nudipennis* and *S. pratorum* (according to BOLD, BIN BOLD:ACY4849). The monophyly of *S. brevipennis* was strongly supported (BPP = 1). The second polytomic clade (not supported) included the remaining species. Moreover, the four morphospecies, S. *aterrima*, S. *edwardsi*, S. *stercoraria* and *S. leucopogon,* were divided into 7, 6, 2 and 2 different molecular operational taxonomic units, respectively.

Extremely low or zero intraspecific distances were found characteristic of few molecular species (BINs) within the genus *Smittia*. To date (accessed on 10 January 2025), 28 266 public records have been deposited for this genus, divided into 221 BINs. Of these, 96 BINs have maximum intraspecific distances of less than 1%, low nucleotide and haplotype diversity values. Selected BINs with low intraspecific distances and wide distribution are presented in Table 3. The results of the test for selective neutrality (Tajima's D) correspond to the model of random accumulation of mutations in the absence of a discriminatory pressure on the all analyzed BINs.

Discussion

Here, we report *S. brevipennis* from two new localities, namely, several sites in the Franz Josef Land Archipelago and a single site on the Vize Isalnd, Western Russian high-Arctic, thus filling the gap in its circumpolar range between Svalbard (Boheman 1856; Stur and Ekrem 2020) and previously known Siberian sites (Sæther 2004). In addition, our findings are the northernmost localities for the entire species range.

Specimens of *S. brevipennis* from the Franz Josef Land were previously incorrectly attributed to of *Metriocnemus sibiricus* (Krasheninnikov and Gavrilo 2013, 2014), which also has flightless females with reduced wings, reduced antenna consisting of 5 flagellomeres, and occurs in similar habitats (Sæther 1995). In chironomids, brachyptery affects many other morphological characteristics and accounts for their high variability (Sæther 2004) thus making difficult morphological identification.

S. brevipennis in the Franz Josef Land was found in different tundra habitats on three islands out of 10 surveyed islands where imago chironomids were revealed (Krasheninnikov and Gavrilo 2013, 2014 (as misidentified *M. sibiricus*), and this study). Observations of female imagoes here were often confined to yellow-coloured flowers (*R. sulphureus, P. r. polare*), which may indicate that the imago probably fed on nectar and/or pollen. It was shown that adult chironomids feed readily on substrates containing glucose and sucrose and that such food consumption increases longevity in females by approximately 40% (Burtt et al. 1986). Such habit, if proved, may increase the reproduction probability of the flightless parthenogenetic *S. brevipennis* living under extreme climatic conditions on high-Arctic islands.

The most peculiar is the discovery of *S. brevipennis* on the Vize Island. Here, it is the only local insect species ever reported, whilst the other one is the vagrant larch tortrix *Zeiraphera griseana* (Hübner 1799) (Insecta, Lepidoptera, Tortricidae) (Gavrilo et al. 2021). Even taking into account that Vize Island is barely studied area, this is a surprising result. Comparably low effort applied during two seasons in Franz Josef Land revealed seven species of chironomids (Krasheninnikov and Gavrilo 2014).

Vize Island is an isolated offshore island at the northern border of the Kara Sea shelf, 575 km from the mainland and 300 km from the nearest large archipelagos of Severnaya

Table 3 Characteristics of the species of the genus *Smittia* with low intraspecific distances

Species	BIN BOLD:	*N*	Average/Maximum Intraspecific distance. %	Nucleotide/Haplotype diversity	Distribution
Smittia brevipennis	AAF4816	32	0/0	0.0/0.0	**Canada**: Nunavut **Norway**: Svalbard **Russia**: Krasnoyarsk Krai **USA**: Alaska
Smittia sp.	ACG9412	23	0/0	0.0/0.0	**Australia**: Western Australia **New Zealand**: Waikato **South Africa**: Western Cape, Northern Cape, Gauteng **USA**: California
Smittia cf. *extrema*	ACI8982	6	0/0	0.0/0.0	**Canada**: Nunavut **Greenland**: Northeast Greenland NP
Smittia sp.	ACN5734	5	0.07/0.17	0.00067/0.400	**Germany**: Bavaria **Norway**: Oppland **Russia**: Primorskiy Kray
Smittia sp.	ACI8913	11	0.03/0.19	0.00033/0.182	**Canada**: Yukon Territory **Greenland**: Northeast Greenland NP
Smittia sp. 25ES	AAM6304	28	0.03/0.35	0.00027/0.00758	**Canada**: Nunavut **Greenland**: Northeast Greenland NP **Norway**: Svalbard
Smittia sp. 26ES	ACA0346	70	0.04/0.36	0.00038/0.00374	**Canada**: Alberta, Nunavut, Yukon Territory **Greenland**: Northeast Greenland NP **Norway**: Svalbard **South Africa**: Northern Cape
Smittia sp.	ACI7905	50	0.02/0.38	0.00018/0.079	**Canada**: Nunavut **Greenland**: Northeast Greenland NP **Thailand**: Nakhon Ratchasima
Smittia sp.	AAG6994	116	0.04/0.55	0.00029/0.131	**Canada**: Alberta, Manitoba, Northwest Territories, Yukon Territory **Costa Rica**: Guanacaste
Smittia sp.	ACO4167	46	0.09/0.56	0.00061/0.243	**Canada**: Newfoundland and Labrador, Nunavut **Norway**: Hordaland, Western Norway **Finland**: Enontekioe
Smittia sp.	ACP4114	299	0.1/0.72	0.00039/0.162	**Canada**: Nunavut **Greenland**: Northeast Greenland NP **Norway**: Svalbard
Smittia aterrima	AAE1362	28	0.15/0.72	0.00153/0.552	**Canada**: Newfoundland and Labrador, Yukon Territory **Norway**: Finnmark, Oppland **Finland**: Enontekioe
Smittia sp. 3ES	AAB0374	50	0.2/0.75	0.00164/0.596	**Canada**: Newfoundland and Labrador, Nunavut, Yukon Territory **Greenland:** Kujalleq **Norway**: Svalbard **Finland**: Enontekioe, Utsjoki
Smittia sp. 14ES	ACW5117	796	0.12/0.98	0.00139/0.514	**Canada**: Alberta, British Columbia, Manitoba, New Brunswick, Nova Scotia, Ontario, Quebec, Saskatchewan, Yukon Territory **Finland**: Southwest Finland **Germany**: Bavaria, Brandenburg **Norway**: Finnmark **Poland:** Łódź Voivodeship **Russia**: Irkutskaya Oblast **USA**: California, Montana, New York

Table 3 (continued)

Species	BIN BOLD:	*N*	Average/Maximum Intraspecific distance. %	Nucleotide/Haplotype diversity	Distribution
Smittia sp. 22ES	AAN5358	1873	0.11/1.02	0.00016/0.045	**Belarus**: Minskaya Voblasts **Canada**: New Brunswick, Ontario **Finland**: Southwest Finland **Germany**: Bavaria, Brandenburg **Norway**: Finnmark, Sor-Trondelag **Poland**: Łódź Voivodeship
Smittia sp. 23ES	AAG1020	564	0.1/1.03	0.00021/0.090	**Argentina**: Buenos Aires **Austria**: Burgenland **Australia**: Australian Capital Territory, Western Australia **Bulgaria**: Sofiya-Grad **Canada**: British Columbia, Ontario **Egypt**: Alexandria **France**: Centre-Val de Loire, Ile-de-France **Germany**: Bavaria **Israel**: Central Coastal Plain **Lebanon**: North **New Zealand**: Waikato **Pakistan**: Baluchistan, Islamabad, Khyber Pakhtunkhwa, Punjab **South Africa**: Free State, Gauteng **South Georgia and the South Sandwich Islands:** South Georgia **United Kingdom** **USA**: California
Smittia aterrima	AAN5356	1822	0.25/1.1	0.00120/0.414	**Argentina** **Australia**: Australian Capital Territory, Western Australia **Canada**: British Columbia, New Brunswick, Nova Scotia, Ontario, Prince Edward Island, Quebec **China**: Beijing Shi, Zhejiang **Costa Rica**: Guanacaste **Gabon**: Ogooue-Lolo **Japan**: Kumamoto, Toyama **New Zealand**: Waikato **Reunion** **Russia**: Primorskiy Kray **South Africa**: Gauteng, Western Cape **Suriname** **USA**: California, District of Columbia, Massachusetts, New York
Smittia sp.	AAG1019	1054	0.17/1.16	0.00141/0.568	**Australia**: Australian Capital Territory, South Australia, Tasmania, Western Australia **Canada**: British Columbia **Colombia**: Bogota Capital District **Ecuador**: Pichincha **Israel**: Central Coastal Plain **New Zealand**: Nelson, Waikato **Portugal**: Porto **South Africa**: Western Cape **South Georgia and the South Sandwich Islands**: South Georgia **United Kingdom** **USA**: California, District of Columbia, Hawaii, Massachusetts, Virginia

N number of studied specimens

Zemlya, Novaya Zemlya, and Franz Josef Land. This small (288 km^2) ice-free and hilly lowland island (the highest elevation is 22 m a.s.l.) has extremely uniform landscapes with many rivers, streams, and wet habitats. The mean air temperatures are positive only in July and August (0.5 °C and 0.1 °C, respectively). The vegetation is dominated by forb and cryptogam high-Arctic tundra.

Different wet habitats in the southern coastal area were examined in search of adult chironomids during the warm season of 2020 under the favourable weather conditions. No imagos could be found anywhere. According to the visual observations, collembolans and mites were common in all examined habitats, but no other arthropods were recorded (Gavrilo 2020, unpublished data).

Only one out of four sediment samples collected in 2022 contained *S. brevipennis* larvae. It was ornithogenic soil taken at a small colony of kittiwakes. In other three samples collected in freshwater habitats, including stream, pond and moss turf overflown with water only enchytraeids (Annelida, Oligochaeta, Enchytraeidae) were recorded in the zoobenthos. This is the first report of freshwater benthos from the Vize Island.

Reported findings raises the question on colonization of the remote Vize Island by the flightless chironomid species.

A number of arctic chironomids are known to have structural modifications such as reduced antennae and wings (Oliver 1983). Brachyptery and macroptery of chironomids can be manifested in the same species depending on the season (Makarchenko 1985). Macropterous forms of *S. brevipennis* have not been found yet. This fact reduces the probability of their wind transfer, but does not exclude it completely. Recent observation of live *Z. griseana* blown in to the Vize Island from the mainland demonstrates viability of such hypothesis (Gavrilo et al. 2021).

The record of *S. brevipennis* larvae only in association with a seabird colony suggested that gulls are involved in insect transfer into this habitat. The possibility of nonparasitic microarthropods phoresy by birds has been discussed in details by N.V. Lebedeva and D.A. Krivolutsky (2003). The authors reported that birds can carry various groups of free-living mites, collembolans, dipterian larvae, and staphylinids in their feathers. For the high-Arctic, N.V. Lebedeva (2012) assumed the seabird colonies to be hotspots of soil biota diversity. Therefore, we firstly hypothesised that *S. brevipennis* larvae were transferred to the colony in kittiwake feathers, and subsequently could fall down from the nests along with the nesting material. The weakness of such a hypothesis is the pelagic lifestyle of kittiwakes (Hatch et al. 2020): these gulls are connected to the land only whilst breeding, they build nests on cliffs or occasionally on buildings (such as on Vize Island), freshwater bodies are used to freshen their plumage, and nesting material is collected on wet tundra. All their terrestrial activities kittiwakes perform nearby their nesting colonies during the breeding season, after which they migrate to the sea and stay there until the next summer; thus, long-distance phoresy of larvae from the areas of known range of *S. brevipennis* to the remote Vize island is unlikely.

Another hypothesis involving kittiwakes is larvae transport with nesting materials. Kittiwakes use primarily wet mosses, mud, and seaweed to build their nests. Given that Vize Island lies at some 300 km from the neighbouring landforms, the finding of *S. brevipennis* larvae under the kittiwake colony suggests only their local transfer with nesting materials from a suitable habitat nearby colony, for example, from a marine beach. In Svalbard, *S. brevipennis* larvae were reported from the intertidal zone with community dominated by the bear sedge *Carex ursina* (Dewey 1835) (Sendstad et al. 1976). Our finding of larvae in ornithogenic soils immediately beneath the nests of the kittiwakes where no vegetation was observed except for a thin film of algae suggested that larvae tolerate guanophication accompanying excessive faecal deposits in seabird colonies (Grant et al. 2022 and references therein). To test this hypothesis, further sampling of beached debris, littoral communities, and other kittiwake colonies on the Vize Island is needed.

Furthermore, this hypothesis is followed by the reasonable question of how flightless midges happened to reach Vize Island beach. We then hypothesize that sea ice-rafted debris could assist such a journey.

Sea ice is one of the most important agents of sediment transport in the Arctic, whilst the shallow Siberian shelves of the Kara and Laptev seas are the major sources of ice formation and sediment entrainment and further export of sediment-laden sea ice to the Arctic Basin (Stein 2008). The general currents system of the Kara Sea with prevailing catabatic currents from the Ob-Enisey estuary system northwards ensures the transport of ice-rafted debris from the mainland coastal area into the Arctic Basin and the northeastern Barents Sea, bypassing Vize Island (McClimans et al. 2000). A considerable amount of dirty ice is observed high-resolution satellite images and in situ in the area surrounding Vize Island (M.V. Gavrilo and D.V. Dobrynin, unpublished data). Such dirty ice floes are believed to contain mineral contamination by sand and/or silt. The dominance of freshwater diatoms (up to 70% of all species observed) in ice floes drifting along Severnaya Zemlya to the Arctic Basin north of the Franz Josef Land and Svalbard (Pfirman et al. 1997) proves the export of incorporated biological material from the Ob–Enisey estuary to the northern Kara Sea. There are two major mechanisms for incorporating materials into sea ice: entrainment via frazil ice and anchor ice entrainment or contact incorporation (Lisitzyn 2022). The latter appeared to be an important source of ice-rafted debris and can involve considerable amounts of bottom sediments, including mollusc

shells and seaweed (Darby et al. 2011). Extensive patches of frozen marine benthic materials, including sediments, macrobenthos, eelgrass and flatfishes, were reported from thick fast ice in river-mouth areas of Arctic Canada (Medcof and Thomas 1974). In this way, the larvae of *S. brevipennis*, along with sediments or with driftwood, can be entrained from their littoral habitats into the bottom fast ice in autumn and, later, after break-up, can be transported northwards and deposited on the shore of the remote Vize Island. Moreover, the general patterns of currents and ice drift in the Arctic Ocean suggest they can assist dispersal of *S. brevipennis* across its high-Arctic range by means of rafting with drifting ice or driftwood (Fig. 5).

The DNA barcoding applied for phylogeographical analysis of genus *Smittia* and to draw light on the historical dispersal of *S. brevipennis* revealed surprisingly low genetic diversity within the species range (specimens were collected in Canada, Alaska, Svalbard, Franz Josef Land, and Vize Island) with intraspecific distances measured in gene COI sequences being zero (K2P = 0). These results are unique to chironomids collected from distant localities of comparable distribution range (approximately 14×10^6 km^2 in

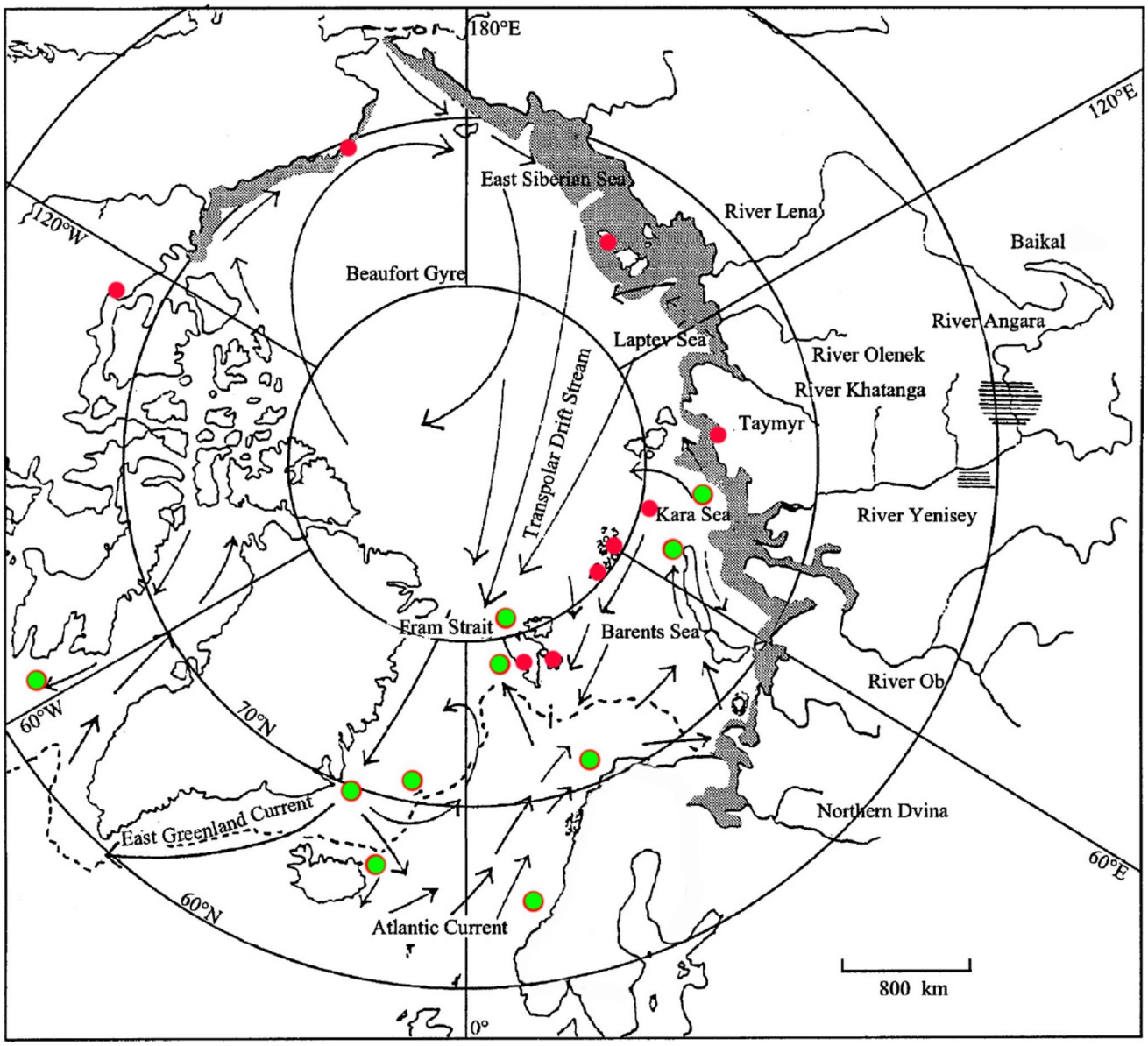

Fig. 5 Map of the distribution of *Smittia brevipennis* (Boheman) (red colour) and major sea ice drift patterns in the Arctic Ocean and prevailing surface ocean currents in adjacent seas. Sites with dendrochronological identification of driftwood from the Yenisey-Angara basins are indicated by green colour after S. Johansen and H. Hytteborn (2001). The source areas in the Yenisey-Angara basins of driftwood dated by dendrochronology are indicated by hatching. Sediment sources in the circumpolar shelf areas are indicated by black colour

our study). For example, for the European (approximately 10×10^6 km^2) orthoclads K2P = 0.75% (Gadawski et al. 2022), for the orthoclads of the Tibetan Plateau (2.5×10^6 km^2) K2P = 2.13% (Han et al. 2023).

Several explanations can be proposed besides our finding, including small sampling size and not an appropriate sequence selected for the DNA barcoding. To evaluate suitability of gene COI for phylogeography of *S. brevipennis*, we compared distribution and intraspecific genetic diversity of *S. brevipennis* to other BINs identified as *Smittia*, mostly those with low intraspecific distances. 53 of the 221 BINs have maximum intraspecific values greater than 1.5%, and their ranges usually do not extend beyond one biogeographic realm which demonstrates the normal mutation rate in the gene COI for orthoclads (Han et al. 2023). Another 110 BINs not only had maximum intraspecific distances of less than 1.5% but also a narrow range, rarely extending beyond one biogeographic realm. The remaining 18 BINs (Table 3) have wide ranges and extremely low, down to zero, variability in the gene COI. Some of these BINs, especially BOLD:AAG1020, BOLD:AAN5356 and BOLD:AAG1019, demonstrate cosmopolitan distribution, which is probably due to their invasive character. The other BINs (BOLD:ACI8982, BOLD:ACI8913, BOLD:AAM6304, BOLD:ACP4114, BOLD:AAB0374, etc.) most likely have a natural range with distribution often tied up with remote Arctic areas. Regardless the invasiveness, an increase in the number of analyzed specimens does not affect intraspecific distances, nucleotide and haplotype diversity. For example, maximum intraspecific distances of BINs BOLD:AAN5358, BOLD:AAN5356, and BOLD:AAG1019 were 1.02%, 1.10% and 1.16% respectively with over 1000 DNA barcodes analyzed.

Even though, the above analysis does not allow drawing a clear conclusion regarding possible changes in COI variability in *S. brevipennis* with an increase of DNA barcodes analyzed, especially in the case of discovery a bisexual populations in the future. However, it can be assumed that the mutation rate will remain extremely low, as in other species of the above discussed group, or that most of the mutations will occur in the bisexual populations. Low genetic diversity, at least in a number of *Smittia* species, may indicate both, rapid dispersal of species across their ranges, and a lack of informativeness of the gene COI for phylogeography due to its disproportionally low mutation rate. Similarly unexpectedly low intraspecific distances for the gene COI were found in two collembolan species inhabiting the intertidal zone as compared to non-marine species of the same genus *Thalassaphorura* (Sun et al. 2018). The molecular mechanisms for a decrease in mutation rate are not known, but the observation of low intraspecific genetic diversity in different taxonomic groups (collembolans and chironomids) but among their representatives with similar ecology (related to marine habitats) is suggestive. We hypothesized that this phenomenon could be related not to the molecular mechanisms but rather to the dispersal mechanisms.

If we accept that the mutation rate of the gene COI in the above discussed group of *Smittia* species is not underestimated, then its low diversity indicates a recent and rapid dispersal of *S. brevipennis* across its circumpolar range. Similar rapid colonization of remote coastal areas with assistance of oceanic transfer may account also for the low intraspecific distances in two marine species of *Thalassaphorura* described in Sun et al. (2018).

Final decision on the ways of historical dispersal of the parthenogenetic brachypterous chironomid, *S. brevipennis,* across its circumpolar range require further studies to increase sample size, search for the possible bisexual populations, and more thoroughly address different working hypothesis. More efforts should be applied to survey different habitats on the isolated islands including intertidal zone, ornithogenic substrates, and different tundra habitats. In addition to the COI sequence genes, other genes should be studied to assess intraspecific genetic diversity and to estimate colonization rate of the remote high-Arctic areas.

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Author contributions Andrey B. Krasheninnikov: collection of material, identification, morphology and systematics. Maria V. Gavrilo: collection of material, ornithological research. Alexander A. Semenchenko: genetic research. All co-authors participated in writing the discussion.

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Data availability Sequence data that support the findings of this study have been deposited in GenBank under numbers OR922272–OR922275.

Declarations

Conflict of interest The authors declare no competing interests.

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