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Chaoborus flavicans Meigen (Diptera, Chaoboridae) is a complex of lake and pond dwelling species: a revision

JUKKA SALMELA[1,2*], OSKARI HÄRMÄ[3] & DEREK J. TAYLOR[4]
[1]*Regional Museum of Lapland, Pohjoisranta 4, 96200 Rovaniemi, Finland*
[2]*Arctic centre, University of Lapland, P.O. Box 122, 96101, Rovaniemi, Finland*
[3]*Forssa Museum of Natural History, Wahreninkatu 4, 30100 Forssa, Finland*
oskari.harma@gmail.com; https://orcid.org/0000-0002-1586-6320
[4]*Department of Biological Sciences, University at Buffalo, Buffalo, NY, 14260, USA*
djtaylor@buffalo.edu; https://orcid.org/0000-0002-2524-0559
[*]*Corresponding author. jukka.e.salmela@gmail.com; https://orcid.org/0000-0001-9462-9624*

Abstract

Chaoborus flavicans (Meigen) is a widespread and much studied lacustrine phantom midge. As larvae, these insects are important aquatic predators. Based on the available type material, morphology of immature stages and adults, their aquatic habitat, and DNA barcodes, *C. flavicans* is shown to be a composite of at least four species, with three of these named here. *Chaoborus flavicans* is primarily a lake-dwelling species with a Holarctic range. *Chaoborus albipes* (Johannsen, 1903 **stat. rev.**) and *C. posio* Salmela **sp. n.** are pond-dwelling Holarctic and north European species, respectively. The position of the larval subordinate mandibular tooth at the vertex of the second and fourth teeth is a synapomorphy of the *Chaoborus flavicans* species complex. We present an identification key to fourth instar larvae, pupae, and adult males. We also designate the lectotype and paralectotypes of *Sayomyia rotundifolia* Felt, 1904 (**syn. nov.** of *C. albipes*). We hypothesize that a fourth species of the species complex is present in Japan. Our revision indicates that Holarctic shallow ponds contain a hidden diversity of predators (*C. albipes* and *C. posio* **sp. n.**).

Key words: phantom midges, taxonomy, DNA barcoding, Holarctic Region

Introduction

Phantom midges of the genus *Chaoborus* Lichtenstein are noted freshwater ecosystem engineers and ecological indicators. In lentic habitats, the predatory larvae are often keystone species that can eliminate or strongly suppress other invertebrates (MacKay *et al.* 1990; Horppila *et al.* 2009; Lindholm *et al.* 2016). Subfossil remains of *Chaoborus* (larval mandibles and pupal respiratory organs are preserved in sediments) have been used to indicate past and present ecological conditions (e.g. Sweetman & Smol 2006; Luoto & Nevalainen 2009; Kurek *et al.* 2010; Palm *et al.* 2011; Ursenbacher *et al.* 2020).

One geographically widespread but problematic species is *Chaoborus flavicans* (Meigen, 1830). The species was described initially from Germany (Meigen 1830, Giles 1902) but remained somewhat obscure because it was partly confused with *Corethra plumicornis* (Fabricius), a synonym of *C. crystallinus* (De Geer). The differing use of the genus-group names *Corethra* Meigen, *Sayomyia* Coquillett, and *Chaoborus* provided another source of confusion. For example, in consecutive articles in a Finnish journal, the names "*Sayomyia*" (Järnefelt 1936) and "*Corethra plumicornis*" (Valle 1936) were used for *C. flavicans*. Wesenberg-Lund (1914, see also Bardenfleth & Ege 1916) noticed that "*Corethra plumicornis*" was composed of two morpho- and ecotypes (from ponds and lakes, *C. obscuripes* (Van der Wulp) and *C. flavicans*, respectively). Valle (1930) was the first to observe that the lake-dwelling species (*C. flavicans*, referred to as *Corethra plumicornis*) performed diel vertical migration.

The taxonomic revision of adult chaoborids by Martini (1929) clarified the definitions of Palaearctic species, and a publication by Peus (1934) did the same for *Chaoborus* larvae. However, Peus (1934) also brought confusion to the taxonomy and ecology of *C. crystallinus* and *C. flavicans* (see Stahl 1966b). He considered *C. flavicans* as

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an inhabitant of ephemeral ponds on the flood-plains of large rivers, and assigned specimens from lakes (profundal zones) to *C. crystallinus*. Spill-over of larvae from larger and permanent water bodies, such as slow-flowing parts of large rivers, may account for the detection of normally lacustrine larvae in such temporary ponds (see Remm 1955, Borkent 1979). The similarity of larval labral blades between *C. crystallinus* and *C. flavicans* may also have caused the misdiagnosis of lacustrine specimens as *C. crystallinus* (Stahl 1966b). Eckstein (1936) followed the taxonomic work of Peus and provided excellent illustrations of larvae and adult males, but was unable to assign the lake-dwelling form of "*crystallinus*" to *C. flavicans*. Berg (1937), in his study of Danish lentic waters, was the first who correctly associated the immature stages and adults of *C. flavicans* and who proposed the species to be lake-dwelling. Peus (1938) then described a new species, *C. alpinus*, from an alpine lake in Germany. He used the name for male specimens with a subapical hyaline crest in the parameres (genital sclerite, penis valve, e.g. Hirvenoja 1960; Ökland 1964; Sikorowa 1967). However, Sæther (1967) treated *C. alpinus* as a synonym of *C. flavicans*. Sæther (1967) also suggested three infrasubspecific names (forms) for Holarctic specimens of *C. flavicans* that he considered geographical and partly ecophenotypic morphotypes. Currently, *C. flavicans* is a very well studied species in Europe: its morphology, life cycles, ecology, and physiology are well characterized (e.g., Parma 1971a; Sikorowa 1973; Berendonk 1999; Horppila *et al.* 2000; Berendonk & Bonsall 2002; Liljendahl-Nurminen *et al.* 2002; Jäger & Walz 2003).

In the Nearctic, *C. flavicans* also has a complicated taxonomic history with several synonyms (Cook 1956; Belkin *et al.* 1966). Cook (1956, p. 23), in his revision of Nearctic chaoborids, considered *C. flavicans* to be variable, "especially in the genitalic structures of the males." Cook figured three parameres (fig. 16H), which he assumed to depict intraspecific variation. However, later in the same paragraph, he continued: "Even this might not invalidate the possibility that two or more species are involved…". In hindsight, the bionomic information given by Cook is also somewhat conflicting, because he reported North American *C. flavicans* as occurring in "water-filled road ruts, temporary ponds and small pools". However, the species is a typical zooplankter of fish-containing lakes in North America, and is only occasionally present in ponds (Borkent 1981; Tsalkitzis *et al.* 1994; Garcia & Mittelbach 2008). In recent checklists, *C. flavicans* is reported to occur in the Nearctic and Palaearctic regions (Borkent 1993; 2014). According to molecular research, North American and Eurasian *C. flavicans* populations are somewhat diverged, most likely due to isolation during the Pleistocene (Wende *et al.* 2006). However, this divergence is rather modest (ca. 2 % in the 3' COI and 5" COII regions; i.e., adjacent to the 5' COI DNA barcoding region). No consistent morphological differences have been reported between populations of the continents (e.g., Sæther 1967; Sæther 1970).

Despite the conspecific North American and Eurasian populations of *C. flavicans*, a closely related and similar-looking taxon *C. cf. flavicans* was recently found from the Nearctic region and Japan (Dupuis *et al.* 2008). This taxon is common on the Seward Peninsula of subarctic Alaska, especially in newly formed thaw ponds, which are permanent but shallow (Taylor *et al.* 2015). It was noted that larvae of *C. cf. flavicans* possess rather large mandibular lateral teeth, the first of them being larger than the subordinate tooth (Dupuis *et al.* 2008). No adults, however, were examined in that study. A current impediment for integrative taxonomy is that genetic studies have yet to use the DNA barcoding region to compare specimens from different continents (Wende *et al.* 2006; Dupuis *et al.* 2008; An *et al.* 2012).

In 2018, JS collected *C. flavicans sensu lato* type larvae from northern Finland that were characterized by large lateral mandibular teeth. Some of the populations were composed of larvae with more than 20 mandibular fan bristles, which is beyond the known variation of *C. flavicans*. In comparison, others had about 16–19 such setae, a number in the upper range of *C. flavicans* or beyond (see e.g., Sæther 1967; Sikorowa 1973). DNA barcoding (analysis of mtDNA COI sequences) of the larvae revealed that the Finnish *C. flavicans s.l.* type specimens split into three distinct clades with very high interspecific K2P distances (15–17 %). In the spring and early summer of 2019 these populations were revisited for the collection of larvae. Rearing of overwintering larvae in the laboratory was successful, and after examination of adult specimens it was clear that molecular clades represented valid taxonomic species.

This study revises the taxonomy of *C. flavicans s.l.* type species using morphological and DNA barcoding evidence at a Holarctic scale. As a result, *C. flavicans* is redescribed, one species is raised from the list of synonymous names to a valid species status, and one species is described as new. An identification key to IV instar larvae, pupae, and adult males is provided.

Material and methods

JS and OH collected most of the new material with a pond-net from lentic water bodies. DJT collected the samples from northwest Alaska and Kodiak Island. Collected larvae or pupae were either stored in 70–80 % ethanol or were kept alive and brought to the laboratory for rearing. The rearing took place at room temperature under a natural photoperiod. Larvae were reared in individual jars. After ecdysis, larval skins were stored in ethanol and given a unique voucher code/museum ID (e.g., NVO.LMM-el-20-1). Later, the pupal exuviae and the adult specimens were given the same museum IDs. Larval skins and pupal exuviae were stored in ethanol or permanently slide-mounted in Euparal. Adults were either stored in ethanol or pinned; wings, heads, legs, and hypopygia of some specimens were slide-mounted in Euparal. Most of the newly collected material was deposited in the LMM and FLHM, and the metadata of this material is available online (www.laji.fi, e.g., http://tun.fi/NVO.LMM-el-20-1). The following abbreviations are used among the studied specimens: BOLD=Barcode of Life Database, indicates that the COI sequence data of the specimen is available; e.l.=ex larva; e.p.=ex pupa; Finnish biogeographical provinces (see e.g. Salmela 2012 for a map), arranged from south to north: Ab=*Regio aboensis*, N=*Nylandia*, Ka=*Karelia australis*, Ta=*Tavastia australis*, Tb=*Tavastia borealis*, Sb=*Savonia borealis*, Oa=*Ostrobottnia australis*, Ok=*Ostrobottnia kajanense*, Ks=*Regio kuusamoensis*, Obb=*Ostrobottnia borealis pars borealis*, Lkor=*Lapponia kemensis pars orientalis*, Lkoc=*Lapponia kemensis pars occidentalis*, Li=*Lapponia inariensis*.

In addition to Finnish material, specimens were studied from Norway, Estonia, Germany, Kazakhstan, Russia, Japan, USA and Canada (larvae, pupae, adults). The material examined is listed below in respective species and the specimens are deposited in the following museums or collections:

ABC	Private collection of Art Borkent, Salmon Arm, Canada (to be deposited in the CNC)
CBG	Centre for Biodiversity Genomics, University of Guelph, Guelph, Canada
CNC	Canadian National Collection of Insects, Arachnids and Nematodes, Ottawa, Canada
CUI	Department of Entomology, Comstock Hall, Cornell University, Ithaca, USA
ELEU	Entomological Laboratory, Faculty of Agriculture, Ehime University, Matsuyama, Japan
FLHM	Forssa Museum of Natural History, Forssa, Finland
KMO	Private collection of Kjell-Magne Olsen, Oslo, Norway
LMM	Regional Museum of Lapland, Rovaniemi, Finland
MNHN	Laboratoire d'Entomologie, Muséum National d'Histoire Naturelle, Paris, France
MZH	Zoological Museum, Finnish Museum of Natural History, University of Helsinki, Helsinki, Finland
NMNS	National Museum of Nature and Science, Ibaraki, Japan
NYSM	New York State Museum, Albany, USA
UBB	Collections of DJT at University at Buffalo, Buffalo NY, USA (will be desposited in the LMM)
USNM	United States National Entomological Collection, U.S. National Museum of Natural History, Washington, USA
ZFMK	Zoologisches Forschungsmuseum Alexander Koenig, Leibniz-Institut für Biodiversität der Tiere, Bonn, Germany
ZMBN	Department of Natural History, University Museum of Bergen, Bergen, Norway

Specimens were studied with Leica Wild M3B stereo and Leica Laborlux S compound microscopes. Measurements were made by using a Moticam +10 camera attached to the compound microscope. The same camera was used to image the specimens. Microphotographic layers were combined using the software Combine ZP and the photos were edited with Photoshop (Adobe). Morphological terminology followed Ogawa (2007) (larvae), Borkent 2012 (pupae) and Cumming and Wood (2017) (adults) or is explained in the figures. One exception for the terminology was the "labral blade" being used instead of head capsule seta 3 in larvae. Measurements (in µm if not otherwise stated) and ratios are given as means followed by ranges (min–max) and the number of measured specimens.

Tissue samples for DNA barcoding were taken from larvae, pupae, and adults. A 658 bp fragment of mitochondrial protein-encoding cytochrome c oxidase subunit I (COI) was sequenced from a total of 220 *Chaoborus flavicans s.l.* specimens (Appendix 1 includes these and other material from BOLD and GenBank). Tissue samples of the specimens were placed in 96% ethanol in 96-well lysis microplates. Extraction and Sanger sequencing was carried out at the Canadian Centre for DNA Barcoding, Biodiversity Institute of Ontario, at the University at Buffalo, NY or at the University of Turku, Finland, using standard protocols and primers (deWaard *et al.* 2008). The fragment was successfully amplified for all taxa treated here. The new sequences are deposited in a public project (FICFL) in BOLD and NCBI Genbank.

Sequences from this study and existing publicly available sequences of the *C. flavicans* complex were assembled and aligned (no gaps were required). A continuous open reading frame using the invertebrate mitochondrial genetic code was verified for all sequences by translating in Geneious 7. Public sequences of *C. crystallinus*, *C. americanus* (Johannsen), *C. nyblaei* (Zetterstedt) and *C. obscuripes* were also added. Sequences of three species of *Mochlonyx* Loew were used to outgroup root the phylogenetic analysis. ModelFinder (Kalyaanamoorthy *et al.* 2017) was used for model fitting and IQTREE 1.6 for the phylogenetic estimation with the optimality criterion of maximum likelihood (Nguyen *et al.* 2015). Branch support was assessed with ultrafast nonparametric bootstrapping (Hoang *et al.* 2017). Figtree 1.4.4 (Andrew Rambaut Institute of Evolutionary Biology, University of Edinburgh. http://tree.bio.ed.ac.uk/) was used to collapse major clades and to visualize the phylogenetic analyses. Subsets of sequences (belonging to species) were exported in nexus format using Geneious 7 and subject to median joining network analysis in Popart (Leigh & Bryant 2015). Geneious was used to estimate DNA barcoding species delimitation metrics. The metrics included measurement of within and among clade genetic distances (using the best fit substitution model) and the probability of identification with confidence intervals. We also estimated the probability of obtaining reciprocal monophyly by random branching alone using a coalescent null model (Rosenberg 2007).

Taxonomy

Culicomorpha Hennig, 1948

Culicoidea Meigen, 1818

Chaoboridae Edwards, 1912

Chaoborus Lichtenstein, 1800

Chaoborus flavicans species complex

We found evidence for at least four species in the *Chaoborus flavicans* complex: *Chaoborus flavicans*, *C. albipes*, *C. posio* **sp. n.** and a lineage from Japan. The monophyly for each of these species is strongly supported by bootstrap values (Fig. 15) and is not attributable to random branching under a coalescent null model (Rosenberg's P(AB) < 0.05 for all species in Table 1). The presence of the subordinate tooth between the second and fourth tooth in the larval mandible is a likely synapomorphy of the *C. flavicans* complex. *Chaoborus crystallinus* has been proposed as a sister species of *C. flavicans* (Sæther 1970, Borkent 1981; note that the close relationship between *C. crystallinus* and *C. flavicans* suggested by Berendonk *et al.* 2003 appears to be a mistake due to *C. flavicans* being confused for *C. crystallinus*). However, we refrained from assessing the proposed sister species of *C. flavicans* complex in this study. Phylogenetic relationships beyond the species complex are not analysed in detail here as COI tends to lack resolution across species groups for *Chaoborus* (Dupuis *et al.* 2008). We also found a lack of resolution at the deeper nodes for *Chaoborus* in the present phylogeny (Fig. 15). Characters that support a close relationship between *C. flavicans* and *C. albipes* are a slender male gonocoxite and gonostylus, a relatively short apical claw of paramere and a subapically constricted pupal respiratory organ. In contrast, *C. posio* **sp. n.** has several autapomorphic character states, such as a wide male gonocoxite and gonostylus, long apical claw of the male paramere and a club-shaped pupal respiratory organ. A high number of larval mandibular fan bristles and conspicuous lateral teeth of the mandibles are shared characters for *C. albipes* and *C. posio* **sp. n.** This sister group relationship also had strong support in our COI phylogeny. A distinct lineage from Japan appears to be more related to *C. posio* + *C. albipes* than to *C. flavicans* sensu stricto (Fig. 15).

It is not known where and when the ancestor of the *C. flavicans* species complex evolved. Divergent selection for habitat seems to be important as species occupy different niches (ponds vs. lakes); Holarctic sister species that occupy the same niche are mostly allopatric (e.g., *C. americanus* and *C. obscuripes*, Borkent 1981). If the pattern of three phylogenetically independent shifts from pond to lake habitats within Holarctic *Chaoborus* (Berendonk *et al.* 2003) is accepted, the ancestor of the *C. flavicans* complex was a pond-dwelling species and *C. flavicans* became a lake-dwelling taxon able to withstand high pressure in deep waters and fish predation. Note that the substantial genetic divergence between *C. flavicans* and other members of the complex (> 30%) indicates that divergence of the complex likely occurred well before the Pleistocene. Moreover, widespread species such as *C. albipes* and *C. flavicans* with two or more closely related geographic clades may also have been present before the Pleistocene.

Chaoborus tertiarius (von Heyden), Upper Oligocene fossil species, is composed of two complete pupae, disarticulated pupal parts, larval mandibles, and anal fans (Borkent 1978). This taxon may be ancestral to *C.* (*Chaoborus* s.str.) and the subgenus *C.* (*Schadonophasma* Dyar & Shannon 1924), or it may be ancestral, or a sister, to species of *C. flavicans* species complex (Borkent 1978). Among the fossil material are two types of larval mandibles: the subordinate tooth is either present between teeth two and four or it branches from the second tooth (Borkent 1978, figs. 3 A-H). However, Borkent admits that the subordinate tooth of the *flavicans*-type "was very difficult to see", and hence it is uncertain if *C. tertiarius* is closely related to the *C. flavicans* species complex.

Diagnosis. Adults male. Penultimate flagellomere slightly longer than ultimate, or about equal in length. Flagellomeres pale or partly darkened, bases of whorls dark, giving annulated appearance. Scutellar stripes bare, orange brown–almost black, pleural sclerites pale yellow and with a varying degree of darker coloration. Legs straw yellow or grayish, apical tarsomeres may be somewhat darkened. Tergites yellowish brown or dark brown, bases of setae with a dark ring. Male epandrium either triangular or broadly rounded in shape, its length about 0.35–0.37 times the length of gonocoxite. Male paramere with a conspicuous apical claw, elongated, almost straight or curved.

Pupa. Outer rib of terminal process smooth, apical spines absent. Mid rib of terminal process usually darker than lateral ribs, margin of inner rib serrated along apical 2/3. Length/width ratio of 8th segment ca. 0.36. Respiratory organ widest medially, constricted apically or not.

IV instar larva. Total length 7–15 mm (e.g. Parma 1971b). Labral blade elongated, degree of serration varied. Mandibular subordinate tooth (3) positioned at the vertex of tooth 2 and tooth 4. Mandibular lateral teeth either small and inconspicuous or larger and distinguishable. Dorsal process pointed.

Key to species of *Chaoborus flavicans* species complex

Note. All species key out as *C. flavicans* in the key by Sæther (1972).

adult males

1 Gonocoxite and gonostylus stout in structure, length:width ratio 2.64 (2.4–3) and 9.43 (8–10.7), respectively (Fig. 14a); apical claw of paramere relatively long (Fig. 14c–e).. . . . . *C. posio* Salmela **sp. n.**

- Gonocoxite and gonostylus slender, length:width ratio ca. 3–3.5 (2.37–3.9) and 12.5–13.7 (10.2–16), respectively (Figs. 6a, 11a); apical claw of paramere relatively short (Figs. 6c–e, 11c–e). 2

2 Paramere medially bent and constricted; apical claw rather narrow, moderately curved (Figs. 6, 8a) . . . .*C. flavicans* (Meigen)

- Paramere medially almost straight or gently curved; apical claw stout, curved (Figs. 8b, 11) . . . . *C. albipes* (Johannsen stat. rev.)

pupae

Separation of pond-dwelling *C. flavicans* and *C. albipes* pupae may be obscured by intraspecific variation

1 Respiratory organ club-shaped, lacking subapical constriction, relatively short (844 (770–930) µm, Fig. 9d . . . . *C. posio* Salmela **sp. n.**

- Respiratory organ with subapical constriction, either slender or voluminous (Figs. 9a–c) 2

2 Length of respiratory horn ≥1000 µm (920–1360), either slender or voluminous (Figs. 9a–b) . . . .*C. flavicans* (Meigen)

- Length of respiratory organ mostly <1000 µm, may exceed 1000 µm (690–1050); slender (Fig. 9c) . . . . *C. albipes* (Johannsen stat. rev)

larvae

Serration of the labral blade may vary in all species.

1 Mandibular lateral teeth inconspicuous; uppermost tooth shorter than subordinate tooth (Figs. 10a–b); number of mandibular fan bristles ≤16. . . . .*C. flavicans* (Meigen)

- Mandibular lateral teeth conspicuous; uppermost tooth about as long as subordinate tooth (Figs. 10d,f); number on mandibular fan bristles almost always >16 2

2 Number of mandibular fan bristles >20, usually >22 (21–29) (Fig. 10h); labral blade finely serrated, rather wide (length:width ratio 3,7 (3–5 Fig. 10g). . . . . *C. posio* Salmela **sp. n.**

- Number of mandibular fan bristles up to 25, usually 15–21; labral blade almost devoid of serration, slender (length:width ratio 5.59 (4.38–6.85, Fig. 10e) . . . . *C. albipes* (Johannsen, stat. rev.)

Chaoborus flavicans **(Meigen, 1830)**

Corethra flavicans Meigen 1830: 243 (original description). Macquart 1834: 47 (short notes on morphology). Gimmerthal 1845: 296 (short notes on morphology). Giles 1900: 362 (identification key to adults, redescription of the holotype, translation of the original description from German to English). Theobald 1901: 294 (translation of the original description from German to English, reference to Giles 1900). Giles 1902: 505 (identification key to adults, redescription of the holotype, translation of the original description from German to English). *Corethra flavicans*: Berg 1937: (ecology, morphology, biology), labral blades fig.1.1, mandible fig.1.2., terminal process fig. 1.3, palpus fig 2.4., two last flagellomeres fig. 2.5., paramere fig. 2.6., egg mass fig. 16, embryos fig. 17, egg mass fig. 18. Berg & Petersen 1956: 184 (ecology, morphology), labral blade fig. 74A, mandible fig. 74B, pupal respiratory organs fig. 74C, terminal process fig. 74D, palpus fig. 75A, two last flagellomeres fig. 75B, paramere fig. 75C.

Chaoborus flavicans: Brunetti 1911: 229 (nomenclature). Séguy 1924: 170 (identification key to adults, comparison to *C. crystallinus*). Séguy 1925: 58 (identification key to adults, comparison to *C. crystallinus*, distribution, ecology). Martini 1929: 56 (identification key to adults, resdescription, distribution), palpus fig. 77a, two last flagellomeres fig. 77b, parameres fig. 77c & c1. Edwards 1930: 164 (notes on adult morphology, in comparison to *C. obscuripes* and *C. crystallinus*). Matheson 1944: 94 (identification key to adults, short notes on morphology), hypopygium plate 10 fig. 2. Sládeček 1952: (larval and pupal morphology, ecology), head fig. 2, mandible fig. 4, labral blade fig. 5c, respiratory organ fig. 7a, terminal process fig. 8a (figs. 5, 7,8 copied from Peus 1934). Aitken 1954: 442 (key to larva, pupa and adult, distribution in Sardinia), labral blade fig. 1.1. Prokešová 1959: (larval morphology, instars, ecology), head capsule fig. 7, mandible fig. 8, thorax fig. 10. Hirvenoja 1961: (identification key). Brindle 1962: (identification key to larvae, ecology), mandible fig. 6. Stahl 1966b: (tentative synonymy of *C. alpinus* with *C. flavicans*). Sæther 1967: forma *flavicans*, forma *alpinus*, forma *infuscatus* (morphology, intraspecific variation), labral blades fig.1A, bifurcate labral setae fig.1 B-E, bristled labral scales fig. 1F-H, plumose labral seta fig. 1J, maxilla fig. 1K, labrum fig. 1L, tergites of pupal exuviae fig. 2A-B, parameres fig. 2C-F. Parma 1969: (larval instars, morphology, ecology, identification key), labral blades fig. 3M-O, labral setae fig. 4B, bifurcate setae fig. 5A-C, bristled scales fig. 6A-F, scales of anal apparatus fig. 7A-C, setae above anal gills fig. 7D-E, anal fan seta fig. 7F, dorsal process fig. 7K, anal papillae fig. 7N, mandible fig. 7O. Parma 1971a: (biology, ecology), embryo fig. 12, newly hatched larvae fig. 13. Parma 1971b: (morphology of larval instars), head capsule, antenna, prelabral appendage, mandible, maxilla, dorsal process fig. 1, last abdominal segments, bristled scales of the labrum, bifurcate setae of the labrum, middle seta of dorsal side of head capsule, details of anal apparatus fig. 2. Balvay 1977a: (identification key, larval instars), labral blade fig. 1C.F., dorsal process and anal tubules fig. 2C.F., mandible fig. 3C.F. Balvay 1977b: (morphometry of larval instars). Balvay 1977c: (morphology of head and mandibles of larval instars), head 1st instar larva fig. 1, post antennal setae 1st instar larva fig. 2a, 4th instar larva fig. 2b, placement of post antennal setae 2nd instar larva fig. 3a, 4th instar larva fig. 3b, mandible 1st instar larva fig. 4, mandible 2nd instar larva fig. 5, mandible 3rd instar larva fig. 6, mandible 4th instar larva fig. 7. Stenson 1978: (ecology), outline of larval head fig. 1. Borkent 1979: (discussion of characters, number of anal fan setae and head capsule length of 4th instar larvae). Stenson 1980: (ecology), head outline fig. 2. Uutala 1990: (paleolimnology, identification key), mandibles fig. 4-5. Wagner 1990: 72 (list of species). Borkent 1993: 15 (list of species, synonymous names, locations of type specimens, distribution). Walker 2001: 46 (paleolimnology), mandible fig. 1e. Berendonk *et al.* 2003: (molecular phylogeny in relation to body size and lake vs. pond-dwelling lifestyle). Sweetman & Smol 2006: (paleolimnology), mandible fig. 3C. Wende *et al.* 2006: (molecular phylogeny, haplotypes). Dupuis *et al.* 2008: (molecular analysis, phylogeny, distribution, ecology, morphology), mandible fig. 2B. An *et al.* 2012: (molecular phylogeny, emphasis on Korean specimens). Borkent 2014: 476 (list of list of species, synonymous names, locations of type specimens, distribution).

Corethra plumicornis: "søform" Wesenberg-Lund 1914: 8 (ecology, life cycle, morphology of larva and pupa), egg mass fig. 6, larval head (lateral view) fig. 7b, dorsal view fig. 8b, anal fan fig. 9b, labral blade fig. 10b, pupal respiratory organ fig. 11b.

Chaoborus eluthera Dyar & Shannon 1924: 211, syn. (description). Stone in Belkin *et al.* 1966: 22 (lectotype designation, syn. of *C. flavicans*).

Chaoborus (Chaoborus) elethera: Edwards 1932: 25 (misspelling, list of species).

Chaoborus (Chaoborus) flavicans: Edwards 1932: 26 (list of species). Peus 1934: (larval morphology, identification key, pupal morphology), mandible fig. 3b, terminal process fig. 9a, apex of respiratory organ fig. 10c. Monchadskii 1936: 114 (identification key, notes on larval morphology), figures copied from Peus 1934. Cook 1956: 23, in part (redescription of *C. flavicans* includes both *C. flavicans* and *C. albipes*), male abdominal tergites 3 and 4 fig. 14B. Enns 1960: 128 (key to larvae, faunistics), labral blade fig. 9 (may also refer to *C. albipes*). Cook 1965: 103 (list of species, distribution). Roth 1967: 65 (identification key to larvae, notes on morphology, ecology), antenna fig. 1.1, dorsal process fig. 1.5, labral blade fig. 1.9, mandible fig. 1.13. Hennig 1968: 73 (list of European species, literature on larvae and pupae). Roth 1968: (identification key to pupae), terminal process fig. 4. Sæther 1970: 35 (measurements and ratios of body parts, phylogeny), upper part of eye fig. 15C. Sæther 1972: (identification keys to larval, pupal and adult stages, ecology), upper part of eye fig. 10A, parameres fig. 11B-C, respiratory organs fig. 12I-J, terminal process fig. 12O, head outline fig. 13J, dorsal process fig. 13M, mandible fig. 13Q, larval antennal 15C, labral blade fig. 15H. Sikorowa 1973: 31 (larval instars, morphology, ecology), parameres fig. 1, larval antenna fig. 4d, labral blade fig. 9d, egg mass fig. 14. Nilssen 1974: (notes on larval morphology, ecology), mandible fig. 3B. Borkent 1981: 126 (distribution, ecology, phylogeny). Sæther 1997a: (identification key to larvae, pupae and adults), figures are the same as in Sæther 2002, except female genitalia figures are lacking. Sæther 1997b: (subgeneric identification key to larvae, pupae and adults), figures are the same as in Sæther 2002, except female genitalia figures are lacking. Sæther 2002: 27 (identification key to larva, pupa and adult, redescription, morphometry), parameres fig. 18e-f, female genitalia fig. 19h, respiratory organs fig. 20c-d, larval antenna fig. 21c, labral blade fig. 21h, mandible fig. 21m, dorsal process fig. 21r, anal tubules fig. 21w.

Chaoborus crystallinus "form aus gr. Madebröken See": Eckstein 1936: (larval and adult morphology, comparison between European and exotic species), dorsal process fig. 1a, labrum and labral blade fig. 3b, bifurcate seta fig. 4c, bristled scale fig. 5c, labral seta fig. 6d, labral blade fig. 7a, labral blades fig. 8b, paramere fig. 9a.

Chaoborus alpinus Peus 1938: 63, syn. (description, larva, pupa, adult male), mandible fig. 1, labral blades fig. 2, dorsal process fig. 3, terminal process fig. 4, respiratory organs fig. 5d-f, parameres fig. 6. Hirvenoja 1960: (identification of museum specimens, ecology), parameres fig. 3. Hirvenoja 1961: (identification key). Ökland 1964: 131 (ecology, notes on morphology or larva, pupa and adult), labral blade fig. 59A, mandible fig. 59B, terminal process fig. 59C, respiratory organs fig. 59D, parameres fig. 59E. Sikorowa 1966: (larval morphology, ecology), anterior part of head fig. 3. Sikorowa 1967: (larval instars, taxonomy), mandibles fig. 1, paramere fig. 2.

Chaoborus: Alhonen & Haavisto 1969: (paleolimnology of a lake), larval mandible (plate 1, fig. 1).

Chaoboridae: Ursenbacher *et al.* 2020: (paleolimnology), pupal respiratory organ fig. 2.

Sayomyia albipes: Felt 1904: 363 (in part, description of larva), mandible fig. 103, labral blades fig. 104, labrum fig. 105, ventral hooks fig. 106.

Sayomyia rotundifolia Felt 1904: 366 (in part, description of larva).

Sayomyia flavicans: Theobald 1905: 43 (list of known species).

Material examined. Type material. Holotype male. ["Corethra flavicans ♂"] (handwritten), ["ISI 40"] (handwritten), ["MNHN, Paris ED946"], pinned (MNHN). Type locality: Germany (Giles 1902, Borkent 2014). The holotype is pinned, in relatively good condition, tip of abdomen missing. Not studied, high quality photos on labels and specimen available at https://science.mnhn.fr/taxon/species/chaoborus/flavicans.

Lectotype male of *Chaoborus eluthera* (Fig. 1). ["Chaoborus" "eluthera" "Dyar & Snn." "Potlatch, Ida." "6.20, 1907" "J.M. Aldrich." "2032" (handwritten)]. ["USNM ENT 1240508" (printed)]. The hypopygium of the lectotype male (Fig. 1a,b) is slide mounted. Designated by Alan Stone in Belkin *et al.* (1966).

FIGURE 1. a) Slide-mounted lectotype of *Chaoborus eluthera* Dyar & Shannon (syn. of *C. flavicans* (Meigen)), male hypopygium. b) Parameres of the lectotype, covered by epandrium. c) *Chaoborus eluthera* lectotype, slide.

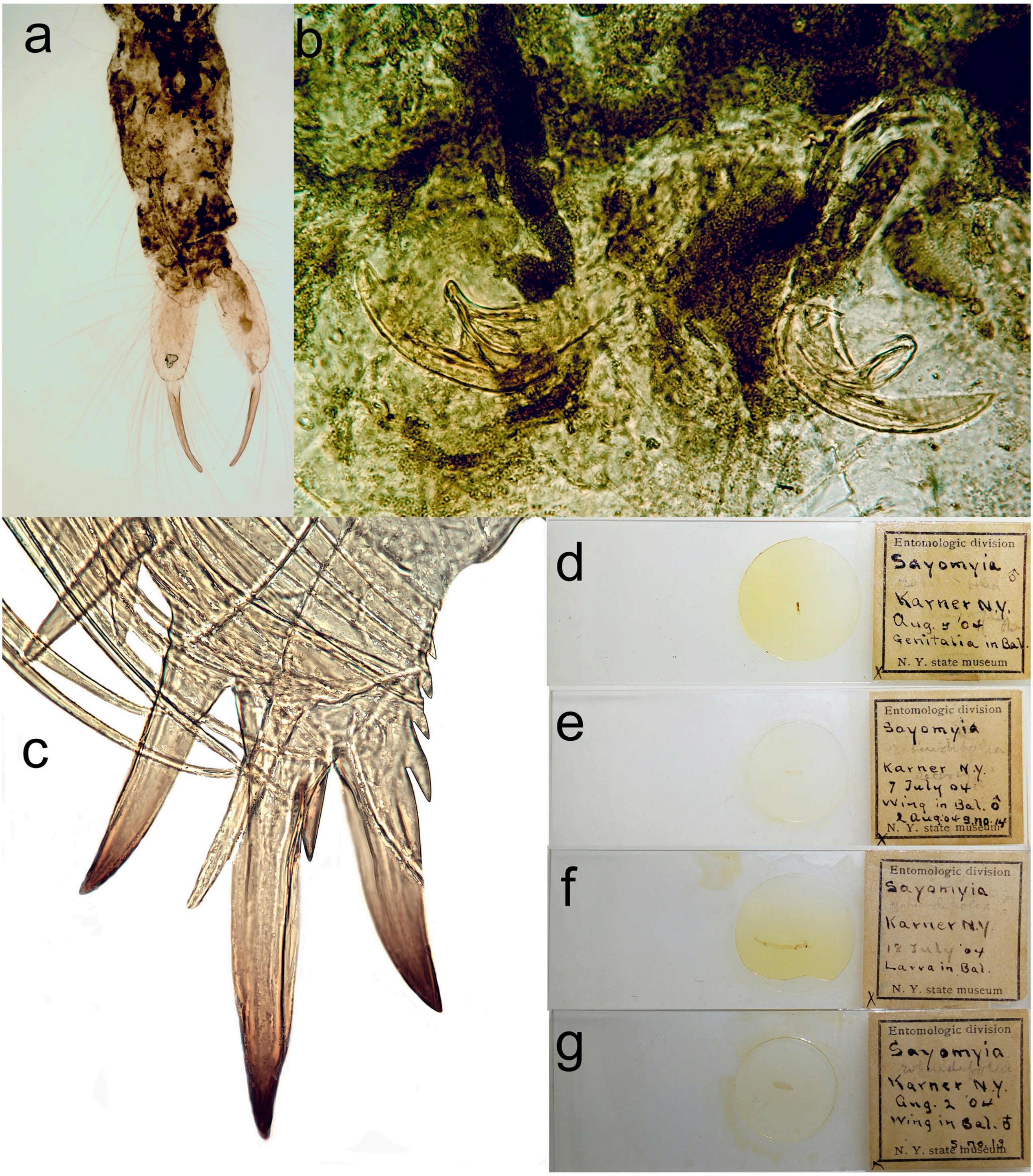

FIGURE 2. a) Slide-mounted lectotype of *Sayomyia rotundifolia* Felt (syn. of *C. albipes* (Johannsen)), male abdominal terminalia. b) *S. rotundifolia* lectotype, parameres. c) *S. rotundifolia* paralectotype, larval mandible. d) *S. rotundifolia* lectotype, slide. e–g) *S. rotundifolia* paralectotypes, e) male wing, f) larva, g) female wing.

***note.** Type material of *C. alpinus* was requested from various institutes and museums in Germany and Canada. It is mentioned in the original description that specimens were deposited in the collection of the author (Peus). It is likely, that Sæther (1967, p. 573) studied the type specimens, because ”Professor Dr. FRITZ PEUS kindly sent me his preparations from the inundation pools of the Oder (Neumark, Bellinchen) and the Rhine (Karlsruhe), and from Lake Eibsee”, Eibsee being the type locality of the species. Besides Sæther, there are no other mention of the type specimens in the literature, except Borkent (1993, 2014) stating that their location is unknown.

Other material. Finland. Ab: Naantali, Tiensuu leg. 12.VIII.1939, 1 female pinned, GV.50520 (MZH). Lohja, A. Luther leg. 23.VI.1901, 1 male pinned, GV.50509; 1 female pinned, GV.50510; 1 female pinned, GV.50511; 1 female pinned, GV.50512 (MZH). Lohja, S. Lindberg leg. 1.VIII.1927, 1 male pinned, GV.50513 (MZH). Lohja, Forsius leg. no date, 1 male, GV.50514 (MZH). Karjalohja, R. Frey leg. no date, 1 female pinned, GV.50508 (MZH). Salo, Märy, Paasivirta L. leg. 7.V.2018, 2 larva, NVO.ins2018-646 (LMM). Lohja, Kärkölä, Viitanen E. leg. 23. VIII.2017, 5 male, parameres of 2 males on slide in glue, NVO.C2020-1; 23.08.2018, 1 male, NVO.ins2018-425; 3 males, 2 females, NVO.ins2018-426; 1 male, wing, legs, head on slide, NVO.ins2018-453; 1 male, legs, head, wings, hypopygium on slide, NVO.CUL-2019-67 (LMM). N: Helsinki, Tiensuu leg. 18.VI.1949, 1 female pinned, GV.50514; 1 male pinned, GV.50515; 1 male pinned, GV.50518 (MZH). Ka: Hamina, Haukilampi, Kymijoen vesi ja ympäristö leg. 24.XI.2015, 2 larvae, NVO.ins2018-786; NVO.CUL-2019-73, 1 larva, BOLD (LMM). Hamina, Kannusjärvi, Ketola M. leg. 1.X.2014, 15 larvae, NVO.ins2018-791 (LMM). Rajala, Saima kanal, von Adelung N. leg. July 1907, 1 male pinned, GV.50519 (MZH). Ta: Iitti, Arrajärvi, Ketola M. leg. 9.X.2014, 15 larvae, NVO.ins2018-788; 1 larva, BOLD, NVO.CUL-2019-69; 1 larva, head & tail on slide, torso EtOH, NVO.CUL-2019-70 (LMM). Iitti, Märkjärvi, Ketola M. leg. 2.X.2014, 15 larvae, NVO.ins2018-790; 1 larva on slide, BOLD, NVO.CUL-2019-71; 1 larva on slide, NVO.CUL-2019-72 (LMM). Iitti, Urajärvi, Ketola M. leg. 3.X.2014, 15 larvae, NVO.ins2018-792 (LMM). Kouvola, Sompanen, Ketola M. leg. 29.IX.2014, 15 larvae, NVO.ins2018-789 (LMM). Hämeenlinna, Ilmoilanselkä, Hämeen ELY leg. 19.X.2018, 5 larvae, NVO.PM2019-01 (LMM). Sysmä, Nuoramoisjärvi, Hämeen ELY leg. 9.X.2018, 10 larvae, NVO.PM2019-02 (LMM). Loppi, Punelia, Hämeen ELY leg. 6.XI.2018, 10 larvae, NVO.PM2019-03 (LMM). Asikkala, Urajärvi, Hämeen ELY leg. 9.X.2018, 8 larvae, NVO.PM2019-04 (LMM). Urjala, Pihlajamäki, Vantanen P. leg. 18.V.2018, 4 larvae 1 pupa, NVO.ins2018-222; 1 larva, BOLD, NVO.ins2018-602; 1 larva, BOLD, NVO.ins2018-603; 1 larva, BOLD, NVO.ins2018-604; 1 larva, BOLD, NVO.ins2018-605; 1 larva on slide, NVO.CUL-2019-74 (LMM). Urjala, Kankaantausta, Vantanen P. leg 02.VI.2018, 3 larvae, NVO.ins2018-228; 1 larva, BOLD, NVO.ins2018-606; 1 larva, BOLD, NVO.ins2018-607 (LMM). Urjala, Kankaanmäki, Härmä O. leg. 30.V.2019, 1 male e.p., pupa exuviae, legs, wings, head, hypopygium on slide; torso EtOH, NVO.CHA047 (LMM). Jokioinen, Luodesuo, Korventie, Härmä O. leg. 28.V.2019, 1 male, NVO.CHA087 (LMM); 11.IV.2020, 3 larvae, LG.6280 (FLHM). Jokioinen, Kuoppatie, Härmä O. leg. 27.III.2020, 1 male e.l., LG.6135 (FLHM). Somero, Piilammi, Härmä O. leg. 18.IV.2020, 1 larva, LG.6159 (FLHM). Tammela, Purinsuo 1, Härmä O. leg. 21.IV.2020, 1 larva, LG. 6195 (FLHM). Tammela, Saarijärvi S, Härmä O. leg. 21.IV.2020, 1 larva (FLHM). Hollola, Silmälammi, Kolcsár L.-P. leg. 01.VIII.2018, 1 male, BOLD, NVO.ins2018-63 (LMM). Orivesi, Laajaanlahti, Salmela J. leg., 15.VII.2020, 1 male e.l., larva skin and pupal exuviae on slide, NVO. LMM-el-20-129; 1 male e.l., larva skin and pupal exuviae on slide, NVO. LMM-el-20-130; 1 female e.l., larva skin and pupal exuviae on slide, NVO. LMM-el-20-134 (LMM). Orivesi, Peräjärvi, Westerling P. & Väisänen A. leg. 4. XII.2017, 1 larva, NVO.ins2018-248 (LMM). Orivesi, Horhanpuro, Westerling P. & Väisänen A. leg. 4. XII.2017, 1 larva, NVO.ins2018-249 (LMM). Pälkäne, Rautajärvi, Mattila K. leg. 22.VII.–28.VII.2018, 1 female, NVO.ins2018-455 (LMM). Tb: Jyväskylä, Tellervonkatu, Linjama T. leg. 10.VIII.–12.VIII.2018, 7 males, NVO.ins2018-209. Sa: Punkaharju, Tiensuu leg. 1950, 1 male pinned, GV.50517 (MZH). Sb: Rautalampi, Pääskylampi, Salmela J. leg. 8.V.2019, 1 larva, NVO.CUL-2019-38 (LMM). Oa: Lappajärvi, Lappajärvi, Konttinen R. leg. 13.IX.2017, 15 larvae, NVO.ins2018-247; 1 larva, NVO.ins2018-611; 1 larva, BOLD, NVO.ins2018-612; 1 larva, NVO.ins2018-613; 1 larva, NVO.ins2018-614; 1 larva, BOLD, NVO.ins2018-615 (LMM). Ok: Kuhmo, Ontojärvi, Kantola L. leg. 4.IX.1984, 4 larva, NVO.chao31, NVO.chao32 (LMM). Kajaani, Nuasjärvi Kantola L. & Tikkanen P. leg. 17.IX.1984, 2 larvae, NVO.chao36 (LMM). Suomussalmi, Vuokkijärvi, Kantola L. & Tikkanen P. leg. 12.IX.1984, 7 larvae, NVO.chao87 (LMM). Suomussalmi, Vuokkijärvi, Kantola L. & Tikkanen P. leg. 13.IX.1984, 10 larvae, NVO.chao89 (LMM). Hyrynsalmi, Latvajärvi, Kolcsár L.-P. leg. 10.VIII.2018, 1 male, legs, wings, head, hypopygium on slide; torso EtOH, BOLD, NVO.ins2018-61 (LMM). Kuhmo, Roukonpuro, Kolcsár L.-P. leg. 9.VIII.2018, 4 males, 1 female, NVO.ins2018-62 (LMM). Kuhmo, Kolcsár L.-P. leg. 08.VIII.2018, 4 males, 2 females, hypopygium of one male on slide, NVO.ins2018-67 (LMM). Kuhmo, Hankaranta, Kolcsár, L-P leg. 08.VIII.2018, 1 male, mid and hind legs, head, wings, hypopygium on slide, torso in EtOH, NVO.CUL-2019-66 (LMM). Kuhmo, Roukonpuro, Kolcsár, L-P leg. 09.VIII.2018, 1 male, hind leg, head, wings, hypopygium on slide, torso EtOH, NVO.CUL-2019-68 (LMM). Obb: Ylitornio, Selkäsaari, Salmela J. leg. 10.VI.2019, 1 female, reared, pupa exuviae in on slide, NVO. LMM-el-265. Ylitornio, Niittysaari, Salmela J. leg. 10.VI.2019, 1 male, reared, pupa exuviae mid and forelegs, wings, head, hypopygium on slide, BOLD, NVO.LMM-el-268 (LMM). Rovaniemi, Erkinlampi, Salmela J. leg. 13.VIII.2019,1 larva II instar, NVO.LMM-el-566 (LMM). Rovaniemi, Hyypiökivalo, Salmela J. leg. 13.VIII.2019, 3 larvae, NVO.LMM-el-568; 8 larva NVO.LMM-el-595; 1 larva, BOLD, NVO.CUL-2019-77; 11.IX.2019, 1 pupa, reared, NVO.CH2020-1 (LMM). Rovaniemi, Hietaperänlampi, Salmela J. leg. 13.VIII.2019, 2 larvae, NVO.LMM-el-569; 5 larvae, NVO.LMM-el-587 (LMM). Rovaniemi, Veitsikangas, Salmela J. leg. 13.VIII.2019, 1 larva, NVO.LMM-el-572 (LMM); 4 larvae, NVO.LMM-el-591; 1 larva, head & tail on slide, NVO.LMM-el-613; 1 larva, head & tail on slide, NVO.LMM-el-614; 1 larva, head & tail on slide, BOLD, NVO.LMM-el-615; 27.V.2020, 1 male e.l., larval skin and pupal exuviae on slide, NVO.LMM-el-20-84; 1 male e.l., NVO.LMM-el-20-88; 1 female e.l., NVO.LMM-el-20-103 (LMM). Rovaniemi, Koivusaari, Salmela J. leg. 7.VI.2019, 1 female, reared, NVO.LMM-el-586 (LMM). Rovaniemi, Kuusilampi, Salmela J. leg. 9.VI.2020, 1 male e.l., NVO.LMM-el-20-115; 1 male e.l., NVO.LMM-el-20-118; 1 male e.l., NVO. LMM-el-20-126 (LMM); 1 larva, 1 pupa (ABC). Rovaniemi, Varjakanlammit, Salmela J. leg. 27.VII.2019, 3 larvae, NVO.LMM-el-609; Salmela J. leg. 26.V.2020,1 male e.l., larval skin and pupal exuviae on slide, adult pinned, NVO.LMM-el-20-80; 1 male e.l., larval skin and pupal exuviae on slide, NVO.LMM-el-20-82; 1 male e.l., larval skin and pupal exuviae on slide, NVO.LMM-el-20-85; 1 female e.l., larval skin and pupal exuviae on slide, NVO.LMM-el-20-87; 1 male e.l., larval skin and pupal exuviae on slide, NVO.LMM-el-20-89; 1 female e.l., larval skin and pupal exuviae on slide, NVO.LMM-el-20-90; 1 pupa e.l., NVO.LMM-el-20-93; 1 male e.l., NVO.LMM-el-20-94; 1 female e.l., NVO.LMM-el-20-95; 1 female e.l., NVO.LMM-el-20-96; 1 male & 1 female e.p., NVO.LMM-el-20-97; 1 pupa e.l., LMM-el-20-98; 1 female e.l., NVO.LMM-el-20-100 (LMM); 2 males e.p. (ABC). Lkoc: Kittilä, Lompola, Salmela J. leg. 27.VII.2019, 1 larva, head & tail on slide, BOLD, NVO.LMM-el-603 (LMM). Lkor: Savukoski, Nimetönselkä, Laine E. leg. 10.VII.2018, 1 larva II instar, NVO.EML2018-02; 1 larva II instar, NVO.EML2018-03; 1 larva II instar, NVO.EML2018-04; 1 larva II instar, NVO.EML2018-05; 1 larva II instar, NVO.ins2019-162 (LMM). Li: Ivalo, R. Frey leg. 1911, 1 male pinned, GV.50522; 1 male pinned, GV.50525; 1 male pinned, GV.50526; 1 male pinned, GV.50527; 1 male pinned, GV.50528; 1 male pinned, GV.50529; 1 male pinned, GV.50530; 1 male pinned, GV.50531; 1 male pinned GV.50535; 1 male pinned, GV.50537; 1 male pinned, GV.50540; 1 male pinned, GV.50546; 1 male pinned GV.50547 (MZH). Inari, Iso-Söimi, Salmela J. leg., 29.VI.2020, 1 pupa, NVO.LMM-el-20-128 (LMM). Utsjoki, Geaidnogeachi, Salmela J. leg., 17.VII.2018, 3 II-III instar larvae, NVO.ins2018-485; 1 larva, BOLD, NVO.ins2018-637; 1 larva, BOLD, NVO.ins2018-638; 1 larva, BOLD, NVO.ins2018-639 (LMM).

Norway. Hordaland (Hoy), Bergen, Milde, Mildevatnet, G. Kvifte & M. Stokkan leg. 21.-24.VIII.2008, 3 males Euparal (ZMBN). Buskerud, Fla, 37, J.P. Nilssen leg., no date, 1 larva III instar on slide (CNC). Ak, Hurdal, Röystrejnet, 32V PM 127 980; EIS 37, 190 masl, K.M. Olsen leg. 19.V.2003, 2 larvae, J.nr.32577 (KMO). AK, Nesodden, Kvistemyrdammen, 32VNM897264, 19 masl, K.M. Olsen leg. 24.V.2007, 5 larvae, 3 pupae, J.nr.KMO 40587 (KMO). Finnmark, Kautokeino, Lahpoluoppal, 69.20992N 23.757661E, 320 masl, Finnmarksprosjektet leg. 25.VI.-9.VII.2010, 1 male Euparal (ZMBN). Finnmark, Sør-Varanger, Pasvik, Russevann, 69.44497N 29.89904E, 60 masl, Finnmarksprosjektet leg. 19.-24.VI.2010, 19 males on slides (ZMBN).

Estonia. Rakujärv, Kolcsár L.-P. leg., 28.VII.2018, 1 male, BOLD, NVO.ins2018-64 (LMM).

Germany. Borken, Jugdenburg Castle, 51.83 6.85, stat.no. 30, A. Borkent leg., 20.VIII.1978, 1 larva (CNC). Brandenburg, Prignitz, Lenzen/Elbe, 53.1122 11.5383, Rulik B. leg. 13.VI.2014, 1 male, ZFMK-TIS-2526022; 1 male, ZFMK-TIS-2526023; 1 female, ZFMK-TIS-2526026; 1 female, ZFMK-TIS-2526028 (ZFMK). Mecklenburg-Vorpommern, Nationalpark Müritz, Boek, 53.42508 12.77963, Heller K. leg. 13.VI.2015, 1 female, ZFMK-TIS-2555532 (ZFMK). Hessen, Sinntal, 50.27362 9.65287, J. Kappert leg. 13.VI.2017, 1 male, ZFMK-TIS-2601121; 1 male, ZFMK-TIS-2588956; 1 male, ZFMK-TIS-2606370 (ZFMK). Mecklenburg-Vorpommern, Insel Rügen, Kniepow, 54.35 13.35, ZFMK Malaise Trap Program leg. 26.VII.2014, 1 male, BOLD, GBOL-224104746; BOLD, GBOL-224101338; BOLD, GBOL-224101362; BOLD, GBOL-224101369; 9.6.2014, 1 male, BOLD, GBOL-224101392; 21.VI.2014, 1 female, BOLD, GBOL-224105295; BOLD, GBOL-224105462; BOLD, GBOL-224105498 (ZFMK).

Poland. Lake near Olsztyn, A. Sikorowa leg. 14.V.1965, 2 larvae on slide, 32 (CNC). Lake Mubek near Olsztyn, A. Sikorowa leg. 20.VI.1963, 1 larva on slide (MZH).

Kazakhstan. Lake Kushmurun, Salokannel J. leg. 09.VIII.2018, 1 female, BOLD, NVO.ins2018-460 (LMM).

Russia. Petsamo, Hellen leg. no date, 1 male, GV.50523 (MZH).

Japan. Shikoku, Matsuyama, Kolcsár L.-P. leg 23.IV.2019, 1 male, BOLD, NVO.C2020-2; 1 male, NVO.C2020-3; 2 females, NVO.C2020-4 (LMM). Shikoku, Matsuyama, T. Ishihara leg. 21.IV.1952, 1 female, pinned (ELEU). Tarumi, Matsuyama, T. Ishihara leg. 2.V.1952, 5 females pinned (ELEU). Honsu, Niigata, Matsunoyama-Kannonji, Kato D. leg. 13.VIII.2020, 1 male, NVO.JAP-08; 1 male, NVO. JAP-10 (LMM).

Canada. Alberta, Siler Lake (unclear handwriting), McMillan & Smith leg. 14.VII.1970, 2 larvae III instar on slide; 1 larva II instar on slide; 1 larva IV instar on slide (CNC). Alberta, near Fort Chipewyan, 58°43′N 111°09′W, D.N. Gallup leg. June-July 1971, 1 larva on slide (CNC). Alberta, Wabumun Lake, 53°33′N 114°29′W, J. Rasmussen leg. 15.V.1972, 1 larva on slide (CNC). Ontario, Kenora, L. 120, 49.75 -93.98, G.J. Brunskill leg. 13.V.1969, emerged 22.V.1969, 1 larva, pupa exuviae, male, (same specimen) on slide, 31 (CNC). Ontario, Marmora, 44.48 -77.68, J.R. Vockeroth leg. 4.VI.1952, 1 male on slide, 40; 7.VI.1952, 1 male pinned, hypopygium in glycerol; 11.VI.1952, 7 males pinned, 1 hypopygium in glycerol; 13.VI.1952, 1 male pinned; 10.VI.1952, 1 male pinned (CNC). Ontario, Kenora, ELA 0.132.2, 49.75 -93.98, collector unknown 3.VI.1968, 1 female on slide, 0-132-2 (CNC). NWT, Mackenzie delta (NWT Pipeline Limnology Project), 68.45 -135.49, N. Snow leg. 19.IV.1972, 5 larvae, 3 in EtOH, 2 on slide, L.7-D (6) (CNC). NWT, Fort Simpson (NWT Pipeline Limnology Project), 61.85 -121.46, Crocker leg. no date, 1 larva in EtOH, RRI-11S190572DN (CNC). Ontario, N. Burgess Twp., Lanark Co., 44.80 -76.28, D.M. Wood leg. 25.VI.1967, 1 male pinned hypopygium in glycerol (CNC). Manitoba, Riding Mountain NP, 50.657 -99.974, 617 masl, BIObus leg. 12.VII.2008, 1 male, BOLD, 08BBDIP-1924 (CBG). Manitoba, Riding Mountain NP, 50.65 -99.94, 582 masl, BIObus leg. 6.VII.2008, 1 male, BOLD, 08BBDIP-2630 (CBG). British Columbia, Gulf Islands National Park Reserve, Near McDonald Campground, 48.673 -123.429, 0 masl, R. Walker & J. Mercer leg. 7.VII.2012, BOLD, BIOUG03103-B03; 1 male, BOLD, BIOUG03103-B06; 15.6.2012, 1 male, BOLD, BIOUG06622-F03; 1 male, BOLD, BIOUG06622-F05; 1 male, BOLD, BIOUG06622-F09; 23.VII.2012, 1 male, BIOUG06622-G02; 2.8.2012, 1 male, BOLD, BIOUG06622-G05 (CBG). Alberta, Elk Island National Park, Astotin Lake, 53.685 -112.86, 719 masl, S. Church leg. 29.VI.2012, 1 male, BOLD, BIOUG03291-E03; 1 male, BOLD, BIOUG03291-F11; 1 male, BOLD, BIOUG03291-G04; 1 female, BOLD, BIOUG03291-G11; 1 female, BOLD, BIOUG03291-H06; 27.VII.2012, 1 male, BOLD, BIOUG03624-G11; 1 male, BOLD, BIOUG03624-G12; 1 male, BOLD, BIOUG03624-H01; 1 male, BOLD, BIOUG03624-H03; 1 male, BOLD, BIOUG03624-H06 (CBG). Prince Edward Island, Prince Edward Island National Park, Woodland Trail / Long Point, 46.4123 -63.085, 6 masl, P. Ayles leg. 26.VI.2013, 1 male, BIOUG10377-H10, (CBG). Nova Scotia, New Glasgow, EQP-CLL-558, 45.567 -62.634, 33 masl, E. Stewart leg. 03.10.2014, 1 female, BOLD, BIOUG16032-D09; 1 female, BOLD, BIOUG16032-E06 (CBG). British Columbia, Gulf Islands National Park Reserve, North Pender Island, Roe Lake Trail, 48.781 -123.301, 108 masl, BIObus leg. 22.VI.2014, 1 male, BOLD, BIOUG23518-B10; 1 male, BOLD, BIOUG23518-D01; 1 male, BOLD, BIOUG23518-D10; 1 female, BOLD, BIOUG23518-G06; 1 female, BOLD, BIOUG23518-H10 (CBG). British Columbia, Victoria, 48.5197 -123.43, 63 masl, D.Faser & L. Ramsay leg. 30.VII.2014, 1 male, BOLD, BIOUG28195-D07; 1 female, BOLD, BIOUG28195-D12 (CBG). Ontario, Perth, Murphy`s Point Provincial Park, 44.7812 -76.2336, 143 masl, CBG Collections Staff leg. 19.VI.2014, 1 male, BOLD, BIOUG35181-F05; 1 male, BOLD, BIOUG35181-F12; 1 male, BOLD, BIOUG35181-H01; 1 male, BOLD, BIOUG35181-H04; 1 male, BOLD, BIOUG35187-A06; 1 male, BOLD, BIOUG35187-A07; 1 male, BOLD, BIOUG35187-A11; 1 male, BIOUG35187-B03; 1 male, BOLD, BIOUG35187-B11; 1 male, BOLD, BIOUG35187-B12; 1 male, BOLD, BIOUG35187-D04; 1 male, BOLD, BIOUG35187-D06; 1 male, BOLD, BIOUG35187-D10; 1 female, BOLD, BIOUG35187-F07 (CBG).

USA. Arizona, Walker L., Green J. leg. 29.VII.1982, 1 larva on slide (CNC).

Redescription. Adult male. Head light brown, bearing pale setae. Non–setose area of occiput whitish, frontal macula bare. Antennal flagellomeres pale. Length of penultimate flagellomere 281 (262–296, n=11), apical flagellomere 239 (214–257, n=9), penultimate/apical 1.18 (1.04–1.36, n=9). Lengths of palpal segments 2–5 (n=10 except 5th palpal segment n=8): 111 (101–129), 218 (201–248), 196 (174–222), 370 (331–409). Thorax. Scutum with orange–dark brown scutellar stripes; ground color straw yellow–light grayish, setae pale (Fig. 3a,b). Scutellum and mediotergite orange–dark brown. Coloration of pleuron composed of pale and dark areas: ventral part of katepisternum about as dark as scutellar stripes; antepronotal lobe, postpronotum, anepimeron, part of metanepisternum and part of anepisternum slightly darkened, halteres whitish (Fig. 4). Thoracic setae (n=5, except katepisternal and postpronotal n=4): antepronotal lobe 32 (25–36), postpronotal 5 (4–5), proepisternal 8 (7–8), katepisternal 4 (3–4), anepisternal 11 (8–15), anepimeron 8 (4–10), supra–alar 2 (2–3). Legs pale–straw yellow, apical tarsomeres slightly darkened. Foreleg, lengths of fe, ti and ta1–ta5 (n=10): fe 1737 (1517–1922), ti 1865 (1559–2097), t1 787 (650–901), t2 496 (420–557), t3 398 (332–455), t4 264 (210–307), t5 193 (169–219). Midleg, lengths of fe, ti and ta1–ta5 (n=10): fe 1606 (1445–1802), ti 1558 (1353–1902), t1 665 (557–815), t2 426 (358–547), t3 342 (301–429), t4 220 (197–281), t5 181 (155–197). Hind leg, lengths of fe, ti and ta1–ta5 (n=8): fe 2002 (1875–2198), ti 1903 (1722–2107), t1 1102 (989–1199), t2 621 (563–698), t3 442 (408–481), t4 246 (229–271), t5 192 (169–205). Wing (n=10). Length 3862 (3394–4170), width 884 (771–952), length/width 4.38 (3.71–4.57); fork of R_{2+3} 423 (330–490), fork of M_{1+2} 402 (322–476), R_3 1302 (1149–1539), M_1 1113 (988–1226), number of setae on squama 35 (30–42, n=9). Abdomen. Ground color of tergites pale yellowish or grayish, first tergite brownish, brown basal band of second tergite very wide, with a median lobe, third–fifth tergites with a subapical brown band, median lobe modest; bases of setae with a dark ring (Fig. 5a). Hypopygium (Fig. 6). Gonocoxite most often yellowish brown, rarely dark brown, length 534 (477–655), width 169 (141–199), length/width 3.05 (2,37–3,46), n=9); gonostylus brown–dark brown, rather narrow, length 428 (364–462), width 31 (27–36), length/width 13.74 (11.86–16, n=10); paramere usually bicolorous, basal part pale, apical claw infuscated, in some specimens dark all over; medially bent and constricted; apical claw rather narrow, slightly curved (viewed from above) (Fig. 6b–e, 8a); subapical crest present or absent; if present may vary in width (Fig. 7); length 141 (118–160, n=9).

Adult female. In general similar to male, with usual sexual differences. Penultimate flagellomere (152–180, n=2), apical flagellomere (195–206, n=2), penultimate/apical 0.78–0.87. Lengths of palpal segments 2–5 (n=3 except 5th palpal segment n=1): 117 (109–129), 224 (207–236), 208 (188–219), 401. Thoracic setae (n=2): antepronotal lobe 31–37, postpronotal 7, proepisternal 7–9, katepisternal 7–8, anepisternal 18–19, anepimeron 15–17, supra–alar 2. Wing length 4503 (4263–4701), width 1216 (1167–1303), length/width 3.71 (3.49–3.99); fork of R_{2+3} 391 (348–467), fork of M_{1+2} 396 (326–450), R_3 1698 (1682–1723), M_1 1512 (1478–1558), number of setae on squama 43 (26–53) (n=3). Foreleg, lengths of fe, ti and ta1–ta5 (n=1–2): fe 1845–1893, ti 1898–1993, t1 930, t2 556, t3 441, t4 292, t5 212. Midleg, lengths of fe, ti and ta1–ta5 (n=3): fe 1671 (1576–1753), ti 1573 (1458–1694), t1 713 (665–712), t2 426 (409–446), t3 298 (251–323), t4 236 (222–250), t5 195 (183–199). Hind leg, lengths of fe, ti and ta1–ta5 (n=3): fe 2085 (1887–2298), ti 2082 (1903–2200), t1 1196 (1140–1239), t2 664 (635–700), t3 459 (443–485), t4 271 (244–301), t5 215 (203–231). Abdominal tergites (Fig. 5b) 3–5 with relatively wide subapical bands, median lobes wider than in males.

Pupa. Thoracic respiratory organ constricted subapically, either slender (pond populations, Fig. 9a, length 1034 (920–1181), width 250 (207–282), length/width 4.16 (3.8–4.47, n=8)) or voluminous (lake populations, Fig. 9b, length 1108 (1011–1364), width 401 (386–413), length/width 2.75 (2.47–3.3), n=4). Lateral ribs of terminal processes brown to light brown, mid rib brown to dark brown; in lake-dwelling specimens all ribs may be pale.

IV instar larva. Mandibular fan bristles 13 (11–15, n=24). Apices of mandibular teeth 1, 2 and 4 darkened, otherwise pale, especially in lake-dwelling populations; in pond populations tips may be more extensively darkened, including tooth 3 (Fig. 10a,b). Average number of lateral teeth 4.3 (3–6, n=23), uppermost tooth smaller than mandibular tooth 3 (Fig. 9a,b). Labral blade (Fig. 10c) almost always serrated, length 276 (245–327), width 59 (48–68), length/width 4.72 (3.77–5.95, n=25). Length of antenna 543 (477–670, n=24). Number of anal fan setae 23 (20–26, n=23). Anal hook pale–brown in color.

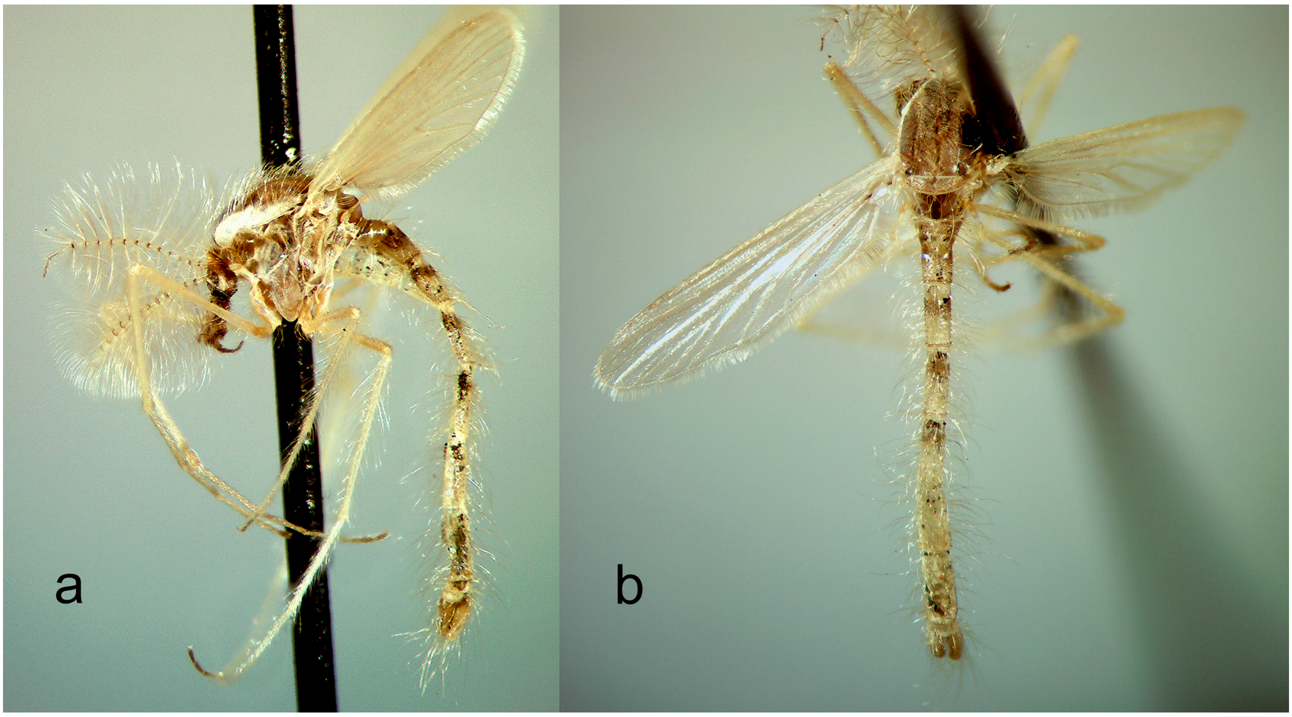

FIGURE 3. *Chaoborus flavicans* (Meigen), pinned male, a) lateral view, b) dorsal view (Canada, Ontario, Marmora).

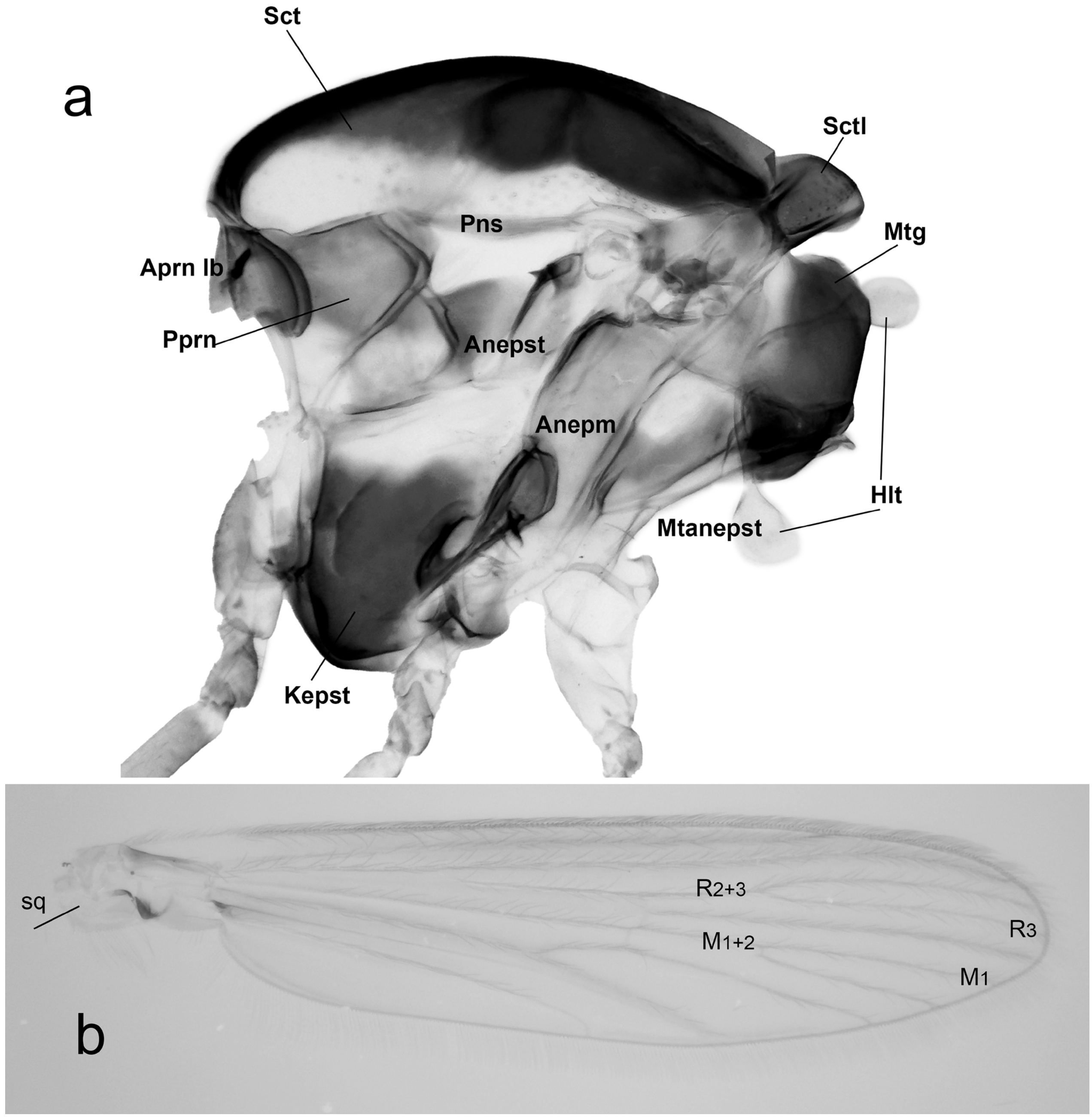

FIGURE 4. a) *Chaoborus flavicans* (Meigen), slide-mounted male, thorax, lateral view (Norway, Russevann). Anepm=anepimeron, Anepst=anepisternum, Aprn lb=antepronotal lobe, Hlt=halteres, Kepst=katepisternum, Mtanepst= metanepisternum, Mtg=mediotergite, Pns=paranotal suture, Pprn=postpronotum, Sct=scutum, Sctl=scutellum. b) *Chaoborus posio* Salmela **sp. n.** (Finland, Tammela), male wing,, sq=squama.

DNA barcoding. *Chaoborus flavicans* was the most genetically divergent member of the complex, being over 30 % divergent from the most closely related congener (Table 1). The average pairwise tree distance of sequences (intra) for this species was modest at 2.4 %. However, this average was inflated by the presence of differentiated geographic clades (Nearctic and Palearctic; Fig. 15). The most basal sequence of *C. flavicans* was from Japan where the divergence was 7 % from Holarctic *C. flavicans*. These geographic clades presumably resulted from survival in separate Pleistocene glacial refugia (although the more divergent Japanese lineage may predate the Pleistocene). There was regional variation within the Palaearctic (Fig. 15). The barcoded Japanese specimen forms a unique BIN in BOLD (BOLD:AEF3847), that is 4.28 % (K2P) distant from the nearest Palaearctic *C. flavicans* specimen. Palaearctic haplotype subgroups formed two BIN clusters in BOLD, BOLD:ACB8413 and BOLD:ADT7895. The members of the former were mainly from ponds and small lakes, collected from Finland, Estonia, Norway, Germany, Kazakhstan and China, while the latter was composed of Finnish and South Korean specimens mostly from large, thermally stratified lakes. Nearctic specimens clustered in a single BIN (BOLD:AAG5462). The probability of identification of *C. flavicans* from barcoding information alone was high (97%).

Comments. Adults of *C. flavicans* are typically relatively light in their coloration. Scutellar stripes and adjoining integument are orange-brown or light brown, ground coloration is pale yellow or straw yellow, and pleural sclerites follow the same pattern. Abdominal tergites are yellowish brown with darker subapical bands on tergites 2–5. Based on these color patterns, adult specimens can be identified to species with high confidence. However, some specimens are darker, and for example, thoracic markings approach black in color (Fig. 4) and abdominal tergites are more uniformly darker. Parameres of adult males are medially bent and constricted, with the apical claw dark and relatively narrow. Pupae of *C. flavicans* are hard to separate from those of *C. albipes*, especially among pond populations that have slender respiratory organs. Larvae of *C. flavicans* are unique in the possession of small lateral mandibular teeth. Additional measurements from larvae and pupae are available e.g. from Parma (1969), Sæther (1967) and Sikorowa (1973).

Sæther (1967) was the first to study the variation of *C. flavicans* in a Holarctic context. His study was mainly based on larvae and pupae, but the parameres of adult males were also examined. First of all, Sæther synonymised *C. alpinus* with *C. flavicans* but he named three forms, *flavicans*, *alpinus* and *infuscatus*. These forms should display differences especially in larval coloration, shape of pupal respiratory organ, and shape and coloration of male paramere (as "genital sclerite"). However, as Sæther himself discusses, these characters are mostly overlapping and at least partly influenced by the environment. It should also be noted that the material studied by Sæther was treated in KOH, which may obscure coloration patterns (Borkent 1979). Sæther did not explicitly assign the studied specimens to these forms, but it may be deduced that f. *flavicans* and f. *alpinus* are European and f. *infuscatus* is North American.

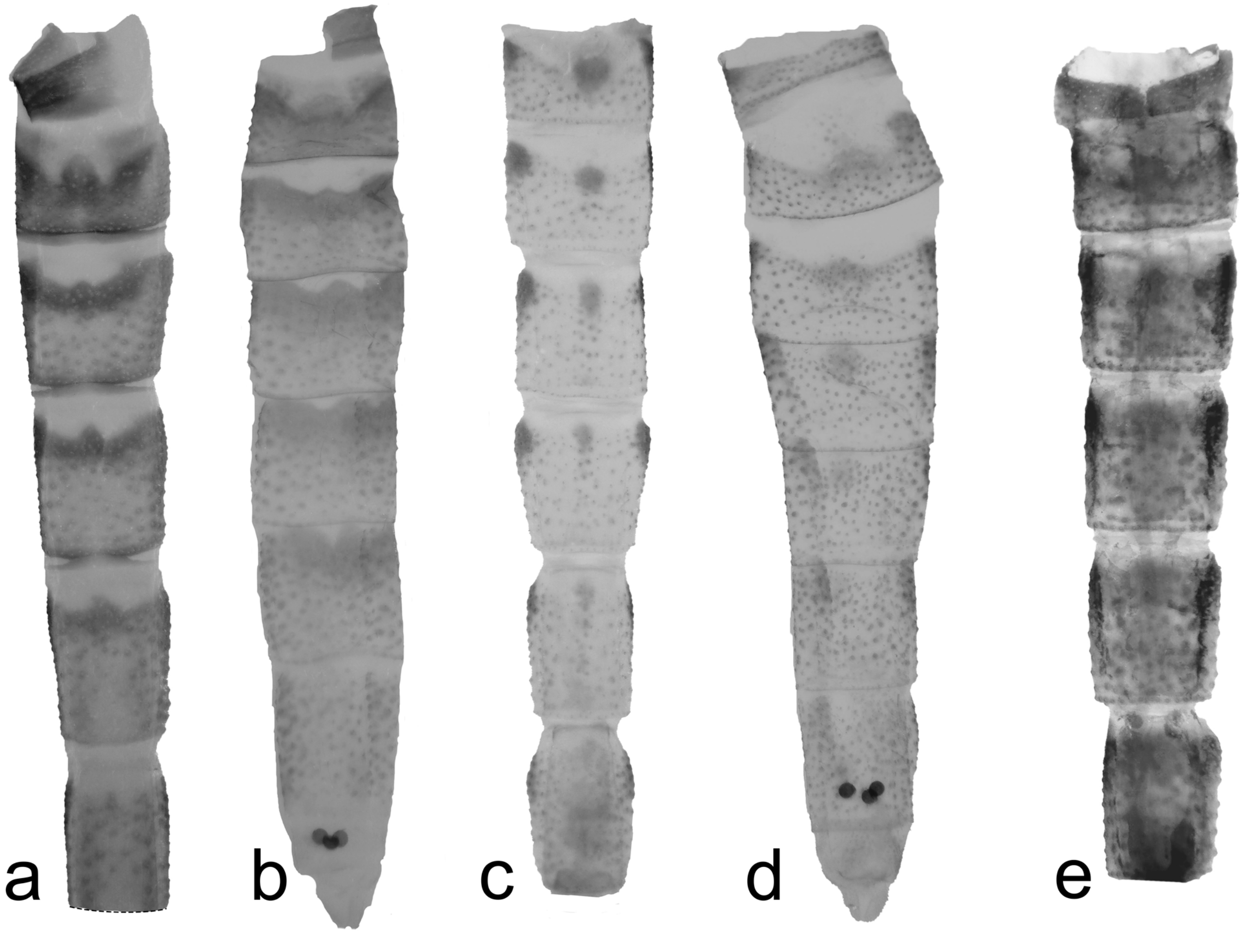

FIGURE 5. Abdominal tergites of adult specimens, *Chaoborus flavicans* (Meigen) (a–b) and *C. albipes* (Johannsen) (c–e). a) male (Germany, Kniepow), b) female (Germany, Kniepow), c), male (Canada, Ontario, Owen Sound) d) female (Canada, New Brunswick, Spingfield), e) male (Norway, Buskerud).

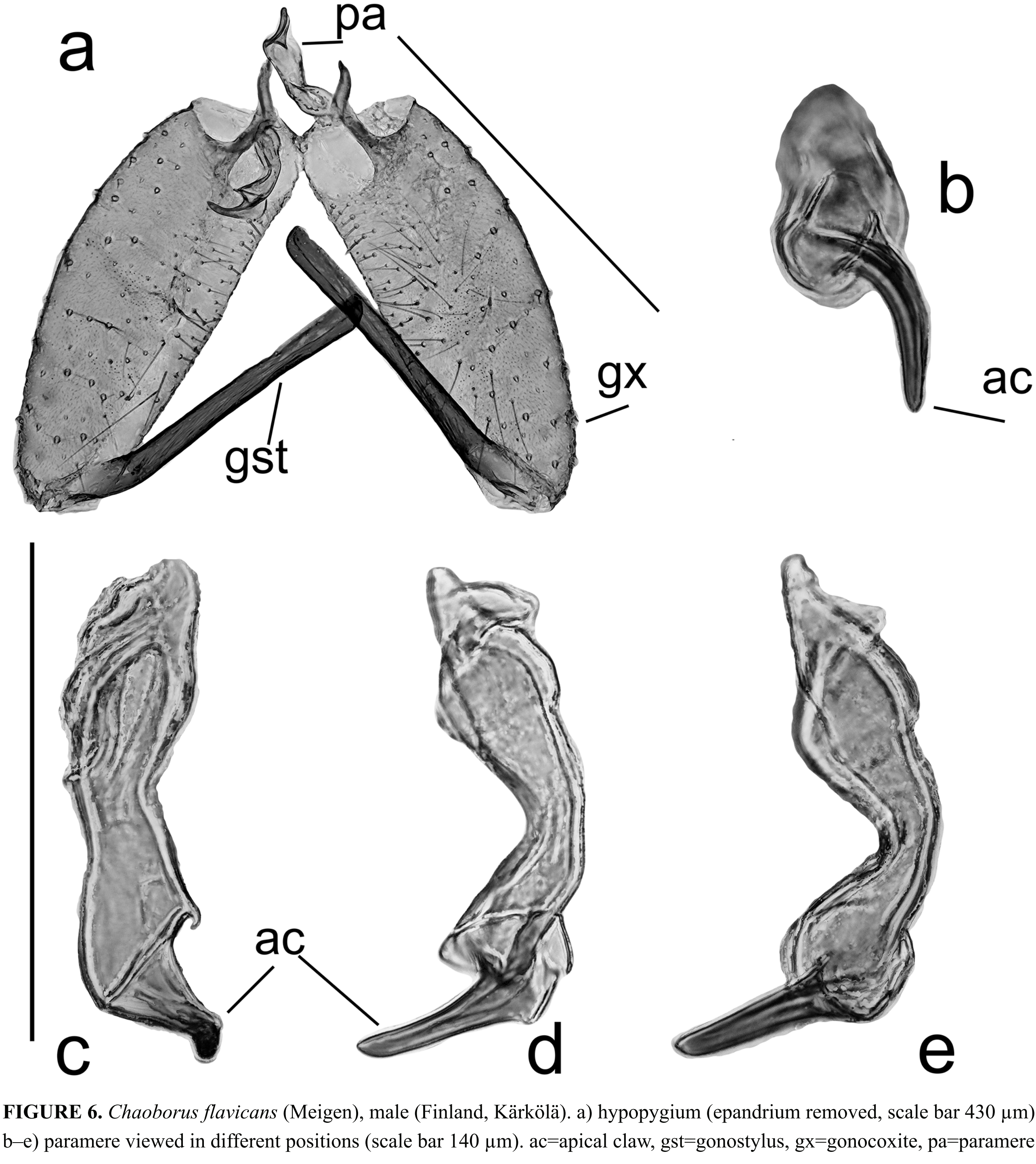

FIGURE 6. *Chaoborus flavicans* (Meigen), male (Finland, Kärkölä). a) hypopygium (epandrium removed, scale bar 430 µm), b–e) paramere viewed in different positions (scale bar 140 µm). ac=apical claw, gst=gonostylus, gx=gonocoxite, pa=paramere.

Above all, it may be assumed that all specimens studied by Sæther (1967) actually belong to *C. flavicans*, not to the two other species covered in the present revision. This is due to the shape of parameres depicted by him and the fact that specimens were mostly collected from larger lakes, not from ponds. Thus, Sæther's study provides a good source to assess intraspecific variation of *C. flavicans*, especially for measurements of specific structures and numbers of setae. Among the characters, the pupal respiratory organ and male paramere are particularly discussed as follows because these are otherwise important in *Chaoborus* taxonomy (e.g. Martini 1929; Peus 1934; Berg 1937; Sæther 1970; Borkent 1979).

The forms that Sæther (1967) described differ in some regards. The respiratory organ is present either as a slender (f. *flavicans*) or a broad form (f. *alpinus*, *infuscatus*) (Fig. 9a,b), and its function is to keep the pupa in upright position in the water (A. Borkent pers.comm.) and provide stability during emergence (Parma 1971a). The f.

infuscatus may have strong spicules on the whole surface and in f. *alpinus* these spicules are apparently lacking. Broad or voluminous respiratory organs are present in lake populations. In contrast, slender organs are present in pond populations, such as among the pupae described by Peus (1934) from the inundation pools along large rivers in Germany (see also Sæther 1967, table 2). Organ volume may be affected by environmental conditions such as wave action (i.e., phenotypic plasticity). In smaller lentic waters, slender organs may suffice for safe emergence. On the other hand, organ width may be a genetically fixed trait. Finally, presence or absence of spicules in the two forms may be at least partly artefactual in nature. If one looks at the surface of the organs with high magnification, it can be seen that such spicules are indeed present on slender organs; instead of protruding, the spicules are appressed to the lamina.

The subapical crest of the male paramere may be present (f. *alpinus*) or absent (f. *flavicans*, *infuscatus*); if present, it may vary in size (Peus 1938; Sæther 1967). Among the material studied in this revision, the presence of a crest is the prevailing character, and we agree that its size may vary (Fig. 7). However, unlike in Sæther (1967), the crest was also present in Nearctic specimens. One male from northern Norway (Kautokeino) possessed the paramere of the f. *infuscatus* (dark, crest absent) type. *Chaoborus flavicans* parameres figured by Cook (1956) actually depict *C. albipes*, and thus Sæther's comment, in reference to Cook (1956), "without having a wing-like crest" for Nearctic specimens is not valid. It should also be noted that the paramere is a complex structure, and its position on the slide or angle to the viewer may influence whether the crest is visible or not. We thus conclude that the formae and their traits presented by Sæther are geographically vastly overlapping and bear only limited or minimal taxonomic importance.

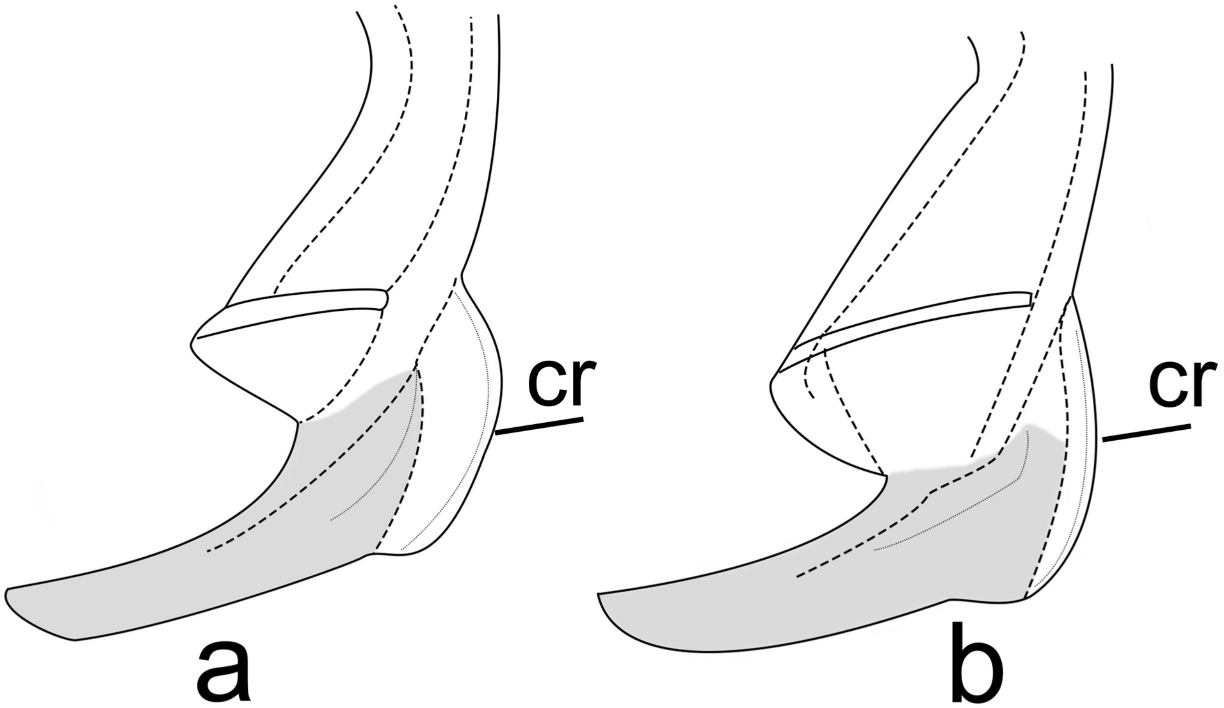

FIGURE 7. *Chaoborus flavicans* (Meigen), apical part of male paramere. a) specimen with wide subapical crest (cr) (Germany, Prignitz), b) specimen with narrow subapical crest (Canada, Ontario, Marmora).

Sikorowa (1973), among other things, studied the larval instars and intraspecific variation of *C. flavicans* in Poland. According to her results, pond and lake populations differ in some larval characters. For example, larvae from lakes are more transparent than those from ponds, which is at least partly explained by the algal growth in the cuticula of pond-dwelling specimens (Sikorowa 1973, p. 15). Moreover, pond larvae are larger than lake larvae (Sikorowa 1973, table 3). However, Sikorowa also examined the presence/absence of the subapical crest of male parameres between pond and lake populations. This data is not quantified, but she states that the subapical crest may be present in both populations, and despite differences in larval characters, this variation should be considered as intraspecific.

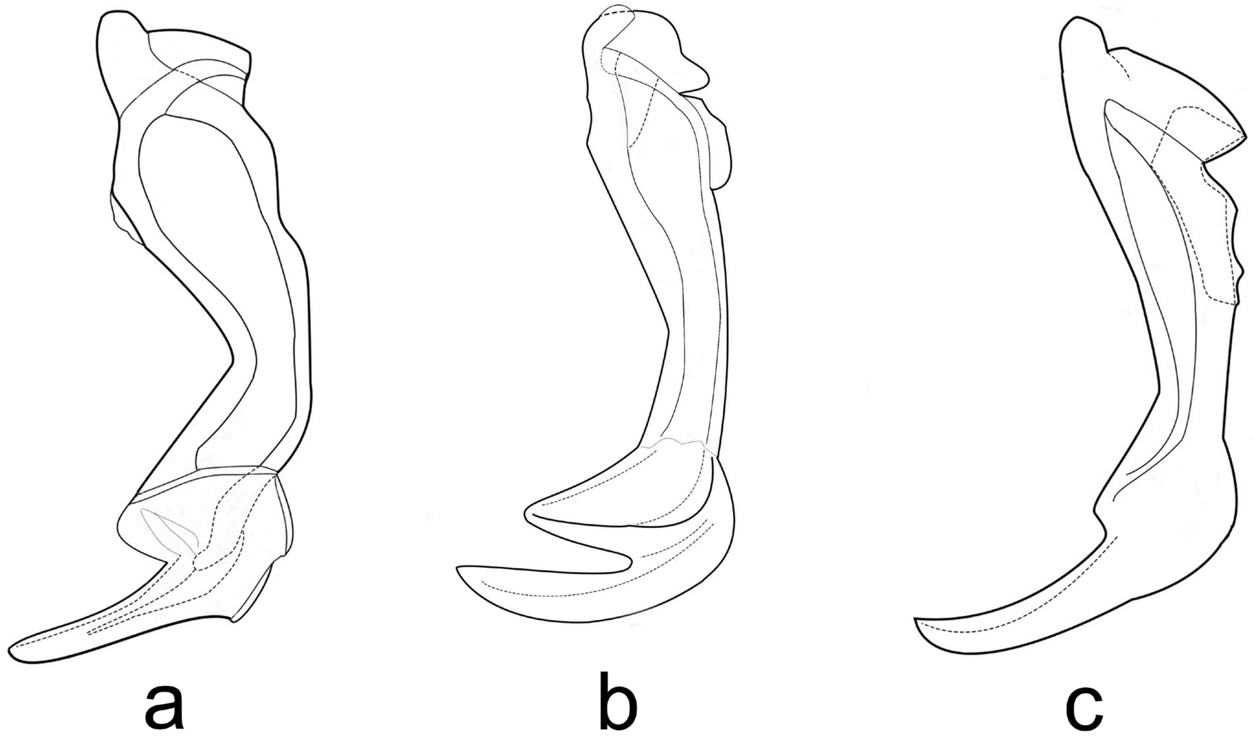

FIGURE 8. Male parameres of a) *Chaoborus flavicans* (Meigen) (Finland, Kärkölä), b) *C. albipes* (Johannsen) (Finland, Joroinen) and c) *C. posio* Salmela **sp. n.** (Finland, Utsjoki).

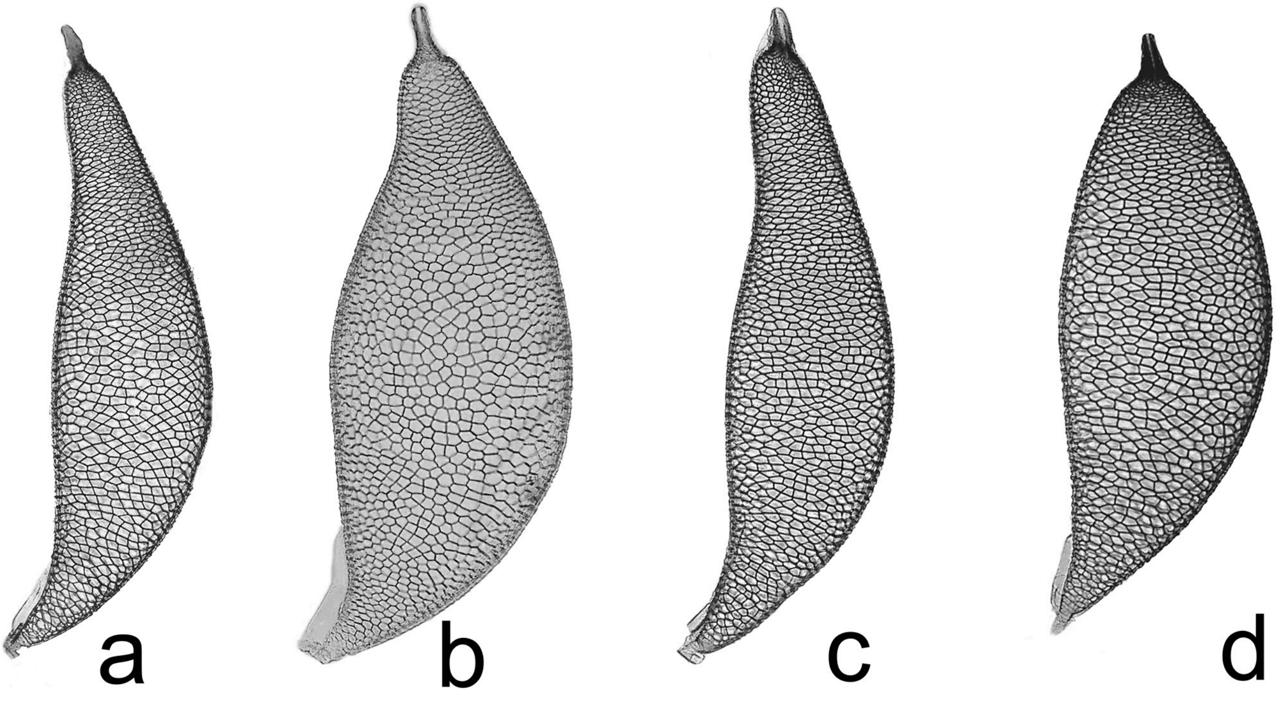

FIGURE 9. Pupal respiratory organs. *Chaoborus flavicans* (Meigen), a) slender type from a pond population (Finland, Urjala), b) voluminous type from a lake population (Canada, Ontario, Kenora), c) *C. albipes* (Finland, Savonlinna), d) *C. posio* Salmela **sp. n.** (Finland, Posio).

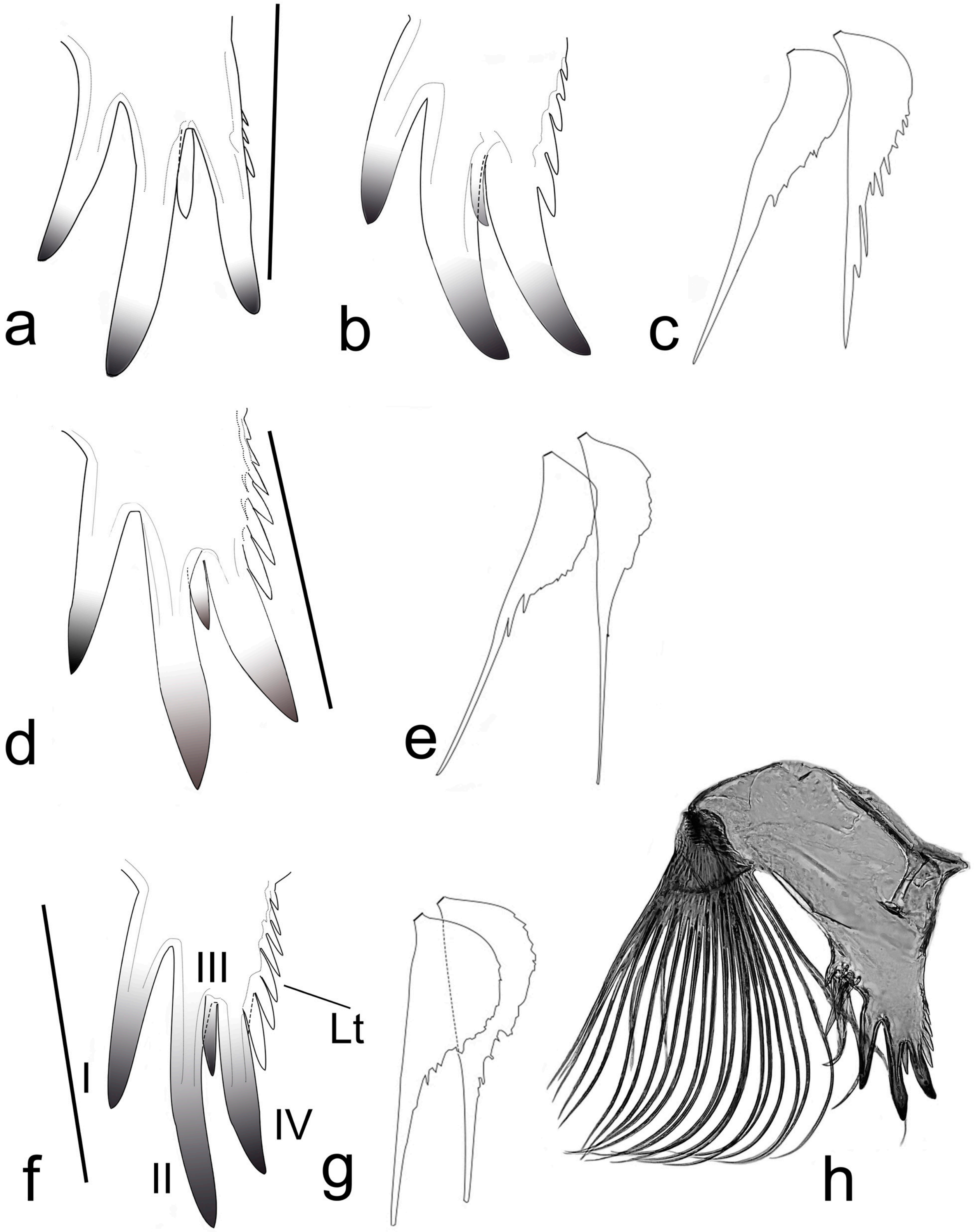

FIGURE 10. Larval mandibles (a,b,d,f;h showing whole mandible with mandibular fan bristles) and labral blades (c,e,g) of *Chaoborus flavicans* (Meigen) (a,c, lake population, Finland, Arrajärvi, b, pond population, Finland, Rovaniemi), *C. albipes* (Johannsen) (d,e, Finland, Savukoski) and *C. posio* Salmela **sp. n.** (f,g,h Finland, Posio). I–IV mandibular teeth (III=subordinate tooth), Lt=lateral teeth. Scale bars a: 200, d: 180 and f: 130 µm. Lengths of labral blades ca. 250 µm.

Distribution. The species has a broad Holarctic range. It is widely distributed in the Nearctic Region, despite hitherto confusion with *C. albipes* (e.g. in Cook 1956; Borkent 1981). In the Palaearctic it occurs from Ireland to Japan and from northern Fennoscandia and western Russia to Italy, Sardinia and Spain (this study, Aitken 1954; Wende *et al.* 2006; Arranz *et al.* 2015; Andersen & Kvifte 2012).

Ecology. Mostly univoltine in the boreal–north temperate region, rarely bivoltine (Berg 1937; Hirvenoja 1960; Regmi *et al.* 2013), but may produce three generations in fishless ponds in Poland (Sikorowa 1973). Records of 5–6 annual generations in Japan (Xie *et al.* 1998) may also concern *C. albipes* or *Chaoborus* sp. (see below). Very common in dystrophic, eutrophic, or turbid lakes and may attain high densities, up to tens of thousands per square metre in bottom samples (Stahl 1966a; 1966b; Parma 1971a; Liljendahl-Nurminen *et al.* 2002). Fourth instar larvae perform diel vertical migrations, i.e., being present in the sediment or hypolimnion during day and epilimnion during night (Valle 1930; Berg 1937; Parma 1971a; Sikorowa 1973). Larvae penetrate the sediment (Gosselin & Hare 2003) and may also feed there (Parma 1971a). Most of the feeding occurs at night in the epilimnion where larvae prey upon planktic crustaceans (Sikorowa 1973; Jäger *et al.* 2011). In ponds of riverine flood-plains, larvae can be present in shallow water close to shore and devour young *Ochlerotatus* mosquito larvae (JS pers.obs.). Larvae respond to the presence of fish via chemical cues (Dawidowicz *et al.* 1990) and are photophobic (orient to darkness) (Parma 1971a). Fourth instar larvae overwinter and pupation in lake populations occurs typically in mid or late summer (Berg 1937). Pupae also perform vertical migrations (Parma 1971a). Adults emerge on the surface at night and live about 1–4 days (Parma 1971a, Sikorowa 1973). Males may form large swarms in the lake shores around sunset (Berg 1937). Females lay eggs in roundish, floating egg masses and a female may lay only one batch of eggs (ca. 300 eggs, Sikorowa 1973). Ovipositing females do not discriminate between lentic habitats with or without fish (Berendonk 1999). First instar larvae hatch from the eggs within a few days and remain mainly in the surface waters during the first three instars (Parma 1971a; Sikorowa 1973). Fourth instar larvae finally aggregate to the deepest parts of the lake and may be present in lake bottoms of several tens of meters deep (Bardenfleth & Ege 1916). From late autumn to spring larvae hibernate in bottom sediments (Kajak & Rybak 1979). Larvae can also be present in fishless ponds (Sikorowa 1973; Garcia & Mittelbach 2008), but at least in some regions, these ponds are close to larger water bodies (JS pers.obs., Borkent 1981). Larvae of pond populations are usually somewhat larger and darker than those in lakes (Sikorowa 1973; JS pers.obs.). The species is also reported to occur in temporary ponds (Peus 1934; Kuper & Verberk 2011; Arranz *et al.* 2015), but these are results of the spill-over of larvae from adjacent water bodies (Borkent 1979) and ovipositing females from permanent populations (Berendonk & Bonsall 2002). Pond populations of *C. flavicans* emerge in late May or early June in Finland, and in late April in Poland (Sikorowa 1973). In Finland, *C. flavicans* is generally very rare or absent from chaoborid communities of fishless ponds. There is evidence that the larger and dominant species *C. obscuripes* (Palaearctic) may displace *C. flavicans* from fishless water bodies (Wissel & Benndorf 1998). However, *C. flavicans* and *C. obscuripes* may coexist if the water body is deep enough to permit spatial segregation of the two species (Hongve 1975).

Chaoborus albipes **(Johannsen, 1903), stat. rev.**

Corethra albipes Johannsen 1903: 398 (original description of female holotype), wing plate 39 fig. 11. Richardson 1912: 202 (redescription of larva, especially in comparison to *C. plumicornis var. americana* (=*Chaoborus americanus*), description of male, short comments on pupa and adult female, biology), larval antennae fig. 1, male wing fig. 2.1, female wing fig. 2.2

Sayomyia albipes: Felt 1904: 363 (in part, description of female copied from Johannsen 1903, description of pupa and male). Felt 1905: 497 (verbal description of male hypopygium). Dyar 1905: 16 (key to larvae, confused with *C. punctipennis*).

Chaoborus (Chaoborus) albipes: Dyar & Shannon 1924: 211 (comparison to *Chaoborus crystallina* and *C. flavicans*, distribution in USA). Hennig 1968: 74 (list of Nearctic species, literature of larvae and pupae).

Chaoborus albipes: Johannsen 1934: 44 (identification key, diagnoses of larva and pupa, var.a. consists of larvae with 25 or more anal fan setae and somewhat broader labral blades), larva habitus plate 43 fig. 166, pupa habitus fig. 167, labral blades fig. 171. Dickinson 1944: 357 (verbal description of adult and larva, perhaps based on earlier references, occurrence in Wisconsin), labral blade fig. 229. Belkin *et al.* 1966: 22 (location of holotype, type locality, bionomics, as a syn. of *C. flavicans*).

Sayomyia rotundifolia Felt 1904: 366 **syn. nov.** (description of female, male, larva and pupa), female wing plate 13 fig. 2, male wing plate 13 fig. 3, male hypopygium plate 40 fig. 2. Felt 1905: 497 (verbal description of male hypopygium). Dyar 1905: 16 (key to larvae).

Chaoborus rotundifolia: Johannsen 1934: 43 (identification key, following the concept by Felt).

Chaoborus (Chaoborus) rotundifolia: Hennig 1968: 74 (list of Nearctic species, literature of larvae and pupae).

Chaoborus crystallina: Matheson 1925: 159 (*Sayomyia rotundifolia* as a new synonym of *C. crystallina*).

Chaoborus crystallinus: Yamada 1932: 230 (redescription of female), habitus photo of adult female on page 230. Matheson 1944: 95 (identification key), male hypopygium plate 10 fig. 4.

Chaoborus (Chaoborus) flavicans: Cook 1956: 23, in part. (redescription of *C. (C.) flavicans* includes both *C. flavicans* and *C. albipes*), parameres (fig. 16H).

Chaoborus flavicans: Strickman 1980: (in vitro copulation and oviposition), egg mass. fig. 1. Likely the species involved here is *C. albipes*, because material studied was from a "shallow, woodland pond". Ogawa 2007: (phylogeny), mandible fig. 2.15b, parameres fig. 2.51b. Luoto & Nevalainen 2009: in part. (paleolimnology), mandibles in fig. 2a represent *C. albipes*.

Chaoborus cf. flavicans: Dupuis *et al.* 2008: (molecular analysis, phylogeny, distribution, ecology, morphology), mandible fig. 2A. An *et al.* 2010: (molecular phylogeny, partly based on same material as in Dupuis et a. 2008). Taylor *et al.* 2015: (distribution, ecology). Ballinger *et al.* 2014: (RNA virus infection, distribution). Ballinger *et al.* 2017: (RNA virus infection, distribution).

Material examined. Type material. Holotype. ["O.A.J. det 1759" "Corethra albipes Jo. Ithaca N.Y. 1901 HOLOTYPE no 2968 (partly hand written)" "Cornell University Dept. of Entomology"] white label on slide. ["HOLOTYPE Cornell U. No. 2968"] red label on slide (CUI). An additional white label is glued on left upper corner, [Chaoborus flavicans (Meig.) det. E.F. Cook 1951]. The holotype of *C. albipes* consists of a slide mounted wing only, the rest of the specimen is lost (J.J. Dombroskie, pers.comm.). The holotype was studied from photos.

Lectotype of *Sayomyia rotundifolia*, by present designation (J. Salmela, Fig. 2a,b,d). ["Entomologic division (printed)" "Sayomyia rotundifolia ♂" "Karner N.Y." "Aug. 5 '04" "Genitalia in Bal. (hand written)" "N.Y. state museum (printed)"]; lectotype of *S. rotundifolia* consists of a slide mounted male abdominal terminalia. Paralectotypes, by present designation. 1 male, ["Entomologic division (printed)" "Sayomyia rotundifolia" "Karner N.Y." "1 July 04" "Wing in Bal. ♂ s.no. 14 (hand written)" "N.Y. state museum (printed)"]; a wing on a slide (Fig. 2e). 1 larva, ["Entomologic division (printed)" "Sayomyia rotundifolia" "Karner N.Y." "18 July '04" "Larva in Bal. (hand written)" "N.Y. state museum (printed)" (Fig. 2c,f); one slide mounted larva, intact, i.e. mouthparts etc. not detached; most likely belong to *C. flavicans*, not *C. albipes*. 1 female, ["Entomologic division (printed)" "Sayomyia rotundifolia" "Karner N.Y." "Aug. 2 04" "Wing in Bal. ♀ (hand written)" "S.no.14 (handwritten)" "N.Y. state museum (printed)"]; one slide-mounted female wing (Fig. 2g). According to the original description Felt studied only one male specimen, but different dates on the labels indicate that lectotype male and paralectotype male are different specimens.

Other material. Finland. Ab: Salo, Härjänsilmä, Salmela J. leg. 2.V.2020, 6 larvae, NVO.LMM-el-20-5; 1 male e.l., NVO.LMM-el-20-15; 1 male e.l., NVO.LMM-el-20-16; 1 male e.l., NVO.LMM-el-20-17; 1 male e.l., NVO.LMM-el-20-18; 1 male e.l., NVO.LMM-el-20-23; 1 female e.l., NVO.LMM-el-20-27; 1 male e.l., NVO.LMM-el-20-28; 1 male e.l., NVO.LMM-el-20-29; 1 male pupa, e.l., NVO.LMM-el-20-34; 4 males e.p., NVO.LMM-el-20-49; 2 males e.p., NVO.LMM-el-20-55 (LMM); 1 male e.p. (ABC). N: Sipoo, Jöusjärv, Salmela J. leg. 2.V.2020, 1 pupa e.l., NVO.LMM-el-20-2; 1 male e.l., NVO.LMM-el-20-19; 1 male e.l., NVO.LMM-el-20-20; 1 male e.l., NVO.LMM-el-20-21; 1 male e.p., NVO.LMM-el-20-31; 1 male e.p., NVO.LMM-el-20-47; 1 female e.p., NVO.LMM-el-20-54 (LMM). Sipoo, Fallträsk, Salmela J. leg. 2.V.2020, 1 larval and pupal exuviae on slide, adult escaped (LMM). Ta: Tammela, Kärjensuo 1, Härmä O. leg. 9.IV.2020, 1 male e.l., LG.6092; 1 male e.l., LG.6092; 1 male e.l., LG.6093; 1 male e.l., LG.6094; 1 male e.l., LG.6109; 1 pupa e.l., LG.6110; 1 female e.l., LG.6111; 1 male e.l., LG.6128; 1 male e.l., LG.6129; 1 male e.l., LG.6130; 1 male e.l., LG.6132; 1 male e.l., LG.6164; 1 female e.l., LG.6165; 6 larva, LG.6165 (FLHM). Tammela, Kärjensuo 2, Härmä O. leg. 9.IV.2020, 1 larva (FLHM). Tammela, Ammeenpohja, Härmä O. leg. 16.IV.2020, 2 larvae, LG.6113; 1 male e.l., LG.6227; 1 male e.l., LG.6228; 1 female e.l., LG.6229; 1 pupa e.l., LG.6230; 1 male e.l., LG.6231; 1 female e.l., LG.6232; 1 pupa, LG.6234; 1 male e.l., LG.6246 (FLHM). Tammela, Lehmälammi, Härmä O. leg. 21.IV.2020, 9 larvae, LG.6193; 1 male e.l., LG.6236; 1 male e.l., LG.6237; 1 female e.l., LG.6238; 1 female e.l., LG.6239; 1 male e.l., LG.6240; 1 female e.l., LG.6241; 1 male e.l., LG.6242; 1 female e.l., LG.6252; 1 pupa e.l., LG.6259; 1 pupa e.l., LG.6260 (FLHM). Tammela, Paskolammi, Härmä O. leg. 30.IV.2020, 5 larvae, LG.6262 (FLHM). Tammela, Vehkala, Härmä O. leg. 21.IV.2020, 10 larvae, LG.6198; 1 female e.l., LG.6243; 1 female e.l., LG.6244; 1 female e.l., LG.6245; 1 female e.l., LG.6253; 1 male e.l., LG.6255; 1 female e.l., LG.6256; 1 female e.l., LG.6257; 1 pupa e.l., LG.6258 (FLHM). Jokioinen, Kaitalammi, Härmä O. leg. 13.IV.2020, 10 larva, LG.6126; 5 larvae, LG.6147; 1 male e.l., LG.6169; 1 male e.l., LG.6170; 1 male e.l., LG.6172; 1 male e.l., LG.6173; 1 female e.l., LG.6173; 1 female e.l., LG.6175; 1 male e.l., LG.6176; 1 male e.l., LG.6177; 1 male e.l., LG.6178; 1 male e.l., LG.6179; 1 male e.l., LG.6180; 1 female e.l., LG.6181; 1

pupa e.l., LG.6182; 9 males e.l., LG.6183; 8 females e.l., LG.6184; 1 male e.l., LG.6202; 1 female e.l., LG.6203; 1 female e.l., LG.6204; 1 male e.l., LG.6205; 1 pupa e.l., LG.6226; 1 pupa e.l., LG.6248; 1 pupa e.l., LG.6249; 1 pupa e.l., LG.6250 (FLHM). Somero, Hossinoja, Härmä O. leg. 10.IV.2020, 1 male e.l., LG.6102; 1 male e.l., LG.6103; 1 male e.l., LG.6104; 1 male e.l., LG.6105; 1 female e.l., LG.6106; 1 female e.l., LG.6107; 1 male e.l., LG.6108; 1 male e.l., LG.6122; 1 male e.l., LG.6124; 4 larva, LG.6125; 1 male e.l., LG.6131; 1 female e.l., LG.6133; 1 pupa e.l., LG.6134; 1 pupa e.l., LG.6166 (FLHM). Somero, Jorri, Härmä O. leg. 18.IV.2020, 2 larvae, LG.6163 (FLHM). Somero, Salakkajärvi W, Salmela J. leg. 2.V.2020, 4 larvae, NVO.LMM-el-20-9; 1 male e.l., NVO.LMM-el-20-12; 1 male e.l., NVO.LMM-el-20-13; 1 male e.l., NVO.LMM-el-20-14; 1 pupa e.l., NVO.LMM-el-20-25; 1 male e.l., NVO.LMM-el-20-26; 5 male e.p., NVO.LMM-el-20-32; 2 male e.p., NVO.LMM-el-20-50; 1 male e.p., NVO.LMM-el-20-56 (LMM). Somero, Salakkajärvi W, Härmä O. leg. 10.IV.2020, 1 male e.l., LG.6095; 1 larva, LG.6114 (FLHM). Somero, Äijämö, Härmä O. leg. 18.IV.2020, 1 larva, LG.6156; 1 larva, LG.6158; 1 male e.l., LG.6212; 1 female e.l., LG.6213; 1 male e.l., LG.6214; 1 male e.l., LG.6215; 1 male e.l., LG.6217; 1 pupa e.l., LG.6218; 1 pupa e.l., LG.6219; 1 pupa e.l., LG.6220; 1 pupa e.l., LG.6221; 1 pupa e.l., LG.6222; 1 pupa e.l., LG.6223 (FLHM). Kouvola, Konttisuo, Salmela J. leg. 6.V.2019, 1 larva, head, tail, respiratory organs of prepupa (taken beneath larval skin) on slide, BOLD, NVO.CUL-2019-26 (LMM); Kymijoen vesi ja ympäristö leg. 18.XI.2015, 1 larva, head & tail on slide, BOLD, NVO.ins2018-783 (LMM); 1 larva, head + tail on slide, NVO.CUL-2019-84 (LMM). Sa: Savonlinna, Ukonlampi, Salmela J. leg. 07.V.2019, 1 male e.l., pinned, larval and pupal exuviae on slide, hypopygium on slide, BOLD, NVO.LMM-el-15; 1 male e.l., pinned, NVO.LMM-el-17; 1 female e.l., larval and pupal exuviae on slide, NVO.LMM-el-42; 1 male e.l., pinned, NVO.LMM-el-57; 1 male e.l., pinned, pupal exuviae on slide, BOLD, NVO.LMM-el-61; 3 males e.p., NVO.LMM-el-64; 1 male e.l., pinned, pupal exuviae and hypopygium on slide, BOLD, NVO.LMM-el-76; 1 male e.l., pinned, NVO.LMM-el-99 (LMM). Sb: Joroinen, Ulminmäki, Salmela J. leg. 07.V.2019, 1 male e.l., pinned, larval and pupal exuviae on slide, hypopygium on slide, BOLD, NVO.LMM-el-10; 1 male e.l., pinned, larval and pupal exuviae on slide, hypopygium on slide, BOLD, NVO.LMM-el-11; 1 male e.l., pinned, larval and pupal exuviae on slide, hypopygium on slide, NVO.LMM-el-13; 1 male e.l., larval and pupal exuviae on slide, hypopygium on slide, NVO.LMM-el-29; 1 female e.p., pinned, pupal exuviae on slide, NVO.LMM-el-39; 1 male e.p., NVO. LMM-el-40; 1 male e.l., pinned, pupal exuviae on slide, NVO.LMM-el-41; 3 males e.p., parameres of two specimens glued on slide, NVO.LMM-el-49; 1 male e.p., pupal exuviae, wings, legs, head, hypopygium on slide, NVO.LMM-el-50 (LMM). Tb: Toivakka, Kataislammit, Salmela J. leg. 1.V.2020, 1 larva, NVO.LMM-el-20-1; 1 male e.l., NVO.LMM-el-20-42; 1 male e.l., NVO.LMM-el-20-43; 1 pupa e.l., NVO.LMM-el-20-44; 1 male e.l., NVO.LMM-el-20-45 (LMM). Obb: Rovaniemi, Pietarinlampi, Salmela J. leg. 5.VI.2020, 1 male e.p., pupal exuviae and hypopygium on slide, NVO.LMM-el-20-105; 1 male e.p., adult pinned, pupa exuviae on slide, NVO.LMM-el-20-107; 1 male e.p., NVO.LMM-el-20-108 (LMM). Lkoc: Kittilä, Muotrikkilehto, Salmela J. leg. 27.VII.2019, 1 larva, NVO.LMM-el-608 (LMM); 1 larva, NVO.LMM-el-610 (LMM); 1 larva, head & tail on slide, BOLD, NVO.CUL-2019-78 (LMM); 1 larva, head & tail on slide, BOLD, NVO.CUL-2019-79 (LMM). Kittilä, Papinmutka, Salmela J. leg. 28.VII.2019, 1 female, pupal exuviae and female in EtOH, BOLD, NVO.LMM-el-526 (LMM). Lkor: Savukoski, Rouvoivanselkä, Salmela J. leg 05.VI.2019, 1 male e.l., larval and pupal exuviae, hypopygium on slide, NVO.LMM-el-206; 1 male e.l., NVO.LMM-el-211; 1 male e.l., larval and pupal exuviae on slide, legs, wings, head on slide, torso EtOH, NVO.LMM-el-212; 1 male e.l., larval and pupal exuviae on slide, legs, wings, head on slide, torso EtOH, NVO.LMM-el-213; 1 male e.l., larval and pupal exuviae on slide, legs, wings, head, hypoopgium on slide, torso EtOH, NVO.LMM-el-214; 1 male e.l., NVO.LMM-el-215; 1 female e.l. pinned, larval & pupal exuviae on slide, NVO.LMM-el-216; 1 male e.l., NVO.LMM-el-217; 1 male e.l., NVO.LMM-el-218; 1 male e.l., NVO.LMM-el-219; 1 male e.l., NVO.LMM-el-220; 1 female e.l., NVO.LMM-el-221; 1 male e.l., NVO.LMM-el-222; 1 male e.l., LMM-el-223; 1 male e.l., NVO.LMM-el-224; 1 male e.l., NVO.LMM-el-225; 1 male e.l., NVO.LMM-el-226; 1 male e.l., NVO.LMM-el-227; 1 pupa e.l., NVO.LMM-el-228; 1 pupa e.l., NVO.LMM-el-229; 1 male e.l., NVO.LMM-el-230; 1 male e.l., NVO.LMM-el-231; 1 female e.l., NVO.LMM-el-232; 1 female e.l., larval and pupal exuviae on slide, NVO.LMM-el-233; 1 pupa e.l., NVO.LMM-el-234; 1 male e.l., NVO.LMM-el-290; Laine E. & Salmela J. leg. 13.VI.2018, 5 larvae 5 pupae, one teneral hypopogium on slide, NVO.ins2018-420; 10 larvae 3 pupae, one teneral hypopogium on slide NVO.ins2018-421; 1 pupa teneral hypopogium on slide, NVO.ins2018-427; 1 pupa, BOLD, NVO.ins2018-624; 1 pupa, BOLD, NVO.ins2018-625; 1 larva, BOLD, NVO.ins2018-626; 1 larva, BOLD; NVO.ins2018-627; 1 larva, BOLD, NVO.ins2018-628; 1 larva, NVO.ins2018-681; Laine E. leg. 12.VII.2018, 7 larvae I and II instar, NVO.ins2019-195 (LMM).

Norway. Buskerud, Kongsberg, Karlshaug - N Svensketjern, 59.5302 9.5642, 495 masl, K.M. Olsen leg. 31.V.-26.VI.2013, 20 males, 1 on slide, J.nr. BAB 470603 (KMO).

Russia. South Urals, Osipovka, Salokannel, J. leg. 05.VIII.2018, 1 female, BOLD, NVO.ins2018-457 (LMM). Primorskiy Kray, Kiparisovo (Tazyozhnyi), 43.4858 131.975, E. Zakharov leg. 7.VII.2014, 1 female, BOLD, BIOUG15361-C01 (CBG)

Japan. Tokyo, Yotsuya, 35.68 139.72, leg? 1948, 3 males 1 female in EtOH (NMNS). Sado Island, 38.03 138.33, I. Tosayabashi leg. 16.VI.1917, 1 male, pinned hypopygium in microvial (NMNS). Shiba, Tokio, 35.65 139.74, S. Yamada leg. 20.VIII.1919, 1 male, pinned (NMNS). Hokkaido, K. Tanaka leg., no date, 3 males, pinned (two hypopygia in microvial), A-0213, (NMNS). Matsuyama-shi, Higashino, 33.8411 132.8111, J. Oku leg. 19.V.2016, 1 male, pinned, hypopygium in microvial (ELEU). Honsu, Niigata, Matsunoyama-Kannonji, Kato D. leg. 13.VIII.2020, 1 male, NVO.JAP-06; 1 male, NVO.JAP-07; 1 male, NVO.JAP-09; 1 male, NVO.JAP-11 (LMM).

Canada. Ontario, Roseneath L., 44.19 -78.05, H.G. James leg. 1963, 1 male on slide, 38 (CNC). Ontario, Carden Alvar, Cameron Ranch, 44.637 -79.058, J. Cossey leg. 6.10.2011, 1 female, BOLD, BIOUG01756-G05 (CBG). Ontario, Rouge National Urban Park, Toronto Zoo, 43.8223 -79.1897, 125 masl, K. Kerr & A. Sritharan leg. 1.VII.2014, 1 female, BOLD, BIOUG20540-A09; 1 male, BOLD, BIOUG20540-B02 (CBG). Ontario, Cambridge, Indian Woods, 43.3736 -80.3652, 304 masl, BIO Collections Staff leg. 14.V.2015, 1 female, BOLD, BIOUG22361-C03 (CBG). Ontario, Charleston Lake Provincial Park, Hemlock Ridge Trail, 44.5054 -76.0275, 108 masl, BIObus leg. 22.VI.2015, 1 III instar larva, BOLD, BIOUG23326-C12 (CBG). Ontario, Owen Sound, Bayview Escarpment Provincial Park, 44.6337 -80.6983, 319 masl, CBG Collections Staff leg. 10.VII.2014, 1 male, BOLD, BIOUG33751-B08; 1 male, BOLD, BIOUG33752-A07 (CBG). Ontario, Tiny, Awenda Provincial Park, 44.8253 -79.9846, 231 masl, CBG Collections Staff leg. 8.VIII.2014, 1 female, BOLD, BIOUG34258-F03 (CBG). Ontario, Morpeth, Rondeau Provincial Park, 42.3021 -81.8531, 239 masl, CBG Collections Staff leg. 13.V.2014, 1 male, BOLD, BIOUG34670-D06; 1 male, BOLD, BIOUG34670-G06; 1 female, BOLD, BIOUG34670-H02 (CBG). Ontario, Perth, Murphy`s Point Provincial Park, 44.7812 -76.2336, 143 masl, CBG Collections Staff leg. 23.V.2014, 1 female, BOLD, BIOUG34683-F08; 1 male, BOLD, BIOUG34694-D02 (CBG). Ontario, Warsaw, Ferris Provincial Park, 44.2829 -77.7963, 131 masl, CBG Collections Staff leg. 12.IX.2014, 1 female, BOLD, BIOUG34924-D04 (CBG). New Brunswick, Springfield, Belleisle Regional High School, 45.669 -65.836, 13 masl, S. Lawson leg. 2.X.2015, 1 male, BOLD, BIOUG25544-C01; 1 female, BOLD, BIOUG25544-F11 (CBG). Prince Edward Island, Prince Edward Island National Park, 46.4123 -63.085, 6 masl, P. Ayles leg. 26.VI.2013, 1 male, BOLD, BIOUG10366-H09; 1 female, BOLD, BIOUG10368-A04; 10.VII.2013, 1 male, BOLD, BIOUG10435-C08; 5.VI.2013, 1 male, BOLD, BIOUG10660-D02; 1 male, BOLD, BIOUG10787-B11 (CBG). British Columbia, Kootenay National Park, Kootenay Pond, 50.892 -116.041, 1188 masl, BIObus 2014 leg. 14.VIII.2014, 1 female pupa, BOLD, BIOUG22761-H04 (CBG). NWT, Nahanni National Park Reserve, Nailicho (Virginia Falls), 61.606 -125.758, 578 masl, Parks Canada leg. 27.VI.2014, 1 male, BOLD, BIOUG16983-G08; 12.VII.2014, 1 female, BOLD, BIOUG17213-H03 (CBG). NWT, Reindeer Depot, Mackenzie delta, 68°42’N 134°07’W, J.R. Vockeroth leg. 5.VII.1948, 7 males (5 pinned, 2 on slide) 1 female on slide; 15.VII.1948, 2 females pinned; 1.VIII.1948, 1 female pinned (CNC).

USA. Alaska, Big Delta, Boleo Lk., 64.14 -145.81, W.R.M. Mason leg. 22.V.1955, 1 male on slide, 32 (CNC). Alaska, pond near Kuzitrin River, 65.396 -164.496, D. J. Taylor leg. 31.VII.2013, 6 larvae in EtOH, Kuzitrin 4 (UBB). Alaska, pond near Nome Airport, 64.514 -165.422, D. J. Taylor leg. 3.VIII.2011, 4 larvae in EtOH, Nome 1 2011 (UBB). North Carolina, Highlands, 35°03′N 83°12′W, 3800’, J.R. Vockeroth leg. 24.VI.1957, 4 males (1 on slide, 3 pinned, 1 hypopygium in microvial); 8.VI.1957, 1 female pinned; 10.VI.1957, 1 female pinned; 21.VI.1957, 1 male pinned (CNC).

Redescription. Adult male. Head light to dark brown, bearing pale setae. Non-setose area of occiput brownish. Clypeus bearing dark setae. Penultimate flagellomere 285 (271–313), apical flagellomere 204 (163–228), penultimate/apical 1.42 (1.21–1.78, n=6). Lengths of palpal segments 2–5: 105 (89–113), 208 (177–234), 181 (172–194), 336 (267–393, n=6). Thorax. Scutellum and mediotergite orange–dark brown (Fig. 11). Coloration of pleuron composed of pale and dark areas: most of the katepisternum darkened; antepronotal lobe, postpronotum, anepimeron, part of metanepisternum and part of anepisternum slightly darkened, halteres whitish. Thoracic setae (n=6): antepronotal lobe 33 (27–45), postpronotal 4 (3–6), proepisternal 5 (4–7), katepisternal 6 (6–7), anepisternal 16 (12–19), anepimeron 8 (7–9), supra–alar 2 (1–2, n=3). Legs pale yellow–light brown. Foreleg, lengths of fe, ti and ta1–ta5 (n=6, except t4 and t5 n=5): fe 1708 (1667–1750), ti 1773 1722–1859), t1 825 (773–864), t2 499 (455–534), t3 397

(344–432), t4 271 (230–291), t5 196 (177–221). Midleg, lengths of fe, ti and ta1–ta5 (n=6): fe 1467 (1360–1556), ti 1413 (1314–1472), t1 689 (619–727), t2 398 (348–443), t3 318 (261–364), t4 218 (188–235), t5 179 (160–193). Hind leg, lengths of fe, ti and ta1–ta5 (n=6, except fe and t4 n=5): fe 1839 (1723–1945), ti 1761 (1639–1933), t1 1012 (869–1114), t2 581 (454–643), t3 404 (318–443), t4 248 (209–271), t5 185 (171–197). Wing (n=7). Length 3485 (2777–3831), width 770 (643–882), length/width 4.52 (4.32–4.73); fork of R_{2+3} 402 (318–448), fork of M_{1+2} 370 (306–424), R_3 1054 (888–1205), M_1 903 (782–979), number of setae on squama 30 (24–39, n=5). Abdomen. Tergal pattern either with dark specks on pale ground or tergites almost uniformly brown (Fig. 5c–e); in former case tergites 2–6 with central and lateral specks that are not connected. Hypopygium (Fig. 11). Gonocoxite brown, length 484 (455–546), width 141 (118–193), length/width 3.47 (2.59–3.91, n=13). Gonostylus brown, somewhat darker than or about as dark as gonocoxite, rather narrow, length 398 (345–432), width 32 (25–39), length/width 12.55 (10.21–13.93, n=14). Paramere (Fig. 11b–e) almost unicolorous, brownish, gently curved medially, apical claw stout and curved; length 132 (122–152, n=13).

Adult female. In general similar to male. Penultimate flagellomere 165 (157–175), apical flagellomere 172 (159–186), ratio penultimate/apical 0.96 (0.91–1.04) (n=4). Lengths of palpal segments 2–5 (n=4 except 5th segment n=3): 99 (79–115), 217 (195–240), 193 (171–209), 345 (324–376). Thoracic setae (n=2): antepronotal lobe 28–34, postpronotal 7–8, proepisternal 5–9, katepisternal 4–11, anepisternal 13–14, anepimeron 5–14, supra–alar 1–3. Wing length 3587 (3025–4337), width 964 (864–1155), length/width 3.72 (3.43–4.20) (n=5); fork of R_{2+3} 372 (134–483), fork of M_{1+2} 330 (257–402), R_3 1292 (1090–1460), M1 1111 (772–1318) (n=4), number of setae on squama 35–47 (n=2). Foreleg, lengths of fe, ti and ta1–ta5 (n=4): fe 1621 (1374–1747), ti 1691 (1397–1856), ta1 790 (717–871), ta2 459 (379–509), ta3 374 (322–407), ta4 257 (202–292), ta5 188 (128–231). Midleg, lengths of fe, ti and ta1–ta5 (n=4 except ta5 n=3): fe 1477 (1301–1643), ti 1352 (1130–1489), ta1 647 (520–736), ta2 365 (255–437), ta3 270 (217–326), ta4 206 (147–240), ta5 188 (175–204). Hind leg, lengths of fe, ti and ta1–ta5 (n=2): fe 1779–1950, ti 1703–1950, ta1 978–1139, t2 542–667, t3 390–433, t4 244–284, t5 185–193. Dark specks of abdominal tergites, if present, blurred, not as clear as in males Fig. 5d).

Pupa. Thoracic respiratory organ slender, subapically constricted (Fig. 9c), length 891 (693–1057), width 220 (170–284), length/width 4.09 (3.31–4.92 n=26). Lateral ribs of terminal processes pale–light brown, mid rib light brown–dark brown.

IV instar larva. Anal fan setae 22 (18–25, n=17). Anal hook pale – brown in color. Mandibular teeth 1–4 darkened in their apical halves. Mandibular fan bristles 17.1 (14–23, n=33). Number of lateral teeth 5.4 (5–6, n=23); uppermost lateral tooth about as long as or longer than subordinate tooth (Fig. 10d). Labral blade elongated, moderately serrated or almost smooth (Fig. 10e), length 268 (228–299), width 49 (39–62), length/width 5.49 (4.38–6.85, n=24). Length of antenna 536 (443–628, n=25).

DNA barcoding. *Chaoborus albipes* was very divergent from other members of the complex (>17%) (Table 1). Intraspecific variation was the greatest within the species complex (Table 1), but as with *C. flavicans*, this divergence was mainly due to the presence of differentiated geographic clades (Fig. 16). Again, these shallow geographic clades presumably resulted from survival in separate Pleistocene glacial refugia. The pattern is not merely an isolation by distance effect as single clades are almost identical over thousands of kilometers (e.g., Nome [Alaska], Kodiak [Alaska], and British Columbia). Interestingly, two Western Nearctic/Beringian clades may presently overlap in range. The probability of identification from barcoding information alone was very high (>98%). Barcoding sequences of Alaskan specimens from the present study were >99.6% similar to the shorter Alaskan sequences of *C. cf. flavicans* of Ballinger *et al.* (2017). *Chaoborus albipes* includes three BIN clusters in BOLD: BOLD:ADT7561 (Finland), BOLD:ADT7894 (Northwest Territories, Central Russia) and BOLD:AAM6295 (eastern Nearctic). The two latter BINs were included in Hebert *et al.* (2016), a study that estimated the species richness of Canadian insects. Because *C. albipes* is composed of two Nearctic BIN clusters, it is possible that there are other phantom midge species with more than one BIN. Hence, the presence of 19 chaoborid species, in contrast to the 12 currently known, in Canada is perhaps an overestimation.

Comments. *Chaoborus albipes* is a widespread and rather common Holarctic species that has been hitherto confused with *C. flavicans*. The species, however, is distinguished from *C. flavicans* on morphological, molecular and ecological grounds. The paramere of adult males has a characteristic apical claw, that is curved and stout in structure. Also, below the apical claw is a large and protruding "lower lip" that is modest in *C. flavicans* and *C. posio* **sp. n.** The pupa is similar to *C. flavicans* (see above) and the larva is similar to *C. posio* **sp. n.** (see below).

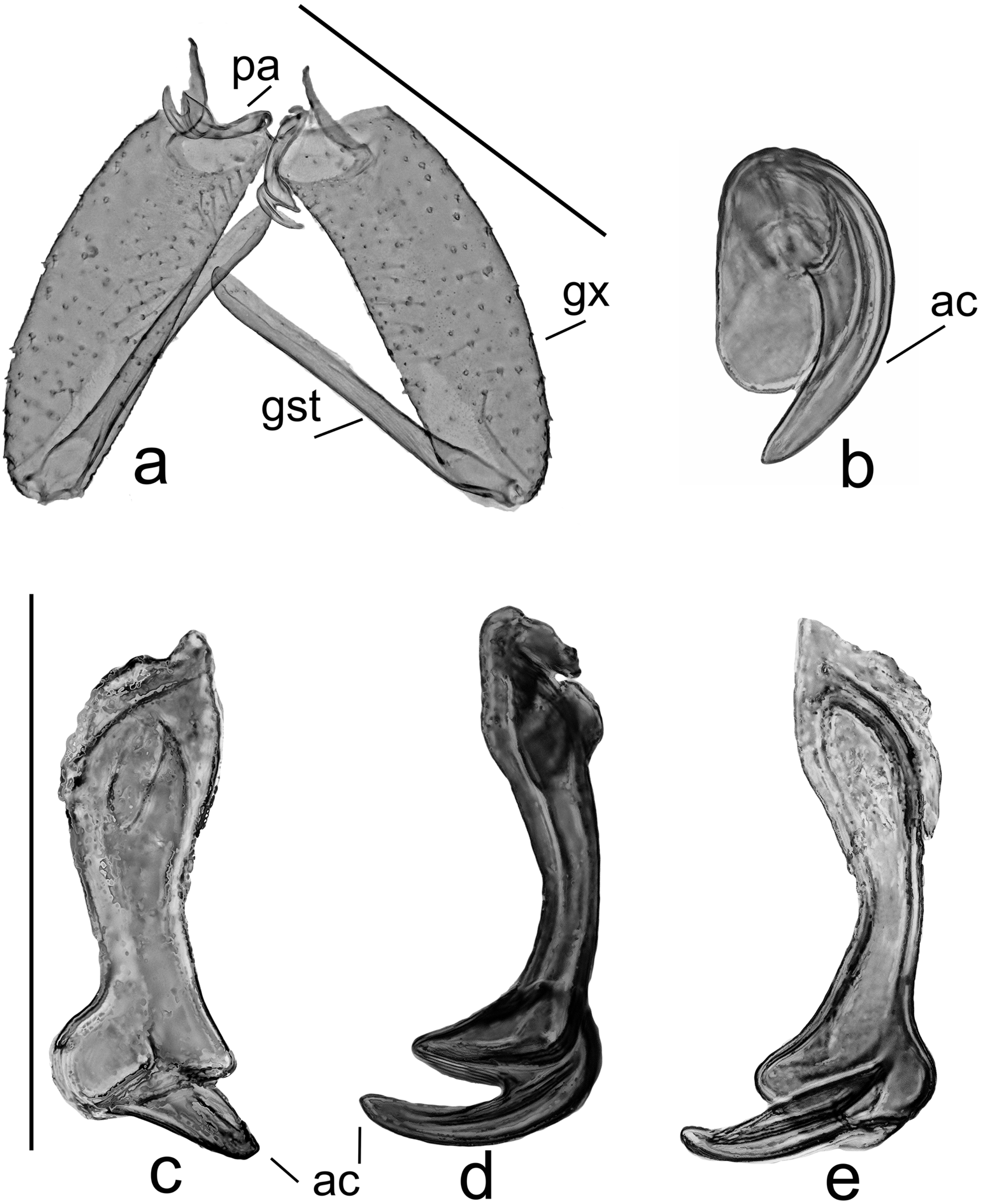

FIGURE 11. *Chaoborus albipes* (Johannsen), male (Finland, Joroinen). a) hypopygium (epandrium removed, scale bar 400 μm), b–e) paramere viewed in different positions (scale bar 130 μm). ac=apical claw, gst=gonostylus, gx=gonocoxite, pa=paramere.

The original description of the species (Johannsen 1903) is quite superficial and is based on an adult female. The holotype female was perhaps pinned and a wing was slide mounted; presently the slide remains, but the rest of the specimen is lost (J.J. Dombroskie pers. comm.). The female holotype was collected from the eastern USA, Ithaca, New York. *Chaoborus albipes* specimens from eastern North America (e.g. Nova Scotia, New Brunswick, Ontario, and Prince Edward Island) have a characteristic pattern on the tergites. Unlike *C. flavicans*, there are no transverse dark subapical bands. Instead, *C. albipes* has have separate lateral and median specks on the tergites 2–6 (Fig. 5c,d). The original description states, "… lateral margin sparsely sprinkled with small irregular black specks." (Johannsen 1903, p. 398). Thus, despite the female sex of the holotype and a partially lost specimen, it is concluded that *C. albipes* is the oldest available name for this taxon. *Chaoborus albipes* was redescribed by Felt (1904) and Richardson (1912) soon after its initial description; the tergal pattern in both publications is consistent with the current concept of *C. albipes*. Lateral specks may also be partly due to the dispersion of chromatophores from the larval air sacs to the tissues of adult flies (Borkent & Borkent 2008), but it is evident that the abdominal patterns in *C. albipes* (especially eastern Nearctic populations) and *C. flavicans* are specific (Fig. 5). *Sayomyia rotundifolia* is treated as a new junior synonym of *C. albipes*. The lectotype male of *S. rotundifolia*, as designated here, consists of a slide mounted abdomen (Fig. 2a,b,d). The hypopygium of the lectotype is in moderately good condition and the shape of the paramere can be seen from the slide (Fig. 2b), despite being somewhat pressed.

In the original description of *Sayomyia rotundifolia*, the larva, pupa, adult female and male are described (Felt 1904). The description of the larva is either erroneous or based on the III instar larva, because, according to Felt (1904, p. 368) there are four pairs of post-antennal filaments, the anal fan (as "ventral tuft") consists of 16 setae and the number of mandibular fan bristles is seven. Nonetheless, the paralectotype larva is a IV instar larva with 10 post-antennal filaments, 21 anal fan and 12 mandibular fan bristles. Felt (1904) implicitly considers the features given by him as diagnostic differences between *S. albipes* and *S. rotundifolia*, a diagnosis later repeated by Johannsen (1934). A further confusion with the paralectotype larvae is its taxonomic identity. That specimen is slide-mounted as a whole, but fortunately the mandibles and labral blades can be clearly seen. The paralectotype larva (Fig. 2c) has four mandibular lateral teeth, and the uppermost of these is somewhat smaller than the subordinate tooth. This character and the low number of mandibular fan bristles (12) taken into account, the paralectotype actually fits the concept of *C. flavicans* better than that of *C. albipes*.

Chaoborus albipes is a widespread species with notable intraspecific variation. This variation is evident in mitochondrial and nuclear DNA (Dupuis *et al.* 2008, see above) and in the coloration of adult specimens (Fig. 12). Adult specimens in temperate North America and Japan have light-orange brown or brown scutellar stripes and pleural markings; abdominal tergites are whitish in ground color with modest medial and lateral dark markings (spots, specks) (Fig. 12b,d,f). Specimens from subarctic North America, Hokkaido and Fennoscandia have dark thoracic markings and brown tergites (Fig. 12a,c,e). The parameres, which are essential characters in the identification of species based on adult males, hardly varies. Despite its small size and apparent simplicity, it is rather complex in structure. The outline of the paramere depends on the angle to the observer (Fig. 11b-d). The differing positions of the character on the slide or petri dish (see below) can be confused with variation. Intraspecific variation in larval and pupal characters is currently not well known due to the scarcity of available material. The number of mandibular fan bristles is variable among the studied material, ranging from 14 to 23. However, this variation seems to be population specific. For example, in Joroinen, Savukoski and Kuzitrin, the average numbers are 20.8 (20–23, n=4), 15.3 (14–16, n=7) and 15.3 (14–17, n=6) respectively.

In his revision of North American chaoborids, Cook (1956) redescribed larvae, pupae, adult males and females of *C. flavicans*. However, it is now clear that Cook mixed two species under the name *C. flavicans*. This can be judged from the material studied by him and reading the descriptions. For example, specimens from MacKenzie Delta, Reindeer Depot are deposited at the CNC and belong to *C. albipes*. On the other hand, the description of the tergal color pattern fits *C. flavicans*. Cook (1956, p. 23) admits that variation in *C. flavicans* is notable in coloration and "… especially in the genitalic structures of the males. The variation in the penis valves of the males is quite marked, so that if only the extremes were available it might seem that two distinct species are involved." Cook states that there is a continuum between the extremes and it is impossible to segregate individual specimens. In retrospect it has to be agreed that the parameres figured by Cook actually depict intraspecific variation; not in *C. flavicans*, but in *C. albipes*. Material studied by Cook was rather extensive, covering ca. 180 specimens (all life stages combined). In this study JS has examined >100 males of *C. albipes* and >100 males of *C. flavicans*, and in all cases identification based on the morphology of parameres has been unambiguous.

Distribution. Holarctic. Probably very widespread and common in North America, from subarctic to temperate vegetation zones. In the Palaearctic known from north boreal to south temperate ecoregions; perhaps absent from Central Europe. In this study verified from USA (Alaska, New York, North Carolina), Canada (North West Territories, British Columbia, Ontario, Nova Scotia, New Brunswick, Prince Edward Island), Norway (Buskerud), Finland (north boreal, south boreal), Russia (South Urals, Far East), and Japan (Hokkaido, Sado Island, Honshu, Shikoku). Also known from Massachusetts (Richardson 1912), New Jersey (Ogawa 2007), Wisconsin (Dickinson 1944), Alaska, Indiana (USA) and Alberta (Canada) (Dupuis *et al.* 2008; Ballinger *et al*. 2014; 2017).

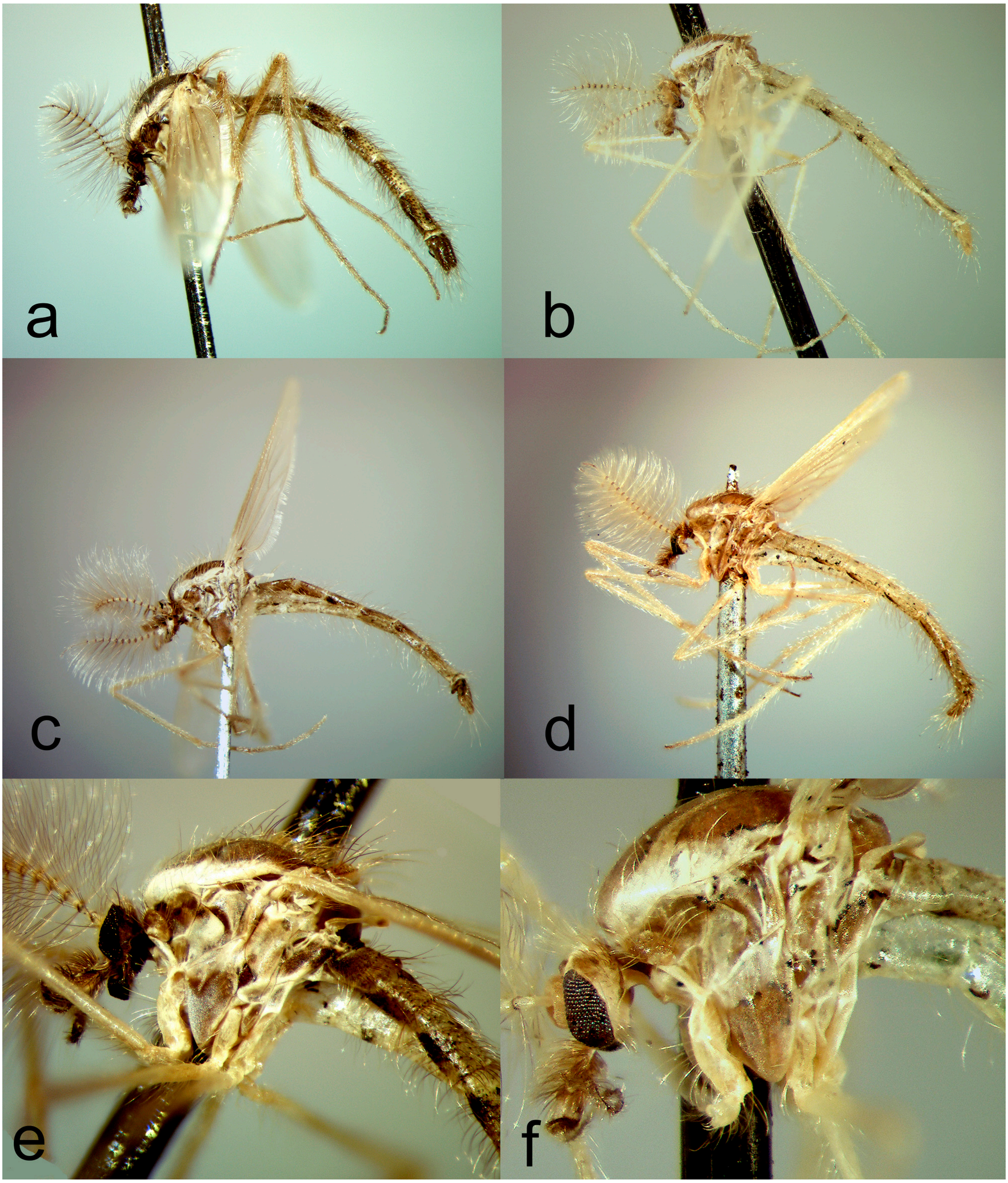

FIGURE 12. *Chaoborus albipes* (Johannsen), pinned males, habitus photos, lateral view. a,e) Canada, Northwest Territories, Reindeer Depot, b,f) USA, North Carolina, Highlands, c) Japan, Hokkaido, d) Japan, Tokyo.

Ecology. In Finland the species is uni- or bivoltine, pupation and emergence of overwintered larvae occur in early summer (only reared material were hitherto available). In a pond in northern Finland, pupae of the overwintering generation were collected in early June, and two months later, in early August, pupal exuviae and first and second instar larvae were observed. This indicates a bivoltine lifecycle or a very long pupation time of the overwintered generation. Habitats are mostly small but permanent fishless ponds, from ca. 20 m^2 to 2700 m^2 in area, and one to a few meters in depth. Ponds are often influenced by humic substances, i.e. water color is brownish, most often with a mire margin (bog or fen vegetation). Larvae occur in sympatry usually with *C. obscuripes* and seldom with *C. nyblaei, C. flavicans* and *C. posio* **sp. n.**. The only known collection site in Norway is near a small lake 495 m above sea level, populated by fish (*Perca fluviatilis* and *Salmo trutta*, K-M Olsen, pers.comm.). However, it is not known whether the specimens in the Malaise trap sample originated from this lake or fishless ponds nearby. Remarkably, one Finnish population is known from a boreal humic pond (area 6900 m^2, max depth 8 m) that is inhabited by a fish (*P. fluviatilis*, J. Salmela, pers.obs.). It is not yet known if the larvae of this population perform diel vertical migration. In North America, *C. albipes* is known from small forest ponds (Felt 1904, Richardson 1912) and from humic tundra pools in Alaska (Taylor *et al.* 2015), where the species may coexist in deeper ponds with *C. americanus*. In Japan it is known from north to south, and is possibly bivoltine (adults collected in May and late August). According to Richardson (1912), larvae eat unicellular organisms and Copepoda. Alaskan larvae do not perform diel vertical migrations in shallow ponds (Dupuis *et al.* 2008), but it is not known if the larvae can withstand higher pressure of deeper waters. The RNA virus family, Phasmaviridae was first described from *C. albipes* and *C. trivittatus* (Loew) in the Nome region of Alaska (Ballinger *et al.* 2014). This family of viruses is now known from most major insect groups and is perhaps maternally inherited in Culicomorpha. Notably phasmaviruses have a high prevalence in larval stages, but little is known of the fitness effects on the host.

Based on indirect evidence it is assumed that *C. albipes* is more common in the Nearctic than in the Palaearctic. First of all, despite the long entomological tradition dating back to 18th century in Europe, the species was first detected from North America. Secondly, *C. albipes* (51) and *C. flavicans* (345) are both well represented among the DNA barcoded specimens from North America (BOLD public data base, accessed 20.VIII.2020), whereas there are only a few barcoded *C. albipes* specimens from the Palaearctic (only one, if the Finnish and Russian specimens that were purposely analyzed are excluded). Finally, it is likely that *C. albipes* prefers shallow (<2 m deep), fishless ponds (Felt 1904; Richardson 1912; Cook 1956 in part; Dupuis *et al.* 2008; Taylor *et al.* 2015; material studied here). In central and southern Europe *C. crystallinus* is a common and abundant *Chaoborus* species in such habitats (e.g. Kuper & Verberk 2011; Arranz *et al.* 2015). In contrast, *C. crystallinus* is not that widespread in the North America, being absent from eastern North America (Borkent 1981) where *C. albipes* seems to be common (see material examined above). It is possible, that the favored habitat of *C. albipes* is largely occupied and dominated by *C. crystallinus* in Europe and the former is either absent or extremely rare there due to competition. However, the species is likely rather common yet overlooked in Fennoscandia. Up to June 2020, the species was known from 22 locations in Finland and Norway, of which 68 % were found during April–June 2020.

Chaoborus posio Salmela sp. n.

Material examined. Type material. Holotype. Male. [“http://tun.fi/” “NVO.LMM-el-164” “FINLAND Posio” “Peuralamminharjut” “etrs-tm35fin: 7350437,” “527225” “23.V.2019” “Salmela, Jukka leg.”] [QR code], printed. Type locality: Finland, Ks: Posio, Peuralamminharjut, 66.27269 27.60633, 311 masl, e.l., larval skin and pupal exuviae in Euparal and adult pinned, NVO.LMM-el-164 (LMM).

Paratypes. Finland. Ta: Tammela, Saarijärvi S, Salmela J. leg. 3.V.2020, 10 larvae, NVO.LMM-el-20-7; 1 male pupa e.l., NVO.LMM-el-20-24; 1 female e.l., NVO.LMM-el-20-33; 1 female e.l., NVO.LMM-el-20-35; 1 male pupa e.l., NVO.LMM-el-20-36; 1 male e.l., NVO.LMM-el-20-37; 1 female e.l., NVO.LMM-el-20-38; 1 male e.l., NVO.LMM-el-20-59; 1 female e.l., NVO.LMM-el-20-60; 1 female e.l., NVO.LMM-el-20-61; 1 female e.l., NVO.LMM-el-20-62 (LMM); Härmä O. leg. 21.IV.2020, 4 larvae, LG.6201; 1 female e.l., LG.6271; 1 male e.l., LG.6272; 1 male e.l., LG.6284 (FLHM). Ok: Suomussalmi, Hoiluankangas, Salmela J. leg. 22.5.2019, 10 larvae, NVO.CUL-2019-9; 1 larva, head & tail on slide, BOLD, NVO.CUL-2019-80; 1 larva, head & tail on slide, BOLD, NVO.CUL-2019-81 (LMM). Ks: Posio, Peuralamminharjut, Salmela J. leg. 23.5.2019, 1 male e.l., larval and pupal exuviae on slide, legs, wings, head, hypopygium on slide, NVO.LMM-el-134; 1 male e.l., larval and pupal exuviae on slide, legs, wings, head, hypopygium on slide, NVO.LMM-el-135; 1 male e.l., larval and pupal exuviae on slide, legs, wings, head, hypopygium on slide, NVO.LMM-el-137; 1 female e.l., larval and pupal exuviae on slide, NVO.LMM-el-138; 1 male e.l., larval and pupal exuviae on slide, hypopygium on slide, NVO.LMM-el-141 (LMM); 1 male e.l., pinned, larval and pupal exuviae on slide, NVO.LMM-el-142; 1 male e.l., pinned, larval and pupal exuviae on slide, LMM-el-142 (LMM); 1 male e.l., NVO.LMM-el-170 (MZH); 1 male e.p., NVO.LMM-el-175 (LMM); 1 pupa e.l., larval exuviae on slide, NVO.LMM-el-136; 1 male pupa e.l., larval exuviae on slide, NVO.LMM-el-139; 1 female, larval and pupal exuviae on slide (adult escaped during rearing) e.l., NVO.LMM-el-140; 1 female, larval and pupal exuviae on slide, NVO.LMM-el-143; 1 male e.l., larval and pupal exuviae on slide, legs, wings, head, hypopygium on slide, NVO.LMM-el-144; 1 male e.l., larval and pupal exuviae on slide, legs, wings, head, hypopygium on slide, NVO.LMM-el-145; 1 female e.l., larval and pupal exuviae on slide, NVO.LMM-el-146; 1 male e.l., pinned, NVO.LMM-el-162; 1 male e.p., NVO.LMM-el-184; 1 female e.p., NVO.LMM-el-185; 1 male e.p., NVO. LMM-el-186; 1 male e.p., NVO.LMM-el-188; 1 male e.p., NVO.LMM-el-193; 1 female e.p., NVO.LMM-el-194; 1 male e.p., NVO.LMM-el-195; 3 males 1 female e.p., parameres of one male in glue on slide, NVO.LMM-el-199; 1 female e.p., NVO.LMM-el-202; 2 males 2 females e.p., NVO.LMM-el-203. 24.5.2018, 20 larvae 5 pupae, NVO.ins2018-384; 7 pupae, NVO.ins2018-386; 15 larvae, NVO.ins2018-387; 1 larva, BOLD, NVO.ins2018-580; 1 larva, BOLD, NVO.ins2018-581; 1 larva, BOLD, NVO.ins2018-582; 1 pupa, BOLD, NVO.ins2018-616; 1 pupa, BOLD, NVO.ins2018-617; 1 pupa, BOLD, NVO.ins2018-618; 1 larva, BOLD, NVO.ins2018-619; 1 larva, BOLD, NVO.ins2018-620; 1 larva, BOLD, NVO.ins2018-621; 1 larva, BOLD, NVO.ins2018-622; 1 larva, BOLD, NVO. ins2018-623; Salmela J. & Ahola J. leg. 20.VIII.2019, 4 larvae, NVO.LMM-el-599; (LMM). Obb: Rovaniemi, Montosenlampi W, Salmela J. leg. 5.VI.2020, 2 male e.p., NVO.LMM-el-20-104; 1 male e.p., adult pinned, pupal exuviae on slide, NVO.LMM-el-20-109; 1 male e.p., NVO.LMM-el-20-111; 1 male e.p., NVO.LMM-el-20-112; 1 female e.p., NVO.LMM-el-20-113; 7 male e.p., NVO.LMM-el-20-114 (LMM); 1 larva, 2 males and pupa exuviae (ABC) Lkoc: Kittilä, Muotrikkilehto, Salmela J. leg. 27.VII.2019, 1 larva, head and tail on slide, BOLD, NVO. LMM-el-574; 3 larvae, NVO.LMM-el-588; 1 larva, NVO.LMM-el-589; 5 larvae, NVO.LMM-el-590; 3 larvae, NVO.LMM-el-600; 1 larva, NVO.LMM-el-612; 1 larva, BOLD, NVO.CUL-2019-75 (LMM). Li: Inari, Latnabuolza, Salmela J. leg. 23.8.2019, 1 larva, NVO.LMM-el-584; 1 larva, NVO.LMM-el-606; 1 larva, head & tail on slide, BOLD, NVO.CUL-2019-76 (LMM). Inari, Iso-Söimi, Salmela J. leg. 29.VI.2020, 6 larvae, NVO.LMM-el-20-137 (LMM). Utsjoki, Geaidnogeachi, Salmela J. leg., 13.6.2019, 1 male e.p., NVO.LMM-el-306 (LMM); 1 male pupa e.l., NVO.LMM-el-293; 1 female pupa e.l., NVO.LMM-el-294; 1 male e.l., larval and pupal exuviae on slide, hypopygium on slide, NVO.LMM-el-295; 1 male e.l., larval and pupal exuviae on slide, hypopygium on slide, NVO. LMM-el-296; 1 female e.l., larval and pupal exuviae on slide, NVO.LMM-el-297; 1 pupa e.l., NVO.LMM-el-299; 1 male e.l., larval and pupal exuviae on slide, legs, wings, head, hypopygium on slide, NVO.LMM-el-302; 2 males 2 females e.p., NVO.LMM-el-307; 1 male e.p., NVO.LMM-el-309; 1 female e.l., NVO.LMM-el-310; 1 female e.l., NVO.LMM-el-311; 1 female, NVO.LMM-el-312; 1 male pupa e.l., NVO.LMM-el-313; 1 male e.l., larval and pupal exuviae on slide, legs, wings, head, hypopygium on slide, NVO.LMM-el-314; 1 female e.l., NVO.LMM-el-315; 1 female pupa e.l., NVO.LMM-el-316; 1 female e.l., NVO.LMM-el-317; 1 male pupa e.l., NVO.LMM-el-318; 1 female pupa e.l., NVO.LMM-el-319; 1 male e.p., NVO.LMM-el-320; 1 male e.p., NVO.LMM-el-321; 1 male e.p., NVO.LMM-el-323; 1 female e.p., NVO.LMM-el-324; 1 male e.p., NVO.LMM-el-326; 1 female e.p., NVO. LMM-el-327; 1 female e.p., NVO.LMM-el-328; 1 male e.p., NVO.LMM-el-329; 1 male e.p., NVO.LMM-el-330; 1 female e.p., NVO.LMM-el-331; 3 male 3 female e.p., NVO.LMM-el-339; 4 males e.p., NVO.LMM-el-340; 1 female e.p., NVO.LMM-el-343; 1 male e.p., NVO.LMM-el-344; 1 female e.l., NVO.LMM-el-365; 4 males 3 females e.p., NVO.LMM-el-372; 2 males e.p., NVO.LMM-el-379; 1 male e.p., hypopygium on slide, NVO.LMM-el-583; 17.VII.2018, 1 larva, BOLD, NVO. ins2018-480 (LMM).

Derivatio nominis. The name of the new species refers to Posio, a municipality in southeastern Lapland. Posio is derived from Sámi languages (*boaššu*), meaning a sacred opening opposite of the main entrance in *lavvu* (a tent-like dwelling). The name is a noun in apposition.

Diagnosis. General coloration of adult specimens dark–almost black. Male hypopygium mostly dark, gonocoxite and gonostylus relatively wide; paramere strongly scleroterized, apical beak long, almost straight. Respiratory organs of pupa club-shaped, widest medially, not constricted subapically. Larval mandible with conspicuous lateral teeth, uppermost about as large as subordinate tooth; number of mandibular fan bristles over 20 (21–29).

Description. Adult male. Head dark with dark setae. Non–setose area of occiput pale, frontal macula bare. Clypeus with numerous dark setae. Antennal flagellomeres slightly infuscated between bases of whorls and apices, basal parts of flagellomeres pale; length of penultimate flagellomere 242 (233–256), apical flagellomere 201 (188–222, n=5), penultimate/apical 1.21 (1.05–1.36). Lengths of palpal segments 2–5: 104 (90–113, n=6), 213 (191–239, n=6), 180 (174–186, n=6), 320 (295–330, n=5). Thorax mostly dark–almost black (Fig. 13). Scutum dark brown–black, scutellar stripes are dark and hard to discriminate expect their non–setosity (Fig. 13b); narrow pale area is present along paranotal suture and anepisternum (Fig. 13a). Scutellum and mediotergite black. Halter whitish. Thoracic setae (n=2): antepronotal lobe 33–34, postpronotal 5–6, proepisternal 5–6, katepisternal 3–5, anepisternal 10–12, anepimeron 5–7, supra–alar 1. Legs pale brown–brown, apices of femora slightly darkened. Foreleg, lengths of fe, ti and ta1–ta5 (n=7): fe 1706 (1653–1778), ti 1889 (1778–2000), t1 875 (807–945), t2 552 (523–591), t3 464 (432–500), t4 299 (278–326), t5 207 (194–225). Midleg, lengths of fe, ti and ta1–ta5 (n=7): fe 1606 (1489–1917), ti 1599 (1486–1917), t1 805 (716–1139), t2 496 (432–695), t3 383 (336–466), t4 247 (225–284), t5 195 (183–217). Hind leg, lengths of fe, ti and ta1–ta5 (n=7): fe 1880 (1806–1972), ti 1815 (1458–1972), t1 1086 (972–1222), t2 641 (580–739), t3 458 (409–517), t4 275 (245–330), t5 200 (188–214). Wing (n=5, Fig. 4b). Length 3655 (3440–3859), width 797 (714–847), length/width 4.59 (4.45–4.82); fork of R_{2+3} 480 (422–531), fork of M_{1+2} 442 (391–484), R_3 1063 (954–1129), M_1 926 (862–971), number of setae on squama 35 (26–45, n=7). Abdomen dark–almost black. Hypopygium dark brown, epandrium rounded apically (Fig. 14a). Gonocoxite stout, bearing dark setae, length 571 (472–625), width 217 (186–239), length/width 2.64 (2.40–3.03, n=10); gonostylus relatively stout, length 495 (466–545), width, 53 (48–59), length/width 9.43 (7.90–10.69); paramere (Fig. 14b–e) strongly sclerotezited, dark, apical claw rather long and straight; length 179 (160–194, n=9).

FIGURE 13. *Chaoborus posio* Salmela **sp. n.**, pinned specimen, a) lateral, b) dorsal view (Finland, Posio).

Adult female. In general, similar to male. Penultimate flagellomere 144–153 (n=2), apical flagellomere 151 (n=1). Lengths of palpal segments 2–5: 98–207, 153–300, 85–176, 171–295 (n=2). Thoracic setae (n=2): antepronotal lobe 20–22, postpronotal 4–6, proepisternal 4, katepisternal 5–8, anepisternal 14–15, anepimeron 10–13, supra–alar 1. Wing length 3647–3898, width 947–1043, length/width 3.73–3.85 (n=2); fork of R_{2+3} 483–539, fork of M_{1+2} 408–454, R_3 1274–1336, M_1 1154–1231 (n=2), number of setae on squama 31 (n=1). Foreleg, lengths of fe, ti and ta1–ta5 (n=2): fe 1611–1651, ti 1744–1768, t1 819–850, t2 482–498, t3 403–453, t4 267–299, t5 202–206. Midleg, lengths of fe, ti and ta1–ta5 (n=2): fe 1550–1579, ti 1476–1479, t1 722–748, t2 420–458, t3 322–360, t4 232–234, t5 189–197. Hind leg, lengths of fe, ti and ta1–ta5 (n=2): fe 1890–1916, ti 1858–1870, t1 1032–1147, t2 586–661, t3 430–466, t4 270–292, t5 196–198.

Pupa. Thoracic respiratory organ rather short, club–shaped, widest medially, not constricted subapically (Fig. 9d); length 844 (773–925), width 243 (214–284), length/width 3.48 (2.92–4.0, n=18). Lateral ribs of terminal processes slightly paler than middle rib.

IV instar larva. Total length circa 12 mm. Anal fan setae 26 (24–28, n=17). Anal hook brown–dark brown in color. Mandibular fan bristles 24 (21–29, n=25, Fig. 10h). Lateral teeth of mandible conspicuous, ultimate tooth about as large as mandibular tooth 3 (Fig. 10f); number of lateral teeth 6.32 (5–8, n=25); mandibular teeth 1–4 darkened along entire length. Labral blade moderately serrated, basal part relatively wide (Fig. 10g), usually darkened; length 268 (228–295, n=25), width 73 (56–84, n=24), length/width 3.7 (3.0–5.0, n=24). Length of antenna 587 (545–682, n=24).

DNA barcoding. *Chaoborus posio* **sp. n.** was also very divergent from other members of the complex (>17%) (Table 1). Intraspecific variation was the lowest for the species complex (Table 1), perhaps indicating that this species survived in a single glacial refugium. Because the within species divergence was weak, the probability of identification from barcoding information was the highest in the complex (>99%). The barcoded specimens formed a unique BIN cluster in BOLD (BOLD:ADT7562).

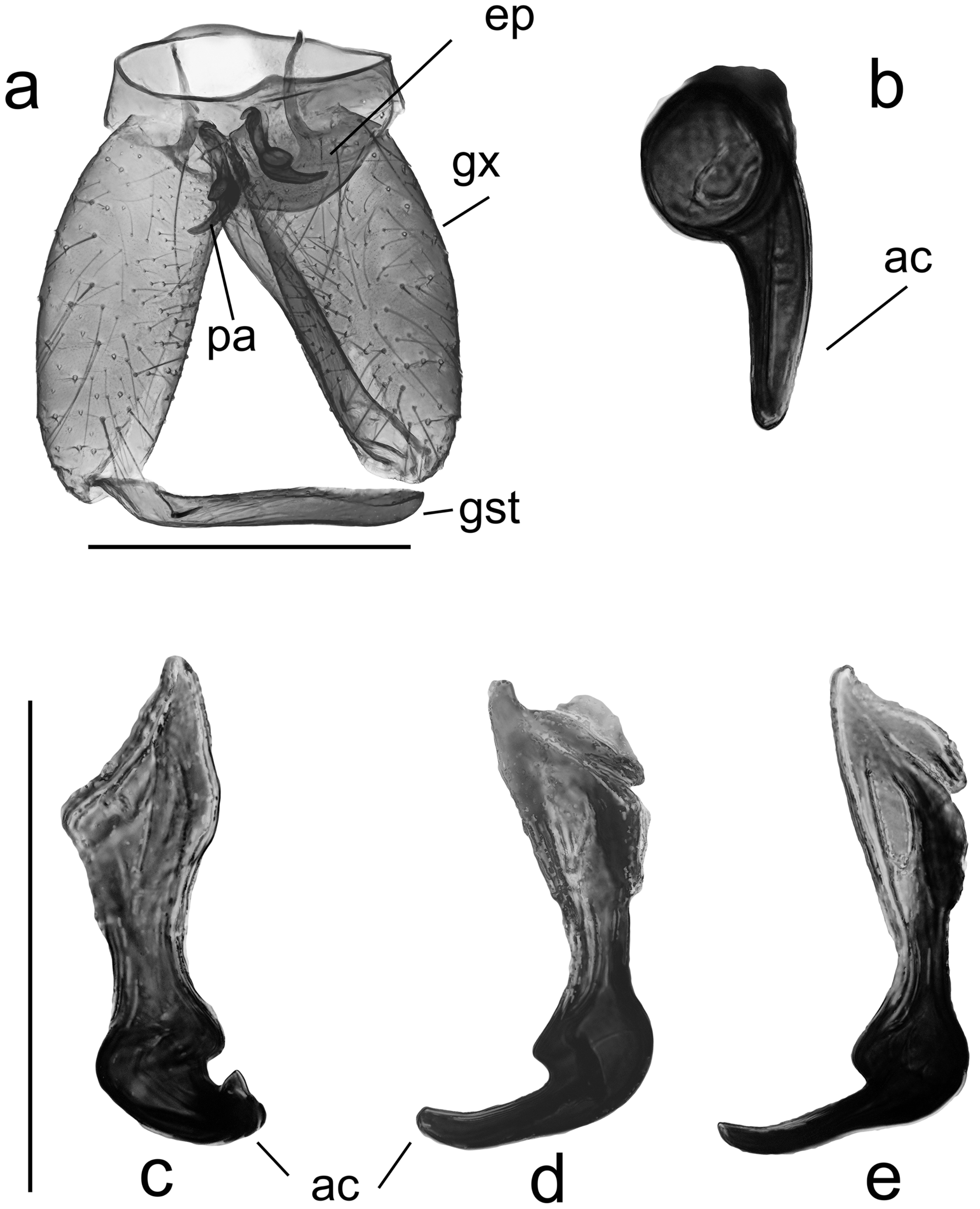

FIGURE 14. *Chaoborus posio* Salmela **sp. n.**, a) hypopygium (scale bar 500 µm), b–e) paramere viewed in different positions (scale bar 170 µm). ac=apical claw, gst=gonostylus, gx=gonocoxite, ep=epandrium, pa=paramere.

Comments. The new species can be readily separated from *C. flavicans* and *C. albipes* in larval, pupal and adult stages. Fourth instar larvae possess a high number, in most cases well over 20 mandibular fan bristles; the number of such bristles is lower in the other species (the averages for *C. flavicans* and *C. albipes* are 13 and 17.7, respectively). The labral blade of the new species is rather wide: length/width ratio is ca. 3.72, whereas 5.55 and 4.73 in *C. albipes* and *C. flavicans*, respectively. The respiratory organ of pupae is not constricted subapically and it is generally rather short and wide. Adults are very darkly colored, almost black, and the thoracic setae are dark. Dark forms of *C. albipes* have a more pale/whitish coloration on the scutum and the thoracic setae are pale. The gonocoxite and gonostylus of the adult male in *C. posio* **sp. n.** are very stout, (i.e., they are more slender in the other species), and the paramere is strongly sclerotized. The apical claw is long and almost straight.

Distribution. Hitherto known from Finland only, but is likely to occur at least in Sweden, Norway and northwestern Russia. Most of the records are from the north boreal ecoregion, yet there is a locality in the south boreal zone, ca. 500 km south of the main area of distribution. It is not yet known if this should be considered a relict population outside of the normal range, or if the species is more widely present in the southern parts of Fennoscandia. The northernmost sites are presently at the subarctic zone, north of the limit of coniferous trees.

Ecology. The life cycle is univoltine, i.e., there is one generation per year. Overwintered, IV instar larvae pupate readily under laboratory conditions at room temperature, and the flying season in nature takes place in early summer. IV instar larvae of the new generation are present by mid-August. Larvae have been collected from fishless, permanent ponds (n=10, plus 8 sites detected in late 2020, J. Salmela *et al.* in prep). These ponds are often rather large (mean area 3400 m^2) and the larvae are absent from smaller yet permanent ponds that are present nearby. Typically the water color is at least moderately humic and the shores are characterized by bog vegetation. The new species often co-occurs with *C. obscuripes*, occasionally with *C. flavicans* (three occasions) and *C. albipes* (two occasions). In Central Lapland, Kittilä, *C. posio* **sp. n.** was observed from a possibly alkaline pond with clear water; the pond is surrounded by a calcareous rich fen vegetation.

TABLE 1. Summary of species delimitation metrics for mitochondrial clades of the *Chaoborus flavicans* species complex and *C. crystallinus*. Taxa were monophyletic with bootstrap values of 100. Genetic distance was estimated using the best fit model: TVM+F+R4. P ID is the probability of identification of an unknown specimen (with confidence intervals) under strict and relaxed criteria. AV is the mean distance between the most recent common ancestor (MRCA) of a species and the extant sequences. P(AB) is the probability of reciprocal monophyly under a null model of random coalescence.

Taxon	Intra distance	Inter distance (closest)	Intra/ inter	P ID (Strict)	P ID (Liberal)	Av (MRCA-tips)	Rosenberg's P(AB)
C. flavicans	0.024	0.327	0.07	0.97 (0.92, 1.0)	0.99 (0.96, 1.0)	0.0531	NA
C. posio	0.003	0.181	0.01	0.99 (0.94, 1.0)	1.00 (0.98, 1.0)	0.0037	5.6E-22
C. albipes	0.025	0.181	0.14	0.94 (0.89, 1.0)	0.98 (0.95, 1.0)	0.0251	5.6E-22
Chaoborus sp. (JPN)	0.000	0.174	0.00	0.00 (0.00, 0.00)	0.96 (0.83, 1.0)	0.0000	1.6E-4
C. crystallinus	0.003	0.352	0.01	0.93 (0.80, 1.0)	0.98 (0.88, 1.0)	0.0042	0.02

Chaoborus sp.

Chaoborus crystallinus: Komyo 1954: 12 (redescription, adult female and male), paramere fig. 1.
Chaoborus cf. flavicans: in part. Dupuis *et al.* 2008 (molecular phylogeny).
Chaoborus flavicans: in part. An *et al.* 2012: (molecular phylogeny).
Chaoborus sp.: Zhang *et al.* 2019: (molecular phylogeny).

This taxon is treated here as a putative undescribed species of the *C. flavicans* complex. Komyo (1954) redescribed Japanese specimens as *C. crystallinus* and illustrated the male paramere. According to Komyo, this species lacks tergal bands and the paramere does not fit *C. crystallinus*, *C. flavicans*, *C. albipes* or *C. posio* **sp. n.** In recent molecular studies (Dupuis *et al.* 2008; An *et al.* 2012; Zhang *et al.* 2019) a few specimens (four in total, see below) seem to form separate clusters or branches, which probably represent a distinct taxonomic species (Fig. 15). This species

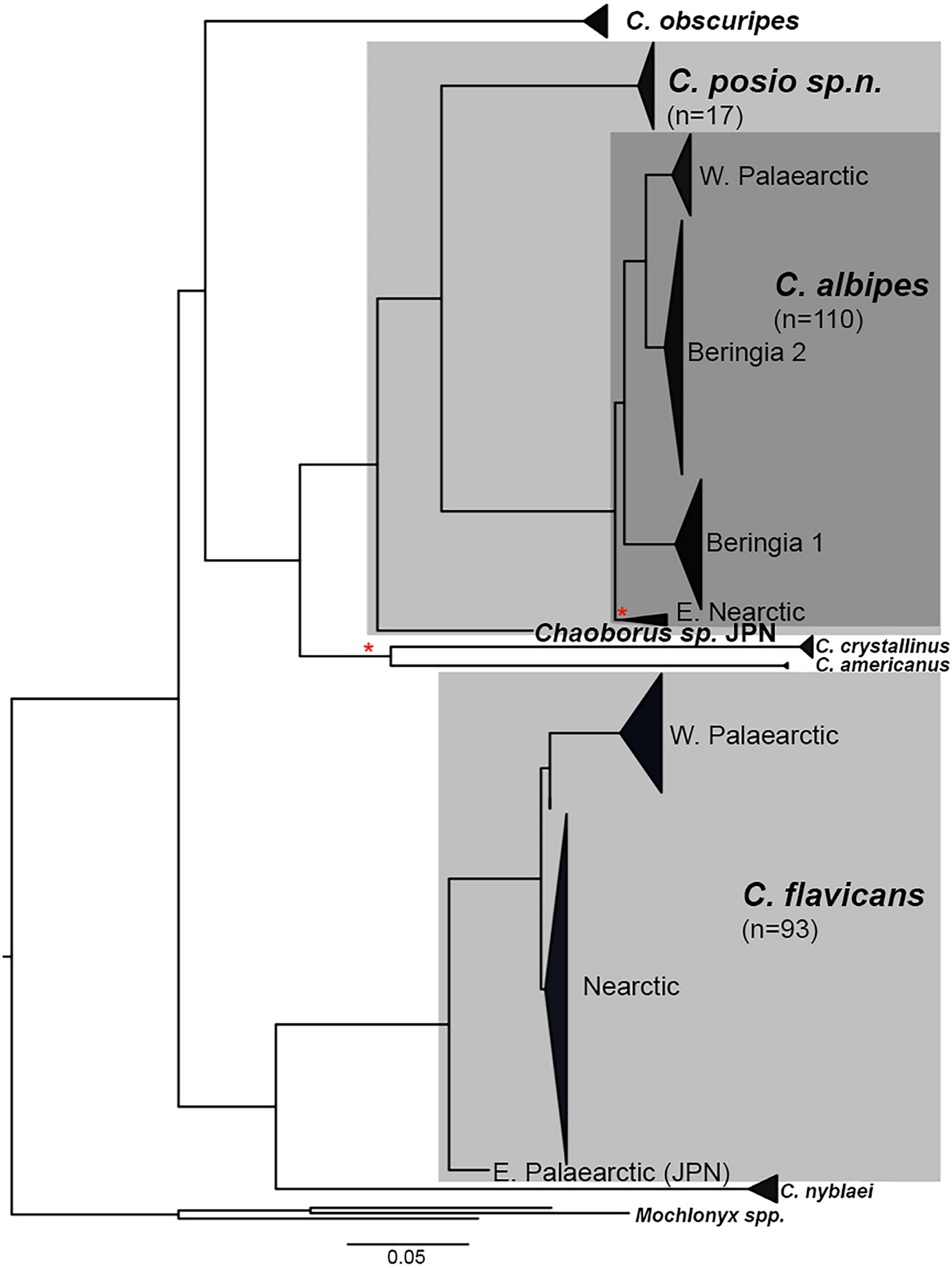

FIGURE 15. A maximum likelihood phylogram of the *Chaoborus flavicans* species complex based on the DNA barcoding region (COI) of mitochondrial DNA. The best fit substitution model of TVM+F+R4 was used. Support values exceeded 90 (transfer bootstrap support) except where asterisks are given. Clade sample sizes are provided. The light gray shading indicates the *C. flavicans* complex and the dark gray box indicates *C. albipes* (also a member of the *C. flavicans* complex). The tree was outgroup rooted using species of *Monchlonyx.* Triangles represent collapsed clades to save space.

may be the *Chaoborus* illustrated by Komyo, but conclusive evidence is still lacking. Further integrative studies are needed to clarify the status of this taxon which may be endemic to Japan. This taxon formed a unique BIN BOLD: AEA6459 in BOLD, composed of the specimen MK281356 analysed by Zhang *et al.* (2019). The collecting data of the specimen is the following: Japan, Kyushu, Fukuoka-shi, Kashii, 2.10.2013, Shigetaka Nonaka leg. (Zhang *et al.* 2019 appendix). Sequencing of the specimens studied by Dupuis *et al.* (2008) and An *et al.* (2012) did not cover the COI barcoding region and are not comparable in the present context. GenBank accession number DQ146274 (Dupuis *et al.* 2008) was collected from Toyama prefecture, N36.81, E136.93, in 2004; JQ277993 and JQ277994 (An *et al.* 2012) lack collection data, except "Japan".

Discussion

The morphological and genetic evidence agree that at least three species (and probably more) in the *Chaoborus flavicans* species complex exist. Among Palaearctic chaoborids, *C. flavicans* has been assigned as the only species to withstand fish predation. The present revision indicates that *C. flavicans* truly is the only lake-dwelling species, whilst *C. albipes* and *C. posio* **sp. n.** are restricted to (fishless) ponds. However, ecological and behavioral studies are needed to verify this. For example, it is unknown whether these two pond species can perform diel vertical migrations in the water column or if the ovipositing females can detect fish kairomones from the water's surface. Because the mandibles and pupal organs differ among members of the complex, there is potential to use these species as paleolimnological proxies. A robust phylogeny of the genus, including a monophyly test for the *C. flavicans* complex, awaits a molecular and morphological analysis. The group also appears to be a promising subject for investigating the effects of Pleistocene glaciation on the biogeography of phantom midges. Our results suggest that pronounced geographic partitioning within and among continents persists despite the presence of potentially dispersing adults.

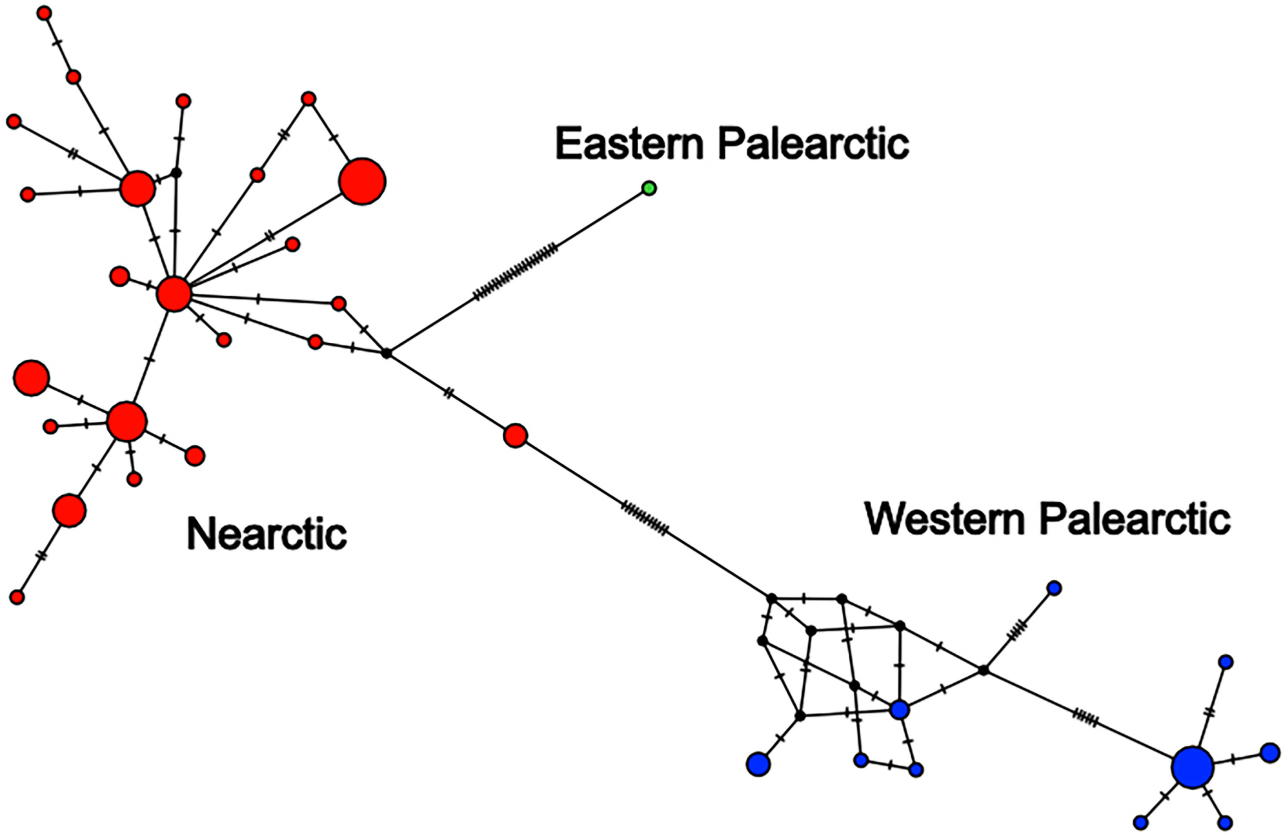

FIGURE 16. A median joining network of *Chaoborus flavicans* (Meigen) sequences from the barcoding region of mitochondrial DNA. 93 sequences were used and the pie diameters are proportional to the number of individuals detected per haplotype. Hash marks on the network represent substitutions and the smallest black circles represent unobserved haplotypes. Colors indicate one of three major geographic regions.

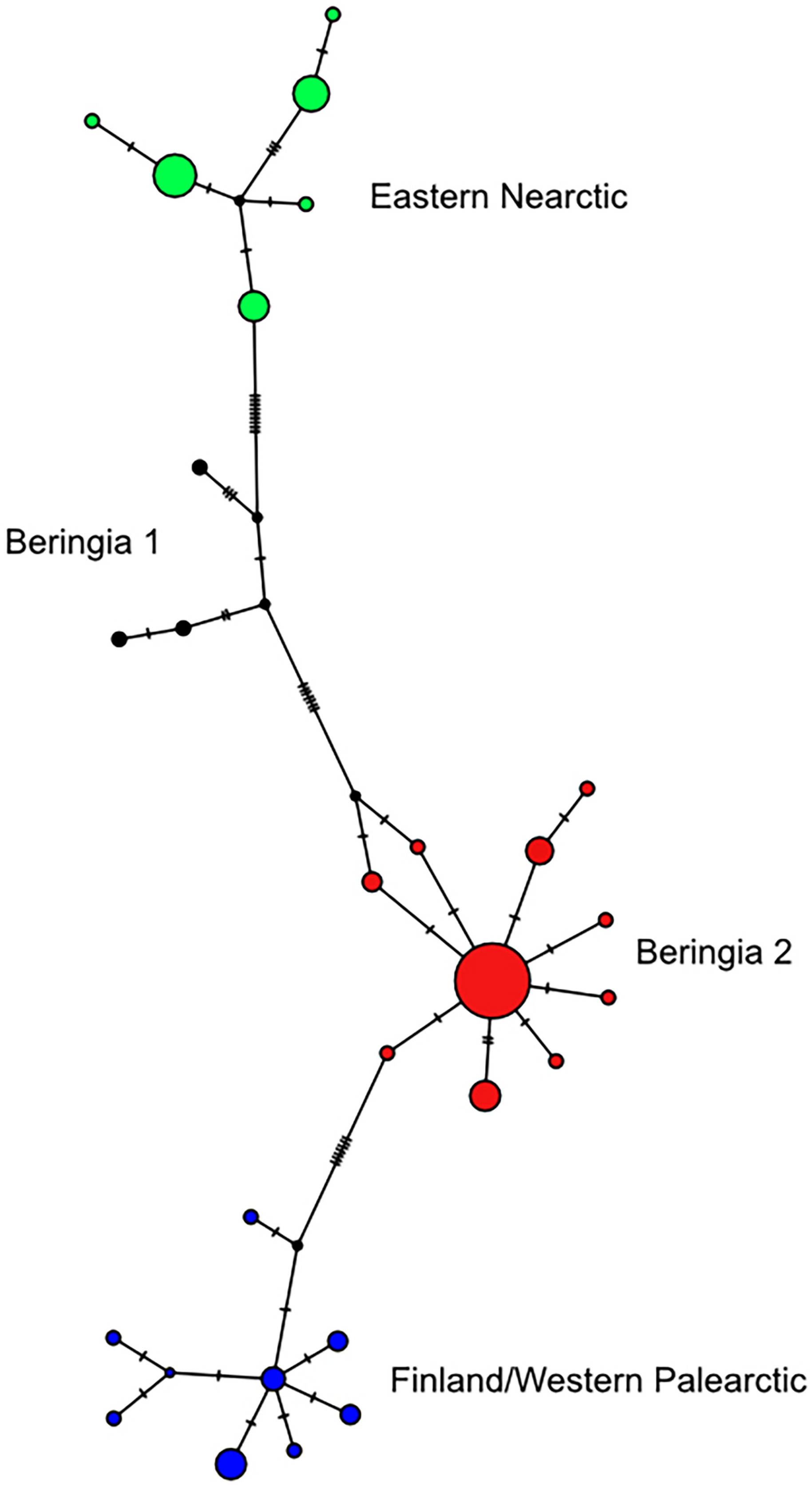

FIGURE 17. A median joining network of *Chaoborus albipes* (Johannsen) sequences from the barcoding region of mitochondrial DNA. 110 sequences were used and the pie diameters are proportional to the number of individuals detected per haplotype. Hash marks on the network represent substitutions and the smallest black circles represent unobserved haplotypes. Other colored haplotypes represent geographic regions.

Stahl (1966b, p. 100) wrote regarding *Chaoborus* that "...the taxonomy of the genus is simple, the larvae can usually be identified to species with accuracy and facility...". In general, the taxonomy of Holarctic chaoborids is well known (Sæther 1970; 1972; Borkent 1979). However, the present taxonomic revision shows that, even in such groups, taxa may be resurrected from synonymy or described as new. *Chaoborus flavicans* is a much-studied lacustrine species, and it may, at first sight, seem unlikely that such a well-known species included two "cryptic" taxa. It is, however, likely that most of the *C. flavicans* records in scientific literature from lakes refer to this species. In smaller lentic waters, however, at least a part of the previous records of *C. flavicans* may actually belong to *C. albipes* or *C. posio* **sp. n.** (see below). It is hoped that the present revision is informative for all students of lentic freshwater ecosystems that aim to identify immature specimens from plankton net hauls or similar samples.

Stahl (1966b) concluded that sympatric species are expected to co-occur in each lake or pond suitable for *Chaoborus*. As Borkent (1981) wrote, this conclusion is hardly correct: sympatric congeneric species may differ widely in their habitats (Borkent 1979) and some species pairs or communities are excluded by intraguild predation (Garcia & Mittelbach 2008). *Chaoborus flavicans* and *C. albipes* are sympatric in a large geographic area, but are seldom known to coexist in the same waterbody. As already noted, the former is primarily a species of large, stratified lakes, the latter prefers fishless ponds. Three species of the *C. flavicans* complex occur in sympatry in Fennoscandia. There are three known cases where *C. flavicans* and *C. posio* **sp. n.** coexist, and two coexisting populations of both *C. flavicans*–*C. albipes* and *C. albipes*–*C. posio* **sp. n.** are known. Thus, the present results are in accordance with Borkent's (1981) theory that sympatric sister species may be present if they have differences in habitat preferences (*C. flavicans*–*C. albipes*/*C. posio* **sp. n.**). Despite *C. posio* **sp. n.** and *C. albipes* have similar habitat preferences, the species seem occur in different kinds of ponds (see above). In addition to Finnish larval records, *C. flavicans* and *C. albipes* adults have been collected from the shore of a pond in Japan, Niigata (see material examined of both species), and are thus likely to coexist in the same waterbody. Clearly there is a need to study the ecology of these sympatric pond-dwelling species to determine if there is further ecological partitioning.

Subfossil *Chaoborus* mandibles in the sediment samples of lakes have been used as indicators of predator-prey interactions and environmental change (Sweetman & Smol 2006). The presence of *C. flavicans* mandibles in lake sediments is commonly used as an indicator of fish presence or hypoxic conditions (Ursenbacher *et al.* 2020). It is, however, likely that at least in some of the studied lakes *C. flavicans* records refer to other species. For example, Luoto and Nevalainen (2009) studied chaoborid remains from surface sediment samples of shallow Finnish lakes. In their article a photograph of a *C. flavicans* mandible (Luoto & Nevalainen 2009, fig. 2a) was published. The mandible, however, possessed large lateral teeth that are atypical for *C. flavicans*, and it was predicted that the species is in reality either *C. albipes* or *C. posio* **sp. n.** To verify the prediction, this small forest pond (Jöusjärv, Sipoonkorpi National Park) was resampled in early May 2020 and the collected larvae were reared to adults. The pond was occupied by two *Chaoborus* species, namely *C. albipes* (see examined material) and *C. obscuripes* with *C. flavicans* apparently absent. Based on the results of this revision, subfossil remains of *C. flavicans* can be confidently separated from the two pond-dwelling species, *C. albipes* and *C. posio* **sp. n.** The two latter species, however, are hard to separate from mandibles alone. If pupal respiratory organs are sieved from the sediment samples (see Ursenbacher *et al.* 2020), the two species become identifiable.

Holarctic shallow ponds (fishless) are among the most sensitive ecosystems to climate change (e.g. Smol & Douglas 2007). A deeper understanding of the ongoing and historical changes in this ecosystem will depend on recognizing that the phantom midges detected here are more than "overflow" of *C. flavicans* from nearby lakes. Instead, our revision indicates that these ponds contain a hidden diversity of predators (*C. albipes* and *C. posio* **sp. n.**) that are ecologically, morphologically, and genetically differentiated from *C. flavicans*.

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References

Aitken, T.H.G. (1954) The Culicidae of Sardinia and Corsica (Diptera). *Bulletin of Entomological Research*, 45 (3), 437–494. https://doi.org/10.1017/S0007485300029564

Alhonen, P. & Haavisto, M.-L. (1969) The biostratigraphical history of Lake Otalampi in southern Finland, with special reference to the remains of subfossil midge fauna. *Bulletin of the Geological Society of Finland*, 41, 157–164. https://doi.org/10.17741/bgsf/41.017

An, H., Jung, G. & Kim, C.-B. (2012) Molecular taxonomy of a phantom midge species (*Chaoborus flavicans*) in Korea. *Animal Systematics, Evolution and Diversity*, 28 (1), 36–41. https://doi.org/10.5635/ASED.2012.28.1.036

Andersen, T. & Kvifte, G.M. (2012) Phantom midges (Diptera, Chaoboridae) from Finnmark, northern Norway. *Norwegian Journal of Entomology*, 59, 155–157.

Arranz, I., Sala, J., Gascón, S., Ruhí, A., Quintana, X.D., Amoedo, J., Martinoy, M. & Boix, D. (2015) Contribution to the knowledge of the distribution of *Chaoborus* species (Diptera: Chaoboridae) in the NE Iberian Peninsula, with notes on the spatial and temporal segregation among them. *Limnetica*, 34, 57–68. https://doi.org/10.23818/limn.34.05

Ballinger M.J., Bruenn, J.A., Hay, J., Czechowski, D. & Taylor, D.J. (2014) Discovery and evolution of Bunyavirids in arctic phantom midges and ancient bunyavirid-like sequences in insect genomes. *Journal of Virology*, 88 (16), 8783–8794. https://doi.org/10.1128/JVI.00531-14

Ballinger M.J., Medeiros, A.S., Qin, J. & Taylor, D.J. (2017) Unexpected differences in the population genetics of phasmavirids (*Bunyavirales*) from subarctic ponds. *Virus Evolution*, 3, vex015. https://doi.org/10.1093/ve/vex015

Balvay, E. (1977a) Détermination des larves de *Chaoborus* (Diptera, Chaoboridae) recontrées en France. *Annales d'hydrobiologie*, 8 (1), 27–32.

Balvay, E. (1977b) Morphologie des stades larvaires de *Chaoborus flavicans* (Diptera chaoboridae) en France. *Annales d'hydrobiologie*, 8 (2), 163–177.

Balvay, E. (1977c) Nouvelle interprétation de la signification de certains appendices céphaliques et de la morphologie de la mandibule chez la larve de premier stade de *Chaoborus flavicans* Meigen (Diptera, Chaoboridae). *Annales d'hydrobiologie*, 8 (2), 179–189.

Bardenfleth, K.S. & Ege, R. (1916) On the anatomy and physiology of the air-sacs of the larva of *Corethra plumicornis*. *Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening i Kjøbenhavn*, 67, 25–42.

Belkin, J.N., Schick, R.X. & Heineman, S.J. (1966) Mosquito studies (Diptera, Culicidae) VI. Mosquitoes originally described from North America. *Contributions of the American Entomological Institute*, 1 (6), 1–39.

Berendonk, T.U. (1999) Influence of fish kairomones on the ovipositing behavior of *Chaoborus* imagines. *Limnology and Oceanography*, 44 (2), 454–458. https://doi.org/10.4319/lo.1999.44.2.0454

Berendonk, T.U. & Bonsall, M.B. (2002) The phantom midge and a comparison of metapopulation structures. *Ecology*, 83, 116–128. https://doi.org/10.1890/0012-9658(2002)083[0116:TPMAAC]2.0.CO;2

Berendonk, T.U., Barraclough, T.G. & Barraclough, J.C. (2003) Phylogenetics of pond and lake lifestyles in *Chaoborus* midge larvae. *Evolution*, 57, 2173–2178. https://doi.org/10.1111/j.0014-3820.2003.tb00395.x

Berg, K. (1937) Contributions to the biology of *Coretha* Meigen (*Chaoborus* Lichtenstein). *Biologiske Meddelser*, 13, 1–101.

Berg, K. & Petersen, J.C. (1956) Studies on the humic, acid Lake Gribsö. *Folia limnologica Scandinavica*, 8, 1–273.

Borkent, A. (1978) Upper Oligocene fossil pupae and larvae of *Chaoborus tertiarius* (von Heyden) (Chaoboridae, Diptera) from West Germany. *Quaestiones Entomologicae*, 14, 491–496.

Borkent, A. (1979) Systematics and bionomics of the species of the subgenus *Schadonophasma* Dyar & Shannon (*Chaoborus*, Chaoboridae, Diptera). *Quaestiones Entomologicae*, 15, 122–255.

Borkent, A. (1981) The distribution and habitat preferences of the Chaoboridae (Culicomorpha: Diptera) of the Holarctic region. *Canadian Journal of Zoology*, 59, 122–133.
https://doi.org/10.1139/z81-019

Borkent, A. (1993) A world catalogue of fossil and extant Corethrellidae and Chaoboridae (Diptera), with a listing of references to keys, bionomic information and descriptions of each known life stage. *Entomologica Scandinavica*, 24, 1–24.
https://doi.org/10.1163/187631293X00019

Borkent, A. (2012) The pupae of Culicomorpha—morphology and a new phylogenetic tree. *Zootaxa*, 3396 (1), 1–98.
https://doi.org/10.11646/zootaxa.3398.1

Borkent, A. (2014) World catalog of extant and fossil Chaoboridae (Diptera). *Zootaxa*, 3796 (3), 469–493.
https://doi.org/10.11646/zootaxa.3796.3.4

Borkent, C.J. & Borkent, A. (2008) Description and phylogenetic interpretation of chromatophore migration from larval air sacs to adult structures in some Chaoboridae (Diptera). *Canadian Entomologist*, 140, 630–640.
https://doi.org/10.4039/n08-049

Brindle, A. (1962) Taxonomic notes on the larvae of British Diptera. 8 – The subfamily Chaoborinae (Culicidae). *The Entomologist*, 95, 178–182.

Brunetti, E. (1911) Further notes on synonymy in Corethrinae. *Records of the Indian Museum*, 6, 227–229.
https://doi.org/10.5962/bhl.part.21334

Cook, E.F. (1956) The Nearctic Chaoborinae (Diptera: Culicidae). *University of Minnesota Agricultural Experiment Station Technical Bulletin*, 218, 1–102.

Cook, E.F. (1965) Family Chaoboridae. *In*: Stone, A., Sabrosky, C.W., Wirth, W.W., Foote, R.H. & Coulson, J.R. (Eds.), *A Catalog of the Diptera of America North of Mexico. United States Department of Agriculture. Agricultural Research Service. Agriculture Handbook 276*. United States Department of Agriculture, Agricultural Research Service, Washington, D.C., pp. 102–105.

Cumming, J.M. & Wood, D.M. (2017) 3. Adult morphology and terminology. *In*: Kirk-Spriggs, A.H. & Sinclair, B.J. (Eds.), *Manual of Afrotropical Diptera. Vol. 1. Introductory chapters and keys to Diptera families. Suricata 4*. South African National Biodiversity Institute, Pretoria, pp. 89–133.

Dawidowicz, P., Pijanowska, J. & Ciechomski, K. (1990) Vertical migration of *Chaoborus* larvae is induced by the presence of fish. *Limnology and Oceanography*, 35, 1631–1637.
https://doi.org/10.4319/lo.1990.35.7.1631

deWaard, J., Ivanova, N., Hajibabaei, M. & Hebert, P.N. (2008) Assembling DNA Barcodes. *In*: Martin, C.C. & Martin, C.C. (Eds.), Environmental Genomics. *Methods in Molecular Biology*, 410, pp. 275–294.
https://doi.org/10.1007/978-1-59745-548-0_15

Dickinson, W.E. (1944) The mosquitoes of Wisconsin. *Bulletin of the Public Museum of the City of Milwaukee*, 8, 269–365.

Dupuis, D., Svensson, J.-E. & Taylor, D.J. (2008) The cryptic origins of environment-indicating phantom midges (*Chaoborus*). *Limnology and Oceanography*, 53, 236–243.
https://doi.org/10.4319/lo.2008.53.1.0236

Dyar, H.G. (1905) Our present knowledge of North American Corethrid larvae. *Proceedings of the Entomological Society of Washington*, 7, 13–16.

Dyar, H.G. & Shannon, R.C. (1924) The American Chaoborinae (Diptera, Culicidae). *Insecutor Inscitiae Menstruus*, 12, 201–216.

Eckstein, F. (1936) Beiträge zur Kenntnis exotischer Chaoborinae (Corethrinae auct.) nebst Bemerkungen über einige einheimische Formen. *Archiv für Hydrobiologie*, Supplement 14, 484–505.

Edwards, F.W. (1930) The British species of *Chaoborus* and *Mochlonyx* (Diptera, Culicidae). *Entomologist's Monthly Magazine*, 66, 163–165.

Edwards, F.W. (1932) Diptera family Culicidae. *Genera Insectorum*, 194, 1–258.

Enns, W.R. (1960) Larval Phantom Midges in Missouri (Diptera: Chaoboridae). *Journal of the Kansas Entomological Society*, 33 (3), 125–128.
https://doi.org/10.2307/25083180

Felt, E.P. (1904) Mosquitos or Culicidae of New York State. *New York State Museum Bulletin*, 79 (Entomology 22), 239–400, 57 pls.

Felt, E.P. (1905) Studies in Culicidae. *New York State Museum Bulletin*, 97 (Entomology 24), 442–497, pls. 1–19.

Garcia, E. & Mittelbach, G. (2008) Regional coexistence and local dominance in *Chaoborus*: species sorting along a predation gradient. *Ecology*, 89 (6), 1703–1713.
https://doi.org/10.1890/07-0737.1

Giles, G.M. (1900) *A handbook of the gnats or mosquitoes giving the anatomy and life history of the Culicidae*. John Bale, Sons & Danielsson, Ltd., London, 374 pp.
https://doi.org/10.5962/bhl.title.101828

Giles, G.M. (1902) *A handbook of the gnats or mosquitoes giving the anatomy and life history of the Culicidae. Together with descriptions of all species notices up to the present data. 2nd Edition. Rewritten and Enlarged*. J. Bale, Sons & Danielsson, London, XI + 530 pp.

Gimmerthal, B.A. (1845) Erster Beitrag zu einer Künftig zu Bearbeitenden Dipterologie Russlands. *Bulletin de la Société Im-*

périale des Naturalistes de Moscou, 18, 287–331.
https://doi.org/10.5962/bhl.title.66007

Gosselin, A. & Hare, L. (2003) Burrowing behavior of *Chaoborus flavicans* larvae and its ecological significance. *Journal of the North American Benthological Society*, 22, 575–581.
https://doi.org/10.2307/1468354

Hebert, P.D.N., Ratnasingham, S., Zakharov, E.V., Telfer, A.C., Levesque-Beaudin, V., Milton, M.A., Pedersen, S., Jannetta, P. & de Waard, J.R. (2016) Counting animal species with DNA barcodes: Canadian insects. *Philosophical Transactions of the Royal Society B*, 371, 20150333.
https://doi.org/10.1098/rstb.2015.0333

Hennig, W. (1968) *Die Larvenformen der Dipteren*. *2. Teil*. Akademie Verlag, Berlin, 458 pp.

Hirvenoja, M. (1960) Ökologische Studien über die Wasserinsekten in Riihimäki (Südfinnland). I. Chaoborinae (Dipt., Culicidae). *Annales Entomologici Fennici*, 26, 31–44.

Hirvenoja, M. (1961) Weitere Studien über Chaoborinen (Dipt., Culicidae). Beschreibung der Larve und der Puppe von *Chaoborus (Schadonophasma) nyblaei*. Zett. *Annales Entomologici Fennici*, 27, 77–83.

Hoang, D.T., Chernomor, O., von Haeseler, A., Minh, B.Q. & Vinh, L.S. (2017) UFBoot2: Improving the Ultrafast Bootstrap Approximation. *Molecular Biology and Evolution*, 35 (2), 518–522.
https://doi.org/10.1093/molbev/msx281

Hongve, D. (1975) On the ecology and distribution of *Chaoborus* (Chaoboridae, Diptera) from the Upper Romerike District, south-east Norway. *Norwegian Journal of Entomology*, 22, 49–57.

Horppila, J., Malinen, T., Nurminen, L., Tallberg, P. & Vinni, M. (2000) A metalimnetic oxygen minimum indirectly contributing to the low biomass of cladocerans in Lake Hiidenvesi – a diurnal study on the refuge effect. *Hydrobiologia*, 436, 81–90.
https://doi.org/10.1023/A:1026594006856

Horppila, J., Eloranta, P., Liljendahl-Nurminen, A., Niemistö, J. & Peckan-Hekim, Z. (2009) Refuge availability and sequence of predators determine the seasonal succession of crustacean zooplankton in a clay-turbid lake. *Aquatic Ecology*, 43, 91–103.
https://doi.org/10.1007/s10452-007-9158-3

Johannsen, O.A. (1903) Aquatic nematocerous Diptera. *New York State Museum Bulletin*, 68 (Entomology 18), 327–448, pls. 32–50.
https://doi.org/10.5962/bhl.title.8531

Johannsen, O.A. (1934) Aquatic Diptera. Part I. Nemocera, exclusive of Chironomidae and Ceratopogonidae. *Memoir, Cornell University Agricultural Experiment Station*, 164, 1–71.

Jäger, I.S. & Walz, N. (2003) Unusual allometry between respiration rate and body size in *Chaoborus* species. *Journal of Plankton Research*, 25 (3), 255–260.
https://doi.org/10.1093/plankt/25.3.255

Jäger, I.S., Hölker, F., Flöder, S. & Walz, N. (2011) Impact of *Chaoborus flavicans*-predation on the zooplankton in a mesotrophic lake – a three year study. *International Review of Hydrobiology*, 96, 191–208.
https://doi.org/10.1002/iroh.201011253

Järnefelt, H. (1936) Zur Limnologie einiger Gewässer Finnlands XIV. *Annales Zoologici, Societatis Zoologicae-Botanicae Fennicae Vanamo*, 4 (3), 1–19.

Kajak, Z. & Rybak, J. (1979) The feeding of *Chaoborus flavicans* Meigen (Diptera, Chaoboridae) and its predation on lake zooplankton. *Internationale Revue der gesamten Hydrobiologie*, 64, 361–378.
https://doi.org/10.1002/iroh.19790640310

Kalyaanamoorthy, S., Minh, B., Wong, T., von Haeseler, A. & Jermiin, L.S. (2017) ModelFinder: fast model selection for accurate phylogenetic estimates. *Nature Methods*, 14, 587–589.
https://doi.org/10.1038/nmeth.4285

Komyo, E. (1954) Japanese Chaoborin Mosquitoes. *The Scientific Reports of the Saikyo University Agriculture*, 6, 11–15.

Kuper, J. & Verberk, W. (2011) Fenologie, habitat en verspreiding van Pluimmuggen in Nederlandse hoogvenen (Diptera: Chaoboridae). *Nederlandse Faunistische Mededelingen*, 35, 73–82.

Kurek, J., Cwynar, L.C., Weeber, R.C., Jeffries, D.S. & Smol, J.P. (2010) Ecological distributions of *Chaoborus* species in small, shallow lakes from the Canadian Boreal Shield ecozone. *Hydrobiologia*, 652, 207–221.
https://doi.org/10.1007/s10750-010-0333-5

Leigh, J.W. & Bryant, D (2015) PopART: full-feature software for haplotype network construction. *Methods in Ecology and Evolution*, 6, 1110–1116.
https://doi.org/10.1111/2041-210X.12410.

Liljendahl-Nurminen, A., Horppila, J., Eloranta, P., Malinen, T. & Uusitalo, L. (2002) The seasonal dynamics and distribution of *Chaoborus flavicans* larvae in adjacent lake basins of different morphometry and degree of eutrophication. *Freshwater Biology*, 47, 1283–1295.
https://doi.org/10.1046/j.1365-2427.2002.00867.x

Lindholm, M., Wolf, R., Finstad, A. & Hessen, D.O. (2016) Water browning mediates predatory decimation of the Arctic fairy shrimp *Branchinecta paludosa*. *Freshwater Biology*, 61, 340–347.
https://doi.org/10.1111/fwb.12712

Luoto, T. & Nevalainen, L. (2009) Larval chaoborid mandibles in surface sediments of small shallow lakes in Finland: implications for palaeolimnology. *Hydrobiologia*, 631, 185–195.
https://doi.org/10.1007/s10750-009-9810-0

MacKay N.A., Carpenter, S.R., Soranno, P.A. & Vanni, M.J. (1990) The impact of two *Chaoborus* species on a zooplankton community. *Canadian Journal of Zoology*, 68 (5), 981–985.
https://doi.org/10.1139/z90-141

Macquart, J. (1834) *Histoire naturelle des Insectes—Diptères. 1*. Librairie Encyclopédique de Roret, Paris, 578 pp. [1834–1835]
https://doi.org/10.5962/bhl.title.14274

Martini, E. (1929) Culicidae. *In*: Lindner, E. (Ed.), *Die Fliegen der palaearktischen Region*, 3, pp. 1–48 (lfg. 33) + pp. 49–96 (lfg. 35).

Matheson, R. (1925) Notes on Chaoborinae (Diptera, Culicidae). *Canadian Entomologist*, 57, 159–160.
https://doi.org/10.4039/Ent57159-7

Matheson, R. (1944) *Handbook of the Mosquitoes of North America. Handbooks of American Natural History. Vol. V. 2nd Edition.* Comstock Publishing Company, Ithaca, New York, 314 pp.

Meigen, J.W. (1830) *Systematische Beschreibung der bekannten europäischen zweiflügeligen Insekten. Vol. 6*. Schulzische Buchhandlung, Hamm, xi + 401 pp., pls. 55–66.

Monchadskii, A.S. (1936) *Larvae of the Culicidae of the USSR and Adjacent Countries. Opredeliteli po faune SSSR. Vol. 24*. Izd. AN SSSR, Moscow-Leningrad, 379 pp. [in Russian]

Nguyen, L.-T., Schmidt, H.A., von Haeseler, A. & Minh, B.Q. (2015) IQ-TREE: A fast and effective stochastic algorithm for estimating maximum-likelihood phylogenies. *Molecular Biology and Evolution*, 32 (1), 268–274.
https://doi.org/10.1093/molbev/msu300

Nilssen, J.P. (1974) On the ecology and distribution of the Norwegian larvae of *Chaoborus* (Diptera, Chaoboridae). *Norsk entomologisk Tidsskrift*, 21, 37–44.

Ogawa, J.R. (2007) *Phylogeny of the "Chaoboriform" genera*. Doctor of Philosophy thesis, Oregon State University, Corvallis, Oregon, xiv + 256 pp.

Palm, F., El-Daoushy, F. & Svensson, J.E. (2011) Fragmented subfossil *Chaoborus* mandibles reveal periods of cyprinid presence in lake histories. *Journal of Paleolimnology*, 45, 101–113.
https://doi.org/10.1007/s10933-010-9483-8

Parma, S. (1969) Notes on the larval taxonomy, ecology, and distribution of the Dutch *Chaoborus* species (Diptera, Chaoboridae). *Beaufortia*, 17, 21–50.

Parma, S. (1971a) Chaoborus flavicans *(Meigen) (Diptera: Chaoboridae): an autecological study*. Doctor of Philosophy Thesis, University of Groningen, Groningen, 128 pp.

Parma, S. (1971b) The morphology of the larval instars of *Chaoborus flavicans* (Meigen, 1818) (Diptera, Chaoboridae). *Beaufortia*, 18, 173–182.

Peus, F. (1934) Zur Kenntnis der Larven und Puppen der Chaoborinae (Corethrinae auct.). *Archiv für Hydrobiologie*, 27, 641–668.

Peus, F. (1938) Über eine neue aufgefundene alpine Büschelmücke, *Chaoborus alpinus*, n.sp. (Dipt., Culicid.). *Encyclopédie Entomologique*, Series B, II, 9, 63–73.

Prokesova V. (1959) Beitrag zur Artenunterscheidung und zum Vorkommen der *Chaoborus*-larven (Diptera). *Časopis Československé společnosti entomologické*, 56, 142–149.

Regmi, B.P., Wivegh, J.S. & Hobæk, A. (2013) Population decline and life-cycle changes in a phantom midge (*Chaoborus flavicans*) after introduction of planktivorous fish. *Freshwater Biology*, 58, 1436–1446.
https://doi.org/10.1111/fwb.12141

Remm, H. (1955) Eesti NSV klaasiksääsklastest. *Eesti NSV teaduste akadeemia juures asuva loodusuurijate seltsi astaraamat*, 1955, 226–233.

Richardson, C.H. (1912) Notes on the life-history of *Corethra albipes* Johannsen. *Psyche: A Journal of Entomology*, 19, 200–203.
https://doi.org/10.1155/1912/74627

Rosenberg, N.A. (2007) Statistical tests for taxonomic distinctiveness from observations of monophyly. *Evolution*, 61, 317–323.
https://doi.org/10.1111/j.1558-5646.2007.00023.x

Roth J.C. (1967) Notes on *Chaoborus* species from the Douglas Lake region, Michigan, with a key to their larvae (Diptera: Chaoboridae). *Papers of the Michigan Academy of Science, Arts and Letters*, 52, 63–68.

Roth J.C. (1968) The pupa of *Chaoborus albatus* with a key to eastern *Chaoborus* pupae. *Entomological News*, 79, 275–277.

Sæther, O.A. (1967) Variation within immature stages of *Chaoborus flavicans* (MEIG.) (syn. *Chaoborus alpinus* Peus syn. nov.). *Internationale Revue der gesamten Hydrobiologie*, 52, 573–587.
https://doi.org/10.1002/iroh.19670520407

Sæther, O.A. (1970) Nearctic and Palaearctic *Chaoborus* (Diptera: Chaoboridae). *Fisheries Research Board of Canada Bulletin*, 174, i–vii + 1–57.

Sæther, O.A. (1972) VI. Chaoboridae. *Zooplankton der Binnengewässer. 1. Tiel. Binnengewässer*, 26, 257–280.

Sæther, O.A. (1997a) Diptera Chaoboridae, Phantom midges. *In*: Nilsson, A. (Ed.), *Aquatic Insects of North Europe*. *Vol. 2*. Apollo Books, Stenstrup, pp. 149–161.

Sæther, O.A. (1997b) 2.17. Family Chaoboridae. *In*: Papp, L. & Darvas, B. (Eds.), *Contributions to a Manual of Palaearctic Diptera (with special reference to the flies of economic importance).* Science Herald, Budapest, pp. 305–317.

Sæther, O.A. (2002) Chaoboridae, phantom midges. *In*: Schwoerbel, J., Schwoerbel, J. & Zwick, P. (Eds.), *Süsswasserfauna von Mitteleuropa*, 21 (10), pp. 1–38.

Salmela, J. (2012) Biogeographic Patterns of Finnish Crane Flies (Diptera, Tipuloidea). *Psyche—A Journal of Entomology*, 2012 (1).
https://doi.org/10.1155/2012/913710

Séguy, E. (1924) Les moustiques de l'Afrique Mineure, de l'Egypte et de la Syrie. *Encyclopedie entomologique (A)*, 1, 1–257.

Séguy, E. (1925) Diptères (Nématocères piqueurs): Ptychopteridae, Orphnephilidae, Simuliidae, Culicidae, Psychodidae Phlebotominae. *Faune de France*, 12, 1–109.

Sikorowa, A. (1966) Beitrag zur Systematik und Ökologie der Chaoborinae. *Internationale Vereinigung für Theoretische und Angewandte Limnologie XI. Ecology of Freshwater Organisms. 3. Aquatic Animals*, 16 (3), 1709–1715.
https://doi.org/10.1080/03680770.1965.11899498

Sikorowa, A. (1967) Occurrence of *Chaoborus alpinus* Peus (Diptera, Culicidae), a new species in Poland. *Polskie Archiwum Hydrobiologii*, 14, 87–90.

Sikorowa, A. (1973) Morfologia, biologia i ekologia gatunkow rodzaju *Chaoborus* Lichtenstein (Diptera, Chaoboridae) wystepujacych w Polsce. *Zeszyty Naukowe Akademii Rolniczo-Technicznej w Olsztynie*, 105, 1–121.

Sládeček, V. (1952) Larvy *Chaoborus (Corethra)* v českých vodách. *Časopis Národního muzea: Oddíl přírodovědný*, 121, 94–102.

Smol, J.P. & Douglas, M.S. (2007) Crossing the final ecological threshold in high Arctic ponds. *Procedings of the National Academy of Sciences USA*, 104, 12395–12397.
https://doi.org/10.1073/pnas.0702777104

Stahl, J. (1966a) The ecology of *Chaoborus* in Myers Lake, Indiana. *Limnology and Oceanography*, 11, 177–183.
https://doi.org/10.4319/lo.1966.11.2.0177

Stahl, J. (1966b) Coexistence in *Chaoborus* and its ecological significance. *Investigations of Indiana Lakes and Streams*, 7, 99–113.

Stenson, J.A.E. (1978) Differential predation by fish on two species of *Chaoborus* (Diptera, Chaoboridae). *Oikos*, 31, 98–101.
https://doi.org/10.2307/3543389

Stenson, J.A.E. (1980) Predation pressure from fish on two *Chaoborus* species as related to their visibility. *In*: Kerfoot, W.C. (Ed.), *Evolution and Ecology of Zooplankton Communities*. University Press of New England, Hanover, pp. 618–622.

Strickman, D. (1980) Observations on adults and eggs of *Chaoborus flavicans* (Diptera: Chaoboridae). *Hydrobiologia*, 74, 195–197.
https://doi.org/10.1007/BF00008752

Sweetman, J.N. & Smol, J.P. (2006) Reconstructing fish populations using *Chaoborus* (Diptera: Chaoboridae) remains – a review. *Quaternary Science Reviews*, 25 (15–16), 2013–2023.
https://doi.org/10.1016/j.quascirev.2006.01.007

Taylor, D.J., Ballinger, M.J., Medeiros, A.S. & Kotov, A.A. (2015) Climate associated tundra thaw pond formation and range expansion of boreal zooplankton predators. *Ecography*, 39, 43–53.
https://doi.org/10.1111/ecog.01514

Theobald, F.V. (1901) *A monograph of the Culicidae or moquitoes*. *Vol. 2*. British Museum (Natural History), London, viii + 391 pp.

Theobald, F.V. (1905) Diptera. Family Culicidae. *Genera Insectorum*, 5 (26), 1–50.

Tsalkitzis, E., Yan, N.D., McQueen, D.J., Popiel, S.A. & Demers, E. (1994) Habitat separation among three temperate *Chaoborus* species. *Archiv für Hydrobiologie*, 129 (4), 385–403.

Ursenbacher, S., Stötter, T. & Heiri, O. (2020) Chitinous aquatic invertebrate assemblages in Quaternary lake sediments as indicators of past deepwater oxygen concentration. *Quaternary Science Reviews*, 231, 106203.
https://doi.org/10.1016/j.quascirev.2020.106203

Uutala, A.J. (1990) *Chaoborus* (Diptera: Chaoboridae) mandibles—paleolimnological indicators of the historical status of fish populations in acid-sensitive lakes. *Journal of Paleolimnology*, 4, 139–151.
https://doi.org/10.1007/BF00226321

Valle, K.J. (1930) Über das Auftreten von *Mysis relicta* und *Corethra plumicornis* während des Sommers in einigen Seen von Südost-Finnland. *Archiv für Hydrobiologie*, 21, 483–492.

Valle, K.J. (1936) Fortgeführte boden- und tiefentierökologische Untersuchungen in einigen südostfinnischen Seen. *Annales Zoologici, Societatis Zoologicae-Botanicae Fennicae Vanamo*, 4 (4), 1–41.

Wagner, R. (1990) Family Chaoboridae. *In*: Soós, A. & L. Papp, L. (Eds.), *Catalogue of Palaearctic Diptera*, 2 (Psychodidae—Chironomidae), pp. 71–74.

Walker, I.R. (2001) 3. Midges: Chironomidae and related Diptera. *In*: Smol, J.P., Birks, H.J.B. & Last, W.M. (Eds.), *Tracking Environmental Change Using Lake Sediments*. *Vol. 4*. Kluwer Academic Publishers, Dordrecht, pp. 43–66
https://doi.org/10.1007/0-306-47671-1_3

Wende, F., Lucas, L.K., Graves, A.M., Swift, M.C. & Berendonk, T.U. (2006) Steps between lakes? Some initial genetic data on the Holarctic planktonic predator *Chaoborus flavicans*. *Archiv für Hydrobiologie*, 167, 169–182. https://doi.org/10.1127/0003-9136/2006/0167-0169

Wesenberg-Lund, C. (1914) Bidrag til nogle myggeslaegters, saerlig *Mochlonyx* og *Corethra*'s biologi. *In*: Jungersen, H.F.E. & Warming, E. (Eds.), *Mindeskrift i anledning af hundreaaret for Japetus Steenstrup fødsel udgivet af en kreds af naturforskere. 2 (34)*. Bianco Lunos Bogtrykkeri, København, pp. 1–25.

Wissel, B. & Benndorf, J. (1998) Contrasting effects of the invertebrate predator *Chaoborus obscuripes* and planktivorous fish on plankton communities of a long term biomanipulation experiment. *Archiv für Hydrobiologie*, 143, 129–146. https://doi.org/10.1127/archiv-hydrobiol/143/1998/129

Xie, P., Iwakuma, T. & Fujii, K. (1998) Studies on the biology of *Chaoborus flavicans* (Meigen) (Diptera: Chaoboridae) in a fish-free eutrophic pond, Japan. *Hydrobiologia*, 368, 83–90. https://doi.org/10.1023/A:1003217325236

Ökland, J. (1964) The eutrophic lake Borrevann (Norway). *Folia Limnologica Scandinavica*, 13, 1–337.

Yamada, S. (1932) *Iconographia insectorum japonicorum*. Tokyo, 230 pp. (in Japanese)

Zhang, X., Kang, Z., Ding, S., Wang, Y., Borkent, C., Saigusa, T. & Yang, D. (2019) Mitochondrial genomes provide insights into the phylogeny of Culicomorpha (Insecta: Diptera). *International Journal of Molecular Sciences*, 2019, 20, 747. https://doi.org/10.3390/ijms20030747

APPENDIX 1. *Chaoborus flavicans* (Meigen) species group and *C. crystallinus* (De Geer) specimens used in DNA barcoding and genetic analyses. BOLD=BOLD sample ID, GenBank=GenBank accession number, year=collecting year.

species	BOLD	GenBank	year	country	locality
Chaoborus flavicans	LMM-el-615		2019	Finland	Rovaniemi
Chaoborus flavicans	CUL-2019-69		2014	Finland	Iitti
Chaoborus flavicans	LMM-el-268		2019	Finland	Ylitornio
Chaoborus flavicans	LMM-el-603		2019	Finland	Kittilä
Chaoborus flavicans	CUL-2019-71		2014	Finland	Iitti
Chaoborus flavicans	CUL-2019-77		2019	Finland	Rovaniemi
Chaoborus flavicans	CUL-2019-73		2015	Finland	Hamina
Chaoborus flavicans	NVO.ins2018-64		2018	Estonia	Rakujärv
Chaoborus flavicans	NVO.ins2018-638		2018	Finland	Utsjoki
Chaoborus flavicans	NVO.ins2018-606		2018	Finland	Urjala
Chaoborus flavicans	NVO.ins2018-460		2018	Kazakhstan	Qostanay
Chaoborus flavicans	NVO.ins2018-602		2018	Finland	Urjala
Chaoborus flavicans	NVO.ins2018-607		2018	Finland	Urjala
Chaoborus flavicans	NVO.ins2018-637		2018	Finland	Utsjoki
Chaoborus flavicans	NVO.ins2018-612		2017	Finland	Lappajärvi
Chaoborus flavicans	NVO.ins2018-63		2018	Finland	Hollola
Chaoborus flavicans	NVO.ins2018-603		2018	Finland	Urjala
Chaoborus flavicans	NVO.ins2018-615		2017	Finland	Lappajärvi
Chaoborus flavicans	NVO.ins2018-249		2017	Finland	Orivesi
Chaoborus flavicans	NVO.ins2018-61		2018	Finland	Hyrynsalmi
Chaoborus flavicans	NVO.ins2018-605		2018	Finland	Urjala
Chaoborus flavicans	NVO.ins2018-604		2018	Finland	Urjala
Chaoborus flavicans	NVO.ins2018-639		2018	Finland	Utsjoki
Chaoborus flavicans	NVO.C2020-02		2019	Japan	Matsuyama
Chaoborus flavicans	BIOUG03103-B06	KM987996	2012	Canada	BC, Gulf Island NP
Chaoborus flavicans	BIOUG23518-D10	MF715683	2014	Canada	BC, Gulf Island NP
Chaoborus flavicans	BIOUG03237-F09	KM989739	2012	Canada	AB, Elk Island NP
Chaoborus flavicans	BIOUG03237-E05	KM993515	2012	Canada	AB, Elk Island NP
Chaoborus flavicans	BIOUG27709-F09	MG172714	2014	Canada	BC, Victoria
Chaoborus flavicans	BIOUG10562-A07	KR384115	2013	Canada	ON, Pukaskwa NP
Chaoborus flavicans	BIOUG03624-H06	KM991891	2012	Canada	AB, Elk Island NP
Chaoborus flavicans	BIOUG04091-F03	KM989258	2012	Canada	AB, Elk Island NP
Chaoborus flavicans	BIOUG17212-F06	KR513961	2014	Canada	NWT, Nahanni NP
Chaoborus flavicans	BIOUG04358-A04	KM995659	2012	Canada	AB, Elk Island NP
Chaoborus flavicans	BIOUG03624-A02	KM990766	2012	Canada	AB, Elk Island NP
Chaoborus flavicans	BIOUG03450-B02	KM988633	2012	Canada	AB, Elk Island NP
Chaoborus flavicans	BIOUG03450-H01	KM994913	2012	Canada	AB, Elk Island NP
Chaoborus flavicans	BIOUG03549-G04	KM991724	2012	Canada	AB, Elk Island NP
Chaoborus flavicans	BIOUG03333-A04	KM990814	2012	Canada	AB, Elk Island NP
Chaoborus flavicans	BIOUG03291-H06	KM988513	2012	Canada	AB, Elk Island NP
Chaoborus flavicans	BIOUG03237-G11	KM990485	2012	Canada	AB, Elk Island NP
Chaoborus flavicans	10BBCDIP-3021	JN291123	2010	Canada	ON, Pukaskwa NP
Chaoborus flavicans	BIOUG03624-H01	KM994984	2012	Canada	AB, Elk Island NP

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APPENDIX 1. (Continued)

species	BOLD	GenBank	year	country	locality
Chaoborus flavicans	08BBDIP-1861	KM569761	2008	Canada	AB, Waterton Lakes NP
Chaoborus flavicans	BIOUG03333-E05	KM990809	2012	Canada	AB, Elk Island NP
Chaoborus flavicans	BIOUG03291-E03	KM988175	2012	Canada	AB, Elk Island NP
Chaoborus flavicans	BIOUG03237-H02	KM990633	2012	Canada	AB, Elk Island NP
Chaoborus flavicans	10BBCDIP-0751	JN290723	2010	Canada	ON, Pukaskwa NP
Chaoborus flavicans	BIOUG21263-D08	MF708604	2014	Canada	SK, Grasslands NP
Chaoborus flavicans	BOLD:AAG5462	KM951626	2012	Canada	AB, Elk Island NP
Chaoborus flavicans	BIOUG06622-F03	KM990832	2012	Canada	BC, Gulf Island NP
Chaoborus flavicans	BIOUG03671-A09	KM994832	2012	Canada	AB, Elk Island NP
Chaoborus flavicans	BIOUG03237-E03	KM989522	2012	Canada	AB, Elk Island NP
Chaoborus flavicans	BIOUG28107-D09	MG177446	2014	Canada	BC, Victoria
Chaoborus flavicans	BIOUG06622-G02	KM989348	2012	Canada	BC, Gulf Island NP
Chaoborus flavicans	BIOUG03450-C09	KM994812	2012	Canada	AB, Elk Island NP
Chaoborus flavicans	BIOUG03624-F01	KM989368	2012	Canada	AB, Elk Island NP
Chaoborus flavicans	BIOUG16032-E06	KR772778	2014	Canada	NS, New Glasgow
Chaoborus flavicans	BIOUG03671-A05	KM990312	2012	Canada	AB, Elk Island NP
Chaoborus flavicans	BBDIQ039-10	HQ552106	2008	Canada	MB, Riding Mountain NP
Chaoborus flavicans	BIOUG17130-F11	KR499600	2014	Canada	NWT, Nahanni NP
Chaoborus flavicans	BIOUG03624-G12	KM993571	2012	Canada	AB, Elk Island NP
Chaoborus flavicans	BIOUG23381-D12	MF712997	2014	Canada	BC, Gulf Island NP
Chaoborus flavicans	BIOUG03291-F11	KM990835	2012	Canada	AB, Elk Island NP
Chaoborus flavicans	BIOUG03624-D04	KM993176	2012	Canada	AB, Elk Island NP
Chaoborus flavicans	BIOUG03450-F12	KM990704	2012	Canada	AB, Elk Island NP
Chaoborus flavicans	BIOUG28102-G10	MG173232	2014	Canada	BC, Victoria
Chaoborus flavicans	BIOUG03237-A05	KM989450	2012	Canada	AB, Elk Island NP
Chaoborus flavicans	08BBDIP-0676	KM570561	2008	Canada	SK, Grasslands NP
Chaoborus flavicans	BIOUG23516-B11	MF714251	2014	Canada	BC, Gulf Island NP
Chaoborus flavicans	BIOUG03624-F10	KM993268	2012	Canada	AB, Elk Island NP
Chaoborus flavicans	08BBDIP-1924	KM571690	2008	Canada	MB, Riding Mountain NP
Chaoborus flavicans	BIOUG03450-B11	KM990490	2012	Canada	AB, Elk Island NP
Chaoborus flavicans	BIOUG11441-B12	KT118897	2013	Canada	BC, New Afton Mine
Chaoborus flavicans	BIOUG03624-F03	KM995571	2012	Canada	AB, Elk Island NP
Chaoborus flavicans	BIOUG21112-F11	MF711270	2014	Canada	SK, Grasslands NP
Chaoborus flavicans	BIOUG03114-B05	KM988754	2012	Canada	AB, Elk Island NP
Chaoborus flavicans	BIOUG23518-G06	MF712684	2014	Canada	BC, Gulf Island NP
Chaoborus flavicans	BIOUG03450-B09	KM991074	2012	Canada	AB, Elk Island NP
Chaoborus flavicans	BIOUG03624-E10	KM993062	2012	Canada	AB, Elk Island NP
Chaoborus flavicans	BIOUG03624-A06	KM990093	2012	Canada	AB, Elk Island NP
Chaoborus flavicans	BARS_2015_34_113	MG177685	2015	Canada	ON, Peterborough
Chaoborus flavicans	BIOUG06622-F05	KM991260	2012	Canada	BC, Gulf Island NP
Chaoborus flavicans	BIOUG03291-G11	KM990290	2012	Canada	AB, Elk Island NP
Chaoborus flavicans	BIOUG03624-F02	KM988618	2012	Canada	AB, Elk Island NP
Chaoborus flavicans	BIOUG04079-B03	KM995713	2012	Canada	AB, Elk Island NP

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APPENDIX 1. (Continued)

species	BOLD	GenBank	year	country	locality
Chaoborus flavicans	BIOUG23466-D01	MF712899	2014	Canada	BC, Gulf Island NP
Chaoborus flavicans	BIOUG07042-G03	KR686326	2013	Canada	BC, New Afton Mine
Chaoborus flavicans	BIOUG28195-D07	MG174618	2014	Canada	BC, Victoria
Chaoborus flavicans	BIOUG04091-E04	KM993568	2012	Canada	AB, Elk Island NP
Chaoborus flavicans		AF425842		Canada	ON, Ottawa
Chaoborus flavicans	BIOUG03624-G11	KM994513	2012	Canada	AB, Elk Island NP
Chaoborus flavicans	BIOUG03624-H03	KM989905	2012	Canada	AB, Elk Island NP
Chaoborus albipes	CUL-2019-26		2019	Finland	Kouvola
Chaoborus albipes	NVO.ins2018-624		2018	Finland	Savukoski
Chaoborus albipes	CUL-2019-84		2015	Finland	Kouvola
Chaoborus albipes	LMM-el-526		2019	Finland	Kittila
Chaoborus albipes	LMM-el-76		2019	Finland	Savonlinna
Chaoborus albipes	CUL-2019-78		2019	Finland	Kittila
Chaoborus albipes	LMM-el-11		2019	Finland	Joroinen
Chaoborus albipes	CUL-2019-79		2019	Finland	Kittila
Chaoborus albipes	ins2018-783		2015	Finland	Kouvola
Chaoborus albipes	LMM-el-10		2019	Finland	Joroinen
Chaoborus albipes	LMM-el-15		2019	Finland	Savonlinna
Chaoborus albipes	LMM-el-61		2019	Finland	Savonlinna
Chaoborus albipes	NVO.ins2018-625		2018	Finland	Savukoski
Chaoborus albipes	NVO.ins2018-626		2018	Finland	Savukoski
Chaoborus albipes	NVO.ins2018-627		2018	Finland	Savukoski
Chaoborus albipes	NVO.ins2018-628		2018	Finland	Savukoski
Chaoborus albipes	BIOUG17213-H03	KR513469	2014	Canada	NWT, Nahanni NP
Chaoborus albipes	BIOUG09060-H05	KR383516	2013	Canada	ON, Rouge
Chaoborus albipes	BIOUG25462-E07	MG173677	2015	Canada	ON, Uxbridge
Chaoborus albipes	BIOUG25544-B02	MG180477	2015	Canada	NB, Springfield
Chaoborus albipes	BIOUG20540-A09	MF709178	2014	Canada	Ontario, Rouge
Chaoborus albipes	BIOUG27451-D04	MF706462	2014	Canada	ON, Point Pelee NP
Chaoborus albipes	BIOUG25544-F11	MG173492	2015	Canada	NB, Springfield
Chaoborus albipes	BIOUG27556-A11	MF715617	2014	Canada	ON, Point Pelee NP
Chaoborus albipes	JSDIQ650-10	JN302365	2010	Canada	ON, Leeds and Greenville
Chaoborus albipes	BIOUG16983-G08	KR508504	2014	Canada	NWT, Nahanni NP
Chaoborus albipes	BIOUG10858-D11	KR385257	2013	Canada	Prince Edward Island
Chaoborus albipes	BIOUG10660-D02	KR399486	2013	Canada	Prince Edward Island
Chaoborus albipes	BIOUG20540-B02	MF713591	2014	Canada	Ontario, Rouge
Chaoborus albipes	BIOUG10366-H09	KR389895	2013	Canada	Prince Edward Island
Chaoborus albipes	BIOUG25544-C01	MG176403	2015	Canada	NB, Springfield
Chaoborus albipes	BIOUG10435-C08	KR386004	2013	Canada	Prince Edward Island
Chaoborus albipes	BARS_2015_41_021	MG178121	2015	Canada	ON, Kawartha Lakes
Chaoborus albipes	BIOUG22361-C03	KT603841	2015	Canada	ON, Cambridge
Chaoborus albipes	TTMDI620-10	HQ981771	2008	Canada	ON, Puslinch
Chaoborus albipes	BIOUG22761-H04	MF709383	2014	Canada	BC, Kootenay NP

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APPENDIX 1. (Continued)

species	BOLD	GenBank	year	country	locality
Chaoborus albipes	BIOUG23326-C12	MG175461	2015	Canada	ON, Charleston Lake
Chaoborus albipes	BIOUG10787-B11	KR397037	2013	Canada	Prince Edward Island
Chaoborus albipes	BIOUG10320-H10	KR394192	2013	Canada	Prince Edward Island
Chaoborus albipes	BARS_2015_41_064	MG172970	2015	Canada	ON, Kawartha Lakes
Chaoborus albipes	TTMDI601-10	HQ981754	2008	Canada	ON, Puslinch
Chaoborus albipes	BIOUG10733-D05	KR390182	2013	Canada	Prince Edward Island
Chaoborus albipes	BIOUG10329-D02	KR397330	2013	Canada	Prince Edward Island
Chaoborus albipes	BIOUG27691-B03	MG172684	2015	Canada	ON, Charleston Lake
Chaoborus albipes		MT524222	2005	USA	AK, Nome
Chaoborus albipes		MT524223	2005	USA	AK, Nome
Chaoborus albipes		MT524230	2005	USA	AK, Nome
Chaoborus albipes		MT524231	2005	USA	AK, Nome
Chaoborus albipes		MT524232	2005	USA	AK, Nome
Chaoborus albipes		MT524194	2005	USA	Kougarok HWY, AK
Chaoborus albipes		MT524195	2005	USA	Kougarok HWY, AK
Chaoborus albipes		MT524196	2005	USA	Kougarok HWY, AK
Chaoborus albipes		MT524197	2005	USA	AK, Kodiak
Chaoborus albipes		MT524198	2005	USA	AK, Kougarok HWY
Chaoborus albipes		MT524199	2005	USA	AK, Kougarok HWY
Chaoborus albipes		MT524200	2005	USA	AK, Kougarok HWY
Chaoborus albipes		MT524201	2005	USA	AK, Kougarok HWY
Chaoborus albipes		MT524202	2005	USA	AK, Kougarok HWY
Chaoborus albipes		MT524203	2005	USA	AK, Kougarok HWY
Chaoborus albipes		MT524204	2005	USA	AK, Kougarok HWY
Chaoborus albipes		MT524205	2005	USA	AK, Kougarok HWY
Chaoborus albipes		MT524206	2005	USA	AK, Kougarok HWY
Chaoborus albipes		MT524207	2005	USA	AK, Kougarok HWY
Chaoborus albipes		MT524208	2005	USA	AK, Kougarok HWY
Chaoborus albipes		MT524209	2005	USA	AK, Kougarok HWY
Chaoborus albipes		MT524210	2005	USA	AK, Kougarok HWY
Chaoborus albipes		MT524211	2005	USA	AK, Council
Chaoborus albipes		MT524212	2005	USA	AK, Pilgrim Hot Springs
Chaoborus albipes		MT524213	2005	USA	AK, Pilgrim Hot Springs
Chaoborus albipes		MT524214	2005	USA	AK, Pilgrim Hot Springs
Chaoborus albipes		MT524215	2005	USA	AK, Kougarok HWY
Chaoborus albipes		MT524216	2005	USA	AK, Kougarok HWY
Chaoborus albipes		MT524217	2005	USA	AK, Kougarok HWY
Chaoborus albipes		MT524218	2005	USA	AK, Kougarok HWY
Chaoborus albipes		MT524219	2005	USA	AK, Kougarok HWY
Chaoborus albipes		MT524220	2005	USA	AK, Kougarok HWY
Chaoborus albipes		MT524221	2005	USA	AK, Kougarok HWY
Chaoborus albipes		MT524224	2005	USA	AK, Teller
Chaoborus albipes		MT524225	2005	USA	AK, Teller

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APPENDIX 1. (Continued)

species	BOLD	GenBank	year	country	locality
Chaoborus albipes		MT524226	2005	USA	AK, Kougarok HWY
Chaoborus albipes		MT524227	2005	USA	AK, Kougarok HWY
Chaoborus albipes		MT524228	2005	USA	AK, Kougarok HWY
Chaoborus albipes		MT524229	2005	USA	AK, Kougarok HWY
Chaoborus albipes		MT524233	2005	USA	AK, Kodiak
Chaoborus albipes		MT524234	2005	USA	AK, Pilgrim Hot Springs
Chaoborus albipes		MT524235	2005	USA	AK, Pilgrim Hot Springs
Chaoborus albipes		MT524236	2005	USA	AK, Pilgrim Hot Springs
Chaoborus albipes		MT524237	2005	USA	AK, Council
Chaoborus albipes		MT524238	2005	USA	AK, Kodiak
Chaoborus albipes		MT524239	2005	USA	AK, Kougarok HWY
Chaoborus albipes		MT524240	2005	USA	AK, Council
Chaoborus posio **sp. n.**	CUL-2019-80		2019	Finland	Suomussalmi
Chaoborus posio **sp. n.**	CUL-2019-76		2019	Finland	Inari
Chaoborus posio **sp. n.**	NVO.ins2018-619		2018	Finland	Posio
Chaoborus posio **sp. n.**	CUL-2019-75		2019	Finland	Kittilä
Chaoborus posio **sp. n.**	CUL-2019-81		2019	Finland	Suomussalmi
Chaoborus posio **sp. n.**	LMM-el-574		2019	Finland	Kittilä
Chaoborus posio **sp. n.**	NVO.ins2018-622		2018	Finland	Posio
Chaoborus posio **sp. n.**	NVO.ins2018-618		2018	Finland	Posio
Chaoborus posio **sp. n.**	NVO.ins2018-580		2018	Finland	Posio
Chaoborus posio **sp. n.**	NVO.ins2018-617		2018	Finland	Posio
Chaoborus posio **sp. n.**	NVO.ins2018-620		2018	Finland	Posio
Chaoborus posio **sp. n.**	NVO.ins2018-616		2018	Finland	Posio
Chaoborus posio **sp. n.**	NVO.ins2018-623		2018	Finland	Posio
Chaoborus posio **sp. n.**	NVO.ins2018-581		2018	Finland	Posio
Chaoborus posio **sp. n.**	NVO.ins2018-582		2018	Finland	Posio
Chaoborus sp.	MK281356	MK281356	2013	Japan	Fukuoka-shi
Chaoborus crystallinus	NVO.ins2018-22		2018	Finland	Inari
Chaoborus crystallinus	NVO.ins2018-600		2018	Finland	Inari
Chaoborus crystallinus	NVO.ins2018-39		2018	Finland	Inari
Chaoborus crystallinus	NVO.ins2018-601		2018	Finland	Kitee
Chaoborus crystallinus	NVO.ins2018-640		2018	Finland	Rovaniemi