

# Revision of Finnish Chaoboridae (Diptera, Culicomorpha)

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The 11 Finnish species of phantom midges (Chaoboridae) are revised. The study included nationwide field sampling, targeted investigations, DNA barcoding, examination of museum specimens and an extensive literature survey. The regional fauna now consists of all European taxa, with *Mochlonyx triangularis* Klink reported here for the first time from Fennoscandia. An illustrated key is provided to fourth instar larvae, pupae and adult males of all species. *Chaoborus flavicans* (Meigen) is noted as the only truly lake-dwelling species, whilst *Ch. albipes* (Johannsen) may also occasionally be present in ponds that contain fish populations, all other species are deemed inhabitants of fishless ponds. Among the pond-dwelling species, *Ch. obscuripes* (Van der Wulp) is dominant, both in terms of numbers of ponds and abundance. The number of chaoborid species in a given pond varies from one to six, with 1–2 taxa found universally. The number of *Chaoborus* species is most often from one to two and the presence of  $\geq 3$  *Chaoborus* species in a pond is quite rare. Reasons for the observed patterns are likely caused by niche differences, biotic interactions, depth and pond permanence. A total of 251 journal articles, reports or academic theses were found to include records on Finnish Chaoboridae. *Chaoborus flavicans* was the most often cited taxon (74 % of the studies), whilst the pond-dwelling species (20 %) were cited far more rarely.

Key words: Diptera, Culicomorpha, Chaoboridae, pond, lake, biodiversity, phantom midges, true flies, plankton, aquatic, predator, Finland

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## Introduction

Chaoboridae, or phantom midges, is a family of lower Diptera (Culicomorpha). A total of 53 species are known globally, of which 11 occur in

Europe (Borkent 1993, Borkent 2014, Salmela *et al.* 2021). Chaoboridae is the sister group of mosquitoes (Culicidae), but the lineages separated at least 200 MYA (Borkent 2012, da Silva *et al.* 2020) or perhaps even before (Lorenz *et al.* 2021).

Despite the rich fossil record with numerous genera, the modern fauna only comprises six extant genera (Borkent 2014). Adult chaoborids are similar to mosquitoes e.g. by wing venation and presence of scale-like setae on the wing margin. However, mouthparts of chaoborids are short and females are not blood-feeding. Notable synapomorphies of the Culicidae + Chaoboridae clade are the pupal terminal processes, i.e. articulated swimming paddles on the abdominal apex, and the precocious adult eyes present in the larval stage (Borkent 2012). European species belong to three genera, *Cryophila* Edwards, *Mochlonyx* Loew and *Chaoborus* Lichtenstein (Edwards 1930a, Borkent 2014).

Larvae and pupae of phantom midges are aquatic and have four larval instars (e.g. Parma 1971a,b). Full-grown, fourth instar larvae are small (6–9 mm) or large (10–22 mm) in size (Sæther 2002). The primitive condition for larval ecology, observed in genera such as *Eucoethra* Underwood (Nearctic), *Mochlonyx* (Holarctic) and *Cryophila* (Palearctic), is the occurrence in small water bodies and presence of metapneustic spiracles for aerial respiration (Cook 1956, Sæther 1992, Ogawa 2007). *Chaoborus*, the only truly lacustrine genus, is apneustic and immature stages obtain dissolved oxygen through their cuticle (Krogh 1911, Cook 1956). All Chaoborinae larvae possess two or three pairs of air sacs that are derived from the tracheal system. These air sacs, or bladders, help larvae to adjust their position in the water column (Teraguchi 1975). Antennae of larvae are prehensile and are adapted to grasp prey animals (Kruppert et al. 2019). Larvae of the genus *Chaoborus* are almost transparent, with only air sacs, gut contents and eyes being visible to the naked human eye (especially so among lake-dwelling species or populations, Sikorowa 1973, Berendonk et al. 2003), larvae of other European genera are translucent (*Mochlonyx*) or orange-brown in colour (*Cryophila*). Pupae, as noted above, possess terminal processes and conspicuous respiratory organs. Among *Chaoborus*, the function of the organs is to keep the pupa in an up-right position and provide stability during emergence (Parma 1971a), in other genera also respiration. Adult males are

characterised by plumose antennae (i.e. long and thick setosity) and distinct flagellomeres; superficially similar Chironomidae males have mostly merged flagellomeres (except subfamily Podonominae). Especially pupae of *Mochlonyx* and *Ochlerotatus* Lynch Arribalzaga (melt-water mosquitoes) are superficially similar to each other, but the long proboscis of the latter and longer respiratory organs of the former are good distinguishing characters.

Larvae of the European Chaoboridae are restricted to lentic waters and are the only truly planktonic insects. However, because the larvae are able to swim rapidly, they are also nektonic animals. *Cryophila* and *Mochlonyx* live mostly in ephemeral, snow-melt ponds, or small but permanent water bodies lacking fish. Larvae hatch from overwintered eggs and are relatively short-lived (a few weeks, but see *M. fuliginosus* (Felt) below, and Lake 1969). *Chaoborus* females lay eggs on the water surface and larvae hatch soon after oviposition (Berg 1937). Overwintering *Chaoborus* larvae are present in permanent ponds and lakes, and at least the larva of *Ch. flavicans* (Meigen) diapause during winter in pond or lake sediment (Rabette & Lair 1998). *Cryophila* and *Mochlonyx* are univoltine, but *Chaoborus* may have two or three generations in Central and northern Europe (Sikorowa 1973, Regmi et al. 2013).

The response of chaoborids to the presence of fish is species-specific (Berendonk et al. 2003). Among the European species, *Ch. flavicans* can be present in ponds and large, stratified lakes, but most other species are restricted to fishless ponds (e.g. Parma 1969a, Sikorowa 1973, Palm & Svensson 2010, Salmela et al. 2021). Pond species such as *Ch. crystallinus* (De Geer) and *Ch. obscuripes* (Van der Wulp) avoid fish-containing waters by chemical cues; females are able to discriminate the presence of fish due to kairomones, and thus lay their eggs in fishless ponds (Berendonk 1999). Furthermore, their larvae do not perform diel vertical migration (DVM) and are not capable of avoiding fish (Stenson 1978, Borkent 1981). Because *Chaoborus* larvae are preferably eaten by planktivorous fish (Stenson 1978, Horppila et al. 2004), lake-species have adaptations that reduce

predation. Larvae can detect fish kairomones and escape toward darkness or the lake or pond bottom if fish are added to a previously fishless habitat (Stenson 1981, Dawidowicz *et al.* 1990). Larvae and pupae perform DVM, that is, they bury themselves in the bottom sediment or are present in the hypoxic hypolimnion during daytime and ascend to the epilimnion after sunset (Berg 1937, Voss & Mumm 1999). By doing this larvae diminish the risk of being captured by high-oxygen demanding and visually feeding fish. Lake species are also generally more transparent and smaller in size than their pond-dwelling relatives (Berendonk *et al.* 2003). As an exception to the general rule, one European *Chaoborus* species, *Ch. nyblaei* (Zetterstedt) overwinter in the egg stage and can be present in ephemeral ponds (Hirvenoja 1961a, Borkent 1979, this study).

Chaoboridae larvae are voracious feeders of other invertebrates, especially Rotifera, Cladocera, Copepoda and Culicidae (Jenkins & Knight 1950, Monchadsky 1964, Sikorowa 1973). Due to their often great abundance, chaoborids have a notable impact on the food-webs of ponds and lakes (MacKay *et al.* 1990, Liljendahl-Nurminen *et al.* 2003). Larvae are gape-limited predators and some cladocerans use inducible morphological defences in order to reduce predation. That is, exposure to *Chaoborus* kairomones induces water fleas (*Daphnia*) to produce neck spines (e.g. Repka *et al.* 1995). In addition, water fleas may alter their life-history parameters such as reproductive size in the presence of *Chaoborus* (Repka *et al.* 1994). As noted above, *Chaoborus* are readily eaten by planktivorous fish, in Fennoscandia these include perch (*Perca fluviatilis*) (Rask 1984, Raitaniemi *et al.* 1988), smelt (*Osperus eperlanus*) (Horppila *et al.* 2004), white bream (*Blicca bjoerkna*) (Pekcan-Hekim & Horppila 2007) and cisco (*Coregonus albula*) (Viljanen 1983), and they may be even eaten by piscivorous fish (pikeperch, *Sander lucioperca*) if suitable fish prey is lacking (Vinni *et al.* 2009).

In addition to food-webs of lakes and ponds, Chaoboridae are also important in environmental monitoring and biodiversity assessment. *Chaoborus flavicans* is often seen as an indicator of eutrophication, because it benefits

from decreased Secchi-depth or oxygen levels (Tuunainen *et al.* 1972, Raunio *et al.* 2007). On the other hand, chaoborids can be used as indicators of the presence of fish (von Ende 1979, Palm & Svensson 2010), and even climate change over time (Lindholm *et al.* 2016), as larval mouthparts (mandibles) and pupal respiratory organs are preserved in lake sediments and these subfossil remains are often included in paleolimnological studies (e.g. Uutala 1990, Luoto & Nevalainen 2009, Ursenbacher *et al.* 2020).

The taxonomy of European phantom midges is relatively well known. Descriptions, keys and illustrations of larvae, especially of *Chaoborus* species have been published in numerous papers (e.g. Martini 1928, 1929, Peus 1934, Monchadsky 1936, Berg 1937, Hirvenoja 1961a, Parma 1969a, Sæther 1970, 1972, Sikorowa 1973, Nilssen 1974, Balvay 1977, Klink 1982). The most recent taxonomic treatment of European species was provided by Sæther (2002, his 1997a and 1997b publications being essentially the same). Before 2020, the number of known species was rather low (9 spp), with the most recent new species described in 1982 (Klink 1982), and before that in 1928 (Martini 1928). However, one new *Chaoborus* species was freshly described from Finland and another was reported for the first time from the Palaearctic Region (Salmela *et al.* 2021). A few species such as *Ch. flavicans* and *Ch. crystallinus* are much studied and well known (e.g. Akerhurst 1922, Berg 1937, Parma 1971a,b, Janz *et al.* 2016), whilst northern species such as *Cr. lapponica* (Martini) and *Ch. nyblaei* are very poorly-known and seldom reported in scientific journals. Another obscure species is *M. triangularis* Klink, hitherto known from the Netherlands alone (Klink 1982, Kuper & Verberk 2011), and whose larval description has been based on a few uncertain specimens only (Sæther 1997a, 2002).

Finland is located in NW Europe, is part of Fennoscandia, and covers over 338 000 km<sup>2</sup> of land area. It is the eight-largest European country, spanning from the hemiboreal (N60°) to the subarctic ecoregion (N70°), and from the southernmost point to the northernmost is 1160 km. Finland's climate is generally cold,

but winter temperatures are much milder than in continental areas of the same latitudes, such as Siberia (Tikkanen 2006a). The mean annual temperature in the hemiboreal zone is about +4–5 C°, and –1–3 C° in the north boreal and subarctic zones (Tikkanen 2006a). Finland's terrain is mostly below 200 m asl., and the highest elevations (>1000 m asl) are present in NW Lapland (Tikkanen 2006b). Most of the country is dominated by boreal forest, i.e. conifers with scattered deciduous trees. Agricultural land is most common in southern and western parts of Finland. In addition to forests, many lakes and mires are prevalent in the landscape. No less than 187 000 lakes  $\geq 0.5$  ha in area being present (Raatikainen & Kuusisto 1990), with the number of smaller ponds innumerable. These lakes and ponds were formed during the last 10 000 years, following the melting of the glacial sheet, either as emergence of their basins below the ice sheet or through isolation from the Baltic basin (Tikkanen 2006c). Finnish lakes are mostly brown in colour, due to humic substances derived from podzolic drainage areas and peatlands. Clay-turbid lakes are however present in southern Finland, whereas clearwater lakes and ponds are more sporadic in occurrence. Calcareous waters are rare due to dominance of acidic bedrock, and the pH of the most small lakes is below seven (Forsius *et al.* 1990).

Due to the high number and natural variation of suitable habitats, i.e. ponds and lakes, and species richness of phantom midges (all European species present), Finland is an optimal region to study the ecology, occurrence and distribution of Chaoboridae. The aim of the present study is to make a synthesis of the Finnish fauna and provide tools for the identification of larvae, pupae and adults. Despite the regional approach, identification keys should be applicable on a European/Palaeartic scale. It is hoped that the present revision inspires entomologists and limnologists to study chaoborids and further increase the knowledge on the ecology and ranges of the species.

## Material and methods

The project “Revision of the Finnish Chaoboridae” was started by JS in 2017. The aim was to i) get an overall picture of the regional fauna, ii) clarify the distribution and ecology of each species, with poorly known taxa such as *Ch. nyblaei* and *Cr. lapponica* emphasized, and iii) provide an identification key to larvae, pupae and adults of the Finnish species. Even before 2017, LP and JS had identified chaoborids from aquatic and Malaise trap samples as a bycatch, but during 2017–2020 fieldwork by JS was focused more intently upon collecting phantom midges.

Most of the samples were collected with a pond-net (0.5 mm mesh size) from permanent and seasonally dry ponds (Figure 1); larger lentic waters were mostly left aside, because only one Palaeartic species (*Ch. flavicans*) is present in large, thermally stratified lakes. However, fresh specimens of that species from lake sediment samples were received from colleagues. In addition, plankton net (0.25 mm mesh size), aerial sweep net and aquatic emergence traps (eclector traps) were used in the fieldwork. Immature stages were stored in 70–80 % ethanol or were kept alive, brought to the laboratory and were reared to adults. Larvae or pupa were reared individually in 200 ml jars. Larval skins and pupal exuvia were collected after pupation and emergence, respectively, and were stored in ethanol or were slide-mounted on Euparal. Most of the adults were stored in ethanol, but a few were pinned. Most of the material collected in this project is deposited in the Regional Museum of Lapland, Rovaniemi (LMM), and Forssa Natural History Museum, Forssa (FLHM). All data, including species and metadata (locality, habitat, date, sampling method) from the identifications and voucher specimens, are available online from [www.laji.fi](http://www.laji.fi). The collections in LMM and FLHM hold 2067 and 290 samples, respectively.

Besides large-scale, nationwide sampling, chaoborids were systematically studied in geographically restricted areas in two MSc theses, by EL (Laine 2021) and JA (Ahola 2021) (University of Jyväskylä). The work of EL (2018) took place in eastern Lapland (Savukoski, Salla,





**FIGURE 1.** Pond habitats of Finnish phantom midges (Chaoboridae). a) Utsjoki, Látnabuolža (69.60, 28.29, 177 m asl, 0.49 ha, subarctic zone), rather large and deep pond, habitat of *Ch. obscuripes* and *Ch. posio*. b) Savukoski, Rouvoivanselkä (67.83, 29.45, 245 m asl, 0.075 ha, north boreal zone), habitat of *Cr. lapponica*, *M. triangularis*, *M. velutinus*, *Ch. albipes*, *Ch. nyblaei* and occasionally of *Ch. obscuripes*. c) Salla, Värriö, Vedenjakajanselkä (67.70, 29.66, 405 m asl, 0.18 ha [early summer water level], north boreal zone), seasonally dry pond, dominated by the grass *Nardus stricta*, habitat of meltwater mosquitoes and *M. velutinus*. d) Posio, Peuralamminharjut (66.27, 27.61, 310 m asl, 0.015 ha, north boreal zone), permanent, ca. 1 m deep flark of an aapamire, habitat of *Ch. obscuripes*. e) Somero, Rantasensuo (60.49, 23.65, 95 m asl, 0.001 ha, south boreal zone), a small, permanent bog pool, perhaps slightly spring-fed, possibly excavated, habitat of *Ch. crystallinus*, *Ch. pallidus* and *Ch. obscuripes*. f) Sipoo, Jöusjärvi (60.33, 25.18, 37 m asl, 0.27 ha, at the border of hemiboreal and south boreal zone), permanent and deep, humic pond, inhabited by *Ch. albipes* and *Ch. obscuripes*.

30 ponds) and JA (2020) in Hossa National Park and surrounding area (Suomussalmi, 19 ponds). Numerous chaoborid samples were also collected and identified by OH, especially from SW Häme (Forssa, Jokioinen, Tammela, n=119), including rearing of immature stages. Additional samples were provided by several of our colleagues and friends; this material was sent to JS for identification and the collectors are named in the acknowledgments. There were a total number of 401 collecting sites visited or identified by us during 2017–2020. The chaoborid collection (148 pinned or slidemounted specimens, a few in ethanol, which are not yet databased) at the Finnish Museum of Natural History, Luomus, University of Helsinki (MZH), was studied by JS in 2018. Besides the chaoborids deposited at the LMM, FLHM and MZH, no other curated collections in Finland are known to us.

In order to assess the diversity and coexistence of phantom midges, a dataset consisting of 305 chaoborid sampling sites was compiled. The material was collected during 2017–2020 as larval samples, mainly from ponds, by JS, OH, EL and JA. The sampled waterbodies spanned from hemiboreal to the subarctic region, and the samples were taken between April and September. It is now assumed that most of these sites have been comprehensively sampled, that is, most of the chaoborid taxa, at least *Chaoborus* spp, of a given waterbody should have been detected. The dataset is therefore suitable to draw robust conclusions on species richness and rarity of the fauna, though it should be noted as a caveat that is possible that some species may have been missed.

All pertinent scientific literature on Finnish chaoborids was searched. All peer-reviewed titles, other journals, PhD and MSc theses and some reports that are electronically available were included. A reference was included if a phantom midge taxon (family, genus, species) was mentioned at least in the results or it was treated in the discussion of review type of papers. Google Scholar was the main instrument used, using search terms “Chaoboridae, Chaoborus, Corethra, Sayomyia, Mochlonyx, Cryophila, Finland”. In the search of older literature the Helda database (University of Helsinki, <https://helda.helsinki.fi/>)

was used. The literature search covered at least most of the peer-reviewed titles up to 31.8.2020 and also Salmela et al. (2021) that was a submitted manuscript while the writing of the present paper took place. Due to the behaviour, abundance and commonness of *Ch. flavicans*, it is regularly collected in daytime profundal zone samples in lake surveys (e.g. Paasivirta 1989, Nurmi 1998). Thus the species is also copiously mentioned in limnological literature, in peer-reviewed journals (e.g. Koskenniemi 1992, Tolonen et al. 2001, Jyväsjärvi et al. 2012) and in so-called grey literature (reports and MSc theses, e.g. Malinen & Vinni 2014, Väisänen 2007), and most often there is just a mention of the presence and abundance of the species in a given waterbody. We acknowledge that the literature search is not complete regarding *Ch. flavicans*, because not all publications, for example of Water Protections Districts, were examined, and we may have missed some pre-2000's MSc theses that are not digitized. However, the goal here was to examine how seldom other species than *Ch. flavicans* are covered in the Finnish entomological, ecological or especially limnological literature. The literature records were tabulated according to the publication year, the chaoborid species involved and the subject of the study (e.g. limnology, taxonomy, faunistics, physiology, ecology) (Table 2).

Distribution maps were gathered for all species. In addition to our own observations, the data were extracted from the [www.laji.fi](http://www.laji.fi) database, which includes e.g. all POHJE-records (macroinvertebrates from environmental monitoring sites of lakes and rivers). Also reliable, species level records from literature were added to the maps. The maps were produced by using the Simplemappr program and were finally edited in Photoshop. In the species section, the original description of the taxon and relevant taxonomic works in the European/Nordic perspective are given. Hence, not all synonymous names are given, and Borkent (2014) should be consulted for these.

Specimens were studied under 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, as well as the Optika SZP-10 CMO compound microscope with an Optika 5Mb camera were used in imaging of the specimens. Layer photos were combined with the Combine ZP software and the photos were finally edited with Adobe Lightroom and/or Photoshop softwares. Morphological terminology follows Cumming and Wood (2017, adults), Ogawa (2007, larvae), Borkent (2012, pupae) or is explained in the figures. As an exception ‘labral blade’ is used instead of head capsule seta 3. If not otherwise stated, measurements are given in  $\mu\text{m}$ . Epandria of *M. triangularis* and *M. velutinus* (Figure 15 d,f) were drawn by Tanja Männistö (Rovaniemi) using the compound microscope mentioned above.

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 114 phantom midge specimens. 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, Canada, 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 two public projects (FICFL, CHAOF) in BOLD.

## Results and discussion

### *Faunistics and biodiversity*

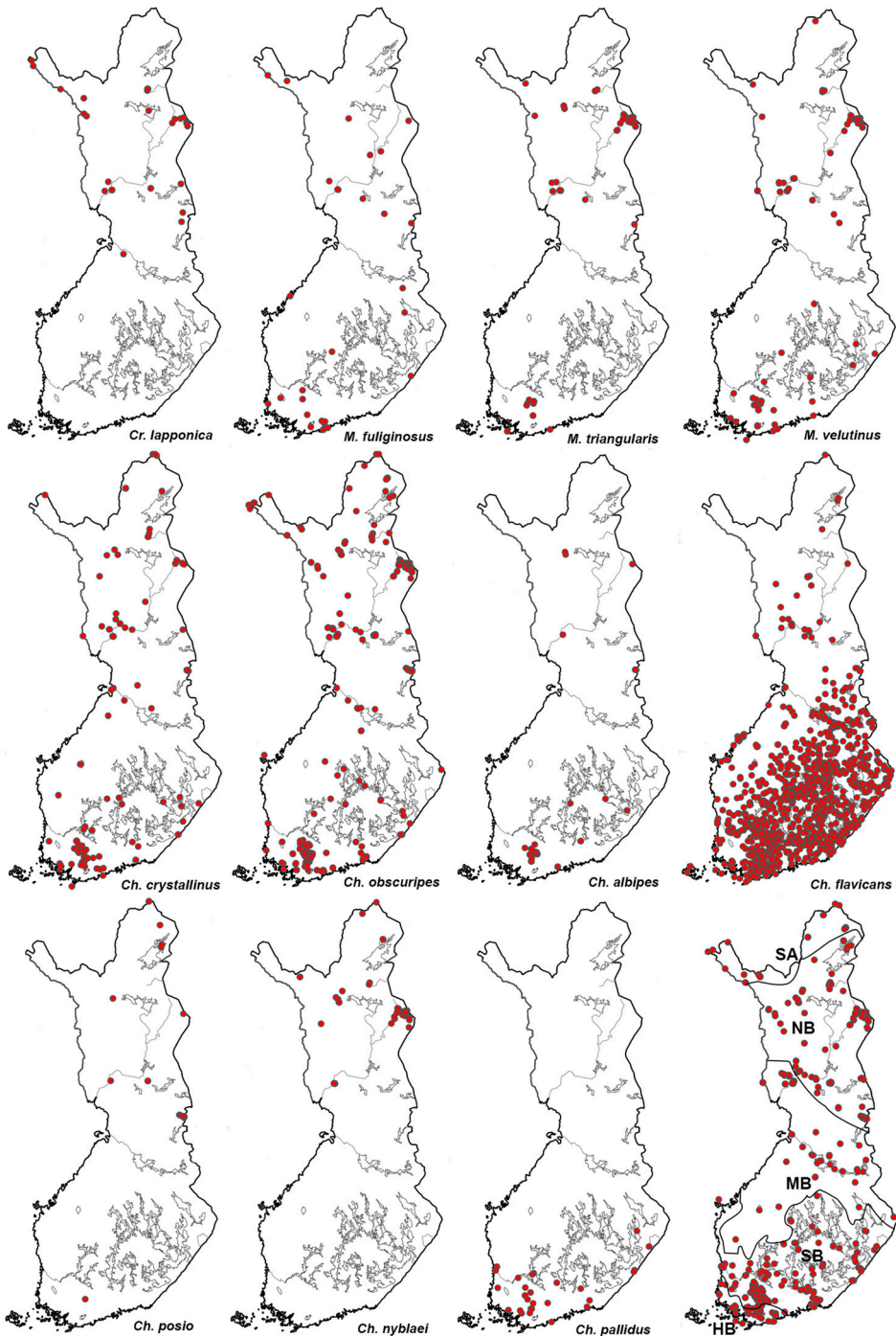
The Finnish fauna was found to consist of 11 species (Table 1). During the project three new species to the regional fauna were discovered: *Ch. albipes* (Johannsen), *Ch. posio* Salmela (Salmela *et al.* 2021), and *Mochlonyx triangularis* (which is here reported for the first time from Fennoscandia). *Chaoborus flavicans* is the only lacustrine species, i.e. being common in thermally stratified large lakes. All other species were found to be confined to fishless ponds, either permanent or temporary in nature. However, *Ch. albipes* was on a single occasion observed from a pond inhabited by perch, but it is not yet known whether this species

commonly coexists with fish (see below for details). *Cryophila lapponica*, *M. triangularis*, *M. velutinus* (Ruthe) and *Ch. nyblaei* were found to be present in both seasonally dry and permanent (often small) ponds, and *M. fuliginosus* was found to inhabit very small pools, such as bog pools and springs.

Six chaoborid species were widespread, that is, their ranges cover all ecoregions (from hemiboreal to the subarctic zone, Table 1). Both middle and north boreal zones harbour 10 species, regional species richness was slightly lower in the hemiboreal (7 spp.), south boreal (9 spp.) and subarctic zone (9 spp.). *Cryophila lapponica* and *Ch. nyblaei* were found to be northern species, being present from the northern parts of the middle boreal zone to the subarctic (Figure 2). *Chaoborus posio* was mostly observed from the middle boreal – subarctic area, but a disjunct population in SW Finland was identified (Figure 2); it is yet to be clarified if the species is more widely present in the south boreal zone. *Chaoborus albipes* appears to be absent from the hemiboreal and subarctic zones, but it seems to be locally common in the south boreal zone, and it may become rare toward northernmost Finland. It should be noted that its absence or rarity may in fact be due to imperfect sampling. *Chaoborus pallidus* (Fabricius) (Figure 2) is the only southern species (hemiboreal – south boreal) among the Finnish chaoborids.

On the European scale, it seems that species richness of phantom midges is the highest in Fennoscandia, especially in the middle and north boreal zones, where all but one (*Ch. pallidus*) of the species occur. About half (6 spp.) of the European species are widespread, i.e. their ranges cover most of the continent. Outside of this more broadly distributed taxa are *Cr. lapponica*, *M. triangularis*, *Ch. albipes*, *Ch. posio* and *Ch. nyblaei*, which are mostly northern species in Europe. However, we predict that at least *M. triangularis* and *Ch. albipes* may prove out to be more widespread than currently known, as both taxa may have been overlooked due to their similarity of closely related species (*M. velutinus* and *Ch. flavicans*, respectively).

In the dataset of 305 generally smaller lentic waterbodies all 11 species were encountered.



**FIGURE 2.** Distribution maps of Finnish species of Chaoboridae (*Cryophila lapponica* – *Chaoborus pallidus*). The map in the lower right corner displays all sites sampled or specimens identified by the authors during 2017–2020. HB=hemiboreal, SB=south boreal, MB=middle boreal, NB=north boreal, SA=subarctic ecoregion.

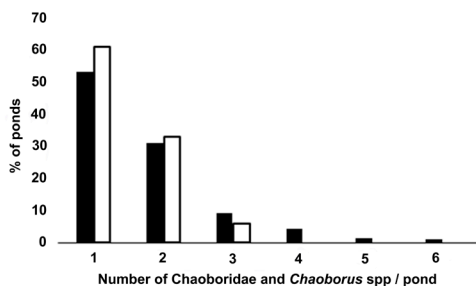
**TABLE 1.** Finnish species of Chaoboridae and their presence in ecoregions. HB=hemiboreal, SB=south boreal, MB=middle boreal, NB=north boreal, SA=subarctic.

	HB	SB	MB	NB	SA
<i>Cr. lapponica</i>			x	x	x
<i>M. fuliginosus</i>	x	x	x	x	x
<i>M. triangularis</i>	x	x	x	x	x
<i>M. velutinus</i>	x	x	x	x	x
<i>Ch. crystallinus</i>	x	x	x	x	x
<i>Ch. obscuripes</i>	x	x	x	x	x
<i>Ch. albipes</i>		x	x	x	
<i>Ch. flavicans</i>	x	x	x	x	x
<i>Ch. posio</i>		x	x	x	x
<i>Ch. nyblaei</i>			x	x	x
<i>Ch. pallidus</i>	x	x			
<b>number of spp</b>	<b>7</b>	<b>9</b>	<b>10</b>	<b>10</b>	<b>9</b>

*Chaoborus obscuripes* was the most common species (62 % of waterbodies), followed by *M. triangularis* (20 %), *M. velutinus* (20 %) and *Ch. crystallinus* (19 %). *Chaoborus pallidus* (1.6 %) and *M. fuliginosus* (3.6 %) were the most infrequently collected species. The number of species present per site varied from one to six with 53 % of the sites were occupied by a single species and 47 % consisted of two or more chaoborid taxa (Figure 3). Interestingly the most species rich sites were not the largest nor the most permanent. In contrast, the seven sites where five or six species were observed, are either small or shallow, and surprisingly included seasonally dry ponds prone to having pond sediments frozen during the winter. It is possible that moderate disturbance (varying water level and wintertime freezing) decimate the abundance of *Ch. obscuripes* especially, which is the largest species to overwinter in a larval stage. There is indirect evidence that *Ch. obscuripes* is competitively superior and it may drive congeneric species locally extinct (Wissel & Benndorf 1998). It is likely that *Ch. obscuripes* is ecologically similar to its putative Nearctic sister species *Ch. americanus* (Johannsen) that is a dominant species in North American fishless ponds (von Ende 1979, Borkent 1981, Garcia & Mittelbach 2008).

Among the dataset of 305 ponds, *Chaoborus* species were present in 254 sites, and of these 154 (61 %) were occupied by a single species (*Ch. obscuripes* 103, *Ch. crystallinus* 24, *Ch. nyblaei* 15, *Ch. flavicans* 10 and *Ch. albipes* 2 sites) (Figure 3). We observed no pond inhabited by more than three *Chaoborus* species, and a pond with four *Chaoborus* has only been observed once in Finland (Korkeamäki *et al.* 2017). This site (Kouvola, Konttisuo, south boreal zone), a small excavated lentic waterbody next to a bog, was revisited by JS in 2019, resulting in a tally of three species. Two (n=84, 33%) or three (n=15, 6%) species *Chaoborus* assemblages consisted of ten and nine combinations, respectively. Among the two-species communities, *Ch. obscuripes* – *Ch. nyblaei* (20), *Ch. obscuripes* – *Ch. crystallinus* (18) and *Ch. obscuripes* – *Ch. albipes* (18) were the most common combinations. Among the three-species assemblages, a combination of *Ch. obscuripes*, *Ch. flavicans* and *Ch. posio* was observed three times, other combinations once or twice. Among the geographically sympatric species, combinations of *Ch. albipes* with *Ch. flavicans* (1), *Ch. posio* (2) or *Ch. crystallinus* (2) were rare. In addition, coexistence of *Ch. crystallinus* with any other species except *Ch. obscuripes* was seldom observed. The ponds with





**FIGURE 3.** Species richness of Chaoboridae (black bars) and *Chaoborus* (white bars) in ponds and pools. Number of observed species (1 – 6) is given in the x-axis and percentage of each richness class in the y-axis. The total number of sampled waterbodies is 305.

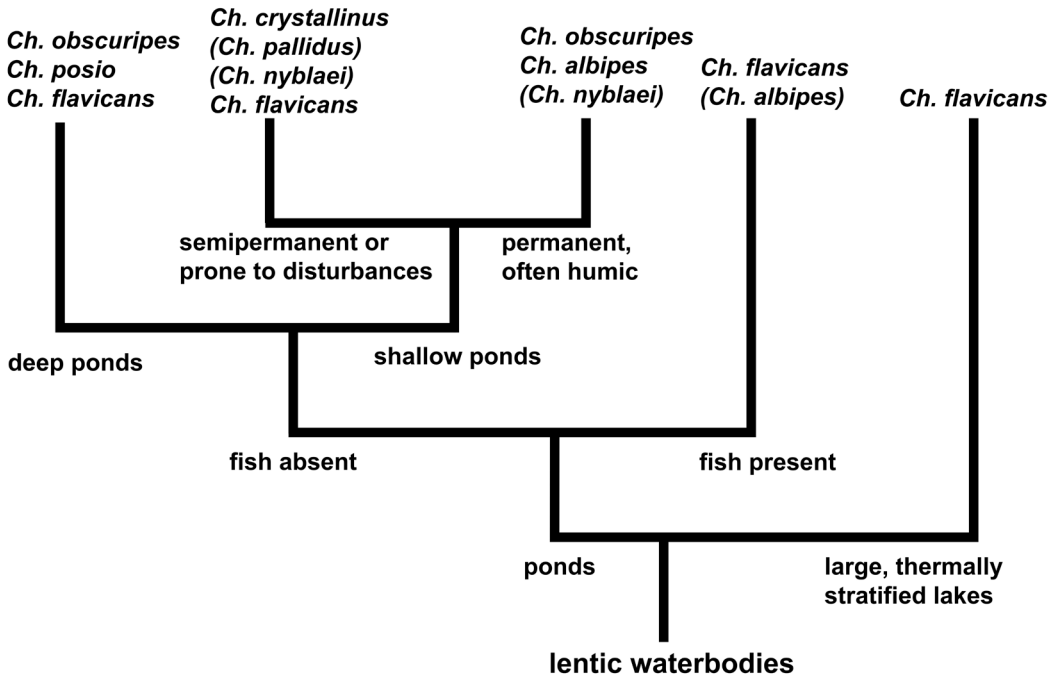
three *Chaoborus* species were either rather small and shallow or deep (3–6 m) permanent ponds. The depth may provide refuge for species such as *Ch. flavicans* and *Ch. posio*. For example, out of the 28 lakes examined by Hongve (1975), *Ch. obscuripes* and *Ch. flavicans* coexisted only in two. Both lakes were deep (5.5–9.5 m) and the larvae of these two species were seemingly spatially segregated (Hongve 1975 fig. 2). Because *Chaoborus* spp. mostly occupy different niches than *Mochlonyx* or *Cryophila*, their coexistence patterns are not discussed here.

As noted by Berendonk and Bonsal (2002), *Chaoborus* assemblages of ponds display a dynamic pattern of local extinction and recolonization. This phenomenon was also observed by us, e.g. in a small and isolated pond in NE Lapland (Nimetönselkä), where *Ch. obscuripes* was absent in 2018 but present in 2020. In some shallow ponds *Ch. obscuripes* was presumed not able to overwinter, because larvae were absent from samples taken in spring. However, small larvae were often observed in midsummer, implying the oviposition of females originated from neighbouring populations. Such ponds are clearly sink habitats (e.g. Johnson 2004) for this species. It should also be mentioned that fishless ponds totally lacking chaoborids were very seldom encountered. For example, in the well-sampled datasets of EL and JA, chaoborid-free ponds were only found singularly for each

recorder (i.e. 3–5 % of the studied sites).

Our results of species coexistence are in great conflict with the hypothesis by Stahl (1966), that competitive exclusion does not occur in natural populations of *Chaoborus* and hence all sympatric (sharing the same geographic area) species should be present in all suitable waterbodies. Furthermore, the lack of species from a pond or lake should only indicate poor sampling effort and all species should have similar niches. However, Stahl accepted that *Ch. flavicans* is the only lake-dwelling taxon in Europe, because hydrostatic organs (air sacs) of other species do not withstand the pressure of deep water. This hypothesis was elaborated by a theory where niche differences between species are constant, and sympatric species may coexist only if they are not phylogenetically related (sister species, Borkent 1981). For example, *Ch. americanus* and *Ch. obscuripes* are (putative) sister species that have similar niches, but the species are allopatric; *Ch. trivittatus* (Loew) and *Ch. cooki* Sæther are closely related, sympatric species, but they have different niches (Borkent 1979, 1981). Our observations from Finland are generally in agreement with Borkent's hypothesis, except that there are three geographically sympatric pond-dwelling species that are most likely closely related (*Ch. flavicans*, *Ch. albipes* and *Ch. posio*, see Salmela et al. 2021). However, these three species do not frequently coexist and it seems that they have niche differences (see below). In most of the Finnish territory, six *Chaoborus* species have overlapping ranges, i.e. they are sympatric. Despite geographic sympatry of so many species, an occurrence of  $\geq 3$  *Chaoborus* in a given pond is a rather rare phenomenon. Clearly, more studies are needed to explain the observed patterns. In addition to niche differences between taxa, we assume that a combination of biotic interactions (presence of fish, intraguild predation), disturbance, and depth of the pond best explain the composition of the local *Chaoborus* community in a given ecoregion (Figure 4).

As discussed above, the number of coexisting *Chaoborus* species in ponds may vary. For example, Arranz et al. (2015) collected *Chaoborus* from 50 lentic waters in the Iberian Peninsula.



**FIGURE 4.** Schematic presentation of habitat preferences of Finnish *Chaoborus* in lakes and ponds. Species in parentheses refer to restricted distribution (i.e. absent from southern or northern parts of the country) or limited knowledge (*Ch. albipes* hitherto known from one pond inhabited by fish).

Among the three species present, 90 % of the sites were occupied by one species, and coexistence of all three species was rare (2 %). In the Netherlands, Parma (1969a) represented data from a total of 38 lentic waterbodies, varying in size. According to him, “coexistence of 2 or 3 is the rule rather than the exception” (Parma 1969a, p. 21). However, if his data (table 12, pp. 38–39) are recalculated, it is clear that the presence of one species is the most common occasion (74 %), and the coexistence of two (18 %) or three (8 %) species is much less frequent. Citing anecdotal sources and his own experiments, Parma (1969a) states that the pond-dwelling taxa (*Ch. crystallinus*, *Ch. obscuripes* and *Ch. pallidus*) display bottom burrowing behaviour as larvae and pupae. It thus possible that some of the ponds and pools we sampled evaded capture during the net sampling due larvae being confined within pond sediment. However, the pond-dwelling species are regularly noted as non-migratory (absence of vertical migration in the

water column) and limnetic, not bottom-dwelling (Hongve 1975, Borkent 1981).

#### Literature survey

Our final list of references included 251 titles of journal articles, reviews, MSc and PhD theses, other articles, faunistic notes and reports (Table 2). The earliest publication we found was by Levander (1900), which treated the planktonic fauna and flora of Finnish inland waters. In the early 1900’s, the genus-group name *Corethra* was used for both *Chaoborus* and *Mochlonyx* (e.g. Luther 1902, Hellevaara 1916). It should be noted that Luther (1902) already observed that *Chaoborus* larvae can be present at great depths, thus preceding Juday (1903) and Wesenberg-Lund (1904, 1914) who has been claimed as the first authors to notice that chaoborids may also occur outside ponds and surface waters (Bardenfleth & Ege 1916). The first Finnish check-list of phantom

**TABLE 2.** A list of references on the studies on Finnish Chaoboridae, 1900–2021. Species names are abbreviations (e.g. *Ch. flav*=*Chaoborus flavicans*). The list is arranged in chronological order.

Author	Contents	Category
Levander 1900	Plankton fauna and flora of lakes, <i>Chaoborus</i> , (as <i>Corethra</i> )	faunistics
Luther 1902	Fauna of the Lake Lohjanjärvi, <i>Ch. flav</i> (as <i>Corethra</i> )	faunistics
Schneider 1902	Food item of <i>Osmerus eperlanus</i> , <i>Ch. flav</i> (as <i>Corethra</i> )	fish biology
Levander 1906	Lake productivity, lake biota, <i>Ch. flav</i> (as <i>Corethra</i> )	limnology
Wahlberg 1914	Lake biota, plankton, <i>Ch. flav</i> (as <i>Corethra</i> )	limnology
Hellevaara 1916	Food web, invertebrates as fish food, <i>Mochlonyx</i> and <i>Chaoborus</i> (both as <i>Corethra</i> )	review
Järnefelt 1916	Biota of a fountain, <i>Chaoborus</i> (as <i>Sayomyia</i> )	faunistics
Järnefelt 1917	food item of <i>Perca fluviatilis</i> , <i>Chaoborus</i> (as <i>Sayomyia</i> )	fish biology
Frey 1921	list of Finnish species, <i>Mo. velu</i> (as <i>culiciformis</i> ), <i>Ch. flav</i> (as <i>plumicornis</i> ), <i>Ch. crys</i> (as <i>fusca</i> ) (3 spp)	faunistics
Järnefelt 1921	limnology of a lake, <i>Ch. flav</i> (as <i>Sayomyia</i> ) as food of <i>Gymnocephalus cernua</i>	limnology, fish biology
Järnefelt 1922	lake typification, <i>Ch. flav</i> (as <i>Sayomyia</i> )	review
Levander 1922	List of Finnish species (3 spp)	faunistics
Järnefelt 1923	Fauna of small ponds, <i>Chaoborus</i> (as <i>Sayomyia</i> )	limnology
Valle 1921	lake typification, <i>Ch. flav</i> (as <i>Corethra</i> )	review
Valle 1923	Notes on lake biota in Evo area, S FIN, <i>Ch. flav</i> (as <i>Corethra</i> )	limnology
Valle 1927a	Lake zoobenthos, <i>Ch. flav</i> (as <i>Corethra plumicornis</i> )	limnology
Valle 1927b	ecology of <i>Ch. flav</i> (as <i>Corethra plumicornis</i> )	review
Valle 1928	Lake zoobenthos, <i>Ch. flav</i> (as <i>Corethra plumicornis</i> )	limnology
Martini 1928	description of <i>Cr. lapp</i> (as <i>Mochlonyx</i> ), faunistics, 4 spp in Finland	taxonomy
Järnefelt 1929	Lake zoobenthos and plankton, <i>Ch. flav</i> (as <i>Sayomyia</i> )	limnology
Valle 1930	DVM, <i>Ch. flav</i> (as <i>Co. plumicornis</i> ); studied lakes belong to modern Russia	limnology
Storå 1935	<i>M. fuli</i> (as <i>M. velu</i> ), collection data, faunistic records	faunistics
Hellén 1936	<i>M. fuli</i> (as <i>M. velu</i> ) (citing records from Kuusamo and Pietarsaari, see Storå 1935)	faunistics
Järnefelt 1936a	Lake studies, <i>Ch. flav</i> (as <i>Sayomyia</i> )	limnology
Järnefelt 1936b	Lake studies, <i>Ch. flav</i> (as <i>Sayomyia</i> )	limnology
Valle 1936	Lake studies, <i>Ch. flav</i> (as <i>Co. plumicornis</i> )	limnology
Frey et al. 1941	list of Finnish species (4 spp)	faunistics
Frey 1946	ecology of larvae, <i>Mochlonyx</i> , <i>Chaoborus</i> (as <i>Corethra</i> )	review
Tiensuu 1951	<i>Ch. pall</i> and <i>Ch. flav</i> from Finland	faunistics
Frey 1953	<i>M. fuli</i> (as <i>M. martini</i> ), specimens donated to MZH	faunistics
Järnefelt 1953	Bottom fauna on lakes, typification, <i>Ch. flav</i> (as <i>Chaoborus</i> )	limnology
Perttunen & Lagerspetz 1956a	larval physiology of <i>Ch. crys</i> (as <i>Co. plumicornis</i> )	physiology
Perttunen & Lagerspetz 1956b	larval physiology of <i>Ch. crys</i> (as <i>Co. plumicornis</i> )	physiology

TABLE 2. *continued*

Hirvenoja 1960	faunistics, ecology, phenology, <i>C. flav.</i> , <i>C. cryst.</i> , <i>C. obsc</i>	ecology, phenology
Krogerus 1960	mire-dwelling arthropods, <i>Chaoborus</i> (as <i>Corethra plumicornis</i> ), <i>M. velu</i> (as <i>M. culiciformis</i> ), <i>M. fuli</i> (as <i>M. velutinus</i> )	faunistics
Hirvenoja 1961a	redescription of <i>Ch. nybl</i> , key to Finnish species	taxonomy, faunistics
Hirvenoja 1961b	<i>M. velu</i> (as <i>Co. culiciformis</i> ), along mosquito survey	ecology, phenology
Hirvenoja 1962	<i>M. velu</i> (as <i>Co. culiciformis</i> ), along mosquito survey	ecology, phenology
Lagerspetz & Perttunen 1962	adult physiology of <i>Ch. crystallinus</i> (as <i>Co. plumicornis</i> )	physiology
Hirvenoja 1963	Further records of <i>Ch. pall</i> from Finland	faunistics
Kostama 1964	<i>M. velu</i> (as <i>Co. culiciformis</i> ), along mosquito survey	faunistics
Hirvenoja 1965	Emergence of <i>Ch. cryst</i> and <i>Ch. flav</i>	ecology, phenology
Bagge & Tulkki 1967	Occurrence of <i>Ch. flav</i> in a non-saline, recently isolated lake	limnology
Nuorteva 1967	Larval cannibalism, a review of Monchadsky 1959	review
Bagge & Jumppanen 1968	Bottom fauna of a large lake, pollution, <i>Ch. flav</i>	limnology
Kolehmainen <i>et al.</i> 1968	137Cs bioaccumulation, <i>Chaoborus</i> (not seen)	ecotoxicology
Alhonen & Haavisto 1969	Lake sediment stratigraphy, <i>Ch. flav</i> (as <i>Chaoborus</i> )	paleolimnology
Tuunainen 1970	Introduced <i>Salmo trutta</i> and <i>Oncorhynchus mykiss</i> in small lakes, <i>Chaoborus</i> as a food item	limnology
Sauvonsaari 1971	Food item of <i>Barbatula barbatula</i> , <i>Chaoborus</i>	fish biology
Särkkä & Paasivirta 1972	Sediment fauna of a lake, <i>Ch. flav</i>	limnology
Tuunainen <i>et al.</i> 1972	Fauna of a lake, eutrophication, <i>Ch. flav</i>	limnology
Jumppanen 1976	Effects of waste waters, <i>Ch. flav</i> (not seen)	limnology
Salonen <i>et al.</i> 1976	Energy and organic carbon content of aquatic invertebrates, <i>Ch. flav</i>	limnology
Hakkari 1978	Zooplankton as fish food (not seen), <i>Ch. flav</i>	fish biology
Honkasalo 1978	DVM, spatial distribution, phenology, <i>Ch. flav</i> , a small meromictic lake	ecology
Häkkilä <i>et al.</i> 1978	Bottom fauna of a brackish estuary, <i>Ch. flav</i> .	limnology
Lagerspetz 1978	Biography of August Krogh, <i>Chaoborus</i> (as <i>Corethra</i> ) physiology, review	review
Paasivirta & Särkkä 1978	Sediment fauna in relation to pollution, <i>Ch. flav</i>	limnology
Salonen & Sarvala 1978	Estimation of inorganic carbon fraction of total carbon in aquatic invertebrates, <i>Ch. flav</i>	limnology
Borkent 1979	redescription of <i>Ch. nybl</i> , Finnish material studied	taxonomy
Meriläinen 1979	Bottom fauna of 3 lakes, <i>Ch. flav</i>	limnology
Särkkä 1979	Mercury and chlorinated hydrocarbons in zoobenthos, <i>Ch. flav</i>	ecotoxicology
Eloranta 1980	Zooplankton of a polluted water course, <i>Ch. flav</i>	limnology
Hackman 1980	list of Finnish species (8 spp), <i>Mochl</i> spp (2) with “?”	faunistics
Yli-Karjanmaa 1980	Limnology of a polluted lake, <i>Ch. flav</i> (as <i>Chaoborus</i> )	limnology

TABLE 2. continued

Paasivirta & Koskenniemi 1980	Bottom fauna of two reservoirs, <i>Ch. flav</i>	limnology
Kansanen 1981	Bottom fauna of a lake, pollution, <i>Ch. flav</i>	limnology
Kansanen & Aho 1981	Bottom fauna of a lake, <i>Ch. flav</i>	limnology
Bagge & Hakkari 1982	Food of fish in deep lakes basins of a lake, <i>Ch. flav</i>	fish biology
Paasivirta 1982	Fauna of small forest lakes, <i>Ch. flav</i> , <i>Ch. obsc</i>	ecology, faunistics
Paasivirta 1983	Fauna of small forest lakes, <i>Ch. flav</i> , <i>Ch. obsc</i>	ecology, faunistics
Viljanen 1983	Food item of <i>Coregonus albula</i> , <i>Ch. flav</i>	fish biology
Meriläinen 1984	Fauna of an estuary in the Bothnian Bay, <i>Ch. flav</i>	limnology
Rask 1984	Diet of <i>Perca fluviatilis</i> in a small, humic forest lake, perhaps <i>Ch. flav</i> (as <i>Chaoborus</i> )	fish biology
Kansanen 1985	Bottom sediment fauna of a lake, <i>Ch. flav</i>	limnology
Ranta & Nuutinen 1985	Diel vertical migration of <i>Daphnia</i> spp in rock pools, <i>Chaoborus</i> as a predator	Crustacean ecology
Rask & Arvola 1985	Food item of <i>Coregonus lavaretus</i> , <i>Ch. flav</i>	fish biology
Arvola et al. 1986	Presence of <i>Chaoborus</i> in a polyhumic lake, S FIN, acidification experiment	limnology
Kankaala 1988	<i>Daphnia</i> study in a polyhumic lake, <i>Chaborus</i> mentioned as a predator	Crustacean ecology
Paasivirta et al. 1988	Fauna of a bog, emergence traps, <i>Ch. obsc</i>	ecology, faunistics
Raitaniemi et al. 1988	lake acidification, sparse <i>Perca fluviatilis</i> population, <i>Ch. obsc</i> in diet, referring Grahn et al. 1974, Erikson et al. 1980	fish biology
Selin & Koskinen 1988	Phyto and zooplankton of sedimentation ponds in peat digging areas, <i>Ch. flav</i>	limnology
Antikainen 1989	Phyto and zooplankton of a eutrophic lake, <i>Ch. flav</i> (as <i>Chaoborus</i> )	limnology
Ketola & Vuorinen 1989	<i>Daphnia</i> experiment, <i>Chaoborus</i> as predators	Crustacean ecology
Marja-aho & Koskinen 1989	Effects of peat mining, lakes, <i>Ch. flav</i>	limnology
Meriläinen & Hynynen 1989	Acidification, indicator species, <i>Ch. flav</i>	limnology
Paasivirta 1989	Lake monitoring, zoobenthos, <i>Ch. flav</i>	limnology
Vuorinen et al. 1989	<i>Daphnia</i> experiment, <i>Ch. cryst</i> as predator	Crustacean ecology
Walls & Ketola 1989	<i>Daphnia</i> experiment, <i>Ch. cryst</i> as predator	Crustacean ecology
Meriläinen & Hynynen 1990	Acidification, indicator species, <i>Ch. flav</i>	limnology
Kansanen et al. 1990	Bottom sediment fauna of a lake, pollution, <i>Ch. flav</i>	limnology
Hirvenoja & Michailova 1991	Presence of <i>Ch. cryst</i> in a garden pond, S FIN	faunistics
Walls et al. 1991	<i>Daphnia</i> experiment, <i>Ch. cryst</i> as predator	Crustacean ecology
Koskenniemi 1992	Profundal fauna of a reservoir, <i>Ch. flav</i>	limnology
Koskenniemi & Sevola 1992	Monitoring of lake bottom fauna, <i>Ch. flav</i>	limnology



TABLE 2. *continued*

Sæther 1992	Redescription of <i>Cr. lapp</i> , examination of Finnish type specimens	taxonomy
Salonen & Lehtovaara 1992	DVM, <i>Daphnia longispina</i> , small polyhumic lake, <i>Chaoborus</i>	Crustacean ecology
Torpström & Lappalainen 1992	Lake biomanipulation, review, <i>Chaoborus</i> discussed	lake biomanipulation
Meriläinen & Hamina 1993	Paleolimnology, pollution, <i>Ch. flav</i>	paleolimnology
Salonen <i>et al.</i> 1993	DVM, <i>Ch. flav</i> (as <i>Chaoborus</i> )	limnology
Harjuntausta 1994	<i>Daphnia</i> experiment, <i>Chaoborus</i> as predator	Crustacean ecology
Koskenniemi 1994	Faunal development of a reservoir, <i>Ch. flav</i>	limnology
Repka <i>et al.</i> 1994	<i>Daphnia</i> experiment, <i>Chaoborus</i> and <i>Mochlonyx</i> as predators	Crustacean ecology
Riihelä 1994	Bottom fauna of 3 lakes, <i>Ch. flav</i> (as Chaoboridae)	limnology
Sarvala 1994	Acidification, forest lakes, review, <i>Chao</i>	limnology, review
Lauren-Määttä <i>et al.</i> 1995	<i>Chaoborus</i> , toxin in a food-web, experiment	limnology
Repka <i>et al.</i> 1995	Predators in an experiment, <i>Daphnia</i> morphological defences, <i>Ch. flav</i> and <i>Ch. obsc</i>	Crustacean ecology
Bagge <i>et al.</i> 1996	Comparison of sampling methods for semipelagic animals, <i>Ch. flav</i>	limnology
Rask <i>et al.</i> 1996	Food-web structure after <i>Perca fluviatilis</i> population collapse in a small lake, <i>Chaoborus</i>	limnology
Repka & Pihlajamaa 1996	<i>Daphnia</i> experiment, <i>Chaoborus</i> as predator	Crustacean ecology
Simola <i>et al.</i> 1996	Paleolimnological analysis of a large lake complex, <i>Ch. flav</i>	paleolimnology
Manninen 1997	DVM, plankton, <i>Chaoborus</i>	ecology
Olander <i>et al.</i> 1997	Paleolimnology, NW Lapland, <i>Chaoborus</i>	paleolimnology
Palomäki & Hynynen 1997	Lake monitoring, zoobenthos, <i>Ch. flav</i>	limnology
Walls <i>et al.</i> 1997	<i>Daphnia</i> experiment, <i>Chaoborus</i> spp as predator, <i>Mochlonyx</i> reported from ponds, SW FIN	Crustacean ecology
Hirvenoja 1998	<i>Cr. lapp</i> , <i>M. velu</i> (as <i>M. culicoformis</i> ), localities from Lapland	faunistics
Nurmi 1998	Lake zoobenthos, monitoring, <i>Ch. flav</i> (as Chaoboridae)	limnology
Rask <i>et al.</i> 1998	Limnology of 4 lakes, <i>Ch. flav</i> (as <i>Chaoborus</i> ) in diet of <i>Perca fluviatilis</i>	limnology
Repka & Walls 1998	<i>Daphnia</i> experiment, <i>Ch. obsc</i> as predator	Crustacean ecology
Walls & Ventelä 1998	<i>Daphnia</i> experiment, <i>Ch. obsc</i> as predator; <i>Mochlonyx</i> mentioned from Åland	Crustacean ecology
Grey & Jones 1999	Carbon stable isotopes, <i>Ch. flav</i>	limnology
Itkonen <i>et al.</i> 1999	Paleolimnology of a large lake, <i>Ch. flav</i>	paleolimnology
Jones <i>et al.</i> 1999	Carbon stable isotopes, <i>Ch. flav</i>	limnology
Horppila <i>et al.</i> 2000	zooplankton, <i>Osmerus eperlanus</i> , DVM, oxycline, <i>Ch. flav</i>	limnology
Vinni <i>et al.</i> 2000	Diet of 5 cyprinid fish species, <i>Ch. flav</i>	fish biology
Arvola & Salonen 2001	Experiment, <i>Daphnia</i> , <i>Chaoborus</i> density in a small lake	limnology

TABLE 2. continued

Malinen et al. 2001	Langmuir circulation, <i>Ch. flav</i> , fish predation	limnology
Meriläinen et al. 2001	Paleolimnology of a lake, pollution, <i>Ch. flav</i>	paleolimnology
Ojala & Salonen 2001	<i>Daphnia</i> study in polyhumic lake, <i>Chaoborus</i> density reported	limnology
Tolonen et al. 2001	Presence of <i>Ch. flav</i> at upper profundal zone, large lake complex	limnology
Liljendahl-Nurminen et al. 2002	<i>Ch. flav</i> spatial distribution in a lake	limnology
Korhola et al. 2002	Temperature reconstructions, lakes, sediment, <i>Chaoborus</i> (as Chaoboridae)	paleolimnology
Keränen 2002	Pollution and recovery history of an impacted lake, <i>Ch. flav</i>	limnology
Paasivirta & Salmela 2002	Aquatic insects, eutrophic lake, ponds, <i>Ch. cryst</i> , <i>Ch. flav</i>	faunistics
Sarmaja-Korjonen 2002	Paleolimnology of a small lake, <i>Chaoborus</i>	paleolimnology
Horppila et al. 2003	<i>C. flav</i> , diet of <i>Osmerus eperlanus</i>	limnology
Liljendahl-Nurminen et al. 2003	Predation and abundance of <i>Ch. flav</i> in a lake	limnology
Meriläinen et al. 2003	Paleolimnology of an urban lake, <i>Ch. flav</i>	paleolimnology
Mettinen 2003	Lake monitoring, zoobenthos, <i>Ch. flav</i>	limnology
Rautio et al. 2003	<i>Daphnia</i> , UV radiation, vertical distribution in a small subarctic pond, <i>Ch. obsc</i>	Crustacean ecology
Uusitalo et al. 2003	Fish, zooplankton, diet, <i>Ch. flav</i>	limnology
Horppila et al. 2004	Predator-prey experiment, turbidity, <i>Osmerus eperlanus</i> , <i>Ch. flav</i>	limnology, ecology
Hynynen et al. 2004	Pollution and recovery history of an impacted lake, <i>Ch. flav</i>	paleolimnology
Vinni et al. 2004	Food-item of <i>Osmerus eperlanus</i> , <i>Ch. flav</i>	fish biology
Horppila 2005	Review of the studies of the Lake Hiidenvesi, <i>Ch. flav</i>	review
Horppila & Liljendahl-Nurminen 2005	Lake management, zooplankton predation in turbid lakes, <i>Ch. flav</i>	lake biomanipulation
Koivisto et al. 2005	Bottom fauna of reservoir lakes, <i>Ch. flav</i>	limnology
Laakkonen 2005	Lake monitoring, zoobenthos, <i>Ch. flav</i> (as <i>sulkasääski</i> )	limnology
Liljendahl-Nurminen et al. 2005	mesocosm experiment, zooplankton, predation, <i>Ch. flav</i>	limnology
Malinen et al. 2005	Hydroacoustics, <i>Ch. flav</i>	fish biology
Nyman et al. 2005	Surface sediment chironomid fauna of lakes in NW Lapland, abundant <i>Chaoborus</i> observed from a lake	ecology
Tolonen et al. 2005	lake assessment, zoobenthos, <i>Ch. flav</i> (as Chaoboridae)	limnology
Lappalainen et al. 2006	Diet of <i>Sander lucioperca</i> , <i>Ch. flav</i>	fish biology
Pekcan-Hekim et al. 2006	<i>Ch. flav</i> ecology in a turbid lake, review	limnology, review
Sarmaja-Korjonen et al. 2006	Paleolimnology of a small subarctic lake, <i>Chaoborus</i>	paleolimnology
Wende et al. 2006	A <i>Ch. flav</i> specimen from Finland in a molecular study	phylogeography
Liljendahl-Nurminen 2006	Ecology of <i>Ch. flav</i> in a turbid lake, PhD thesis	limnology

TABLE 2. *continued*

Aarniosalo 2007	Plankton fauna of a small lake, <i>Ch. flav</i> discussed, not caught	limnology
Leppä 2007	Bottom fauna of 14 lakes, Eastern FIN, <i>Ch. flav</i>	limnology
Li 2007	Stable isotope analysis, <i>Chaoborus</i>	limnology
Pekcan-Hekim & Horppila 2007	Predation experiment, turbidity, <i>Blicca bjoerkna</i> , <i>Ch. flav</i>	fish biology
Horppila & Nurminen 2007	<i>Ch. flav</i> larvae, in relation spectral composition of upwelling light	limnology
Raunio <i>et al.</i> 2007	<i>Ch. flav</i> as an indicator of impacted lakes	limnology
Sarmaja-Korjonen & Seppä 2007	Paleolimnology of a lake, <i>Chaoborus</i>	paleolimnology
Väisänen 2007	Bottom fauna, humic lakes, status assessment, <i>Ch. flav</i>	limnology
Yakovlev <i>et al.</i> 2007	Faunistics, NE Finnish Lapland, <i>Ch. obsc</i>	limnology
Jurvelius <i>et al.</i> 2008	Echo-sounding, <i>Ch. flav</i>	fish biology
Liljendahl-Nurminen <i>et al.</i> 2008	<i>Ch. flav</i> larvae in relation to depth and turbidity	limnology
Luoto <i>et al.</i> 2008	Paleolimnology of a lake, <i>Ch. flav</i>	paleolimnology
Mettinen 2008	Lake zoobenthos, monitoring, <i>Ch. flav</i>	limnology
Taipale <i>et al.</i> 2008	Dissolved inorganic C, isotopes, <i>Chaoborus</i> presence mentioned	limnology
Alahuhta <i>et al.</i> 2009	Small lakes, status assessment, eastern Finland, <i>Ch. flav</i>	limnology
Estlander <i>et al.</i> 2009	Humic lakes, zooplankton, fish, <i>Ch. flav</i> , predation	limnology
Hagman 2009	Lake restoration, profundal fauna, <i>Ch. flav</i>	lake biomanipulation/restoration
Horppila <i>et al.</i> 2009	Turbid lake, zooplankton, predation, <i>Ch. flav</i>	limnology
Jyväsjärvi <i>et al.</i> 2009	Natural variation of profundal lake communities, <i>Ch. flav</i> (as Chaoboridae)	limnology
Luoto 2009	Paleolimnology, modelling, <i>Ch. flav</i>	paleolimnology
Luoto & Nevalainen 2009	<i>Ch. flav</i> ( <i>Ch. albi</i> in part) and <i>Ch. obsc</i> (as <i>obscurripes</i> ) mandibles in lake sediments	limnology, biogeography
Saxen <i>et al.</i> 2009	<sup>137</sup> Cs concentrations in small lakes, <i>Chaoborus</i>	ecotoxicology
Valtonen 2009	Zooplankton and <i>Ch. flav</i> in 4 small lakes, S FIN	limnology
Vinni <i>et al.</i> 2009	<i>Ch. flav</i> in the diet of <i>Sander lucioperca</i> in a lake	fish biology
Estlander <i>et al.</i> 2010	Diet of <i>Perca fluviatilis</i> and <i>Rutilus rutilus</i> , <i>Ch. flav</i>	fish biology
Liljendahl <i>et al.</i> 2010	Zooplankton samples, preservation time lag, <i>Ch. flav</i>	limnology
Luoto <i>et al.</i> 2010	Paleolimnology of a small lake, <i>Ch. flav</i>	paleolimnology
Nevalainen & Luoto 2010	Surface sediment fauna of small lakes, presence-absence of fish, <i>Ch. flav</i> ( <i>Ch. albi</i> in part)	paleolimnology
Hagman 2011	Restoration plan of a lake, <i>Ch. flav</i>	lake biomanipulation/restoration
Horppila <i>et al.</i> 2011	Feeding experiment, <i>Perca fluviatilis</i> , <i>Ch. flav</i>	fish biology
Jyväsjärvi <i>et al.</i> 2011	Profundal macroinvertebrate assemblages, <i>Ch. flav</i>	limnology
Luoto 2011	Indicator value, midges, boreal lakes, <i>Ch. flav</i>	limnology
Luoto & Nevalainen 2011	Paleolimnology of a lake, <i>Ch. flav</i>	paleolimnology

TABLE 2. continued

Mettinen & Könönen 2011	Lake monitoring, zoobenthos, <i>Ch. flav</i>	limnology
Nevalainen et al. 2011	Paleolimnology of a lake, <i>Chaoborus</i>	paleolimnology
Syväranta et al. 2011	C and N stable isotopes, biomanipulation, <i>Ch. flav</i>	lake biomanipulation
Aroviita et al. 2012	Assessment of surface waters, indicator species, <i>Ch. flav</i>	limnology
Estlander et al. 2012	<i>Perca fluviatilis</i> , <i>Chaoborus</i> abundance, humic lakes, predation experiment, <i>Ch. flav</i>	limnology, fish biology
Jyväsjärvi et al. 2012	Lake monitoring, zoobenthos, <i>Ch. flav</i>	limnology
Mutyaba 2012	Stable carbon isotopes, meromictic lake, <i>Chaoborus</i>	limnology
Luoto et al. 2012	Midge distribution on varying spatial scales, <i>Ch. flav</i>	limnology, biogeography
Aalto et al. 2013	Mesocosm experiment, presence of <i>Ch. flav</i> in a small lake	limnology
Jyväsjärvi et al. 2013a	Sedimentation, profundal fauna, <i>Ch. flav</i>	limnology
Jyväsjärvi et al. 2013b	Lake restoration, profundal fauna, <i>Ch. flav</i>	lake biomanipulation
Joensuu et al. 2013	Experiment, effect of turbulence on <i>Ch. flav</i> larvae	limnology
Lilja et al. 2013	DVM, food-item of <i>Coregonus albula</i> , <i>Ch. flav</i>	limnology, fish biology
Luoto 2013a	Paleolimnology, <i>Ch. flav</i>	paleolimnology
Luoto 2013b	Dystrophy in small boreal lakes, <i>Ch. flav</i>	limnology
Nevalainen & Luoto 2013	Paleolimnology of a lake, <i>Ch. flav</i>	limnology
Pekcan-Hekim et al. 2013	Predation experiment, turbidity, <i>Perca fluviatilis</i> , <i>Ch. flav</i>	fish biology
Rantala 2013	Paleolimnology of a lake, <i>Ch. flav</i>	paleolimnology
Estlander et al. 2014	Predation experiment, <i>Perca fluviatilis</i> , <i>Ch. flav</i>	fish biology
Härkönen et al. 2014	<i>Ch. flav</i> , predation experiment	limnology, ecology
Härkönen et al. 2014a	<i>Ch. flav</i> , predation experiment, turbulence, environmental change	limnology
Härkönen 2014b	Predation, turbulence, <i>Ch. flav</i>	limnology, ecology
Ketola 2014a	Restoration plan of a lake, <i>Ch. flav</i> abundance	lake biomanipulation
Ketola 2014b	Restoration plan of a lake, <i>Ch. flav</i> abundance	lake biomanipulation
Lehtovaara et al. 2014	Long-term environmental change in a lake, <i>Ch. flav</i>	limnology
Luoto & Ojala 2014	Paleolimnology of a lake, pollution, <i>Ch. flav</i>	paleolimnology
Malinen & Vinni 2014	<i>Ch. flav</i> abundance, fish diet, eutrophic lake, S FIN	limnology
Malinen et al. 2014	<i>Ch. flav</i> abundance in a large lake, echo-sounding	limnology
Nurminen et al. 2014	Predation experiment, <i>Perca fluviatilis</i> , <i>Rutilus rutilus</i> , <i>Ch. flav</i>	fish biology
Nykänen et al. 2014	Recycling and fluxes of carbon gases, <i>Ch. flav</i>	limnology
Rahkola-Sorsa et al. 2014	Comparison of zooplankton sampling methods, <i>Ch. flav</i>	limnology
Rask et al. 2014	Growth of <i>Perca fluviatilis</i> in a lake, 20 yr period, <i>Ch. flav</i> (as <i>Chaoborus</i> )	fish biology
Saari 2014	Food consumption of <i>Esox lucius</i> , stable isotopes, <i>Ch. flav</i>	fish biology
Salmela et al. 2014	list of Finnish species (8)	faunistics
Ahokas 2015	Paleolimnology of two lakes, Central FIN, <i>Ch. flav</i>	paleolimnology
Devlin et al. 2015	Methane efflux, fish introduction, experiment, <i>Chaoborus</i>	limnology

TABLE 2. *continued*

Hiltunen <i>et al.</i> 2015	Food-web, fatty acid composition, <i>Ch. flav</i> (as <i>Chaoborus</i> )	limnology
Malinen & Vinni 2015	Pelagic fish stock of two lakes, <i>Ch. flav</i> in food-web, SW Finland	fish biology
Strandberg <i>et al.</i> 2015	Fatty-acids, food-web, eastern FIN, <i>Ch. flav</i> (as <i>Chaoborus</i> )	limnology
Lensu <i>et al.</i> 2016	Profundal fauna of reservoirs, <i>Ch. flav</i>	limnology
Kangasniemi <i>et al.</i> 2016	Bottom fauna of two bog pools, Ekman-grab, <i>Chaoborus</i>	faunistics
Milardi <i>et al.</i> 2016	Effects of <i>Salmo trutta</i> introduction of food-web, <i>Ch. posi</i> (as <i>Ch. flav</i> ) in a control lake, Värriö SNR	ecology, limnology
Nevalainen <i>et al.</i> 2016	Paleolimnology of two small lakes, eastern FIN, <i>Ch. flav</i>	paleolimnology
Rinta <i>et al.</i> 2016	Carbon isotopes, methanogenic carbon, food-web, <i>Chaoborus</i>	limnology
Vesala 2016	hypolimnetic oxygenation, profundal macroinvertebrates, <i>Ch. flav</i> , Central Finland	lake biomanipulation/restoration
Arvola <i>et al.</i> 2017	Artificial mixing of a boreal lake, foodweb response, <i>Ch. flav</i>	lake biomanipulation/restoration
Hietala 2017	Bottom fauna of a lake, restoration, <i>Ch. flav</i>	lake biomanipulation
Korkeamäki <i>et al.</i> 2017	<i>Ch. flav</i> ( <i>Ch. albi</i> in part), <i>Ch. cryst.</i> , <i>Ch. obsc.</i> , <i>Ch. pall.</i> , mire inventory, SE FIN	faunistics
Luoto & Ojala 2017	Paleolimnology, paleotemperature proxy, sediment, <i>Chaoborus</i>	paleolimnology
Luoto <i>et al.</i> 2017	Paleolimnology of a lake, <i>Ch. flav</i>	paleolimnology
Horppila <i>et al.</i> 2018	Visual and physiological refuges, day time distribution, <i>C. flav</i> larvae	limnology
Kotila <i>et al.</i> 2018	faunistic record from NW Lapland, insect survey, <i>Ch. nybl</i>	faunistics
Malinen 2018	Hydroacoustics, <i>Ch. flav</i>	fish biology
Vesterinen <i>et al.</i> 2018	Metabarcoding, bat diet, <i>Ch. flav</i>	ecology
Horppila <i>et al.</i> 2019	Rotifer abundance, turbulence, <i>Ch. flav</i> predation, experiment	limnology, ecology
Luoto <i>et al.</i> 2019	Polluted lake, presence of <i>Ch. flav</i> in sediment samples	limnology
Mettinen 2019	lake zoobenthos, monitoring, <i>Ch. flav</i>	limnology
Mykrä <i>et al.</i> 2019	Bottom fauna of a lake, <i>Ch. flav</i> , W FIN	limnology
Salmela <i>et al.</i> 2019	Red-list assessment, <i>Ch. nybl</i> and <i>Cr. lapp</i>	conservation biology
Ståhl 2020	Occurrence of <i>Ch. flav</i> in Åland, faunistic survey	faunistics, limnology
Salmela <i>et al.</i> 2021	Taxonomy, <i>Ch. flav</i> , <i>Ch. albi</i> , <i>Ch. posi</i>	taxonomy

midges was published by Frey (1921, 3 spp), then considered a subfamily as a part of the mosquitoes. Renowned Finnish limnologists, H. Järnefelt and K.J. Valle, published several limnological studies in the 1920's and 1930's (e.g. Järnefelt 1923, 1929, Valle 1928, 1936). In their publications, *Ch. flavicans* was referred to as “*Sayomyia*” by Järnefelt and as “*Corethra plumicornis*” by Valle. Among other discoveries, Valle (1930) was perhaps the first to document DVM in *Ch. flavicans*. The first proper taxonomic work on Finnish phantom midges was by Martini (1928), who described *Cryophila lapponica* (as *Mochlonyx*) based on

Finnish and Russian specimens deposited at the MZH. Before Martini, these specimens were examined and tentatively named by the Finnish entomologist E.E. Bergroth, who was probably in correspondence with Martini (“in litt.”, Martini 1928) and even wrote a manuscript on that species (“MS”, Edwards 1930a). So perhaps the binomial “*Cryophila lapponica*” was invented by Bergroth, but the actual authors of the species and genus are Martini and Edwards, respectively. Ragnar Storå (1935) reported *M. fuliginosus* (as *M. velutinus*) for the first time based on his own collection from western Finland and that of R. Krogerus from



Kuusamo. It is likely that Storå identified phantom midges from the mire samples of Krogerus (1960). The Finnish list of species was published once more by Frey *et al.* (1941, 4 spp) and Frey (1946) also wrote a review of mosquito and phantom midge larvae. Lauri Tiensuu (1951) reported *Ch. pallidus* from Finland and verified the status of *Ch. flavicans* as a part of the regional fauna. In the 1960's M. Hirvenoja published a series of important papers, such as the emergence of *Chaoborus* from lentic waterbodies at Riihimäki (S Finland, Hirvenoja 1960) and the redescription of *Ch. nyblaei* and its first record from Finland (Utsjoki, Lapland, Hirvenoja 1961a). In his paper (1961a) he also provided an identification key to all European *Chaoborus* species; in his keys *Ch. alpinus* was still considered a valid species, but we now consider it to be a synonym of *Ch. flavicans* (Sæther 1967, Salmela *et al.* 2021).

Starting from the late 1960's, several articles on pollution and eutrophication of Finnish lakes were published (e.g. Bagge & Jumppanen 1968, Tuunainen *et al.* 1972, Paasivirta & Särkkä 1978). Wastewaters especially from the wood pulp industry and other municipal sources impacted the quality of lakes, e.g. by lowering oxygen levels and causing fish kills in wintertime. *Chaoborus flavicans* is often reported as an indicator of pollution, because it is frequently present in the oxygen poor profundal samples (Paasivirta 1989, Nurmi 1998, Jyväsjärvi *et al.* 2013a). Another environmental impact was acidification, and *Ch. flavicans* was also seen as an indicator of acidified waters (Meriläinen & Hynynen 1989). In limnological studies *Chaoborus* (almost invariably *Ch. flavicans*) is often just briefly mentioned, as a part of the lake bottom fauna or planktonic community. Notable exceptions are studies from the Lake Hiidenvesi (SW Finland), where the ecology of *Ch. flavicans* has been studied in several sample-based and experimental studies (e.g. Liljendahl-Nurminen *et al.* 2002, 2003, Horppila *et al.* 2003, Pekcan-Hekim & Horppila 2007). In addition to limnology, phantom midges play a part in studies focusing on fish biology (e.g. Viljanen 1983, Rask 1984, Rask & Arvola 1985, Vinni *et al.* 2004) and crustacean ecology (Ranta & Nuutinen 1985, Ketola & Vuorinen 1989,

Rautio *et al.* 2003). There are also numerous studies on paleolimnology or lake bottom fauna inferred from subfossil sediment samples (e.g. Alhonen & Haavisto 1969, Meriläinen & Hamina 1993, Luoto *et al.* 2008). The most recent Finnish checklist was published by Salmela *et al.* (2014), listing 8 spp as reliably recorded. The family was also recently assessed for the Finnish red-list for the first time (Salmela *et al.* 2019).

It is not a surprise that *Ch. flavicans* is the most often mentioned species in the literature. Among 240 titles (with 11 review papers and checklists excluded from the total 251 searched), *Ch. flavicans* occurs 173 times (72 %), whilst all the remaining species are referred to just 49 times in total (20 %). In other references 8 % of mentions are chaoborids at family or genus level. However, some of these references are based on misidentifications, here corrected. For example, despite some authors originally referring to *Ch. flavicans* (Luoto & Nevalainen 2009, Nevalainen & Luoto 2010, Milardi *et al.* 2016) resampling of the study site indicated that most likely another species was involved (see below and Table 2). In general, the literature survey shows how biased the ecological studies of Finnish species have hitherto been. Most of the studies are from lakes and only a minority have been carried out in smaller lentic waters. The recent discovery of two (to date) previously unknown species from ponds (Salmela *et al.* 2021) also supports this conclusion.

## Taxonomy

- List of Finnish Chaoboridae Edwards, 1912
- Chaoborinae Edwards 1912: 48 (as a subfamily of Culicidae)
- Cryophila* Edwards, 1930
  - lapponica* (Martini, 1928)
- Mochlonyx* Loew, 1844
  - fuliginosus* (Felt, 1905)
  - triangularis* Klink, 1982
  - velutinus* (Ruthe, 1831)
- Chaoborus* Lichtenstein, 1800
  - sg. *Chaoborus*
    - crystallinus* (De Geer, 1776)
    - obscuripes* (Van der Wulp, 1859)

*flavicans*-group

*albipes* (Johannsen, 1903)

*flavicans* (Meigen, 1830)

*posio* Salmela in Salmela et al. 2021

sg. *Schadonophasma* Dyar & Shannon, 1924

*nyblaei* (Zetterstedt, 1838)

sg. *Sayomyia* Coquillett, 1903

(syn. *Peusomyia* Sæther, 1970)

*pallidus* (Fabricius, 1781)

Note: Author of the genus *Cryophila* and its nominotypic species *lapponica* varies in the systematic literature (see Borkent 1993, 2014). We follow the concept proposed by Borkent (1993), that the author of the genus is Edwards (Edwards 1930a) and the species is Martini (Martini 1928), not Bergroth (Sæther 1992, Borkent 2014). Based on Ogawa (2007) we consider the subgenus *Peusomyia* as a synonym of *Sayomyia*; the subgenus *Sayomyia* is paraphyletic if *Peusomyia* and *Neochaoborus* Edwards are treated as valid subgenera.

**A key to fourth instar larvae, pupae and adults of Finnish Chaoboridae**

*IV instar larvae*

1. Larva apneustic, siphon absent (Figure 5a,b). Mandibular teeth long, dispersed (Figure 5c). Antennal bases proximate (Figure 5c). Larvae 10–22 mm in length, transparent, bearing two pairs of air sacs ..... 5 *Chaoborus*
  - Larva metapneustic, siphon present on abdominal tergite VII (Figure 5d,e,g,h). Mandibular teeth stout and short. Antennal bases spaced. Larvae 6–13 mm in length, translucent or brownish, bearing two or three pairs of air sacs ..... 2
2. Siphon conspicuous, protruding, tube-like (Figure 5d,e). Mandibular teeth as in Figure 5f. Mandibular seta 2 group setae comb-like, hypostoma absent (Figure 5f). Larvae about 6–10 mm in length, translucent, bearing two pairs of air sacs (thoracic and abdominal) ..... 3 *Mochlonyx*
  - Siphon inconspicuous, plate-like minor bulge (Figure 5g,h). Mandibular teeth as in Figure

- 5i. Mandibular seta 2 group setae simple, not comb-like. Hypostoma present, bearing an anterior row of teeth (Figure 5i). Larvae 11–13 mm, three pairs of air-sacs present (thoracic and two abdominal) ..... *Cryophila lapponica*
3. Apex of siphon with two long setae (Figure 6a) ..... *M. fuliginosus*
  - Apex of siphon lacking long setae (Figure 6c,e) ..... 4
4. Anterior seta of mandibular seta 2 group about as dark as mandibular teeth, comb teeth relatively long and thin (Figure 6d). Larvae usually very pale, almost transparent ..... *M. triangularis*
  - Anterior seta of mandibular seta 2 group pale, not as dark as mandibular teeth, comb teeth rather short (Figure 6f). Larvae usually darker, not pale ..... *M. velutinus*
5. Inner basal margin of antenna straight (Figure 7f). Labral blade narrow, needle-like (Figure 9g) ..... *Ch. pallidus*
  - Inner basal margin of antenna notched (Figure 7a–e). Labral blade wider, leaf-like (Figure 8a,d,h, 9a,c,e) ..... 6
6. Subordinate tooth of mandible (III tooth) exactly between teeth II and IV (Figure 8b,e,i) ..... 7 (*Ch. flavicans*-group)
  - Subordinate tooth of mandible (III tooth) attached to tooth II (Figure 9b,d,f,h) ..... 9
7. Mandibular lateral teeth inconspicuous, uppermost tooth shorter than subordinate tooth (Figure 8e). Number of mandibular fan bristles  $\leq 16$  ..... *Ch. flavicans*
  - Mandibular lateral teeth conspicuous, uppermost tooth at least as long as subordinate tooth (Figure 8b,i) ..... 8
8. Number of mandibular fan bristles  $> 20$ , usually 22–29 (Figure 8i). Labral blade finely serrated, rather wide (length:width ratio 3.7, Figure 8h) ..... *C. posio*
  - Number of mandibular fan bristles up to 23, usually 15–21. Labral blade almost devoid of serration – modestly serrated, slender (length:width ratio 5.5, Figure 8a) ..... *C. albipes*
9. Outline of anterior part of head pointed in lateral view (Figure 7e). Anal fan with  $> 30$

- setae (Figure 7j). Larvae large, 18–22 mm. ...  
..... *Ch. nyblaei*
- Outline of anterior part of head more or less rounded in lateral view (Figure 7c,d). Anal fan with less than 30 setae (Figure 7g–i). Larva  $\leq 16.5$  mm in length ..... 10
- 10. Labral blade rather narrow, serration weak (Figure 9a). Dorsal process of 9th abdominal segment pointed (Figure 7h) .....  
..... *Ch. crystallinus*
- Labral blade wide, strongly serrated (Figure 9c). Dorsal process of 9th abdominal segment blunt, rounded (Figure 7i) ..... *Ch. obscuripes*

*Pupae*

1. Terminal process with delicate, transparent membrane. Lateral and mid ribs very strong (Figure 10b) ..... *Chaoborus* 5
- Membrane of pupal paddle more robust and with some pigmentation. Lateral ribs rather weak (Figure 10e,g) ..... 2
2. Respiratory organ rather wide, sinuous (Figure 10f,h). Terminal processes widest apically (Figure 10g). Membrane between abdominal sternites conspicuous, with darkened specks (Figure 10f) ..... *Cryophila lapponica*
- Respiratory organ rather long and narrow, curved or rather straight (Figure 10d). Terminal process widest medially (Figure 10e). Membrane between abdominal sternites inconspicuous (Figure 10d) ..... *Mochlonyx* 3
3. Longest setae on tergites II–IV over twice as long as respective tergite, setae curved (Figure 11f). Respiratory organ slightly curved, pale brownish, rather elongate, length:width ratio ca. 12.5 (Figure 11g) ..... *M. triangularis*
- Longest setae on tergites II–IV about 1.5–2 times as long as respective tergite, setae straight (Figure 11j). Respiratory organ straight or curved ..... 4
4. Respiratory organ curved, long and narrow, dark, length:width ratio ca. 13 (Figure 11c) ....  
..... *M. fuliginosus*
- Respiratory organ straight, club-shaped, pale brownish, length:width ratio ca. 5.1 (Figure 11k) ..... *M. velutinus*
5. Mid rib of terminal process straight (Figure 12h). Respiratory organ relatively short (ca.

- 730–760) and wide (length:width ratio ca. 2.9–3.3), dark-brown in color .....  
..... *Ch. pallidus*
- Mid rib of terminal process apically curved (Figure 12e–g). Respiratory organ mostly more elongate in shape (e.g. Figure 8c,f,j) ....  
..... 6
- 6. Abdominal tergites very wide, width:length ratio ca. 1.8 (Figure 12g). Terminal process basally infuscated (Figure 12g) .....  
..... *Ch. nyblaei*
- Abdominal tergites more elongate, width:length ratio ca. 1–1.14 (Figure 12e,f). Base of terminal process usually unpigmented .....  
..... 7
- 7. Median rib of terminal process darker than lateral ribs. Apex of outer rib smooth (Figure 8k) ..... *Ch. flavicans*-group 8
- Median and lateral ribs of terminal process equally dark (Figure 12e,f). Apex of outer rib with either distinct serration (Figure 12i) or bearing inconspicuous bristles (Figure 12j) ..... 10
- 8. Respiratory organ club-shaped, lacking subapical constriction, relatively short (Figure 8j) ..... *Ch. posio*
- Respiratory organ with subapical constriction, either slender or voluminous (Figure 8c,f,g) ..  
..... 9
- 9. Length of respiratory organ  $>1000$   $\mu\text{m}$ , either slender (pond populations) or voluminous (lake populations) (Figure 8f,g) .....  
..... *Ch. flavicans*
- Respiratory organ slender, length mostly  $<1000$   $\mu\text{m}$ , but may exceed  $1000$   $\mu\text{m}$  (Figure 8c) .....  
..... *Ch. albipes* [note: separation of pond-dwelling *C. flavicans* and *C. albipes* pupae may be obscured by intraspecific variation]
- 10. Apex of outer rib of pupal paddle with distinct serration (Figure 12i). Inner margin of respiratory organ with subapical constriction (Figure 12a) .....  
..... *Ch. crystallinus*
- Apex of outer rib of pupal paddle at most with inconspicuous bristles (Figure 12j). Respiratory organ without subapical constriction, inner margin almost straight (Figure

- 12b) ..... *Ch. obscuripes*  
*Adult males*
1. First tarsomere longer than second (Figure 13c) ..... *Chaoborus* 5
  - First tarsomere shorter than second (Figure 13f,i) ..... 2
  2. Mid and hind tibial spurs present (Figure 13i). Antennae short, antennal plume reduced (Figure 13g). Gonostylus with two small apical spines (Figure 14b) ..... *Cryophila lapponica*
  - Tibial spurs absent (Figure 13f). Antenna longer, male antennal plume normal (i.e. long verticils on flagellomeres, Figure 13d). Gonostylus with an elongated apical spine (Figure 15a–c) ..... *Mochlonyx* 3
  3. Gonocoxite elongate. Parameres short, medially bent. Epandrium rounded, with no median projections (Figure 15a) ..... *M. fuliginosus*
  - Gonocoxite rather wide. Parameres long, somewhat sinuous and strongly sclerotized. Epandrium either with finger-like median projection or triangular (Figure 15b,c) ..... 4
  4. Epandrium with a finger-like median projection (Figure 15c). Paramere as in Figure 15c ..... *M. velutinus*
  - Epandrium medially triangular (Figure 15b). Paramere as in Figure 15b ..... *M. triangularis*
  5. Wings patterned (Figure 16g). Legs with either numerous transverse bands or apices of femur, tibia and tarsomeres darkened (Figure 16g,i) ..... 6
  - Wings without distinct pigmentation. Legs lacking transverse bands or apically darkened leg joints (Figure 16a,b,d,e) ..... 7
  6. Large (wing length ca. 4.5–6.3 mm), brownish species. Wing patterned. Joints of legs darkened (Figure 16g,h). Paramere long and narrow, apically bent (Figure 17e,f) ..... *Ch. nyblaei*
  - Small (wing length ca. 3–3.5 mm), pale species. Wing medially weakly patterned. Femorae and tibiae with numerous transverse dark bands (Figure 16i). Paramere rather inconspicuous, aedeagus present (Figure 17g–i) ..... *Ch. pallidus*
  7. Apical claw not exceeding the tip of paramere

- in lateral view (Figure 17b,d) ..... 8
- Apical claw exceeding the tip of paramere in lateral view (Figure 19b,d,f) ..... 9
8. Paramere rather small, simple in structure, apical claw modestly curved (Figure 17a,b) ..... *Ch. crystallinus*
- Paramere rather large, complex in structure, apical claw loop-like (Figure 17c,d) ..... *Ch. obscuripes*
9. Gonocoxite and gonostylus stout in structure (Figure 19e). Paramere very dark, strongly sclerotized, apical claw of paramere relatively long (Figure 19f) ..... *C. posio*
- Gonocoxite and gonostylus slender (Figure 196a,c). Paramere pale yellowish or brownish, apical claw of paramere relatively short (Figure 19b,d) ..... 10
10. Paramere medially bent and constricted. Apical claw usually infuscated, with a modest lower lip (Figure 19d) ..... *C. flavicans*
- Paramere medially almost straight or gently curved. Apical claw stout, curved, more or less the same coloration throughout, with a protruding lower lip (Figure 19b) ..... *C. alipes*

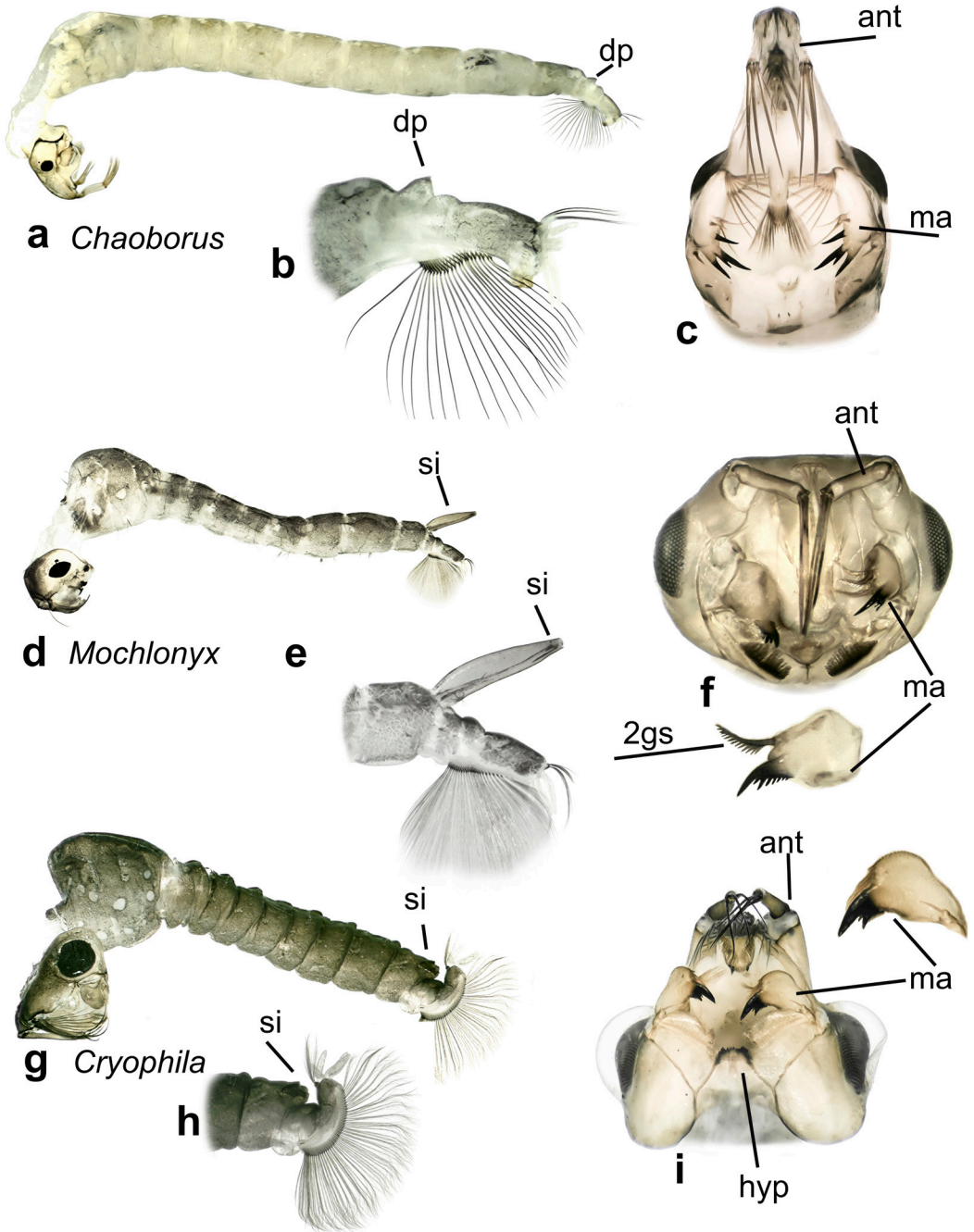
## The species

### *Cryophila lapponica*

*Mochlonyx lapponicus* Martini 1928: 33 (original description). *Cryophila lapponica* Martini: Edwards 1930a: 540 (establishment of the genus-group name); Monchadsky 1939: 142 (description of larva). Sæther 1992: 5 (as *Cr. lapponica* Bergroth, redescription, phylogeny); Sæther 2002: 22 (as *Cr. lapponica* Bergroth morphology).

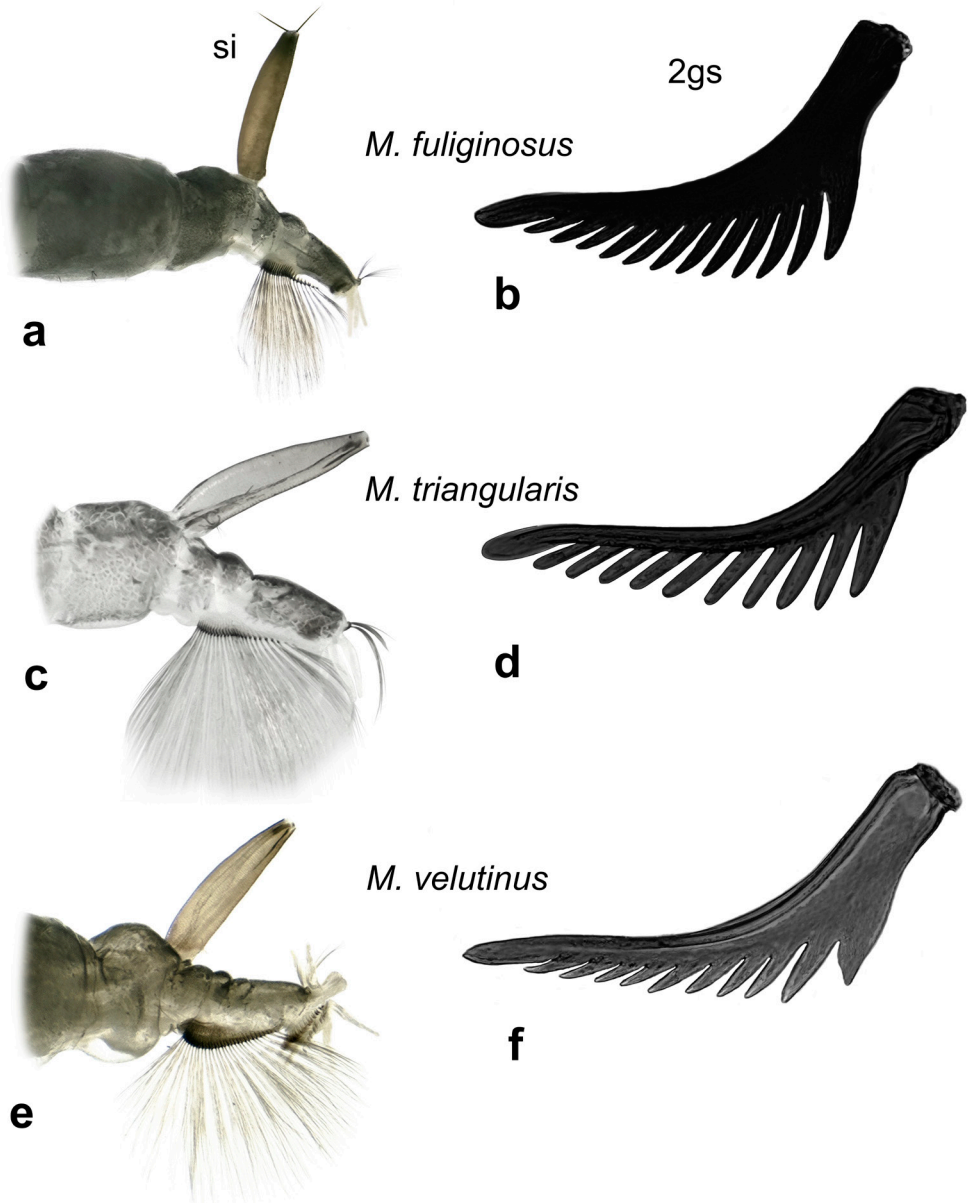
Larva is relatively large and robust, length ca. 11–13 mm, coloration brownish or orange brown. Pairs of air sacs present in thorax and abdominal segments VI and VII, antennal bases spaced. Anal fan with dense setosity, bearing ca. 90 setae (Figure 5h). Siphon is small and inconspicuous, plate-like (Figure 5h). Mandible with a large black tooth, comb-like setae absent (Figure 5i).

Pupa: Respiratory organs are large (length ca. 1120) and medially bent (Figure 10f, 14a). Membranes between sternites are conspicuous, with darkened specks (Figure 10f). Terminal process is widest apically (Figure 10g).



**FIGURE 5.** Larvae of Chaoboridae genera. Habitus, lateral view (a, d, g), abdominal apex, lateral view (b, e, h) and head, ventral view (c, f, i). *Chaoborus* (a–c), *Mochlonyx* (d–f), *Cryophila lapponica* (g–i). ant=antenna, dp=dorsal process, hyp=hypostoma, ma=mandible, si=siphon, 2gs=uppermost of the mandibular seta 2 group setae (i.e. third seta of the mandibular pectinate setae).



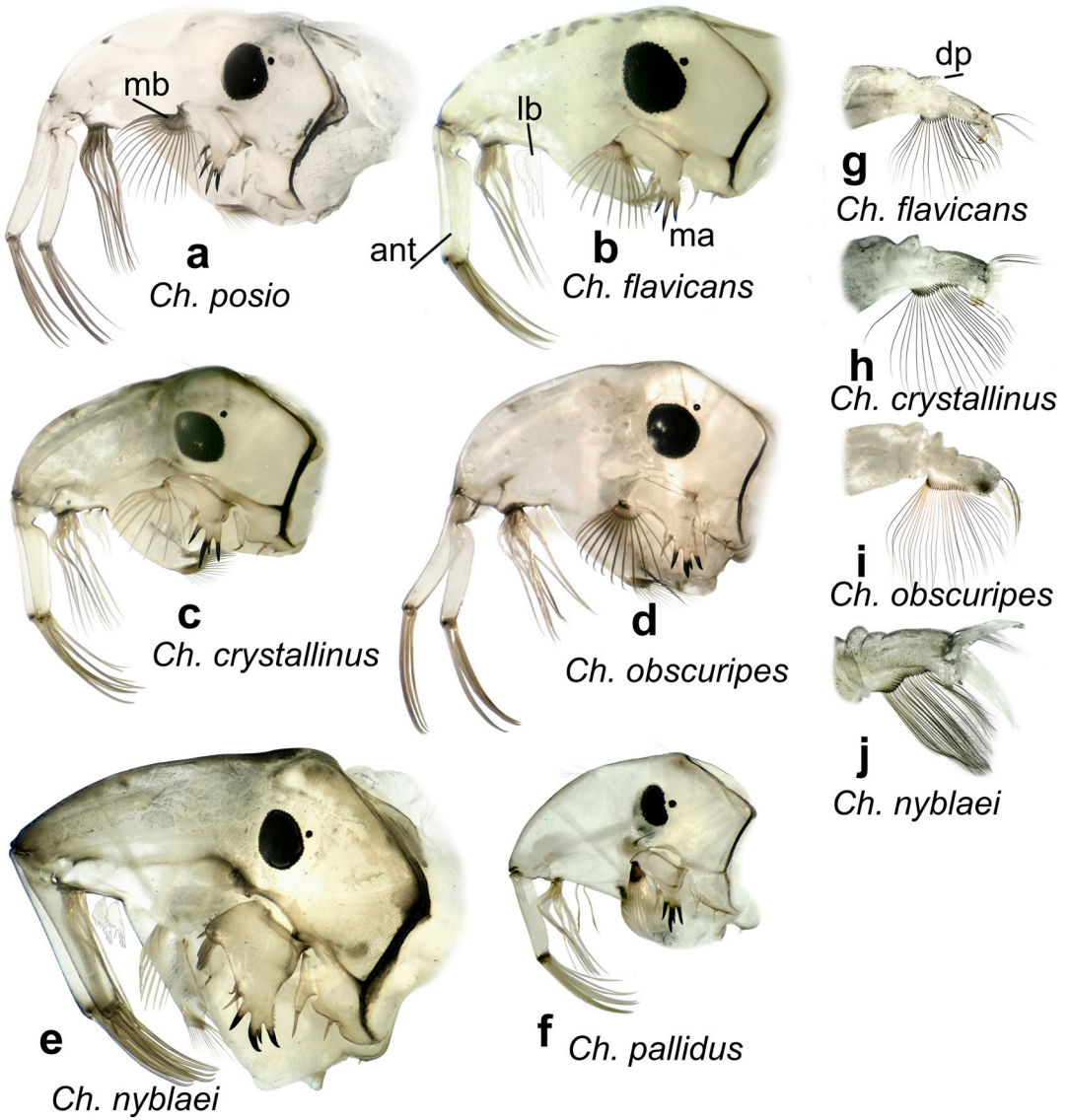


**FIGURE 6.** *Mochlonyx*, larvae. Abdominal apices, lateral view (a, c, e) and uppermost of the mandibular seta 2 group setae (i.e. third seta of the mandibular pectinate setae) (b, d, f). *Mochlonyx fuliginosus* (a, b), *M. triangularis* (c, d) and *M. velutinus* (e, f). si=siphon, 2gs=uppermost of the mandibular seta 2 group setae (i.e. third seta of the mandibular pectinate setae)

Adult: Mid and hind tibiae with spurs (Figure 13i). First tarsomere is shorter than the second. Antennae are relatively short, with reduced plume in male (Figure 13g,h). Hypopygium is brown or almost dark brown. Gonostylus bearing several

long setae that exceed the width of gonostylus and two minor apical spines are present. Parameres are rather short and curved, apically truncated (Figure 14b).

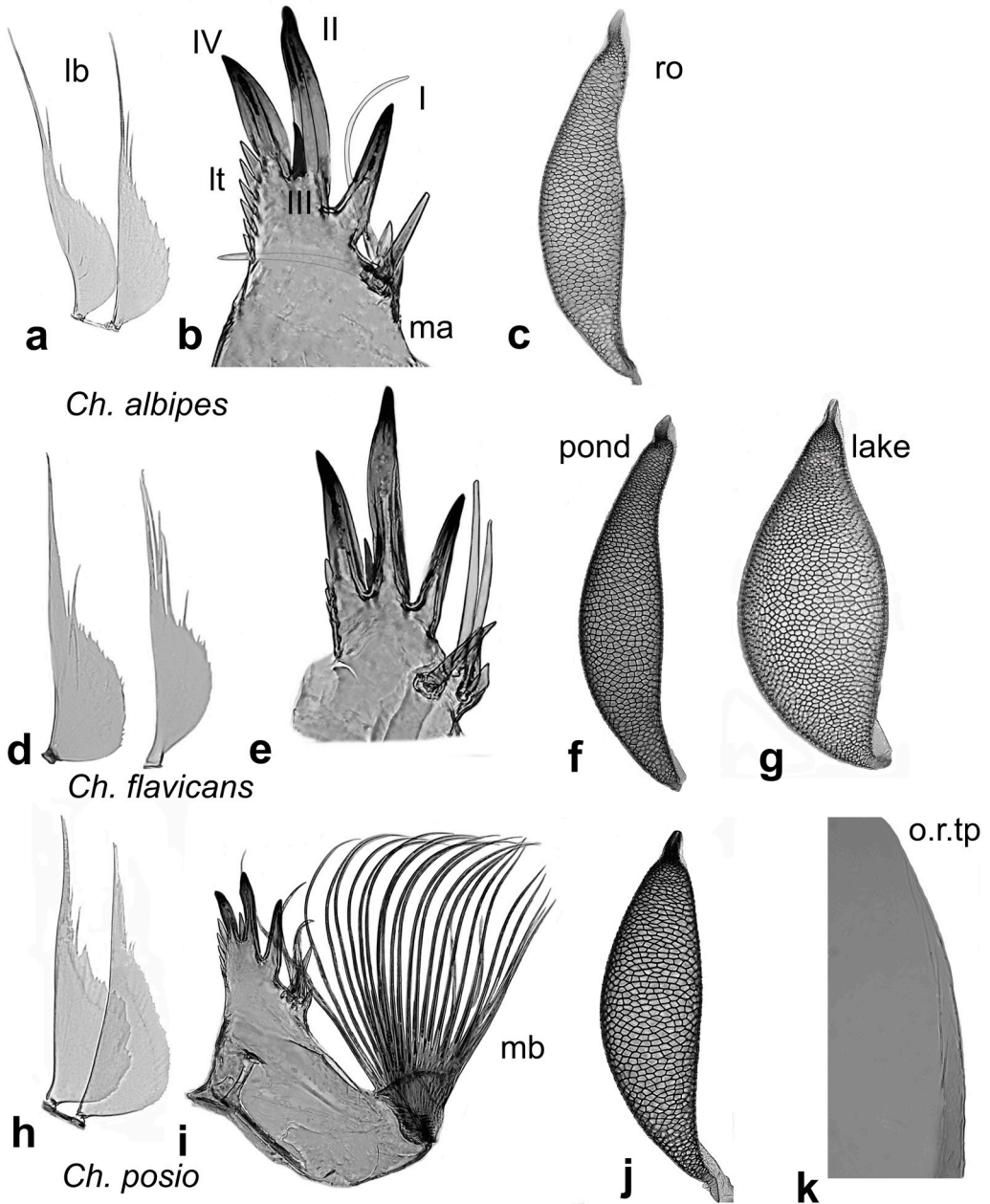
Biology: This is a univoltine species. Larvae



**FIGURE 7.** *Chaoborus*, larvae. Head, lateral view (a–f) and abdominal apices (g–j). *Chaoborus posio* (a), *Ch. flavicans* (b, g), *Ch. crystallinus* (c, h), *Ch. obscuripes* (d, i), *Ch. nyblaei* (e, j) and *Ch. pallidus* (f). ant=antenna, dp=dorsal process, lb=labral blade, ma=mandible, mb=mandibular bristles.

hatch from overwintering eggs in spring, roughly in synchrony with snow-melt mosquitoes (*Ochlerotatus* spp.). Larvae are present in larger temporary melt-water pools, that retain water for at least a two-month period, and in semipermanent pools, and are seldom found in permanent pools. Larvae eat mosquito and chironomid larvae, small crustaceans and are cannibalistic (Monchadsky

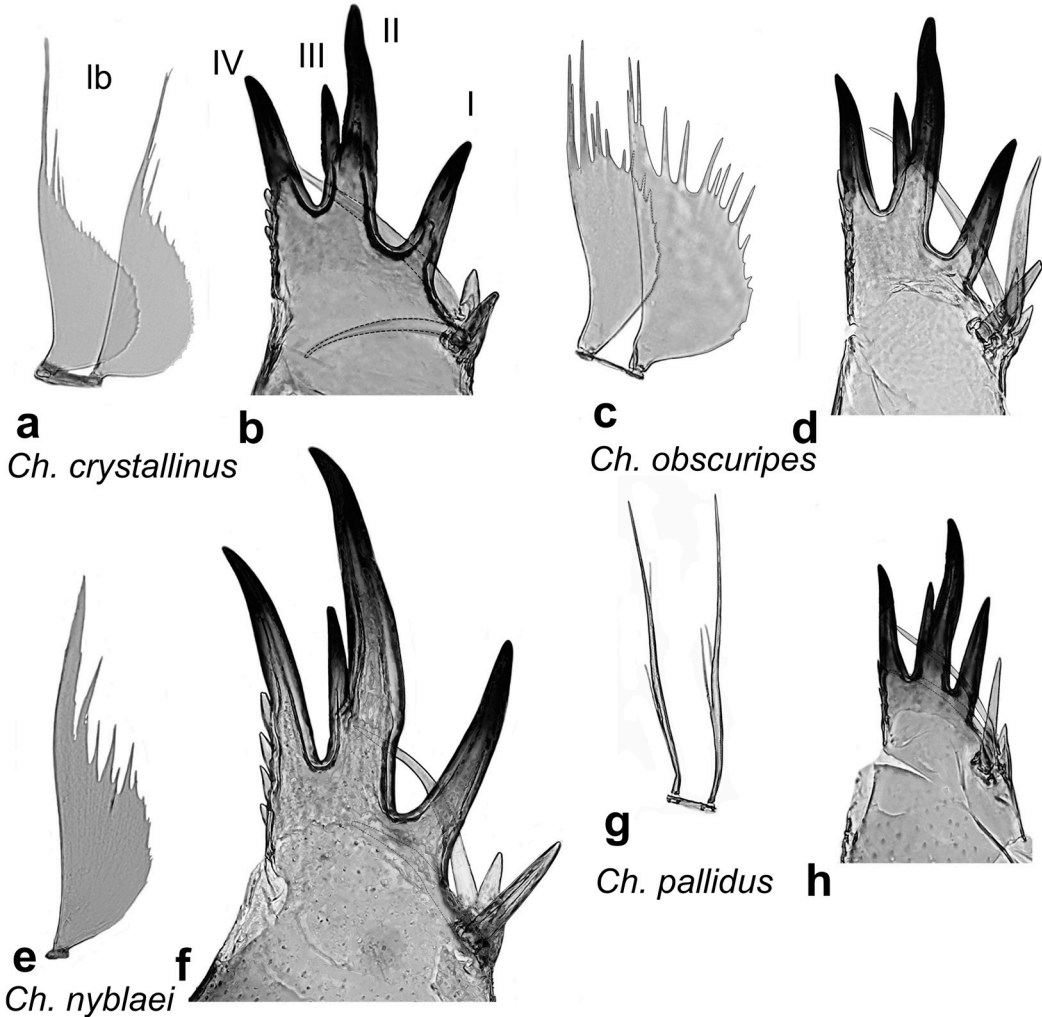
1959, 1964, JS pers.obs.). The specific gravity of the larvae is less than that of water and motionless larvae slowly ascend toward the surface. Close to the surface larvae resume swimming motion to descend again: larvae are thus constantly in motion and are prone to cannibalism as well as predation by *Mochlonyx* larvae (Monchadsky 1959). Pupation takes place in late June – mid July,



**FIGURE 8.** *Chaoborus flavicans* group, larvae and pupae. Labral blades (a, d, h), mandibles (b, e, i), respiratory organs (c, f=*Ch. flavicans*, pond population, g=*Ch. flavicans*, lake population, j) and apex of outer rib of terminal process (k). *Chaoborus albipes* (a–c), *Ch. flavicans* (d–g) and *Ch. posio* (h–k). lt=lateral teeth, I–IV mandibular tooth, III being the subordinate tooth, lb=labral blade, ma=mandible, mb=mandibular bristles, o.r.tp=outer rib of terminal process, ro=respiratory organ.

perhaps even in August in late or cold summers or in climatically cold NW Lapland (Martini 1928). Adults are perhaps day active and can be found

close to the larval sites, nocturnal activity is unknown. Their behaviour is not well known, but both sexes can stride on the water surface and fly



**FIGURE 9.** *Chaoborus*, larvae. Labral blades (a, c, e, g) and mandibles (b, d, f, h). *Chaoborus crystallinus* (a–b), *Ch. obscuripes* (c–d), *Ch. nyblaei* (e–f) and *Ch. pallidus* (g–h). lb=labral blade, I–IV=mandibular tooth, III being the subordinate tooth.

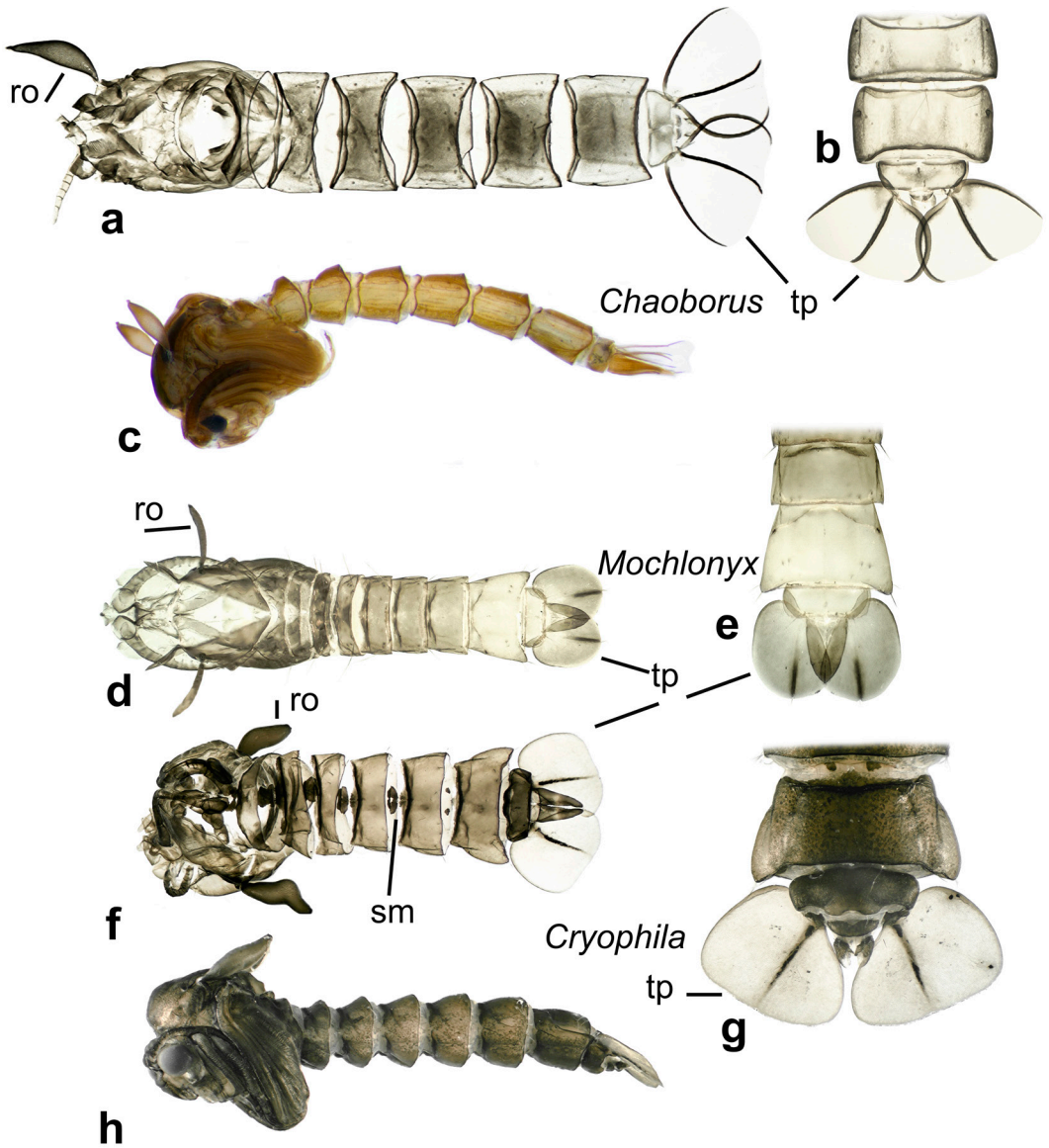
short distances e.g. between emergent vegetation. Swarming probably does not take place as suggested by the presence of the reduced antennal plume of males. Longevity of adults or egg-laying behaviour is not known.

**Distribution:** Western Palaearctic. Known from Finland, Sweden, Norway and in Russia as far east as western Siberia (Borkent 1981, Andersen & Kvifte 2012). It is a northern species with boreal and subarctic distribution. In Finland known from the mid and north boreal and subarctic ecoregions, from a total of 31 collecting sites (Figure 2).

**DNA barcoding:** A total of six Finnish specimens were barcoded. All specimens belong to a BIN cluster BOLD:ACG2270, composed of seven specimens (Finnish ones barcoded here and a specimen from Norway). The average within-group distance is 0.18 %, maximum distance is 0.48 % and the distance to the nearest BIN cluster is 12.86 %.

**Comments:** Due to its large size, brownish coloration and constant motion, *Cr. lapponica* larvae are easy to observe in the field. Larvae are present in shallow water bodies and in larger





**FIGURE 10.** Chaoboridae, pupae and exuvia. Exuvia, ventral view (a, d, f), details of abdominal terminalia (b, e, g) and pupa, lateral view (c, h). *Chaoborus* (a–c), *Mochlonyx* (d–e) and *Cryophila lapponica* (f–h). sm=sternal membrane, ro=respiratory organ, tp=terminal process.

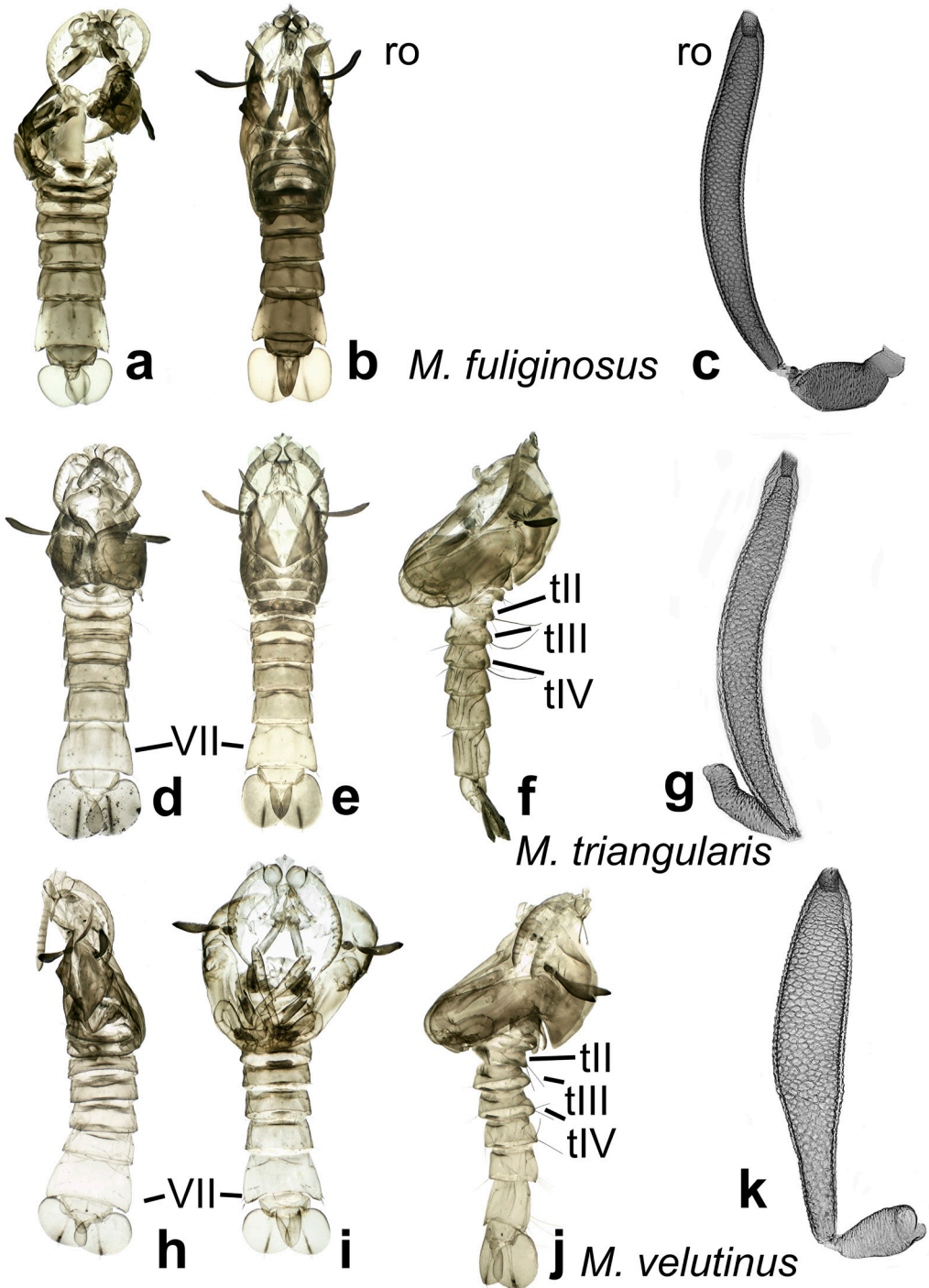
pools and they are to be found close to the surface and not far from the shore. Larvae can also be confidently identified in the field and it could be thus effectively monitored e.g. as part of mosquito surveys. The species was collected some 90 years ago close to St. Petersburg, Russia, from the south boreal zone (Monchadsky 1936, 1939), but it is not known if the population is still present. The

species is most likely adapted to (middle–north) boreal climatic conditions, where shallow snow-melt pools are abundant and persist long enough for the development of the immature stages.

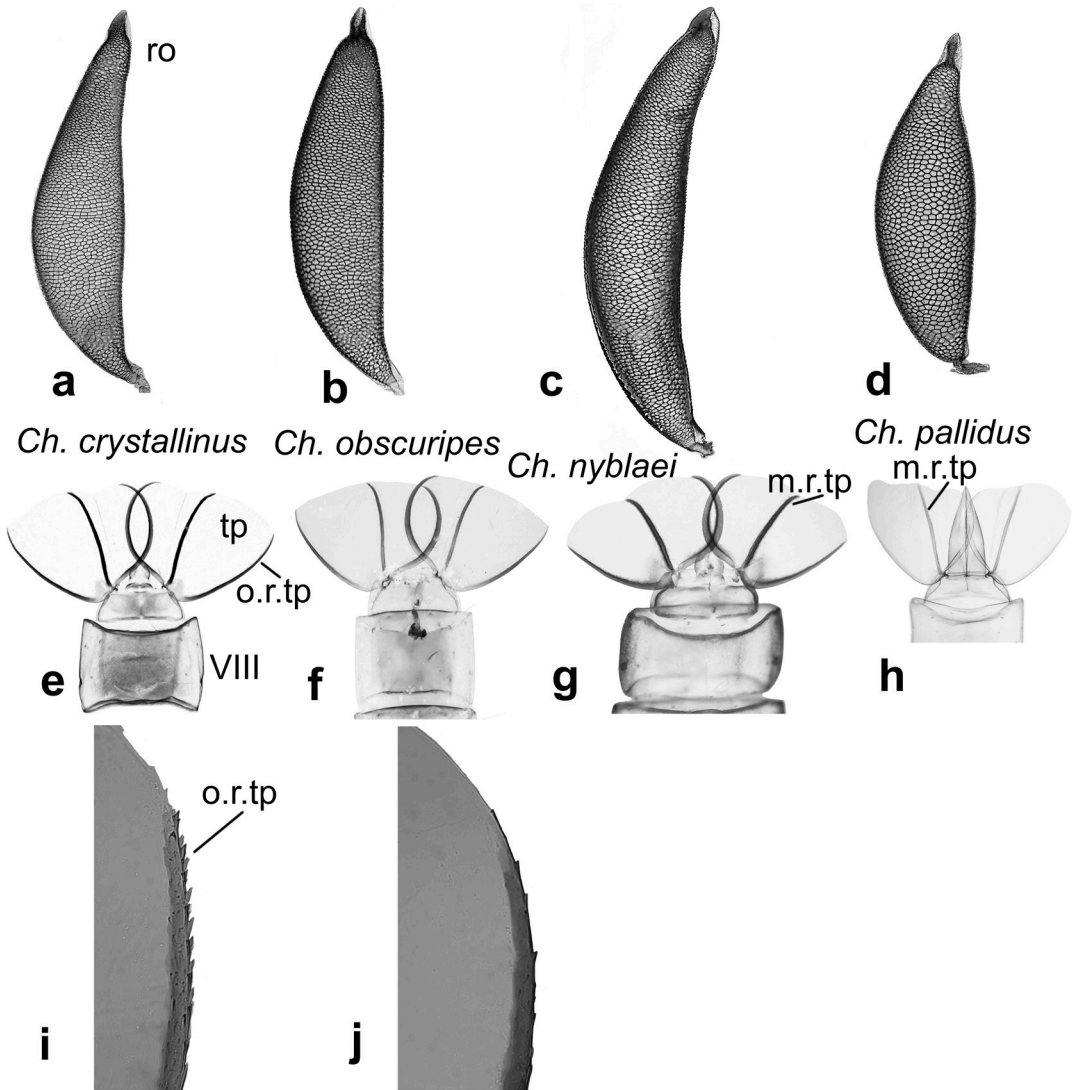
***Mochlonyx fuliginosus***

*Corethra fuliginosus* Felt 1905: 458 (original description).  
*Mochlonyx velutinus* Ruthe (auct. nec): Martini 1929: 49





**FIGURE 11.** *Mochlonyx*, pupal exuvia. Exuvia, ventral (a, d, h), dorsal (b, e, i), lateral view (f, j) and respiratory organs (c, g, k). *Mochlonyx fuliginosus* (a–c), *M. triangularis* (d–g) and *M. velutinus* (h–k). VII=7<sup>th</sup> abdominal segment, ro=respiratory organ, tII–tIV=3<sup>rd</sup>–4<sup>th</sup> tergite.



**FIGURE 12.** *Chaoborus*, pupae. Respiratory organs (a–d), terminal processes (e–h) and apices of outer ribs of terminal processes (i–j). *Chaoborus crystallinus* (a, e, i), *Ch. obscuripes* (b, f, j), *Ch. nyblaei* (c, g) and *Ch. pallidus* (d, h). VIII=eighth abdominal segment, m.r.tp=median rib of terminal process, o.r.tp=outer rib of terminal process, ro=respiratory organ, tp=terminal process.

(redescription). *Mochlonyx martinii* Edwards 1930b: 165 (a new name for the *M. velutinus* in Martini 1929). Klink 1982: (morphology). *Mochlonyx fuliginosus*: Cook 1956: 48 (morphology). Freeman 1962: 42 (nomenclature, synonymous names). Lake 1969: (morphology, biology). Sæther 2002: 16 (morphology).

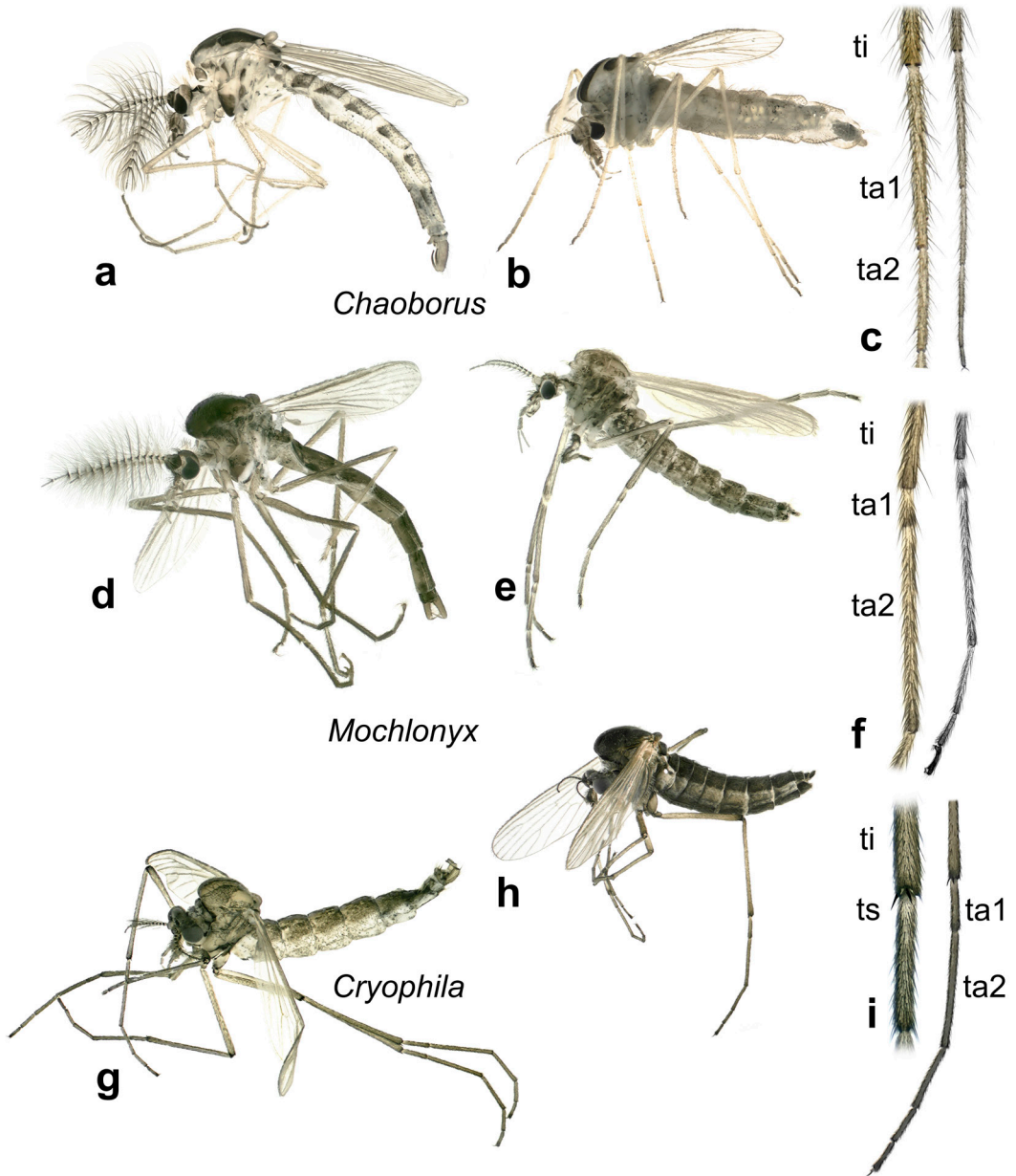
**Larva:** Length of larva is ca. 7–8 mm. Siphon bearing two conspicuous apical setae (Figure 6a). Uppermost of the mandibular seta 2 group setae is

black (Figure 6b).

**Pupa:** Respiratory organs are very long and narrow, infuscated (Figure 11c). Setae on tergites 2–4 are short.

**Adult:** General coloration is dark. Male hypopygium with elongate gonocoxites, gonostyli is narrow and epiandrium is rounded, parameres are short (Figure 15a).

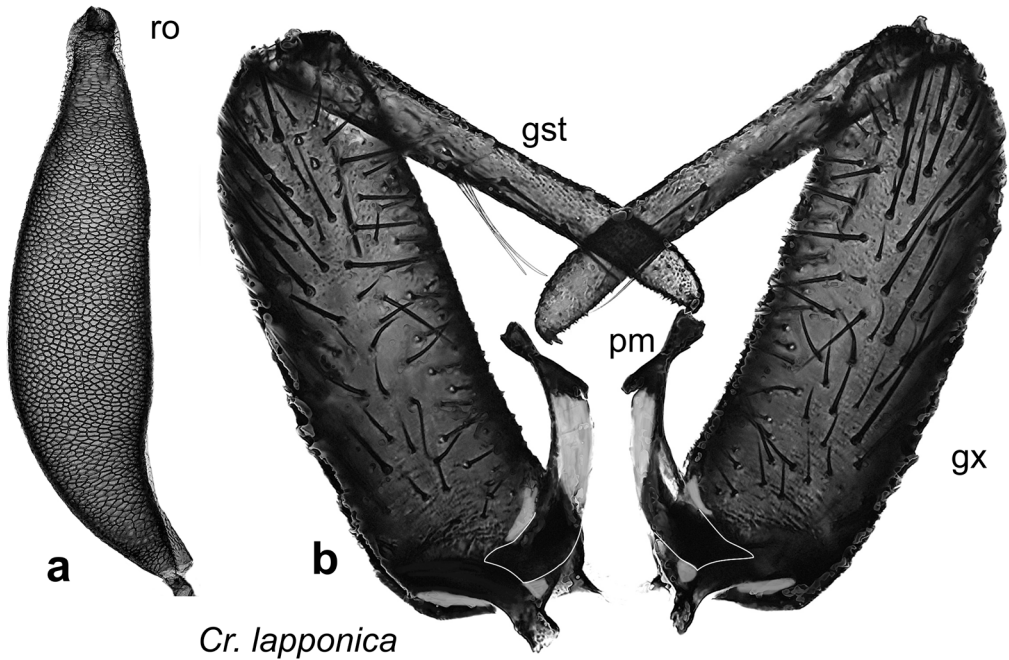
**Biology:** The species is uni- or bivoltine



**FIGURE 13.** Chaoboridae genera, adults. Male habitus, lateral view (a, d, g), female habitus, lateral view (b, e, h), apices of tibiae and tarsomeres (c, f, i). *Chaoborus* (a–c), *Mochlonyx* (d–f) and *Cryophila lapponica* (g–i).

with overwintering eggs or larvae. Larvae have been found in very small water bodies, such as springs and shallow pools of bogs, aapa mires (patterned fens) and palsa mires (subarctic fens with frozen hummocks). Usually absent from larger ponds and thus seldom co-occurring with

other chaoborids. IV instar larvae have been found in early May, late July and late October, adults from early summer to late August. It is yet to be resolved whether the species overwinters in the egg or larval stage, or both, in Finland. In eastern North America *M. fuliginosus* is deemed to be



*Cr. lapponica*

**FIGURE 14.** *Cryophila lapponica*. Pupal respiratory organ (a) and male hypopygium, tergal view (b, epandrium removed).

as a multivoltine species, but the overwintering stage was not identified (Lake 1969). According to Kuper & Verberk (2011) the larvae of the species are present in spring and autumn, and two generations may be produced. In addition, larvae may occasionally overwinter. It is however obvious that the development is not in synchrony with melt-water mosquitoes, and larvae most likely feed mainly on small crustaceans. Usually met in low numbers as larvae in pond-net and as adults in Malaise trap samples.

**Distribution:** Holarctic. In Europe known from Fennoscandia, Lithuania, United Kingdom, Germany (Wagner 2013), Czech Republic (Jedlička & Országh 1997), Russia (Leningrad area, Monchadsky 1936) and the Netherlands (Kuper & Verberk 2011). In Finland the species is known from the hemiboreal to the subarctic ecoregions, from a total of 31 localities (Figure 2). **DNA barcoding:** A total of four specimens (three from Finland, one from Norway) were barcoded. All specimens belong to the BIN cluster BOLD:ADJ8614, composed of six specimens

(Finland, Norway). The average within-group distance is 0.33 %, maximum distance is 0.64 and the nearest BIN cluster is apparently composed of Nearctic *M. fuliginosus*; average distance of the clusters is low, 1.77 %.

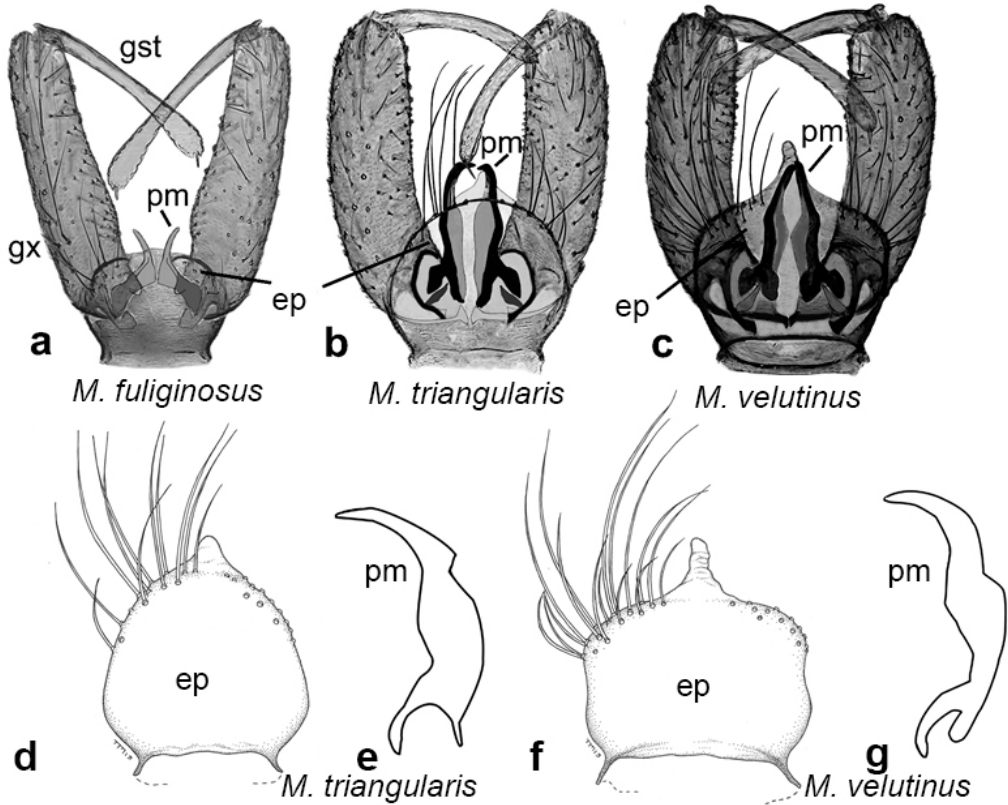
**Comments:** The species is readily distinguished from its congeners in larval, pupal and adult stages. *Mochlonyx fuliginosus* is also one of the few European chaoborids able to live in thermally constant cold limnocrone springs. At the first glance the species may appear rare, given the low number of observations (<40). Nevertheless, the species is probably very common in Finland and is most likely overlooked.

#### ***Mochlonyx triangularis***

*Mochlonyx triangularis* Klink 1982: 150 (original description). Sæther 2002: 14 (morphology).

**Larva:** Fourth instar larva is rather transparent, pale yellowish in colour, its length is length ca. 6–7 mm. Siphon lacking long apical setae (Figure 6c). Uppermost of the mandibular seta 2 group setae is very dark, and the are teeth relatively narrow (Figure 6d).





**FIGURE 15.** *Mochlonyx*, males. Hypopygia, tergal view (a–c), epandrium, tergal view (d, f) and parameres, lateral view (e, g). *Mochlonyx fuliginosus* (a), *M. triangularis* (b, d, e) and *M. velutinus* (c, f, g). ep=epandrium, gst=gonostylus, gx=gonocoxite, pm=paramere.

**Pupa:** Respiratory organs are elongate (length ca. 715), mostly curved (Figure 11g). Tergite VIII is rather narrow in both sexes, width:length ratio is 1.4 and 1.7 in male and females, respectively. Long setae are present on tergites II–IV (Figure 11f).

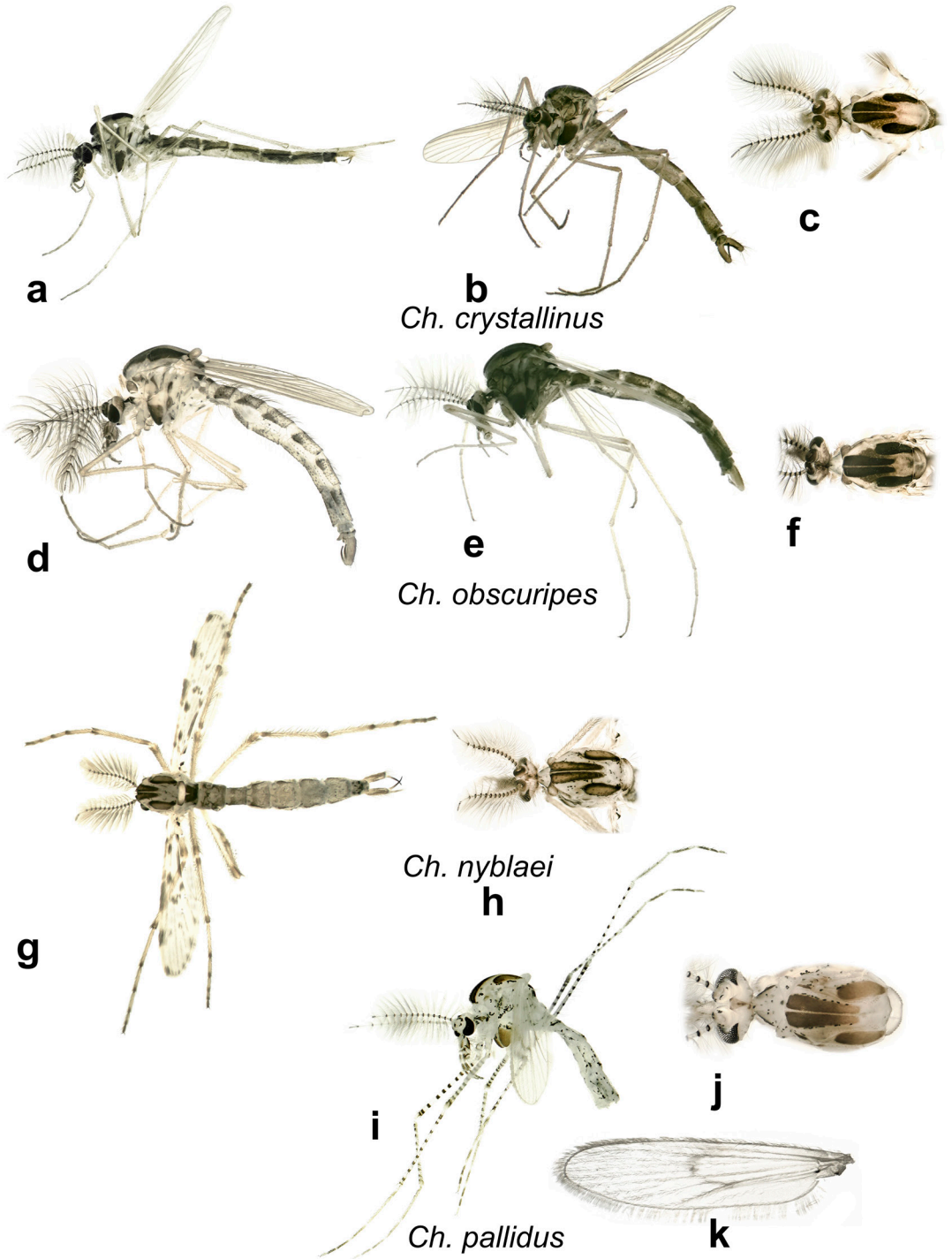
**Adult:** General coloration is yellowish brown. Male epandrium is caudally triangular, lacking finger-like median projection (Figure 15b,d). Paramere is elongate, its ventral edge is angular in lateral view (Figure 15d).

**Biology:** This is a univoltine species with overwintering eggs. Larval development takes place later than in *M. velutinus*, and the species often co-occur in the same ponds. II instar larvae of *M. triangularis* are present in early summer while larvae of *M. velutinus* are already full-grown. IV instar larvae and pupae are present in late June or early to mid July. Adults can be

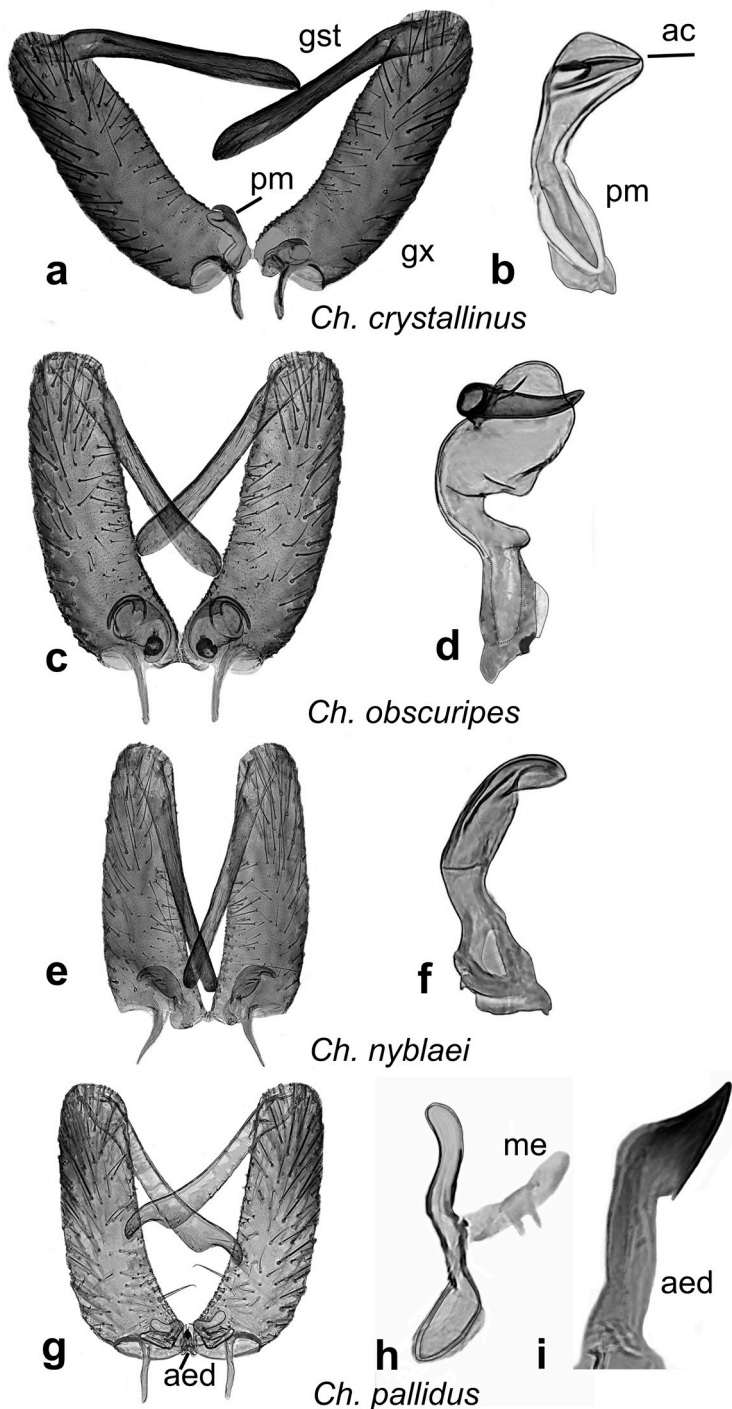
found close to breeding ponds. In daytime adults stay in the vegetation and swarming has been once observed circa 11pm (daylight conditions) in late July in Kittilä, Lapland; adults formed low-flying swarms next to ponds and swarming ceased if wind velocity was too high. Larvae are present in temporary pools but are also common in larger ponds, often being numerous. It is most likely that this species does not primarily feed upon melt-water mosquito larvae due to mosquito larvae size and their principal absence in July when *M. triangularis* larvae are full grown.

**Distribution:** European, hitherto known from the Netherlands (Klink 1982, Kuper & Verberk 2011) alone; here reported for the first time from Fennoscandia. The species is reported from Germany in Fauna Europaea (Wagner 2013), but this record is doubtful and any literature of such record is lacking (R. Wagner, pers.comm.). In

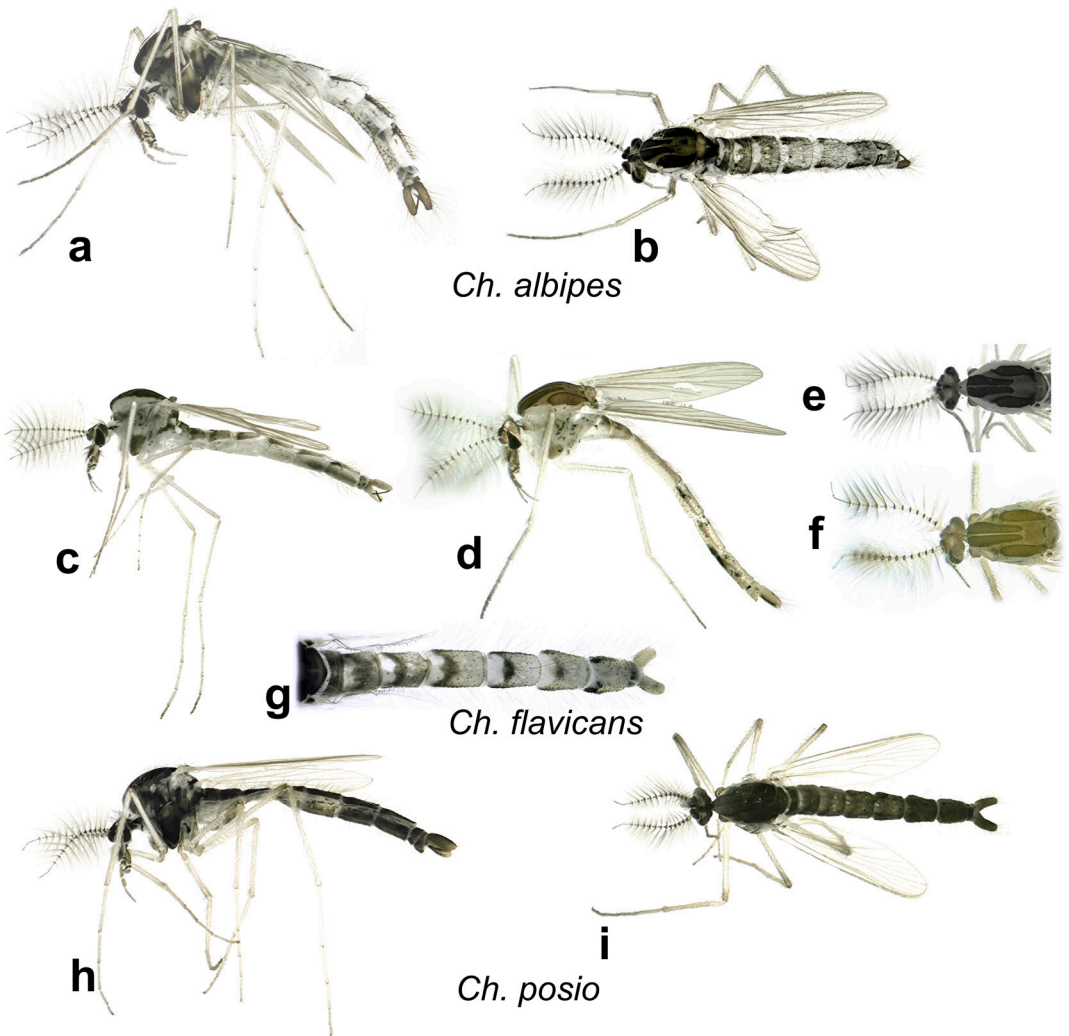




**FIGURE 16.** *Chaoborus*, males. Habitus, lateral view (a, b, d, e, g, i) and dorsal view (c, f, h, j). *Chaoborus crystallinus* (a–c), *Ch. obscuripes* (d–f), *Ch. nyblaei* (g–h) and *Ch. pallidus* (i–j).



**FIGURE 17.** *Chaoborus*, males. Hypopygia, tergal view (a, c, e, g), parameres, lateral view (b, d, f, h) and aedeagus, lateral view (i). *Chaoborus crystallinus* (a–b), *Ch. obscuripes* (c–d), *Ch. nyblaei* (e–f) and *Ch. pallidus* (g–i). ac=apical claw, aed=aedeagus, gst=gonostylus, gx=gonocoxite, me=median hyaline bridge connecting parameres, pm=paramere.



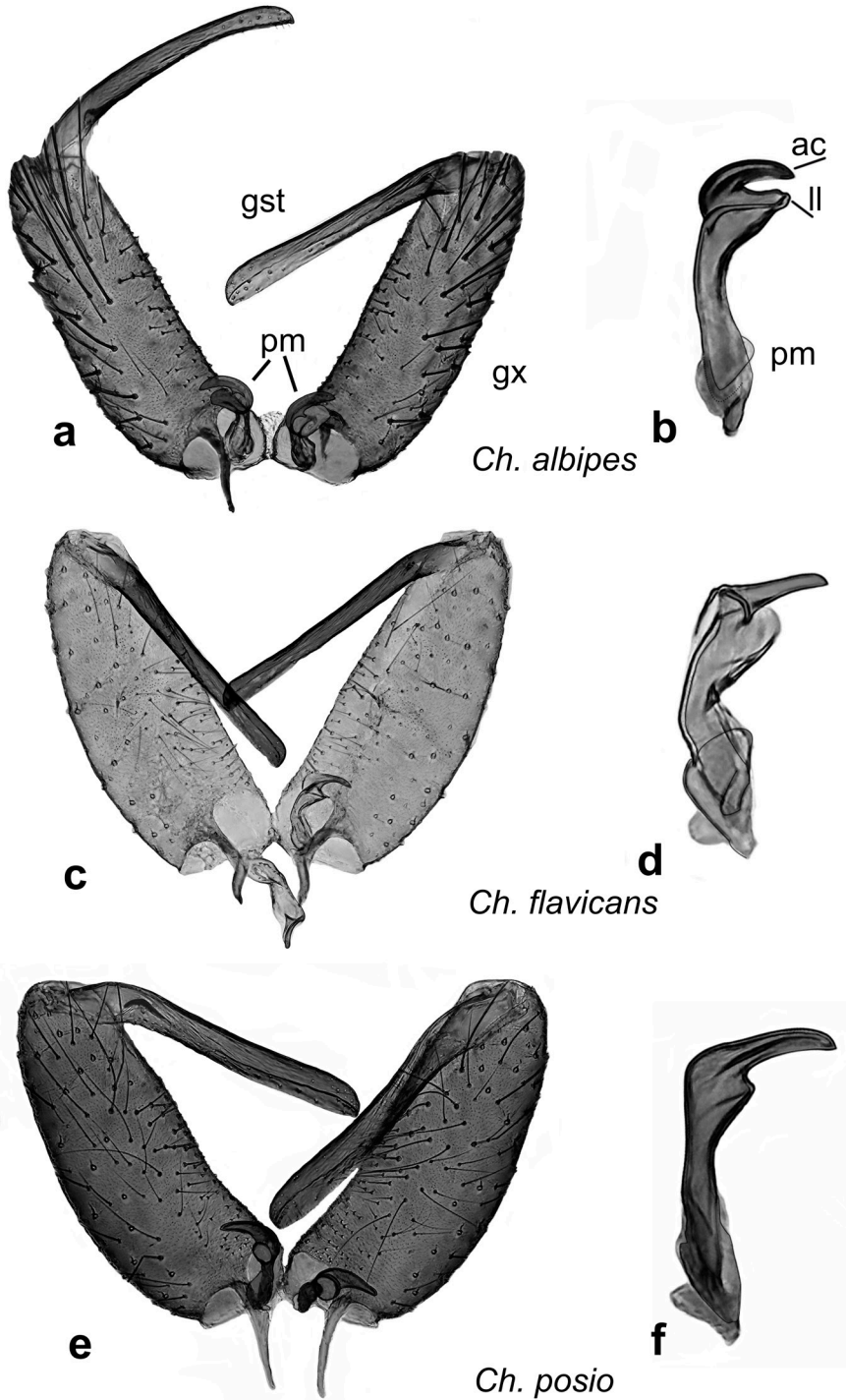
**FIGURE 18.** *Chaoborus flavicans* group, males. Habitus, lateral view (a, c, d, h), dorsal view (b, e, f, i) and abdomen, dorsal view (g). *Chaoborus albipes* (a–b), *Ch. flavicans* (c–g) and *Ch. posio* (h–i).

Finland it is recorded from the hemiboreal to north boreal ecoregions, absent or not yet collected from the subarctic zone, and observed from a total of 68 sites (Figure 2).

DNA barcoding: A total of 13 Finnish specimens were barcoded. The specimens form a unique BIN cluster BOLD:ADD2442, characterised by a low within-group variation (average distance 0.19 %, maximum distance 0.48 %). The average distance to the nearest BIN cluster is 10.94 %.

Comments: Most likely *M. triangularis* and

*M. velutinus* are sister species, based on their close similarity. These two species look quite similar but are nevertheless separable in larval, pupal and adult stages. Differences between larvae are usually very clear due to coloration and shape of mandibles, even from II instar onwards. Because the species is widespread and common in Finland, it is likely to occur in neighbouring territories as well. For example, perhaps the late hatching “third wave larvae” of *M. velutinus* (as *M. culiciformis*, in Monchadsky 1964) in truth represents *M. triangularis*. These two species are



**FIGURE 19.** *Chaoborus flavicans* group, males. Hypopygia, tergal view (a, c, e) and parameres, lateral view (b, d, f). *Chaoborus albipes* (a–b), *Ch. flavicans* (c–d) and *Ch. posio* (e–f). ac=apical claw, gst=gonostylus, gx=gonocoxite, ll=lower lip of paramere, pm=paramere.



often in sympatry but temporally segregated.

Sæther (1997a, 2002) was the first to describe the larva of the species. It is not explicitly expressed, but it is apparent that he studied the type material from the Netherlands. According to Sæther (2002, p. 15) “all pectinate setae yellowish brown”, but in our material these setae are darkened. Sæther’s description is based on a few larvae (2 IV instar, and 4 III instar larvae in the type material, Klink 1982), and it is still to be clarified if there is geographical variation in this character. It is also possible that the larvae studied by Sæther were cleared and slidemounted, thus explaining the light color of pectinate setae. Nevertheless, the shape of the third pectinate seta (i.e. the uppermost of the mandibular seta 2 group setae) depicted by Sæther (2002, figure 13d) fits well to our material (Figure 6d).

### ***Mochlonyx velutinus***

*Corethra velutina* Ruthe 1831: 1205 (original description). *Tipula culiciformis* De Geer 1776: 372 (original description, preoccupied name) *Corethra rufa* Zetterstedt 1838: 808 (original description). Wahlgren 1904: 14 (taxonomic interpretation). *Mochlonyx culiciformis* ssp. *vernalis* Monchadsky 1953: 371, syn. (original description, biology of larva). *Mochlonyx culiciformis*: Martini 1929: 46 (morphology). Klink 1982: (morphology). *Mochlonyx velutinus*: Cook 1956: 44 (morphology). James 1957: (larval instars, ecology). Sæther 2002: 13 (morphology).

Larva: Brownish or brownish-gray in color, not particularly transparent, its length is ca. 6.5–8.5 mm. Siphon lacking long apical setae (Figure 6e). Uppermost of the mandibular seta 2 group setae is light brown – brown, teeth are relatively wide (Figure 6f).

Pupa: Respiratory organ is stout and almost straight (length ca. 680), club-shaped (Figure 11k). Tergite VIII rather wide in both sexes, width:length ratio is 1.8 and 1.9 in male and female, respectively. Setae on tergites II–IV are short (Figure 11j).

Adult: General coloration is brownish. Male epandrium bearing a medial, conspicuous finger-like projection (Figure 15c,f). Parameres are elongated, ventral edge is rounded in lateral view (Figure 15g). Gonocoxite is characterised apicomediaally by numerous long, hyaline setae (not shown).

Biology: This is a univoltine species with overwintering eggs. Development of larvae are in synchrony with melt-water mosquitoes, and among the European *Mochlonyx*, this species seems to be most clearly associated with temporary waters that support abundant mosquito populations. Pupation takes place in early summer, e.g. in Rovaniemi (at the border of mid and north boreal ecoregions) during late May and early June. Larvae devour mosquitoes and small crustaceans. The larvae inhabit small and larger temporary ponds, including small, open waters in flood plains of large rivers; also present in semipermanent ponds, but mostly absent from large ponds. May attain high densities in certain localities.

Distribution: Holarctic. In Europe known from Fennoscandia, United Kingdom, Central and southern Europe (Wagner 2013, Kuper & Verberk 2011). Widespread in Finland, records (n=90) extending from the hemiboreal to the subarctic zone (Figure 2).

DNA barcoding: A total of 19 Finnish specimens were barcoded. The specimens fall into two BIN clusters, BOLD:ACG1345 and BOLD:ADJ8074, but these are very closely related (average distance 1.28 %). The former consists of 15 specimens (13 Finnish, singletons from Norway and Germany), the latter of seven specimens (6 Finnish, 1 Norwegian). If Finnish specimens from these to BIN clusters are combined, the average intraspecific distance is 0.97 % (min 0, max 2.19 %). Members of both BIN clusters can be present in sympatry, and no geographical pattern is evident. The species has perhaps colonised Fennoscandia from two different glacial refugia, resulting in the observed intraspecific divergence.

Comments: Common and widespread species. Perhaps some of the older records in Fennoscandia mistakenly represent *M. triangularis*.

### ***Chaoborus crystallinus***

*Tipula crystallina* De Geer 1776: 386 (original description). *Tipula plumicornis* Fabricius 1794:246 (as a new name for *Tipula pilicornis* Fabricius). *Chaoborus crystallinus*: Martini 1929: 55 (redescription). *Chaoborus (Chaoborus) crystallinus*: Edwards 1932: 25 (subgeneric assignment). Peus 1934: (description of larva and pupa). Parma 1969a: (larval

morphology). Sæther 1970: 31 (morphology). Sæther 2002: 26 (morphology).

Larva: Length of the fourth instar larva is ca. 12–14 mm. Subordinate mandibular tooth (III) is situated on the tooth II (Figure 9b). Labral blade is elongate and slightly sinuous (Figure 9a). Dorsal process is pointed (Figure 7h).

Pupa: Respiratory organ is constricted subapically, its length is ca. 880–1130 (Figure 12a). Lateral ribs of terminal processes are rather narrow and all ribs equally dark (Figure 12e). Outer rib bearing relatively strong apical bristles (Figure 12i).

Adult: The ultimate flagellar segment in male is clearly shorter than the penultimate segment, length ratio is ca. 1.3. Scutellar stripes are very dark, adjoining integument of scutum is about equally dark; in teneral specimens the integument is pale (Figure 16c). Abdominal tergites lacking dark transverse bands. Gonocoxite is yellowish brown, gonostylus is black (Figure 17a). Paramere is rather inconspicuous, apical claw is small and curved (Figure 17a,b).

Biology: The species is bi- or multivoltine in southern Finland, bivoltine in middle boreal ecoregion and univoltine in northern and subarctic ecoregions. Larvae are present in a wide array of lentic waters, but the species is most common in small pools and ponds. Among the Finnish *Chaoborus* s. str. species, *Ch. crystallinus* is most often associated with man-made or disturbed habitats (such as ditches and artificial pools), sporadically collected from spring pools. In Finland it is seldom found to co-occur with *Ch. obscuripes* in pristine ponds, and it seems to be the less numerous species in such cases. Larvae are not able to perform DVM (Borkent 1981) and are thus prone to fish predation. However, larvae may migrate shorter distances in the water column in order to locate optimal thermal conditions (Büns & Ratte 1991). Ovipositing females can detect fish kairomones and avoid laying their egg batch in ponds that have fish (Berendonk 1999). Larvae eat mosquitoes and small crustaceans.

Distribution: Holarctic. One of the most widespread species in Europe, from mediterranean to the northernmost Fennoscandia (Wagner 2013). In Finland observed from all ecoregions and

recorded from a total of 122 sites (Figure 2).

DNA barcoding: A total of five Finnish specimens were barcoded. The specimens belong to a BIN cluster BOLD:ACK5185, consisting of eight specimens (Finnish ones and 3 from Norway, average distance 0.33 %, maximum 0.96 %). The nearest BIN (BOLD:ACI7830), consisting of one female from Canada, is about 7.4 % distant to the European specimens. If this specimen represents Nearctic *Ch. crystallinus*, it may indicate that the lineages of the two continents have split before Pleistocene glaciations. If further studies show that there are two distinct species, the name *Ch. borealis* Cook, 1956 is available for the Nearctic taxon.

Comments: *Chaoborus crystallinus* is the type species of the genus and it also has the highest number of synonymous names among chaoborids (9, Borkent 2014). One of the synonymous names, *Corethra plumicornis*, may in some cases also refer to *Ch. flavicans* (e.g. Valle 1930). The species is one of the most well-known chaoborids regarding ecology and physiology (e.g. Akerhurst 1922, Parma 1969b, Swift 1992, Burrows & Dosorenko 2014).

### *Chaoborus obscuripes*

*Corethra obscuripes* Van der Wulp 1859: 160 (original description). *Chaoborus obscuripes*: Martini 1929: 58 (redescription). *Chaoborus (Chaoborus) obscuripes*: Edwards 1932: 26 (subgeneric assignment). Peus 1934: (description of larva and pupa). Sæther 1970: 29 (morphology). Sæther 2002: 28 (morphology).

Larva: The largest species of the European *Chaoborus* s.str., length of fourth instar larva is ca. 15–16.5 mm. Coloration of living larvae is yellowish. Subordinate mandibular tooth (III) is situated on the tooth II (Figure 9d). Labral blade is rather wide and serrated (Figure 9c). Dorsal process is globular, blunt (Figure 7i).

Pupa: Respiratory organ is about equally wide along most of its length (Figure 12b). Outer lateral rib of anal paddle has a few modest bristles (Figure 12j).

Adult: Relatively large species with black setosity. Scutum is very dark and pleural sclerites are predominantly infuscated (Figure 16d,e). Paramere with a strong, sclerotized apical claw

that looks either rounded or angular, depending on view (Figure 17c,d); subapical membrane area is large.

**Biology:** The species is uni- or bivoltine in Finland (Paasivirta et al. 1988). Bivoltine populations were observed in 2018, during an exceptionally warm summer in southern Lapland, north boreal and subarctic populations are likely univoltine. Pupation takes place very early in the season, soon after the melting of ice cover. Larvae are common in poly- and oligohumic ponds, also in permanent flarks (pools) of aapamires and hollows of ombrotrophic bogs. This is the most common chaoborid in fishless ponds in Finland, yet usually not present in the smallest permanent ponds or man-made pools. Larvae stay mostly in surface waters and are present in depths up to five metres (Hongve 1975). The species is relatively tolerant of UV-radiation (Nagiller & Sommaruga 2009). Larvae eat mosquitoes, rotifers and small crustaceans, and also other *Chaoborus* larvae.

**Distribution:** Palaearctic. In Europe recorded from central and northern parts (Wagner 2013), absent from Spain (Arranz et al. 2015). In Finland occurring in all ecoregions, collected from a total of 301 localities (Figure 2).

**DNA barcoding:** A total of seven Finnish specimens were barcoded. The specimens fall into a BIN cluster BOLD:ADD1228, which consists of ten specimens (the Finnish ones and 3 from Slovakia, average distance 0.96 %, maximum 2.09 %). It seems that *Ch. obscuripes* is very distantly related to the other European congeners: its nearest neighbour in the BOLD database is a fungus gnat (Mycetophilidae) and its K2P distance to the other European Chaoboridae species varies between 17–20 %.

**Comments:** *Chaoborus obscuripes* is a good indicator of ponds that lack fish populations (Palm & Svensson 2010). Due to its large size, yellowish coloration and the lack of vertical migration, larvae are highly vulnerable to fish predation (Stenson 1978). The species is very common and abundant in the whole of Finland, and it is abundant especially in ponds that are either polyhumic or associated with mires.

### *Chaoborus albipes*

*Corethra albipes* Johannsen 1903: 398 (original description). *Sayomyia rotundifolia* Felt 1904: 366, syn., in part. *Chaoborus* (*Chaoborus*) *flavicans*: Cook 1956: 23, in part (morphology). *Chaoborus cf. flavicans*: Dupuis et al. 2008: (molecular analysis, phylogeny). *Chaoborus albipes*: Salmela et al. 2021: 169 (redescription).

**Larva:** Length of the fourth instar larva is ca. 10–12 mm. Subordinate mandibular tooth (III) is situated exactly between II and IV teeth (Figure 8b). Lateral teeth of mandibles are conspicuous, uppermost tooth is at least as large as the subordinate tooth (Figure 8b). Labral blade elongate, length:width ratio 4.4–6.8, with moderate serration (Figure 8a). Number of mandibular fan setae almost always  $\geq 15$ , usually 15–21.

**Pupa:** Respiratory organ is constricted subapically (Figure 8c), its length is mostly <1000 (700–1060). Outer rib of anal paddle is smooth, mid rib is darker than the lateral ribs. Very similar and practically impossible to separate from the pond populations of *Ch. flavicans*.

**Adult:** Coloration of Fennoscandian specimens is quite dark, including abdomen that is brownish throughout (Figure 18b). Male paramere with a stout apical claw and a protruding lower lip beneath the claw (Figure 19a,b).

**Biology:** The species is perhaps univoltine or bivoltine in Fennoscandia, with overwintering fourth instar larvae. Most often present in small woodland ponds (0.1–0.3 ha in area) with mire or bog vegetation on shores, rarely in large fishless ponds. However, one population was found from a humic pond (Rovaniemi, Lapland, 0.6 ha in area, max depth 8 m) with perch, and the species is therefore able to withstand at least a moderate fish predation. Thus, the species should be able to perform DVM and penetrate the bottom sediment in such ponds to avoid predation. Pupation takes place in early summer in May or June. Feeding ecology is not well known, but in laboratory larvae feed on mosquitoes and small crustaceans. Larvae do not perform vertical migrations in shallow ponds (Taylor et al. 2015) and can be collected from surface waters during daytime.

**Distribution:** Holarctic. In Europe known from Finland and Norway (Salmela et al. 2021). Widely

distributed in Finland, from hemiboreal to north boreal zones, collected from a total of 28 sites (Figure 2).

DNA barcoding: For details, see Salmela et al. 2021. The Finnish specimens (n=16) form a BIN clade BOLD:ADT7561 (average distance 0.33 %, maximum 0.68 %). The nearest BIN cluster is composed of *Ch. albipes* specimens from Kazakhstan, Russian Far East and Canada. The average distance of the two BIN clusters is 1.25 %.

Comments: This species was recently reinstated from synonymy with *Ch. flavicans* (Salmela et al. 2021). Together with *Ch. flavicans* and *Ch. posio*, the three species likely form a monophyletic group within *Chaoborus* s.str., referred to above as the *Ch. flavicans* species group. *Chaoborus albipes* is readily distinguishable from the closely related species in larva and adult male, but pupal stages between *Ch. albipes* and *Ch. flavicans* are highly similar. It is likely that some of the records of *Ch. flavicans*, especially from fishless ponds, actually belong to *Ch. albipes* or *Ch. posio* (see below). Likely to occur at least in Sweden, Russian Karelia and the Baltic countries.

### ***Chaoborus flavicans***

*Corethra flavicans* Meigen 1830: 243 (original description). Berg 1937: (ecology, morphology). *Chaoborus flavicans*: Martini 1929: 56 (redescription). Sæther 1967: (morphology, variation). Parma 1969a: (morphology). *Chaoborus (Chaoborus) flavicans*: Peus 1934: (description of larva). Sæther 1970: 35 (morphology, phylogeny). Sæther 1972: (morphology). Sæther 2002: 27 (morphology). *Chaoborus alpinus* Peus 1938: 63. Hirvenoja 1960: (ecology, male parameres). Hirvenoja 1961: (identification key). Ökland 1964: 131 (ecology, notes on morphology).

Larva: Length of fourth instar larvae is ca. 10–12 mm. The subordinate mandibular tooth (III) is situated exactly between II and IV teeth (Figure 8e). Lateral teeth of mandibles are inconspicuous, uppermost of these is smaller than the subordinate tooth (Figure 8e). Number of mandibular fan setae is almost always <16, usually 12–14. Labral blade is elongated, length:width ratio 3.77–5.95, with irregular serration (Figure 8d).

Pupa: Respiratory organ is constricted subapically, either slender (Figure 8f, in pond populations) or voluminous (Figure 8g, lake

populations), average length:width ratio is 4.16 and 2.75, respectively. Terminal processes as in *Ch. albipes*.

Adult male: Scutellar stripes and the adjoining integument are mostly light brown (Figure 18d,f), rarely darker (Figure 18e). Abdominal tergites 2–5 with subapical transverse dark band (Figure 18g). Gonocoxite is elongate, gonostylus is rather narrow, dark brown – black (Figure 19c). Paramere medially bent and constricted, apical claw darkened, narrow (Figure 19d).

Biology: The species is possibly univoltine in Finland, at least populations of large lakes invariably univoltine. *Chaoborus flavicans* is the only Eurasian truly lacustrine species; larvae perform DVM and can penetrate bottom sediments in deep lakes (e.g. Voss & Mumm 1999, Liljendahl-Nurminen et al. 2002). Ovipositing females do not discriminate between fishless and fish containing water bodies (Berendonk 1999). Populations in ponds emerge in late spring or early summer, those in lakes mostly in July and August. Larvae can be found from ponds, but the species is typically absent from permanent but shallow (<3 m depth) woodland ponds. Especially in north boreal and subarctic Finland, the species is typically absent from lake and pond communities. Instead, larvae are often present in ponds close to larger water bodies, such as oxbow lakes in alluvial zones of large rivers. The species is also present in slow-flowing parts of large rivers (at least occasionally) and brackish water of the Baltic Sea (estuaries, e.g. Meriläinen 1984). Most likely the most common and abundant of the Finnish species, lake populations may attain densities up to several thousands per m<sup>2</sup> (Parma 1971a, Liljendahl-Nurminen et al. 2002). Larvae eat mosquitoes, small zooplanktic organisms and even oligochaete worms in sediments (Parma 1971a). Emergence of adults takes place at nighttime and adults form swarms along shores at dusk (Berg 1937, Hirvenoja 1965, Goldspink & Scott 1971).

Distribution: Holarctic. Widespread and common in Europe, from the mediterranean to the northernmost Fennoscandia (Wagner 2013, Salmela et al. 2021). In Finland present in all ecoregions, known from a total of 1372 localities.



Absent or very rare in NW Lapland (Figure 2), and generally rare in the north boreal zone (see also Luoto & Nevalainen 2009). It is possible that the combination of predominantly oligohumic waters and nocturnal lightness (midnight sun above the Arctic Circle) prevent the occurrence of the species in most fish containing lakes in central and northern Lapland.

DNA barcoding: For details, see Salmela et al. (2021). Finnish specimens belong into two BIN-clusters, BOLD:ACB8413 and BOLD:ADT7895. The former is composed of 32 specimens, collected from Finland (12 specimens), Norway, Germany, Kazakhstan and China. The Finnish specimens of this group are collected from ponds. The latter is composed of specimens from Finland (8 specimens), South Korea and Montenegro, Finnish material being mainly from large, stratified lakes. If Finnish specimens from both BINs are combined, their average within species distance is 0.94 % (min 0, max 2.03 %). We assume that the observed intraspecific divergence is due to isolated refuges during Pleistocene glaciations. Nevertheless, it would be interesting to know if there really are haplotypes that consistently occur either in ponds or lakes and is the slender vs. voluminous type pupal respiratory organ a genetically fixed trait or is it influenced by the environment. Among the species of the *flavicans*-group, *Ch. flavicans* is very distantly related to the other taxa (ca. 30 % distance), whereas *Ch. albipes* and *Ch. posio* are about 17 % distant to each other.

Comments: *Chaoborus flavicans* is a Holarctic species that was recently revised (Salmela et al. 2021). It is likely that most of the pre 2021 records in literature belong to *Ch. flavicans* if the studied specimens originate from lakes. In pond habitats, some of the records may actually represent either *Ch. albipes* or *Ch. posio*, and two such cases were found by us. Firstly, Luoto & Nevalainen (2009) and Nevalainen & Luoto (2010) reported *Ch. flavicans* from a pond at the Sipoonkorpi National Park, Jöusjärvi, and figured a larval mandible in their 2009 article (*op. cit.* p. 189 fig. 2a). The mandible in question, however, displayed large lateral teeth, typical of either *Ch. albipes* or *Ch. posio*. This pond was revisited by JS in May

2020 and larvae were collected for rearing. No *Ch. flavicans* was present in the samples, and instead all *flavicans*-group specimens belonged to *Ch. albipes*. Secondly, *Chaoborus flavicans* was reported by Milardi et al. (2016) from the Värriö Strict Nature Reserve, a pond called “Lake Tippakurulampi”. Such a pond name does not exist in maps, but the exact location of the pond can be deduced from the article (*op. cit.* fig. 1). This pond is a rather deep, spring-fed and fishless habitat, inhabited by an abundant population of *Ch. obscuripes*, a species not detected by Milardi et al. (2016). Despite this, the pond was revisited (JS) in mid-August 2020, and only a few, small *flavicans s.l.* larvae were collected. It is possible that the relatively high altitude and influence of groundwater kept the water cool and delayed the development of *flavicans s.l.* population, that is usually in the III–IV larval stage in that time of year. However, the collected larvae belonged to *Ch. posio*, and it is likely that *Ch. flavicans* is absent in that particular site.

### *Chaoborus posio*

*Chaoborus posio* Salmela in Salmela et al. 2021: 177 (original description).

Larva: Length of fourth instar larvae is ca. 11–12.5 mm. Subordinate mandibular tooth (III) is situated exactly between II and IV teeth, mandibular teeth are extensively darkened (Figure 8i). Lateral teeth of mandibles are conspicuous, the uppermost of these is about as large as the subordinate tooth (Figure 8i). Number of mandibular fan setae is almost always >20, usually 21–28 (Figure 8i). Labral blade is relatively wide, average length:width ratio is 3.7 (range 3–5), with fine serration (Figure 8h).

Pupa: Respiratory organ is rather short, club-shaped, not constricted subapically (Figure 8j). Terminal process as in *Ch. albipes*.

Adult: General coloration is very dark, including scutum, thoracic pleura and abdomen (Figure 18h,i). Gonocoxite is brown and rather wide. Gonostylus is dark brown and relatively wide (Figure 19e). Epandrium is broadly rounded. Paramere is very dark and strongly sclerotized; apical claw is long and stout, almost straight (Figure 19e,f).

**Biology:** Most likely this is a univoltine species. Pupation takes place in early summer. Larvae are associated with rather large and fishless ponds, with mire vegetation on their shores. In one case collected from an alkaline, clear water pond surrounded by rich fen. The species almost always co-occurs with *Ch. obscuripes* and it is presumed that large surface area or depth permits their coexistence. It is not known if the larvae are able to perform vertical migrations. Larval diet is not well known, but at least consists of planktonic crustaceans.

**Distribution:** European, hitherto known from Finland only, but it is likely to occur at least in Norway, Sweden and NW Russia. In Finland mostly collected from the north boreal and subarctic ecoregions, but there is a disjunct population in the south boreal zone; observed from a total of 18 localities (Figure 2).

**DNA barcoding.** For details, see Salmela et al. (2021). A total of 17 Finnish specimens were sequenced, being assigned to the unique BIN-group BOLD:ADT7562 (average intraspecific distance 0.21 %, min 0, max 0.67 %).

**Comments:** *Chaoborus posio* was recently described from Finland. This is a third member of the *Ch. flavicans*-complex of species, and it can be readily identified in larval, pupal and adult stages. The species may have a northern range in the Eurasian taiga. Phylogenetic relationships between the three species and within *Chaoborus* s.str. are still unresolved.

### ***Chaoborus nyblaei***

*Erioptera nyblaei* Zetterstedt 1838: 830 (original description). *Chaoborus (Schadonophasma) nyblaei*: Edwards 1930a: 533 (valid species, assignment to the subgenus). Hirvenoja 1961a: 80 (redescription). Borkent 1979: 152 (redescription, phylogeny). Sæther 2002: 28 (morphology).

**Larva:** The largest of the Eurasian species, length of fully grown larvae ca. 18–22 mm, coloration of living larvae yellowish. Mandible as in Figure 9f. Labral blade rather narrow, strongly serrated (Figure 9e). Outline of head rather pointed in lateral view (Figure 7e).

**Pupa:** Respiratory organ sausage shaped (Figure 12c), length ca. 1300. Abdominal tergites very wide, width:length ratio ca. 2.5 (Figure 12g).

**Adult:** Coloration of thorax and abdomen light brown – greyish, scutellar stripes light brown – orange brown; legs brown, apices of femorae and tarsi infuscated, wings patterned (Figure 16g,h). Gonocoxite and gonostylus light brown, rather narrow (Figure 17e). Paramere elongated, apically curved (Figure 17e,f).

**Biology:** Univoltine species with overwintering eggs. Larvae are present in seasonally dry and permanent ponds. Larvae hatch from the eggs in spring and are full-grown within roughly a six to eight week period, depending the temperature during this time. Larvae eat planktonic Crustacea, mosquito larvae and pupae, other chaoborids and even other *Ch. nyblaei* larvae of the same size. It has been observed that the larvae can devour fairy-shrimps (Lindholm et al. 2016). Adults have been observed from late June to August. Swarming and oviposition behaviour in natural conditions have not been observed.

**Distribution:** European, so far known from Fennoscandia only (Norway, Sweden, Finland, Hirvenoja 1961a, Borkent 1979). In Finland observed from the northern part of the middle boreal, north boreal and subarctic ecoregions, a total of 50 localities (Figure 2).

**DNA barcoding:** A total of six Finnish specimens were barcoded. The specimens fall into a BIN cluster BOLD:ADD1227, which consists of no other records (average distance 0.6 %, maximum 1.12 %). It seems that *Ch. nyblaei* is distantly related to the other European congeners, because the nearest neighbour in the BOLD database is a Nearctic *Schadonophasma* cluster of specimens (perhaps *Ch. cooki*, average distance 11.24 %).

**Comments:** The species is either a Fennoscandian endemic or, more likely, it may have a more widespread taiga and subarctic range extending to NW Russia and Siberia. The species may have been overlooked due to its life cycle (univoltine, eggs overwintering) and generally northern distribution. Hence, the immature stage of the species is relatively short, from May to August, depending on latitude and yearly thermal conditions and thus the species will remain undetected if samples are collected too late in the season.

A tentative synonym of the species *Corethra pilipes*, was described from Riga, Latvia (Gimmerthal 1845). The original description is inadequate by present day standards, and e.g. it is not mentioned if wings are patterned or not. The key characters that fit well to *Ch. nyblaei* are the infuscated apices of femorae and tarsi. Apparently, the type specimen is lost (Borkent 2014) and the conspecificity of the two names cannot be established. Based on the current range of the species, *Ch. nyblaei* is not likely to occur in the Baltic countries. Nevertheless, the species should be searched for from southern Fennoscandia and the Baltic states, too.

The species is assessed as VU (vulnerable) in the Finnish red-list (Salmela *et al.* 2019). The assessment was made in early 2018, predating the large-scale collecting effort in that year. Hence, at that time, it was not known how common the species actually is especially in eastern Lapland. However, *Ch. nyblaei* is seemingly rare along its southern range, despite its several populations in an upland area south of the Arctic circle in Rovaniemi. The species may also be negatively impacted by global warming (but see Lindholm *et al.* 2016, 2018).

Lindholm *et al.* (2016, 2018) presented novel and interesting results on *Ch. nyblaei* in relation to climate change and predation. These studies are summarized in the following way: global warming increases vegetation in the arctic-alpine landscapes, which in turn leads to browning effect of lentic waters (increased TOC levels). Because UV-radiation deteriorates DNA of *Chaoborus* (Nagiller & Sommaruga 2009), larvae have a threshold in regard to TOC, which attenuates UV-radiation. In effect, browning of arctic-alpine waters may lead to a range extension of *Chaoborus* spp. According to their results (Lindholm *et al.* 2016), *Ch. nyblaei* may occur up to altitudes of 1175 m asl, and locally it can drive extinct the arctic fairy-shrimp (*Brachynecta paludosa*). Moreover, in laboratory ovipositing *Ch. nyblaei* females preferred humic water over clear, giving experimental support to the range extension of the species (Lindholm *et al.* 2018). However, it is not known if the females were allowed to mate in the laboratory or whether the adults copulate in

small cages without the possibility of swarming. Hence, the females may have just laid infertile egg batches on the containers. On the other hand, it is still to be solved if the species lays eggs in soil or on the water surface. The oviposition behaviour of the putative Nearctic sister species, *Ch. cooki*, has been observed in the laboratory, where the females laid eggs with thick protective layer on the walls of vials, not on the water surface (Borkent 1979, p. 190). Such eggs may also be possessed by *Ch. nyblaei* females.

### ***Chaoborus pallidus***

*Tipula pallidus* Fabricius 1781:407 (original description). *Chaoborus pallidus*: Martini 1929: 58 (redescription). *Chaoborus (Sayomyia) pallidus*: Edwards 1930a: 533 (subgeneric assignment). *Chaoborus (Peusomyia) pallidus*: Sæther 1970: 11 (redescription, new subgenus). Sæther 2002: 33 (morphology).

Larva: Length of fourth instar larva is ca. 10–11 mm. Antenna is ventrobasally straight, i.e. without a notch (Figure 7f). Labral blade is very narrow, needle-like, with a few serrations (Figure 9g).

Pupa: Respiratory organ is ovoid in shape, rather short (730–760) (Figure 12d). Median rib of terminal process is straight (Figure 12h).

Adult: A small, pale species. Wings with a weak median pattern. Femorae and tibiae are with numerous dark rings (Figure 16i). Gonocoxite is apically infuscated, bearing numerous stout, apically hooked setae ventromesially (only one of these shown in Figure 17g). Gonostylus is notched apically (Figure 17g). Aedeagus is present (Figure 17g,i), absent in all other European species. Parameres are finger-like and angular, being connected by a hyaline bridge (Figure 17g,h).

Biology: The species is perhaps bivoltine in Finland, adults have been collected in early (May–June) and late (July–September) season. Larvae occur in small, permanent ponds, ranging from polyhumic forest pools to eutrophic ditches and turbid, artificial ponds. Larvae may seek refuge among vegetation (Edwards 1920).

Distribution: Palaearctic, widespread in Europe (Wagner 2013), including Spain (Arranz *et al.* 2015), Norway (Olsen 2008) and Sweden (Liungman 2005). In Finland the distribution is

restricted to the hemi- and south boreal ecoregions (Figure 2), and is recorded from a total of 27 localities.

DNA barcoding: Only one Finnish specimen was successfully barcoded, and that specimen is the sole member of the BIN BOLD:AEC0470. *Chaoborus pallidus* is distant to all other European *Chaoborus*, its K2P interspecific distance varies between ca. 19–21 %. In the BOLD database, however, its nearest neighbor is Nearctic *Ch. albipes*, average distance being 13.22 %. It should be noted that Japanese *Ch. pallidus* specimens are very distant to the European specimens (18.45 %), and there are also morphological differences; it is likely that Japanese specimens represent an undescribed species (J. Salmela et al., in prep.).

Comments: *Chaoborus pallidus* is seemingly rare in Finland, given the low number of observed localities. Most likely, however, the species is common in small ponds and lentic ditches in southern Finland. The northern range of the species in Finland is still to be resolved.

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