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**TAXONOMY, SPECIES RICHNESS AND
BIOGEOGRAPHY OF FINNISH CRANE FLIES
(DIPTERA, TIPULOIDEA)**

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**Dedicated to the memory of Professor Carl Lundström (1844–1914),
the first student of Finnish crane flies**

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LIST OF ORIGINAL PAPERS

This thesis is a summary of the following publications and manuscripts, which are referred to by their Roman numerals in the text:

- I** Salmela J (2012) Revision of *Tipula (Yamatotipula) stackelbergi* Alexander (Diptera, Tipulidae), and a short discussion on subspecies among crane flies. *ZooKeys* 162: 43–58.
- II** Pilipenko V, Salmela J & Vesterinen EJ (2012) Description and DNA barcoding of *Tipula (Pterelachisus) recondita* sp. n. from the Palaearctic region. *ZooKeys* 192: 51–65.
- III** Salmela J (2012) Annotated list of Finnish crane flies (Diptera: Limoniidae, Tipulidae, Pediciidae & Cylindrotomidae). *Entomologica Fennica* 22: 219–242.
- IV** Salmela J (2012) Biogeographic patterns of Finnish crane flies (Diptera, Tipuloidea). *Psyche: A Journal of Entomology* 2012: Article ID 913710, 1–20.

	II
Original idea	JS
Field work	JS, VP
Preparation of material	JS, VP
Identification of specimens	JS, VP
DNA analyses	EJV
Other analyses	JS
Writing of the manuscript	JS, VP, EJV
Comments of the manuscript	VP, EJV

JS: Jukka Salmela, VP: Valentin Pilipenko, EJV: Eero J. Vesterinen

ABSTRACT

Biodiversity is unequally spread throughout terrestrial ecosystems. The highest species richness of animals and plants is encountered around the Equator, and naturalists observe a decrease in the number of creatures with increasing latitude. Some animal groups, however, display an anomalous species richness pattern, but these are exceptions to the general rule. Crane flies (Diptera, Tipuloidea) are small to large sized, non-biting nematoceran insects, being mainly associated with moist environments. The species richness of crane flies is highest in the tropics, but these insects are species rich and abundant in all biogeographic realms, boreal and arctic biomes included. The phylogeny and systematics of crane flies are still at an early stage and somewhat controversial. New species are constantly discovered even from temperate Europe, faunistically the best known continent. Crane flies have been rather neglected group of insects in Finland. The history of Finnish crane fly taxonomy and faunistics started in 1907, the year when Carl Lundström published his two first articles on tipuloids. Within roughly 100 years there have been only a handful of entomologists studying the Finnish fauna, and the species richness and natural history of these flies have remained poorly understood and mapped. The aim of this thesis is to clarify the taxonomy of Finnish crane flies, present an updated and annotated list of species and seek patterns in regional species richness and assemblage composition.

Tipula stackelbergi Alexander has been revised (I). This species was elevated to a species rank from a subspecific rank under *T. pruinosa* Wiedemann and *T. stackelbergi* was also deleted from the list of European crane flies. Two new synonyms were found: *T. subpruinosa* Mannheims is a junior synonym of *T. freyana* Lackschewitz and *T. usuriensis* Alexander is a junior synonym of *T. pruinosa*. A new species *Tipula recondita* Pilipenko & Salmela has been described (II). Both morphology and COI (mtDNA) sequences were used in the assessment of the status of the species. The new species is highly disjunct, known from Finland and Russian Far East. A list of Finnish crane flies was presented, including the presence of species in the Finnish biogeographical provinces (III). A total of twenty-four species were formally reported for the first time from Finland and twenty-two previously reported species were deleted from the list. A short historical review on the studies of Finnish crane flies has been provided. The current list of Finnish species consists of 338 crane flies (IV, Appendix I). Species richness of all species and saproxylic/fungivorous species is negatively correlated with latitude, but mire-dwelling species show a reversed species richness gradient (i.e. an increase in the number of species toward north). Provincial assemblages displayed a strong latitudinal gradient and faunistic distance increased with increasing geographical distance apart of the provinces. Nearly half (48 %) of the Finnish crane flies are Trans-Palaeartic, roughly one-third (34 %) are West Palaeartic and only 16 and 2 % are Holarctic and Fennoscandian, respectively. Due to the legacy of Pleistocene glaciations, endemic Fennoscandian species are problematic and it is thus concluded that there are probably no true endemic crane flies in this region. Finally, there are probably species living within Finnish borders that have hitherto remained unnoticed. Based on subjective assessment, the number of “true” (i.e. recorded + unknown species) species count of Finnish crane flies is at minimum 350.

1. INTRODUCTION

1.1. Taxonomists never die

Let us imagine a taxonomist describing a new species, an insect for example. The taxonomist has gone through thousands of specimens, perhaps pinned or preserved in ethanol, and named all of them to the lowest possible taxonomic rank. Genus is better than family, but species is better than genus. Subspecific and infrasubspecific ranks are ambiguous, and ignored here. If our taxonomist is working on a material collected in the temperate zone or from an industrialized country, most of the material, 90 % or more, could perhaps be named to known species. Working on material collected from the tropics, the situation may be almost the opposite: 10 % or less are known species, i.e. already described, whereas 90 % or more are without a scientific name, i.e. unknown species. One may think that the next step is easy: the taxonomist should just draw illustrations / take photographs, write a description, give a Latin binomial and submit the manuscript to a journal. Indeed, many have done this, and recklessly. Depending on taxonomic group or biogeographic realm, there may be several scientific names for a given species (Gaston 2003, Jones et al. 2012). Such synonymous names are problematic. If the nomenclature has remained uncorrected, species richness estimates will be inflated for larger areas (e.g. Europe, Palearctic region).

In many cases morphological differences between species are small, microscopic. Old descriptions may be of poor quality according to present day standards and identification keys may be outdated. It follows that the procedure of describing a new species is not straightforward. Hence, in order to maintain good taxonomic standards, the taxonomist should loan and examine all relevant type material, at least holotypes or lectotypes, to be sure that the new name proposed for the species is valid and not synonymous. The oldest types in entomology date back to 1758 and Linnaeus, older material or literature is not useful for taxonomic purposes (ICZN 1999). Types may be preserved in various museums all over the globe, some types maybe missing, lost in fire or eaten by beetle larvae, leaving only a pin and dusty labels. In dipterology, a discipline within entomology devoted to true flies (order Diptera), taxonomy is heavily based on male specimens. Thus, especially among nematoceran families females are often difficult, laborious or impossible to identify (e.g. Hippa et al. 2010). Nevertheless, some holotypes may be females, providing an additional source of frustration. It is also possible that a holotype is in otherwise good condition, but important body part (e.g. hypopygium) is missing or dissected in a manner not allowing examination of morphological details (I).

Let us imagine further. Our taxonomist has studied specimens from some restricted region, say a one hectare plot of rainforest, Great Smoky Mountains National Park or New Zealand, for instance. The taxonomist has also studied relevant types and associated literature and become confident that, yes, this is a new species. Then, accidentally, the taxonomist receives an email from a colleague. The colleague, studying similar fauna in another area, is asking “Have you seen this kind of creature?” There is an attached photo,

depicting a specimen very similar to the one that the taxonomist was about to describe. A new problem arises: are the specimens conspecific or do they belong to different species. In most cases, there are only a few specimens available. Most species are rare, either in their numbers in local assemblages, or restricted in their occurrence (with a small total range or a low area of occupancy). In addition, species may be elusive, hard to collect and bring to natural history museums. This means that usually most descriptions are based on a rather small number of studied specimens (May et al. 1995). However, the decision made, whether specimens are conspecific or not, is largely a working hypothesis, based on expert opinion. As Grimaldi and Engel (2005, p. 6) put it: “*They [systematists] assess variation and then lump individuals on the basis of consistent similarities*”. A group of taxonomists may later be lucky enough to collect larger number of specimens from the whole range of the species, and thus obtain a better understanding of intraspecific variation (one species) or interspecific characteristics (two or more species). There is no rule how many specimens one should examine before giving a name to a new species. It is also possible that the single specimen in hand may just be an aberrant individual, morph (e.g. short winged or apterous specimen of a species that usually have normal wings) or gynandromorphic (that is, displaying both male and female characteristics simultaneously). In general, the higher the number of studied specimens, the higher the validity of the description. Practically all systematic entomologists are studying dead animals, and the species concept used is based on phenotypic, and perhaps also genetic, variation among the examined specimens. Thus, although implicitly stated, the species concept in most entomological descriptions is either a Genotypic Cluster Species Concept or a Phylogenetic Species Concept(s) (see e.g. Coyne & Orr 2004, and also de Queiroz 2005 for a discussion of species concepts). Our taxonomist and his/her colleague are probably well aware of the fact that speciation is not tidy (cf. Burns et al. 2007). Of course there are many sympatric taxa that are well distinguished based on their morphology and DNA sequences. But there are also many allopatric and parapatric populations in the early stages of divergence, still exchanging genes with the ancestral population. In taxonomy scientists draw lines between populations; some lines are thick and resist all efforts of interbreeding but some lines are thin and may vanish due to the lack of proper isolating mechanisms.

To conclude, taxonomic ranks may change and new taxa may be discovered, from rain forests, boreal springs or even from one’s backyard. Hopefully, step by step, we are improving our understanding of how many species there are on the Earth, which species are rare and which are common. Despite the fact that there is no single, universally accepted species concept (but see de Queiroz 2005), without taxonomy ecologists, managers of natural resources, decision-makers and conservationists could not communicate. In short, the species is the most important concept in biology.

It has been noted that taxonomy is in crisis (e.g. Agnarsson & Kutner 2007). Natural history museums, buildings where most taxonomists work, are struggling with financial problems. Scientific journals that publish taxonomic papers have usually a low impact factor, or no impact factor at all (Agnarsson & Kutner 2007, Valdecasas 2011). Young

scientists may thus think that taxonomy is not a good career to choose: if you publish in low-impact journals you may have poor chances to get grants or paid work. It is also clear that there are many more species living out there without a scientific name, than there are named ones (Mora et al. 2011) and global biodiversity is declining in alarming rate (Sala et al. 2000). It is thus likely that many small bodied and elusive creatures are lost before they were named by taxonomists. Hence, taxonomy is important. Moreover, only if we have a reasonable taxonomic knowledge are we able to do meaningful ecological research. In addition, if there are many erroneous identifications or synonyms, as there may well be (see e.g. Gaston 2003, Gaston & Mound 1993), we may make spurious assumptions about species' range, rarities and diversity patterns.

A decade ago the technique of DNA barcoding was presented, as a possible new tool to accelerate the discovery of new species (Hebert et al. 2003, Tautz et al. 2003). This new method has been successful in many cases, e.g. in the identification of cryptic species that are difficult to diagnose with traditional methods (Smith et al. 2006). In addition, DNA barcoding can be used to associate sexes of the same species or used in the identification of immature stages (e.g. Hubert et al. 2010) that are usually harder to identify than sexually mature specimens. However, considering taxonomy, barcoding is almost useless without a solid reference library (Meier et al. 2006). Specimens older than 20 years are notorious in not yielding comparable, high quality DNA sequences: this fact alone prevents straightforward sequencing of most of the existing holotypes. Nevertheless, DNA barcoding is a useful method in taxonomy and biodiversity studies, especially if used together with morphological understanding (e.g. Emery et al. 2009).

1.2. Natural history of crane flies

Crane flies (Diptera, Tipuloidea) are small to large-sized true flies, belonging to the infraorder Nematocera. Classification of crane flies is controversial. Following Starý (1992), most European authors distinguish four families: Limoniidae, Tipulidae, Pediciidae and Cylindrotomidae. North American authors, strongly influenced by C.P. Alexander, usually prefer a single family, Tipulidae; other families, *sensu* Starý, are there subfamilies or tribes (Byers 1992, Petersen et al. 2010). According to a recent phylogenetic analysis (Petersen et al. 2010), two families are recognized, Tipulidae and Pediciidae, but the consensus tree of that analysis had many unresolved polytomies. Hence, the higher classification of crane flies is still problematic. Within Nematocera, however, monophyly of Tipulomorpha (Tipuloidea + Trichoceridae) is well supported (Wiegmann et al. 2011). In this thesis, Starý (1992) is followed, mainly because of the long Fennoscandian tradition of separating the limoniids (including pediciids) from the tipulids (e.g. Lundström 1907a,b, 1912, Tjeder 1955, Mendl 1974).

The global crane fly taxonomy was greatly dominated by C.P. Alexander, a man who described over 10 000 species (Oosterbroek 2009). In the Palaearctic region, two prominent figures should be mentioned, namely B. Mannheims (Reusch & Oosterbroek 2009)

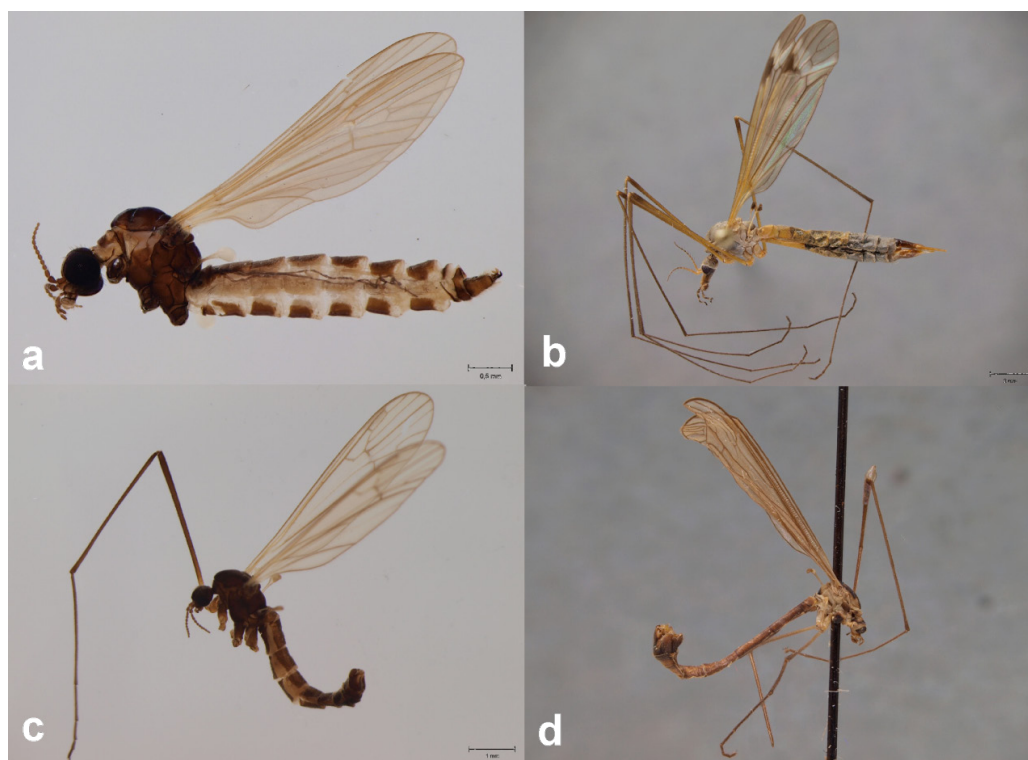


Fig. 1. **a)** *Symplecta lindrothi* Tjeder, Limoniidae, male specimen (Finland). This species is so far known only from Finland and Sweden. The species is typically found around springs and headwater streams. **b)** *Tipula jutlandica* Nielsen, Tipulidae, female specimen (Russia). This is a poorly known and rare Palearctic species. This female specimen was identified based on COI gene sequences; the female of this species has not been described. **c)** *Dicranota robusta* Lundström, Pediciidae, male specimen (Finland). This is a northern species in Finland, living in streams. **d)** *Cylindrotoma borealis* Peus, Cylindrotomidae, male specimen (Norway). This is the holotype, loaned from the Museum für Naturkunde, Berlin (MFN). This taxon may be a northern–eastern haplotype within the wide-spread Holarctic species *C. distinctissima* Meigen.

and E.N. Savchenko (Lantsov 2009), who produced several high quality descriptions and monographs (e.g. Mannheims 1952, Savchenko 1961). Globally, literature for identification is scattered and hard to find. The Catalogue of the Craneflies of the World (Oosterbroek 2012) is a magnificent source of information, and more and more scanned publications (e.g. all >1000 Alexander's papers) and figures on male hypopygia etc. are being added there. Because of the i) inaccessible literature, ii) a high number of species and iii) high number of undescribed species, especially outside Europe, crane flies are a challenging group to study. However, taxonomy and nomenclature of North European fauna are relatively stable. In recent years, despite large sampling efforts (see below), only two new species have been described from here (Salmela & Starý 2008, II).

There are over 15 000 described crane fly species (de Jong et al. 2008, Oosterbroek 2012), and the number is about to increase. New species are constantly discovered even from Europe (e.g. Starý 2011a,b, Ujvarosi & Balint 2012) which is faunistically the best known continent.



Fig. 2. Limoniid crane fly *Dicranomyia aperta* Wahlgren visiting on *Parnassia palustris* flower. The fly species is associated with calcareous fens and springs, currently classified as Near Threatened (NT) in Finland (Penttinen et al. 2010). Photo J. Salmela 8/2012.

Tipuloidea is the most species rich dipteran superfamily, and most species are known from the neotropics and oriental region (Pape et al. 2009). Among Tipuloidea, Limoniidae is the most species rich family (10 512 spp.), followed by Tipulidae (4272), Pediciidae (490) and Cylindrotomidae (71). In the West-Palaeartic region, a total of 1549 species are known, and the species richness increases with decreasing latitude. For example, 494 species are known from Italy, 465 from Germany and 338 from Finland (Oosterbroek 2012, Fig. 3).

Members of the family Limonidae (Fig. 1a) vary in their size, but generally have short last palpal segment and wing vein S_c ending on the Costa. Apparently there are many lineages or tentative subfamilies within “Limoniidae” (Petersen et al. 2010), at least many more than the four proposed by Starý (1992). Limoniids dwell in moist, and even in aquatic habitats, but some genera are associated with fungal fruiting bodies or decaying wood; most larvae eat decaying organic material or other invertebrates. Adults of some genera have an elongated rostrum (e.g. *Elephantomyia*), and their adults visit flowers, as do several other species with a “normal” short rostrum (Fig. 2). The appearance of adults is usually darkish or drab brown, having pruinosity on thorax and abdomen, but some are bright yellow or green and may be shining. Many forest-dwelling species have patterned wings (e.g. *Discobola*, *Metalimnobia*). *Chionea* adults, so called snow crane flies, are wingless and are active from late autumn to early spring.

Tipulidae (Fig. 1b) are among the largest crane flies, wing span may be over 60 mm. Tipulids have an elongated last palpal segment and S_c ending on R_1 . Larval habitats range from riffles to desert soils, while some species are associated with mosses or decaying wood. Adults of the subfamily Ctenophorinae are coloured by shining black, orange

or yellow, mimicking parasitoid wasps, males having pectinate antennal flagellomeres. Tipulines are mostly darkish-gray or brownish in their coloration, wings may be clear or patterned. The females of some species (e.g. *Tipula gimmerthali*) have rudimentary wings, while the males are capable of flying. Dolichopezinae adults have white tarsi. It should be noted that the classification of Ctenophorinae, Dolichopezinae and Tipulinae as separate subfamilies was not supported by Petersen et al. (2010).

Pediciids (Fig. 1c) are similar to limoniids, but their eyes (ommatidia) are hairy. Most species of Pediciidae are predatory in their larval stages, living mostly in fresh water or moist habitats, but the larvae of the genus *Ula* are confined to fungal fruiting bodies. Adult pediciids are mainly small and inconspicuous (e.g. *Dicranota*), but some species are large bodied with contrasting wing pattern (e.g. *Pedicia rivosa*).

Cylindrotomids (Fig. 1d) are unique among crane flies, given their herbivorous mode of life. Some genera are associated with mosses, some with terrestrial vascular plants. Those moss-eating genera may be aquatic (*Phalacrocer*), semiaquatic (*Triogma*) or terrestrial (*Diogma*). Larvae are sluggish, bearing spines on their dorsal side. Adult males have trifid aedeagal apices and female cerci are specialized to oviposit eggs on plant tissues. The tip of the abdomen exceeds the wing length, giving a long-bodied appearance.

C. Lundström was the first who studied Finnish crane flies seriously (III). His four major publications (Lundström 1907a,b, 1912, Lundström & Frey 1916) formed the basis for Finnish crane fly taxonomy and faunistics. Lundström described several new species and many of these are still valid. After his short but prolific era, there were no Finnish crane fly specialists during the following decades (see III for details). R. Frey, with his co-authors, recorded 227 crane fly species from Finland (Frey et al. 1941). Since then the accumulation of Finnish species has seen periods stagnations and rises (Fig. 3), caused

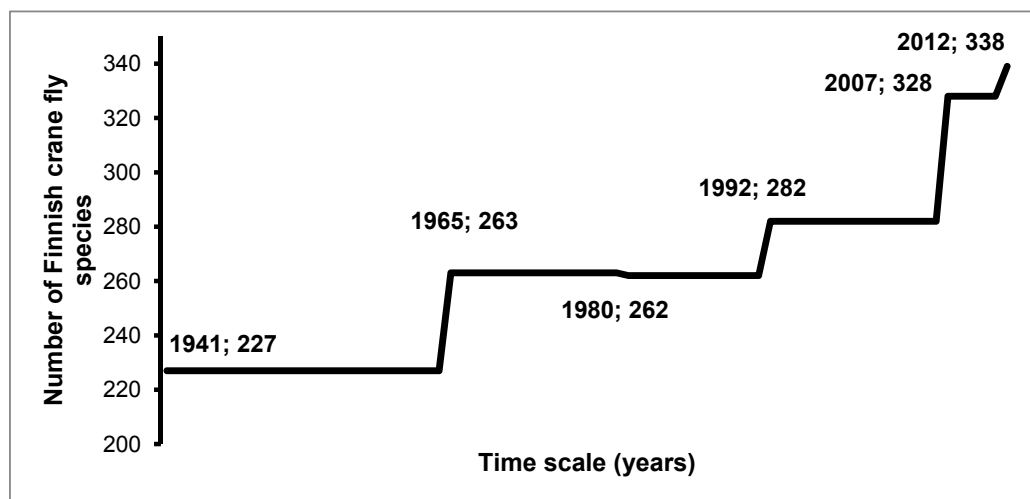


Fig. 3. Accumulation of Finnish crane fly (Diptera, Tipuloidea) species, following Salmela (2008, fig. 1, 1941–2007) and IV (2012). Four limoniid species have been discovered new for Finland after the publication of paper IV, see Appendix I for details.

by the activity of a few people each decade. At present, 338 species are known from Finland, and it is likely that there still are species awaiting discovery. Hence, 338 is an observed number based on cumulative collecting effort starting from Lundström and ending with Salmela. Because the observed number of species in a given geographic area is usually an underestimate (Magurran 2004), it would be interesting to estimate the total number of Finnish crane flies. That is, based on expert opinion, to give an academic guess whether there are 1, 10 or 100 regionally unrecorded species. I will come back to this issue in the Conclusions.

1.3. What is species richness?

Species richness, that is the number of species in a taxonomic group in a given geographic area, is an easy concept. However, the distribution of individuals among species is usually highly skewed. In most assemblages, a few species are abundant and many more occur in low numbers (Magurran 2004, McGill et al. 2007). Diversity, instead of species richness, is a concept which takes into account the variation in abundance between species. In general, the more similar the abundances of each species, the higher the diversity in a given area (Magurran 2004, Jost 2006, Tuomisto 2011). In the present thesis, diversity is not discussed further since only presence – absence data is used (IV); all species have equal weight in the analyses because satisfactory abundance data was lacking.

Despite species richness being an easily understood and straightforward concept, it may be hard to measure in practice. As noted above, species differ in their abundance. A modest sampling effort may yield most of the common species, but the rarest ones, occurring in low abundance, will be missed. For example, in inventories of forest-dwelling beetles in the boreal zone, one has to collect ca. 200 species in order to detect at least one red-listed species (Martikainen & Kouki 2003). As showed by Longino et al. (2002), a representative view on species richness may be achieved if several trapping methods of intensive collecting are used. However, large samples containing tens of thousands of specimens may still have many singletons (Novotny & Basset 2000, Hyvärinen et al. 2006, Coddington et al. 2009), and a large proportion of singletons in a sample usually indicates the presence of unseen species (Colwell & Coddington 1994, Magurran 2005, 2007, Coddington et al. 2009). In other words, there are species present in the sampled area but they were not detected; true species richness is thus higher than the observed one. To conclude, it is important to understand the quality of the species richness data. If there are many unseen species, one may obtain erroneous estimates of the conservation value and beta diversity, for example.

On a global scale, species richness is highest around the equator, decreasing gradually toward the poles. Hence, in most animal and plant groups, the tropics harbour far more species than do the temperate or arctic zones (Gaston 2000). The most likely explanations for this pattern are related to the productivity and biomass, being determined by the amount of available energy (sun light) and moisture (Clarke 2007). In addition, historical

factors have an impact on the pattern: Pleistocene glaciations totally eradicated fauna and flora from most high latitude areas, while the tropics probably experienced less severe climatic stress (Cox & Moore 2005). In addition, the tropics have the largest geographical land area, and larger areas invariably support more species than smaller areas (Rosenzweig 1995, Gaston & Blackburn 2000).

Despite the predominance of the general trend, some taxa show a reversed latitudinal pattern in species richness. For instance, sawflies (Kouki et al. 1994) and aphids (Dixon et al. 1987) are richer in species in the north boreal and temperate zones than in the tropics. Within northwestern Europe, the species richness of stone flies (Lillehammer 1985, Heino 2002), waders (Järvinen & Väisänen 1978) and mire-dwelling bird communities (Järvinen & Sammalisto 1976, Järvinen et al. 1987) increases toward the north. It has been discussed that the availability of resources best explains the reversed patterns. For example, environmental complexity, total area of flark fens and abundance of invertebrate food explains species richness of mire-dwelling birds and waders in the north Fennoscandia (Järvinen & Väisänen 1978, Järvinen et al. 1987). In a related vein, the high diversity and abundance of willows (*Salix*), the most important food plant for sawfly larvae, accounts for the reversed pattern of sawfly richness (Kouki et al. 1994, Kouki 1999).

1.4. Finnish biogeography

Finland is geographically part of Fennoscandia, being located in the northernmost Europe. Current Fennoscandian biota is much influenced by the legacy of Pleistocene glaciations (Pekkarinen 2001). The latest glacial maximum (Weichselian) took place about 18 000 years ago and only a small part of the Fennoscandia was free of ice by some 11 000 years ago (Pekkarinen 2001, Cox & Moore 2005). However, considering Finland alone, all terrestrial biota must have had colonized Finland during the last circa 10 000 years. Because of this recent origin of Finnish biota, endemic species (i.e. taxa only present in Fennoscandia and nowhere else) are exceptions (e.g. Brüstle & Muona 2009). European, or West Palaearctic species currently present in Finland are descendants from South European glacial refugia (Hewitt 2004, Knopp & Merilä 2009). In addition to southern species, the list of Finnish biota has a strong taiga element, i.e. boreal species of eastern origin, and also an arctic element, i.e. circumpolar species (e.g. Hultén 1950, Mikkola 1996, Mikkola et al. 1991, Mönkkönen 1994).

Finland is part of the Holarctic biome called the boreal zone, that is, a belt of coniferous forests. Southernmost parts of the country are hemiboreal, with mixed broad-leaved (e.g. *Quercus*, *Ulmus*, *Fraxinus*) and coniferous stands (see Fig. 3b). The south boreal zone is the northern limit for some broad-leaved trees, such as *Tilia cordata* and *Acer platanoides*. The middle boreal zone possesses increasing amount of northern elements, such as *Picea abies* ssp. *obovata*, and a decreasing number of southern elements (e.g. *Alnus glutinosa* occurs there at its northern limit). The north boreal zone is mostly coniferous,

Picea abies and *Pinus sylvestris* dominate, but *Betula* spp., *Populus tremula* and *Alnus incana* occur in the whole region. Northernmost subalpine Finland is characterized by mountain birch (*Betula pubescens* ssp. *czerepanovii*) forests and tree-less fells (Euroala 1999). Due to this latitudinal variation, Finland is an optimal region for biogeographic studies (see e.g. Järvinen & Väisänen 1973, 1980). Composition and species richness of Finnish fauna and flora are mainly driven by latitudinal variations in climate and local environmental factors (Lahti et al. 1988, Väisänen et al. 1992, Väisänen & Heliövaara 1994, Heino et al. 2002, Luoto et al. 2006, Heino & Toivonen 2008, Ilmonen et al. 2009, Eronen et al. 2011). In addition, some plant species reflect increasing continentality from western to northeastern Fennoscandia (Ahti et al. 1968, Pedersen 1990), but among insects longitude is a poor biogeographic predictor in NW Europe (Väisänen et al. 1992).

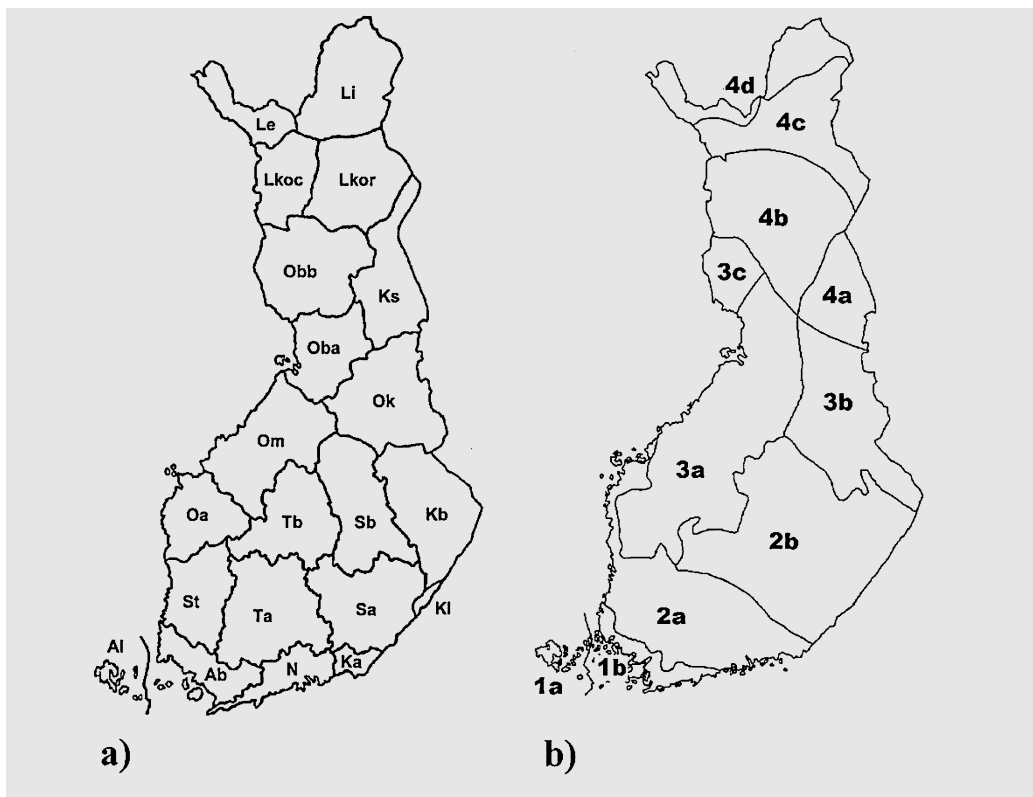


Fig. 4. a) Finnish biogeographical provinces, **b)** Finnish ecoregions or vegetation zones: 1= hemiboreal, 2= south boreal, 3= middle boreal, 4= north boreal. Abbreviations of the Figure 4a are explained in paper IV.

2. AIMS OF THE THESIS

Why crane flies? Tipuloids are usually abundant in moist or shaded habitats, and given their generally large size, they are important in detritus processing. They also serve as prey items for vertebrate animals, especially for birds. The species richness of crane flies in Europe is relatively high, definitely high enough for reasonable biogeographic assessment. Furthermore, the taxonomy of the North European species is quite well known, lowering the probability of obtaining erroneous macroecological patterns. The vast majority of all identifications used in this thesis have been either made or controlled by me, hopefully improving the consistency of identifications. Many crane flies are associated with some specific habitat type. For example, some species dwell invariably on decaying aspen trees, calcareous fens or alpine wetlands. For these reasons crane flies are suitable organisms for biodiversity studies and macroecological research in the boreal zone.

The aim of this thesis is to clarify the taxonomy and faunistics of Finnish crane flies and to seek patterns in regional species richness. *Tipula stackelbergi*, a poorly known Palaearctic species has been revised (I). By studying the holotype of *T. stackelbergi* and type material of two other *Tipula* species, I wanted to clarify the nomenclature and ranges of *T. stackelbergi* and related taxa. In the same vein, subspecific ranks among tipuloids were discussed. Based on material collected from Finland and Russia, one new species has been described (II). Alongside the description, 17 closely related species were examined and their DNA barcoding region was sequenced. Based on the barcodes, the status of the new species was verified and a Maximum Likelihood tree was constructed to show graphically the relatedness of the species. Lists of Finnish crane fly species have been published since Frey et al. (1941) and, in addition, dozens of species have been reported as new for Finland in various notes (Siitonen 1983, Rautio 1986) and papers (Mannheims 1965, Salmela 2001, Salmela & Härmä 2004, Salmela & Autio 2009). Although Silfverberg (1986, 1996) has been keeping track of these changes, Finnish list of species needed thorough revision (III). For the first time, this revision (III) also included presence/absence data of the species in the Finnish biogeographical provinces. Biogeographic patterns of the Finnish crane fly fauna were studied by pooling species' occurrences into 20 biogeographic provinces (IV). The main aim was to evaluate the latitudinal gradient in species richness of i) all species, ii) saproxylic/fungivorous and iii) mire-dwelling species. I also used multivariate methods to analyze the divergence of provincial assemblages and to study whether the faunal turnover was associated with latitude or longitude. Furthermore, distribution types of the Finnish species were assessed and a special attention was laid on "endemics", i.e. species hitherto known from Fennoscandia only. Thus, despite the taxonomic emphasis in the Introduction, this PhD thesis is not solely taxonomic. Two papers (I, II) are taxonomic in their scope, the others are related to faunistics (III) and biogeography (IV). However, the taxonomy is always supporting the work, and the conclusions reached. Without the revised check-lists and occurrence data, assessments of rarity and species richness gradients (IV) would be spurious.

3. MATERIALS AND METHODS

3.1. Study area and data sets

Finland is located between 59°30'N and 70°05'N and 19°07'E and 31°35'E, being part of the boreal zone, i.e. zone of coniferous forests. Finland is divided into four major ecoregions or vegetation zones, namely (from south to north) hemiboreal, south boreal, middle boreal and north boreal (Fig. 4b). This zonation is mainly controlled by climate (e.g. decreasing mean annual temperature towards the north, differences in the length of the growing season, duration of snow cover) and also topographic relief. Differences in vegetation structure between neighboring zones are not clear-cut but gradual changes take place along a latitudinal gradient (e.g. change of mire massif types from peat bogs to aapamires across the border of the southern and middle boreal regions). Finnish bedrock is mainly composed of acidic siliceous rocks, intermediate (e.g. mica schist, amphibolite) or calcareous (marbles, dolomite) rocks are generally rare. For further information, see e.g. Ahti et al. (1968), Euroala (1999), Ruuhijärvi et al. (2000), Lindholm and Heikkilä (2006). A traditional way to map species' occurrences in Finland is to use biogeographical provinces (see e.g., Heikinheimo & Raatikainen 1971, Fig. 3a). There are a total of 21 such provinces, their surface areas ranging from 1500 to 25 500 km². Boundaries of the provinces mainly follow borderlines of Finnish municipalities and are thus administrative rather than "natural".

The data for papers III and IV is based on a personal database of Finnish crane flies. Data from literature, Finnish museum specimens and author's personal observations were entered in to this database, which includes e.g. locality data and ecological information, if available. This database, first created in 2006, has since been updated and by the end of March 2012 it included 14 782 entries for the families Limoniidae, Tipulidae, Pediciidae and *Cylindrotomidae* (entry= data from a museum specimen or an observation from a single locality). An important source of occurrence data has been accumulated from Malaise trapping, performed between the years 2000 – 2011, totaling 476 Malaise trapping sites and circa 1670 Malaise trapping months. This is one of the largest sets of Malaise trap samples so far collected and has yielded 101081 crane fly specimens and 301 species. NMS ordination of these sample sites reveals a coarse biogeographic pattern, implying that a north–south gradient is influencing assemblage composition (Fig. 5). A succinct review of this data is provided in the Table 1. Malaise trapping was performed in a wide spatial scale, ranging from the Aland Islands to northernmost Finland (Utsjoki and Enontekiö), and from the Russian border (Lieksa) to western Finland (Kälviä). Headwater streams (Fig. 6) and springs surrounded by boreal forests and northern aapamires are quite well sampled habitats, but meadows, shores of large rivers and Baltic coastal meadows south of Oulu are poorly represented in the trapping material. Additional material (not counted, but several thousands of specimens) comes from sweep net samples, pit fall traps, window traps and trunk-emergence traps.

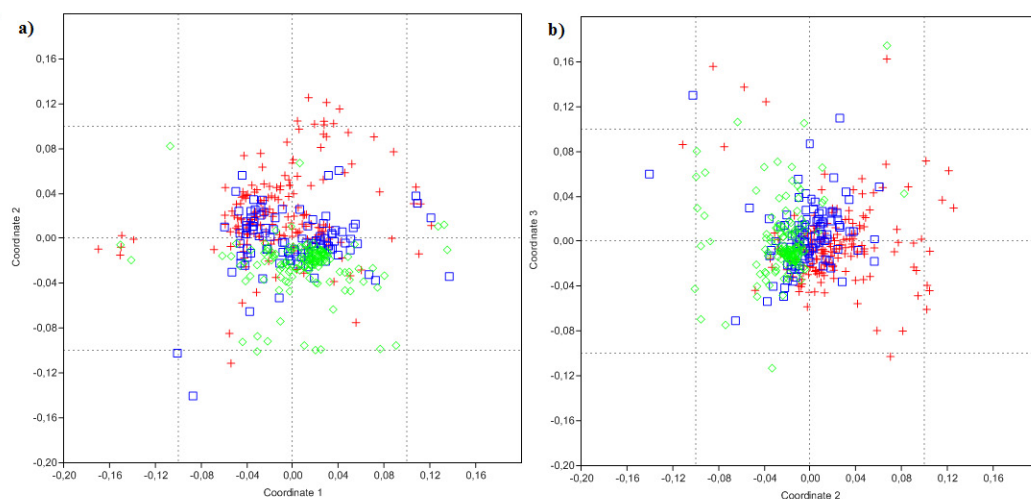


Fig. 5. NMS ordination on nation-wide Malaise trapping data, based on 421 sites, 301 species and 101081 crane fly (Diptera, Tipuloidea) specimens. Symbols refer to the location of a study site in Finland: red cross=hemi/south boreal, blue square=middle boreal and green diamond=north boreal ecoregion. a) Ordination according to 1st and 2nd axes and b) 2nd and 3rd axes. Pair-wise distances were calculated by using Bray-Curtis distance measure, raw abundances were used. Stress value 1.27.

Table 1. The most abundant and frequent (occupancy frequency % in the trapping sites) crane fly species in the Malaise trapping data, including data on rare species (number of singletons and number of species collected only from a single trap site) and species richness of the trapping sites.

abundant spp.	frequent spp. (%)
<i>Molo. flavus</i> , 17253	<i>Tric. immaculata</i> , 77,2
<i>Tric. immaculata</i> , 11310	<i>Ormo. ruficauda</i> , 67,7
<i>Ormo. ruficauda</i> , 6531	<i>Pedi. rivosa</i> , 55,8
<i>Ormo. depilata</i> , 2597	<i>Dicr. separatum</i> , 52,3
<i>Scle. sororcula</i> , 2283	<i>Molo. flavus</i> , 50,3
<i>Molo. ater</i> , 2222	<i>Meta. zetterstedti</i> , 50,1
<i>Tipu. subnodicornis</i> , 2063	<i>Tipu. variicornis</i> , 48,7
<i>Phyl. squalens</i> , 1967	<i>Tipu. subnodicornis</i> , 43,7
<i>Dicr. separatum</i> , 1963	<i>Dicr. distendens</i> , 41,6
<i>Tric. unicolor</i> , 1766	<i>Phyl. fulvonervosa</i> , 41,1

number of singletons: 22

number of spp. in one site: 32

lowest number of species/site: 2

highest number of species/site: 75

average number of species/site: 22,8 (SD ±11,7)



Fig. 6. Malaise trap in Li: Utsjoki, Kaldoaivi, Skalvejavri, headwater stream surrounded by an extensive snow bed. Malaise is a passive trap suitable for collecting low-flying insects, especially dipterans and hymenopterans. Photo J. Salmela 7/2007.

Occurrence of crane flies in the Finnish provinces mainly follows paper number III. However, after that publication three species were recorded as new to the regional fauna (*Dicranomyia klefbecki*, *Ormosia hederæ*, *Tipula pauli*) and *Tipula recondita* was described as a new to science (paper II). In addition, some provincial occurrences were added and corrected. The Finnish list of crane flies now consists of 338 species (IV, Appendix I), of which only one (*Tipula peliostigma*, doubtful species) lacks provincial data (see III).

3.2. Taxonomy of selected *Tipula* species groups

The morphological terminology used in the papers I and II mainly follows Alexander and Byers (1981). The terminology of some special parts of male genitalia was taken from Frommer (1963) or is explained in the figures. The following acronyms for museums and collections are used in the text: ZMKU – Zoological Museum of National Museum of Natural History, National Academy of Science of Ukraine, Kiev, Ukraine; NCBN – Netherlands Centre for Biodiversity Naturalis, Leiden, the Netherlands; ZMUM – Zoological Museum, Moscow State University, Moscow, Russia; MZHF – Finnish

Museum of Natural History (Zoological Museum), University of Helsinki, Helsinki, Finland; PVM – Private Collection of V.-M. Mukkala, Kaarina, Finland; USNM – Smithsonian Institution, National Museum of Natural History, Washington DC, USA; ZMUC – Zoological Museum, University of Copenhagen, Copenhagen, Denmark; ZMUT – Zoological Museum, University of Turku, Turku, Finland; VPM – Private collection of Valentin Pilipenko, Moscow, Russia; ZISP – Zoological Institute Russian Academy of Sciences, St. Petersburg, Russia.

Layer photos (paper I) were taken using an Olympus SZX16 stereomicroscope attached to an Olympus E520 digital camera. Digital photos were captured using the programmes Deep Focus 3.1 and Quick PHOTO CAMERA 2.3. Layer photos were finally combined with the program Combine ZP. For paper II, photos were taken with a Canon PowerShot A640 camera and processed using Combine ZP software. All drawings were prepared from photographs.

In paper II, DNA barcoding was used. The DNA of three specimens was extracted in the University of Turku, using a modified non-destructive salt extraction method (Aljanabi & Martinez 1997, Gilbert et al. 2007). Whole adult specimens were placed on 250 µl 96-plate wells. Ethanol-stored samples were briefly dried at 60 °C. First 118 µl of sterile salt homogenizing buffer (0.4 M NaCl, 10 mM Tris-HCl pH 8.0, 2 Mm EDTA pH 8.0 and 2% SDS) containing 8 µl of 20 mg/ml proteinase K (400 µg/ml final concentration) was added into each well. The samples were incubated overnight in the buffer at 55–65 °C. After the incubation, the intact samples were removed from the buffer and placed into 99.5% ethanol to stop further digestion. Then 80 µl of 6 M NaCl (NaCl saturated H₂O, pH 8) was added to each well. Samples were vortexed for 1 min at maximum speed, and then centrifuged for 20 minutes at 4000 rpm. Thereafter 100 µl of supernatant was transferred to wells on a new plate. An equal volume (100 µl) of isopropanol was added to each sample and the plate was briefly vortexed. Then the plate was placed into freezer (-20 °C) for 1 hour. After freezing, the samples were centrifuged for 20 minutes at 4000 rpm. The supernatant was discarded and the pellet was washed by adding 150 µl of ice-cold 70% ethanol and centrifuging for 20 min at 4000 rpm. The ethanol was then carefully pipetted out and the pellet was dried for overnight at room temperature. The next day, the DNA pellet was dissolved in 50 µl of previously warmed ultrapure water. The DNA barcode region (*cythochrome oxidase subunit I*) was amplified and sequenced from all specimens using universal primers LCO1490: 5'-GGGTCAACAAATCATAAAGATATTGG-3' and HCO2198: 5'-TAAACTTCAGGGTGACCAAAAAATCA-3' (Folmer et al. 1994). All PCR reactions were performed in a 20 µl volume containing 1 µl of DNA extract, 12.5 µl ddH₂O, 2.0 µl 10x buffer, 2.0 µl MgCl₂, 1.0 µl primer1 (LCO), 1.0 µl Primer 2 (HCO), 0.4 µl dNTPs, and 0.1 µl AmpliTaq Gold polymerase. The cycling profile was 95°C for 5 min, 40 cycles of 94 °C for 30 sec, 50 °C for 30 sec, 72°C for 1 min 30 sec and a final extension period of 72 °C for 10 min. Sterile water samples were used as controls in each PCR batch. All of the controls were negative. Successful PCR products were purified and sequenced by Macrogen Incorporated (South Korea).

For the rest of the 26 specimens, DNA barcodes were obtained at the Canadian Centre for DNA Barcoding. Legs or 2–3 abdominal segments of the specimens were placed in 96% ethanol in a 96-well lysis microplate and dispatched to the Biodiversity Institute of Ontario where DNA was extracted and sequenced using standard protocols and primers (deWaard et al. 2008). The resultant sequence data was placed into a project (HOLPT) on BOLD (<http://www.boldsystems.org>, Ratnasingham & Hebert 2007). These sequence records are now publically available on both BOLD and on GenBank.

For paper II, Kimura 2-parameter (K2P) (Kimura 1980) distances between all sequenced specimens were calculated. Based on K2P distances a Neighbor-Joining (NJ) tree was also produced to visualize the degree of similarity of the studied species. The relatedness of the species was also inferred with the character-based Maximum Likelihood (ML) method (GTR + gamma as the evolutionary model, 1000 Bootstrapping replicates). K2P distances, NJ and ML were produced by using the MEGA5 program (Tamura et al. 2011). Because one gene is far too small for reasonable phylogenetic analysis (Gatesy et al. 2007), the ML tree presented in paper II does not reliably illustrate the evolutionary relationships among the sequenced taxa.

3.3. Biogeographic patterns of Finnish crane flies

A traditional way to map species' occurrences in Finland is to use biogeographical provinces (see e.g., Heikinheimo & Raatikainen 1971). There are a total of 21 such provinces, their areal extents ranging from 1500 to 25 500 km². In the paper IV, the very small province K1 (*Karelia ladogensis*) was merged to Sa (*Savonia australis*). Because the provinces were unequal in size, the number of species in each province was corrected using formula:

$$S_{cor} = S_{obs} / A^z$$

where S_{cor} is the corrected number of species, S_{obs} the observed number of species in a province, A is the area of a province and z is a constant taken from species–area relationship (0.15 was chosen, see Lahti et al. 1988, Heino 2002).

Observed and corrected provincial species numbers were calculated for i) all species, ii) mire-dwelling species and iii) saproxylic/fungivorous species. Ombrotrophic bogs and poor – rich fens, mostly open or sparsely wooded, are the principal habitats for mire-dwelling species as defined here. Springs were not taken into account, although most springs fall into mire types in Finnish mire ecology (Lindholm & Heikkilä 2006). The crane fly fauna of springs, however, may be very similar to headwater streams, not mires (Salmela 2011). Subjective assessment of mire-dwellers is unavoidable, but it is based on my careful consideration. Less subjective is the classification of crane flies into saproxylic and fungivorous species. Some genera are strictly fungivorous (e.g. *Metalimnobia*, *Ula*) or dependent on decaying wood (e.g. *Gnophomyia*, *Lipsothrix*)

(Yakovlev 1994, Hancock et al. 2009, Krivosheina & Krivosheina 2011). Classification of some species as saproxylic is based on my personal observations (*Limonia badia*, *Tipula pseudoirrorata*, *T. stenostyla*). Because some species are both saproxylic and fungivorous (i.e. larvae feeding on wood-decaying polyporous fungi), their combination here is justified. A total of 51 and 42 species were classified as mire-dwellers and saproxylic/fungivorous, respectively.

Occupancy of crane flies in the provinces was calculated (i.e. number of species present in one, two, three, ..., 20 provinces). No statistical fitting of occupancy frequency distribution was applied (e.g. McGeoh & Gaston 2002), and the shape of the distribution was assessed based on visual examination.

Biogeographical provinces were further classified into three groups, roughly corresponding the delineation to ecoregions or vegetation zones: (i) hemiboreal and south boreal (Al, Ab, N, Ka, Ta, Tb Sa, St, Sb), (ii) middle boreal (Oa, Kb, Ok, Om, Oba, Obb) and (iii) north boreal (Ks, Lkoc, Lkor, Le, Li). For each zone, i) total species richness of crane flies, ii) number of species present only in one of the zones, iii) number of species present in all three zones and iv) numbers of species representing four different distribution types were calculated. Data for the distribution types were taken from Oosterbroek (2012) and are the following: Holarctic, Trans-Palaeartic, West Palaeartic and Fennoscandian. Holarctic species occur in both Nearctic and Palaeartic realms, Trans-Palaeartic species are recorded from both eastern and western part of the Palaeartic region, West Palaeartic species occur west of Ural mountains and Fennoscandian species are not recorded outside Finland, Sweden, Norway, Kola Peninsula and Russian Karelia. Further, numbers of crane flies that are absent from Central Europe (occurrence in the Baltic countries was allowed) were recorded for the three zones.

The faunistic composition of provincial crane fly assemblages was examined using non-metric multidimensional scaling (NMS) ordination. NMS is an ordination method, in which the original ranked distances (based on distance measure) of the sample units in the p -dimensional species space are forced to a reduced, k -dimensional ordination (Legendre and Legendre 1998; McCune and Grace 2002). The Jaccard coefficient was used as a distance measure. Spearman's correlation coefficient was calculated between the ordination's coordinates of the provinces and latitudinal and longitudinal coordinates. It has been questioned (McCune and Grace 2002, pp. 107–108) whether it is appropriate to present p -values in this connection because coordinate points of the sampling units along the dimensions are not independent variables. By calculating correlation, however, it is possible to interpret the geographical variation of provincial assemblages.

The Mantel test was used to examine the relationship between the faunistic similarity and the geographical distance between the provinces. The Mantel test is used to test the null hypothesis of no relationship between two distance matrices, i.e. the test evaluates linear correlation between two distance matrices. Each matrix is calculated from a

different set of variables, measured for the same sample units (here provinces) (Legendre and Legendre 1998, McCune and Grace 2002). The test value r_M is analogous to the Pearson correlation coefficient (range -1 and 1). Statistical significance is calculated by permutation (9000 permutations were used). The Jaccard coefficient was used as a distance measure for crane flies and Euclidean distance for geographic coordinates of the provinces.

In order to analyze the relationship between latitude and species richness (observed and corrected richness, see above), Spearman's (R_s) correlations were calculated. However, because observed provincial species richness correlated positively with provincial Malaise trapping effort ($R_s=0.54$, $p=0.014$), a partial correlation was also applied. This method can be defined as the correlation of the residuals after regression on the controlling variable. In other words, correlation between observed species richness (all species, saproxylic/fungivorous species, mire-dwellers) and latitude was controlled for Malaise trapping effort. Furthermore, Malaise trapping effort was accounted for by using sample-based rarefaction. Malaise trapping sites were gathered to a single sites \times species matrix, and were arranged according to ecoregions. The aim of this analysis was to evaluate whether rarefaction, i.e. a method to standardize trapping effort (Colwell & Coddington 1994), yields similar results as raw species richness counts for the ecoregions. It was thus predicted that hemi and south boreal ecoregions have the highest rarefied richness, followed by middle and north boreal regions. NMS, Mantel test, rarefaction and correlations were computed using the program PAST 2.14 (Hammer et al. 2001).

4. RESULTS AND DISCUSSION

4.1. Taxonomy of selected *Tipula* species groups

Tipula (Yamatotipula) stackelbergi Alexander, formerly known as a subspecies of *T. (Y.) pruinosa* Wiedemann, was elevated to a species rank (I). By studying the type material of *T. usuriensis* Alexander and *T. subpruinosa* Mannheims, it was concluded that these two species are not synonymous with *T. (Y.) stackelbergi*, as was suggested by Savchenko (1961) and followed by Oosterbroek & Theowald (1992). Instead, *T. usuriensis* is a new junior synonym of *T. (Y.) pruinosa* and *T. subpruinosa* is a new junior synonym of *Tipula (Y.) freyana* Lackschewitz. Based on available material and literature records, *Tipula (Y.) stackelbergi* does not occur in Europe; the range of the species covers East Siberia and the Russian Far East (Alexander 1934, Savchenko 1961, Pilipenko 2009). Thus, the species is deleted from the list of Finland and Sweden (I). With no doubt, *T. (Y.) stackelbergi* and *T. (Y.) pruinosa* are closely related species. There are, however, clear differences in the structure of male hypopygium (general shape and presence of spines on inner gonostylus, structure of sperm pump). Differences between female specimens were also found (internal structures of the ovipositor), but more *T. (Y.) stackelbergi* and *T. (Y.) pruinosa* females should be studied in order to validate the diagnostic differences presented in paper I.

It remains questionable whether *T. (Y.) pruinosa sinapruinosa*, known from China, is a valid subspecies. Based on the original description (Yang & Yang 1993) it is likely that Chinese specimens are conspecific with other eastern Palaearctic *T. (Y.) pruinosa* specimens. If these eastern Palaearctic specimens are to be ranked as subspecies below *T. (Y.) pruinosa*, *T. usuriensis* is the oldest available name for the taxon. However, as discussed in paper I, subspecies should be delineated using several criteria, such as ecology and genetics, and not based solely on small differences in body coloration, for example. (see Appendix II for some minor corrections).

Tipula (Pterelachisus) recondita Pilipenko & Salmela was described based on specimens collected from two localities: Finland, Kittilä (North boreal ecoregion) and Russia, Primorski kray (Zone of temperate broadleaf and mixed forests) (II). Although differences in the structure of the male hypopygium between the Finnish and Russian populations were observed, DNA barcode sequences between the populations differed only by three nucleotides (0.2 % K2P distance), supporting presence of one widespread species. K2P minimum distances between the new species and 17 other species of the subgenus ranged from 5.3 to 16.1 % (mean 8.8 %). The new species is forest-dwelling, known from an old-growth herb-rich forest (Finland) and *Quercus mongolica* forest (Russia). The new species is perhaps closest to *T. (P.) imitator* Alexander and in lesser extent to *T. (P.) pauli* Mannheims (II).

Tipula (P.) recondita is rather easily distinguished from other Holarctic *Tipula (Pterelachisus)* species. The new species is distinctive in its characters of the male hypopygium, especially that of the 9th tergite. There are several *Tipula (Pterelachisus)*

species with a U-shaped median notch or an emargination in the caudal margin of the tergite, but usually having a tooth or other elevated structures at the mid-point (e.g. *T. (P.) angulata* [Alexander 1919, p. 984, Salmela & Autio 2009, p. 55], *T. (P.) varipennis* [Savchenko 1964, p. 56], *T. (P.) imitator* [Alexander 1953, Plate 1]. The new species is peculiar having no such structures in the 9th tergite. There are some morphological differences between Finnish and Russian specimens, perhaps due to the long distance and lack of gene flow between the populations. These differences, however, are here considered to be intraspecific variation. Very small K2P divergence of COI gene (0.2 %) between Finnish and Russian specimens also substantiates the presence of one widespread, but disjunct, species. Based on K2P distances, *Tipula (P.) recondita* is rather distant from the other species of the same subgenus, being closest to *T. (P.) winthemi* (5.3 %) and *T. (P.) jutlandica* (5.5 %). However, it must be noted that *T. (P.) imitator* was not included in the COI analysis, due to the lack of fresh material. Given the morphological similarity of the new species and *T. imitator*, it is likely that their barcoding distances would be smaller than 5 %. In many cases, closely related insects may have pair-wise barcoding distances ranging from 0 to 2 % (Hausmann et al. 2011, Park et al. 2011, J. Salmela, unpublished data). Thus, besides morphology, barcoding may be used as an additional character, but the taxonomy should not rely on it to the exclusion of other criteria. Unfortunately we were not able to examine the holotype of *T. (P.) imitator* while writing the paper II. However, after publication a loan of the holotype was arranged and I studied the holotype. Figures are provided in Appendix III.

4.2. List of Finnish crane flies

Based on all available information from museum specimens, literature records and material identified by me by the end of September 2011, the list of Finnish crane flies was found to consist of 331 species (III). Twenty-four species were formally reported for the first time from Finland and twenty-two previously reported species were deleted from the list. One species, *Tipula peliostigma*, was included in the list but due to the lack of any relevant museum specimen, was considered as a doubtful record. Thus, provincial occurrence records were given for 330 crane fly species. The provincial data was analyzed in another context (IV).

In addition to the revised list and occurrence of the species in Finnish provinces a short historical account on Finnish crane fly research was provided. According to that review (III), C. Lundström was the first who studied Finnish crane flies seriously. His publications (Lundström 1907a, 1907b, 1912, Lundström & Frey 1916) formed the basis for Finnish crane fly taxonomy and faunistics. His taxonomic descriptions and illustrations were good and many of his species are still valid. After Lundström's short but productive years, advancement of Finnish crane fly research was rather modest. Some species were added to the Finnish list (Frey 1932, 1934, Krogerus 1936) and then Frey et al. (1941) produced a full list of Finnish crane flies, as known at that time. Krogerus (1960) collected arthropods, including crane flies, from Finnish mires and Mannheims (1954, 1967) listed Finnish

tipulids and reported several new Finnish records from SW Häme (biogeographical province of Ta) (Mannheims 1964, 1965). Hackman (1980) updated the list of Finnish crane flies and species found from Inari Lapland (Li) were listed by Siitonen (1984). Siitonen, his surname was later Rautio, reported several crane flies new for Finland in short communications (Rautio 1985, 1987). Viramo (1992), based on the identifications of Siitonen and the collections in MZHF, listed the species from northeast Finland (biogeographical province of Ks). During the years 2000–2011 Finnish crane flies have been studied by me and co-authors, and consequently, our knowledge of habitat associations and the extent of species' occurrence have much improved. During this time period, over 50 species have been added to list of Finnish crane flies (Fig. 3), indicating the importance of Malaise trapping and other collecting efforts for enhancing faunistic knowledge (see e.g. Salmela 2001, 2004, 2008, 2011, Starý & Salmela 2004, Salmela & Ilmonen 2005, Salmela et al. 2007, Salmela & Autio 2007, 2009, Salmela & Starý 2008, Starý & Brodo 2009, Autio & Salmela 2010).

4.3. Biogeographic patterns of Finnish crane flies

Species richness and assemblage composition of Finnish crane flies varies according to latitude (IV). Species richness of all species and saproxylic and fungivorous species decreases with increasing latitude, but among mire-dwellers this relationship is reversed. Provincial assemblages of Finnish crane flies also display a strong latitudinal gradient, as evidenced by NMS ordination. According to the Mantel test, similarities of provincial assemblages decrease with increasing geographic distance between them. Considering occupancy, 104 species are known from four or fewer number of provinces ($\leq 20\%$), and could be regarded as rare, and 52 species could be regarded as common, known from 17–20 provinces ($\geq 80\%$). The finding that species richness and assemblage composition of a taxon or biotic group in Fennoscandia is associated with latitude is not surprising (e.g. Väisänen et al. 1992, Pekkarinen & Teräs 1993, Väisänen & Heliövaara 1994, Heino et al. 2002, Heino & Toivonen 2008, Ilmonen et al. 2009). Latitudinal gradient is correlated with climate, and it is likely that higher average monthly temperatures, effective temperature sum, and longer vegetative period promote generally higher species richness in southern Finland. Saproxylic and fungivorous species are favored by the presence of larger number of tree species in the south than in the north. It is also apparent that species richness of fungal groups such as agarics and boletes decreases with increasing latitude (Salo et al. 2010). Following Kouki (1999), one may assume that the availability of resources best explains the reversed species richness gradient of mire-dwelling crane flies. That is, total surface area of mires and environmental heterogeneity (area of flark fens, presence of calcareous bedrocks) account for the higher species richness of mire-dwellers in the northern provinces.

In addition, after the provincial data is clumped according to the ecoregions, it is clear that hemi and south boreal Finland is the most species rich (278 spp.), followed by middle (244) and north boreal (235) zones. In a similar way, based on rarefied Malaise trapping data, ecoregions are ranked similarly as raw species richness. Rarefied richness at the level of 101 trapping sites (the number of trap sites in the middle boreal ecoregion) is 220 (SD

± 4.9) for the hemi and south boreal region, 195 (SD ± 4.8) and 186 (SD ± 4.2) for the middle and north boreal zones, respectively. However, standard deviations of the two latter zones overlap, indicating a similar level of species richness. Nevertheless, when raw-values are considered, the absolute difference between hemi and south boreal and north boreal zones is 43 species. Over 40 species are truly southern, not occurring in the middle or north boreal zones, and 30 north boreal species display an opposite pattern. The middle boreal zone harbours only a few (6 spp.) species recorded only there, implying that this zone is mainly a mixture of northern and southern elements (see also Fig. 5). In other words, there is a true turnover, not merely a gradient created by regional differences in alpha diversity (e.g. Harrison et al. 1992). It thus follows that southern and northern Finland are composed of divergent species pools, differing in their size and the identity of their members. This notion leads to the predictions that composition of local communities is partly determined by the latitude, and that local communities should be richer in species in the south than in the north. However, open mires should display a reversed species richness pattern.

Forty-eight % of the Finnish crane fly fauna is composed of Trans-Palaeartic species, roughly one third (34 %) of the species are West Palaeartic and only 16 and 2 % are Holarctic and Fennoscandian, respectively (IV). Considering regional faunae (i.e. hemi and south, middle, north boreal zones), proportions of different distribution types remain roughly similar. There is however a trend in that the proportion of West Palaeartic species is decreasing from the south to the north and, correspondingly, the proportion of Holarctic and Trans-Palaeartic species is increasing from south to north. The proportion of Fennoscandian species is low (1 or 2 %) in each zone. The above mentioned distribution types are somewhat ambiguous and not too much weight should be given to those figures: assignment of a species as Holarctic, for instance, may change after a taxonomic revision. In addition, some Holarctic species are very rare, only known from Fennoscandia and from a handful of localities in the Nearctic. Some Trans-Palaeartic species may be very common (e.g. *Nephrotoma scurra*) and some may be very rare (e.g. *Tipula recondita*, II). Thus, distribution types used here provide very little predictive power for macroecological analysis, such as testing a relationship between regional and global range sizes (e.g. Gaston & Blackburn 2000). There is, however, a pattern where proportions of i) Trans-Palaeartic species and ii) species not occurring in Central Europe increase toward north boreal zone. This result may be caused by survival of circumpolar and taiga species in the arctic and continental climates prevailing in the northernmost Finland. Finally there is the question, are those species that are currently known only from Fennoscandia endemic or relictual (surviving in Fennoscandian but extinct elsewhere) crane flies for that region? The most likely answer is: no they are not. I suggest (see IV for details) that these species also occur outside Fennoscandia and have hitherto not been recorded from European or Asian parts of Russia, which is the most predicted range of most species (e.g. *Dicranomyia lulensis*, *Symplecta lindrothi*, *Tipula fendleri*). In addition, recent DNA barcoding results point to the conclusion that the Fennoscandian endemic *Cylindrotoma borealis* is an intraspecific haplotype within the wide-ranging *C. distinctissima*, and not a valid species (J. Salmela & N. Paramonov, unpublished).

5. CONCLUSIONS

The taxonomy of North European crane flies is now relatively stable. However, examination of type specimens may yield changes in nomenclature, range-sizes and taxonomic affinities of species studied in the future (I). DNA barcoding seems to work well among crane flies (II, J. Salmela unpublished), but the use of this method should go in hand with sound morphological understanding. Nevertheless, the barcoding method is a useful tool and it may be helpful in taxonomic studies of crane flies (II). It should be briefly mentioned that there may be hidden diversity among the Finnish crane flies, based on my preliminary barcoding results on ca. 700 specimens and 311 species examined so far (see Appendix I). However, this a subject that needs to be studied with a better geographic coverage of specimens and simultaneous examination of old names and their type specimens. We may otherwise just leave confusion and muddied water for the next generation of taxonomists.

Observed species richness is seldom the same as real species richness. The sampling devices we use may not be optimal to detect all species and some rare species may have very small ranges, or low population densities, lowering their catchability. This is equally true with Finnish crane flies. In the estimation of true species richness of Finnish crane flies, I have compared the occurrences of species in neighboring countries. I examined Swedish and Norwegian check-lists (extracted from Oosterbroek 2012) and simply listed species that may well occur in Finland but are not yet recorded. I came up with a rather conservative list of 15 species, consisting of mainly alpine and northern crane flies (e.g. *Nephrotoma ramulifera*, *Tipula boreosignata*, *T. persignata tofina*). It is also likely that some eastern Palearctic and Central European species have populations in Finland, but have hitherto avoided traps and nets. To conclude, it is reasonable to think that there currently are, at minimum, about 15–20 species lurking in Finland, but not yet collected and recorded. Despite this possibility that the check-list should be longer than it actually is, I think the addition of new species would not cause dramatic changes to the general patterns presented in papers III and IV. Climate change may bring about changes in the Finnish fauna, including new species, but this subject is outside the scope of this thesis.

The Finnish crane fly fauna varies according to latitude. Species richness generally decreases with increasing latitude, but among mire-dwelling species this pattern is reversed. Based on these findings, it may be concluded that the needs for nature conservation are highest in the south. Finnish conservation areas are not evenly spaced within the country, the number of protected hectares being instead biased toward the north of Finland (e.g. Ruuhijärvi et al. 2000). I think one interesting direction for an applied research among crane flies would be studying the demands of some focal species, e.g. threatened saproxylic tipuloids. What resources, exactly, they need and what are their prospects within the scattered network of conservation areas in south Finland? Can

restoration of forests enhance their population sizes or range-sizes? The network of mire reserves is rather good in north Finland, and one may assume that mire-dwelling crane flies are safe. However, many northern crane flies may face problems with a warming climate, either because of rising temperature or changing biotic conditions (moisture regime, vegetation, interactions with other species). As noted in paper IV, there are several Finnish crane fly species that are absent in Central Europe. Finland should pay a special attention to these species, and some of these could be assessed as National Responsibility Species. If they vanish from Finland, it would mean that, consequently, a large proportion of their European population will vanish.

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APPENDICES**Appendix I: Additions to the list of Finnish Limoniidae**

BOLD Sample IDs (JES-20...) given below refer to DNA barcoded specimens.

Dicranomyia (Idiopyga) cf. intricata Alexander, 1927

There are two sibling species close to *Dicranomyia intricata* in Finland. The other one is northern, most likely conspecific with *D. suecica* (Nielsen, 1953, at the present a synonym of *D. intricata*). This northern species is known from the provinces Obb, Lkor, Lkoc, Le and Li, occurring mainly in aapamires (JES-20110082, JES-20120082). The other species is only known from Oba, being collected around Baltic coastal meadows in Hailuoto and Oulunsalo (JES-20120094); this may be “true” *D. intricata*. Names proposed here are tentative because the type material of either *D. intricata* or *D. suecica* is not yet studied. These species are separated based on differences in male hypopygia and COI sequences (J. Salmela & S. Vanhakylä in prep.).

Eloeophila mundata (Loew, 1871)

Locality: FIN, N: Nurmijärvi, Kiljavan lähteikkö, 6.8.2009 A. Rinne leg., Malaise trap, boreal spring, 1 female, J. Starý det. (JES-20120373). This specimen was originally identified as *E. submarmorata*. The latter species should be removed from the province N and replaced by *E. mundata*.

Dicranophragma (Brachylimnophila) adjunctum (Walker, 1848)

Locality: FIN, Le: Enontekiö, Tarvantovaaran erämaa, Pulkanoja, 22.7.2009 J. Salmela leg., Malaise trap, 37 specimens, J. Starý det. (JES-20110108). These specimens were originally identified as *D. separatum* (Walker, 1848). New for Fennoscandia.

Appendix II: Corrections to the paper II

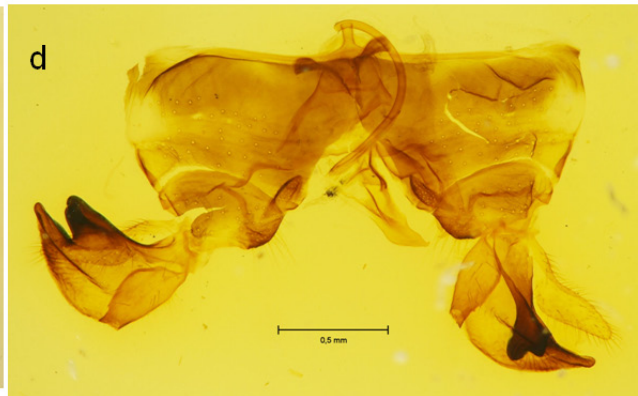
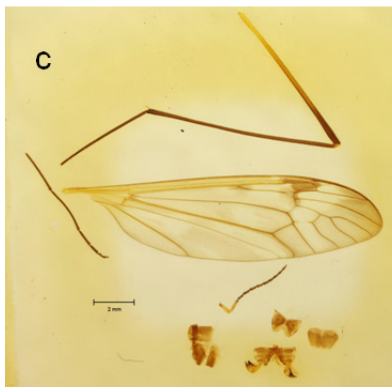
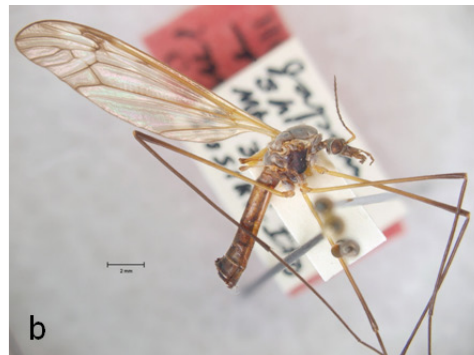
Page 50, Figure 3, Figure legend. Legends for the Figures 3 e, f and g are lacking from the original paper. Outer and inner gonostyli, *Tipula (Y.) stackelbergi* (e) and *Tipula (Y.) pruinosa* (f, g), e) (Primorski kray), f) Altay and g) Moscow (photo courtesy V. Pilipenko).

Appendix III: Holotype of *Tipula (Pterelachisus) imitator* Alexander, 1953

Collection: USNM – Smithsonian Institution, National Museum of Natural History, Washington DC, USA.

Original description: Alexander CP (1953) Records and descriptions of Japanese Tipulidae (Diptera). Part I. The crane-flies of Shikoku. I. Philippine Journal of Science 82: 21–75.

As *Tipula (Oreomyza) imitator*. Type locality: Japan, Shikoku, Mount Tsurugi, Awa, altitude 1400 to 1955 meters, May 31 1950, Issiki-Ito leg.



Holotype of *Tipula (P.) imitator* a) slide mounted antenna and abdominal terminalia, b) pinned specimen, c) slide mounted leg, wing, antenna, abdominal terminalia and d) slide mounted hypopygium (excluding 9th tergite). Photo courtesy V. Rinne.