Flying jewels

Taxonomy and distribution of Northern European cuckoo wasps
(Hymenoptera: Chrysididae)

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Academic Dissertation

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Revitalizing taxonomy is the noblest contribution that our generation can make to humankind. No future generation will ever have access to the number and diversity of species that we have.

– Quentin D. Wheeler, 2008
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Abstract

Cuckoo wasps (Chrysidae) comprise a relatively large cosmopolitan group of aculeate hymenopterans, with more than 2500 described species. They are all parasitoids or kleptoparasites of other insects, mainly solitary wasps and bees, and usually have highly sculptured bodies with bright metallic colours. Their diversity is highest in the desert and steppe regions of the world, since they prefer warm, dry and sunny habitats. Currently, about 490 species are known from Europe, but the true number of European species may be as high as 550–600.

In Northern Europe, the study of cuckoo wasps began with Linnaeus’ work in the 18th century, and since then several taxonomic and faunistic studies have been published, especially in Sweden and Finland. However, a comprehensive revision of the Northern European fauna has been lacking, and the taxonomy of the family has remained unstable, due to indistinct morphological differences between species. The distribution areas, life histories and population changes of most species have also remained poorly known. The main aims of this thesis are 1) to determine which species of cuckoo wasp occur in Northern Europe, i.e. Fennoscandia, Denmark and the Baltic countries, 2) to assess their valid names according to the International Code of Zoological Nomenclature, 3) to investigate their morphological differences and present an identification key for all species and 4) to study their distribution, abundance and long-term population trends.

The morphology, distribution and abundance of cuckoo wasps were studied, based on an extensive survey of museum and private collections. All available name-bearing type specimens were also investigated, and published data of Northern European taxa were compiled. Molecular analysis using two mitochondrial DNA (mtDNA) markers (cytochrome c oxidase I (COI) gene sequences, length 750 base pairs (bp), and ribosomal RNA gene sequences, length 2017–2057 bp, respectively) was used to identify and delimit species of the taxonomically challenging Chrysis ignita group and resolve their phylogenetic relationships. The population trends of Finnish cuckoo wasps were assessed by studying changes in the occupancy of 10 x 10 km grid squares between two periods, 1840–1967 and 1968–2015. Comparative analysis was performed to investigate the correlation between the population trends and shared species traits.

A total of 74 cuckoo wasp species were found in the study area, while 17 previously reported species were deleted from the region, due to erroneous identifications. Four species, Elampus foveatus (Mocsáry, 1914), Chrysis borealis Paukkunen, Ødegaard & Soon, 2015, Chrysis gracillima Förster, 1853 and Chrysis pulcherrima Lepeletier, 1806, were new to Northern Europe. Of these, Chrysis borealis was also described as new to science. Another new species, Cleptes striatipleuris Rosa, Forshage, Paukkunen & Soon, 2015 was described from central Europe. Lectotypes were designated for five nominal species, and two new synonyms were established. Chrysis terminata Dahlbom, 1854 represented the valid name for C. ignita Form A sensu Linsenmaier, 1959, and Cleptes semiauratus (Linnaeus, 1761) was re-established as a senior synonym of Cleptes pallipes Lepeletier, 1806.

The mtDNA markers proved to be useful for the identification and delimitation of the morphologically similar species of the Chrysis ignita group. The results strongly supported the validity of the most currently recognized Northern European species and suggested the existence of several additional cryptic species. Only the taxonomic status of Chrysis mediata Linsenmaier, 1951 vs. Chrysis solida Haupt, 1957 remained unresolved.

Decreasing populations were found in 11 Finnish cuckoo wasp species, while significant increases were not observed for any species. Scarce and small-sized species that are dependent on sun-exposed dead wood have declined more than abundant and large-sized species that live in open sandy habitats.

The results of this thesis form a solid taxonomy and nomenclature for Northern European cuckoo wasps, and the illustrated key remarkably facilitates species identification for amateur and professional entomologists. The declining populations of many species indicate that cuckoo wasps are vulnerable to environmental changes and need conservation measures to maintain viable future populations.
Preface

This PhD thesis was prepared as a part of the project *Cuckoo Wasps of Finland: Fauna, Population Trends and Conservation* funded by the Finnish Ministry of the Environment through the research programme of deficiently known and threatened forest species (PUTTE II) in 2012–2015. The main aim of the project was to increase the information available on Finnish cuckoo wasps not only in the form of a doctoral thesis, but also by producing a popular style identification book. The thesis was designed so that its results would be directly applicable in the book. Although we planned that the project would focus only on Finland, clearly a thorough understanding of the fauna of Finland would not be possible without studying neighbouring areas in addition. Therefore, the geographical scope of this thesis was expanded to cover all the Nordic and Baltic countries and northwestern Russia. Collaboration with foreign, mainly Northern European, Hymenoptera experts has been indispensable for the successful progress of this study.

1. Introduction

The variety of life on Earth is declining globally at an alarming rate, due to human impact, and therefore protection efforts are increasingly urgent (Mang *et al.* 2000, Secretariat of the Convention on Biological Diversity 2014). The need to maintain biodiversity is often justified by ecological and economic arguments that emphasize ecosystem functioning and benefits for human welfare. However, many groups of organisms that are threatened by human activity have little economic or even ecological importance. Cuckoo wasps, the topic of this PhD thesis, are a good example of such a group: they are scarce insects that occur in restricted habitats and parasitize other relatively scarce insects. Why should we care for them, study their biology and take them into account in environmental conservation?

In addition to economic and ecological reasons, the preservation of biodiversity also includes ethical and aesthetic motivations (Tisdell 2014). While the ethical argument highlights the intrinsic value of all forms of life, the aesthetic argument underlines the visual and auditory experiences that biodiversity provides. Cuckoo wasps, with their brilliant metallic colours, have an aesthetic appeal that not many other groups of organisms possess. This feature, together with their vulnerability, also makes them useful for promoting environmental conservation. Beautiful organisms attract people and generate interest towards biology and environmental issues. The importance of the aesthetic argument for environmental conservation should not be underestimated, especially during times when scientific knowledge is increasingly neglected by the media and decision makers.

1.1. Taxonomy and faunistics

This thesis is especially concerned with the taxonomy and distribution of cuckoo wasps. Taxonomy is usually defined as a branch of science that encompasses the description, identification, nomenclature and classification of organisms (Narendran 2006). It is often considered as a part of systematics, which also includes the study of phylogeny, i.e. the investigation of evolutionary relationships among organisms (Mayr & Ashlock 1991). However, the definitions of taxonomy and systematics are variable and sometimes have the same or slightly different meanings. In this study, the focus is on species descriptions, identification and nomenclature, while less attention is given to phylogenetic analysis and classification.

The discipline of taxonomy can be divided into two main branches. Alpha taxonomy is concerned about finding, describing and naming taxa, particularly species, while beta taxonomy deals with classification, i.e. the sorting of species and higher taxa into groups of relatives and arranging them in a hierarchy of higher categories (Mayr 1968). Taxonomic studies usually include information about
the geographic distribution of taxa, e.g. by providing regional species lists for administrative or biogeographic areas. Therefore, taxonomy is closely associated with faunistics and biogeography, which are the disciplines that study the local diversity or geographic distribution of organisms.

Although taxonomy and faunistics are often not regarded as ‘big science’, and journals publishing studies in these fields typically have low impact factors (e.g. Agnarsson & Kutner 2007), taxonomic and faunistic information is indispensable for conducting meaningful ecological and applied biological research. Assessment of biodiversity would be impossible without taxonomic descriptions, classifications and regional inventories. The importance of taxonomic and faunistic research is increasing, because biodiversity is declining rapidly and many species may become extinct before they are even discovered (Sala et al. 2000).

According to the biological species concept, species are groups of actually or potentially interbreeding natural populations that are reproductively isolated from other such groups (de Queiroz 2005). Species can also be defined as evolutionary lineages of organisms that can share genes and maintain their integrity through both time and space (Simpson 1951). In practice, species are usually detected and described by their structural and morphological traits. Delimitation of species can be difficult, if their morphological differences are indistinct. This is the case in closely related cryptic species, which are similar in appearance, but nevertheless do not, or only exceptionally, interbreed and share genes (Fišer et al. 2018).

In many groups of organisms, including cuckoo wasps, the existence of cryptic species has often been overlooked (Pfenninger & Schwenck 2007). New molecular methods, such as DNA barcoding, have recently become widely adopted in taxonomic studies, because they are especially useful not only for the detection, but also for the delimitation, of cryptic species (e.g. Hebert et al. 2016). DNA barcoding is based on the observation that a fragment of the mitochondrial DNA (mtDNA) gene COI in animals possesses both very conservative regions enabling its unequivocal delineation and sufficient variation that is suitable for separating species (Hebert et al. 2003). In this study, DNA barcoding was used as a tool for testing the validity of Northern European cuckoo wasp species.

1.2. Cuckoo wasps

Cuckoo wasps, the Chrysididae, sometimes also referred to as ruby-tailed wasps or jewel wasps, represent one of the largest families of aculeate hymenopterans within the superfamily Chrysidoidea (Kimsey & Bohart 1991). More than 2,500 species are known worldwide (Aguiar et al. 2013), and approximately 490 of these have been recorded in Europe (Mitroiu et al. 2015). Their species richness decreases northwards, and fewer than 100 species have been reported from the area consisting of Fennoscandia, Denmark and the Baltic countries. Cuckoo wasps, excluding the non-European subfamilies Amiseginae and Loboscelidiinae, are well known for their bright metallic colours and parasitic mode of life. In Northern Europe, species of the subfamily Chrysidinae parasitize other aculeate wasps and solitary bees, whereas species of Cleptinae attack sawflies (Symphyta). Members of the Amiseginae and Loboscelidiinae parasitize the eggs of walking sticks (Phasmatodea). The biology of most cuckoo wasps is still poorly known, but many species are known to be highly specialized in their host selection (Pärn et al. 2014).

Although all cuckoo wasps parasitize other insects, they differ significantly in the ways they utilize their hosts. While parasitoids feed directly on the host larvae or pupae, kleptoparasites (or brood parasites) mainly forage the food items stored in the host brood cell (O’Neill 2001). Both modes of development practically always result in the death of the host. When occasionally more than one host brood cell is destroyed, the kleptoparasite can also be considered a predator. Most Northern European species of the subfamily Chrysidinae are kleptoparasites of solitary wasps of the families Vespidae and Crabronidae (Figure 1), whereas a few species are ectoparasitoids of solitary bees of the Megachilidae. Species of the subfamily Cleptinae are ectoparasitoids of sawfly prepupae of the Tenthredinidae and Diprionidae. Some kleptoparasitic cuckoo wasps of the tribe Elampini oviposit in living aphids or true bugs at the hunting site of their hosts, and the egg is brought into the host’s nest.
concealed in the prey (Winterhagen 2015). Thus, the females of these species do not enter the nest of their host for oviposition.

![Figure 1. Life cycles of a kleptoparasitic cuckoo wasp of the genus *Chrysis* Linnaeus, 1761 and its potter wasp host (Vespidae: Eumeninae). Illustration by Alexander Berg.](image)

Most cuckoo wasps are thermophilous and heliophilous, inhabiting warm sunny habitats with sun-exposed dead wood and/or bare sandy patches that provide nesting sites for their hosts. Globally, their diversity is highest in warm desert and steppe regions, as well as areas with Mediterranean woodland and scrub vegetation (Kimsey & Bohart 1991). In regions with cooler climates, cuckoo wasps usually occur patchily in forest edges, sandy shores and various artificial habitats, such as gardens, dry meadows and road verges. They are mostly found in low numbers, but locally can be relatively abundant. In Northern Europe, cuckoo wasps are only active during the summer months on warm and sunny days. They are often seen on the walls of wooden buildings or on sandy patches searching for nests of their hosts. Some species also commonly visit flowers, especially of the families Apiaceae and Asteraceae, but their role as pollinators is rather insignificant.

In Northern Europe, the habitats of cuckoo wasps have been declining during recent decades, due to large-scale industrial forestry and agriculture, including efficient prevention of forest fires and abandonment of traditional animal husbandry (Stoate *et al.* 2009, Paillet *et al.* 2010). The sensitivity of cuckoo wasps to environmental changes has become evident, as the proportion of Red-Listed cuckoo wasp species is exceptionally high in all the Nordic countries (Paukkunen 2010, Larsson 2015, Ødegaard *et al.* 2015). For example, nearly half of the cuckoo wasp species known from Finland were considered near threatened, threatened or regionally extinct in the latest national Red List assessment (Paukkunen 2010). Since the hosts of most cuckoo wasps themselves are highly specialized predators or pollen feeders, cuckoo wasps as their natural enemies may be particularly vulnerable to environmental changes.

1.3. Study region

This study focuses on Northern Europe, as defined by the borders of Fennoscandia, Denmark and the Baltic countries, i.e. Estonia, Latvia and Lithuania. Fennoscandia encompasses Finland, Norway and Sweden, as well as north-western Russia, including the Republic of Karelia, Murmansk Oblast, the
northern part of Leningrad Oblast and the westernmost corner of Arkhangelsk Oblast (Figure 2). While Fennoscandia forms a geologically relatively uniform region (Baltic Shield) mainly composed of ancient Archaean and Proterozoic gneisses and greenstones, Denmark and the Baltic countries are situated on younger Phanerozoic sedimentary rocks, mostly formed of limestone, shale and sandstone deposits (Ager 1980). The geological variety of Northern Europe strongly influences the flora and fauna of the region.

Coniferous forest of the taiga biome is the predominant vegetation type in Fennoscandia, whereas broadleaved forests are more common in Denmark, southern Sweden and the Baltic countries. Alpine tundra and tundra vegetation are found in the mountainous regions of the Scandinavian Peninsula and northern Kola Peninsula (Hallanaro & Pylvänäinen 2001). According to the vegetation zone classification of Ahti et al. (1968), most of the study region belongs to the Arctic and Boreal vegetation zones. Southern Scandinavia, southernmost Finland and the Baltic countries belong mostly to the Boreonemoral (or Hemiboreal) zone, while Denmark, Scania in Sweden and the southern part of Lithuania belong to the Nemoral zone.

During the last glacial period (Weichselian glaciation) that started about 115,000 years ago and ended about 10,000 years ago, practically the entire study region was covered for long periods by
extensive ice sheets. Therefore, nearly all terrestrial animal and plant species occurring in the area have dispersed from the south and east after the glaciation. Due to the relatively short duration of the current post-glacial era, endemic species have been expected to be missing or rare in Northern Europe. In insects, the presence of endemic species in Northern Europe has not been confirmed, although potentially endemic taxa have been proposed by some entomologists (e.g. Brüstle & Muona 2009).

1.4. Historical review

The beginning of cuckoo wasp research in the Nordic countries dates back to the mid-18th century, when the first three species were described by Carolus Linnaeus (later Carl von Linné) in his famous volume of *Systema Naturae* (Linnaeus 1758). Linnaeus (1761) described the genus *Chrysis* and listed six cuckoo wasp species in his classic publication of Swedish animals. Later, he described two additional species from the country. One of the first lists of insects in Finland, published by Johan Julin, included four cuckoo wasp species from northern and central Finland (Julin 1792).

Anders Gustaf Dahlbom published the first Northern European monograph on cuckoo wasps, in which he listed 16 species from Sweden and two new species from Finland (Dahlbom 1829). A couple years later, he increased the number of Swedish species to 23 (Dahlbom 1831). In his third study on the Chrysididae, Dahlbom presented information on 80 species and 12 genera from different parts of the world (Dahlbom 1845). Finally, he compiled all of the information on cuckoo wasps published at the time and provided detailed keys to all known genera and species (Dahlbom 1854). In total, 213 new taxa were described, of which more than 150 are still valid (Kimsey & Bohart 1991). Some of the new taxa were from the Nordic countries.

Several other studies dealing with Northern European cuckoo wasps were also published during the 19th century. These include faunistic studies and checklists from Sweden (e.g. Boheman 1853, Thomson 1862, 1870), Finland (Woldstedt 1875), Denmark (Borries 1891) and Norway (Siebke 1880, Strand 1898). The first chrysidid records from Latvia (e.g. Kawall 1864) and Lithuania (Radoszkowski 1866) were also published during this time.

In the first half of the 20th century, cuckoo wasps were relatively actively collected and studied in Finland and Sweden, but not as much in the other countries of the region. In Finland, Sahlberg (1910) and Hellén (1920) published faunistic reports, and a similar publication of the Swedish fauna was prepared by Aurivillius (1911). Scattered minor observations were reported by several authors in Finland and Sweden. Several new records from Norway and Latvia were also published. Woldemar Trautmann’s monograph on the European fauna (Trautmann 1927) included several records from the Nordic countries.

In the 1950s, the Swiss chrysidid expert Walter Linsenmaier published his extensive revisions of the European fauna and described a large number of new taxa, many of which belong to the taxonomically difficult *Chrysis ignita* group (Linsenmaier 1951, 1959). Some of Linsenmaier’s taxa were from the Nordic countries. In Finland, Erkki Valkeila worked extensively with cuckoo wasps in the 1960s and 1970s and described two new species from Sweden and Finland (Valkeila 1971). Valkeila’s contribution to the knowledge of the Finnish fauna was significant, since he also reported many new records from the country.

Stellan Erlandsson published a checklist of Swedish cuckoo wasps that included 46 species and information on their distribution in the Swedish biogeographical provinces (Erlandsson 1971). In the same publication, he also presented species lists for Denmark, Norway and eastern Fennoscandia, with a total of 25, 25 and 46 species, respectively.

Tumšs & Maršakovs (1970) published an article on the cuckoo wasps of Latvia that included records of 31 species. Later, Tumšs (1976) reported an additional 10 species from the country. In Lithuania, Wengris (1962) published several records of the Chrysidae, and a comprehensive faunistic study was later published by Svetlana Orlovskyté and her colleagues (Orlovskyté *et al.* 2010). In that study, a total of 50 species were reported from Lithuania. In Estonia, almost nothing was published regarding cuckoo wasps before 2004, when Villu Soon finished his MSc thesis on the
Estonian fauna (Soon 2004). A total of 40 species were reported from Estonia in his thesis, and several new species from other Baltic and Nordic countries were also listed.

Most published records of cuckoo wasps from the Russian part of Fennoscandia date back to the 19th and early 20th centuries, when parts of the region belonged to Finland. However, several Russian articles have been published in recent decades, which include scattered information on cuckoo wasps from the area. Most of them were published by Andrei Humala and his colleagues from the Republic of Karelia, northwestern Russia.

The early 21st century has been a period of active chrysidid research in the Nordic and Baltic countries. A large number of faunistic inventories of aculeate hymenopterans have been published especially in Sweden, many of which also include records of cuckoo wasps. In 2014, Villu Soon finished his PhD thesis on the phylogeny of the *Chrysis ignita* species group, which focused on the Northern European fauna (Soon 2014). Svetlana Orlovskytė and her colleagues also published a study on the *Chrysis ignita* species group, in which they described two new species from the Baltic region (Orlovskytė et al. 2016). An important contribution to the knowledge of the hosts of Northern European species was recently made by Pärn et al. (2014) in Estonia.

### 2. Aims of the thesis

The main aim of this thesis was to clarify the taxonomy and distribution of Northern European cuckoo wasps, with emphasis on the fauna of Finland. Another major objective was to investigate the long-term population trends of Finnish cuckoo wasps and assess the factors behind these trends.

More specifically the aims of this thesis were:

1) to determine which species of cuckoo wasp occur in Northern Europe, i.e. Fennoscandia, Denmark and the Baltic countries (I–IV),
2) to assess their valid names according to the International Code of Zoological Nomenclature (II, III),
3) to investigate their morphological and molecular differences and present an identification key for all species (I, III, IV) and
4) to study their distribution, abundance and changes in occurrence in Finland and investigate which shared species traits are associated with these changes (II, IV, V).

Additionally, this thesis aims at promoting environmental conservation and giving guidelines for the protection of threatened species. Hopefully, this thesis will also increase knowledge and interest in cuckoo wasps among amateur entomologists and other naturalists.

### 3. Materials and methods

#### 3.1. Collections and literature examined

The distributional, ecological, morphometric and molecular data of cuckoo wasps and their hosts, as well as type specimens, were mostly acquired from private and public European entomological collections (I–V). Public collections that contain the material studied are listed below:

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<td>HNHM</td>
<td>Hungarian Natural History Museum, Budapest, Hungary</td>
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<td>IRSNB</td>
<td>Royal Belgian Institute of Natural Sciences; Brussels, Belgium</td>
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The private collections consulted consisted of app. 30, mainly Finnish, entomological collections of amateur and professional entomologists (V). The number of specimens examined was notably lower in the private than in the public collections. Additional data were obtained from ecological studies conducted by the Finnish Environment Institute (SYKE) and the Finnish Forest and Park Service (Metsähallitus) in 2004–2006. All materials were identified by me and my coauthors.

Northern European entomological and zoological journals, European faunistic publications, internet databases and other sources were thoroughly inspected to locate all published records of cuckoo wasps from the study region. These records were then critically assessed and listed for all taxa (II).

### 3.2. Molecular and morphometric analyses

Molecular analyses were carried out to evaluate the taxonomic status of Northern European species of the *Chrysis ignita* group (I) and to delineate a newly detected cryptic species, *Chrysis borealis* Paukkunen, Ødegaard & Soon, 2015, by mtDNA characters (IV). All known species and subspecific taxa of the *C. ignita* group from Fennoscandia and the Baltic countries were sampled. Additionally, samples of two outgroup species, as well as specimens that could not be identified reliably using morphological characters were included in the analysis.
Samples for mtDNA analyses were gathered from all the Fennoscandian and Baltic countries, except Latvia. Additional samples from neighbouring countries as well as some other parts of Europe, were included for better evaluation of intraspecific variability. Only recently collected and properly preserved (air-dried or 96% ethanol-stored) specimens were used for molecular analyses, due to difficulties in extracting DNA from old specimens. Although fresh samples were available for all Northern European species, the number of samples for some rare species remained low.

Some publicly available standard DNA barcode sequences, i.e. fragments of the mitochondrial COI gene, from the Barcode of Life database (BOLD, Ratnasingham & Hebert 2007) were also included in the analysis. These were accepted only if they consisted of more than 90% of the standard barcode sequence (658 base pairs) and if species identification could be verified from the original specimens or photos available at BOLD. In total, nearly 400 standard DNA barcode sequences were analysed (I, IV).

In addition to the COI gene sequences (length 750 bp), sequences from mitochondrial ribosomal RNA (rRNA) genes (16S rRNA, transfer RNA for valine (tRNAVal), 12S rRNA and NADH dehydrogenase subunit 4 (ND4), combined length 2017–2057 bp) were also used for resolving the relationships between Northern European species of the *Chrysis ignita* group. DNA was extracted from the thoracic muscle tissue and legs of the specimens studied. All rRNA sequences and most of the COI sequences were obtained, using standard extraction and sequencing methods at the University of Tartu (I). DNA barcode sequences were also received from the Canadian Centre for DNA Barcoding (CCDB), where a high-throughput protocol was used for extraction, including polymerase chain reaction (PCR) amplification and sequencing (I, IV).

Two approaches were employed for testing the validity of Northern European species of the taxonomically challenging *Chrysis ignita* group. These included (1) genetic distance analysis based on the standard COI barcode sequences and; (2) phylogenetic analysis of the COI fragment together with rRNA genes.

Morphometric measurements were taken to find useful morphological characters for identification of the cryptic species of the *Chrysis ignita* group (IV). The characters examined included length and width of the antennal segments, width of the head and length of the forewing. These characters were chosen, because they preliminarily showed distinct interspecific differentiation (proportions of antennal segments) or accounted for intraspecific variation in body size (head width and wing length). Ocular micrometers on the Wild M5 microscope (Wild Heerbrugg, Heerbrugg, Switzerland) and Leica MZ75 microscope (Leica Microsystems GmbH, Wetzlar, Germany) were used for the measurements. Student’s t-test was used for studying differences in the characters measured between species.

### 3.3. Construction of the identification key

An illustrated dichotomous key for all Nordic and Baltic cuckoo wasp species was prepared by examining all previously published morphological diagnostic characters of the Northern European species and critically assessing their suitability for species identification of Northern European specimens (IV). Species identification of European cuckoo wasps has largely relied on the works of Linsenmaier (1951, 1959, 1997), Morgan (1984), Kunz (1994) and van der Smissen (2010), which focus primarily on the central European fauna. If new and useful diagnostic characters were detected, they were also added to the key.

### 3.4. Analysis of population trends and species traits

The population trends of 48 Finnish cuckoo wasp species and 8 selected host species were assessed by studying changes in the occupancy of 10 x 10 km grid squares between two periods: 1840–1967 and 1968–2015 (V). The periods were selected so that the number of individuals observed (proxy of study effort) was as equal as possible in both periods. The cut-off point (late 1960s) also coincided well with
a major shift in land-use practices in Finland, including intensification of agriculture and forestry, as well as accelerating urbanization (Luoto et al. 2003). The final dataset included data on 18,584 specimens of cuckoo wasps collected within the current (i.e. post-WW II) borders of Finland in 1840–2015. The first period included 9186 individuals and the second period 9398 individuals (Figure 3).

Figure 3. Locations of cuckoo wasp records during the two study periods (A) 1840–1967 and (B) 1968–2015 in Finland. Well-studied 10 x 10 km grid squares, with at least 10 individuals, are shown by black dots. Other squares are shown by grey dots. The thin grey lines indicate the borders of the biogeographical provinces.

Occupancy was calculated separately for both study periods as the proportion of occupied squares (with at least one observed individual) to all studied squares of the period. The population trends of each species were then assessed by measuring the relative change in occupancy between the two periods. To assess the temporal changes more reliably, poorly studied grid squares were omitted, and only squares with at least 10 individuals observed per period were included in the analysis. These well-studied squares comprised less than half the total number of squares in both periods, but approximately 90% of all individuals. The significance of change in occupancy was tested for each species statistically.

Data on five species traits were included in a comparative analysis to determine their effects on the population trends. The traits included 1) abundance, 2) size of the distribution area, 3) body length, 4) host specificity and 5) nesting type of the host. These traits influenced the responses to environmental changes in hymenopterans and other insects in previous studies (e.g. Kotiaho et al. 2005, Öckinger et al. 2010, Williams et al. 2010, Bartomeus et al. 2013, Powney et al. 2015).
Abundance was assessed according to the total number of individuals during both observation periods, while distribution size was measured as the total number of occupied biogeographical provinces (see Figure 3). Body length was measured as the average of the minimum and maximum body lengths (mm) for each species. Host specificity was presented as an ordinal variable with three categories (low, moderate and high), depending on the number and relatedness of host species in Finland. Finally, each cuckoo wasp species was classified into two categories according to the nesting type of its host species: 1) ground-nesting (endogeic) or 2) above ground/cavity-nesting (epigeous).

Comparative analysis between the occurrence changes (dependent variable) and species traits (explanatory/independent variables) was performed to determine whether they were associated. To disentangle which combinations of explanatory variables showed the most parsimonious fit to the data and to explore the overall relative importance of the explanatory variables, the model selection approach was applied (Burnham & Anderson 2002). A total of 30 generalized estimation equation (GEE) models were fitted, including all possible combinations of the five explanatory variables while accounting for phylogenetic relatedness among the cuckoo wasp species. The models fitted were ranked according to their quasi-information criterion (QIC) value from the smallest to the highest. For each model, the likelihood that it showed the best fit in the data was calculated. Following this, the relative importance of each explanatory term was estimated.

To compare the population trends of cuckoo wasps with that of their hosts, data on eight host species were collected. They were selected to represent both cavity-nesting potter wasps (Vespidae: Eumeninae) as well as ground-nesting digger wasps (Crabronidae). Each of these species has at least one specialist or near-specialist cuckoo wasp kleptoparasite species in Finland, enabling direct comparison of occurrence trends between the hosts and their natural enemies. The host data were collected from the same sources as the cuckoo wasp data. The host dataset consisted of 4229 individuals, all collected within the current borders of Finland in 1840–2015.

The population trends of the eight host species selected were analysed in a manner similar to that of the cuckoo wasps. The dependence between the trends of the hosts and their specialist cuckoo wasp kleptoparasites (10 species) was studied with Spearman’s correlation analysis. Additionally, Wilcoxon’s signed-rank test was used to determine whether the changes in occurrence were larger in cuckoo wasps than in their hosts.

4. Results and discussion

4.1. Taxonomic findings and species identification

Both the genetic distance analysis and the phylogenetic analysis of the mtDNA sequences supported the validity of 15 out of 18 Northern European species of the Chrysis ignita group (I). Nearly all presumably conspecific samples formed well-supported monophyletic clades, and most species also exhibited interspecific genetic distances of over 2%, which is often suggested as an indication of status as a valid species in insects. Only within the group containing C. ignita (Linnaeus, 1758), C. impressa Schenck, 1856 and C. sp. (= C. borealis), as well as the group with C. mediata Linsenmaier, 1951 and C. solida Haupt, 1956, were the interspecific genetic distances substantially lower than 2%. In C. terminata Dahlbom, 1854, the minimal interspecific distance was 1.85%.

The specific status of Chrysis mediata Linsenmaier, 1951 and C. solida Haupt, 1956 remained unresolved, and samples of C. pseudobrevitarsis Linsenmaier, 1951 likewise did not cluster as supposed, but instead formed a paraphyletic group with respect to C. brevitarsis Thomson, 1870. The high intraspecific genetic divergence of C. pseudobrevitarsis, including up to five more or less distinct haplotypes, suggested the existence of cryptic species within this taxon. Chrysis schencki Linsenmaier, 1968 likewise showed high intraspecific divergence and formed two distinct clades with considerable
genetic distance between them. Unidentified specimens that were included in the analyses clustered into three groups, two of which were distinctly delimited and apparently represented cryptic species.

Five lectotypes were designated to maintain nomenclatural stability (II): *Hedychrum cupreum* Dahlbom, 1845 (= *Hedychridium cupreum* (Dahlbom, 1845)); *Chrysis zetterstedti* Dahlbom, 1845; *Chrysis succincta* var. *chrysoprasina* Trautmann, 1927 (= *Chrysis illigeri* Wesmael, 1839); *Chrysis succincta* var. *virideocincta* Trautmann, 1927 (= *Chrysis bicolor* Lepeletier, 1806) and *Chrysis succincta* var. *nordstromi* Trautmann, 1927 (= *Chrysis westerlundii* Trautmann, 1927), and two new synonymies were found: *Chrysis integra* Dahlbom, 1829 = *Hedychridium ardens* (Coquebert, 1801) and *Chrysis scintillans* Valkeila, 1971 = *Chrysis solida* Haupt, 1957. *Chrysis terminata* Dahlbom, 1854 represented the valid name for *C. ignita* Form A sensu Linsenmaier, 1959.

The lectotype of *Sphex semiaurata* Linnaeus, 1761 (= *Cleptes semiauratus* (Linnaeus, 1761)) was identical with *Cleptes pallipes* Lepeletier, 1806 and thus the old synonymy, already proposed by Dahlbom (1854), was re-established (III). The central and Southern European species with which *C. semiauratus* had been confused by several authors, i.e. *Cleptes semiauratus* sensu Lepeletier, 1806, *nec* Linnaeus, 1761, or *C. splendens* sensu Linsenmaier, 1959, *nec* Fabricius, 1798, had no available name and, therefore, to be able to designate a suitable type specimen, the species was described with a new name *Cleptes striatipleuris* Rosa, Forshage, Paukkunen & Soon, 2015 (III). A holotype male and a paratype female from Hungary were selected and deposited in the collection of TUZ, Estonia (Figure 4).

During the preparation of the identification key for Northern European cuckoo wasps (IV), many previously published diagnostic characters proved unsuitable for species determination, due to wide intraspecific variation, but some new characters were found and included in the key. For example, the relative length of the first and second flagellomere was considered useful for the identification of several morphologically similar species of the *Chrysis ignita* group.

Thorough morphological examination of Northern European cuckoo wasp specimens revealed a potentially undescribed and overlooked species of the *Chrysis ignita* group, closely related to *C. ignita* and *C. impressa*. Several specimens were DNA-barcoded, and the results supported the existence of a new species, which was described as *C. borealis* (IV) (Figure 5). However, not all specimens of *C.
borealis could be distinguished from other species, using morphological characters only. Therefore, information on the diagnostic positions of the DNA barcode sequence was also provided in the description. Two nucleotide mutations were conserved in all sequences of C. borealis, unlike in its closest species, C. ignita and C. impressa, and thus species identification with DNA barcoding is recommended, especially when morphology is doubtful.

Chrysis borealis is mainly found in cooler habitats than C. impressa, so it could be claimed to constitute only a darker coloured ecological form of C. impressa, not a distinct species. The slight, but constant divergence in the DNA barcode sequence and the statistically significant difference in the length ratio of the first and second flagellomere, however, supported the treatment of C. impressa and C. borealis as distinct, but evolutionarily young sibling species. Previous studies also indicated that morphological and molecular differences between biologically well-defined species can be extremely small or even nonexistent in the C. ignita group (I), a phenomenon typical of cryptic species in general.

4.2. Fauna of Fennoscandia, Denmark and the Baltic countries

The cuckoo wasp fauna of the study region consisted of 74 species in 14 genera (Table 1) (II, IV). The highest number of species is known from Sweden (53), while species richness is slightly lower in Estonia (51), Latvia (49), Lithuania (48), Finland (48) and Denmark (47). The lowest species numbers are found in Russian Fennoscandia (39) and Norway (38). The relatively high number of species in Denmark and the Baltic countries is noteworthy, due to their geographically smaller size compared with Finland, Norway and Sweden. Of the nearly 500 known European species approximately 15% were found in the study area. Six genera (Chrysidea Bischoff, 1913, Euchrooeus Latreille, 1809, Pentachrysis Lichtenstein 1876, Praestochrysis Linsenmaier, 1959, Spintharina Semenov, 1892 and Stilbum Spinola, 1806), which are known from Southern or central Europe, have not been found from Fennoscandia, Denmark or the Baltic countries. A recent phylogenetic study (Pauli et al. 2018) suggested that six of the European genera (Chrysidea, Chrysura Dahlbom, 1845, Pentachrysis, Praestochrysis, Spintharina and Trichyris Lichtenstein, 1876) should be synonymized with Chrysis to render the genus monophyletic. The genus Pseudospinolia Linsenmaier, 1951 was also recently synonymized with Pseudochrysis Semenov, 1891 (Rosa et al. 2017), and therefore the name Pseudochrysis neglecta (Shuckard, 1837) is now used for Pseudospinolia neglecta of chapters II and III.

As with species richness, species composition was also relatively similar in the various Nordic and Baltic countries. The most notable differences are found between the Nordic and Baltic regions. While 13 species have only been found in the Nordic countries, 8 species are known only from the Baltic countries. It is likely that many of the Nordic species will later be found in the Baltic region, when the area becomes better studied. Overall, the potential for finding new species is higher in the Baltic countries, due to less research activity and several species that are already known to occur in the adjacent areas.

More than half (app. 51%) of the species found in the study area have Trans-Palaearctic distribution areas, while the proportion of Western Palaearctic species is slightly smaller (app. 42%). However, many of the Western Palaearctic species are difficult to identify and may have been overlooked in the eastern parts of the Palaearctic region. Therefore, it is likely that the proportion of Trans-Palaearctic species is somewhat larger.

While four European species have been recorded in North America, only one of them, Omalus aeneus (Fabricius, 1787), is considered to be a truly Holarctic species (Kimsey 2006). The other three species, Cleptes semiauratus, Pseudochrysis neglecta and Pseudomalus auratus (Linnaeus, 1758), were probably been introduced accidentally into North America with timber, plant material etc. (Kimsey & Bohart 1991). Recently, unpublished DNA studies have shown that Nearctic and Palaearctic populations of O. aeneus widely differ genetically and possibly may represent distinct species. Therefore, it is questionable if any truly Holarctic cuckoo wasp species exist.
Table 1. Number of cuckoo wasp species in the Nordic and Baltic countries and Russian Fennoscandia.

<table>
<thead>
<tr>
<th>Country/Region</th>
<th>Previously reported species¹</th>
<th>Deleted species²</th>
<th>New species</th>
<th>Total³</th>
</tr>
</thead>
<tbody>
<tr>
<td>Denmark</td>
<td>48</td>
<td>4</td>
<td>3</td>
<td>47</td>
</tr>
<tr>
<td>Estonia</td>
<td>46</td>
<td>1</td>
<td>6</td>
<td>51</td>
</tr>
<tr>
<td>Finland</td>
<td>59</td>
<td>13</td>
<td>2</td>
<td>48</td>
</tr>
<tr>
<td>Latvia</td>
<td>51</td>
<td>13</td>
<td>11</td>
<td>49</td>
</tr>
<tr>
<td>Lithuania</td>
<td>51</td>
<td>4</td>
<td>1</td>
<td>48</td>
</tr>
<tr>
<td>Norway</td>
<td>39</td>
<td>7</td>
<td>6</td>
<td>38</td>
</tr>
<tr>
<td>Sweden</td>
<td>67</td>
<td>17</td>
<td>3</td>
<td>53</td>
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<tr>
<td>Russian Fennoscandia</td>
<td>26</td>
<td>2</td>
<td>15</td>
<td>39</td>
</tr>
<tr>
<td>Total</td>
<td>86</td>
<td>17</td>
<td>5</td>
<td>74</td>
</tr>
</tbody>
</table>

¹ Includes all correctly and falsely reported species (also misinterpreted species) over time.
² Some of the deleted species were already removed from regional faunae in previous studies.
³ The total number of species does not include new faunistic records published by Orlovskytė et al. (2016) and Paukkunen et al. (2016), which increase the number in Finland to 49, Lithuania to 50 and Norway to 39, and the total number of species to 75 (by adding Chrysis parietis Budrys, 2016 to the region).

Two species, Holopyga metallica (Dahlbom, 1854) and Chrysis westerlundi Trautmann, 1927, have not been found outside eastern Fennoscandia. However, it is unlikely that they represent Fennoscandian endemics, because their habitats also occur in Eastern Europe and Siberia, where cuckoo wasps are still relatively poorly studied. Chrysis westerlundi and H. metallica may actually be conspecific with the Eastern Palaearctic species C. cavaleriei du Buysson, 1908 and H. sibirica Semenov, 1967, respectively. To confirm this hypothesis, molecular and morphological studies as well as examination of type specimens are needed.

Four species, Elampus foveatus (Mocsáry, 1914), Chrysis borealis, C. gracillima Förster, 1853 and C. pulcherrima Lepeletier, 1806, were recorded for the first time from the Nordic and Baltic countries. Of these, C. borealis was also new to science, as noted above. Additionally, Chrysis terminata can be included in the list of new species, because previously it was treated as a form of C. ignita (“Form A” of Linsenmaier). The Danish record of Hedychridium purpurascens (Dahlbom, 1854) was erroneous, but the species was found in Estonia in our study.

A total of 17 species were incorrectly reported from the region, due to erroneous identifications in previous publications. However, some of these species had already been removed from the regional faunae in previous studies (Table 1).

4.3. Temporal patterns and frequency distribution in Finnish cuckoo wasps

The number of cuckoo wasp individuals collected in Finland remained low throughout the 19th century (V, Figure 6). From the early 20th century to the 1960s and 1970s interest in cuckoo wasps, as well as other aculeate wasps, rose rapidly among entomologists. However, during the last two decades of the century, interest decreased and little material was collected. After the 1990’s many entomologists in Finland have begun collecting cuckoo wasps again.
Figure 6. Number of (A) individuals, (B) species, (C) 10 x 10 km squares and (D) collectors of cuckoo wasps in different decades during 1840–2015. The accumulation of species observed in Finland is shown with a solid line in panel B.

The number of species recorded per decade tended to increase, reflecting a similar trend in collection activity. However, the cumulative species number has not risen significantly after the 1950s, which indicates that the fauna of Finland, with a total of 49 recorded species, is already relatively well known. The spatial coverage of cuckoo wasp data, as displayed by the number of 10 x 10 km squares, has increased especially after the 1990s, since it has become easier and more popular for entomologists to travel and collect throughout the country. The accuracy of reporting collection localities has also improved, especially after implementation of the national coordinate system in the early 1970s. The number of collectors was high from the 1930s to the 1960s and has increased once again after the 1990s. However, most collectors have focused on other groups of insects and have collected cuckoo wasps only sporadically.

The frequency distribution of Finnish cuckoo wasps is strongly skewed, with only a few common species and many rare species (Figure 7). The clearly most abundant species is *Chrysis angustula* Schenck, 1856, which comprised 17% of all individuals studied, while the next most abundant species, *Hedychrum nobile* (Scopoli, 1763), constituted 8% of all individuals. Commonness, as measured by the number of 10 x 10 km squares with records, was strongly correlated with abundance (Spearman’s correlation coefficient 0.94, P < 0.001).
Figure 7. (A) Relative abundance (total number of individuals) and (B) commonness (total number of 10 x 10 km squares) of Finnish cuckoo wasps, based on the study material.

4.4. Species traits and population trends

Quantitative analysis showed that 11 Finnish cuckoo wasp species (23%) declined significantly between the two time periods studied (1840–1967 and 1968–2015), whereas none increased significantly, although the increase in one species was nearly significant (V). The proportion of declining species versus increasing species was unusually high compared with the other insect groups examined, even in a global perspective. For example, in a long-term study of Finnish butterflies, the proportion of declining species was estimated to be 31%, while 36% of species were considered as increasing (Kuussaari et al. 2007).

In the comparative analysis of species traits abundance, body size and nesting type of the host were associated with occurrence changes in cuckoo wasps. Abundant species declined less than scarce species, which may have been due to their less demanding environmental requirements and thus stronger resilience to environmental changes (Warren et al. 2001). Body size was positively associated with occurrence trend, indicating that small species generally declined more than large species. Small body size may correlate with poor dispersal ability and therefore result in vulnerability to environmental changes, such as habitat fragmentation (e.g. Greenleaf et al. 2007, Bommarco et al. 2010). Small body size is also linked with high temporal fluctuations in population size (Henle et al. 2004), which may further increase sensitivity to habitat loss.
Cuckoo wasps that have hosts nesting above ground (cavity nesters) had more negative occurrence trends than those with ground-nesting hosts (ground nesters). While both groups of species have probably suffered from habitat loss in Finland, the emergence of secondary habitats, such as road verges and sand pits, may have benefitted species living in sandy areas and compensated for the negative impact of habitat destruction. Cavity nesters, on the other hand, have not been able to find suitable habitats in intensively managed forests or modern agricultural areas. The loss of traditional log barns and houses has had especially adverse effects on many cavity nesters (Szczepko et al. 2013). The higher vulnerability of cavity-nesting compared with ground-nesting hymenopterans has also been observed in previous studies (Steffan-Dewenter et al. 2006, Williams et al. 2010).

Host specificity was not linked with the population trends of cuckoo wasps, although previous studies have shown that food/nutritional specialists are often more vulnerable to environmental changes than generalists (e.g. Bommarco et al. 2010, Öckinger et al. 2010, Bartomeus et al. 2013). The lack of this dependence could have resulted from specialized cuckoo wasps tending to use common host species that probably retained stable populations during the study period. A study on butterflies also indicated that moderately generalist species can be more sensitive than specialists or extreme generalists (Dapporto & Dennis 2013).

Changes in occurrence were generally larger in cuckoo wasps than in their hosts, although the difference statistically was only marginally significant, due to the small number of host species studied. This result is in accordance with expectations, since species at higher trophic ranks may be more sensitive to environmental changes than species at lower ranks (Hawkins 1994, Holt 1996). Komonen et al. (2000) found that habitat loss and fragmentation in boreal forests truncated food chains, and parasitoid wasps were more affected than their hosts. Moreover, Roslin et al. (2013) showed that food chain length decreased from large to small islands and parasitoid wasps were more sensitive to island size variation than organisms at lower trophic levels. Kruss and Tscharntke (2000) also observed that parasitoids suffered more from habitat loss and isolation than their phytophagous hosts.

A possible source of bias in the Finnish cuckoo wasp dataset could have been caused by changes in sampling methods during the past 175 years. Traditionally, cuckoo wasps have been collected with nets, but in recent decades, different types of traps have gained popularity. Yellow pan traps have become especially popular in entomological surveys. Ground-nesting wasps are probably more attracted to pan traps than are cavity-nesting wasps, since the traps are usually placed on sparsely vegetated spots on the ground. Consequently, the proportion of ground-nesting species could have been overrepresented in recently collected material compared with older collections. This bias is, however, difficult to assess, because the collection method is usually not known for older collected specimens.

Another potential source of bias is caused by changes in the accuracy of reporting collection localities. The national coordinate system (YKJ or GRID27E) was introduced in the early 1970s, and before this, only locality names were used for reporting the collection localities for Finnish entomological specimens. Usually, only the name of the municipality was mentioned, which may have led to an artificial aggregation of old records into some 10 x 10 km squares in the dataset. The problem of spatial aggregation of records during the first observation period could have been somewhat mitigated by applying a larger grid, e.g. of 50 x 50 km squares. This, however, would have caused a loss in resolution and lowered the number of significant trend estimates. A sufficiently fine-scaled grid is essential for the reliable assessment of rarity, trends and extinction risk in species (Hartley & Kunin, 2003; Wilson et al. 2004).

Trend assessments based on natural history collections can be particularly difficult for popular and attractive groups, such as butterflies, moths and beetles, in which rarity and charisma strongly influence collection probability (Jeppsson et al. 2010). In cuckoo wasps, most species are rather similar in general appearance and species identification is often difficult or impossible without a microscope. Therefore, they are collected relatively randomly, while the proportions of specimens in collections probably reflect actual abundances more reliably than in, e.g. butterflies that are skewed
towards rare species (Kuussaari et al. 2007). Pekkarinen and Huldén (1991) noted that specimens of eumenine wasp species that are similar in general appearance are also caught more randomly in collections than specimens of insect groups with greater specific differences in external morphology.

The population trends in cuckoo wasps were assessed here by comparing the relative occupancies in two study periods with approximately equal numbers of records. Since there were only two long study periods (length 128 and 48 years) that were compared, possible shorter temporal fluctuations in population sizes could have remained unnoticed in the study. However, most species are likely to have substantial fluctuations in their population sizes during shorter time-scales, and therefore the changes in occurrence observed represent a rough estimate of long-term population trends.

5. Conclusions

This thesis revises and summarizes what has been known about Northern European cuckoo wasps to date. The aim of this work was not to present a final list of cuckoo wasp species in the region, but rather to provide a solid basis for future investigations of the family. Clearly, the regional cuckoo wasp faunas of the various countries of Northern Europe have been very unevenly studied. While cuckoo wasps have been relatively actively studied in Finland and Sweden for decades, few studies have been published in the Baltic region, Norway and Russian Fennoscandia. However, even having a long history of research does not necessarily indicate that the fauna of a region is well known, since taxonomic errors are often repeated in publications and most studies have consisted of only small-scale species inventories.

In this study, a total of 74 cuckoo wasp species belonging to 14 genera were found in the Nordic and Baltic countries. Although some of the species have probably disappeared from the region, the actual number of species currently occurring in Northern Europe is probably close to 80, or somewhat higher. More than 10 species not yet found in the region, are known to occur in northern Belarus, Poland and Germany, and some of them have likely been overlooked in the Nordic and especially Baltic countries. Climate change is expected to increase the future number of species, since many southern species will probably be distributed in the north, but only few of the currently known species are likely to suffer from a warming climate. However, the indirect effects of climate change can be difficult to predict.

Genetic studies, and especially the increasing use of DNA barcoding, will probably also reveal several new future species of cuckoo wasps in Northern Europe. Such cryptic species are still expected to be found, especially in the *Chrysis ignita* group. In this study, possible cryptic species diversity was found in *C. pseudobrevitarsis*, *C. schencki* and in the clade consisting of *C. ignita* and *C. impressa*. One such cryptic species, *C. borealis*, was described in this study, although its distinctiveness was initially suggested from its morphological characteristics. Another new cryptic species, *Chrysis parietis* Budrys, 2016, was recently described, based on specimens collected from Finland, Lithuania and Norway, and *Chrysis horridula* Orlovskytė, 2016 was found in Belarus close to the Lithuanian border (Orlovskytė et al. 2016). Both species were detected by studying mtDNA sequences.

While molecular studies of cuckoo wasps have mainly focused on the *Chrysis ignita* group, other cuckoo wasps have remained much less extensively studied. Molecular analyses of Northern European species have shown that cryptic diversity can be widespread in the family. For example, the COI barcodes of *Omalus aeneus* (Fabricius, 1787) clustered into distinct clades, indicating the existence of possibly as many as five cryptic species (J. Paukkunen, F. Ødegaard and N. Johansson, unpublished). Clearly, further molecular and morphological studies of cuckoo wasps are needed, and the coverage of groups studied should be expanded. New studies are also needed to identify new DNA markers and morphological features, since the characters currently available cannot fully resolve the species limits and phylogeny of cuckoo wasps.

The identification keys prepared in this study were mainly based on external morphological characters. Although exhaustive efforts were put into finding stable and reliable diagnostic features,
many specimens, especially males of the *Chrysis ignita* group, remain difficult or even impossible to identify by morphological characters only. Detailed morphometric measurements of concealed terga and sternae, as well as genital capsules in males, could possibly reveal new useful characters for future species identification (e.g. Noskiewicz & Lorenkowa 1963, van der Smissen 2010). The application of these characters, however, is time-consuming and requires special slide-mounting and microscopy skills. Other diagnostic characters will probably be found from cuticular hydrocarbon profiles (e.g. Wurdack *et al.* 2015), but these, too, will be impractical for most entomologists.

Since DNA barcoding is very useful for identifying cuckoo wasps, we recommend it for the study of specimens that are especially difficult to identify by morphological characters, such as those of the *C. ignita* group. The barcodes that were used in this study have been deposited in the BOLD database (Ratnasingham & Hebert 2007) and are thus available for research purposes and as references for identification. DNA barcodes are also useful for species delimitation, as has been shown in this study. Entomologists studying cuckoo wasps should always focus on collecting and preserving their specimens so that the DNA is not destroyed, e.g. by placing tissue samples in ethanol. Since the future geographical and taxonomic coverage of DNA-barcoded specimens and species will improve, assessment of species limits and diagnostic morphological characters will also become more reliable.

Although much work remains in solving the taxonomic problems of cuckoo wasps, there is even more to be gained by a study of their biology and ecology. The life histories of most Northern European species are still poorly known, which is partly due to difficulties in finding and rearing their immature stages. Some progress has recently been made in assessing host relationships by rearing cuckoo wasps in artificial trap nests (Pärn *et al.* 2014). Future use of DNA barcoding will probably facilitate this work significantly, since the eggs, larvae and pupae of cuckoo wasps will become easily identifiable to species level.

As discussed above, climate warming will probably benefit many cuckoo wasps and bring new species to Northern Europe, but many species are also vulnerable to human impacts and threatened by the intensification of agriculture and forestry. The percentage of Red-Listed species is exceptionally high in cuckoo wasps in all the Nordic countries, and this study has showed that many more species have declined than increased in abundance during recent decades in Finland. The same factors that cause problems for cuckoo wasps represent significant threats for numerous other species of hymenopterans, such as many bees and other important pollinators. Therefore, it is important that these factors are addressed seriously and taken into account in land use and environmental conservation. The retention of sun-exposed deadwood on forest edges and open habitats, as well as the preservation of old wooden structures in agricultural landscapes, are especially important measures that will benefit cuckoo wasps.

During the preparation of this thesis, cuckoo wasps have received increased attention in the media, and many people have become interested in the group. The illustrated identification key that was published as a part of this study has become popular and widely used, which can be observed in viewer statistics at the ZooKeys website. Less than three years after its publication, it had already been viewed over 18.000 times, and it was scored by popularity in the top 5% of all research outputs by the Altmetric website. Additionally, a printed version of the key has become available at the British NHBS bookstore, and the Norwegian Biodiversity Information Centre, Artsdatabanken, prepared a user-friendly digital version of the key. Clearly, many entomologists have found the key useful for identifying cuckoo wasps, but without doubt, many have also just enjoyed its pictures of these attractive insects. This has indeed been one aim of this study: to offer positive aesthetic experiences that increase interest in the environment and its conservation.
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