

VILLU SOON

A phylogenetic revision of
the *Chrysis ignita* species group
(Hymenoptera: Chrysididae)
with emphasis on the northern
European fauna



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European fauna



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Disclaimer: this dissertation is not issued for purpose of public and permanent scientific record, and remains unpublished for the purposes of zoological nomenclature (ICZN, 1999: 8.2.)



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LIST OF ORIGINAL PUBLICATIONS

This dissertation is a summary of the listed papers, which are referred to in the text using the respective roman numerals:

- I. **Soon, V.;** Saarma, U. (2011) Mitochondrial phylogeny of the *Chrysis ignita* (Hymenoptera: Chrysididae) species group based on simultaneous Bayesian alignment and phylogeny reconstruction. *Molecular Phylogenetics and Evolution*, 60(1), 13–20.
- II. **Soon, V.;** Budrys, E.; Orlovskitè, S.; Paukkunen, J.; Ødegaard, F.; Ljubomirov, T. & Saarma, U. (2014) Testing the validity of Northern European species in the *Chrysis ignita* species group (Hymenoptera: Chrysididae) with DNA Barcoding. *Zootaxa*, 3786(3), 301–330.
- III. **Soon, V.** (2010) *Chrysis tripotini* sp. n., a new cuckoo wasp (Hymenoptera, Chrysididae) from South Korea. *Deutsche Entomologische Zeitschrift*, 57(1), 37–41.
- IV. Paukkunen, J.; Rosa, P.; **Soon, V.;** Johansson, N. & Ødegaard, F. Faunistic review of the cuckoo wasps of Fennoscandia, Denmark and the Baltic countries (Hymenoptera: Chrysididae). (Submitted manuscript).

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The author of this thesis is responsible for the following contributions to the included papers:

- I original idea, data collection, designing experiment, data analysis and paper writing
- II original idea, data collection, designing experiment, data analysis and paper writing
- III original idea, data analysis and paper writing
- IV data collection, data analysis and paper writing: mostly sections related to the *C. ignita* species group and the fauna of the entire family in Estonia, Latvia and Denmark

I. INTRODUCTION

The Chrysididae, commonly known as cuckoo wasps, is a cosmopolitan Hymenoptera family that includes about 3000 named species plus around 1000 species that are as yet unnamed or need to be resurrected from synonymy (Kimsey & Bohart 1991). All species of Chrysididae exhibit a parasitic lifestyle, being cleptoparasites or cleptoparasitoids of various Hymenoptera families, with a few exceptional groups that are parasitoids of Phasmatodea eggs or limacodid moths. Life cycle of typical representatives of the *Chrysis ignita* species group is illustrated in figure 1. In many languages cuckoo wasps are also known as gold wasps, reflecting their characteristic colouration, which resembles a metallic sheen (Figures 2–4; I, Figure 2). Despite their attractive appearance, cuckoo wasps have not been particularly popular objects of study for entomologists, mostly due to their relatively small size. Therefore the family has remained little studied, with many taxonomic uncertainties remaining, and its life strategies poorly understood. As cuckoo wasps are vulnerable to habitat changes and many of the poorly known taxa represent declining and threatened species in Europe, there is an urgent need to revise their taxonomy and distribution.

The Chrysididae family consists of four subfamilies: Cleptinae, Amiseginae, Loboscelidinae and Chrysidinae, of which only Cleptinae and Chrysidinae occur in temperate parts of Eurasia. Chrysidinae is by far the largest of the subfamilies, and it is divided into four tribes, of which three (Elampini, Chrysidini and Parnopini) occur in temperate parts of Eurasia and the fourth (Allocoelini) is endemic to the southern part of Africa. Compared with other regions, the European cuckoo wasp fauna is relatively well known (Rosa & Soon 2014), but our knowledge is still largely incomplete. Moreover, even existing knowledge is outdated and in need of revision. In order to improve our understanding of European cuckoo wasps, the *C. ignita* (Linnaeus, 1758) species group requires most attention.

Genus *Chrysis* belongs to the Chrysidini tribe and is by far the largest genus in the family in terms of the number of species it comprises. Species groups in the genus *Chrysis* were first introduced by Linsenmaier (1951), and this included the *Chrysis ingita* species group. In 1951 he included 9 species and 14 subspecific taxa from European fauna into this newly established group. Eight years later (Linsenmaier 1959a) he focused on the Palaearctic fauna and included 32 species and 30 subspecific taxa in the *C. ignita* group. Although the similar morphology of taxa throughout the group was noted quite early, the New World species of this group were treated as the *C. coerulans* species group in older publications (Moore 1966; Bohart & Kimsey 1982). A modern diagnosis of the group is given by Kimsey and Bohart (1991). Currently more than 150 species are ascribed to the group, making it the largest species group in the whole family. The group is widespread, with the majority of species inhabiting the Palaearctic region. The Palaearctic fauna is also the focus of this thesis, although the Old and New World representatives are closely related and don't

form separate entities. No overall treatment of the *C. ignita* group exists; however there are some regional works with keys to species in the group (Tsuneki 1957; Linsenmaier 1959a, 1994, 1997; Moore 1966; Bohart & Kimsey 1982; Morgan 1984; Kunz 1994; Rosa 2006)

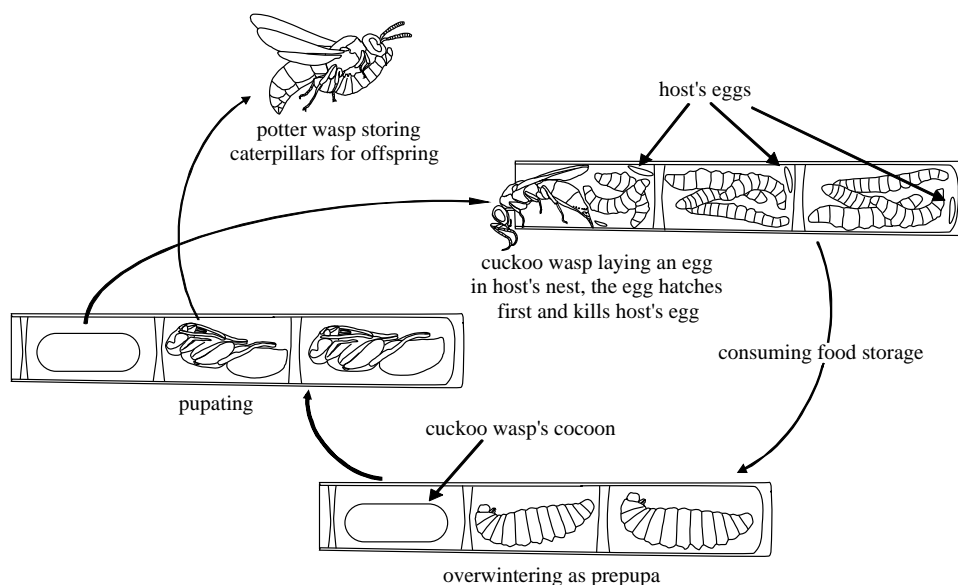


Figure 1. Life cycle of typical representatives of the *Chrysis ignita* species group.

Compared with the rest of Chrysididae, the *C. ignita* species group is remarkably homogenous in terms of morphology, and this has hindered species discrimination within the group. Shuckard (1836) made the earliest attempt to split what was up to then known as *Chrysis ignita* into separate taxa. Based mainly on colour, sculpturing and the shape of the abdominal terminal teeth he described and illustrated six varieties of *C. ignita* – var. *alcione* Shuckard, 1836, var. *asterope* Shuckard, 1836, var. *celeno* Shuckard, 1836, var. *electra* Shuckard, 1836, var. *maja* Shuckard, 1836 and var. *taygeta* Shuckard, 1836 – and one new species – *C. ruddii* Shuckard, 1836. Despite the limited descriptions and the lack of existing type specimens, Shuckard's study is noteworthy since it is clear that he genuinely observed different species, and one of his taxa, *C. ruddii*, is still treated as a valid species.

Shuckard was followed by Dahlbom (1845, 1854), who named four new European species belonging to the group: *C. obsoleta* Dahlbom, 1845, *C. curvidens* Dahlbom, 1854, *C. terminata* Dahlbom, 1854 and *C. soluta* Dahlbom, 1854. None of these names remain in use and it appears likely that Dahlbom was relying on exceptional aberrant specimens. Since Dahlbom's types have not been studied thoroughly, these names have been treated as synonyms of *C. ignita* (Kimsey & Bohart 1991).

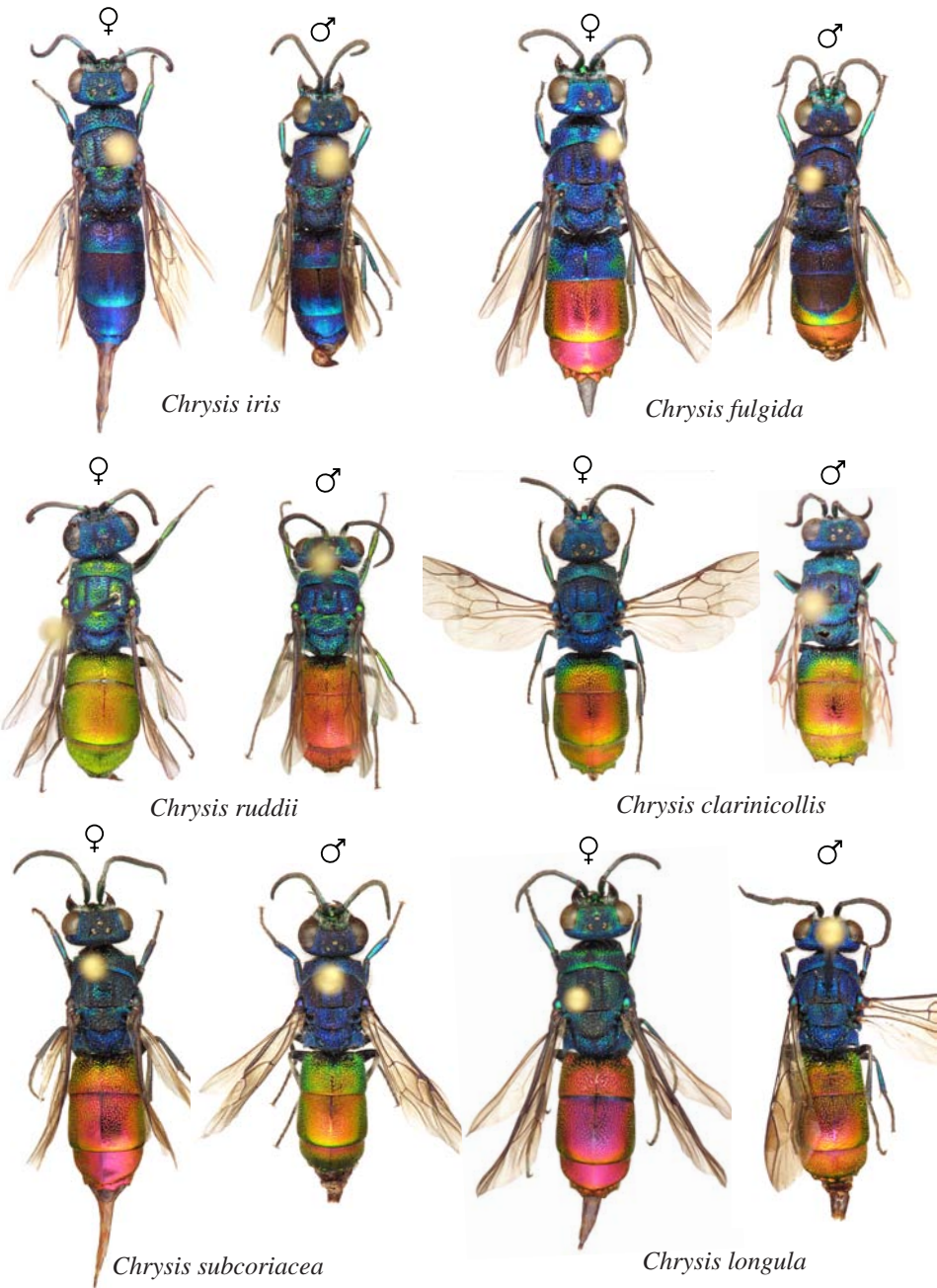


Figure 2. Estonian species of the *Chrysis ignita* species group.

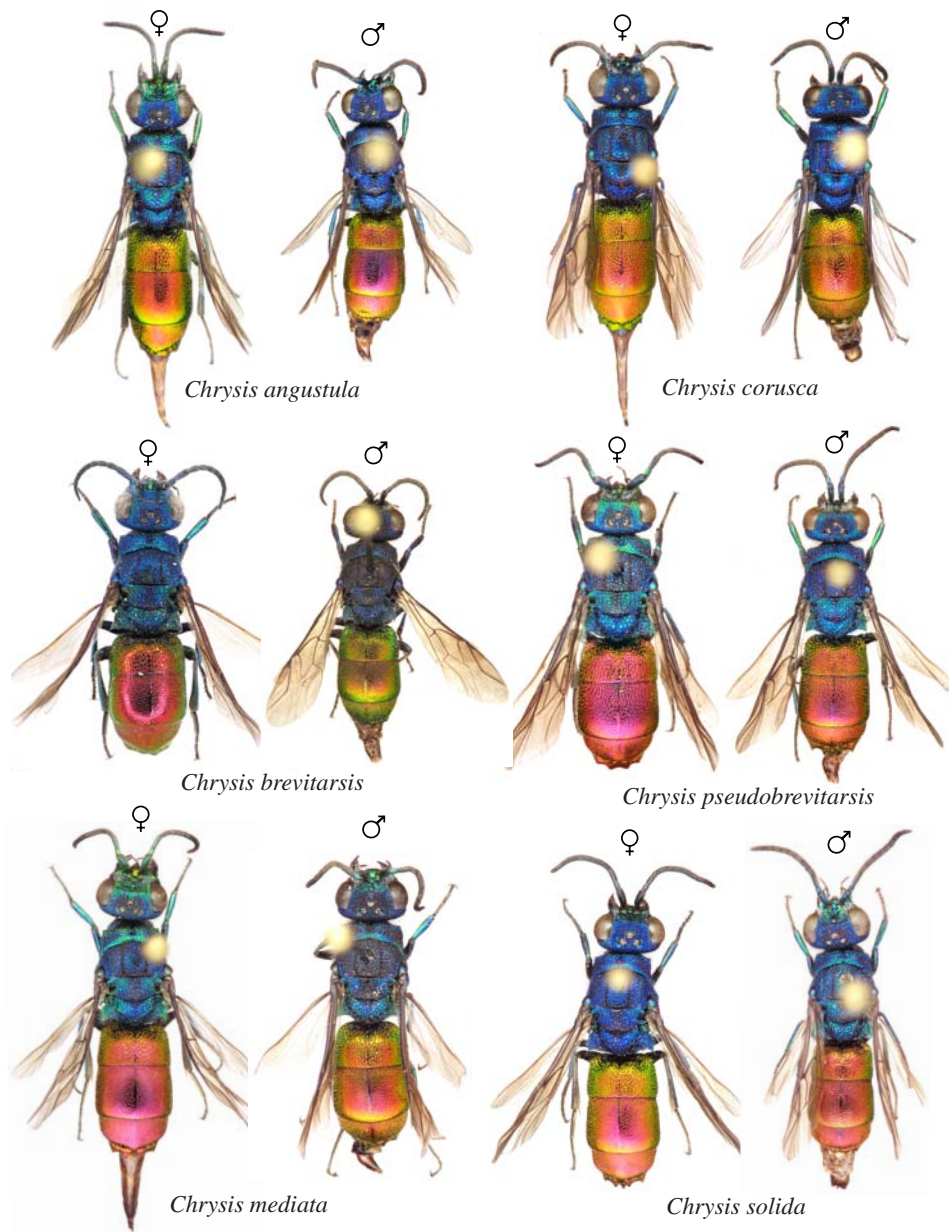


Figure 3. Estonian species of the *Chrysis ignita* species group.

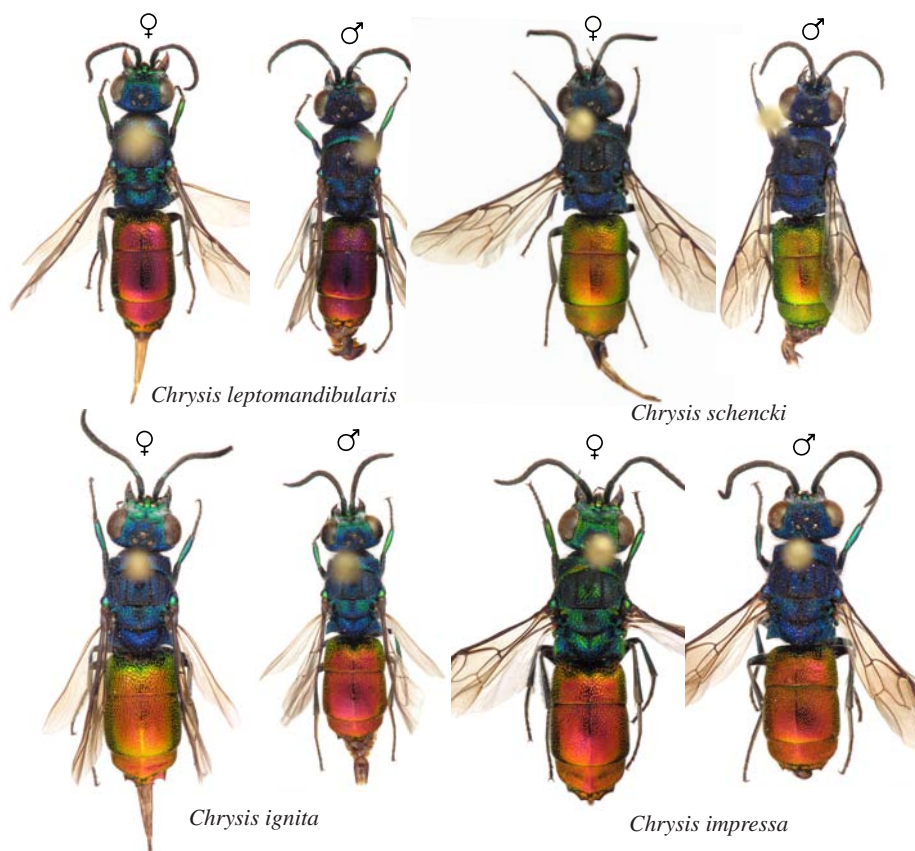


Figure 4. Estonian species of the *Chrysis ignita* species group.

Two years later Schenck (1856) published his interpretation of the group, wherein he described five new species: *C. angustula* Schenck, 1856, *C. impressa* Schenck, 1856, *C. gracilis* Schenck, 1856, *C. brevidentata* Schenck, 1856 and *C. vitripennis* Schenck, 1856. Two of these (*C. angustula* and *C. impressa*) are currently treated as valid species, although in a later publication Schenck (1861) himself relegated all of his new taxa to merely variations of *C. ignita*. In the following years specialists described several new taxa, but treated most existing names simply as varieties of *C. ignita* (Abeille de Perrin 1879; Mocsáry 1889; Buysson 1891; Bischoff 1913; Trautmann 1927). By the end of the 19th century, investigation of insect faunas outside Europe had become more active and many new species in the *C. ignita* species group were published from Asia and elsewhere (Smith 1874; Cameron 1887; Mocsáry 1889, 1893, 1912, 1914; Semenov-Tian-Shanskij 1892, 1967; Buysson 1898, 1908; Bischoff 1910; Uchida 1927). Tsuneki deserves special attention as he was the most important contributor of information about East Asian wasps and published descriptions

of many new taxa in the *C. ignita* species group (Tsuneki 1950, 1952, 1953, 1954).

The most important contribution to knowledge of the *C. ignita* species group was provided in a series of publications by Walter Linsenmaier (Linsenmaier 1951, 1959a, 1959b, 1968, 1987, 1994, 1997). He published descriptions of many new species and subspecies with accompanying keys. Unfortunately his work does not include a critical review of all previous descriptions and types, and his descriptions are sometimes difficult to interpret. This has resulted in misinterpretations of several species and raised doubts about the specific status of many of the taxa that Linsenmaier separated.

Since the middle of the 20th century, relatively few authors besides Linsenmaier have contributed to the taxonomy of the *C. ignita* species group by adding new descriptions or taxonomical notes (Móczár 1965; Valkeila 1971; Morgan 1984; Niehuis 2000). Currently, many taxa in the group have uncertain taxonomic status, being treated either as species or intraspecific forms by different authors (Kimsey & Bohart 1991; Kunz 1994; Linsenmaier 1997; Rosa 2006; Rosa & Soon 2014). Meanwhile, new species within the group continue to be described (Niehuis 2000; Tarbinsky 2000; Strumia & Yildirim 2008; I).

Nearly all attempts to resolve the taxonomy of the *C. ignita* species group have relied on the personal opinions of experienced authors regarding the limits of within-taxon variability in morphological characters. To test if previously described taxa are distinct from each other Kunz (1994) reviewed species in the *C. ignita* group in a more comprehensive manner by including biological data, examining the morphology of internal segments and conducting a morphometrical analysis. As his results did not support the distinctness of most included taxa, Kunz dropped these into synonymy. Although this result was accepted by some authors (Tscharntke *et al.* 1998; Gathmann & Tscharntke 1999; Kruess & Tscharntke 2002; Holzschuh *et al.* 2009), it was rejected by others (Linsenmaier 1997; Niehuis 2001; Rosa 2006; Smissen 2010). Nevertheless, Kunz's results have not yet been tested by an independent study.

Since morphological approaches have resulted in inconsistent treatment of many taxa in this group, I used molecular phylogenetic analysis, which has proven to be especially successful for resolving relationships between cryptic species (Hebert *et al.* 2003, 2004). Molecular characters have frequently been used to resolve taxonomic questions in insects, but have never been used to delimit species of cuckoo wasps. Most molecular studies incorporating cuckoo wasps have focused on resolving the higher level phylogenies of other insect taxa, with cuckoo wasps often used merely as an outgroup. Such studies have included phylogenetic reconstructions of: the entire Hymenoptera (Carpenter & Wheeler 1999), suborder Apocrita (Dowton & Austin 2001; Pilgrim *et al.* 2008), superfamily Apoidea (Ohl & Bleidorn 2006) and family Bethyridae (Carr *et al.* 2010). Molecular methods have only been successfully used to directly study Chrysididae in a few instances (Niehuis & Wägele 2004; Niehuis & Korb 2010).

Knowledge about the cuckoo wasp fauna in Fennoscandia, Denmark and the Baltic countries accumulate tightly together investigations of this family. That includes first species described by Linnaeus (1758) from Sweden as well as numerous taxonomic inconsistencies which are reflected in the studies. Linnaeus was followed by another Swedish entomologist Dahlbom, who provided high level cuckoo wasp studies in the region and whose monograph (Dahlbom 1854) is considered as a landmark in Chrysididae research. In the following years cuckoo wasps were actively collected and studied in Sweden and Finland, though such activity was far lower in other countries in the region (Norway, Denmark, Estonia, Latvia, Lithuania and NW Russia). From 1758 to the present day, nearly 250 studies on cuckoo wasps have been published in this region. Due to recent developments in cuckoo wasp taxonomy, as well as the study of type materials and nomenclature, it is evident that a number of these publications include significant errors. Therefore revision of the existing literature is needed in order to establish a solid overview about the current state of knowledge of this fauna. Moreover, revision of insect collections (partly in order to confirm the identifications of published works) has revealed new occurrence records, which ought to be published for the sake of better understanding the cuckoo wasp fauna of the region and elsewhere.

The aims of this thesis are:

1. To find suitable molecular markers and analytical methods for reconstructing the molecular phylogeny of the *C. ignita* group and for identifying its species **(I–II)**
2. To reveal taxonomic subgroupings and their phylogenetic relationships in the *C. ignita* group **(I)**
3. To assess the validity of current treatments of species and the nomenclature used for *C. ignita* group **(I–IV)**
4. To detect and describe unrecognized species in this species group **(I–III)**
5. To revise published literature regarding the cuckoo wasp fauna of Denmark, Fennoscandia and the Baltic countries (i.e. Denmark, Estonia, Finland, Latvia, Lithuania, Norway, Russian Fennoscandia and Sweden) **(IV)**
6. To provide updated species lists of cuckoo wasps for Denmark, Fennoscandia and the Baltic countries (i.e. Denmark, Estonia, Finland, Latvia, Lithuania, Norway, Russian Fennoscandia and Sweden) **(IV)**

2. MATERIALS AND METHODS

2.1. Taxon sampling for molecular phylogenetic analysis

Although the *C. ignita* species group is widespread and absent only from the Australasian ecozone, the majority of its species are confined to the Palaearctic and Nearctic ecozones. Since the emphasis of this thesis is on the northern European fauna, samples were mostly collected from Eurasia, especially the European part of it. Although insect collections in museums are rich, finding suitable samples for extracting DNA has proven difficult. The main problem is DNA degradation due to sample age and storage conditions, which leaves most collection materials unsuitable for DNA analysis with standard methods. Since cuckoo wasps are also not very abundant in nature and therefore sparsely collected, the availability of properly preserved and recently collected specimens sets great restrictions on taxon sampling.

Paper **I** was designed with the aim of finding suitable loci as well as analysis methods for the *C. ignita* species group and to reveal patterns of its phylogeny. Therefore as many different species from this species group as possible were included into the analysis. Since only fresh samples could be used, it was impossible to cover the whole group, and the study is therefore biased towards the European fauna. Only one sample per species was included into the analysis in paper **I** to provide sufficient interspecific diversity within species group. Moreover, the computer-program that was used (Bali-Phy) is computationally exhaustive and therefore including a single sample from each species (or subspecies) allowed the calculation to remain manageable. As an illustration of this, generating the initial alignment for 51 sequences (2018–2058 nucleotides long) for the phylogeny presented in paper **II** (Figures 3 and 4) took well over 6 months (for a single continuous run; the program can only use one processor at a time and thus a computer cluster would not speed up the process).

Though an emphasis is placed on European species, the ingroup taxa analysed in paper **I** originated from throughout the range of the *C. ignita* species group, including areas at the distributional limits of the group (**I**, Table 2) in order to test its monophyly. This was not straightforward to accomplish since collection materials were often unsuitable for DNA analysis. Consequently, fresh materials from distant areas were most valuable. For example, the rich cuckoo wasp material collected from South Korea by Pierre Tripotin proved highly valuable for DNA analysis (**I**) as well as for investigation of the cuckoo wasp fauna of this area (**III**).

Samples from taxa that are often treated as subspecific or possible cryptic species (with only minor distinguishing features) were included in addition to the widely accepted species in order to test the relationships between these morphologically similar taxa. Specimens representing each taxon were carefully selected to ensure that they were truly representative and, in addition to the use of published identification keys (Linsenmaier 1959a, 1997; Morgan 1984;

Smitsen 2010), the type materials of most included species were studied in order to maintain nomenclatural stability.

Paper **II** was designed with the aim of verifying the specific status of described species in the *C. ignita* species group using molecular methods. This study was limited to the North European fauna largely because the sampling allowed this region to be evaluated best but also because of the high interest in this fauna due to ongoing studies of the whole cuckoo wasp family in this region. While fresh samples of all northern European species were available, the number of available specimens for each species was uneven. Regrettably some species are very rare, which makes it hard to obtain a fresh sample for DNA extraction. For example *Chrysis brevitarsis* Thomson, 1870, is a very rare species throughout its entire distribution area: central and northern Europe. Analysed samples were pre-identified (relying on morphological characters) before conducting the molecular analysis. In order to increase the volume of samples, publicly available COI barcodes were included from the Barcode of Life Data System website (Ratnasingham & Hebert 2007). I did not rely on the specimen identifications of published barcode sequences unless I was able to study the specimen morphology in person or from suitable photographs. Otherwise the identity of published barcodes was based on comparison with barcodes of reliably identified specimens.

2.2. Studied collections

Materials (including type materials) were studied and samples loaned for DNA extraction from the following public collections:

- HNHM** Hungarian Natural History Museum, Budapest, Hungary (S. Csósz)
- IBER** Institute of Biodiversity and Ecosystem Research, Sofia, Bulgaria (T. Ljubomirov)
- IZBE** Institute of Agricultural and Environmental Science, Estonian University of Life Sciences, Tartu, Estonia (O. Kurina)
- LMSZ** Museum of Zoology, University of Latvia; Riga, Latvia (M. Cinītis)
- MNHN** Muséum National d'Histoire Naturelle, Paris, France (C. Villemant)
- MZH** Finnish Museum of Natural History, Helsinki, Finland (P. Malinen; J. Paukkunen)
- NRM** Naturhistoriska Riksmuseet, Stockholm, Sweden (H. Vårdal)
- NINA** Norwegian Institute for Nature Research, Trondheim, Norway (F. Ødegaard)
- NMLS** Natur-Museum Luzern, Luzern, Switzerland (D. Wyniger)
- NMW** Naturhistorisches Museum Wien, Wien, Austria (D. Zimmermann)
- NRC** Nature Research Centre, Vilnius, Lithuania (E. Budrys)
- RMNH** Naturalis Biodiversity Centre, Leiden, Netherlands (C. van Achterberg)
- TUZ** Zoological Museum of the University of Tartu, Estonia (J. Luig)

- ZMHB** Museum für Naturkunde der Humboldt-Universität, Berlin, Germany
(F. Koch, V. Richter)
- ZMUC** University of Copenhagen, Zoological Museum, Copenhagen,
Denmark (L. Vilhelmsen)

Besides institutional collections, materials were studied and loaned for DNA extraction from the following private collections: Paolo Rosa (Bernareggio, Italy), Johan Abenius (Nynäshamn, Sweden), Jaan Luig (Tartu, Estonia), Allan Selin (Tallinn, Estonia), Peeter Tarlap (Kanama, Estonia), Villu Soon (Tartu, Estonia), Sven Hellqvist (Umeå, Sweden), Ilkka Teräs (Helsinki, Finland), Christian Schmid-Egger (Berlin, Germany) and Pierre Tripotin (Rouen, France).

2.3. DNA sequencing

Extraction of total genomic DNA, purification methods and PCR parameters are described in papers **I** and **II**, being identical in both studies aside from the primers, which are provided separately in each paper (**I**, Table 2; **II**, Table 2). DNA cycle sequencing was performed using a DYEnamic ET Terminator Cycle Sequencing Kit (Amersham Biosciences, Uppsala, Sweden) (papers **I–II**) or Big Dye Terminator v.3.1 Cycle Sequencing Kit (Applied Biosystems, Foster City, USA) (paper **II**) using the cycling parameters recommended by the manufacturers, and the same annealing temperature as for PCR. Sequences were resolved using either an ABI PRISM 377 automated sequencer (papers **I–II**) or 3730xl DNA Analyzer (Applied Biosystems) (paper **II**). Standard COI barcodes were also obtained with high throughput methods at the Canadian Centre for DNA Barcoding (Ivanova *et al.* 2006; deWaard *et al.* 2008).

2.4. Sequence verification and identification

Sequence verification and identification methods were identical in papers **I** and **II**. Consensus sequences were created with Consed (Gordon *et al.* 1998), using sequence data from both DNA strands. Sequences were double-checked by eye and edited if necessary with BioEdit (Hall 1999). In papers **I** and **II** the tRNA genes were identified using tRNA-Scan SE version 1.21 (Lowe & Eddy 1997) and the ND4 gene using a nucleotide Blast search (Altschul *et al.* 1990).

2.5. Sequence alignment

Basic methods of alignment and phylogeny estimation were similar in papers **I** and **II**, varying only in the number of bootstrap pseudoreplications and iterations in Bayesian analyses, and the additional COI data included in the paper **II**. In order to avoid possible erroneous results caused by inadequately aligned rRNA genes, two approaches were employed to infer the phylogeny in

papers **I** and **II**: 1) a conservative limited dataset including only those positions of rRNA genes aligned with posterior probability over 0.95 according to the results of Bali-Phy. 2) The complete dataset, using the maximum a posteriori (MAP) alignment of rRNA genes gained from the run with Bali-Phy. Phylogenetic analysis of both datasets was performed using PAUP* (v. 4.0b10, Swofford 2003) for maximum-parsimony (MP), PhyML 3.0 (Guindon & Gascuel 2003) for maximum-likelihood (ML) and MrBayes 3.1.2 (Huelsenbeck & Ronquist 2001) for Bayesian analysis.

2.6. Analysis of genetic divergence and phylogeny reconstruction

Genetic divergences were analysed for COI barcodes in order to estimate the applicability of specimen identification based on these sequences (**II**). A neighbour-joining (NJ) Kimura-2-Parameter (K2P) (Kimura 1980) tree was constructed in order to reveal clustering of species. Although tree-based analysis of COI barcodes can be misleading (e.g. Meier *et al.* 2006; Zhang *et al.* 2012), it was employed in order to reveal the affiliations of numerous unidentified specimens (possibly unrecognized cryptic species). K2P corrected distances (calculated using TaxonDNA; Meier *et al.* 2006) were employed for estimating genetic divergences because this metric has been standard in barcoding studies.

Various algorithms were used to resolve the phylogeny of the same data-matrix in order to gain greater confidence in the results: Neighbour-joining (**II**), maximum-parsimony (**I–II**), maximum-likelihood (**I–II**) and Bayesian analysis methods (**I–II**). Detailed analysis parameters are given in papers **I** and **II**.

3. RESULTS

3.1. Results of the phylogenetic analyses

The monophyly of the *C. ignita* group was generally well-supported, and the majority of its species clustered into four well-supported clades (papers **I–II**). Only four species remained outside these clades; namely, *C. inflata* Aaron, 1885, *C. obtusidens* Dufour & Perris, 1840, *C. indigotea* Dufour & Perris, 1840 and one unidentified species from southern Africa. The latter three species were placed at the stem of the *C. ignita* group, while placement of the Nearctic species *C. inflata* remains ambiguous, since different analyses placed it differently, but none of the placements had high posterior probability support (paper **I**).

Altogether 43 species from the *C. ignita* species group, including some newly found cryptic species, were included in the phylogenetic analyses in papers **I–II**. Five previously undescribed species were sufficiently distinct and are considered as separate species. One of these is formally described and named in paper **III** (*Chrysis tripotini* Soon, 2010), another was already recognized by some earlier authors (as *C. ignita* form A) but did not have a proper name. The valid name for this species (*Chrysis terminata*) was identified among the synonyms of *C. ignita* (sensu Kimsey & Bohart 1991) thanks to the study of type materials (**IV**). Additional cryptic species remain without names; such species are referred to as *Chrysis* sp. 1 in paper **II**, *Chrysis* sp. 2 in paper **II** or erroneously as *C. ignita bischoffi* Linsenmaier, 1959 in paper **I** and *Chrysis* sp. 3 in paper **I**.

Nearly all conspecific samples or haplotypes (**II**, Figures 1–4) formed well supported monophyletic clades with all four methods of phylogeny reconstruction. Considering that these species also exhibited sufficient interspecific genetic distance (>2%) it can be concluded that molecular analysis supported their specific status. Only *C. mediata* Linsenmaier, 1951, *C. solida* Haupt, 1956 and *C. pseudobrevitarsis* Linsenmaier, 1951 did not cluster according to the prescribed species identities and instead formed paraphyletic groups (**II**). Minimal interspecific genetic diversity was mostly above 2% except in *C. terminata* and five other species in two clusters: *C. ignita*, *C. impressa*, *C. sp.* and *C. mediata*, *C. solida* (**II**).

Potential cryptic diversity was also noted in several other instances. Two species with high intraspecific genetic divergence grouped into distinct clades with considerable genetic distance between the clades (**II**): *C. schencki* Linsenmaier, 1968, which formed two distinct clades; and *C. pseudobrevitarsis*, which included up to five more or less distinct groups and haplotypes. The poorly resolved clade consisting of *C. ignita* and *C. impressa* also contained some unrecognized cryptic diversity but due to the low genetic divergence exhibited the relationships remained unresolved (**I–II**).

Many species that have previously been considered as subspecies appeared distant from the nominal species according to molecular analysis. The subspecific status of some of them has been disputed earlier with the taxa in

question often treated as species instead (i.e. *C. impressa*, *C. schencki* or *C. subcoriacea* Linsenmaier, 1959). However two of them have rarely been treated as species in the earlier literature: *C. melaensis* Linsenmaier, 1968 (I) and *C. vanlithi* Linsenmaier, 1959 (II).

3.2. Taxonomy, nomenclature and faunistics

Following the extensive studies on insect collections with special attention to type materials, results with important implications for nomenclature and taxonomy were gained. These include the description of one new species (III: *Chrysis tripotini*), which was detected among the South Korean materials collected by Pierre Tripotin. Although its species status was confirmed using molecular analysis (I), its distinctiveness was already apparent from its morphological characteristics (being most similar with *Chrysis brevitarsis*). Also, five lectotypes were designated in order to maintain nomenclatorial stability (IV: *Hedychrum cupreum* Dahlbom, 1845; *Chrysis zetterstedti* Dahlbom, 1845; *Chrysis succincta* var. *chrysoprasina* Trautmann, 1927; *Chrysis succincta* var. *virideocincta* Trautmann, 1927 and *Chrysis succincta* var. *nordstromi* Trautmann, 1927) and three new synonymies were found (IV: *Chrysis integra* Dahlbom, 1829 = *Hedychridium ardens* (Coquebert, 1801), *Chrysis scintillans* Valkeila, 1971 = *Chrysis solida* Haupt, 1957 and *Chrysis terminata* Dahlbom, 1854 = *Chrysis ignita* Form A *sensu* Linsenmaier, 1959).

A review of the cuckoo wasp fauna of Fennoscandia, Denmark and the Baltic countries led to the deletion of 13 taxa from the species list of the region (IV). Earlier reports of taxon occurrence were found to be incorrect due to misidentifications or changes to taxonomic treatment or nomenclature. The results of molecular phylogenetic analysis published in papers I and II and unpublished analysis of COI barcodes confirmed the treatment of five names as independent species in paper IV rather than subspecies or synonyms of other species as they have often been considered. These species were: *Omalus puncticollis* (Mocsáry, 1887), *Chrysis clarinicollis* Linsenmaier, 1951, *C. vanlithi*, *C. terminata* and *C. zetterstedti* Dahlbom 1845. The study of collection materials revealed new species records for all countries in the studied region except Lithuania (IV, Table 1) while three species (*Elampus foveatus* Mocsáry 1914, *Chrysis pulcherrima* Lepeletier, 1806 and *C. clarinicollis*) were reported for the first time in the whole area. The number of species recorded in the region increased to 73. Label data for the newly recorded species for each country are given in paper IV and also in papers I and II in cases where they are included in molecular analysis.

4. DISCUSSION

This thesis represents the first phylogenetic study of the *C. ignita* species group with sufficiently extensive taxon sampling to determine evolutionary relationships over a wide geographic scale. Although there were some limitations to the sampling (i.e. some species were unavailable, some had low quality DNA, and the size of data matrices that could realistically be analysed using Bali-Phy) the aims of this thesis were sufficiently fulfilled. On the basis of the results, I can conclude that the *C. ignita* species group indeed forms a monophyletic entity, separate from other species groups included in the study (I). Nearly all analysed Palaearctic species fall into four distinct clades (I–IV), which only partly match with earlier subdivisions of the species group. The apparently low success of previous attempts to divide the group into subgroups could be explained by insufficient data and/or convergent evolution in these parasitoid species (i.e. homoplasy), which could render subgroupings based merely on morphological characters unreliable. This is also well illustrated by the fact that the newly described species *C. tripotini* (IV) appears to be most closely related with *C. brevitarsis* on the basis of morphological characters but not according to mitochondrial DNA analysis (I).

The methods and results of papers I and II are to some extent similar, but the aims of the two papers are fundamentally different. As paper I was designed to reveal relationships between species, i.e. phylogeny, only single samples from each species were included. This allowed the relationships between many species to be comprehensively assessed, but it did not provide information about the integrity of included taxa. On the other hand, paper II focused on this latter characteristic: the status of species in the phylogeny. Therefore, multiple samples from each species were included in this analysis. Thus the two papers had different aims. It would have been preferable to meet the aims of both papers with a single comprehensive analysis, but this was not feasible due to the slow process of sample collection and the increase in time taken to perform analysis with Bali-Phy.

The results of this thesis help to resolve numerous problems regarding the taxonomy and nomenclature of cuckoo wasps. It is now possible to have confidence in the specific treatment of most northern (and central) European species in the *C. ignita* species group. Molecular phylogenetic and distance methods both appear suitable for delimiting and identifying species of this group while the COI barcoding approach has particularly high practical value. The COI sequences published within this thesis allow species in the *C. ignita* species group to be identified; a process that would otherwise be complicated, even for the experienced taxonomist.

All molecular analyses in this thesis were based on mitochondrial markers. This might be viewed as a limitation, especially since mitochondrial and nuclear DNA phylogenies may not coincide (e.g. Saarma *et al.* 2009; Prous *et al.* 2011). Discrepancies between marker systems are to be expected because the evolutionary mechanisms of the different types of DNA are fundamentally different.

Nevertheless, nuclear DNA was not analysed for three main reasons: 1) there were no suitable nuclear markers developed for cuckoo wasps when the laboratory analyses were initiated; 2) many of the samples had severely damaged DNA making amplification of even mitochondrial DNA difficult and making successful amplification of nuclear DNA highly unlikely (at least for some of the samples); 3) the results from mitochondrial DNA alone appeared reliable, as they matched very well with identifications based on morphology. In light of this last point it seems that although analysis of additional nuclear markers would have been desirable for verification of the results, it may well have provided little additional information for phylogeny reconstruction of the species in the *C. ignita* group.

While most species can be reliably identified using molecular characters it has no practical use if DNA sequencing methods are not available. This may be a problem for investigators on low budgets, such as amateurs, or in cases where materials contain low quality DNA, such as samples killed and stored using chemicals that damage DNA or old collection material. The latter point is especially critical when examining type materials. Therefore the morphology of species in the *C. ignita* species group should be further investigated with the aim of finding usable characters for species identification. The morphology of these species has long been inspected with only partial success: for example the cryptic species detected in this thesis were not recognized earlier. It is likely that minor morphological characters did not enable recognition of these taxa among all the material available for this species group. Having confirmed taxonomic identifications with DNA analysis, it should now be possible to search for such morphological characters with greater focus. The ability to recognize newly found cryptic species will also enable them to be identified among type materials.

The cuckoo wasp faunas of Fennoscandia, Denmark and the Baltic countries are very unevenly studied. While the faunas of Finland and Sweden have been extensively studied for centuries, there are relatively few studies published for Estonia, Latvia, Lithuania, Norway and Russian Fennoscandia. However, even having a long history of study does not necessarily indicate that these faunas are well known, since the gradual development of knowledge about cuckoo wasp taxonomy, including taxonomic inconsistencies, is reflected in the studies. In this thesis many of the taxonomic problems regarding species of the *C. ignita* species group were resolved in papers **I** and **II**, and the nomenclature of the whole family was revised in paper **IV**. Revision of all relevant literature as well as numerous collection materials in light of current knowledge resulted in an updated faunistic overview of the cuckoo wasp fauna in Fennoscandia, Denmark and Baltic countries (**IV**). This revisionary work does not purport to present a conclusive list of cuckoo wasp species in the region; rather it should generate a solid basis for future investigations of the family.

Despite resolving numerous taxonomic issues, this thesis also identified several new problem areas which require further study. Such problems are related to cryptic species in the *C. ignita* group, which remained unnamed and

undescribed. In addition, possible cryptic species diversity was found under *C. pseudobrevitarsis*, *C. schencki* and in the clade consisting of *C. ignita* and *C. impressa* (II, Figures 2–4). Thus the fauna of the studied area is far from being completely understood. Moreover, species outside the *C. ignita* species group are far less extensively studied. In fact, clustering into distinct clades was found among *Omalus aeneus* (Fabricius, 1787) in unpublished analysis of COI barcodes, which possibly indicates splitting into separate species. Therefore, further molecular and morphological studies of cuckoo wasps are needed, and the coverage of studied groups needs to widen. It would also be beneficial if further studies identified new DNA markers and morphological features, since the currently available characters (molecular and morphological) cannot fully resolve the taxonomy.

In addition to the new species described in this thesis (III), the studied material contained some potentially cryptic species that did not exhibit sufficiently distinct morphological characters. Analysis of these potentially new species requires further sampling and detailed morphological and molecular examination. Moreover, more extensive sampling and DNA analysis of *C. ignita* species group from new areas will most likely also reveal further diversity.

Investigators of northern European cuckoo wasps are often discouraged by the numerous problems related with the *C. ignita* group. Such problems include difficulties in identification as well as unstable taxonomy. The results of this thesis now allow species to be reliably identified using COI barcodes and a taxonomy that is verified for most species in the group. Hopefully these improvements can inspire future investigations of cuckoo wasps in northern Europe and elsewhere and help to reveal many more of the secrets of these interesting insects.

SUMMARY

Cuckoo wasps (Hymenoptera: Chrysididae) form a medium sized family of parasitic Hymenoptera. All species are parasitoids or cleptoparasites of other insects, mainly solitary wasps and bees. Despite their attractive appearance they have been insufficiently studied. Within the northern European fauna the most problematic group of cuckoo wasps is the *Chrysis ignita* species group. Problems include the unstable treatments of species, their names, difficulties associated with their identification and insufficient knowledge about their distribution. These problems are mostly derived from their subtle morphological characters, which are often insufficient to reliably distinguish species.

The aims of this thesis were to overcome these problems by means of molecular phylogenetic and distance analysis (I–II) as well as the study of collection materials (III–IV). Therefore, methods suitable for phylogeny reconstruction and delimitation of cuckoo wasp species needed to be developed first. Molecular analysis was used to delimit species in the *C. ignita* species group (with emphasis on northern European species) and resolve their phylogeny (I–II). In addition, studies of collection materials (especially type specimens) based on the confirmed taxonomy was conducted in order to revise the cuckoo wasp fauna of Fennoscandia, Denmark and Baltic countries (IV).

All northern European species in this species group, plus additional species from outside this area when available, were included in a dataset for molecular analysis (I–II). Mitochondrial DNA markers (COI, 16S rRNA, t-RNA^{val}, 12 rRNA, ND4) were used to reconstruct the phylogeny since mitochondrial markers: 1) have been widely used for similar purposes; 2) are sufficiently described, allowing design of primers when markers are not developed for a particular study object and 3) can be readily amplified even if DNA is somewhat degraded in samples. In order to gain greater confidence in the results, four different analysis methods were used: maximum parsimony, maximum likelihood, Bayesian and distance methods (I–II).

The molecular phylogeny and distance analysis designed and conducted in this thesis enabled a reliable phylogeny of the studied insects to be constructed, revealing four major clades, into which all northern European species fall (I–II). Most importantly, DNA sequence analysis proved to be effective tool for delimiting and identifying species in this group. Numerous species, that earlier had an unstable taxonomy (being treated either as species, subspecies or synonyms), were shown to be distinct species. Moreover, new cryptic species were identified, of which one was also formally described and named. Therefore, the methods used here can be considered as practical and effective for establishing a solid taxonomy of the *C. ignita* species group. The COI sequences published in the frame of this thesis enable reliable identification of species in the *C. ignita* species group, which is otherwise difficult and unreliable even in the hands of an experienced taxonomist (II).

Revision of the cuckoo wasp fauna of Fennoscandia, Denmark and the Baltic countries resulted in increasing the total number of species in the area to 73

(IV). This result was based on an updated taxonomy and nomenclature of the *C. ignita* species group as well as study of collection materials of all cuckoo wasps.

The results of the current thesis establish a solid taxonomy and nomenclature for the northern European cuckoo wasps. Although some uncertainties regarding species nomenclature and taxonomy remain, this thesis has generated a solid basis for future studies of this insect family in northern Europe and elsewhere.

SUMMARY IN ESTONIAN

Kuldherilaste (Hymenoptera: Chrysididae) *Chrysis ignita* liigirühma fülogeneetiline revisjon rõhuasetusega Põhja-Euroopa faunal

Kuldherilased (Hymenoptera: Chrysididae) on keskmise suurusega parasiitse eluviisiga kiletiivaliste sugukond. Valdavalt on tegemist kleptoparasitoididega, mis tähendab, et kuldherilase vastne areneb ennekõike peremehe vastse toiduvastu tarbides, surmates siiski peremehe vastse kui toidukonkurendi. Kuldherilaste sugukond jagatakse neljaks alamsugukonnaks, millest Euraasia parasvöötmes leidub vaid kahte: Cleptidea ja Chrysididea. Neist viimane on liikide hulga poolest suurim, kuna sisaldab liigirikkaimat perekonda *Chrysis*. Põhja-Euroopa faunas on enamik taksonoomia ja nomenklatuuri probleeme seotud *Chrysis ignita* liigirühmaga sellest perekonnast. Probleemid on ennekõike põhjustatud selle liigirühma liikide välisest sarnasusest, mis ei ole võimaldanud liike välistunnuste põhjal selgelt piiritleda. *C. ignita* liigirühma suurt liigirikkust märgati juba 19. sajandil, kuid erinevad katsed seda kirjeldada on olnud vaid osaliselt edukad. Taolised katsed on küll genereerinud hulgaliselt kirjeldusi ja nimesid, kuid nende nimede käsitlemine ei ole olnud üksmeelne.

Kuna eelnevad katsed *C. ignita* liigirühma liike eristada morfoloogilistele tunnustele tuginedes on olnud vaid osaliselt edukad, keskendun oma dissertatsioonis ennekõike molekulaarsetele tunnustele. Dissertatsiooni eesmärgiks on välja töötada kuldherilaste (ennekõike *C. ignita* liigirühma) fülogeneesi rekonstrueerimiseks ja liikide eristamiseks sobilikud molekulaarse analüüsi meetodid (I–II). Molekulaarsete tunnuste abil selgitada välja uuritava liigirühma üldisem fülogenees ning liigirikkus ning seeläbi stabiliseerida liikide käsitus (I–III). Ühtlasi revideerida kogu Fennoskandia, Taani ning Baltimaade kuldherilaste faunat käsitlev kirjandus ja selle piirkonna kuldherilaste nomenklatuur eesmärgiga selgitada välja piirkonna kuldherilaste fauna liigiline koosseis tuginedes rühma kaasaegsele süstemaatikale (II, IV).

Molekulaarsesse analüüsi kaasati kõik Põhja-Euroopas leitud *C. ignita* liigirühma liigid (I–II). Täiendavalt analüüsiti ka kõiki kättesaadavaid liike väljastpoolt seda ala, peamiselt Palaearktisest (I). Proovide kogumine muuseumite kollektsioonidest oli vaid osaliselt edukas, sest enamasti ei sobinud kollektsioonimaterjalid DNA analüüsiks. Liiga vanad, ebasobivates tingimustes hoitud või DNA-d lagundava kemikaaliga kokku puutunud isenditel on DNA ahelad liiga degradeerunud, et markereid saaks standardsete meetodite abil amplifitseerida ja sekveneerida.

Kuigi sedalaadi uurimustes on soovitatav kasutada ka rakutuuma DNA markereid, kasutati käesolevas töös vaid mitokondriaalseid markereid (COI, 16S rRNA, t-RNA^{val}, 12 rRNA, ND4). Mitokondriaalseid markereid eelistati kolmel peamisel põhjusel: 1) mitokondriaalseid markereid on laialdaselt kasutatud analoogsetes uurimustes; 2) mitokondriaalsed markerid on piisavalt

tuntud, võimaldades sobilike praimerite väljatöötamist ka juhul, kui vastavaid DNA järjestusi ei ole selles sugukonnas varem sekveneeritud; 3) mitokonriaalse DNA amplifitseerimine on tuuma omast oluliselt edukam, kui kasutada on halva kvaliteediga DNA (vanad kollektsioonimaterjalid). DNA järjestuste analüüsil rakendati erinevaid meetodeid, et tagada tulemuste usaldusväärsus; kasutati maksimaalse parsimoonia, maksimaalse tõepärasuse, bayesi ning distantsmeetodeid (I–II).

Fülogeneesi rekonstrueerimine paljastas, et Põhja-Euroopa *C. ignita* liigirühma kuldherilased jagunevad nelja suurde klaadi (I–II). Uuritavatest liikidest leidis enamik tugevat toetust monofüleetilise grupi moodustamise ja piisava geneetilise distantsi näol (II). Samuti leidis kinnitust mitme seni sageli alamliigi või vormina tunnustatud taksoni tegelik liigi staatus. Vaid kolme liigi (*C. pseudobrevitarsis*, *C. solia*, *C. mediata*) puhul ei moodustunud monofüleetilist klaadi. *C. mediata* ja *C. solida* ei eristunud teineteisest ilmselt andmete vähesuse tõttu, kuna mõlema liigi omavaheline ja liikide sisene geneetiline distants oli võrdlemisi väike (II). Seevastu *C. pseudobrevitarsis* jagunes mitmesse klaadi ennekõike suure geneetilise divergentsi tõttu, mis tõenäoliselt viitab eri liikide olemasolule, mida hetkel ühe liigina tuntakse. Samuti jagunes *C. schencki* kahte selgesse klaadi, mis viitab võimalusele, et tegemist on kahe erineva liigiga. Leiti ka neli täiendavat krüptilist liiki, millistest ühele liigile anti ka kirjeldus ning nimi (III). Ülejäänud kolme uue krüptilise liigi formaalne kirjeldamine ning nimetamine nõuab täiendavaid morfoloogia uuringuid. Käesolevas dissertatsioonis avaldatud COI järjestused võimaldavad ka mittespetsialistil teostada seni vaid suure kogemusega spetsialistile jõukohaseks osutunud *C. ignita* rühma liikide määramist.

C. ignita liigirühma taksonoomia väljaselgitamine Põhja-Euroopas võimaldas Fennoskandia, Taani ja Baltimaade kuldherilaste fauna revideerimist uutel alustel (IV). Piirkonna erialase kirjanduse ja liikide nomenklatuuri revisjon koos arvukate kollektsioonimaterjalide läbivaatamisega võimaldas teha kindlaks piirkonna kuldherilaste fauna liigilise koosseisu riikide kaupa. Selle käigus tuli mitmeid liike eri riikide liiginimekirjadest kustutada ning samas lisandus neisse ka uusi liike. Kolm liiki olid uued kogu piirkonna jaoks (IV). Ühtlasi tuli zooloogilise nomenklatuuri stabiilsuse huvides määrata viis lektotüüpi ning leiti ka kolm sünonüümset nime.

Käesoleva dissertatsiooni tulemusena on lahenenud mitmed probleemid kuldherilaste taksonoomias ja nomenklatuuris ning ühtlasi on selgitatud liikide levikut. Sellest hoolimata ei ole kuldherilaste juures need suunad kaugeltki lõpuni uuritud ning käesoleva dissertatsiooni põhiväärtus ehk seisnebki hea aluse loomisel kuldherilaste edasiseks uurimiseks nii Põhja-Euroopas kui ka mujal.

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PUBLICATIONS

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- Soon, V. (2011). North European species of the *Chrysis ignita* species group (Hymenoptera: Chrysididae). (oral presentation, invited speaker). Swedish Malaise Trap Project 3rd Hymenoptera Workshop, May 26–29, Öland, Sweden.

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