



<http://dx.doi.org/10.11646/zootaxa.3786.3.4>

<http://zoobank.org/urn:lsid:zoobank.org:pub:6DB0B910-4711-4566-80D9-3FC88CBEE88D>

Testing the validity of Northern European species in the *Chrysis ignita* species group (Hymenoptera: Chrysididae) with DNA Barcoding

VILLU SOON^{1,2,7}, EDUARDAS BUDRYS³, SVETLANA ORLOVSKYTĚ³, JUHO PAUKKUNEN⁴,
FRODE ØDEGAARD⁵, TOSKO LJUBOMIROV⁶ & URMAS SAARMA¹

¹Department of Zoology, Institute of Ecology and Earth Sciences, University of Tartu, Vanemuise 46, Tartu 51014, Estonia.
E-mail: villu.soon@ut.ee

²Museum of Natural History, University of Tartu, Vanemuise 46, 51014 Tartu, Estonia

³Nature Research Centre, Akademijos g. 2, LT-08412, Vilnius, Lithuania

⁴Finnish Museum of Natural History, Zoology Unit, P.O. Box 17, FI-00014 University of Helsinki, Finland

⁵Norwegian Institute for Nature Research NINA, P.O. Box 5685 Sluppen, NO-7485 Trondheim, Norway

⁶Institute of Biodiversity and Ecosystem Research, Bulgarian Academy of Sciences, 1, Tzar Osvoboditel Boulevard, Sofia, 1000, Bulgaria

⁷Corresponding author: E-mail: villu.soon@ut.ee

Abstract

Containing more than a hundred species, the *Chrysis ignita* species group is the largest and one of the most taxonomically challenging groups in its genus. It has not been possible to resolve the taxonomy of the group using traditional methods due to the lack of robust diagnostic morphological characters. Here we present the results of a molecular analysis designed to delimit species in the *Chrysis ignita* group for the first time; using mitochondrial sequence data for 364 in-group specimens consisting of all 18 species known to occur in Northern Europe. Two mitochondrial loci were analysed: a COI gene fragment, and a continuous DNA sequence consisting of 16S rRNA, tRNA^{Val}, 12S rRNA and ND4. Two approaches were employed for delimiting species: (1) genetic distance analysis based on the standard COI barcode sequences and; (2) phylogenetic analysis of the COI fragment together with rRNA genes. Both analyses yielded trees with similar topology, but support values for nodes were higher using the second approach. Fifteen species were distinguished in all analyses: *Chrysis angustula* Schenck, 1856, *C. brevitarsis* Thomson, 1870, *C. clarinicolis* Linsenmaier, 1951, *C. corusca* Valkeila, 1971, *C. fulgida* Linnaeus, 1761, *C. ignita* (Linnaeus, 1758), *C. impressa* Schenck, 1856, *C. iris* Christ, 1791, *C. leptomandibularis* Niehuis, 2000, *C. longula* Abeille de Perrin, 1879, *C. ruddii* Shuckard, 1837, *C. schencki* Linsenmaier, 1968, *C. subcoriacea* Linsenmaier, 1959, *C. terminata* Dahlbom, 1854 and *C. vanlithi* Linsenmaier, 1959. The specific status of *C. mediata* Linsenmaier, 1951 and *C. solida* Haupt, 1957 was not resolved. Included unidentified specimens grouped in three clusters, two of which are distinctly delimited and apparently represent cryptic species. The specific status of the unidentified samples in the third cluster remained unclear. Moreover, our data suggest the existence of additional cryptic species currently lumped under the names *C. pseudobrevitarsis* Linsenmaier, 1951 and *C. schencki* Linsenmaier, 1968. In conclusion, our results derived from analysis of mitochondrial loci strongly support the specific status of the majority of currently recognised species in the *Chrysis ignita* species group, and suggest the existence of additional cryptic species in Northern Europe. Thus, considering the difficulties that often arise during species determination based on morphological characters, the mtDNA loci used here appear highly suitable for assisting species delimitation in this group as well as identification of specimens.

Key words: barcoding, cryptic species, Bali-Phy, cuckoo wasps, molecular phylogeny

Introduction

Commonly known as cuckoo wasps, the Hymenoptera family Chrysididae is a medium sized cosmopolitan group including more than 3000 described species. All members of the family are parasitoids or cleptoparasites, whose hosts belong to various families of Hymenoptera, Phasmatodea or Lepidoptera. The largest genus in the family, *Chrysis* Linnaeus, 1761, is diverse and cosmopolitan, and contains several taxonomically unresolved species

groups. The most recent review and key to species groups within *Chrysis* was published by Kimsey & Bohart (1991) in their systematic treatise of the world's cuckoo wasps. Containing more than a hundred known species, the *Chrysis ignita* species group is the most species-rich and taxonomically challenging group in the genus. This group is widespread, it is absent only from Australasia but is most diverse in the Palaearctic region (Kimsey & Bohart 1991). No overall treatment of the *C. ignita* group exists though there are some regional works with keys to species in the group (Tsuneki 1957; Linsenmaier 1959a, 1994, 1997; Bohart & Kimsey 1982; Morgan 1984; Kunz 1994; Tarbinsky 2000; Rosa 2006; Smissen 2010) Northern European species of the *Chrysis ignita* species-group have not been revised separately, but have been included in several treatments of European fauna (Linsenmaier 1959a, 1997; Morgan 1984; Kunz 1994; Rosa 2006; Smissen 2010).

Shuckard (1836) made the earliest attempt to split what was up to then known as *Chrysis ignita* (L.) 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 were retained and in general it appears likely that Dahlbom was relying on exceptional aberrant specimens. Since Dahlbom's types have not been studied thoroughly, the names have been treated as synonyms of *C. ignita* (Kimsey & Bohart 1991). However, *C. terminata* should be reinstated as a valid species, as the holotype was found to be conspecific with *C. ignita* Form A sensu Linsenmaier (1959a) (Paukkunen *et al.* in prep.).

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 Perrein 1879; Mocsáry 1889; du Buysson 1891; Bischoff 1913; Trautmann 1927).

The most important contribution to knowledge of Northern European species in the *C. ignita* species group was provided in a series of publications by Walter Linsenmaier (1951, 1959a, 1959b, 1968, 1987, 1997). He published descriptions of numerous new species and subspecies with a key to the European species. Unfortunately, his work did not include a critical review of all previous descriptions and types, and his descriptions can be difficult to interpret. This resulted in misinterpretations of several species and raised doubts about the specific status of many of the taxa that Linsenmaier separated (Kimsey & Bohart 1991; Kunz 1994; Mingo 1994). Since the middle of the 20th century only four authors besides Linsenmaier contributed to the taxonomy of the European species of the *C. ignita* species group by adding new descriptions or taxonomical notes (Móczár 1965; Valkeila 1971; Morgan 1984; Niehuis 2000).

Due to similarities in adult morphology, it is difficult to distinguish species and subspecies in the *C. ignita* species group. Therefore, newly described species and subspecies often remain unrecognised and their status questioned by other specialists. Bischoff (1934) discussed this problem and explained the situation with a hypothesis of freely crossbreeding ecological races, with each specialised to different host species.

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 data on the morphology of internal segments and conducting a morphometric analysis. As his results did not support the distinctness of most included taxa, Kunz dropped these into synonymy. These results are accepted by some authors (Tschartke *et al.* 1998; Gathmann & Tschartke 1999; Kruess & Tschartke 2002; Holzschuh *et al.* 2009), but not by others (Linsenmaier 1997; Niehuis 2001; Rosa 2006; Smissen 2010), though his results have not been falsified with independent analysis. Rather than relying on specialist opinion, which can be conflicting, independent analysis is required to rigorously assess the validity of these species.

Molecular characters have frequently been used to resolve taxonomic questions in insects, but have never been used to delimit species of cuckoo wasps. Most studies using molecular markers 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 been used to directly study Chrysididae in a few instances (Niehuis & Wägele 2004; Niehuis & Korb 2010; Soon & Saarma 2011) but none of these have attempted to delimit species. While the study by Soon & Saarma (2011) that dealt with the phylogeny of the *C. ignita* species group suggested some taxonomical changes, it did not assess the distinctness or species rank of each included species. As only single specimens of each species or subspecies were included in that study, it was only possible to suggest elevation of subspecies to species rank in cases where different subspecies of the same species did not form monophyletic group. However, without additional samples for every taxon it was impossible to estimate their taxonomic validity.

In order to evaluate Kunz's results with an independent analysis and stabilize the taxonomy of the *C. ignita* group, we attempt to test the distinctness of Northern European species in the *C. ignita* species group using mtDNA sequences. Since the morphology of the species in this group has been thoroughly discussed in numerous publications including Smissen's (2010) comprehensive descriptions with identification keys, and Kunz's (1994) phenetic analysis based on morphological characters we do not focus on morphological characters in this paper. Instead, we use molecular characters to delimit species in the *C. ignita* group of the Northern European fauna, including the species recorded in Fennoscandia, the Baltic States, NW Russia, Denmark and the British Isles.

Since we assess the validity of an existing system we analyze specimens pre-identified according to morphological characters. We then examine whether intraspecific genetic divergence remains within the 2% threshold value that has been suggested for congeneric species in most invertebrate taxa (Hebert *et al.* 2003) i.e. the genetic species concept as well as whether samples of each species form monophyletic apical clades within the phylogenetic tree, i.e. the phylogenetic species concept. Although these approaches may not give results in precise accordance with the biological species concept, they are practical and reliable methods for delimiting species. The applied approaches are especially useful in groups that are difficult to distinguish using morphological characters and may thus include unrecognised cryptic species.

Material and methods

Specimen identification. Specimens representing each taxon were carefully selected to ensure that they were truly representative. In addition to utilization of the published identification keys (Linsenmaier 1959a, 1997; Morgan 1984; Smissen 2010) type materials of most included species were studied by the first author in order to maintain nomenclatural stability.

List of analysed species complemented with studied type materials

Chrysis angustula Schenck, 1856

= *Chrysis ignita sparsepunctata* Zimmermann 1944, 1 ♀ Maria Luggau, Kärnten, Austria, lectotype (design. Niehuis 2000); Naturhistorisches Museum Wien, Wien, Austria (NMW).

Chrysis brevitarsis Thomson, 1870

Chrysis clarinicollis Linsenmaier, 1951

Chrysis ignita var. *clarinicollis* Linsenmaier 1951, 1 ♀ Martigny, Wallis, Switzerland (6.IX.1937, leg. R. Matthey), lectotype (design. Linsenmaier 1959a); Natur-Museum Luzern, Luzern, Switzerland (NMLS).

Chrysis corusca Valkeila, 1971

Chrysis corusca Valkeila 1971, 1 ♀ Åsbro, Lerbäck, Sweden (1968, leg. G. Hallin), holotype; Naturhistoriska riksmuseet, Stockholm, Sweden (NRM).

Chrysis fulgida Linnaeus, 1761

= *Chrysis fulgida* var. *concolor* Mocsáry 1912, 1 ♂ Raddefka, Sibiria orientalis, Russia, lectotype (design. Bohart in Bohart & French 1986); Hungarian Natural History Museum, Budapest, Hungary (HNHM).

= *Chrysis fulgida* var. *aurolimbata* Móczár 1946, 1 ♂ Félegyháza, Hungary (leg. L. Móczár), lectotype (design. Móczár 1965); Hungarian Natural History Museum, Budapest, Hungary (HNHM).

Chrysis ignita (Linnaeus, 1758)

Chrysis impressa Schenck, 1856

= *Chrysis aurifera* Linsenmaier 1951, ♀♀ Switzerland, syntypes; Natur-Museum Luzern, Luzern, Switzerland (NMLS).

Chrysis iris Christ, 1791

Chrysis leptomandibularis Niehuis, 2000

Chrysis leptomandibularis Niehuis 2000, 1 ♀ Wallis, Switzerland (2.VII.1951, leg. W. Linsenmaier), paratype; Natur-Museum Luzern, Luzern, Switzerland (NMLS).

Chrysis longula Abeille de Perrin, 1879

Chrysis ignita var. *longula* Abeille de Perrin 1879, 1 ♀ Frankfurt, Germany, lectotype (design. Morgan 1984); Muséum National d'Histoire Naturelle, Paris, France (MNHN).

= *Chrysis longula sublongula* Linsenmaier 1951, 1 ♀ Champex, Wallis, Switzerland (10.VI.1950), lectotype (design. Linsenmaier 1959a); Natur-Museum Luzern, Luzern, Switzerland (NMLS).

= *Chrysis longula aeneopaca* Linsenmaier 1959a, 1 ♀ Transcaspia, Russia, holotype; Natur-Museum Luzern, Luzern, Switzerland (NMLS).

Chrysis mediata Linsenmaier, 1951

Chrysis mediata Linsenmaier 1951, 1 ♀ Wallis, Switzerland (12.VI.1948, leg. W. Linsenmaier), lectotype (design. Linsenmaier 1959a); Natur-Museum Luzern, Luzern, Switzerland (NMLS).

Chrysis pseudobrevitarsis Linsenmaier, 1951

C. pseudobrevitarsis Linsenmaier 1951, 1 ♀ Wallis, Switzerland (13.VI.1950, leg. W. Linsenmaier), lectotype (design. Linsenmaier 1959a); Natur-Museum Luzern, Luzern, Switzerland (NMLS).

Chrysis ruddii Shuckard, 1837

= *Tetrachrysis ruddii* var. *viridis* Trautmann 1926 [= *C. viroris* Bohart in Kimsey & Bohart 1991 repl. name], 1 ♀ Germany, lectotype (design. Bohart in Kimsey & Bohart 1991); Museum für Naturkunde der Humboldt-Universität, Berlin, Germany (ZMHB).

Chrysis schencki Linsenmaier, 1968

= *Chrysis schenckiana* Linsenmaier 1959a [= *C. schencki* Linsenmaier 1968 repl. name], 1 ♀ Klosters, Kraubünden, Switzerland (8.VIII.1946, leg. W. Linsenmaier), holotype; Natur-Museum Luzern, Luzern, Switzerland (NMLS).

Chrysis solida Haupt, 1957

= *Chrysis mediata fenniensis* Linsenmaier 1959a, 1 ♀ Hattula, Finland, holotype; Natur-Museum Luzern, Luzern, Switzerland (NMLS).

= *Chrysis scintillans* Valkeila 1971, 1 ♀ Vanaja, Finland (23.VII.1962, leg. E. Valkeila), holotype; Finnish Museum of Natural History, Helsinki, Finland (MZH).

Chrysis subcoriacea Linsenmaier, 1959

Chrysis subcoriacea Linsenmaier 1959a, 1 ♀ Kyrkslätt, Finland, holotype; Natur-Museum Luzern, Luzern, Switzerland (NMLS).

Chrysis vanlithi Linsenmaier, 1959

Chrysis rutiliventris vanlithi Linsenmaier 1959a, 1 ♀ Wallis, Switzerland, holotype; Natur-Museum Luzern, Luzern, Switzerland (NMLS).

Chrysis terminata Dahlbom, 1854

Chrysis terminata Dahlbom 1854, 1 ♂ Austria, holotype; Naturhistorisches Museum Wien, Wien, Austria (NMW).

Taxon sampling for genetic analysis. All known species of the *C. ignita* species group from Fennoscandia and the Baltic states (Paukkunen *et al.* in prep.) were sampled. In addition, we included numerous Northern European samples which we could not identify reliably using morphological characters. Samples for standard COI barcoding were gathered from all Fennoscandian and Baltic countries except Latvia with the aim of sampling all species evenly from the study area (Table 1). Additional samples from neighbouring countries as well as the rest of Europe were included for better evaluation of intraspecific variability. We also used closely related (div. < 2%) publicly available barcodes, of which more than 90% of the standard barcode sequence (568 bp) was available. We did not rely on the specimen identifications of published barcode sequences unless we were able to study the specimen's morphology or they were identifiable on the photos available at the Barcode of Life Data System website (Ratnasingham & Hebert 2007). In total we analysed 364 standard COI barcode sequences.

As the analysis software used in this study, Bali-Phy, is computationally exhaustive, only a limited number of samples from each firmly known taxon were included into phylogenetic analysis with additional mitochondrial DNA sequence data (16S rRNA, tRNA^{Val}, 12S rRNA, ND4). We also included three unidentified samples with relatively small interspecific COI barcode genetic distances in order to evaluate their distinctness from closely related species. Unidentified specimens that formed distinct clusters in barcoding (referred to as *Chrysis* sp. 1 and *C. sp. 2* in this paper) as well as *C. clarinicornis* and *C. vanlithi* were not included in the phylogenetic analysis mainly in order to limit the size of data-matrix but also due to the limited number of available fresh samples from the study area. We selected at most four specimens per species, preferably from distant parts of the species distribution area. Only *C. brevitarsis* was represented by a single specimen since we could not find more fresh specimens of this rare species. Nevertheless, the specific status of this species has never been under question. We based outgroup selection on the study by Soon & Saarma (2011), selecting one distantly related species (*C. indigotea* Dufour & Perris, 1840) from the same species group and one representative of another closely related species group, namely *C. graelsii* Guérin-Meneville, 1842 from the *C. graelsii* species group. Both air-dried specimens from collections and fresh material collected and stored in 96% ethanol were used to extract genomic DNA. In addition to 35 newly sequenced specimens, 16 previously published (Soon & Saarma 2011) sequences from Northern European species were included in this analysis. Altogether, 51 specimens from 12 European countries were included in this analysis; these belonged to 16 ingroup species (plus three additional specimens of unknown identity) and two outgroup species. Since females in the *Chrysis ignita* species group are morphologically more conservative (i.e., easier to identify), we selected female specimens whenever possible.

DNA sequencing. All rRNA sequences were obtained using the methods given below; standard COI barcodes were obtained either with the same methods or with high throughput methods at the Canadian Centre for DNA Barcoding (Ivanova *et al.* 2006; deWaard *et al.* 2008).

The High Pure PCR Template Preparation Kit (Roche Diagnostics GmbH, Mannheim, Germany) was used to extract and purify genomic DNA from thoracic muscle tissue. The manufacturer's instructions were followed with the exception that the first incubation step was extended to 2 hours if the sample was not fully dissolved during the prescribed 1 hour period.

PCR conditions and primers to amplify 12S and 16S rRNA genes, tRNA^{Val} and a small fragment of the ND4 gene of mtDNA were exactly as described in Soon & Saarma (2011); primers used for amplification of a fragment of COI are given in Table 2. After PCR the solution was treated with shrimp alkaline phosphatase and exonuclease I (USB, Cleveland, USA). One unit of both enzymes was added to 10 µl of the PCR solution and incubated for 30 min at 37°C, followed by inactivation at 80°C for 15 min. DNA cycle sequencing was performed using a DYEnamic ET Terminator Cycle Sequencing Kit (Amersham Biosciences, Uppsala, Sweden) or Big Dye Terminator v.3.1 Cycle Sequencing Kit (Applied Biosystems, Foster City, USA). Depending on the kit used, 33 cycles (15 s at 95°C, 15 s at 45°C and 60 s at 60°C) (DYEnamic ET) or denaturation for one min at 96°C followed by 25 cycles (10 s at 95°C, 15 s at 47°C and 1–2 min at 60°C) (Big Dye) were performed in a total volume of 10 µl.

Both DNA strands were sequenced with 5 pmol (DYEnamic ET kit) or 1.6 pmol (Big Dye kit) of primers. Sequences were resolved using either an ABI PRISM 377 automated sequencer or 3730xl DNA Analyzer (Applied Biosystems).

Sequence verification and identification. Sequence data from both DNA strands was used to generate consensus sequences with Consed (Gordon *et al.* 1998). Sequences were double-checked by eye and edited, if necessary, with BioEdit (Hall 1999). All tRNA genes were identified with tRNA-Scan SE version 1.21 (Schattner *et al.* 2005) and the ND4 gene with a nucleotide Blast search (Geer *et al.* 2010).

Sequence alignment. COI sequences were aligned manually, while the computer program Bali-Phy 2.0.2 (Suchard & Redelings 2006) was used for difficult-to-align rRNA genes. An initial run of 3000 iterations, starting from unaligned sequences, the default settings and the GTR + INV + G sequence evolution model, was performed to determine well aligned regions in the rRNA sequences. After examination of log-likelihood scores using Tracer 1.4 (Drummond & Rambaut 2007), the first 500 iterations were discarded as “burn in” to ensure that a stationary distribution was sampled.

Analysis of genetic divergence. A neighbour-joining (NJ) Kimura-2-Parameter (K2P) (Kimura 1980) tree for all COI barcode haplotypes was constructed and bootstrapped with 1000 pseudoreplicates using PAUP* (v. 4.0b10, Swofford 2003). This analysis included all 177 different haplotypes, while incomplete sequences matching with any of the longer haplotypes were considered as belonging to this haplotype and thus not included in analysis. Although the tree-based analysis of COI barcodes has been shown to be misleading (e.g. Meier *et al.* 2006; Zhang *et al.* 2012), we employed it in order to reveal affiliation of numerous unidentified specimens (possibly unrecognized cryptic species). We employed the K2P corrected distances (calculated using TaxonDNA; Meier *et al.* 2006) in our study for estimating genetic divergences because this metric has been standard in barcoding studies.

Phylogeny estimation. In order to study the relationships between known species and the distinctness of the most closely related species in depth, phylogenetic analysis including additional mitochondrial data was designed. Two approaches were employed to infer the phylogeny using COI and rRNA nucleotides in the same data-matrix: 1) a conservative limited dataset including the full COI sequence but only those positions of rRNA genes aligned with posterior probability over 0.95 according to the results of Bali-Phy (highly-supported alignment, 2187 bp). 2) The full dataset, using the maximum a posteriori (MAP) alignment of rRNA genes gained from the initial run with Bali-Phy together with COI (2899 bp).

Phylogenetic analysis of both datasets was performed using PAUP* for maximum-parsimony (MP), PhyML 3.0 (Guindon & Gascuel 2003) for maximum-likelihood (ML) and MrBayes 3.1.2 (Huelsenbeck *et al.* 2001) for Bayesian analysis.

Maximum-parsimony analysis was executed with a heuristic search with 100 random sequence stepwise additions, holding 10 trees at each step and using tree bisection and reconnection (TBR) branch swapping. Node support was estimated using the same methods as for the heuristic search with 10 000 bootstrap pseudoreplicates.

The best fit model of DNA sequence evolution for ML analyses was determined using jModeltest v0.1.1 (Posada 2008). On the basis of the Akaike Information Criterion (AIC) the best model was either TIM3 + I + G (limited dataset) or TIM1 + G (complete dataset). Since neither of these models is implemented in the phylogenetic software we used, we selected the second best models for reconstructing phylogenies: GTR + I + G (limited dataset) and GTR + G (full alignment). Node support in ML analyses was assessed using bootstrapping with 1 000 pseudoreplicates, while Bayesian analyses were run for 10 000 000 iterations, and the first 2 500 000 iterations discarded as “burn in”. Phylograms were visualized using Tree-View 1.6.6 (Page 1996).

Results

Depending on the combination of primers used (listed in Table 2), sequences of various lengths were obtained from the region covering ~ 1800 bp of mitochondrial DNA containing partial tRNA^{Met}, complete tRNA^{Ile}, tRNA^{Cys} and tRNA^{Tyr} followed by full sequence of the COI gene and 228 bp of COII gene. However, as the DNA was somewhat degraded in some samples, we were unable to sequence DNA of this length from all specimens. In phylogenetic analysis we included only the 750 bp sequence of COI gene, which was obtained for all samples. This sequence matches the widely used barcoding region with only 37 bp missing at the 5' end while extending 128 bp beyond this region at the 3' end.

TABLE 1. Specimens of *Chrysis ignita* species group used for molecular analyses.

The identity of most specimens was verified by the authors except those identified by O. Niehuis and housed in his private collection (ON). Specimens, which were identified using COI barcodes alone, are marked with asterisk (*). Boldsystems sequence ID or Genbank accession number is given for DNA sequences used in this study. Abbreviations: AS, Coll. Selin, Tallinn, Estonia; FMNH, Finnish Museum of Natural History, Helsinki, Finland; IBER, Institute of Biodiversity and Ecosystem Research, Sofia, Bulgaria; JA, Coll. Abenius, Nynäshamn, Sweden; NINA, Norwegian Institute for Nature Research, Trondheim, Norway; NMLS, Natur-Museum Luzern, Luzern, Switzerland; NRC, Nature Research Centre, Vilnius, Lithuania; NRM, Naturhistoriska riksmuseet, Stockholm, Sweden; ON, Coll. Niehuis, Albersweiler, Germany; SH, Coll. Hellqvist, Umeå, Sweden; TUZ, Museum of Natural History, University of Tartu, Tartu, Estonia; ZSM, Bavarian State Collection of Zoology, Munich, Germany.

Species	Sex	Locality	Latitude	Longitude	Date	Collector	Voucher ID (depository)	Haplo-type	COI	rRNA
<i>C. angustula</i>	♀	Estonia, Aa	59°25'52"N	27°09'46"E	16.07.2004	V. Soon	VS023 (TUZ)	H1	JX292220	JX292179
<i>C. angustula</i>	♂	Estonia, Väike-Maarja	59°09'04"N	26°16'58"E	7.05-17.09.2007	M. Moora	TNH07-996-1 (NRC)	H2	KJ398851	
<i>C. angustula</i>	♂	Finland, Ikaalinen Vehuvarpee	61°44'02"N	22°50'42"E	28.06.2001	J. Paukkunen	GP.72824 (FMNH)	H2	ACUF1459-12	
<i>C. angustula</i>	♀	Lithuania, Karvelinkai	54°29'45"N	24°07'59"E	9.06-26.08.2009	E. Budrys	TNH09-850-8 (NRC)	H2	KJ398856	
<i>C. angustula</i>	♀	Lithuania, Vėžiongirė forest	54°32'16"N	24°09'10"E	5.06-22.09.2010	E. Budrys	TNH10-493-5 (NRC)	H2	KJ398855	
<i>C. angustula</i>	♀	Finland, Lappeenranta Melkkola	60°56'02"N	28°07'26"E	30.06.2008	J. Paukkunen	GP.66582 (FMNH)	H3	ACUF1460-12	
<i>C. angustula</i>	♀	Finland, Mikkelä	61°37'37"N	27°03'58"E	18.07.2009	M. Koponen	GP.66877 (FMNH)	H4	ACUF1461-12	
<i>C. angustula</i>	♂	Lithuania, Takniškiai	54°24'23"N	24°06'50"E	26.05-22.09.2010	E. Budrys	TNH10-201-7 (NRC)	H4	KJ398853	
<i>C. angustula</i>	♂	Lithuania, Bukta forest	54°26'10"N	23°28'05"E	2.06-28.08.2009	E. Budrys	TNH09-976-11 (NRC)	H5	KJ398858	
<i>C. angustula</i>	♀	Lithuania, Taraldžiai	55°46'11"N	25°21'49"E	02.08.2010	Ž. Nevronytė	ZN2010-08-02 (NRC)	H6	KJ398854	
<i>C. angustula</i>	♀	Lithuania, Varnupys	55°23'38"N	25°16'20"E	10.05-29.08.2009	E. Budrys	TNH09-731-2 (NRC)	H7	KJ398861	
<i>C. angustula</i>	♂	Lithuania, Trakas forest	54°13'44"N	23°45'28"E	5.06-9.09.2010	E. Budrys	TNH10-1051-5 (NRC)	H8	KJ398848	
<i>C. angustula</i>	♂	Lithuania, Musteika	53°54'29"N	24°24'34"E	21.05-20.08.2007	E. Budrys	TNH07-2568-5 (NRC)	H9	KJ398850	
<i>C. angustula</i>	♂	Lithuania, Perloja	54°13'24"N	24°22'58"E	27.05-22.09.2010	E. Budrys	TNH10-1078-1 (NRC)	H9	KJ398862	
<i>C. angustula</i>	♂	Lithuania, Virbalgiris	54°36'18"N	22°47'30"E	6.06-10.09.2010	E. Budrys	TNH10-805-3 (NRC)	H9	KJ398849	
<i>C. angustula</i>	♀	Norway, Gyllvatnet	63°05'55"N	10°17'58"E	28.07.2010	F. Ødegaard	Chrysis071 (NINA)	H9	NOCHR071-13	
<i>C. angustula</i>	♂	Norway, Myra	62°37'12"N	8°53'52"E	2.07.2010	F. Ødegaard	Chrysis055 (NINA)	H9	NOCHR055-13	
<i>C. angustula</i>	♂	Lithuania, Dūkštos oak forest	54°50'31"N	24°57'48"E	26.05-24.08.2009	E. Budrys	TNH09-1129-2 (NRC)	H10	KJ398857	
<i>C. angustula</i>	♂	Lithuania, Trakas forest	54°13'44"N	23°45'28"E	5.06-9.09.2010	E. Budrys	TNH10-1066-3 (NRC)	H11	KJ398859	
<i>C. angustula</i>	♀	Norway, Fatlaberga	61°09'50"N	6°54'31"E	5.07.2011	F. Ødegaard	Chrysis070 (NINA)	H11	NOCHR070-13	
<i>C. angustula</i> *	♀	Germany, Bavaria	48°54'54"N	12°27'18"E	24.05.2008	G. Merkel-Wallner	BC ZSM HYM 17475 (ZSM)	H12	GBACU3130-13	
<i>C. angustula</i>	♀	Norway, Heggnes	59°26'24"N	8°46'59"E	5.06.2009	F. Ødegaard	Chrysis 115 (NINA)	H13	NOCHR110-13	
<i>C. angustula</i>	♀	Norway, Kjevikveien	58°12'32"N	8°05'17"E	3.09.2009	F. Ødegaard	Chrysis146 (NINA)	H13	NOCHR141-13	

..... continued on the next page

TABLE 1. (Continued)

Species	Sex	Locality	Latitude	Longitude	Date	Collector	Voucher ID (depository)	Haplo-type	COI	rRNA
<i>C. angustula</i>	♂	Norway, Magnor	59°57'08"N	12°10'34"E	27.06.2012	F. Ødegaard	Chrysis066 (NINA)	H13	NOCHR066-13	
<i>C. angustula</i>	♀	Norway, Bergsland	59°36'29"N	8°42'40"E	23.06.2010	F. Ødegaard	Chrysis143 (NINA)	H14	NOCHR138-13	
<i>C. angustula</i>	♀	Bulgaria, Sofia, Simeonovo	42°37'12"N	23°19'50"E	20.06.2007	T. Ljubomirov	CCDB-05795-E12 (IBER)	H15	CRABR535-10	
<i>C. angustula</i>	♂	Belgium, Liedekerke	50°51'38"N	4°03'58"E	18.05.2007	M. Pollet	VS057 (TUZ)	H16	JX292237	HM071104
<i>C. angustula</i>	♀	Bulgaria, Sofia, Simeonovo	42°37'12"N	23°19'50"E	21.08.2007	T. Ljubomirov	CCDB-05795-F06 (IBER)	H17	CRABR541-10	
<i>C. angustula</i>	♂	Finland, Vihti Tervalampi	60°19'12"N	24°29'35"E	17.07.2002	J. Paukkunen	GP.72829 (FMNH)	H18	ACUFI458-12	
<i>C. angustula</i>	♀	Lithuania, Varnupys	55°23'39"N	25°16'19"E	19.05-25.08.2007	E. Budrys	TNH07-2256-1 (NRC)	H19	KJ398860	
<i>C. angustula</i>	♀	Lithuania, Arliškės	54°58'21"N	25°21'03"E	31.05-21.09.2008	A. Košel	TNH08-558-1 (NRC)	H20	KJ398852	
<i>C. angustula</i>	♂	Italy, Mezzanino	45°08'00"N	9°13'00"E	25.05.2005	P. Rosa	VS022 (TUZ)	H21	JX292219	JX292178
<i>C. angustula</i>	♀	Norway, Aurfjern	60°13'42"N	11°07'42"E	12.08.2011	F. Ødegaard	Chrysis068 (NINA)	H22	NOCHR068-13	
<i>C. angustula</i>	♀	Norway, Stokkanhaugen	63°24'21"N	10°28'56"E	4.07.2009	F. Ødegaard	Chrysis069 (NINA)	H23	NOCHR069-13	
<i>C. brevitarsis</i>	♀	Finland, Hatula Elillä	61°02'46"N	24°26'10"E	27.06.2011	M. Raekunnas	GP.76506 (FMNH)	H24	ACUFI466-12	
<i>C. brevitarsis</i>	♀	Sweden, Sävar sn, Osmåsfjärden	63°49'55"N	20°40'57"E	23.07.1995	S. Hellqvist	VS140 (SH)	H25	JX292241	HM071110
<i>C. clarinicornis</i>	♀	Ukraine, Lelyaky	50°19'40"N	32°29'30"E	19.07.2005	A. Drozdovskaya	VS152 (TUZ)	H26	KJ398934	
<i>C. clarinicornis</i>	♂	Estonia, Väike-Pakri	59°20'19"N	23°58'41"E	11-12.08.2004	A. Selin	VS511 (AS)	H27	KJ398924	
<i>C. clarinicornis</i>	♀	Italy, Pineta di San Vitale	44°29'29"N	12°13'45"E	20.05.2001	A. Mingazzini	VS085 (TUZ)	H27	KJ398930	
<i>C. clarinicornis</i>	♀	Slovakia, Kopáčky ostrov	48°05'45"N	17°09'40"E	25.05.2006	O. Majzlan	VS524 (TUZ)	H27	KJ398897	
<i>C. corusca</i>	♀	Austria, Reichraming	47°52'46"N	14°30'39"E	29.06-21.09.2007	S. Heinrich	TNH07-882-1 (NRC)	H28	KJ398883	
<i>C. corusca</i>	♀	Belarus, Giry	54°38'31"N	26°12'03"E	13.07.2010	S. Orlovskiyé	SO2010-07-13-2 (NRC)	H29	KJ398863	
<i>C. corusca</i>	♀	Great Britain, Goring	51°30'45"N	1°06'47"W	13-17.06.1999	C.M.T. Raper	VS221 (TUZ)	H30	JX292255	JX292205
<i>C. corusca</i>	♀	Norway, Hellaasen	59°03'58"N	9°41'40"E	25.07.2010	F. Ødegaard	Chrysis019 (NINA)	H31	NOCHR019-13	
<i>C. corusca</i>	♀	Norway, Nenset	59°10'18"N	9°37'33"E	25.07.2010	F. Ødegaard	Chrysis042 (NINA)	H31	NOCHR042-13	
<i>C. corusca</i>	♀	Finland, Lappeenranta Melkkola	60°55'52"N	28°06'58"E	11.07.2006	M. Raekunnas	GP.70892 (FMNH)	H32	ACUFI467-12	
<i>C. corusca</i>	♀	Germany, Messel	49°55'37"N	8°45'27"E	4.06.1998	O. Niehuis	ON054 (ON)	H32	JX292212	HM071096
<i>C. corusca</i>	♀	Lithuania, Paališė	54°48'16"N	24°52'42"E	24.06.2012	A. Petrašiūnas	AP2012-06-24 (NRC)	H32	KJ398907	
<i>C. corusca</i>	♀	Estonia, Kukruse	59°23'09"N	27°21'36"E	14.07.2004	V. Soon	VS024 (TUZ)	H33	JX292221	JX292180
<i>C. fulgida</i>	♀	Germany, 4 km NWW of Freyung	48°49'20"N	13°29'53"E	1.07.2008	J. Mueller	BC ZSM HYM 06295 (ZSM)	H34	FBACA1165-10	
<i>C. fulgida</i>	♀	Germany, 6 km N of Grafenau	48°54'36"N	13°23'24"E	14.08.2008	J. Mueller	BC ZSM HYM 06292 (ZSM)	H34	FBACA1162-10	

.....continued on the next page

TABLE 1. (Continued)

Species	Sex	Locality	Latitude	Longitude	Date	Collector	Voucher ID (depository)	Haplo-type	COI	rRNA
<i>C. fulgida</i>	♀	Germany, 8 km E of Passau	48°34'19"N	13°35'24"E	1.08.2008	J. Mueller	BC ZSM HYM 06293 (ZSM)	H34	FBACA1163-10	
<i>C. fulgida</i>	♀	Germany, Baden-Wuerttemberg	47°52'12"N	7°33'36"E	18.07.2012	C. Schmid-Egger	BC ZSM HYM 17346 (ZSM)	H34	GBACU3001-13	
<i>C. fulgida</i>	♂	Lithuania, Karklupėnai	54°34'13"N	22°49'24"E	6.06-10.09.2010	E. Budrys	TNH10-689-7 (NRC)	H34	KJ398864	
<i>C. fulgida</i>	♀	Germany, 8 km E of Passau	48°34'19"N	13°35'24"E	1.08.2008	J. Mueller	BC ZSM HYM 06294 (ZSM)	H35	FBACA1164-10	
<i>C. fulgida</i>	♀	Germany, Messel	49°55'37"N	8°45'27"E	4.06.1998	O. Niehuis	ON055 (ON)	H36	JX292213	HM071078
<i>C. fulgida</i>	♀	Germany, Berlin	52°29'24"N	13°13'48"E	30.06.2012	C. Schmid-Egger	BC ZSM HYM 14958 (ZSM)	H37	GBACU993-12	
<i>C. fulgida</i>	♀	Estonia, Jõepera	58°16'41"N	27°25'14"E	1.06-15.09.2009	T. Vallisoo & V. VS212 (TUZ)		H38	KJ398932	
<i>C. fulgida</i>	♀	Estonia, Leistu	59°09'44"N	25°12'10"E	22.07.2004	V. Soon	VS025 (TUZ)	H38	JX292222	JX292181
<i>C. fulgida</i>	♀	Finland, Länsi-Turunmaa	60°10'08"N	22°03'00"E	23.06.2010	J. Paukkunen	GP.69761 (FMNH)	H38	ACUF1470-12	
<i>C. fulgida</i>	♂	Finland, Parikkala	61°28'12"N	29°26'38"E	3.07.2009	J. Paukkunen	GP.66099 (FMNH)	H38	ACUF1469-12	
<i>C. fulgida</i>	♂	Finland, Parikkala	61°31'23"N	29°22'08"E	1.07.2007	J. Paukkunen	GP.72807 (FMNH)	H38	ACUF1468-12	
<i>C. fulgida</i>	♂	Lithuania, Papiškiai	55°55'59"N	24°16'35"E	7.06-16.08.2008	E. Budrys	TNH08-1004-1 (NRC)	H38	KJ398867	
<i>C. fulgida</i>	♂	Lithuania, Virbalgris	54°36'18"N	22°47'30"E	6.06-10.09.2010	E. Budrys	TNH10-800-3 (NRC)	H38	KJ398865	
<i>C. fulgida</i>	♂	Norway, Solbergfjell	59°45'32"N	10°02'28"E	8.06.2012	F. Ødegaard	NOCHR247 (NINA)	H38	NOCHR248-13	
<i>C. fulgida</i>	♂	Lithuania, Takniškiai	54°24'23"N	24°06'50"E	26.05-22.09.2010	E. Budrys	TNH10-219-2 (NRC)	H39	KJ398870	
<i>C. fulgida</i>	♂	Lithuania, Kiemėliai	54°51'30"N	25°01'00"E	20.05-30.08.2010	E. Budrys	TNH10-921-8 (NRC)	H40	KJ398871	
<i>C. fulgida</i>	♀	Finland, Lapinjärvi	60°38'13"N	26°09'58"E	8.08.2004	J. Paukkunen	GP.72804 (FMNH)	H41	ACUF1471-12	
<i>C. fulgida</i>	♂	Lithuania, Vilkaraisčiai	55°08'14"N	25°21'24"E	31.05-26.09.2009	A. Košel	TNH09-372-4 (NRC)	H41	KJ398869	
<i>C. fulgida</i>	♀	Lithuania, Kartuvėlė	55°05'58"N	25°21'18"E	7.06-21.09.2008	A. Košel	TNH08-593-2 (NRC)	H42	KJ398866	
<i>C. fulgida</i>	♀	Finland, Kalkkima	65°54'06"N	24°27'54"E	18.07.2009	V. Soon	VS226 (TUZ)	H43	JX292256	JX292206
<i>C. fulgida</i>	♂	Lithuania, Varnupys	55°23'44"N	25°16'07"E	19.05-25.08.2007	E. Budrys	TNH07-2390-4 (NRC)	H43	KJ398874	
<i>C. fulgida</i>	♀	Lithuania, Varnupys	55°23'38"N	25°16'20"E	12.07-23.08.2008	E. Budrys	TNH08-1450-2 (NRC)	H44	KJ398872	
<i>C. fulgida</i>	♀	Lithuania, Varnupys	55°23'38"N	25°16'20"E	10.05-29.08.2009	E. Budrys	TNH09-1166-2 (NRC)	H45	KJ398873	
<i>C. fulgida</i>	♂	Lithuania, Papiškiai	55°55'59"N	24°16'35"E	13.05-4.07.2007	E. Budrys	TNH07-2665-2 (NRC)	H46	KJ398868	
<i>C. ignita</i>	♀	Belarus, Griy	54°38'31"N	26°12'03"E	24.06-2.07.2011	S. Orlovskiyė	SO2011-06-24-2 (NRC)	H47	KJ398887	
<i>C. ignita</i>	♀	Bulgaria, N Nova Cherna	44°00'50"N	26°26'47"E	24.05.2007	M. Ilieva	CCDB-05794-G01 (IBER)	H47	CRABR453-10	
<i>C. ignita</i>	♀	Estonia, Vellavere	58°15'45"N	26°24'40"E	25.06.2003	V. Soon	VS028 (TUZ)	H47	JX292224	JX292183
<i>C. ignita</i>	♀	Italy, Turlin, Aosta	45°41'29"N	7°15'59"E	17.08.2006	P. Rosa	VS171 (TUZ)	H47	JX292249	HM071088

... continued on the next page

TABLE 1. (Continued)

Species	Sex	Locality	Latitude	Longitude	Date	Collector	Voucher ID (depository)	Haplo-type	COI	rRNA
<i>C. ignita</i>	♀	Lithuania, Vistoriai	54°45'11"N	25°15'47"E	23.05.2010	A. Budrienė	AB2010-05-23 (NRC)	H47	KJ398878	
<i>C. ignita</i>	♀	Sweden, Öja, Landsort	58°44'40"N	17°52'03"E	6.07.1990	J. Abernitus	VS141 (JA)	H47	JX292242	JX292199
<i>C. impressa</i>	♂	Finland, Längelmäki Kuusjärvi	61°49'01"N	24°54'14"E	3.07.2001	J. Paukkunen	GP.70882 (FMNH)	H48	ACUF1511-13	
<i>C. impressa</i>	♀	Estonia, Aa	59°25'52"N	27°09'46"E	16.07.2004	V. Soon	VS030 (TUZ)	H49	JX292225	JX292184
<i>C. impressa</i>	♀	Finland, Hämeenlinna Voutila	60°58'59"N	24°24'14"E	6.06.2008	T. Vainio	GP.66686 (FMNH)	H49	ACUF1486-13	
<i>C. impressa</i>	♂	Finland, Orivesi Uihertla	61°34'08"N	24°32'38"E	3.07.2001	J. Paukkunen	GP.70872 (FMNH)	H49	ACUF1485-13	
<i>C. impressa</i>	♂	Finland, Parikkala	61°28'12"N	29°26'38"E	3.07.2009	J. Paukkunen	GP.66105 (FMNH)	H49	ACUF1512-13	
<i>C. impressa</i>	♀	Finland, Parikkala	61°31'23"N	29°22'08"E	2.07.2008	J. Paukkunen	GP.66591 (FMNH)	H49	ACUF1487-13	
<i>C. impressa</i> *	♀	Melkoniemä								
<i>C. impressa</i> *	♀	Germany, Hesse	49°55'16"N	8°28'52"E	3.05.2007	G. Reeder	BC_ZSM_HYM_07999 (ZSM)	H49	FBACB399-11	
<i>C. impressa</i> *	♂	Germany, Thuringia	51°19'23"N	11°01'55"E	6.06.2011	F. Burger	BC_ZSM_HYM_12743 (ZSM)	H49	GBACU2483-13	
<i>C. impressa</i> *	♀	Germany, Thuringia	51°19'23"N	11°01'55"E	6.07.2011	F. Burger	BC_ZSM_HYM_12751 (ZSM)	H49	GBACU2491-13	
<i>C. impressa</i>	♂	Lithuania, Dūkštos oak forest	54°50'00"N	24°57'50"E	20.05-30.08.2010	E. Budrys	TNH10-607-1 (NRC)	H49	KJ398890	
<i>C. impressa</i>	♀	Lithuania, Puvočiai	54°06'57"N	24°18'21"E	30.06.2009	E. Budrys	EB2009-06-30 (NRC)	H49	KJ398885	
<i>C. impressa</i>	♀	Lithuania, Puvočiai	54°06'57"N	24°18'21"E	10.06-25.08.2009	E. Budrys	TNH09-334-1 (NRC)	H49	KJ398884	
<i>C. impressa</i>	♀	Norway, Asakmoen	59°59'06"N	11°06'36"E	27.06.2010	F. Ødegaard	Chrysis122 (NINA)	H49	NOCHR117-13	
<i>C. impressa</i>	♂	Norway, Bergsland	59°36'30"N	8°42'38"E	23.06.2010	F. Ødegaard	Chrysis012 (NINA)	H49	NOCHR012-13	
<i>C. impressa</i>	♀	Norway, Bergsland	59°36'29"N	8°42'40"E	23.06.2010	F. Ødegaard	Chrysis128 (NINA)	H49	NOCHR123-13	
<i>C. impressa</i>	♂	Norway, Blika	59°35'28"N	8°33'22"E	23.06.2010	F. Ødegaard	Chrysis134 (NINA)	H49	NOCHR129-13	
<i>C. impressa</i>	♀	Norway, Blika	59°35'28"N	8°33'23"E	23.06.2010	F. Ødegaard	Chrysis016 (NINA)	H49	NOCHR016-13	
<i>C. impressa</i>	♂	Norway, Blika	59°35'28"N	8°33'23"E	23.06.2010	F. Ødegaard	Chrysis039 (NINA)	H49	NOCHR039-13	
<i>C. impressa</i>	♂	Norway, Heggnes	59°26'24"N	8°46'59"E	5.06.2009	F. Ødegaard	Chrysis108 (NINA)	H49	NOCHR103-13	
<i>C. impressa</i>	♂	Norway, Heggnes	59°26'24"N	8°46'59"E	5.06.2009	F. Ødegaard	Chrysis113 (NINA)	H49	NOCHR108-13	
<i>C. impressa</i>	♂	Norway, Heggnes	59°26'26"N	8°47'00"E	5.06.2009	F. Ødegaard	Chrysis038 (NINA)	H49	NOCHR038-13	
<i>C. impressa</i>	♀	Norway, Heggnes	59°26'24"N	8°46'59"E	3.07.2009	F. Ødegaard	Chrysis107 (NINA)	H49	NOCHR102-13	
<i>C. impressa</i>	♀	Norway, Heggnes	59°26'24"N	8°46'59"E	3.07.2009	F. Ødegaard	Chrysis114 (NINA)	H49	NOCHR109-13	
<i>C. impressa</i>	♀	Norway, Heggnes	59°26'24"N	8°46'59"E	3.07.2009	F. Ødegaard	Chrysis116 (NINA)	H49	NOCHR111-13	
<i>C. impressa</i>	♀	Norway, Leirsjoen	59°53'23"N	12°09'59"E	22.06.2010	F. Ødegaard	Chrysis030 (NINA)	H49	NOCHR030-13	
<i>C. impressa</i>	♂	Norway, Omdal	59°14'35"N	10°14'24"E	8.05.2011	A. Staverlokk	NOCHR261 (NINA)	H49	NOCHR262-13	

..... continued on the next page

TABLE 1. (Continued)

Species	Sex	Locality	Latitude	Longitude	Date	Collector	Voucher ID (depository)	Haplo-type	COI	rRNA
<i>C. impressa</i>	♀	Norway, Raufoss	60°43'49"N	10°37'26"E	17.07.2010	F. Ødegaard	Chrysis018 (NINA)	H49	NOCHR018-13	
<i>C. impressa</i>	♂	Norway, Solbergfjell	59°45'32"N	10°02'28"E	8.06.2012	F. Ødegaard	Chrysis123 (NINA)	H49	NOCHR118-13	
<i>C. impressa</i>	♀	Norway, Solbergfjell	59°45'32"N	10°02'28"E	8.06.2012	F. Ødegaard	Chrysis131 (NINA)	H49	NOCHR126-13	
<i>C. impressa</i>	♂	Norway, Solbergfjell	59°45'34"N	10°02'29"E	8.06.2012	F. Ødegaard	Chrysis036 (NINA)	H49	NOCHR036-13	
<i>C. impressa</i>	♂	Norway, Solbergfjell	59°45'32"N	10°02'28"E	11.06.2012	F. Ødegaard	NOCHR265 (NINA)	H49	NOCHR266-13	
<i>C. impressa</i>	♂	Norway, Solbergfjell	59°45'32"N	10°02'28"E	25.06.2013	F. Ødegaard	NOCHR208 (NINA)	H49	NOCHR209-13	
<i>C. impressa</i>	♂	Norway, Tranby	59°48'58"N	10°14'06"E	3.06.2009	F. Ødegaard	Chrysis011 (NINA)	H49	NOCHR011-13	
<i>C. impressa</i>	♀	Norway, Utstrandra	59°59'53"N	10°17'18"E	13.07.2011	F. Ødegaard	Chrysis035 (NINA)	H49	NOCHR035-13	
<i>C. impressa</i>	♀	Norway, Utstrandra	59°59'53"N	10°17'17"E	2.08.2011	F. Ødegaard	Chrysis119 (NINA)	H49	NOCHR114-13	
<i>C. impressa</i>	♀	Norway, Venannsaas	59°08'05"N	9°57'03"E	20.07.2009	F. Ødegaard	Chrysis031 (NINA)	H49	NOCHR031-13	
<i>C. impressa</i>	♀	Norway, Venannsaas	59°08'06"N	9°57'04"E	25.08.2009	F. Ødegaard	Chrysis133 (NINA)	H49	NOCHR128-13	
<i>C. impressa</i>	♂	Sweden, Marna skjutfält	60°31'27"N	17°27'05"E	17.06-2.07.2003	SMTP	VS530 (NRM)	H49	KJ398926	
<i>C. impressa</i>	♀	Sweden, Öland, Persnäs	57°03'25"N	16°54'51"E	07.2007	J. Abenius	VS504 (TUZ)	H49	IX292260	HM071113
<i>C. iris</i>	♂	Lithuania, Papiškiai	55°55'59"N	24°16'35"E	7.06-16.08.2008	E. Budrys	TNH08-1028-3 (NRC)	H50	KJ398877	
<i>C. iris</i>	♀	Estonia, Prangli	58°10'06"N	26°46'13"E	17.07.2003	V. Soon	VS031 (TUZ)	H51	IX292226	IX292185
<i>C. iris</i>	♂	Bulgaria, Sofia, Bossnek	42°29'43"N	23°10'40"E	27.06.1999	T. Ljubomirov	VS163 (TUZ)	H52	IX292245	HM071080
<i>C. iris</i>	♀	Lithuania, Dūdai	55°05'44"N	24°45'25"E	1.06-24.08.2008	E. Budrys	TNH08-1105-1 (NRC)	H52	KJ398876	
<i>C. iris</i>	♂	Finland, Joutseno Kuurmanpohja	61°04'37"N	28°43'55"E	12.02.2012	M. Raekunnas	GP.86317 (FMNH)	H53	ACUF1488-13	
<i>C. iris</i>	♀	Finland, Joutseno Kuurmanpohja	61°04'37"N	28°43'55"E	14.02.2012	M. Raekunnas	GP.86320 (FMNH)	H54	ACUF1489-13	
<i>C. iris</i>	♀	Poland, Piekary	50°01'49"N	19°48'11"E	7.05-27.09.2007	H. Szentgyörgyi	TNH07-1217-1 (NRC)	H55	KJ398875	
<i>C. iris</i>	♀	Bulgaria, Blagoevgrad, Yurukovo	41°58'56"N	23°38'07"E	30.06.2004	O. Todorov	CCDDB-05795-A06 (IBER)	H56	CRABR481-10	
<i>C. leptomandibularis</i>	♀	Estonia, Nurmetu	59°14'30"N	26°20'19"E	20.07.2004	V. Soon	VS032 (TUZ)	H57	IX292227	IX292185
<i>C. leptomandibularis</i>	♂	Italy, Mezzanino	45°08'00"N	9°13'00"E	25.05.2005	P. Rosa	VS165 (TUZ)	H58	IX292246	HM071082
<i>C. leptomandibularis</i>	♀	Lithuania, Darsūniškis	54°43'21"N	24°06'42"E	17.07.2010	E. Budrys	EB2010-07-17-1 (NRC)	H58	KJ398895	
<i>C. leptomandibularis</i>	♀	Belarus, Giry	54°38'31"N	26°12'03"E	13.07.2010	S. Orlovskytė	SO2010-07-13-1 (NRC)	H59	KJ398894	
<i>C. leptomandibularis</i>	♀	Lithuania, Kaunas	54°54'15"N	23°54'14"E	5.06-9.09.2010	E. Budrys	TNH10-1102-6 (NRC)	H60	KJ398846	
<i>C. longula</i>	♂	Finland, Lieksa Koli	63°04'12"N	29°50'20"E	27.06.2010	M. Raekunnas	GP.69400 (FMNH)	H61	ACUF1490-13	
<i>C. longula</i>	♂	Lithuania, Puvočiai	54°06'34"N	24°18'50"E	11.06-24.09.2011	E. Budrys	TNH11-1243-1 (NRC)	H62	KJ398842	
<i>C. longula</i>	♀	Lithuania, Varnupys	55°23'38"N	25°16'20"E	10.05-29.08.2009	E. Budrys	TNH09-720-2 (NRC)	H63	KJ398840	

... continued on the next page

TABLE 1. (Continued)

Species	Sex	Locality	Latitude	Longitude	Date	Collector	Voucher ID (depository)	Haplo-type	COI	rRNA
<i>C. longula</i>	♀	Germany, Filsen	50°14'15"N	7°35'34"E	25.06.1999	M. Niehuis	ON269 (ON)	H64	JX292217	HM071084
<i>C. longula</i> *	♀	Germany, Thuringia	51°19'23"N	11°01'55"E	6.07.2011	F. Burger	BC ZSM HYM 12750 (ZSM)	H64	GBACU2490-13	
<i>C. longula</i>	♀	Italy, Ozein	45°40'41"N	7°14'16"E	15.08.2002	P. Rosa	VS034 (TUZ)	H64	JX292229	JX292188
<i>C. longula</i>	♀	Lithuania, Varnupys	55°23'38"N	25°16'20"E	19.05-25.08.2007	E. Budrys	TNH07-349-1 (NRC)	H64	KJ398891	
<i>C. longula</i>	♀	Norway, Sohol	60°04'30"N	10°12'36"E	24.07.2010	F. Ødegaard	NOCHR229 (NINA)	H64	NOCHR230-13	
<i>C. longula</i>	♀	Finland, Länsi-Turunmaa Nauvo	60°10'08"N	22°03'00"E	23.06.2010	J. Paukkunen	GP.69760 (FMNH)	H65	ACUFI493-13	
<i>C. longula</i>	♂	Lithuania, Bilšiai	55°08'01"N	25°16'16"E	23.05-28.08.2010	E. Budrys	TNH10-73-1 (NRC)	H66	KJ398889	
<i>C. longula</i>	♀	Belarus, Giry	54°38'31"N	26°12'03"E	24.06-7.10.2011	S. Orlovskytė	TNH11-817-1 (NRC)	H67	KJ398847	
<i>C. longula</i>	♂	Lithuania, Bilšiai	55°08'01"N	25°16'16"E	23.05-28.08.2010	E. Budrys	TNH10-15-2 (NRC)	H68	KJ398888	
<i>C. longula</i>	♀	Lithuania, Kiemeliai	54°51'08"N	25°00'17"E	17.05-19.08.2008	E. Budrys	TNH08-1339-2 (NRC)	H69	KJ398892	
<i>C. longula</i>	♀	Lithuania, Bilšiai	55°08'01"N	25°16'16"E	12.07-23.08.2008	E. Budrys	TNH08-1245-1 (NRC)	H70	KJ398893	
<i>C. longula</i>	♀	Finland, Ylämaa Nurmela	60°40'44"N	27°59'13"E	2.07.2009	J. Paukkunen	GP.66098 (FMNH)	H71	ACUFI491-13	
<i>C. longula</i>	♂	Lithuania, Puvočiai	54°04'55"N	24°19'25"E	10.06-25.08.2009	E. Budrys	TNH09-203-4 (NRC)	H72	KJ398841	
<i>C. longula</i>	♂	Lithuania, Škėvonys	54°36'17"N	24°00'09"E	10.06-2.10.2011	E. Budrys	TNH11-1152-1 (NRC)	H73	KJ398843	
<i>C. mediata</i>	♀	Germany, Landau in der Pfalz	49°11'33"N	8°05'07"E	8.06.1999	O. Niehuis & S. Schulmeister	ON121 (ON)	H74	JX292216	HM071093
<i>C. mediata</i>	♀	Estonia, Raadi airfield	58°23'48"N	26°48'35"E	22.06.2006	V. Soon	VS036 (TUZ)	H75	JX292231	JX292190
<i>C. mediata</i> *	♀	Germany, Brandenburg	52°49'48"N	14°41'24"E	21.05.2012	C. Schmid-Egger	BC ZSM HYM 13901 (ZSM)	H75	GBACU1646-12	
<i>C. mediata</i> *	♀	Germany, Brandenburg	52°49'48"N	14°41'24"E	21.05.2012	C. Schmid-Egger	BC ZSM HYM 13904 (ZSM)	H75	GBACU1649-12	
<i>C. mediata</i>	♀	Lithuania, Kaunas	54°50'49"N	23°56'08"E	31.05.2008	E. Budrys	EB2008-05-31 (NRC)	H75	KJ398898	
<i>C. mediata</i>	♀	Lithuania, Škėvonys	54°36'17"N	24°00'09"E	29.06.2010	S. Orlovskytė	SO2010-06-29 (NRC)	H75	KJ398896	
<i>C. mediata</i> *	♂	Germany, Brandenburg	52°49'48"N	14°05'24"E	21.05.2012	C. Schmid-Egger	BC ZSM HYM 17471 (ZSM)	H76	GBACU3126-13	
<i>C. mediata</i> *	♂	Germany, Rhineland Palatinate	49°38'10"N	8°12'11"E	20.05.2002	G. Reder	BC ZSM HYM 07864 (ZSM)	H76	FBACB359-11	
<i>C. mediata</i> *	♀	Germany, Rhineland Palatinate	49°38'10"N	8°12'11"E	6.05.2003	G. Reder	BC ZSM HYM 07862 (ZSM)	H76	FBACB357-11	
<i>C. mediata</i> *	♀	Germany, Rhineland Palatinate	49°38'10"N	8°12'11"E	6.05.2003	G. Reder	BC ZSM HYM 07863 (ZSM)	H76	FBACB358-11	
<i>C. mediata</i> *	♂	Germany, Rhineland Palatinate	49°32'02"N	8°03'58"E	20.05.2009	G. Reder	BC ZSM HYM 07865 (ZSM)	H76	FBACB360-11	
<i>C. pseudobrevitarsis</i>	♀	Germany, Stolpe/ Oder	52°58'47"N	14°06'50"E	30.06.2001	C. Schmid-Egger	VS127 (TUZ)	H77	JX292239	JX292197
<i>C. pseudobrevitarsis</i>	♀	Lithuania, Tilže	55°39'37"N	26°33'57"E	7.08.2004	V. Soon	VS168 (TUZ)	H77	JX292248	HM071085
<i>C. pseudobrevitarsis</i>	♀	Russia, Kurkijoki Soskua	61°18'00"N	29°58'12"E	3.07.2005	J. Paukkunen	GP.72815 (FMNH)	H77	ACUFI501-13	

..... continued on the next page

TABLE 1. (Continued)

Species	Sex	Locality	Latitude	Longitude	Date	Collector	Voucher ID (depository)	Haplo-type	COI	rRNA
<i>C. pseudobrevitarsis</i>	♀	Belarus, Giry	54°38'31"N	26°12'03"E	15-19.08.2011	S. Orlovskiytė	SO2011-08-15-19 (NRC)	H78	KJ398900	
<i>C. pseudobrevitarsis</i>	♀	Estonia, Võhunnõmme	59°15'02"N	26°35'43"E	15.07.2004	V. Soon	VS037 (TUZ)	H78	JX292232	JX292191
<i>C. pseudobrevitarsis</i>	♂	Finland, Imatra Mellonmäki	61°09'29"N	28°45'18"E	2.07.2007	M. Raekunnas	HE.708 (FMNH)	H78	ACUF1499-13	
<i>C. pseudobrevitarsis</i>	♀	Finland, Parikkala Saari	61°39'50"N	29°40'19"E	14.07.2010	J. Paukkunen	GP.69780 (FMNH)	H78	ACUF1502-13	
<i>C. pseudobrevitarsis</i> *	♀	Germany, Thuringia	51°19'23"N	11°01'55"E	6.06.2011	F. Burger	BC ZSM HYM 12745 (ZSM)	H79	GBACU2485-13	
<i>C. pseudobrevitarsis</i>	♀	Germany, Messel	49°55'37"N	8°45'27"E	4.06.1998	O. Niehuis	ON052 (ON)	H80	JX292218	JX292177
<i>C. pseudobrevitarsis</i> *	♂	Germany, Thuringia	51°19'23"N	11°01'55"E	6.06.2011	F. Burger	BC ZSM HYM 12742 (ZSM)	H80	GBACU2482-13	
<i>C. pseudobrevitarsis</i> *	♂	Germany, Thuringia	51°13'59"N	11°19'23"E	7.07.2011	F. Burger	BC ZSM HYM 12748 (ZSM)	H81	GBACU2488-13	
<i>C. pseudobrevitarsis</i>	♀	Estonia, Vehendi	58°13'48"N	26°09'17"E	3-9.07.2010	V. Soon	VS002798 (TUZ)	H82	KJ398927	
<i>C. pseudobrevitarsis</i>	♀	Norway, Kviljo	58°04'32"N	6°40'35"E	14.08.2008	F. Ødegaard	Chrysis073 (NINA)	H83	NOCHR073-13	
<i>C. pseudobrevitarsis</i>	♀	Italy, Sardegna, Barchidda mt	SS40°47'99"N	9°08'87"E	14.05-4.06.2002	F. Strumia	VS222 (TUZ)	H84	KJ398933	
<i>C. ruddii</i>		Norway, Solbergfjell	59°45'32"N	10°02'28"E	25.05.2012	F. Ødegaard	NOCHR279 (NINA)	H85	NOCHR280-13	
<i>C. ruddii</i>	♀	Finland, Halikko Rikala	60°23'31"N	23°04'05"E	16.07.2004	J. Paukkunen	GP.72797 (FMNH)	H86	ACUF1506-13	
<i>C. ruddii</i>	♂	Norway, Heggneset	59°26'24"N	8°46'59"E	8.07.2013	F. Ødegaard	NOCHR281 (NINA)	H87	NOCHR282-13	
<i>C. ruddii</i>	♂	Norway, Rauer	59°13'26"N	10°41'42"E	9.06.2013	F. Ødegaard	NOCHR282 (NINA)	H88	NOCHR283-13	
<i>C. ruddii</i>	♂	Norway, Rauer	59°13'26"N	10°41'42"E	9.06.2013	F. Ødegaard	NOCHR283 (NINA)	H88	NOCHR284-13	
<i>C. ruddii</i>	♂	Norway, Lilleby	59°46'44"N	9°55'59"E	8.06.2012	F. Ødegaard	NOCHR278 (NINA)	H89	NOCHR279-13	
<i>C. ruddii</i>	♀	Sweden, Öland, Persnäs	57°02'42"N	16°56'13"E	20.07.2007	J. Abernitus	VS501 (TUZ)	H90	JX292258	JX292208
<i>C. ruddii</i>	♀	Italy, S Barrea	41°44'36"N	13°59'06"E	17.06.2011	T. Ljubomirov	CCDB-12229-D04 (IBER)	H91	CRABR1655-11	
<i>C. ruddii</i>	♀	Bulgaria, Sofia, Tchuypetlovo	N42°32'14"N	23°14'25"E	26.06.1999	T. Ljubomirov	VS038 (TUZ)	H92	JX292233	JX292192
<i>C. ruddii</i>	♀	Estonia, Jõeääre	58°43'36"N	26°49'55"E	8.07.2004	V. Soon	VS173 (TUZ)	H93	JX292250	HM071090
<i>C. ruddii</i> *	♂	France, La Foux d'Allos	44°17'38"N	6°33'50"E	15.07.2010	C. Schmid-Egger	BC ZSM HYM 07798 (ZSM)	H94	FBACB293-11	
<i>C. ruddii</i>	♂	Norway, Hjøllhagan	62°03'04"N	9°07'37"E	10.06.2013	F. Ødegaard	NOCHR276 (NINA)	H95	NOCHR277-13	
<i>C. ruddii</i>	♂	Norway, Hjøllhagan	62°03'04"N	9°07'37"E	10.06.2013	F. Ødegaard	NOCHR277 (NINA)	H95	NOCHR278-13	
<i>C. ruddii</i> *	♂	Germany, Rhineland Palatinate	49°32'35"N	8°08'13"E	24.04.2010	G. Reder	BC ZSM HYM 07877 (ZSM)	H96	FBACB372-11	
<i>C. ruddii</i> *	♀	Germany, Rhineland Palatinate	49°38'10"N	8°08'13"E	30.05.2006	G. Reder	BC ZSM HYM 07874 (ZSM)	H97	FBACB369-11	
<i>C. ruddii</i> *	♂	Germany, Rhineland Palatinate	49°32'35"N	8°08'13"E	21.05.2005	G. Reder	BC ZSM HYM 07876 (ZSM)	H98	FBACB371-11	
<i>C. ruddii</i> *	♀	Germany, Rhineland Palatinate	49°38'10"N	8°08'13"E	22.05.2007	G. Reder	BC ZSM HYM 07875 (ZSM)	H98	FBACB370-11	

... continued on the next page

TABLE 1. (Continued)

Species	Sex	Locality	Latitude	Longitude	Date	Collector	Voucher ID (depository)	Haplo-type	COI	rRNA
<i>C. schencki</i>	♀	Norway, Lovbergmoen	60°54'04"N	11°35'31"E	23.08.2007	F. Ødegaard	NOCHR260 (NINA)	H99	NOCHR261-13	
<i>C. schencki</i>	♀	Finland, Tammissaari Gästans	59°52'34"N	23°41'46"E	12.07.2010	L. Kaila	GP.80590 (FMNH)	H100	ACUF1513-13	
<i>C. schencki</i> *	♂	Germany, Thuringia	51°11'53"N	11°15'11"E	23.06.2011	F. Burger	BC ZSM HYM 12759 (ZSM)	H100	GBACU2499-13	
<i>C. schencki</i>	♀	Italy, Aymavilles	45°42'04"N	7°14'33"E	16.06.2007	V. Soon	VS102 (TUZ)	H100	JX292238	JX292196
<i>C. schencki</i>	♀	Norway, Asakmoen	59°59'06"N	11°06'36"E	27.08.2010	F. Ødegaard	Chrysis121 (NINA)	H100	NOCHR116-13	
<i>C. schencki</i>	♀	Norway, Botnahaugen	62°46'48"N	7°51'58"E	19.09.2008	F. Ødegaard	Chrysis129 (NINA)	H100	NOCHR124-13	
<i>C. schencki</i>	♀	Norway, Busund	60°07'44"N	10°14'35"E	18.08.2008	F. Ødegaard	NOCHR259 (NINA)	H100	NOCHR260-13	
<i>C. schencki</i>	♀	Norway, Fagerhaug	62°39'32"N	9°53'17"E	6.07.2007	F. Ødegaard	Chrysis145 (NINA)	H100	NOCHR140-13	
<i>C. schencki</i>	♀	Norway, Faksfall	62°02'13"N	9°10'05"E	27.06.2008	F. Ødegaard	Chrysis181 (NINA)	H100	NOCHR176-13	
<i>C. schencki</i>	♀	Norway, Gyllvatnet	63°05'56"N	10°17'56"E	4.07.2009	F. Ødegaard	Chrysis179 (NINA)	H100	NOCHR174-13	
<i>C. schencki</i>	♂	Norway, Gyllvatnet	63°05'55"N	10°17'58"E	28.07.2010	F. Ødegaard	Chrysis008 (NINA)	H100	NOCHR008-13	
<i>C. schencki</i>	♀	Norway, Jakopsmyran	63°11'07"N	9°37'43"E	18.07.2010	F. Ødegaard	Chrysis044 (NINA)	H100	NOCHR044-13	
<i>C. schencki</i>	♀	Norway, Jakopsmyran	63°11'06"N	9°37'44"E	18.07.2010	F. Ødegaard	Chrysis120 (NINA)	H100	NOCHR115-13	
<i>C. schencki</i>	♀	Norway, Langoya V	59°00'29"N	9°45'22"E	18.08.2009	O. Gammelmo	NOCHR270 (NINA)	H100	NOCHR271-13	
<i>C. schencki</i>	♀	Norway, Leirsjoen	59°53'27"N	12°09'43"E	28.07.2010	F. Ødegaard	Chrysis046 (NINA)	H100	NOCHR046-13	
<i>C. schencki</i>	♀	Norway, Leirsjoen	59°53'28"N	12°09'43"E	28.07.2010	F. Ødegaard	Chrysis186 (NINA)	H100	NOCHR181-13	
<i>C. schencki</i>	♂	Norway, Magnor	59°57'08"N	12°10'34"E	27.06.2012	F. Ødegaard	Chrysis002 (NINA)	H100	NOCHR002-13	
<i>C. schencki</i>	♀	Norway, Munkvoll	62°36'36"N	9°26'56"E	20.07.2013	F. Ødegaard	NOCHR274 (NINA)	H100	NOCHR275-13	
<i>C. schencki</i>	♀	Norway, Ormsset	62°52'16"N	8°09'54"E	14.08.2005	F. Ødegaard	Chrysis127 (NINA)	H100	NOCHR122-13	
<i>C. schencki</i>	♂	Norway, Ormsset	62°52'15"N	8°09'55"E	14.08.2005	F. Ødegaard	Chrysis052 (NINA)	H100	NOCHR052-13	
<i>C. schencki</i>	♂	Norway, Smaasetran	62°34'21"N	11°24'45"E	23.07.2007	F. Ødegaard	Chrysis001 (NINA)	H100	NOCHR001-13	
<i>C. schencki</i>	♂	Norway, Smaasetran	62°34'21"N	11°24'45"E	23.07.2007	F. Ødegaard	Chrysis022 (NINA)	H100	NOCHR022-13	
<i>C. schencki</i>	♀	Norway, Starmoen	60°51'07"N	11°41'53"E	13.06.2007	F. Ødegaard	NOCHR257 (NINA)	H100	NOCHR258-13	
<i>C. schencki</i>	♀	Sweden, Norberg, Halvarsbänning	60°06'02"N	15°47'18"E	10.07.2007	J. Abenius	VS046 (TUZ)	H100	JX292235	JX292194
<i>C. schencki</i>	♂	Norway, Jakopsmyran	63°11'07"N	9°37'43"E	18.07.2010	F. Ødegaard	Chrysis010 (NINA)	H101	NOCHR010-13	
<i>C. schencki</i>	♂	Norway, Gyllvatnet	63°05'56"N	10°17'56"E	6.07.2008	F. Ødegaard	Chrysis137 (NINA)	H102	NOCHR132-13	
<i>C. schencki</i>	♀	Finland, Janakkala Hakoinen	60°52'41"N	24°35'49"E	1.01.2003	J. Paukkunen & Söderman	G.GP.70855 (FMNH)	H103	ACUF1514-13	
<i>C. schencki</i>	♀	Lithuania, Merkinė	54°09'46"N	24°11'38"E	12.06-24.09.2011	E. Budrys	TNH11-407-1 (NRC)	H103	KJ398844	
<i>C. schencki</i>	♀	Lithuania, Musteika	53°59'22"N	24°25'51"E	21.05-20.08.2007	E. Budrys	TNH07-2522-1 (NRC)	H103	KJ398839	

..... continued on the next page

TABLE 1. (Continued)

Species	Sex	Locality	Latitude	Longitude	Date	Collector	Voucher ID (depository)	Haplo-type	COI	rRNA
<i>C. schencki</i>	♂	Lithuania, Puvočiai	54°06'01"N	24°18'39"E	10.06-25.08.2009	E. Budrys	TNH09-769-1 (NRC)	H103	KJ398906	
<i>C. schencki</i>	♂	Norway, Bratsberg	63°20'46"N	10°31'50"E	19.06.2011	F. Ødegaard	Chrysis006 (NINA)	H103	NOCHR006-13	
<i>C. schencki</i>	♀	Norway, Fatlaberga	61°09'50"N	6°54'31"E	5.07.2011	F. Ødegaard	Chrysis048 (NINA)	H103	NOCHR048-13	
<i>C. schencki</i>	♀	Lithuania, Puvočiai	54°06'32"N	24°18'37"E	10.06-25.08.2009	E. Budrys	TNH09-542-2 (NRC)	H104	KJ398905	
<i>C. schencki</i>	♀	Lithuania, Bagdononys	54°37'37"N	24°42'32"E	24.06.2012	S. Orlovskytė	SO2012-06-24 (NRC)	H105	KJ398908	
<i>C. schencki</i>	♀	Norway, Lovbergmoen	60°54'04"N	11°35'31"E	13.06.2007	F. Ødegaard	Chrysis188 (NINA)	H106	NOCHR183-13	
<i>C. schencki</i>	♀	Bulgaria, Sofia, Batulya	42°53'52"N	23°25'28"E	17.11.2002	S. Lazarov	CCDB-05795-G07 (IBER)	H107	CRABR554-10	
<i>C. schencki</i>	♀	Lithuania, Juodkrantė	55°31'06"N	21°06'32"E	24.05-6.09.2011	E. Budrys	TNH11-234-1 (NRC)	H108	KJ398845	
<i>C. schencki</i>	♀	Estonia, Vormsi, Förby	58°59'48"N	23°10'05"E	11.07.2006	V. Soon	VS157 (TUZ)	H109	JX292243	HM071074
<i>C. schencki</i>	♀	Great Britain, Goring	51°30'45"N	1°06'47"W	13-17.06.1999	C.M.T. Raper	VS213 (TUZ)	H110	JX292252	JX292202
<i>C. solida</i>	♀	Lithuania, Kiemeliai	54°51'30"N	25°01'00"E	20.05-30.08.2010	E. Budrys	TNH10-918-2 (NRC)	H111	KJ398914	
<i>C. solida</i>	♂	Lithuania, Babrai	54°08'47"N	23°42'05"E	26.06-25.09.2011	E. Budrys	TNH11-1098-2 (NRC)	H112	KJ398919	
<i>C. solida</i>	♀	Lithuania, Perloja	54°13'24"N	24°22'58"E	27.05-22.09.2010	E. Budrys	TNH10-1093-1 (NRC)	H113	KJ398913	
<i>C. solida</i>	♀	Lithuania, Dūkštos forest	oak54°50'00"N	24°57'50"E	25.05-19.08.2008	E. Budrys	TNH08-856-1 (NRC)	H114	KJ398904	
<i>C. solida</i>	♀	Lithuania, Bilšiai	55°08'02"N	25°16'15"E	23.05-29.08.2010	E. Budrys	TNH10-668-2 (NRC)	H115	KJ398909	
<i>C. solida</i>	♀	Lithuania, Dūkštos forest	oak54°49'49"N	24°57'35"E	13.05-31.08.2007	E. Budrys	TNH07-923-2 (NRC)	H116	KJ398901	
<i>C. solida</i>	♀	Lithuania, Varnupys	55°23'44"N	25°16'07"E	22.05-28.08.2010	E. Budrys	TNH10-286-2 (NRC)	H116	KJ398902	
<i>C. solida</i>	♀	Lithuania, Bilšiai	55°08'02"N	25°16'15"E	23.05-29.08.2010	E. Budrys	TNH10-668-1 (NRC)	H117	KJ398915	
<i>C. solida</i> *	♀	Germany, Thuringia	51°01'08"N	11°18'14"E	31.05.2011	F. Burger	BC ZSM HYM 12753 (ZSM)	H118	GBACU2493-13	
<i>C. solida</i> *	♂	Germany, Thuringia	51°01'08"N	11°18'14"E	31.05.2011	F. Burger	BC ZSM HYM 12754 (ZSM)	H118	GBACU2494-13	
<i>C. solida</i> *	♀	Germany, Thuringia	51°13'59"N	11°19'23"E	7.07.2011	F. Burger	BC ZSM HYM 12752 (ZSM)	H118	GBACU2492-13	
<i>C. solida</i>	♀	Germany, Waldleiningen	49°23'30"N	7°52'43"E	6.08.1999	M. Niehuis	ON112 (ON)	H118	JX292215	JX292176
<i>C. solida</i>	♂	Lithuania, Žemaitkiemis	54°14'55"N	23°26'55"E	5.06-09.09.2010	E. Budrys	TNH10-96-1 (NRC)	H118	KJ398911	
<i>C. solida</i>	♂	Norway, Solbergfjell	59°45'32"N	10°02'28"E	11.06.2012	F. Ødegaard	NOCHR264 (NINA)	H119	NOCHR265-13	
<i>C. solida</i>	♀	Finland, Lapinjärvi Vasarankylä	60°38'13"N	26°09'58"E	8.08.2004	J. Paukkunen	GP.72802 (FMNH)	H120	ACUF1518-13	
<i>C. solida</i>	♀	Finland, Loviisa Harmaakallio	60°25'12"N	26°12'40"E	2.07.2009	J. Flinck	GP.64796 (FMNH)	H120	ACUF1517-13	
<i>C. solida</i>	♂	Finland, Somero Talvisilta	60°34'23"N	23°23'20"E	7.06.2008	J. Paukkunen	GP.66671 (FMNH)	H120	ACUF1516-13	
<i>C. solida</i>	♂	Lithuania, Kiemeliai	54°51'30"N	25°01'00"E	20.05-30.08.2010	E. Budrys	TNH10-905-1 (NRC)	H120	KJ398910	
<i>C. solida</i>	♀	Norway, Asakmoen	59°59'06"N	11°06'36"E	27.08.2010	F. Ødegaard	Chrysis162 (NINA)	H120	NOCHR157-13	

.....continued on the next page

TABLE 1. (Continued)

Species	Sex	Locality	Latitude	Longitude	Date	Collector	Voucher ID (depository)	Haplo-type	COI	rRNA
<i>C. solida</i>	♂	Norway, Hoelsand	62°39'23"N	8°40'04"E	2.07.2010	F. Ødegaard	Chrysis003 (NINA)	HI20	NOCHR003-13	
<i>C. solida</i>	♀	Norway, Hoelsand	62°39'22"N	8°40'05"E	8.07.2010	F. Ødegaard	Chrysis156 (NINA)	HI20	NOCHR151-13	
<i>C. solida</i>	♂	Norway, Hoelsand	62°39'22"N	8°40'05"E	8.07.2010	F. Ødegaard	Chrysis157 (NINA)	HI20	NOCHR152-13	
<i>C. solida</i>	♂	Norway, Hoelsand	62°39'22"N	8°40'05"E	8.07.2010	F. Ødegaard	Chrysis160 (NINA)	HI20	NOCHR155-13	
<i>C. solida</i>	♂	Norway, Langoya N	59°00'29"N	9°45'07"E	24.06.2009	O. Gammelmo	NOCHR268 (NINA)	HI20	NOCHR269-13	
<i>C. solida</i>	♂	Norway, Langoya V	59°00'29"N	9°45'22"E	24.06.2009	O. Gammelmo	NOCHR269 (NINA)	HI20	NOCHR270-13	
<i>C. solida</i>	♀	Norway, Leirsjoen	59°53'28"N	12°09'43"E	28.07.2010	F. Ødegaard	Chrysis163 (NINA)	HI20	NOCHR158-13	
<i>C. solida</i>	♀	Norway, Oreiman	62°40'12"N	8°36'01"E	24.06.2001	F. Ødegaard	Chrysis026 (NINA)	HI20	NOCHR026-13	
<i>C. solida</i>	♀	Norway, Orekroken	59°01'59"N	11°00'32"E	22.08.2007	F. Ødegaard	Chrysis147 (NINA)	HI20	NOCHR142-13	
<i>C. solida</i>	♀	Norway, Skipstadkilen	59°03'07"N	10°56'28"E	4.07.2011	F. Ødegaard	Chrysis144 (NINA)	HI20	NOCHR139-13	
<i>C. solida</i>	♂	Norway, Solbergfjell	59°45'34"N	10°02'29"E	8.06.2012	F. Ødegaard	Chrysis007 (NINA)	HI20	NOCHR007-13	
<i>C. solida</i>	♂	Norway, Solbergfjell	59°45'34"N	10°02'29"E	8.06.2012	F. Ødegaard	Chrysis050 (NINA)	HI20	NOCHR050-13	
<i>C. solida</i>	♂	Norway, Solbergfjell	59°45'32"N	10°02'28"E	11.06.2012	F. Ødegaard	NOCHR263 (NINA)	HI20	NOCHR264-13	
<i>C. solida</i>	♀	Sweden, Norberg, Halvarsbenning	60°05'09"N	15°46'09"E	16.06.2007	J. Abenius	V505 (TUZ)	HI20	JX292261	JX292210
<i>C. solida</i>	♂	Lithuania, Bilšiai	55°08'02"N	25°16'15"E	23.05-29.08.2010	E. Budrys	TNH10-676-4 (NRC)	HI21	KJ398912	
<i>C. solida</i>	♂	Lithuania, Bilšiai	55°08'02"N	25°16'15"E	23.05-29.08.2010	E. Budrys	TNH10-1225-1 (NRC)	HI22	KJ398935	
<i>C. solida</i>	♀	Norway, Orod	59°06'58"N	11°26'06"E	20.08.2009	F. Ødegaard	Chrysis150 (NINA)	HI23	NOCHR145-13	
<i>C. solida</i>	♂	Lithuania, Gerkiskės	54°30'41"N	24°10'52"E	9.06-26.08.2009	E. Budrys	TNH09-488-5 (NRC)	HI24	KJ398922	
<i>C. solida</i>	♀	Lithuania, Kiemeliai	54°51'30"N	25°01'00"E	17.05-19.08.2008	E. Budrys	TNH08-1203-1 (NRC)	HI25	KJ398920	
<i>C. solida</i>	♀	Lithuania, Ambraziskiai	55°08'28"N	25°18'06"E	23.05-28.08.2010	E. Budrys	TNH10-830-14 (NRC)	HI26	KJ398916	
<i>C. solida</i>	♂	Lithuania, Perloja	54°13'24"N	24°22'58"E	27.05-22.09.2010	E. Budrys	TNH10-1080-1 (NRC)	HI27	KJ398917	
<i>C. solida</i>	♂	Lithuania, Bilšiai	55°08'02"N	25°16'15"E	10.05-30.08.2009	E. Budrys	TNH09-921-5 (NRC)	HI28	KJ398918	
<i>C. solida</i>	♂	Lithuania, N. Verikiai	54°45'14"N	25°19'08"E	21.05-15.09.2009	A. Košel	TNH09-380-1 (NRC)	HI29	KJ398921	
<i>C. solida</i>	♀	Norway, Hellaasen	59°03'58"N	9°41'40"E	20.08.2010	F. Ødegaard	Chrysis054 (NINA)	HI30	NOCHR054-13	
<i>C. solida</i>	♀	Great Britain, Goring	51°30'45"N	1°06'47"W	2-5.07.1999	C.M.T. Raper	V5220 (TUZ)	HI31	JX292254	JX292204
<i>C. solida</i>	♀	Norway, Utstrandra	59°59'53"N	10°17'17"E	13.07.2011	F. Ødegaard	Chrysis151 (NINA)	HI31	NOCHR146-13	
<i>C. solida</i>	♀	Norway, Utstrandra	59°59'55"N	10°17'19"E	2.08.2011	F. Ødegaard	Chrysis058 (NINA)	HI31	NOCHR058-13	
<i>C. solida</i>	♂	Poland, Piekary	50°02'09"N	19°48'25"E	7.05-27.09.2007	E. Budrys	TNH07-181-1 (NRC)	HI31	KJ398903	
<i>C. solida</i>	♂	Norway, Myra	62°37'12"N	8°53'53"E	2.07.2010	F. Ødegaard	Chrysis161 (NINA)	HI32	NOCHR156-13	
<i>C. solida</i>	♀	Estonia, Tartu	58°23'42"N	26°42'42"E	1.08.2004	V. Soon	V5035 (TUZ)	HI33	JX292230	JX292189

..... continued on the next page

TABLE 1. (Continued)

Species	Sex	Locality	Latitude	Longitude	Date	Collector	Voucher ID (depository)	Haplo-type	COI	rRNA
<i>C. solida</i> *	♂	Germany, Brandenburg	52°49'48"N	14°05'24"E	21.05.2012	C. Schmid-Egger	BC.ZSM.HYM.17472 (ZSM)	H133	GBACU3127-13	
<i>C. solida</i> *	♂	Germany, Brandenburg	52°49'48"N	14°05'24"E	21.05.2012	C. Schmid-Egger	BC.ZSM.HYM.17473 (ZSM)	H133	GBACU3128-13	
<i>C. solida</i> *	♂	Germany, Brandenburg	52°49'48"N	14°05'24"E	21.05.2012	C. Schmid-Egger	BC.ZSM.HYM.17474 (ZSM)	H133	GBACU3129-13	
<i>C. solida</i> *	♀	Germany, Brandenburg	52°49'48"N	14°41'24"E	21.05.2012	C. Schmid-Egger	BC.ZSM.HYM.13902 (ZSM)	H133	GBACU1647-12	
<i>C. sp.</i>	♀	Bulgaria, Hasskovo, Garvanovo	N41°58'38"N	25°27'40"E	6.07.2005	T. Ljubomirov	CCDB-05795-E02 (IBER)	H134	CRABR525-10	
<i>C. sp.</i>	♀	Bulgaria, Sofia, S Kladnitsa	42°31'36"N	23°11'23"E	24.09.1999	T. Ljubomirov	VS027 (TUZ)	H135	KJ398899	
<i>C. sp.</i>	♀	Bulgaria, Hasskovo, N Garvanovo	41°58'38"N	25°27'40"E	6.07.2005	T. Ljubomirov	CCDB-05795-E04 (IBER)	H136	CRABR527-10	
<i>C. sp.</i>	♀	Bulgaria, Hasskovo, N Garvanovo	41°58'38"N	25°27'40"E	6.07.2005	T. Ljubomirov	CCDB-05795-E05 (IBER)	H137	CRABR528-10	
<i>C. sp.</i>	♀	Bulgaria, Hasskovo, N Garvanovo	41°58'38"N	25°27'40"E	6.07.2005	T. Ljubomirov	CCDB-05795-H08 (IBER)	H137	CRABR567-10	
<i>C. sp.</i>	♀	Slovakia, Kopačský ostrov	48°05'45"N	17°09'40"E	5.09.2006	O. Majzlan	VS029 (TUZ)	H137	KJ398925	
<i>C. sp.</i>	♀	Norway, Nedre Timenes	58°09'41"N	8°06'01"E	18.06.2009	F. Ødegaard	Chrysis028 (NINA)	H138	NOCHR028-13	
<i>C. sp.</i>	♂	Norway, Solbergfjell	59°45'32"N	10°02'28"E	8.06.2012	F. Ødegaard	Chrysis118 (NINA)	H138	NOCHR113-13	
<i>C. sp.</i>	♂	Norway, Ornes	61°17'10"N	7°20'28"E	4.07.2011	F. Ødegaard	Chrysis183 (NINA)	H139	NOCHR178-13	
<i>C. sp.</i>	♀	Norway, Smaasetran	62°34'23"N	11°24'43"E	23.07.2007	F. Ødegaard	Chrysis187 (NINA)	H139	NOCHR182-13	
<i>C. sp.</i>	♂	Norway, Smaasetran	62°34'23"N	11°24'43"E	23.07.2007	F. Ødegaard	Chrysis189 (NINA)	H139	NOCHR184-13	
<i>C. sp.</i>	♂	Norway, Smaasetran	62°34'21"N	11°24'45"E	11.07.2010	F. Ødegaard	Chrysis021 (NINA)	H139	NOCHR021-13	
<i>C. sp.</i>	♂	Norway, Stordalsberget	61°35'12"N	9°49'10"E	1.06.2009	F. Ødegaard	Chrysis089 (NINA)	H139	NOCHR089-13	
<i>C. sp.</i>	♂	Finland, Kolari	67°35'10"N	24°14'20"E	9.07.1989	M. Koponen	GP.3907 (FMNH)	H140	ACUFI494-13	
<i>C. sp.</i>	♀	Norway, Stordalsberget	61°35'13"N	9°49'08"E	1.09.2009	F. Ødegaard	Chrysis180 (NINA)	H141	NOCHR175-13	
<i>C. sp.</i>	♀	Sweden, Öland, Persnäs	57°02'47"N	16°55'51"E	20.07.2007	J. Abenius	VS053 (TUZ)	H142	JX292236	JX292195
<i>C. sp.</i>	♀	Finland, Mailla	69°03'36"N	20°45'31"E	14.07.2009	V. Soon	VS210 (TUZ)	H143	JX292251	JX292201
<i>C. sp.</i>	♀	Finland, Enontekiö Anjaloanji	69°10'08"N	21°26'24"E	11.07.2007	R. Jussila	GP.86304 (FMNH)	H144	ACUFI497-13	
<i>C. sp.</i>	♀	Finland, Rymättylä	60°22'28"N	21°56'56"E	21.07.1971	A. K. Merisuo	VS130 (FMNH)	H145	JX292240	JX292198
<i>C. sp.</i>	♂	Norway, Lilleby	59°46'44"N	9°55'59"E	1.05.2012	F. Ødegaard	Chrysis132 (NINA)	H145	NOCHR127-13	
<i>C. sp.</i>	♂	Norway, Solbergfjell	59°45'34"N	10°02'29"E	28.06.2012	F. Ødegaard	Chrysis004 (NINA)	H145	NOCHR004-13	
<i>C. sp. 1</i>	♀	Lithuania, Visoriai	54°45'11"N	25°15'47"E	21.07.2010	E. Budrys	TNH10-7-0 (NRC)	H146	KJ398882	
<i>C. sp. 1*</i>	♀	Germany, Rhineland Palatinate	49°39'04"N	8°12'40"E	3.06.2007	G. Reder	BC.ZSM.HYM.07998 (ZSM)	H147	FBACB398-11	

... continued on the next page

TABLE 1. (Continued)

Species	Sex	Locality	Latitude	Longitude	Date	Collector	Voucher ID (depository)	Haplo-type	COI	rRNA
<i>C. sp. 1</i>	♀	Portugal, Azores, Flores, Fajã de Lopo Vaz	39°22'28"N	31°12'16"W	21.09.2009	N. Fritzen	VS211 (TUZ)	HI48	KJ398931	
<i>C. sp. 1</i>	♂	Norway, Lade	63°26'49"N	10°26'02"E	23.06.2010	F. Ødegaard	Chrysis112 (NINA)	HI49	NOCHR107-13	
<i>C. sp. 1</i>	♀	Bulgaria, Plovdiv, Plovdiv	42°09'06"N	24°48'10"E	23.09.2003	O. Todorov	CCDB-05794-G05 (IBER)	HI50	CRABR457-10	
<i>C. sp. 1</i>	♀	Turkey, Isparta, W Çiflik	37°44'27"N	30°49'43"E	29.07.2008	T. Ljubomirov	CCDB-05794-G06 (IBER)	HI50	CRABR458-10	
<i>C. sp. 2*</i>	♀	Germany, Thuringia	51°09'14"N	11°04'19"E	19.07.2011	F. Burger	BC ZSM HYM 12747 (ZSM)	HI51	GBACU2487-13	
<i>C. sp. 2*</i>	♀	Germany, Brandenburg	52°33'36"N	14°28'48"E	4.08.2012	C. Schmid-Egger	BC ZSM HYM 15251 (ZSM)	HI52	GBACU2236-13	
<i>C. sp. 2</i>	♀	Slovakia, Kopátsky ostrov	48°05'45"N	17°09'40"E	30.09.2006	O. Majzlan	VS172 (TUZ)	HI53	KJ398923	
<i>C. sp. 2</i>	♀	Spain, Teruel, Albarracin	40°24'26"N	1°26'33"W	22.04.1995	W. Linsenmaier	VS063 (NMLS)	HI53	KJ398928	
<i>C. sp. 2</i>	♀	Belarus, Giry	54°38'31"N	26°12'03"E	12.06.2010	S. Orlovskiytė	SO2010-06-12-1 (NRC)	HI54	KJ398880	
<i>C. sp. 2</i>	♀	Belarus, Giry	54°38'31"N	26°12'03"E	24.06-2.07.2011	S. Orlovskiytė	SO2011-06-24-1 (NRC)	HI54	KJ398886	
<i>C. sp. 2</i>	♀	Belarus, Giry	54°38'31"N	26°12'03"E	17.07.2010	S. Orlovskiytė	SO2010-07-17 (NRC)	HI55	KJ398881	
<i>C. sp. 2</i>	♀	Bulgaria, Blagoevgrad, S Paril	41°25'58"N	23°40'39"E	24.06.2009	T. Ljubomirov	CCDB-05795-G12 (IBER)	HI56	CRABR559-10	
<i>C. subcorticea</i>	♂	Finland, Lieksa Koli	63°03'36"N	29°52'40"E	4.08.2010	M. Raekunmas	GP.69401 (FMNH)	HI57	ACUF1503-13	
<i>C. subcorticea</i>	♀	Finland, Rantasalmi Linnasaari	62°06'22"N	28°31'19"E	19.07.2010	J. Paukkunen	GP.69743 (FMNH)	HI57	ACUF1522-13	
<i>C. subcorticea</i>	♂	Finland, Tammissaari Koski	60°10'59"N	23°17'53"E	24.05.2008	J. Paukkunen	GP.66648 (FMNH)	HI57	ACUF1520-13	
<i>C. subcorticea</i>	♂	Finland, Äetsä Leikkuu	61°20'46"N	22°45'58"E	16.07.2001	J. Paukkunen	GP.72821 (FMNH)	HI57	ACUF1519-13	
<i>C. subcorticea</i>	♀	France, Queyras	44°43'59"N	6°49'02"E	22-23.07.1998	O. Niehuis & Schulmeister	S.ON066 (ON)	HI57	JX292214	HM071073
<i>C. subcorticea</i>	♂	Norway, Lilleby	59°46'44"N	9°55'59"E	8.05.2012	F. Ødegaard	NOCHR266 (NINA)	HI57	NOCHR267-13	
<i>C. subcorticea</i>	♀	Sweden, Öland, Persnäs	57°02'47"N	16°55'51"E	20.07.2007	J. Abenius	VS500 (TUZ)	HI57	JX292257	JX292207
<i>C. subcorticea</i>	♀	Estonia, Võhunnõmme	59°15'02"N	26°35'43"E	15.07.2003	V. Soon	VS039 (TUZ)	HI58	JX292234	JX292193
<i>C. subcorticea</i>	♂	Norway, Solbergfjell	59°45'34"N	10°02'29"E	28.06.2012	F. Ødegaard	Chrysis063 (NINA)	HI59	NOCHR063-13	
<i>C. terminata</i>	♀	Lithuania, Tilže	55°39'37"N	26°33'57"E	7.08.2004	V. Soon	VS166 (TUZ)	HI60	JX292247	JX292200
<i>C. terminata</i>	♀	Bulgaria, Boyana	42°38'26"N	23°16'50"E	1.05.2002	T. Ljubomirov	CCDB-05794-F12 (IBER)	HI61	CRABR452-10	
<i>C. terminata</i>	♀	Bulgaria, N Gorna Breznitsa	41°46'54"N	23°04'30"E	15.08.2003	T. Ljubomirov	CCDB-05794-H07 (IBER)	HI62	CRABR471-10	
<i>C. terminata</i>	♀	Belarus, Giry	54°38'31"N	26°12'03"E	15.07.2010	S. Orlovskiytė	SO2010-07-15 (NRC)	HI63	KJ398879	
<i>C. terminata</i>	♀	Bulgaria, Sofia, W Baykalsko	42°23'46"N	22°48'18"E	3.05.2010	T. Ljubomirov	CCDB-05795-H06 (IBER)	HI63	CRABR565-10	
<i>C. terminata</i>	♀	Bulgaria, Yurukovo	41°58'56"N	23°38'07"E	30.06.2004	O. Todorov	CCDB-05795-G10 (IBER)	HI63	CRABR557-10	
<i>C. terminata*</i>	♀	Germany, Thuringia	51°00'50"N	11°20'24"E	22.05.2010	F. Burger	BC ZSM HYM 12738 (ZSM)	HI63	GBACU2478-13	

... continued on the next page

TABLE 1. (Continued)

Species	Sex	Locality	Latitude	Longitude	Date	Collector	Voucher ID (depository)	Haplo-type	COI	rRNA
<i>C. terminata</i> *	♀	Germany, Thuringia	51°13'59"N	11°19'23"E	18.04.2011	F. Burger	BC ZSM HYM 12739 (ZSM)	H163	GBACU2479-13	
<i>C. terminata</i> *	♂	Germany, Thuringia	51°13'19"N	10°52'30"E	15.06.2011	F. Burger	BC ZSM HYM 12749 (ZSM)	H163	GBACU2489-13	
<i>C. terminata</i> *	♂	Germany, Thuringia	51°13'59"N	11°19'23"E	7.07.2011	F. Burger	BC ZSM HYM 12740 (ZSM)	H163	GBACU2480-13	
<i>C. terminata</i> *	♂	Germany, Thuringia	51°13'59"N	11°19'23"E	7.07.2011	F. Burger	BC ZSM HYM 12741 (ZSM)	H163	GBACU2481-13	
<i>C. terminata</i>	♀	Norway, Heggenes	59°26'24"N	8°46'59"E	5.06.2009	F. Ødegaard	Chrysis102 (NINA)	H163	NOCHR097-13	
<i>C. terminata</i>	♀	Norway, Heggenes	59°26'24"N	8°46'59"E	5.06.2009	F. Ødegaard	Chrysis105 (NINA)	H163	NOCHR100-13	
<i>C. terminata</i>	♀	Norway, Heggenes	59°26'24"N	8°46'59"E	3.07.2009	F. Ødegaard	Chrysis101 (NINA)	H163	NOCHR096-13	
<i>C. terminata</i>	♀	Norway, Lilleby	59°46'44"N	9°53'59"E	1.05.2012	F. Ødegaard	Chrysis109 (NINA)	H163	NOCHR104-13	
<i>C. terminata</i>	♂	Norway, Nedre Timenes	58°09'41"N	8°06'01"E	25.07.2009	F. Ødegaard	Chrysis041 (NINA)	H163	NOCHR041-13	
<i>C. terminata</i>	♀	Sweden, Ösmo	58°56'20"N	17°49'56"E	15.04.2007	J. Abenius	VSS03 (TUZ)	H163	JX292259	JX292209
<i>C. terminata</i>	♀	Norway, Heggenes	59°26'24"N	8°46'59"E	5.06.2009	F. Ødegaard	Chrysis111 (NINA)	H164	NOCHR106-13	
<i>C. terminata</i>	♂	Ukraine, Kiev, Holosiiv Raion	50°19'25"N	30°33'33"E	17.07.2005	A. Drozdovskaya	VSO26 (TUZ)	H165	JX292223	JX292182
<i>C. terminata</i>	♀	Bulgaria, Sofia, Simeonovo	42°37'12"N	23°19'50"E	25.05.2008	T. Ljubomirov	CCDB-05795-F07 (IBER)	H166	CRABR542-10	
<i>C. terminata</i>	♀	Bulgaria, Sofia, Potop	42°44'56"N	23°39'31"E	15.05.2002	S. Lazarov	CCDB-05795-H05 (IBER)	H167	CRABR564-10	
<i>C. terminata</i>	♀	Great Britain, Goring	51°30'45"N	1°06'47"W	13-17.06.1999	C.M.T. Raper	VS215 (TUZ)	H168	JX292253	JX292203
<i>C. terminata</i>	♀	Bulgaria, Sofia, Sofia	42°41'45"N	23°19'44"E	16.04.2009	T. Ljubomirov	CCDB-05795-G11 (IBER)	H169	CRABR558-10	
<i>C. terminata</i>	♀	Bulgaria, S Stara Kressna	41°44'56"N	23°09'29"E	3.05.2003	M. Langourov	CCDB-05795-F10 (IBER)	H170	CRABR545-10	
<i>C. terminata</i>	♀	Bulgaria, E Gorno Ossenovo	42°02'32"N	23°23'16"E	6.07.2002	T. Ljubomirov	CCDB-05794-G07 (IBER)	H171	CRABR459-10	
<i>C. terminata</i>	♂	Bulgaria, S Krupnik	41°47'30"N	23°04'03"E	5.07.2003	T. Ljubomirov	CCDB-05794-F09 (IBER)	H172	CRABR449-10	
<i>C. terminata</i>	♀	Bulgaria, Sofia, Slatina	42°41'00"N	23°21'37"E	29.04.2003	T. Ljubomirov	CCDB-05794-G08 (IBER)	H173	CRABR460-10	
<i>C. terminata</i> *	♀	France, Rhone-Alpes	46°40'21"N	7°06'41"E	15.06.2013	M. Balke & co.	GBOL 01977 (ZSM)	H174	GBCOU359-13	
<i>C. terminata</i>	♀	Italy, N San Sebastiano	41°56'43"N	13°45'13"E	19.06.2011	T. Ljubomirov	CCDB-12229-C11 (IBER)	H175	CRABR1650-11	
<i>C. terminata</i>	♀	Italy, Pescasseroli	41°48'34"N	13°47'27"E	27.06.2011	T. Ljubomirov	CCDB-12233-B04 (IBER)	H175	CRABR2011-11	
<i>C. vanlithi</i>	♀	Norway, Asmaloy	59°03'07"N	10°56'28"E	5.07.2013	F. Ødegaard	NOCHR273 (NINA)	H176	NOCHR274-13	
<i>C. vanlithi</i>	♀	Switzerland, Ayer	46°11'24"N	7°35'40"E	25.08.1999	W. Linsenmaier	VS070 (NMLS)	H177	KJ398929	
<i>C. longula aeneopaca</i>	♀	Russia, Chita Oblast, Kunaleja	50°25'29"N	109°45'51"E	22.08.1998	A. Anichtchenko	VS033 (TUZ)	H178	JX292228	JX292187
<i>C. graelsii</i>	♀	Estonia, Vellavere	58°15'45"N	26°24'40"E	25.06.2003	V. Soon	VS162 (TUZ)		JX292244	HM071079
<i>C. indigolea</i>	♀	Germany, Messel	49°55'37"N	8°45'27"E	4.06.1998	O. Niehuis	ON050 (ON)		JX292211	HM071094

TABLE 2. Primers used to amplify and sequence the mitochondrial COI gene. Position numbering is based on the *Primeuchroeus* sp. mitochondrial gene fragment (GenBank accession no. DQ302101.1), f/r forward or reverse primer.

Gene	Primer	f/r	Sequence (5'-3')	Position	Source
tRNA ^{Met}	Kuld6R	f	TTTATCGWYAGGGTATGAAC	3158	this study
COI	LepF1-chrys	f	TCAACWAATCATAARGATATTGG	3443	Hebert <i>et al.</i> 2004 modified
	AP-L-2013	f	TATAGTTATACCATTTTAATTG	3622	Pedersen 1996
	AP-L-2013chrys	f	TATAGTWATACCWTTTATAATYGG	3622	Pedersen 1996 modified
	COI2Chr2-f	f	TACTCGGGCTTATTTTACTTCAG	4318	this study
	KuldCO1F	r	AATCAAATCTYATATTATTYATTCG	3729	this study
	AP-H-2650chrys	r	ACAGTAAAYATATGATGWGCTC	4302	Pedersen 1996 modified
	AP-H-2650	r	TCCGACTGTAAATATGTGATGTGCTC	4306	Pedersen 1996
	A2590	r	GCTCCTATTGATARWACATARTGRAAATG	4572	Normark <i>et al.</i> 1999
COII	COI2Chr2-r	r	CGTCCAAATTACCTCAATTATATG	5231	this study
COII	COI2Chr4-r	r	AAAATTTGTAATGATGGGATAGC	5284	this study

Obtained rRNA sequences consisted of the nearly complete sequence of 16S rRNA, the complete sequence of tRNA^{Val}, the complete sequence of 12S rRNA and part of the ND4 gene. The rRNA gene sequences varied considerably in length (2017–2057 bp) due to numerous indel events.

Nearly all haplotypes clustered with conspecific haplotypes forming well supported monophyletic clades according to the neighbour-joining (NJ) K2P analysis (Figs 1, 2). However, relationships between these clades remained unsupported according to the bootstrapping results. Some of the unidentified samples formed two distinct clusters that were genetically distant from all other included species according to the branch lengths. Although further analysis is needed to gain confidence in their status, we treat these two clusters as separate species and name them as *C. sp. 1* and *C. sp. 2* hereafter in order to avoid confusion with other species. Additional clusters were formed by unidentified samples near *C. ignita* and *C. impressa*, but due to the relatively short branch lengths we hesitate to treat these as separate species and leave them as *C. sp.* All included published barcodes from the Barcode of Life Datasystems website grouped within included species and hence we treat them as members of these species hereafter ignoring their original identification. Only *C. mediata*, *C. solida* and *C. pseudobrevitarsis* samples did not cluster according to the prescribed species and formed paraphyletic groups instead.

Maximum intraspecific divergence remained below 2% in all species except *C. pseudobrevitarsis*, *C. schencki* and *C. fulgida*, where the divergence was 4.06%, 2.08% and 2.01%, respectively (Table 3). *C. pseudobrevitarsis* formed a paraphyletic group with respect to *C. brevitarsis*, while several of its samples were also relatively distant to each-other. *C. schencki* clustered into two relatively distinct clades with maximum genetic divergence within each clade of 0.61% and 1.12% and minimal divergence between them of 1.85%. Also, *C. fulgida* grouped in two clusters with maximum genetic divergences of 0.45% and 0.92% and minimal divergence between these clusters of 0.91%.

Minimal interspecific divergence was mostly above 2% except in *C. terminata* (1.85%) and five other species in two clusters: *C. ignita* (0.61%) / *C. impressa* (0.45%) / *C. sp.* (0.45%) and *C. mediata* (0.15%) / *C. solida* (0.15%).

Aligning mitochondrial rRNA genes for phylogenetic analysis with Bali-Phy produced a 2149 positions long maximum a posteriori (MAP) alignment. However, fewer than 50% of those positions were supported with posterior probabilities over 0.95. Removing poorly supported positions with probability below 0.95 resulted in a 1437 bp alignment, which was used as a “limited dataset” in phylogenetic analysis.

Maximum Parsimony, Maximum Likelihood and Bayesian analyses of the alignment consisting of only well supported positions produced the phylogeny presented in Figure 3. The topologies of the phylogenetic trees produced by the three methods were nearly identical and all were relatively well supported. Nevertheless, most of the major nodes gained high support except a few, which were sufficiently supported only by the Bayesian analysis. Ten species that were represented by more than one sample (*C. iris*, *C. fulgida*, *C. ruddii*, *C. subcoriacea*, *C. longula*, *C. angustula*, *C. corusca*, *C. terminata*, *C. schencki* and *C. leptomandibularis*) formed monophyletic

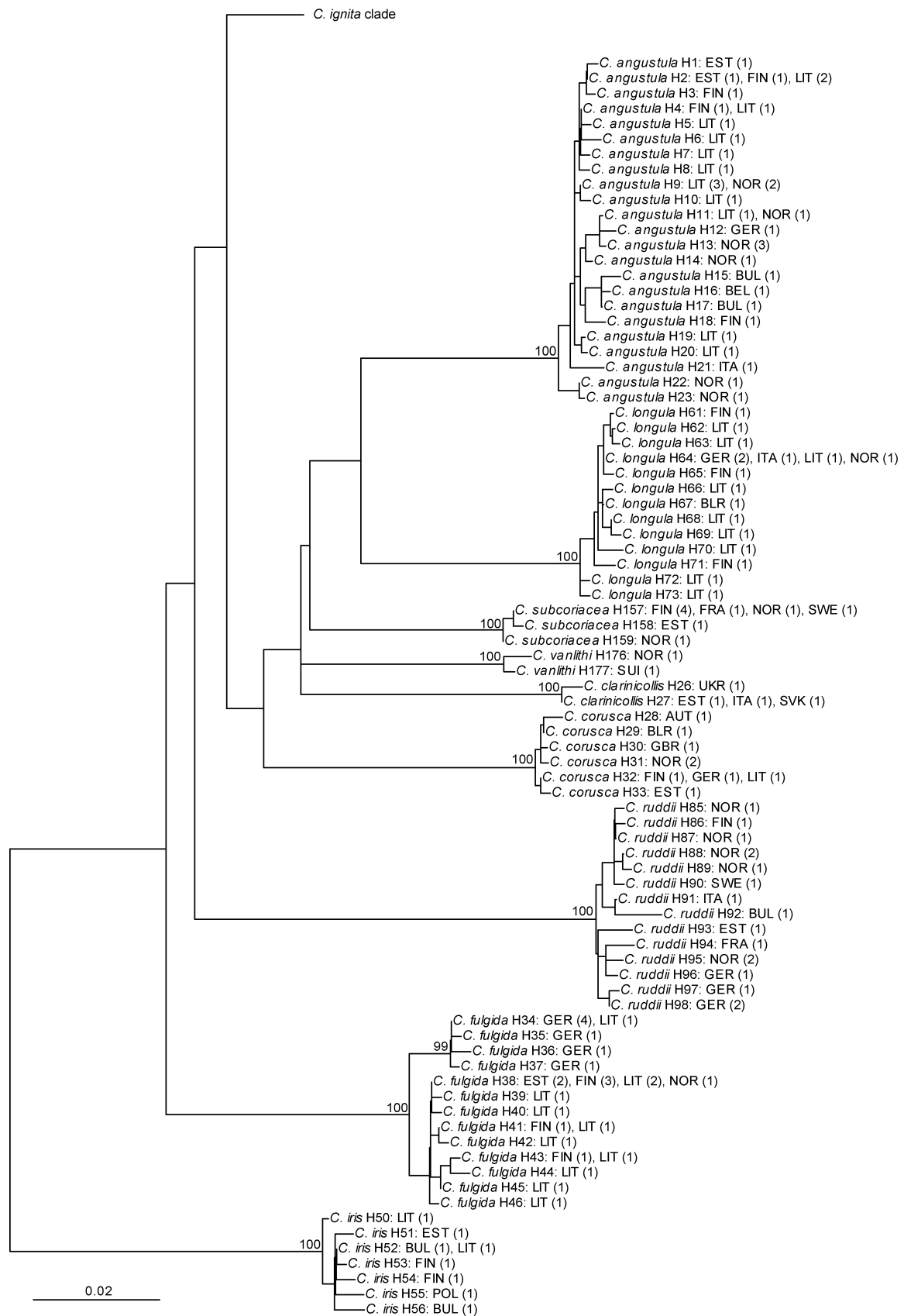


FIGURE 1. Kimura-2-parameter neighbour joining tree of all ingroup haplotypes: the *C. fulgida*, *C. ruddii* and *C. longula* clades. Bootstrap values below 90 are not shown. For each haplotype the species name and haplotype number is given followed by a list of countries (three digit code) where the haplotype is found, with the number of sequences from each country in parentheses (Table 1).

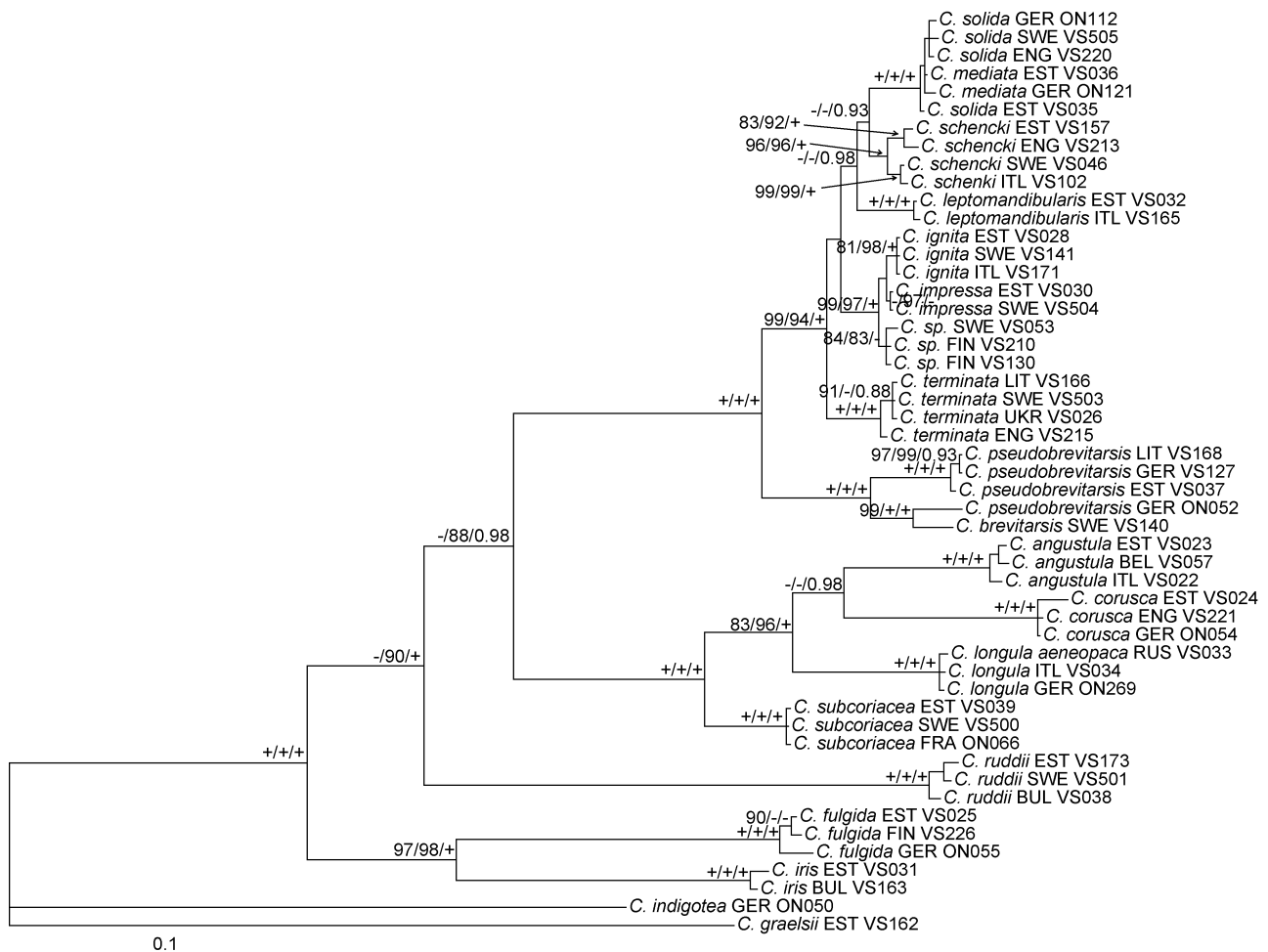


FIGURE 3. Phylogeny of Northern European species in the *C. ignita* group based on 2187 bp: COI (750 bp) and positions of the rRNA locus that could be aligned with strong posterior probability (1437 bp). The topology is taken from the Bayesian analysis; support values indicate bootstrap values for maximum-parsimony and maximum-likelihood, and posterior probabilities for the Bayesian analysis, respectively. ML and Bayesian analyses were both performed using the GTR + I + G sequence evolution model. Bootstrap values below 75 and posterior probabilities below 0.90 are indicated with minus (-). Bootstrap and posterior probability values indicating 100 percent reliability are indicated with plus (+).

clades. Moreover, all of these clades were well supported with all three methods. One species, namely *C. pseudobrevitarsis*, appears to be paraphyletic. Three samples of *C. pseudobrevitarsis* formed a separate well supported clade, with genetic divergence within the clade below 0.6%, while one specimen initially identified as *C. pseudobrevitarsis* grouped together with another species, *C. brevitarsis*. Relationships between species remained poorly resolved only in two highly supported clades. One of these clades consisted of *C. ignita*, *C. impressa* and *C. sp.*; although these three taxa grouped into separate clades, these were only sufficiently supported by one or two methods, but never by all three. The other clade included samples of *C. mediata* and *C. solidus*, which did not group according to their initial identification with any of the methods used.

A phylogenetic tree based on the full alignment is presented in Figure 4. Despite the risk of obtaining a misleading result from the ambiguous alignment, the general topology of this tree was the same as obtained using the reduced alignment. Moreover, support values for the major clades were higher using the full alignment. In common with the analysis based on only well-aligned positions of rRNA genes, the same ten species formed well supported clades and *C. pseudobrevitarsis* appeared paraphyletic. Including data from ambiguously aligned positions also improved support for the clades consisting of *C. ignita*, *C. impressa* and *C. sp.*, though resolution within the clade consisting of *C. mediata* and *C. solidus* did not improve considerably.

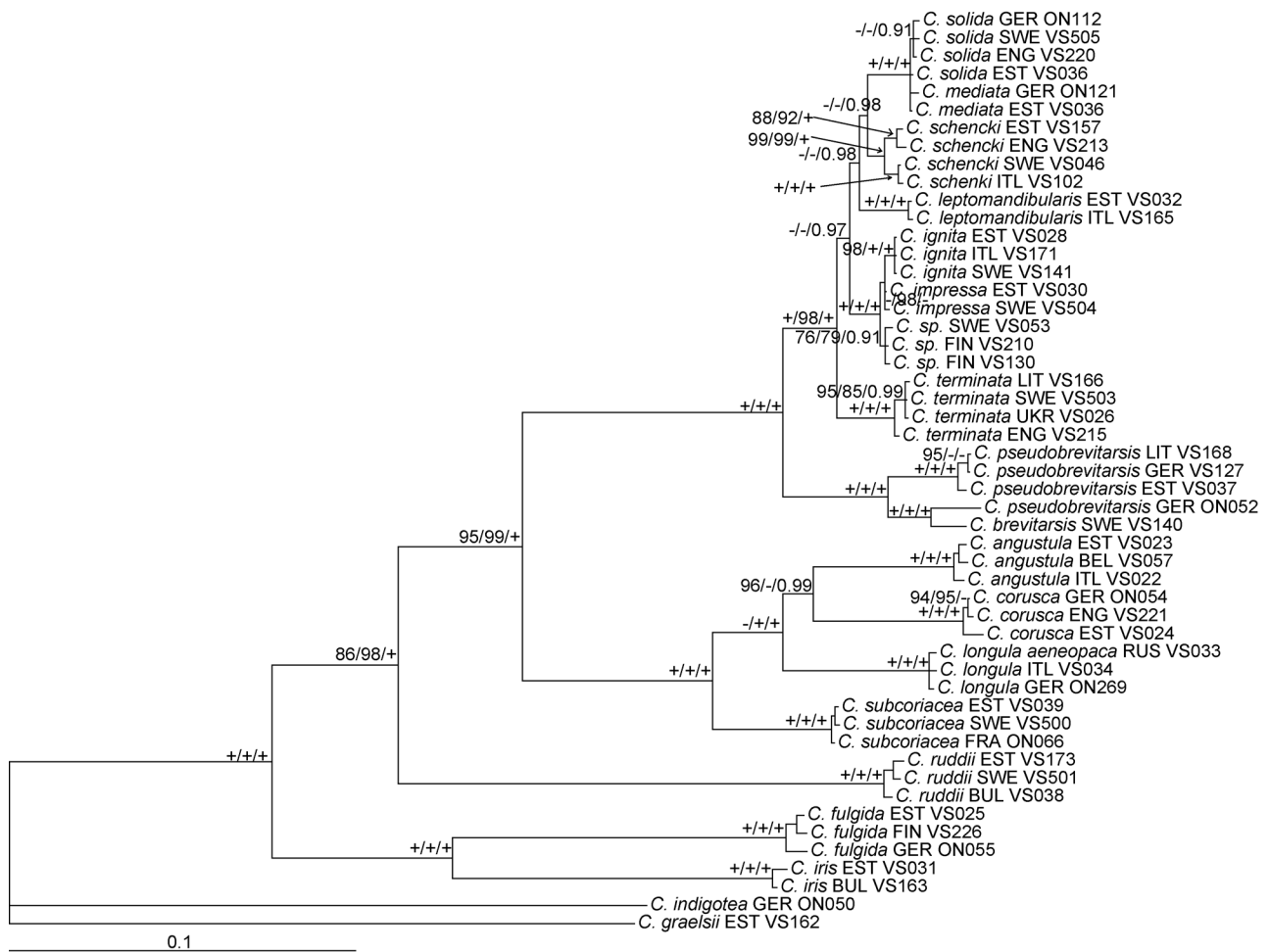


FIGURE 4. Phylogeny of Northern European species in the *C. ignita* group based on 2899 bp: COI (750 bp) and complete alignment of the rRNA locus (2149 bp). The topology is taken from the Bayesian analysis; support values indicate bootstrap values for maximum-parsimony and maximum-likelihood, and posterior probabilities for the Bayesian analysis, respectively. ML and Bayesian analyses were both performed with the GTR + G sequence evolution model. Bootstrap values below 75 and posterior probabilities below 0.90 are indicated with minus (-). Bootstrap and posterior probability values indicating 100 percent reliability are indicated with plus (+).

Discussion

While the species as well as specimen identification in the *Chrysis ignita* group remains difficult using external morphology, most of the species analysed in this study can be reliably identified using the DNA barcoding approach due to the sufficient difference in intra- and inter-specific genetic divergence present in the COI gene. Some species exhibited very low intraspecific genetic divergence. For example, all available sequences of *C. ignita* belonged to the same haplotype despite relatively wide geographical sampling (Table 1), and all sequences of *C. impressa* belonged to just two haplotypes. While some species (e.g. *C. pseudobrevitarsis*, *C. schencki*) had relatively high intraspecific divergence they could still be identified using the “Best match” or “Best close match” methods for barcode identification (Meier *et al.* 2006), unless new genetically distant haplotypes are identified. However, the low interspecific genetic divergence between *C. mediata* and *C. solida* meant that these two species could not be reliably identified using standard COI barcoding methods. Moreover, additional mitochondrial markers did not enable these species to be separated.

The deep genetic intraspecific divergence of *C. pseudobrevitarsis* and *C. schencki* may indicate hitherto unknown cryptic species currently lumped together under a single species name. That is also consistent with *C. pseudobrevitarsis* forming a paraphyletic group with respect to *C. brevitarsis* and the two distinct clusters of *C. schencki* appearing to be sympatric rather than isolated populations (Fig. 2). Deep intraspecific genetic divergence

in *C. fulgida* may however reflect long-term isolation between different populations of a single species since maximal divergence within two of the clusters is higher than the minimal divergence between them. Moreover, these two clusters appear to be largely allopatric: one originating from Central Europe (Germany) and the other from Northern Europe (Estonia, Finland, Norway), with the clusters coexisting in Lithuania. The reasons for the high intraspecific genetic divergence in these three species can hopefully be resolved with additional genetic and morphological analysis, and the inclusion of more samples.

TABLE 3. Maximum intraspecific divergence and minimal interspecific divergence for each species. Kimura-2-Parameter (K2P) (Kimura 1980) corrected distances were calculated with TaxonDNA (Meier *et al.* 2006). The species with the minimal interspecific distance is given in the fourth column.

	Max. intrasp. distance	Min. intersp. distance	Species with min. intersp. distance
<i>Chrysis angustula</i>	1.5	6.68	<i>Chrysis longula</i>
<i>Chrysis brevitarsis</i>	0.15	2.24	<i>Chrysis pseudobrevitarsis</i>
<i>Chrysis clarinicollis</i>	0.22	7.53	<i>Chrysis subcoriacea</i>
<i>Chrysis corusca</i>	0.61	8.31	<i>Chrysis vanlithi</i>
<i>Chrysis fulgida</i>	2.01	8.86	<i>Chrysis pseudobrevitarsis</i>
<i>Chrysis ignita</i>	N/A	0.61	<i>Chrysis impressa</i>
<i>Chrysis impressa</i>	0.15	0.45	<i>Chrysis sp.</i>
<i>Chrysis iris</i>	0.97	9.04	<i>Chrysis fulgida</i>
<i>Chrysis leptomandibularis</i>	0.3	2.32	<i>Chrysis sp.</i>
<i>Chrysis longula</i>	0.92	6.68	<i>Chrysis angustula</i>
<i>Chrysis mediata</i>	0.3	0.15	<i>Chrysis solida</i>
<i>Chrysis pseudobrevitarsis</i>	5.21	2.24	<i>Chrysis brevitarsis</i>
<i>Chrysis ruddii</i>	1.85	9.9	<i>Chrysis subcoriacea</i>
<i>Chrysis schencki</i>	2.56	2.09	<i>Chrysis sp. 1</i>
<i>Chrysis solida</i>	1.07	0.15	<i>Chrysis mediata</i>
<i>Chrysis sp.</i>	0.92	0.45	<i>Chrysis impressa</i>
<i>Chrysis sp. 1</i>	1.53	2.09	<i>Chrysis schencki</i>
<i>Chrysis sp. 2</i>	1.3	6.05	<i>Chrysis sp.</i>
<i>Chrysis subcoriacea</i>	0.3	6.34	<i>Chrysis vanlithi</i>
<i>Chrysis terminata</i>	1.53	1.85	<i>Chrysis impressa</i>
<i>Chrysis vanlithi</i>	0.61	6.34	<i>Chrysis subcoriacea</i>

The previously unidentified specimens grouped into three separate clades (Fig. 2), two of which formed distinct clades with sufficiently high interspecific divergence from all other species, while the remaining unidentified specimens formed a poorly resolved clade which also included *C. ignita* and *C. impressa*. We consider that the former two clades represent unrecognised cryptic species and thus refer to them as *C. sp. 1* and *C. sp. 2*. It is possible that either of these species is already named but that the name is currently synonymised; thus further morphological study of these species and of the type materials of known species is required prior to describing them as new.

It is possible that the unidentified specimens placed in the clade of *C. ignita* and *C. impressa* also represent unrecognised cryptic species, but the low level of divergence between all species in this clade makes it difficult to resolve reliably. Curiously, the divergence between the numerous unidentified samples in this clade exceeds the interspecific divergence of the two known species in the clade. Although phylogenetic analysis with additional DNA sequences enabled us to resolve this group better than with COI barcode alone, the resulting three clades were well supported only by some of the analysis methods.

The general topologies of phylogenetic trees generated in this study correspond relatively well with those in Soon & Saarma (2011), and include the same four major clades. This is unsurprising since the genes and methods

used for analysis in both studies are largely identical. However, inclusion of the COI gene fragment in this study affected the phylogenetic signal to some extent, resulting in slightly better and somewhat different resolution of the relationships between species within the *ignita*-clade. Nevertheless, the relationships between these species remain poorly resolved.

Although the study by Soon & Saarma (2011) suggested the existence of some unknown species and a distinct status for a few disputable species, their analysis did not allow robust taxonomic conclusions to be drawn since only single specimens per species were included. Analysing more samples from different geographic locations now enables us to demonstrate the specific status of the included species. On the basis of adequate interspecific genetic distances as well as the formation of well supported apical clades consisting of specimens with the same identity, we propose *C. iris*, *C. fulgida*, *C. ruddii*, *C. subcoriacea*, *C. longula*, *C. angustula*, *C. corusca*, *C. terminata*, *C. leptomandibularis*, *C. ignita*, *C. schencki*, *C. vanlithi*, *C. clarinicornis*, *C. brevitarsis*, *C. sp. 1* and *C. sp. 2* to be considered as well established species.

The presence of an unresolved clade consisting of *C. mediata* and *C. solida* (Figs 2–4) reflects the fact that these species exhibit almost identical morphology. Morphological similarities have given rise to confusion about the rank of these two species, the latter being treated either as a subspecies (Linsenmaier 1997 (as *C. mediata fenniensis*)) or a synonym (Kunz 1994) of the former, or both treated as separate species (Smitsen 2010). Although our results favour synonymization of these two names, we suggest that further study should be undertaken before doing so. The strongest argument for treating these taxa as separate species is their specialisation on host species. *C. mediata* is known to be a specialised nest parasite of the ground-nesting potter wasps from the genus *Odynerus* Latreille (Linsenmaier 1959a; Smitsen 2001; Wickl 2001), while *C. solida* is known to be a nest parasite of wood-nesting wasp species *Ancistrocerus parietinus* (Linnaeus) (Stefan-Dewenter & Leschke 2003), *A. gazella* (Panzer) (Smitsen 2010) and *Symmorphus bifasciatus* (Linnaeus) (Wickl 2001). These two taxa need further study including not only additional molecular data, but also detailed study of their biology and morphology.

Cases where species remained unresolved or did not accord with the existing taxonomy might also be the result of incomplete lineage sorting or horizontal gene transfer. These are plausible explanations since such species are likely to have split from each other recently. Confirming the identity of the most recently split species with DNA sequence analysis requires additional analysis with more characters from both mtDNA and nuclear loci. Evidently, analysis based on nuclear markers is needed to gain further insight into the detailed phylogeny of the *Chrysis ignita* species group. Nevertheless, a good overlap between the morphological identification and the molecular data analysis based on mitochondrial genes indicates that in most cases nuclear markers may not eventually be necessary for delimiting species of this group.

Our results, derived from analysis of mitochondrial loci, strongly disagree with the conservative approach presented by Kimsey & Bohart (1990), Mingo (1994) and Kunz (1994). Rather, our results support the more exhaustive treatment of the *C. ignita* species group as proposed by W. Linsenmaier (1997), O. Niehuis (2001), P. Rosa (2006) and J. van der Smitsen (2010). Moreover, the existence of new cryptic species is proposed, demonstrating the usefulness of mtDNA analysis in studies of this species group as well as the necessity of confirming specimen identifications using COI barcodes.

Acknowledgements

We are grateful to Denise Wyniger (Natur Museum, Luzern), Sándor Csósz (Hungarian Natural History Museum), Hege Vårdal (Swedish Museum of Natural History), Claire Villemant (Muséum National d'Histoire Naturelle, Paris) and Viola Richter (Berlin Museum of Natural History) for assistance and specimen loans. We are also indebted to Oliver Niehuis, Johan Abenius, Alina Drozdovskaya, Alexander Anischenko, Paolo Rosa, Marc Pollet, Christian Schmid-Egger, Chris Raper and Sven Hellqvist, who collected and/or loaned specimens for DNA analysis. We thank the three anonymous reviewers and Arkady Lelej for their critical and thoughtful comments and John Davison for correcting the English of the manuscript.

This study was supported by the Estonian Ministry of Education and Research (target-financed project SF0180122s08 and institutional research funding grant no. IUT20-33), the Estonian Science Foundation (grants no. 6598, 7558 and 9174) and the European Union through the European Regional Development Fund (Center of Excellence FIBIR). A part of the study was supported by the EC Framework Programme 7, project SCALES

(contract No 226852), the Taxonomy Initiative of the Norwegian Biodiversity Information Centre, project ACUNOR, Canadian Centre for DNA Barcoding, University of Guelph and the Research Council of Lithuania (contracts MIP-115/2010 and MIP-033/2011).

References

- Abeille de Perrein, E. (1879) ["1878"] Synopsis critique et synonymique des Chrysidés de France. *Annales de la Société linnéenne de Lyon*, 26, 1–108.
- Bischoff, H. (1913) Hymenoptera. Fam. Chrysididae. *Genera insectorum*, 151, 1–86.
- Bischoff, H. (1934) Die Ökologische Rassenkreis der *Chrysis ignita* L. *Entomologische Beihefte aus Berlin-Dahlem*, 1, 72–75.
- Bohart, R.M. & French, L.D. (1986) Designation of Chrysidid Lectotypes in the Mocsáry Collection at the Hungarian National Museum, Budapest (Hymenoptera: Chrysididae). *Pan-Pacific Entomologist*, 62, 340–343.
- Bohart, R.M. & Kimsey, L.S. (1982) Chrysididae in America North of Mexico. *Memoirs of the American Entomological Institute* 33, 266 pp.
- Buysson, R. du (1891–1896) Les Chrysidés. In: André, E. (Ed.), *Species des Hyménoptères d'Europe & d'Algérie. Tome Sixième*. V^e Duboscq, Paris, I–XII + 13–758 + 64 unnumbered pages + 32 pls. (1891) 1–88, (1892) 89–208, (1893) 209–272, (1894) 273–400, (1895) 401–624, (1896) 625–756 + 1*–22*, (1891–1896) 64 unnumbered pages + 32 pls.
- Carpenter, J.M. & Wheeler, W.C. (1999) Towards simultaneous analysis of morphological and molecular data in Hymenoptera. *Zoologica Scripta*, 28, 251–260.
<http://dx.doi.org/10.1046/j.1463-6409.1999.00009.x>
- Carr, M., Young, J.P.W. & Mayhew, P.J. (2010) Phylogeny of bethylid wasps (Hymenoptera: Bethyridae) inferred from 28S and 16S rRNA genes. *Insect Systematics & Evolution*, 41, 55–73.
<http://dx.doi.org/10.1163/187631210x486995>
- Christ, J.L. (1791) *Naturgeschichte, Klassifikation und Nomenclatur der Insekten vom Bienen, Wespen und Ameisengeschlecht: als der fünften Klasse fünfte Ordnung des Linneischen Natursystems von den Insekten, Hymenoptera: mit häutigen Flügeln*. Hermannischer Buchhandlung, Frankfurt am Main, 535 pp. + 60 pls.
- Dahlbom, A.G. (1845) *Dispositio Methodica Specierum Hymenopterorum, secundum Familias Insectorum naturales. Particula secunda*. Dissert. Berlingianis, Lund, 20 pp.
- Dahlbom, A.G. (1854) *Hymenoptera Europaea praecipue borealia, formis typicis nonnullis specierum generumve Exoticorum aut Extraneorum propter nexum systematicum associatis, per familias, genera, species et varietates disposita atque descripta. 2. Chrysis in sensu Linnæano*. Friedrich Nicolai, Berlin, XXIV + 412 pp. + 12 pls.
- deWaard, J.R., Ivanova, N.V., Hajibabaei, M. & Hebert, P.D.N. (2008) Assembling DNA barcodes: analytical protocols. In: Martin, C. (Ed.), *Methods in molecular biology: environmental genetics*. Humana Press, Totowa, N.J., pp. 275–293.
- Dowton, M. & Austin, A.D. (2001) Simultaneous analysis of 16S, 28S, COI and morphology in the Hymenoptera: Apocrita evolutionary transitions among parasitic wasps. *Biological Journal of the Linnean Society*, 74, 87–111.
<http://dx.doi.org/10.1111/j.1095-8312.2001.tb01379.x>
- Drummond, A.J. & Rambaut, A. (2007) BEAST: Bayesian evolutionary analysis by sampling trees. *BMC evolutionary biology*, 7, 214.
<http://dx.doi.org/10.1186/1471-2148-7-214>
- Dufour, L. & Perris, E. (1840) Mémoire sur les Insectes Hyménoptères qui nichent dans l'intérieur des tiges sèches de la Ronce. *Annales de la Société Entomologique de France*, 9, 5–53.
- Gathmann, A. & Tschamtkke, T. (1999) Landschafts-Bewertung mit Bienen und Wespen in Nisthilfen: Artenspectrum, Interaktionen und Bestimmungsschlüssel. *Naturschutz und Landschaftspflege Baden-Württemberg*, 73, 277–305.
- Geer, L.Y., Marchler-Bauer, A., Geer, R.C., Han, L., He, J., He, S., Liu, C., Shi, W. & Bryant, S.H. (2010) The NCBI BioSystems database. *Nucleic Acids Research*, 38, D492–D496.
<http://dx.doi.org/10.1093/nar/gkp858>
- Gordon, D., Abajian, C. & Green, P. (1998) Consed: a graphical tool for sequence finishing. *Genome Research*, 8, 195–202.
<http://dx.doi.org/10.1101/gr.8.3.195>
- Guérin-Meneville, M. (1842) Description de quelques Chrysidides nouvelles. *Revue Zoologique*, 5, 144–150.
- Guindon, S. & Gascuel, O. (2003) A simple, fast, and accurate algorithm to estimate large phylogenies by maximum likelihood. *Systematic Biology*, 52, 696–704.
<http://dx.doi.org/10.1080/10635150390235520>
- Hall, T.A. (1999) BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucleic Acids Symposium Series*, 41, 95–98.
- Haupt, H. (1957) ["1956"] Die unechten und echten Goldwespen Mitteleuropas (*Cleptes* et Chrysididae). *Abhandlungen und Berichte aus dem Staatlichen Museum für Tierkunde in Dresden*, 23, 15–139.
- Hebert, P.D.N., Penton, E.H., Burns, J.M., Janzen, D.H. & Hallwachs, W. (2004) Ten species in one: DNA barcoding reveals cryptic species in the neotropical skipper butterfly *Astraptes fulgerator*. *Proceedings of the National Academy of Sciences of the United States of America*, 101, 14812–14817.

- <http://dx.doi.org/10.1073/pnas.0406166101>
- Hebert, P.D.N., Ratnasingham, S. & DeWaard, J.R. (2003) Barcoding animal life: cytochrome c oxidase subunit 1 divergences among closely related species. *Proceedings of the Royal Society B*, 270, S96–S99.
<http://dx.doi.org/10.1098/rsbl.2003.0025>
- Holzschuh, A., Steffan-Dewenter, I. & Tschamtkke, T. (2009) Grass strip corridors in agricultural landscapes enhance nest-site colonization by solitary wasps. *Ecological applications: a publication of the Ecological Society of America*, 19, 123–132.
<http://dx.doi.org/10.1890/08-0384.1>
- Huelsenbeck, J.P., Ronquist, F., Posada, D. & Crandall, K.A. (2001) MRBAYES: Bayesian inference of phylogeny. *Bioinformatics*, 17, 754–755.
<http://dx.doi.org/10.1093/bioinformatics/17.8.754>
- Ivanova, N.V., deWaard, J.R. & Hebert, P.D.N. (2006) An inexpensive, automation-friendly protocol for recovering high-quality DNA. *Molecular Ecology Notes*, 6, 998–1002.
<http://dx.doi.org/10.1111/j.1471-8286.2006.01428.x>
- Kimsey, L.S. & Bohart, R. (1991) ["1990"] *The Chrysidids wasps of the World*. Oxford University Press, New York, 652 pp.
- Kimura, M. (1980) A simple method for estimating evolutionary rate of base substitutions through comparative studies of nucleotide sequences. *Journal of Molecular Evolution*, 16, 111–120.
<http://dx.doi.org/10.1007/bf01731581>
- Kruess, A. & Tschamtkke, T. (2002) Grazing Intensity and the Diversity of Grasshoppers, Butterflies, and Trap-Nesting Bees and Wasps. *Conservation Biology*, 16, 1570–1580.
<http://dx.doi.org/10.1046/j.1523-1739.2002.01334.x>
- Kunz, P.X. (1994) Die Goldwespen (Chrysididae) Baden-Württembergs. Taxonomie, Bestimmung, Verbreitung, Kartierung und Ökologie. Mit einem Bestimmungsschlüssel für die deutschen Arten. *Beihefte zu den Veröffentlichungen für Naturschutz und Landschaftspflege in Baden-Württemberg*, 77, 1–188.
- Linnaeus, C. (1758) *Systema Naturae per Regna tria Naturae, secundum Classes, Ordines, Genera, Species, cum characteribus, differentiis, synonymis, locis. Editio Decima, Refurmata, Tomus I. Laurentii Salvii, Holmiae*, 824 pp + IV.
- Linnaeus, C. (1761) *Fauna Svecica sistens Animalia Sveciae Regni: Mammalia, Aves, Amphibia, Pisces, Insecta, Vermes. Distributa per Classes et Ordines, enera et Species, cum Differentiis, Specierum, Synonymis, Auctorum, Nominibus Incolarum, Locis natalium, Descriptionibus Insectorum. Editio Altera, Auctior. Laurentius Salvius, Stockholmiae*, 578 pp. + 2 pl.
- Linsenmaier, W. (1951) Die europäischen Chrysididen (Hymenoptera). Versuch einer natürlichen Ordnung mit Diagnosen. *Mitteilungen der Schweizerischen entomologischen Gesellschaft*, 24, 1–110.
- Linsenmaier, W. (1959a) Revision der Familie Chrysididae (Hymenoptera) mit besonderer Berücksichtigung der europäischen Spezies. *Mitteilungen der Schweizerischen entomologischen Gesellschaft*, 32, 1–232 pp.
- Linsenmaier, W. (1959b) Revision der Familie Chrysididae. Nachtrag. *Mitteilungen der Schweizerischen entomologischen Gesellschaft*, 32, 233–240.
- Linsenmaier, W. (1968) Revision der Familie Chrysididae. Zweiter Nachtrag. *Mitteilungen der Schweizerischen entomologischen Gesellschaft*, 41, 1–144.
- Linsenmaier, W. (1987) Revision der Familie Chrysididae. (Hymenoptera). 4. Teil. *Mitteilungen der Schweizerischen entomologischen Gesellschaft*, 60, 133–158.
- Linsenmaier, W. (1994) Grundriss der *Chrysis ignita* - Gruppe von Nordamerika. (Hymenoptera, Chrysididae). *Entomofauna*, 15, 481–500.
- Linsenmaier, W. (1997) Die Goldwespen der Schweiz. *Veröffentlichungen aus dem Natur-Museum Luzern*, 9, 1–139.
- Meier, R., Kwong, S., Vaidya, G. & Ng, P.K.L. (2006) DNA Barcoding and Taxonomy in Diptera: a Tale of High Intraspecific Variability and Low Identification Success. *Systematic Biology*, 55, 715–728.
- Mingo, E. (1994) *Hymenoptera Chrysididae*. Fauna Iberica, Musao Nacional de Cencias Naturales Consejo Superior de Investigaciones Cientificas, 256 pp.
- Mocsáry, A. (1889) *Monographia Chrysididarum orbis terrarium universi*. Musæi Nat. Hungarici Adiuncto, Academiae Scientiarum Hungaricae Socio. Typis Societatis Franklinianæ, Budapest, 643 pp.
- Mocsáry, A. (1912) Species Chrysididarum novae. III. *Annales Musei Nationalis Hungarici*, 10, 549–592.
- Móczár, L. (1946) Über einige seltene südliche Hymenopteren aus meinen Sammelausbeuten beuten. *Folia Entomologica Hungarica*, 1, 27–28.
- Móczár, L. (1965) Weitere Ergebnisse der Revision der Goldwespenfauna des Karpatenbeckens (Hymenoptera, Genus: Chrysis). *Acta Zoologica Hungarica*, 11, 168–180.
- Morgan, D. (1984) Cuckoo-Wasps. (Hymenoptera, Chrysididae). *Handbooks for the Identification of British Insects*, 6 (5), 1–37.
- Niehuis, O. (2000) The European species of the *Chrysis ignita* group: Revision of the *Chrysis angustula* aggregate (Hymenoptera, Chrysididae). *Mitteilungen aus dem Museum für Naturkunde in Berlin, Deutsche Entomologische Zeitschrift*, 47, 181–201.
- Niehuis, O. (2001) Chrysididae. In: Dathe, H.H., Taeger, A. & Blank, S.M. (Eds.), *Verzeichnis der Hautflügler Deutschlands (Entomofauna Germanica 4)*. *Entomologische Nachrichten und Berichte*, 7, 119–123.
- Niehuis, O. & Korb, J. (2010) Isolation and characterization of seventeen polymorphic microsatellite markers in the

- cleptoparasitic cuckoo wasp *Hedychrum nobile* (Hymenoptera: Chrysididae). *Conservation Genetics Resources*, 2, 253–256.
<http://dx.doi.org/10.1007/s12686-009-9167-8>
- Niehuis, O. & Waegele, J.-W. (2004) Phylogenetic analysis of the mitochondrial genes LSU rRNA and COI suggests early adaptive differentiation of anal teeth in chrysidine cuckoo wasps (Hymenoptera: Chrysididae). *Molecular Phylogenetics and Evolution*, 30, 615–622.
[http://dx.doi.org/10.1016/s1055-7903\(03\)00231-8](http://dx.doi.org/10.1016/s1055-7903(03)00231-8)
- Normark, B.B., Jordal, B.H. & Farrell, B.D. (1999) Origin of a haplodiploid beetle lineage. *Proceedings of the Royal Society B Biological Sciences*, 266, 2253–2259.
<http://dx.doi.org/10.1098/rspb.1999.0916>
- Ohl, M. & Bleidorn, C. (2006) The phylogenetic position of the enigmatic wasp family Heterogynaidae based on molecular data, with description of a new, nocturnal species (Hymenoptera: Apoidea). *Systematic Entomology*, 31, 321–337.
<http://dx.doi.org/10.1111/j.1365-3113.2005.00313.x>
- Page, R.D.M. (1996) Tree-View: an application to display phylogenetic trees on personal computers. *Computer applications in the biosciences CABIOS*, 12, 357–358.
<http://dx.doi.org/doi:10.1093/bioinformatics/12.4.357>
- Pedersen, B.V. (1996) A phylogenetic analysis of cuckoo bumblebees (*Psithyrus*, Lepeletier) and bumblebees (*Bombus*, Latreille) inferred from sequences of the mitochondrial gene cytochrome oxidase I. *Molecular Phylogenetics and Evolution*, 5, 289–297.
<http://dx.doi.org/10.1006/mpev.1996.0024>
- Pilgrim, E., von Dohlen, C. & Pitts, J. (2008) Molecular phylogenetics of Vespoidea indicate paraphyly of the superfamily and novel relationships of its component families and subfamilies. *Zoologica Scripta*, 37, 539–560.
<http://dx.doi.org/10.1111/j.1463-6409.2008.00340.x>
- Ratnasingham, S. & Hebert, P.D.N. (2007) BOLD: The Barcode of Life Data System. *Molecular Ecology Notes*, 7, 355–364. Available from: <http://www.barcodinglife.org> (Accessed 8 Apr. 2014)
- Rosa, P. (2006) *I Crisidi della Valle d'Aosta (Hymenoptera, Chrysididae)*. Monografie del Museo Regionale di Scienze Naturali, 6, St.-Pierre, Aosta, 368 pp., I–XVI + 32 pl.
- Schattnner, P., Brooks, A.N. & Lowe, T.M. (2005) The tRNAscan-SE, snoscan and snoGPS web servers for the detection of tRNAs and snoRNAs. *Nucleic Acids Research*, 33, W686–W689.
<http://dx.doi.org/10.1093/nar/gki366>
- Schenck, A. (1856) Beschreibung der in Nassau aufgefundenen Goldwespen (Chrysididae) nebst Einleitung und einer Kurzen Beschreibung der ubrigen deutschen Arten. *Jahrbücher des Vereins für Naturkunde im Herzogthum Nassau, Wiesbaden*, 11, 13–89.
- Schenck, A. (1861) Zusatz und Berichtigungen. *Jahrbücher des Vereins für Naturkunde im Herzogthum Nassau, Wiesbaden*, 16, 174–178.
- Shuckard, W.E. (1836) Description of the genera and species of the British Chrysididae. *The Entomological magazine*, 4, 156–177.
- Smitsen, J. van der (2001) *Die Wildbienen und Wespen Schleswig-Holsteins Rote Liste Band I–III*. Landesamt für Natur und Umwelt des Landes Schleswig-Holstein, Flintbek, 138 pp
- Smitsen, J. van der (2010) Bilanz aus 20 Jahren entomologischer Aktivitäten (1987–2007) (Hymenoptera Aculeata). *Verhandlungen des Vereins für Naturwissenschaftliche Heimatforschung zu Hamburg e. V.*, 43, 1–426.
- 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, 13–20.
<http://dx.doi.org/10.1016/j.ympev.2011.04.005>
- Steffan-Dewenter, I. & Leschke, K. (2003) Effect of habitat management on vegetation and above-ground nesting bees and wasps of orchard meadows in Central Europe. *Biodiversity & Conservation*, 12, 1953–1968.
- Suchard, M.A. & Redelings, B.D. (2006) Bali-Phy: simultaneous Bayesian inference of alignment and phylogeny. *Bioinformatics*, 22, 2047–2048.
<http://dx.doi.org/10.1093/bioinformatics/btl175>
- Swofford, D.L. (2003) *PAUP*. Phylogenetic Analysis Using Parsimony (*and Other Methods)*. Version 4. Sinauer Associates, Sunderland, Massachusetts.
- Tarbinsky, Yu.S. (2000) [The golden wasp genus *Chrysis* [gr. *ignita*] (Hymenoptera, Chrysididae) in Tien Shan and adjacent territories]. *Thethys Entomological Research*, 2, 193–204. [in Russian]
- Thomson, C.G. (1870) Öfversigt af de i Sverige funna arter af Slägtet *Chrysis* Lin. *Opuscula Entomologica*, 2, 101–108.
- Trautmann, W. (1926) Untersuchungen an einigen Goldwespenformen. *Entomologische Zeitschrift*, 40, 4–12.
- Trautmann, W. (1927) *Die Goldwespen Europas*. Uschman, Weimar, 194 pp.
- Tscharntke, T., Gathmann, A. & Steffan-Dewenter, I. (1998) Bioindication using trap-nesting bees and wasps and their natural enemies: community structure and interactions. *Journal of Applied Ecology*, 35, 708–719.
<http://dx.doi.org/10.1046/j.1365-2664.1998.355343.x>
- Tsuneki, K. (1957) Ecological problems centering around the microdistribution of the cuckoo wasp populations. Appendix: key to the Japanese Species of the Holonychinae. *The Insect Ecology*, 6, 11–23. [in Japanese]

- Valkeila, E. (1971) Two new North European species of genus *Chrysis*. *Entomologisk Tidskrift*, 92, 82–93.
- Wickl, K.-H. (2001) Goldwespen der Oberpfalz (Hymenoptera: Chrysididae). *Galathea*, 17, 57–72.
- Zhang, A.B., Muster, C. & Liang, H.B. (2012) A fuzzy-set-theory-based approach to analyse species membership in DNA barcoding. *Molecular Ecology*, 21, 1848–1863.
<http://dx.doi.org/10.1111/j.1365-294x.2011.05235.x>
- Zimmermann, S. (1944) *Chrysis käufeli*, eine neue Goldwespe aus den Ostalpen. *Annalen des Historischen Museums in Wien*, 53, 82–88.