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„The cryptic species of the *Bombus lucorum*-complex in Austria“

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Contents

Abstract

Over the past decades there has been great disagreement about the taxonomy of the cryptic bumblebee species *Bombus lucorum* and the closely related *Bombus cryptarum* and *Bombus magnus*. Presently, the status of these three distinct species in the so-called *Bombus lucorum*-complex is widely accepted, primarily due to investigations of nucleotide sequences of the mitochondrial COI gene. In contrast, the restricted possibilities of reliable identification based on morphology led to an uncertain and fragmentary knowledge about the autecology of these bumblebee species and their distribution in Austria. I analyzed COI sequences of 387 specimens collected all over the country including the Austrian Alps to clarify the situation. I analyzed genetic divergences and variation, species distributions and ecological differentiation, as well as other relevant topics. The results confirm previous findings of three distinct genotypic groups within the species complex. The genetic variation within *B. lucorum* and *B. cryptarum* is very low, indicating a past bottleneck phenomenon. *Bombus lucorum* and *B. cryptarum* co-occur in several areas all over the country, with *B. lucorum* being the most common and most widespread species. The less common species, *B. cryptarum*, mainly occurs in the high mountains and is the predominant species above altitudes of 2100 m a.s.l. Further, *B. cryptarum* is almost absent from woodlands and is relatively more abundant in habitats with colder climate than *B. lucorum*. The present study provides no evidence for the presence of *B. magnus* in Austria.

Zusammenfassung

Der taxonomische Status des kryptischen Artenkomplexes von *Bombus lucorum* und der nah verwandten Taxa *Bombus cryptarum* und *Bombus magnus* war lange Zeit Gegenstand von Diskussion. Heutzutage ist der Artstatus dieser drei Spezies innerhalb des *Bombus lucorum*-Komplexes weitgehend gesichert, nicht zuletzt dank der guten Abgrenzbarkeit der Arten anhand von Nukleotidsequenzen des mitochondriellen COI Gens. Trotzdem ist aufgrund der schwierigen und unsicheren morphologischen Bestimmbarkeit der Kenntnisstand bezüglich der Ökologie und der Verbreitung dieser Hummelarten in Österreich lückenhaft. Zu diesem Zweck wurden in dieser Studie die Nukleotidsequenzen des COI Gens von 387 Belegexemplaren aus verschiedenen Regionen Österreichs und der österreichischen Alpen untersucht. Hierbei wurden unter anderem die genetischen Distanzen sowieso die Variabilität anhand der Nukleotid- und Haplotypendiversität ermittelt. Es wurden die Zusammensetzung der Arten, deren Verteilung im Untersuchungsgebiet sowie deren ökologische Differenzierung untersucht. Im Einklang mit den Resultaten der aktuellen Studien lassen sich die österreichischen Tiere zweifelsfrei trennen. Die Nukleotiddiversität von *B. lucorum* und *B. cryptarum* ist sehr gering, was einen zurückliegenden Populationseinbruch und einen damit verbundenen genetischen Flaschenhals vermuten lässt. *Bombus lucorum* und *B. cryptarum* kommen sympatrisch in diversen Gebieten Österreichs vor. *Bombus lucorum* ist hierbei die am weitesten verbreitete und häufigste Art des Artenkomplexes. Die weniger häufige *B. cryptarum* ist hauptsächlich im Alpenraum verbreitet und ist ab etwa 2100 m Seehöhe die häufigere Art. *Bombus cryptarum* meidet Waldgebiete, während *B. lucorum* häufig in diesem Habitattyp gefunden wurde. Es lassen sich Verteilungsmuster der Arten anhand der klimatischen Bedingungen im Untersuchungsgebiet erkennen, wobei *B. cryptarum* in durchschnittlich kühleren Gebieten vorkommt. Die Studie liefert keinen Hinweis auf ein Vorkommen von *B. magnus* in Österreich.

Introduction

Bumblebees (*Bombus*, LATREILLE 1802) represent a striking feature of Europe's pollinator fauna (e.g. MAUSS 1994; CORBET et al. 1991; GOULSON 2010). Their main areas of distribution are cool moderate and cold climate zones (WILLIAMS 1994; WILLIAMS 1996; HINES 2008). They occur in several mountainous regions of the world and are particularly abundant and diverse in the European mountains (WESTRICH 1990; OBESO 1992; NEUMAYER & PAULUS 1999; NEUMAYER & KOFLER 2005). In contrast to most other bee genera, bumblebees are considered to be intuitively recognizable and are rarely confused with other bees (AMIET 1996; GOKCEZADE et al. 2010; AMIET & KREBS 2012). Yet species determination requires expertise, and reliable identification in the field is often impossible. Reasons for this are the relatively monotonous morphology (MICHENER 2007), enormous variability in coloration and size which is often associated with biogeographical distribution (e.g. VOGT 1909; VOGT 1911; KRÜGER 1951; LØKEN 1973; PEKKARINEN 1979) and the fact that the same or similar color-patterns often repeated in various species (DALLA TORRE 1880; REINIG 1939; AMIET 1996; WILLIAMS 2007 and references therein). Some authors suppose these patterns are a consequence of Müllerian mimicry (PLOWRIGHT & OWEN 1980; WILLIAMS 2007). However, one of these groups with very similar morphology consists of the European species of the subgenus *Bombus* s. str.: *Bombus terrestris* L., *B. lucorum* L., *B. cryptarum* FABR., *B. magnus* VOGT and *B. sporadicus* NYL. In the past decades, there has been much disagreement on the taxonomy of this group. Especially the status of *B. lucorum* and the closely related *B. cryptarum* and *B. magnus*, forming the so-called *Bombus lucorum*-complex (hereinafter 'LCMc'), has been intensively discussed. Nowadays, their species status is widely accepted, primarily due to investigations of nucleotide sequences (BERTSCH et al. 2005; MURRAY et al. 2008; BERTSCH 2009; CAROLAN et al. 2012; WILLIAMS et al. 2012; BARDAKJI 2013) and marking pheromones (BERTSCH 1997; BERTSCH et al. 2004; BERTSCH et al. 2005). In contrast, there is serious doubt concerning the validity of species identification based on morphology with several authors claiming the species are morphologically indistinguishable (e.g. WILLIAMS 2000; WATERS et al. 2011; CAROLAN et al. 2012). In addition, information about diagnostic characters in the literature are often confusing or even contradictory. As a consequence of the doubtful delineation, our current knowledge about their autecology is an unsolved puzzle: one the one hand the literature is full of unreliable data from literally hundreds of authors over the centuries. On the other hand, there are very few studies focusing on their ecology which provide reliable species identification using biochemical methods.

The same situation applies to Austria, where *B. lucorum* and *B. cryptarum* are widely distributed and co-occur in several areas (NEUMAYER & PAULUS 1999; NEUMAYER & KOFLER 2005; BARDAKJI 2013; GEREBEN-KRENN et al. 2013). A reliable proof for the presence of *B. magnus* has not been recorded yet (NEUMAYER & KOFLER 2005; GUSENLEITNER et al. 2012). NEUMAYER & PAULUS (1999) suppose *B. cryptarum* to occur predominantly in the mountains, whereas *B. lucorum* is more widespread in the lowland. However, the data concerning the ecology and niche differentiation of the species in the Austrian Alps is fragmentary. This is additionally challenged by the unreliability of data achieved by morphological identification, since BARDAKJI (2013) recently showed that the identification of workers in the field is not trustworthy.
The phylogenetic analyses using nucleotide sequences of the mitochondrial cytochrome oxidase I gene (COI) for species recognition is the method of choice: it has been successfully applied in various insect groups and found its way into entomological textbooks (GRIMALDI & ENGEL 2005; SAMWAYS et al. 2009; GULLAN & CRANSTON 2010). Aside from some justified criticisms, COI analyses and COI barcoding are reliable methods for species identification in the LCMc (BERTSCH et al. 2005; MURRAY et al. 2008; BERTSCH 2009; CAROLAN et al. 2012; WILLIAMS et al. 2012).

In summary, this study consists of two major emphases: At first, a critical review about the taxonomy and the distinguishability of the LCMc provides an urgently required reappraisal to pave the way for future issues. Secondly, this study is a contribution to sharpen the ecological profile of the species in Austria, based on identification with genetic methods.

Reviewing species recognition and identification of the *Bombus lucorum*-complex

Bombus lucorum vs. Bombus magnus

Bombus lucorum and *B. terrestris* were described by LINNAEUS in 1761 and 1758, respectively. Their species status has been widely accepted in the last century. Only single authors doubted their status and lumped them together (e.g. WARNCKE 1981; WARNCKE 1986). More than a century later, *B. magnus* was described by VOGT (1911) in a single sentence as a 'forma nova *magnus*' without detailed information. It was probably the same species that was described as *Bombus terrestris* var. *flavoscutellaris* by TRAUTMANN & TRAUTMANN (1915). The species description of *B. magnus* was conducted by KRÜGER (1951; 1954) with detailed description of all castes and several *races* and *ethna*, which are difficult to comprehend from today's view. Some earlier experts failed to distinguish *B. lucorum* and *B. magnus* (ELFVING 1960; ANDER 1965), others primarily highlighted the need of further studies (ALFORD 1975; DELMAS 1981). LØKEN (1973) conducted a grand morphometric analysis and advocated the species status, primarily based on measurements of queens, whereas the distinguishability of workers and males remained uncertain. Her work was confirmed and enhanced by further specific indices by TKALCŮ (1974). At that time the first biochemical results in form of male labial gland marking pheromones emerged (KULLENBERG et al. 1970; BERGSTRÖM et al. 1973; BERGSTRÖM et al. 1981): For *B. lucorum,* two similar but distinctly different profiles could be identified concerning a 'dark' and a 'blonde' form, supporting LØKEN´S (1973) view. However, common to all of the above mentioned literature is the fact that a previously unknown species, *B. cryptarum*, occurs sympatrically, a fact that probably biased their results due to a species mix in their samples. This is probably the reason why the results from PEKKARINEN (1979) are not in line with the others. Even though other authors misconceived a possible third taxon, as well (SCHOLL & OBRECHT 1983; PAMILO et al. 1984), their results based on enzyme electrophoresis were convincing that *B. lucorum* is not a single species.

A third species comes into play

Using morphological/morphometric methods, RASMONT (1981a; 1981b) was the first who recognized a putative third species and described it as *Bombus lucocryptarum* BALL which was later been synonymized with *Bombus cryptarum* FABR. (RASMONT 1983). Interestingly it seems that this taxon was also described as *Bombus lucorum* var. *pseudocryptarum* SKORIKOV from Russia and Poland before (SKORIKOV 1913). Anyway, RASMONT (1981b) provides a determination table for queens. The tables for both female castes (RASMONT 1984) and males (RASMONT et al. 1986) followed, even if the latter one has a rather limited applicability. His keys are supported by remarkable crossing experiments between the three putative species (DE JONGHE 1982; DE JONGHE & RASMONT 1983): hereby crossing between the three putative taxa failed, even though copulation and egg deposition were observed. In contrast, breeding within the taxa succeeded. Similar results were achieved by BUČÁNKOVÁ et al. (2011) recently. However, due to the limited sample size these results give great hints for reproductive isolation but are not completely reliable. Even though the evidence for more than one taxon in *B. lucorum* were broadly accepted at that time, the species were still lumped together by several authors, sometimes as an interim solution (WARNCKE 1986; WESTRICH 1990; WILLIAMS 1991; WILLIAMS 1998). The confirmation of a third species with biochemical methods remained open for some time (OBRECHT & SCHOLL 1984; SCHOLL et al. 1990; SCHOLL et al. 1992; PAMILO et al. 1997), probably due to the similar enzyme genetic profiles of *B. cryptarum* and *B. magnus*. However, it was possible that the samples of *B. cryptarum* and *B. magnus* used for analyses became mixed up again, a point that BERTSCH et al. (2004) presupposes for PAMILO et al. (1997). It is a recurring theme: the morphometric attempts of BAKER (1996) were of restricted value, since *B. cryptarum* was not considered as a separate species and the same applies for MACDONALD (1999). He advocated *B. lucorum* and *B. magnus* as good species based on the coloration of the pile (extended yellow collar and a "pinkish-buff" on the tail of queens of *B. magnus*; for a review of morphological traits see below) and observations concerning their ecology. In retrospect, it seems highly likely that at least some of the examined specimens from his study were in fact *B. cryptarum,* since this species occurs most frequently in the mainland of northern Scotland (MACDONALD, pers. comm.). This might be the explanation why WILLIAMS (2000) could not find a clear gap in collar extending between *B. lucorum* and *B. magnus*: *B. cryptarum* queens have on average a collar extension between the latter two species (CAROLAN et al. 2012) which may have critically biased the measurements. However, the first sufficient biochemical evidence for all three species was conducted by BERTSCH (1997) and BERTSCH et al. (2004) by the identification of three distinct male labial gland secretion profiles: the profiles of *B. cryptarum* and *B. magnus* are similar and share ethyl dodecanoate as the main component. Yet they clearly differ in minor components such as alcohols (BERTSCH et al. 2004; BERTSCH et al. 2005). Recently the great stability of the labial gland secretion composition of *B. cryptarum* over great geographical ranges was shown, a fact that supports their value for species recognition (BERTSCH & SCHWEER 2012).

Nucleotide sequence data improved the understanding

The debate gained new life with the application of phylogenetic analyses using nucleotide sequences of the mitochondrial cytochrome oxidase I gene (COI). With this method, the composition of three distinct molecular operational taxonomic units (MOTUs) in the European LCMc was convincingly confirmed multiple times (BERTSCH et al. 2005; MURRAY et al. 2008; BERTSCH 2009; CAROLAN et al. 2012; BARDAKJI 2013), even if the taxonomic state of knowledge remains incomplete in the global context (WILLIAMS et al. 2012). Admittedly, COI barcoding and its applicability for species recognition has been criticized (e.g. WILL &

RUBINOFF 2004; DESALLE et al. 2005; MEYER & PAULAY 2005; for a review see TAYLOR & HARRIS 2012), yet the results for this species complex seems to be clear: the interspecific and intraspecific genetic divergences, based on Kimura 2-parameter (KIMURA 1980), combined from CAROLAN et al. (2012) and BARDAKJI (2013), are 0.03-0.044 and 0-0.005, respectively. For BERTSCH et al. (2005) combined with MURRAY et al. (2008), based on Tamura-Nei (TAMURA & NEI 1993), they are slightly smaller: 0.023-0.043 and 0.001-0.004, respectively. In summary, the divergences between the species are considerably larger than within the species and these patterns are stable over wide geographic ranges of Europe. BERTSCH et al. (2005) calculated a distance of about 7000 km between two collection sites. Certainly one must face a number of unresolved taxonomic problems, especially within *B. lucorum* and *B. cryptarum* when dealing with the species from whole Holarctic (WILLIAMS et al. 2012). Additionally, the COI sequences are suitable for inexpensive and fast analyses with restriction fragment length polymorphisms (RFLP), if only the species identity and not the individual sequence is of interest. Therefore MURRAY et al. (2008) provided a protocol which was successfully applied in WATERS et al. (2011). An enhanced version was published recently (VESTERLUND et al. 2014). This more time consuming approach works well with smaller COI fragments and hence is better suited for degraded DNA. However, it should be mentioned that due to different primers, none of the RFLPs protocols worked with the so-called *Folmer region* (derived from the primers presented in FOLMER et al. (1994)), which is widely used for DNA 'barcode' collections such as BOLD (RATNASINGHAM & HEBERT 2007).

In conclusion, both the labial gland secretion profiles and the results from the analyses of the nucleotide sequences reveal sufficient support for three distinct species within the European LCMc. Additional indications arise from the morphological and phenological implications and the crossing experiments. Against this background, the debate about the species status of *B. lucorum*, *B. cryptarum* and *B. magnus* can be meaningfully continued by discussing species concepts, in general.

Can the species be distinguished by morphology?

While the biochemical and genetic methods for determination are widely accepted today, the published information on the morphological distinguishability is confusing. Fortunately the combination of the methods used nowadays allow the positive verification or contradiction of potential traits. Currently, the key in RASMONT (1984) is the most important reference for the determination of females since most other keys (e.g. MAUSS 1994; AMIET 1996; BERTSCH et al. 2004; DOROW 2004, pp. 173; NEUMAYER & MAUSS, in prep.) share crucial traits or are based on them. The key in RASMONT (1984) includes two tables: the first one provides morphological characters with several indices and the other one shows indications about the coloration. The characters of color have been examined much more intensively. It must be mentioned that using RASMONT (1984), the entirety of characters are only cognizable in queens. In this respect, the occurrence of the first collar is particularly important, since this may be the only character that is accessible in the field (RASMONT 1984; BERTSCH 1997; BERTSCH et al. 2004).

Identification of queens

Three distinct forms of the first collar have been suggested to identify queens from the LCMc. The first describes the lateral border of the yellow collar, which has been described as a characteristic trait multiple times (e.g. SKORIKOV 1913; BALL 1914; TRAUTMANN & TRAUTMANN 1915; ALFORD 1975; RASMONT 1981b; RASMONT 1984; AMIET 1996; BERTSCH 1997; BERTSCH et al. 2004): if the border extends far down on the episternum, it is associated with *B. magnus* (Fig. 1c) and *B. cryptarum* (Fig. 1b). For *B. magnus*, the collar was reported to become very broad below the tegulae. In contrast, a higher lateral border that is almost exclusively restricted to the pronatallobus argues for *B. lucorum* (Fig. 1a & 1d). In the literature, this trait is often vaguely described as "below tegula" or not, which is not entirely correct, since the border of the episternum is slightly below the tegula (Fig. 1d). The second trait is a so-called "S"— or "5"—shape that can be found within the collar: the pile along the border of the pronatallobus and the episternum is black and forms the "S" (Fig. 1b). It is associated with *B. cryptarum*. Another hint comes from a strong melanization of the collar which has been reported for *B. cryptarum*. However, this trait is regionally restricted (BERTSCH et al. 2004; BERTSCH et al. 2005) and on rare occasions can occur in the other species, too (CAROLAN et al. 2012).

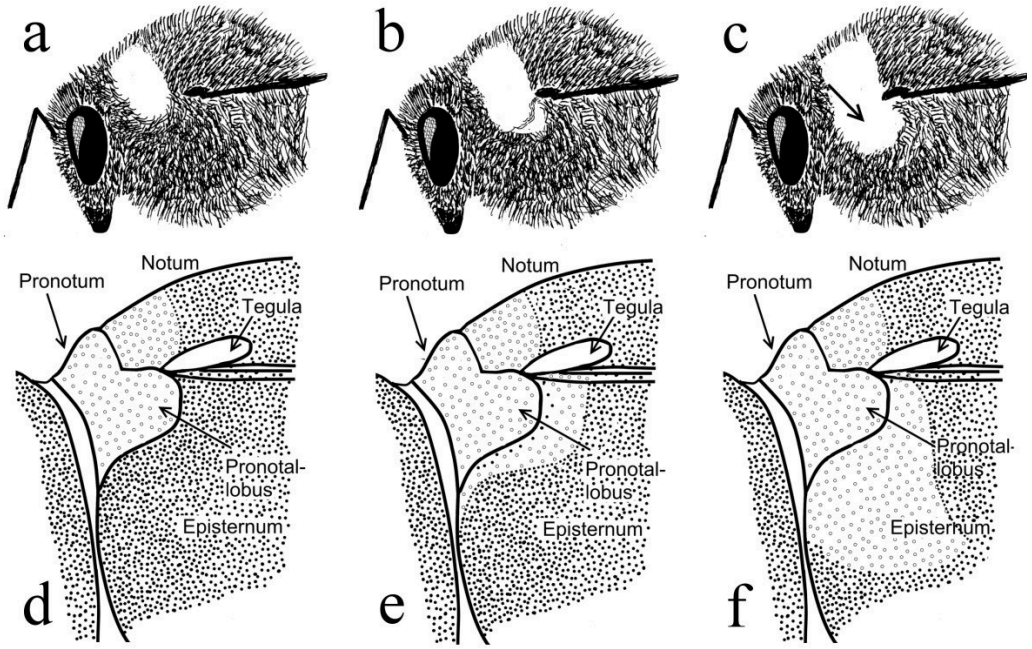


Fig. 1: The shape of the first collar as described in the text: *B. lucorum* (a, d), *B. cryptarum* (b, e) and *B. magnus* (c, f). Drawings taken from NEUMAYER & MAUSS (in prep.).

BERTSCH (2009) was able to assign all but one investigated queen to the correct species with the above mentioned characters, according to the biochemical evidence (n=25). In contrast, using a larger sample from the British Isles and Denmark (n=67), CAROLAN et al. (2012) showed that especially the collar-characters are not reliable for species diagnosis since they show overlap. However, not every voucher of their study was convincing: A close look at specimen "h" from Fig. 2, identified by morphology as "*lucorum*", reveals an obvious collar extension far below the tegula and onto the episternum. There is no "S"-shape, it should therefore be associated with *B. magnus*, which is actually the case according to the DNA barcode. Moreover, specimen "c", which was identified as "*magnus*" based on morphology reveals a faint black "S"-shape, exactly as described in BERTSCH et al. (2004). It remains unclear why this voucher was assigned to *B. magnus* and not *B. cryptarum*. Thirdly, specimen "f" is not a typical *B. magnus*-morphotype since it does not show a clear broad collar below the tegula. Additionally, the authors could have prepared the voucher more carefully, since it seems questionable why a leg of specimen "h" blocks the view on the crucial part of the collar extension beneath the tegula. However, against this background, their conclusion that "each species can be morphologically identified as belonging to all 3 taxa." cannot be upheld.

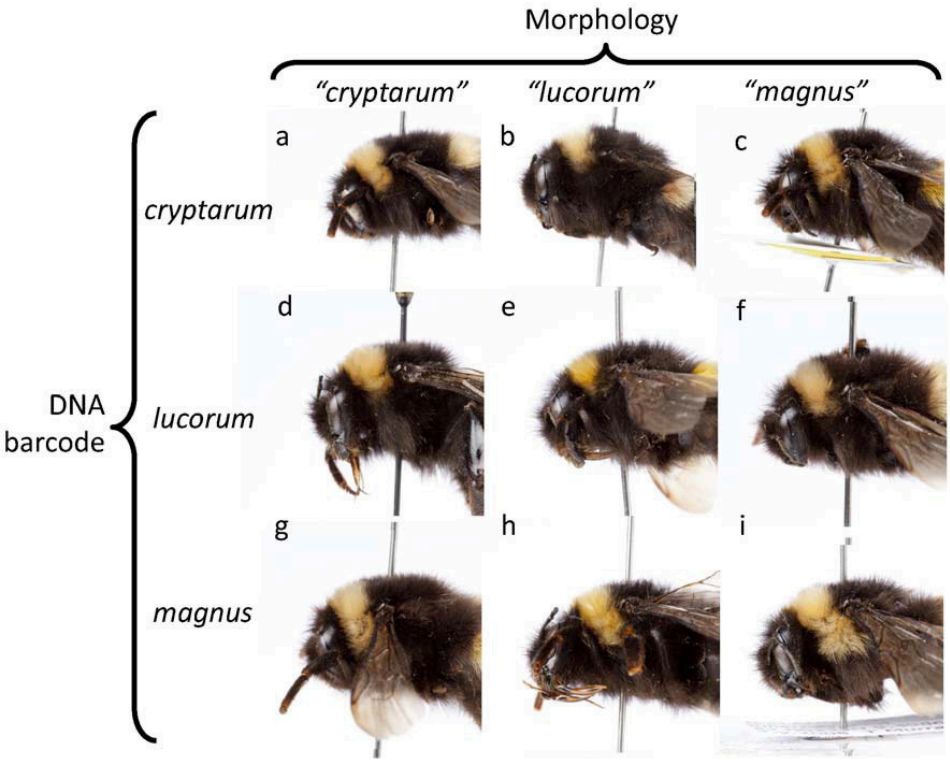


Fig. 2: Figure 4 from CAROLAN et al. (2012). Original description: „[…]. Horizontal rows indicate species as identified by barcoding, whilst vertical columns show how molecularly identified specimens of each species can be morphologically identified as belonging to all 3 taxa. […]"

Aside from the confusing information, the work from CAROLAN et al. (2012) provided sufficient indication that the collar characters are unreliable and should not be exclusively taken into account for species identification. Still it remains debatable if it is purposeful[? useful] to mix up samples from numerous regions. However, the key in RASMONT (1984) provides several characters aside from the coloration of the pile, such as the form of the labrum, punctuations of several structures and the shape of the hindleg metatarsus. The reliability of these characters has not been examined yet against a biochemical control and on an adequate scale (BERTSCH 2009). Thus the distinguishability of queens of the LCMc can solely be presumed, even if most specimens are probably easily determined as described previously (BERTSCH 1997; BERTSCH et al. 2004; BERTSCH et al. 2005).

Identification of workers

The current state of knowledge concerning the identification of workers is worse than that for queens. RASMONT (1984) postulated that the coloration of workers corresponds approximately to the coloration of queens, implying a potential distinguishability by the shape and extension of the first collar. Unfortunately, the "S"-shape of *B. cryptarum* workers can be inconspicuous or absent (RASMONT, pers. comm., related to ssp. *reinigianus*). Indications for the recognition of *B. magnus* can arise if yellow hair is mixed in the black pile of the first tergum (RASMONT 1984). However, the distinguishability of the first collar was examined quantitatively with Scottish (WATERS et al. 2011) and Austrian specimens (BARDAKJI 2013) and was verified with RFLPs and DNA barcodes, respectively. Both studies revealed an uncertain connection of the traits to the species. In Scotland, where all three species occur sympatrically, WATERS et al. (2011) was unable to properly distinguish *B. cryptarum* from the other two species. Still there was significant difference in collar extension between *B. lucorum* and *B. magnus*. It seems that the collar extension of the Scottish *B. cryptarum* is moderately variable and therefore constrains the possibility to recognize the other two species. However, data on the pile coloration of the first tergum were not recorded, therefore the accuracy of this potential character remains uncertain.
In the study with the Austrian specimens (BARDAKJI 2013), the sample consisted of *B. lucorum* and *B. cryptarum* individuals only. Regarding the extension of the collar, BARDAKJI (2013) was able to identify a great part (85.5%, 47 of n=55) of the workers correctly. There were considerably more identification errors in *B. cryptarum*, supporting the view that the extension of the collar of workers of *B. cryptarum* is more variable in contrast to the others species. Aside from coloration, RASMONT (1984) describes two groups of morphological characters that are accessible in queens and workers. (**I**) The first distinguishes characters of the labrum, e. g. the form of the basal area, especially if it is "U"-shaped (*B. lucorum* and *B. magnus*, Fig. 3a and 3c, respectively) or "V"-shaped (*B. cryptarum*, Fig. 3b). Further, the form of the lamella and punctuation. (**II**) The second group describes the punctuations of the second tergum. Unfortunately, it is not possible to distinguish *B. cryptarum* and *B. magnus* based on the second tergum.
BARDAKJI (2013) tested the reliability of these traits and could correctly assign every worker on the basis of the labrum characters. The characters of the second tergum failed in about 1 of 5 cases, confirming the view of DOROW (2004), who found greater variation on the second tergum than described in RASMONT (1984). In any case, *B. magnus* was not present in the sample from BARDAKJI (2013) and therefore no general statements can be made, since RASMONT (1984) has highlighted the difficulties between workers of *B. magnus* and *B. cryptarum*. Still, it strongly suggested to test these traits on a larger scale with all three species. To avoid misunderstandings it is important to separately name the essential structures, since BARDAKJI (2013) described the form of the lamella "U"- or "V"-shaped. The wording may be confusing since the "U"- or "V"-shape is used to describe the "basal area of the labrum" (after MICHENER 2007; German: Labrummittelfurche; French: Fossé labral), and the lamella is the lateral structure directly below the basal area (Fig. 3). This is important because the form of the lamella is a separate characteristic in the key from RASMONT (1984).
In summary, the general possibility to identify workers of all three species based on morphology has not been verified until now. Yet the characters of the labrum and the second tergum are particularly promising. Further comparative examinations, e.g. supported by DNA barcodes, are necessary to verify the supposed characters and can help find potential new traits. In the field, the extension of the first collar may be an indication but is definitely not reliable, especially if all three species co-occur. Additionally, the reliability of the yellowish coloration of the first tergum for workers of *B. magnus* is worthy of further investigations.

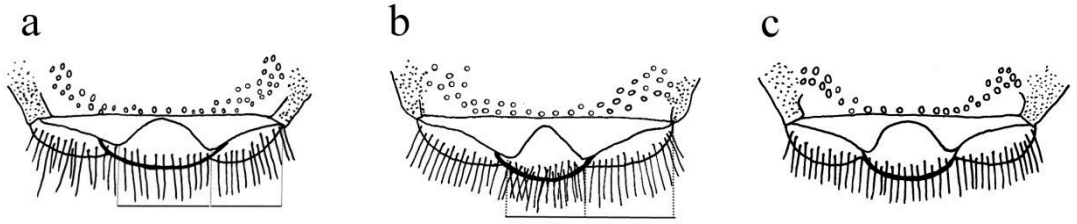


Fig. 3: Labrum characters of *B. lucorum* (a), *B. cryptarum* (b) and *B. magnus* (c). Drawings taken from NEUMAYER & MAUSS (in prep.).

Identification of males

Identification of the males is probably the most difficult caste. Authors of recently published studies agreed that they are indistinguishable by morphology (MURRAY et al. 2008; BERTSCH 2009; WATERS et al. 2011). All three taxa are very similar and show extensive and overlapping variation in color and male genitalia (RASMONT et al. 1986). Therefore, keys based on coloration of the pile of the "face" (e.g. AMIET 1996; DOROW 2004, pp. 174; GOKCEZADE et al. 2010) are of restricted value, even if they may work for certain geographic regions. Aggravating this situation, the males of *B. terrestris* may also be confusing, especially when compared with specimens of *B. cryptarum* having a dark pile. However, *B. cryptarum* males often show the "S"-shape, but it also seems to be geographically restricted, e.g. it is absent in specimens from northern Scandinavia (RASMONT, pers. comm., related to ssp. *reinigianus*). Aside from coloration, RASMONT et al. (1986) described several potential morphological characters. In this respect, he highlighted the punctuation of the second tergum as a distinguishing character for *B. lucorum* against *B. cryptarum* and *B. magnus*. Additional characters concern the diameter of the ocelli and the shape of the eighth tergum. However, the reliability of these traits in the wider European context remains uncertain. As long as no new insights in the distinguishability of the males are gained, completely reliable identification can only be achieved by biochemical or genetic approaches.

Material & Methods

Taxon sampling

A total of 312 bumblebees was sampled from May 28 to August 22, 2013 by the collectors listed in Tab. 6 (appendix). Specimens were collected from 14 areas all over Austria. The region of the Hohe Tauern was subdivided into three distinct sites due to the different conditions of the sites on the main ridge of the Alps. For every collection area, altitudinal categories were defined to cover a broad altitudinal range. Each category covered 300 m of elevation and was assigned a unique letter: Y (300-600 m), Z (600-900 m), A (900-1200 m), B (1200-1500 m), C (1500-1800 m), D (1800-2100 m), E (2100-2400 m) and F (2400-2700 m). A maximum of 10 specimens for one altitudinal category per area was collected, whereas some transects contained slightly more samples due to parallel sampling by two or more persons. To avoid excessive sampling of siblings, a maximum of two specimens was collected at any site. Additionally, no further collecting was conducted in a radius of at least 100 m surrounding the site. Seven habitat categories were defined: bogs together with fens, buffer stripes such as green way- and roadsides, dwarf shrub and krummholz communities, scree areas, woodlands together with forest edges and tall forb meadows. The different kinds of grassland communities, such as lowland and alpine pastures, grasslands with poor and rich nutrient levels, dry and wet meadows, were placed together in the category *meadows*. Specimens from all castes, in particular workers, were captured manually, killed in 99% ethanol and stored at -20°C prior to DNA extraction. A total of 77 complete samples from BARDAKJI (2013) are integrated into the present study and are highlighted in Tab. 6. In summary, a total of 387 samples from 18 collection sites were analyzed, consisting of 275 specimens of

Tab. 1: Comprehensive collection table. The abbreviations in the brackets refer to the respective federal states within Austria: V = Vienna, LA = Lower Austria, ST = Styria, UA = Upper Austria, SA = Salzburg, C = Carinthia, T = Tyrol and VA = Vorarlberg.

Collection site	Number of females			Number of males			Total
	B. lucorum	*B. cryptarum*	*B. terrestris*	*B. lucorum*	*B. cryptarum*	*B. terrestris*	
Vienna Woods (V)	17	0	10	1	0	1	29
Blockheide (LA)	9	3	0	0	0	0	12
Lunz am See (LA)	27	0	0	1	0	0	28
Raxalpe and Schneeberg (LA)	50	3	0	6	0	0	59
Rottalmoos (LA)	2	3	0	0	0	0	5
Dachstein (ST)	0	2	0	2	0	0	4
Gesäuse (ST)	8 (1 queen)	0	1	29	0	3	41
Tannermoor (UA)	11	2	0	0	0	0	13
Hohe Tauern, main ridge (SA)	4	7	0	0	0	0	11
Hohe Tauern, northern slope (SA)	2	17	0	0	0	0	19
Tennen Mountains (SA)	17	0	1	0	0	0	18
Hohe Tauern, southern slope (C)	6	21	0	0	5	0	32
Karawanks (C)	34	1	0	0	0	0	35
Karwendel (T)	2	2	10	1	1	0	16
Ötztal Alps (T)	17	13	0	0	2	0	32
Zillertal Alps (T)	2	1 queen	0	8	0	0	11
Silvretta Alps (VA)	19 (3 queens)	3	0	0	0	0	22
Total	227	78	22	48	8	4	387

B. lucorum, 86 *B. cryptarum* and 26 *B. terrestris* (see Tab. 1). Additionally, a single specimen of *B. magnus* and one of *B. soroeensis* (#388 & #389, respectively) were collected from Norway and included in the phylogenetic analyses only. For each specimen, a set of information was recorded: elevation, collection date, potential flower visit with details such as pollen or nectar foraging, and the habitat type of the collection site.

Genetic analyses

DNA extraction was conducted using two different methods. In general, a single crushed midleg was used. For very small specimens or if the extraction had to be repeated, a second or more legs were clipped. For most specimens, DNA was extracted using a Proteinase K digestion prior to a phenol-chloroform protocol (SAMBROOK et al. 1989). For the others, the extraction was performed using a DNeasy® Blood & Tissue Kit (QIAGEN GmbH, Hilden, Germany), according to the manufacturer´s manual. Hereby, the second elution step was skipped. Polymerase chain reactions (PCR) of a partial COI sequence were conducted using the universal primers LCO1490 and HC02198 (FOLMER et al. 1994). The other PCR components were provided by using the DreamTaq™ PCR Mastermix (2x) (Thermo Fisher Scientific Inc., Waltham, MA, USA). Each reaction mixture and the amplification profile were conducted according to the manufacturer´s protocol. The PCR amplicons were purified using the GeneJET™ PCR Purification Kit (Thermo Fisher Scientific Inc., Waltham, MA, USA) and sent to VBC-Biotech Service GmbH (Vienna, Austria) for sequencing. Sequences were manually checked and aligned using BioEdit 7.2.5 (HALL 1999). The alignment to the full mitochondrial genome of *Apis mellifera* (CROZIER & CROZIER 1993; GenBank acc. no. NC_001566) and *Bombus ignitus* (CHA et al. 2007; acc. no. DQ870926) were conducted automatically with ClustalX 2.1 (LARKIN et al. 2007). For the total of 387 samples with 619 comparable positions, the genetic distances between and within the species were computed using MEGA 5.2 (TAMURA et al. 2011) with the Maximum Composite likelihood model and gamma distribution. The variance was estimated with the bootstrap method and 10,000 bootstraps. Additionally, the net evolutionary divergence between and within the species was estimated based on the Tamura-Nei model (TAMURA & NEI 1993), gamma distribution and 10,000 bootstraps. To determine significant differences between the COI sequences from *B. lucorum* and *B. cryptarum*, an analyses of molecular variance (AMOVA) (EXCOFFIER et al. 1992) was conducted as implemented in ARLEQUIN 3.5.1.3 (EXCOFFIER & LISCHER 2010). The software was also used to estimate the nucleotide diversity (π) and haplotype diversity (h) in the sample.

To calculate phylogenetic trees, a more comprehensive dataset was used: to avoid extensive calculation time, identical sequences were removed, resulting in one individual sequence for every haplotype shown in Tab. 2. Therefore, a haplotype was defined as an individual, whose COI sequence had at least one individual polymorphic site. Since there were no specimens of *B. magnus* in the Austrian samples, the *B. magnus* sample from Norway (#388) was included and four additional sequences for *B. magnus* were taken from GenBank (GenBank acc. nos. JN872620, JQ843552, JQ692958 and JN872607). *B. soroeensis* (#389) was used as the outgroup, resulting in 29 sequences with 609 positions. The Bayesian phylogeny based on the Markov Chain Monte Carlo method (MCMC) was computed using MRBAYES 3.2.2 (RONQUIST et al. 2012). The calculation was computed with the Generalised time reversible model (GTR), gamma-distributed rate variation, 400,000 generations with a sample frequency of 10 and a "burn in" of 25%. The Neighbor Joining (NJ) analyses was conducted using MEGA 5.2 (TAMURA et al. 2011) based on the Tamura-Nei model (TAMURA & NEI 1993), gamma distribution and 10,000 bootstraps. The Bayesian phylogram and the bootstrap consensus tree for the NJ analyses (Fig. 4a & b, respectively) were visualized with TREEGRAPH 2.0.50 (STÖVER & MÜLLER 2010).

Tab. 2: The estimated haplotypes and their frequency.

Species	Haplotype	Number of specimens
Bombus lucorum	L1	231
	L2	1
	L3	1
	L4	1
	L5	3
	L6	1
	L7	1
	L8	2
	L9	1
	L10	1
	L11	7
	L12	1
	L13	16
	L14	3
	L15	2
	L16	1
	L17	2
Bombus cryptarum	C1	2
	C2	67
	C3	16
	C4	1
Bombus terrestris	T1	1
	T2	25

Biogeographical and ecological analyses

To decipher the ecological differences between *B. lucorum* and *B. cryptarum*, the data collected on their distribution and foraging were compared against the determination using COI analyses. Therefore, the respective proportions of the species of every habitat category (Fig. 5), every altitudinal category (Fig. 6) and every area (Fig. 7 & Fig. 8) were calculated. To test if the proportion of the species was effected by habitat, an analysis of variance (ANOVA) was performed. Additionally, a likelihood ratio test of independence (*G* test) was computed to compare the proportions of the two species in the category "Woodland / Forest edge". As in MURRAY et al. (2008), a *G* test was used to examine the species composition below and above an altitudinal threshold, which in this study was 1200 m. Since crucial climatic factors, such as precipitation and temperature, considerably change with increasing altitude, these factors were also included into the analyses. Given the importance of dependable data concerning the altitudinal climate changes, the high resolution Austrian climate maps for 1971-2000 (HIEBL et al. 2011) were used, since the grids consider altitudinal changes by a digital elevation model. On this basis, together with the collected GPS data, it was possible to assign the mean annual precipitation sum and the mean annual air temperature of this period for each collection site where at least one specimen was collected. Further, it was examined if these assigned values differ between the investigated species. Since both, the mean annual precipitation sum and the mean annual air temperature data, do not follow a normal distribution, differences were tested with two-sample Wilcoxon rank sum tests. The GIS grids were kindly provided by Alexander Orlik from the *Zentralanstalt für Meteorologie und Geodynamik* (ZAMG) and handled with QGIS 2.2 (QGIS DEVELOPMENT TEAM 2014).
Furthermore, the distribution of the species was examined in respect to the geology of the particular collection areas. Therefore, the areas were categorized into two categories: mountains consisting of limestone and mountains primarily of crystalline, slate or sedimentary rock. Since geological implications seem to be unlikely when the basement rocks are covered with thick soil horizons, the collection areas located in the low and wetland areas were excluded from these analyses. The groups were compared with a *G* test. Statistical analyses were performed using R (R CORE TEAM 2013). For the *G* tests, the DEDUCER package (FELLOWS 2012) was used.

Results

Nucleotide composition, haplotypes, genetic distances and phylogeny

Partial COI sequences for 314 samples were obtained and successfully aligned. Overall, the 619 comparable positions revealed 67 polymorphic sites, 40 sites with transitions and 29 sites with transversions. The sequences revealed no gaps and indels. The relative values concerning the nucleotide composition were C = 13.62 %, T = 43.19 %, A = 33.29 % and G = 9.90 %, revealing the strong A + T bias that has been reported for the mitochondrial genome of several insect groups (CLARY & WOLSTENHOLME 1985; CROZIER et al. 1989; LIU & BECKENBACH 1992; BROWER & DESALLE 1998) and for the COI of the species of the LCMc (e.g. BERTSCH et al. 2005; BERTSCH 2009).
23 different haplotypes were found consisting of 17 haplotypes for *B. lucorum*, four haplotypes for *B. cryptarum* and two for *B. terrestris* (Tab. 2). For *B. lucorum*, the haplotype L1 is by far the most common and the sequences of all other haplotypes were highly similar. Only two haplotypes differed in more than one substitution, namely L9 with three and L14 with two substitutions. Due to these positions, the 206 amino acids long sequence revealed 13 polymorphic sites. The most common haplotype of *B. cryptarum*, C2, shared all except one position with C1 and C3 and the rare haplotype C4 has two individual positions (Tab. 4). The amino acid sequence showed only one polymorphic site, the other substitutions were at silent positions.
As shown in Tab. 3a and 3b, the interspecific divergence between *B. lucorum*, *B. cryptarum* and *B. terrestris* ranged from 0.044 to 0.080 for the net mean divergence and from 0.049 to 0.10 for the divergence based on maximum composite likelihood model. The divergences within the species were considerably smaller and ranged from 0.0001 to 0.0007, revealing a clear "barcoding gap". The smallest interspecific divergence was estimated between *B. lucorum* and *B. cryptarum*. However, the divergence between these species in comparison with the divergence within the species was significantly greater as confirmed by the AMOVA (F_{ST} = 0.986; d.f. = 1,360; p = 0.0000). The nucleotide diversity (π) and haplotype diversity (h) for *B. lucorum* was 0.00062 ± 0.00057 and 0.29 ± 0.0358, whereas 0.00067 ± 0.00064 and 0.362 ± 0.056 for *B. cryptarum*, respectively. Aside from the barcoding gap, the taxa of the LCMc were clearly separated into three distinct branches in both calculated trees, in the Bayesian phylogram and in the bootstrap consensus tree (Fig. 4a & b, respectively). With respect to this, the patterns of both trees were highly similar, revealing *B. cryptarum* and *B. magnus* as the most closely related taxa with *B. lucorum* as sister group. *B. terrestris* emerged as the sister group to the clade of these LCMc. All important nodes show great support in both trees, strongly suggesting four distinct groups.

Tab. 3a: Inter- & intraspecific divergence of the COI gene based on the maximum composite likelihood model ± S.E.

	B. lucorum	*B. cryptarum*	*B. terrestris*
B. lucorum	0.0006 ± 0.0002		
B. cryptarum	0.0491 ± 0.0139	0.0007 ± 0.0005	
B. terrestris	0.1015 ± 0.0282	0.0846 ± 0.0229	0.0001 ± 0.0001

Tab. 3b: Net mean divergence of the COI gene based on the Tamura-Nei model ± S.E.

	B. lucorum	*B. cryptarum*	*B. terrestris*
B. lucorum			
B. cryptarum	0.0436 ± 0.0091		
B. terrestris	0.0800 ± 0.0136	0.0696 ± 0.0123	

Tab. 4: Distinctive nucleotide positions of the determined haplotypes based on the full mitochondrial genome of *Bombus ignitus* from CHA et al. (2007). Positions with empty fields do not differ from the reference, whereas positions that solely differ in *B. ignitus* are not shown.

Nucleotide position		1723	1734	1741	1742	1750	1762	1768	1771	1813	1816	1846	1852	1861	1864	1880	1895	1903	1918	1948	1949	1954	1960	1966	1969	1972	1976	1985	2000	2005	2018	2020	2023	2038
*Bombus ignitus**		A	C	A	T	A	T	A	A	A	A	T	A	T	A	T	T	T	T	A	T	T	A	T	A	A	T	T	G	T	A	T	T	A
Bombus lucorum	L1		T		C			T		T	T	A		C			C	A	C	T											G		C	
	L2		T		C			T		T	T	A		C			C	A	C	T											G		C	
	L3		T		C			T		T	T	A		C			C	A	C	T		C									G		C	
	L4		T		C			T		T	T	A		C			C	A	C	T									A		G		C	
	L5		T		C			T		T	T	A		C			C	A	C	T													C	
	L6		T		C			T		T	T	A		C			C	A	C	T											G		C	
	L7		T		C			T		T	T	A		C			C	A	C	T											G		C	
	L8		T		C			T		T	T	A		C			C	A	C	T											G		C	
	L9		T	G	C			T		T	T	A		C			C	A	C	T											G		C	
	L10		T	G	C			T		T	T	A		C			C	A	C	T											G		C	
	L11		T		C			T		T	T	A		C			C	A	C	T					G						G		C	
	L12		T		C			T		T	T	A		C			C	A	C	T											G		C	
	L13		T		C			T		T	T	A		C			C	A	C	T											G		C	
	L14		T		C			T		T	T	A		C			C	A	C	T											G		C	
	L15		T		C			T		T	T	A					C	A	C	T											G		C	
	L16		T		C			T		T	T	A		C			C	A	C	C											G		C	
	L17		T		C			T		T	T	A		C			C	A	C	T											G		C	
Bombus cryptarum	C1	T	T					T		T		A							C	T						T	A	A		A	G	A		T
	C2	T	T					T		T		A							C	T						T	A	A		A	G	A		T
	C3	T	T			G		T		T		A							C	T						T	A	A		A	G	A		T
	C4	T	T			G		T		T		A							C	T						T	A	A		A	G	A		T
Bombus terrestris	T1	T	T				A		T				T		T	C		C		T	C		T	C				A			G	A		T
	T2	T	T				A		T				T		T	C		C		T	C			C				A			G	A		T

Nucleotide position		2050	2056	2059	2072	2083	2086	2091	2101	2107	2125	2131	2144	2182	2198	2209	2225	2230	2245	2248	2257	2264	2266	2287	2296	2299	2302	2308	2311	2317	2323	2324	2326	2329
Bombus ignitus		T	A	A	G	T	A	T	C	T	T	T	A	T	G	A	T	A	C	A	T	T	A	T	T	T	T	A	A	T	T	C	T	T
Bombus lucorum	L1		C			C			T					C		T		T	T			C	T	C		C		T				T	A	
	L2		C		A	C			T					C		T		T	T			C	T	C		C		T				T	A	
	L3		C			C			T					C		T		T	T			C	T	C		C		T				T	A	
	L4		C			C			T					C		T		T	T			C	T	C		C		T				T	A	
	L5		C			C			T					C		T		T	T			C	T	C		C		T				T	A	
	L6		C			C	G		T					C		T		T	T			C	T	C		C		T				T	A	
	L7		C			C			T					C		T		T	T	G		C	T	C		C		T				T	A	
	L8		C			C			T					C		T	C	T	T			C	T	C		C		T				T	A	
	L9		C			C		C	T					C		T	C	T	T			C	T	C		C		T				T	A	
	L10		C			C			T					C		T		T	T			C	T	C		C		T				T	A	
	L11		C			C			T					C		T		T	T			C	T	C		C		T				T	A	
	L12		C			C			T		C			C		T		T	T			C	T	C		C		T				T	A	
	L13		C						T					C		T		T	T			C	T	C		C		T				T	A	
	L14		C						T					C		T		T	T			C	T	C	C	C		T				T	A	
	L15		C			C			T					C		T		T	T			C	T	C		C		T				T	A	
	L16		C			C			T					C		T		T	T			C	T	C		C		T				T	A	
	L17		C			C			T					C		T		T	T			C	T	C		C		T				T	A	C
Bombus cryptarum	C1	C							T							T		C	A		A	C	T									T	A	
	C2	C							T							T		C	A		A	C	T						G			T	A	
	C3	C							T							T		C	A		A	C	T						G			T	A	
	C4	C							T						A	T		C	A		A	C	T						G			T	A	
Bombus terrestris	T1			T						A		C	T				C	T		T						C	A			C	C			
	T2			T						A		C	T				C	T		T						C	A			C	C			

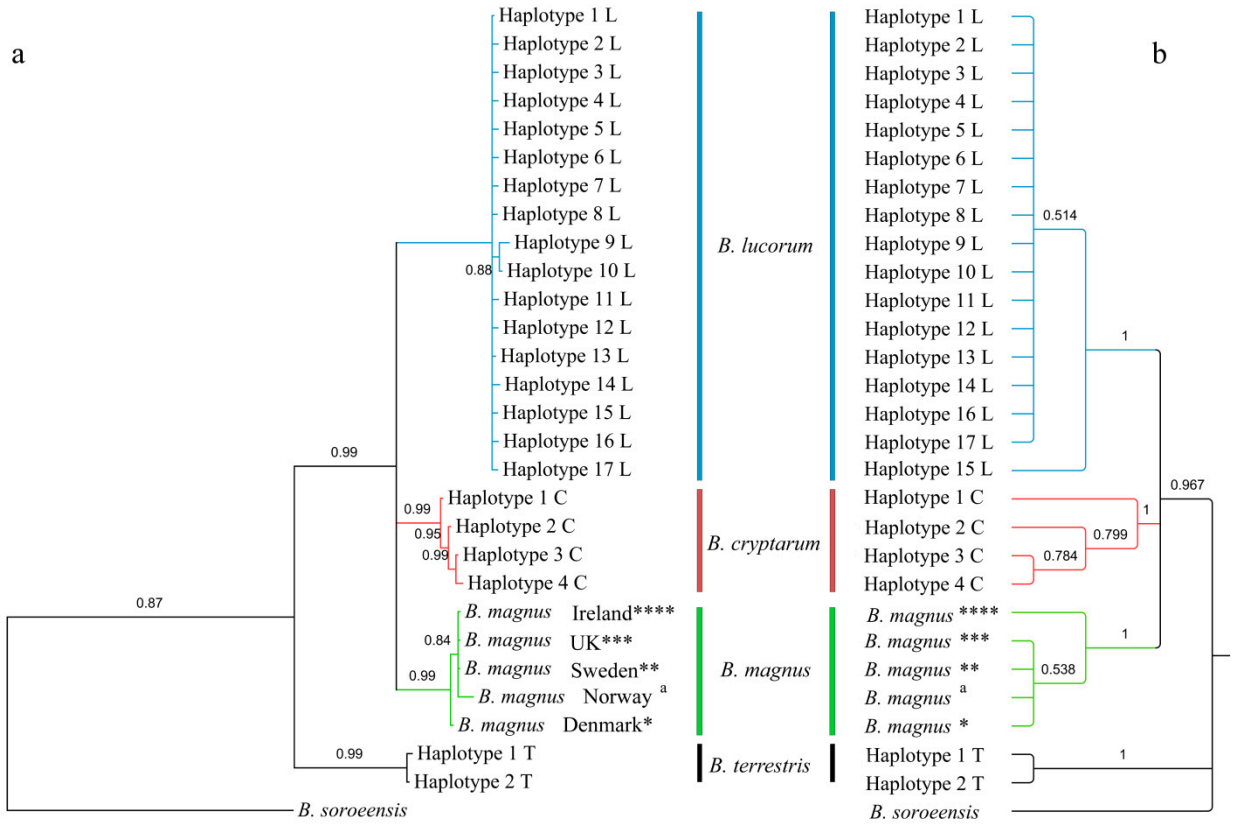


Fig. 4: Calculated phylogenetic trees. Samples with an asterisk are imported from GenkBank: JN872620 (*), JQ843552 (**), JQ692958 (***) and JN872607 (****). The sample with a superscript [a] corresponds to voucher #388. Phylogenetic analyses were based on 609 bp of the COI gene. (a): Bayesian phylogram. Values at branches show Bayesian posterior probabilities (PP), only those values that are belowe 1.00 are shown. (b): Bootstrap consensus tree for the neighbor joining analyses. Numbers show the bootstrap values, whereby the cutoff value is 50.

Ecological implications

Bombus lucorum and *Bombus cryptarum* appear widespread in Austria, whereas no evidence for *B. magnus* was found. *B. lucorum* and *B. cryptarum* co-occur in 13 of 18 study areas, in the remaining five areas only *B. lucorum* was found. With 275 specimens, *B. lucorum* is by far the most common species, followed by *B. cryptarum* with 86 specimens. *B. lucorum* is more abundant in the majority of study areas, only the three areas in the Hohe Tauern and the small sample from Litschau show greater proportions of

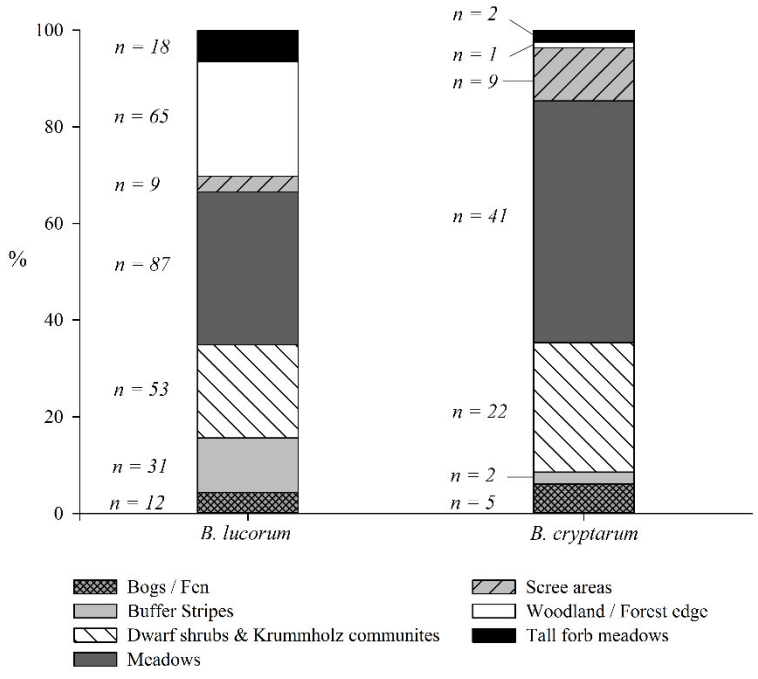


Fig. 5: The distribution of *Bombus lucorum* and *Bombus cryptarum* along the examined habitats. Both species occurred in every habitat type and most often on the various meadow types. *B. lucorum* seems to occur often in woodlands and forest edges whereas *B. cryptarum* seems to avoid these habitats. The figure shows the respective proportion of both species and is designed after Fig. 3 from WATERS et al. (2010).

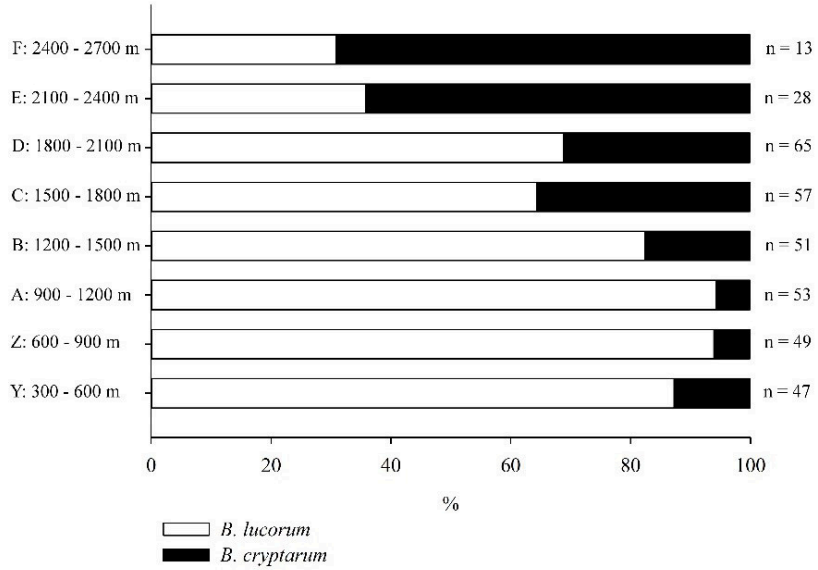
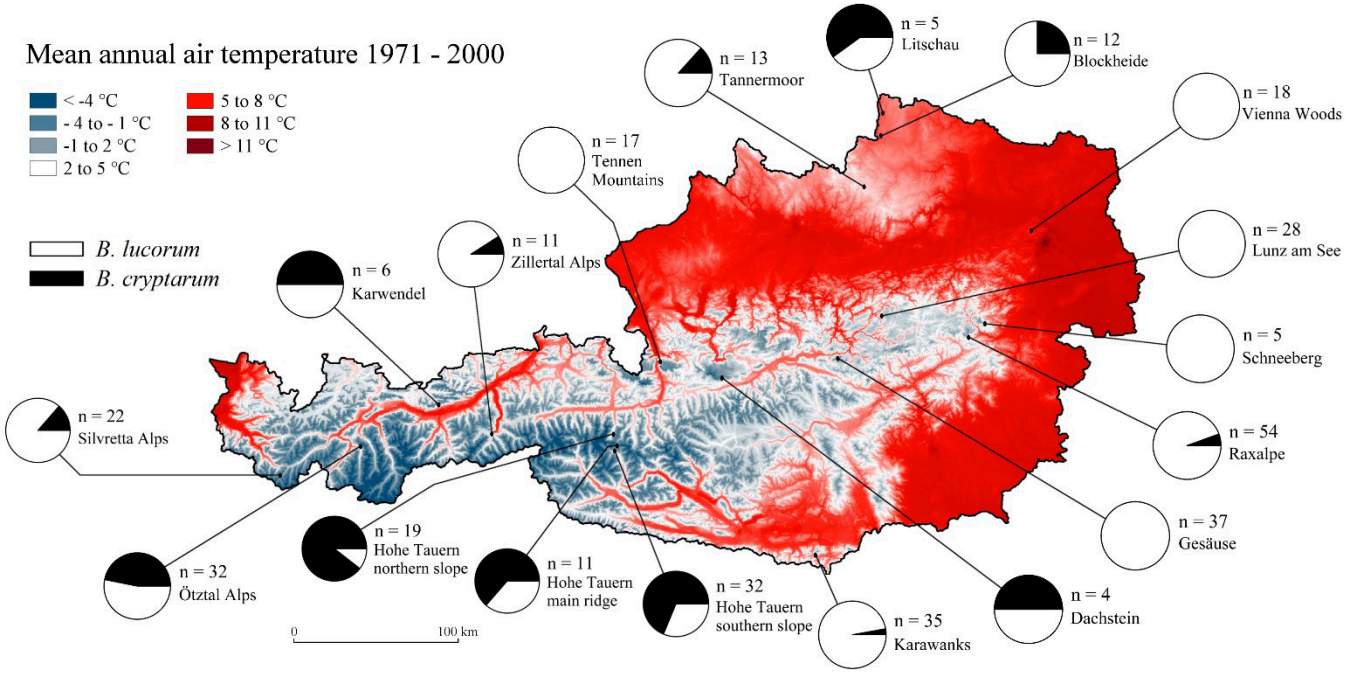


Fig. 6: The proportions of *Bombus lucorum* and *Bombus cryptarum* in the respective altitudinal categories reveal a shift in the species abundances along the altitudinal gradient. The proportion of *B. cryptarum* rises with increasing altitude.

B. cryptarum. Most specimens of *B. cryptarum* were collected in the Central Eastern Alps, located in western Austria, especially in the Hohe Tauern and Ötztal Alps. *B. cryptarum* seems to be very rare in eastern Austria, whereas there are remarkable findings in wetlands in the north. Both species occurred in all seven habitat categories. Neither the number of collected specimens of *B. lucorum* ($F = 0.276$; $p = 0.606$), nor of *B. cryptarum* ($F = 0.734$; $p = 0.402$) was significantly affected by the habitat. However, most individuals of both species were captured in meadow habitats and *B. cryptarum* seems to be relatively more abundant in scree areas. With only one collected individual, it appears conspicuous, that *B. cryptarum* is almost completely absent from woodlands, whereas *B. lucorum* was found there frequently. The proportion of the two species found in woodlands, compared to all other habitats, shows *B. lucorum* to be highly significantly more abundant in woodlands than *B. cryptarum* ($G = 30.225$; $p < 0.0001$). As shown in Fig. 6, both species occurred along the complete altitudinal range, whereas the proportion of *B. cryptarum* clearly rises with increasing altitude. *B. lucorum* is more abundant in all altitudinal categories except the two highest categories, in which *B. cryptarum* occurred more often. Comparing the species composition below and above the altitudinal threshold of 1200 m reveals a significant inhomogeneity ($G = 40.193$; $p < 0.0001$). Based on the mean annual air temperature for 1971-2000 (Fig. 7), the mean of the annual air temperature for all collection sites is 2.53 °C for sites of *B. cryptarum* and 4.49 °C for sites of *B. lucorum* (Fig. 9a). The Wilcoxon rank sum tests demonstrates the difference between these groups as statistically significant ($W = 6273.5$; $p < 0.0001$). *B. lucorum* occurs in the warmest and coldest study areas, whereas *B. cryptarum* is absent from regions with a mean annual air temperature

Fig. 7: The large-scale distribution of *Bombus lucorum* and *Bombus cryptarum* in Austria on a climate map. The pie charts show the respective proportions of the species in the study areas. The climate map shows the mean annual air temperature for the period 1971 – 2000 with linearized color interpolation and is based on the data of HIEBL et al (2011).



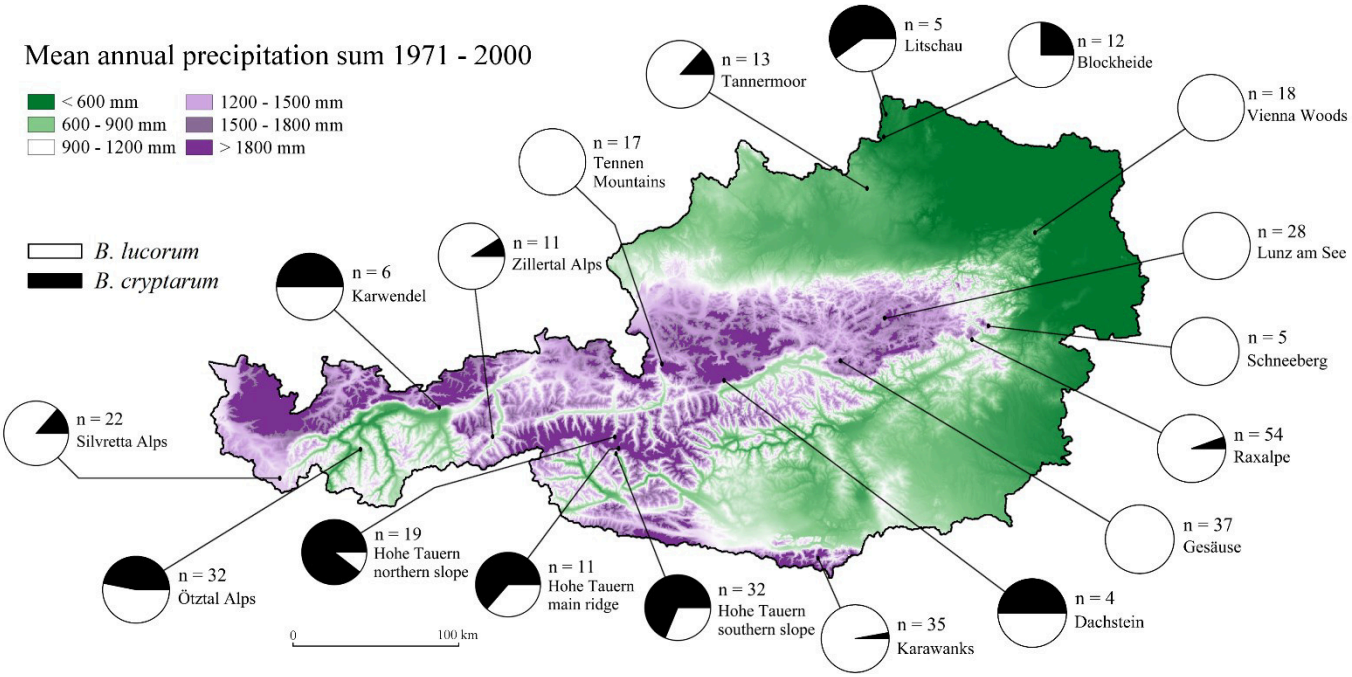


Fig. 8: The distribution of *Bombus lucorum* and *Bombus cryptarum* based on a climate map showing the mean annual precipitation sum for the period 1971-2000. The map has linearized color interpolation and is based on the data of HIEBL et al (2011).

higher than 7.1 °C. This includes great parts of eastern Austria. In addition, most findings of *B. cryptarum* in areas with a mean annual air temperature higher than 5.6 °C are located in the northern wetlands, which may not be representative since the special climatic condition of wetlands were not considered in the used climatic maps. The mean annual precipitation seems to have no detectable effect on the species composition ($W = 10897$; $p = 0.2722$). Both species occurred in areas with high and low precipitation (Fig. 8), resulting in a mean precipitation of 1356 mm per year for the collection localities of *B. cryptarum* and 1410 mm per year for the sites of *B. lucorum* (Fig. 9b). Significant heterogeneity was revealed by the *G* test ($G = 91.81$; $p < 0.0001$) concerning the distribution of the species with respect to the geology of the collection areas. Only 9 specimens of *B. cryptarum* were found in mountains consisting of limestone, in contrast, 69 specimens could be found in mountains comprised primarily of crystalline, slate or sedimentary rock. 168 specimens of *B. lucorum* were found on limestone mountains and 67 on crystalline, slate or sedimentary rock mountains.

Both *B. lucorum* and *B. cryptarum* could be found foraging on a variety of plant species (Tab. 5). A total of 216 flower visits were recorded for *B. lucorum* and 74 flower visits were observed for *B. cryptarum*. In total, *B. lucorum* visited 59 different plant species, and 53 species from 19 different plant families were used for collecting pollen. This includes uncommon plant visits on species of *Rumex* (Polygonaceae) and *Dactylis glomerata* (Poaceae) for pollen collection. *B. cryptarum* was found on flowers of 30 plant species, of which 18 species from 11 families were used for collecting pollen. The majority of plant species were observed to be visited by both bumblebee species. The two plant species for which most visits were observed are shared along the two species, namely *Calluna vulgaris* and *Rhinanthus glacialis*. Other plants that were frequently used by *B. lucorum* and *B. cryptarum* are species of *Vaccinium* and *Trifolium*. However, due to the great number of the different plant species visited, there are many plant species for which only one visit could be observed. Both bumblebee species could be observed performing nectar robbery, especially on flowers of *Rhinanthus*. Consulting Tab. 5, it appears that *B. lucorum* performs buzz pollination more frequently with 35 observed flower visits with buzzing, in contrast to *B. cryptarum,* with only one single observation. However, it should be noted, that the majority of plant species on which *B. lucorum* performed buzzing were not visited by *B. cryptarum* in this study.

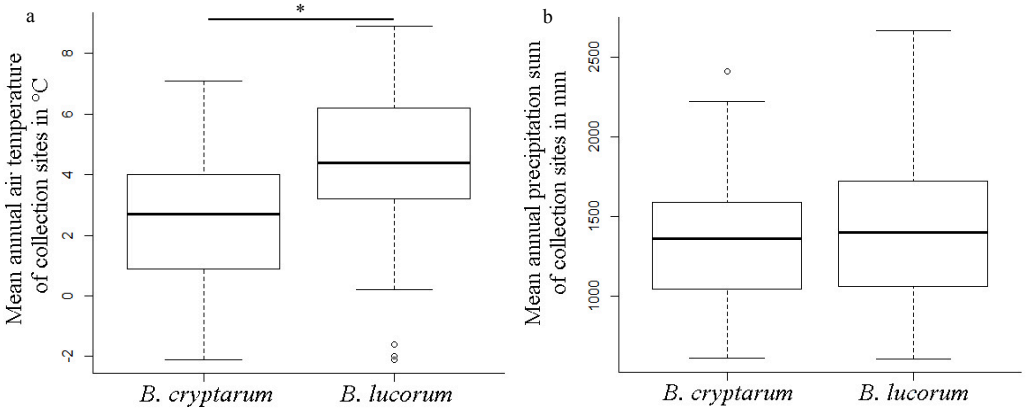


Fig. 9: (a) The mean annual air temperature and (b) the mean annual precipitation sum of the collection sites of all collected *B. cryptarum* and *B. lucorum* for the period 1971-2000. Box-Whisker-Plot, range = 1.5 * IQR. The asterisk indicates a significant difference between the groups based on a Wilcoxon rank sum test ($W = 6273.5$; $p < 0.0001$).

Tab. 5: The recorded flower visits of females of *B. lucorum* and *B. cryptarum* and the numbers of individuals collecting pollen, foraging nectar, foraging nectar by nectar robbery and buzzing.

	B. lucorum	#pollen	#nectar	#nectar robbery	#buzzing	*B. cryptarum*	#pollen	#nectar	#nectar robbery	#buzzing
Acinos alpina	1	1	1							
Aegopodium podagraria						1		1		
Angelica sylvestris	1		1							
Anthyllis sp.						1	1	1		
Anthyllis vulneraria	1	1		1	1	1		1		
Aruncus dioicus	3	3								
Betonica alopecuros	2	2	1	1	1					
Buphthalmum salicifolium	1	1								
Calluna vulgaris	23	6	20			15		15		
Carduus sp.	1	1	1							
Centaurea pseudophrygia	1	1	1							
Centaurea scabiosa	1	1								
Centaurea sp.	2	2	2							
Cirsium arvense						1		1		
Cirsium oleraceum	1	1	1							
Dactylis glomerata	1	1								
Dryas octopetala	1	1			1					
Echium sp.						1	1	1		
Epilobium angustifolium						1		1		
Filipendula ulmaria	1		1							
Genista sagittalis	3	3			3					
Gentiana germanica						1	1	1		
Geranium sylvaticum						1		1		
Helianthemum alpestre	3	3			2	3	3			1
Helianthemum nummularium	5	5			3	2	2			
Helianthemum sp.	2	2			1	1	1			
Hypericum maculatum	2	2				1	1			
Hypericum perforatum	4	4								
Impatiens glandulifera	1	1	1							
Inula sp.	1	1								
Leontodon hispidus	1	1	1							
Ligusticum mutellina	2	2								
Lotus corniculatus	14	14	11	1		2	1	2		
Lupinus polyphyllus	6	6	6			1	1	1		
Melampyrum pratense	1	1	1							
Melampyrum sylvaticum	1	1	1		1					
Myosotis alpestris	1	1	1							
Onobrychis arenaria	1		1							
Origanum vulgare	1		1							
Oxytropis campestris						2			2	
Pedicularis verticillata	1	1			1					
Pedicularis sp.	9	9			1					
Plantago media	1	1								
Potentilla aurea	1	1				1	1			
Pulicaria dysenterica	1	1								
Ranunculus acris	6	6			5					
Rhinanthus alectorolophus	6	6	5	1						
Rhinanthus glacialis	19	19	6	13	4	13	13	2	10	
Rhinanthus sp.	10	10	1	8	1					
Rhododendron ferrugineum						1	1	1		
Rhododendron hirsutum	5	5	4	1	2					
Rosa canina agg.	5	5			4					
Rumex alpinus	1	1			1					
Rumex obtusifolius	1	1								
Saxifraga rudolphiana	1	1	1			2	2	1		
Securigera varia	2	2	1	1						
Silene acaulis	1	1	1			3	2	3		
Silene vulgaris	1		1			1		1		
Solanum dulcamara	1	1			1					

Tab. 5: Continued.

Spiraea x *bumalda*	2	2								
Stachys sp.	1	1	1							
Symphoricarpos albus	2		2							
Telekia speciosa	4	4	4							
Thymus praecox agg.	8	3	8			2	1	2		
Trifolium montanum						1		1		
Trifolium pratense	12	4	9	2		5	2	3	2	
Trifolium repens	9	8	7			1		1		
Trollius europaeus	1	1			1					
Vaccinium oxycoccus	10	10	8			5	5	2		
Vaccinium vitis-ideae	1	1			1					
Valeriana officinalis	1	1								
Veronica sp.						1		1		
Viccia cracca	1	1		1		2	1		2	
Viccia sp.	1		1			1		1		
Viccia tenuifolia	1	1								
Total	216	177	113	30	35	74	40	45	16	1

Discussion

Genetic variation and the haplotypes in the European context

The species of the cryptic European *Bombus lucorum*-complex can clearly be separated with the phylogenetic analyses of the COI gene. Therefore, the results based on the Austrian specimens are in accord with the results of the recently published studies from Europe (BERTSCH et al. 2005; MURRAY et al. 2008; BERTSCH 2009; CAROLAN et al. 2012). The data on inter- and intraspecific distances from these studies and from the present study (Tab. 3a & b) reveal meaningful divergences, which is also reflected in the results of the AMOVA. However, when comparing the results from the different studies, it must be mentioned that almost all studies were carried out with different primer sets. Therefore comparisons are restricted to the sequence overlap (Fig. 10).

The intraspecific divergences from this study are considerably smaller than in the previous studies. This is not surprising since they were carried out with specimens collected in a variety of regions in Europe (BERTSCH et al. 2005; MURRAY et al. 2008; BERTSCH 2009; CAROLAN et al. 2012): increasing intraspecific genetic variation along geographic gradients is a general pattern in phylogeographic studies (AVIS 2000; BERGSTEN et al. 2012). Therefore the intraspecific divergences from this study are expected to be smaller due to the more narrow geographic range. However, even if the geographic scale is restricted to Austria, the genetic variation within the species is surprisingly small as indicated by the very low nucleotide diversity (π) and haplotype diversity (h). The *B. lucorum* specimens from MURRAY et al. (2008) reveal greater genetic variation, but variation is still very low with an average substitution rate of 1.4 substitutions for a 700 bp long segment. Combining data from the other studies, there seems to be one main haplotype group for *B. lucorum* that consists of relatively few and highly similar haplotypes indicating a low nucleotide diversity in Europe: L1 from this study is identical with the most common haplotype 1 (acc. no. JN872605.1) from CAROLAN et al. (2012) and with three of four haplotypes from BERTSCH et al. (2005), namely luc-menz-1 (acc. no. AY530009), luc-menz-2 (acc. no. AY530010) and luc-yakutsk (acc. no. AF279497). The fourth haplotype (acc. no. AY181117) is from Austria and differs only in one single substitution. Interestingly, this substitution is not shared by a haplotype from this study (Tab. 4). Further, the L1 haplotype is the predominant one in the study of WILLIAMS et al. (2012), e.g. it occurs in Turkey (acc. no. JQ843510), Sweden (acc. no. JQ843547), Iceland (acc. no. JQ843513) and Mongolia (acc. no. JQ843504). In conclusion, this means that the most common haplotype from this study, L1, belongs to the same haplotype group that is predominant in Austria, Ireland, Scotland, Germany,

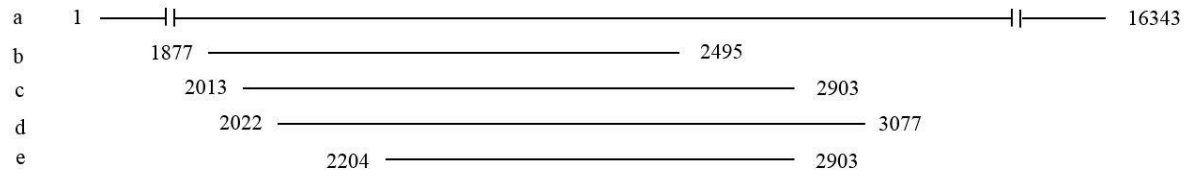


Fig. 10: Overview about the positions of the COI sequences of relevant studies based on a full mitochondrial genome of *Apis mellifera* (a) from CROZIER & CROZIER (1993). b shows the position of the partial COI sequences from this study and from BARDAKJI (2013). Further, the positions obtained in studies from BERTSCH et al. (2005) (c), PEDERSEN (2002) (d), and MURRAY et al. (2008) (e) are given. Numbers indicate the exact codon position based on a. The strains are not in scale.

Denmark, Sweden and Finland and even occurs in Iceland, Turkey, Mongolia, China and great parts of Russia. Low nucleotide diversity, together with low haplotype diversity has been reported to characterize populations that suffered strong genetic bottleneck conditions or drastic population decreases (AVIS 2000). In this case the situation is probably caused by the dramatic climatic changes in the Pleistocene and the related multiple glaciations of great parts of Western Palaearctic. All European areas mentioned above were surely recolonized by *B. lucorum* after the last deglaciation, which began approx. 14 kyr ago (RANDI 2007). Indicated by the diversity indices, the postglacial recolonization event was most likely conducted by a single genealogical linage that expanded toward central and northern Europe. The high frequency of haplotypes that differ exclusively in one, or rarely two positions, suggests a sudden and rapid expansion of a more or less small population. During the postglacial population an increase in the number of slightly different haplotypes could occurred, whereas the time was too short to develop great nucleotide diversity. However, it remains unclear where the recolonization event began. A south European refugium suggests itself because of the small geographic distance. However, bumblebees are very mobile organisms and can spread quickly over great distances as revealed by the recent spreading of *Bombus haematurus* (e.g. NEUMAYER 2004; SÁROSPATAKI, NOVÁK & MOLNÁR 2005; ŠIMA & SMETANA 2009; JENIČ, GOGALA & GRAD 2010; TEPPNER 2010) and *Bombus semenoviellus* (e.g. RASMONT et al. 2005; STREINZER 2010; ŠIMA & SMETANA 2012). Therefore, potential non-Mediterranean refugia, as mentioned by BILTON et al. (1998) for mammals, should be taken into account. A postglacial expansion originating from the hills of Crimea or the southwestern Ural Mountains might explain the presence of the haplotype in great parts of Russia and the same applies to the Altai Mountains and its geographical proximity to China and Mongolia.

The situation for *B. cryptarum* is slightly different. Several studies revealed greater intraspecific divergences as in *B. lucorum* (MURRAY et al. 2008; CAROLAN et al. 2012; WILLIAMS et al. 2012). This could not be confirmed in the present study and by BERTSCH (2009), but a closer look at the haplotypes reveals the reason for this inconsistence. The recent studies (CAROLAN et al. 2012; WILLIAMS et al. 2012) revealed two major haplotype groups with distinct COI sequences and diagnostic positions of substitutions. Interestingly, haplotype groups 1 and 2 from CAROLAN et al. (2012) differ in 8 of 642 positions. The extensive sample of WILLIAMS et al. (2012) allowed the authors to draw distributional patterns of the haplotype groups: haplotype 1 occurs on the British Isles, Central Europe, Turkey and further east reaching central Asia, whereas haplotype 2 has a more widespread boreal distribution in Scandinavia, Russia, Mongolia, China and even reaches western North America. Interestingly, both haplotypes co-occur in Scotland (WILLIAMS et al. 2012). In line with these patterns, all haplotypes of *B. cryptarum* from this study belong to group 1, thereby decreasing the genetic variation of the sample and reducing the intraspecific divergence. Due to the remarkable number of stable diagnostic positions, it can safely be assumed that both haplotype groups represent separated genealogical lineages that recolonized great parts of the Palaeartic on different dispersal routes. As discussed for *B. lucorum*, potential refugia remain unclear. Based on today's patterns, it can be assumed that the ancestral lineage of the haplotype 2 group was not contracted in a Mediterranean refugium and originated from a refugium in eastern Europe or Asia. Additionally, cryptic northern refugia as suggested by STEWART & LISTER (2001), can be considered. In contrast, today's distribution of haplotype group 1 indicates a Mediterranean or southeastern refugium. However, the current data does not allow one to clarify the phylogeography of the species with certainty.

The species status of *B. cryptarum* with respect to *B. lucorum* is widely accepted nowadays. This view was decisively influenced by the distance-based delineation with sequence data of the COI gene. Concerning the delineation of the species based on the sequence data, this study resampled the results from the other recently published studies about the LCMc (BERTSCH et al. 2005; MURRAY et al. 2008; BERTSCH 2009; CAROLAN et al. 2012; WILLIAMS et al. 2012). In summary, the clear "barcoding gap" between the intra- and interspecific divergences, together with the results from the AMOVA and the clearly separated and highly supported tree branches (Fig. 4) provide overwhelming evidence for four distinct taxa in the European subgenus *Bombus* s. str. Since there are no intermediates between the taxa, the hypothesis of MURRAY et al. (2008) that their results "provide strong support for the existence of *B. cryptarum*, *B. lucorum*, *B. magnus* and *B. terrestris* as species that are discrete genotypic clusters", with respect to the Genotypic Cluster Concept of species (MALLET 1995), is completely in line with the results from this study.

Ecological implications

Aside from the phylogeographic insights, the results of this study contribute to sharpen the ecological profile of the species of the LCMc. When dealing with the available data of the species of the LCMc from the literature, one is confronted with three major problems. First, the last taxon, *B. cryptarum*, was redescribed in 1981 (RASMONT 1981a). All data before the redescription is unreliable since it is not possible to distinguish the species by the debatable morphological traits. Against this background, it seems unnecessary to make uncommented use of references published before that date, such as the textbook of ALFORD (1975) in MURRAY et al. (2008) and WATERS et al. (2011). The same applies for the study area: most Austrian specimens mentioned as *Bombus magnus* from Austria before the redescription were checked recently and belong to *B. cryptarum* based on morphology (NEUMAYER, pers. comm.). Second, many authors did not immediately accept *B. cryptarum* as a valid taxon and pooled the available data. In a strict sense, many reference textbooks (e.g. PRŶS -JONES & CORBET 1987; VON HAGEN 1990; WESTRICH 1990) cannot be taken in account for reliable data. Third, the species determination based on morphology is at least extremely difficult and the reliability of the used traits must be confirmed with biochemical methods. Until then, most studies based on morphological identification should be considered critically.

In light of these problems, the number of applicable studies strongly decreases. Reliable ecological data is primarily available in the recent studies based on biochemical methods (BERTSCH 1997; BERTSCH et al. 2004; BERTSCH et al. 2005; MURRAY et al. 2008;

BERTSCH 2009; WATERS et al. 2011; CAROLAN et al. 2012). Additionally the data from Pierre RASMONT (RASMONT 1981a; RASMONT 1981b; RASMONT 1983; RASMONT 1984; RASMONT et al. 1986) should be considered, since he is probably the world's leading expert in the morphological identification of the European species of the LCMc.

Bombus lucorum and Bombus cryptarum

Overall, *Bombus lucorum* is the most abundant species of the LCMc in Austria. This agrees with the results from other geographic regions in Europe, e.g. Czech Republic (URBANOVÁ et al. 2001), Poland (BANASZAK & RASMONT 1994), Ireland (MURRAY et al. 2008) and Finland (PAMILO et al. 1997; VESTERLUND et al. 2014). In contrast, *B. cryptarum* is more abundant in a study from north-western Scotland (WATERS et al. 2011). In Austria, *B. lucorum* and *B. cryptarum* are not geographically evenly distributed. A factor that have been claimed to be of importance is the altitude: *B. cryptarum* is referred to as a high mountain species (NEUMAYER & PAULUS 1999). The results from this study reveal a gradual increase of the proportion of *B. cryptarum* along an altitudinal gradient (Fig. 6), strongly indicating a higher abundance of *B. cryptarum* in the high-lying habitats of the Austrian Alps. *B. cryptarum* reaches altitudes up to 2570 m a.s.l. but is not restricted to high mountains as the records in northern Austria reveal. Therefore the classification as a high mountain species cannot be entirely upheld, a finding described in DOROW (2004). MURRAY et al. (2008) revealed altitudinal distribution patterns with similar tendencies as in this study, but their altitudinal range is restricted from 150 m to 550 m a.s.l. However, the facts that *B. cryptarum* and *B. lucorum* co-occur in all examined altitudinal categories and that both species can be found sympatric in various lowland habitats all over Europe (e.g. BERTSCH 1997; BERTSCH et al. 2004; MURRAY et al. 2008; WATERS et al. 2011) denies that altitude is the striking factor that determines the species distribution. This suggests the existence of influencing factors that change along the examined altitudinal gradient, e.g. the changing climatic conditions. Two climatic parameters were examined in this study and reveal interesting results: the mean annual precipitation sum does not seem to have an effect on the abundance of the species (Fig. 9b). Both species occur in areas with high and low annual precipitation, e.g. the Hohe Tauern and the Ötztal Alps (Fig. 8). In contrast, the mean annual air temperature reveals distributional differences between the species (Fig. 9a): as a trend, the localities that *B. cryptarum* inhabits are colder than the those where *B. lucorum* is found. This pattern can be traced along the colder habitats in the Alps (Fig. 7): *B. cryptarum* occurs mainly in western Austria along the main ridge of the Alps, whereas it is very rare or absent in the lower mountains and foothills of the Alps in the eastern regions. Exceptions are findings *B. cryptarum* in the wetlands in northern Austria. In these cases, the mean air temperature of the collection sites are considerably higher than those in the Alps. However, the special climatic conditions of wetlands are not considered in the climate maps. Therefore, the climatic data of the findings in northern Austria are of restricted value.

It seems unusual that the species composition of *B. lucorum* and *B. cryptarum* differs witht respect to the geology of the collection areas. Such a pattern is typical for many sibling plant species in the Alps but is widely unknown for insects. Even though the statistical test provides a significant result, it remains unclear in which way the geology of the basement rocks should interact with the bumblebees and how this may influence their abundance. However, one should bear in mind that these results might be due to a distortive sampling: approx. 75% of all *B. cryptarum* specimens were collected in the non-limestone areas of the Hohe Tauern and the Ötztal Alps. In contrast, there are regions based on limestone, such as the Dachstein and the Karwendel, where *B. cryptarum* comprises half of all sampled specimens. With four and six collected specimens, respectively, the total number of samples from these regions are far too small to have a decisive impact on the statistical test. Nonetheless, *B. cryptarum* occurs in areas based on limestone and might not be less abundant there than *B. lucorum.*

The collection sites of this study show that both *B. lucorum* and *B. cryptarum* may appear in all specified habitat categories. The species had different abundances: *B. cryptarum* seemed to avoid woodlands and was relatively more abundant in scree areas than *B. lucorum*. These findings are linked to the altitudinal patterns: several high-lying collection sites where *B. cryptarum* was abundant lay above the treeline, and scree areas are typical environments of the alpine level. Therefore, this observation is in agreement with the greater abundance of *B. cryptarum* in the highest habitat categories. In contrast, *B. cryptarum* was not sampled in regions that were dominated by woodlands, such as the Gesäuse or Lunz am See. In a study in northwestern Scotland, WATERS et al. (2011) also showed that *B. cryptarum* rarely occurs in woodlands but the same applies to *B. lucorum*. Nonetheless, it remains unclear how extensive the woodlands were sampled, since they provide a small number of specimens from that category. Additionally, they reported both species to occur frequently in heathlands, a habitat type that is not relevant in Austria. In contrast, BERTSCH et al. (2004) collected queens of all LCMc taxa in a pine forest. However, many bumblebees are probably opportunistic reacting organisms and are rarely restricted to a single habitat type: a radio-tracking study showed that bumblebees can travel great distances for food resources and frequently change the used habitats (HAGEN et al. 2011).

With very limited available data, RASMONT (1984) attempted the first ecological characterization of *B. cryptarum* as an stenoecious ericophilous species. Against the background of the currently available data, this categorization is too narrow. The species is not restricted to habitats dominated by Ericaeae nor does it rely on Ericaceae for flower visits. The results of this study and from WATERS et al. (2011) reveal that *B. cryptarum* occurs in many different habitats and forages on a wide range of plant species from various families. Due to its widespread distribution in the Palaearctic and even in parts of the Nearctic, a distinct definition would not contribute significantly to the ecology of the species at our current state of knowledge. Therefore, furthar ecological data from other regions of the Palaearctic is necessary.

As described in the literature and in previous studies, both species clearly show polylectic foraging. The many flower visits on a large number of plant species from several families indicate a wide breadth of diet. Both species show similar preferences, however, the present study design does not allow calculating reliable diet breadths of the respective species.

Bombus magnus

The third species of the LCMc is either extremely rare or absent in Austria. The present study provided no evidence for the presence of *B. magnus* in Austria. Nonetheless, the literature provides records of *B. magnus* in Austria (e.g. findings from W.F. REINIG in AISLEITNER 2000; findings from B. TKALCŮ in NEUMAYER & KOFLER 2005). However, as mentioned above, these findings probably belong to *B. cryptarum* and are not reliable. For Austria, no specimens of *B. magnus* are available that could be used for species identification ensured by a genetic or pheromonal evidence.

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Appendix

Tab. 6: Collection table of all collected specimens, collection sites, habitats, individual specimen numbers, sex, genetic haplotypes, GPS coordinates, elevations, dates, visited plant species and the collectors. Collector abbreviations: Silas Bossert (S.B.), Johann Neumayer (J.N.), Joseph F. Gokcezade (J.F.G.), Barbara-Amina Gereben-Krenn (B.-A. G.-K.), Hannes F. Paulus (H.F.P.). Specimens from BARDAKJI (2013) are marked with an asterik.

Region / Collection site	Habitat	#S.	Species	Haplo type	Lat. / Long.	Elevation (m) / category	Date	Flower visit / feeding	Collector
Vienna, Vienna Woods / Gütenbachtal	Meadow	1	*B. lucorum* ♀	L1	N48.143468 E16.237725	300 / Y	28.05.2013	*Onobrychis arenaria* / nectar	S.B.
	Meadow	2	*B. terrestris* ♀	T2	N48.143411 E16.239259	301 / Y	28.05.2013	*Onobrychis arenaria* / nectar	S.B.
	Meadow	3	*B. terrestris* ♀	T2	N48.143926 E16.240622	308 / Y	28.05.2013	*Onobrychis arenaria* / nectar	S.B.
	Meadow	4	*B. terrestris* ♀	T2	N48.142938 E16.240954	317 / Y	28.05.2013	*Onobrychis arenaria* / nectar	S.B.
	Meadow	5	*B. terrestris* ♂	T2	N48.144341 E16.242531	301 / Y	28.05.2013	*Salvia pratense*, nectar	S.B.
Lower Austria, Vienna Woods / Kierlinger Forst	Meadow	6	*B. lucorum* ♀	L1	N48.278773 E16.261049	428 / Y	09.06.2013	*Rhinantus alectorolophus* / pollen & nectar	S.B.
	Meadow	7	*B. lucorum* ♀	L1	N48.279145 E16.259161	414 / Y	09.06.2013	*R. alectorolophus* / pollen & nectar	S.B.
	Meadow	8	*B. lucorum* ♀	L1	N48.278231 E16.259118	429 / Y	09.06.2013	*R. alectorolophus* / pollen & nectar	S.B.
	Meadow	9	*B. lucorum* ♀	L1	N48.278188 E16.257080	424 / Y	09.06.2013	*R. alectorolophus* / pollen & nectar	S.B.
Lower Austria, Vienna Woods / Weidlingsbach	Meadow	10	*B. terrestris* ♀	T2	N48.272176 E16.230268	330 / Y	12.06.2013	*Trifolium repens* / pollen	S.B.
	Meadow	11	*B. lucorum* ♀	L1	N48.272947 E16.229110	352 / Y	12.06.2013	*Filipendula ulmaria* / pollen & nectar	S.B.
	Meadow	12	*B. terrestris* ♀	T2	N48.273747 E16.227833	372 / Y	12.06.2013	*T. repens* / pollen	S.B.
	Meadow	13	*B. lucorum* ♀	L1	N48.273754 E16.229914	374 / Y	12.06.2013	*T. repens* / pollen	S.B.
	Meadow	14	*B. lucorum* ♀	L1	N48.264299 E16.232807	391 / Y	12.06.2013	*T. repens* / pollen & nectar	S.B.
	Meadow	15	*B. lucorum* ♀	L1	N48.263013 E16.231413	412 / Y	12.06.2013	*Lotus corniculatus* / pollen	S.B.
	Meadow	16	*B. lucorum* ♀	L1	N48.263013 E16.231413	412 / Y	12.06.2013	*L. corniculatus* / pollen	S.B.
	Meadow	17	*B. terrestris* ♀	T2	N48.260242 E16.229760	440 / Y	12.06.2013	*T. repens* / pollen & nectar	S.B.
	Meadow	18	*B. terrestris* ♀	T2	N48.261699 E16.228602	430 / Y	12.06.2013	*Trifolium pratense* / pollen	S.B.
	Meadow	19	*B. lucorum* ♀	L1	N48.262613 E16.229546	432 / Y	12.06.2013	*Ranunculus acris* / pollen	S.B.
	Meadow	20	*B. lucorum* ♀	L1	N48.264570 E16.232228	393 / Y	12.06.2013	*Dactylis glomerata* / pollen	S.B.
Lower Austria, Vienna Woods / Sophienalpe	Meadow	21	*B. lucorum* ♀	L1	N48.242153 E16.226585	446 / Y	13.06.2013	*L. corniculatus* / pollen	S.B.
	Meadow	22	*B. lucorum* ♀	L1	N48.244211 E16.226155	464 / Y	13.06.2013	*Rhinantus alectorolophus* / pollen & nectar	S.B.
	Meadow	23	*B. lucorum* ♀	L1	N48.245597 E16.230125	472 / Y	13.06.2013	*T. repens* / pollen & nectar	S.B.
	Meadow	24	*B. lucorum* ♀	L1	N48.246004 E16.230699	466 / Y	13.06.2013	*T. repens* / pollen & nectar	S.B.
Lower Austria / Perchtoldsdorf	Meadow	25	*B. lucorum* ♀	L1	N48.126108 E16.249428	323 / Y	28.06.2013	*Centaurea* sp. / pollen & nectar	S.B.
Vienna / Schafbergwiese	Meadow	26	*B. terrestris* ♀	T2	N48.238109 E16.293856	337 / Y	19.07.2013	*Oxytropis* sp. / pollen & nectar	S.B.
	Meadow	27	*B. lucorum* ♂	L1	N48.239146 E16.292182	370 / Y	19.07.2013	*Centaurea* sp. / nectar	S.B.
	Meadow	28	*B. terrestris* ♀	T2	N48.238375 E16.293824	342 / Y	19.07.2013	*Stachys* sp. / nectar	S.B.
	Meadow	29	*B. terrestris* ♀	T1	N48.238650 E16.291276	353 / Y	19.07.2013	*Stachys* sp. / nectar	S.B.
Lower Austria / Blockheide	Buffer stripes	30	*B. cryptarum* ♀	C2	N48.775389 E14.994750	486 / Y	19.06.2013	*Aegopodium podagraria* / nectar	S.B.

Tab. 6: Continued.

	Buffer stripes	31	*B. lucorum* ♀	L9	N48.776177 E14.996651	496 / Y	19.06.2013	*Lupinus polyphyllus* / pollen & nectar	S.B.
	Buffer stripes	32	*B. lucorum* ♀	L11	N48.785090 E14.990072	475 / Y	19.06.2013	*Symphoricarpos albus* / nectar	S.B.
	Buffer stripes	33	*B. lucorum* ♀	L11	N48.785090 E14.990072	475 / Y	19.06.2013	*Symphoricarpos albus* / nectar	S.B.
	Buffer stripes	34	*B. lucorum* ♀	L1	N48.786817 E14.992345	487 / Y	19.06.2013	*Rosa canina* agg. / nectar	S.B.
	Buffer stripes	35	*B. cryptarum* ♀	C2	N48.779797 E14.997898	499 / Y	19.06.2013	*Lupinus polyphyllus* / pollen & nectar	S.B.
	Buffer stripes	36	*B. lucorum* ♀	L1	N48.779797 E14.997898	499 / Y	19.06.2013	*Lupinus polyphyllus* / pollen & nectar	S.B.
	Buffer stripes	37	*B. lucorum* ♀	L14	N48.776993 E15.004288	514 / Y	19.06.2013	*Lupinus polyphyllus* / pollen & nectar	S.B.
	Meadow	38	*B. lucorum* ♀	L13	N48.786972 E15.004046	541 / Y	19.06.2013	*Lupinus polyphyllus* / pollen & nectar	S.B.
	Meadow	39	*B. lucorum* ♀	L1	N48.788819 E15.004934	548 / Y	19.06.2013	*Lupinus polyphyllus* / pollen & nectar	S.B.
	Meadow	40	*B. cryptarum* ♀	C2	N48.788527 E15.002641	547 / Y	19.06.2013	*L. corniculatus* / nectar	S.B.
	Meadow	41	*B. lucorum* ♀	L1	N48.788527 E15.002641	547 / Y	19.06.2013	*T. repens* / nectar	S.B.
Lower Austria / Rottalmoos	Bog / Fen	42	*B. cryptarum* ♀	C2	N48.913130 E15.020017	553 / Y	20.06.2013	*Vaccinium oxycoccus* / pollen & nectar	S.B.
	Bog / Fen	43	*B. lucorum* ♀	L1	N48.913130 E15.020017	553 / Y	20.06.2013	*V. oxycoccus* / pollen & nectar	S.B.
	Bog / Fen	44	*B. cryptarum* ♀	C2	N48.913300 E15.020199	552 / Y	20.06.2013	*V. oxycoccus* / pollen & nectar	S.B.
	Bog / Fen	45	*B. cryptarum* ♀	C2	N48.913072 E15.021213	551 / Y	20.06.2013	*V. oxycoccus* / pollen & nectar	S.B.
	Bog / Fen	46	*B. lucorum* ♀	L1	N48.912461 E15.020518	552 / Y	20.06.2013	*V. oxycoccus* / pollen & nectar	S.B.
Upper Austria / Tannmoor	Bog / Fen	47	*B. cryptarum* ♀	C1	N48.507287 E14.862935	910 / A	01.07.2013	*V. oxycoccus* / pollen & nectar	S.B.
	Bog / Fen	48	*B. lucorum* ♀	L1	N48.507283 E14.863015	910 / A	01.07.2013	*V. oxycoccus* / pollen & nectar	S.B.
	Bog / Fen	49	*B. lucorum* ♀	L1	N48.507063 E14.864383	915 / A	01.07.2013	*V. oxycoccus* / pollen & nectar	S.B.
	Bog / Fen	50	*B. lucorum* ♀	L1	N48.506686 E14.865993	919 / A	01.07.2013	*Melampyrum pratense* / pollen & nectar	S.B.
	Bog / Fen	51	*B. lucorum* ♀	L13	N48.506885 E14.866266	920 / A	01.07.2013	*V. oxycoccus* / pollen & nectar	S.B.
	Bog / Fen	52	*B. lucorum* ♀	L1	N48.506080 E14.867095	917 / A	01.07.2013	*V. oxycoccus* / pollen & nectar	S.B.
	Bog / Fen	53	*B. lucorum* ♀	L1	N48.506061 E14.866975	917 / A	01.07.2013	*V. oxycoccus* / pollen & nectar	S.B.
	Bog / Fen	54	*B. cryptarum* ♀	C2	N48.506029 E14.866917	917 / A	01.07.2013	*V. oxycoccus* / pollen & nectar	S.B.
	Bog / Fen	55	*B. lucorum* ♀	L1	N48.506590 E14.872275	909 / A	01.07.2013	*Lupinus polyphyllus* / pollen & nectar	S.B.
	Bog / Fen	56	*B. lucorum* ♀	L5	N48.506636 E14.872033	909 / A	01.07.2013	*V. oxycoccus* / pollen & nectar	S.B.
	Bog / Fen	57	*B. lucorum* ♀	L1	N48.507651 E14.871362	915 / A	01.07.2013	*V. oxycoccus* / pollen & nectar	S.B.
	Bog / Fen	58	*B. lucorum* ♀	L1	N48.507709 E14.871360	915 / A	01.07.2013	*V. oxycoccus* / pollen & nectar	S.B.
	Buffer stripes	59	*B. lucorum* ♀	L1	N48.501738 E14.872543	937 / A	01.07.2013	*T. repens* / pollen & nectar	S.B.
Lower Austria, Lunz am See / Steinbachtal	Woodland / Forest edge	60	*B. lucorum* ♀	L1	N47.790870 E15.006343	907 / A	22.07.2013	*Rhinanthus* sp. / pollen & nectar robbery	S.B.
	Buffer stripes	61	*B. lucorum* ♀	L1	N47.79105 E15.00793	924 / A	22.07.2013	*Rhinanthus* sp. / pollen & nectar robbery	S.B.
	Buffer stripes	62	*B. lucorum* ♀	L1	N47.79105 E15.00793	924 / A	22.07.2013	*Rhinanthus* sp. / pollen & nectar robbery	S.B.
	Woodland / Forest edge	63	*B. lucorum* ♀	L1	N47.793099 E15.010906	961 / A	22.07.2013	*Hypericum perfloratum* / pollen	S.B.
	Woodland / Forest edge	64	*B. lucorum* ♀	L1	N47.792920 E15.01282	965 / A	22.07.2013	*Rhinanthus* sp. / pollen & nectar robbery	S.B.
	Woodland / Forest edge	65	*B. lucorum* ♀	L1	N47.79515 E15.01041	1009 / A	22.07.2013	*Rhinanthus* sp. / pollen & nectar robbery	S.B.
	Woodland / Forest edge	66	*B. lucorum* ♀	L3	N47.79592 E15.00989	1006 / A	22.07.2013	*Hypericum perfloratum* / pollen	S.B.
	Woodland / Forest edge	67	*B. lucorum* ♀	L1	N47.79768 E15.01030	1040 / A	22.07.2013	*Rhinanthus* sp. / pollen & nectar robbery	S.B.
	Woodland / Forest edge	68	*B. lucorum* ♀	L1	N47.79976 E15.01137	1097 / A	22.07.2013	*Rhinanthus* sp. / pollen & nectar robbery	S.B.

Tab. 6: Continued.

Lower Austria, Lunz am See / Rechberg	Woodland / Forest edge	69	*B. lucorum* ♀	L1	N47.80482 E15.01841	1290 / B	22.07.2013	*Carduus* sp. / pollen & nectar	S.B.
	Woodland / Forest edge	70	*B. lucorum* ♀	L1	N47.80296 E15.01688	1312 / B	22.07.2013	*Trifolium repens* / pollen & nectar	S.B.
	Woodland / Forest edge	71	*B. lucorum* ♀	L13	N47.80379 E15.01706	1309 / B	22.07.2013	*Hypericum perfloratum* / pollen	S.B.
	Woodland / Forest edge	72	*B. lucorum* ♀	L8	N47.80206 E15.01631	1290 / B	22.07.2013	*Thymus* sp. / pollen & nectar	S.B.
	Woodland / Forest edge	73	*B. lucorum* ♀	L1	N47.80020 E15.01684	1325 / B	22.07.2013	*Buphthalmum salicifolium* / pollen	S.B.
	Woodland / Forest edge	74	*B. lucorum* ♀	L1	N47.800033 E15.015215	1273 / B	22.07.2013	*Rhinanthus* sp. / pollen & nectar robbery	S.B.
	Woodland / Forest edge	75	*B. lucorum* ♀	L15	N47.80690 E15.02614	1349 / B	22.07.2013	*Inula* sp. / pollen	S.B.
	Woodland / Forest edge	76	*B. lucorum* ♀	L1	N47.80759 E15.02580	1341 / B	22.07.2013	*Lotus corniculatus* / pollen & nectar robbery	S.B.
	Woodland / Forest edge	77	*B. lucorum* ♂	L1	N47.807618 E15.023192	1337 / B	22.07.2013	*Stachys alopecuros*	S.B.
	Woodland / Forest edge	78	*B. lucorum* ♀	L1	N47.805397 E15.018965	1289 / B	22.07.2013	*Hypericum perfloratum* / pollen	S.B.
	Buffer stripes	79	*B. lucorum* ♀	L1	N47.86306 E15.06798	768 / Z	21.07.2013	*Solanum dulcamare* / pollen (buzzing)	S.B.
	Buffer stripes	80	*B. lucorum* ♀	L1	N47.86306 E15.06798	768 / Z	21.07.2013	*Trifolium pratense* / pollen & nectar	S.B.
	Buffer stripes	81	*B. lucorum* ♀	L1	N47.86373 E15.06944	774 / Z	21.07.2013	*Lotus corniculatus* / pollen & nectar	S.B.
	Buffer stripes	82	*B. lucorum* ♀	L1	N47.86559 E15.07120	777 / Z	21.07.2013	*Valeriana officinalis* / pollen	S.B.
	Buffer stripes	83	*B. lucorum* ♀	L8	N47.86559 E15.07120	777 / Z	21.07.2013	*Securigera varia* / pollen & nectar robbery	S.B.
	Meadow	84	*B. lucorum* ♀	L1	N47.86238 E15.07355	811 / Z	21.07.2013	*Lotus corniculatus* / pollen & nectar	S.B.
	Meadow	85	*B. lucorum* ♀	L1	N47.86014 E15.07298	820 / Z	21.07.2013	*Trifolium repens* / pollen & nectar	S.B.
	Meadow	86	*B. lucorum* ♀	L1	N47.86157 E15.07072	776 / Z	21.07.2013	*Lotus corniculatus* / pollen & nectar	S.B.
	Woodland / Forest edge	87	*B. lucorum* ♀	L1	N47.782750 E14.985236	604 / Z	22.07.2013	*R. alectorolophus* / pollen & nectar robbery	S.B.
Carinthia / Heiligenblut	Buffer stripes	88*	*B. lucorum* ♀	L13	-	1050 / A	17.07.2012	*Viccia cracca* / pollen & nectar robbery	H.F.P.
	Buffer stripes	89*	*B. cryptarum* ♀	C2	-	1050 / A	17.07.2012	*V. cracca* / pollen & nectar robbery	H.F.P.
	Buffer stripes	90*	*B. lucorum* ♀	L16	-	1050 / A	17.07.2012	*V. cracca*	H.F.P.
Carinthia / Hohe Tauern, southern slope	Meadow	91*	B. cryptarum ♂	C2	N47.043194 E12.853667	1650 / C	28.08.2012	*C. scabiosa* / pollen & nectar robbery	J.N.
	Meadow	92	*B. cryptarum* ♀	C2	N47.05448 E12.82762	1728 / C	16.07.2013	*Rhinanthus glacialis* / pollen & nectar	S.B.
	Meadow	93	*B. cryptarum* ♀	C2	N47.05230 E12.82520	1681 / C	16.07.2013	*Trifolium repens* / nectar	S.B.
	Meadow	94	*B. cryptarum* ♀	C2	N47.05230 E12.82520	1640 / C	16.07.2013	*Helianthemum nummularium* / pollen	S.B.
	Buffer stripes	95	*B. cryptarum* ♀	C2	N47.054167 E12.833333	1910 / D	17.07.2012	*Vicia cracca* / nectar robbery	J.N.
	Meadow	96	*B. cryptarum* ♀	C2	N47.061194 E12.827278	1910 / D	17.07.2012	*Trifolium montanum* / nectar	J.N.
	Meadow	97	*B. cryptarum* ♀	C2	N47.056889 E12.805694	1910 / D	17.07.2012	*Trifolium pratense*/ pollen & nectar	J.N.
	Meadow	98	*B. lucorum* ♀	L11	N47.064389 E12.827139	1910 / D	18.07.2012	*Rhinanthus glacialis* / pollen & nectar robbery	J.N.
	Meadow	99	*B. lucorum* ♀	L17	N47.064306 E12.826194	1989 / D	18.07.2012	*Trifolium pratense* / nectar robbery	J.N.
	Dwarf shrub community	100	*B. cryptarum* ♀	C2	N47.064972 E12.825222	2020 / D	28.08.2012	*Calluna vulgaris* / nectar	J.N.
	Meadow	101	*B. cryptarum* ♀	C2	N47.056917 E12.805694	1935 / D	17.07.2012	*Thymus* sp. / nectar	J.N.
	Meadow	102	*B. cryptarum* ♀	C2	N47.056722 E12.805361	1965 / D	18.07.2012	*Silene vulgaris* / nectar	J.N.
	Meadow	103	*B. cryptarum* ♂	C2	N47.056722 E12.805361	1965 / D	18.07.2012	*Geranium sylvaticum* / nectar	J.N.
	Meadow	104	*B. lucorum* ♀	L1	N47.056722 E12.805361	1965 / D	18.07.2012	*Silene vulgaris* / nectar	J.N.
	Meadow	105	*B. cryptarum* ♀	C2	N47.056722 E12.805361	1965 / D	18.07.2012	*Geranium sylvaticum* / nectar	J.N.
	Meadow	106	*B. cryptarum* ♀	C2	N47.06915 E12.84006	2282 / E	18.07.2013	*Oxytropis* sp. / nectar robbery	S.B.

Tab. 6: Continued.

	Meadow	107	*B. cryptarum* ♀	C2	N47.06915 E12.84006	2282 / E	18.07.2013	*Helianthemum nummularium* / pollen	S.B.
	Meadow	108	*B. cryptarum* ♀	C2	N47.07047 E12.84109	2254 / E	18.07.2013	*Oxytropis* sp. / nectar robbery	S.B.
	Meadow	109	*B. cryptarum* ♀	C2	N47.07047 E12.84109	2254 / E	18.07.2013	*Thymus* sp. / pollen & nectar	S.B.
	Meadow	110	*B. cryptarum* ♀	C2	N47.066514 E12.841237	2185 / E	18.07.2013	*Rhinanthus glacialis* / pollen	S.B.
	Dwarf shrub community	111*	*B. cryptarum* ♂	C2	N47.064083 E12.830639	2122 / E	28.08.2012	*Calluna vulgaris* / nectar	J.N.
	Dwarf shrub community	112*	*B. cryptarum* ♀	C2	N47.064083 E12.830639	2122 / E	28.08.2012	*C. vulgaris* / nectar	J.N.
	Dwarf shrub community	113*	*B. lucorum* ♀	L1	N47.064083 E12.830639	2122 / E	28.08.2012	*C. vulgaris* / nectar	J.N.
	Dwarf shrub community	114*	*B. cryptarum* ♂	C3	N47.064083 E12.830639	2122 / E	28.08.2012	*C. vulgaris* / nectar	J.N.
	Dwarf shrub community	115*	*B. cryptarum* ♀	C2	N47.064083 E12.830639	2122 / E	28.08.2012	*C. vulgaris* / nectar	J.N.
	Dwarf shrub community	116*	*B. cryptarum* ♀	C2	N47.064083 E12.830639	2122 / E	28.08.2012	*C. vulgaris* / nectar	J.N.
	Dwarf shrub community	117*	*B. cryptarum* ♀	C6	N47.064083 E12.830639	2122 / E	28.08.2012	*C. vulgaris* / nectar	J.N.
	Scree area	118*	*B. cryptarum* ♂	C2	N47.064083 E12.830639	2126 / E	18.07.2012	*Anthyllis vulneraria* / nectar	J.N.
	Scree area	119*	*B. cryptarum* ♀	C2	N47.064083 E12.830639	2126 / E	18.07.2012	*Anthyllis vulneraria* / nectar	J.N.
Carinthia / Hohe Tauern, main ridge	Scree area	120	*B. cryptarum* ♀	C2	N47.082453 E12.848383	2570 / F	17.07.2013	*Helianthemum alpestre / Pollen*	S.B.
	Scree area	121	*B. cryptarum* ♀	C2	N47.081453 E12.850347	2569 / F	17.07.2013	*Silene acaulis* / pollen & nectar	S.B.
	Scree area	122	*B. lucorum* ♀	L1	N47.084588 E12.842134	2484 / F	18.07.2013	*Saxifraga rudolphiana* / pollen & nectar	S.B.
	Scree area	123	*B. cryptarum* ♀	C2	N47.08074 E12.84590	2579 / F	18.07.2013	*Saxifraga rudolphiana* / pollen	S.B.
	Scree area	124	*B. cryptarum* ♀	C2	N47.08097 E12.85140	2567 / F	18.07.2013	*Helianthemum alpestre* / pollen	S.B.
	Scree area	125	*B. lucorum* ♀	L1	N47.08221 E12.85030	2563 / F	18.07.2013	*Pedicularis* sp. / pollen	S.B.
	Scree area	126	*B. lucorum* ♀	L1	N47.08195 E12.85032	2567 / F	18.07.2013	*Silene acaulis* / pollen & nectar	S.B.
	Scree area	127	*B. lucorum* ♀	L1	N47.08081 E12.85100	2566 / F	18.07.2013	*Pedicularis* sp. / pollen	S.B.
	Scree area	128	*B. cryptarum* ♀	C2	N47.083885 E12.842571	2510 / F	18.07.2013	*Saxifraga rudolphiana* / pollen & nectar	S.B.
	Scree area	129	*B. cryptarum* ♀	C2	N47.081768 E12.851642	2562 / F	17.07.2013	*Silene acaulis* / nectar	J.N.
	Scree area	130	*B. cryptarum* ♀	C2	N47.081768 E12.851642	2562 / F	17.07.2013	*Silene acaulis* / pollen & nectar	J.N.
Salzburg / Hohe Tauern, northern slope	Tall forb meadow	131*	*B. lucorum* ♀	L1	N47.151667 E12.811667	1400 / B	17.07.2012	*Trifolium pratense* / pollen & nectar robbery	J.N.
	Meadow	132	*B. cryptarum* ♀	C2	N47.152253 E12.812831	1430 / B	15.07.2013	*Anthyllis* sp. / pollen & nectar	S.B.
	Meadow	133	*B. cryptarum* ♀	C2	N47.150265 E12.809967	1386 / B	17.07.2013	*Rhinanthus glacialis* / pollen	S.B.
	Meadow	134	*B. cryptarum* ♀	C2	N47.152436 E12.813112	1428 / B	17.07.2013	- (collected from nest)	S.B.
	Meadow	135	*B. cryptarum* ♀	C2	N47.152436 E12.813112	1428 / B	17.07.2013	- (collected from nest)	S.B.
	Meadow	136	*B. cryptarum* ♀	C2	N47.152253 E12.812831	1430 / B	15.07.2013	*Rhinanthus glacialis* / pollen	S.B.
	Buffer stripes	137*	*B. lucorum* ♀	L1	N47.160833 E12.815278	1631 / C	18.07.2012	*R. glacialis* / pollen & nectar robbery	J.N.
	Meadow	138	*B. cryptarum* ♀	C2	N47.134197 E12.808822	1783 / C	17.07.2013	*R. glacialis* / pollen & nectar robbery	S.B.
	Meadow	139	*B. cryptarum* ♀	C2	N47.134197 E12.808822	1783 / C	17.07.2013	*R. glacialis* / pollen	S.B.
	Meadow	140	*B. cryptarum* ♀	C2	N47.135223 E12.809069	1770 / C	17.07.2013	*R. glacialis* / pollen & nectar robbery	S.B.
	Meadow	141	*B. cryptarum* ♀	C2	N47.135223 E12.809069	1770 / C	17.07.2013	*R. glacialis* / pollen & nectar robbery	S.B.
	Meadow	142	*B. cryptarum* ♀	C2	N47.133708 E12.807476	1755 / C	17.07.2013	*R. glacialis* / pollen & nectar robbery	S.B.
	Meadow	143	*B. cryptarum* ♀	C2	N47.133708 E12.807476	1755 / C	17.07.2013	*R. glacialis* / pollen & nectar robbery	S.B.
	Meadow	144	*B. cryptarum* ♀	C2	N47.134960 E12.807556	1727 / C	17.07.2013	*R. glacialis* / pollen & nectar robbery	S.B.

Tab. 6: Continued.

	Meadow	145	*B. cryptarum* ♀	C2	N47.144454 E12.814417	1611 / C	17.07.2013	*Viccia* sp. / nectar	S.B.
	Meadow	146	*B. cryptarum* ♀	C2	N47.123828 E12.808382	1914 / D	17.07.2013	*R. glacialis* / pollen & nectar robbery	S.B.
	Meadow	147	*B. cryptarum* ♀	C2	N47.123828 E12.808382	1914 / D	17.07.2013	*R. glacialis* / pollen & nectar robbery	S.B.
	Meadow	148*	*B. cryptarum* ♀	C2	N47.122778 E12.825556	2265 / E	17.07.2012	*Trifolium pratense* / pollen & nectar robbery	J.N.
	Meadow	149*	*B. cryptarum* ♀	C2	N47.122778 E12.825556	2265 / E	17.07.2012	*Trifolium pratense* / nectar robbery	J.N.
Lower Austria / Raxalpe	Woodland / Forest edge	150	*B. lucorum* ♂	L1	N47.716196 E15.084208	538 / Y	25.07.2013	*Origanum vulgare* / nectar	S.B.
	Woodland / Forest edge	151	*B. lucorum*	L1	N47.71619 E15.80411	538 / Y	25.07.2013	*Origanum vulgare* / nectar	S.B.
	Woodland / Forest edge	152	*B. lucorum* ♂	L1	N47.717920 E15.807018	519 / Y	25.07.2013	*Origanum vulgare* / nectar	S.B.
	Woodland / Forest edge	153	*B. lucorum* ♀	L1	N47.718928 E15.807159	517 / Y	25.07.2013	*Pulicaria dysenterica* / pollen	S.B.
	Woodland / Forest edge	154	*B. lucorum* ♂	L1	N47.719865 E15.804117	539 / Y	25.07.2013	*Origanum vulgare* / nectar	S.B.
	Woodland / Forest edge	155	*B. lucorum* ♂	L1	N47.719993 E15.803920	542 / Y	25.07.2013	*Origanum vulgare* / nectar	S.B.
	Woodland / Forest edge	156	*B. lucorum* ♀	L13	N47.712883 E15.806107	509 / Y	25.07.2013	*Lotus corniculatus* / pollen & nectar	S.B.
	Woodland / Forest edge	157	*B. lucorum* ♀	L1	N47.669677 E15.751336	850 / Z	25.07.2013	*Securigea varia* / pollen & nectar	S.B.
	Woodland / Forest edge	158	*B. cryptarum* ♀	C2	N47.67066 E15.74789	829 / Z	25.07.2013	*Echium sp.* / pollen & nectar	S.B.
	Woodland / Forest edge	159	*B. lucorum* ♀	L1	N47.67066 E15.74788	829 / Z	25.07.2013	*Lotus corniculatus* / pollen & nectar	S.B.
	Buffer stripes	160	*B. lucorum* ♀	L1	N47.675257 E15.748735	739 / Z	25.07.2013	*Telekia speciosa* / pollen & nectar	S.B.
	Buffer stripes	161	*B. lucorum* ♀	L1	N47.675257 E15.748735	739 / Z	25.07.2013	*T. speciosa* / pollen & nectar	S.B.
	Buffer stripes	162	*B. lucorum* ♀	L1	N47.674141 E15.758252	699 / Z	25.07.2013	*T. speciosa* / pollen & nectar	S.B.
	Buffer stripes	163	*B. lucorum* ♀	L1	N47.674141 E15.758252	699 / Z	25.07.2013	*T. speciosa* / pollen & nectar	S.B.
	Buffer stripes	164	*B. lucorum* ♀	L1	N47.67437 E15.75658	698 / Z	25.07.2013	*Thymus sp.* / pollen & nectar	S.B.
	Buffer stripes	165	*B. lucorum* ♀	L1	N47.676448 E15.770279	651 / Z	25.07.2013	*Lotus corniculatus* / pollen & nectar	S.B.
	Woodland / Forest edge	166	*B. lucorum* ♀	L1	N47.66925 E15.74116	970 / A	24.07.2013	*Rhinanthus glacialis* / pollen & nectar	S.B.
	Woodland / Forest edge	167	*B. lucorum* ♀	L1	N47.67449 E15.72426	1063 / A	24.07.2013	*R. glacialis* / pollen & nectar robbery	S.B.
	Woodland / Forest edge	168	*B. lucorum* ♀	L1	N47.673909 E15.724606	1062 / A	24.07.2013	*R. glacialis* / pollen & nectar robbery	S.B.
	Buffer stripes	169	*B. lucorum* ♀	L1	N47.67601 E15.72366	1065 / A	24.07.2013	*Lotus corniculatus* / pollen & nectar	S.B.
	Buffer stripes	170	*B. lucorum* ♀	L1	N47.676002 E15.723400	1065 / A	24.07.2013	*Lotus corniculatus* / pollen & nectar	S.B.
	Woodland / Forest edge	171	*B. lucorum* ♀	L1	N47.67568 E15.72192	1069 / A	24.07.2013	*R. glacialis* / pollen & nectar robbery	S.B.
	Woodland / Forest edge	172	*B. lucorum* ♀	L1	N47.67649 E15.72218	1076 / A	24.07.2013	*R. glacialis* / pollen & nectar	S.B.
	Woodland / Forest edge	173	*B. lucorum* ♀	L1	N47.67682 E15.72098	1099 / A	24.07.2013	*R. glacialis* / pollen & nectar	S.B.
	Woodland / Forest edge	174	*B. lucorum* ♀	L1	N47.67778 E15.72056	1120 / A	24.07.2013	*R. glacialis* / pollen & nectar robbery	S.B.
	Woodland / Forest edge	175	*B. lucorum* ♀	L2	N47.67888 E15.71967	1153 / A	24.07.2013	*R. glacialis* / pollen, nectar robbery & buzz	S.B.
	Woodland / Forest edge	176	*B. lucorum* ♀	L1	N47.68211 E15.71792	1227 / B	24.07.2013	*R. glacialis* / pollen & nectar	S.B.
	Tall forb meadow	177	*B. lucorum* ♀	L1	N47.684553 E15.715540	1301 / B	24.07.2013	*Hypericum maculatum* / pollen	S.B.
	Tall forb meadow	178	*B. lucorum* ♀	L1	N47.68432 E15.71577	1290 / B	24.07.2013	*Hypericum maculatum* / pollen	S.B.
	Tall forb meadow	179	*B. lucorum* ♀	L1	N47.685778 E15.714411	1349 / B	24.07.2013	*R. glacialis* / pollen & nectar	S.B.
	Tall forb meadow	180	*B. lucorum* ♀	L1	N47.68572 E15.71527	1324 / B	24.07.2013	*Origanum vulgare* / nectar	S.B.
	Tall forb meadow	181	*B. lucorum* ♀	L1	N47.68682 E15.71537	1327 / B	24.07.2013	*Trifolium repens* / pollen & nectar	S.B.
	Tall forb meadow	182	*B. lucorum* ♀	L1	N47.68833 E15.71434	1363 / B	24.07.2013	*Trifolium pratense* / pollen & nectar	S.B.

Tab. 6: Continued.

	Krummholzzone	183	*B. lucorum* ♀	L1	N47.68994 E15.71066	1486 / B	24.07.2013	*Thymus* sp. / nectar	S.B.
	Meadow	184	*B. cryptarum* ♀	C2	N47.716981 E15.774133	1571 / C	22.06.2013	*Potentilla aurea* / pollen	S.B.
	Meadow	185	*B. cryptarum* ♀	C2	N47.718294 E15.773189	1580 / C	22.06.2013	*Veronica* sp. / nectar	S.B.
	Meadow	186	*B. lucorum* ♀	L1	N47.718698 E15.773167	1582 / C	22.06.2013	*Potentilla aurea* / pollen	S.B.
	Meadow	187	*B. lucorum* ♀	L13	N47.719074 E15.771429	1599 / C	22.06.2013	*Lotus corniculatus* / pollen & nectar	S.B.
	Krummholzzone	188	*B. lucorum* ♀	L1	N47.691388 E15.710374	1546 / C	24.07.2013	*R. glacialis* / pollen & nectar	S.B.
	Krummholzzone	189	*B. lucorum* ♀	L1	N47.69206 E15.71016	1570 / C	24.07.2013	*R. glacialis* / pollen, nectar robbery & buzz	S.B.
	Krummholzzone	190	*B. lucorum* ♀	L1	N47.69049 E15.70720	1656 / C	24.07.2013	*Stachys* sp. / pollen & nectar	S.B.
	Meadow	191	*B. lucorum* ♀	L1	N47.69014 E15.70402	1771 / C	24.07.2013	*Pedicularis* sp. / pollen	S.B.
	Meadow	192	*B. lucorum* ♂	L1	N47.69014 E15.70402	1770 / C	24.07.2013	*Cerastium* sp. / nectar	S.B.
	Krummholzzone	193	*B. lucorum* ♀	L12	N47.69320 E15.70381	1801 / D	25.07.2013	*Pedicularis* sp. / pollen & buzzing	S.B.
	Krummholzzone	194	*B. lucorum* ♀	L1	N47.69320 E15.70381	1801 / D	25.07.2013	*R. glacialis* / pollen, nectar & buzz	S.B.
	Krummholzzone	195	*B. lucorum* ♀	L15	N47.71185 E15.70429	1819 / D	25.07.2013	*Pedicularis* sp. / -	S.B.
	Krummholzzone	196	*B. lucorum* ♀	L1	N47.71005 E15.70928	1870 / D	25.07.2013	*Pedicularis* sp. / pollen & buzzing	S.B.
	Krummholzzone	197	*B. lucorum* ♀	L13	N47.70485 E15.71340	1870 / D	25.07.2013	*Pedicularis* sp. / pollen & buzzing	S.B.
	Krummholzzone	198	*B. lucorum* ♀	L1	N47.70293 E15.71298	1844 / D	25.07.2013	*Helianthemum* sp. / pollen & buzzing	S.B.
	Krummholzzone	199	*B. lucorum* ♀	L1	N47.70220 E15.71425	1842 / D	25.07.2013	*Pedicularis* sp. / pollen & buzzing	S.B.
	Krummholzzone	200	*B. lucorum* ♀	L5	N47.70206 E15.71450	1840 / D	25.07.2013	*Pedicularis* sp. / pollen & buzzing	S.B.
	Krummholzzone	201	*B. lucorum* ♀	L1	N47.70088 E15.71537	1831 / D	25.07.2013	*Rhododendron hirsitum* / pollen & nectar	S.B.
	Krummholzzone	202	*B. lucorum* ♀	L1	N47.69975 E15.71496	1826 / D	25.07.2013	*Rosa canina* agg. / pollen & buzzing	S.B.
	Krummholzzone	203	*B. lucorum* ♀	L1	N47.69975 E15.71496	1826 / D	25.07.2013	*Rosa canina* agg. / pollen & buzzing	S.B.
Lower Austria / Schneeberg	Woodland / Forest edge	204*	*B. lucorum* ♀	L1	N47.779167 E15.898778	608 / Z	31.07.2012	*Centaurea scabiosa* / pollen	J.F.G.
	Woodland / Forest edge	205*	*B. lucorum* ♀	L1	N47.753194 E15.854083	1358 / B	31.07.2012	*Vicia tenuifolia* / pollen	J.F.G.
	Meadow	206*	*B. lucorum* ♀	L1	N47.754333 E15.857528	1297 / B	31.07.2012	*Trifolium pratense* / nectar	J.F.G.
	Krummholzzone	207*	*B. lucorum* ♀	L1	N47.757333 E15.835667	1770 / C	31.07.2012	*Leontodon hispidus* / pollen & nectar	J.F.G.
	Krummholzzone	208*	*B. lucorum* ♀	L1	N47.757333 E15.835667	1770 / C	31.07.2012	*Rhinanthus* sp. / pollen	J.F.G.
Tyrol, Zillertal Alps / Zemmtal	Scree area	209	*B. lucorum* ♀	L1	N47.14568 E11.82788	787 / Z	05.08.2013	*Impatiens glandulifera* / pollen & nectar	S.B.
	Woodland / Forest edge	210	*B. lucorum* ♂	L1	N47.13952 E11.82058	845 / Z	05.08.2013	*Knautia dipsacifolia* / nectar	S.B.
	Woodland / Forest edge	211	*B. lucorum* ♂	L1	N47.15235 E11.83188	693 / Z	08.08.2013	*Origani vulgare* / nectar	S.B.
	Scree area	212	*B. lucorum* ♂	L1	N47.14568 E11.82788	787 / Z	08.08.2013	*Impatiens glandulifera* / nectar	S.B.
	Woodland / Forest edge	213	*B. lucorum* ♂	L1	N47.14741 E11.82605	824 / Z	08.08.2013	*Impatiens glandulifera* / nectar	S.B.
	Woodland / Forest edge	214	*B. lucorum* ♂	L5	N47.143626 E11.828132	794 / Z	08.08.2013	*Knautia dipsacifolia* / nectar	S.B.
	Meadow	215	*B. lucorum* ♂	L1	N47.08329 E11.77256	1112 / A	07.08.2013	*Cirsium* sp. / pollen	S.B.
	Meadow	216	*B. lucorum* ♂	L1	N47.146733 E11.820962	911 / A	08.08.2013	*Trifolium repens* / pollen	S.B.
	Meadow	217	*B. lucorum* ♀	L1	N47.14655 E11.82122	913 / A	08.08.2013	*Angelica sylvstris* / pollen	S.B.
	Tall forb meadow	218	*B. lucorum* ♂	L13	N47.039515 E11.772315	1483 / B	05.08.2013	*Leontodon hispidus* / nectar	S.B.
Tyrol, Zillertal Alps Zemmgrund	Dwarf shrub community	219	*B. cryptarum* ♀	C3	N47.022678 E11.813367	2006 / D	05.07.2013	*Rhododendron ferrugineum* / pollen &	S.B.
Styria / Gesäuse	Woodland / Forest edge	220	*B. lucorum* ♂	L1	N47.605048 E14.727811	503 / Y	14.08.2013	*Eupatorium canabinum* / -	S.B.

Tab. 6: Continued.

Woodland / Forest edge	221	*B. lucorum* ♂	L1	N47.60205 E14.72785	508 / Y	14.08.2013	*Eupatorium canabinum* / -	S.B.
Woodland / Forest edge	222	*B. lucorum* ♂	L1	N47.580285 E14.593567	590 / Y	14.08.2013	*Cirsium oleraceum* / nectar	S.B.
Woodland / Forest edge	223	*B. lucorum* ♂	L1	N47.58001 E14.59522	598 / Y	14.08.2013	*Cirsium oleraceum* / nectar	S.B.
Woodland / Forest edge	224	*B. lucorum* ♂	L1	N47.58091 E14.59094	598 / Y	14.08.2013	*Cirsium oleraceum* / nectar	S.B.
Woodland / Forest edge	225	*B. lucorum* ♂	L1	N47.58367 E14.61205	608 / Z	14.08.2013	*Mentha* sp. / nectar	S.B.
Woodland / Forest edge	226	*B. lucorum* ♂	L1	N47.583032 E14.612454	622 / Z	14.08.2013	*Anthericum ramosum* / nectar	S.B.
Woodland / Forest edge	227	*B. lucorum* ♂	L1	N47.56145 E14.58003	667 / Z	14.08.2013	*Rhinanthus sp.* / pollen, nectar & buzzing	S.B.
Woodland / Forest edge	228	*B. lucorum* ♂	L1	N47.537840 E14.588802	789 / Z	14.08.2013	*Cirsium oleraceum* / nectar	S.B.
Meadow	229	*B. terrestris* ♀	T2	N47.532161 E14.617310	888 / Z	14.08.2013	*Galeopsis speciosa* / pollen & nectar	S.B.
Woodland / Forest edge	230	*B. lucorum* ♂	L13	N47.500702 E14.548080	844 / Z	14.08.2013	*Angelica sylvestris* / nectar	S.B.
Woodland / Forest edge	231	*B. lucorum* ♂	L1	N47.500702 E14.548080	844 / Z	14.08.2013	*Angelica sylvestris* / nectar	S.B.
Tall forb meadow	232*	*B. lucorum* ♀	L1	N47.588333 E14.737778	770 / Z	25.08.2012	*Cirsium oleraceum* / pollen & nectar	J.N.
Tall forb meadow	233*	*B. lucorum* ♂	L1	N47.590556 E14.741389	690 / Z	25.08.2012	*Cirsium oleraceum* / nectar	J.N.
Tall forb meadow	234	*B. lucorum* ♂	L1	N47.53978 E14.62351	1122 / A	14.08.2013	*Centaurea* sp. / nectar	S.B.
Tall forb meadow	235	*B. lucorum* ♂	L1	N47.540162 E14.622830	1156 / A	14.08.2013	*Centaurea* sp. / nectar	S.B.
Tall forb meadow	236	*B. lucorum* ♂	L1	N47.54123 E14.62680	1186 / A	14.08.2013	*Mentha longifolia* / nectar	S.B.
Tall forb meadow	237	*B. lucorum* ♂	L1	N47.541393 E14.627293	1179 / A	14.08.2013	*Mentha longifolia* / nectar	S.B.
Tall forb meadow	238	*B. lucorum* ♂	L1	N47.538576 E14.621274	1065 / A	15.08.2013	*Knautia* sp. / nectar	S.B.
Meadow	239	*B. lucorum* ♀	L1	N47.535840 E14.622552	976 / A	15.08.2013	*Centaurea* sp. / pollen & nectar	S.B.
Meadow	240	*B. lucorum* ♂	L1	N47.532970 E14.618677	918 / A	15.08.2013	*Carduus* sp. / nectar	S.B.
Woodland / Forest edge	241	*B. lucorum* ♂	L1	N47.510076 E14.553709	1129 / A	15.08.2013	*Calluna vulgaris* / nectar	S.B.
Dwarf shrub community	242	*B. lucorum* ♀	L1	N47.52521 E14.55557	1498 / B	20.08.2013	*C. vulgaris* / nectar	S.B.
Dwarf shrub community	243	*B. lucorum* ♀	L1	N47.52521 E14.55557	1498 / B	20.08.2013	*C. vulgaris* / pollen & nectar	S.B.
Dwarf shrub community	244	*B. lucorum* ♀	L1	N47.52057 E14.55689	1417 / B	20.08.2013	*C. vulgaris* / pollen & nectar	S.B.
Dwarf shrub community	245	*B. lucorum* ♂	L1	N47.52057 E14.55689	1417 / B	20.08.2013	*C. vulgaris* / nectar	S.B.
Dwarf shrub community	246	*B. lucorum* ♀	L1	N47.51860 E14.55758	1362 / B	20.08.2013	*C. vulgaris* / pollen & nectar	S.B.
Dwarf shrub community	247	*B. lucorum* ♂	L1	N47.51860 E14.55758	1362 / B	20.08.2013	*C. vulgaris* / nectar	S.B.
Tall forb meadow	248	*B. terrestris* ♂	T2	N47.51083 E14.55577	1212 / B	20.08.2013	*Angelica sylvestris* / nectar	S.B.
Tall forb meadow	249	*B. lucorum* ♂	L1	N47.51083 E14.55577	1212 / B	20.08.2013	*A. sylvestris* / nectar	S.B.
Tall forb meadow	250	*B. terrestris* ♂	T2	N47.51083 E14.55577	1212 / B	20.08.2013	*A. sylvestris* / nectar	S.B.
Krummholzzone	251	*B. terrestris* ♂	T2	N47.56367 E14.64878	1753 / C	15.08.2013	*Cirsium* sp. / nectar	S.B.
Krummholzzone	252	*B. lucorum* ♂	L1	N47.56147 E14.65099	1712 / C	15.08.2013	*Cirsium* sp. / nectar	S.B.
Krummholzzone	253	*B. lucorum* ♂	L1	N47.561553 E14.651722	1705 / C	15.08.2013	*Scabiosa* sp. / nectar	S.B.
Krummholzzone	254	*B. lucorum* ♂	L1	N47.56145 E14.65272	1690 / C	15.08.2013	*Scabiosa* sp. / nectar	S.B.
Krummholzzone	255	*B. lucorum* ♂	L1	N47.55653 E14.65440	1630 / C	15.08.2013	*Stachys alopecuros* / nectar	S.B.
Krummholzzone	256	*B. lucorum* ♂	L1	N47.55537 E14.65357	1603 / C	15.08.2013	*Carduus defloratus* / nectar	S.B.
Woodland / Forest edge	257	*B. lucorum* ♂	L1	N47.54678 E14.64252	1550 / C	15.08.2013	*C. defloratus* / nectar	S.B.
Woodland / Forest edge	258	*B. lucorum* ♂	L1	N47.54678 E14.64252	1550 / C	15.08.2013	*C. defloratus* / nectar	S.B.

Tab. 6: Continued.

	Meadow	259	*B. lucorum* ♂	L1	N47.529508 E14.552615	1501 / C	20.08.2013	*Calluna vulgaris* / nectar	S.B.
	Meadow	260	*B. lucorum* ♂	L1	N47.529508 E14.552615	1501 / C	20.08.2013	*Calluna vulgaris* / nectar	S.B.
Tyrol, Ötztal Alps / Kaunertal	Tall forb meadow	261	*B. cryptarum* ♂	C3	N47.076083 E10.729194	1196 / A	20.08.2013	*Mentha longifolia* / nectar	B.-A.G.-K.
	Buffer stripes	262*	*B. lucorum* ♀	L1	N47.029361 E10.744111	1311 / B	09.08.2012	*Vicia* sp. / nectar	B.-A.G.-K.
	Buffer stripes	263*	*B. cryptarum* ♀	C3	N47.028889 E10.743833	1313 / B	09.08.2012	*Epilobium angustifolium* / nectar	B.-A.G.-K.
	Buffer stripes	264*	*B. cryptarum* ♂	C3	N47.030194 E10.742	1386 / B	09.08.2012	*Knautia arvensis* / nectar	B.-A.G.-K.
	Meadow	265*	*B. cryptarum* ♀	C3	N47.019611 E10.739111	1313 / A	09.08.2012	*Trifolium pratense* / nectar	B.-A.G.-K.
	Tall forb meadow	266	*B. lucorum* ♀	L1	N47.023417 E10.743361	1305 / B	20.08.2013	*Epilobium angustifolium* / -	B.-A.G.-K.
	Meadow	267	*B. cryptarum* ♀	C3	N47.0275 E10.741611	1367 / B	20.08.2013	*Trifolium pratense* / nectar	B.-A.G.-K.
	Tall forb meadow	268	*B. cryptarum* ♀	C3	N47.074 E10.746472	1659 / C	19.08.2013	*Cirsium arvense* / nectar	B.-A.G.-K.
	Dwarf shrub community	269	*B. cryptarum* ♀	C3	N47.0765 E10.745583	1723 / C	19.08.2013	*Calluna vulgaris* / nectar	B.-A.G.-K.
	Dwarf shrub community	270	*B. cryptarum* ♀	C2	N47.076083 E10.746361	1736 / C	19.08.2013	*C. vulgaris* / nectar	B.-A.G.-K.
	Dwarf shrub community	271	*B. lucorum* ♀	L1	N47.076694 E10.746694	1760 / C	19.08.2013	*C. vulgaris* / -	B.-A.G.-K.
	Dwarf shrub community	272	*B. cryptarum* ♀	C3	N47.076639 E10.746889	1766 / C	19.08.2013	*C. vulgaris* / -	B.-A.G.-K.
	Dwarf shrub community	273	*B. lucorum* ♀	L1	N47.076139 E10.745056	1701 / C	20.08.2013	*C. vulgaris* / nectar	B.-A.G.-K.
	Dwarf shrub community	274*	*B. lucorum* ♀	L1	N46.889861 E10.734694	1925 / D	08.08.2012	*C. vulgaris* / nectar	B.-A.G.-K.
	Dwarf shrub community	275*	*B. lucorum* ♀	L13	N46.890028 E10.734778	1926 / D	08.08.2012	*C. vulgaris* / nectar	B.-A.G.-K.
	Dwarf shrub community	276*	*B. lucorum* ♀	L1	N46.887889 E10.734556	1935 / D	08.08.2012	*C. vulgaris* / pollen	B.-A.G.-K.
	Dwarf shrub community	277*	*B. lucorum* ♀	L13	N46.887917 E10.73475	1930 / D	08.08.2012	*C. vulgaris* / pollen	B.-A.G.-K.
	Dwarf shrub community	278*	*B. lucorum* ♀	L1	N46.885917 E10.734556	1988 / D	08.08.2012	*C. vulgaris* / nectar	B.-A.G.-K.
	Dwarf shrub community	279*	*B. lucorum* ♀	L1	N46.886528 E10.73475	1963 / D	08.08.2012	*C. vulgaris* / -	B.-A.G.-K.
	Dwarf shrub community	280	*B. cryptarum* ♀	C3	N47.04525 E10.732861	2034 / D	21.08.2013	*C. vulgaris* / nectar	B.-A.G.-K.
	Dwarf shrub community	281	*B. cryptarum* ♀	C3	N47.045111 E10.732944	2030 / D	21.08.2013	*C. vulgaris* / nectar	B.-A.G.-K.
	Dwarf shrub community	282	*B. cryptarum* ♀	C3	N47.047111 E10.735694	1942 / D	21.08.2013	*C. vulgaris* / nectar	B.-A.G.-K.
	Dwarf shrub community	283*	*B. lucorum* ♀	L1	N46.890028 E10.720556	2255 / D	08.08.2012	*C. vulgaris* / nectar	B.-A.G.-K.
	Dwarf shrub community	284*	*B. lucorum* ♀	L1	N46.890139 E10.720611	2287 / D	08.08.2012	*C. vulgaris* / nectar	B.-A.G.-K.
	Dwarf shrub community	285*	*B. lucorum* ♀	L1	N46.889333 E10.719611	2265 / D	08.08.2012	*C. vulgaris* / nectar	B.-A.G.-K.
	Dwarf shrub community	286*	*B. lucorum* ♀	L1	N46.889333 E10.719194	2275 / D	08.08.2012	*C. vulgaris* / nectar	B.-A.G.-K.
	Dwarf shrub community	287*	*B. lucorum* ♀	L18	N46.888528 E10.716333	2301 / D	08.08.2012	*C. vulgaris* / nectar	B.-A.G.-K.
	Dwarf shrub community	288	*B. cryptarum* ♀	C3	N46.888056 E10.7265	2159 / D	18.08.2013	*C. vulgaris* / nectar	B.-A.G.-K.
	Dwarf shrub community	289	*B. cryptarum* ♀	C3	N46.888 E10.726667	2161 / D	18.08.2013	*C. vulgaris* / nectar	B.-A.G.-K.
	Dwarf shrub community	290	*B. cryptarum* ♀	C3	N46.889194 E10.725611	2158 / D	18.08.2013	*C. vulgaris* / nectar	B.-A.G.-K.
	Dwarf shrub community	291	*B. lucorum* ♀	L1	N47.039472 E10.730028	2119 / D	21.08.2013	*C. vulgaris* / nectar	B.-A.G.-K.
	Dwarf shrub community	292	*B. lucorum* ♀	L1	N47.044694 E10.72925	2156 / D	21.08.2013	*C. vulgaris* / nectar	B.-A.G.-K.
Tyrol / Karwendel	Buffer stripes	293*	*B. lucorum* ♂	L1	N47.3375 E11.389722	1480 / B	11.08.2012	*Carduus defloratus* / -	B.-A.G.-K.
	Tall forb meadow	294	*B. terrestris* ♀	T2	N47.297389 E11.39525	1220 / B	10.07.2013	*Acinos alpinus* / nectar	B.-A.G.-K.
	Tall forb meadow	295	*B. terrestris* ♀	T2	N47.298556 E11.399056	1214 / B	10.07.2013	No flower visit	B.-A.G.-K.
	Tall forb meadow	296*	*B. terrestris* ♀	T2	N47.301389 E11.383333	1600 / C	10.08.2012	*Cirsium erisithales* / nectar	B.-A.G.-K.

Tab. 6: Continued.

	Meadow	297*	*B. terrestris* ♀	T2	N47.303611 E11.388333	1690 / C	10.08.2012	*Prunella grandiflora* / pollen & nectar robbery	B.-A.G.-K.
	Meadow	298*	*B. cryptarum* ♀	C2	N47.336944 E11.404167	1540 / C	11.08.2012	*Hypericum maculatum* / pollen	B.-A.G.-K.
	Krummholzzone	299	*B. terrestris* ♀	T2	N47.304944 E11.387472	1726 / D	11.07.2013	*Thymus* sp. / pollen & nectar	B.-A.G.-K.
	Krummholzzone	300	*B. cryptarum* ♀	C2	N47.304472 E11.387861	1697 / D	11.07.2013	*Helianthemum* sp. / pollen	B.-A.G.-K.
	Meadow	301*	*B. cryptarum* ♂	C2	N47.308056 E11.386111	1905 / D	10.08.2012	*Cirsium spinosissimum* / nectar	B.-A.G.-K.
	Meadow	302	*B. terrestris* ♀	T2	N47.305028 E11.377806	1900 / D	11.07.2013	*Anthyllis* sp. / pollen	B.-A.G.-K.
	Meadow	303	*B. terrestris* ♀	T2	N47.304778 E11.376056	1908 / D	11.07.2013	*Globularia* sp. / pollen	B.-A.G.-K.
	Meadow	304	*B. terrestris* ♀	T2	N47.305222 E11.376	1925 / D	11.07.2013	*Anthyllis* sp. / pollen	B.-A.G.-K.
	Scree area	305	*B. terrestris* ♀	T2	N47.306639 E11.381861	1872 / D	11.07.2013	*Gallium* sp. / pollen	B.-A.G.-K.
	Scree area	306	*B. lucorum* ♀	L1	N47.306456 E11.386667	1820 / D	11.07.2013	*Helianthemum* sp. / pollen	B.-A.G.-K.
	Scree area	307	*B. terrestris* ♀	T2	N47.306167 E11.386556	1802 / D	11.07.2013	*Helianthemum* sp. / pollen	B.-A.G.-K.
	Meadow	308*	*B. lucorum* ♀	L13	N47.326667 E11.439444	2150 / E	11.08.2013	*Thymus* sp. / nectar	B.-A.G.-K.
Vorarlberg / Silvretta Alps	Meadow	309*	*B. lucorum* ♀	L13	N46.994472 E10.017611	1000 / A	05.08.2012	*Trifolium pratense* / pollen	J.N.
	Meadow	310*	*B. lucorum* ♀	L1	N46.993444 E10.018111	1000 / A	05.08.2012	*T. pratense* / -	J.N.
	Meadow	311*	*B. lucorum* ♀	L1	N46.984611 E10.025	968 / A	05.08.2012	*T. pratense* / -	J.N.
	Meadow	312*	*B. lucorum* ♀	L1	N46.983667 E10.024806	972 / A	05.08.2012	*T. pratense* / -	J.N.
	Meadow	313*	*B. lucorum* ♀	L1	N46.976361 E10.035806	999 / A	05.08.2012	*T. pratense* / nectar	J.N.
	Meadow	314*	*B. lucorum* ♀	L1	N46.976361 E10.035806	999 / A	05.08.2012	*T. pratense* / nectar	J.N.
	Meadow	315*	*B. lucorum* ♀	L1	N46.966139 E10.071917	1079 / A	05.08.2012	*T. pratense* / nectar	J.N.
	Meadow	316*	*B. lucorum* ♀	L1	N46.966417 E10.071306	1078 / A	05.08.2012	*T. pratense* / nectar	J.N.
	Meadow	317*	*B. lucorum* ♀	L1	N46.962083 E10.076528	1119 / A	05.08.2012	*T. pratense* / nectar	J.N.
	Meadow	318*	*B. lucorum* ♀	L11	N46.962556 E10.077	1118 / A	05.08.2012	*T. pratense* / nectar	J.N.
	Dwarf shrub community	319*	*B. lucorum* ♀	L1	N46.93525 E10.054306	1770 / C	06.08.2012	*Thymus* sp. / -	J.N.
	Dwarf shrub community	320*	*B. lucorum* ♀	L1	N46.934833 E10.053667	1740 / C	06.08.2012	*Thymus* sp. / -	J.N.
	Dwarf shrub community	321*	*B. lucorum* ♀	L1	N46.933917 E10.053139	1766 / C	06.08.2012	*Thymus* sp. / nectar	J.N.
	Dwarf shrub community	322*	*B. lucorum* ♀	L11	N46.933917 E10.053139	1766 / C	06.08.2012	*Thymus* sp. / nectar	J.N.
	Buffer stripes	323*	*B. lucorum* ♀	L1	N46.918889 E10.0895	2030 / D	04.08.2012	-	J.N.
	Dwarf shrub community	324*	*B. cryptarum* ♀	C2	N46.920028 E10.085194	2007 / D	04.08.2012	-	J.N.
	Dwarf shrub community	325*	*B. cryptarum* ♀	C2	N46.920528 E10.081889	1999 / D	04.08.2012	*C. vulgaris* / nectar	J.N.
	Dwarf shrub community	326*	*B. lucorum* ♀	L1	N46.920278 E10.082361	1998 / D	04.08.2012	*C. vulgaris* / nectar	J.N.
	Dwarf shrub community	327*	*B. lucorum* ♀	L1	N46.916778 E10.081028	1945 / D	04.08.2012	*C. vulgaris* / nectar	J.N.
	Dwarf shrub community	328*	*B. lucorum* ♀	L1	N46.916806 E10.080861	1958 / D	04.08.2012	*C. vulgaris* / nectar	J.N.
	Dwarf shrub community	329*	*B. cryptarum* ♀	C2	N46.917083 E10.079	1956 / D	04.08.2012	*C. vulgaris* / nectar	J.N.
	Buffer stripes	330*	*B. lucorum* ♀	L13	N46.917528 E10.090222	2012 / D	04.08.2012	*C. vulgaris* / pollen	J.N.
Styria / Dachstein	Woodland / Forest edge	331	*B. lucorum* ♂	L1	N47.418762 E13.729461	832 / Z	21.08.2013	-	S.B.
	Tall forb meadow	332	*B. lucorum* ♂	L1	N47.439882 E13.714398	1170 / A	22.08.2013	*Knautia dipsacifolia* / nectar	S.B.
	Meadow	333	*B. cryptarum* ♀	C2	N47.424045 E13.692426	1060 / A	22.08.2013	*Lotus corniculatus* / pollen & nectar	S.B.
	Meadow	334	*B. cryptarum* ♀	C2	N47.45437 E13.70356	2020 / D	22.08.2013	*Gentianella germanica* / pollen & nectar	S.B.

Tab. 6: Continued.

Salzburg / Tennen Mountains	Meadow	335	*B. terrestris* ♀	T2	N47.539916 E13.196569	1150 / B	18.07.2013	*Betonica alopecuros* / pollen, nectar & buzz.	J.N.
	Meadow	336	*B. lucorum* ♀	L1	N47.5399163 E13.196569	1150 / B	18.07.2013	*Betonica alopecuros* / pollen & nectar	J.N.
	Scree area	337	*B. lucorum* ♀	L1	N47.543640 E13.199049	1300 / B	18.07.2013	*B. alopecuros* / pollen, nectar & buzzing	J.N.
	Meadow	338	*B. lucorum* ♀	L14	N47.541348 E13.196988	1200 / B	20.07.2013	*Rhinanthus glacialis* / pollen & nectar	J.N.
	Scree area	339	*B. lucorum* ♀	L1	N47.545746 E13.204870	1400 / C	18.07.2013	*Helianthemum nummularium* / pollen	J.N.
	Meadow	340	*B. lucorum* ♀	L1	N47.5434278 E13.2075065	1600 / C	18.07.2013	*Helianthemum nummularium* / pollen	J.N.
	Meadow	341	*B. lucorum* ♀	L1	N47.5303257 E13.2127177	1756 / C	18.07.2013	*Myosotis alpestris* / pollen & nectar	J.N.
	Meadow	342	*B. lucorum* ♀	L1	N47.5303257 E13.2127177	1756 / C	20.07.2013	*Helianthemum alpestre* / pollen & buzzing	J.N.
	Meadow	343	*B. lucorum* ♀	L11	N47.5452080 E13.2065626	1500 / C	20.07.2013	*R. glacialis* / pollen, nectar robbery & buzz.	J.N.
	Meadow	344	*B. lucorum* ♀	L1	N47.5257186 E13.2152036	1800 / D	18.07.2013	*Rhododendron hirsutum* / pollen, nectar & buzzing	J.N.
	Meadow	345	*B. lucorum* ♀	L1	N47.5257186 E13.2152036	1800 / D	18.07.2013	*Ligusticum mutellina* / pollen	J.N.
	Meadow	346	*B. lucorum* ♀	L1	N47.5257186 E13.2152036	1800 / D	18.07.2013	*R. hirsutum* / pollen, nectar & buzzing	J.N.
	Meadow	347	*B. lucorum* ♀	L11	N47.5236533 E13.2174623	1900 / D	18.07.2013	*Ligusticum mutellina* / pollen	J.N.
	Meadow	348	*B. lucorum* ♀	L1	N47.5236533 E13.2174623	1900 / D	18.07.2013	*Rhododendron hirsutum* / pollen & nectar	J.N.
	Meadow	349	*B. lucorum* ♀	L1	N47.5240379 E13.2203261	1925 / D	18.07.2013	-	J.N.
	Meadow	350	*B. lucorum* ♀	L4	N47.5236533 E13.2174623	1900 / D	19.07.2013	*R. hirsutum* / pollen & nectar robbery	J.N.
	Meadow	351	*B. lucorum* ♀	L1	N47.5236533 E13.2174623	1900 / D	20.07.2013	*H. nummularium* / pollen & buzzing	J.N.
	Meadow	352	*B. lucorum* ♀	L1	N47.5236533 E13.2174623	1900 / D	20.07.2013	*H. nummularium* / pollen & buzzing	J.N.
Carinthia / Karawanks	Buffer stripes	353	*B. lucorum* ♀	L1	N46.46638 E14.3775	814 / Z	09.07.2013	*Spiraea* x *bumalda* / pollen	J.N.
	Woodland / Forest edge	354	*B. lucorum* ♀	L1	N46.46638 E14.3775	814 / Z	09.07.2013	*R. glacialis* / pollen & nectar robbery	J.N.
	Woodland / Forest edge	355	*B. lucorum* ♀	L1	N46.46638 E14.3775	814 / Z	09.07.2013	*R. glacialis* / pollen & nectar robbery	J.N.
	Buffer stripes	356	*B. lucorum* ♀	L6	N46.46638 E14.3775	814 / Z	09.07.2013	*Spiraea* x *bumalda* / pollen	J.N.
	Woodland / Forest edge	357	*B. lucorum* ♀	L1	N46.47694 E14.46027	1000 / A	09.07.2013	*Melampyrum sylvaticum* / pollen, nectar & buzz.	J.N.
	Woodland / Forest edge	358	*B. lucorum* ♀	L1	N46.47861 E14.4675	1050 / A	09.07.2013	*Centaurea pseudophrygia* / pollen & nectar	J.N.
	Woodland / Forest edge	359	*B. lucorum* ♀	L1	N46.47861 E14.48055	930 / A	09.07.2013	*Aruncus dioicus* / pollen	J.N.
	Woodland / Forest edge	360	*B. lucorum* ♀	L13	N46.47861 E14.48055	930 / A	09.07.2013	*Aruncus dioicus* / pollen	J.N.
	Woodland / Forest edge	361	*B. lucorum* ♀	L1	N48.48083 E14.47305	1015 / A	09.07.2013	*Aruncus dioicus* / pollen	J.N.
	Woodland / Forest edge	362	*B. lucorum* ♀	L1	N46.49277 E14.51555	1230 / B	09.07.2013	*Rosa canina* / pollen & buzzing	J.N.
	Meadow	363	*B. lucorum* ♀	L1	N46.49277 E14.50777	1310 / B	09.07.2013	*Plantago media* / pollen	J.N.
	Meadow	364	*B. lucorum* ♀	L1	N46.49277 E14.50777	1310 / B	09.07.2013	*Genista sagittalis* / pollen & buzzing	J.N.
	Meadow	365	*B. lucorum* ♀	L1	N46.49388 E14.5075	1325 / B	09.07.2013	*Genista sagittalis* / pollen & buzzing	J.N.
	Meadow	366	*B. lucorum* ♀	L10	N46.49388 E14.5075	1325 / B	09.07.2013	*Genista sagittalis* / pollen & buzzing	J.N.
	Meadow	367	*B. lucorum* ♀	L1	N46.49222 E14.50611	1260 / B	09.07.2013	*Ranunculus acris* / pollen & buzzing	J.N.
	Meadow	368	*B. lucorum* ♀	L1	N46.49222 E14.50611	1260 / B	09.07.2013	*Rosa canina* / pollen & buzzing	J.N.
	Meadow	369	*B. lucorum* ♀	L1	N46.50194 E14.51111	1560 / C	09.07.2013	*Thymus* sp. / pollen & nectar	J.N.
	Meadow	370	*B. lucorum* ♀	L1	N46.50388 E14.51056	1600 / C	09.07.2013	*Ranunculus acris* / pollen & buzzing	J.N.
	Meadow	371	*B. lucorum* ♀	L1	N46.50388 E14.51056	1600 / C	09.07.2013	*Ranunculus acris* / pollen & buzzing	J.N.

Tab. 6: Continued.

	Meadow	372	*B. lucorum* ♀	L1	N46.50388 E14.51056	1600 / C	09.07.2013	*Acinos alpina* / pollen & nectar	J.N.
	Meadow	373	*B. lucorum* ♀	L1	N46.50388 E14.51056	1600 / C	09.07.2013	*Thymus* sp. / nectar	J.N.
	Meadow	374	*B. lucorum* ♀	L1	N46.50388 E14.51056	1600 / C	09.07.2013	*Lotus corniculatus* / pollen & nectar	J.N.
	Meadow	375	*B. lucorum* ♀	L13	N46.50416 E14.50666	1700 / C	09.07.2013	*Rumex obtusifolius* / pollen	J.N.
	Krummholzzone	376	*B. lucorum* ♀	L1	N46.50361 E14.49917	1900 / D	09.07.2013	*H. nummularium* / pollen	J.N.
	Meadow	377	*B. lucorum* ♀	L1	N46.50361 E14.49917	1900 / D	09.07.2013	*Ranunculus acris* / pollen & buzzing	J.N.
	Meadow	378	*B. lucorum* ♀	L14	N46.50361 E14.49917	1900 / D	09.07.2013	*Ranunculus acris* / pollen & buzzing	J.N.
	Meadow	379	*B. lucorum* ♀	L1	N46.50361 E14.49917	1900 / D	09.07.2013	*Trollius europaeus* / pollen & buzzing	J.N.
	Meadow	380	*B. lucorum* ♀	L1	N46.50361 E14.49917	1900 / D	09.07.2013	*Pedicularis verticillata* / pollen & buzzing	J.N.
	Meadow	381	*B. lucorum* ♀	L1	N46.50361 E14.49917	1900 / D	09.07.2013	*Rumex alpinus* / pollen & buzzing	J.N.
	Meadow	382	*B. lucorum* ♀	L1	N46.50361 E14.49917	1900 / D	09.07.2013	*Dryas octopetala* / pollen & buzzing	J.N.
	Meadow	383	*B. lucorum* ♀	L1	N46.50361 E14.49917	1900 / D	09.07.2013	*Helianthemum alpestre* / pollen	J.N.
	Meadow	384	*B. lucorum* ♀	L1	N46.50361 E14.49917	1900 / D	09.07.2013	*Helianthemum alpestre* / pollen & buzzing	J.N.
	Krummholzzone	385	*B. cryptarum* ♀	C1	N46.50361 E14.49917	1900 / D	09.07.2013	*Helianthemum alpestre* / pollen & buzzing	J.N.
	Krummholzzone	386	*B. lucorum* ♀	L1	N46.50611 E14.48722	1850 / D	09.07.2013	*Vaccinium vitis-idaea* / pollen & buzzing	J.N.
	Meadow	387	*B. lucorum* ♀	L1	N46.50305 E14.50306	2139 / E	09.07.2013	*Anthyllis vulneraria* / pollen, nectar robbery & buzzing	J.N.
Norway, Narvik	-	388	*B. magnus* ♀	-	N68.44010 E17.42620	51 / -	06.08.2013	*Trifolium pretense* / nectar robbery	J.N.
	-	389	*B. soroeensis* ♀	-	N68.44010 E17.42620	51 / -	06.08.2013	*Trifolium pretense* / nectar robbery	J.N.

Curriculum Vitae

Bossert, Silas

School Education

August 1993 - June 1997	Primary school in Wiesbaden - Kohlheck
August 1997 - June 2003	**Elly-Heuss-Schule** (Gymnasium) in Wiesbaden
August 2003 - June 2006	**Martin-Niemöller-Schule** (Oberstufengymnasium) in Wiesbaden

Alternative military service

August 2006 - May 2007	As an assistant in a workshop for disabled persons (EVIM-Rehawerkstatt)

Academic Education

October 2007 - June 2011	**University of Constance** / Biological Science *BSc. in Biological Sciences (Thesis Title: Auswirkungen von Herbivorie aquatischer Invertebraten auf Myriophyllum spicatum L. (Haloragaceae))*
April 2010- July 2010	Assistent student at the Institute for Marine Biology in Giglio, Italy, supervised by Dr. Claus Valentin
October 2011 -	**University of Vienna** / Zoology M. Sc.

Grants

October 2011 - September 2012	Performance scholarship of the University of Vienna ("Leistungsstipendium")
June 2013	Supporting scholarship of the University of Vienna ("Förderstipendium")

Publications

Bossert, S. (2014). "Shelter usage by males of *Hylaeus nivalis* (Morawitz 1867) (Hymenoptera: Apidae) and notes on flower records." Linzer biol. Beiträge **46**(1) (*in press*).

Bossert, S. (2014). "The high alpine bee fauna (Hymenoptera: Apoidea) of the Zillertal Alps, Austria." Biodiversity Data Journal (*in prep*.).

Published Posters

Gereben-Krenn, B.A., Neumayer J., Bardakji S., Timelthaler G., Gokcezade J.F., **Bossert S.** and Krenn H.W. (2013): Cryptic bumblebee species of the *Bombus lucorum*-complex in the Austrian Alps.

[Poster, BioSyst.EU 2013, Vienna, Feb. 21, 2013]

Gereben-Krenn, B.A., Neumayer J., Bardakji S., Timelthaler G., Gokcezade J.F., **Bossert S.** and Krenn H.W. (2013): Cryptic bumblebee species of the *Bombus lucorum*-complex in the Austrian Alps.

[Poster, Symposium Bienen und Wespen Europas, Wien, April 10, 2013]

Language abilities

German	Mother tongue
English	9 years school education, several courses at University
French	6 years school education

Additional qualifications

Driver licenses:	cars (class A), motorboats ("Bootsschein See")
Software skills:	MS Office, R, Arlequin, MEGA, MrBayes, BioEdit, ClustalX, TreeGraph, QGIS