Identification of Bombus species based on wing venation structure

Peter Kozmus, Meta Virant-Doberlet, Vladimir Meglič, Peter Dovč

Apidologie (2011) 42:472–480

DOI: 10.1007/s13592-011-0037-5

Original article

Identification of *Bombus* species based on wing venation structure

Peter Kozmus[1], Meta Virant-Doberlet[2], Vladimir Meglič[1], Peter Dovč[3]

[1]Agricultural Institute of Slovenia, Hacquetova 17, Ljubljana, Slovenia
[2]National Institute of Biology, Večna pot 111, Ljubljana, Slovenia
[3]Biotechnical Faculty, University of Ljubljana, Groblje 3, Domžale, Slovenia

Received 2 February 2010 – Revised 3 August 2010 – Accepted 4 August 2010

Abstract – About 250 bumblebee species in 15 subgenera are known in the world. Identification of some species is difficult due to small morphological differences. In this study, wing venation patterns were analysed to obtain characters for species identification. Four hundred and sixty-nine bumblebees from 121 localities in Slovenia and 61 imported individuals were included in the analyses. The coordinates of 19 vein junctions on the forewings were measured and used in the calculation of 37 wing characters. Based on discriminate method, more than 97% of all analysed bumblebees were assigned to the correct species. The most informative characters were angles J16, A4 and discoidal shift. Wing venation pattern also differed between autochthonous and imported *Bombus terrestris* individuals.

bumblebees / identification / wing venation / Slovenia

1. INTRODUCTION

The world bumblebee fauna consists of approximately 250 species (Williams 1998). All species of the genus *Bombus* have been assigned to 15 subgenera (Williams et al. 2008). The majority of these species are known as true bumblebees. The remaining 45 species are known as cuckoo bumblebees, and belong to the subgenus *Psithyrus* (Pedersen 2002).

Correct species identification is very important especially when bumblebee species are used as an environment indicator. As a genus, *Bombus* is morphologically monotonous (Michener 1990), and species are difficult to identify due to variations in colour, size and morphology (Krüger 1958; Pekkarinen et al. 1979; Reinig 1981). Early classifications depended mostly on colour patterns (Dalla Torre 1980), but these were generally regarded as being of limited value, particularly since most species exhibit considerable colour variation within and between populations. Also, there is often convergent evolution of coat colour driven by Mullerian mimicry (Plowright and Owen 1980; Williams 2007). Many morphological keys exist for bumblebee determination (e.g. Faester 1959; Løken 1973; Milliron 1973; Alford 1975; Delmas 1976; Erlandsson 1979; Svensson 1979; Løken 1984; Rasmont 1984; Prys-Jones and Corbet 1991; Amiet 1996; Bertsch 1997); however, only the species from limited geographic regions are included in these keys. Species are often distinguished only by small differences in morphology and therefore, a lot of practice is needed for correct determination.

The subgenus *Bombus* with the European species *Bombus terrestris, Bombus lucorum, Bombus cryptarum, Bombus magnus, Bombus maderensis* and *Bombus sporadicus* varies so

Corresponding author: P. Kozmus,
peter.kozmus@kis.si
Manuscript editor: Marla Spivak

little that only typical specimens and queens can be identified (Pedersen 2002). Despite considerable intraspecific variation, studies based on morphology (Krüger 1958; Pekkarinen et al. 1979; Rasmont 1984), cross-breeding experiments (De Jonghe and Rasmont 1983), enzyme electrophoretic data (Scholl and Obrecht 1983; Pamilo et al. 1987) and analysis of the compounds of the secretion from male labial glands (Bertsch 1997) confirmed the existence of these species. Also, comparison of mtDNA sequences within the subgenus *Bombus* showed that species can be characterised using specific mtDNA polymorphisms (Pedersen 2002; Murray et al. 2008). However, reliable identification based exclusively on morphological traits is still problematic and numerous discrepancies in classification and identification are still present.

In the present study, we examined the wing venation patterns of 18 bumblebee species to determine if this approach is sufficient for species identification and determination. Wing venation characters have been applied in morphometric analyses and taxonomic classification of the honeybee *Apis mellifera* L. (Ruttner et al. 1978). Compared to honeybees, bumblebees have similar wing venation structure (differences exist only in one vein junction) and therefore the same wing characters could be used for species determination. We also assessed the suitability of this approach to distinguish specimens of imported *B. terrestris* from the Netherlands, which are used for commercial pollination, from native specimens of the same species from Slovenia.

2. MATERIALS AND METHODS

2.1. Collecting samples and identification

Altogether, 530 specimens (workers and queens) were analysed (Table I). While in some species (e.g. *Bombus pascuorum*), many specimens were found and included in the analyses; in others (e.g. *Bombus barbutellus*), only few specimens were collected and analysed. Four hundred and sixty-nine specimens were collected from different sites in Slovenia (Figure 1) and 61 specimens (*B. terrestris*) were from commercial colonies imported from the Netherlands. All specimens were collected over three years, 2004–2006, from June through September each year. Species identification was made using morphological keys (Amiet 1996; Prys-Jones and Corbet 1991). Before and after analysis, specimens were stored at −80°C.

2.2. Wing venation analysis

The right side forewing was removed from each specimen, attached to paper and scanned into a digital image. Coordinates of 19 vein junctions (Figure 2) were used for analysis, following Ruttner (1988), to obtain 37 wing characters (Tables II and III). For calculating wing characters, BeeWings 1.20 (Farny 1999) was used.

All data were analysed with the statistical programme SAS (version 8.02). Analysis of variance was calculated for 37 characters. Following discriminate analysis, based on Mahalanobis distances, each specimen was assigned to a group. In addition, canonical discriminate analysis was performed and three components with the most variability were calculated. 3D graphs were constructed using the KyPlot programme (ver. 2.0 beta; Yoshioka 2001). Finally, multiple variance analysis based on LSD (least significant difference) test was performed and statistical differences between species in wing venation characteristics were calculated.

3. RESULTS

Explained variability (R^2) and values of statistical significance (p) for each of 37 characters are shown in Table IV. The highest R^2 was calculated for angles J16 (0.64), A4 (0.62) and for the discoidal shift (0.60). The least informative were angles O26 (0.16) and A1 (0.15). Altogether 30 characters had R^2 above 0.30 and for subsequent calculations only the most informative characteristics were used (Table IV).

Using discriminate analysis, all specimens in 13 out of 18 species were classified into correct species groups (Figure 3). In five species, a few specimens were classified incorrectly. The highest error rate was found in *Bombus sylvarum*, where two out of 17 specimens were classified

Table I. Number of specimens of each bumblebee species included in the wing venation analyses.

Species	Number	Species	Number
B. pascuorum (w)	102	*B. pratorum* (w)	16
B. lapidarius (w)	65	*B. wurfleinii* (w)	12
B. terrestris (imported) (w)	61	*B. soroeensis* (w)	9
B. lucorum (w)	56	*B. hypnorum* (w)	8
B. hortorum (w)	52	*B. monticola* (w)	7
B. humilis (w)	40	*B. argillaceus* (w)	6
B. terrestris (w)	30	*B. sylvestris* (q)	6
B. ruderarius (w)	20	*B. rupestris* (q)	5
B. sylvarum (w)	17	*B. barbutellus* (q)	2
B. bohemicus (q)	16	Total	530

w workers, *q* queens

incorrectly (11.8%), while in native *B. terrestris* (30), *Bombus hortorum* (52), *Bombus humilis* (40) and *B. pascuorum* (102), only one specimen was assigned incorrectly. Analysis also revealed differences between Slovenian and imported populations of *B. terrestris*. Two native specimens were assigned to the group of imported *B. terrestris* and similarly, three imported bumblebees out of 61 were classified in the native population.

Using canonical discriminate analysis, three variables were created to separate the species into groups based on wing morphology. Due to high degree of overlap, plotting all 18 species in one graph showed only basic differences between species. To demonstrate that morphologically similar species can have significantly different wing morphology, we grouped together only the most morphologically similar species (Figure 4). A comparison between *B. lucorum* and *B. terrestris* is shown in Figure 4a. Although both species are morphologically very similar in other characters, the specimens fell into separate groups that overlapped only slightly. Species

Figure 1. *Dots* indicate sites in Slovenia where bumblebees were collected for analyses.

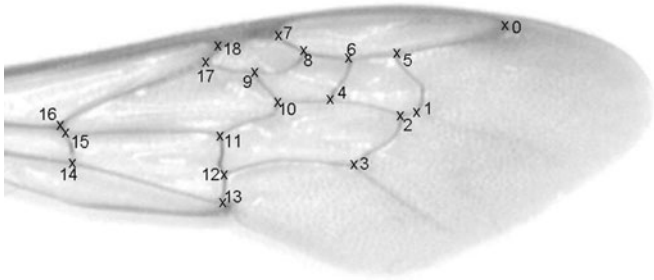

Figure 2. Right bumblebee forewing with 19 measured points at vein junctions.

Bombus lapidarius, *Bombus monticola*, *Bombus ruderarius*, *Bombus rupestris* and *Bombus wurfleinii* are all black with red pile on the terminus of the abdomen, but based on wing venation these species can be discriminated (Figure 4b). A comparison between *B. hortorum, B. lapidarius, B. lucorum* and *B. pascuorum* is shown in Figure 4c. Differences among species are clearly seen; only specimens *B. lucorum* and *B. lapidarius* overlap. Again, analysis revealed differences between autochthonous and imported populations of *B. terrestris*, although populations overlapped in the middle (Figure 4d).

Difference in wing venation characters and statistical significance among bumblebees species, based on *t* test and LSD criterion are shown in Table V. Four species (*B. humilis, B. lucorum, Bombus pratorum* and *B. terrestris*) and the group of the imported *B. terrestris* were significantly different from all other species. Also, the difference in wing venation between autochthonous and imported *B. terrestris* was significant. However, differences among *B. barbutellus* and the other nine species were not significant.

4. DISCUSSION

Nearly all measured wing pattern characters were informative (average R^2=0.43). Unlike in honey bee species and subspecies determination, the most informative character for *Bombus* determination was not cubital index (Ruttner 1988), but angles J16, A4 and discoidal shift. The least informative characters were angles A1 and O26. Angle O26 is related to a vein junction where differences between honeybee and bumblebee wings occur, and therefore a low informativeness was expected. In angle A1, one length is too small for accurate measurements

Table II. Measured angles, lengths and indices of the vein patterns and their boundary points.

Angles	Points	Angles	Points	Length	Points	Index	Points
A1	2, 1, 4	J10	6, 9, 10	Radial field	0, 7	Cubital (CI)	2; 4/1; 2
A4	4, 1, 5	J16	8, 9, 18	A	2, 4	Precubital (PCI)	4; 9/8; 10
B3	1, 4, 3	K19	12, 11, 14	B	1, 2	Dumb-bell (DBI)	1; 4/5; 6
B4	1, 4, 5	L13	5, 7, 6	C	3, 4	Radial (RI)	0,7,3
D7	4, 3, 13	M17	7, 8, 18	D	11, 15	Surface of 6 fields (AREA6)	1, 2, 3, 12, 13, 14, 15, 16, 17, 18, 7, 8, 6, 5
E9	6, 5, 10	N23	9, 18, 17	Inner length	1, 14		
G7	3, 13, 4	O26	15, 14, 16	Inner width	7, 13		
G18 H12	12, 13, 14 11, 10, 12	Q21	11, 16, 17	Discoidal schift (DisA), (DisD)	0, 7, 3		

In angles, the vertex is denoted by the second number in the series and the first and last numbers are the end points of line segments

Table III. Measured cells in the vein patterns and their boundary points.

CELL	Points	Measured lengths
Cub cell 1 (CUB1)	7, 8, 9, 17, 18	7–8, 7–9, 7–18, 8–9, 9–17, 9–18, 17–18
Cub cell 2 (CUB2)	4, 6, 8, 9, 10	4–6, 4–10, 6–8, 6–10, 8–9, 8–10, 9–10
Cub cell 3 (CUB3)	1, 2, 4, 5, 6	1–2, 1–5, 2–4, 2–5, 4–5, 4–6, 5–6
Discoidal cell 1 (DIS1)	9, 10, 11, 16, 17	9–10, 9–11, 9–17, 10–11, 11–16, 11–17, 16–17
Discoidal cell 2 (DIS2)	2, 3, 12, 11, 10, 4	2–3, 2–4, 3–4, 3–10, 3–11, 3–12, 4–10, 10–11, 11–12
Brachial cell (BRA1)	11, 12, 13, 14, 15, 16	11–12, 11–16, 12–13, 12–16, 13–14, 13–15, 13–16, 14–15, 15–16

and low informativeness was a consequence of a high scoring error.

Results of the discriminate analyses were very promising. Based on this method, more than 97% of analysed bumblebees were assigned to the correct species. In 13 species, all specimens (100%) were correctly assigned. With some optimization and programme for wing measuring adjustments this method will undoubtedly yield even better results. The results may further improve

Table IV. Values of explained variability (R^2) and statistical significance (p) calculated by analysis of variance.

Characteristics	R^2	p value	Characteristics	R^2	p value
J16	0.6382	<0.0001	N23	0.4489	<0.0001
A4	0.6191	<0.0001	Area6	0.4479	<0.0001
DisD	0.6030	<0.0001	BRA1	0.4203	<0.0001
DBI	0.5840	<0.0001	A	0.4151	<0.0001
K19	0.5831	<0.0001	B4	0.3943	<0.0001
L13	0.5746	<0.0001	CI	0.3942	<0.0001
CUB3	0.5493	<0.0001	DIS1	0.3820	<0.0001
D7	0.5456	<0.0001	RI	0.3758	<0.0001
G7	0.5283	<0.0001	Inner width	0.3750	<0.0001
H12	0.5223	<0.0001	PCI	0.3677	<0.0001
D	0.5117	<0.0001	CUB2	0.3613	<0.0001
CUB1	0.5067	<0.0001	Q21	0.2620	<0.0001
DisA	0.4956	<0.0001	G18	0.2475	<0.0001
B3	0.4941	<0.0001	E9	0.2444	<0.0001
DIS2	0.4885	<0.0001	J10	0.1965	<0.0001
Inner length	0.4884	<0.0001	M17	0.1730	<0.0001
Radial field	0.4765	<0.0001	O26	0.1588	<0.0001
C	0.4752	<0.0001	A1	0.1546	<0.0001
B	0.4598	<0.0001			

Characters in shadowed fields were omitted from further analysis

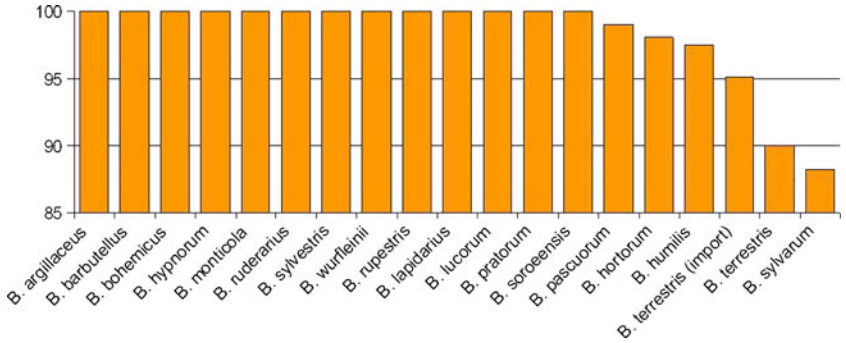

Figure 3. Percentage (%) of correctly assigned specimen based on discriminate analysis.

if more specimens could have been included in the analyses, specifically where only a few bees represented a species (e.g. *B. barbutellus*). The method also appears useful to compare or distinguish populations of the same species, because we distinguished imported *B. terrestris* individuals from the native Slovenian *B. terrestris* population.

Based on these results, bumblebee wing venation pattern is an appropriate tool for species determination. The method is especially

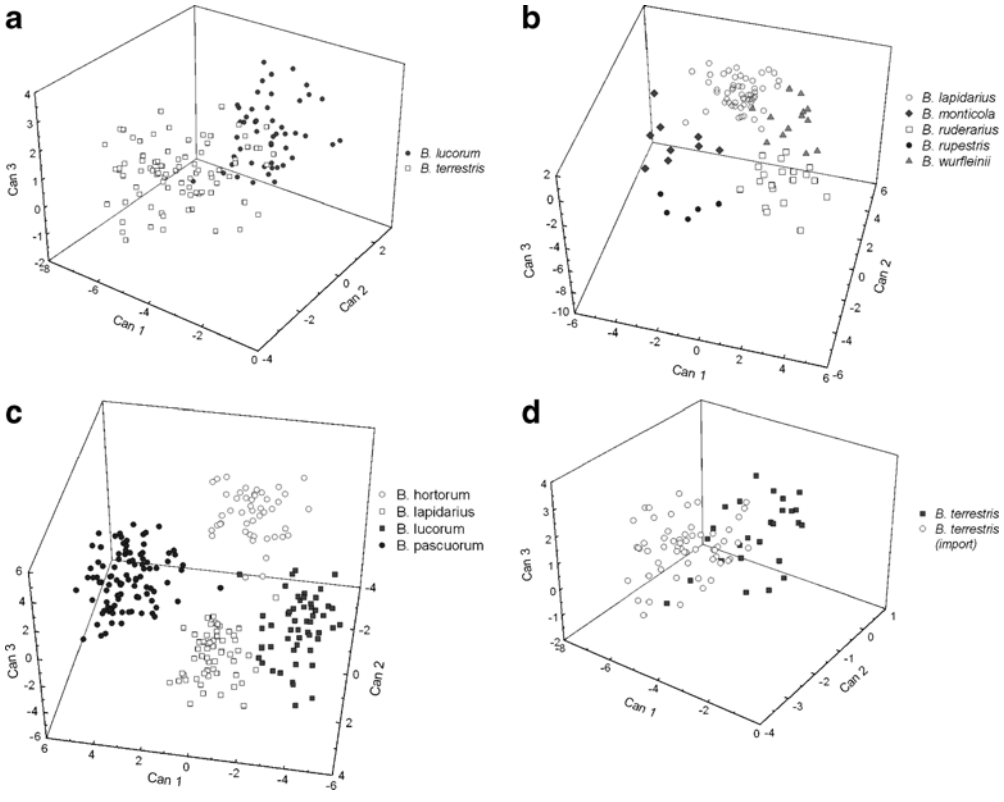

Figure 4. Differences in wing venation pattern based on discriminate analysis between different bumblebees species.

Table V. Difference in wing venation characters among bumblebees species, based on analysis of variance and *t* test for Canonical variable 1 (below diagonal) and statistical significance (above diagonal).

	Can1	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
1	*B. argillaceus*		ns	[a]	[a]	[a]	[a]	[a]	[a]	ns	[a]	[a]	[a]	ns	[a]	[a]	ns	[a]	[a]	[a]
2	*B. barbutellus*	−0.85		ns	ns	[a]	ns	ns	[a]	ns	[a]	[a]	[a]	ns	ns	[a]	ns	[a]	[a]	[a]
3	*P. bohemicus*	−1.15	−0.31		ns	[a]	[a]	[a]	[a]	[a]	[a]	[a]	[a]	[a]	ns	[a]	ns	[a]	[a]	[a]
4	*B. hortorum*	−1.65	−0.8	−0.5		[a]	ns	ns	[a]	[a]	[a]	[a]	[a]	[a]	ns	[a]	ns	[a]	[a]	[a]
5	*B. humilis*	−7.34	−6.49	−6.19	−5.69		[a]	[a]	[a]	[a]	[a]	[a]	[a]	[a]	[a]	[a]	[a]	[a]	[a]	[a]
6	*B. hypnorum*	−2.27	−1.42	−1.12	−0.62	5.07		ns	[a]	[a]	[a]	[a]	[a]	[a]	ns	[a]	[a]	[a]	[a]	[a]
7	*B. lapidarius*	−2	−1.15	−0.84	−0.35	5.35	0.27		[a]	[a]	[a]	[a]	[a]	[a]	ns	[a]	[a]	[a]	[a]	[a]
8	*B. lucorum*	1.23	2.07	2.38	2.88	8.57	3.5	3.22		[a]	[a]	[a]	[a]	[a]	[a]	[a]	[a]	[a]	[a]	[a]
9	*B. monticola*	0.39	1.24	1.54	2.04	7.73	2.66	2.39	−0.84		[a]	[a]	[a]	ns	[a]	[a]	[a]	[a]	[a]	[a]
10	*B. pascuorum*	−6.36	−5.51	−5.21	−4.71	0.98	−4.09	−4.36	−7.59	−6.75		[a]	[a]	[a]	[a]	ns	[a]	[a]	[a]	[a]
11	*B. pratorum*	−3.73	−2.88	−2.58	−2.08	3.61	−1.46	−1.73	−4.96	−4.12	2.63		[a]	[a]	[a]	[a]	[a]	[a]	[a]	[a]
12	*B. ruderarius*	−5.19	−4.34	−4.04	−3.54	2.15	−2.92	−3.19	−6.42	−5.58	1.17	−1.46		[a]	[a]	[a]	[a]	[a]	[a]	ns
13	*B. rupestris*	−0.03	0.82	1.12	1.62	7.31	2.24	1.97	−1.26	−0.42	6.33	3.7	5.16		[a]	[a]	ns	[a]	[a]	[a]
14	*B. soroeensis*	−1.51	−0.66	−0.36	0.14	5.83	0.76	0.49	−2.74	−1.9	4.85	2.22	3.68	−1.48		[a]	ns	[a]	[a]	[a]
15	*B. sylvarum*	−6.36	−5.51	−5.2	−4.7	0.99	−4.08	−4.36	−7.58	−6.74	0	−2.63	−1.16	−6.32	−4.85		[a]	[a]	[a]	[a]
16	*P. sylvestris*	−1.12	−0.27	0.04	0.53	6.23	1.15	0.88	−2.34	−1.51	5.24	2.61	4.07	−1.09	0.39	5.24		[a]	[a]	[a]
17	*B. terrestris*	1.79	2.64	2.94	3.44	9.13	4.06	3.79	0.56	1.4	8.15	5.52	6.98	1.82	3.3	8.14	2.91		[a]	[a]
18	*B. terrestris* (im.)	2.93	3.78	4.08	4.58	10.27	5.2	4.93	1.7	2.54	9.29	6.66	8.12	2.96	4.44	9.28	4.05	1.14		[a]
19	*B. wurfleinii*	−4.64	−3.79	−3.49	−2.99	2.7	−2.37	−2.64	−5.87	−5.03	1.72	−0.91	0.55	−4.61	−3.13	1.72	−3.52	−6.43	−7.57	

Numbers in the first row indicate bumblebee species in the same order as in the first column

ns not significant

[a] Significant

useful for species which, based on others morphological characteristics, are hard to determine (e.g. *B. terrestris, B. lucorum*). Using a full classical morphological approach can be time-consuming and ultimately results in the destruction of the specimen; therefore, the use of a single forewing for species determination is more appropriate if many specimens must be determined and the material is to be retained in an entomological collection. This method is not very expensive, compared to genetic analyses, due to low-capital investment needed (scanner, computer and software). It is also appropriate for researchers who do not have enough experience with bumble bee taxonomy as they could use wing venation analysis to confirm morphological identification.

Identification des espèces de bourdon (*Bombus*) à partir de la structure des nervures alaires.

bourdon / identification / Slovénie / nervures alaires

Bestimmung von *Bombus*-Arten anhand der Struktur des Flügelgeäders.

Hummeln / Artbestimmung / Flügelgeäder / Slowenien

REFERENCES

Alford D.V. (1975) Bumblebees. London, Davis-Poynter: 352 str.

Amiet, F. (1996) Hymenoptera: Apidae, 1.Teil. Insecta helvetica **12**, 1–98

Bertsch, A. (1997) Abgrenzung der Hummel-Arten *Bombus cryptarum* und *B. lucorum* mittels männlicher Labialdrüsen-Sekrete und morphologischer Merkmale (Hymenoptera; Apidae). Entomol. Gen. **22**, 129–145

Dalla Torre, K.W. (1980) Unsere hummel-(*Bombus*) Arten. Naturhistoriker **2**, 40–41

De Jonghe, R., Rasmont, P. (1983) Kreuzungsexperiment mit Hummeln des Genus *Bombus* Latreille Sensu Stricto (Hymenoptera; Apidae). Phegea **11**, 7–10

Delmas, R. (1976) Contribution à l'étude de la faune française des Bombinae (Hymenoptera, Apoidea, *Bombidae*). Ann. Soc. Entomol. Fr. (Nouvelle serie) **12**, 247–290

Erlandsson, A. (1979) *Bombus canariensis* Pérez, 1895 n. stat and *Bombus maderensis* n. sp. from the Macaronesian Islands. Entomol. Scand. **10**, 187–192

Faester, K. (1959) In Dänemark getroffene Arten von *Bombus* und *Psithyrus* (Hym., Apidae). Entomol. Medd. **29**, 152–153

Farny R. (1999) BeeWings v. 1.20.902.56 computer program distributed by the author and Bee research institute in Dol. Czech Republic.

Krüger, E. (1958) Phaenoanalytische studien an einigen arten der untergattung Terrestribombus O. Vogt (Hymenoptera, Bombidae) III. Tijdschr. Entomol. **101**, 283–344

Løken, A. (1973) Studies on Scandinavian bumblebees (Hymenoptera, Apidae). Norsk entomologisk tidsskr. **20**, 1–218

Løken, A. (1984) Scandinavian species of the genus *Psithyrus* Lepeletier (Hymenoptera: Apidae). Entomol. Scan. (supplement) **23**, 1–45

Michener, C.D. (1990) Classification of the Apidae. University of Kansas Science Bull. **54**, 75–164

Milliron, H.E. (1973) A Monograph of the Western Hemisphere Bumblebees (Hymenoptera: Apidae: *Bombinae*). II. The Genus *Megabombus* Subgenus *Megabombus*. Mem. Entomol. Soc. Can. **89**, 81–237

Murray, T.E., Fitzpatrick, U., Brown, M.J.F., Paxton, R.J. (2008) Cryptic species diversity in a widespread bumble bee complex revealed using mitochondrial DNA RFLPs. Conserv. Genet. **9**, 653–666

Pamilo, P., Pekkarinen, A., Varvio, S.L. (1987) Clustering of bumblebee subgenera based on interspecific genetic relationships (Hymenoptera: Apidae: *Bombus* and *Psithyrus*). Ann. Zool. Fenn. **24**, 19–27

Pedersen, B.V. (2002) European bumblebees (Hymenoptera: Bombini)—phylogenetic relationship inferred from DNK sequences. Insect. Syst. Evol. **33**, 361–386

Pekkarinen, A., Varvio-Aho, S.L., Pamilo, P. (1979) Evolutionary relationships in northern European *Bombus* and *Psithyrus* species (Hymenoptera: Apidae) studied on the base of allozymes. Ann. Entomol. Fenn. **45**, 77–80

Plowright, R.C., Owen, R.E. (1980) The evolutionary significance of bumble bee colour patterns—a mimetic interpretation. Evolution **34**, 622–637

Prys-Jones, O.E., Corbet, S.A. (1991) Bumblebees. Naturalists Handbooks 6. Richmonds Publishing Co, Slough, England. 92 str

Rasmont, P. (1984) Les bourdons du sous-genre *Bombus* Latreille sensu stricto en Europe Occidentale et Centrale (Hymenoptera, Apidae). Spixiana **7**, 135–160

Reinig, W.F. (1981) Synopsis der in Europa nachgewiesen Hummel—und schmarotzerhummelarten. Spixiana **4**, 159–164

Ruttner, F. (1988) Biogeography and taxonomy of honeybees, pp. 251–257. Springler-Verlag, Berlin

Ruttner, F., Tassencourt, L., Louveaux, J. (1978) Biometrical-statistical analsis of the geographical variability of *Apis mellifera* L. Apidologie **9**, 363–381

Scholl, A., Obrecht, E. (1983) Enzymelektrophoretische Untersuchungen zur Artsabgrenzung im *Bombus lucorum*-Komplex (Apidae, *Bombini*). Apidologie **14**, 65–78

Svensson, B.G. (1979) *Pyrobombus lapponicus* auct. in Europe recognized as two species: *P. lapponicus* (Fabricius, 1793) and *P. monticola* (Smith, 1849) (Hymenoptera, Apoidea, *Bombinae*). Entomol. Scan. **10**, 275–296

Williams, P.H. (1998) An annotated checklist of bumble bees with an analysis of patterns of description (Hymenoptera: Apidae, *Bombini*). Bull. Brit. Museum (Natural History) Entomol. **67**, 79–152

Williams, P.H. (2007) The distribution of bumblebee colour patterns world-wide: possible significance for thermoregulation, crypsis, and warning mimicry. Biol. J. Linn. Soc. **92**, 97–118

Williams, P.H., Cameron, S.A., Hines, H.M., Cederberg, B., Rasmont, P. (2008) A simplified subgeneric classification of the bumblebees (genus *Bombus*). Apidologie **39**, 46–74

Yoshioka K. (2001) KyPlot v. 2.0 computer program distributed by the author at http://kyplot.software.informer.com/2.0/. Accesseed 12 May 2008).