



The bumblebees of the subgenus *Subterraneobombus*: integrating evidence from morphology and DNA barcodes (Hymenoptera, Apidae, *Bombus*)

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Although bumblebees have received a lot of attention, some taxonomic problems have persisted for many years. One particularly obdurate case has been the species of the subgenus *Subterraneobombus*. We revise the bees of this subgenus by integrating evidence from both morphology and, for a 5% subsample, from DNA (cytochrome *c* oxidase subunit 1, *COI*) barcodes from pinned museum specimens. We apply a reciprocal illumination procedure: (1) taxa recognized previously from morphology are used to stratify samples for DNA subsampling; (2) DNA barcodes from these subsamples are used to recognize groups of phylogenetically related specimens; and (3) for these groups, we re-examine morphological characters in order to recognize and diagnose species. A total of 3854 specimens from 1535 samples from across the geographic range of the subgenus throughout the Holarctic and northern Oriental regions are identified to 11 species. This includes one species newly recognized from Mongolia, *Bombus mongolensis* Williams sp. nov. Taxon concepts are modified substantially for four species, seven lectotypes are designated, and four new synonyms are recognized. The prevailing usage of *Bombus distinguendus* is maintained as valid by designating *Bombus elegans* as a *nomen oblitum* and designating *B. distinguendus* as a *nomen protectum*. Identification keys and colour-pattern diagrams are provided, and geographic distributions, elevational ranges, and phenological activity periods are described to characterize the species. An estimate of the biogeographic history is reconstructed with dispersal–vicariance analysis. In this study, DNA barcode data have been a cost-effective source of additional characters for diagnosing groups of specimens. The barcode data contributed directly to recognizing the one new species, of which females remain difficult to identify from morphology alone.

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INTRODUCTION

Bumblebees are among the best-sampled groups of insects worldwide (Williams, 1998). They have attracted a lot of attention because they are large, brightly coloured, and active at the same times and places as many entomologists. But bumblebees also combine a homogeneity in morphology that is unusual among bees (Michener, 2007) with an impressive variability in colour pattern (Williams, 2007). So, unsur-

prisingly, all the attention they have received over more than two centuries of study has resulted in a plethora of nominal taxa, the status of which in many cases remains uncertain (Williams, 1998). The status of taxa has become an important question because of recent declines in the range or abundance of some of these valuable pollinators, which means that there is a pressing need to monitor all bumblebee species (Williams & Osborne, 2009). One group of bumblebees that presents a particular taxonomic impediment for monitoring is the subgenus *Subterraneobombus*. All of the European and some of the North American

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species of this subgenus are among those in decline. But in Asia, where the majority of the species in the subgenus occur, there has been persistent confusion in our understanding of a series of similarly coloured nominal taxa (Tkalců, 1961), so that both the species and their conservation status have remained unclear. Consequently there is a need to revise the species of this subgenus as a priority.

HISTORY

The subgenus *Subterraneobombus* was first named and diagnosed by Vogt (1911), to include: *Bombus subterraneus* (Linnaeus, 1758); *Bombus distinguendus* Morawitz, 1869; *Bombus melanurus* Lepeletier, 1835; and *Bombus fertoni* Vogt, 1911 (= *Bombus fedtschenkoi* Morawitz, 1875). The subgeneric type species, *B. subterraneus*, was designated subsequently by Frison (1927). The species of *Subterraneobombus* have never been comprehensively revised. One difficulty has been that many of the nominal taxa were described from the mountains and steppes of Central Asia and the Tibetan Plateau, where access has long been limited.

Skorikov ([1923]), in his review of all bumblebees, treated *Subterraneobombus* as a genus, and increased the number of species to 12, including all of the previously described species recognized in this paper except *Bombus amurensis* Radoszkowski, 1862, plus two others: *Bombus breviceps* Smith, 1852 and *Bombus flaviventris* Friese, 1905. When Richards (1968) came to review all of the bumblebee subgenera, his diagnosis of *Subterraneobombus* excluded *B. breviceps* (this species is now considered to be part of the subgenus *Alpigenobombus*). However, from the 1985 arrangement of the collection in the Natural History Museum (BMNH), London, it appeared that Richards still (as in Richards, 1930) followed Skorikov in including *B. flaviventris* in *Subterraneobombus*. In contrast, Williams (1991) excluded *B. flaviventris* from *Subterraneobombus*, recognizing it as being part of the species *Bombus sibiricus* (Fabricius, 1781), which although superficially similar in morphology, is part of the subgenus *Sibiricobombus*. Another species of *Sibiricobombus* that was often confused with species of *Subterraneobombus* is *Bombus oberti* Morawitz, 1883 (e.g. Friese, 1911b; Skorikov, 1912; Skorikov, 1931; Wang, 1982).

Reinig (1930, 1934) reviewed several of the European and Asian species of *Subterraneobombus* in the course of describing a collection of bumblebees from the Pamir. He illustrated variation in the sculpturing of metasomal tergum 6 (his Abb. 4) and variation in the male genitalia (his Abb. 5). From this he described three groups of species: (1) *subterraneus* + *distinguendus* + *fragrans*; (2) *melanurus* + *tshitscherini* + *griseofasciatus*; and (3) *fedtschenkoi*.

Tkalců (1961, 1969a, 1974b) considered several other taxa described previously in *Subterraneobombus* to be separate species (*Bombus chaharensis* Yasumatsu, 1940, *Bombus lantschouensis* Tkalců, 1961 *Bombus maidli* Pittioni, 1939 *Megabombus subdistinctus* Richards, 1928, and *Megabombus tshitscherini* (Radoszkowski, 1862)). Tkalců (1961) also included *Bombus filchnerae* Vogt, 1908 until the male was described (Tkalců, 1974b), thereby placing it in *Thoracobombus*. Summarising, Tkalců (1961) wrote that although many *Subterraneobombus* taxa are relatively widely distributed and common in the Asian steppes, their taxonomy was still not satisfactorily resolved (i.e. from morphological characters; cf. Table 1).

Williams (1991, 1998) attempted brief reviews of *Subterraneobombus* species from their morphology and from explicit criteria for recognizing species. But with no new major sources of characters and a lack of material for some of the taxa, there could be no substantial advance in understanding. More recently, data from five genes have provided a well-supported phylogenetic analysis for most bumblebee species (Cameron, Hines & Williams, 2007), including eight species of a monophyletic subgenus *Subterraneobombus* (Fig. 1). This at last permits the morphological diagnosis of a well-founded subgenus *Subterraneobombus* (given in keys in Williams *et al.*, 2008). The most distinctive of the group's morphological synapomorphies is the spoon-shaped male penis valve with its paddle- or trident-shaped lateral extension.

Identification keys for the Asian species of *Subterraneobombus* have been published only by Richards (1930) and Skorikov (1931). Richards' key depends primarily on colour. Early authors had noticed subtle variations in the length of the hair and in the hue of the yellow bands, and had used these to distinguish several taxa that they named as species. However, even within what is interpreted here to be a single species, *B. melanurus*, pronounced variation in hue is observed (between a vivid lemon yellow in Iran, a pale sandy yellow in Ladakh, and a mid brown in the Himalaya). A similar variation in hue is shown by other species. As used in Richards' key, relying on scoring the hue of the yellow confounds some species (e.g. some individuals of *B. melanurus* were assigned to *Bombus difficillimus* Skorikov, 1912) and splits others (e.g. separating *Bombus roborowskyi* Morawitz, 1887 and *Bombus personatus* Smith, 1879), although Richards did write that he had not examined all of the species listed in his key. Skorikov's (1931) key placed greater emphasis on morphology, especially on characters of the sculpturing of metasomal tergum 6. However, this sculpturing also appears to vary within species, especially among workers, where it covaries in strength with body size, causing

Table 1. Names accepted by a selection of authors over the last century as valid species names for two of the Asian species recognized in this paper

Source	Depository	Focal region†	Species 1	Species 2
This paper	See text	Global	<i>melanurus</i> *	<i>difficillimus</i> *
Williams (1991)	BMNH	Kashmir	<i>melanurus</i> (part)*	<i>melanurus</i> (part)*
Tkalců (1974b)	NMP	Mongolia	<i>melanurus</i> , <i>tshitscherini</i> (♂)* <i>difficillimus</i> (♀)*	
Tkalců (1974a)	NMS	Nepal	<i>difficillimus</i> *	
Tkalců (1969a)	Brno	Afghanistan	<i>melanurus</i> (dark wings), <i>subdistinctus</i> (light wings)	
Tkalců (1961)	lost‡	Qinghai		<i>tshitscherini</i> *
Skorikov (1931)	ZISP	Central Asia	<i>melanurus</i> , <i>tshitscherini</i> (part)	<i>difficillimus</i> , <i>tshitscherini</i> (part)
Richards (1930)	BMNH	Himalaya	<i>melanurus</i> ,* <i>tshitscherini</i> ,*§ <i>difficillimus</i> (part)§	<i>difficillimus</i> * (part)

Misidentifications are shown in bold.

*Specimens examined (or for Tkalců, 1961, photos).

†The region studied, which does not mean that both species occur there, so some species are mentioned as separate by the author without being recorded from the same sample.

‡From a search by JH.

§Based on applying the keys by Richards (1930).

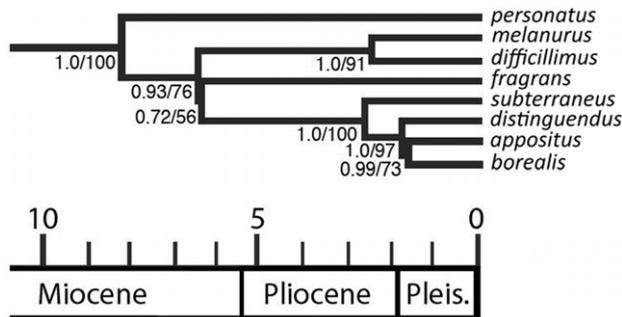


Figure 1. Estimate of phylogeny for eight of the 11 *Subterraneobombus* species (vouchers identified by PW) by Bayesian analysis of five genes (*opsin*, *EF-1 α* , *arginine kinase*, *PEPCK*, and *16S*) from Cameron *et al.* (2007), with divergence times estimated by Hines (2008) (the time scale is in millions of years before the present; values next to the nodes are Bayesian posterior probabilities/parsimony bootstrap values). Redrawn from Hines (2008).

problems for diagnosis. More reliable keys to the three species of Europe to the west of Turkey [*Bombus fragrans* (Pallas, 1771), *B. subterraneus*, and *B. distinguendus*] were published by Pittioni (1939a), and to the three North American species (*Bombus appositus* Cresson, 1878, *Bombus borealis* Kirby, 1837, and *B. distinguendus*) by Williams & Thomas (2005).

AIMS

The primary aim of this paper is to revise the species of the subgenus *Subterraneobombus*. The

secondary aim is to assess the value of the new information that widely available DNA (cytochrome *c* oxidase subunit 1, *COI*) barcode data can contribute to easing difficult taxonomic decisions regarding bumblebees. Previous studies by the most experienced bumblebee taxonomists have recognized the limitations to what has been achieved using morphology (e.g. Tkalců, 1961). Because integrated approaches have helped with other bees (Gibbs, 2009), here we seek to integrate evidence based on morphology with new data from *COI* barcodes. Our general procedure is to use *COI* barcodes to identify groups of phylogenetically related individuals that can then be assessed for whether they are morphologically diagnosable. Greater attention is paid to sampling the regions of Asia where the taxonomic problems have been most severe, both by collecting much new material from China and by re-examining museum material from previous studies. The contributions of the present authors are as follows: PW, collecting material, database design and input, data analysis and manuscript preparation; JA, organizing the collecting surveys in North China and collecting material; JH, collecting material and database input.

MATERIAL AND METHODS

RECOGNIZING SPECIMENS OF *SUBTERRANEOBOMBUS*

Subterraneobombus specimens were diagnosed from morphological characters based on the characters given in the keys of Williams *et al.* (2008).

Males

Males of *Subterraneobombus* are diagnosed easily by the form of the penis valve head, which is uniquely turned in towards the body midline distally, as an incurved, bowl-shaped spoon; in addition, the penis-valve shaft has the ventral angle about halfway along its length produced ventrally and laterally as a broad, transverse, paddle- or trident-like process. Otherwise, the species of this subgenus differ from *some* species of otherwise similar subgenera in: having the mandible with a dense posterior fringe of long hairs ('beard', cf. some *Thoracobombus*); antennal segments 5–15 more than twice as long as broad, slightly curved, but without pronounced swellings on one side (cf. many *Thoracobombus*); and hind tibia with outer surface concave in part and only weakly convex in part.

Females

As for bumblebees of many subgenera, there is no single morphological character of females that can be used to diagnose all *Subterraneobombus*. Three characters come closest to being diagnostic: (1) the clypeus is often predominantly smooth and shiny, the strongly flattened central area has only widely scattered micropunctures, with larger punctures only at the edges, but if the clypeus is more extensively and densely covered with many small and medium punctures (*B. fragrans*, *B. amurensis*, and *B. fedtschenkoi*), then the ocello-ocular area of the vertex of the head has the unpunctured shiny area small, extending for half or less of the distance between the eye and the lateral ocellus; (2) metasomal sternum 6 has a raised, smooth, and often shiny median longitudinal keel in the posterior one third (not always obvious in small workers, and less shiny and only slightly weaker keels occur in, for example, some *Thoracobombus*); and (3) the labrum has the median longitudinal furrow wide (0.27–0.5 times the labral breadth), deep, and rounded like a bowl. Otherwise the species of this subgenus differ from *some* species of similar subgenera in: having the oculo-malar distance at least equal to the breadth of the mandible proximally between the outer ends of its articulations, and often much longer, usually with small, shallow, widely spaced punctures in a weak band across its entire breadth; clypeus without a median longitudinal groove in the dorsal quarter (cf. most *Megabombus*); mid basitarsus with distal posterior corner extended to form a sharp angle of 45° or less, often produced as a narrow tooth or spine; hind basitarsus with proximal posteriorly directed process with dense plume of moderately long branched hairs on its proximal surface, not continuing onto its adjacent outer surface, which is shiny and often bare (cf. *Sibiricobombus*); metasomal tergum 6 usually with a shallow longitudinal groove on the

midline (absent from many smaller specimens and from most *B. fedtschenkoi* and *B. amurensis*); and this is the only subgenus in which none of the species have bands of red hair on the thorax or metasoma.

MATERIAL EXAMINED

Material was examined from 41 collections (Table 2). Emphasis was placed on reviewing material from Central Asia, Mongolia, and China (less from North America and Europe). This includes recent, well-documented surveys by the authors from across North China, which provide many new records supported by GPS data. Specimens were given unique database identifiers (referred to here by DB#), and data were recorded in an ACCESS database (v.2003) and mapped with ARCVIEW GIS (v.3.3), and with a program written in C by PW. Data in the database are not literal transcriptions of the labels. Chinese and Russian characters have been transliterated and abbreviations expanded. For specimens from the Bruno Pittioni collection (BMNH), additional data were added from entries in Pittioni's card index for those specimens. In some cases, current names for places were added where these have changed. In cases where GPS data were unavailable, some geographic coordinates and elevations were estimated from GOOGLEEARTH (v.5.0, accessed 2009), and these indirect data were registered in the database with lower precision estimates. The locality data for all specimens examined are available online in an ACCESS database (<http://www.nhm.ac.uk/bombus/downloads/subterraneobombus.mdb>).

DNA BARCODE DATA

Subsamples from groups of individuals showing differing morphology and colour patterns, and representing almost all of the named taxa within *Subterraneobombus*, had their DNA sequenced for the short 5' barcode region of the mitochondrial *COI* gene. This gene has a relatively high substitution rate that can be used to identify groups of divergent specimens within closely related taxa (e.g. Hebert, Ratnasingham & deWaard, 2003; Baker, Tavares & Elbourne, 2009; Gibbs, 2009). Sequences from this region, even as short as 100 nucleotides, can be diagnostic for 90% of species in other groups (Meusnier *et al.*, 2008). The sequenced subsamples consisted of specimens collected mostly within the last 15 years, and where possible included specimens from across the entire breadth of the geographic ranges of the nominal taxa. Specimens were sequenced at the Biodiversity Institute of Ontario, University of Guelph, as part of the BEE-BOL campaign to barcode the bees of the world (Packer, 2008). DNA extraction,

Table 2. Collections from which material has been examined

Abbreviation	Address
AM	Dr Alireza Monfared, Tehran, Iran
AMNH	American Museum of Natural History, New York, USA
ANSP	Academy of Natural Sciences, Philadelphia, USA
BMNH	Natural History Museum, London, UK
BT	Dr Borek Tkalců, Prague, Czech Republic
DG	Prof. Dave Goulson, Stirling, UK
GE	George Else, Hampshire, UK
HMB	Hungarian Natural History Museum, Budapest, Hungary
HUM	Hokkaido University Museum, Sapporo, Japan
IAB	Institute of Apiculture, Chinese Academy of Agricultural Sciences, Beijing, PRC
ISEAK	Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Kraków, Poland
IZB	Institute of Zoology, Chinese Academy of Sciences, Beijing, PRC
KUK	Kyushu University, Kyushu, Japan
LP	Prof. Laurence Packer, Toronto, Ontario, Canada
LSL	Linnean Society, London, UK
MA	Prof. Murat Aytekin, Hacettepe University, Ankara, Turkey
ME	Mike Edwards, Midhurst, UK
MNHU	Museum für Naturkunde an der Humboldt-Universität, Berlin, Germany
NME	Naturkundemuseum Erfurt, Erfurt, Germany
NMP	National Museum, Prague, Czech Republic
NMS	Naturmuseum Senckenberg, Frankfurt, Germany
NMV	Naturhistorisches Museum, Vienna, Austria
OLL	Oberösterreichs Landesmuseum, Linz, Austria
PR	Prof. Pierre Rasmont, Mons, Belgium
PUI	Purdue University, West Lafayette, Indiana, USA
PW	Dr Paul Williams, London, UK
ROM	Royal Ontario Museum, Toronto, Ontario, Canada
SC	Dr Sydney Cameron, Urbana, Illinois, USA
SR	Stuart Roberts, Reading, UK
SZMN	Siberian Zoological Museum, Novosibirsk, Russia
TP	Dr Tadeusz Pawlilowski, Toruń, Poland
TY	Prof. Tang Ya, Chengdu, Sichuan, PRC
UKK	University of Kansas, Kansas, USA
UMO	University Museum, Oxford, UK
UOG	University of Guelph, Guelph, Ontario, Canada
USNM	US National Museum of Natural History, Washington DC, USA
ZIH	Zoological Institute, University of Halle, Halle, Germany
ZISP	Zoological Institute, Russian Academy of Sciences, St Petersburg, Russia
ZMA	Zoological Museum Amsterdam, Amsterdam, The Netherlands
ZMMU	Zoological Museum of the Moscow State University, Moscow, Russia
ZSM	Zoologische Staatssammlung, München, Germany

polymerase chain reaction (PCR), and sequencing used the standard protocols described by Hebert *et al.* (2003). Universal primers for amplifying the *CO1* barcode sequence for insects were used (variants

LepF1 and LepR1; Hebert *et al.*, 2004). Data for the sequenced specimens have been uploaded to the BOLD online database (Ratnasingham & Hebert, 2007). Only sequences of at least 500 nucleotides were accepted for analysis (Ratnasingham & Hebert, 2007). The *CO1* sequence data, sample-site data, and photographs of specimens are available online in the BOLD database (<http://www.boldsystems.org>) within the project on bumblebees of the subgenus *Subterraneobombus* (BBST).

MORPHOLOGICAL DATA

Among the divergent groups of specimens identified from the molecular analysis, morphological characters were re-examined and compared using optical microscopes. These characters were then checked across all of the remaining material. Morphological terms follow Williams *et al.* (2009). Pubescence is referred to as hair for simplicity. Several terms are used as shorthand when describing components of the colour pattern that do not correspond precisely with particular segments or sclerites. On the head, the 'face' is used for the patch of hair around the antennal bases between the eyes, dorsal to the clypeus and ventral to the ocelli (frons + supraocular area + paraocular area). The 'sides' of the thorax refers to the long hair covering the lateral parts of the thorax ventral to the wing bases (on the lateral pronotum + mesepisternum + metepisternum + lateral propodeum). On the abdomen, the term 'tail' is used more flexibly, referring to the palest long hair covering all or parts of metasomal terga 4–6. Metasomal terga 1–7 and sterna 1–6 are abbreviated to T1–T7 and S1–S6. Body lengths were measured in lateral aspect from the base of the antenna to the posterior edge of T6 (females) or T7 (males).

ESTIMATING PHYLOGENY

Nucleotide sequences (without primer sequences) for *CO1* barcodes were aligned with the CLUSTALW function within BIOEDIT (v.7.0.9.0; <http://www.mbio.ncsu.edu/BioEdit/bioedit.html>, accessed 2010) and trimmed to a common frame length of 658 nucleotides that was shared by most samples. Four estimates of the phylogenetic tree were made.

1. We estimated a tree from all *CO1* sample sequences with MRBAYES (v.3.1.2; Huelsenbeck & Ronquist, 2001; Ronquist & Huelsenbeck, 2003). We found the nucleotide substitution model that fitted our *CO1* data best according to JMODELTEST (v.0.1.1; Posada, 2008) to be the general time-reversible (GTR) model with an inverse-gamma frequency distribution of changes among sites. We searched for 20 million generations of

the metropolis-coupled Markov-chain Monte Carlo algorithm with four chains, chain temperature set to 0.2, and with sampling of the trees every 1000 generations. Burn-in was set initially to 10%, with convergence between two separate runs of the analysis judged to have occurred when the average standard deviation of the split frequencies approached stationarity. The post burn-in stability of the log likelihood of the cold chain was confirmed using TRACER (v.1.5.0; Drummond & Rambaut, 2007), and the stability of the sample groups was examined using AWTY (v.0.8.1; Nylander *et al.*, 2008). Post burn-in trees from both replicates were combined and trees were rooted using data for *Bombus (Orientalibombus) haemorrhoidalis* Smith, 1852 to represent an out-group, based on the results of Cameron *et al.* (2007).

2. Before proceeding to a total-evidence estimate, we used BIOEDIT to derive single consensus *COI* sequences for each species, recording ambiguous nucleotides at particular sites where required, and obtained a tree from searching 20 million generations.
3. To estimate a tree from the morphological data, rates of change were set to be the same among all characters and we searched for 10 million generations. Autapomorphies were excluded from the data.
4. For the total-evidence estimate of the phylogenetic tree, the *COI* consensus data were entered along with the morphological data. Rates of change were unlinked between the consensus *COI* and morphological data, and again we searched for 10 million generations. The NEXUS files are available from PW and from TreeBASE (<http://www.treebase.org>).

RECOGNIZING SPECIES

For the purposes of this review, species are recognized operationally by unique combinations of two or more fixed morphological character states (reviewed for bumblebees in Williams, 1998), which may include characters of the colour pattern. Multiple concordant fixed states are likely to be evidence of a lack of recombination, and therefore of a lack of interbreeding. If an established species separated into discrete well-supported groups with substantial *COI* distances between them, then we looked for morphological character states that might diagnose those groups. If two or more diagnostic morphological character states could be found for those groups, then the groups would be recognized as separate species. However, a large genetic distance in *COI* orthologous sequence divergence alone is unreliable as evidence of separate species

(Meyer & Paulay, 2005; Meier *et al.*, 2006; Schmidt & Sperling, 2008), and is not accepted here as sufficient justification. To minimize inconsistencies, all material was identified or confirmed to species level by one author (PW).

RECONSTRUCTING BIOGEOGRAPHIC HISTORY

A scenario of biogeographic history was reconstructed using the dispersal–vicariance analysis implemented in DIVA (v.1.1; Ronquist, 1997). This estimates the ancestral distributions at each node of the supplied phylogenetic tree from the current distributions of terminal taxa by using a cost matrix to minimize the number of dispersal and extinction events, attributing no cost to vicariance events. Area units were chosen by projecting the point distribution data from the database into a coarse-scale equal-area grid, and then agglomerating cells with similar faunas into larger areas of endemism. The distribution of the out-group was not included. The number of ancestral areas recovered for each node was left unconstrained, but when ancestral area reconstructions were ambiguous, the more inclusive solution was accepted.

RESULTS

In total, 3854 specimens of *Subterraneobombus* were examined and databased. A subsample of 286 specimens was sequenced for *COI* barcode data, of which 214 (75%) succeeded in yielding sequences of at least 500 nucleotides (most include more than 600 nucleotides). The failures were concentrated among the older specimens, particularly those collected in India during the 1980s. This reduced the representation spanning the breadth of the geographic range, particularly for *B. personatus* and *B. difficillimus*. No amplification of *Wolbachia* (or other obviously non-target DNA) was detected. All sequences lacked indels, in-frame stop codons, and had closely similar GC% (22.47%, SE ± 0.037), with a strong AT-bias in the third codon position (97.88%, SE ± 0.082), providing no apparent evidence for the amplification of nuclear mitochondrial pseudogenes ('numts'; Song *et al.*, 2008).

An estimate of phylogenetic relationships from all of the individual *COI* sample data of *Subterraneobombus* is shown in Figure 2 (groups with a posterior probability < 0.9 should be considered unreliable). Multiple morphological characters (see the species diagnoses) were found to diagnose the groups of specimens that correspond to the previously described taxa (from the top of Fig. 2): *B. personatus*, *B. melanurus* (in a broad sense), *B. difficillimus*, *B. amurensis*, *B. fragrans*, *B. subterraneus* (in a

broad sense), *B. distinguendus*, *B. appositus*, and *B. borealis*. Consequently these taxa are recognized here as species. Only a single sequence is available for the rare and morphologically distinctive *B. fedtschenkoi*. A new taxon is recognized as a distinct monophyletic group, supported with multiple *CO1* nucleotide and morphological changes, and named *Bombus mongolensis* sp. nov.

There is substantial variation within some of species of *Subterraneobombus*. First, within *B. melanurus s.l.*, there is a large group of specimens from eastern Asia (Fig. 2) that have a strong band of black hair between the wing bases (a character state that corresponds to the type specimen of the taxon *tschitscherini*). A very similar, if weaker, black band occurs among a group of specimens from Nepal and among other specimens from China (Fig. 2). Considering these specimens together, the evidence from *CO1* is consistent with them being at best a paraphyletic group with respect to *B. melanurus s.s.* (although Fig. 2 does not support this directly, because it does not resolve the grouping of all *tschitscherini* specimens – they appear polyphyletic but the posterior probabilities are far too low to be reliable). But the crucial issue is that no *CO1* or morphological character state other than the black band has been found to diagnose the black-banded specimens (or to diagnose the remaining unbanded specimens). Consequently, until more evidence is available, the taxon *tschitscherini* is interpreted as part of the broader species *B. melanurus s.l.* Second, no morphological characters were found to diagnose the two most basal and strongly divergent *CO1* groups within *B. melanurus s.l.* In another case, the *CO1* data show no strong divergence among the described subspecific taxa of *B. subterraneus* (*dlabulai*, *latreillellus*, and *subterraneus s.s.*), and indeed provide no evidence to support intraspecific groups (Fig. 2). Again, these taxa are at present diagnosable only by their colour patterns. Consequently, until more evidence is available, they are interpreted as part of the species *B. subterraneus*. No morphological characters were found to diagnose the strongly divergent basal *CO1* groups within *B. distinguendus*.

Comparing intra- and interspecific variation for what we infer to be orthologous *CO1* data for the morphological species of *Subterraneobombus* we recognize, the maximum intraspecific variation is 2.67% (within *B. distinguendus*), and the minimum interspecific variation is 1.20% (between *B. melanurus* and *B. mongolensis* sp. nov.). Consequently, for these morphological species, some of which are relatively widespread, this appears to be another example of broad overlap between intra- and interspecific barcode variation ranges, rather than supporting the proposed

'barcoding gap' around the species rank (Meyer & Paulay, 2005; Meier *et al.*, 2006). The *CO1* distances between *B. distinguendus* and either *B. appositus* (1.55%) or *B. borealis* (1.86%) are low, even though the three have long and consistently been recognized as separate species (e.g. Franklin, 1913; Milliron, 1973). If they were considered together and a simple barcode divergence threshold criterion applied, then all three might have been considered parts of a single species. This shows that a simple distance threshold criterion used alone is problematic for diagnosing what are currently widely accepted to be good morphological species.

An estimate of phylogenetic relationships from the consensus *CO1* data for each species of *Subterraneobombus* is shown in Figure 3, and an estimate from the morphological data (Appendix 1) is shown in Figure 4. But the best estimate of phylogenetic relationships is shown in Figure 5, from the total evidence combined from both the *CO1* consensus sequences for each species and the morphological data (the topology from Fig. 5 with the morphological character changes optimized on it is shown in Appendix 2, Figure 106). Trees estimated from repeat runs of the same analysis were identical in topology. Figure 5 shows that in this case in the combined analysis the information from the 27 morphological characters is not swamped by the information from the 141 variable DNA nucleotide positions. Some groups in Figure 5 are well supported with high posterior probabilities, although there are distinct exceptions for the positions of *B. personatus* and *B. fedtschenkoi*, and for relationships within the *distinguendus* complex. Both *B. personatus* and *B. fedtschenkoi* show strong independent divergence in *CO1* (Figs 2, 3; these are more likely to have included multiple changes for any one nucleotide, which could obscure relationships), but have few morphological synapomorphies (Appendix 2). Therefore, further evidence from other molecules and from morphology would be highly desirable to increase the reliability of the estimated phylogeny.

The distribution of all of the geographically locatable samples (91% of all 1535 samples) for the material examined of *Subterraneobombus* is plotted in Figure 6. Maps for individual species are plotted in Figures 7–17, and diagrams of the colour patterns of the dorsal pubescence are shown in Figures 18–98. These diagrams represent particular specimens and are not expected to be exhaustive.

A scenario of biogeographic history for *Subterraneobombus* is plotted in Figure 99 using the phylogenetic estimate from Figure 5. The relationships of *B. personatus* and *B. fedtschenkoi* in this estimate are unreliable, but this estimate remains the best available for all species at present. Unsurprisingly, the



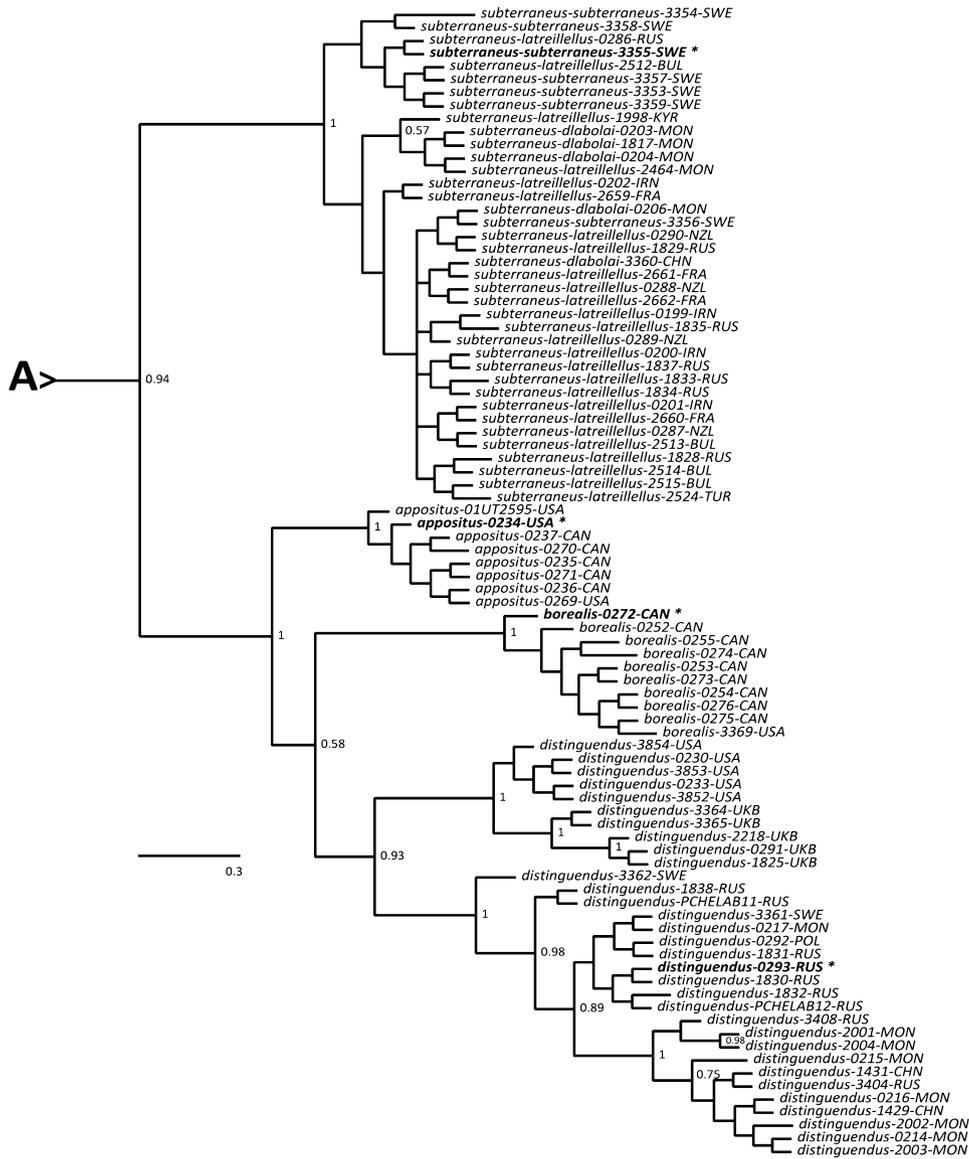


Figure 2. Estimate of phylogeny for 212 samples of all 11 *Subterraneobombus* species by Bayesian analysis of *CO1* barcode data (frame length 658 nucleotides, sequence data available from BOLD, specimen data available from the DB#) from a consensus of 36 002 sample trees after burn-in. The out-group (*Bombus haemorrhoidalis*) was chosen using the results of Cameron *et al.* (2007). The codes following the taxon names are the four-figure specimen identifiers (DB#), or longer IDs from BOLD, with country abbreviations: BUL, Bulgaria; CAN, Canada; CHN, China; FRA, France; IND, India; IRN, Iran; KAZ, Kazakhstan; KYR, Kyrgyzstan; MON, Mongolia; NEP, Nepal; NZL, New Zealand; POL, Poland; RUS, Russia; SWE, Sweden; SYR, Syria; THA, Thailand; TUR, Turkey; UKB, Britain; USA, United States of America. Values next to the nodes are Bayesian posterior probabilities for groups (groups with values of less than 0.9 are considered unreliable); values of less than 0.5 within species have been removed. Asterisks mark individuals from sites closest to the type localities of the primary types for each of the species names, which were regarded as informal proxies for types when applying names within this analysis. The scale bar represents 0.3 expected substitutions per nucleotide site.

minimum number of dispersal events required depends on which areas of endemism are chosen for encoding the data. One trade-off between simplicity and informativeness is obtained when the Tibet + Pamir highlands are treated as one area

unit (defined by the range of *B. difficillimus*, including the Himalaya + Alai) with the Central Asian + Mongolian highlands as another unit (defined by the range of *B. melanurus*, excluding Tibet + Pamir but including the Turkish + northern Iranian +

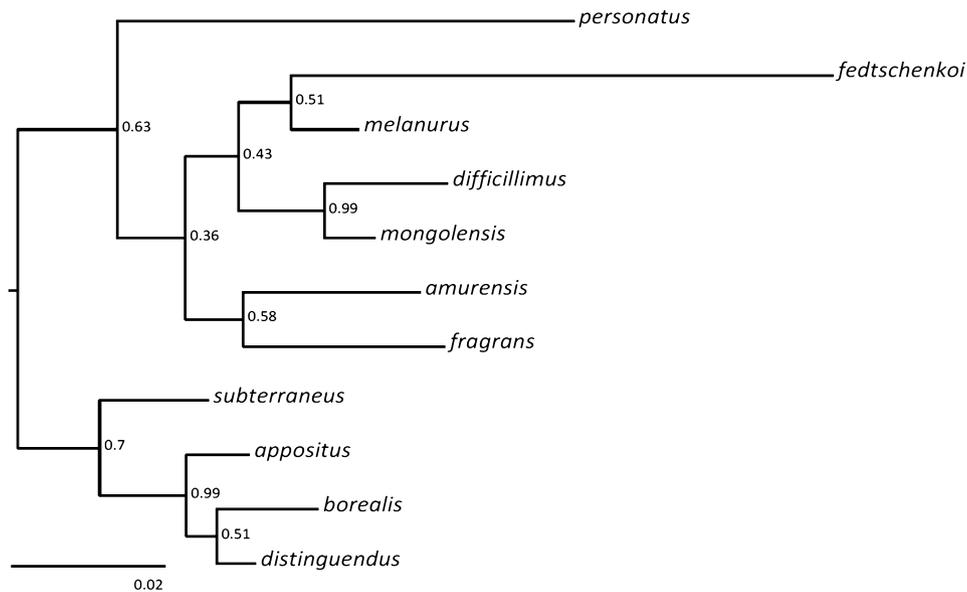


Figure 3. Estimate of phylogeny for all 11 *Subterraneobombus* species by Bayesian analysis of a single consensus *CO1* barcode sequence for each species (derived from the sequences in Figure 2), from a consensus of 18 002 sample trees after burn-in. The out-group (*Bombus haemorrhoidalis*, not shown) was chosen using the results of Cameron *et al.* (2007). Values next to the nodes are Bayesian posterior probabilities (see Fig. 2). The scale bar represents 0.02 expected substitutions per nucleotide site.

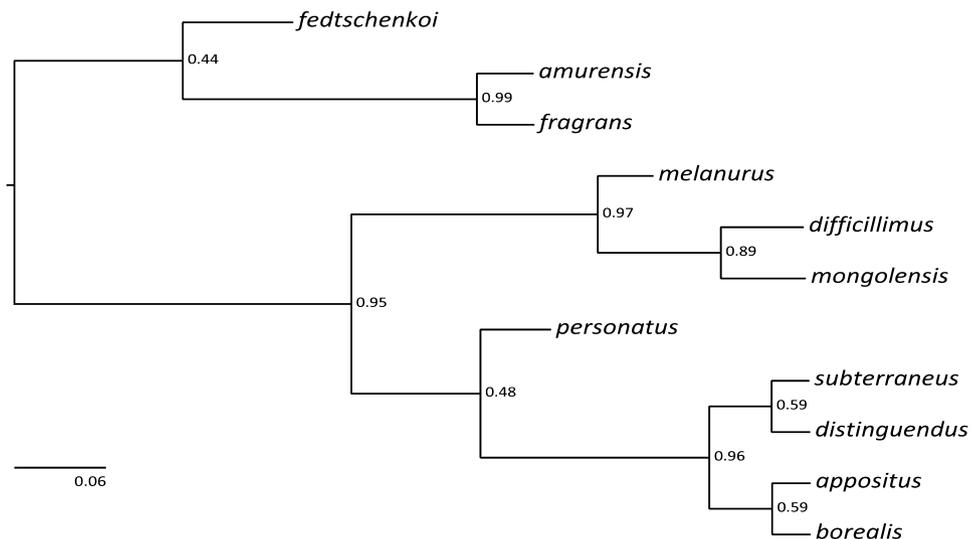


Figure 4. Estimate of phylogeny for all 11 *Subterraneobombus* species by Bayesian analysis of 27 morphological characters (excluding autapomorphies, data in Appendix 1) from a consensus of 18 002 sample trees after burn-in. The out-group (*Bombus haemorrhoidalis*, not shown) was chosen using the results of Cameron *et al.* (2007). Values next to the nodes are Bayesian posterior probabilities (see Fig. 2). The scale bar represents 0.06 expected state changes per character.

Tianshan + Altai + North China highlands), with lowland areas of Central Asia as a third unit (defined by the ranges of *B. amurensis* + *B. fragrans*). For this scheme (Fig. 99), an exact optimal solution was found requiring a minimum of six dispersal events. Among the principal results are: (1) an

initial divergence between a Tibet + Pamir ancestor (to the ?*personatus* + *melanurus* + ?*fedtschenkoi* + *fragrans* groups) and a northern Holarctic ancestor (to the *subterraneus* group); (2) a subsequent divergence between an Alai + Pamir ancestor (to ?*B. fedtschenkoi*) and a Central Asian ancestor (to the

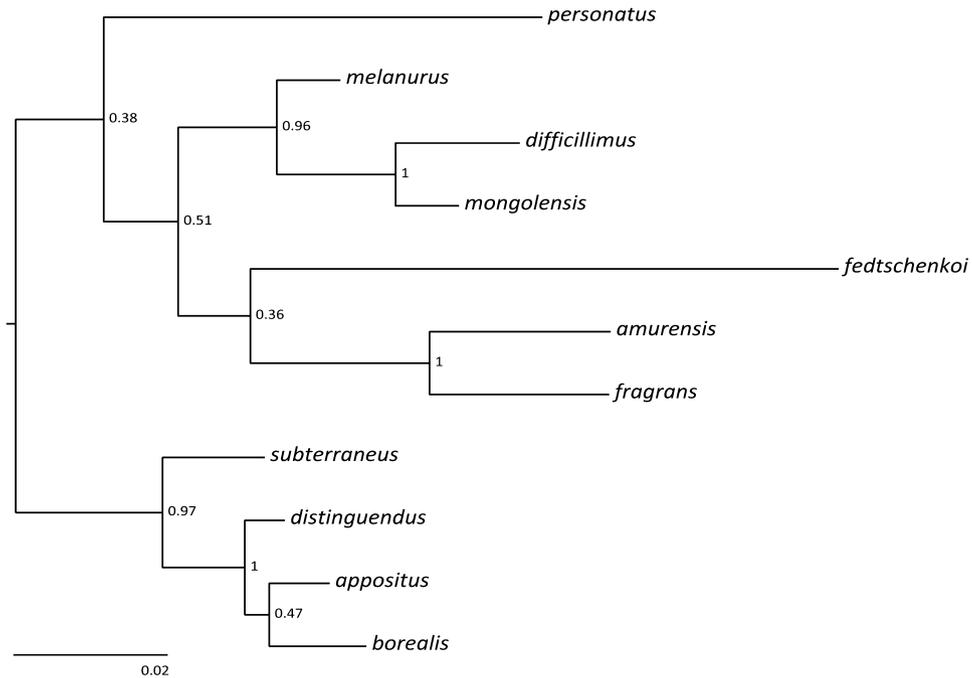


Figure 5. Estimate of phylogeny for all 11 *Subterraneobombus* species by Bayesian analysis of the total evidence of 658 *CO1* nucleotides (Fig. 2), reduced to a single consensus sequence for each species, in combination with the 27 morphological characters for the species (Fig. 4), from a consensus of 18 002 sample trees after burn-in. The out-group (*Bombus haemorrhoidalis*, not shown) was chosen using the results of Cameron *et al.* (2007). Values next to the nodes are Bayesian posterior probabilities (see Fig. 2). The scale bar represents 0.02 expected changes per nucleotide site or character.

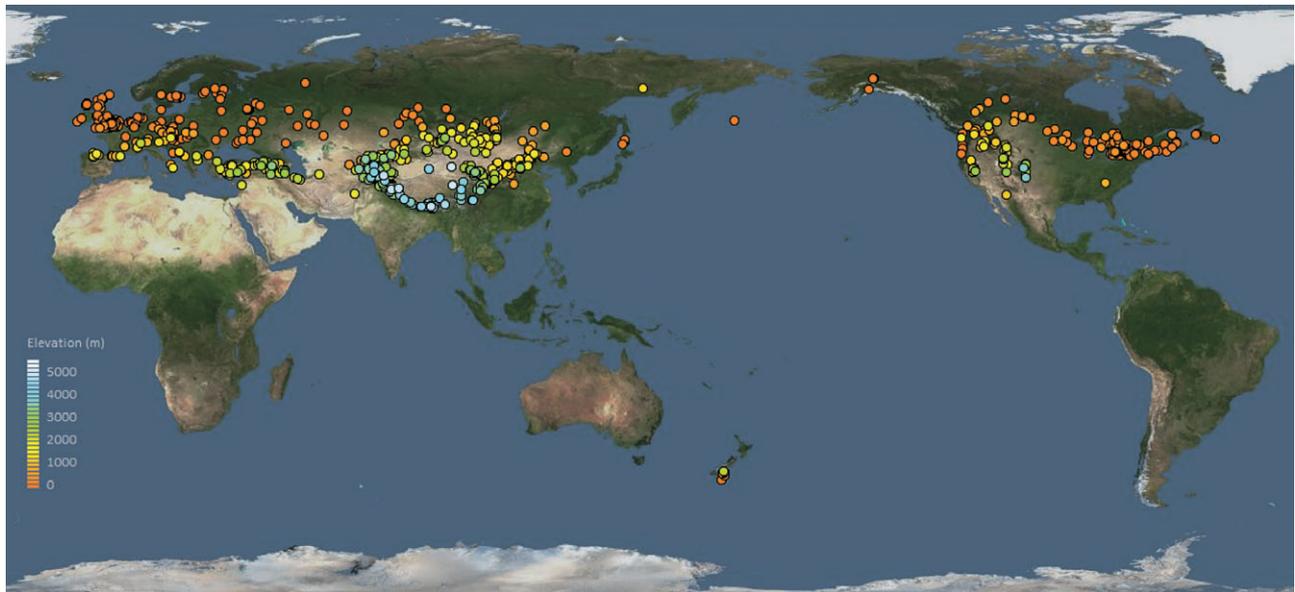
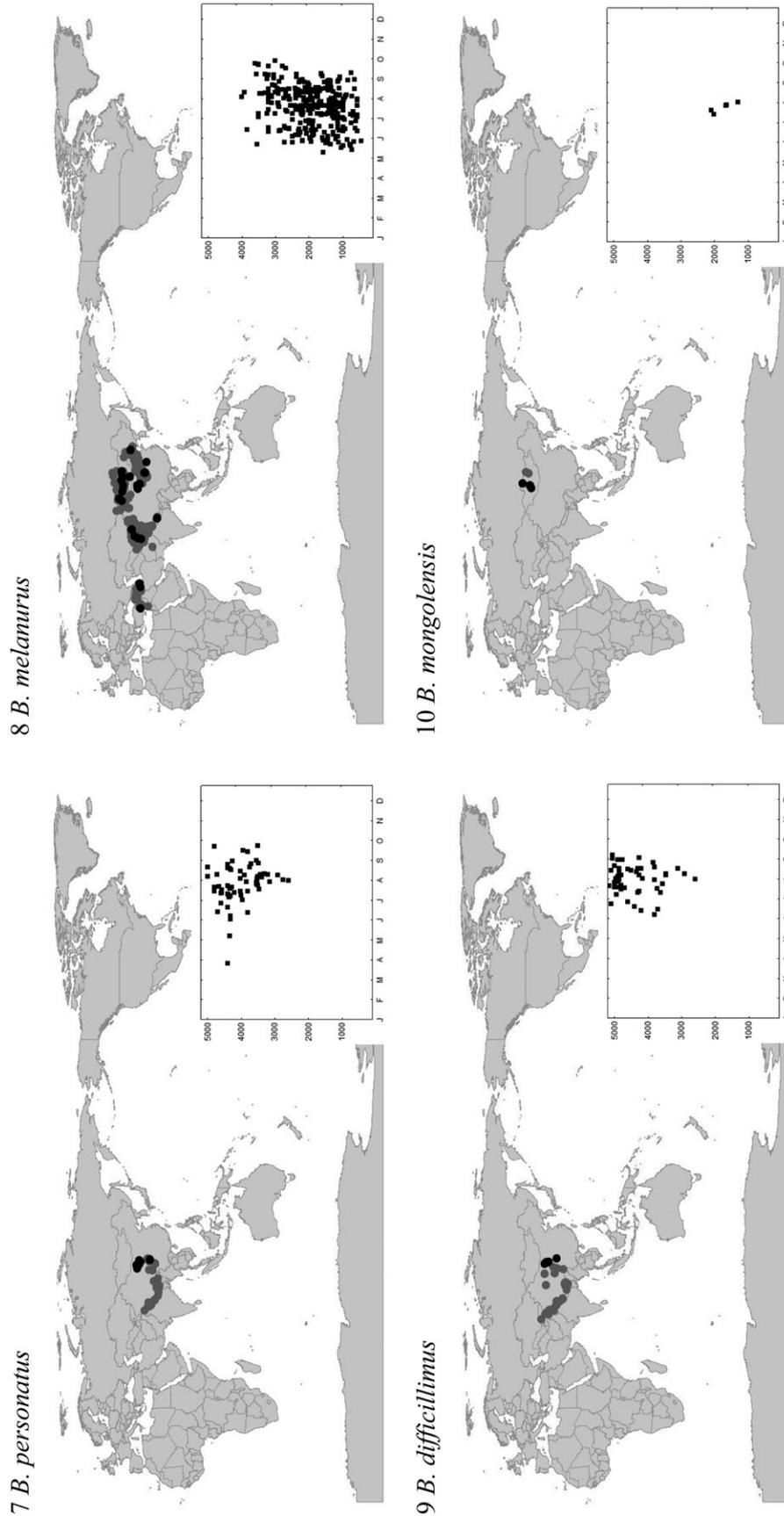


Figure 6. Global distribution of sample sites indicated as coloured spots, with the colours showing the elevation (scale at left). Cartesian orthonormal projection (as for the following maps): north at the top of the map.

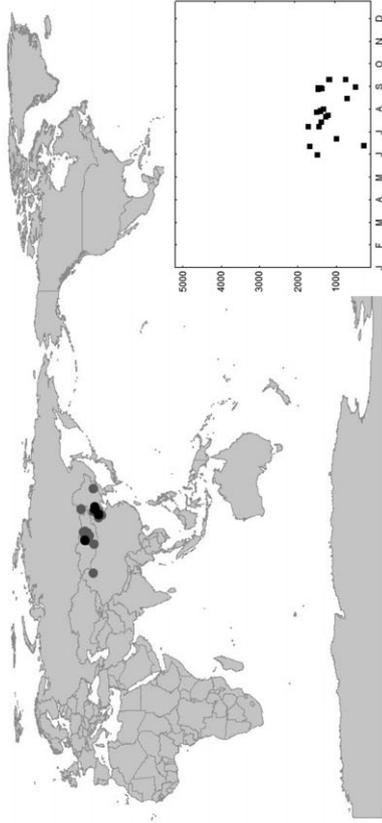
fragrans group); and (3) a relatively recent divergence between a Palaearctic ancestor (*B. distinguendus*) and a Nearctic ancestor (*B. appositus* + *B. borealis*) (see the Discussion for an interpretation). What

appears to emerge from this analysis is that a high proportion of reconstructed ancestral distributions are associated primarily with the Tibet + Pamir block when these areas are treated together.

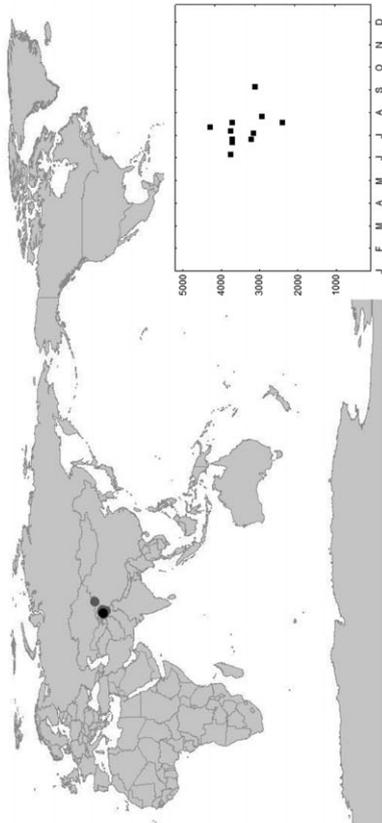


Figures 7–10. Global distribution of material examined (grey spots) and successfully sequenced (black spots) for *Bombus personatus*, and for the species of the *melanurus* group. The inset scatter plots show activity by phenology (x-axis: day of the year, letters refer to months) and elevation (y-axis: metres).

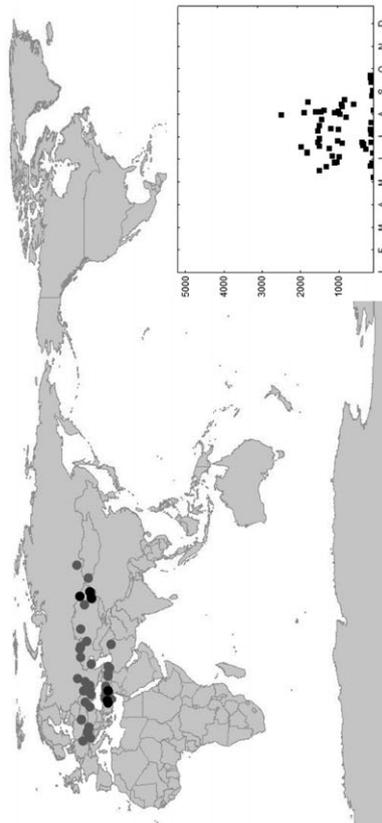
12 *B. amurensis*



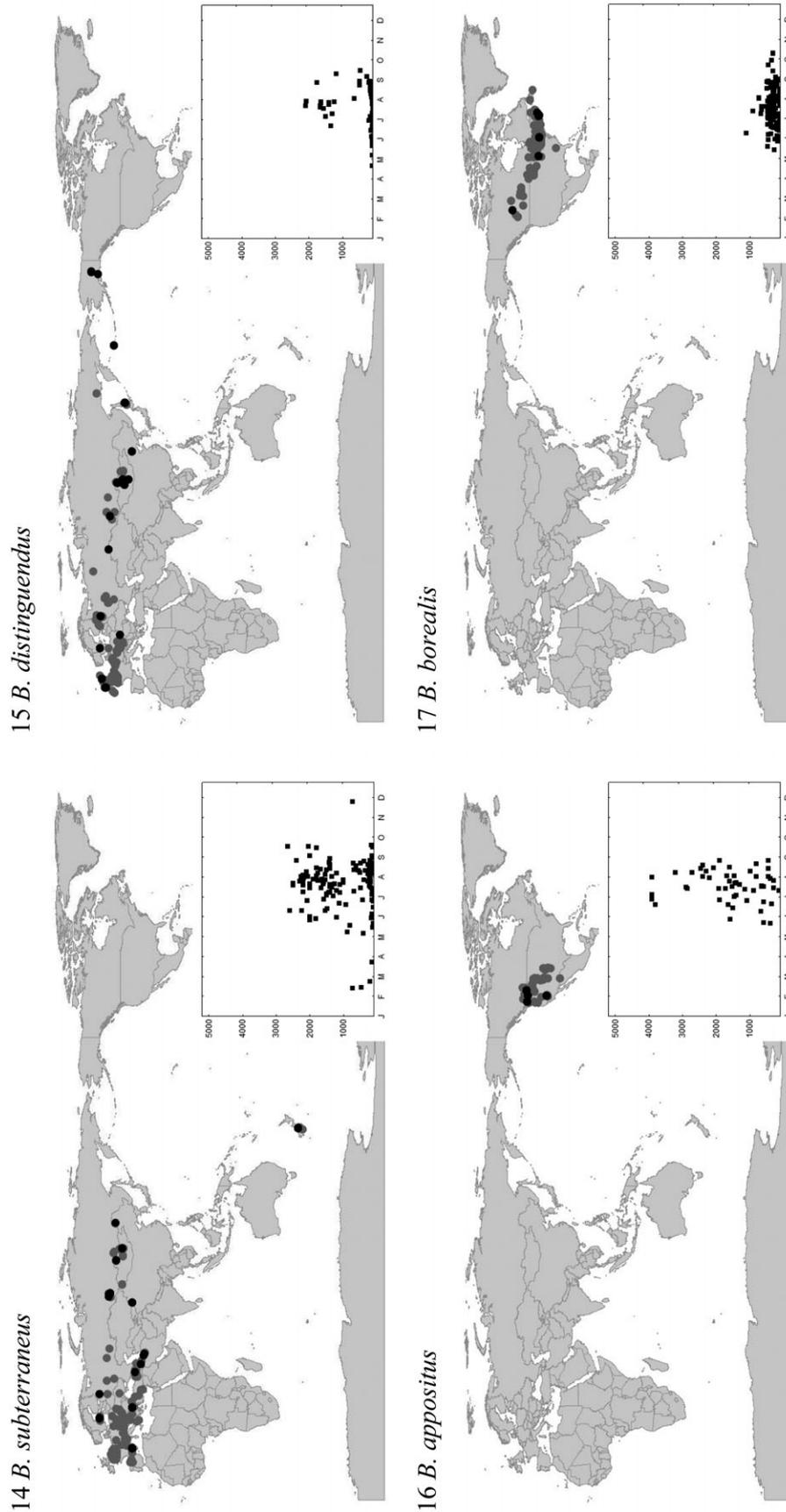
11 *B. fedtschenkoi*



13 *B. fragrans*



Figures 11–13. Global distribution of material examined (grey spots) and successfully sequenced (black spots) for the species of the *fragrans* group. The inset scatter plots show activity by phenology (x-axis: day of the year, letters refer to months) and elevation (y-axis: metres).



Figures 14–17. Global distribution of material examined (grey spots) and successfully sequenced (black spots) for species of the *subterraneus* group. The inset scatter plots show activity by phenology (x-axis: day of the year, letters refer to months) and elevation (y-axis: metres).

KEY TO FEMALES

Specimens of *Subterraneobombus* for which *CO1* barcode data are available can now be identified from our reference database on the BOLD website by using the sequence comparison tool on the homepage. Keys using morphological characters follow (also see the tree in Appendix 2). Identifications from the key or figures should be checked against the diagnoses within the species accounts.

1. Clypeus smooth and shiny, with only micropunctures in its central half.....4
 - Clypeus rough and matt, with small and large punctures scattered throughout.....2
- 2 (1). Oculo-malar distance 1.5 times as long as the basal breadth of the mandible; T4–T5 hair black (Figs 30–34).....*Bombus fedtschenkoi*
 - Oculo-malar distance 1.0 times as long as the basal breadth of the mandible; T4–T5 hair predominantly yellow, at most each tergum with a few black hairs in a triangle medially adjacent to the anterior edge (Figs 35–38)3
- 3 (2). Labrum with the breadth of the median furrow less than 0.33 times the total breadth of the labrum; thoracic dorsum with a broad band of black hairs between the wing bases; T3–T5 with few or no black hairs (Figs 37, 38).....*Bombus fragrans*
 - Labrum with the breadth of the median furrow more than 0.5 times the total breadth of the labrum; thoracic dorsum with an isolated spot of black hairs between the wing bases; T3–T5 each with black hairs in a small triangle medially at the anterior edge (Figs 35, 36).....*Bombus amurensis*
- 4 (1). Clypeus with the micropunctures sparse, most separated by more than twice their own breadths; T1–T2 hair either extensively black or, if T1–T2 entirely yellow or white, then either T3–T4 entirely black or T3–T4 predominantly yellow (Figs 23–29, 39–62).....5
 - Clypeus with many micropunctures, many separated by only twice their own breadths; T1–T2 hair entirely yellow or cream–yellow, T3–T4 usually black with broad posterior fringes of long white hairs, or, if only a few pale hairs, then the black band between the wing bases is nearly as broad as the yellow thoracic bands combined, and black hairs intermixed throughout the posterior half of the anterior yellow thoracic band (Figs 18–22)*Bombus personatus*
- 5 (4). T1–T2 hair entirely yellow or white, T3–T5 usually entirely black, although rarely with a yellow posterior fringe on T3 (Figs 23–29).....6
 - T1–T2 hair either extensively black or, if T1–T2 entirely yellow, then T3–T4 also predominantly yellow (Figs 39–62).....8
- 6 (5). Clypeus with a few sparse small punctures in its central half; thoracic dorsum either entirely yellow or brown, or, if a black band is present between the wing bases, then it is less than 0.8 times the breadth of the anterior yellow or brown thoracic band; pale hair of the thorax lemon yellow, or straw yellow, but usually only cream–yellow if faded by the sun; hair (short) on T2 straight and erect over the anterior one-quarter (or less), curved and more decumbent over the posterior three-quarters; T5 with longest hairs projecting beyond the posterior edge by less than the greatest breadth of the hind basitarsus; distal area of forewing beyond the closed cells greyish or mid brown, as dark as or darker than the proximal area*Bombus melanurus*
 - Clypeus almost devoid of even micropunctures in its central half; thoracic dorsum with a black band between the wing bases, which is 0.75–1.0 times the breadth of the anterior yellow or white thoracic band; pale hair of the thorax cream–yellow or white; hair (long) of T2 straight and erect over the anterior two-thirds, curved and more decumbent along the posterior edge; T5 with longest hairs projecting beyond the posterior edge by more than the greatest breadth of the hind basitarsus; distal area of forewing beyond the closed cells nearly clear, often paler than the proximal area7
- 7 (6). Gena in the area just lateral to the dorsal furrow with sparse shallow medium punctures scattered almost to the anterior edge next to the eye; dense pale hair on the sides of the thorax (pronotum + mesepisternum) extending halfway or nearly halfway from the wing base to the mid-leg bases.....*Bombus difficillimus*
 - Gena in the area just lateral to the dorsal furrow smooth and shiny, with almost no punctures (very shallow) in the anterior third; dense pale hair on the sides of the thorax (pronotum + mesepisternum) extending three-quarters of the way from the wing base to the mid-leg bases***Bombus mongolensis sp. nov.***
- 8 (5). Terga 1–3 hair predominantly yellow or brown, usually at most with black hairs intermixed anteriorly on each, T4–T5 with yellow, brown, or black hair, but never with white hair (Figs 48–62).....9
 - Terga 1–3 hair with extensive and conspicuous areas of black, usually with very narrow posterior fringes of short white or yellow hairs, T3–T5 usually with conspicuous white hair, or occasionally T1–T5 almost entirely black (Figs 39–47).....*Bombus subterraneus*
- 9 (8). Pale hair of the face (if present) at least slightly lighter than the hair on T1; hair short, the longest hair near the posterior edge of T5 laterally about equal to the greatest breadth of the hind basitarsus (Figs 53–62).....10

- Pale hair of the face (if present) the same colour as T1; hair long, the longest hair near the posterior edge of T5 laterally about 1.5 times as long as the greatest breadth of the hind basitarsus (Figs 48–52).....*Bombus distinguendus*
- 10 (9). Tergum 5 hair entirely sand yellow or coffee brown; pale hair at the anterior of the thoracic dorsum usually greyish white, or rarely yellow, but usually paler than T1–T4, which are sand yellow or coffee brown (Figs 53–57).....*Bombus appositus*
- Tergum 5 hair usually entirely or predominantly black, rarely predominantly yellow with some black hair; pale hair at the anterior of the thoracic dorsum the same golden yellow as T1–T4 (Figs 58–62).....*Bombus borealis*

KEY TO MALES

1. Gonocoxa with a sharp dorsal ridge reaching all the way to the distal edge, on its inner side distally with a dorsally flat or concave triangular inwardly directed process.....7
- Gonocoxa with sharp dorsal ridge subsiding into the rounded convex dorsal surface before the distal edge, so that the distal portion is finger like, or if the sharp dorsal ridge subsides into the convex dorsal surface only just before the distal edge, then the gonostylus lacks a distinct and narrowed inner proximal process.....2
- 2 (1). Gonostylus approximately or nearly as long as broad, with the apex truncate with two weakly marked angles, the inner proximal process at its narrowest point almost as broad as the length of the gonostylus; penis valve head proximal outer corner with a long proximally directed process; penis valve ventrolateral process often with teeth but without long spines.....3
- Gonostylus much shorter than broad and triangular with the apex with one angle, the inner proximal process at its narrowest point half as broad as the length of the gonostylus; penis valve head proximal outer corner without a long proximally directed process; penis valve ventrolateral process with a dorsal and a ventral long spine.....5
- 3 (2). Gonostylus with the inner proximal process turned posteriorly at the distal end; penis valve with the ventrolateral process broadly and evenly rounded without teeth, like a manatee tail.....4
- Gonostylus with the inner proximal process indistinct and not turned posteriorly at the distal end; penis valve with the ventrolateral process with the dorsal tooth very weak or absent, the middle area broadly triangular or rounded, and with a ventral spine (Figs 74–77).....*Bombus fedtschenkoi*
- 4 (3). Hair on the metasoma ventrally long, the long hairs in the median half of S3 nearly as long as the greatest breadth of the mid basitarsus; T3–T5 without black hair (Figs 81–83).....*Bombus fragrans*
- Hair on the metasoma ventrally unusually short, the long hairs in the median half of S3 less than half as long as the greatest breadth of the mid basitarsus; T3–T5 each with a well-defined but often inconspicuous small triangular patch of black hair anteriorly near the midline, the apices of the triangles pointing posteriorly (Figs 78–80).....*Bombus amurensis*
- 5 (2). Hair of the face yellow or if black then there is no band of black hairs between the wing bases; gonostylus with the inner proximal process at its narrowest as broad as a quarter of the length of the gonostylus (Figs 65–69).....*Bombus melanurus*
- Hair of the face usually black, but if with many pale hairs then there are few or no pale hairs just above the wing base in the black band between the wing bases; gonostylus with the inner proximal process at its narrowest as broad as nearly a half of the length of the gonostylus.....6
- 6 (5). Hair on top of the head mostly yellow, without any black hairs intermixed in the middle; clypeus almost covered in hair and large punctures, at most with only a narrow median longitudinal stripe free of these and shiny; hind tibia outer surface with widely separated scarcely overlapping decumbent almost unbranched hairs; gonostylus distally broadly rounded (Figs 70, 71).....*Bombus difficillimus*
- Hair on top of the head either black or intermixed with black hairs throughout; clypeus in the median third for most of its length free of hair and large punctures, and shiny; hind tibia outer surface with dense extensively overlapping decumbent obviously branched hairs; gonostylus distally abruptly right angled (Figs 72, 73).....*Bombus mongolensis* sp. nov.
- 7 (1). Penis-valve head on its outer proximal corner with a toothed ridge, with two distinct anteriorly-directed flattened teeth or processes.....8
- Penis-valve head on its outer proximal corner with a simple anteriorly-directed long conical or cylindrical spine (Figs 63, 64).....*Bombus personatus*

- 8 (7). Penis-valve head on its outer proximal corner with a toothed ridge, either with small indistinct teeth or with a ventral process that is longer than a dorsal process; penis valve with the trident-like ventrolateral process with the middle tooth broadly rounded and only weakly marked.....9
- Penis-valve head on its outer proximal corner with a toothed ridge, the more dorsal process longer than the ventral process; penis valve with the trident-like ventrolateral process with the middle tooth produced as an equilateral triangle.....10
- 9 (8). Penis valve with the ventrolateral process with a strong dorsal tooth; the majority of the hairs just dorsal to the antennal base and anterior to the ocelli black; T2 with black hairs usually intermixed for at least half of the length from the anterior to the posterior edges, so as to appear as a conspicuous brown band, but occasionally reduced to inconspicuous patches of a few black hairs intermixed laterally near the anterior edge (Figs 84–88).....*Bombus subterraneus*
- Penis valve with the ventrolateral process with a weak dorsal tooth; the majority of at least the shorter hairs just dorsal to the antennal base usually yellow; T2 without any black hair (Figs 89–92).....*Bombus distinguendus*
- 10 (8). Pale hair of the head and of the anterior thoracic dorsum a similar grey–white or yellow; T1–T6 hair coffee brown or straw yellow, without a black band on T5 or at most with a few scattered black hairs (Figs 93–95).....*Bombus appositus*
- Pale hair of the face (rarely almost absent) between the clypeus and the ocelli cream–yellow, pale hair of the vertex and of the anterior thoracic dorsum a distinctly darker sand yellow; T1–T6 hair golden yellow except for broad anterior black bands on T5–T6 (Figs 96–98).....*Bombus borealis*

SPECIES ACCOUNTS

Treatment of names follows the rules of the ICZN (1999). Unavailable names are shown in brackets, and only the first incidences of misspellings are listed. Misidentifications are generally not included except in Table 1.

BOMBUS PERSONATUS SMITH, 1879
(FIGS 7, 18–22, 63, 64)

Bombus personatus Smith, 1879: 132, lectotype queen by designation of Richards (1930: 656), BMNH examined. India: Himachal Pradesh.

Bombus Roborowskyi Morawitz, 1887: 197, syntype queen, ZISP examined. China: Qinghai. Synonymized with *Bombus personatus* Smith by Williams, 1991: 64.

[*Subterraneobombus roborowskii* (Morawitz); Skorikov, 1923: 154, incorrect subsequent spelling.]

[*Subterraneobombus robororskii* (Morawitz); Skorikov, 1933a: 244, incorrect subsequent spelling.]

[*Bombus presonatus* Smith; Wu, 1941: 282, incorrect subsequent spelling.]

[*Bombus* (*Subterraneobombus*) *roborowskyi* f. *tenuiciliata*, f. *nigricans* Tkalcù, 1961: 362, infrasubspecific.]

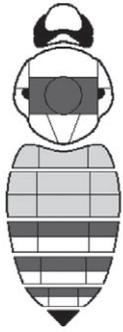
[*Bombus* (*Subterraneobombus*) *robrowskii* Morawitz; Wang, 1982: 443, incorrect subsequent spelling.]

History: Until 1991, this species was usually referred to (albeit rarely) by the name *B. roborowskyi*.

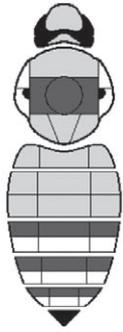
Diagnosis: Female. Head with clypeus weakly shiny, in its central half lacking medium or large punctures, but with many widely scattered micropunctures. Hair long: the longest hair of T5 longer than the greatest

breadth of the hind basitarsus. Colour pattern (Figs 18–22). Hair of the head black, with pale hairs inconspicuously intermixed, except laterally posterior to the eye where the hairs are exclusively black, and in queens between the base of the antenna and the clypeus where pale hairs predominate; the side of the thorax, all of the dorsum except for a band between the wing bases, and T1–T2 yellow (a pale grey–yellow or cream, although queens sometimes distinctly more lemon yellow on T1–T2; young workers often more pale yellow); the black band between the wing bases usually sharply defined and equal to the greatest breadth of the anterior pale band (measured from anterior to posterior on the body midline), but sometimes with black hairs intermixed in the posterior half of the anterior pale band; T3–T5 black with posterior fringes of white hairs, which may occupy half the length of the terga for queens, or may be narrow or almost lacking for some workers.

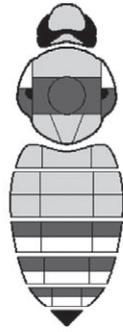
Male. Head with clypeus nearly covered in dense and moderately long hair, except in a narrow median band occupying the median quarter in the anterior ventral quarter adjacent to the labrum; antennal scape with hairs longer than the breadth of the scape in the distal third; genitalia with gonocoxa with proximal inner process particularly broad and rounded, almost semicircular; gonocoxa with sharply defined dorsal ridge reaching the distal outer edge before the distal extremity, which is flat dorsally; gonostylus weakly triangular, the distal apex hardly marked beyond the moderately broad inner process; volsella distally moderately broad; penis valve with the ventrolateral process broad, with a weak dorsal tooth, a strong ventral tooth, with an almost right-angled pronounced central projection; penis valve head 1.3



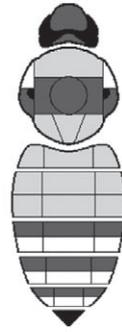
18 *B. personatus*



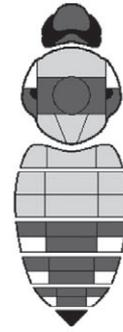
19 *B. personatus**



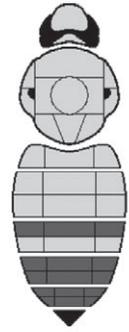
20 *B. personatus*



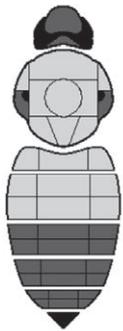
21 *B. personatus*



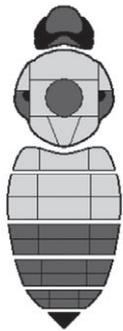
22 *B. personatus*



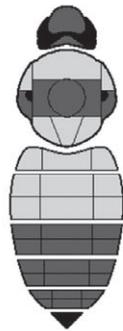
23 *B. melanurus*



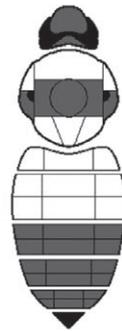
24 *B. melanurus**



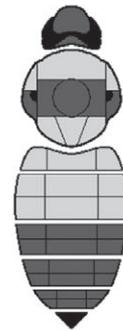
25 *B. melanurus*



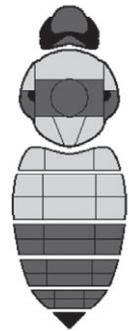
26 *B. melanurus*



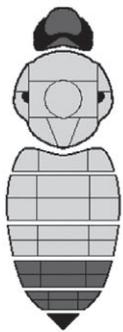
27 *B. difficillimus*



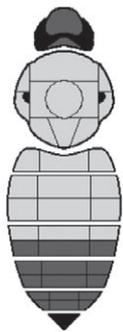
28 *B. difficillimus**



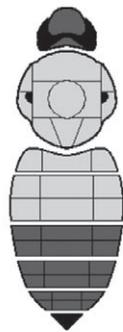
29 *B. mongolensis*



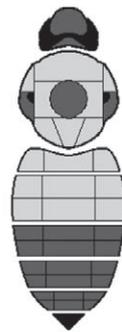
30 *B. fedtschenkoi*



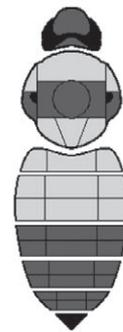
31 *B. fedtschenkoi*



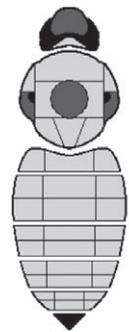
32 *B. fedtschenkoi**



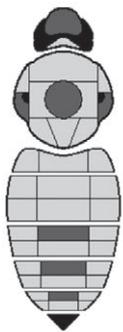
33 *B. fedtschenkoi*



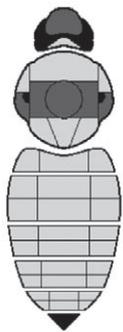
34 *B. fedtschenkoi*



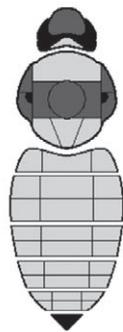
35 *B. amurensis**



36 *B. amurensis*



37 *B. fragrans*



38 *B. fragrans**

Figures 18–38. Simplified colour pattern diagrams for the dorsal pubescence of females (*most frequent pattern). Dark grey indicates black; light grey indicates yellow or brown; white indicates white or pale cream. Figure (DB#) country: 18 (0036) India; 19 (0031) India; 20 (1283) China; 21 (0035) India; 22 (0007) China; 23 (1873) Mongolia; 24 (0142) Iran; 25 (0076) India; 26 (1311) China; 27 (2593) Tajikistan; 28 (0009) China; 29 (1921) Mongolia; 30 (2545) Kyrgyzstan; 31 (2546) Kyrgyzstan; 32 (0295) Tajikistan; 33 (2075) Kyrgyzstan; 34 (1967) Kyrgyzstan; 35 (0171) China; 36 (0177) China; 37 (1993) Kazakhstan; 38 (2522) Turkey.

times as long as broad (cf. *B. melanurus*, *B. difficilinus*, and *B. mongolensis* sp. nov.), distally broadly rounded on its outer edge, its outer proximal corner with an anteriorly directed long conical spine. Colour pattern (Figs 63, 64). Hair predominantly pale grey–yellow, with black hair intermixed on the head, especially along the edge of the clypeus and along inner eye edge, posteriorly and laterally to the eye, on the thoracic dorsum in a more or less distinct band between the wing bases, and anteriorly on T3–T7.

Material examined: A total of 52 queens, 78 workers, and 12 males (BMNH, HUM, IAB, IZB, MNHU, PW, SC, and YT; see Table 2 for a list of institutional abbreviations), 16 specimens barcoded in the BOLD database. Details can be found at <http://www.nhm.ac.uk/bombus/downloads/subterraneobombus.mdb>.

Distribution: Material examined from China, India, Nepal, and Pakistan (2585–5000 m a.s.l.; Fig. 7). Regional maps are available for Kashmir (Williams, 1991) and Sichuan (Williams *et al.*, 2009).

Variation: Primarily among workers in how many pale hairs are present as pale fringes at the posterior of T3–T5. Also in the hue of the yellow, which may be light yellow among workers, but is more grey–yellow, cream, or nearly white among queens, except on T1–T2, where it often remains lemon yellow. The palest queens examined are from Ladakh in the west and the darkest workers are from Qinghai in the east. No geographic pattern to *CO1* variation is apparent.

BOMBUS MELANURUS LEPELETIER, 1835
(FIGS 8, 23–26, 65–69, 100)

Bombus melanurus Lepeletier de Saint-Fargeau, 1835: 469, lectotype queen by designation of Tkalců (1969a: 202), UMO examined. Syria.

Bombus altaicus Eversmann 1846: 436, holotype queen by monotypy (Skorikov, 1910: 572), ZISP not seen. Altai. Synonymized with *Bombus melanurus* Lepeletier by Morawitz (in Fedtschenko, 1875: 5).

Bombus Tschitscherini Radoszkowski, 1862: 591, by indication of Radoszkowski (1860: 485, as *B. attaicus*, an incorrect subsequent spelling of *B. altaicus*

Eversmann), **lectotype** queen by present designation (note 1), ISEAK examined. Russia: Siberia. Regarded as conspecific (in the form *Bombus melanurus tschitscherini* Radoszkowski) by Vogt (1909: 53); synonymized with *Bombus melanurus* Lepeletier by Williams (1991: 62).

[*Bombus æltaicus* Eversmann; Smith, 1878: 9, incorrect subsequent spelling.]

Bombus tschitscherinii Radoszkowski; Dalla Torre, 1896: 560, unjustified emendation (multiple similar emendations).

[*Bombus melanurus tschitscherini* var. *lantschouensis* Vogt, 1909: 53, infrasubspecific.]

Bombus (Subterraneobombus) melanurus ssp. *subdistinctus* Richards, 1928: 333, holotype queen by original designation, BMNH examined. India: Kashmir.

[*Bombus (Subterraneobombus) melanurus* ab. *ciliatus* Reinig, 1930: 82, infrasubspecific.]

[*Bombus (Subterraneobombus) melanurus ciliatus* Form *postzonatus* Reinig, 1930: 122, infrasubspecific.]

Subterraneobombus melanurus ssp. *maljuschenkoi* Skorikov, 1931: 231, **lectotype** queen by present designation (note 2), ZISP examined. Armenia.

Bombus (Subterraneobombus) maidli Pittioni, 1939b: 246, lectotype worker by designation of Williams (1991: 62), NMV examined. Mongolia. Synonymized with *Megabombus subdistinctus* (Richards) by Tkalců (1969a: 203); synonymized with *Bombus melanurus* Lepeletier by Williams (1991: 62).

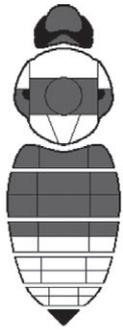
Bombus (Subterraneobombus) lantschouensis Tkalců, 1961: 360, by indication of Vogt, 1909: 53, lectotype (note 3) queen by designation of Tkalců (1974b: 48), MNHU examined. China: Gansu. Junior primary homonym of *B. lucorum* var. *lantschouensis* Vogt, 1908: 101 (= *B. patagiatus* Nylander); **syn. nov.**

Megabombus (Subterraneobombus) subdistinctus (Richards); Tkalců, 1969a: 203, change of status. Synonymized with *Bombus melanurus* Lepeletier by Williams (1991: 62).

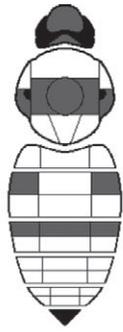
[*Bombus melanurus* Lepeletier; Yefremova, 2001: 273, incorrect subsequent spelling.]

[*Bombus (Subterraneobombus) schitscherini* Radoszkowski; An *et al.*, 2008: 85, incorrect subsequent spelling.]

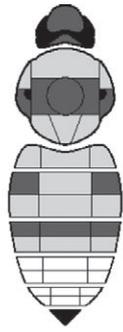
[*Bombus (Subterraneobombus) tshitscherini* Radoszkowski; Proshchalykin & Kupianskaya, 2009: 65, incorrect subsequent spelling.]



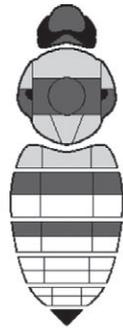
39 *B. subterraneus*



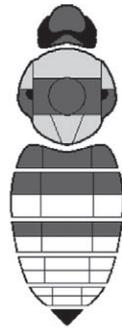
40 *B. subterraneus*



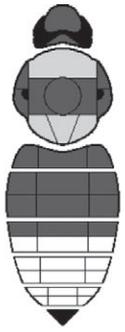
41 *B. subterraneus*



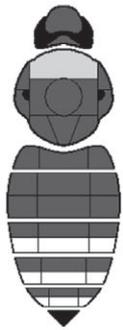
42 *B. subterraneus**



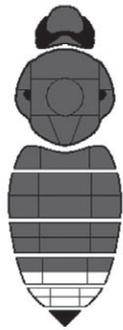
43 *B. subterraneus*



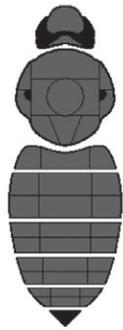
44 *B. subterraneus*



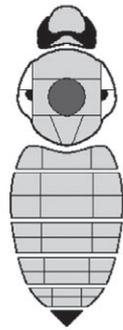
45 *B. subterraneus*



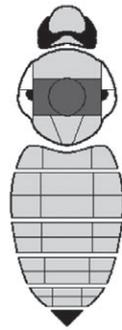
46 *B. subterraneus*



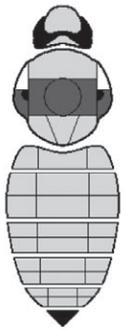
47 *B. subterraneus*



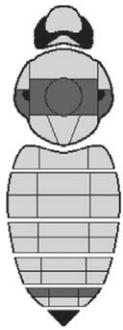
48 *B. distinguendus**



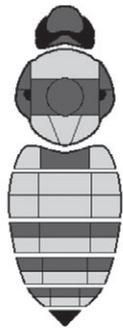
49 *B. distinguendus*



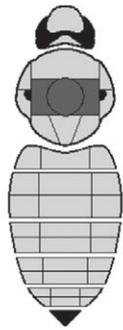
50 *B. distinguendus*



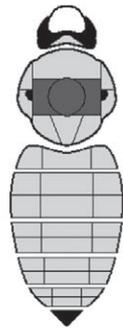
51 *B. distinguendus*



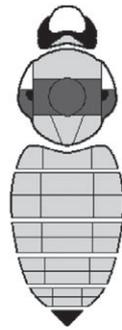
52 *B. distinguendus*



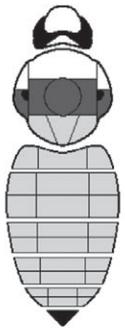
53 *B. appositus*



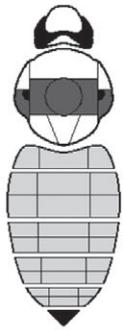
54 *B. appositus*



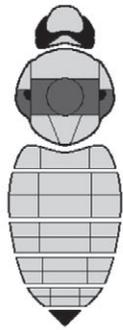
55 *B. appositus*



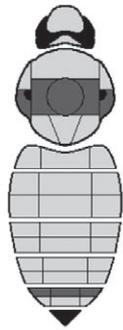
56 *B. appositus**



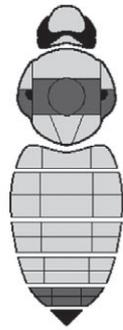
57 *B. appositus*



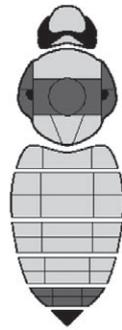
58 *B. borealis*



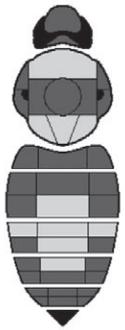
59 *B. borealis*



60 *B. borealis**



61 *B. borealis*



62 *B. borealis*

Figures 39–62. Simplified colour pattern diagrams for the dorsal pubescence of females (*most frequent pattern). Dark grey indicates black; light grey indicates yellow or brown; white indicates white or pale cream. Figure (DB#) country: 39 (2000) Mongolia; 40 (0203) Mongolia; 41 (0198) Iran; 42 (1197) Spain; 43 (0182) UK; 44 (0185) UK; 45 (0190) UK; 46 (0195) Sweden; 47 (0194) Sweden; 48 (0209) UK; 49 (2055) Russia; 50 (0215) Mongolia; 51 (0230) USA; 52 (0232) USA; 53 (3084) USA; 54 (3083) USA; 55 (3082) USA; 56 (0238) USA; 57 (0240) USA; 58 (2275) Canada; 59 (0255) Canada; 60 (0251) Canada; 61 (0262) USA; 62 (3367) USA.

Note 1 (*tschitscherini*). Although named by Behr, the description making the name available was by Radoszkowski (1860, 1862), who is therefore the author (ICZN, 1999: article 50.1.1). According to Pesenko & Astafurova (2003), after his death Radoszkowski's collection went to the Polish Academy of Sciences in Krakow (ISEAK). Radoszkowski's original description gives the type locality as 'Sibirie' (Radoszkowski, 1862, also referring back to Radoszkowski, 1860, where a second specimen is described from 'Transoural'). There is a single queen in the ISEAK collection with the labels: (1) handwritten, illegible; (2) handwritten '*Bombus/altaicus/Evm.* ♀'; (3) discoloured red printed 'Sibiria.'; (4) red unmarked; (5) handwritten '*tschitscherinii*'; (6) handwritten in pencil '*B. Tschitscherini* Behr'; (7) white printed 'HOLOTYPE ♀/*Bombus tschitscherini*/Behr in/ Radoszkowski 1862/det. PH Williams 2009'; (8) printed '*Subterraneobombus*/DB# 3079. det. PHW/*Bombus melanurus*'. Therefore this queen with appropriate locality and determination labels, and which lacks the left forewing and left hind tibia and tarsus, is designated here as the lectotype (ICZN, 1999: article 74.1).

Note 2 (*maljuschenkoi*). Skorikov's (1931) description of *Subterraneobombus melanurus* ssp. *maljuschenkoi* gives the type locality as 'kaukasische' [of the Caucasus]. A queen in the ZISP collection is labelled *malushenkoi* [sic], apparently by Skorikov, but despite the original description, the head is not substantially shorter than for individuals from Central Asia or Mongolia (a similar comment about the lack of difference among MNHU material is made by Tkalců, 1969a: 202, footnote). This queen has a locality label for Armenia, which was referred to by Russians at the time as the Transcaucasus. This queen bears the labels: (1) printed '[Tsamakapert, on/Gokcha, Erivan g./Bryanskii 8.VI.09]'; (2) printed '[K. Skorikov]'; (3) 'Ssp./*malushenkoi*/Skor.' (probably in A. Skorikov's handwriting); (4) 'Rasmont det. 2002/*Bombus/melanurus*'; (5) red '*Lectotypus S. melanu-irus maljuschenkoi*/Skorikov/design. Podbolo. ♀' (handwriting of M. Podbolotskaya, designation unpublished); (6) printed '*Subterraneobombus*/DB# 3071. det. PHW/*Bombus melanurus*'; (7) white printed 'LECTOTYPE ♀/*Subterraneobombus/melanurus* ssp./*maljuschenkoi*/Skorikov 1931/det. PH Williams 2009'. From the original publication, this and any other specimens of similar date and region in the ZISP collection (the original description does not specify that there was just

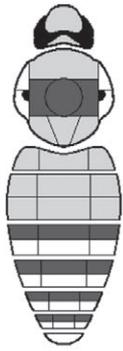
one) must be regarded as syntypes. Therefore this queen, which lacks the right antenna and the distal tarsal joints of the right hind leg, is designated here as the lectotype (ICZN, 1999: article 74.1).

Note 3 (*lantschouensis*). Vogt's (1909) name *B. melanurus tschitscherini* var. *lantschouensis* is unavailable, and so does not have type specimens or synonyms according to the code (ICZN, 1999). The multiple specimens described by Vogt (1909) and then indicated by Tkalců (1961) must then be considered syntypes of the name *lantschouensis* made available from the publication by Tkalců (1961). Tkalců (1974b) subsequently designated a queen in the MNHU collected by W. Filchner as the lectotype of his name. As noted by Tkalců (1974b), this queen has a red printed label 'Type', but no determination label from Vogt. Another of Filchner's specimens, a worker not mentioned by Tkalců (1974b), is in the ZMA (examined), and has a pencilled label 'lan/tschou/ensis/O.V.'. This is considered to be a paralectotype.

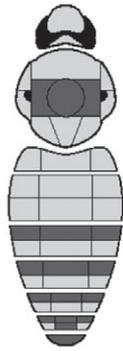
History: In Asia, this species has often been confused with *B. difficillimus* (Table 1). For example, B. Tkalců labelled some specimens of *B. melanurus* from Mongolia in the OLL collection as *B. melanurus*, and others as *B. difficillimus*; whereas in the NMP collection he labelled some as *B. difficillimus* and others as *B. tschitscherini*. Williams (1991) did not have males of *B. difficillimus* available for examination, and from females of *B. difficillimus*, a series of unbanded and banded females of *B. melanurus*, and from an accompanying series of what proved to be unbanded and banded males of *B. melanurus* alone, mistakenly concluded that they were all of a single species.

Bombus melanurus var. *apicatus* Friese (1911a: 457) is a synonym of *B. (Sibiricobombus) oberti* Morawitz (syntype queen, MNHU examined; see comments on *B. difficillimus*).

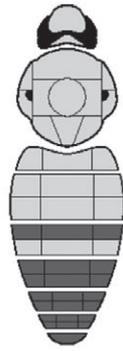
Diagnosis: Female. Head with clypeus shiny, in its central half lacking medium or large punctures, but with a few widely scattered micropunctures (cf. *B. difficillimus*, *B. mongolensis* sp. nov.); gena in the area just outside the dorsal furrow laterally with sparse shallow or deep medium punctures, scattered almost to the anterior edge next to the eye (cf. *B. mongolensis* sp. nov.). Fore wing with the distal area beyond the closed cells greyish or mid brown (cf. *B.*



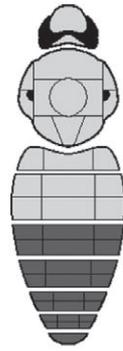
63 *B. personatus**



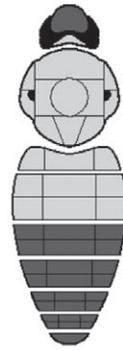
64 *B. personatus*



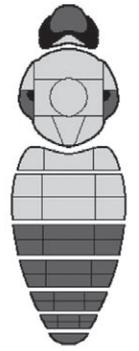
65 *B. melanurus*



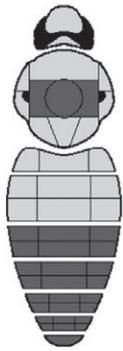
66 *B. melanurus**



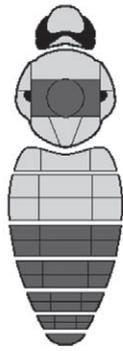
67 *B. melanurus*



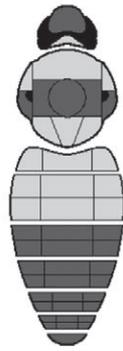
68 *B. melanurus*



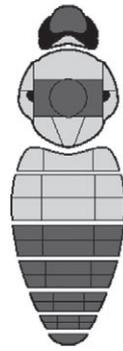
69 *B. melanurus*



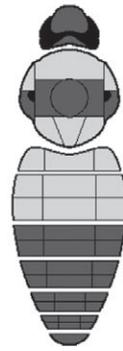
70 *B. difficillimus*



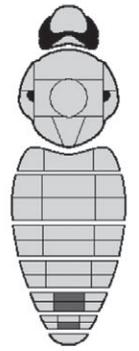
71 *B. difficillimus**



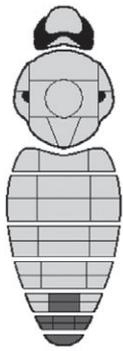
72 *B. mongolensis*



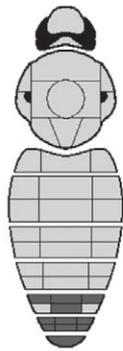
73 *B. mongolensis**



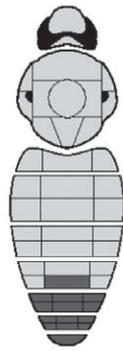
74 *B. fedtschenkoi*



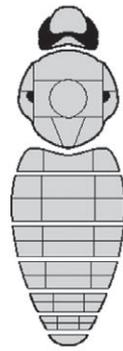
75 *B. fedtschenkoi*



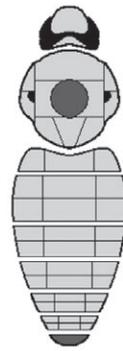
76 *B. fedtschenkoi**



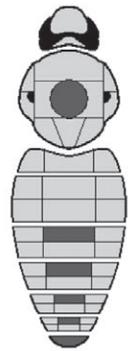
77 *B. fedtschenkoi*



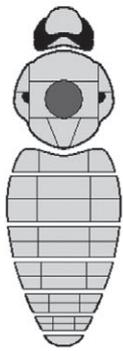
78 *B. amurensis*



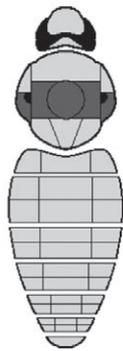
79 *B. amurensis**



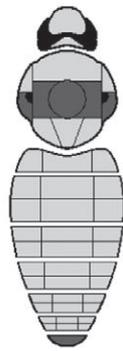
80 *B. amurensis*



81 *B. fragrans*

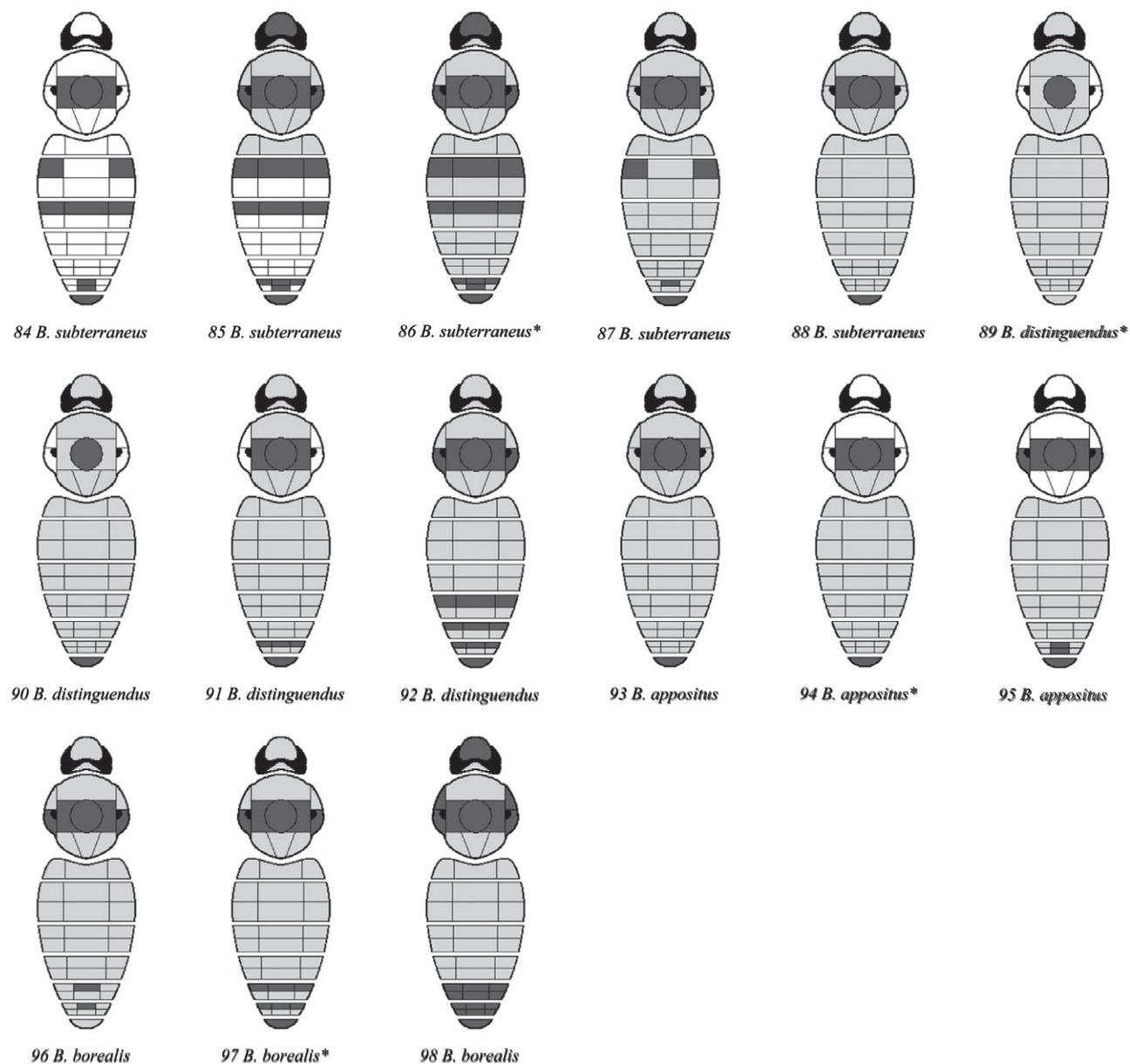


82 *B. fragrans**



83 *B. fragrans*

Figures 63–83. Simplified colour pattern diagrams for the dorsal pubescence of males (*most frequent pattern). Dark grey indicates black; light grey indicates yellow or brown; white indicates white or pale cream. Figure (DB#) country: 63 (0037) India; 64 (2656) India; 65 (2588) Kyrgyzstan; 66 (1821) China; 67 (0083) India; 68 (0080) India; 69 (0136) China; 70 (2594) Tajikistan; 71 (1582) China; 72 (2597) Mongolia; 73 (0169) Mongolia; 74 (2618) Kyrgyzstan; 75 (2549) Kyrgyzstan; 76 (2547) Kyrgyzstan; 77 (2007) Kyrgyzstan; 78 (0176) China; 79 (0175) China; 80 (0180) China; 81 (0801) Austria; 82 (0800) Austria; 83 (1984) Turkey.



Figures 84–98. Simplified colour pattern diagrams for the dorsal pubescence of males (*most frequent pattern). Dark grey indicates black; light grey indicates yellow or brown; white indicates white or pale cream. Figure (DB#) country: 84 (0207) Mongolia; 85 (0193) UK; 86 (1816) UK; 87 (3062) UK; 88 (3065) UK; 89 (1838) Russia; 90 (1831) Russia; 91 (0226) Mongolia; 92 (3362) Sweden; 93 (3081) USA; 94 (0243) USA; 95 (0245) USA; 96 (0261) USA; 97 (0259) Canada; 98 (3373) USA.



Figure 99. A biogeographic scenario for all 11 species of *Subterraneobombus* by dispersal–vicariance analysis with DIVA using the tree from Figure 5 as an estimate of the phylogeny. Shaded branches above show simplified reconstructions of the ancestral distributions for each of the nodes that they precede (where area reconstructions are ambiguous, the more inclusive/widespread solution is accepted). See the text for details of the area units.

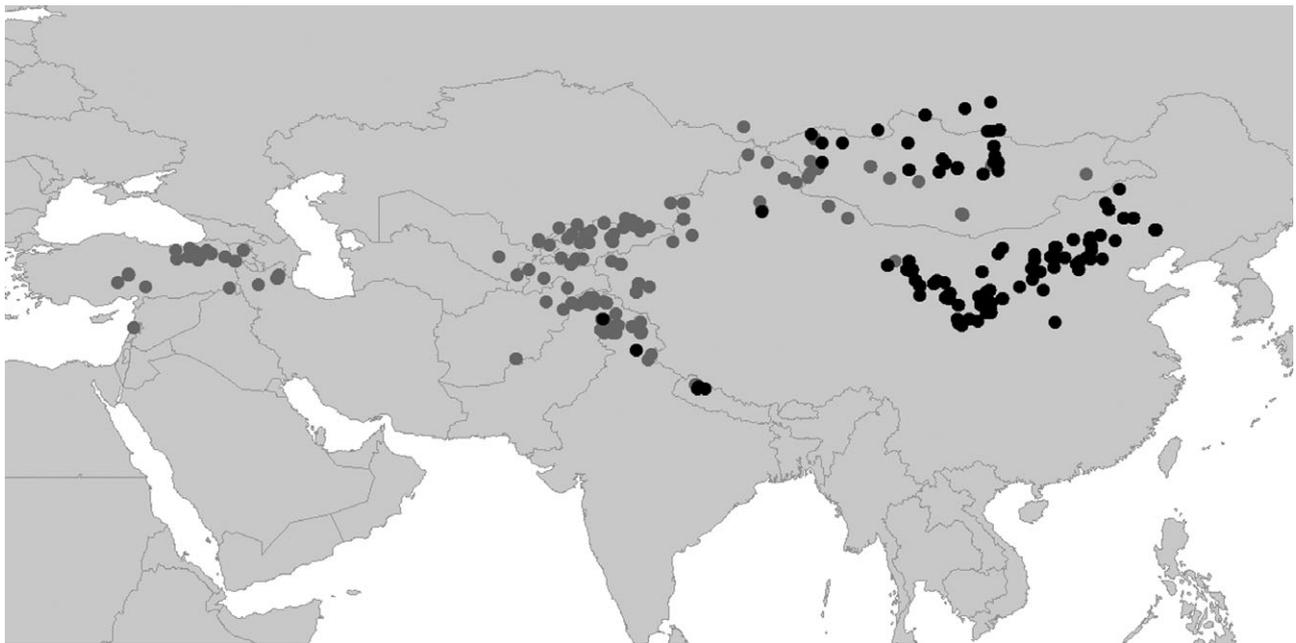


Figure 100. Distribution of the principal colour patterns of *Bombus melanurus*. Grey spots show specimens without an obvious spot or band of black hair between the wing bases on the thoracic dorsum (Figs 23, 24, 65–68; *melanurus* s.s.); black spots show specimens with an obvious spot or band of black hair between the wing bases on the thoracic dorsum (Figs 25, 26, 69; *tschitscherini*).

difficillimus and *B. mongolensis* sp. nov.). Hair medium or short: hair on T2 straight and erect over the anterior one-third, curved and more decumbent over the posterior two-thirds, the longest hair of T5 shorter than the greatest breadth of the hind basitarsus (cf. *B. difficillimus*). Colour pattern (Figs 23–

26). Hair of the head, legs, ventral surfaces, and T3–T6 usually black, sometimes with grey tips, especially on the metasoma; the side of the thorax in its dorsal two-thirds, either all of the dorsum of the thorax, or all of the thoracic dorsum except for a band between the wing bases, and T1–T2 yellow (bright

lemon, sandy, or mid brown, cf. *B. difficillimus* and *B. mongolensis* sp. nov.), sometimes with some short pale hairs intermixed on the head; if there is a black band between the wing bases then it is either sharply or weakly defined, but is not more than two-thirds of the greatest breadth of the anterior pale band (measured from anterior to posterior on the body midline, cf. *B. difficillimus* and *B. mongolensis* sp. nov.).

Male. Head with clypeus nearly covered in dense and moderately long hair, except in a narrow median band occupying the median quarter in the anterior ventral quarter adjacent to the labrum; antennal scape with hairs longer than the breadth of the scape in the distal third; hind tibia outer surface without a longitudinal concavity in the posterior half, usually flat or weakly convex, the surface with widely separated non-overlapping decumbent unbranched hairs (cf. *B. difficillimus* and *B. mongolensis* sp. nov.); genitalia with gonocoxa with proximal inner process longer than broad, apically obliquely truncate; gonocoxa with sharply defined dorsal ridge subsiding before the distal extremity, which is convex dorsally; gonostylus broadly triangular, breadth of the inner proximal process at its narrowest about a quarter of the length of the gonostylus (cf. *B. difficillimus* and *B. mongolensis* sp. nov.); volsella distally moderately broad; penis valve with the ventrolateral process almost trident-like, with a spine-like dorsal tooth, a spine-like ventral tooth, and a weaker central projection; penis valve head 1.7 times as long as broad (cf. *B. personatus*, *B. difficillimus*, and *B. mongolensis* sp. nov.), distally with a distinct rounded corner on its outer edge, its outer proximal corner rounded, without an anteriorly directed spine. Colour pattern (Figs 65–69). Hair of the head often black, except on the vertex, upon which the long hairs are almost exclusively yellow, and the hair of the clypeus varying among individuals from black to predominantly yellow, with more yellow hair present when there is conspicuous black hair on the thorax between the wing bases (e.g. Mongolia, Neimenggu) and absent only when there is not (e.g. Kashmir), but sometimes hair of head mostly yellow; hair of T3–T7 usually black, but occasionally T3 yellow in the posterior half.

Material examined: In total, 267 queens, 954 workers, and 264 males (AMNH, BMNH, HMB, HUM, IAB, ISEAK, IZB, KUK, MNHU, NME, NMP, NMS, OLL, PUI, PW, SC, UMO, USNM, ZIH, ZISP, ZMA, and ZMMU), with 73 specimens barcoded in the BOLD database. Details can be found at <http://www.nhm.ac.uk/bombus/downloads/subterraneobombus.mdb>.

Distribution: Material examined from Afghanistan, Armenia, China, India, Iran, Kazakhstan, Kyr-

gyzstan, Lebanon, Mongolia, Nepal, Pakistan, Russia, Syria, Tajikistan, Turkey, and Uzbekistan (433–4200 m a.s.l.; Figs 8, 100). The distribution is strongly disjunct, with an absence between the east of Iran and the west of Afghanistan, a gap mirrored by *B. (Melanobombus) keriensis* Morawitz (Williams, 1991). Vicarious with *B. difficillimus* at higher elevations. Skorikov (1931: fig. 9) mapped the distribution of *B. melanurus* within Central Asia, although his records labelled with *tschitscherini* from Russia and Mongolia may be confused in part with *B. mongolensis* sp. nov. and *B. difficillimus*. Regional or national maps are available for Kashmir (Williams, 1991) and Turkey (Rasmont & Flagother, 1996).

Variation: There is substantial variation within this species.

1. Individuals from North China and from Iran have short even hair, whereas in the Himalaya and Tibet it is longer and less even.
2. Individuals from North China and from Iran have the pale hair vivid lemon yellow, whereas on the south side of the Himalaya the pale hair tends to be brown, especially for large queens.
3. Individuals from Turkey and from Iran lack a black band between the wing bases, whereas in the Himalaya and Tibet (especially towards the east) there may be a poorly defined band, and in parts of Mongolia and in North China the band is very sharply defined, although individuals with weak bands also occur there (Fig. 100). The *COI* results show that specimens with either a black spot or band on the thorax (*tschitscherini*) are just possibly a paraphyletic group with respect to the unbanded specimens (*melanurus* s.s.; Fig. 2), because of the low reliability of groups within the unbanded specimens. If these groups were collapsed, then it would allow the single weakly banded specimen (IAB: DB#3823 that appears to make the banded *tschitscherini* polyphyletic) instead make *tschitscherini* paraphyletic. The subset of specimens that have both a distinct black band and are from Mongolia or northern China form a strongly divergent monophyletic group (Fig. 2) that deserves further investigation, although so far this group has not been diagnosed with even a single morphological character state.
4. Some of the workers without a black band between the wing bases from Mongolia have many of the short feathery hairs at the dorsal posterior of the head and on the face yellowish ('yellow' in Fig. 2). A worker (OLL: DB#1873) from Mongolia has the hair of the head and the posterior half of T3 intermixed with yellow. A male (ZMMU: DB#2588) from Kyrgyzstan has the hair of the head and the posterior

half of T3 almost completely yellow. There is no support from *COI* for these forming a monophyletic or paraphyletic group.

5. Some of the workers without a black band between the wing bases from Mongolia and some queens with more black hair from Uzbekistan and Kyrgyzstan have more punctures on the clypeus than normal.
6. Richards (1928) described a subspecies *subdistinctus* from 'India and Tibet', characterized as 'the wings of the female are, on average, much less dark than usual'. Although this is true, and shared by females from both Kashmir south of the Himalaya and from Ladakh, what is perhaps more noticeable is that the females (especially queens) from south of the Himalaya (rather than Ladakh) have the pale hair darker and more brown, rather than yellow. Queens from western Nepal are intermediate in (a) hue of the pale hair; (b) darkening of the wings; and (c) strong intermixing of black hair on the thoracic dorsum as a band between the wing bases.
7. A queen and a series of workers from Mongolia (OLL) have the wings pale, the yellow hair is pale and often cream, and there is a band of black hair between the wings. B. Tkalců has labelled these as *B. difficillimus*. However, many of these individuals are small, the clypeus has a few scattered punctures, the black band between the wings is narrow, and the hair of T5 is relatively short. In addition, the wing edges are in every case frayed, so that these specimens are interpreted as *B. melanurus* that have been bleached by prolonged exposure to the sun (but see the comments on *B. mongolensis* sp. nov. for other specimens from this sample).

Specimens with the palest yellow hair appear to occur at the higher elevations (Tibetan Plateau), whereas those with the darkest yellow appear to occur at the lower elevations in the south (lower Himalaya), although both light and dark forms occur in parts of Mongolia and China. Broadly, the geographic trends in thoracic banding patterns (Fig. 100) are towards having a black band between the wing bases in the north-east of the range (Mongolia and northern China) and lacking it in the south-west (Turkey and Afghanistan). The *COI* results (Fig. 2) are consistent with the black-banded individuals from Mongolia and northern China being at best a paraphyletic group with respect to the unbanded individuals (although Fig. 2 does not support this directly, see above). But crucially, so far, no morphological character state has been found to be associated with either the banded or unbanded groups, and individuals with intermediate weak thoracic bands have been found in Gansu (IAB:

DB#3823) and in the Himalaya (NME: DB#0283–0285). Therefore, at present these colour forms are regarded as belonging to a single species.

BOMBUS DIFFICILLIMUS SKORIKOV, 1912

(FIGS 9, 27, 28, 70, 71)

Bombus difficillimus Skorikov, 1912: 609, **lectotype** queen by present designation (note 1), ZISP examined. ?Kyrgyzstan (note 2).

Bombus (*Subterraneobombus*) *melanurus* ssp. *griseofasciatus* Reinig, 1930: 83, **lectotype** queen by present designation (note 3), ZMA examined. Tajikistan. Synonymized with *Subterraneobombus difficillimus* (Skorikov) by Skorikov (1931: 239).

[*Bombus* (*Subterraneobombus*) *difficillimus* Skorikov; Panfilov, 1957: 236, incorrect subsequent spelling.]

Note 1 (*difficillimus*). Skorikov's (1912) description of *B. difficillimus* is of a series of syntype queens, workers, and a male from the 'Pamir', and a series of localities extending eastwards to the Tibetan Plateau. There is a queen in the ZISP collection that agrees with the original description and bears the labels: (1) handwritten '[Pass Naiza-Tam]/3700 mts. [Pamir]/15.VI.09 [Makarjin]'; (2) printed '[K. Skorikov]'; (3) white '**LECTOTYPUS**/*B. difficillimus*/Skor. ♀ Tkalců det.' (handwriting of B. Tkalců, designation unpublished); (4) red '*Lectotypus Bombus/difficillimus* Skor./design. ♀ Tkalců' (handwriting of M. Podbolotskaya, designation unpublished); (5) printed '*Subterraneobombus*/DB# 3067. det. PHW/*Bombus difficillimus*'; (6) white printed '**LECTOTYPE** ♀/*Bombus difficillimus*/Skorikov 1912/det. PH Williams 2009'. From the original publication, this and the other specimens mentioned in the ZISP collection must be regarded as syntypes. Therefore this queen, which lacks the distal tarsal joints of the right hind leg, is designated here as the lectotype (ICZN, 1999: article 74.1).

Note 2 (*difficillimus*). The locality of the lectotype of *B. difficillimus* is given on the label as 'Naiza-Tam pass, 3700 m, Pamir Mountains'. We have been unable to locate a locality of this name in the Pamir as it is known today (Tajikistan). However, there are localities named Naiza and Tam approximately 70 km apart to the north in Kyrgyzstan, separated by a mountain ridge reaching above 3700 m a.s.l. This area is accepted provisionally as the type locality.

Note 3 (*griseofasciatus*). Reinig's (1930) description of *B. melanurus* ssp. *griseofasciatus* is of a series of syntype queens, workers, and males from the modern Pamir (Tajikistan). Reinig described a very similar colour form (infrasubspecific) of *B. oberti* Morawitz in the same paper (Reinig, 1930: 109), also under a name *griseofasciatus* (ZMA exam-

ined). There is a series of 34 queens of the subgenus *Subterraneobombus* with Reinig's Pamir labels in the ZMA collection that agree with the original description. However, only one specimen has a large red 'Type' label. This queen bears the labels: (1) 'Zentral – Pamir/VII. – VIII.28/leg.Reinig'; (2) handwritten 'Schor-Kul/17.VII.3720m' (Reinig's paper gives 3750 m a.s.l.); (3) red typed 'Type'; (4) handwritten '*B. melanurus/griseofasciatus*/det. W. F. Reinig'; (5) printed 'Collectie/C. et O. Vogt/Acq. 1960'; (6) red printed 'Bombus/melanurus griseofasciatus/Reinig 1930/ZMAN type HYME.0107.1'; (7) printed '*Subterraneobombus*/DB# 2593. det. PHW/*Bombus difficillimus*'; (8) white printed 'LECTOTYPE ♀/*Bombus melanurus* ssp./*griseofasciatus*/Reinig 1930/det. PH Williams 2009'. From the original publication, this and the other Pamir queens from Reinig in the ZMA collection must be regarded as syntypes. Therefore this queen, which lacks the distal tarsal joints of the left hind leg, and which has a Reinig determination label and the unique red label interpreted as indicating the type, is designated here as the lectotype (ICZN, 1999: article 74.1).

History: This species has often been confused with *B. melanurus* (Table 1). Some queens of *B. (Sibiricobombus) oberti* Morawitz with little or no red hair on the metasoma (ZISP, MNHU examined) have also been confused with *B. difficillimus* as *B. difficillimus* var. *pamirus* Skorikov (1912) (infrasubspecific, ZISP examined; see comments on *B. melanurus*).

Diagnosis: Female. Head with clypeus shiny, in its central half lacking medium or large punctures, almost devoid of micropunctures, and entirely smooth (cf. *B. melanurus*); gena in the area just outside the dorsal furrow laterally with sparse shallow medium punctures scattered almost to the anterior edge next to the eye (cf. *B. mongolensis* sp. nov.). Forewing with the distal area beyond the closed cells nearly clear (cf. *B. melanurus*). Hair long: hair of T2 usually straight and erect over the anterior two-thirds, curved and more decumbent along the posterior edge, the longest hair of T5 longer than the greatest breadth of the hind basitarsus (cf. *B. melanurus*). Colour pattern (Figs 27, 28). Hair of the head, legs, ventral surfaces, a band between the wing bases, and T3–T6 entirely black; the side of the thorax in its dorsal half (cf. *B. mongolensis* sp. nov.), dorsum of the thorax except for the band between the wing bases, and T1–T2 creamy yellow (varying from cream or almost white in large queens, to a pale lemon yellow in workers); the black band between the wing bases sharply defined and equal in its greatest breadth to the anterior pale band (measured from anterior to posterior along the

body midline; cf. *B. melanurus*), or narrower (three-quarters) in individuals from the Pamir; propodeum with lateral hair black with pale hairs intermixed.

Male. Head with the clypeus almost entirely covered in dense and moderately long hair (cf. *B. melanurus* and *B. mongolensis* sp. nov.); antennal scape with hairs longer than the breadth of the scape in the distal third; hind tibia outer surface with a longitudinal concavity in the posterior half, the surface with sparse scarcely overlapping decumbent almost unbranched hairs (cf. *B. melanurus* and *B. mongolensis* sp. nov.); genitalia with gonocoxa with proximal inner process narrowly triangular or broader; gonocoxa with sharply defined dorsal ridge subsiding before the distal extremity, which is convex dorsally; gonostylus broadly triangular, the distal corner broadly rounded, the breadth of the inner proximal process less than half of the length of the gonostylus; volsella distally moderately broad; penis valve with the ventrolateral process almost trident-like, with a spine-like dorsal tooth, a spine-like ventral tooth, and a weaker central projection; penis valve head twice as long as broad (cf. *B. personatus* and *B. melanurus*), distally with a distinct rounded corner on its outer edge, its outer proximal corner rounded, without an anteriorly directed spine. Colour pattern (Figs 70, 71). Hair of the head black, except on the vertex, on which medially the long hairs are exclusively yellow (cf. *B. melanurus* and *B. mongolensis* sp. nov.), or (Pamir) with a minority of yellow–grey hairs on the face (but the pale hair bands of the thorax and T1–T2 yellow rather than the white of the females).

Material examined: In total, 33 queens, 85 workers, and four males (AMNH, BMNH, HMB, IAB, IZB, MNHU, PW, USNM, ZISP, and ZMA), with six specimens barcoded in the BOLD database. Details available at <http://www.nhm.ac.uk/bombus/downloads/subterraneobombus.mdb>.

Distribution: Material examined from China, India, Kyrgyzstan, Pakistan, and Tajikistan (2585–5150 m a.s.l.; Fig. 9). A record from 1477 m a.s.l., according to a label on a specimen from Gansu in the IZB collection (DB#1786), may just represent the county town nearest to the collecting site (which was presumably at a higher elevation), because it is more than 1000 m lower than the next highest record, and it is therefore excluded. Vicarious with *B. melanurus* at lower elevations, and vicarious with the north Mongolian *B. mongolensis* sp. nov. Regional maps are available for Kashmir (Williams, 1991: as banded *B. melanurus*) and for Sichuan (Williams *et al.*, 2009).

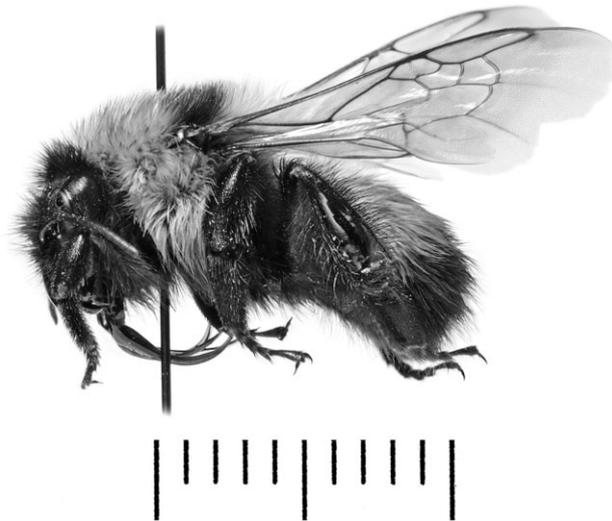
Variation: Primarily in the hue of the yellow, which is darkest for workers from the north-east (Gansu), and palest for queens from the south (Qomolangma) and from the far west (Alai-Pamir). In the Alai-Pamir, females have the black band between the wing bases narrower and males have yellow hairs intermixed within this band. Females also vary in the extent of the pale pubescence on the sides of the thorax, so that not all are easy to separate from *B. mongolensis* sp. nov. with this character (pragmatically the two can be distinguished by their disjunct distributions).

***BOMBUS MONGOLENSIS* WILLIAMS SP. NOV.**

(FIGS 10, 29, 72, 73, 101, 102)

[*Bombus* (*Subterraneobombus*) *tschitscherini* Radoszkowski [cited as Behr]; Williams *et al.*, 2009: 139 male only, misidentification.]

Note (*mongolensis*). The usual neo-latin adjective for inhabitants of Mongolia is *mongolicus* (M. Alonso-Zarazaga, pers. comm.). This name is preoccupied by the senior homonyms: *Bombus hortorum* var. *mongolicus* Friese, 1916: 110 (? = *B. diversus* Smith); *Lapidariobombus alagesianus* ssp. *mongolicus* Skorikov, 1931: 226 (= *B. keriensis* Morawitz); and *Bombus magnus* Rasse *mongolicus* Krüger, 1954: 276 [not infrasubspecific after Tkalčú, 1974b: 31; = *B. lucorum* (Linnaeus) complex]. Therefore, the name *mongolensis* is proposed (following previous usage of the neologism, e.g. *Halictus rubicundus* var. *mongolensis* Blüthgen, 1936) to convey the current knowledge of this species as an endemic of Mongolia.



Figures 101, 102. Photographs of *Bombus mongolensis* sp. nov. from the left lateral aspect with scale bars in mm: 101, worker (DB#1934, BOLD 1550B04-1934-MON), body length 15 mm; 102, holotype male (DB#0169, BOLD B3262-D05), body length 19 mm.



Figures 101, 102. *Continued*

History: This species was first collected as one specimen in 1892 by H. Leder in northern Mongolia (label: 'N. Mongolei/Leder 92'). Leder's route is described by Kerzhner (1972). Although there is no direct information about where along this route the specimen was collected, from the locality given as northern Mongolia it is likely to have been from the section of the route between Kyakhta and Ulaanbaatar. This large, relatively pale male (DB#2597, ZMA; Fig. 72) was confused with *B. melanurus* (label: 'melanurus/det. Kohl'), and so appears subsequently to have been ignored. The species was first recognized as a new species during the present study from the two large darker males (Fig. 73) collected by D. Sheppard near Khovsgol Nuur (= Hövsgöl Nuur), in the far north of Mongolia (west of Kyakhta). Initially the large body size and divergent male genitalia were recognized as distinctive. This was confirmed from their divergent *CO1* sequences and then from the morphological differences in the male hind legs. The workers were later recognized and associated from their *CO1* data, and only subsequently from their morphology and colour pattern, although the latter characters are at best subtle and difficult to use. Eleven of the workers from Mongolia in the OLL collection labelled as *Megabombus* (*Subterraneobombus*) *difficillimus* by Tkalčú (no date) are interpreted here from *CO1* data as *B. mongolensis* sp. nov. One worker and one queen in addition from this same series are tentatively associated with *B. mongolensis* sp. nov. from morphology and colour pattern (although they failed to sequence for *CO1*). Another 25 workers from this series are

interpreted from *COI* data as *B. melanurus*, along with one queen and three workers tentatively associated from morphology and colour pattern (they failed to sequence for *COI*). There are also four workers from Mongolia in the NMP collection, also described by Tkalcú (1974b) under the name *M. (St.) difficillimus*, that are revised here to *B. melanurus*.

Diagnosis: Female (Fig. 101). Head with clypeus shiny, in its central half lacking medium or large punctures, almost devoid of micropunctures and entirely smooth (cf. *B. melanurus*); gena in the area just outside the dorsal furrow laterally smooth and shiny, with almost no punctures (which are very shallow) in the anterior third (cf. *B. melanurus* and *B. difficillimus*). Forewing with the distal area beyond the closed cells nearly clear, often distinctly lighter than the proximal area (cf. *B. melanurus*). Hair long; hair of T2 usually straight and erect over the anterior two-thirds, curved and more decumbent along the posterior edge, the longest hair of T5 longer than the greatest breadth of the hind basitarsus (cf. *B. melanurus*). Colour pattern (Fig. 29). Hair of the head, legs, ventral surfaces, a band between the wing bases, and T3–T6 entirely black; the side of the thorax in its dorsal three-quarters (cf. *B. difficillimus*), the dorsum of the thorax except for the band between the wing bases, and T1–T2 creamy yellow; the black band between the wing bases sharply defined and equal in its greatest breadth to the anterior pale band (measured from anterior to posterior along the body midline) (cf. *B. melanurus*); propodeum with the lateral hair black with pale hairs intermixed.

Male (Fig. 102). Head with hair of clypeus confined to the lateral thirds, the central third throughout most of its length smooth and shiny with only widely scattered micropunctures (cf. *B. difficillimus*); antennal scape with no hairs longer than the breadth of the scape in the distal third; hind tibia outer surface with a longitudinal concavity in the posterior half, the surface with dense, extensively-overlapping decumbent obviously branched hairs (cf. *B. melanurus* and *B. difficillimus*); genitalia with gonocoxa with proximal inner process broadly triangular; gonocoxa with sharply defined dorsal ridge subsiding before the distal extremity, which is convex dorsally; gonostylus broadly triangular, the distal angle a pointed right angle, the breadth of the inner proximal process at its narrowest just less than half of the length of the gonostylus (cf. *B. melanurus*); volsella distally moderately broad; penis valve with the ventrolateral process almost trident-like, with a spine-like dorsal tooth, a spine-like ventral tooth, and a weaker central projection; penis valve head twice as long as broad (cf. *B. personatus* and *B. melanurus*), distally with a distinct rounded corner on its outer edge, its outer

proximal corner rounded, without an anteriorly directed spine. Colour pattern (Figs 72, 73). Hair of the head black, sometimes with an inconspicuous minority of long yellow hairs intermixed on the vertex, and at most with only a few yellow hairs on the face (cf. *B. melanurus* and *B. difficillimus*); black band between the wings with some yellow hairs intermixed anteriorly.

Material examined: In total, one queen, 12 workers, and three males (BMNH, OLL, PW, and ZMA). Holotype: adult male (Fig. 102), body length 19 mm, deposited in the BMNH collection, London, with labels: (1) white printed 'Khovsgol Nuur/Mongolia. Kh. [Kh. crossed out in pencil]/51N 100E/28.vii.2004 [28 in pencil]/D.A.Sheppard'; (2) white printed 'B3262-D05' (BOLD number); (3) green printed 'BOLD# (BEE-BOL/BBW/PHW)/B3262-D05'; (4) printed '*Subterraneobombus*/DB# 169. det. PHW/*Bombus mongolensis*'; (5) white printed 'HOLOTYPE ♂/*Bombus mongolensis*/Williams/det. PH Williams 2009'; (6) large red plain label. Paratypes: one male (ZMA) labels: (1) white printed 'N. Mongolei/Leder 92'; (2) handwritten/printed 'melanurus/det. Kohl'; (3) white printed 'Collectie/C. et O. Vogt/Acq. 1960'; (4) printed '*Subterraneobombus*/DB# 2597. det. PHW/*Bombus mongolensis*'; (5) white printed 'Paratype ♂/*Bombus mongolensis*/Williams/det. PH Williams 2009'; one male (PW) labels: (1) white printed 'Khovsgol Nuur/Mongolia. Kh. 172 [172 in pencil]/51N 100E/27.vii.2004 [27 in pencil]/D.A.Sheppard'; (2) green printed 'BOLD#/(BEE-BOL/BBW/PHW)/595B11-0168-MON'; (3) printed '*Subterraneobombus*/DB# 168. det. PHW/*Bombus mongolensis*'; (4) white printed 'Paratype ♂/*Bombus mongolensis*/Williams/det. PH Williams 2009'. Thirteen specimens barcoded in the BOLD database. Details available at <http://www.nhm.ac.uk/bombus/downloads/subterraneobombus.mdb>.

Distribution: Material examined from Mongolia (1300–2100 m a.s.l.; Fig. 10), where the species appears to be endemic. Vicarious with the Tibetan *B. difficillimus*.

Variation: Males with hair of the propodeum, metepisternum, and ventrolateral mesepisternum varying from predominantly black to predominantly yellow. Only one paler male has a conspicuous predominance of yellow hairs on the vertex. Females with the extent of the pale pubescence on the side of the thorax varying from covering three-quarters of the distance to the mid leg base to covering just the dorsal half, so that not all are easy to separate from *B. difficillimus*.

with this character (pragmatically the two can be distinguished by their disjunct distributions).

BOMBUS FEDTSCHENKOI MORAWITZ, 1875
(FIGS 11, 30–34, 69–72)

Bombus Fedtschenkoi Morawitz in Fedtschenko, 1875: 5, holotype female by monotypy, ZMMU examined. ‘Samarkand’ but probably Kyrgyzstan.

Bombus (Subterraneobombus) fertoni Vogt, 1911: 63, **lectotype** male by present designation (note 1), HMB examined. Kyrgyzstan (Alai Mountains). Junior primary homonym of *Bombus terrestris fertoni* Pérez, 1909: 158 and *Bombus hortorum fertoni* Krausse, 1909: 85 [= *Bombus ruderatus* (Fabricius, 1775)]. Synonymized with *Subterraneobombus fedtschenkoi* (Morawitz) by Skorikov (1914: 289).

Subterraneobombus fedtschenkoi var. *cinguliferus* Skorikov, 1914: 291, syntype queens, ZISP not seen. Kyrgyzstan.

Subterraneobombus fedtschenkoi var. *ciliogereus* Skorikov, 1914: 291, syntype queens and workers, ZISP not seen. Kyrgyzstan.

Subterraneobombus fedtschenkoi var. *oshaninellus* Skorikov, 1914: 291, syntype queens, ZISP not seen. Kyrgyzstan.

Subterraneobombus fedtschenkoi var. *aterrimus* Skorikov, 1914: 292, syntype workers, ZISP not seen. Kyrgyzstan.

Subterraneobombus fedtschenkoi var. *ambiguus* Skorikov, 1914: 292, syntype queen and males ZISP not seen. Kyrgyzstan (including ‘Samarkand region, Voru’). Junior secondary homonym in *Bombus* of *B. ambiguus* Franklin, 1911: 159 (= *B. pleuralis* Nylander).

Subterraneobombus fedtschenkoi var. *subconcolor* Skorikov, 1914: 292, holotype male by monotypy, ZISP not seen. Kyrgyzstan.

[*Bombus fedtschenkoi* ab. *zonatoides* Reinig, 1930: 84, infrasubspecific.]

[*Bombus fedtschenkoi* (var.) *ciliogereus* (Skorikov); Reinig, 1930: 84, incorrect subsequent spelling.]

[*Subterraneobombus vertoni* (Vogt); Skorikov, 1931: 232, incorrect subsequent spelling.]

Note 1 (*fertoni*). Vogt’s (1911) description of *B. fertoni* is based on a series of ‘einige’ [a few] syntype males from the Alai Mountains sent by Major Fertton-Bonifacio. One male of the subgenus *Subterraneobombus* labelled Alai Mountains in the HMB collection agrees with the original description in having T1–T3 pale, T4–T7 with many black hairs, although two other males with the same locality data have more pale hair on T4. The one male matching the original description bears the labels: (1) printed ‘Alai mont./1906 Korb’; (2) handwritten ‘*B. Fertoni* ♂/nov. spec. O.V./det. O. Vogt.’ (the only specimen labelled in this

way); (3) ‘LECTOTYPE/*Bombus/fertoni* Vogt/Tkalcù det.’ (handwriting of B. Tkalcù, designation unpublished); (4) printed red ‘Lecto-/typus’; (5) handwritten ‘*M. (S.)/fedtschenkoi*/(Mor.) Tkalcù det.’; (6) printed ‘*Subterraneobombus*/DB# 2007. det. PHW/*Bombus fedtschenkoi*’; (7) printed ‘LECTOTYPE ♂/*Bombus fertoni*/Vogt 1911/det. PH Williams 2008’. From the original publication, this and the other Alai males in the HMB collection must be regarded as syntypes. Therefore, this male, which is complete and has Vogt’s determination label, is designated here as the lectotype (ICZN, 1999: article 74.1).

History: This species remains rare in collections and is poorly known. Perhaps because of this, the concept and name of the species have been stable for more than half a century. *Bombus fedtschenkoi* is named after the Russian entomologist Aleksey Fedtschenko (1844–1873; brief biography in Pesenko & Astafurova, 2003).

Diagnosis: Female. Head with clypeus dull, in its central half with many medium or large punctures and dense micropunctures; oculo-malar distance 1.5 times as long as the basal breadth of the mandible. Hair short: the longest hair of metasomal T5 shorter or equal to the greatest breadth of the hind basitarsus. Colour pattern (Figs 30–34). Hair of the head, legs, ventral surfaces, and at least T5–T6 black; the side of the thorax, either all of the dorsum of the thorax (usually with a few black hairs between the wing bases), or all of the thoracic dorsum except for a spot or band between the wing bases, and at least T1–T2 sandy yellow; propodeum with the lateral hair yellow.

Male. Head with clypeus almost entirely covered in dense hair; antennal scape with hairs longer than the breadth of the scape in the distal third; genitalia with gonocoxa with proximal inner process finger shaped, apically bluntly rounded; gonocoxa with sharply defined dorsal ridge subsiding just before the distal edge, which is distally narrowly rounded and convex dorsally; gonostylus enlarged with the apex truncate with weakly marked angles, the inner proximal process as broad as the length of the gonostylus and not distinct from it (cf. all other *Subterraneobombus* species); volsella distally not broadened or narrowed; penis valve with the ventrolateral process with the dorsal tooth very weak or absent, the middle area broadly triangular or rounded laterally, and with a ventral spine; penis valve head distally broadly rounded on its outer edge, its outer proximal corner with an anteriorly-directed flattened process, which in lateral aspect is triangular and acute. Colour pattern (Figs 69–72). Hair predominantly pale yellow; black hair intermixed on the head, especially along

the edge of the clypeus and along the inner edge of the eye, and posteriorly and laterally to the eye; T1–T3, sometimes T4, and T5 laterally, predominantly pale yellow, but with black hairs often broadly intermixed.

Material examined: In total, 24 queens, four workers, and seven males (BMNH, HMB, MNHU, OLL, PW, ZMA, and ZMMU), with one specimen barcoded in the BOLD database. Details available at <http://www.nhm.ac.uk/bombus/downloads/subterraneobombus.mdb>.

Distribution: Material examined from Kazakhstan, Kyrgyzstan, and Tajikistan (2400–4274 m a.s.l.; Fig. 11). Only a single worker is recorded from Kazakhstan ('Wernyi' = Almaty), so occurrence there needs to be confirmed.

Variation: Primarily in whether T3–T4 are black or yellow, but also in whether a black spot or band is present between the wing bases. Available samples are too small to assess whether there is any geographic pattern to this variation.

BOMBUS AMURENSIS RADOSZKOWSKI, 1862
(FIGS 12, 35, 36, 78–80)

Bombus Amurensis Radoszkowski, 1862: 590, **lectotype** queen by present designation (note 1), MNHU examined. Russia: southern Siberia.

Bombus fragrans ssp. *mongol* Skorikov, 1912: 607, syntype male, ZISP examined. Mongolia; **syn. nov.**

Bombus (*Subterraneobombus*) *chaharensis* Yasumatsu, 1940: 94, holotype male by original designation, presumed lost (note 2) not seen. China: Neimenggu; **syn. nov.**

Note 1 (*amurensis*). According to Pesenko & Astafurova (2003), General O. Radoszkowski's collection went to the Polish Academy of Sciences in Krakow (ISEAK) after his death, although many syntypes went by exchange to the MNHU collection. Radoszkowski's (1862) original description of *B. amurensis* is written in the singular, as though referring to just one queen ('*Femelle* long. 38 mil.'). In the ISEAK collection no queen can be found (D. Moron, pers. comm.). Two workers labelled *B. amurensis*, possibly by Radoszkowski, are of the South American species *Bombus* (*Thoracobombus*) *dahlbomii* Guérin-Méneville, 1835, and do not agree with the original description of *B. amurensis* in size or in colour pattern. However, two possible candidates for syntype queens of *B. amurensis* have been examined. The first specimen (BMNH, length 25 mm) has large handwritten labels '*Nor. Gob.*' (?= northern Gobi) and '*amurensis/♀ Rad.*' (reverse side accession number '90.26') that are in a 19th century hand. The BMNH

accession catalogue contains a letter from Radoszkowski dated 11 March 1890, which mentions this specimen. The second specimen (MNHU, length > 24 mm, lacking T5–T6) bears the labels: (1) small circular gold label; (2) small discoloured pink label printed 'Sibir.'; (3) printed label '31102'; (4) handwritten '*Sibirien/Coll. Rad.*'; (5) handwritten '*Bombus/amurensis/Rad. Type.*'; (6) red printed 'Type'; (7) handwritten '*amurensis*'; (8) printed 'Radachk.'; (9) white 'LECTOTYPE/*Bombus/amurensis* ♀/Rad. Tkalčú det.' (handwriting of B. Tkalčú, designation unpublished); (10) yellow printed 'Zool. Mus./Berlin'; (11) printed '*Subterraneobombus/DB# 2627. det. PHW/Bombus amurensis*'; (12) white printed 'LECTOTYPE ♀/*Bombus amurensis/Radoszkowski 1862/det. PH Williams 2009*'. Because there are at least two possible syntypes, the queen in the MNHU collection that has locality data matching the original description and a type label is designated here as lectotype (ICZN, 1999: article 74.1).

Note 2 (*chaharensis*). Yasumatsu's (1940) type of *B. chaharensis* is not in the Kyushu University collection (O. Tadauchi, pers. comm.) or in the National Museum in Tokyo (A. Shinohara, pers. comm.). It may have been in the collection of the Musée Heude in Shanghai, and might then have been transferred to the IZB (A. Shinohara, pers. comm.), but it has not been located in the collection there (J. Yao, pers. comm.). Nonetheless, the identity of the taxon appears clear from the original description, so a neotype is unjustified.

History: This species has rarely been recognized in the literature. It has been confused with *B. fragrans* following the description by Skorikov of *B. fragrans* ssp. *mongol*. For Williams (1998), with no specimens of *mongol* in the BMNH collection (a ZISP syntype male was examined but had been damaged, obscuring its identity), *mongol* was accepted following Skorikov as being conspecific with *B. fragrans*. At the same time, two large queens in the BMNH collection, one of which has an old label *B. amurensis*, were found to be morphologically distinct from *B. fragrans*, so these were assumed to differ from *mongol*, and were interpreted as a separate species. However, during fieldwork in central Neimenggu in 2007, workers were collected that match the *B. amurensis* queens in morphology, but that also match the descriptions of *mongol* in colour pattern (e.g. Skorikov, 1933b). Males in the same samples have genitalia that are morphologically distinct from *B. fragrans*. Thus it appeared that *mongol* might be a junior synonym of *B. amurensis* and a species separate from *B. fragrans*.

Diagnosis: Female. Head with the labrum with the breadth of the median furrow more than half of the total breadth of the labrum (cf. *B. fragrans*); clypeus dull, in its central half with many medium punctures and micropunctures; oculo-malar distance 1.0 times as long as the basal breadth of the mandible. Hair short: the longest hair of T5 shorter than the greatest breadth of the hind basitarsus; hind tibia with the longest hairs of the posterior fringe shorter than the greatest breadth of the tibia. Colour pattern (Figs 35, 36). Hair of the head (except for the vertex posterior to the ocelli), legs, ventral surfaces, and T6 black; the dorsal half of the side of the thorax, the thoracic dorsum except for a spot between but isolated from the wing bases, and T1–T5 yellow (sandy yellow, or more brownish in queens); T3–T5 each with a well-defined but usually inconspicuous small triangular patch of black hair anteriorly near the midline, the apices pointing posteriorly (cf. *B. fragrans*); propodeum with the lateral hair predominantly black.

Male. Head with clypeus almost entirely covered in dense short hair; antennal scape with no hairs longer than the breadth of the scape in the distal third; hair on the metasoma ventrally unusually short, the long hairs in the median half of S3 less than half as long as the greatest breadth of the mid basitarsus (cf. *B. fragrans*); genitalia with gonocoxa with proximal inner process finger shaped, apically bluntly rounded; gonocoxa with sharply defined dorsal ridge subsiding before the distal extremity, which is convex dorsally; gonostylus enlarged with the apex truncate with two weakly marked angles, the inner proximal process almost as broad as the length of the gonostylus; volsella distally broadened; penis valve with the ventrolateral process broadly and evenly rounded without teeth, like a manatee's tail; penis valve head distally broadly rounded on its outer edge, its outer proximal corner with an anteriorly-directed flattened process, which in lateral aspect is triangular and sharp. Colour pattern (Figs 78–80). Hair predominantly lemon yellow, or more golden yellow on the thoracic dorsum; black hair intermixed on the head, especially along the edge of the clypeus and along the inner edge of the eye, and posteriorly and laterally to the eye, and sometimes in an inconspicuous small spot between, but isolated from, the wing bases, and on the legs; T3–T6 each with a well-defined but usually inconspicuous small triangular patch of black hair anteriorly near the midline, the apices pointing posteriorly (cf. *B. fragrans*), T7 black in its median half.

Material examined: In total, 18 queens, 68 workers, and 13 males (AMNH, BMNH, HMB, IAB, IZB, MNHU, NMP, OLL, and PW), with 11 specimens

barcoded in the BOLD database. Details available at <http://www.nhm.ac.uk/bombus/downloads/subterraneobombus.mdb>.

Distribution: Material examined from China, Mongolia, and Russia (266–2600 m a.s.l.; Fig. 12). Vicarious with the western *B. fragrans*. Skorikov (1931: fig. 5) mapped the distribution of this species, as his records labelled *mongol* in Russia and Mongolia, recording it (p. 177) from as far west as the Burchan Gorge.

Variation: Primarily in the size of the black spot between the wing bases, which is largest in workers, smaller in queens, and absent in many males. Also in the hue of the yellow, which is palest in workers, and darker and brownish in queens and on the thoracic dorsum of larger males. No geographic pattern to colour (or *CO1*) variation is apparent, although there may be a relationship between colour and body size.

BOMBUS FRAGRANS (PALLAS, 1771)

(FIGS 13, 37, 38, 81–83)

APIS fragrans Pallas, 1771: 474, syntypes, presumed lost (note 1) not seen. Russia: Volga region.

[*BOMBUS FRAGRANS* variété d'Orenbourg Radoszkowski, 1860: 484, incorrectly formed name.]

[*Bombus fragrans* (Pallas); Hoffer, 1883: 28, incorrect subsequent spelling.]

[*Bombus fragrans* var. *sulfureus* Skorikov, 1908: 111, infrasubspecific.]

[*Bombus (Subterraneobombus) fragrans* f. *mongoloides* Pittioni, 1939a: 77, infrasubspecific.]

Note 1 (*fragrans*). At the time of the description of *A. fragrans*, Peter Simon Pallas was a professor at the St Petersburg Academy of Sciences. Pallas' (1771) original description refers to both queens and males (syntypes). No possible syntype specimens have been found in the ZISP collection (S. Belokobylskij, pers. comm.). Nonetheless, the concept and name of this species in Europe and western Russia have been consistently stable. Consequently, the designation of a neotype is unjustified (ICZN, 1999: article 75).

History: In Asia, this species has been confused with *B. amurensis* (see the comments on that species).

Diagnosis: Female. Head with the labrum with the breadth of the median furrow less than a third of the total breadth of the labrum (cf. *B. amurensis*); clypeus dull, in its central half with many large punctures and dense medium punctures; oculo-malar distance 1.0' times as long as the basal breadth of the mandible. Hair short: the longest hair of T5 shorter than the greatest breadth of the hind basitarsus; hind tibia with the longest hairs of the posterior fringe shorter

than the greatest breadth of the tibia. Colour pattern (Figs 37, 38). Hair of the head (except for the vertex posterior to the ocelli), legs, side of the thorax, ventral surface, and T6 black; the dorsal quarter or less of the side of the thorax, the thoracic dorsum except for a broad band between the wing bases (cf. *B. amurensis*), and T1–T5 yellow (sandy); T3–T5 with few or no black hairs anteriorly near the midline (cf. *B. amurensis*); propodeum with the lateral hair predominantly black.

Male. Head with clypeus almost entirely covered in dense short hair; antennal scape with no hairs longer than the breadth of the scape in the distal third; hair on the metasoma long, the long hairs in the median half of S3 nearly as long as the greatest breadth of the mid basitarsus (cf. *B. amurensis*); genitalia with gonocoxa with proximal inner process finger shaped, apically bluntly rounded; gonocoxa with sharply defined dorsal ridge subsiding before the distal extremity, which is convex dorsally; gonostylus enlarged with the apex truncate with two weakly marked angles, the inner proximal process almost as broad as the length of the gonostylus; penis valve with the ventrolateral process broadly and evenly rounded without teeth, like a manatee's tail; volsella distally broadened; penis valve head distally broadly rounded on its outer edge, its outer proximal corner with an anteriorly-directed flattened process, which in lateral aspect is broadly rounded. Colour pattern (Figs 81–83). Hair predominantly sandy yellow; black hair intermixed on the head, especially along the edge of the clypeus and along the inner edge of the eye, and posteriorly and laterally to the eye, and in a narrow band between the wing bases, which is occasionally largely intermixed with yellow, and on the legs; T3–T5 without black hair (cf. *B. amurensis*), T6 with variable quantities of black in its median quarter, T7 black in its median half.

Material examined: In total, 88 queens, 123 workers, and 21 males (BMNH, HMB, ISEAK, IZB, MA, MNHU, NMP, OLL, PR, PW, SC, SZMN, and ZMMU), with eight specimens barcoded in the BOLD database. Details available at <http://www.nhm.ac.uk/bombus/downloads/subterraneobombus.mdb>.

Distribution: Material examined from Austria, China, Czech Republic, Hungary, Iran, Kazakhstan, Moldova, Poland, Russia, Turkey, and Ukraine (from –25 to +2500 m a.s.l.; Fig. 13). Vicarious with the eastern *B. amurensis*. Skorikov (1931: fig. 5) mapped the distribution of this species, but confused it with *B. amurensis* (i.e. excluding his records labelled *mongol*). National maps are available for, e.g. Poland

(Pawlikowski, 2008), Russia (Panfilov, 1984), Turkey (Rasmont & Flagthier, 1996), and the Ukraine (Panfilov, 1984).

Variation: Primarily in the breadth of the black band between the wing bases. Pittioni's infrasubspecific form *mongoloides* has the black band between the wing bases much less apparent because of intermixed yellow hair, and so converges superficially with *B. amurensis*. However, the name *mongoloides* was applied originally to a male from Austria (BMNH: DB#0801) that has character states of the genitalia typical of *B. fragrans*. Some worker specimens from Kazakhstan have an inconspicuous minority of short hairs on the face pale.

BOMBUS SUBTERRANEUS (LINNAEUS, 1758)
(FIGS 14, 39–47, 84–88, 103)

APIS acervorum Linnaeus, 1758: 579, species 34, type believed by Day (1979: 48) to be lost. Sweden. Synonymized with *B. subterraneus* (Linnaeus, 1758) by Løken (1973: 186) as *Apis acervorum* Linnaeus (note 1).

APIS subterranea [*subterranea*] Linnaeus, 1758: 579, species 35, holotype queen, LSL examined. Sweden.

APIS Nemorum Scopoli, 1763: 307, species 821, type worker not seen. Austria. Regarded as conspecific [in the form *Bombus subterraneus* ssp. *nemorum* (Scopoli, 1763)] by Warncke (1986: 106).

Apis bomb. grifea [*grisea*] Christ, 1791: 130, type queen not seen. Europe. Synonymized with *B. subterraneus* ssp. *nemorum* (Scopoli, 1763) by Warncke (1986: 100).

APIS Latreillella Kirby, 1802: 330, holotype male, BMNH examined. UK. Synonymized with *B. subterraneus* (Linnaeus, 1758) by Dalla Torre (1879: 12).

Bombus Latreillanus Illiger, 1806: 165, unjustified emendation.

?*BOMBUS HORTORUM* [var.] β . *bicingulatus* Evermann, 1852: 132, type not seen. Type locality not given.

[*Bombus Latreillellus* (Kirby); Radoszkowski, 1877: 208, incorrect subsequent spelling.]

Bombus Latreillellus var. *borealis* Schmiedeknecht, 1878: 375, holotype male by monotypy not seen. Germany. Junior primary homonym of *Bombus borealis* Kirby, 1837: 272 (= *B. borealis* Kirby). Regarded as conspecific (in the form *Bombus subterraneus* var. *borealis* Schmiedeknecht) by Dalla Torre (1896: 552).

Bombus subterraneus ssp. *germanicus* Friese, 1905: 522, type not seen. Type locality not given.

[*Bombus subterraneus* var. *latreillellus* ab. *runderatiiformis*, ab. *propedistinguendus* Vogt, 1909: 74, infrasubspecific.]

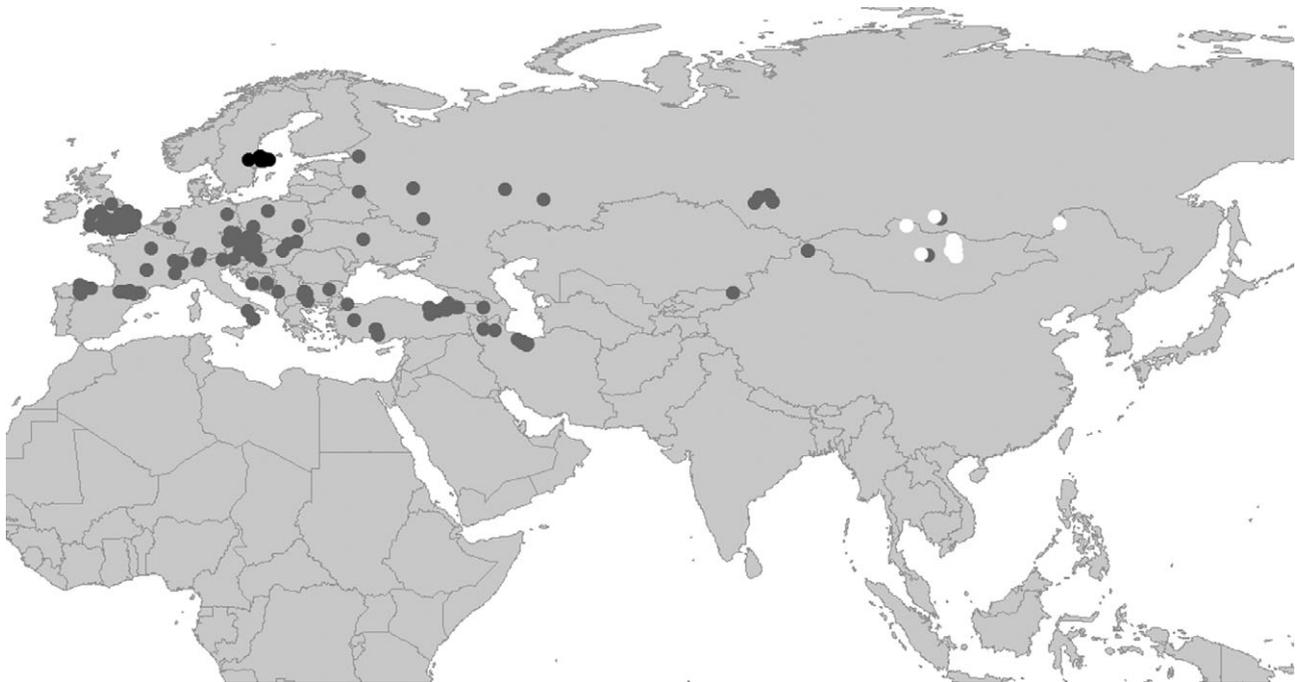


Figure 103. Distribution of the principal colour patterns of *Bombus subterraneus*. White spots show specimens with bands of white hair on the thoracic dorsum (Figs 39, 40, 84; *dlabolai*); grey spots show specimens with bands of yellow hair on the thoracic dorsum (Figs 41–45, 85–88; *latreillellus*); black spots show female specimens with no obvious bands of pale hair on the thoracic dorsum (Figs 46, 47; *subterraneus* s.s.; males from this region have yellow bands). Introductions to New Zealand are not shown.

Bombus (*Subterraneobombus*) *subterraneus* var. *geogr. latocinctus* Vogt, 1911: 62, syntypes, not seen. 'Zentraleuropa. Kleinasien. Turkestan.'

[*Bombus* (*Subterraneobombus*) *subterraneus* f. *flavotaeniatus*, f. *flavodisjunctus*, f. *sulphureofasciatus*, f. *sulphureociliatus* Vogt, 1911: 62–63, infrasubspecific.]

[*Bombus* *subt.*[*erraneus*] var. *amoenus* Scholz, 1924: 7, infrasubspecific.]

Bombus (*Subterraneobombus*) *subterraneus* ssp. *pallidofasciatus* C.&O. Vogt 1938: 296, type female not seen. Type locality eastern Siberia. Junior primary homonym of *Bombus asiaticus pallidofasciatus* Vogt, 1909: 51 (= *B. asiaticus* Morawitz).

Bombus (*Subterraneobombus*) *subterraneus* *Schmiedeknechtianus* C.&O. Vogt 1938: 296, replacement name for *Bombus subterraneus borealis* Schmiedeknecht, 1878.

[*Bombus* (*Subterraneobombus*) *subterraneus* m.[*orpha*] *mongolicus* Pittioni, 1939a: 245, infrasubspecific.]

[*Bombus* (*Subterraneobombus*) *subterraneus* f. *bistigmatus*, f. *fasciatus*, f. *alboanalisis*, f. *superborealis*, f. *soroensiooides*, f. *fasciolatus*, f. *taeniatus*, f. *flavescens*, f. *flavus*, f. *distinguendiformis* Pittioni, 1939a: 76–77, infrasubspecific.]

Bombus subterraneus [ssp.] *tectosagorum* Kruseman, 1958: 162, holotype queen by original designation, ZMA not seen. France.

Megabombus (*Subterraneobombus*) *subterraneus* [ssp.] *dlabolai* Tkalčů, 1974b: 47, holotype queen by original designation (note 2), BMNH examined. Mongolia.

Megabombus (*Subterraneobombus*) *subterraneus* ssp. *liguriensis* Rasmont, 1988: 70, holotype queen by original designation, ZSM not seen. Italy.

Note 1 (*acervorum*). Løken (1973: 186) appears to have been the first to explicitly recognize *Apis acervorum* Linnaeus, 1758 and *Apis subterranea* Linnaeus, 1758 as conspecific and, as the first reviser, to select the latter name as the valid name for the species *Bombus subterraneus* (Linnaeus, 1758).

Note 2 (*dlabolai*). Because it is the name of a morph, the name *B. subterraneus* morpha *mongolicus* Pittioni cannot be made available by any subsequent nomenclatural action, except by the intervention of the ICZN. Therefore, the name *M. subterraneus dlabolai* Tkalčů is not a replacement name for *mongolicus* Pittioni as a junior homonym of *mongolicus* Vogt, 1909: 42 (which is itself actually infrasubspecific) as proposed (see also the note on *B. mongolensis* sp. nov.), but is a name for a new (if identical) taxon.

Consequently Tkalců's designation of a lectotype for *mongolicus* Pittioni is construed as a designation of a holotype for *dlabolai* Tkalců.

History: The concept of this species has been stable for more than a century. In Europe, both sexes are sometimes confused with *Bombus* (*Megabombus*) *rud-eratus* (Fabricius, 1775), and pale males are often confused with *B. distinguendus*.

Diagnosis: Female. Head with clypeus shiny, in its central half lacking medium or large punctures, with only a few widely scattered micropunctures. Hair short: the longest hair of T5 about equal to the greatest breadth of the hind basitarsus. Colour pattern (Figs 39–47). Hair colour very variable: the darkest individuals almost entirely black, but with hair of T4–T5 dark chocolate brown with white tips; the palest individuals with head black [cf. the similar *Bombus* (*Thoracobombus*) *exil* Skorikov, 1923], at most with one or two yellow hairs on the vertex posterior to the ocelli; black band between the wing bases very rarely with pale hair intermixed laterally; T2–T3 with conspicuous transverse bands of black hair often occupying half of the length from the anterior to the posterior edges, the posterior fringe white or yellow (rarely absent), and the hair of T4–T5 usually completely white (cf. *B. distinguendus*).

Male. Head with clypeus with sparse moderately long hair, except absent in a median band occupying the median third in the anterior ventral third adjacent to the labrum; antennal scape with hairs longer than the breadth of the scape in the distal third; genitalia with gonocoxa with proximal inner process finger shaped, apically bluntly rounded; gonocoxa with the sharply defined dorsal ridge reaching the distal outer edge before the distal extremity, which is flat dorsally; gonostylus broadly triangular, breadth of the inner proximal process about half of the length of the gonostylus; volsella distally narrowed; penis valve with the ventrolateral process almost trident-like, with a strong dorsal tooth (cf. *B. distinguendus*), a strong ventral tooth, and a rounded scarcely marked central projection; penis valve head distally broadly rounded on its outer edge, its outer proximal corner with a flattened process, reduced to a dorso-ventral ridge with at least one small tooth. Colour pattern (Figs 84–88). Hair colour variable, but usually with extensive pale hair (yellow or white, or both), except with the majority of the hairs just dorsal to the antenna base and anterior to the ocelli black (cf. *B. distinguendus*), the black band between the wing bases with few or no pale hairs intermixed, black hairs usually intermixed on T2–T3 for at least half of the length from the anterior to posterior edges, so as to appear as conspicuous brown bands, but

occasionally reduced to inconspicuous patches of black hairs intermixed laterally near the anterior edge of T2 (cf. *B. distinguendus*).

Material examined: In total, 202 queens, 173 workers, and 427 males (AMNH, BMNH, DG, HMB, IZB, MA, MNHU, NMP, OLL, PR, PUI, PW, SC, SR, TP, UOG, ZIH, and ZMMU), with 38 specimens barcoded in the BOLD database. Details available at <http://www.nhm.ac.uk/bombus/downloads/subterraneobombus.mdb>.

Distribution: Material examined from Austria, Azerbaijan, Belarus, Bosnia, Bulgaria, China, Croatia, Czech Republic, Denmark, France, Germany, Hungary, Iran, Italy, Kyrgyzstan, Mongolia, Montenegro, the Netherlands, New Zealand, Poland, Russia, Spain, Sweden, Switzerland, Turkey, UK, and Ukraine (1–3000 m a.s.l.; Fig. 14, records from February and November are from New Zealand). This species was introduced from the UK into New Zealand, and became established between 1885 and 1914 (Gurr, 1957). Recently, it appears to have been extirpated from the UK, where it was last recorded in 1988 (Williams & Osborne, 2009). National maps are available for, e.g. Belgium (Rasmont, 1988), Finland (Pekkarinen *et al.*, 1981), France (Rasmont, 1988), Italy (Reinig, 1970), the Netherlands (Peeters, Raemakers & Smit, 1999), New Zealand (Macfarlane & Gurr, 1995), Norway (Løken, 1973), Poland (Pawlikowski, 2008), Sweden (Løken, 1973), Switzerland (Amiet, 1996), Turkey (Rasmont & Flagothier, 1996), and the UK (Benton, 2006).

Variation: There is pronounced colour variation in the extent of the black or pale hair (Fig. 103). In the north-west of the range in Sweden, queens and workers may be almost completely black, although the males are yellow banded (*subterraneus* s.s.). In the rest of Europe, female colour patterns are variable, with between one and three yellow bands (*latreillellus*). For example, female colour patterns with between one and three yellow bands have been found in Britain, although there is a strong tendency towards lighter three-banded females further south in Europe (from Spain to Turkey) and Iran. For males from areas as far apart as Britain and Russia, a minority have the metasoma almost entirely yellow, and have often been confused with *B. distinguendus*. At the far east of the range in Mongolia, the yellow hue in both sexes may be partly or completely replaced by cream for the queens and males, and grey–white for the workers (*dlabolai*). This pale appearance is not a result of the fading of old specimens in sunlight. It is also variable within a long series of queens from near Ulaanbaatar. In Mongolia, just as in Britain, some females have a pale T1,

some have T1 with only a pale posterior fringe, and some have T1 entirely black, but in Mongolia all have a narrow pale band on the scutellum. Although these black, yellow-banded, and white-banded forms have been regarded as regional subspecies (*subterraneus*, *latreillellus*, *dlabolai*, respectively; Fig. 103), the distinctions between them in colour are not discrete.

The intraspecific *COI* variation is weak, with no evidence from our *COI* results for reliable internal groups (Fig. 2). However, there is geographic pattern in the colour variation, which presumably has a genetic basis (Fig. 103).

BOMBUS DISTINGUENDUS MORAWITZ, 1869
(FIGS 15, 48–52, 89–92)

APIS nemorum Fabricius, 1775: 382 species 19, type female, LSL (Zimsen, 1964: 416) not seen. Denmark. Junior primary homonym of *Apis nemorum* Scopoli, 1763: 307 [= *B. subterraneus* (Linnaeus, 1758)]; junior primary homonym of *Apis nemorum* Fabricius, 1775: 380 (= *Bombus bohemicus* Seidl, 1837). Synonymized provisionally with *B. distinguendus* Morawitz, 1869 by Dalla Torre (1896: 517).

Apis pratorum Fabricius, 1781: 478, species 23, replacement name for Fabricius, 1775: 382, species 19 (*Apis nemorum*). Junior primary homonym of *Apis pratorum* Linnaeus, 1761: 424 [= *Bombus pratorum* (Linnaeus, 1761)].

Bombus elegans Seidl, 1837: 67, type believed by Tkalců (1969b: 901) to be lost (note 1). Czech Republic. Synonymized with *Megabombus distinguendus* (Morawitz, 1869) by Tkalců (1969b: 902) (note 2); **nomen oblitum** (note 2).

Bombus distinguendus Morawitz, 1869: 32, **lecto-type** male by present designation (note 3), ZISP examined. Russia: St Petersburg; **nomen protectum** (note 2).

[*Bombus distinguendus* Morawitz; Radoszkowski, 1884: 89, incorrect subsequent spelling.]

Bombus Latreillellus Rasse *frisius* Verhoeff, 1891: 204, holotype male by monotypy not seen. Germany. Synonymized with *B. subterraneus* var. *distinguendus* Morawitz by Friese & Wagner (1914: 175).

Bombus subterraneus var. *flavidissimus* Friese & Wagner, 1914: 175, type not seen. Type locality unknown. Regarded as conspecific [in the form *Subterraneobombus distinguendus* var. *flavidissimus* (Friese)] by Skorikov (1922: 40).

[*Subterraneobombus distinguendus* var. *eurynotus*, var. *laesoides* Skorikov, 1922: 40, infrasubspecific.]

Bombus (*Subterraneobombus*) *alinae* Reinig, 1936: 3, holotype queen by original designation, one of

several believed lost when the Reinig personal collection was destroyed (Williams, 1991: 77). China: Neimenggu; **syn. nov.**

Note 1 (*elegans*). The name *B. elegans* has been applied to several taxa by different authors. Tkalců (1969b: 901–903) reasoned that Seidl had originally described *B. elegans* from an individual of the species that has been known recently by the name *B. distinguendus*, although Seidl's original type is lost. According to Tkalců, a specimen of the species recently known by the name *Bombus mesomelas* Gerstaecker, 1869 may then have been substituted as the type of *B. elegans*, but now this specimen cannot be found either.

Note 2 (*distinguendus*). Although *B. elegans* has been accepted as the oldest available name for this species (note 1), no publication using the name *B. elegans* has been known for this species since 1899 (ICZN, 1999: article 23.9.1.1), except for *B. mesomelas* Gerstaecker, 1869 as a misidentification, whereas the name *B. distinguendus* has been in common use for the species since 1960, e.g. Tkalců, 1969b; Løken, 1973; Tkalců, 1974b; Alford, 1975; Delmas, 1976; Sakagami, 1976; Pekkarinen, 1979; Pekkarinen *et al.*, 1981; Reinig, 1981; Panfilov, 1982; Rasmont, 1983; Pekkarinen & Teräs, 1993; Kosior, 1992; Rasmont *et al.*, 1995; Amiet, 1996; Berezin, Beiko & Berezina, 1996; Williams, 1998; Peeters *et al.*, 1999; Hagen & Aichhorn, 2003; Edwards & Williams, 2004; Benton, 2006; Fitzpatrick *et al.*, 2006; Kosior *et al.*, 2007; Pawlikowski, 2008; Goulson, 2010 (ICZN, 1999: article 23.9.1.2). Because both of these conditions of the code apply, it is suggested that, in the interests of stability (ICZN, 1999: article 23), and to prevent further confusion with *B. mesomelas*, the prevailing usage of *B. distinguendus* be maintained as valid by designating *B. elegans* Seidl, 1837 as a *nomen oblitum*, and designating *B. distinguendus* Morawitz, 1869 as a *nomen protectum* (ICZN, 1999: article 23.9.2).

Note 3 (*distinguendus*). Morawitz's (1869) description of *B. distinguendus* is of queen, worker, and male syntypes from St Petersburg. Løken (1973: 182), citing Ponomareva (pers. comm., 1964), lists a worker and a male syntype from Leningrad (St Petersburg) in the ZISP collection. A male from St Petersburg in the ZISP collection labelled as *distinguendus*, in what appears to be Morawitz's handwriting, lacks the antennal flagella and genitalia, but agrees with the original description. It bears the labels: (1) handwritten '*Petrop.*' (i.e. Petropolis or St Petersburg); (2) '*distinguen-/dus* F. Mor.' (handwriting of F. Morawitz); (3) '*B. subterraneus/v. distinguendus/♂* 1904 Friese det.'; (4) printed '[K.F. Morawitz]'; (5) red '*Paralectotypus Bombus/distinguendus/Morawitz/* design. Podbolots. ♂' (handwriting of M. Podbolotskaya, designation unpublished); (6) printed

'*Subterraneobombus*/DB# 3069. det. PHW/*Bombus distinguendus*'; (7) white printed 'LECTOTYPE ♂/*Bombus distinguendus*/Morawitz 1869/det. PH Williams 2009'. This male, which matches the original description, has the correct locality data and a Morawitz determination label, and is regarded as a syntype. It is designated here as the lectotype (ICZN, 1999: article 74.1). The worker, which is complete but lacks a Morawitz determination label, is considered a likely syntype and is labelled as a paralectotype.

History: The concept of this species has been stable for more than a century. Nonetheless, the species is often confused in both sexes with other similarly coloured species, e.g. *B. (Thoracobombus) mesomelas* Gerstäcker, 1869 and *Bombus (Thoracobombus) laesus* Morawitz, 1875. It is also confused in Europe with pale males of *B. subterraneus*. The identification of the dark females from Attu in the Aleutian Islands with this species (Williams & Thomas, 2005), and more recent records from continental North America, at Fairbanks and Palmer, Alaska (DB#3852–3854; C. Sheffield, pers. comm.), are now confirmed from *COI* data.

Diagnosis: Female. Head with clypeus shiny, in its central half lacking medium or large punctures, with only a few widely scattered micropunctures. Hair long: mid basitarsus with the longest hairs of the posterior edge as long as or longer than the greatest breadth of the basitarsus, the longest hair near the posterior edge of T5 about 1.5 times as long as the greatest breadth of the hind basitarsus. Colour pattern (Figs 48–52). Hair of the head often predominantly yellow, but variable, with at least some yellow hair intermixed on the vertex posterior to the ocelli; dorsum of the thorax and of the metasoma predominantly straw yellow, paler posteriorly, T2 always yellow with at most a few inconspicuous anterior black hairs (cf. *B. subterraneus*), black hair forming a band between the wing bases, although usually with yellow hair strongly intermixed in a lateral longitudinal band next to the tegula, legs distally, and T6 predominantly black, although the extent of the black on the metasoma is variable, sometimes with black hair intermixed on T1–T5 anteriorly, and especially broadly on T5, although this black hair rarely forms conspicuous black bands; the ventral surface varying from entirely grey–cream to almost entirely black.

Male. Head with clypeus nearly covered in dense moderately long hair, except in a narrow median band occupying the median quarter in the anterior ventral quarter adjacent to the labrum; antennal scape with the hairs longer than the breadth of the scape in the distal third; genitalia with gonocoxa with proximal inner process shorter than broad, apically obliquely

truncate; gonocoxa with sharply defined dorsal ridge reaching the distal outer edge before the distal extremity, which is flat dorsally; gonostylus broadly triangular, breadth of the inner proximal process about half of the length of the gonostylus; volsella distally narrowed; penis valve with the ventrolateral process almost trident-like, usually with only a weak dorsal tooth (cf. *B. subterraneus*), a strong ventral tooth, and a rounded scarcely marked central projection; penis valve head distally broadly rounded on its outer edge, its outer proximal corner with a flattened process reduced to a dorsoventral ridge, dorsally with a small tooth and ventrally with a more triangular process. Colour pattern (Figs 89–92). Hair usually predominantly straw or lemon yellow, paler ventrally, usually with the majority of at least the shorter hairs just dorsal to the antenna base yellow (cf. *B. subterraneus*), except for a black band between the wing bases, although this black band usually has yellow hairs intermixed at least laterally next to the tegula, and sometimes throughout, legs distally and T7 often predominantly black, and although the extent of the black on the metasoma is variable, T2 without black hair (cf. *B. subterraneus*).

Material examined: In total, 109 queens, 109 workers, and 93 males (BMNH, DG, GE, HMB, HUM, IAB, LP, ME, NMP, OLL, PUI, PW, SC, UKK, ZIH, ZISP, and ZMMU), with 31 specimens barcoded in the BOLD database. Details available at <http://www.nhm.ac.uk/bombus/downloads/subterraneobombus.mdb>.

Distribution: Material examined from Austria, China, Czech Republic, Finland, Germany, Ireland, Mongolia, the Netherlands, Poland, Russia, Sweden, UK, and the USA (1–2100 m a.s.l.; Fig. 15). National maps are available for, e.g. Belgium (Rasmont, 1988), Finland (Pekkarinen *et al.*, 1981), France (Rasmont, 1988), Ireland (Fitzpatrick *et al.*, 2006), the Netherlands (Peeters *et al.*, 1999), Norway (Løken, 1973), Poland (Pawlikowski, 2008), Russia (Panfilov, 1982), Sweden (Løken, 1973), Switzerland (Amiet, 1996), and the UK (Benton, 2006).

Variation: Colour variation is primarily in the replacement of yellow with black hair, especially between the wing bases, but sometimes with black hair intermixed on T1–T5 anteriorly, and especially broadly on T5, although this black hair rarely forms conspicuous black bands. Also, the hair of the ventral surface varies from entirely grey–cream to almost entirely black. The lightest individuals occur in the west of the range (UK and Ireland), and the darkest individuals occur in the Far East (Magadan and Attu).

Compared with *B. subterraneus*, *B. distinguendus* shows less intraspecific variation in colour pattern, but stronger structure in the *COI* results (Fig. 2), with the more reliable basal groups showing a strong geographic pattern across: (1) Alaska; (2) the UK; and (3) Europe and Asia. What is most intriguing is the strong divergence of the UK population from other European populations (giving it potentially greater priority for conservation), and its apparent relationship to the population from Alaska, on the other side of the North Pole (a pattern of *COI* variation that does not match the colour variation, see above). These groups might indicate a fragmentation of the more northern range for *B. distinguendus* into a series of isolated refugia, where populations diverged, perhaps during the ice ages, followed by a more recent trend towards merging into a broad northern distribution.

BOMBUS APPOSITUS CRESSON, 1878
(FIGS 16, 53–57, 93–95)

Bombus appositus Cresson, 1878: 183, lectotype queen by designation of Cresson, 1916: 111, ANSP not seen. USA: Colorado.

History: The concept and name of this species have been consistently stable.

Diagnosis: Female. Head with clypeus shiny, in its central half lacking medium or large punctures, with only a few widely scattered micropunctures. Hair short: mid basitarsus with the longest hairs of the posterior edge as long as or shorter than the greatest breadth of the basitarsus, the longest hair near the posterior edge of T5 about 1.0 times as long as the greatest breadth of the hind basitarsus. Colour pattern (Figs 53–57). Hair of the head grey–white, or rarely yellow, with few black hairs; the upper half of the side of the thorax grey–white or rarely yellow, and the thoracic dorsum anterior to a black band between the wing bases grey–white, or sometimes yellow, the lateral eighth of the black thoracic band intermixed with grey–white or yellow, the posterior of the thoracic dorsum either grey–white with brownish tips, or a coffee brown, or yellow; the hair of T1–T5 yellow or (especially for queens) a coffee brown; the hair of the propodeum, of the ventral surface of the thorax and legs, and of T6 black or yellow.

Male. Head with clypeus with sparse moderately long hair, except in a median band occupying the median third in the anterior ventral third adjacent to the labrum; antennal scape with the hairs longer than the breadth of the scape in the distal third; genitalia with gonocoxa with proximal inner process shorter than broad, apically obliquely truncate; gonocoxa with sharply defined dorsal ridge reaching the

distal outer edge before the distal extremity, which is flat dorsally; gonostylus broadly triangular, breadth of the inner proximal process less than half of the length of the gonostylus; volsella distally narrowed; penis valve with ventrolateral process almost trident-like, with a strong dorsal tooth, a strong ventral tooth, and a strong triangular central projection; penis valve head distally broadly rounded on its outer edge, its outer proximal corner with a flattened process, reduced to a dorsoventral ridge, but dorsally with an extended anteriorly-directed flattened sharp process and a weaker ventral process. Colour pattern (Figs 93–95). Hair of the head usually predominantly grey–white, or rarely yellow; the side and ventral surface of the thorax grey–white, or rarely yellow, the thoracic dorsum anterior to a black band between the wing bases grey–white or sometimes yellow, the lateral eighth of the black thoracic band intermixed with grey–white or yellow, the posterior of the thoracic dorsum either grey–white with brownish tips, yellow, or a coffee brown; hair of T1–T6 straw yellow or a coffee brown; hair of the distal parts of the legs, and of T7, and the median quarter of T6 black.

Material examined: In total, 158 queens, 142 workers, and 21 males (BMNH, LBL, LP, PW, ROM, SC, UOG, and USNM), with seven specimens barcoded in the BOLD database. Details available at <http://www.nhm.ac.uk/bombus/downloads/subterraneobombus.mdb>.

Distribution: Material examined from Canada and the USA (1–3900 m a.s.l.; Fig. 16). Stephen (1957: map 1) mapped the entire distribution of this species and Thorp, Horning & Dunning (1983: map 6) mapped its distribution within California.

Variation: Primarily in the hue of the hair of the thoracic dorsum, from grey–white, to straw yellow, to a coffee brown, and in the extent of the replacement of the pale hair with black on the sides of the thorax. Replacement of all grey–white hair with yellow is predominant among many specimens from near Corvallis, Oregon (Figs 53, 93), so that these individuals resemble *B. distinguendus* closely. No geographic pattern to *COI* variation is apparent (but see comments on variation in *B. distinguendus*).

BOMBUS BOREALIS KIRBY, 1837
(FIGS 17, 58–62, 96–98)

BOMBUS BOREALIS Kirby, 1837: 272, syntype workers (note 1), believed by Milliron (1973: 118) to be lost. Canada.

Note 1 (*borealis*). The females in the description by Kirby (1837) were said to be eight (English) lines long (17 mm), and so appear to have been workers.

History: The concept and name of this species have been consistently stable. Consequently the designation of a neotype is unjustified (ICZN, 1999: article 75). Nonetheless, this species is often confused with *Bombus (Thoracobombus) fervidus* (Fabricius, 1798), which has an overlapping but more southerly distribution.

Diagnosis: Female. Head with clypeus shiny, in its central half lacking medium or large punctures, with only a few widely scattered micropunctures. Hair short: mid basitarsus with the longest hairs of the posterior edge as long as or shorter than the greatest breadth of the basitarsus, the longest hair near the posterior edge of T5 about 1.0 times as long as the greatest breadth of the hind basitarsus. Colour pattern (Figs 58–62). Hair of the face between the ocelli and the clypeus cream–yellow, usually with very few black hairs (cf. eastern *B. fervidus*), hair posterior to the ocelli predominantly a slightly darker sand yellow; the upper half or quarter of the side of the thorax, and the thoracic dorsum, except for a black band between the wing bases, and T1–T4 a golden yellow; the hair of the propodeum, of the ventral surface of the thorax and legs, and of T5–T6 black, sometimes with yellow hairs in a narrow posterior fringe on T5, or rarely more extensively on T5, sometimes with black hairs laterally on T4 or even T3.

Male. Head with clypeus with sparse moderately long hair, except in a median band occupying the median third in the anterior ventral third adjacent to the labrum; antennal scape with hairs longer than the breadth of the scape in the distal third; genitalia with gonocoxa with proximal inner process shorter than broad, apically obliquely truncate; gonocoxa with sharply defined dorsal ridge reaching the distal outer edge before the distal extremity, which is flat dorsally; gonostylus broadly triangular, breadth of the inner proximal process less than half of the length of the gonostylus; volsella distally narrowed; penis valve with the ventrolateral process almost trident-like, with a strong dorsal tooth, a strong ventral tooth, and a triangular central projection; penis valve head distally broadly rounded on its outer edge, its outer proximal corner with a flattened process, reduced to a dorso-ventral ridge but dorsally with an extended anteriorly-directed flattened sharp process and a weaker ventral process. Colour pattern (Figs 96–98). Hair of face between the ocelli and the clypeus cream–yellow, with black hairs intermixed, hair of the vertex predominantly a slightly darker sand yellow; the side of the thorax and the thoracic dorsum, except for a black band between the wing bases, and T1–T7 golden yellow; many hairs of the ventral surface of the thorax, proximally on the legs, and in anterior

bands on T5–T7 black (T5 varies from predominantly black with a few fringing yellow hairs, to predominantly yellow with a few black hairs intermixed anteriorly, sometimes T6 also predominantly yellow).

Material examined: In total, 136 queens, 98 workers, and 51 males (BMNH, LP, PUI, PW, ROM, SC, UOG, and USNM), with ten specimens barcoded in the BOLD database. Details available at <http://www.nhm.ac.uk/bombus/downloads/subterraneobombus.mdb>.

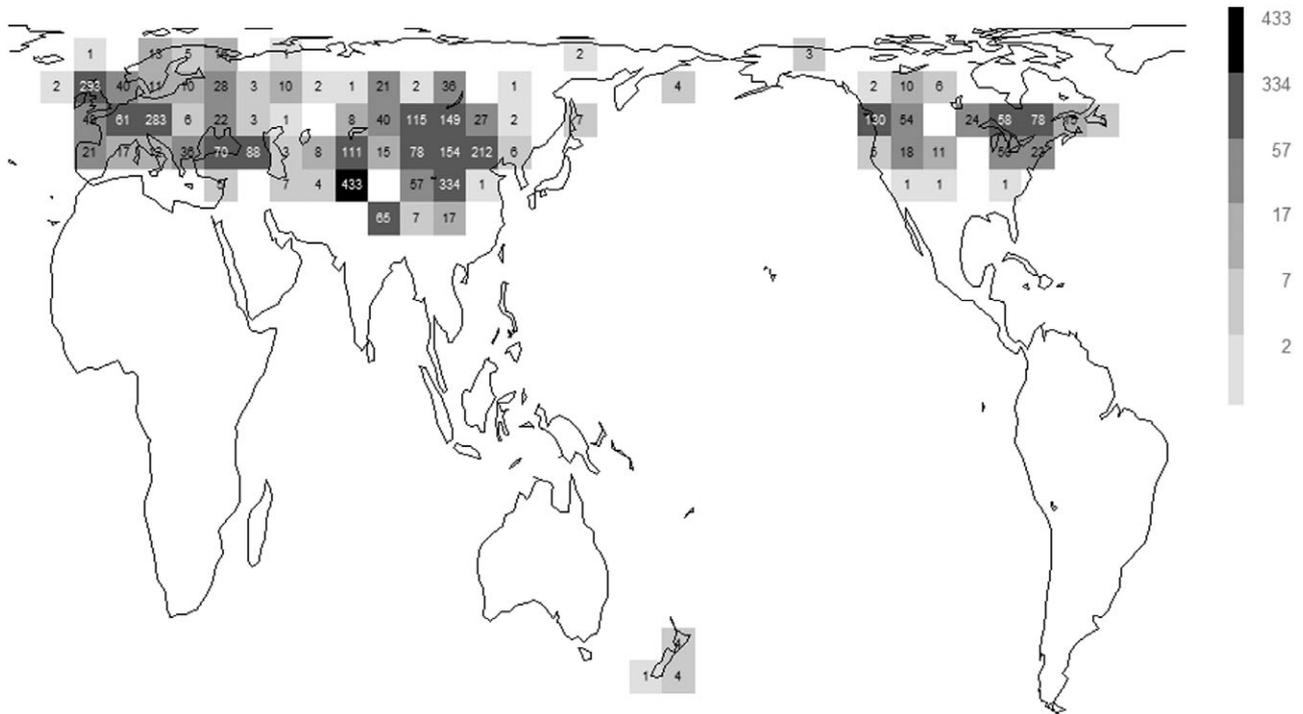
Distribution: Material examined from Canada and the USA (1–1113 m a.s.l.; Fig. 17). A worker (UOG: DB#2412) labelled ‘Van. B.C.’ (? = Vancouver British Columbia) is assumed to be mislabelled because no other records are known from southern British Columbia (R. Thorp, pers. comm.). This record is excluded from Figure 17. Lavery & Harder (1988: map 19) mapped the distribution of this species within eastern Canada.

Variation: Primarily in the relative extent of black and yellow hair. At the dark extreme, a queen from Wisconsin (UOG: DB#3367; Fig. 62) has only a few short hairs on the head yellow, the posterior pale band on the thorax and on T1 are extensively intermixed with black, and there is black hair anteriorly and laterally on T2, laterally on T3, and laterally and posteriorly on T4. At the light extreme, a worker from Toronto (UOG: DB#2275; Fig. 58) has T1–T5 almost entirely yellow, with only a few black hairs on T5. Occasionally an individual has the pale hair of the head and anterior thorax so pale and greyish as to show some similarity to *B. appositus*, but these individuals have T5 black and T1–T4 yellow. No geographic pattern to colour (or *COI*) variation is apparent (but see comments on variation in *B. distinguendus*).

DISCUSSION

Historically, the greatest sampling effort for bumblebee taxonomy has been in Europe and North America (Williams, 1998). Fortunately, we have been able to assemble reasonably large samples of material from Asia (Fig. 104), which is where the greatest species richness of *Subterraneobombus* is recorded (Fig. 105). This map of species richness for *Subterraneobombus* (Fig. 105) is similar to one published previously (Williams, 1998), although the centre of greatest richness (at this scale) is shown from our data to be in Mongolia rather than in the Tien Shan.

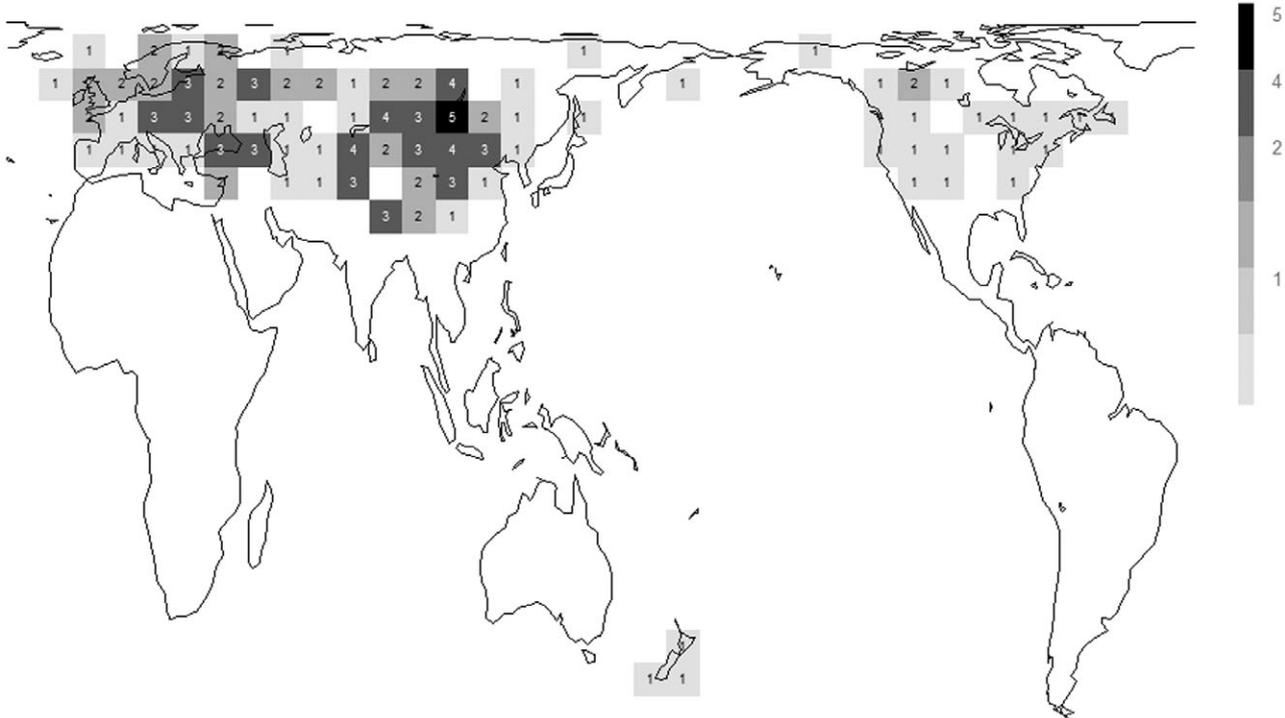
VALUE OF DNA BARCODE DATA FOR BUMBLEBEES
Obtaining and databasing the *COI* data for about 5% of the specimens in this review is estimated to have



Figures 104, 105. Global distribution of (104) numbers of specimens examined and (105) numbers of species recognized for *Subterraneobombus* among equal-area grid cells (grey scale at right; from georeferenced specimens in the database). The grid is based on longitudinal intervals of 10°, which are used to calculate graduated latitudinal intervals to provide equal-area cells (each cell approximately represents 611 000 km²). The grey scale is used to group the counts (numbers on map) into six classes. The maximum count is shown in black, and otherwise counts are divided into five classes of approximately equal size by numbers of grid cells. Cylindrical equal-area projection, with north at the top of the map.

accounted for about 10% of the total cost of the project (excluding any of the original costs of collecting, mounting, and labelling of specimens). Very few (< 20) of the specimens were collected with the intention of barcoding them, although the specimens used were all dry-mounted recent specimens (maximum age 23 years). Amplification and sequencing were successful for 75% of those selected. In this study, *CO1* data contributed particularly to supporting: (1) the discovery of the new species, *B. mongolensis* sp. nov., especially of the females and their diagnostic morphological character; (2) *B. fragrans* and *B. amurensis* as separate species; and (3) the specimens of *B. melanurus* with and without a black band on the thorax as conspecific, implying that in this case this colour character may be uninformative in relation to species status. Consequently we conclude that *CO1* data are a cost-effective source of additional characters for informing these long-standing problems where morphological information has been insufficient. However, it would be misleading to claim that *CO1* data alone had resolved these taxonomic problems. Progress can be credited in part to the larger samples of specimens now available for morphological analysis.

For the subgenus *Subterraneobombus* at least, the expectation of discovering many species considered previously to be morphologically cryptic, as suspected for some other bumblebee subgenera (e.g. Rasmont, 1984; Murray *et al.*, 2008), is unfulfilled. Only one new species is identified, in part as a result of barcoding, and several previously described taxa of contentious status are synonymized or confirmed as synonyms (e.g. within *B. melanurus*). Therefore, from our results there is no reason to expect that the rate of species discovery for bumblebees as a whole will increase dramatically with the use of DNA barcode (*CO1*) data above the rate found previously with morphological data (e.g. species-discovery curves in Williams, 1998). Indeed, there have been warnings that paralogous genes might sometimes give the impression of greater numbers of species than actually exist (Song *et al.*, 2008). We suspect that representative sampling of the entire global distributions of each species may also be important to reduce the number of false cryptic species claimed. An example from our data is that the *B. distinguendus* samples from the UK and from the USA did not form an exclusive monophyletic group with the other samples of this species, in the tradi-



Figures 104, 105. *Continued*

tional broad sense, until the Swedish samples were added late in the analysis. However, even if this subgenus proves to be unrepresentative, it is nonetheless reassuring that the traditional morphological approach has provided a reasonable first approximation to the present interpretation of the *COI* data in this case. Next, we need to explore the patterns shown by other genes, particularly the nuclear genes, and to find out more about the relationships between populations within species.

COLOUR PATTERNS

The two most basal species in Figure 5 (*B. personatus* and *B. subterraneus*) are the only two species of the subgenus to show a colour pattern consisting of yellow bands anteriorly and a white tail. This pattern is shown by the majority of temperate species in the closely related subgenus *Megabombus*. Otherwise, species within the subgenus *Subterraneobombus* fall into two colour pattern groups (Fig. 5): first, the *melanurus* group and *B. fedtschenkoi*, with black tails, are associated with high-elevation mountain grasslands (up to 5200 m a.s.l.; Fig. 6); and second, the *fragrans* and *distinguendus* groups, with extensively yellow or pale colour patterns, are associated with lower elevation grasslands and steppes. Among bumblebees generally, an extensively yellow pattern among females appears to be associated with open lower elevation

grasslands, where in summer it may help to provide cryptic defence against predators as the long grass dries and yellows (Williams, 2007). This is the only subgenus of bumblebees to have no species with any individuals with red tails.

HISTORY OF SPREAD AND SPECIATION

Speciation within the subgenus *Subterraneobombus* appears to be associated with the history of mountain building and aridification in Central Asia, as part of the more general divergence between the Palearctic and Oriental bumblebee faunas (Williams, 1996). The subgenus most closely related to *Subterraneobombus* is *Orientalibombus* (or possibly *Megabombus*; Cameron *et al.*, 2007), the species of which are found particularly in forests, especially at lower elevations, in China and in the Himalaya (Williams, 1998; Williams *et al.*, 2009). In contrast, *Subterraneobombus* species are generally associated with open grasslands further north, extending into semi-desert areas in the middle of their latitudinal range, and into high alpine areas nearer the equator (Fig. 6). Their centre of diversity is at higher elevations in Mongolia and in the mountains of Asia (Fig. 105). This may reflect a vicariance event between *Subterraneobombus* and *Orientalibombus* (or *Megabombus*) at approximately

22–20 Mya (Hines, 2008), which coincided with a period of increasing uplift of the Tibetan Plateau and of the mountains of Central Asia (Ruddiman, 1998; An *et al.*, 2001).

Although the precise relationships of *B. personatus* and *B. fedtschenkoi* remain very uncertain, the best available estimate of the phylogeny for all species (Fig. 5) is used in Figure 99 to reconstruct estimates of ancestral distributions. The initial divergence between the ?*personatus* + *melanurus* + ?*fedtschenkoi* + *fragrans* groups and the *subterraneus* group is likely to have occurred between 9 and 6 Mya (Fig. 1). The ancestral distribution for the ?*personatus* + *melanurus* + ?*fedtschenkoi* + *fragrans* groups appears to have been Tibet + Pamir, whereas the ancestral distribution of the *subterraneus* group appears to have been further north in the Holarctic region. This divergence coincides with the late phase of higher uplift (> 5000 m a.s.l.) of the Tibetan Plateau (An *et al.*, 2001), and the profound aridification of Central Asia (forming the Taklimakan and Gobi deserts). These deserts now form a barrier between the Holarctic bumblebee fauna to the north and the divergent Tibetan and Oriental bumblebee fauna to the south (Williams, 1996).

One interpretation of Figure 99 is that ancestors of *B. melanurus*, *B. difficillimus*, and *B. mongolensis* sp. nov. could have spread through grassland habitats at higher elevations along the mountain chains, and crossed from the Tibetan and Pamir plateaux into the more northerly mountains of Central Asia and Mongolia. There is then likely to have been a vicariance event between a primarily Central Asian *B. melanurus* ancestor (Fig. 8) and a primarily Tibetan + Mongolian *B. difficillimus* + *B. mongolensis* sp. nov. ancestor (Figs 9, 10). This may have been followed by another vicariance event in the east, between the Tibetan *B. difficillimus* and the Mongolian *B. mongolensis* sp. nov. Within *B. melanurus*, black-banded individuals are distributed primarily in the eastern part of the species range (in Mongolia and North China), which could be evidence of an east–west divergence (Fig. 100). Intriguingly, this east–west division within *B. melanurus* presumably pre-dates the current disjunction across the deserts between Central Asia + Mongolia in the north and Tibet + North China in the south, because both banded and unbanded colour forms occur on both sides of the desert (Fig. 100). It may be that during periods when the desert barrier was less pronounced and more mesic (Yu *et al.*, 1998), the species was able to colonize the southern areas in the east, which are now isolated. There is also a major disjunction further to the west, between Turkey + Iran in the west and Central Asia + China in

the east. Neither of these disjunctions, presumably caused by the continuing recent aridification, is associated with strong divergence in colour pattern or in *CO1* (Fig. 2).

Although *B. fedtschenkoi* has a narrow endemic distribution at intermediate elevation in the Alai-Pamir (Fig. 11), the other species of the *fragrans* group are associated with lowland open steppes (Figs 12, 13). Both the western *B. fragrans* and the eastern *B. amurensis* occur on both the northern and the southern edges of the broad Asian central arid belt. The divergence of this group from the *melanurus* group may have occurred fairly early (Figs 1, 99). During subsequent wetter periods these steppes may have extended into the region now occupied by the deserts (Yu *et al.*, 1998), so that the current desert-edge distribution may be a relic of an earlier, more continuous distribution.

The more northern Holarctic species of the *subterraneus* group are often associated with forest meadows within the more mesic lowland zone north of the arid-zone barriers. Again, there are records from isolated mesic sites for *B. distinguendus* within arid regions of Mongolia and Neimenggu that may be relics from less arid periods. Further north in the Palaearctic, the two species are widespread from the Atlantic almost to the Pacific. The more southern *B. subterraneus* shows relatively less variation in *CO1* despite strong colour variation (Figs 2, 39–47). In contrast, the more northern *B. distinguendus* is more variable in *CO1* (Fig. 2), possibly because further north the populations became more fragmented and diverged within multiple refugia during glacial cold periods. *Bombus distinguendus* as well as the ancestors of *B. borealis* and of *B. appositus* (as parts of an ancestral *distinguendus* complex) presumably spread from Asia into the Nearctic in the last 2 Myr through a belt of suitable habitat along the Bering land bridge (Williams, 1985; Sanmartin, Enghoff & Ronquist, 2001; Hines, 2008).

RECENT CHANGES

Bombus subterraneus was introduced from Britain into New Zealand in the 19th century (Gurr, 1957). It has recently been extirpated from Britain (Williams & Osborne, 2009), but persists in New Zealand, although populations there might also soon be lost (Goulson, 2007). There are currently plans to reintroduce it to Britain from New Zealand (Anonymous, 2009).

Rather than being invasive, species of *Subterraneobombus* show ecological characteristics (e.g. late emergence and narrow climatic ranges) that may predispose them to be particularly susceptible to decline in the face of environmental changes (Will-

iams & Osborne, 2009). In Central Europe, the three species of this subgenus have all declined during the latter half of the twentieth century. In Britain, *B. subterraneus* has become extinct since 1988, and *B. distinguendus* has become restricted to the far north-west. *Bombus distinguendus* has been adopted as a flagship of bumblebee conservation in Britain, and has become the subject of conservation projects involving the Bumblebee Conservation Trust (which currently uses it in its logo), the Royal Society for the Protection of Birds, and Scottish National Heritage. It has also declined throughout northern Europe (e.g. Berezin *et al.*, 1996). Both species may soon start to suffer either similar or increasing declines in the EU accession countries of eastern Europe, where they have until now remained relatively common, if new agricultural subsidies encourage similar land-use changes to those adopted throughout western Europe (Goulson, 2007). The contrasting pattern of relative *COI* variation between *B. subterraneus* and *B. distinguendus* (Fig. 2) needs to be explored in other genes. It may have consequences for conservation priorities if *B. distinguendus* populations are confirmed to be highly structured geographically in other genes as well. In particular, the populations in Britain and on Attu Island are not only genetically divergent from other populations and small, but could easily be threatened by environmental changes, including climate change (Williams, Araújo & Rasmont, 2007). Much remains to be clarified about the distribution of *B. distinguendus* in North America. But whereas both *B. subterraneus* and *B. distinguendus* are still locally common in parts of continental Europe and in Mongolia, the southern steppe species, *B. fragrans*, seems to have become extirpated or extremely scarce throughout its range from south-eastern Europe (P. Rasmont, pers. comm.) to Siberia (A. Byvaltsev, pers. comm.), and can now be found reliably only in Turkey (M. Aytakin, pers. comm.). In North America, declines have also been described for *B. borealis* (Grixti *et al.*, 2009), although not for *B. appositus* (R. Thorp, pers. comm.; J. Strange, pers. comm.). We have no evidence for similar changes in Asia, but surveys for the IAB will continue to monitor the situation in North China (Williams *et al.*, 2010).

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APPENDIX 1

Morphological character matrix excluding autapomorphies for *B. haemorrhoidalis* and all *Subterraneobombus* species (see Fig. 3).

character	111111111122222222
species	123456789012345678901234567
<i>haemorrhoidalis</i>	000000101110010000000101???
<i>personatus</i>	0000100000001001000100000??
<i>melanurus</i>	000010001001100110010011???
<i>difficillimus</i>	010010101001100110010111???
<i>Mongolensis</i> sp. nov.	010010011001100110010111???
<i>fedtschenkoi</i>	10001110111000010001000010?
<i>amurensis</i>	10110111111011010101000010?
<i>fragrans</i>	10110011111011010101000010?
<i>subterraneus</i>	00000000000101100111000110
<i>distinguendus</i>	00000000000101100111000110
<i>appositus</i>	00000000000101100111000111
<i>borealis</i>	00000000000101100111000111

1	female	clypeus small and large punctures in centre	0	absent
			1	present
2		clypeus micropunctures in centre	0	present
			1	absent
3		oculo-malar area length/breadth ratio	0	> 1
			1	= 1
4		T4 hair short even and strongly decumbent	0	absent
			1	present
5		T4 hair medially sparse	0	absent
			1	present
6		T6 median longitudinal furrow	0	present
			1	absent
7	male	clypeus hair in median anterior area	0	absent
			1	present
8		scape hair in distal third	0	long
			1	short
9		gonocoxa dorsal ridge	0	reaching distal edge
			1	not reaching distal edge
10		gonostylus distally	0	triangular
			1	truncate
11		gonostylus inner process	0	medium
			1	broad
12		gonostylus inner process	0	medium
			1	narrow
13		gonostylus inner process	0	reduced
			1	extended

APPENDIX 1 *Continued*

14	male	volsella distally	0	medium
			1	broad
15		volsella distally	0	medium
			1	narrow
16		penis valve ventrolateral process	0	marked only as an angle
			1	produced as spatula or trident
17		penis valve ventrolateral process	0	with 1–3 teeth
			1	with at least 2 long spines
18		penis valve ventrolateral process	0	with 1–3 teeth
			1	broadly rounded
19		penis valve ventrolateral process	0	base broad
			1	base narrow
20		penis valve head shape	0	arrow-shaped
			1	spoon-shaped
21		penis valve head dip angle	0	45° to shaft axis
			1	90° to shaft axis
22		penis valve head length	0	< 2× as long as broad
			1	2× as long as broad
23		penis valve head distal outer corner	0	rounded
			1	angled
24		penis valve head proximal outer corner	0	extended as a long process
			1	process absent
25		penis valve head proximal outer corner	0	with a conical spine
			1	with a flattened process
26		penis valve head proximal outer corner	0	with a flattened process
			1	process reduced to 2+ teeth
27		penis valve head proximal outer corner	0	dorsal tooth short
			1	dorsal tooth extended

APPENDIX 2

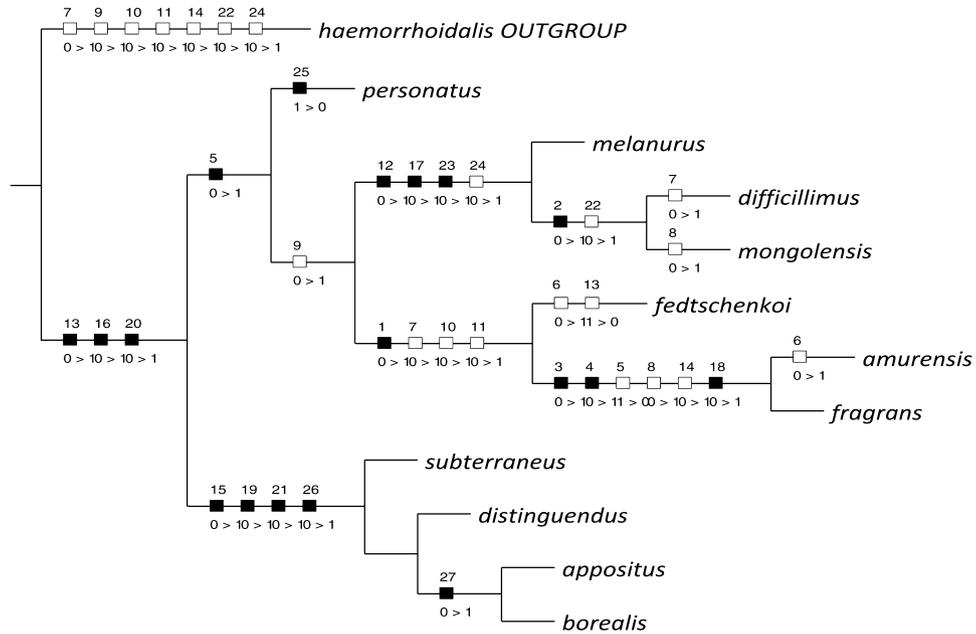


Figure 106. Estimate of the phylogeny for all 11 *Subterraneobombus* species by Bayesian analysis of the total evidence of 658 *CO1* nucleotides, reduced to consensus sequences for each species, and of 27 morphological characters for the species (Fig. 4), but with morphological character-state changes (Appendix 1) optimized with WINCLADA (ASADO v.1.7; <http://www.cladistics.com>, accessed 2009): numbers above the branches are the character numbers; numbers below the branches are the character-state changes; solid squares show unique character-state changes; open squares show parallel or reverse character-state changes.