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The steppe bumblebees of the subgenus *Sibiricobombus* revised world-wide from species' gene coalescents and morphology despite numts (Hymenoptera, Apidae, genus *Bombus*)

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Abstract. Bumblebees of the subgenus *Sibiricobombus* Vogt, 1911 of the genus *Bombus* Latreille, 1802 are associated with dry grasslands in the montane regions of Mongolia, Central Asia, the Qinghai-Tibetan Plateau and surrounding mountains, to as far west as Greece. Many of the taxa in this group were described initially from their colour patterns and have at different times been regarded as separate species or have been put into different combinations that were variously regarded as species. We examine integrated evidence for species as evolutionarily independent lineages, comparing evidence from species' gene coalescents, based on fast-evolving barcode-like DNA sequences, and from discontinuous variation in skeletal morphology and in colour patterns. Many sequences of *Sibiricobombus* taxa appear from their AT bias at the third codon position to be recent low-divergence numts. Higher frequencies of these numts may be associated with more substitutions within the barcode-primer-binding regions of the mitogenome since the divergence of bumblebees from the lepidopteran source of the primers. Nonetheless, in this particular case, all but one of the 12 species' gene coalescents support candidate species that are corroborated by morphological diagnoses. For the 11 corroborated species, the status of three species is revised and one new replacement name is proposed: *Bombus sibiricus* (Fabricius, 1781), *B. semenovi* Morawitz, 1887 stat. rev., *B. oberti* Morawitz, 1883, *B. morawitzi* Radoszkowski, 1876, *B. sulfureus* Friese, 1905, *B. niveatus* Kriechbaumer, 1870, *B. obtusus* Richards, 1951, *B. tescorum* Williams nom. nov. et stat. rev., *B. longiceps* Smith, 1878 stat. rev., *B. falsificus* Richards, 1930 stat. rev., and *B. asiaticus* Morawitz, 1875. Nine new synonyms are recognised. Estimates are provided for (1) an evolutionary tree for species and (2) for the ancestral species' distributions.

Keywords. Barcode, coalescent, distribution, integrative, species.

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Introduction

It is currently considered that there are approximately 294 extant species of bumblebees world-wide, all included in the single genus *Bombus* Latreille, 1802 (unpublished PW, updated from a global list in Williams 1998). Based on an evolutionary tree from five genes by Cameron *et al*. (2007), bumblebees are divided into 15 monophyletic groups named as subgenera, each of which tends to have different morphological and behavioural characteristics (Williams *et al.* 2008). Bumblebees of the subgenus *Sibiricobombus* Vogt, 1911 are distributed relatively narrowly through the high montane regions of Asia (Vogt 1911): from Mongolia, Central Asia, the Qinghai-Tibetan Plateau (QTP), the Himalaya, and Hindu Kush, to as far west as Iran, Turkey, and Greece (Skorikov 1923; Richards 1968; Williams 1998). They occur at low, intermediate, and high elevations, especially in dry grassland steppes, where they can be locally abundant.

Much of the information known about *Sibiricobombus* comes from the single species (*B. niveatus* Kriechbaumer, 1870), which occurs in south-eastern Europe (Rasmont *et al.* 2021). *Bombus niveatus* is unusual among European bumblebees because the males have especially large eyes (Streinzer & Spaethe 2014) and unusually long antennae. These antennae distinguish them from males of the other bumblebee groups in the Old World with strongly enlarged eyes (in the subgenera *Mendacibombus* Skorikov, 1914, *Bombias* Robertson, 1903, and some species of *Melanobombus* von Dalla Torre, 1880), all of which have much shorter antennae (Williams *et al.* 2008). The males of *B. niveatus* show a characteristic mate-searching behaviour, which has been described in more detail for the related species *B. longiceps* Smith, 1878 stat. rev. in Kashmir as "racing behaviour" (Williams 1991: under the name *B. asiaticus* Morawitz, 1875). Although this involves chasing of other bees, it is distinct from true territorial behaviour in that it does not result in male displacement and turnover in male perch occupancy. This behaviour appears to have advantages for encountering more females when unmated queens are expected to occur at high and uniform densities in open habitats, described from particular hill slopes in short grassland (Williams

1991). A few other species of *Sibiricobombus* have males with unenlarged eyes, sharing the form typical of most bumblebee species (see below).

The subgenus *Sibiricobombus* is part of a larger monophyletic group that has been described as the "short-faced" (Cameron *et al.* 2007) or "short-tongued" (Kawakita *et al.* 2004) bumblebees (including also the subgenera *Pyrobombus* Skorikov, 1914, *Bombus* s. str., *Alpinobombus* Skorikov, 1914, *Alpigenobombus* Skorikov, 1914, *Melanobombus* Skorikov, 1914, and *Cullumanobombus* Vogt, 1911). Nonetheless, in contrast to most of their close relatives within this group (Kawakita *et al.* 2004: fig. 2), species of *Sibiricobombus* actually have relatively long faces and tongues. This (and their short hair) may explain why they have sometimes been mistaken for species of the long-tongued bumblebees of the subgenus *Subterraneobombus* Vogt, 1911 (Richards 1930). Tongue length in bumblebees is ecologically important because it governs flower choice, diet, and competitive interactions for food resources with other bumblebee species (Heinrich 1979).

A few species of *Sibiricobombus*, often at lower elevations and in drier habitats, have extensively yellow colour patterns (especially the species *B. sulfureus* Friese, 1905 and *B. sibiricus* (Fabricius, 1781)), which may provide camouflage in dry summer grassland or desert habitats (Williams 2007). The majority of species of *Sibiricobombus*, particularly in the higher mountains, have colour patterns with strongly contrasting coloured bands in the hair (e.g., most *B. niveatus* and species of the *asiaticus*-group), which for the females (which sting) have been interpreted as parts of regional protective Müllerian mimicry groups (Richards 1929; Plowright & Owen 1980; Williams 2007). These patterns can be quite different among different geographical regions (even within species), which has contributed to a lack of agreement regarding the number of species accepted within the subgenus. Many of the taxa in this group have at different times been regarded as separate species or have been put into different combinations that were variously regarded as species (e.g., Skorikov 1923, 1931, 1933; Richards 1951; Wang 1982, 1985; Williams 1991, 1998) (Table 1). However, there has never been a complete revision of the group. Consequently, there is a need to review more evidence, including from genes, in order to ascertain which of these taxa are indeed most strongly supported as separate species.

There are two principal obstacles when seeking to compile a revised list of bumblebee species for use in (for example) conservation assessments: (1) the difficulty in recognising species; and (2) the huge area of the world, much of it difficult to access, that needs to be sampled in order to represent their full range of genetic and morphological variation.

For the first problem, ideas of what species are have changed greatly through time (Wilkins 2018, 2023), resulting in profound effects when applied to bumblebees with the lumping or splitting of the taxa named as species (Williams 2022c). For many bumblebees, ideas of species have until recently depended on interpretations developed in the nineteenth century based on morphology (Williams 1998). The approach used was not the one currently preferred and has rarely been quantitative, so decisions on species status may sometimes be difficult to judge other than by trusting to the authority of experienced specialists. This can be inconsistent, especially when declining numbers of taxonomic specialists and academic pressures (Hochkirch *et al.* 2022) cause taxonomy to be practiced increasingly in short-term studies that are not supervised by taxonomic specialists (Williams 2022b). However, in the last decade there has been a change, as a concept and definition of species for taxonomic purposes as 'evolutionarily independent lineages' (EILs) (de Queiroz 2007; Maddison & Whitton 2023) has become widely adopted by bumblebee specialists. These species are recognised in practice using an integrative approach, which allows for consideration of a variety of operational methods, the results of which can be assessed within a comparative framework (Padial *et al.* 2010; Schlick-Steiner *et al.* 2010). Among the methods used, some, like species' gene-coalescent analysis, have the advantages of: (1) being especially closely allied to the theory of EILs through the direct relationship between evolutionary independence and species'

Table 1. Previous lists of taxa interpreted as species of the subgenus *Sibiricobombus* Vogt, 1911 in its present broad sense (to include *Obertobombus* Reinig, 1930), to show equivalence among studies. * names of taxa published without descriptions.

Skorikov 1923	Williams 1991, 1998	This study
asiaticus	*asiaticus*	*asiaticus*
*avinovi**		
*immitator**		
	asiaticus	*falsificus*
miniatocaudatus	*asiaticus*	*tescorum* nom. nov. et stat. rev.
morawitzi	*morawitzi*	*morawitzi*
niveatus	*niveatus*	*niveatus*
vorticosus	*niveatus*	*niveatus*
oshanini	*asiaticus*	*longiceps* stat. rev.
semenovi	*oberti*	*semenovi* stat. rev.
	oberti	*oberti*
sibiricus	*sibiricus*	*sibiricus*
sulfureus	*sulfureus*	*sulfureus*
	obtusus	*obtusus*

coalescents; (2) being quantitative; and (3) providing the quantitative assessments of the uncertainty that are expected of scientific methods. A discussion of best practice for how these methods can be applied to bumblebees in order to address some of the inherent problems is summarised in Williams *et al*. (2020). Global revisions of other subgenera of bumblebees have also been provided by Williams *et al*. (2011, 2012, 2016, 2019, 2023), through which the application of these approaches to bumblebees has been refined.

The second problem is that the area to be sampled is huge, with the area of Asia alone, in which most of the species occur, covering ca 44.5 million km² (The Times 2001). The problem is compounded because there are large parts of Asia that are difficult to access, due both to topography and to restrictions on collecting and on specimen use, while the resources available for sampling are inevitably limited. Fortunately, a historically unparalleled geographic sampling coverage has been possible recently through partnerships with local researchers, helped by improved online communications. This has been developed as a collaborative network during previous revisionary studies. It is now timely to convert this potential into the identification tools that are in demand to support conservation surveys.

This study

We revise the species of the monophyletic subgenus *Sibiricobombus* by taking a global over view. We examine evidence from: (1) species' gene coalescents based on seeking sequences of a fast-evolving gene (appropriate for closely related taxa), mitochondrial cytochrome *c* oxidase subunit I (COI), and using the standard 'barcode' region COI-5 that can be aligned unambiguously; (2) discontinuous variation in skeletal morphology; and (3) discontinuous variation in colour patterns of the hair. For the 11 species supported, the status of three species is revised and one new name is proposed. Nine new synonyms are recognised. Estimates are provided for (1) an evolutionary tree for species and for (2) the ancestral species' distributions.

Material and methods

Sampling

The area of geographical distribution of species of the subgenus *Sibiricobombus* is known to extend across mountains throughout Central Asia, extending into Mongolia, North China, the QTP, the Himalaya, West Asia, and to as far west as Greece in Europe (Skorikov 1923; Williams 1998: map on page 134). Some of the greatest variation in bumblebees is restricted to areas in remote mountain ranges (such as within the QTP and the Tian Shan system), where access for sampling can be difficult (Williams *et al.* 2017a) and where species of *Sibiricobombus* may not always be abundant. Revisionary studies need sample sizes that are sufficiently large to detect all constituent species while keeping costs within reasonable bounds (Phillips *et al.* 2018).

For this study, several thousands of specimens of the subgenus *Sibiricobombus* were identified by PW, by including existing collections, new collections made during this study, and from as many individuals again seen in the field during work in Asia. Together these form the 'hypodigm' samples that are the basis for the 'species-taxon concepts' revised here (Simpson 1940, 1961; Mayo 2022). However, much of the material examined for this project cannot be listed or databased because permission is limited by the policies of some institutions. National policies in some countries also prevent specimens or samples from leaving the country of origin, even for identification. These constraints reduce the accountability of the species-taxon concepts.

To reduce sampling costs and to facilitate access permissions, we use a global coalition of collaborators to contribute samples from a network of sites that are spaced deliberately widely (following the practice of Williams *et al.* 2012). In particular, this coalition has given us unparalleled access to new material from the QTP and Central Asia. Other collections have been examined from Central Asia (e.g., Williams 2011; Williams *et al.* in prep.). There has also been extensive field work by many of the authors in China and India between 1980–2019. An indication of the total sample size can be seen from the many field observations plus more than 50000 bumblebees identified from surveys across all of the provinces of China in one collection (IAR) alone (Williams *et al.* 2017a).

Sampling effort for this project has been directed in a 'taxonomically stratified' pattern, based iteratively on accumulating knowledge, in order to achieve representation of as much as possible of the range of variation across even the rarest taxa known at each step (Williams 2022b). This approach could risk biasing the analysis, so a random component to sampling is important. We believe that this is contributed, in effect, by the older museum collections, collected mostly from named field sites in the Asian mountains. Decimal latitude and longitude coordinates are given for the specimens, using hand-held GPS for recent material, and focussing on the material that could be sequenced for each species.

Abbreviations for depositories

The material upon which this study is based is deposited in the collections of the following institutions, acronyms based on GRSciColl (https://scientific-collections.gbif.org/).

AB = A. Byvaltsev research collection, Novosibirsk
AM = A. Monfared research collection, Yasouj
EA = E. Akulov research collection, Krasnoyarsk
EB E. Borisova research collection, Krasnoyarsk
GG = G. Ghisbain research collection, Mons
IAR = Institute of Apicultural Research, Chinese Academy of Agricultural Sciences, Beijing
IEAUG = Institute of Entomology, Agricultural University of *Georgia*, Tbilisi
IZCAS = Institute of Zoology, Chinese Academy of Sciences, Beijing

KSEM = University of Kansas, Lawrence
LMOB = Oberösterreichisches Landesmuseum, Linz
MM = M. Mei research collection, Rome
NHMUK = Natural History Museum, London
NKME = Naturkundemuseum Erfurt, Erfurt
Naturalis = National Museum of Natural History, Leiden
NZSI = Zoological Survey of India, Kolkata
PW = P. Williams research collection, London
RJ = R. De Jonghe research collection, Westerloo
SJ = S. Jaffar research collection, Guangzhou
SMF = Naturmuseum Senckenberg, Frankfurt am Main
SNM = Natural History Museum of Denmark, Copenhagen
UMons = University of Mons, Mons
UUH = Institute of General and Experimental Biology, Ulan-Ude
VLA = Federal Scientific Center of the East Asia Terrestrial Biodiversity, Vladivostok
ZIN = Russian Academy of Sciences Zoological Institute, St Petersburg
ZMB = Museum für Naturkunde an der Humboldt-Universität, Berlin
ZMMU = Zoological Museum of Moscow State University, Moscow
ZSM = Zoologische Staatssammlung, München

Species concept and species discovery methods

We view species in theory for this revision as evolutionarily independent lineages (de Queiroz 2007; Maddison & Whitton 2023), which we seek to discover in practice by using an integrative procedure (Schlick-Steiner *et al.* 2010), specifically by comparing evidence for species' coalescents in a fast-evolving gene (COI) with evidence from skeletal morphology. The choice of methods is discussed in more detail by Williams *et al*. (2020).

Subspecies

We do not recognise taxa at the rank of subspecies because these do not have a consistent underlying concept and often confound different *kinds* of entity (Wilson & Brown 1953; Barrowclough 1982; Zink 2004; Williams *et al.* 2015b). In practice, as applied to bumblebees, subspecies are usually labels for different colour patterns, sometimes with different regional distributions, often from islands, but also from arbitrarily defined segments of clines (Williams 2007; Williams *et al.* 2015b). We prefer to label different colour patterns directly and informally (e.g., 'yellow-banded' cf. 'white-banded'), when necessary, to avoid adding unnecessary formal names that require time-consuming nomenclatural treatments. We are also especially keen to avoid slipping into imposing unknown and unjustified assumptions about unstudied differences in their history, possible futures, behaviour, or physiology: such differences will need to be explicitly demonstrated.

Candidate species from species' gene coalescents

For a fast-evolving gene that is most likely to be informative for relationships near the species level, we seek DNA sequences for the 657-nucleotide barcode segment (the standard COI-5 'barcode') of the COI gene, the functional copy of which is located in the mitochondrial genome. Many COI-barcode-like sequences can be obtained by downloading data from online databases (BOLD: www.boldsystems.org; and GenBank: www.ncbi.nlm.nih.gov/nucleotide/). We also used the standard barcode-sequencing protocols (Hebert *et al.* 2004) in the labs of: (1) the Canadian Centre for DNA Barcoding (CCDB) at Guelph (sequences now in their BOLD database); (2) IAR; and (3) NHMUK. Because orthologous COI barcodes include no indels, they can be aligned by eye using a sequence editor such as the BioEDIT software (ver. 7.0.9.0, www.mbio.ncsu.edu/BioEdit/bioedit.html). All barcode-like sequences were tested using the GenBank BLAST procedure to confirm that they are most similar to known sequences of species of the subgenus *Sibiricobombus* and not from misidentified specimens or contaminants.

Interpreting COI-like barcodes is not always as straightforward as is sometimes claimed. A fundamental assumption of the coalescent approach is that all of the sequences used for estimating evolutionary relationships should be from homologous genes (Brigandt & Griffiths 2007; Baum & Smith 2012). Some studies have applied coalescent analysis to ultra-conserved elements ('UCEs'), but this use does not fit the assumptions of coalescent analysis and so far there is no theoretical justification (Williams *et al.* 2024).

One kind of problem that can be present is the accidental sequencing of paralogous copies of COI genes (i.e., pseudogenes) called 'numts': copies of mitochondrial genes (like COI barcodes) that have been transferred to the nucleus (Lopez *et al.* 1994; Zhang & Hewitt 1996; Bensasson *et al.* 2001; Funk & Omland 2003; Leite 2012). In their new, nuclear location these sequences are no longer expressed. Freed from stabilising selection, they may then diverge more rapidly from the original mitochondrial copy, which still persists in parallel. Consequently, if divergent paralogous numts are accidentally but preferentially amplified when sequencing some of the samples, they can give very misleading results, which often appear as 'pseudospecies' on relationship trees (Song *et al.* 2008, 2014; Leite 2012).

Older 'palaeonumts' may sometimes be easily identified when sequences have in-frame stop codons or indels, for example in some Crustacea Brünnich, 1772 (Song *et al.* 2008, 2014). These numts are often filtered out as standard practice in databases like BOLD (Ratnasingham & Hebert 2007). Some older numts may lack these features, but nonetheless their greater age may be betrayed by their strongly separated positions on trees of estimated evolutionary relationships, often appearing as 'basal' groups, close-to-root on trees, because of their strong divergence (Funk & Omland 2003; Magnacca & Brown 2010).

More recent 'neonumts' are usually more difficult to identify because they do not show stop codons or indels, for example in some insects (Moulton *et al.* 2010; Song *et al.* 2014). Numts may start to diverge as soon as they are copied to the nucleus. Low-divergence neonumts might still be detectable because there is normally an extreme bias in the nucleotides at codon position three of functional COI sequences towards the nucleotides adenine ('A') or thymine ('T'). Random mutation from the extreme AT3% bias of the functional gene may reduce this bias in numts (Song *et al.* 2008), because there is no longer stabilising selection on these non-functional copies to maintain the translation, synthesis, and hence the function of the protein subunit (Carlini *et al.* 2001). Consequently a reduction in AT3% could be used to detect recent neonumts (Song *et al.* 2008; Williams *et al.* 2023), although in principle there can be no absolute threshold in reduced AT3% for detecting numts (Williams *et al.* 2024). Additional criteria that can be helpful for indicating numts include: (1) what appears to be splitting of taxa into groups widely separated on the tree when this is not supported by morphological differences (or unsupported by other characters often associated with species, although these are unavailable here); (2) close-to-root positions of some of the split taxa; and (3) unusually long branches (divergence) on the evolutionary tree to the groups consisting of likely numts (Song *et al.* 2014; Williams *et al.* 2023).

Although numts have been dismissed as unimportant for barcode-based studies (Hebert *et al.* 2004), evidence for their importance in some groups is increasing (Song *et al.* 2008; Williams *et al.* 2023). In insects, neonumts are more common than palaeonumts (Song *et al.* 2014). Their diversity might also be promoted, because unlike orthologous COI, numts are inherited from both parents, as well as undergoing duplication within the nucleus (Song *et al.* 2014).

Obtaining a representative gene tree could also be difficult if just some of the (often more common) species were relatively 'over-sampled' (Zhang *et al.* 2013; Williams *et al.* 2020). If many closely similar sequences within these species gave rise to many short (or zero-length) branches between them on the gene tree, then this could lead (through mis-calibration of the models) to any groups of sequences separated by slightly longer branches within other less well-sampled species being interpreted falsely as separate species (Zhang *et al.* 2013). This problem can be reduced by retaining only unique haplotypes, to remove zero-difference sequences (Williams 2022b). Unique haplotypes are identified here using the COLLAPSE software (ver. 1.2: https://www.softpedia.com/get/Science-CAD/Collapse.shtml), after ranking sequences from longest to shortest. This ranking avoids matching longer to shorter sequences, which could reject longer sequences that might otherwise obscure real differences.

Metric evolutionary gene trees (suitable for PTP below) for the COI-barcode region among samples are estimated here with MrBayes (ver. 3.1.2; Ronquist & Huelsenbeck 2003), which is preferred for estimating evolutionary relationships because it applies explicit evolutionary models and uses a Bayesian approach to assess uncertainty (Baum & Smith 2012). The best-fit nucleotide-substitution model available in MrBayes for this gene fragment is selected for the best fit using the Bayesian information criterion (BIC) from MEGA (ver. 6.06; Tamura *et al.* 2013), in this case as the general time-reversible model with a gamma-frequency distribution of changes among sites (GTR+Γ). For MrBayes we use four Markov-chain Monte-Carlo (MCMC) chains with the 'temperature' set to 0.2 for 10 million generations. The tree is rooted by including a sequence for the outgroup *B.* (*Cullumanobombus*) *rufocinctus* Cresson, 1863. A sample of 10 000 resulting trees is examined for convergence using Tracer (ver. 1.6.0, www.beast.bio.ed.ac.uk/Tracer; Drummond & Rambaut 2007).

To examine support for species' gene coalescents, we apply Poisson-tree-process (PTP) models to the summary metric evolutionary gene tree (Zhang *et al.* 2013), as PTP has performed well when applied to bumblebees previously when compared with general mixed Yule-coalescent models (GMYC: Williams *et al.* 2015b, 2016). PTP analysis depends on fitting models to a gene tree in order to model: (1) branch lengths on the tree within species; and (2) branch lengths on the tree between species (Zhang *et al*. 2013). For the PTP technique to perform properly, the models in each analysis need to be fitted and calibrated to data that include at least five separate, verified, most-closely-related species (Reid & Carstens 2012; Fujisawa & Barraclough 2013; Talavera *et al.* 2013; Zhang *et al.* 2013; Leliaert *et al.* 2014; Dellicour & Flot 2015). Fortunately, the subgenus *Sibiricobombus* has sufficient a priori recognised species, with at least five species in the tree by Cameron *et al*. (2007). Evidence for initial candidate species as supported by species' gene coalescents is obtained using the online bPTP server (https://species.h-its.org/; Zhang *et al.* 2013). We do not use the mPTP version (Kapli *et al.* 2017) because it appears to over-split bumblebee taxa by comparison with morphology (Williams *et al.* 2020). Sequence data are available in the online file (Supp. file 1).

Morphology

PW examined morphological characters using a light microscope (Wild model M5A). Morphological terms follow Michener (2000) and Williams *et al.* (2009), with terms for the components of the male genitalia following homologies identified by Williams (1985, 1994). Setae, pile or pubescence is referred to as 'hair' for simplicity, following Michener (2000). Metasomal terga 1–7 and sterna 1–6 are abbreviated to T1–7 and S1–6 respectively (male S7 and S8 are not examined here in detail because intraspecific variation in bumblebees can be substantial). Antennal segments 1–13 are abbreviated to A1–13.

Integrative assessment of species

We begin by comparing samples from across the entire geographical range of the subgenus *Sibiricobombus* in order to examine evidence for species' coalescents in the COI gene. Where such species' coalescents are discovered, these indicate candidate species that then become the focus for examining specimens to discover diagnostic morphological characters. The candidate species are accepted as species only if the two patterns of evidence coincide to corroborate one another. The assumption behind this order of searching is that morphology evolves more slowly and is therefore likely to be more conservative and less variable. This is not the same as employing a more conservative, purely morphological criterion alone, because any morphological variation that does not coincide with a gene coalescent is not accepted as evidence of species. Consequently, we accept neither morphological variation, nor COI coalescents, nor colour pattern alone as sufficient evidence to support separate species.

Note that this method with just two sources of evidence would be unable to discover species if they were perfectly cryptic in morphology. However, we are unaware of any such cases being known for bumblebees. Even the several closely similar European species widely described as cryptic within the subgenus *Bombus* s. str. (revised in Williams *et al.* 2012; Williams 2021) do show subtle morphological differences (Rasmont *et al.* 2021).

Where available from other studies, we include evidence as to whether there are reported differences in the composition of cephalic labial gland secretions (CLGS) of the males (Rasmont *et al.* 2005), even though there is no theoretically defined threshold criterion to establish a biologically significant level of these differences between species.

Assigning names to species

We seek to represent the major formally named taxa of the subgenus *Sibiricobombus* in our analysis with COI-like sequences in order to assign these names to the species we recognise and we then seek to identify the oldest available (valid) names for those species (ICZN 1999). Particular attention is paid to whether the status of taxon names is considered to be within the ‘species group’ in the sense of ICZN, or whether they are considered to have infrasubspecific status.

Because permission is rarely granted to extract gene sequences from older primary type specimens, we follow a pragmatic procedure (Williams *et al.* 2012) of associating the original name-bearing primary type specimens with gene sequences via the identification of more recently collected, informal proxy-type specimens for which we do have gene sequences (Table 2). Informal proxy specimens for the primary types should ideally be as nearly identical as possible with the primary type specimen and are chosen here by: (1) matching morphology and colour pattern of the hair; (2) proximity of the proxy collection locality to the original type locality; (3) having long COI sequences; and (4), for some taxa, it is desirable to match the sex and caste of the proxies with the original type specimens, because of occasional difficulties in associating sexes and castes among species from morphology alone. Our proxies are not intended to have any formal or persistent nomenclatural status beyond this study and are not recognised by the ICZN (1999). Aside from the lack of formal status and persistence, our process is otherwise similar to some of the ‘epitypification’ procedures used by botanists when primary types cannot be sequenced for genes (Hyde & Zhang 2008). Although still subjective, our process at least provides explicit accountability in applying names, because the proxies can be examined, re-interpreted, and, if necessary, the application of the names can be corrected in future studies.

It has long been common practice for taxonomists revising the taxonomy of a group to re-examine material in museum collections that had been identified by previous specialists in order to understand their earlier concepts of particular taxa (part of the ‘hypodigm’ samples, above). Our proxy procedure differs from this practice in emphasising a particular specimen in relation to the name. This process is especially important when revising the subgenus *Sibiricobombus* because separate species can be closely similar in morphology and in colour pattern. New proxy types are likely to be needed in future studies that require fresh material for more demanding genetic sampling.

Table 2. List of selected available formal names in the species group for the taxa studied of the subgenus *Sibiricobombus* Vogt, 1911 (for details of the references, see the text). These names are associated informally with barcoded specimens as proxies for types. Specimen ID refers to the specimen number (SB#*n*) of the proxy type in the *Sibiricobombus* project database.

Taxon name	Species name	Original type locality	Barcode proxy locality	Specimen / sequence ID
asiaticus	*asiaticus*	Tajikistan	Tajikistan	06/1552H01
falsificus	*falsificus*	Xizang	Qinghai	62/6880D01
flaviventris	*sibiricus*	Xizang	Qinghai	02/NHMC06
huangcens	*longiceps*	Xizang	Kashmir	51/1552D07
iranensis	*niveatus*	Alborz	Alborz	10/NHMI010
longiceps	*longiceps*	Ladakh	Ladakh	50/1552D10
morawitzi	*morawitzi*	Uzbekistan	Tajikistan	77/6880F04
niveatus	*niveatus*	Palaestina	Greece	86/6880G01
oberti	*oberti*	Kazakhstan	Tajikistan	42/NHMK01
obtusus	*obtusus*	Afghanistan	Afghanistan	68/6880D07
pamirensis	*asiaticus*	Tajikistan	Tajikistan	72/6880D11
persiensis	*niveatus*	Alborz	Alborz	09/NHMI008
semenovi	*semenovi*	Qinghai	Qinghai	03/NHMC08
sibiricus	*sibiricus*	Siberia	Neimenggu	60/6880C11
sulfureus	*sulfureus*	Asia Minor	Iran	08/NHMI027
tescorum	*tescorum*	Mongolia	Mongolia	66/6880D05
vorticosus	*niveatus*	unknown	Greece	87/6880G02

Estimating the species' evolutionary tree

We are essentially extending the most widely accepted estimate of the evolutionary tree of bumblebee species (Cameron *et al*. 2007), which was obtained from five genes for 208 of the world species as currently recognised. Their aligned, concatenated data are available for re-analysis: mitochondrial 16S rRNA ('16S'); nuclear long-wavelength rhodopsin copy 1 ('opsin'); elongation factor-1 alpha F2 copy ('Ef-1α'); arginine kinase ('ArgK'); and phosphoenolpyruvate carboxykinase ('PEPCK'). The older relationships (tree topology) in the Cameron *et al*. (2007) tree have now been largely supported and further resolved for subgenera by using much more broadly sampled genomic data for a representative of each subgenus (Sun *et al*. 2020).

Data for the five genes used by Cameron *et al*. (2007) are still unavailable for some of the species (*B. oberti* Morawitz, 1883, *B. morawitzi* Radoszkowski, 1876, *B. obtusus* Richards, 1951, *B. tescorum* Williams nom. nov. et stat. rev., *B. falsificus* Richards, 1930 stat. rev., *B. asiaticus* Morawitz, 1875). However, we can extend the Cameron *et al*. (2007) tree by using it as a 'backbone' (Trunz *et al.* 2016; Talavera *et al.* 2021), on which the remaining species accepted here can be interpolated by using data for the rapidly evolving COI-like sequences (available for all of the species) (Williams *et al.* 2022). The aligned data include 5420 nucleotide positions with a maximum of data for 4475 of these nucleotide positions. For full data see the online material (Supp. file 1).

The species' tree was estimated from the combined six-gene dataset (excluding the morphological data from Cameron *et al*. 2007) using the Bayesian procedure BEAST (ver. 2.6.6, Drummond & Bouckaert

2015). The XML settings were scripted using BEAUTi (ver. 2.6.6, Drummond & Bouckaert 2015): the best evolutionary model from the Bayesian information criterion in MEGA6 (ver. 6.06, Tamura *et al.* 2013) is the general time-reversible model with a gamma-frequency distribution of changes among sites, with the site model with four gamma categories, with invariant sites (GTR+Γ+I), a log-normal relaxed clock model, a calibrated Yule model, a prior added to identify the outgroup (*B. rufocinctus*) and monophyletic ingroup, with the MCMC set to 100 million generations sampled every 100 000 generations. Analyses were repeated in at least two separate runs to confirm that consistent results were obtained. Tracer (ver. 1.6.0, Drummond & Rambaut 2007) was used to examine the trace files. TreeAnnotator (ver. 2.6.6) was used to find a maximum-clade-credibility tree with mean node heights after burn-in. Trees were drawn with FigTree (ver. 1.4.4, http://tree.bio.ed.ac.uk/software/figtree/) and Illustrator (Adobe, ver. 26.0.1).

Age calibration of the tree is based on the dated tree of Hines (2008), which used the Cameron *et al.* (2007) data together with molecular rates and point calibration from fossils from outside of the genus *Bombus* (fossils within *Bombus* are not closely related to the subgenus *Sibiricobombus*: Dehon *et al.* 2019). The date for the crown node of the subgenus *Sibiricobombus* was obtained by re-estimating the tree from the 208 currently known and accepted species of the genus *Bombus* that are represented in the data from Cameron *et al*. (2007) supplemented with additional COI barcodes (Williams *et al.* 2022). We follow the procedure of Hines (2008) in fixing the date of the crown divergence within the genus *Bombus* at 34 Ma. From this we estimate a crown date here for *Sibiricobombus* with a mean age of 10.2 Ma (95% highest posterior density interval ±2 Ma, approximated with a sigma of 1.0 Ma). This two-step process makes the extraction of separate estimates of 10 000 sample trees tractable for the subsequent biogeographic analysis.

Estimating species' ancestral distributions

To seek the most likely explanation for current bumblebee distributions if only short-distance dispersal with establishment were possible (Williams *et al.* 2017b, 2022), a model of potential corridors for dispersal (assuming suitable climates and habitats in all appropriate periods) is defined specifically for the subgenus *Sibiricobombus* in its specific montane habitats. This model summarises a set of short-distance-dispersal events (excluding long-distance dispersal 'jumps') permitted between neighbouring areas of endemism, assuming that suitable habitat and climate are present. Ideally, the modelled climate preferences of the ancestral lineages should be combined with the modelled habitat suitability of past potential dispersal corridors with changing climates, considering also the abilities of populations to disperse over appropriate distances and found new populations, so that the overall likelihood of dispersal and establishment can be assessed, as described for ancestral species of *Mendacibombus* in Central Asia (Williams *et al.* 2017b).

Area units for biogeographic analysis are chosen by agglomerating species' distribution data into a few areas with shared, often nested, faunas with unique endemic species or combinations of species. Such areas often appear as areas of high species' richness and as areas with high endemism. The number of areas recognised within a species' range is kept low because the biogeographic analysis does not have mechanisms by which two daughter species can both inherit ranges consisting of many areas (Lamm & Redelings 2009; Ree & Sanmartín 2009). Ancestral ranges are constrained to be a maximum of three contiguous areas so as: (1) to exclude long-distance-dispersal jumps between non-contiguous areas; (2) to not exceed the size (as number of area units) coded for current ranges of species; (3) to offset the tendency of analyses towards combining all areas from daughter species into widespread ancestral ranges; and (4) to prevent reconstructed ranges from being highly disjunct (Ronquist 1996; Ree & Smith 2008; Lamm & Redelings 2009; Ree & Sanmartín 2009).

To assess explanations of current distributions from phylogeny, dispersal, and extinction, we use the statistical version (from samples of trees) of the BioGeoBEARS methods (Matzke 2013a, 2013b, 2014) from a library in R (R Core Team 2017) within the RASP package (ver. 4.4 win64, accessed 2024: Yu *et al.* 2020). S-BioGeoBEARS uses a sample of 10 000 ultrametric trees in the results from BEAST. The DIVALIKE+J option was selected a priori because it assumes that distribution changes occur at nodes (associated with speciation: Yu *et al*. 2020), as S-DIVA has been found to perform better with bumblebee data (Williams *et al.* 2017b) than S-DEC (Yu *et al.* 2014), which assumes that changes occur along branches (S-DIVA has also been applied to the present data although the results did not change the inferences).

Results

Candidate species from species' gene coalescents

An initial evolutionary tree was estimated for *Sibiricobombus* with MrBayes from a sample of 64 barcode-like sequences representing the range of principal nominal taxa. The number of species' coalescents in this initial tree was estimated by PTP to represent 18 candidate species. Several of these candidates are not supported by diagnostic morphological character states and are likely to be pseudospecies.

Standard filters were applied to these raw sequences to reduce the number of pseudospecies by retaining only the unique haplotypes and longer (> 90% of the barcode region) sequences, with an exception made for the single available sequence for the taxon *obtusus*. This left a sample of 26 *Sibiricobombus* barcode-like sequences. The number of species' coalescents in this initial tree was then estimated by PTP to represent 12 candidate species (Fig. 1; for morphological support, see the following section). In only one case (the taxon *morawitzi*) does a nominal taxon appear within more than one candidate species (groups linked in the figure by blue lines) as two possible candidate species. In addition, the PTP scores for the samples of *B. longiceps* stat. rev. appear to show borderline uncertainty as to whether they represent one or two species.

The distribution of AT3% scores for the subgenus *Sibiricobombus* in Fig. 1 is low compared with those from studies of the subgenera *Subterraneobombus* and *Alpinobombus*, and similar to *Alpigenobombus* (Figs 2–5). The distribution of AT3% scores for many *Subterraneobombus* and *Alpinobombus* sequences matches the expectation of high AT3 bias for orthologous COI barcodes, whereas the lower AT3% scores for many *Alpigenobombus* and *Sibiricobombus* sequences raises the possibility that many of their sequences might be low-divergence neonumts (Song *et al.* 2008; Williams *et al.* 2023).

In Fig. 6, comparison of the Lep primer sequences (from Hebert *et al.* 2004) that are often used to extract bumblebee barcodes with the corresponding Lep-primer-binding regions of the mitogenomes (data from Illumina sequencing by Sun *et al.* 2020) shows that for bumblebees the species from the subgenera with more of the likely numts in Figs 2–5 (*Alpigenobombus* and *Sibiricobombus*) have primer-binding regions with: (1) more total substitutions (highlighted in colours, yellow+red); (2) with particular unique substitutions (in bold); and (3) with more substitutions of G or C for A or T, or vice versa, resulting in purine-pyrimidine mismatches (highlighted in red) that would further reduce binding strength (GC also binds more strongly than AT: Borah 2011).

The substitutions in the Lep-primer-binding regions have occurred over the long period since the divergence of bumblebees from the lepidopteran source of the Lep primers. Because of the relatively much shorter period since the divergence of low-divergence neonumts from their orthologous sequences, it is unlikely that there will have been many additional substitutions in the short Lep-primer-binding regions, either for the orthologous sequences or for the numts sequences. Substitution rates are expected

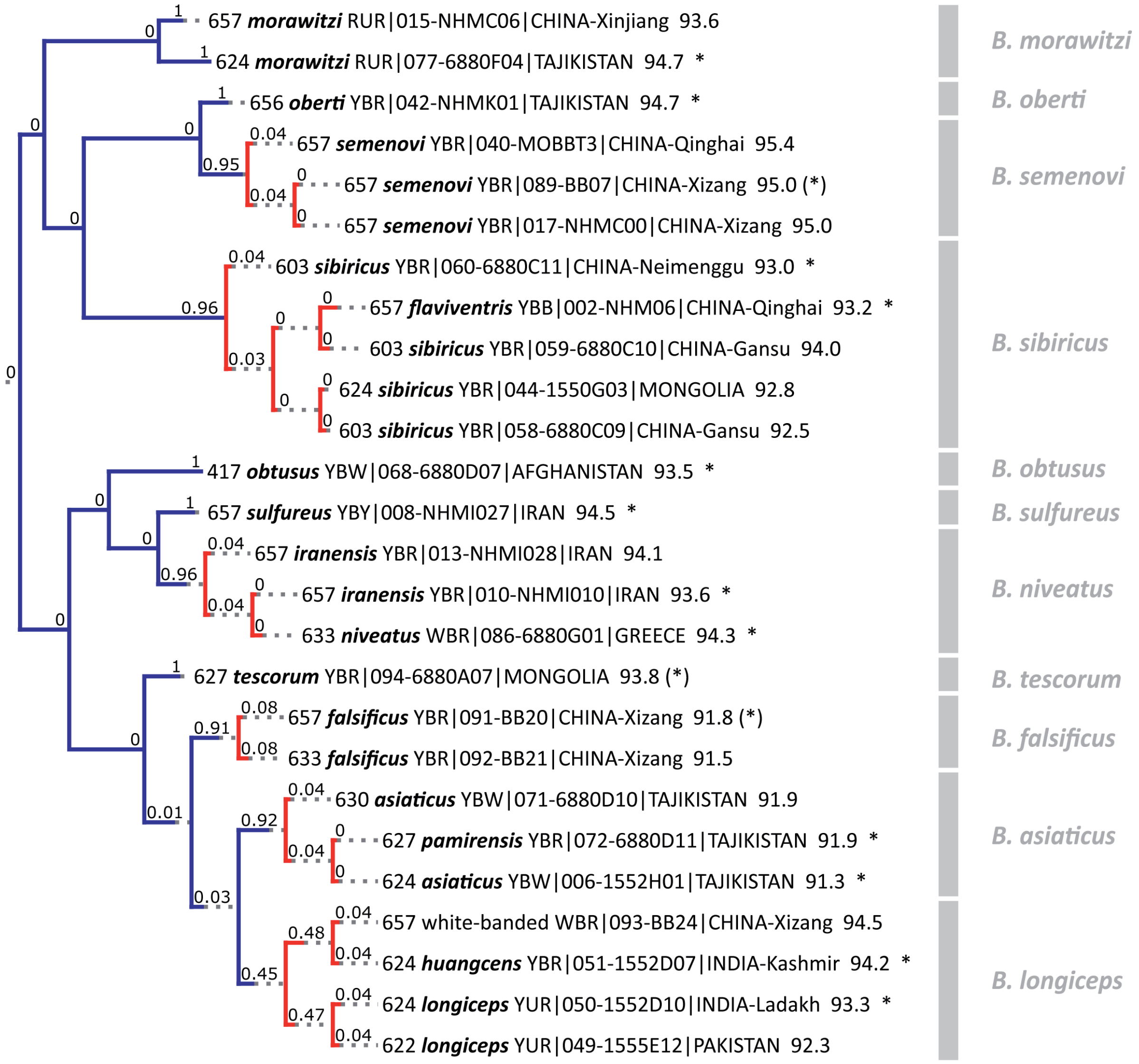
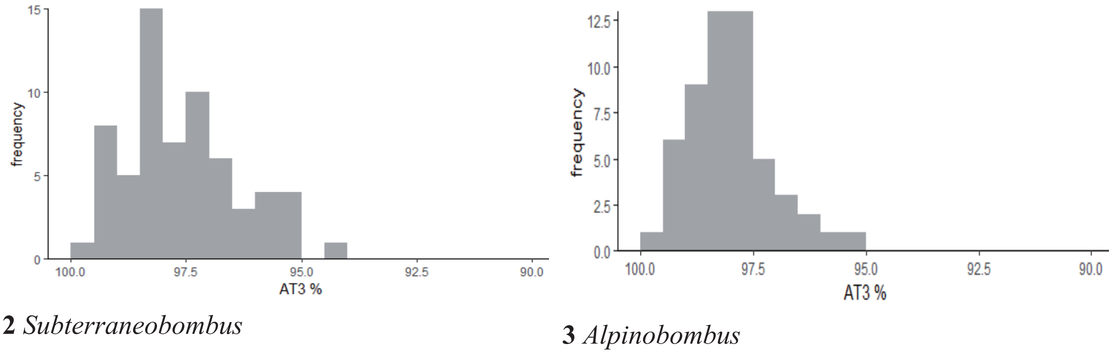


Fig. 1. Support for apparent species' gene coalescents within the subgenus *Sibiricobombus* Vogt, 1911 from unique longer haplotypes for COI barcode-like sequences (with the exception of the single short sequence of the taxon *obtusus* Richards, 1951) including likely numts (nuclear copies of mitochondrial sequences), obtained from an evolutionary tree estimated with MrBayes and using maximum likelihood to fit Poisson-Tree-Process (PTP) models. Numbers at each node show the probability that all daughter sequences to the right are parts of a single unique species. Branches change from blue to red at the node with the best fit (maximum local probability) for the change from inter-species to intra-species branching PTP models (species' coalescent nodes) (grey dots artificially extend branches to make the tree easier to read). Each sequence is labelled with: sequence length; a morphological taxon name; a code for the colour pattern consisting of three characters: Y[ellow]/W[hite]/R[ed]band anteriorly + B[anded]/U[nbanded]between the wing bases + W[hite]/R[ed]/B[lack]-tailed metasoma; a code consisting of a sequence identifier from the project database and a specimen identifier from the online database; its country and (for larger countries) state or province of origin. The sequence AT3% score is shown to the right of each sequence label. Sequences marked with '*' are proxy types for names (Table 2) and sequences marked with '(*)' match haplotypes for proxy types when the proxy types are not included in this tree. To the right in grey is the interpretation as the 11 species of the subgenus from the integrative analysis (see the text).

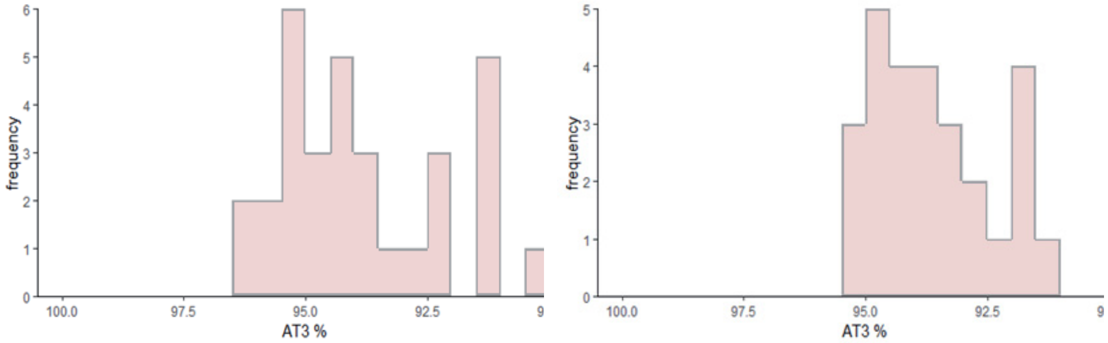
to be higher in orthologous DNA than in the nuclear numts DNA (Song *et al.* 2014), so this might contribute to primers binding to the conserved numts preferentially. Indeed, primer-binding sites for numts can sometimes be very highly conserved (Song *et al.* 2014).

The data for Lep-primer-binding regions in Fig. 6 are very few and this comparison is in any case not proof of the suggested mechanism. But the comparison is consistent with the idea that more (or



2 *Subterraneobombus*

3 *Alpinobombus*



4 *Alpigenobombus*

5 *Sibiricobombus*

6

LepF1 + LepR1 primers		ATTCAACCAATCATAAAGATATTGG + TGATTTTTTGGACATCCAGAAGTTTA	Δ	ΔGC
Subterraneobombus	*difficillimus*	TATCTACTAATCATAAAAATATTGG + TGATTTTTTGGACATCCTGAAGTTTA	6	2
Alpinobombus	*polaris*	TATCAACAAATCATAAAAATATTGG + TGATTTTTTGGACATCCTGAAGTTTA	5	2
Alpigenobombus	*breviceps*	TATCCACTAACCA**C**AAAAATATTGG + TGATTTTTTGG**T**CATCCAGAAGTTTA	8	5
Sibiricobombus	*sibiricus*	TATCAACTAATCA**C**AAAAATATTGG + TGATTTTTTGG**T**CATCCAGAAGTTTA	6	3

Figs 2–6. Distribution of AT3% scores from COI barcode-like sequences used for analyses of species in a selection of previous studies of bumblebee subgenera (lower AT3% is associated with numts). **2**. *Subterraneobombus* Vogt, 1911 from Williams *et al*. (2011). **3**. *Alpinobombus* Skorikov, 1914 from Williams *et al*. (2019). **4**. *Alpigenobombus* Skorikov, 1914 from Williams *et al*. (2023). **5**. *Sibiricobombus* Vogt, 1911 from Fig. 1. **6**. The top row shows the 51 nucleotides in the primer LepF1 and the reverse complement of the primer LepR1 (primers from Hebert *et al.* 2004), the rows below showing the equivalent mitogenome Lep-primer-binding regions for an example species of each of the four subgenera by Illumina sequencing from Sun *et al.* (2020): the coloured markers (red+yellow) together highlight total nucleotide substitutions relative to the Lep primers, the red markers highlighting the numbers of substitutions of G/C for A/T or vice versa relative to the Lep primers, with the columns on the right showing (Δ) the total numbers of substitutions and (ΔGC) the numbers of substitutions of G/C for A/T or vice versa relative to the Lep primers (substitutions unique to *A. breviceps* + *S. sibiricus* are shown in bold).

particular) substitutions in the Lep-primer-binding region might reduce the binding strength of the Lep primer to the Lep-primer-binding region for the orthologous barcodes and that this might therefore reduce orthologous binding specificity and in contrast promote binding to the conserved numts. More Lep-primer-binding-region substitutions do appear to be associated with groups of bumblebee species that show more frequent sequencing of numts.

Integrative analysis

In an integrative analysis, examples of the specimens from the two '*morawitzi*'-taxon candidate species in Fig. 1 show no detected morphological difference. These sequences come from distant sites within the nominal taxon's range, from Xinjiang in the north and from Tajikistan in the south. Until further information is available, the two *morawitzi* sequences are interpreted as divergent individuals from two ends within one broad population, which could be consistent with them being conspecific.

Similarly, the samples of the taxon *longiceps* that have borderline PTP support for one or two groups (Fig. 1) have no known morphological differences between them (Williams 1991). The two colour-pattern groups on either side of the Great Himalaya range (unbanded-yellow in Ladakh/Zanskar and banded-white in the Kashmir valley) also show extensive recombination of their colour-pattern characters in samples from a couple of high valleys where the populations are in contact (Williams 1991: table 9), which is consistent with them being parts of a single species.

All other candidate species in Fig. 1 are morphologically diagnosable (see the key). Consequently, even if the COI barcode-like sequences in Fig. 1 were all numts, then for the purpose of estimating the evolutionary tree, these sequences appear to be sufficiently low-divergence that they behave like orthologous sequences. Therefore, with the exception of the uncorroborated split within *B. morawitzi*, the 11 candidate species in Fig. 1 are accepted as true species.

Estimating the species' evolutionary tree

The six-gene tree (Fig. 7) places several species in different positions from those in the COI-barcode-like tree (Fig. 1). Most interesting is that the group of species with large-eyed males (*morawitzi*–*asiaticus*) appears to be monophyletic in the six-gene tree (providing morphological corroboration). Least well supported on this tree is the position of *B. morawitzi*, so obtaining nuclear gene sequences for this rare species to improve the support in Fig. 7 would be highly desirable. Four attempts to sequence PEPCK from recent samples of this species provided sequences that could not be aligned.

Estimating species' ancestral distributions

The explicit model for dispersal among areas of species' endemism is shown in Fig. 10. There is no order implicit in the area names: the polarity of dispersals is estimated from the phylogenetic tree that is rooted by the outgroup. The distribution of the outgroup, *B. rufocinctus*, is given as AB (reducing this to A has no substantial effect on the results) because, although the species is North American, the distribution of the common ancestor is likely to be in Central Asia (Williams *et al.* 2022: fig. 14). The permissible short-distance dispersal corridors in this model are: AB AD AE BC CD DE EF. Because of the geological and climatic uncertainties, the model is fully open, allowing free dispersal both in either direction and in all time periods.

The most likely solution for ancestral distributions of lineages for the subgenus *Sibiricobombus* from the DIVALIKE+J analysis is shown in Fig. 11. All of these events can be resolved, requiring only the short-distance dispersal if suitable habitat were available at the appropriate times in all of the corridors (Williams *et al.* 2016), as proposed in Fig. 10 (which allows a range size of just two areas for each ancestor, matching the current species' range sizes). However, the large sectors of black in the pie

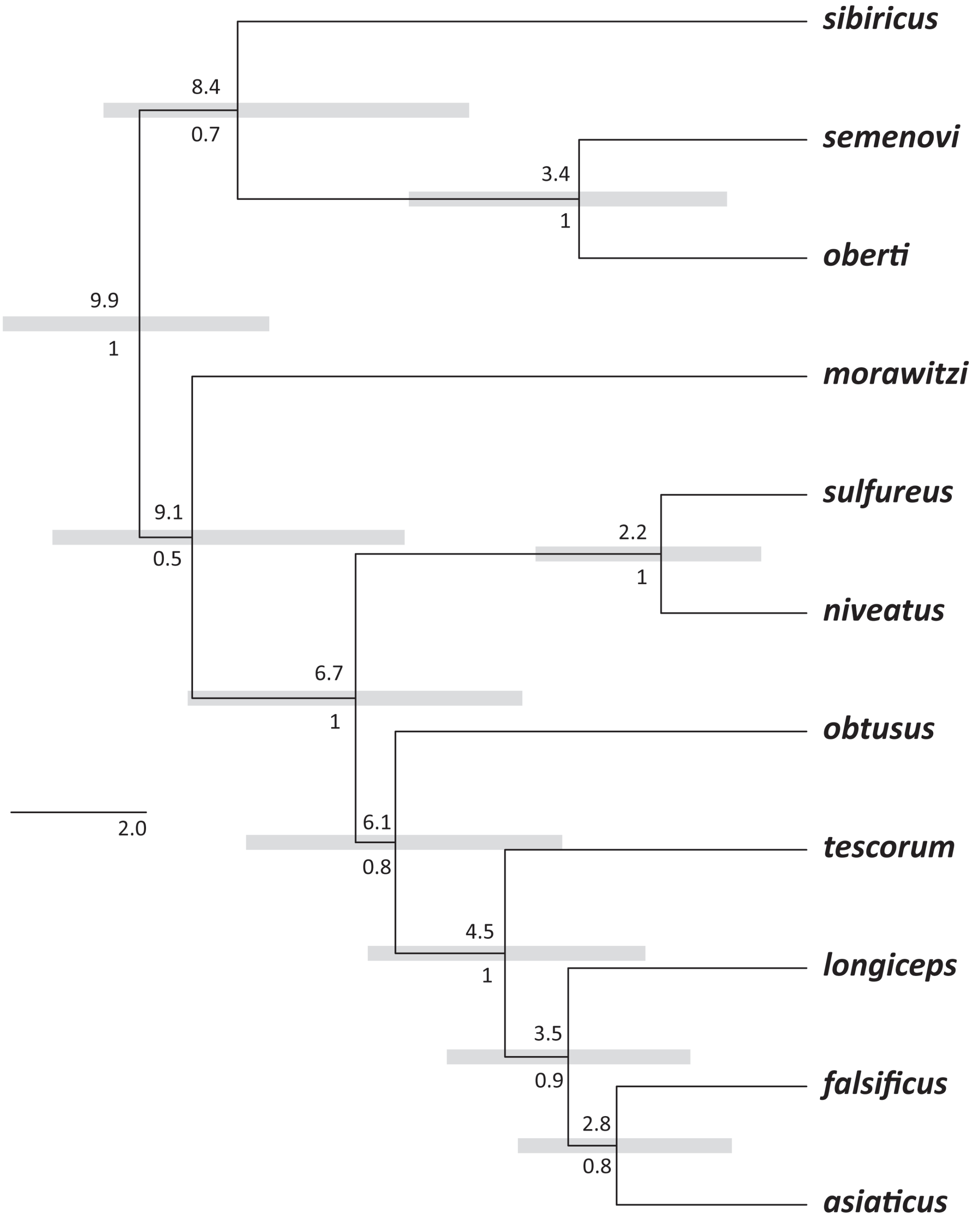
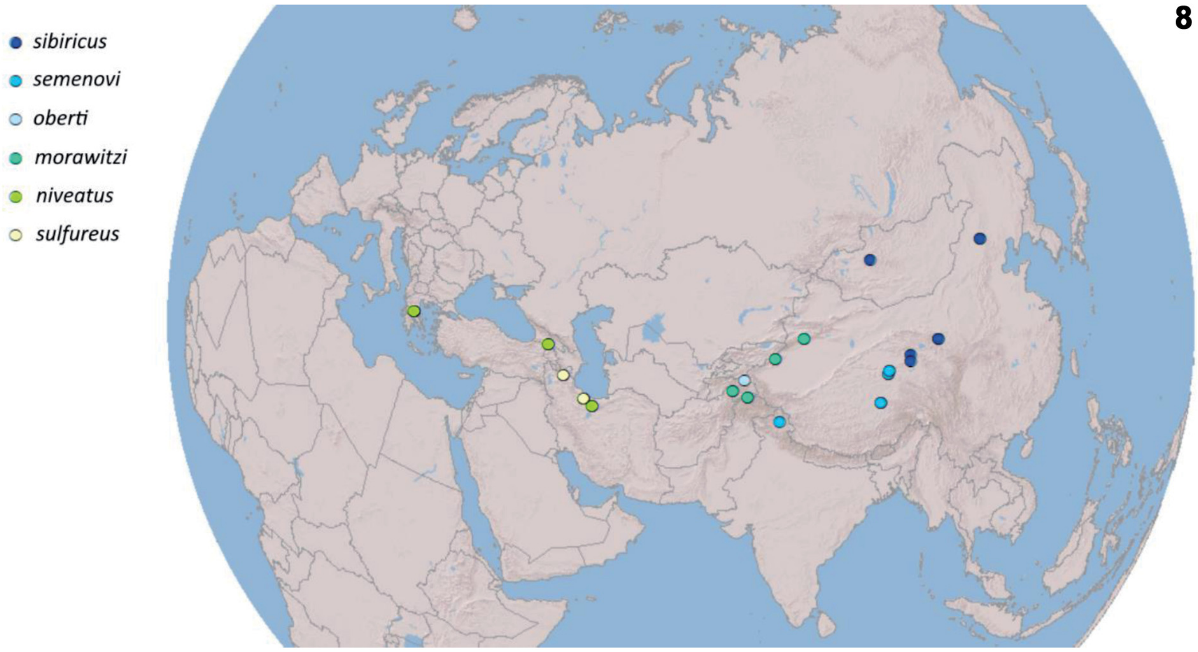


Fig. 7. BEAST estimate of dated relationships as an ultrametric tree (outgroup *B. rufocinctus* Cresson, 1863 not shown) from six genes (COI, 16S, opsin, Ef-1α, ArgK, PEPCK) for species of the subgenus *Sibiricobombus* Vogt, 1911, estimated with a GTR+Γ+I model over 100 million MCMC generations and a 5% burn-in. Numbers below nodes are support values. Numbers above nodes are estimates of the age of a node in Ma before the present, with grey node bars representing the 95% highest posterior density interval of the age estimates. Note added in proof: the estimate has been re-run to include a PEPCK sequence for *B. morawitzi*, which increases the Bayesian posterior support for the group of *morawitzi* + *niveatus*-group + *asiaticus*-group from 0.5 to 0.75.

diagrams (indicating multiple low-probability alternative solutions for ancestral areas) show substantial uncertainties in the results.

The most recent common ancestor of the subgenus *Sibiricobombus* is most likely to have been distributed in mountains broadly in the region of the current Hindu Kush. Several of the early descendent-lineage

8



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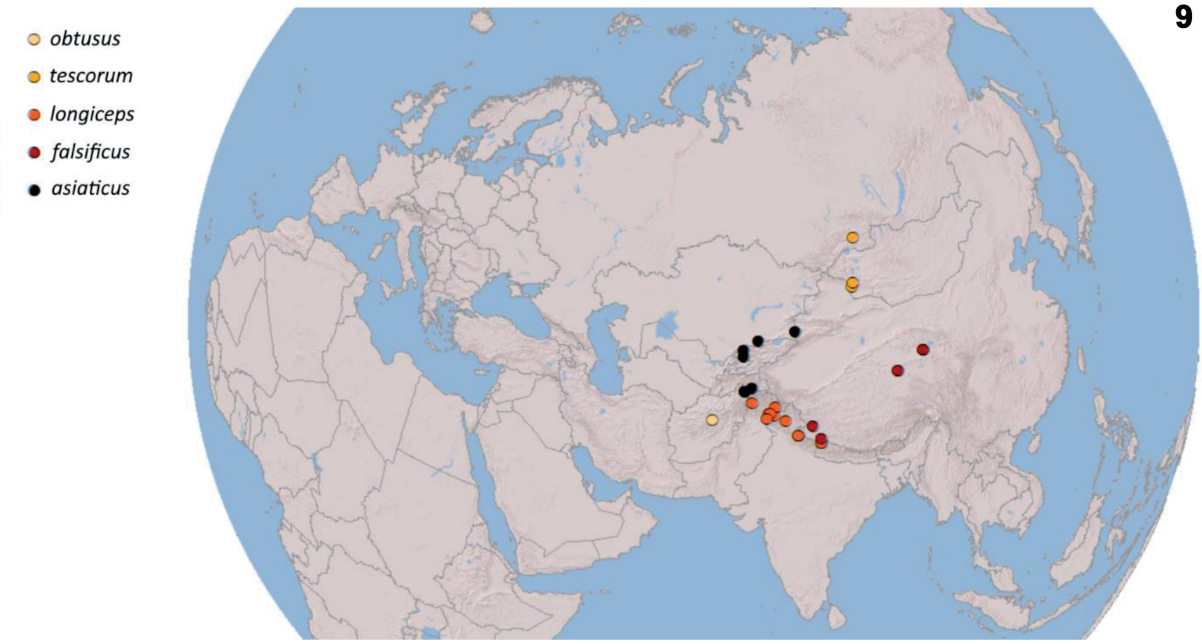


Figs 8–9. Geographical distribution of the sites from which *Sibiricobombus* Vogt, 1911 samples have been barcoded, mapped to indicate the approximate location and a part of the extent of occurrence (EOO) for each corresponding species as accepted in Fig. 7. Spherical projection with international boundaries as recognized by the UN shown as grey lines. Map projected in ArcGIS using the World_Shaded_Relief basemap © 2014 ESRI.

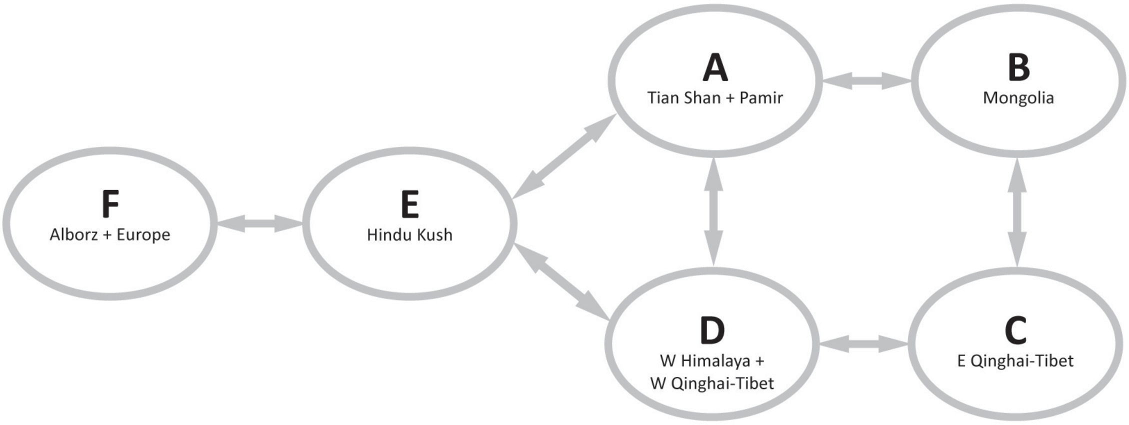


Fig. 10. Diagram representing a corridor-dispersal model, encompassing a set of short-distance dispersal events permitted (in either direction) between the proposed areas of endemism, based on unique taxa, the geographical proximity of these areas, and the likely disposition of corridors with suitable habitat and favourable climates in the past.

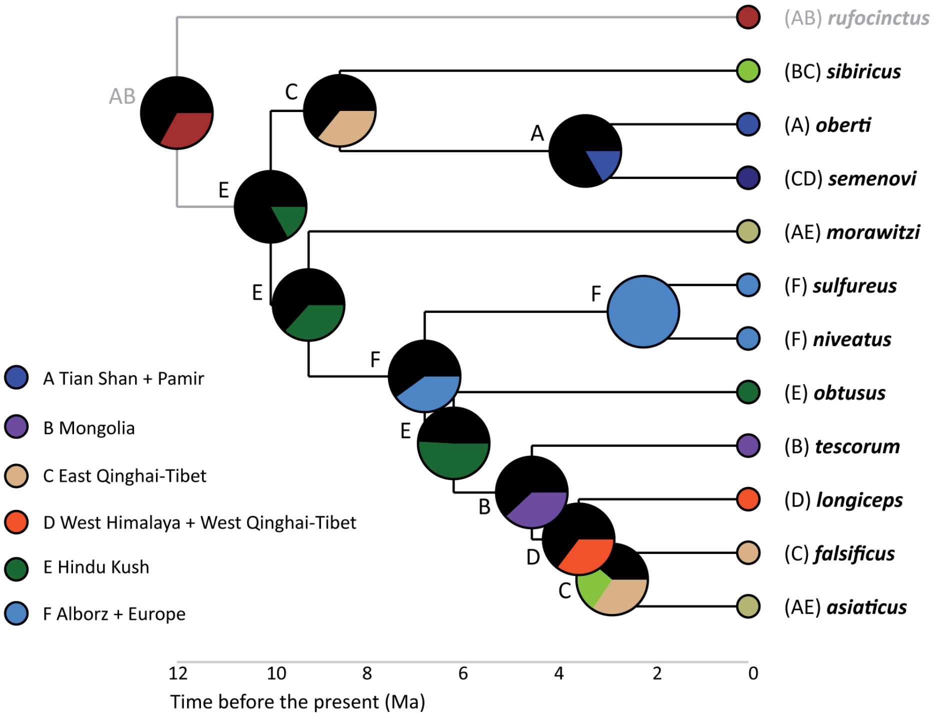


Fig. 11. Most likely ancestral ranges reconstructed for all extant currently recognised species of the subgenus *Sibiricobombus* Vogt, 1911 from the dispersal model in Fig. 10, using the model DIVALIKE+J in S-BioGeoBEARS from a sample of 10 000 trees from BEAST used to make the estimates of species phylogenies from the six genes in Fig. 7. Letters represent the area units in Fig. 10: letter combinations at terminals show species' current distributions (key lower left shows the colour codes used for the principal areas of endemism, other colours not in the key represent combinations of areas e.g., olive for area combination AE); letter combinations at nodes show the most likely reconstructions for ancestral distributions, with pies indicating the percentage of solutions for that node in which solutions occur (with black for a mixture of subsidiary solutions each with $p < 0.25$). Numbers on the *x*-axis are ages in Ma before present. The outgroup is shown in grey.

distributions are estimated to include the Hindu Kush area and this is also close to where several of the extant species persist (Figs 8–9, 11). The ancestor of the *sibiricus*-group appears to have dispersed eastwards through the Qinghai-Tibetan Plateau, but with *B. oberti* reaching the Tian Shan and *B. sibiricus* reaching Mongolia. The ancestor of the *niveatus*-group dispersed westwards through the Alborz mountains and into eastern Europe. The ancestor of the *asiaticus*-group dispersed and speciated into the mountains that surround the QTP, with different daughter lineages reaching each of Mongolia, the Himalaya, and the Tian Shan.

Synopsis of world species

Class Insecta Linnaeus, 1758
Order Hymenoptera Linnaeus, 1758
Family Apidae Linnaeus, 1758
Genus *Bombus* Latreille, 1802

Subgenus ***Sibiricobombus*** Vogt, 1911

Sibiricobombus Vogt, 1911: 60.
Obertobombus Reinig, 1930: 110.

We associate a total of 82 published formal names with species of the subgenus *Sibiricobombus* (including misspellings and infrasubspecific names). Below is a list of the 11 species recognised from the integrative analysis together with the synonyms that occur most frequently in the literature (identified from morphology) with the changes since the last checklist labelled (Williams 1998).

The subgenus *Obertobombus* (Reinig 1930) is included within the subgenus *Sibiricobombus* (Richards 1968), based on evidence from morphology (Richards 1968; Williams 1991) and from genes (Cameron *et al.* 2007; Williams *et al.* 2008, 2022). The species of *Obertobombus* are recognised here as part of the *sibiricus*-group of species.

***sibiricus*-group**

Bombus sibiricus (Fabricius, 1781)
  = *melinoides* Fischer de Waldheim, 1843
  = *flaviventris* Friese, 1905
  = *ochrobasis* Richards, 1930
  = *nikiforuki* Tkalců, 1961
Bombus semenovi Morawitz, 1887 stat. rev.
  = *xionglaris* Wang, 1982 syn. nov.
  = *duanjioaoris* Wang, 1982 syn. nov.
  = *zhadaensis* Wang, 1982 syn. nov.
Bombus oberti Morawitz, 1883
  = *apicatus* Friese, 1911 syn. nov.
  = *griseofasciatus* Reinig, 1930: 108, not of Reinig, 1930: 83

***morawitzi*-group**

Bombus morawitzi Radoszkowski, 1876
  = *oppositus* Smith, 1878
  = *hydrophthalmus* Morawitz, 1883

***niveatus*-group**

Bombus sulfureus Friese, 1905
  = *aureocorbicularis* Pittioni, 1937
Bombus niveatus Kriechbaumer, 1870
  = *vorticosus* Gerstaecker, 1872
  = *parnassius* von Dalla Torre, 1882
  = *araraticus* Radoszkowski, 1890
  = *pallidofasciatus* Vogt, 1909
  = *postzonatus* Vogt, 1911: 61, not of Vogt, 1911: 57
  = *skorikowi* Friese, 1911
  = *iranensis* Pittioni, 1937
  = *persicus* Pittioni, 1937, not of Radoszkwski, 1881
  = *persiensis* (Rasmont, 1983)

***asiaticus*-group**

Bombus obtusus Richards, 1951
  = *badakshanensis* (Tkalců, 1968)
Bombus tescorum Williams nom. nov. et stat. rev.
  = *miniatocaudatus* Vogt, 1911, not of Vogt, 1909
Bombus longiceps Smith, 1878 stat. rev.
  = *flavodorsalis* (Skorikov, 1933), not of Franklin, 1913, syn. nov.
  = *oshanini* (Skorikov, 1933) syn. nov.
  = *huangcens* Wang, 1982 syn. nov.
Bombus falsificus Richards, 1930 stat. rev.
  = *heicens* Wang, 1982 syn. nov.
Bombus asiaticus Morawitz, 1875
  = *bizonatus* Smith, 1878, syn. nov.
  = *regeli* Morawitz, 1880
  = *pamirensis* Friese, 1913
  = *diversocaudatus* Reinig, 1932
  = *flavicollis* Wang, 1985
  = *baichengensis* Wang, 1985

Key to species for females of the subgenus Sibiricobombus

Future identification of species of the subgenus *Sibiricobombus* will be most reliable for specimens from which COI-barcode-like data are available for comparison of nucleotide differences with the reference data in our Supp. file 1. Keys using morphological skeletal shape, surface sculpturing, and hair-colour-pattern characters follow below. The couplets of the keys are differential diagnoses, in that (because of variation) for each couplet, it is the best fit for the majority of characters (and especially for those near the beginning of the couplet) that points to a decision for progressing to the next numbered couplet or to a species' identification. Our results imply that in some cases (in at least one sex) we should be able to assign most reliably the specimens with locality labels to the next couplets or to species on the basis of their collection locality alone. All identifications of species from the key or from the figures should be checked against the species' diagnoses within the accounts of each species.

Diagrams showing the major aspects of variation in the colour-patterns of the dorsal hair are presented in Figs 12–89. These diagrams summarise only the major differences (Williams 2007) rather than finer details (e.g., Williams 1991: figs 371–391). This is a simplification to aid quantitative comparisons and inevitably requires compromises. Colour-pattern variation within species is established with reference to particular individuals identified whenever possible from COI barcodes for each diagram. Morphology of the male genitalia is illustrated in Figs 90–100.

1. Thoracic dorsum with the hair anterior to the wing bases and T1–2 orange-red .... ***B. morawitzi*** Radoszkowski, 1876
– Thoracic dorsum with the hair anterior to the wing bases and T1–2 *either* yellow *or* white *or* black 2

2. From the region including Iran and Europe to its west 3
– From the region including Afghanistan and Asia to its east 4

3. Metasomal T4–5 with the hair orange-red; clypeus in its centre with few widely spaced large punctures but with many more small punctures, often spaced by only their own diameters, so that much of the surface between the large punctures is uneven and locally convex (not flat, smooth and shining); hindleg basitarsus outer surface with the short branched hairs long so that they are just overlapping and the shining surface is partly obscured .... ***B. niveatus*** Kriechbaumer, 1870
– Metasomal T4–5 with the hair yellow; clypeus in its centre with few widely spaced large punctures and few small punctures, so that much of the surface between the large punctures is flat, smooth and shining; hindleg basitarsus outer surface with the short branched hairs so short that they are not overlapping and the surface is conspicuously brightly shining .... ***B. sulfureus*** Friese, 1905

4. Metasomal T3 with the hair entirely yellow .... ***B. sibiricus*** (Fabricius, 1781)
– Metasomal T3 with the hair *either* black *or* orange *or* white, at most with a narrow posterior yellow fringe 5

5. Antennal A3 length $\leq 2 \times$ greatest breadth; hind basitarsus outer surface with the short hairs dense and strongly overlapping so that reflections from the outer surface are partly obscured and only weakly visible; (in large individuals) T6 subapically medially with a longitudinal groove 6
– Antennal A3 length $\geq 2.5 \times$ greatest breadth; hind basitarsus outer surface with the short hairs not especially dense and weakly overlapping so that reflections from the outer surface are clearly visible; (in large individuals) T6 subapically medially with a raised boss 7

6. Labral furrow broad, 0.35 × the entire breadth of the labrum; hair of T3 often extensively orange, T4–5 dull orange (Qinghai-Tibetan Plateau) ....***B. semenovi*** Morawitz, 1887 stat. rev.
– Labral furrow narrow, 0.25 × the entire breadth of the labrum; hair of T3 black at most with a narrow posterior pale fringe, T4–5 *either* dull orange *or* dark brown *or* black (Tian Shan, Pamir) .... ***B. oberti*** Morawitz, 1883

7. Hindleg basitarsus outer surface with few widely separated non-overlapping short weakly branched pale hairs so that the surface is conspicuously brightly shining; hair of T4 black at most with a few white hairs along the posterior margin (Afghanistan) ....***B. obtusus*** Richards, 1951
– Hindleg basitarsus outer surface with many overlapping short weakly branched pale hairs so that the surface is partly obscured and weakly shining; hair of T4 *either* black *or* orange *or* white 8

8. Clypeus with the anterior lateral corners with a small patch of large punctures spaced by their own breadths with only a very few widely spaced small punctures between them; T2 with the hair dorsally almost entirely yellow without black hairs even in the posterior lateral quarter (Xizang, Qinghai, Gansu) .... ***B. falsificus*** Richards, 1930 stat. rev.

– Clypeus with the anterior lateral corners with a large patch of large punctures spaced by their own breadths with a dense patch of many small and medium punctures between them; T2 with the hair dorsally with some black hairs along the posterior margin or in the posterior lateral quarter 9

9. Ocello-ocular area with a broad band of dense fine punctures along the inner eye margin, this band along its inner edge without medium and large punctures; hair beneath the base of the hind wing *either* usually yellow *or* white *or* rarely black, thoracic dorsum *either* bright yellow *or* bright yellow with a black band between the wing bases *or* white with a black band between the wing bases, T4–5 *either* predominantly white *or* orange-red *or* black but usually not noticeably paler at the tips (China, Central Asia, India) 10

– Ocello-ocular area with a broad band of dense fine punctures along the inner eye margin, this band along its inner edge with a few medium and large punctures; hair beneath the base of the hind wing usually black, thoracic dorsum *either* dull yellow with a black band between the wing bases *or* almost entirely black, T4–5 pale pinkish-orange, the hairs often conspicuously paler at the tips (Mongolia, Russia) .... ***B. tescorum*** Williams nom. nov. et stat. rev.

10. Hind tibia outer corbicular surface in its upper proximal half weakly sculptured and smooth, so that the shining reflections are scarcely interrupted by the sculpturing; T2 with the hair *either* usually nearly entirely yellow without black hairs intermixed along the midline *or* only rarely extensively black, T4 usually in the anterior half black, T5 *either* usually nearly white *or* rarely pale pinkish-orange (Tian Shan, Pamir, Afghanistan) .... ***B. asiaticus*** Morawitz, 1875

– Hind tibia outer corbicular surface in its upper proximal half coarsely sculptured and rough or matt, so that reflections are much interrupted by the prominent sculpturing; T2 with the hair *either* part yellow *or* part white, with black at least intermixed along the midline, *or* black throughout, T4–5 *either* usually predominantly orange *or* rarely white *or* black (western Himalaya, Ladakh) .... ***B. longiceps*** Smith, 1878 stat. rev.

Key to species for males of the subgenus Sibiricobombus

1. Eye not or scarcely enlarged relative to the eye of a female bumblebee, from the dorsal aspect the eye separated from the lateral ocellus by more than 2 × the ocellar breadth 2

– Eye greatly enlarged relative to the eye of a female bumblebee, from the dorsal aspect the eye separated from the lateral ocellus by 1 × the ocellar breadth 4

2. Metasomal T3 with the hair entirely yellow; penis-valve head recurved section very broad, only narrowing at the tip .... ***B. sibiricus*** (Fabricius, 1781)

– Metasomal T3 with the hair *either* black *or* orange; penis-valve head recurved section narrow, broadening towards just before the tip 3

3. Volsella with the inner distal corner as a broad but pointed hook projecting posteriorly almost as far as the outer distal corner (Qinghai-Tibetan Plateau) .... ***B. semenovi*** Morawitz, 1887 stat. rev.

– Volsella with the inner distal corner broadly and evenly rounded and much shorter than the outer distal corner (Tian Shan, Pamir) .... ***B. oberti*** Morawitz, 1883

4. Clypeus with the hair black, thoracic dorsum anterior to the wing bases and T1–2 orange-red; penis-valve head recurved section narrow finger-like and curved, concave posteriorly at the base .... ***B. morawitzi*** Radoszkowski, 1876

– Clypeus with the hair *either* yellow *or* white *or* at least with some grey hair anteriorly, thoracic dorsum anterior to the wing bases and T1–2 yellow; penis-valve head recurved section broad triangular and straight, convex posteriorly at the base 5

5. Volsella posterior to the gonostylus greatly broadened and weakly curved, penis-valve head on its inner side ventrally at the base marked by a projecting angle, this angle also marked dorsally (Iran and Europe to its west) 6
– Volsella posterior to the gonostylus narrowed and angled inwards towards the body midline, penis-valve head on its inner side ventrally at the base without a projecting angle, this angle only marked dorsally (Afghanistan and Asia to its east) 7

6. Metasomal T5–7 with the hair orange-red; penis-valve head recurved section narrowing abruptly just before the tip, volsella just beyond gonostylus 2 × its distal posterior breadth .... ***B. niveatus*** Kriechbaumer, 1870
– Metasomal T5–7 with the hair yellow; penis-valve head recurved section narrowing gradually towards the tip, volsella just beyond gonostylus 3 × its breadth between the distal posterior corners .... ***B. sulfureus*** Friese, 1905

7. Volsella beyond the gonostylus narrowing to less than its breadth between the distal posterior corners, gonostylus distal lobe approximately square, gonocoxa from the dorsal aspect distally as broad as adjacent spatha, S6 with the posterior margin in the middle with a deep concave indentation 8
– Volsella beyond the gonostylus nearly parallel-sided and consistently broader than its breadth between the distal posterior corners, gonostylus distal lobe approximately circular, gonocoxa from the dorsal aspect distally narrower than adjacent spatha, S6 with the posterior margin in the middle nearly straight and hardly concave (Afghanistan) ....***B. obtusus*** Richards, 1951

8. Penis-valve head recurved section nearly straight posteriorly at the base 9
– Penis-valve head recurved section strongly concave posteriorly at the base (Mongolia, Russia) ....***B. tescorum*** Williams nom. nov. et stat. rev.

9. Penis-valve shaft at its proximal base on its outer side with a deeply marked ‘S’-shaped step 10
– Penis-valve shaft at its proximal base on its outer side with only a shallowly marked ‘S’-shaped step (Xizang, Qinghai, Gansu) .... ***B. falsificus*** Richards, 1930 stat. rev.

10. Metasomal T2 with the hair in part *either* yellow *or* white *or* black, T5–6 *either* usually orange-red *or* rarely white *or* black (western Himalaya, Ladakh) .... ***B. longiceps*** Smith, 1878 stat. rev.
– Metasomal T2 with the hair *either* usually nearly entirely yellow *or* rarely extensively black, T5–6 white (Tian Shan, Pamir, Afghanistan) ....***B. asiaticus*** Morawitz, 1875

Accounts of the species

Accounts of the 11 species accepted after integrative assessment follow below. Square brackets [*Bombus xus*] are used to indicate transliterations, translations, and interpretations.

1. ***Bombus* (*Sibiricobombus*) *sibiricus*** (Fabricius, 1781)

Figs 1, 7–8, 12–17, 90, 101

Apis ſibirica [= *sibirica*] Fabricius, 1781: 478.
BOMBUS MELINOIDES Fischer de Waldheim, 1843: pl. 122 n. 1.
Bombus flaviventris Friese, 1905: 514.
Bombus (*Subterraneobombus*) *flaviventris* subsp. *ochrobasis* Richards, 1930: 655.
Bombus (*Pyrobombus*) *nikiforuki* Tkalců, 1961: 354.

Diagnosis

Females

Queens body length 20–21 mm, workers 12–14 mm. Colour pattern of the hair with the head predominantly black, the thoracic dorsum anterior and posterior bands and metasomal T1–3 entirely yellow, *and* hair of the band between the wing bases *either* yellow *or* orange *or* black, *and* hair of T4–5 *either* orange *or* black, the lower side of thorax and legs black (Figs 12–14). Morphology with hind basitarsus outer surface in the centre with short branched hairs dense, black and strongly overlapping so that reflections from the outer surface are interrupted; (in large individuals) T6 subapically medially with a longitudinal ridge with a flattened crest.

Males

Body length 14–17 mm. Colour pattern of the hair similar to the female, with the head black but with yellow on the vertex and on the clypeus, the thoracic dorsum anterior and posterior bands and metasomal T1–3 entirely yellow, *and* hair of the band between the wing bases *either* yellow *or* orange *or* black, *and* hair of T4–6 *either* orange *or* black, the coxae and legs predominantly black (Figs 15–17). Morphology with the eye scarcely enlarged relative to the eye of a female bumblebee, from the dorsal aspect the eye separated from the lateral ocellus by more than 2 × the ocellar breadth; S6 with the posterior margin in the middle with a deep concave indentation; penis-valve head with the recurved section broad, narrowing gradually towards the tip (Fig. 90).

Type material

Lectotype of *Apis sibirica* (designated here)

RUSSIA • ♀ (worker); “Sibiria”; P. Pallas leg.; NHMUK Banks Collection (examined PW).

Holotype of *Bombus melinoides* (by monotypy?)

RUSSIA • ♀ (queen); Irkutsk; (type not seen but identity not in doubt).

Syntypes of *Bombus flaviventris*

CHINA • 2 ♀♀ (queen, worker); ZMB (examined PW).

Holotype of *Bombus* (*Subterraneobombus*) *flaviventris* subsp. *ochrobasis* (by original designation)

CHINA • ♀ (queen); [not] Sikkim [Xizang], “Khamba Jong” [Gampa Dzong]; 15-30 Jul. 1903; NHMUK (examined PW).

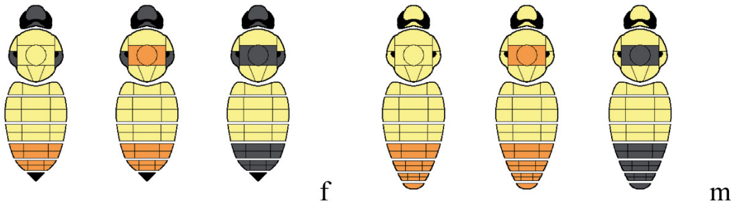
Holotype of *Bombus* (*Pyrobombus*) *nikiforuki* (by original designation)

CHINA • ♀ (worker); Qinghai, “Hsi-li-gou” north of Dulan; 31 Aug. 1950; C. Yang leg.; LMOB (examined PW).

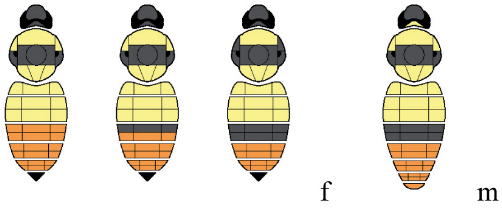
Material examined

CHINA – **Gansu** • 2 ♂♂; Yongden, Tongyuan; 36.6767° N, 103.0472° E; 2 Sep. 2010; P. Williams leg.; BOLD nos: 6880C09, 6880C10 (COI); PW, SB058, SB059. – **Inner Mongolia** • 1 ♀ (worker), 1 ♂; Majiazi; 43.2176° N, 117.3153° E; 10 Sep. 2007; P. Williams leg.; BOLD nos: 6880C11, 6880C12 (COI); PW, SB060, SB061. – **Qinghai** • 1 ♀ (worker); Xingfucan; 35.8993° N, 97.8892° E; 10 Aug.

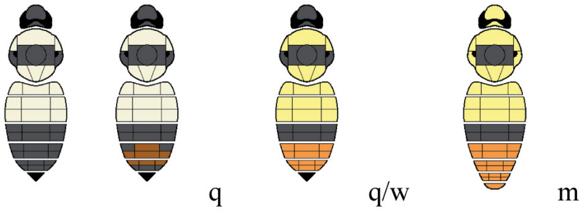
Figs 12–44 (on next page). Simplified diagrams for the colour patterns of the hair on the dorsum for particular female (f, or q/w for queen/worker) and male (m) specimens of the species of the subgenus *Sibiricobombus* Vogt, 1911 from Figs 1, 7. The dorsum is divided into regions, each of which shows only the predominant or most apparent colour for that region, using a simplified colour palette, with olive indicating a mixture of black and yellow hair, and grey indicating a mixture of black and white hair.



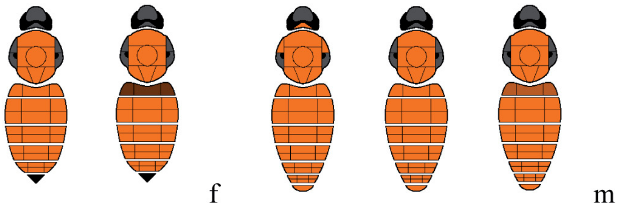
12–17 *sibiricus*



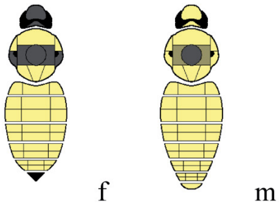
18–21 *semenovi*



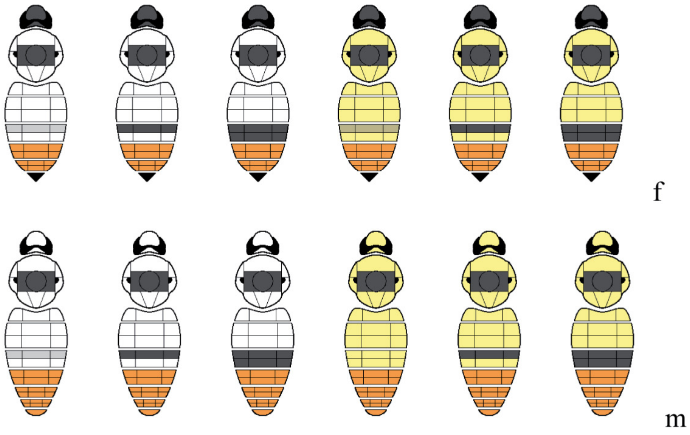
22–25 *oberti*



26–30 *morawitzi*



31–32 *sulfureus*



33–44 *niveatus*

2013; P. Williams leg.; PW, SB002/NHMC06 • 1 ♀ (worker); NW of Dulan; 36.6689° N, 98.1181° E; 14 Aug. 2013; P. Williams leg.; PW, SB001/NHMC07. –

MONGOLIA – **Zavkhan** • 1 ♀ (worker); Tegshiin Gol; 48.3313° N, 97.8645° E; 22 Jul. 2004; J. Gelhaus leg.; BOLD no.: 1550G03 (COI); KSEM, SB044.

Distribution

Asian desert-edge and Tibetan Plateau species: Fig. 101 – North Asia: KAZAKHSTAN, MONGOLIA, RUSSIA: East Siberia. – East Asia: CHINA: Xinjiang, Xizang, Qinghai, Gansu, Ningxia, Shaanxi, Hebei, Inner Mongolia. One of the highest recorded bumblebee species in the world at 5640 m a.s.l., along with *B. tibeticus* Williams, 2020 (recorded in 2018 under the name *B. keriensis* Morawitz s. lat.) and *B. tanguticus* Morawitz, 1887 from a site beside the West Rongbuk Glacier in Tibet [= Xizang], at 28.061160° N, 86.847273° E (Williams 2018). The species is so far unrecorded from central Xizang, e.g., in collections from the Tanggu La mountains. (AB, EA, EB, IAR, IZCAS, LMOB, NHMUK, PW, RDJ, UUH, VLA, ZIN, ZMB.)

Behaviour

Because the male eye is scarcely enlarged relative to the eye of a female, as in most bumblebees, the male mate-searching behaviour is expected to be similar to the most widespread male "patrolling" behaviour (Awram 1970; Svensson 1979), as for *B. tunicatus* Smith, 1852, compared with "racing" behaviour (below) (Williams 1991). It is also possible, but unrecorded, that the males might seek out colonies with young females.

Taxonomic remarks

Note on the lectotype of *Apis sibirica* Fabricius, 1781: this would appear to be (one of?) the specimen(s) referred to by Fabricius (1781) in the original description as being in the Banks Collection ("*Dr. Pallas. Muſ. Dom. Banks.*"). Because the number of specimens of *Apis sibirica* in this collection seen by Fabricius was not explicit in the original description and others may have existed, this individual which lacks the left hind tarsi and has some glue on the underside (with a later red-edged, round NHMUK label printed with "Type / H.T.", a recent printed label identifying *B. sibiricus*: "BMNH(E) #668744", and an old drawer label "Apis Sibirica / Fabr. Sp. ruf.[?] N<u>o</u> 22.") is designated as lectotype in order to reduce uncertainty in the identity of the taxon and in the application of the name.

The taxon concept of the species *B. sibiricus* here agrees with the recent interpretation (Williams 1998), presenting evidence that: (1) our PTP analysis supports independent species-level coalescents in the COI gene (Fig. 1); corroborated by (2) diagnostic morphological character states (see the keys).

The species-level coalescent in the COI gene (Fig. 1) also supports as conspecific the red-tailed taxon *sibiricus* s. str. from Mongolia and the black-tailed taxon *flaviventris* from the QTP. This conspecificity is corroborated by their closely similar morphology (see the key). Surprisingly, the black-tailed taxon *flaviventris* has had unusually widely different interpretations by previous authors: (1) as part of a "Gruppe *confusus*" (Friese 1905); (2) as part of the subgenus *Subterraneobombus* (Richards 1930); or (3) as part of the subgenus *Sibiricobombus* (Williams 1991, 1998).

Individuals of the orange-tailed colour pattern vary from having a distinct orange band in the hair between the wing bases (taxon *sibiricus* s. str.) to having the thoracic dorsum entirely yellow (taxon *melinoides*).

2. ***Bombus* (*Sibiricobombus*) *semenovi*** Morawitz, 1887 stat. rev.

Figs 1, 7–8, 18–21, 91

Bombus Semenovi Morawitz, 1887: 198. Note 1.

Bombus (*Sibiricobombus*) *xionglaris* Wang, 1982: 432. **Syn. nov.**
Bombus (*Subterraneobombus*) *duanjiaoris* Wang, 1982: 444. **Syn. nov.**
Bombus (*Subterraneobombus*) *zhadaensis* Wang, 1982: 444. **Syn. nov.**

Bombus semenowii – von Dalla Torre 1896: 546, unjustified emendation.
Bombus (*Sibiricobombus*) *oberti* – Williams 1991: 92, (in part) misidentification.

Diagnosis

Females

Queens body length 20–23 mm, workers 12–13 mm. Colour pattern of the hair with the head, lower side of the thorax and legs predominantly black, metasomal T3–4 *either* black *or* more or less extensively dull orange, thoracic dorsum anterior and posterior bands and T1–2 yellow, T5 dull orange (Figs 18–20). Morphology with labral furrow broad, 0.35 × the entire breadth of the labrum; antennal A3 length 2 × greatest breadth; hind basitarsus outer surface in the centre with short branched hairs dense, black and strongly overlapping so that reflections from the outer surface are interrupted; (in large individuals) T6 subapically medially with a deep narrow longitudinal groove.

Males

Body length 16 mm. Colour pattern of the hair similar to the female, with the head except the yellow vertex, legs predominantly black, thoracic dorsum anterior and posterior bands, anterior sides of the thorax, and T1–2 yellow, metasomal T3 *either* black *or* more or less extensively dull orange, T4–6 dull orange (Fig. 21). Morphology with the eye scarcely enlarged relative to the eye of a female bumblebee, from the dorsal aspect the eye separated from the lateral ocellus by more than 2 × the ocellar breadth; S6 with the posterior margin in the middle with a shallow narrow concave indentation; volsella with the inner distal corner as a broad but obtusely pointed hook projecting posteriorly almost as far as the outer distal corner (Fig. 91).

Type material

Syntype of *Bombus semenovi* (lectotype designation by Podbolotskaya unpubl.)
CHINA • ♀ (queen); Qinghai, “im Thale des gelben Flusses” [Yellow River, Huang He]; [1884]; N. Przhevalsky leg.; ZIN (examined PW).

Holotype of *Bombus* (*Sibiricobombus*) *xionglaris* (by original designation)
CHINA • ♂; Xizang, Nyalam; 31 May 1974; X. Zhang leg.; IZCAS (examined PW).

Holotype of *Bombus* (*Subterraneobombus*) *duanjiaoris* (by original designation)
CHINA • ♀ (worker); Xizang, Rutog; 23 Aug. 1976; F. Huang leg.; IZCAS (examined PW).

Holotype of *Bombus* (*Subterraneobombus*) *zhadaensis* (by original designation)
CHINA • ♀ (queen); Xizang, Zanda; 25 Jun. 1976; F. Huang leg.; IZCAS (examined PW).

Material examined

CHINA – **Qinghai** • 1 ♀ (worker); Kunlun Shan Pass; 35.6920° N, 94.0520° E; 13 Aug. 2013; P. Williams leg.; PW, SB003/NHMC08 • 2 ♀♀ (workers); Kunlun Shan; 35.9063° N, 94.4052° E; 18 Jul. 2017; IZCAS, SB040/MOBBT3, SB089/BB07 • 1 ♀ (worker); Kunlun Shan Pass; 35.6917° N, 94.0533° E; 19 Aug. 2013; IAR, SB016/JH8. – **Xizang** • 1 ♂; Tanggula Shan; 32.8614° N, 91.9174° E; 18 Aug. 2015; IAR, SB004/JH13 • 1 ♀ (queen); Tanggula Shan; 32.8614° N, 91.9174° E; 29 Jun. 1999; K. Huber leg.; BOLD no.: 1552A07 (COI); LMOB, SB041 • 1 ♂; near Zhilong; 32.8614° N, 91.9174° E; 18 Aug. 2015; IAR, SB017/JHNEW.

INDIA – **Jammu & Kashmir** • 1 ♀ (queen); Zanskar, Nimaling; 33.7927° N, 77.5881° E; 18 Aug. 1980; P. Williams leg.; BOLD no.: 1555D11 (COI); PW, SB014.

Distribution

Tibetan high montane species – East Asia: INDIA: Kashmir & Jammu; CHINA: Xizang, Qinghai. (IAR, IZCAS, NHMUK, PW, ZIN.)

Behaviour

Because the male eye is scarcely enlarged relative to the eye of a female, as in most bumblebees, the male mate-searching behaviour is expected to be similar to the most widespread male "patrolling" behaviour (Awram 1970; Svensson 1979), as for *B. tunicatus*, compared with "racing" behaviour (below) (Williams 1991). It is also possible, but unrecorded, that the males might seek out colonies with young females.

Taxonomic remarks

Note 1 on the name *B. semenovi* Morawitz, 1887 stat. rev.: the type locality of *B. semenovi* is probably near the source of the Yellow River, in the river valley downstream from the Zhaling Hu in Qinghai. See the discussion of the type locality of *B.* (*Melanobombus*) *tanguticus* Morawitz, 1887 in Williams (2018).

The taxon concept of the species *B. semenovi* stat. rev. here agrees with the recent interpretation of a species separate from *B. oberti* (Williams 2022a), presenting evidence that: (1) our PTP analysis supports independent species-level coalescents in the COI gene (Fig. 1); corroborated by (2) diagnostic morphological character states (see the keys).

Queens show some variation from T3 black (Qinghai) to T3 predominantly orange-red, or at least with an orange-red fringe posteriorly (Zanskar, Kashmir, India).

The taxa *xionglaris*, *duanjiaoris* and *zhadaensis* are re-descriptions of the taxon *semenovi*.

3. ***Bombus* (*Sibiricobombus*) *oberti*** Morawitz, 1883

Figs 1, 7–8, 22–25, 92

Bombus Oberti Morawitz, 1883: 238.
Bombus melanurus var. [= subsp.] *apicatus* Friese, 1911: 457. **Syn. nov.**
Bombus (*Obertobombus*) *oberti* var. [= subsp.] *griseofasciatus* Reinig, 1930: 108, not of Reinig, 1930: 83 (= *B. difficillimus* Skorikov, 1912).

Bombus obertii – von Dalla Torre 1896: 538, unjustified emendation.

Diagnosis

Females

Queens body length 20–23 mm, workers 13 mm. Colour pattern of the hair with the head, lower side of the thorax and legs predominantly black, thoracic dorsum anterior and posterior bands and T1–2 *either* yellow (workers and some queens) *or* grey-white (some queens), metasomal T3 black, at most with a narrow posterior pale fringe, T4–5 *either* dull orange *or* dark brown *or* black (Figs 22–24). Morphology with labral furrow narrow, 0.25 × the entire breadth of the labrum; antennal A3 length 2 × greatest breadth; hind basitarsus outer surface with short branched hairs dense, black and strongly overlapping so that reflections from the outer surface are interrupted; (in large individuals) T6 subapically medially with a deep narrow longitudinal groove.

Males

Body length 17 mm. Colour pattern of the hair with the head black with yellow on the vertex and on the clypeus, the legs with many pale hairs, thoracic dorsum anterior and posterior bands and T1–2 yellow, metasomal T3 black, T4–6 dull orange (Fig. 25). Morphology with S6 with the posterior margin in the middle with a shallow narrow indentation; volsella with the inner distal corner broadly and evenly rounded and much shorter than the outer distal corner (Fig. 92).

Type material

Lectotype of *Bombus oberti* (by designation of Williams 1991: 92)
KAZAKHSTAN • ♂; "im Hochgebirge bei Wernoye" [Almaty]; A. Kuschakewitsch leg.; ZIN (examined PW).

Holotype of *Bombus melanurus* var. [= subsp.] *apicatus* (by monotypy)
KYRGYZSTAN • ♀ (queen); "Pamir Hochland am Alai"; ZMB (examined PW).

Lectotype of *Bombus* (*Obertobombus*) *oberti* var. [= subsp.] *griseofasciatus* (designated here)
TAJIKISTAN • ♀ (queen); Pamir, "Pass Naisa-Tasch"; 31 Jul. 1928; W. Reinig leg.; Naturalis (examined PW).

Material examined

TAJIKISTAN • 1 ♀ (queen); Pamir, SE Kara-Kul; 38.9537° N, 73.5076° E; 12 Jul. 1928; W. Reinig leg.; Naturalis, SB042/NHMK01.

Distribution

Rare Central Asian high montane species – Central Asia: KAZAKHSTAN, KYRGYZSTAN, TAJIKISTAN. (Naturalis, PW, ZIN, ZMB.)

Behaviour

Because the male eye is scarcely enlarged relative to the eye of a female, as in most bumblebees, the male mate-searching behaviour is expected to be similar to the most widespread male "patrolling" behaviour (Awram 1970; Svensson 1979), as for *B. tunicatus*, compared with "racing" behaviour (below) (Williams 1991). It is also possible, but unrecorded, that the males might seek out colonies with young females.

Taxonomic remarks

Note on the name *B. oberti* var. *griseofasciatus* Reinig, 1930: although Reinig used both "subsp." and "var.' in his 1930 publication, which would imply infrasubspecific status for taxa described as "var.", he gave the taxon *griseofasciatus* a geographically defined distribution in the "Pamir-Gebiet" (p. 109) and also used the name as a simple trinomen "*Bombus oberti griseofasciatus*" (p. 73), both of which would appear to confer subspecific status.

Note on the lectotype of *B. oberti* var. *griseofasciatus* Reinig, 1930: the label data matches the data for one of the specimens referred to by Reinig 1930 in the original description. Because others were listed, this individual, which lacks the right hind terminal joint of the tarsus and has a bald patch on T2 (labels: (1) printed "Zentral – Pamir / VII.-VIII.28 / leg. Reinig"; (2) hand-written "Pass Naisa-Tasch / 4100m 31.VI.28"; (3) hand-written "*B.oberti* / *griseofasciatus* / det. W. F. Reinig"; (4) printed "Collectie / C. et O. Vogt / Acq. 1960"; (5) red printed "*Bombus* / *oberti griseofasciatus* / Reinig, 1930 / ZMAN type HYME.0106.7"; (6) printed "ZMA.INS.959151 [square barcode]"; (7) printed "*Bombus* / (*Sibiricobombus*) / *oberti* / det. PH Williams 2018"; (8) red hand-written "LECTOTYPE ♀ / *Bombus* *oberti* / var. [= ssp.] / *griseofasciatus* / Reinig, 1930 / det. PH Williams 2023") is designated as lectotype in order to reduce uncertainty in the identity of the taxon and in the application of the name.

The taxon concept of the species *B. oberti* here agrees with the recent interpretation of a species separate from *B. semenovi* stat. rev. (Williams 2022a), presenting evidence that: (1) our PTP analysis supports independent species-level coalescents in the COI gene (Fig. 1); corroborated by (2) diagnostic morphological character states (see the keys).

In the Tian Shan, queens, workers, and males all have yellow bands and an orange-red tail. However, in the Pamir, while workers and males retain a similar colour pattern, queens have the yellow replaced by grey-white and the tails are either black or dark brown (the colour-pattern taxon *apicatus*; Reinig 1930, 1932, 1934).

4. ***Bombus* (*Sibiricobombus*) *morawitzi*** Radoszkowski, 1876

Figs 1, 7–8, 26–30, 93

Bombus Morawitzi Radoszkowski, 1876: 101.
BOMBUS OPPOSITUS Smith, 1878: 9.
Bombus hydrophthalmus Morawitz, 1883: 240.

Bombus morawitzii – von Dalla Torre 1896: 535, unjustified emendation.

Diagnosis

Females

Queens body length 19–23 mm, workers 12–18 mm. Colour pattern of the hair with the head predominantly black with only a few brown hairs intermixed on the vertex, the thoracic dorsum and metasomal T1–5 bright orange-red, the side of the thorax and legs predominantly black (Figs 26–27). Morphology with the hind basitarsus outer surface in the centre with short branched hairs dense, black and strongly overlapping so that reflections from the outer surface are interrupted; (in large individuals) T6 subapically medially with a raised boss.

Males

Body length 14–18 mm. Colour pattern of the hair with the head predominantly black including the clypeus, often with orange hairs more or less intermixed on the vertex, the thoracic dorsum and metasomal T1–6 bright orange-red, *either* the side *or* the lower side of the thorax and the legs predominantly black (Figs 28–30). Morphology with the eye greatly enlarged relative to the eye of a female bumblebee, from the dorsal aspect the eye separated from the lateral ocellus by 1 × the ocellar breadth; S6 with the posterior margin in the middle nearly straight; penis-valve head recurved section narrow curved and finger-like, concave posteriorly at the base (Fig. 93).

Type material

Lectotype of *Bombus morawitzi* (by designation of Tkalců 1968: 199)
UZBEKISTAN • ♀ (queen); "Samarkand"; ZMB (examined PW).

Holotype of *Bombus oppositus* (by monotypy)
CHINA • ♀ (queen); Xinjiang, "Yark. Exp." "No precise locality indicated" [mountains west of Yarkant?]; F. Stoliczka leg.; NZSI (examined PW).

Syntype of *Bombus hydrophthalmus*
KAZAKHSTAN • ♂; "im Hochgebirge bei Wernoye" [Almaty]; A. Kuschakewitsch leg.; NHMUK (examined PW).

Material examined

AFGHANISTAN • 1 ♀ (worker); Wakhan, N of Borak; 37.09° N, 73.63° E; 9 Jul. 1971; GG, SB095/GG002.

CHINA – **Xinjiang** • 1 ♀ (worker); Kuqa, Ku'ergan; 42.4358° N, 83.2538° E; 31 Jul. 2011; IAR, SB015/NHMC06 • 1 ♀ (worker); Akqi, Sumutashi; 40.9055° N, 78.3568° E; 15 Jul. 2012; IAR, SB019/NHMC01.

TAJIKISTAN • 1 ♀ (worker); Pamir, Rushan; 37.9901° N, 71.5846° E; Jul. 2000; Gurko leg.; BOLD no.: 6880F04 (COI); MM, SB077.

Distribution

Central Asian high montane species – Central Asia: AFGHANISTAN, TAJIKISTAN, KYRGYZSTAN, KAZAKHSTAN, CHINA: Xinjiang. (AB, GG, IAR, IZCAS, Naturalis, NHMUK, NZSI, PW, UMons, ZIN, ZMB.)

Behaviour

Because the male eye is greatly enlarged relative to the eye of a female bumblebee and the male antenna is strongly elongated, the male mate-searching behaviour is expected to be similar to the "racing" behaviour described for "*B. asiaticus*" (actually *B. longiceps* stat. rev.) with these morphological characteristics by Williams (1991).

Taxonomic remarks

The taxon concept of the species *B. morawitzi* here agrees with the recent interpretation as a distinctive species (Tkalců 1968; Williams 1998; Ghisbain *et al.* 2020). We present evidence that: (1) our PTP analysis supports independent species-level coalescents in the COI gene (Fig. 1); corroborated by (2) diagnostic morphological character states (see the keys).

The colour pattern of this species shows little variation, although there is some variation in both sexes in how much black hair is intermixed on T1 and in males in the extent of the black hair on the side of the thorax.

5. ***Bombus* (*Sibiricobombus*) *sulfureus*** Friese, 1905

Figs 1, 7–8, 31–32, 94

Bombus vorticosus subsp. *sulfureus* Friese, 1905: 521.
Bombus (*Sibiricobombus*) *sulfureus* var. [= subsp.] *aureocorbicularis* Pittioni, 1937: 121.

Diagnosis

Females

Queens body length 16–19 mm, workers 15 mm. Colour pattern of the hair with the head predominantly black, the thoracic dorsum anterior and posterior bands and metasomal T1–6 yellow, lower side of thorax and legs black (Fig. 31). Morphology with the clypeus in its centre with scattered large and few small punctures, so that the surface has smooth shining areas; hindleg basitarsus outer surface with short branched hairs so short and sparse that they are not overlapping and the surface is conspicuously brightly shining; (in large individuals) T6 subapically medially slightly but irregularly raised.

Males

Body length 15 mm. Colour pattern of the hair with the entire body predominantly yellow, except for the thoracic dorsum with black hair between the wing bases (Fig. 32). Morphology with the eye greatly enlarged relative to the eye of a female bumblebee, from the dorsal aspect the eye separated from the lateral ocellus by 1 × the ocellar breadth; S6 with the posterior margin in the middle with a deep concave indentation; volsella posterior to the gonostylus greatly broadened and nearly straight, penis-valve head on its inner side ventrally at the base marked by a ridge with a projecting angle, this angle also marked dorsally on a parallel dorsal ridge; penis-valve head recurved section narrowing gradually towards the tip, volsella just beyond gonostylus 3 × its breadth between its distal posterior corners (Fig. 94).

Type material

Type of *B. vorticosus* subsp. *sulfureus*
"Asia minor"; (type not seen but identity not in doubt).

Holotype of *Bombus* (*Sibiricobombus*) *sulfureus* var. [= subsp.] *aureocorbicularis* (by monotypy)
IRAN • (worker); Alborz, "Keredj-Mazanderan"; Brandt leg.; 12 Aug.; (type not seen but identity not in doubt).

Material examined

IRAN • 1 ♀ (queen); Qazvin, Werk; 38.5488° N, 47.2609° E; 6 Jun. 2007; A. Monfared leg.; PW, SB008/NHMI027 • 1 ♀ (worker); Qazvin, Bala Rouch; 36.3870° N, 50.6639° E; 19 Aug. 2012; A. Monfared leg.; PW, SB007/NHMI025.

Distribution

Rare West Asian montane species – West Asia: TURKEY, IRAN. (AM, NHMUK, PW, UMons.)

Behaviour

Because the male eye is greatly enlarged relative to the eye of a female bumblebee and the male antenna is strongly elongated, the male mate-searching behaviour is expected to be similar to the "racing" behaviour described for "*B. asiaticus*" (actually *B. longiceps* stat. rev.) with these morphological characteristics by Williams (1991). Similar "racing" behaviour has been observed in Turkey (Rasmont *et al*. 2021).

Taxonomic remarks

The taxon concept of the species *B. sulfureus* here agrees with the recent interpretation (Williams 1998; Monfared *et al.* 2007; Rasmont *et al.* 2021) of a species separate from *B. niveatus*, presenting evidence that: (1) our PTP analysis supports independent species-level coalescents in the COI gene (Fig. 1); corroborated by (2) diagnostic morphological character states (see the keys). This separation of *B. sulfureus* from *B. niveatus* is also supported by a difference in CLGS (Rasmont *et al.* 2005).

The colour pattern of this species shows little variation.

6. ***Bombus* (*Sibiricobombus*) *niveatus*** Kriechbaumer, 1870

Figs 1, 7–8, 33–44, 95

Bombus niveatus Kriechbaumer, 1870: 101.
Bombus vorticosus Gerstaecker, 1872: 290.
Bombus (*Kallobombus*) *Parnassius* von Dalla Torre, 1882: 21.
Bombus araraticus Radoszkowski, 1890: 502.
Bombus (*Sibiricobombus*) *asiaticus* [subsp.] *pallidofasciatus* Vogt, 1909: 51.
Bombus (*Sibiricobombus*) *vorticosus* Forma [= subsp.] *postzonatus* Vogt, 1911: 61, not of Vogt, 1911: 57 (= *B. cullumanus* (Kirby, 1802)).

Bombus (*Sibiricobombus*) *niveatus* var. [= subsp.] *skorikowi* Friese, 1911: 572, not of Vogt, 1911: 51 (= *B. pratorum* (Linnaeus, 1761)).

Bombus (*Sibiricobombus*) *vorticosus* morpha [= subsp.] *iranensis* Pittioni, 1937: 120.

Bombus (*Sibiricobombus*) *niveatus* morpha [= subsp.] *persicus* Pittioni, 1937: 121, not of Radoszkowski, 1881: v (= *B. persicus* Radoszkowski, 1881).

Pyrobombus (*Sibiricobombus*) *niveatus* [subsp.] *persiensis* Rasmont, 1983: 168, replacement name for *B. niveatus* subsp. *persicus* Pittioni, 1937.

Diagnosis

Females

Queens body length 17–22 mm, workers 9–16 mm. Colour pattern of the hair with the head predominantly black, legs black, the thoracic dorsum anterior and posterior bands, side of thorax, and metasomal T1–2 *either* yellow *or* white, T3 at least in part *either* black *or* yellow *or* white, T4–5 orange-red (Figs 33–38). Morphology with the clypeus in its centre with scattered large and very many small punctures, so that the surface is uneven; hindleg basitarsus outer surface with short branched hairs long so that they are just overlapping and the shining surface is only partly obscured; (in large individuals) T6 subapically medially slightly but irregularly raised.

Males

Body length 15–17 mm. Colour pattern of the hair with the head, side of thorax, legs, thoracic dorsum anterior and posterior bands and metasomal T1–2 *either* yellow *or* white, T3 at least in part *either* black *or* yellow *or* white, T4–7 orange-red (Figs 39–44). Morphology with the eye greatly enlarged relative to the eye of a female bumblebee, from the dorsal aspect the eye separated from the lateral ocellus by 1 × the ocellar breadth; S6 with the posterior margin in the middle with a deep concave indentation; volsella posterior to the gonostylus greatly broadened and weakly curved, penis-valve head on its inner side ventrally at the base marked by a ridge with a projecting angle, this angle also marked dorsally on a parallel dorsal ridge; penis-valve head recurved section narrowing abruptly just before the tip, volsella just beyond gonostylus 2 × its breadth between its distal posterior corners (Fig. 95).

Type material

Lectotype of *Bombus niveatus* (by designation of Tkalců 1969: 897)
ISRAEL • ♀ (queen), “Palaestina”; ZSM (type not seen but identity not in doubt).

Syntypes of *Bombus vorticosus*
UNKNOWN • (syntypes of both sexes and castes); most from ”Krakau” [locality likely in error]; Nowicki leg.; (types not found by Tkalců 1969: 897, but identity not in doubt).

Syntypes of *Bombus* (*Kallobombus*) *parnassius*
GREECE • “Parnass”; (types not seen but identity not in doubt).

Lectotype of *Bombus araraticus* (by designation of Tkalců 1969: 897)
TURKEY • ♂; “Ararat”; O. Radoszkowski leg.; ZMB (type not seen but identity not in doubt).

Syntypes of *Bombus* (*Sibiricobombus*) *asiaticus* [subsp.] *pallidofasciatus*
RUSSIA • “Kaukasus”; unknown repository (types not seen but identity not in doubt).

Syntypes of *Bombus* (*Sibiricobombus*) *vorticosus* Forma [= subsp.] *postzonatus*
TURKMENISTAN • 2 ♀♀ (queens); “Krassnowodsk” [Turkmenbashi]; unknown repository (types not seen but identity not in doubt).

Lectotype of *Bombus* (*Sibiricobombus*) *vorticosus* morpha [= subsp.] *iranensis* (designated here)
IRAN • ♀ (queen); Alborz, Nissa; 1–10 Aug. 1936; Brandt leg.; NHMUK (examined PW).

Lectotype of *Bombus* (*Sibiricobombus*) *niveatus* morpha [= subsp.] *persicus* (designated here)
IRAN • ♀ (queen); Alborz, Nissa; 20 Jul.–1 Aug. 1936; Brandt leg.; NHMUK (examined PW).

Material examined

GEORGIA • 1 ♀ (queen); Calka, Bashdashi; 41.5891° N, 44.1330° E; 27 May 2011; BOLD no.: 1555A02 (COI); IEAUG, SB053.

GREECE • 3 ♀♀ (workers); N of Lamia; 38.9365° N, 22.4300° E; 8 Jun. 2016; M. Halada leg.; BOLD nos: 6880G01 to 6880G03 (COI); PW, SB086 to SB088.

IRAN • 1 ♀ (worker); Qazvin, Vikan; 36.3754° N, 50.6893° E; 9 Aug. 2011; A. Monfared leg.; PW, SB010/NHMI010 • 1 ♀ (queen); Qazvin, Wikan [Vikan]; [36.3754° N, 50.6893° E]; 30 Jul. 2006; A. Taghavi leg.; PW, SB013/NHMI028 • 1 ♀ (worker); Tehran, Damavand; 35.7013° N, 52.0586° E; 14 Jun. 2015; A. Monfared leg.; PW, SB009/NHMI008 • 2 ♀♀ (worker, queen); Qazvin, Vikan; 36.3754° N, 50.6893° E; 9 Aug. 2011; A. Monfared leg.; PW, SB011/NHMI011, SB012/NHMI009.

Distribution

West Asian and European montane species – Europe: ALBANIA, GREECE, UKRAINE, RUSSIA: Caucasus. – West Asia: TURKEY, GEORGIA, SYRIA, LEBANON, ISRAEL, IRAN, TURKMENISTAN. (AM, GG, Naturalis, NHMUK, PW, UMons, ZIN, ZMB.)

Records of *B. niveatus* from Xizang (Wang 1982) are misidentifications of *B.* (*Melanobombus*) *keriensis* Morawitz, 1887 (Williams *et al.* 2020).

Behaviour

Because the male eye is greatly enlarged relative to the eye of a female bumblebee and the male antenna is strongly elongated, the male mate-searching behaviour is expected to be similar to the "racing" behaviour described for "*B. asiaticus*" (actually *B. longiceps* stat. rev.) with these morphological characteristics by Williams (1991).

Taxonomic remarks

Note on the syntypes of *B. vorticosus* Gerstaecker, 1872: described as most syntypes from "Krakau" [locality likely in error]; Nowicki leg.; (types not found by Tkalců 1969: 897, but identity not in doubt). The given type locality is very unlikely to be either Kraków (Poland) or Krakau (Austria) as these are far too far north for this species.

Note on the lectotype of *B. vorticosus* morpha *iranensis* Pittioni, 1937 designated here: the original description data from Pittioni (1937) match one of the specimens in the NHMUK collection. Because other specimens were listed, this individual, which lacks both antennae (labels: (1) printed "IRAN: ELBURS-GEB. / NISSA, (CA.3000 M.) / 1.8. – 10.8.1936 / LEG.BRANDT"; (2) hand-written "*vortic. ira-* / ♀ *nensis* Pitt / det. Pittioni"; (3) hand-written with black border "f. *iranensis* / Pitt typ."; (4) printed "Pittioni Coll. / Turner Bequest / B.M. 1954-76"; (5) printed "[barcode] / NHMUK 013380602"; (6) printed "*Bombus* / (*Sibiricobombus*) / *niveatus* / det. PH Williams 2022"; (7) red hand-written "LECTOTYPE ♀ / *Bombus vorticosus* / morpha [= ssp.] / *iranensis* / Pittioni, 1937 / det. PH Williams 2023") is designated as lectotype in order to reduce uncertainty in the identity of the taxon and in the application of the name.

Note on the lectotype of *B. niveatus* morpha *persicus* Pittioni, 1937 designated here: the original description data from Pittioni (1937) match one of the specimens in the NHMUK collection. Because other specimens were listed, this individual, which lacks the right antenna (labels: (1) red hand-written "Type"; (2) printed "B.M. TYPE / HYM / 17b.1318"; (3) printed "IRAN: ELBURS-GEB. / NISSA, (CA.3000 M.) / 20.7. – 1.8.1936 / LEG.BRANDT"; (4) hand-written "*niveatus per*- / ♀ *sicus* Pitt / det. Pittioni"; (5) printed "Pittioni Coll. / Turner Bequest / B.M. 1954-76"; (6) printed "[barcode] / NHMUK 013380602"; (7) printed "*Bombus* / (*Sibiricobombus*) / *niveatus* / det. PH Williams 2022"; (8) red hand-written "LECTOTYPE ♀ / *Bombus niveatus* / morpha [= ssp.] / *persicus* / Pittioni, 1937 / det. PH Williams 2023") is designated as lectotype in order to reduce uncertainty in the identity of the taxon and in the application of the name.

The taxon concept of the species *B. niveatus* here agrees with the recent interpretation (e.g., Williams 1998; Monfared *et al.* 2007; Rasmont *et al.* 2021) of a species separate from *B. sulfureus*, presenting evidence that: (1) our PTP analysis supports independent species-level coalescents in the COI gene (Fig. 1); corroborated by (2) diagnostic morphological character states (see the keys). This separation of *B. niveatus* from *B. sulfureus* is also supported by a difference in CLGS (Rasmont *et al.* 2005).

The species-level coalescent in the COI gene (Fig. 1) also supports as conspecific the white-banded taxon *niveatus* s. str. and the yellow-banded taxon *vorticosus*. Conspecificity is corroborated by their morphology (see the keys) and by their similar male CLGS mixtures (Rasmont *et al.* 2005). It has been claimed that the two taxa "differ significantly" in habitat (Rasmont *et al*. 2021), although it also appears that their distributions are broadly overlapping and geographically concentric, with the white-banded colour pattern the more frequent at higher elevations (where it co-occurs with other white-banded bumblebees). This might be explained by mimetic selection in favour of different mimetic model patterns at different elevations. It is common for pale-banded mountain bumblebees to have both yellow- and white-banded colour patterns that are more frequent in different areas (Williams 2007). There are several examples of this in the subgenus *Melanobombus* (Williams *et al.* 2020).

Both the yellow-banded and the white-banded colour patterns also vary in whether T3 is entirely black (Greece, Turkey, Lebanon) or, in the Alborz mountains of northern Iran, has more extensive pale hair (yellow taxon *iranensis*, white taxon *persiensis*), varying from a posterior fringe on T3 to covering T3 entirely in the male (Pittioni's infrasubspecific taxon *brandti*). Individuals with T3 extensively yellow resemble *B. sulfureus*.

7. ***Bombus* (*Sibiricobombus*) *obtusus*** Richards, 1951

Figs 1, 7, 9, 45–48, 96

Bombus (*Sibiricobombus*) *obtusus* Richards, 1951: 196.
Pyrobombus (*Sibiricobombus*) *obtusus* [subsp.] *badakshanensis* Tkalců, 1968: 201.

Diagnosis

Females

Queens unknown, body length workers 12–14 mm. Colour pattern of the hair with the head and legs usually predominantly black sometimes with some yellow intermixed, the thoracic dorsum anterior and posterior bands, side of thorax, and metasomal T1–2 bright sulphur yellow, metasomal T3–4 black, T4 at most with a few white hairs along the posterior margin, T5 white (Figs 45–46). Morphology with the oculo-malar area anteriorly sparsely covered with large punctures regularly spaced; antennal A3 length 3 × greatest breadth; hind basitarsus outer surface with the short branched hairs few and very widely spaced so that they are not overlapping, with reflections from the outer surface clearly visible and brightly shining; (in large individuals) T6 subapically medially weakly raised.

Males

Body length 12–14 mm. Colour pattern of the hair similar to the female but with yellow hair on the head, more often intermixed between the wing bases, on the legs, and with metasomal T3–4 black, at most with a few white hairs along the posterior margins (Figs 47–48). Morphology with the eye greatly enlarged relative to the eye of a female bumblebee, from the dorsal aspect the eye separated from the lateral ocellus by 1 × the ocellar breadth; S6 with the posterior margin in the middle nearly straight and hardly concave; gonocoxa from the dorsal aspect distally narrower than adjacent spatha, gonostylus distal lobe approximately circular, volsella beyond gonostylus strongly inwardly curved, nearly parallel-sided, and consistently just broader than its breadth between the distal posterior corners (Fig. 96).

Type material

Holotype of *Bombus* (*Sibiricobombus*) *obtusus* (by original designation)

AFGHANISTAN • ♂; Koh-i-Baba, Puistagoli; 2 Aug. 1948; N. Haarløv leg.; SNM, 00240323 (photos examined PW).

Material examined

AFGHANISTAN • 1 ♀ (worker); Hindu Kush; [34.3824° N, 66.8670° E]; 8 Aug. 1968; M. Tong leg.; BOLD no.: 6880D07 (COI); NHMUK, SB068.

Distribution

Rare endemic Afghan montane species – Central Asia: AFGHANISTAN. (NHMUK, UMons.)

Behaviour

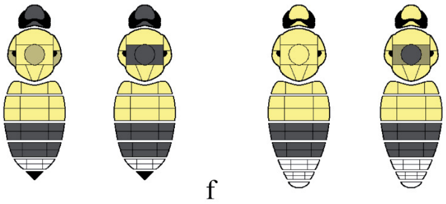
Because the male eye is greatly enlarged relative to the eye of a female bumblebee and the male antenna is strongly elongated, the male mate-searching behaviour is expected to be similar to the “racing” behaviour described for “*B. asiaticus*” (actually *B. longiceps* stat. rev.) with these morphological characteristics by Williams (1991).

Taxonomic remarks

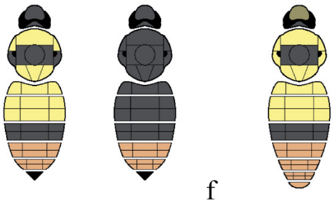
The taxon concept of the species *B. obtusus* here agrees with the recent interpretation (Tkalců 1968; Williams 1998) of a species separate from *B. asiaticus*, presenting evidence that: (1) our PTP analysis supports independent species-level coalescents in the COI gene (Fig. 1); corroborated by (2) diagnostic morphological character states (see the keys).

Richards (1951: 198) described the females of *B. obtusus* as “Structurally apparently identical with *B. asiaticus* F. Mor. and only differing in that all the hairs of abdominal tergite 4 are black”. Tkalců (1968: 198) described this species only as being morphologically more closely related to *B. morawitzi* than to *B. asiaticus*. To support these groups he cites differences in the incisura of the mandible, although these differences appear to be at best subtle and inconsistent. However, Williams (1991: 90) described a character difference between *B. obtusus* and *B. asiaticus* in the hairs of the hind basitarsus that is more reliable (see the key). Richards (1951) and Tkalců (1969) appear to have been, in effect, using colour pattern alone to determine what they considered to be “*B. obtusus*”, which could explain why some of their descriptions of its colour-pattern variation may be inconsistent with those reported here based

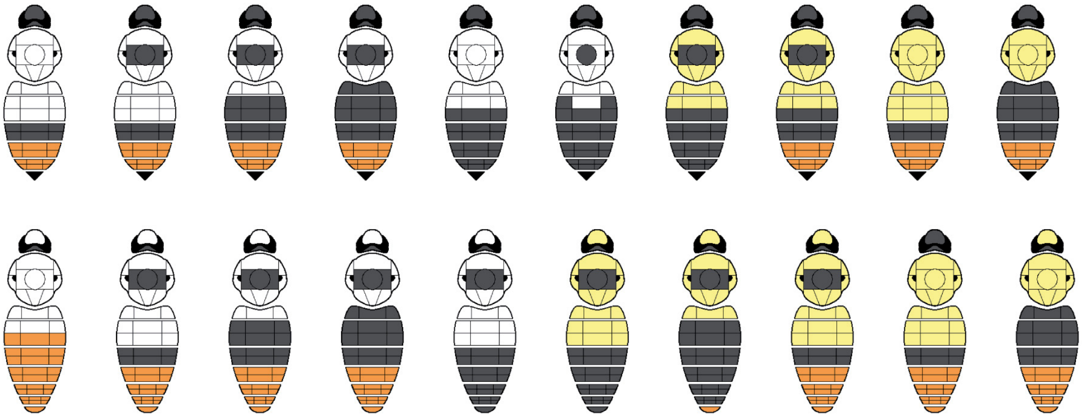
Figs 45–89 (on next page)**.** Simplified diagrams for the colour patterns of the hair on the dorsum for particular female (f, or q/w for queen/worker) and male (m) specimens of the species of the subgenus *Sibiricobombus* Vogt, 1911 from Figs 1, 7. The dorsum is divided into regions, each of which shows only the predominant or most apparent colour for that region, using a simplified colour palette, with olive indicating a mixture of black and yellow hair, and grey indicating a mixture of black and white hair.



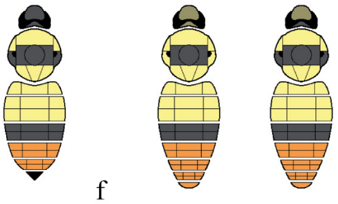
45–48 *obtusus*



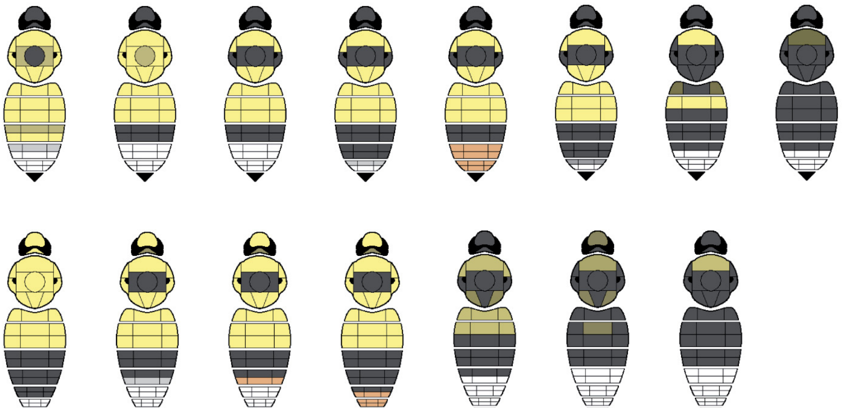
49–51 *tescorum*



52–71 *longiceps*



72–74 *falsificus*



75–89 *asiaticus*

on morphology, because they may have been including some individuals considered here to be part of *B. asiaticus*.

Variation in the colour pattern of *B. obtusus* has been described in three aspects. First, the black band between the wing bases varies from narrower than the yellow anterior band, but distinct with a sharp boundary, to indistinct with a mixture of yellow, to being replaced by yellow (taxon *badakshanensis*), especially for males (Richards 1951; Tkalců 1968).

Second, one worker (collection site unspecified) was described as having the T5–6 pale hairs with their bases "brownish-red" (Richards 1951; Tkalců 1968). This has not been seen by us for *B. obtusus*, although we have seen this colour pattern for Afghan *B. asiaticus*.

Third, based on a description of material from two sites identified as *B. asiaticus* by Reinig (1940) (prior to Richards' description of *B. obtusus*), Tkalců (1969) suggested that there might also be a black-tailed colour pattern of *B. obtusus*, with a colour pattern resembling of *B.* (*Subterraneobombus*) *melanurus* Lepeletier, 1835 (thoracic dorsum and T1–2 yellow, T3–6 black). This material was described by Tkalců as most likely lost. This colour pattern has not been seen by us, although we have seen this colour pattern for Afghan *B. asiaticus*.

8. ***Bombus* (*Sibiricobombus*) *tescorum*** Williams nom. nov. et stat. rev.

urn:lsid:zoobank.org:act:E2A94219-04F9-43C9-9F8A-EF80E36FFF78

Figs 1, 7, 9, 49–51, 97

Bombus (*Sibiricobombus*) *regeli* [?Forma] [= subsp.] *miniatocaudatus* Vogt, 1911: 61, not of Vogt, 1909: 56 (= *B. soroeensis* (Fabricius, 1777)).

Bombus (*Sibiricobombus*) *regeli* Ab. *miniatocaudatus* – Vogt 1909: 50 footnote 1, infrasubspecific.
Bombus (*Sibiricobombus*) *asiaticus* – Williams 1991: 87, (in part) misidentification.

Diagnosis

Females

Queens body length 17–20 mm, worker 14 mm. Colour pattern with the hair beneath the base of the hind wing black, thoracic dorsum varying from *either* dull yellow with a narrow black band between the wing bases *to* almost entirely black, metasomal T2 varying from *either* dorsally with at least a few black hairs intermixed along the posterior margin and in the posterior lateral quarter with no black along the midline *to* predominantly black, T4–5 pinkish-orange (Figs 49–50). Morphology with the oculo-malar area anteriorly only sparsely covered with small to medium punctures scattered irregularly; clypeus in the anterior lateral corners with a large patch of large punctures spaced by their own breadths with a dense patch of many small and medium punctures between them; antennal A3 length 3 × greatest breadth; ocello-ocular area with a broad band of dense fine punctures along the inner eye margin, this band along its inner edge with a line of medium and large punctures; hind basitarsus outer surface with short branched hairs not especially dense and partly overlapping so that reflections from the outer surface are partly obscured; (in large individuals) T6 subapically medially with a raised boss.

Males

Body length 16 mm. Colour pattern with the hair on the head black except on the clypeus yellow and the vertex with a few yellow hairs intermixed, side of the thorax yellow, thoracic dorsum dull yellow with a narrow black band between the wing bases, legs black with some yellow, metasomal T1–2 yellow, T2 dorsally usually with at least a few black hairs along the posterior margin and in the posterior lateral quarter but no black along the midline, T4–6 pinkish-orange (Fig. 51). Morphology with the eye greatly enlarged relative to the eye of a female bumblebee, from the dorsal aspect the eye separated from the lateral ocellus by 1 × the ocellar breadth; S6 with the posterior margin in the middle with a deep concave indentation; gonocoxa from the dorsal aspect distally narrower than adjacent spatha, gonostylus distal lobe approximately square, volsella posterior to the gonostylus narrowed and angled inwards towards the body midline, volsella beyond the gonostylus nearly parallel-sided and consistently just broader than its breadth between the distal posterior corners, penis-valve head on its inner side ventrally at the base without a projecting angle, this angle only marked dorsally (Fig. 97).

Type material

Holotype of *Bombus* (*Sibiricobombus*) *regeli* [subsp.] *miniatocaudatus* (by monotypy: Williams 1991)

MONGOLIA • ♂; "Septentrionalis"; Naturalis (examined PW).

Material examined

MONGOLIA • 1 ♂; Hovd, Tsenkher; 46.9676° N, 91.6496° E; 9 Aug. 2014; D. Altanchimeg leg.; BOLD no.: 6880A07 (COI); DA, SB094 • 1 ♀ (queen); Bayan Ölgiy, Bulgan River; 46.5833° N, 91.3667° E; 26 Jul. 1992; A. Culverwell leg.; BOLD no.: 6880D05 (COI); PW, SB066.

RUSSIA – **Tuva** • 1 ♀ (queen); Kaa-Khem, Mt Apedek; 51.7090° N, 94.7869° E; 16–17 Aug. 2010; Y. Danilov leg.; BOLD no.: 6880E03 (COI); PW, SB076.

Distribution

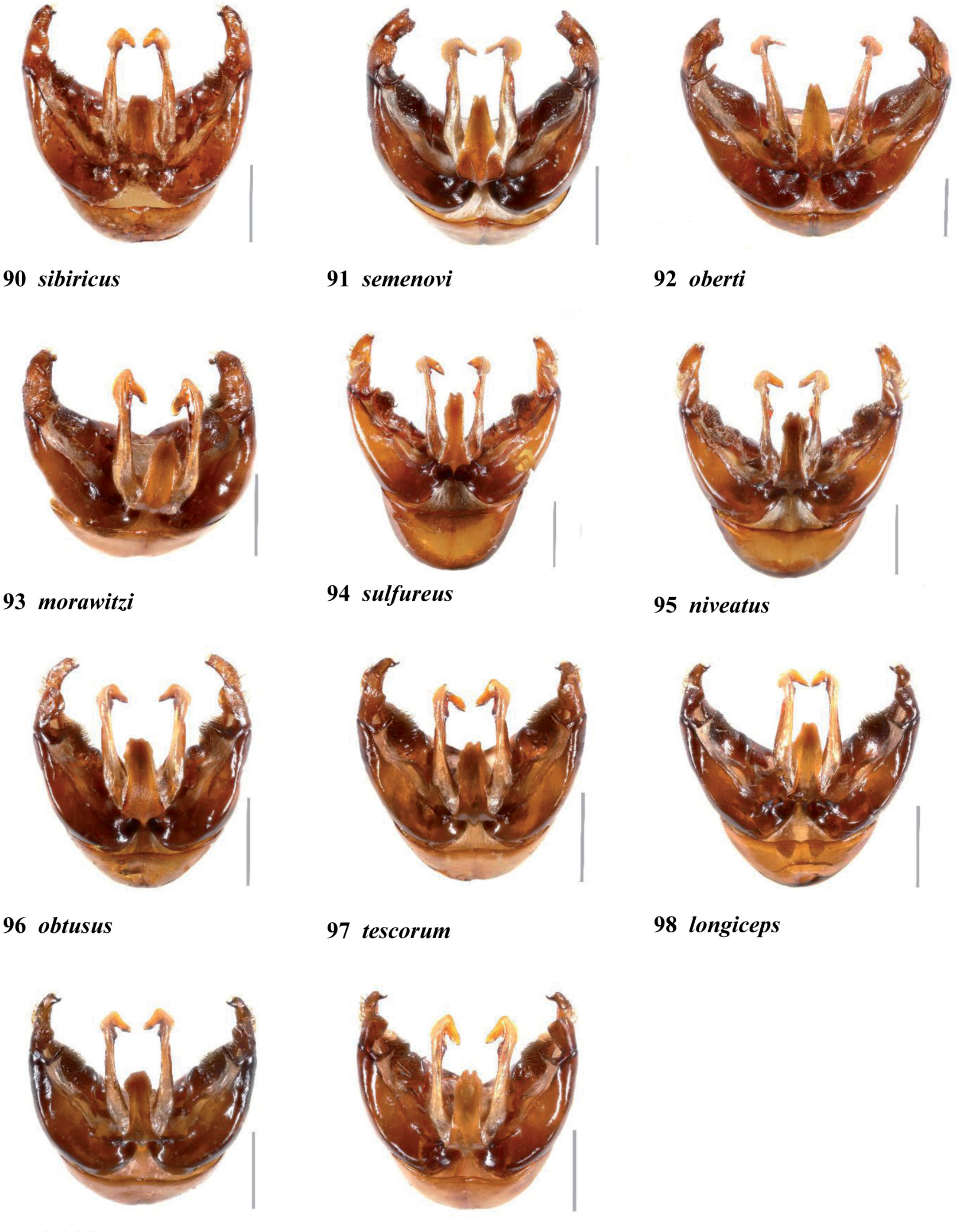
North Asian montane species – North Asia: RUSSIA: Tuva, Altai (Republic); MONGOLIA. (AB, Naturalis, NHMUK, PW.)

Behaviour

Because the male eye is greatly enlarged relative to the eye of a female bumblebee and the male antenna is strongly elongated, the male mate-searching behaviour is expected to be similar to the "racing" behaviour described for "*B. asiaticus*" (actually *B. longiceps* stat. rev.) with these morphological characteristics by Williams (1991).

Taxonomic remarks

Note 1 on the name *B. regeli* ?Forma *miniatocaudatus* Vogt 1911: 61. Vogt (1911) named a taxon "*Sb. regeli miniatocaudatus*", although he gave no explicit reference connecting this name as an indication of his earlier use of a similar name that as an 'Ab.'[erration] was clearly of infrasubspecific in rank (Vogt 1909, see Note 3 below). The 1911 name can be considered as a new proposal at a new status and includes a minimal description to distinguish it from *B. vorticosus* (= *B. niveatus*): *B. regeli* is distinguished from *B. vorticosus* by its consistently longer hair and black pleurae; and *B. regeli* s. str. is distinguished from the taxon *miniatocaudatus* by the latter having the hair of the "Kaudalsegmenten" (tail) red rather than white. The nomenclatural rank of the taxon *miniatocaudatus* Vogt (1911) is not specified explicitly, although in a section on "Neue Hummelformen" and as a trinomen it can by default be considered to be of subspecific rank (ICZN 1999: Article 45.6). Vogt (1911) writes that red-tailed individuals (taxon *miniatocaudatus*) never occur in the "Siebenstromgebiet" [Semirechye] region of Central Asia, implying that it is geographically restricted, which is consistent with subspecific status in the sense of ICZN (see also the comments on type material below), making it an available name. However, while the name *miniatocaudatus* Vogt (1911) may be available, it cannot be the valid name for a bumblebee species because it is a junior homonym in *Bombus* of *B. soroeensis* var. [= subsp.] *miniatocaudatus* Vogt, 1909 (Vogt 1911: 50 footnote 1 states that he intends "*Varietas geographica*" to be equivalent to subspecies in rank; this "variety" is interpreted as having subspecific status because it is also described as regionally restricted: ICZN 1999: Article 45.6.4). Therefore, a new replacement


90 ***sibiricus***

91 ***semenovi***

92 ***oberti***

93 ***morawitzi***

94 ***sulfureus***

95 ***niveatus***

96 ***obtusus***

97 ***tescorum***

98 ***longiceps***

99 ***falsificus***

100 ***asiaticus***

Figs 90–100. Morphology of the male genitalia for species of the subgenus *Sibiricobombus* Vogt, 1911 from the dorsal aspect, anterior at the bottom of the image, posterior at the top. **90**. *B. sibiricus* (Fabricius, 1781). **91**. *B. semenovi* Morawitz, 1887 stat. rev. **92**. *B. oberti* Morawitz, 1883 (left penis-valve head recurved hook missing). **93**. *B. morawitzi* Radoszkowski, 1876. **94**. *B. sulfureus* Friese, 1905 (left penis-valve head recurved hook missing). **95**. *B. niveatus* Kriechbaumer, 1870. **96**. *B. obtusus* Richards, 1951. **97**. *B. tescorum* Williams nom. nov. et stat. rev. **98**. *B. longiceps* Smith, 1878 stat. rev.. **99**. *B. falsificus* Richards, 1930 stat. rev.. **100**. *B. asiaticus* Morawitz, 1875. Images taken by L. Berridge. Scale bars = 1 mm.

name (not a description of a new species) is required for the taxon *miniatocaudatus* Vogt (1911) in the subgenus *Sibiricobombus* (see Note 3 and the comments on type material below).

Note 2 on the replacement name for the name *B. regeli* ?Forma *miniatocaudatus* Vogt, 1911: 61. Because *B. regeli miniatocaudatus* Vogt, 1911 is a junior homonym in the genus *Bombus* of *B.* (*Kallobombus*) *soroeensis* subsp. *miniatocaudatus* Vogt, 1909, the replacement name *B. tescorum* nom. nov. et stat. rev. is proposed here (ICZN 1999: Article 60.3) in order to reduce the confusion that is likely to follow if the name *miniatocaudatus* Vogt, 1911 in the subgenus *Sibiricobombus* were to be propagated in the literature. The replacement name '*tescorum*' (from a meaning of rough or barren regions, wastes, or deserts: thanks to I. Beavis pers. com.) describes what is known of the hilly dry steppe habitat of this species. Vogt (1909) named two taxa "*miniatocaudatus*", a name he used in both cases for red-tailed colour patterns (also in part replaced by more extensive black?). The name for a taxon in the subgenus *Sibiricobombus* was described in the category of 'Ab.', which is specifically given infrasubspecific status by the ICZN (1999: Article 45.6.2).

Note 3 on the type of *B. regeli* ?Forma *miniatocaudatus* Vogt 1911: 61: Vogt (1911) did not designate a holotype or a series of syntypes. However, Vogt (1909) specified that he had a single male with the colour pattern of the taxon *miniatocaudatus* in the subgenus *Sibiricobombus* from Central Asia. Williams (1991) examined a single male in the Vogt collection at the Naturalis, Leiden, that agrees with Vogt's descriptions of the taxon *miniatocaudatus* in the subgenus *Sibiricobombus* from 1911 and carries a hand-written red label "*regeli*=Gruppe / *miniatocaudatus* / Type" and a label Mongolia "Septentrionalis". This specimen is regarded as a syntype of *miniatocaudatus* Vogt, 1911.

The taxon concept of the species *B. tescorum* nom. nov. et stat. rev. here supports it as a species separate from *B. asiaticus*, *B. falsificus* stat. rev., *B. longiceps* stat. rev., and *B. obtusus*, presenting evidence that: (1) our PTP analysis supports independent species-level coalescents in the COI gene (Fig. 1); corroborated by (2) diagnostic morphological character states (see the keys). That the *asiaticus*-group might consist of a series of species has been anticipated by Reinig (1940).

Our concept of the species *B. tescorum* nom. nov. et stat. rev. is considerably narrower than the application of the name *miniatocaudatus* Vogt, 1911 by some authors, which has included yellow-banded and orange-tailed individuals belonging to other species of the *asiaticus*-group, especially of *B. falsificus* stat. rev. (Richards 1930; Wang 1982) and of some *B. asiaticus* (Richards 1930). Reinig (1934) distinguished "dem mongolischen *miniatocaudatus* Vogt" from his taxon "*B. regeli rufocaudatus*" in the Pamir (= *B. asiaticus*) by the lighter (yellow) bands of the latter.

A queen of *B. tescorum* nom. nov. et stat. rev. from Tuva (Russia, SB076) shows almost complete replacement of the yellow hair with black, with only some dull yellow hair remaining intermixed in a transverse band in the middle of T2.

9. ***Bombus* (*Sibiricobombus*) *longiceps*** Smith, 1878 stat. rev.

Figs 1, 7, 9, 52–71, 98

Bombus longiceps Smith, 1878: 8. **Stat. rev**.
Sibiricobombus flavodorsalis Skorikov, 1933: 248, not of Franklin, 1913 (= *B. pensylvanicus* (DeGeer, 1773)). **Syn. nov.**
Sibiricobombus oshanini Skorikov, 1933: 248. **Syn. nov.**
Bombus (*Sibiricobombus*) *huangcens* Wang, 1982: 430. **Syn. nov.**

Bombus (*Sibiricobombus*) *asiaticus* – Williams 1991: 87, (in part) misidentification.

Diagnosis

Females

Queens body length 17–20 mm, workers 11–15 mm. Colour pattern with the hair of the head and legs black, beneath the base of the hind wing bases *either* usually yellow *or* white *or* rarely black, thoracic dorsum *either* bright yellow *or* bright yellow with a black band between the wing bases *or* white with a black band between the wing bases, metasomal T2 *either* part yellow *or* part white, with black at least intermixed along the midline, T3 black, T4–5 *either* usually predominantly orange *or* rarely white *or* black (Figs 52–61). Morphology with the oculo-malar area anteriorly only sparsely covered with small to medium punctures scattered irregularly; clypeus with the anterior lateral corners with a large patch of large punctures spaced by their own breadths with a dense patch of many small and medium punctures between them; antennal A3 length 3 × greatest breadth; ocello-ocular area with a broad band of dense fine punctures along the inner eye margin, this band along its inner edge without medium and large punctures; hind tibia outer corbicular surface in its upper proximal half coarsely sculptured and matt, so that reflections are much interrupted by the prominent sculpturing; hind basitarsus outer surface with short branched hairs not especially dense and partly overlapping so that reflections from the outer surface are partly obscured; (in large individuals) T6 subapically medially with a raised boss.

Males

Body length 13–17 mm Colour pattern with the hair on the head black except on the clypeus *either* yellow *or* white, hair of the side of the thorax *either* yellow *or* white, thoracic dorsum *either* bright yellow *or* bright yellow with a black band between the wing bases *or* white with a black band between the wing bases, hair of the legs predominantly black, metasomal T2 in part *either* yellow *or* white *or* black, T4–6 *either* usually predominantly orange *or* rarely black (Figs 62–71). Morphology with the eye greatly enlarged relative to the eye of a female bumblebee, from the dorsal aspect the eye separated from the lateral ocellus by 1 × the ocellar breadth; S6 with the posterior margin in the middle with a deep concave indentation; gonocoxa from the dorsal aspect distally as broad as adjacent spatha, gonostylus distal lobe approximately square, volsella posterior to the gonostylus narrowed and angled inwards towards the body midline, volsella beyond the gonostylus narrowing to less than its breadth between the distal posterior corners, penis-valve head on its inner side ventrally at the base without a projecting angle, this angle only marked dorsally, penis-valve shaft at its proximal base on its outer side with a deeply marked ‘S’-shaped step, penis-valve head recurved section nearly straight posteriorly at the base (Fig. 98).

Type material

Lectotype of *Bombus longiceps* (by designation of Frison 1935: 340)

INDIA • ♀ (large worker, not a queen); Kashmir, Ladakh Leh; [Aug. to Sep.]; F. Stoliczka leg.; NZSI (examined PW).

Syntypes of *Sibiricobombus flavodorsalis*

INDIA • ♀♀ (queens), Kashmir, Ladakh, Suru valley; ZIN (type not seen but identity not in doubt).

Syntypes of *Sibiricobombus oshanini*

INDIA • ♀♀ (queens), 1 ♂, Kashmir; Ladakh, Nubra valley; ZIN (type not seen but identity not in doubt).

Holotype of *Bombus* (*Sibiricobombus*) *huangcens* (by original designation)

CHINA • ♀ (queen); Xizang, Zanda; 28 Jun. 1976; F. Huang leg.; IZCAS (examined PW).

Material examined

CHINA – **Xizang** • 2 ♀♀ (workers); Burang, Lalongba; 30.2060° N, 81.2523° E; 22 Jul. 2018; IZCAS, SB093/BB24, SB090/BB02.

INDIA – **Himachal Pradesh** • 1 ♀ (queen), 2 ♂♂; Saichu Nalla; 31.6000° N, 78.2670° E; 8 Sep. 1986; A. Hutchings leg.; BOLD nos.: 6880D12, 6880E01, 6880E02 (COI); PW, SB073 to SB075. – **Kashmir & Jammu** • 1 ♀ (queen); Zanskar, Padum; 33.4746° N, 76.8871° E; 30 Jul. 2007; R. Raina leg.; BOLD no.: 1552D10 (COI); RR, SB050 • 1 ♀ (queen); Kashmir, Kazalwan; 34.6464° N, 74.7171° E; 19 Jun. 2007; R. Raina leg.; BOLD no.: 1552E03 (COI); RR, SB046 • 2 ♀♀ (queens); Kashmir, Shah Pora; 34.6552° N, 74.8942° E; 28 Jun. 2009; R. Raina leg.; BOLD nos: 1552D07, 1552D09 (COI); RR, SB047, SB051 • 1 ♀ (queen); Kashmir, Baltal; 34.2648° N, 75.4366° E; 14 Jul. 2008; R. Raina leg.; BOLD no.: 1552D06 (COI); RR, SB048 • 1 ♀ (worker); Kashmir, Gulmarg; 34.0548° N, 74.3856° E; Aug. 1985; P. Williams leg.; BOLD no.: 6880C05 (COI); PW, SB054.

PAKISTAN • 1 ♀ (worker); Skardu; 35.2903° N, 75.6444° E; 31 Aug. 2017; S. Jaffar leg.; BOLD no.: 1552E12 (COI); SJ, SB049 • 1 ♀ (worker); Hindu Kush, Shanduz Pass; 36.0756° N, 72.5200° E; 5 Jul. 2004; V. Gurko leg.; BOLD no.: 6880F07 (COI); MM, SB080.

Distribution

West Himalayan species – East Asia: AFGHANISTAN; PAKISTAN; INDIA: Kashmir & Jammu, Himachal Pradesh, Uttarakhand, Sikkim; NEPAL; CHINA: Xizang. (IZCAS, NHMUK, NKME, PW, SMF, ZIN, ZSI.)

Behaviour

The male eye is greatly enlarged relative to the eye of a female bumblebee and the male antenna is strongly elongated, which is related to the male mate-searching behaviour described for this species (under the misidentified name of *B. asiaticus*) as “racing behaviour” by Williams (1991).

Uniquely (as far as is known), males of this species were found to congregate in groups of up to 10 individuals among grass roots to spend the night torpid, with individually numbered males switching between clusters on successive nights (although this could be the result of disturbance) (Williams 1991: 23).

Taxonomic remarks

The taxon concept of the species *B. longiceps* stat. rev. here agrees with the recent interpretation of a species separate from *B. asiaticus*, *B. falsificus* stat. rev., *B. obtusus*, and *B. tescorum* nom. nov. et stat. rev. (Williams 2022a), presenting the details of evidence that: (1) our PTP analysis supports independent species-level coalescents in the COI gene (Fig. 1); corroborated by (2) diagnostic morphological character states (see the keys). That the *asiaticus*-group might consist of a series of species has been anticipated by Reinig (1940).

The taxa *flavodorsalis* and *oshanini* are re-descriptions of the taxon (yellow unbanded colour pattern) *longiceps* stat. rev.

The species-level coalescent in the COI gene (Fig. 1) also supports as conspecific the yellow-unbanded taxon *longiceps* s. str., the yellow-banded taxon *huangcens*, and the white-banded taxon (*callophenax* of authors other than Cockerell (1917) (= *B. avinoviellus* Skorikov, 1914, see Williams *et al.* 2016)). Sculpturing of the female hind tibia is slightly more coarse and the wings are darker in Kashmir white-banded bees than in yellow unbanded Ladakh bees. Conspecificity is corroborated by their clypeal sculpturing (see the keys). Williams (1991: 115–118) also described how in high mountain passes (near Nigagar and Lal Pani) of the Great Himalaya in Kashmir, where “white-banded” (Kashmir valley) and “yellow-unbanded” (Ladakh) populations meet and produce apparent intermediate colour patterns (and also show some black-tailed colour patterns), the frequencies of states for two out of three colour-pattern characters (for presence/absence of a black thoracic band; and tail red/black) in the haploid males predicted the frequencies in the diploid females (the prediction failed for white/yellow bands). These predictions would be expected to hold if there were simple bi-allelic coding with simple dominance. Crucially, this is consistent with the two regional populations interbreeding as parts of a single species.

10. ***Bombus* (*Sibiricobombus*) *falsificus*** Richards, 1930 stat. rev.

Figs 1, 7, 9, 72–74, 99

Bombus (*Sibiricobombus*) *miniatocaudatus* race [= subsp.] *falsificus* Richards, 1930: 652. **Stat. rev**.
Bombus (*Sibiricobombus*) *heicens* Wang, 1982: 430. **Syn. nov.**

Bombus (*Sibiricobombus*) *asiaticus* – Williams 1991: 87, (in part) misidentification.

Diagnosis

Females

Queens body length 17–18 mm, workers 12–15 mm. Colour pattern with the hair beneath the base of the hind wing black, thoracic dorsum yellow with a narrow black band between the wing bases, lower side of the thorax and legs black, metasomal T1–2 dorsally entirely yellow without black hairs even in the posterior lateral quarter, T4–5 orange (Fig. 72). Morphology with the oculo-malar area anteriorly only sparsely covered with small to medium punctures scattered irregularly; clypeus with the anterior lateral corners with a small patch of large punctures spaced by their own breadths with only a very few scattered small punctures between them; antennal A3 length 3 × greatest breadth; hind basitarsus outer surface with short branched hairs not especially dense, but partly overlapping so that reflections from the outer surface are partly obscured; (in large individuals) T6 subapically medially with a raised boss.

Males

Body length 15–16 mm. Colour pattern with the hair on the head black except on the clypeus yellow, thoracic dorsum yellow with a narrow black band between the wing bases, metasomal T2 dorsally entirely yellow without black hairs even in the posterior lateral quarter, T4–6 orange (Figs 73–74). Morphology with the eye greatly enlarged relative to the eye of a female bumblebee, from the dorsal aspect the eye separated from the lateral ocellus by 1 × the ocellar breadth; S6 with the posterior margin in the middle with a deep concave indentation; gonocoxa from the dorsal aspect distally as broad as adjacent spatha, gonostylus distal lobe approximately square, volsella posterior to the gonostylus narrowed and angled inwards towards the body midline, beyond the gonostylus narrowing to less than its breadth between the distal posterior corners, penis-valve head on its inner side ventrally at the base without a projecting angle, this angle only marked dorsally, penis-valve shaft at its proximal base on its outer side with only a shallowly marked ‘S’-shaped step (Fig. 99).

Type material

Holotype of *Bombus* (*Sibiricobombus*) *miniatocaudatus* race [= subsp.] *falsificus* (by original designation)

CHINA • ♀ (queen); Xizang, Tingri; 4 Jul. 1924; R. Hingston leg.; NHMUK (examined PW).

Holotype of *Bombus* (*Sibiricobombus*) *heicens* (by original designation)

CHINA • ♀ (queen), Xizang, Rutog; 26 Aug. 1976; F. Huang leg.; IZCAS (examined PW).

Material examined

CHINA – **Qinghai** • 1 ♂; Yakou, Nangguanxiu; 36.6821° N, 98.7751° E; 30 Aug. 2010; P. Williams leg.; BOLD no.: 6876C02 (COI); PW, SB052 • 2 ♀♀ (workers); ridge S of Caka; 36.6671° N, 98.7737° E; 9 Aug. 2013; P. Williams leg.; BOLD nos.: 6880D01, 6880D02 (COI); PW, SB062, SB063 • 2 ♀♀ (workers); Kunlun Shan pass; 35.6920° N, 94.0520° E; 13 Aug. 2013; P. Williams leg.; BOLD nos.: 6880D03, 6880D04; PW, SB064, SB065. – **Xizang** • 1 ♀ (queen); Mapang Yongcuo, Sere; 30.7151° N, 81.3662° E; 23 Jul. 2018; IZCAS, SB091/BB20 • 1 ♀ (worker); Xindisang; 32.3551° N, 80.4848° E; 29 Jul. 2018; IZCAS, SB092/BB21

Distribution

East Tibetan Plateau species – East Asia: CHINA: Xizang, Qinghai, Gansu. (IAR, IZCAS, NHMUK, PW.)

Behaviour

Because the male eye is greatly enlarged relative to the eye of a female bumblebee and the male antenna is strongly elongated, the male mate-searching behaviour is expected to be similar to the "racing" behaviour described for "*B. asiaticus*" (actually *B. longiceps* stat. rev.) with these morphological characteristics by Williams (1991). Male perching and "racing" behaviour has been observed on one occasion in Qinghai (PW).

Taxonomic remarks

Note on the name *B. miniatocaudatus* race *falsificus* Richards, 1930: 652: although Richards (1930) uses the term "Subsp." as well as "var." and "race", he states that the taxon *falsificus* is characteristic of a particular geographical area, so this nominal taxon is therefore deemed to be of subspecific rank (ICZN 1999: Article 45.6.4) (Williams 1991).

The taxon concept of the species *B. falsificus* stat. rev. here agrees with the recent interpretation of a species separate from *B. asiaticus*, *B. longiceps* stat. rev., *B. obtusus*, and *B. tescorum* nom. nov. et stat. rev. (Williams 2022a), presenting evidence that: (1) our PTP analysis supports independent species-level coalescents in the COI gene (Fig. 1); corroborated by (2) diagnostic morphological character states (see the keys). That the *asiaticus*-group might consist of a series of species was anticipated by Reinig (1940).

The colour pattern of this species shows little variation. The taxon *heicens* is a re-description of the taxon *falsificus* stat. rev.

11. ***Bombus* (*Sibiricobombus*) *asiaticus*** Morawitz, 1875

Figs 1, 7, 9, 75–89, 100

Bombus hortorum var. [= subsp.] *asiatica* [= *asiaticus*] Morawitz in Fedtschenko, 1875: 4.
BOMBUS BIZONATUS Smith, 1878: 9. **Syn. nov.**
Bombus Regeli Morawitz, 1880: 337.
Bombus regeli var. [= subsp.] *pamirensis* Friese, 1913: 87.
Bombus (*Sibiricobombus*) *regeli* subsp. *diversocaudatus* Reinig, 1932: 257.
Bombus (*Sibiricobombus*) *flavicollis* Wang, 1985: 163.
Bombus (*Sibiricobombus*) *asiaticus* [subsp.] *baichengensis* Wang, 1985: 164.

Bombus regelii – von Dalla Torre 1896: 544, unjustified emendation.

Diagnosis

Females

Queens body length 16–21 mm, workers 9–18 mm. Colour pattern with the hair of the head black and the legs predominantly black, beneath the base of the hind wing *either* usually yellow *or* rarely black, thoracic dorsum bright yellow usually with a narrow black band between the wing bases, metasomal T2 *either* usually nearly entirely yellow without black hairs intermixed along the midline *or* rarely extensively black, T3 black, T4 *either* white *or* buff *or* orange *or* black, T5 *either* white *or* buff *or* orange (Figs 75–82). Morphology with the oculo-malar area anteriorly only sparsely covered with small to medium punctures scattered irregularly; clypeus with the anterior lateral corners with a large patch of large punctures spaced by their own breadths with a dense patch of many small and medium punctures between them; antennal A3 length 3 × greatest breadth; ocello-ocular area with a broad band of dense fine punctures along the inner eye margin, this band along its inner edge without medium and large punctures; hind tibia outer corbicular surface in its upper proximal half weakly sculptured and smooth, so that the shining reflections are scarcely interrupted by the sculpturing; hind basitarsus outer surface with short branched hairs not especially dense but partly overlapping so that reflections from the outer surface are partly obscured; (in large individuals) T6 subapically medially with a raised boss.

Males

Body length 13–18 mm. Colour pattern with the hair of the head and the legs *either* yellow *or* black, the hair beneath the base of the hind wing *either* usually yellow *or* rarely black, thoracic dorsum *either* bright yellow *or* bright yellow with a black band between the wing bases *or* predominantly black with a yellow anterior band, metasomal T1–2 *either* usually nearly entirely yellow without black hairs intermixed along the midline *or* rarely extensively or entirely black, T3 black, T4–6 *either* white *or* orange *or* black (Figs 83–89). Morphology with the eye greatly enlarged relative to the eye of a female bumblebee, from the dorsal aspect the eye separated from the lateral ocellus by 1 × the ocellar breadth; S6 with the posterior margin in the middle with a deep concave indentation; gonocoxa from the dorsal aspect distally as broad as adjacent spatha, gonostylus distal lobe approximately square, volsella posterior to the gonostylus narrowed and angled inwards towards the body midline, beyond the gonostylus narrowing to less than its breadth between the distal posterior corners, penis-valve shaft at its proximal base on its outer side with a deeply marked 'S'-shaped step, penis-valve head on its inner side ventrally at the base without a projecting angle, this angle only marked dorsally, penis-valve head recurved section nearly straight posteriorly at the base (Fig. 100).

Type material

Lectotype of *Bombus hortorum* var. [= subsp.] *asiaticus* (by designation of Williams, 1991)
TAJIKISTAN • ♀ (worker); "Tschiburgan"; 26 Jun. 1871; ZMMU (examined PW).

Holotype of *Bombus bizonatus* (by monotypy)
CHINA • ♀ (queen); Xinjiang, "No locality indicated" [mountains west of Yarkant?]; F. Stoliczka leg.; NZSI (examined PW).

Syntype of *Bombus regeli* (lectotype designation by Podbolotskaya unpubl.)
CHINA • 1 ♀ (queen); Xinjiang, near "Kuldsha" [Yining]; E. Regel leg.; ZIN (examined PW).

Holotype of *Bombus regeli* var. [= subsp.] *pamirensis* (by monotypy)
TAJIKISTAN • ♂; "Pamir-Hochlande"; O. Staudinger leg.; unknown repository (type not seen but identity not in doubt).

Syntypes of *Bombus* (*Sibiricobombus*) *regeli* subsp. *diversocaudatus*
TAJIKISTAN • 13 ♀♀; 'Pamir-darja-Gebiet'; Aug. 1928; W. Reinig leg.; unknown repository (types not seen but identity not in doubt).

Holotype of *Bombus* (*Sibiricobombus*) *flavicollis* (by original designation)
CHINA • ♀ (queen); Xinjiang, Zhaosu; 24 Jul. 1978; Y. Han leg.; IZCAS (examined PW).

Holotype of *Bombus* (*Sibiricobombus*) *asiaticus* [subsp.] *baichengensis* (by original designation)
CHINA • ♀ (queen); Xinjiang, Baicheng; 19 May 1978; X. Zhang leg.; IZCAS (examined PW).

Material examined

KAZAKHSTAN • 1 ♀ (worker); Korday; 43.01° N, 74.01° E; 18 Jun. 2003; BOLD no.: 1549F06 (COI); KUK, SB045 • 1 ♂; Ketmen Mts; [43.3309° N, 80.2188° E]; 14 Jun. 1998; V. Gurko leg.; BOLD no.: 6880F11 (COI); MM, SB084.

KYRGYZSTAN • 1 ♂; Ketmen Mts, Tujuk; [41.4532° N, 71.9314° E]; 6 Jul. 1999; V. Gurko leg.; BOLD no.: 6880F08 (COI); PW, SB081 • 1 ♀ (queen); Sari-Tzelek; [42.10° N, 72.00° E]; 4 Jun. 1995; BOLD no.: 6880F09 (COI); MM, SB082.

TAJIKISTAN • 2 ♀♀ (queens); E of Khorog; 37.4814° N, 71.5938° E; 3 Jun. 2009; L. Best leg.; BOLD nos: 1552H01, 1552H02 (COI); PW, SB005, SB006 • 1 ♀ (worker); E of Khorog; 37.4814° N, 71.5938° E; 16 Jun. 2009; L. Best leg.; BOLD no.: 6880D10 (COI); PW, SB071 • 1 ♀ (queen); E of Khorog; 37.4814° N, 71.5938° E; 17 Jun. 2009; L. Best leg.; BOLD no.: 6880D09 (COI); PW, SB070 • 1 ♀ (queen); Okmamad; 37.6968° N, 72.6968° E; 25 Jun. 2009; L. Best leg.; BOLD no.: 6880D11 (COI); PW, SB072.

Distribution

Central Asian montane species – Central Asia: KAZAKHSTAN, KYRGYZSTAN, TAJIKISTAN, AFGHANISTAN, CHINA: Xinjiang. (IAR, IZCAS, NHMUK, NZSI, PW, UMons, ZIN, ZMMU.)

Behaviour

Because the male eye is greatly enlarged relative to the eye of a female bumblebee and the male antenna is strongly elongated, the male mate-searching behaviour is expected to be similar to the "racing" behaviour described for "*B. asiaticus*" (actually *B. longiceps* stat. rev.) with these morphological characteristics by Williams (1991).

Taxonomic remarks

Note on the name *B. hortorum* var. *asiatica* Morawitz in Fedtschenko 1875: 4: mandatory change in an incorrect original spelling to *asiaticus* (Williams 1991).

The taxon concept of the species *B. asiaticus* here agrees with the recent interpretation of a species separate from *B. falsificus* stat. rev., *B. longiceps* stat. rev., *B. obtusus*, and *B. tescorum* nom. nov. et stat. rev. (Williams 2022a), presenting evidence that: (1) our PTP analysis supports independent species-level coalescents in the COI gene (Fig. 1); corroborated by (2) diagnostic morphological character states (see the keys). That the *asiaticus*-group might consist of a series of species has been anticipated by Reinig (1940).

The species-level coalescent in the COI gene (Fig. 1) also supports as conspecific the white-tailed taxon *asiaticus* s. str. and the orange-tailed taxon *pamirensis*. Conspecificity of these taxa is corroborated by their morphology (see the keys). In addition, (1) some individuals (especially from Afghanistan) have the black band between the wing bases ('inter-alar' band) much reduced or replaced by yellow; (2) some have the pale tail colour replaced by black; and (3) some (especially from Kyrgyzstan and Kazakhstan) have the yellow bands reduced by replacement of yellow hair with black. Colour-pattern variation in Afghanistan and the Pamir is described in more detail by Reinig (1930, 1932, 1940).

The taxon *flavicollis* is a re-description of the taxon (colour pattern) *pamirensis* and the taxon *baichengensis* is a re-description of the taxon (colour pattern) *asiaticus* s. str. (Williams 1998).

Discussion

Numts and species' recognition

When seeking to recognise species by methods such as PTP that use estimates of evolutionary relationships from COI barcodes, it is a basic requirement that orthologous sequences should be used and that paralogous numts should be excluded in order to achieve reliable estimates of evolutionary trees (Song *et al.* 2008; Moulton *et al.* 2010; Williams *et al.* 2023).

Avoiding numts may be difficult to achieve completely (Song *et al.* 2014). The most careful approach would be to use data only with the high AT3% scores (Figs 2–3) and to avoid the lower AT3% scores (Figs 4–5). In revisions of some groups of bumblebees, it may be possible to exclude selectively all of the sequences with the lower AT3% that are likely to be numts (Williams *et al.* 2024). In other groups of bumblebees, for many taxa and with the techniques currently available to us, it may be possible to exclude only the highest-divergence numts (lowest AT3%), because currently it is not straightforward to obtain consistently high AT3% sequences (Williams *et al.* 2023). The justification for including any of the lower-divergence numts here is that lower-divergence numts may be sufficiently similar to orthologous sequences that they will still yield a good approximation to the evolutionary trees that would be obtained from orthologous sequences (although this has yet to be demonstrated).

It may be that there is another explanation for the low AT3% scores in general and that some of them at least are indeed genuine orthologous sequences, but we are unaware of any such explanation. Pragmatically, it does appear that using what appear from their AT3% scores to be lower-divergence numts in coalescent analyses of species for bumblebees of the subgenera *Alpigenobombus* and *Sibiricobombus* supports candidate species that are corroborated by morphological diagnoses. In our results, there are substantially fewer PTP coalescents interpreted as pseudospecies for *Sibiricobombus* (Fig. 1: only one, that splits the taxon *morawitzi*) than was the case for *Alpigenobombus* (Williams *et al*. 2023: fig. 11). However, accepting any likely numts to include in the analysis is not ideal, and a better understanding of these systems and improved barcode extraction are clearly needed.

Steppe specialisation, desert edges, disjunctions, and ancient climate change

More precisely than for many other 'montane grassland' bumblebees (Williams *et al.* 2022), at least some *Sibiricobombus* species are indicators of the transition zones consisting of drier flower-rich grassland between arid deserts and wetter forest meadows. This particular association is shown by several species of *Sibiricobombus* (*B. sibiricus*, *B. semenovi* stat. rev., *B. falsificus* stat. rev., *B. longiceps* stat. rev.) at high elevations in different parts within the QTP, with their distributions tracing broadly the diagonal band of the steppe transition zone (northeast to southwest) between the desert of the north-western corner of the QTP and the forests of the south-eastern corner (Figs 8–9) (supported by field work in Qinghai, China, and Zanskar, India). These species are all absent even from meadows in the wetter forests and meadows of the eastern Himalaya, the south-eastern QTP, and the Hengduan mountains. *Bombus longiceps* and *B. semenovi* also occur in 'islands' of flower-rich refuges isolated amid the drier areas of the western Himalaya and Zanskar (Figs 8–9) (Williams 1991; Williams *et al.* 2015a). Their population genetics and history will be interesting to explore.

A similar pattern of association with steppe transition zones is also continued at lower elevation by *B. sibiricus* in Mongolia and Neimenggu (Fig. 101). This species occurs in the drier steppe zones on either side of the highly arid deserts that cross Central Asia, Mongolia, and North China: i.e., in the northern transitional steppe zone with the forests of northern Mongolia, and in the southern transitional steppe zone with the forests of the North China hills (Fig. 101) (supported by observations during field work in Neimenggu and Gansu).

There are of course broadly similar amphi-desertic patterns shown by many other bumblebee species. The rare *B.* (*Subterraneobombus*) *amurensis* Radoszkowski, 1862 comes closest to *B. sibiricus* in spanning the Asian deserts between Mongolia and Neimenggu (it is also similar in appearance, as a very large, short-haired, and predominantly yellow bumblebee), but it is less abundant and extends less far to the

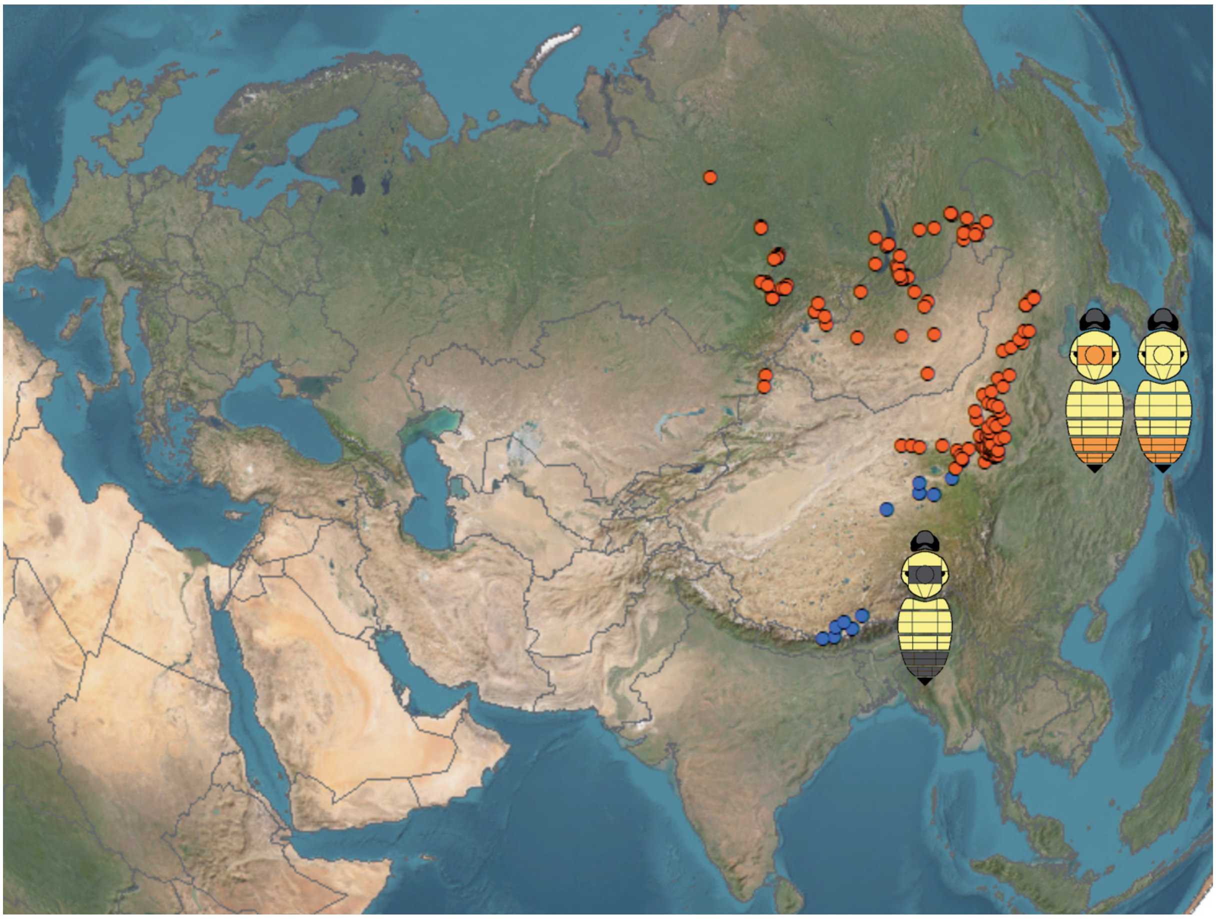


Fig. 101. Map of the distribution of all samples examined for *B. sibiricus* (Fabricius, 1781) s. lat., showing the distributions of the red-tailed taxon (colour pattern) *sibiricus* s. str. (orange spots) and the black-tailed taxon (colour pattern) *flaviventris* Friese, 1905 (blue spots) on either side of the Mongolian deserts (data from the collections of the AB, EA, EB, IAR 2006–2012, IZCAS, LMOB, NHMUK, PW, RJ, UUH, and VLA, all non-Russian specimens identified or checked by PW, together with Russian records identified by AB). The southern border of Mongolia runs through the middle of the desert region where no bumblebees have been found. The yellow area is classified as desert. Spherical projection with international boundaries as recognized by the UN shown as grey lines. Map projected in ArcGIS using the World_Shaded_Relief basemap © 2014 ESRI. The background map is international boundaries on the 'World Imagery' from ESRI with credits to ESRI, Maxar, Earthstar Geographics, and the GIS User Community.

west, at least to the south of the Chinese deserts (Williams *et al.* 2011: fig. 12; An *et al.* 2014: fig. 14). In Russia, both species have at least in the past extended west to Khakassia (AB). It is possible that *B. sibiricus* and *B. amurensis* are both specialising in nesting in the burrows of steppe ground squirrels, because in Neimenggu these squirrels are abundant sunning themselves on the roads in the semi-desert where these bees occur, although the bumblebee nests have not been recorded. A distribution centred on grassland habitats, but broader, is shown by another species of *Subterraneobombus* that often co-occurs with *B. sibiricus*, of the more widespread yellow-and-black-banded *B. melanurus* complex (Williams *et al*. 2012: fig. 100). In addition, several yellow/grey species of the subgenus *Thoracobombus* also span the Asian deserts in a variety of grasslands (most notably *B. laesus* Morawitz, 1875, *B. filchnerae* Vogt, 1908, *B. deuteronymus* Schulz, 1906, and *B. humilis* Illiger, 1806*:* An *et al*. 2014: figs 40, 42, 50, 52). These species are not quite such narrow habitat specialists, but by analogy with their European relatives, they are likely to nest often on the surface of the ground among grass.

There are yet other species that show intriguing amphi-desertic disjunct distributions, but at higher elevations. Some of these species are concentrated in the north-eastern corner of the QTP and in the Mongolian mountains to the north. They include *B. lantschouensis* Vogt 1908 and *B. sichelii* Radoszkowski, 1859, with perhaps the most extreme case being the rare high-elevation *B. margreiteri* Skorikov, 1910 (Williams *et al.* 2016: fig. 65). This particular repeated pattern of disjunction across the deserts has long been known (Panfilov 1957; Williams *et al.* 2017b: figs 1, 6). The pattern may be the result of cooler, wetter periods in the past that provided a bridge of suitable habitat southwards from Mongolia via the North China hills (running from Gansu, to the north of Beijing, towards Harbin) and possibly through part of what is currently the adjacent Neimenggu desert (Barbolini *et al.* 2020).

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Contributions of the authors

Design of the study, PW; collecting specimens for this project, PW, AB, RJ, AM, RR; arranging sequencing of specimens, PW, JH, MO; identification of sequenced specimens, analysis of genetic data and morphological data, and writing of the manuscript and keys, PW; comment and discussion of the manuscript, PW, JA, AB, GG, RJ, JH, MM, AM, MO, RR, MS.

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Supplementary file

Supp. file 1. Gene-sequence data used to produce Fig. 7.
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