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Monograph

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Bumblebees with big teeth: revising the subgenus *Alpigenobombus* with the good, the bad and the ugly of numts (Hymenoptera: Apidae)

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Abstract. The mountain bumblebees of the subgenus *Alpigenobombus* Skorikov, 1914, are uniquely distinctive because the females have enlarged mandibles with six large, evenly spaced teeth, which they use to bite holes in long-corolla flowers for nectar robbing. Recognition of species in this subgenus has been uncertain, with names used in various combinations. To revise the species, we examined COI-like barcodes for evidence of species' gene coalescents using MrBayes and PTP and we compare the coalescent groups with morphological variation for integrative assessment. While we seek to include only orthologous barcodes (the 'good') and exclude all of the more strongly divergent barcode-like numts (the 'bad'), for some nominal taxa only low-divergence numts could be obtained (the 'ugly'). For taxa with no orthologous sequences available, using a minimum number of the lowest divergence numts did yield coalescent candidates for species that were consistent with morphologically diagnosable groups. These results agree in recognising 11 species within this subgenus, supporting: (1) recognising the widespread European *Bombus mastrucatus* Gerstaecker, 1869 **stat. rev.** as a species separate from the west Asian *B. wurflenii* Radoszkowski, 1860 s. str.; (2) the recently recognised *B. rainai* Williams, 2022, as a species separate from *B. kashmirensis* Friese, 1909, within the western Himalaya; (3) the recognition once again of *B. sikkimi* Friese, 1918 **stat. rev.** and *B. validus* Friese, 1905 **stat. rev.** as species separate from *B. nobilis* Friese, 1905 s. str. within the eastern Himalaya and Hengduan regions; (4) confirming the recognition of *B. angustus* Chiu, 1948, *B. breviceps* Smith, 1852 s. lat., *B. genalis* Friese, 1918, and *B. grahami* (Frison, 1933) as separate species within the Himalaya, China, and Southeast Asia; (5) recognising the conspecificity of the nominal taxa (not species) *channicus* Gribodo, 1892 (Southeast Asia) and *dentatus* Handlirsch, 1888 (Himalaya) as parts of the species *B. breviceps* s. lat. (southern and eastern China); and (6) recognising the conspecificity of the rare taxon *beresovskii* (Skorikov, 1933) **syn. n.** as part of the species *B. grahami* within China. Nectar robbing by bumblebees is reviewed briefly and prospects for future research discussed.

Keywords. Calibrated phylogeny, coalescent, integrative, robbing, taxonomy.

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Introduction

Management of crops and conservation of wild ecosystems in north-temperate regions of the world depends in substantial part on bumblebees as some of the most important pollinators (Dias *et al.* 1999; Winter *et al.* 2006; Goulson 2010; Ollerton 2020). But because both conservation and management often focus on particular species, it is vital to know both the characteristics of all of the different bumblebee species and also where each of these species occurs (Williams 2022c).

It is estimated currently that there are ca 294 extant species of bumblebees world-wide (PW), all included in the single genus *Bombus* Latreille, 1802 (updated from a global list reviewed in Williams 1998). More than half of this global diversity of bumblebees is in Asia (Williams 1998; Williams & Jepsen 2014),

although despite continuing efforts (Kupyanskaya 1995; Williams *et al.* 2017a; Williams 2022a), we do not yet have a complete published list of species revised according to the current concept of species as evolutionarily independent lineages. The present study is one in a series that addresses this need by revising the species within each of the bumblebee subgenera world-wide.

Alpigenobombus

Bumblebees are divided into 15 monophyletic groups of species, named as subgenera (Williams *et al.* 2008). This review of subgenera includes a broad interpretation of the subgenus *Alpigenobombus* Skorikov, 1914, to include as a synonym *Nobilibombus* Richards, 1968. The subgenus *Alpigenobombus* is a group that is best known for including primarily montane species with females characterised by having mandibles with six large, evenly-spaced teeth. Most of the information known about *Alpigenobombus* comes from the single species of the group that occurs in Europe (e.g., Løken 1973; Rasmont *et al.* 2021) (revised here to *B. mastrucatus* Gerstaecker, 1869). This species is unusual among European bumblebees for routinely biting holes in flowers to rob them of nectar (Løken 1950; see the Discussion), so it is important to understand how the *Alpigenobombus* species as a group affect pollination.

Species of the subgenus *Alpigenobombus* are associated primarily with habitats in mountains, some reaching high into the alpine zone (Williams *et al.* 2009; Williams 2022a). Like many other bumblebees of high mountains, these bees have especially bright colour patterns of the hair with strongly contrasting coloured bands (Figs 1–9). For females, which can sting, these colour patterns have been interpreted as parts of regional Müllerian mimicry groups, whereas the stingless males are Batesian mimics (Williams 2007). These bright patterns can also be quite different both within and between species among different regions, which has contributed to a lack of agreement regarding the number of species accepted within the subgenus. Consequently many of the taxa in this group have at different times been regarded as separate species, or have been put into different combinations that have been regarded as species (e.g., Skorikov 1933b; Bischoff 1936; Tkalců 1968; Wang 1979, 1992; Wang & Yao 1993; Williams 1998, 2022a; Williams *et al.* 2009; Hines & Williams 2012). There has been no complete revision of the group, although from the faunal lists, which were all based on morphological comparisons alone, 11 species were listed by Skorikov (1923), 13 species were listed by Wang *et al.* (Wang 1979; Wang & Yao 1993), and six by Williams (1998) (Table 1). Consequently, there is a need to review the evidence, including more broadly now from genes, in order to ascertain which of these taxa are indeed most strongly supported as separate species.

Obstacles

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

For the first problem, ideas of what species are as applied to bumblebees have changed through time, resulting in profound effects on the lumping and splitting of the taxa named as species (Williams 2022d). For many bumblebees, ideas of species still depend on interpretations based on morphology developed in the nineteenth century (Williams 1998). The approach used was not that 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 cause taxonomy to be practiced increasingly by students in short-term studies that are not supervised by taxonomic specialists (Williams 2022b). In the last decade there has been a change, as a theoretical unified concept of species as ‘evolutionarily independent lineages’ (EILs) (de Queiroz 2007) has become widely adopted. These species are recognised in practice by 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 being: (1) especially closely allied to the theory of EILs through the direct relationship between evolutionary independence and species' coalescents; (2) quantitative; and (3) providing the quantitative assessments of uncertainty that are expected of scientific methods. A more detailed discussion of best practice for how these methods can be applied to bumblebees in order



1 *mastrucatus*



2 *kashmirensis*



3 *kashmirensis*



4 *sikkimi*



5 *nobilis*



6 *genalis*



7 *breviceps*



8 *breviceps*



9 *grahami*

Figs 1–9. Individuals of the subgenus *Alpigenobombus* Skorikov, 1914 (with photo credits). 1. *Bombus mastrucatus* Gerstaecker, 1869, worker Norway robbing (P. Haringsma). 2. *B. kashmirensis* Friese, 1909 s. str., worker China-Sichuan robbing (PW). 3. *B. kashmirensis* (taxon *meinertzhageni* Richards, 1928) worker India-Kashmir-Zanskar (PW). 4. *B. sikkimi* Friese, 1918, worker India-Arunachal (MS). 5. *B. nobilis* Friese, 1905 s. str., worker China-Yunnan (ZR). 6. *B. genalis* Friese, 1918, worker India-Arunachal (MS). 7. *B. breviceps* Smith, 1852 (taxon *dentatus* Handlirsch, 1888) worker China-Yunnan (PW). 8. *B. breviceps* (taxon *channicus* Gribodo, 1892) worker Thailand (CT). 9. *B. grahami* (Frison, 1933) worker India-Arunachal (MS). Some images reversed.

Table 1. Previous lists of taxa interpreted previously as species of the subgenus *Alpigenobombus* Skorikov, 1914, in its present broad sense (to include *Nobilibombus* Richards, 1968) to show equivalence among studies. The last six rows are for species that are no longer interpreted as parts of *Alpigenobombus*.

Skorikov 1923	Wang 1979 + Wang & Yao 1993	Williams 1998	This study
<i>alpigenus</i>		<i>wurflenii</i>	<i>wurflenii</i>
<i>mastrucatus</i>	<i>mastrucatus</i>	<i>wurflenii</i>	<i>mastrucatus</i>
<i>kashmirensis</i>		<i>kashmirensis</i>	<i>kashmirensis</i>
<i>pulcherrimus</i>		<i>kashmirensis</i>	<i>kashmirensis</i>
	<i>meinertzhageni</i>	<i>kashmirensis</i>	<i>kashmirensis</i>
	<i>tetrachromus</i>	<i>kashmirensis</i>	<i>kashmirensis</i>
	<i>sikkimi</i>	<i>nobilis</i>	<i>sikkimi</i>
	<i>chayaensis</i>	<i>nobilis</i>	<i>nobilis</i>
	<i>xizangensis</i>	<i>nobilis</i>	<i>nobilis</i>
	<i>morawitziides</i>	<i>nobilis</i>	<i>validus</i>
	<i>genalis</i>	<i>genalis</i>	<i>genalis</i>
	<i>breviceps</i>	<i>breviceps</i>	<i>breviceps</i>
	<i>channicus</i>	<i>breviceps</i>	<i>breviceps</i>
	<i>dentatus</i>	<i>breviceps</i>	<i>breviceps</i>
	<i>rufocognitus</i>	<i>breviceps</i>	<i>breviceps</i>
	<i>grahami</i>	<i>grahami</i>	<i>grahami</i>
<i>beresovskii</i>			<i>grahami</i>
<i>crotchii</i>		(<i>Crotchiibombus</i>) <i>crotchii</i>	[(<i>Cullumanobombus</i>) <i>crotchii</i>]
<i>haueri</i>		(<i>Brachycephalibombus</i>) <i>haueri</i>	[(<i>Cullumanobombus</i>) <i>haueri</i>]
<i>longiceps</i>		(<i>Sibiricobombus</i>) <i>asiaticus</i>	[(<i>Sibiricobombus</i>) <i>longiceps</i>]
<i>mormonorum</i>		(<i>Separatobombus</i>) <i>griseocollis</i>	[(<i>Cullumanobombus</i>) <i>griseocollis</i>]
<i>morrisoni</i>		(<i>Separatobombus</i>) <i>morrisoni</i>	[(<i>Cullumanobombus</i>) <i>morrisoni</i>]
<i>separatus</i>		(<i>Separatobombus</i>) <i>griseocollis</i>	[(<i>Cullumanobombus</i>) <i>griseocollis</i>]

to address some of the inherent problems is summarised by Williams *et al.* (2020). Global revisions of other subgenera of bumblebees have also been provided by Williams *et al.* (2011, 2012, 2016, 2019), through which these approaches have been refined.

The second problem is that the area to be sampled is huge, with the area of Asia alone, where most of the species occur, covering ca 44.5 million km² (Anonymous 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 specimen use, while the resources available for sampling are very limited. Species of the subgenus *Alpigenobombus* are also not the most abundant among bumblebees, with some species being quite rare. Fortunately, an historically unparalleled geographic sampling coverage has been possible recently through partnerships with local researchers, helped by improved online communications, and 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.

In the subgenus *Alpigenobombus* we have encountered a third problem: that many barcode-like sequences violate the fundamental assumption of homology (Brigandt & Griffiths 2007; Baum & Smith 2012) that is required for the methods to recognise species: by including paralogous ‘numts’ (nuclear copies of mitochondrial sequences: Lopez *et al.* 1994; Zhang & Hewitt 1996; Bensasson *et al.* 2001; Funk & Omland 2003; Leite 2012). Although known from other bees, these pseudogene sequences have been rare or unacknowledged in most previous revisions of bumblebee subgenera.

This study

We revise the species of the subgenus *Alpigenobombus* by taking a broad global over-view. We re-examine evidence from: (1) species’ gene coalescents by seeking sequences of a fast-evolving gene, mitochondrial cytochrome *c* oxidase subunit I (COI), and using the standard ‘barcode’ region; (2) discontinuous variation in skeletal morphology; and (3) discontinuous variation in colour patterns of the hair.

Revising the subgenus *Alpigenobombus* requires developing new best practices for integrating morphological and molecular evidence in circumstances in which sequences can have questionable origin. We assume that we should avoid including obvious numts in our analyses wherever we can use the related orthologous sequences, in order to preserve homology among the samples compared. However, in cases for which we have (so far) been unable to obtain orthologous sequences, we ask: (1) whether we can identify the lowest-divergence numts (most similar to the orthologous sequences); (2) whether including these low-divergence numts in our analyses can yield results that still agree with the morphological evidence; and (3) is this useful?

Material and methods

Sampling

The area of geographical distribution of species of the subgenus *Alpigenobombus* is known to extend across mountains throughout much of Europe and Asia (Skorikov 1923; Williams 1998: map page 122). Some of the greatest diversity in bumblebees is restricted to areas in remote mountain ranges, where access for sampling can be difficult (Williams *et al.* 2017a) and where *Alpigenobombus* species 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 *Alpigenobombus* were identified by PW, including existing collections, new collections made during this study, and many individuals seen in the field in Europe and Asia. Together these form the ‘hypodigm’ samples that are the basis for the ‘species-taxon concepts’ revised here (Simpson 1940; 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 Qinghai-Tibetan Plateau. There has also been extensive field work by 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 50 000 bumblebees identified from surveys across all of the provinces of China in one collection (IAR) alone (Williams *et al.* 2017a).

Sampling effort 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 largely supplied 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 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:

BEEP	=	Bee Protection Laboratory, Chiang Mai University, Chiang Mai, Thailand
CAU	=	China Agricultural University, Beijing, China
CUNHM	=	Chulalongkorn University Museum of Natural History, Bangkok, Thailand
HNS	=	Haus der Natur, Salzburg, Austria
IAR	=	Institute of Apicultural Research, Chinese Academy of Agricultural Sciences, Beijing, China
IEAUG	=	Institute of Entomology, Agricultural University of Georgia, Tbilisi, Georgia
IOZ	=	Institute of Zoology, Chinese Academy of Sciences, Beijing, China
KIB	=	Kunming Institute of Botany, Chinese Academy of Sciences, Kunming, China
LSL	=	Linnean Society of London, London, UK
MCSN	=	Museo Civico di Storia Naturale, Genova, Italy
NCBS	=	National Centre for Biological Sciences, Bengaluru, India
NHMUK	=	Natural History Museum, London, UK
NME	=	Naturkundemuseum Erfurt, Erfurt, Germany
PCYU	=	Packer Collection at York University, Toronto, Canada
PW	=	P. Williams research collection, London, UK
RMNH	=	National Museum of Natural History, Leiden, Netherlands
SC	=	S. Cameron research collection, Urbana, IL, USA
SEHU	=	Hokkaido University & Hokkaido University Museum, Sapporo, Japan
SNSB	=	Zoologische Staatssammlung, München, Germany
SS	=	S. Schoder collection, Wien, Austria
TARI	=	Taiwan Agricultural Research Institute, Taipei, Taiwan
TFRI	=	Taiwan Forestry Research Institute, Taipei, Taiwan
USNM	=	United States National Museum of Natural History, Washington DC, USA
ZIN	=	Russian Academy of Sciences Zoological Institute, St Petersburg, Russia
ZMHB	=	Museum für Naturkunde an der Humboldt-Universität, Berlin, Germany
ZSC	=	Zoological Survey of India, Kolkata, India

Species concept and species-discovery methods

We view species in theory for this revision as evolutionarily independent lineages (de Queiroz 2007), which we seek to discover in practice by using an integrative procedure (Schlick-Steiner *et al.* 2010): by comparing evidence for species’ coalescents in a fast-evolving gene (COI) with evidence from morphology and from colour patterns. 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.* 2015). 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 arbitrary segments of clines (Williams 2007). We prefer to label these different colour patterns directly and informally (e.g., ‘yellow-banded’ vs ‘white-banded’) when necessary, to avoid adding unnecessary names requiring time-consuming, formal nomenclatural treatments. We are also especially keen to avoid slipping into imposing 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 ‘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 from online databases (e.g., BOLD: www.boldsystems.org; and GenBank: www.ncbi.nlm.nih.gov/nucleotide/). We used standard barcoding protocols (Hebert *et al.* 2004) implemented in the labs of: (1) the Canadian Centre for DNA Barcoding (CCDB) at Guelph (sequences now in their BOLD database); (2) IAR; (3) KIB; (4) NCBS; (5) CAU; and (6) 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 *Alpigenobombus* 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). One kind of problem that can be present is the formation 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 they are no longer expressed. Now free from stabilising selection, they may then diverge 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 as sequences with in-frame stop codons or indels (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 age may be betrayed by their strongly separated positions on estimated trees, often appearing as basal groups because of their strong divergence (Funk & Omland 2003; Magnacca & Brown 2010).

More recent ‘neonumts’ may be detected by smaller divergences despite lacking indels and stop codons (Moulton *et al.* 2010; Song *et al.* 2014). For example, they may be detected because the normal extreme bias of the bases at codon position three towards the nucleotides adenine (‘A’) or thymine (‘T’) is reduced (Song *et al.* 2008: referred to here as ‘AT3’: orthologous sequences are expected to have an AT bias of around 98–99%). Decay from the extreme AT3 bias of the functional gene may be explained when there is no longer stabilising selection on the non-functional copies to maintain the translation, synthesis and hence function of the protein unit (Carlini *et al.* 2001). In our data, we suspect any sequences with an AT3 bias of <95% (even when lacking stop codons or indels) of being cryptic neonumts, based on extensive unpublished testing against morphological patterns in other groups of bumblebees.

Obtaining a representative gene tree could also be difficult if just some of the 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 branches between them on the gene tree, then this could lead to 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 including only unique haplotypes (Williams 2022b). Unique haplotypes are identified here using the COLLAPSE software (ver. 1.2: <http://collapse.sharewarejunction.com/>), 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 phylogenetic gene trees for the COI-barcode region among samples are estimated here with MrBayes (ver. 3.1.2; Ronquist & Huelsenbeck 2003), which is preferred for estimating phylogeny because it applies explicit evolutionary models and uses a Bayesian approach to uncertainty (Baum & Smith 2012). The best-fit nucleotide-substitution model available in MrBayes for this gene fragment is selected using the Bayesian information criterion (BIC) from MEGA (ver. 6.06; Tamura *et al.* 2013) 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. (Melanobombus) festivus* Smith, 1861. A sample of 10 000 resulting trees is examined for convergence using Tracer (ver. 1.6.0, <https://beast.community/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 they have performed well when applied to bumblebees previously when compared with general mixed Yule/coalescent models (Williams *et al.* 2015, 2016). PTP analysis depends on fitting models to a gene tree in order to model: (1) branching rates on the tree within species; and (2) branching rates 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 representing 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 *Alpigenobombus* has sufficient a priori recognised species, with 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).

Morphology

PW (first author) examined morphological characters of the exoskeleton 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 because intraspecific variation in bumblebees may be substantial).

Integrative assessment of species

The procedure followed here has been to start by comparing samples from across the entire geographical range of the subgenus *Alpigenobombus* 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 separate species only if both any discontinuities in morphology and any fast-gene coalescents 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 alone as sufficient evidence to support separate species.

Assigning names to species

We seek to represent all of the major formally named taxa of the subgenus *Alpigenobombus* in our analysis with COI-like sequences in order to assign these names to the species we recognise and then 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. However, 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 for: (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 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 procedure differs from this traditional practice primarily in emphasising a particular specimen. This process is especially important when revising the subgenus *Alpigenobombus* because species can be closely similar in morphology and in colour pattern. New proxy types may be needed in future studies that require fresh material for more demanding genetic sampling.

Estimating species’ phylogeny

We are essentially extending the most widely accepted estimate for the phylogeny 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’) and nuclear long-wavelength rhodopsin copy 1 (‘opsin’), elongation factor-1 alpha F2 copy (‘Ef-1 α ’), arginine kinase (‘ArgK’), and phosphoenolpyruvate carboxykinase (‘PEPCK’). The older relationships (tree topology) in the Cameron *et al.* tree has 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 Cameron *et al.*’s five genes are still unavailable for some of the species (*B. angustus* Chiu, 1948, *B. genalis* Friese, 1918, *B. sikkimi* Friese, 1918, *B. rainai* Williams, 2022, *B. validus* Friese, 1905, and *B. wurflenii* Radoszkowski, 1860). 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.* 2022a). The aligned data include 5420 base positions with a maximum of data for 4475 base positions. For full data see the online material (Supp. file 1).

Table 2. List of selected available formal names in the species group for the taxa studied of the subgenus *Alpigenobombus* Skorikov, 1914 (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 (AG#n) of the proxy type in the *Alpigenobombus* project database.

Taxon name	Species name	Original type locality	Barcode proxy locality	Specimen ID
<i>angustus</i>	<i>angustus</i>	Taiwan	Taiwan	#074
<i>beresovskii</i>	<i>grahami</i>	Sichuan	Sichuan	#001
<i>breviceps</i>	<i>breviceps</i>	Zhejiang	Zhejiang	#069
<i>brevigena</i>	<i>mastrucatus</i>	Sweden	Norway	#067
<i>channicus</i>	<i>breviceps</i>	Myanmar	Thailand	#155
<i>chayaensis</i>	<i>nobilis</i>	Xizang	Xizang	#087
<i>dentatus</i>	<i>breviceps</i>	India	Arunachal	#041
<i>flavicante</i>	<i>mastrucatus</i>	Pyrenees	France	#066
<i>genalis</i>	<i>genalis</i>	Sikkim	Xizang	#184
<i>grahami</i>	<i>grahami</i>	Sichuan	Yunnan	#076
<i>kashmirensis</i>	<i>kashmirensis</i>	Kashmir	Sichuan	#083
<i>mastrucatus</i>	<i>mastrucatus</i>	Germany	Austria	#165
<i>meinertzhageni</i>	<i>kashmirensis</i>	Kashmir	Qinghai	#084
<i>nobilis</i>	<i>nobilis</i>	Sichuan	Sichuan	#143
<i>rainai</i>	<i>rainai</i>	Kashmir	Kashmir	#081
<i>sikkimi</i>	<i>sikkimi</i>	Sikkim	Arunachal	#206
<i>stramineus</i>	<i>kashmirensis</i>	Kashmir	Xizang	#085
<i>validus</i>	<i>validus</i>	Gansu	Gansu	#091
<i>wurflenii</i>	<i>wurflenii</i>	Caucasus	Georgia	#065
<i>xizangensis</i>	<i>nobilis</i>	Xizang	Xizang	#183

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 substitution 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, a log-normal relaxed clock model, a calibrated Yule model, a prior added to identify the outgroup (*B. (Melanobombus) festivus*) and monophyletic ingroup, with the MCMC set to 10 million generations, sampled every 10 000 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 (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 *Alpigenobombus*: Dehon *et al.* 2019). The date for the crown node of the subgenus *Alpigenobombus* 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 of Cameron *et al.* (2007). We follow the procedure of Hines (2008) in fixing the date of the crown divergence within the genus *Bombus* at 34 Ma in order to estimate a crown date here for *Alpigenobombus* with a mean age of 6.33 Ma (95% highest posterior density interval 2.5 Myr, approximated with a sigma of 0.65 Myr). 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 were possible (reviewed by Williams *et al.* 2017b, 2022a), a model of potential corridors for dispersal (assuming suitable climates and habitats in all appropriate periods) is defined specifically for the subgenus *Alpigenobombus* 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 when 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 colonisation can be assessed, as illustrated in an example for ancestral *Mendacibombus* species in Central Asia (Williams *et al.* 2017b).

Area units 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 individual species; (3) to offset the bias 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 a sample of trees) of the BioGeoBEARS methods (Matzke 2013a, 2013b, 2014) from a library in *R* (*R_Core_Team* 2017) within the RASP package (ver. 4.2, accessed 2020: Yu *et al.* 2020). S-BioGeoBEARS uses a sample of 10 000 ultrametric trees in the results from BEAST. The DIVALIKE+J model 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

Sampling

The sampling programme for the subgenus *Alpigenobombus* yielded 207 sequences (of which only 21 sequences are from Europe, so that Europe with a low diversity of *Alpigenobombus* is not highly over-sampled relative to Asia). Five sequences were rejected after GenBank BLAST identification checks for being non-*Alpigenobombus* contaminants or misidentifications (three other sequences were also similar

to *Pyrobombus* Dalla Torre, 1880, AG#204–206). Many of the remaining sequences are identical to one another for the available barcode-like segments. Excluding identical sequences leaves 73 sequences that are available for use by this project.

Preliminary analysis of gene coalescents

MrBayes analysis of the 73 available COI-like sequences over 10 million MCMC generations after a 10% burn-in had converged on stable traces. The best estimate from PTP analysis of these data (Fig. 10) for the number of candidate species is 17 (95% confidence-interval estimate 14–23 species). In this tree, some nominal taxa (identified from morphology) occur in more than one PTP candidate species across the tree (*sikkimi*, *xizangensis* Wang, 1979). One of the groups identified as PTP candidate species also includes a diversity of morphology as indicated by including both of these nominal taxa.

Minimising the more divergent numts

Our first tree (Fig. 10) can be re-drawn (Fig. 11) with interpretations of each sequence's numts status shown in different colours.

Highlighted in purple are those sequences within MrBayes groups that: (a) are recognised by PTP as what appear to be duplicate candidate species that include nominal taxa also appearing elsewhere in the tree in other PTP candidate species, but which are not supported as separate species by being morphologically diagnosable from these other PTP candidate species (Fig. 10); and (b) branch earlier than the other duplicate PTP candidate species containing the same nominal taxa, nearer to the base of the tree. These purple sequences are interpreted as likely to be older and more divergent numts, which are supporting PTP pseudospecies.

Our second tree (Fig. 11) also shows the AT3% of each sequence at the right-hand end of each sequence's label. Some sequences have high AT3% ($\geq 95\%$), as expected for orthologous COI sequences, and these are shown in black (or grey for *sikkimi* AG#204, see below). For example, the sequences of the nominal taxon *sikkimi* AG#204–206, with higher AT3% (in black or grey), are interpreted as orthologous sequences of a PTP candidate species, *B. sikkimi*. In contrast, the sequences of the nominal taxa *sikkimi* AG#005, 207 and *xizangensis* AG#148 (in purple) all have distinctly lower AT3% than the other PTP candidate species that includes the nominal taxon *sikkimi* and these purple sequences are interpreted as likely to be numts within a pseudospecies.

Similar earlier-diverging and lower AT3% distinctions are shown (Fig. 11) by the sequence *genalis* AG#40 (purple, as a likely pseudospecies) compared with the sequences *genalis* AG#184, 185.

In contrast, the early-diverging sequences for *grahami* (Frison, 1933) AG#94, 150, 203 (purple) are not distinguished from another later-diverging sequence *grahami* AG#76 by lower AT3%, but only by their isolated relationships, as three separate single-sequence, early-branching PTP candidate species (interpreted as likely to be three pseudospecies).

The remaining sequences of the *breviceps*-group and the PTP candidate species *mastrucatus* and *rainai* (Fig. 11) all have low AT3% ($< 95\%$) and these are interpreted as likely to be younger (less divergent) numts. These sequences are highlighted in red (or orange or brown). Among these likely numts, we seek to identify the longest sequences with the least divergence from the unknown (but preferred) orthologous sequences, as evidenced by their higher AT3% (shown in orange or brown in Fig. 11). These sequences have an AT3% of preferably 94–93%, although for some nominal taxa the maximum AT3% attained among the available sequences is lower (as shown to the right of each sequence label in Fig. 11 for the taxa *angustus*, *beresovskii* Skorikov, 1933, *breviceps* Smith, 1852, *channicus* Gribodo, 1892, *dentatus* Handlirsch, 1888, *grahami*).

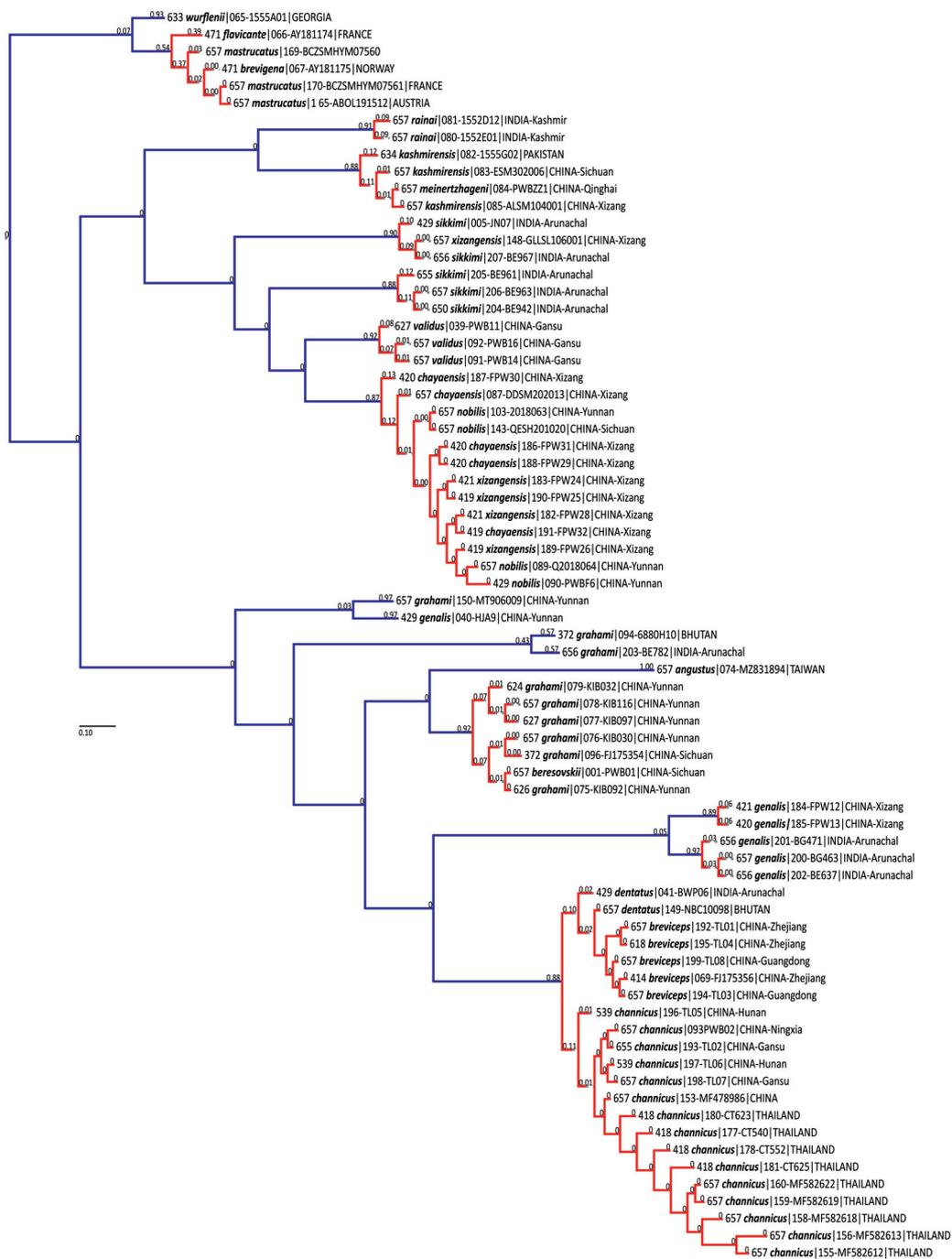


Fig. 10. Default interpretation of MrBayes estimate of phylogeny as a metric tree (outgroup *B. festivus* Smith, 1861, not shown) for the subgenus *Alpigenobombus* Skorikov, 1914, from COI-like sequences from GenBank and BOLD databases with additions from the authors, analysed with Bayesian Poisson-tree-process (PTP) models for assessing support for species' gene coalescents by maximum likelihood (PTP scores are shown above branches: scores approaching 1, and where branches change from blue to red, indicates where the most likely species' gene coalescents are identified for 17 candidate species). The scale bar is calibrated in substitutions per nucleotide site. Each sequence is labelled with: sequence length; a morphological taxon name; 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.

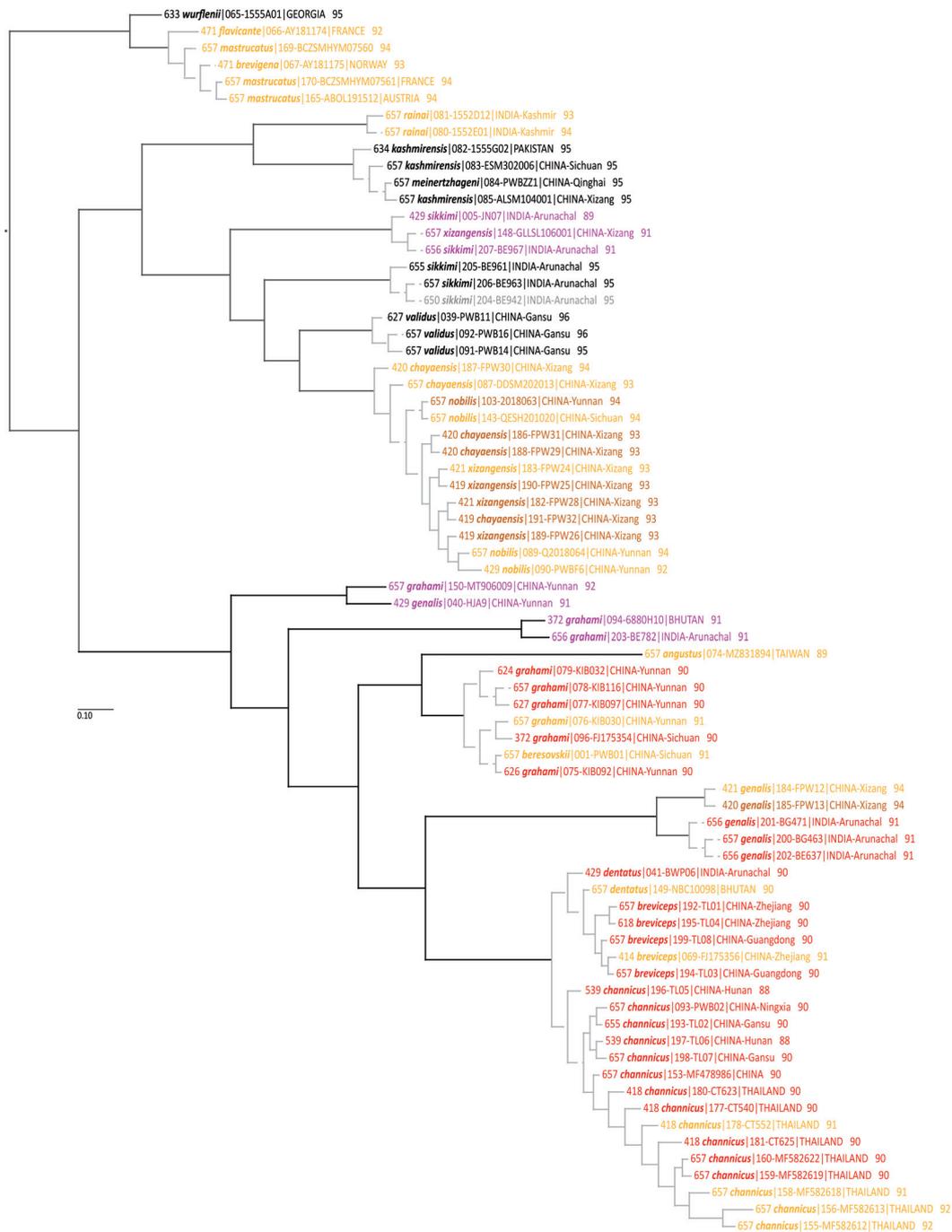


Fig. 11. Re-interpretation of sequences from Fig. 10, re-drawn with the percentage of nucleotides A and T at codon position 3 (AT3%) for each sequence given after the sequence label. Sequences are classified: (a) in purple – earlier-diverging groups of sequences without unique morphology that often have lower AT3% and shorter sequences that appear to duplicate species as pseudospecies in Fig. 10 – these sequences are interpreted as older, more divergent numts; (b) red – remaining sequences with low AT3% (<95%) – these are interpreted as younger, less divergent numts; (c) orange – sequences from the red group but with the highest AT3% available for some taxa, selected to retain these taxa in the analysis; (d) grey and brown – sequences that are duplicate haplotypes for the black and orange sequences above and often shorter; (e) black – likely orthologous sequences with high AT3% ($\geq 95\%$) and unique haplotypes.

In order to avoid using what are likely to be the most misleading numts sequences (shown in purple and red in Fig. 11) for recognising candidate species (and to reduce over-sampling), we remove the purple and red sequences from further analysis. We minimise the number of orange sequences used to represent the nominal taxa by removing the shorter duplicate sequences (shown in brown or grey; although a single sequence is retained to represent each of the nominal taxa *brevigena* Thomson, 1870, and *xizangensis*) and then re-assess the remaining black and orange sequences for a separate ‘filtered’ MrBayes and PTP analysis (Fig. 12). Ideally, we would not use any of the orange sequences, but then the majority of nominal taxa (*angustus*, *beresovskii*, *breviceps*, *brevigena*, *channicus*, *chayaensis* Wang, 1979, *dentatus*, *flavicante* Pérez, 1890, *genalis*, *grahami*, *mastrucatus*, *nobilis* Friese, 1905, *rainai*, *xizangensis*) would be lost from the analysis. Therefore, including a minimum number of orange sequences is considered the least-worst compromise, with the imperfect data available at present, for representing all of the principal nominal taxa.

Candidate species from species’ gene coalescents in the filtered data

Tracer showed that the last MrBayes analysis of the 33 COI-like haplotypes (filtered as described above) over 10 million MCMC generations after a 10% burn-in had converged on stable traces. After 10% burn-in the traces were stable and the minimum effective sample size (ESS) was 7320. The best estimate from PTP analysis (Fig. 12) for the number of candidate species is 11 (95% confidence-interval estimate 10–19 species). The 11 candidate species are represented by between one and six unique haplotypes.

If the orange sequences in Fig. 11 are numts, then the tree in Fig. 12 should include sequence-transfer events from the mitochondria to nuclei in order to properly represent the gene tree. There is a minimum of four events. These are likely to be associated (Fig. 12: grey spots) with the branches leading to: (1) the most recent common ancestor (MRCA) of *B. mastrucatus*; (2) the MRCA of *B. rainai*; (3) the MRCA of *B. nobilis*; and (4) the MRCA of the *breviceps*-group.

Morphology and integrative assessment

The 11 PTP candidate species in Fig. 12 are all diagnosable by morphology as described in the key below, including those with single haplotypes. The differences among some species pairs in the sculpturing of the exoskeleton are in some cases subtle, but they are consistent for the samples studied. Maps of the geographical distribution of the sequenced samples for the 11 candidate species (Figs 13–15) indicate the species’ approximate geographical range extents. These maps show that the distributions of the 11 candidate species are spatially coherent, in the sense that they do not show the very wide, inter-continental disjunctions that might (in some cases) indicate falsely lumped species. Several of the different candidate species are also overlapping while maintaining their distinct morphological character, which appears to confirm a lack of interbreeding (a necessary, but no longer sufficient, property of species). Therefore the 11 PTP candidates in Fig. 12 are all accepted as species.

Assigning names to species

The 11 species of the subgenus *Alpigenobombus* recognised from the integrative assessment are named by adopting as the valid name for each species the oldest available name with reference to our sequenced proxy types (from Table 2) in Fig. 12, based on the primary types. In only one case, that of *B. sikkimi*, have we been unable to obtain a representative gene sequence from the taxon with the oldest available name in its narrowest sense. The nomenclature of species is summarised in outline in the Synopsis section below.

Species’ phylogeny estimation

After ten million MCMC generations with BEAST, a sample of 10 000 trees with a 10% burn-in shows ESS values from Tracer that are > 305 for all of the trace statistics.

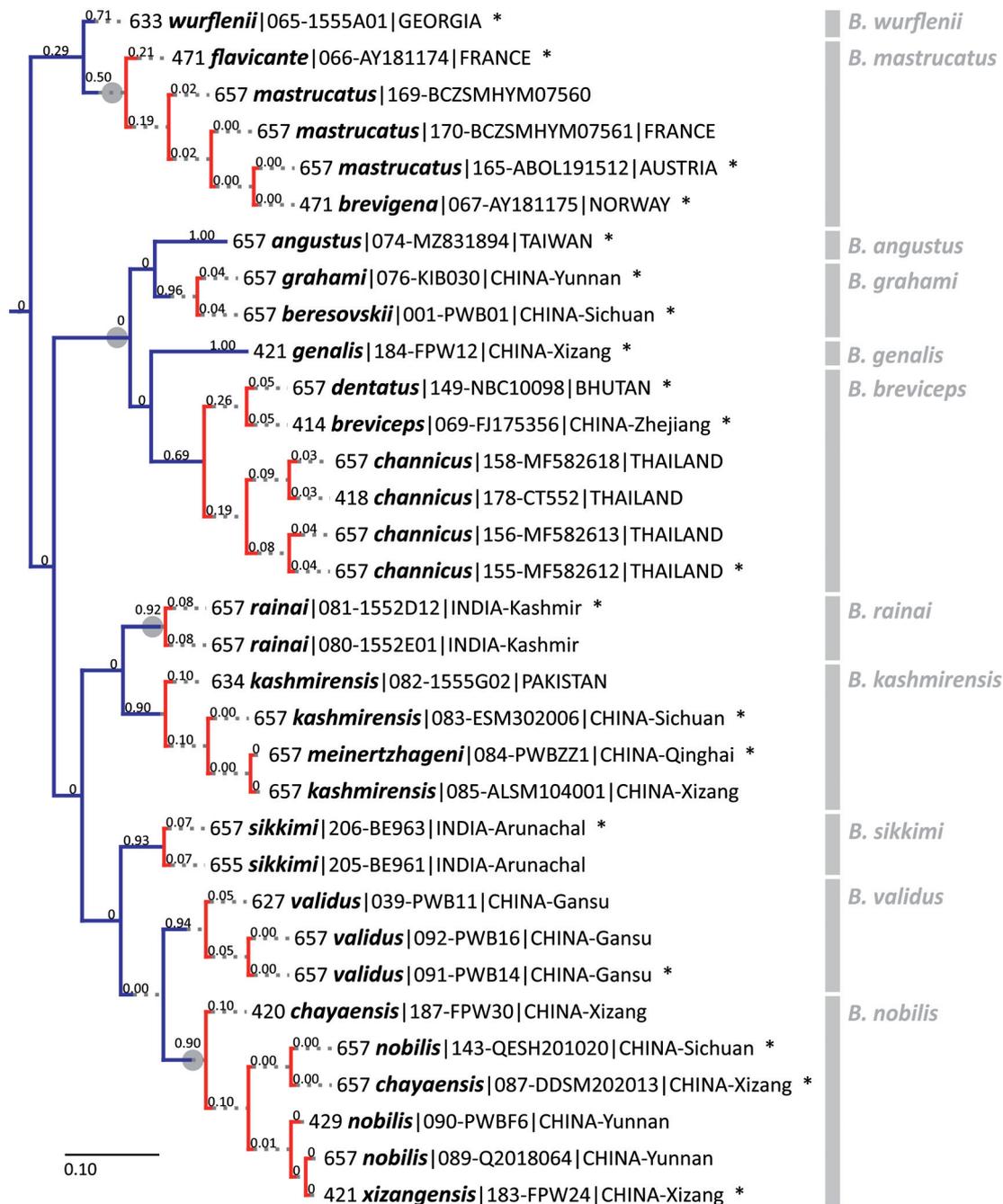
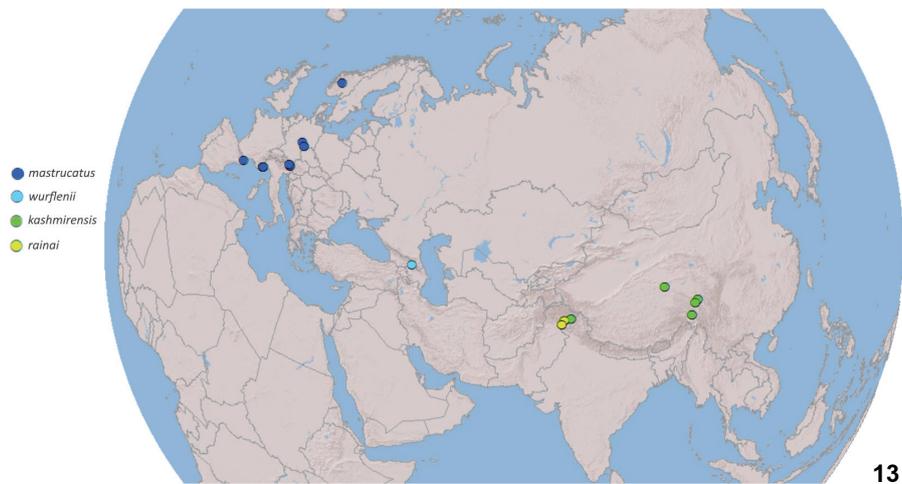


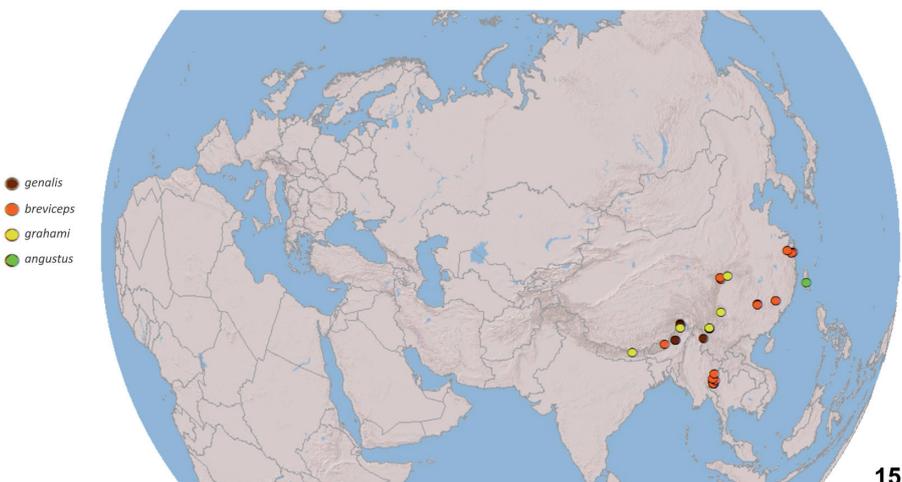
Fig. 12. Interpretation of filtered MrBayes estimate of phylogeny as a metric tree (outgroup *B. festivus* Smith, 1861, not shown) for the subgenus *Alpigenobombus* Skorikov, 1914, from COI-like sequences from the sequences identified in black and orange in Fig. 11 together with Bayesian Poisson-tree-process (PTP) models re-applied for assessing support for species' gene coalescents by maximum likelihood (for the 11 most likely candidate species). The scale bar is calibrated in substitutions per nucleotide site. Sequence labels and branch colours as in Fig. 10. Numbers above nodes are the Bayesian support values that all daughter haplotypes are parts of a single species. Grey spots show likely mitochondrial-to-nuclear transfers of the low-divergence numts accepted for estimating this tree. Asterisks mark sequences used as informal proxies for the type specimens of each of the taxon names in Table 2. To the right in grey are shown the interpretations of the PTP results as candidate species using the oldest available names for the species.



13



14



15

Figs 13–15. Distribution of the barcoded samples (and matching haplotypes) of the subgenus *Alpigenobombus* Skorikov, 1914, from Fig. 10 with their interpretation as the 11 species from Fig. 12 and from the associated morphology in the keys, shown as differently coloured spots as in the colour keys on the left, to indicate the approximate relative range extent among the species. **13.** The *wurflenii*-group and *kashmirensis*-group. **14.** The *nobilis*-group. **15.** The *breviceps*-group. Relief map with hill shading, Cartesian orthonormal projection, the international boundaries shown as narrow grey lines. Images created in ArcGIS using World_Shaded_Relief basemap which is Copyright: ©2014 Esri.

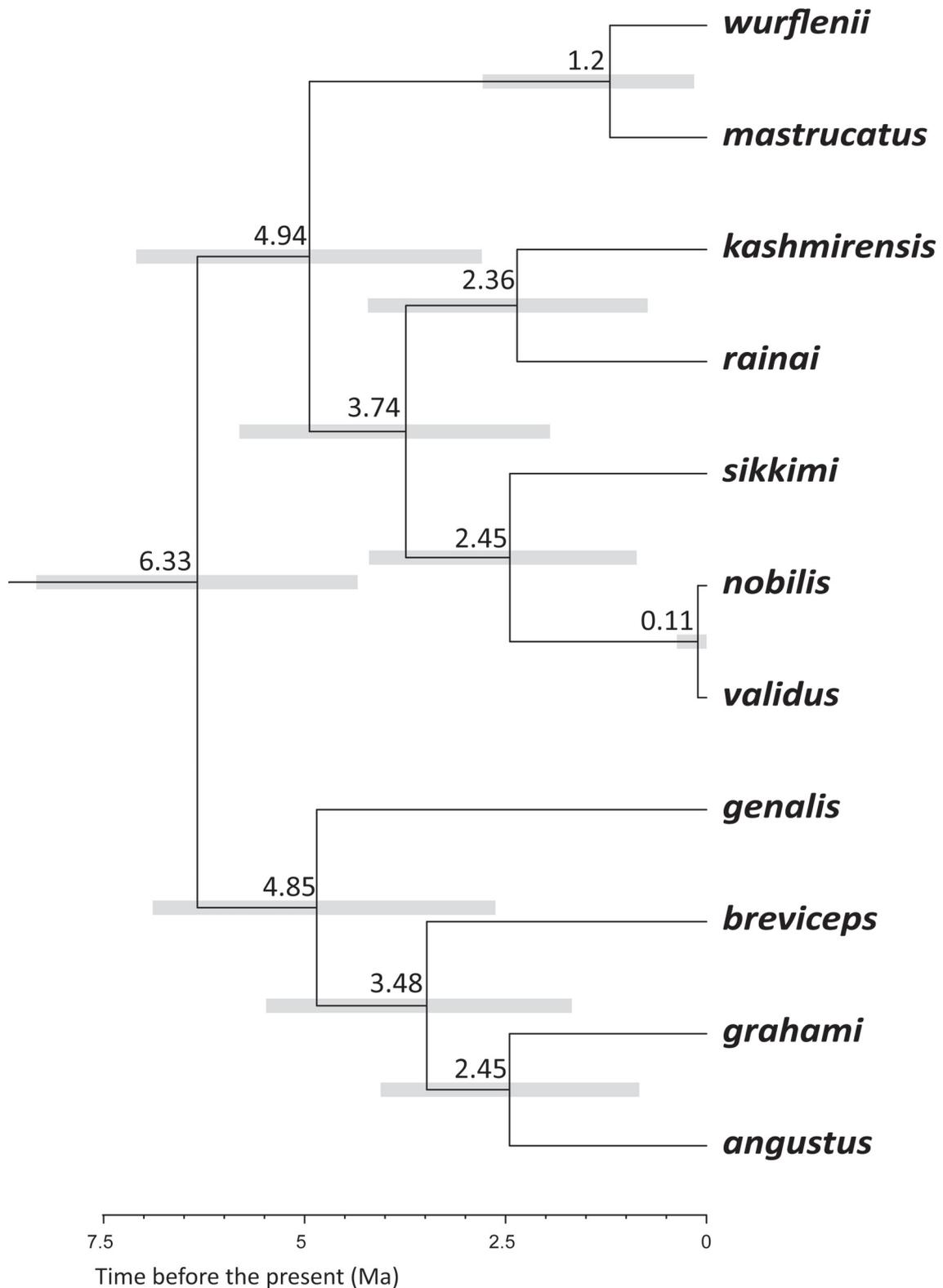


Fig. 16. BEAST estimate of species' dated phylogeny as an ultrametric tree (outgroup *B. festivus* Smith, 1861, not shown) from six genes for the subgenus *Alpigenobombus* Skorikov, 1914. All nodes have support values >0.98 . Numbers at nodes are estimates of the age of a node in Ma before the present, with grey node bars representing the 95% highest posterior density interval of the age estimates.

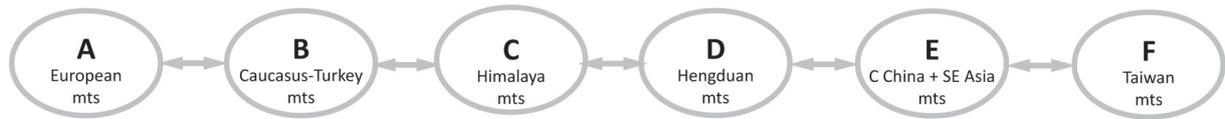


Fig. 17. Diagram representing a corridor-dispersal model, encompassing a set of short-distance dispersal events permitted (in either direction) between the proposed areas of endemism, based on unique taxa, the geographical proximity of these areas, and the likely disposition of corridors with suitable habitat and favourable climates in the past.

From the estimate of the species tree for the subgenus *Alpigenobombus* in Fig. 16 we recognise: (1) a *wurflenii*-group of two species; (2) a *kashmirensis*-group of two species; (3) a *nobilis*-group of three species; and (4) a *breviceps*-group of four species.

Ancestral distribution estimation

The explicit model for dispersal among areas of species' endemism is shown in Fig. 17. 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 permissible dispersal corridors in this model are: AB ABC BC BCD CD CDE DE DEF 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 *Alpigenobombus* from the DIVALIKE+J analysis is shown in Fig. 18. All of these events can be resolved, requiring only the short-distance dispersal as proposed in Fig. 17, if suitable habitat were available at the appropriate times in all of the corridors.

The earliest, most recent common ancestor of the subgenus *Alpigenobombus* is most likely to have been distributed in the Himalayan area (which includes the adjacent part of southern Xizang). Notably, all of the early descendent lineage distributions are estimated to include the Himalayan area. This is where most of the extant species persist (Fig. 18). Later divergences within the *wurflenii*-group are centred on the Caucasus and European areas (the common ancestor of the *wurflenii*-group is likely to have dispersed westwards from the Himalaya through the Iranian and Armenian highlands and into Europe). In addition, the group of *B. nobilis* + *B. validus* shows the most recent divergence within the Hengduan area.

Synopsis of world species

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

Subgenus *Alpigenobombus* Skorikov, 1914

= *Mastrucatobombus* Krüger, 1917.

= *Nobilibombus* Richards, 1968.

We associate a total of 83 published formal names with species of the subgenus *Alpigenobombus* (including misspellings and infrasubspecific names). Applying the ICZN (1999) rules for an assessment of the status of these names under Article 45.6, just 55 names are considered to be

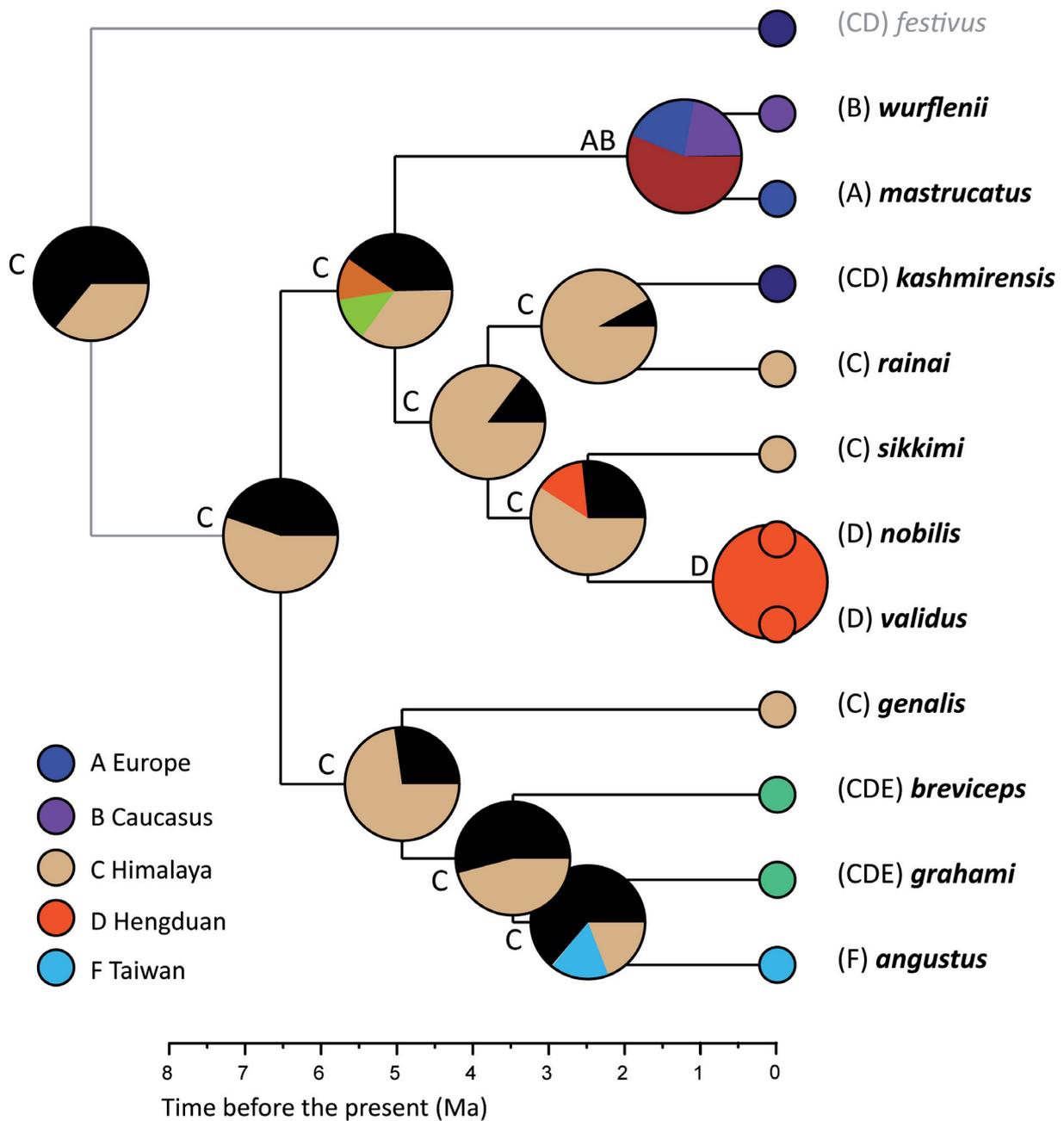


Fig. 18. Most likely ancestral ranges reconstructed for all extant currently recognised species from the dispersal model in Fig. 17, using the model DIVALIKE+J in S-BioGeoBEARS from a sample of 10000 trees from BEAST used to make the estimates of species phylogenies from the six genes in Fig. 16. Letters represent the area units in Fig. 17: letter combinations at terminals show species' current distributions (key lower left show the colour codes used for the principal areas of endemism, other colours not in the key represent combinations of areas e.g., darker green for area combination CDE, with black for a mixture of other areas); letter combinations at nodes show the most likely reconstructions for ancestral distributions; pies at nodes indicate the percentage of solutions for that node in which solutions occur (area E does not occur alone in any ancestor distribution). Numbers on the x-axis are ages in Ma before present. Outgroup shown in grey.

available (most unavailable names are not listed here, but are in a database, PW in prep.). 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 (Williams 1998). There are few novel arrangements of the names here because there have been so many different re-arrangements in the past, although our results show the currently supported interpretation.

The subgenus *Mastrucatobombus* Krüger, 1917 is a synonym of *Alpigenobombus*. The subgenus *Nobilibombus* Richards, 1968 has been included within the subgenus *Alpigenobombus* (Williams *et al.* 2008), based on evidence from the five genes obtained by Cameron *et al.* (2007). The name *Nobilibombus* was published initially without fixation of a type species (Skorikov 1933b), or as a junior synonym (Bischoff 1936; Milliron 1961), so the first valid publication is by Richards (1968). The species of *Nobilibombus* are recognised here as the *nobilis*-group of species.

wurflenii-group

- Bombus wurflenii* Radoszkowski, 1860 s. str.
 - = *alpigenus* Morawitz, 1874
 - = *uralicus* (Tkalčů, 1969)
- Bombus mastrucatus* Gerstaecker, 1869 stat. rev.
 - = *brevigena* Thomson, 1870
 - = *flavicante* Pérez, 1890
 - = *pyrenaicus* Vogt, 1909
 - = *collaris* Friese, 1909
 - = *transitorius* Friese, 1909
 - = *lutescens* Friese, 1909
 - = *luteus* Friese, 1909
 - = *tirolensis* Friese, 1911
 - = *apfelbecki* Reinig in Reinig & Rasmont, 1988
 - = *knechteli* Reinig in Reinig & Rasmont, 1988
 - = *balcaniensis* Rasmont, Ghisbain & Terzo, 2021

kashmirensis-group

- Bombus kashmirensis* Friese, 1909
 - = *stramineus* Friese, 1909
 - = *tetrachromus* Cockerell, 1909
 - = *pulcherrimus* (Skorikov, 1914)
 - = *meinertzhageni* Richards, 1928
- Bombus rainai* Williams, 2022

nobilis-group

- Bombus sikkimi* Friese, 1918 stat. rev.
- Bombus nobilis* Friese, 1905 s. str.
 - = *xizangensis* Wang, 1979
 - = *chayaensis* Wang, 1979
- Bombus validus* Friese, 1905 stat. rev.
 - = *morawitziides* (Skorikov, 1933)

breviceps-group

- Bombus genalis* Friese, 1918
- Bombus breviceps* Smith, 1852 s. lat.

- = *nasutus* Smith, 1852
- = *dentatus* Handlirsch, 1888
- = *simulus* Gribodo, 1892
- = *channicus* Gribodo, 1892
- = *laticeps* Friese, 1905
- = *orichalceus* Friese, 1916
- = *brevigenalis* Friese, 1918
- = *rufocognitus* Cockerell, 1922
- = *pretiosus* Bischoff, 1936
- = *cantonensis* Bischoff, 1936
- = *coloricontrarius* Tkalcù, 1968
- = *colorilaetus* Tkalcù, 1968
- = *vicinus* Tkalcù, 1968
- = *bischoffiellus* Tkalcù, 1977
- Bombus grahami* (Frison, 1933) s. lat.
- = *beresovskii* (Skorikov, 1933) syn. nov.
- = *melani* Wang & Yao, 1993 syn. nov.
- Bombus angustus* Chiu, 1948

Key to species for females of the subgenus *Alpigenobombus*

Future identification of species of the subgenus *Alpigenobombus* will be most reliable for specimens from which COI-barcode-like data are available for comparison of nucleotide differences with the reference data we provide in supplementary data. Keys using morphological shape, surface sculpturing, and hair-colour-pattern characters follow below. Our results imply that in some cases we should be able to assign most reliably the specimens with locality labels to groups or 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 for each species.

Diagrams showing the major aspects of variation in the colour-patterns of the dorsal hair are presented in Figs 19–105. These diagrams summarise only the major differences (Williams 2007) rather than finer details (e.g., Williams 1991: figs 295–310). 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 from COI barcodes for each diagram. Morphology of the male genitalia is illustrated in Figs 106–115.

1. Oculo-malar area (= malar area) shorter than broad (OM length measured as the minimum distance between the eye ventrally and concave margin between the mandibular condyles (hinges); OM breadth measured as the distance between and including the mandibular condyles) 2
 - Oculo-malar area longer than broad 9
2. Clypeus adjacent to the labrum not raised in the centre but flat so that the transverse anterior groove is not interrupted, this central area uniformly with many small punctures and not shining (Europe, Turkey, Caucasus, Urals) 3
 - Clypeus adjacent to the labrum slightly raised in the centre so that the transverse anterior groove is interrupted, this central area with few small punctures and more shining than the surrounding areas (Asia east of Pakistan) 4
3. Ocello-ocular area (= ocellocular area) with the punctures anterior to the unpunctured area (adjacent to the lateral ocellus and between it and towards the inner ocular margin) less dense than posterior to it; hair of the thoracic dorsum *either* entirely black *or* sometimes with bands anteriorly and

- posteriorly yellow (Figs 26–30) (Europe, in Scandinavia, Pyrenees, Alps, Carpathians, Greece) **B. mastrucatus** Gerstaecker, 1869 stat. rev.
- Ocello-ocular area with the punctures anterior to the unpunctured area at least as dense as posterior to it; hair of the thoracic dorsum black with bands anteriorly and usually posteriorly white (Figs 19–22) (Turkey, Caucasus, Urals) **B. wurflenii** Radoszkowski, 1860 s. str.
4. Wings *either* clear *or* very lightly clouded with brown, T1-2 with hair predominantly (nearly completely) *either* white *or* yellow (occurring at elevations above 3000 m) 5
- Wings *either* darkly clouded with brown *or if* pale yellow *or* nearly clear *then* T1-2 with hair black (occurring at elevations below 3000 m) 6
5. Oculo-ocular area in its outer half with large and medium punctures; hair of T5 orange with white tips, the side of the thorax in at least its upper half and the scutellum *either* white *or* yellow (Figs 35–41) (Himalaya, Hengduan) **B. kashmirensis** Friese, 1909
- Oculo-ocular area in its outer half with only a few small shallow punctures, any larger punctures confined to the eye margin; hair of T5 entirely orange without paler tips, the side of the thorax in no more than its upper third white and the scutellum predominantly black (Figs 49–51) (Kashmir) **B. rainai** Williams, 2022
6. Wings very darkly clouded with brown, hair of T1 *either* yellow *or* grey *or* white 7
- Wings *either* pale yellow *or* nearly clear, hair of T1 black 8
7. Clypeus in its central area with many small punctures, many spaced by only their own widths; hair of the thoracic dorsum black, often with orange bands anteriorly and posteriorly, T1 yellow (Figs 76–84) **B. breviceps** Smith, 1852
- Clypeus in its central area with only a few large and small punctures, most spaced by more than their own widths; hair of the thoracic dorsum black, *either* usually with many grey hairs intermixed so as to appear silvery olive-grey, with the majority of the hair along the longitudinal midline white, *or if* entirely black *then* T1 predominantly grey-white (Figs 94–100) **B. grahami** (Frison, 1933)
8. Mid and hind tibiae with exoskeleton and hair bright orange; wings pale yellow with the veins orange; clypeus in its central area with widely-scattered large punctures and only a few micro-punctures that are more widely-spaced than their own widths (Fig. 74) (Himalaya) **B. genalis** Friese, 1918
- Mid and hind tibiae with the exoskeleton and hair predominantly black; wings nearly clear with the veins black; clypeus in its central area with widely-scattered large punctures and many small punctures that are as widely spaced as their own widths (Fig. 104) (Taiwan) **B. angustus** Chiu, 1948
9. Oculo-ocular area sparsely punctured with few scattered medium-sized punctures with few small punctures between them with broad smooth areas; hair of the side of the thorax and scutellum predominantly black, T2–3 with only a few black hairs along the midline (Figs 70–71) (Sichuan, Gansu) **B. validus** Friese, 1905 stat. rev.
- Oculo-ocular areas densely punctured with scattered medium-sized punctures with many small punctures between them and lacking smooth areas; hair of the side of the thorax and scutellum predominantly *either* grey *or* yellow, T2–3 usually with a few black hairs along the midline and a transverse band of black hairs (Himalaya, Hengduan) 10
10. Oculo-ocular area antero-lateral to the lateral ocellus with large and small punctures sufficiently separated to have flat shining areas in between (= interspaces) (at least for queens, differences weaker for workers); hair on the anterior dorsum of the thorax *and* of the side of the thorax *and* scutellum

- either* golden yellow *or* grey-white, on the scutellum the yellow hair anteriorly incompletely divided in the middle by black, T1 yellow, T2 *either* predominantly black *or* with anterior lateral patches yellow (Figs 61–66) (Hengduan) ***B. nobilis*** Friese, 1905
- Oculo-ocellar area antero-lateral to the lateral ocellus with large, medium and many small punctures almost coalescing and without flat shining areas in between (= interspaces) (at least for queens, differences weaker for workers); hair on the anterior dorsum of the thorax *and* of the side of the thorax *and* scutellum *and* T1 *either* grey *or* olive-yellow, on the scutellum the pale hair anteriorly often deeply divided in the middle by a triangle of black, T2 *either* predominantly yellow *or* with large anterior lateral patches yellow (Figs 54–57) (Himalaya) ***B. sikkimi*** Friese, 1918 stat. rev.

Key to species for males of the subgenus *Alpigenobombus*

1. Oculo-malar area shorter than broad (OM length measured as the minimum distance between the eye ventrally and concave margin between the mandibular condyles (hinges); OM breadth measured as the distance between and including the mandibular condyles); genitalia with the gonocoxa with the distal (posterior) inner corner not projecting inwards (Figs 106–109, 113–115) 2
 - Oculo-malar area longer than broad; genitalia with the gonocoxa with the distal (posterior) inner corner projecting strongly inwards (Figs 110–112) 9
2. From the region including European, Turkish, Caucasus and Ural mountains 3
 - From the region including the mountains of Asia east of Pakistan 4
3. Hair of the thoracic dorsum between the wing bases predominantly black, usually with few or no yellow hairs (Figs 31–34) (Europe, especially in Scandinavia, Pyrenees, Alps, Carpathians, Greece) ***B. mastrucatus*** Gerstaecker, 1869 stat. rev.
 - Hair of the thoracic dorsum between the wing bases *either* predominantly yellow *or* with many yellow hairs (Figs 23–25) (Turkey, Caucasus, Urals) ***B. wurflenii*** Radoszkowski, 1860 s. str.
4. Genitalia with the penis valve distally recurved as a sickle by more than 90° with the hook much longer than broad (Figs 108–109) (occurring at elevations above 3000 m) 5
 - Genitalia with the penis valve distally recurved as a sickle by just 90° with the hook scarcely longer than broad (Figs 113–115) (occurring at elevations below 3000 m) 6
5. Hair of the side of T5–6 orange at the base but white-tipped, T3 predominantly black, the side of the thorax *either* yellow *or* white, the pale hair reaching to the midleg bases (Figs 42–48); genitalia with the penis valve recurved head broad, the recurved section narrowing only just before the tip, gonostylus on its outer side less than half as long as on its inner side (Fig. 108) (Himalaya including Kashmir, Hengduan) ***B. kashmirensis*** Friese, 1909
 - Hair of the side of T5–6 orange, T3 predominantly orange, the side of the thorax with black and white intermixed, but often predominantly black in its lower half (Figs 52–53); genitalia with the penis valve recurved head narrow, the recurved section tapering gradually to the tip, gonostylus on its outer side about half as long as on its inner side (Fig. 109) (Kashmir) ***B. rainai*** Williams, 2022
6. Wings very darkly clouded with brown (Figs 85–93) ***B. breviceps*** Smith, 1852
 - Wings *either* pale yellow *or* nearly clear 7
7. Hair of the thoracic dorsum predominantly black 8
 - Hair of the thoracic dorsum yellow, often between the wing bases with many black hairs intermixed (Figs 101–103) ***B. grahami*** (Frison, 1933)

8. Wings pale yellow with the veins orange, the mid and hind tibiae with exoskeleton and hair bright orange (Fig. 75) (Himalaya) **B. genalis** Friese, 1918
– Wings weakly clouded with brown with the veins brown, exoskeleton and hair of the mid and hind tibiae predominantly black (Fig. 104) (Taiwan) **B. angustus** Chiu, 1948
9. Hair of the side of the thorax and scutellum predominantly black, T2–3 with *either* very few *or* no black hairs along the midline and no transverse band of black hairs (Figs 72–73); genitalia with the gonostylus on its outer side less than half its greatest length (Fig. 112) (Sichuan, Gansu)
..... **B. validus** Friese, 1905 stat. rev.
– Hair of the side of the thorax and scutellum predominantly *either* grey *or* yellow, T2–3 usually with many black hairs along the midline and at least a narrow transverse band of black hairs *either* posteriorly on T2 *and/or* anteriorly on T3; genitalia with the gonostylus on its outer side more than half its greatest length (Fig. 110–111) (Himalaya, Hengduan) 10
10. Hair on the anterior dorsum of the thorax *and* of the side of the thorax *and* scutellum *either* golden yellow *or* grey-white, T1 *either* yellow *or* if nearly white *then* T2 antero-laterally also nearly white, on the scutellum in the middle the yellow only shallowly divided by black (Fig. 67–69); genitalia with the gonostylus with the distal edge concave (Fig. 111) (Hengduan) **B. nobilis** Friese, 1905 s. str.
– Hair on the anterior dorsum of the thorax *and* of the side of the thorax *and* scutellum *and* T1 *either* grey-white *or* dull olive-yellow, T2 antero-laterally yellow, on the scutellum in the middle the grey or yellow nearly completely divided by black (Figs 58–60); genitalia with the gonostylus with the distal edge weakly convex (Fig. 110) (Himalaya) **B. sikkimi** Friese, 1918 stat. rev.

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 (Alpigenobombus) wurflenii*** Radoszkowski, 1860 s. str.
Figs 19–25, 106

Bombus WURFLENI [sic] Radoszkowski, 1860: 482.

Bombus alpigenus Morawitz, 1874: 132.

Alpigenobombus wurfleini subsp. *uralicus* Tkalců, 1969: 891, by indication of Pittioni (1938). Note 1.

Bombus Wurfleini – Radoszkowski 1877: 191, incorrect subsequent spelling.

Bombus Wurflenii – Radoszkowski 1877: 191, incorrect subsequent spelling.

Bombus mastrucatus morpha [not subsp.] *uralicus* – Pittioni 1938: 66, infrasubspecific.

NOTE 1. *Alpigenobombus wurfleini* subsp. *uralicus* Tkalců, 1969: 891, by indication of Pittioni (1938). Lectotype by designation of Tkalců (1969: 893): ♀ (queen) central Ural Mountains (‘Sojmonowsk’), Russia (NHMUK), examined. According to A. Byvaltsev (pers. com.), the type queen of the taxon *uralicus* was collected on the territory of modern Karabash, in Chelyabinsk Oblast (55.4465° N, 60.2151° E, ca 320 m a.s.l., but with ridges 20 km to the southwest that reach to ca 1100 m a.s.l.). The Soymonovsky goldmine (named after V.Yu. Soymonov, chairman of the Temporary Mining Commission responsible for the development of gold in the Middle Urals) and the small settlement Sak-Elginsky Vyselok were located here. Later copper deposits were discovered in the area and the Soymonovsky copper smelter was founded in 1834. The Sak-Elginsky settlement then began to be called Soymonovsky or simply Soymonovsk [= ‘Sojmonowsk’].

Species-taxon concept and variation

The taxon concept of the species *B. wurflenii* is revised here from the widely-cited interpretation since Tkalců (1969), to distinguish *B. wurflenii* from the separate taxon concept for the species *B. mastrucatus* (see the comments below on *B. mastrucatus*), based on: (1) our PTP analysis supports independent species-level coalescents in the COI gene (Fig. 12); corroborated by (2) diagnostic morphological character states (see below and the keys).

The morphological results (see the keys) support the interpretation that the individuals with the divergent colour patterns of the taxa *wurflenii* s. str. (Figs 20–25) and *uralicus* (lectotype queen Fig. 19) are conspecific, although only a single queen of the taxon *uralicus* is available. Only two other individuals of the taxon *uralicus* from the Urals are definitely known at present (A. Byvaltsev pers. com.): a male from 1909 and a female from 1929 (both ZIN).

Variation in the colour-pattern diagrams for *B. wurflenii* in Figs 19–25 is arranged approximately from north (Urals) to south (Turkey). *Bombus wurflenii*, with its white-banded red-tailed female colour pattern in Turkey and the Caucasus, appears to mimic the more abundant *B. (Melanobombus) incertus* Morawitz, 1881, *B. (Ml.) eriophorus* Klug, 1807, and similar species (Williams 2007: fig. 51).

Type material

Bombus WURFLENII Radoszkowski, 1860: 482. Type not seen, but identity not in doubt.

Morphological diagnosis

Female

Wings nearly clear with veins dark brown, hair long, oculo-malar area shorter than broad, clypeus adjacent to the labrum not raised in the centre but flat so that the shallow transverse anterior groove is not interrupted, this central area uniformly with many small punctures and not shining, oculo-ocular area with the punctures anteriorly to the unpunctured area at least as dense as posterior to it (cf. *B. mastrucatus*); hair of the thoracic dorsum black, with bands anteriorly and usually posteriorly grey-white.

Male

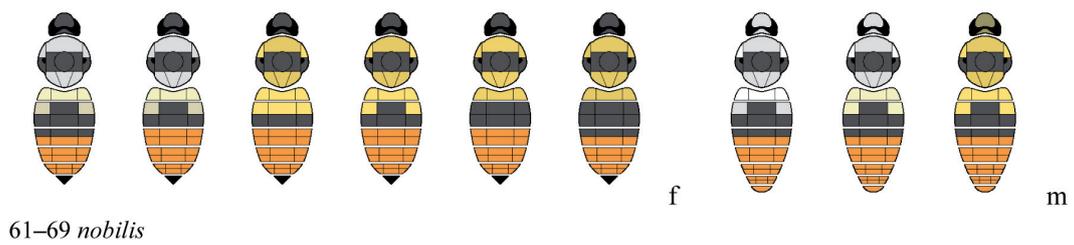
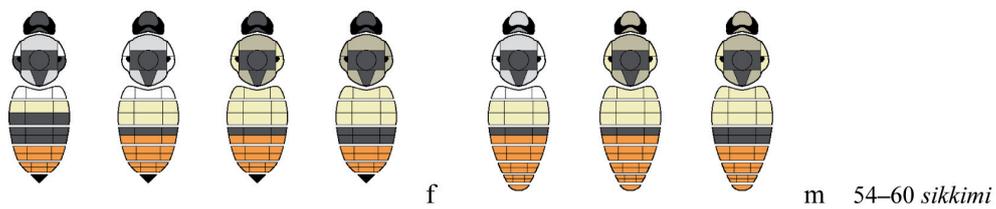
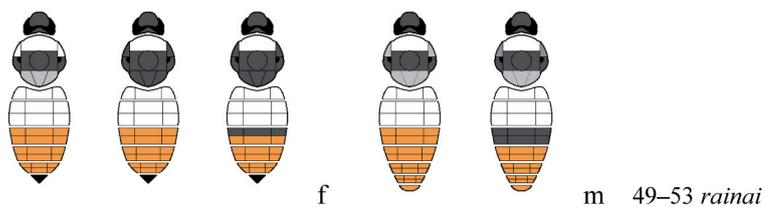
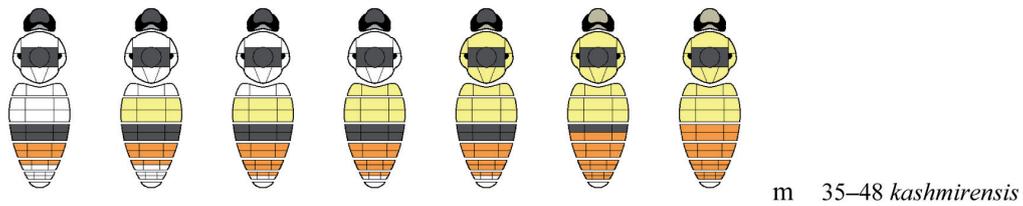
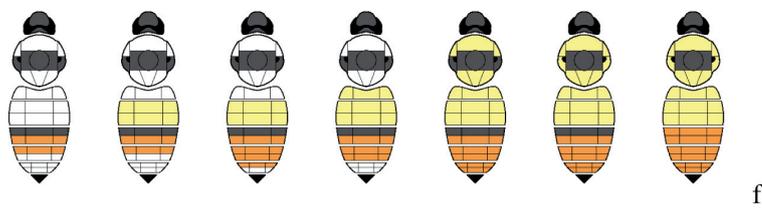
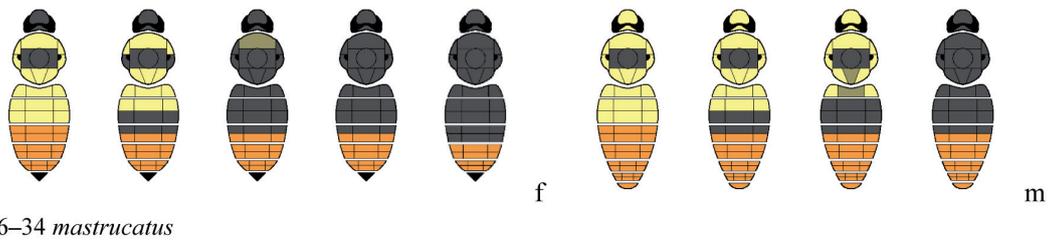
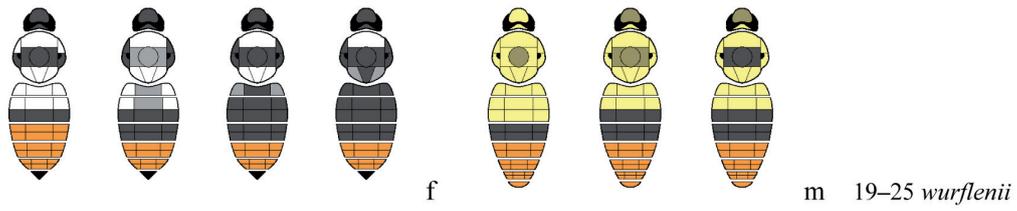
Wings nearly clear with veins dark brown, hair long, oculo-malar area shorter than broad; genitalia (Fig. 106) with the gonostylus long and distally near its midline axis convexly rounded, length on its outer side about a quarter as long as on its inner side with the two inner corners of the distal lobe rounded, the margin between them nearly straight, penis-valve head strongly recurved, the recurved hook much longer than broad and distally at the end of the hook broadly rounded (cf. *B. mastrucatus*); hair of the thoracic dorsum between the wing bases *either* predominantly pale cream-yellow *or* with many pale cream-yellow hairs.

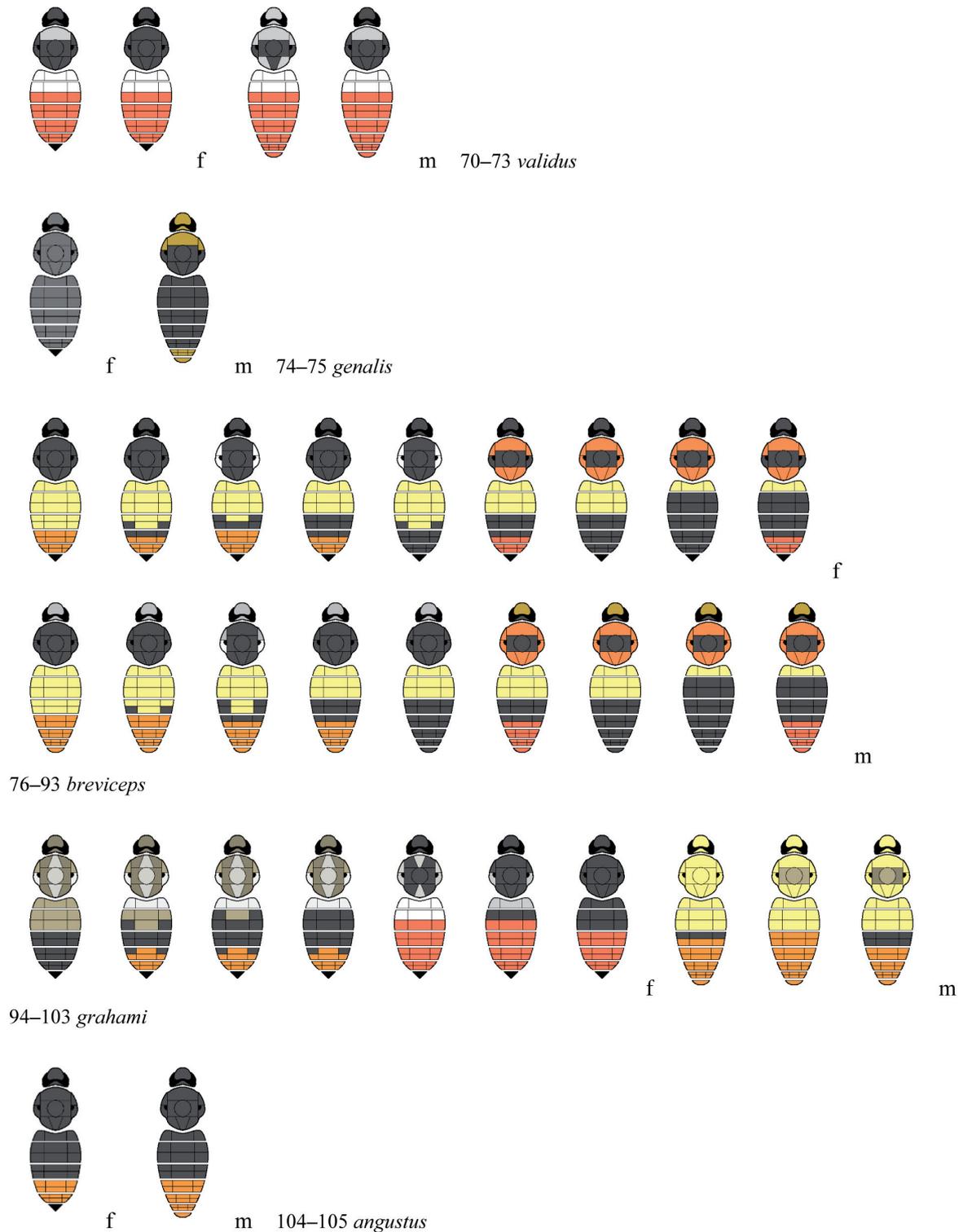
Material sequenced in Fig. 12

GEORGIA • 1 ♀ (queen); Lagodekhi; 41.8714° N, 46.3645° E; 22 Jun. 2015; G. Kirkitadze leg.; BOLD seq: 1555A01; IEAUG: AG#065.

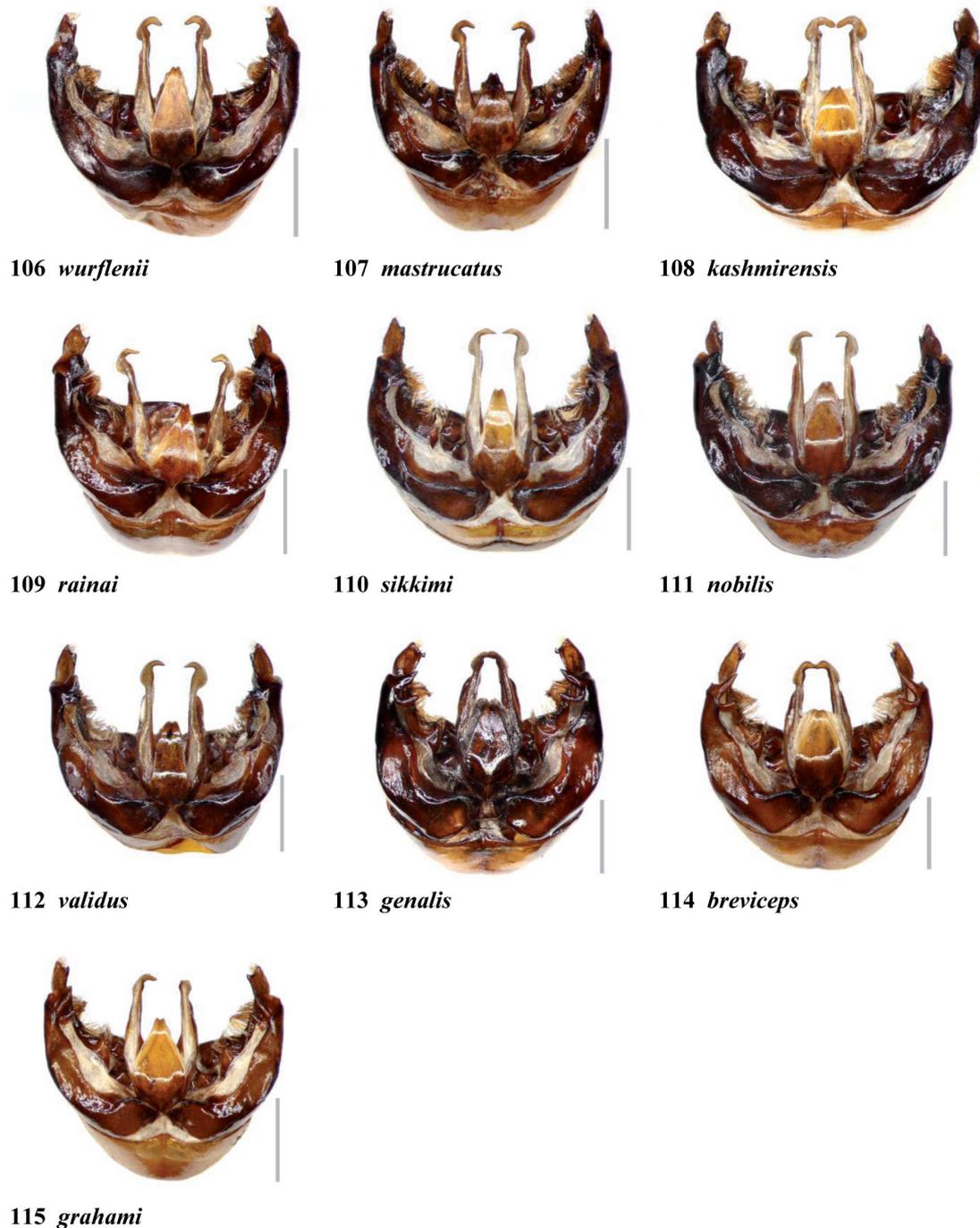
Global distribution

Western Asia: Turkey, Georgia, Armenia, Azerbaijan, Iran, Russia (Caucasus, Urals): IEAUG, NHM, PW, ZIN.





Figs 19–105 (see pages 28–29). Simplified diagrams for the colour patterns of the hair on the dorsum for particular female (f) and male (m) specimens of the species from Fig. 12. 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.



Figs 106–115. Morphology of the male genitalia for species of the subgenus *Alpigenobombus* Skorikov, 1914, from the dorsal aspect, anterior at the bottom of the image, posterior at the top. **106.** *Bombus wurflenii* Radoszkowski, 1860, Turkey. **107.** *B. mastrucatus* Gerstaecker, 1869, Austria. **108.** *B. kashmirensis* Friese, 1909, India-Kashmir. **109.** *B. rainai* Williams, 2022, India-Kashmir. **110.** *B. sikkimi* Friese, 1918, Nepal. **111.** *B. nobilis* Friese, 1905, China-Sichuan. **112.** *B. validus* Friese, 1905, China-Gansu. **113.** *B. genalis* Friese, 1918, China-Yunnan. **114.** *B. breviceps* Smith, 1852, China-Sichuan. **115.** *B. grahami* (Frison, 1933) China-Sichuan (left penis-valve recurved hook missing). Scale bars = 1 mm.

This species is recorded at elevations of 1600–2570 m in Turkey in the montane and subalpine coniferous forest zone (Rasmont & Flagothier 1996) and in the alpine zone in the northern Caucasus (Skorikov 1910).

Behaviour

Male eye not obviously enlarged relative to female eye: males are expected to show ‘patrolling’ behaviour in search of mates (Williams 1991).

2. *Bombus (Alpigenobombus) mastrucatus* Gerstaecker, 1869 stat. rev. Figs 1, 26–34, 107

Bombus mastrucatus Gerstaecker, 1869: 326.

Bombus brevigena Thomson, 1870: 255.

Bombus mastrucatus var. [subsp.] *flavicante* Pérez, 1890b: 475.

Bombus lefebvrei [subsp.] *pyenaicus* Vogt, 1909: 50.

Bombus mastrucatus var. [subsp.] *collaris* Friese, 1909: 673 (not of Scopoli 1763: 306 = *B. pratorum* (Linnaeus)).

Bombus mastrucatus var. [subsp.] *transitorius* Friese, 1909: 673.

Bombus mastrucatus var. [subsp.] *lutescens* Friese, 1909: 673 (not of Pérez 1890a: 154 = *B. flavidus* Eversmann).

Bombus mastrucatus var. [subsp.] *luteus* Friese, 1909: 673.

Bombus mastrucatus var. [subsp.] *tiroloensis* Friese, 1911b: 684, replacement name for *B. mastrucatus* [subsp.] *collaris* Friese, 1909.

Alpigenobombus wurfleini [subsp.] *apfelbecki* Reing in Reing & Rasmont, 1988: 48.

Alpigenobombus wurfleini [subsp.] *knechteli* Reing in Reing & Rasmont, 1988: 49.

Bombus mastrucatus morpha [not subsp.] *kriechbaumeri* – Pittioni 1938: 66, infrasubspecific.

Bombus (Alpigenobombus) wurflenii [subsp.] *balcaniensis* – Rasmont *et al.* 2021: 155, unjustified replacement name. Note 1.

NOTE 1. The earlier name *B. helferanus* f.[orma] *apfelbecki* Pittioni, 1939: 87 (= *B. humilis* Illiger) was given infrasubspecific status (Pittioni 1939: 51), so that the name *apfelbecki* Reing, 1988 remains available and a replacement name is unjustified.

Species-taxon concept and variation

The taxon concept of the species *B. mastrucatus* is revised here from the widely-cited interpretation (since Tkalců 1969), to distinguish *B. mastrucatus* from the separate taxon concept of the species *B. wurflenii* (see the comments above on *B. wurflenii*), based on: (1) our PTP analysis supports independent species-level coalescents in the COI gene (Fig. 12); corroborated by (2) diagnostic morphological character states (see the keys).

Bombus mastrucatus is a widespread European species that had long been well-known by the use of this name by many authors (e.g., von Dalla Torre 1896; Friese & von Wagner 1912; Skorikov 1923; Reing 1935; Pittioni 1937; aside from occasional confusion with *B. lefebvrei* Lepeletier de Saint-Fargeau, [1835] (= *B. pomorum* (Panzer, 1805)) by Strand 1901).

Then Tkalců (1969) reduced the taxon *mastrucatus* to the status of a subspecies within *Alpigenobombus wurfleini* [sic], although without a detailed justification. Subsequently, the name *B. wurflenii* (in various spellings) has been used in most publications for this bumblebee species in Europe (e.g., in influential keys by Løken 1973; Hagen & Aichhorn 2003; Ornosá & Ortiz-Sánchez 2004; Rasmont *et al.* 2021).

Nonetheless, the name *mastrucatus* remains familiar to European bee workers from these same publications, even if only as what has often been interpreted as a subspecies.

The PTP and morphological results (Fig. 12, keys) both support the interpretation that *B. mastrucatus* and *B. wurflenii* are separate species. The available COI-barcode-like sequences may all be low-divergence neonumts (Fig. 11). The PTP and morphological analysis results (Fig. 12, keys) also support the interpretation that the divergent colour patterns of the taxa *mastrucatus* s. str. (Alps: Figs 28–29, 32–33) and *flavicante* (Pyrenees: Figs 26–27, 31–32), as well as the disjunct population of the taxon *brevigena* (Scandinavia: Figs 30, 33–34) are conspecific (no fresh samples were available from eastern Europe for sequencing). No diagnostic characters published for the other named taxa for this group in Europe provide any reason to consider them as candidates for separate species.

Variation in the colour-pattern diagrams of *B. mastrucatus* in Figs 26–34 is arranged approximately from south-west (Pyrenees) to north-east (Norway). *Bombus mastrucatus*, with its unbanded red-tailed colour pattern in northern Europe and its yellow-banded red-tailed colour pattern especially in south-western Europe, appears to mimic the local colour patterns of the abundant *B. (Melanobombus) lapidarius* (Linnaeus, 1758) and similar species (Williams 2007: fig. 5e, j).

Type material

Bombus mastrucatus Gerstaecker, 1869: 326. Type not seen (not found by Tkalců 1969: 892), but identity not in doubt.

Morphological diagnosis

Female

Wings nearly clear with veins dark brown, hair long, oculo-malar area shorter than broad, clypeus adjacent to the labrum not raised in the centre but flat so that the shallow transverse anterior groove is not interrupted, this central area uniformly with many small punctures and not shining, ocello-ocular area with the punctures anteriorly to the unpunctured area in the outer half less dense than posterior to it (cf. *B. wurflenii*); hair of the thoracic dorsum *either* entirely black *or* sometimes with bands anteriorly and posteriorly yellow.

Male

Wings nearly clear with veins dark brown, hair long, oculo-malar area shorter than broad; genitalia (Fig. 107) with the gonostylus long and distally near its midline axis convexly rounded, length on its outer side about a quarter as long as on its inner side with the two inner corners of the distal lobe rounded, the margin between them nearly straight, penis-valve head strongly recurved, the recurved hook much longer than broad and distally at the end of the hook weakly pointed (cf. *B. wurflenii*); hair of the thoracic dorsum between the wing bases predominantly black, usually with few or no yellow hairs.

Material sequenced in Fig. 12

AUSTRIA • 2 ♀♀ (queens); Carinthia, Innere Eben; 46.978° N, 12.759° E; 26 Jul. 2019; W. Wallner leg.; BOLD seq: ABOL19-1511 ABOL19-1512; HNS: AG#164, AG#165 • 1 ♀ (worker); Tyrol, Hohe Tauern; 47.023° N, 12.238° E; 20 Jul. 2020; S. Schoder leg.; BOLD seq: ABOLHT20-S038; SS: AG#166.

FRANCE • 1 ♀ (queen); Roussillon, Prats de Mollo; [42.400° N, 2.483° E]; 25 Aug. 1993; GenBank seq: AY181174; AG#066 • 1 ♀ (queen); Alpes Maritimes, Col Turini; 43.999° N, 7.429° E; 11 Jul. 2010; C. Schmid-Egger leg.; BOLD seq: BCZSMHYM07560; SNSB: AG#169 • 1 ♀ (queen); Alpes Maritimes, Tende; 44.105° N, 7.448° E; 9 Jul. 2010; C. Schmid-Egger leg.; BOLD seq: BCZSMHYM07561; SNSB: AG#170.

NORWAY • 1 ♀ (queen); Buskerud, Mørkedalen; [60.9° N, 8.3° E]; 2 Jul. 1994; GenBank seq: AY181175; AG#067.

Additional sequences in Fig. 10 and haplotype duplicates

FRANCE • 1 ♀ (queen); Alpes Maritimes, Col Turini; 43.999° N, 7.429° E; 11 Jul. 2010; C. Schmid-Egger leg.; BOLD seq: BCZSMHYM07559; SNSB: AG#168.

GERMANY • 1 ♀ (worker); Saxony, Carlsfeld; 50.435° N, 12.585° E; 16 Jul. 2004; F. Burger leg.; BOLD seq: BCZSMHYM08976; SNSB: AG#171 • 1 ♂; Thuringia, Orlamünde; 50.775° N, 11.541° E; 19 Sep. 2001; F. Burger leg.; BOLD seq: BCZSMHYM08978; SNSB: AG#172 • 1 ♂; Saxony, Carlsfeld; 50.435° N, 12.585° E; 16 Jul. 2004; F. Burger leg.; BOLD seq: BCZSMHYM08979; SNSB: AG#173.

Global distribution

Europe: Spain, France, Belgium, Italy, Bosnia and Herzegovina, Montenegro, Serbia, Macedonia, Greece, Germany, Switzerland, Austria, Czechia, Slovakia, Poland, Bulgaria, Romania, Moldova, Ukraine, Norway, Sweden, Russia (Murmansk): HNS, NHMUK, PW, RMNH, SNSB, SS, ZMHB.

This species is recorded at elevations of 1740–2740 in the Eyrer Pyrenees (Iserbyt *et al.* 2008), at 1000–2450 m in Languedoc-Roussillon, France (Rasmont 1988), and at 1500–2600 m in the Alps (Pittioni 1937; Neumayer 1998; Neumayer & Paulus 1999). It has been associated in general with the mountain-forest zone (Løken 1973; Rasmont *et al.* 2021).

Behaviour

Male eye not obviously enlarged relative to female eye: males show ‘patrolling’ behaviour when searching for mates in Austria (Williams 1991).

3. *Bombus (Alpigenobombus) kashmirensis* Friese, 1909

Figs 2–3, 35–48, 108

Bombus mastrucatus var. [subsp.] *kashmirensis* Friese, 1909 [September: Tkalčů 1974]: 673. Note 1.

Bombus mastrucatus var. [subsp.] *stramineus* Friese, 1909 [September: Tkalčů 1974]: 673.

Bombus tetrachromus Cockerell, 1909 [November: Tkalčů 1974]: 397.

Alpigenobombus pulcherrimus Skorikov, 1914: 128.

Bombus (Mastrucatorobombus) mastrucatus subsp. *meinertzhageni* Richards, 1928: 335.

Bombus mastrucatus var. [subsp.] *kashmirensis* – redescribed by Friese & von Wagner 1910: 47.

Bombus mastrucatus var. [subsp.] *stramineus* – redescribed by Friese & von Wagner 1910: 47.

Alpigenobombus pulcherrimus var. [not subsp.] *albidocaudatus* – Skorikov 1914: 129, infrasubspecific.

NOTE 1. Acceptance of *B. kashmirensis* as the valid name in preference to *B. stramineus* follows Skorikov (1923) as the First Reviser (ICZN 1999: Article 24).

Species-taxon concept and variation

The taxon concept of the species *B. kashmirensis* here agrees with the recent interpretation (Williams 2022a) that it is separate from the taxon concept of the species *B. rainai* (see the comments below on *B. rainai*), based on: (1) our PTP analysis supports independent species-level coalescents in the COI gene (Fig. 12); corroborated by (2) diagnostic morphological character states (see the keys).

The PTP and morphological results (Fig. 12, keys) support the interpretation that the divergent colour patterns of the taxa *kashmirensis* s. str., *stramineus*, and *meinertzhageni* are parts of a single species

(Williams 1991). The other named taxa (*tetrachromus*, *pulcherrimus*) appear to be re-descriptions of this species.

Variation in the colour-pattern diagrams of *B. kashmirensis* in Figs 35–48 is arranged approximately from the Hengduan and outer Himalayan ranges (e.g., Pir Panjal: Figs 35–37, 42–44) to the trans-Himalaya (e.g., Zaskar: Figs 39–41, 46–48). *Bombus kashmirensis*, with the white-banded colour pattern in the south (Himalaya) and east (Hengduan) more mesic parts of its range, appears to mimic the abundant *B. (Melanobombus) rufofasciatus* Smith, 1852, and *B. (Ml.) prshewalskyi* Morawitz, 1880 (Williams 2007: fig. 5g), whereas the yellow-banded colour pattern in the north-west (trans-Himalayan mountains) more arid parts of its range appears to mimic the abundant *B. (Ml.) keriensis* Morawitz, 1887, and similar species (Williams 2007: fig. 5j).

Type material

Bombus mastrucatus var. [subsp.] *kashmirensis* Friese, 1909 [September: Tkalců 1974]: 673. Lectotype by designation of Tkalců 1974: ♀ (queen) Kashmir, India (ZMHB). Examined.

Morphological diagnosis

Female

Wings nearly clear with veins dark brown, hair medium to long, oculo-malar area shorter than broad, clypeus adjacent to the labrum slightly raised in the centre so that the transverse anterior groove is interrupted, this central area with few small punctures and more shining than the surrounding areas, oculo-ocellar area in almost its outer half with large and medium punctures (cf. *B. rainai*); hair of the side of the thorax in at least its upper half and the scutellum *either* white *or* yellow, hair of T5 orange with white tips.

Male

Wings nearly clear with veins dark brown, hair medium to long, oculo-malar area shorter than broad; genitalia (Fig. 108) with the gonostylus long and distally near its midline axis convexly rounded, length on its outer side about a quarter as long as on its inner side with the two inner corners of the distal lobe rounded, the margin between them nearly straight, penis-valve head strongly recurved, the recurved hook much longer than broad, but broad and narrowing only just before the apex (cf. *B. rainai*); male eye distinctly enlarged relative to female eye; hair of the side of the thorax *either* yellow *or* white with the pale hair reaching to the midleg bases, hair of T3 usually predominantly black, hair at the side of T5–6 orange at the base but white-tipped.

Material sequenced in Fig. 12

CHINA • 1 ♀ (worker); Sichuan, Queer Mountain; 31.8969° N, 99.1485° E; 5 Aug. 2018; Z. Ren *et al.* leg.; KIB seq: QESM302006; KIB: AG#083 • 1 ♀ (worker); Xizang, Ailashan; 31.6142° N, 98.4803° E; 4 Aug. 2018; Z. Ren *et al.* leg.; KIB seq: ALSM104001; KIB: AG#085 • 1 ♀ (worker); Qinghai, Kunlun Pass road; 35.6917° N, 94.0533° E; 19 Aug. 2013; PW seq: PWK1; IAR: AG#084.

PAKISTAN • 1 ♂; Baltistan [Olthingthang]; 34.7093° N, 76.1208° E; 16 Sep. 2016; S. Jaffar leg.; BOLD seq: 1555G02; PW: AG#082.

Additional sequences in Fig. 10 and haplotype duplicates

CHINA • 1 ♀ (worker); Xizang, Yelanshan; 30.1489° N, 97.3091° E; 22 Jul. 2018; Z. Ren *et al.* leg.; KIB seq: YLSH308001; KIB: AG#130.

Global distribution

Himalaya and Hengduan: Pakistan, India (Kashmir, Himachal Pradesh, Uttarakhand, Sikkim), Nepal, China (Xizang, Qinghai, Sichuan, Gansu): IAR, IOZ, KIB, NHMUK, PW, RMNH, SC, ZMHB.

This species is recorded at elevations of 2400–4800 m in the Himalaya and trans-Himalaya, and of 2272–4700 m in the Hengduan mountains (Williams 1991; Williams *et al.* 2009, 2010; An *et al.* 2014). In Kashmir, Sichuan, and Gansu, *B. kashmirensis* occurs primarily above the tree line and high into the alpine zone (queens have been seen to forage from flowers at 4000 m in Kashmir even when it was snowing heavily, PW pers. obs.) and even in the semi-arid trans-Himalaya (Williams 1991; Williams *et al.* 2009).

Behaviour

Male eye slightly enlarged relative to female eye: males show ‘cruising’ behaviour when searching for mates in Kashmir (Williams 1991).

4. *Bombus (Alpigenobombus) rainai* Williams, 2022
Figs 49–53, 109

Bombus (Alpigenobombus) rainai Williams, 2022a: 132.

Bombus (Alpigenobombus) kashmirensis – Williams 1991: 66, (in part) misidentification.

Species-taxon concept and variation

The taxon concept of the species *B. rainai* here agrees with the recent interpretation (Williams 2022a) that it is separate from the taxon concept of the species *B. kashmirensis* (see the comments above on *B. kashmirensis*), based on: (1) our PTP analysis supports independent species-level coalescents in the COI gene (Fig. 12); corroborated by (2) diagnostic morphological character states (see the keys).

This taxon was discussed as divergent from *B. kashmirensis* by Williams (1991: 68–69, figs 308–310), although it was not then named as a separate species.

Although the PTP and morphological results (Fig. 12, keys) support the interpretation that *B. rainai* and *B. kashmirensis* are separate species (Williams 2022a), the available COI-barcode-like sequences may all be low-divergence neonumts (Fig. 11).

Variation of *B. rainai* is shown in the colour-pattern diagrams in Figs 49–53. *Bombus rainai*, with its white-banded red-tailed colour pattern in the Himalaya, appears to mimic the abundant *B. (Sibiricobombus) longiceps* Smith, 1878 (until recently regarded as part of *B. asiaticus* Morawitz, 1875), and similar species (Williams 2007: fig. 51).

Type material

Bombus (Alpigenobombus) rainai Williams 2022a: 132. Holotype by original designation: ♀ (queen) Kashmir, India (ZSC). Examined.

Morphological diagnosis**Female**

Wings nearly clear with veins dark brown, hair medium length, oculo-malar area shorter than broad, clypeus adjacent to the labrum slightly raised in the centre so that the transverse anterior groove is interrupted, this central area with few small punctures and more shining than the surrounding areas, oculo-ocellar area in its outer half with only a few small shallow punctures, any larger punctures confined

to the eye margin (cf. *B. kashmirensis*); hair of the side of the thorax in no more than its upper third white and the scutellum predominantly black, hair of T5 entirely orange without obviously paler tips.

Male

Wings nearly clear with veins dark brown, hair medium length, oculo-malar area shorter than broad; genitalia (Fig. 109) with the gonostylus long and distally near its midline axis convexly rounded, length on its outer side about a quarter as long as on its inner side with the two inner corners of the distal lobe rounded, the margin between them convex, penis-valve head strongly recurved, the recurved hook much longer than broad and narrow, tapering gradually to the apex (cf. *B. kashmirensis*); male eye distinctly enlarged relative to female eye; hair of the side of the thorax with black and white intermixed, but often predominantly black in its lower half, hair of the sides of T5–6 orange, hair of T3 often predominantly orange.

Material sequenced in Fig. 12

INDIA • 1 ♀ (queen); Kashmir, Achoora; 34.636° N, 74.864° E; 26 Jun. 2009; R. Raina leg.; BOLD seq: 1552E01; ZSC: AG#080 • 1 ♀ (queen); Kashmir, Apharwat; 34.055° N, 74.386° E; 21 Aug. 2009; R. Raina leg.; BOLD seq: 1552D12; ZSC: AG#081.

Global distribution

Western Himalaya: Pakistan, India (Kashmir): NHMUK, PW, ZSC.

This species is recorded at elevations of 2542–4200 m, primarily above the tree line and high into the alpine zone (Williams 1991).

Behaviour

Male eye distinctly enlarged relative to female eye: males are expected to show ‘cruising’ behaviour when searching for mates in Kashmir (Williams 1991).

5. *Bombus (Alpigenobombus) sikkimi* Friese, 1918 stat. rev. Figs 4, 54–60, 110

Bombus sikkimi Friese, 1918: 82. Examined.

Bombus (Alpigenobombus) nobilis – Burger *et al.* 2009: 460, misidentification. — Williams *et al.* 2010: 130, misidentification. — Streinzer *et al.* 2019: table 1, misidentification.

Species-taxon concept and variation

The taxon concept of the species *B. sikkimi* here agrees with the recent interpretation (Williams 2022a) that it is separate from the taxon concept of the species *B. nobilis* (see the comments below on *B. nobilis*), based on: (1) our PTP analysis supports independent species-level coalescents in the COI gene (Fig. 12); corroborated by (2) diagnostic morphological character states (see the keys).

The morphological results (Fig. 12, keys) support the interpretation that the divergent colour patterns of the yellow-banded taxa *sikkimi* s. str. and individuals from the Himalaya with an unnamed white-banded colour pattern are conspecific. We have been able to obtain COI barcode sequences so far only from the white-banded individuals, not the yellow-banded individuals. The latter will be needed to confirm the conspecific relationship.

Variation in the colour-pattern diagrams of *B. sikkimi* in Figs 54–60 is arranged approximately from east to west within the Himalaya. *Bombus sikkimi*, with the yellow-banded colour pattern in the west

(central Himalaya) of its range (Figs 56–57, 59–60), appears to mimic the common *B. (Melanobombus) eurythorax* Wang, 1982, and similar species (Williams 2007: fig. 5j), whereas the white-and-yellow-banded colour pattern in the east (eastern Himalaya: Figs 54–55, 58) appears to mimic the abundant *B. (Ml.) prshewalskyi* (Williams 2007: fig. 5p).

Type material

Bombus sikkimi Friese, 1918: 82. Syntype: ♀ (queen) Sikkim, India (ZMHB). Examined.

Morphological diagnosis

Female

Wings nearly clear with veins dark brown, hair long, oculo-malar area longer than broad, oculo-ocellar areas densely and broadly punctured with scattered medium-sized punctures with many small punctures between them, antero-laterally to the lateral ocellus with large, medium and many small punctures almost coalescing and without flat shining areas in between (cf. *B. nobilis*, *B. validus*); hair on the anterior dorsum of the thorax *and* of the side of the thorax *and* scutellum *and* T1 *either* grey *or* olive-yellow, on the scutellum the pale hair anteriorly often deeply divided in the middle by a triangle of black, T2 *either* predominantly yellow *or* with large anterior lateral patches yellow.

Male

Wings nearly clear with veins dark brown, hair long, oculo-malar area longer than broad; genitalia (Fig. 110) with the gonostylus short and distally near its midline axis nearly consistently weakly convexly rounded, its outer side about a half as long as its inner side with the two inner corners of the distal lobe rounded, the margin between them concave, penis-valve head weakly recurved, the recurved section only slightly longer than broad at the base (cf. *B. nobilis*, *B. validus*); hair on the anterior dorsum of the thorax *and* of the side of the thorax *and* scutellum *and* T1 *either* grey-white *or* dull olive-yellow, T2 antero-laterally yellow, on the scutellum in the middle the grey or yellow nearly completely divided by black.

Material sequenced in Fig. 12

INDIA • 1 ♂; Arunachal Pradesh, Donyi La; 28.9819° N, 95.2403° E; 4 Sep. 2017; NCBS seq: BE961; NCBS: AG#205 • 1 ♀ (worker); Arunachal Pradesh, Sango-Camp; 28.9814° N, 95.2482° E; 4 Sep. 2017; NCBS seq: BE963; NCBS: AG#206.

Additional sequences in Fig. 10 and haplotype duplicates

INDIA • 1 ♀ (worker); Arunachal Pradesh, Sela Lake; 27.5050° N, 92.1016° E; 24 Sep. 2015; J. Neumayer leg.; NCBS seq: BE968; NCBS: AG#005 • 1 ♀ (worker); Arunachal Pradesh, Sango-Camp; 28.9744° N, 95.2542° E; 2 Sep. 2017; NCBS seq: BE942; NCBS: AG#204 • 1 ♀ (queen); Arunachal Pradesh, Nagula; 27.6981° N, 91.8486° E; 30 May 2016; NCBS seq: BE967; NCBS: AG#207.

Global distribution

Himalaya: India (Himachal Pradesh, Uttarakhand, Sikkim, Arunachal Pradesh), Nepal: NCBS, NHMUK, PW, ZMHB.

This species is recorded (under the name *B. nobilis*) at elevations of 2700–4300 m in the Himalaya, mostly above the tree line and into the subalpine zone (especially rich in *Rhododendron* L. species) (Williams *et al.* 2010; Streinzer *et al.* 2019). MS identified two nests, at 3860 m (near BE963) and one near Sela Pass at 4230 m.

Behaviour

Male eye not obviously enlarged relative to female eye: males are expected to show ‘patrolling’ behaviour in search of mates (Williams 1991).

6. *Bombus (Alpigenobombus) nobilis* Friese, 1905 s. str. Figs 5, 61–69, 111

Bombus nobilis Friese, 1905: 513.

Bombus (Nobilibombus) xizangensis Wang, 1979: 188.

Bombus (Nobilibombus) chayaensis Wang, 1979: 189.

Species-taxon concept and variation

The taxon concept of the species *B. nobilis* here agrees with the recent interpretation (Williams 2022a) that it is separate from the taxon concept of the species *B. sikkimi* (see the comments above on *B. sikkimi*), based on: (1) our PTP analysis supports independent species-level coalescents in the COI gene (Fig. 12); corroborated by (2) diagnostic morphological character states (see the keys).

The PTP and morphological results (Fig. 12, keys) support the interpretation that *B. nobilis*, *B. sikkimi*, and *B. validus* are separate species (Williams 2022a). The available COI-barcode-like sequences may all be low-divergence neoneumts (Fig. 11).

From the morphology and colour pattern it appears likely that the yellow-banded holotype queen of the taxon *chayaensis* (Fig. 63, from Chagyab, north-eastern Xizang) and the white-banded holotype worker of the taxon *xizangensis* (Fig. 62, from Zayü, southern Xizang) are conspecific with *B. nobilis*. A small collection from northern Myanmar (Adung valley, 1931) of both yellow-banded (NHMUK: 3 ♀♀ (2 queens, 1 worker), Figs 65–66) and white-banded (NHMUK: 2 ♀♀ (workers), Fig. 61) individuals matches this species in morphology.

Variation of *B. nobilis* is shown in the colour-pattern diagrams in Figs 61–69. *Bombus nobilis*, with the yellow-banded colour pattern in the north (northern Hengduan) of its range (Figs 63–64, 69), appears to mimic the abundant *B. (Melanobombus) friseanus* Skorikov, 1933 (Williams 2007: fig. 5j), whereas the white-and-yellow-banded colour pattern in the south (southern Hengduan: Figs 61–62, 67–68) appears to mimic the abundant *B. (Ml.) prshewalskyi* (Williams 2007: fig. 5p).

Type material

Bombus nobilis Friese, 1905: 513. Type not found, but identity not in doubt (Williams *et al.* 2009).

Bombus (Nobilibombus) xizangensis Wang, 1979: 188. Holotype by original designation: ♀ (worker) Zayü, Xizang, China (IOZ). Examined.

Bombus (Nobilibombus) chayaensis Wang, 1979: 189. Holotype by original designation: ♀ (queen) Chagyab, Xizang, China (IOZ). Examined.

Morphological diagnosis

Female

Wings lightly clouded with brown with the veins dark brown, hair of medium length, oculo-malar area longer than broad, oculo-ocellar areas densely punctured with scattered medium-sized punctures with many small punctures between them, antero-laterally to the lateral ocellus with large and small punctures sufficiently separated to have flat shining areas in between (cf. *B. sikkimi*, *B. validus*); hair on the anterior dorsum of the thorax *and* of the side of the thorax *and* scutellum *either* golden yellow *or*

grey-white, on the scutellum the yellow hair anteriorly scarcely divided in the middle by a triangle of black, T1 yellow, T2 *either* predominantly black *or* with large anterior lateral patches yellow.

Male

Wings lightly clouded with brown with the veins dark brown, hair of medium length, oculo-malar area longer than broad; genitalia (Fig. 111) with the gonostylus short and distally near its midline axis deeply concavely rounded, its outer side about a half as long as its inner side with the two inner corners of the distal lobe rounded, the margin between them concave, penis-valve head weakly recurved, the recurved section about as long as broad at the base (cf. *B. sikkimi*, *B. validus*); hair on the anterior dorsum of the thorax *and* of the side of the thorax *and* scutellum *either* golden yellow *or* grey-white, T1 *either* yellow *or if* nearly white *then* T2 antero-laterally also nearly white, on the scutellum in the middle the yellow only shallowly divided by black.

Material sequenced in Fig. 12

CHINA • 1 ♀ (worker); Yunnan, Lijiang; 27.0156° N, 100.1714° E; 12 Aug. 2017; H. Liang leg.; KIB seq: #2018064; KIB: AG#089 • 1 ♂; Xizang, Zhougoin; 28.3469° N, 98.0102° E; 3 Sep. 2014; Q.-T. Wu leg.; IOZ seq: FPW30; IOZ: AG#187 • 1 ♀ (worker); Sichuan, Queershan; 29.5718° N, 98.1847° E; 5 Aug. 2018; Z. Ren *et al.* leg.; KIB seq: QESH201020; KIB: AG#143 • 1 ♀ (worker); Xizang, Dongdashan; 29.5718° N, 98.1847° E; 21 Jul. 2018; Z. Ren *et al.* leg.; KIB seq: DDSM202013; KIB: AG#087 • 1 ♂; Xizang, Zhougoin; 28.3469° N, 98.0102° E; 2 Sep. 2014; Q.-T. Wu leg.; IOZ seq: FPW24; IOZ: AG#183 • Yunnan; IAR seq: HJF6; IAR: AG#090.

Additional sequences in Fig. 10 and haplotype duplicates

CHINA • 1 ♀ (worker); Yunnan, Lijiang; 27.0156° N, 100.1714° E; 2 Sep. 2012; Y. Zhao leg.; KIB seq: #218628241; KIB: AG#108 • 1 ♀ (worker); Xizang, Zhougoin; 28.3469° N, 98.0102° E; 3 Sep. 2014; Q.-T. Wu leg.; IOZ seq: FPW31; IOZ: AG#186 • 1 ♂; Xizang, Zhougoin; 28.4853° N, 97.3634° E; 30 Aug. 2014; Q.-T. Wu leg.; IOZ seq: FPW29; IOZ: AG#188 • 1 ♀ (worker); same collection data as for preceding but 31 Aug. 2014; IOZ seq: FPW28; IOZ: AG#182 • 1 ♀ (worker); Xizang, Zhougoin; 28.3469° N, 98.0102° E; 3 Sep. 2014; Q.-T. Wu leg.; IOZ seq: FPW26; IOZ: AG#189 • 1 ♀ (worker); same collection data as for preceding but 2 Sep. 2014; IOZ seq: FPW25; IOZ: AG#190 • 3 ♂♂; Xizang; 29.6114° N, 94.6441° E; 10 Aug. 2012; IAR seq: ZA3 ZA4 ZA5; IAR: AG#010 to AG#012 • 3 ♀♀ (workers); Xizang, Lulang; 29.6414° N, 94.6982° E; 26 Jul. 2018; Z. Ren *et al.* leg.; KIB seq: SJLSM108001, SJLSM104001, SJLSM104002; KIB: AG#086, AG#146, AG#147 • 1 ♀ (worker); Xizang, Galonglashan; 29.8219° N, 95.7110° E; 24 Jul. 2018; Z. Ren *et al.* leg.; KIB seq: GLLSL106001; KIB: AG#148 • 1 ♀ (worker); Yunnan, Lijiang; 27.0156° N, 100.1714° E; 12 Aug. 2017; H. Liang leg.; KIB seq: #2018063; KIB: AG#103 • 1 ♀ (worker); Xizang, Markam; 29.7432° N, 95.6753° E; 2 Sep. 2014; Q.-T. Wu leg.; IOZ seq: FPW32; IOZ: AG#191.

Global distribution

Hengduan: China (Qinghai, Xizang, Yunnan, Sichuan, Gansu), Myanmar: IAR, IOZ, KIB, NHMUK, PW, SC, ZMHB.

This species is recorded at elevations of 2600–4500 m in Sichuan, mostly above the tree line and into the subalpine zone (especially rich in *Rhododendron* species) (Williams *et al.* 2009).

Behaviour

Male eye not obviously enlarged relative to female eye: males are expected to show ‘patrolling’ behaviour in search of mates (Williams 1991).

7. *Bombus (Alpigenobombus) validus* Friese, 1905 stat. rev.
Figs 70–73, 112

Bombus validus Friese, 1905: 510.

Nobilibombus morawitziides Skorikov, 1933b: 62, by indication of *Bombus haemorrhoidalis* Morawitz, 1880: 344 (specifically the worker from ‘Gan-su’).

Bombus haemorrhoidalis – Morawitz 1880: 344 (not of Smith, 1852: 43, misidentification = *B. haemorrhoidalis* Smith).

Alpigenobombus morawitziides – Skorikov 1923: 159, published without description or indication, unavailable name.

Alpigenobombus morawitziides – Skorikov 1931: 203, published without description or indication, unavailable name.

Bombus (Alpigenobombus) nobilis – Williams *et al.* 2009: 170, (in part) misidentification.

Species-taxon concept and variation

The taxon concept of the species *B. validus* here agrees with the recent interpretation (Williams 2022a) that it is separate from the taxon concept of the species *B. nobilis* (see the comments above on *B. nobilis*), based on: (1) our PTP analysis supports independent species-level coalescents in the COI gene (Fig. 12); corroborated by (2) diagnostic morphological character states (see the keys).

The PTP and morphological results (Fig. 12, keys) support the interpretation that *B. validus*, *B. sikkimi*, and *B. nobilis* are separate species (Williams 2022a).

Morawitz’s taxon *haemorrhoidalis*, with the oculo-malar area longer than for *B. mastrucatus*, matches closely with *B. validus*. The collection locality for one worker was given by Morawitz as ‘Gan-su’ (used in a much broader sense than currently) and this individual was later referred to by Skorikov (1933b) is consistent with *B. validus*. It is intriguing that Skorikov (1933b) mentioned *B. validus* in his comments on *morawitziides* without giving any distinguishing characters. The other location for *haemorrhoidalis* given by Morawitz is ‘Ordoss’ (= Mu Su Shamo, referring to the Ordos desert, in Shaanxi), which is unexpected because it is at a much lower elevation and mostly more arid. This raises the possibility that Morawitz also had some rare paler individuals of the taxon *beresovskii* (not seen; but see the comments on *B. grahami*) in front of him, although this species has a shorter oculo-malar area that does not match Morawitz’s description, which is more likely to refer to *B. (Melanobombus) pyrosoma* Morawitz, 1890.

Variation of *B. validus* is shown in the colour-pattern diagrams in Figs 65–68. *Bombus validus*, with its black-thorax and largely-orange-metasoma colour pattern in northern Hengduan, appears to mimic the abundant *B. (Melanobombus) pyrosoma* (Williams 2007: close to fig. 5m).

Type material

Bombus validus Friese, 1905: 510. Syntype (Tkalčů 1987: 60): ♀ (queen) ‘Turkestan Kashgar’, but probably Sichuan (ZMHB). Examined.

Morphological diagnosis

Female

Wings nearly clear with the veins dark brown, hair of medium length, oculo-malar area longer than broad, oculo-ocellar area sparsely punctured with few scattered medium-sized punctures with few small punctures between them with broad smooth areas (cf. *B. sikkimi*, *B. nobilis*); hair of the side of the thorax and scutellum predominantly black with only a few scattered grey hairs, T2–3 with only a few black hairs along the midline.

Male

Wings nearly clear with the veins dark brown, hair of medium length, oculo-malar area longer than broad; genitalia (Fig. 112) with the gonostylus short and distally near its midline axis concavely rounded, its outer side about a half as long as its inner side with the two inner corners of the distal lobe rounded, the margin between them nearly straight, penis-valve head weakly recurved, the recurved section about as long as broad at the base (cf. *B. sikkimi*, *B. nobilis*); hair of the side of the thorax and scutellum varying from predominantly black to predominantly grey-white, T2–3 with only a few black hairs along the midline.

Material sequenced in Fig. 12

CHINA • 3 ♀♀ (workers); Gansu, Zhagana; 34.2477° N, 103.1329° E; 24 Jul. 2009; JH seq: PWB11, PWB14, PWB16; IAR: AG#039, 091, 092.

Additional sequences in Fig. 10 and haplotype duplicates

CHINA • 1 ♂; Gansu, Shangbaimu Xia; 36.9620° N, 102.8209° E; 14 Aug 2011; JH seq: PWZA1; IAR: AG#008.

Global distribution

Northern Hengduan: China (Sichuan, Gansu): IAR, IOZ, PW, ZIN, ZMHB.

This species has an unusually restricted distribution, recorded at elevations of 2196–3524 m in Sichuan and Gansu, mostly above the tree line and into the subalpine zone (Williams *et al.* 2009; An *et al.* 2014).

Behaviour

Male eye not obviously enlarged relative to female eye: males are expected to show ‘patrolling’ behaviour in search of mates (Williams 1991).

8. *Bombus (Alpigenobombus) genalis* Friese, 1918
Figs 6, 74–75, 113

Bombus genalis Friese, 1918: 84.

Species-taxon concept and variation

The taxon concept of the species *B. genalis* here agrees with the long-standing interpretation (Williams 2022a) that it is separate from the taxon concepts of other species in the subgenus *Alpigenobombus*, based on: (1) our PTP analysis supports independent species-level coalescents in the COI gene (Fig. 12); corroborated by (2) diagnostic morphological character states (see the keys).

The PTP and morphological results (Fig. 12, keys) support the interpretation that *B. genalis* and *B. breviceps* are separate species. The available COI-barcode-like sequences may all be low-divergence neoneumts (Fig. 11).

No substantial colour-pattern variation is known for *B. genalis* (Figs 74–75). *Bombus genalis*, with its black with orange-legged colour pattern, appears to mimic the common *B. (Pyrobombus) flavescens* Smith, 1852, and *B. (Melanobombus) eximius* Smith, 1852 (Williams 2007: fig. 5a).

Type material

Bombus genalis Friese, 1918: 84. Syntypes: ♀♀ (queen and worker) Sikkim, India (ZMHB). Examined.

Morphological diagnosis

Female

Wings pale yellow with the veins light orange (unique within the subgenus *Alpigenobombus*), hair short, oculo-malar area shorter than broad, clypeus in its central area shining with only a few small and large widely-spaced punctures (cf. *B. breviceps*); mid and hind tibiae exoskeleton and hair bright orange, hair of the thoracic dorsum and T1 black.

Male

Wings pale yellow with the veins light orange (unique within the subgenus *Alpigenobombus*), hair short, oculo-malar area shorter than broad; genitalia (Fig. 113) with the gonostylus nearly equally short on both its outer side and its inner side but with the distal lobe projecting inwards as a long broadly triangular acutely pointed process, triangular in section (cf. *B. breviceps*, *B. grahami*); mid and hind tibiae exoskeleton and hair bright orange, the hair of the scutellum and T1 predominantly black.

Material sequenced in Fig. 12

CHINA • 1 ♀ (worker); Xizang, Linzhi; 29.5710° N, 95.4633° E; 29 Aug. 2015; Q.-T. Wu leg.; IOZ seq: FPW12; IOZ: AG#184.

Additional sequences in Fig. 10 and haplotype duplicates

CHINA • 1 ♀ (worker); Yunnan, Guanshizhai; 25.9334° N, 98.8008° E; 18 Aug. 2011; PW seq: PWB9; IAR: AG#040 • 1 ♀ (worker); Xizang, Miyuecun; 29.4065° N, 95.3721° E; 18 Aug. 2015; Q.-T. Wu leg.; IOZ seq: FPW13; IOZ: AG#185.

INDIA • 2 ♀♀ (workers); Arunachal Pradesh, Salaya; 27.5969° N, 93.851° E; 22 Jun. 2018; J. Narah leg.; NCBS seq: BG463 BG471; NCBS: AG#200, AG#201 • 1 ♀ (worker); Arunachal Pradesh, Hari; 27.5838° N, 93.8446° E; 27 Sep. 2015; NCBS seq: BE637; NCBS: AG#202.

Global distribution

Himalaya and borders of southern Hengduan: India (Sikkim, Arunachal Pradesh), China (Xizang, Yunnan), Myanmar: IAR, IOZ, NCBS, NHMUK, PW, ZMHB.

This is an uncommon species and few individuals have been recorded. This species is recorded at elevations of 1561–1852 m in the Himalaya in the middle forest zone (Streinzer *et al.* 2019).

Behaviour

Male eye very slightly enlarged relative to female eye, male mate-searching behaviour unknown.

9. *Bombus (Alpigenobombus) breviceps* Smith, 1852

Figs 7–8, 76–93, 114

Bombus nasutus Smith, 1852: 44.

Bombus breviceps Smith, 1852: 44. Note 1.

Bombus dentatus Handlirsch, 1888: 227.

Bombus simulus Gribodo, 1892: 114.

Bombus Channicus Gribodo, 1892: 116.

Bombus laticeps Friese, 1905: 513.

Bombus orichalceus Friese, 1916: 107.

Bombus channicus var. [subsp.] *brevigenalis* Friese, 1918: 81.

BOMBUS RUFOCOGNITUS Cockerell, 1922: 4.

Bombus (Alpigenobombus) dentatus [subsp.] *pretiosus* Bischoff, 1936: 11, not of Friese 1911a: 572 (= *B. polaris* Curtis).

Bombus (Alpigenobombus) channicus [subsp.] *cantonensis* Bischoff, 1936: 14.

Alpigenobombus breviceps [subsp.] *coloricontrarius* Tkalčú, 1968: 14.

Alpigenobombus breviceps [subsp.] *colorilaetus* Tkalčú, 1968: 14.

Alpigenobombus breviceps [subsp.] *vicinus* Tkalčú, 1968: 21.

Alpigenobombus breviceps [subsp.] *bischoffiellus* Tkalčú, 1977: 224. Replacement name for *Bombus (Alpigenobombus) dentatus* [subsp.] *pretiosus* Bischoff, 1936.

Bombus rufocognitus var. [not subsp.] *nefandus* – Cockerell 1931: 6, infrasubspecific.

Bremus (Alpigenobombus) dentatus var. [not subsp.] *concinus* – Frison 1935: 352, infrasubspecific.

Bremus (Alpigenobombus) dentatus var. [not subsp.] *surdus* – Frison 1935: 353, infrasubspecific.

Bremus (Alpigenobombus) orichalceus var. [not subsp.] *conjunctus* – Frison 1935: 355, infrasubspecific.

NOTE 1. Acceptance of *B. breviceps* as the valid name in preference to *B. nasutus* follows Tkalčú (1968) as the First Reviser (ICZN 1999: Article 24).

Species-taxon concept and variation

The taxon concept of the species *B. breviceps* here agrees with the long-standing interpretation (Williams 2022a) that it is separate from the taxon concepts of other species in the subgenus *Alpigenobombus*, based on: (1) our PTP analysis supports independent species-level coalescents in the COI gene (Fig. 12); corroborated by (2) diagnostic morphological character states (see the keys).

The PTP and morphological results (Fig. 12, keys) support the interpretation that *B. breviceps* and *B. genalis* are separate species. The available COI-barcode-like sequences may all be low-divergence neoneumts (Fig. 11).

The PTP and morphological results (Fig. 12, keys) support and confirm the interpretation that the divergent colour patterns of the taxa *breviceps* s. str., *channicus*, and *dentatus* are conspecific as parts of the species *B. breviceps* (Tkalčú 1968; Williams *et al.* 2009; Hines & Williams 2012).

Variation in the colour-pattern diagrams of *B. breviceps* in Figs 76–93 is arranged for the black-thorax Himalayan individuals approximately from west (Kashmir) to east (Myanmar) and for the orange-banded Chinese and Southeast Asian individuals from north (Gansu) to south (Thailand). *Bombus breviceps*, with the black-thorax colour pattern in the west (Himalaya) and centre (Hengduan) of its range (Figs 76–80, 85–89) and the orange-banded colour pattern in the south-east (Southeast Asia: Figs 81–84, 90–93), appears to mimic the abundant *B. (Orientalibombus) haemorrhoidalis* Smith, 1852, and *B. (Megabombus) montivagus* Smith, 1878 (Williams 2007: fig. 5h–i). The black-tailed colour patterns occur on the India/Myanmar border (Figs 80, 89) and in southern China (Figs 82–83, 91–92).

Type material

Bombus breviceps Smith, 1852: 44. Holotype by monotypy: ♀ (worker) Zhejiang, China (NHMUK). Examined.

Morphological diagnosis

Female

Wings very darkly clouded with brown with the veins dark brown, hair short, oculo-malar area shorter than broad, clypeus in its central area with many small punctures (cf. *B. genalis*, *B. grahami*); hair of the thoracic dorsum black, often with orange bands anteriorly and posteriorly, hair of T1 yellow.

Male

Wings very darkly clouded with brown with the veins dark brown, hair short; genitalia (Fig. 114) with the gonostylus nearly equally short on both its outer side and its inner side but with the distal lobe projecting inwards as a long narrowly pointed almost spine-like process, rounded in section (cf. *B. genalis*, *B. grahami*).

Material sequenced in Fig. 12

BHUTAN • 1 ♀ (worker); Trashigang, Doksum; 27.4377° N, 91.5833° E; 23 May 2017; W. Klein leg.; PW seq: NBC10098; RMNH: AG#149.

CHINA • 1 ♂; Zhejiang, [Huangjiaotang]; 28.805° N, 120.961° E; GenBank seq: FJ175356; SC: AG#069.

THAILAND • 1 ♀ (worker); Chiang Mai, Doi Inthanon; 18.545° N, 98.516° E; 10 Aug. 2016; C. Sinpoo leg.; GenBank seq: MF582612; BEEP: AG#155 • 1 ♀ (worker); Chiang Mai, Doi Inthanon; 18.554° N, 98.582° E; 19 Jul. 2016; C. Sinpoo leg.; GenBank seq: MF582613; BEEP: AG#156.

Additional sequences in Fig. 10 and haplotype duplicates

CHINA • 1 ♀ (worker); Zhejiang, Gaolaoshan; 28.9043° N, 120.5496° E; 4 Apr. 2021; Y. Chen leg.; CAU seq: TL01; CAU: AG#192 • 1 ♀ (worker); Gansu, Qingyugou; 32.7734° N, 105.4137° E; 23 Jun. 2021; Y. Chen leg.; CAU seq: TL02; CAU: AG#193 • 1 ♀ (worker); Guangdong, Nanxiang; 24.7677° N, 113.5932° E; 18 Jul. 2021; Y. Chen leg.; CAU seq: TL03; CAU: AG#194 • 1 ♀ (worker); Zhejiang, Pingding cun; 29.6615° N, 120.0088° E; 1 Oct. 2020; L. Tian leg.; CAU seq: TL04; CAU: AG#195 • 1 ♀ (worker); Hunan, Dazhushan; 26.1662° N, 110.1746° E; 23 Jul. 2021; L. Tian leg.; CAU seq: TL05; CAU: AG#196 • 1 ♀ (worker); Hunan, Nanshan; 26.1513° N, 110.1644° E; 22 Jul. 2021; L. Tian leg.; CAU seq: TL06; CAU: AG#197 • 1 ♀ (worker); Gansu, Liushuwan; 33.0474° N, 105.2562° E; 21 Jun. 2021; Y. Chen leg.; CAU seq: TL07; CAU: AG#198 • 1 ♀ (worker); Guangdong, Nanxiang; 24.7677° N, 113.5932° E; 18 Jul. 2021; Y. Chen leg.; CAU seq: TL08; CAU: AG#199 • same collection data as for preceding; GenBank seq: KP259094; IOZ: AG#152 • same collection data as for preceding; GenBank seq: MF478986; IAR: AG#153 • Ningxia; IAR seq: NX2; IAR: AG#093.

INDIA • 1 ♀ (worker); Arunachal Pradesh, Jang; 27.5821° N, 91.9704° E; 24 Sep. 2015; J. Neumayer leg.; NCBS BE653 seq: PWB6; NCBS: AG#041.

THAILAND • 1 ♀; Chiang Mai, Doi Inthanon; 18.5893° N, 98.4859° E; 21 Sep. 2006; Y. Areeluck leg.; BOLD seq: 3261H02; PCYU: AG#102 • 1 ♀ (worker); Chiang Mai, Doi Suthep; 18.815° N, 98.4920° E; 26 Jun. 2016; C. Sinpoo leg.; GenBank seq: MF582617; BEEP: AG#157 • 2 ♀♀ (workers); Chiang Mai, Doi Inthanon; 18.543° N, 98.548° E; 19 Jul. 2016; C. Sinpoo leg.; GenBank seq: MF582618, MF582619; BEEP: AG#158, AG#159 • 1 ♀ (worker); Chiang Mai, Doi Inthanon; 18.545° N, 98.516° E; 10 Aug. 2016; C. Sinpoo leg.; GenBank seq: MF582622; BEEP: AG#160 • 1 ♀ (worker); Chiang Mai, Doi Inthanon; 18.5892° N, 98.48872° E; 21 Jul. 2015; N. Warrit *et al.* leg.; CT seq: CT540; CUNHM: AG#177 • 1 ♀ (worker); Chiang Mai, Doi Inthanon; 18.5447° N, 98.5179° E; 21 Jul. 2015; N. Warrit *et al.* leg.; CT seq: CT552; CUNHM: AG#178 • 1 ♀ (worker); Chiang Mai, Khun Chang Khian; 18.8387° N, 98.8965° E; 18 Jul. 2015; N. Warrit *et al.* leg.; CT seq: CT607; CUNHM: AG#179 • 1 ♀ (worker); Chiang Mai, Doi Kiew Lom; 19.3175° N, 98.6006° E; 20 Nov. 2017; N. Warrit *et al.* leg.; CT seq: CT623; CUNHM: AG#180 • 1 ♀ (worker); Chiang Mai, Doi Ang Khang; 19.8823° N, 99.0437° E; 21 Nov. 2017; N. Warrit *et al.* leg.; CT seq: CT625; CUNHM: AG#181.

Global distribution

One of the most widespread Oriental species, in the Himalaya, Hengduan, Central and southern China, and Southeast Asia: India (Kashmir, Himachal Pradesh, Uttarakhand, Sikkim, Arunachal Pradesh), Nepal, Bhutan, China (Xizang, Yunnan, Sichuan, Gansu, Shaanxi, Chongqing, Hubei, Jiangxi, Hunan, Guizhou, Zhejiang, Fujian, Guangdong, Guangxi), Myanmar, Vietnam, Laos, Thailand: BEEP, CAU, CUNHM, IAR, IOZ, MCSN, NCBS, NHMUK, PCYU, PW, RMNH, SC, USNM, ZMHB.

This species is recorded at elevations of 484–3000 m in the Himalaya (Williams *et al.* 2010; Streinzer *et al.* 2019), and at 270–3350 m in the Hengduan and in Shaanxi (Williams *et al.* 2009; An *et al.* 2014). It is one of the few bumblebee species that occurs down to lower elevations in subtropical habitats, where it may be relatively common, even inside cities. However, in the warmer habitats it may be active only in the early morning and evening (Yunnan and Guangdong, PW pers. obs.; Thailand, C. Thanosing pers. obs.).

Behaviour

Male eye very slightly enlarged relative to female eye, male mate-searching behaviour unknown.

10. *Bombus (Alpigenobombus) grahami* (Frison, 1933) Figs 9, 94–103, 115

Bremus (Alpigenobombus) grahami Frison, 1933 [[30] September]: 334. Note 1.

Alpigenobombus beresovskii Skorikov, 1933a [30 September: Pesenko & Astafurova 2003]: 248.

Syn. nov.

Bombus Alpigenobombus grahami [subsp.] *melani* Wang & Yao, 1993: 422. **Syn. nov.**

Alpigenobombus (Alpigenobombus) beresovskii – Skorikov 1923: 156, published without description or indication, unavailable name.

Alpigenobombus berezovskii – Skorikov 1931: 204, published without description or indication, unavailable name.

Bremus (Alpigenobombus) grahami var. [not subsp.] *ordinatus* – Frison 1935: 353, infrasubspecific.

NOTE 1. Acceptance of *B. grahami* as the valid name in preference to *B. beresovskii* follows Williams (2022a) as the First Reviser (ICZN 1999: Article 24). *Bombus grahami* is the name in most widespread use for this species in the literature.

Species-taxon concept and variation

The taxon concept of the species *B. grahami* here is modified from the long-standing interpretation (Williams 2022a), in that it includes the taxon *beresovskii*, based on: (1) our PTP analysis supports independent species-level coalescents in the COI gene (Fig. 12); corroborated by (2) diagnostic morphological character states (see the keys).

The PTP and morphological results (Fig. 12, keys) support the interpretation that the divergent colour patterns of the taxa *grahami* s. str. and *beresovskii* are conspecific (Williams 2022a). The available COI-barcode-like sequences may all be low-divergence neoneumts (Fig. 11). From morphology, the taxon *melani* (holotype queen Fig. 99) is closely similar to the taxon *beresovskii* (syntype queen Fig. 100).

For the typically coloured individuals of *B. grahami*, the wings of the males are (unusually among bumblebees) much paler than the wings of the females. The wings are also slightly paler for females of the taxon *beresovskii* (males not seen).

Some females with the *beresovskii* colour pattern (from northern Sichuan: Figs 99–100) have a dark colour pattern that resembles *B. angustus*, but others (from Shaanxi: Fig. 98) have a light colour pattern that resembles *B. validus*. One worker (Fig. 98) has a distinct band of grey hairs fringing the thoracic dorsum anteriorly and posteriorly with some grey hairs along the midline. Males of the taxa *beresovskii* and *melani* are unknown to us.

Bombus grahami females, with the grey-thorax colour pattern in the west (Himalaya) and centre (Hengduan) of its range (Figs 94–97), appear to mimic the commoner *B. (Orientalibombus) funerarius* Smith, 1852 (Williams 2007: fig. 5g). In contrast, the more extensively black-thorax colour pattern in the north-east (in the hills to the north of the Sichuan Basin: Figs 98–100) appears to mimic the abundant *B. (Melanobombus) pyrosoma* (Williams 2007: close to fig. 5m). Some of these females (Fig. 98) resemble closely *B. validus* (Figs 70–71) in colour pattern, but can be distinguished easily by the shorter oculo-malar distance of *B. grahami*.

Type material

Bremus (Alpigenobombus) grahami Frison, 1933 [[30] September]: 334. Holotype by original designation: ♀ (worker) Sichuan, China (USNM). Examined.

Alpigenobombus beresovskii Skorikov, 1933a [30 September: Pesenko & Astafurova 2003]: 248. Syntype (unpublished Podbolotskaya lectotype): ♀ (queen) Sichuan, China (ZIN). Examined.

Bombus (Alpigenobombus) grahami [subsp.] *melani* Wang & Yao, 1993: 422. Holotype by original designation: ♀ (queen) Henan, China (IOZ). Examined.

Morphological diagnosis

Female

Wings very darkly clouded with brown with the veins dark brown, hair short, oculo-malar area shorter than broad, clypeus in its central area with only a few large and small widely-spaced punctures (cf. *B. breviceps*); hair of the thoracic dorsum black, *either* usually with many grey hairs intermixed so as to appear silvery olive-grey, with the majority of the hair along the longitudinal midline white, *or if* entirely black, *then* T3 predominantly orange-red.

Male

Wings nearly clear with the veins dark brown, hair short; genitalia (Fig. 115) with the gonostylus half as long on its outer side than on its inner side with the distal lobe slightly reduced and broadly flattened, appearing as a triangular pointed inwardly-projecting process only from the inner aspect (cf. *B. genalis*, *B. breviceps*); hair of the thoracic dorsum yellow, often between the wing bases with many black hairs intermixed.

Material sequenced in Fig. 12

CHINA • 1 ♀ (queen); Sichuan, Taoyuan; 32.6924° N, 106.8336° E; 21 Sep. 2011; PW seq: PWB01; IAR: AG#001 • 1 ♀ (worker); Yunnan, Lijiang; 27.0156° N, 100.1714° E; 12 Jul. 2017; H. Liang leg.; KIB seq: KIB030; KIB: AG#076.

Additional sequences in Fig. 10 and haplotype duplicates

BHUTAN • 1 ♀ (worker); Thimpu, Dochu-La; [27.4898° N, 89.7504° E]; 7 Jul. 1996; L. Blommers leg.; BOLD seq: 6880H10; RMNH: AG#094.

CHINA • 2 ♀♀ (workers); Yunnan, Lijiang; 27.0156° N, 100.1714° E; 2 Aug. 2017; H. Liang leg.; KIB seq: KIB092, KIB097; KIB: AG#075, AG#077 • 2 ♀♀ (workers); same collection data as for preceding

but 12 Aug. 2017; KIB seq: KIB116, KIB032; KIB: AG#078, AG#079 • 1 ♀ (worker); Sichuan, Meigu; 28.329° N, 103.129° E; GenBank seq: FJ175354; SC: AG#096 • Yunnan, Yulong Snow Mountain; [27.047° N, 100.261° E]; H. Liang leg.; GenBank seq: MT906009; KIB: AG#150.

INDIA • 1 ♀ (worker); Arunachal Pradesh, 1300 m E of Lama Tukkut; 28.9949° N, 95.2926° E; 30 Aug. 2017; NCBS seq: BE782; NCBS: AG#203.

NEPAL • 1 ♂; Janakpur, Dongo Kharka; 27.9022° N, 86.2865° E; 23 Aug. 1983; I. Kudo leg.; BOLD seq: 1551H05; SEHU: AG#119.

Global distribution

Himalaya, Hengduan, and into Central China: Nepal, India (Sikkim, Arunachal Pradesh), China (Xizang, Yunnan, Sichuan, Gansu, Shaanxi, Chongqing, Hubei, Henan, Guizhou): IAR, IOZ, KIB, NCBS, NHMUK, PW, RMNH, SEHU, USNM, ZIN.

This species is recorded at elevations of 2650–2800 m in the Himalaya (Williams *et al.* 2010; Streinzer *et al.* 2019), and 858–3040 m in the Hengduan and in Shaanxi (Williams *et al.* 2009; An *et al.* 2014). *Bombus grahami* is active in open areas in the middle and upper forest zones, but also inside the forest. Individuals with a black-thorax colour pattern (taxon *beresovskii*) occur in the hills to the north of the Sichuan basin, where they appear to be extremely rare (only three queens and three workers have been examined: IAR, IOZ, PW) and are not known to co-occur with individuals with the olive-thorax colour pattern (although many more data are needed to clarify the situation).

Behaviour

Male eye slightly enlarged relative to female eye, male mate-searching behaviour unknown.

11. *Bombus (Alpigenobombus) angustus* Chiu, 1948

Figs 104–105

Bombus (Alpigenobombus) angustus Chiu, 1948: 59.

Species-taxon concept and variation

Evidence for the taxon concept of the species *B. angustus* here provides further support for the interpretation (Williams *et al.* 2022b) that this is separate from the taxon concept of the species *B. breviceps* (Williams 1998), based on: (1) our PTP analysis supports independent species-level coalescents in the COI gene (Fig. 12); corroborated by (2) diagnostic morphological character states (see the keys).

The PTP and morphological results (Fig. 12, keys) support the interpretation that *B. angustus* and *B. breviceps* are separate species (Williams *et al.* 2022b). The available COI-barcode-like sequences may all be low-divergence neoumuts (Fig. 11).

The female mandible of *B. angustus* has been imaged by Starr (1992: fig. 6a).

No substantial colour-pattern variation of *B. angustus* is known (Figs 104–105). *Bombus angustus*, with its black with red-tailed colour pattern from Taiwan, appears to mimic the commoner local *B. (Megabombus) trifasciatus* Smith, 1852 (Williams 2007: fig. 5e).

Type material

Bombus (Alpigenobombus) angustus Chiu, 1948: 59. Holotype by original designation: ♂ Taiwan (TARI). Photographic images examined.

Morphological diagnosis

Female

Wings very weakly clouded with brown, nearly clear, with the veins dark brown (cf. *B. genalis*, *B. breviceps*, *B. grahami*), hair of medium length, oculo-malar area shorter than broad, clypeus in its central area with many small punctures (cf. *B. genalis*, *B. grahami*); mid and hind tibiae with the exoskeleton and hair predominantly black, hair of the thoracic dorsum and T1–3 black, T4–6 orange-red.

Male

Examined from photographic images, also described and genitalia illustrated by Chiu (1948: fig. 1) (genitalia of the type not found by C.-F. Lee, pers. com.): wings very weakly clouded with brown, nearly clear, with the veins light brown; genitalia with the gonostylus nearly equally short on both its outer side and its inner side but with the distal lobe projecting inwards as a long broadly triangular pointed process; hair of the thoracic dorsum and T1–3 'black' (on the type specimen, which is in poor condition, hair of the thorax in part ?faded to brown), T4–7 orange-red.

Material sequenced in Fig. 12

TAIWAN • 1 ♀ (worker); Chiayi, Alishan; [23.446° N, 120.794° E]; 14 Jul. 2020; Y. Lin leg.; GenBank seq: MZ831894; TFRI: AG#074.

Global distribution

Taiwan endemic (Williams *et al.* 2022b): PW, TARI, TFRI.

This is a rare species with few individuals recorded: Chiu (1948) lists three individuals from three localities; Starr (1992) lists 21 individuals from eight localities (mapped in Starr: fig. 7) among a total sample of 4555 Taiwanese bumblebees (<0.5%; from his map fig. 7, most *B. angustus* appear to be from elevations around 1000–2000 m, although one individual in the north may be from ca 100 m).

Behaviour

Male behaviour not seen.

Discussion

Our estimate of phylogeny (Fig. 16) for the species of the subgenus *Alpigenobombus*, after ten years of compiling data, has achieved stability and broadly supports expectations from earlier work by others. For example, our tree (for 11 species) matches the topology for the tree for the subset of five species that was presented by Cameron *et al.* (2007) (although this may be partly because we use some of the same gene-sequence data). We observe that the *nobilis*-group of species in our gene-tree is supported by morphology, most notably by the longer oculo-malar distance (related to visiting deeper flowers), which was recognised previously in the former subgenus *Nobilibombus*; the *kashmirensis*-group is supported most notably by the enlarged male eye (related to mate-searching behaviour, Williams 1991); and the *breviceps*-group is supported by the shorter hair (related to living at lower elevations) and reduced male gonostylus. In contrast, the *wurflenii*-group is supported by only a subtle synapomorphy of exoskeletal sculpturing, despite being remotely vicariant in western Asia and in Europe (see the keys). At the species level, all of the PTP species' coalescents in the gene tree of Fig. 12 are supported by morphology as valid species, as described in the species' diagnoses. We consider that this results in a more consistent approach for resolving the status of taxa as species or parts of species than could be achieved previously (Table 1). We hope that more genomic data become available from more sample sites in the future to re-assess all of these taxa.

Numts: the good, the bad, and the ugly

Filtering out numts is an attempt to select only those sequence data that meet the assumptions that are required by the methods used in order to estimate phylogeny: to meet the requirement for comparing homologous sequences (the ‘good’) (Brigandt & Griffiths 2007). Strongly divergent numts are well recognised as a problem (because they are paralogous) when trying to obtain data for estimating phylogenetic trees and ideally should be excluded (the ‘bad’) (Song *et al.* 2014).

If numts were assumed to be always misleading, then our decision here to deliberately retain some numts when seeking to estimate an evolutionary relationship tree (Fig. 12) is apparently paradoxical. Our repeated attempts to sequence species like *B. breviceps* from fresh material in four different labs using a variety of different primers have consistently yielded nothing but numts. More frustrating still, our attempts to obtain orthologous COI barcodes by next-generation Illumina sequencing to obtain entire mitochondrial genomes for some problematic bumblebee species have so far also failed to solve this problem (in prep.). Unfortunately, because we do not at present have access to fresh specimens of these species, we cannot sequence them for other genes or using other techniques.

We sought here to assess whether low-divergence numts (the ‘ugly’) might retain enough information representative of species’ phylogeny to be useful for estimating the relationships of the missing taxa and for assessing their status as separate species without being misleading. Our results support an association between some of the lowest AT3% values and the likely older numts (in purple and red in Fig. 11). Therefore, we interpret intermediate AT3% values as indicating likely numts with low divergence (orange and brown in Fig. 11). However, support is weak from our Fig. 11 that absolute thresholds in AT3% values can be established even within this one subgenus of bumblebees. Our results in Fig. 11 show that it is comparisons between closely related PTP candidate species that are more likely to be informative.

When the PTP analysis is filtered to remove the high-divergence numts, and only the minimum number of low-divergence numts is retained so that all of the nominal taxa are represented (Fig. 12), then the candidate species identified by PTP are all corroborated by morphology (see the keys). However, full confirmation of this will require obtaining orthologous barcode sequences for the sister taxa that are represented here only by low-divergence numts: *B. mastrucatus*, *B. nobilis*, *B. rainai* (and for species within the *breviceps*-group). These species are not recognised solely from their barcode-like sequences, but are also distinct in morphological characters, so it is unlikely that they will be rejected.

Equal care and caution must be taken in any future instance where such an approach is leveraged. When no better data are available, using a minimum number of low-divergence numts (for which no orthologous sequences are available at present) may be a least-worst compromise. This should not be followed in practice unless unavoidable and should be used only when other aspects of variation are extensively surveyed for comparison, such as morphology (see comments above on Sample size). The PTP analysis should be repeated as soon as orthologous sequences can be obtained.

Even if retaining a minimum number of low-divergence numts for PTP analysis can give an estimate of species that is consistent with morphology, is it a useful approach? There is a substantial cost incurred from the filtering out of the older numts to the availability of data for representing population variation. We started with >200 sample sequences, but only 33 sequences were left to estimate the PTP tree, which is low compared to the 11 candidate species detected (Fig. 12). Ideally, many more of the truly orthologous sequences with different haplotypes should be included for each species. Such sequences might be found in other parts of the species’ ranges, but they might take a great deal more effort to acquire. Much more work is needed to understand the limits to the usefulness of low-divergence numts.

Homologous sequences should always be preferred. It is to be hoped that improved methods will be found for securing orthologous sequences in the future. No doubt other genomic methods will be advocated instead, but these should also need to be shown to satisfy requirements for homology in comparisons.

Problems from heteroplasmy

Some bumblebee species are known to have multiple different heteroplasmic haplotypes within their mitochondria (Françoso *et al.* 2016; Ricardo 2017). Strong divergence between heteroplasmic haplotypes could lead to pseudospecies being falsely recognised, although comparison with other genes can demonstrate that a single species is involved (Williams *et al.* 2019). More often, it should be a lack of morphological corroboration that prevents strongly-diverging heteroplasmic haplotypes from being recognised falsely as separate species. Where heteroplasmic divergence is weaker, they are less likely to be identified as apparent coalescents of pseudospecies and so would appear in the trees as part of the intraspecific variation in haplotypes. Such lesser haplotype variation, whether heteroplasmic or fixed within a population, should not present a challenge to taxonomic revisions.

Nectar robbing by bumblebees

Bumblebees are well known for collecting nectar from meadow flowers, particularly as a source of sugars for energy for flight (Heinrich 1976). The deeper and more tubular flowers tend to have more nectar, and foraging bumblebees are extraordinarily good at choosing to visit the deepest available flowers to which the length of their tongues will allow them access so as to optimise the rate of energy profit per unit time (Harder 1983). Restricting energy rewards in this way by flowers results in greater specialisation by particular bumblebee species in visiting flowers of particular plant species (Harder 1983). Such specialisation should in turn promote pollen transfer between flowers within the same plant species and improve pollination (Darwin 1877). However, some flower visitors will cheat on this mutually beneficial relationship in order to gain access by other routes to greater nectar rewards, with the result of not pollinating the flowers. These visitors are referred to as ‘nectar robbers’ (Inouye 1980).

Some short-tongued bumblebee species that cannot reach the nectar in the deeper, more nectar-rich flowers may circumvent the nectar protection (selective visitor exclusion) provided by longer corollas (the fused bases of petals) by biting holes in the lower part of the corolla in order to access nectar more easily through the side of the corolla (although some bumblebees also pierce softer corollas with their tongues, Free & Butler 1959). This is a behaviour known as (‘primary’) nectar robbing (Free 1962). The bumblebees that rob are predominantly the species with the shorter tongues (Brian 1954; Free & Butler 1959). These same bumblebees on subsequent visits to the same flower, as well as other bumblebees that are not biting holes (including some species with long tongues, as well as honeybees), may also use these same pre-formed holes to gain access as (‘secondary’) nectar robbers (Free 1962), apparently facultatively. Robbing behaviour can sometimes be acquired by copying other bumblebees (Kugler 1943; Leadbeater & Chittka 2008). Because nectar robbers do not visit flowers from the entrance opening at the front, where they would make contact with the stamens and stigmas, they are unlikely to cause pollination directly and may reduce pollination (although simply disturbing the flowers, or reducing the standing crop of nectar, could conceivably also help to promote pollination: Soper 1952; Free & Butler 1959; Zimmerman & Cook 1985; Richardson 2004; Irwin *et al.* 2010).

An alternative adaptive path to robbing behaviour may not be linked to head and tongue length. One of us (ZR) has observed *B. nobilis* in Sichuan visiting *Gentiana* L. flowers legitimately from the front entrance of the open flowers during sunny weather. When it rains, the flowers close, restricting access. Then, the *B. nobilis* foragers turn to robbing the closed flowers by biting holes at the base of the corolla. Flowers of some other species also close at particular times of day, especially in the evenings. It is not known whether these are then regularly robbed.

My, what big teeth you have

From our own field observations in Europe, India, and China, the arch nectar-robbers of meadow flowers in mountains of the Old World are bumblebees of the subgenus *Alpigenobombus*. These are the most specialised ‘cheaters’ among the many flower-visiting bumblebees. This has often been recorded previously of course, for example in Europe by Løken (1950), who observed that where *B. mastrucatus* was abundant in Norway, nearly all of the *Aconitum* L. flowers had been robbed (Løken 1949). In what may be an arms race, it is likely that the flowers of some plant species have evolved protective structures (e.g., a thickened calyx of sepals) to reduce robbing (Irwin *et al.* 2010).

Most female bumblebees, even *B. terrestris* (Linnaeus, 1758), have the distal edge of the mandible broadly curved (which may be suited to manipulating pollen and wax within the nest), with only two small basal teeth and sometimes one small apical tooth. In contrast, and uniquely among bumblebees, females of the subgenus *Alpigenobombus* have the distal edge of the mandible armed with six large, evenly-spaced, triangular teeth (Williams 1991: fig. 33), which these bees use routinely to bite holes in long-corolla flowers (especially *Aconitum*: Fig. 1; *Delphinium* L.: Fig. 2). Bees of *Alpigenobombus* have not only strong mandibular teeth, but also a slightly larger genal area posterior to the compound eye (especially noticeable in *B. breviceps*), which accommodates enlarged mandibular muscles. This resembles (if on a smaller scale) the great enlargement of the same area of the head of the giant Asian hornet, *Vespa mandarinia* Smith, 1852, which uses its powerful mandibles instead to crush large numbers of honeybees in rapid succession during group raids at hive entrances (Matsuura & Yamane 1990).

In the core region of the distribution of the subgenus, in the Himalaya and Hengduan mountains, robbing takes place throughout the elevational range of bumblebees, but is carried out by different *Alpigenobombus* species in different elevational zones. These range from *B. breviceps* and *B. genalis* at the lower elevations to the *nobilis*-group and especially the *kashmirensis*-group at the higher elevations, with *B. grahami* at intermediate elevations (see the comments on each species separately). However, species of this subgenus are not especially widespread and are not especially abundant among bumblebees, so presumably the cost/benefit balance for fitness of this form of robbing is not usually overwhelmingly favourable.

Costs and benefits of nectar-robbing

Much remains to be done to quantify the costs and benefits to fitness of floral larceny, including assessing the memory requirements. Biting holes might give early access to a larger standing crop of nectar if nectar is secreted primarily in the early morning. Part of the costs and benefits of robbing will depend on the daily profile of nectar secretion and on how this is affected by robbing. So far, there have been only casual observations of the time required to bite holes of sufficient size in flowers for nectar robbing. Both the time and the energy required to bite these holes are likely to be important costs that should be measured, because bumblebee foragers have been demonstrated to make decisions that maximise closely their energy profit per unit time (Harder 1983). Bumblebees visiting flowers as secondary robbers may do so twice as quickly as when making non-robbing visits (Free & Butler 1959). Stronger mandibles would be an advantage (Kugler 1943) when biting holes if they reduced the costs in time of biting holes in flowers. We are unaware of any evidence as to whether flowers in montane environments are likely to have their nectar more strongly protected by thickened corollas or by other surrounding thickened structures such as sepals. It does appear to be the case that individual foragers return to flowers that they have robbed previously (PW pers. obs. for *B. mastrucatus*, *B. kashmirensis*, *B. nobilis*, *B. breviceps*, *B. grahami*), presumably to reap the rewards of the forager’s prior investment in hole-biting and avoid repeating the costs of the biting process. It is unknown whether there are any greater challenges in learning the positions of the many robbed flowers, or the extent to which these foragers then reject shallower or less remunerative un-robbed flowers, or how any added costs of travelling along ‘trapline’ flights (Heinrich 1979; Sahel & Chittka 2007) between robbed flowers at learned locations are traded-

off against varying rewards. Furthermore, if bumblebees when making ‘legitimate’ visits to the front of flowers regularly scent-mark the flowers they visit (Leadbeater & Chittka 2008), can this scent-marking be reduced or obscured by robbing bumblebees in order to help hide their robbing holes and reduce the likelihood that other visitors will detect and benefit from their investment?

One common bumblebee species not of the subgenus *Alpigenobombus* but well known for nectar robbing is the widespread European, commercially reared, and invasive *B. terrestris* (Free 1962). Its robbing behaviour, where it has been introduced into southern South America, has even been suggested to contribute to substantial competitive pressure on the declining indigenous ‘giant’ bumblebee, *B. dahlbomii* (Guérin-Méneville, 1835) (Rosenberger *et al.* 2021; Chalcoff *et al.* 2022). However, in other situations, robbing may give access for bees to flowers that are normally visited primarily by birds (Pyke 1982).

Evolution of *Alpigenobombus*

Our estimates of dated relationships (Fig. 16) and ancestral distributions (Fig. 18) imply that the crown divergence of the lineages to most of the extant species of the subgenus *Alpigenobombus* is most likely to have taken place in the Himalayan region (including the adjacent forested and mesic grassland region of south-eastern Tibet) ca 6.3 Ma. This is a period when global temperatures were mostly within one degree of recent but with a slow cooling trend (Zachos *et al.* 2001).

Reaching beyond the Himalaya-Hengduan region there have been two principal dispersal events (Figs 16, 18): (1) for the *wurflenii*-group-lineage into Caucasus-Turkey-Europe after ca 4.9 Ma; and (2) for the *angustus*-lineage into Taiwan after ca 2.5 Ma. For bumblebee dispersal into Europe along corridors of suitable habitat from the Himalaya, according to models of ancestral habitat preference and ancestral habitat suitability with changing climate (Williams *et al.* 2017b), high mountain bumblebees of the subgenus *Mendacibombus* are likely to have had a corridor of potentially suitable habitat extending via the Hindu Kush and Alborz mountains within a cooler period from ca 8–3 Ma. In contrast, Taiwan endemic bumblebee species like *B. angustus* are generally montane species, and they may have arrived via a land bridge corridor much later and when sea levels were lower during the cooler Pleistocene glaciations (Huang 2011; Williams *et al.* 2022b).

Many extant species of the subgenus *Alpigenobombus* occur in and are most abundant in open (grass/herb) areas around the upper edge of the coniferous forest zone and alpine zone (e.g., Williams *et al.* 2009: figs 277–279; where they often co-occur with other more abundant montane ‘grassland’ bumblebee species, most often of the subgenus *Melanobombus* Dalla Torre, 1880). Two groups of *Alpigenobombus* species extend to lower elevations: (1) *B. mastrucatus* in some north temperate forested highland regions in Europe (in Germany, Norway and Sweden); and (2) *B. breviceps* in some southern subtropical forested highlands (in southern China and Southeast Asia, where there are fewer species or individuals of *Melanobombus*). In Guangdong, no foragers of *B. breviceps* could be seen during the middle of the day, but dead workers were found (PW) as evidence that the species is present, so it may be that in subtropical regions they are active primarily near dawn and dusk (which is confirmed for *B. breviceps* in Thailand by Thanosing 2022). At the opposite extreme, the species *B. kashmirensis*, *B. rainai*, *B. sikkimi*, and *B. nobilis* occur primarily above the tree line and in some cases extend well above 4000 m into the alpine zone. The divergence of *B. validus* on the north-eastern edge of the Qinghai-Tibetan Plateau is estimated to be especially recent, at 1.1 Ka (Figs 16, 18). This divergence is well supported by morphological differences.

Once strongly-toothed mandibles had arisen in the stem lineage to the subgenus *Alpigenobombus*, it is easy to envisage how this would have given an advantage to these bees in allowing them access to a greater range of deeper flowers that contain more nectar. This may have been important to these bees

where they occur at relatively high elevations that have shorter seasons for colony development (when the benefits of robbing outweigh the costs). Extensively forested habitats in these regions appear to be relatively resource-poor, in having lower densities of suitable flowers than open subalpine meadows, at least when *Rhododendron* is not in flower. What is intriguing is that the particular lineage of the *nobilis*-group also has a longer oculo-malar distance (longer face), which is usually associated with having a longer tongue, giving (legitimate) direct access to deeper-corolla flowers from the front (Heinrich 1979), which would seem redundant for specialists in robbing (unless perhaps there were some deep-corolla robust flowers that were slow to open (some *Rhododendron* species?) or too well protected, e.g., by thick sepals, to be otherwise easily robbed). Also intriguing is that the (short-faced) European *B. mastrucatus* is unusual for having a relatively long tongue (Neumayer & Paulus 1999), disproportionately so for its head length when compared with other bumblebees (Pekkarinen 1979). This may help it access more nectar through small corolla holes higher in flowers with longer corollas when the far inner end of the corolla is better protected (e.g., *Aconitum*). Exploring variation in the shape and size of the tongue and head among *Alpigenobombus* species and the shape and size of the flowers visited (with morphometric analysis) would repay further study.

Just as many questions remain for the subgenus *Alpigenobombus* around the extent to which they rob flowers and the possible costs and benefits of specialising in robbing flowers, so too there may be unusual specialisations in the behaviour and morphology associated with male mate-searching behaviour (Williams 1991) in high mountains (see the comments on *B. kashmirensis*), all of which remain to be investigated.

Conclusions

First, our results support the idea that we can identify some of the lowest-divergence COI-barcode-like numts from mid-range values of the percentage of nucleotides A+T at codon position three (in our data, 94–93%). Second, when orthologous sequences cannot be obtained for some taxa, nonetheless including these low-divergence numts in our analyses did yield candidate species that are corroborated by morphological evidence. Third, whether this is useful can only be fully confirmed when orthologous sequences can be obtained. At the least, it does incur an additional cost in terms of the number of sequences required for the analysis. Using this approach, we recognise 11 species in the subgenus *Alpigenobombus* and are able to estimate phylogenetic relationships among the extant species and then estimate ancestral distributions to reconstruct their historical biogeography. Many aspects of the nectar-robbing behaviour in which *Alpigenobombus* species specialise remain almost completely unexplored.

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Contributions of the authors

Design of the study, PW; collecting specimens for this project, PW JA PD JH SJ GJ JN ZR MS CT LT; arranging sequencing of specimens, PW JH JN ZR MS CT LT MO; identification of specimens, analysis

of genetic data and morphological data, and writing of the manuscript and keys, PW; comment and discussion of the manuscript, PW JA PD JH SJ GJ JN ZR MS CT LT MO.

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Supplementary material

Supp. file 1. Aligned concatenated sequence data for six genes used to estimate evolutionary relationships among species in fasta format (see text for details). <https://doi.org/10.5852/ejt.2022.892.2283.9849>