

## Research article

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**Bumblebees of the *hypnorum*-complex world-wide including two new near-cryptic species (Hymenoptera: Apidae)**Paul H. WILLIAMS<sup>1,\*</sup>, Phurpa DORJI<sup>2</sup>, Zongxin REN<sup>3</sup>, Zhenghua XIE<sup>4</sup> & Michael ORR<sup>5</sup><sup>1</sup>Natural History Museum, Cromwell Road, London SW7 5BD, UK.<sup>2</sup>Royal Society for Protection of Nature, Thimphu, Bhutan.<sup>3</sup>Kunming Institute of Botany, Chinese Academy of Sciences, 132 Lanhei Road, Kunming, Yunnan 650201, China.<sup>4</sup>Institute of Highland Forest Science, Chinese Academy of Forestry, Kunming, Yunnan 650224, China.<sup>4</sup>Key Laboratory of Breeding and Utilization of Resource Insects of National Forestry and Grassland Administration, Kunming, Yunnan 650224, China.<sup>5</sup>Institute of Zoology, Chinese Academy of Sciences, 1 Beichen West Road, Chaoyang, Beijing 100101, China.<sup>5</sup>Staatliches Museum für Naturkunde Stuttgart, Rosenstein 1, D-70191 Stuttgart, Germany.

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**Abstract.** The *hypnorum*-complex of bumblebees (in the genus *Bombus* Latreille, 1802) has been interpreted as consisting of a single widespread Old-World species, *Bombus hypnorum* (Linnaeus, 1758) s. lat., and its closely similar sister species in the New World, *B. perplexus* Cresson, 1863. We examined barcodes for evidence of species' gene coalescents within this species complex, using the closely related *vagans*-group to help calibrate Poisson-tree-process models to a level of branching appropriate for discovering species. The results support seven candidate species within the *hypnorum*-complex (*Bombus taiwanensis* Williams, Sung, Lin & Lu, 2022, *B. wolongensis* Williams, Ren & Xie sp. nov., *B. bryorum* Richards, 1930, *B. hypnorum*, *B. koropokkrus* Sakagami & Ishikawa, 1972, and *B. hengduanensis* Williams, Ren & Xie sp. nov., plus *B. perplexus*), which are comparable in status to the currently accepted species of the *vagans*-group. Morphological corroboration of the coalescent candidate species is subtle but supports the gene coalescents if these candidates are considered near-cryptic species.

**Keywords.** Barcode, bumblebee, coalescent, distribution, species.

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## Introduction

Bumblebees are some of the most intensively studied and well-known insects globally and yet new species continue to be discovered (patterns reviewed by Williams 1998; 2022b). Some of the most widespread bumblebee species within Europe and Asia have in the last decade been examined for genetic variation across their ranges (Dellicour *et al.* 2015, 2017; Lecocq *et al.* 2016; Martinet *et al.* 2021). Part of the interest for this kind of work comes from the intriguing case of obscure cryptic species that are now well established from multiple lines of evidence to exist among the relatives of *Bombus lucorum* (Linnaeus, 1761) within Europe, but which remain difficult to distinguish from morphology (reviewed by Rasmont 1984; Williams *et al.* 2012, 2021). However, in a contrasting case, the widespread European *B. lapidarius* (Linnaeus, 1758) has also been shown to have intriguing patterns of variation in different kinds of characters within its continental distribution (e.g., Lecocq *et al.* 2013; 2019), although re-analysis of the different lines of evidence has recently shown that these patterns do not agree with one another in supporting the same set of individuals as a separate species (the nominal taxon *bisiculus*: Williams *et al.* 2020). In the present study, we examine what has hitherto appeared to be another of the most widespread but not especially variable bumblebee species, *B. hypnorum* (Linnaeus, 1758).

*Bombus hypnorum* (in the previous broad sense) is of particular interest because it is one of the few bumblebee taxa to have increased substantially in its European distribution range without any deliberate introductions having been documented (Prŷs-Jones 2019; Huml *et al.* 2021; Rasmont *et al.* 2021). Quantitative comparative analyses have the potential to allow us to understand more about such ‘winners’ and to better contrast them with the ‘losers’ that have shown range declines (Williams *et al.* 2009a). During this century, the *hypnorum*-complex has expanded in range within Europe, for example establishing for the first time in Britain (Goulson & Williams 2001; Crowther *et al.* 2014; Prŷs-Jones 2014; Huml *et al.* 2021), in Ireland (O’Donnell 2018), and in Iceland (Prŷs-Jones *et al.* 2016). There have been suggestions that these bees are associated, in some regions of Europe at least, especially with human activities within the forests (Løken 1973) or within tree-rich suburbs of towns (Rasmont *et al.* 2021). The *hypnorum*-complex has otherwise been described as being associated more broadly with the temperate and boreal coniferous forest zones (Løken 1973), extending into coniferous forest high in mountains in warmer regions further to the south (Williams 1991, 2022a; Starr 1992). However, these analyses must depend on reliable taxonomy.

There are approximately 288 species of bumblebees world-wide, all placed in a single genus *Bombus* Latreille, 1802 (Williams 1998; 2022a). When discussing evolutionary and ecological patterns, it is often convenient to name smaller, monophyletic groups of the more closely-related species, such as subgenera (using the estimate of phylogeny from Cameron *et al.* 2007: fig. 1). *Bombus hypnorum* belongs to the subgenus *Pyrobombus* Dalla Torre, 1880 (in the subgeneric system revised by Williams *et al.* 2008), which includes at least 56 species (updated from the estimate in Williams 1998). Within this subgenus, a *hypnorum*-group can be recognised, which is most closely related to the *vagans*-group, *lapponicus*-group, and *lepidus*-group (Hines *et al.* 2006; Cameron *et al.* 2007). The *hypnorum*-group includes: *B. hypnorum* s. lat., which is widespread in Europe and Asia (Reinig 1939; Williams 1991); its closely similar sister-species *B. perplexus* Cresson, 1863, which is widespread in North America (Williams *et al.* 2014); and *B. haematurus* Kriechbaumer, 1870, a close relative from eastern Europe and western Asia (Biella *et al.* 2020). But because it has been suggested that *B. hypnorum* s. lat. may

actually consist of several species that may be difficult to distinguish (see below), the former broad interpretation of the species should instead be referred to in the interim as the *hypnorum*-complex, to include the closely similar *B. perplexus* (but to exclude *B. haematurus* of the larger *hypnorum*-group). When compared with other species complexes of bumblebees, there have been surprisingly few attempts over the last 150 years to assess whether this complex might include additional species. The exceptions are *B. bryorum* Richards, 1930, postulated as a separate species from the Himalaya by Tkalců (1974); *B. fletcheri* Richards, 1934, postulated as a separate species also from the Himalaya by Richards (1934); and most recently, *B. taiwanensis* Williams, Sung, Lin & Lu, 2022, postulated as a separate species from Taiwan by Williams *et al.* (2022). The status of these taxa as separate species has not always been accepted because their morphological divergence from the broadly distributed *B. hypnorum* s. str. is subtle (Reinig 1939; Williams 1991; Starr 1992).

Here we re-assess the species of the *hypnorum*-complex by taking a global over-view of the variation and by providing a context appropriate for discovering patterns at the species level. Enabled by unparalleled geographic sampling, founded in partnerships with local researchers, we provide a revised interpretation for this challenging species complex. We re-examine variation in: (1) sequences of a fast-evolving gene (Hebert *et al.* 2003; Baker *et al.* 2009), the ‘barcode’ region of the mitochondrial cytochrome *c* oxidase subunit I (COI) gene; (2) exoskeletal morphology; and (3) colour patterns of the hair.

## Material and methods

### Species concept and discovery methods

We view species in theory as evolutionarily independent lineages (de Queiroz 2007) and seek to discover species 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 morphology, and with 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 (Williams 2007). We prefer to label these different colour patterns directly and informally (e.g., ‘yellow-banded’ versus ‘white-banded’) when necessary, to avoid adding unnecessarily to the burden of formal classification. We are especially keen to avoid slipping into imposing unjustified assumptions about unstudied differences in their history, possible futures, genetics, physiology, or behaviour: such differences should instead need to be demonstrated.

### Sampling

The area of geographical distribution of the *hypnorum*-complex extends across most of the large Palaearctic Region of Europe and Asia, as well as across much of the northern Oriental Region of Asia and extending into the northern Nearctic Region (Reinig 1939; Williams 1991). Some of the greatest variation is restricted to areas in remote mountain ranges of Asia, where access for sampling can be difficult (Williams *et al.* 2017). Studies need sample sizes that are sufficiently large to detect species while keeping costs within reasonable bounds (Phillips *et al.* 2018). To reduce sampling costs and to facilitate access permissions, we formed a global coalition of collaborators to contribute samples from a network of sites that are spaced deliberately widely across taxon distributions (following the practice of Williams *et al.* 2012). Much of the material examined for this project is not listed here because permission to publish data was limited by local policies. All specimens were identified by PW, where possible by comparison with primary type specimens. Decimal latitude and longitude coordinates are

given in the material sequenced for each species. The holotype specimens of the two new species from China have been deposited in the Chinese national collection at the Chinese Academy of Sciences' Institute of Zoology, Beijing, China.

### Institutional abbreviations

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
NHMUK	=	Natural History Museum, London, UK
NME	=	Naturkundemuseum Erfurt, Erfurt, Germany
PW	=	P. Williams research collection, London, UK
RMNH	=	National Museum of Natural History, Leiden
TFRI	=	Taiwan Forestry Research Institute, Taipei, China

### Species' gene coalescents

To find sufficient differences from DNA sequences to enable informative comparison of closely related taxa, we need a fast-evolving gene (Hebert *et al.* 2003; Baker *et al.* 2009). We use the 657-nucleotide barcode segment of the COI gene, which is located in the mitochondrial genome. COI-barcode sequences were obtained by downloading data from online databases BOLD (<https://www.boldsystems.org>) and GenBank (<https://www.ncbi.nlm.nih.gov/nucleotide/>) or by using standard protocols (Hebert *et al.* 2004) in the labs of: (1) the Canadian Centre for DNA Barcoding (CCDB) at Guelph (sequences now in their BOLD database); and (2) the KIB. Because orthologous COI barcodes include no indels, they can be aligned by eye using a sequence editor, BioEDIT ver. 7.0.9.0 (<https://www.mbio.ncsu.edu/BioEdit/bioedit.html>). An in-frame length threshold of 480 base-pairs was applied to exclude short sequences (Williams *et al.* 2016). No sequences had in-frame stop codons or indels that might indicate strongly-divergent numts (Magnacca & Brown 2010).

Obtaining a gene tree with representative branch lengths could pose a challenge if just some of the species were relatively 'over-sampled' (Williams *et al.* 2020). If many closely similar sequences within these species can give 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). The problem is reduced by including only the unique haplotypes (Williams *et al.* 2020). These unique haplotypes are identified using the software COLLAPSE ver. 1.2 (<https://www.darwin.uvigo.es/software/collapse.html>), 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 with MRBAYES ver. 3.1.2 (Ronquist & Huelsenbeck 2003), which is preferred for estimating phylogeny because it applies explicit and well-tested evolutionary models for genes as well as using 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+ $\Gamma$ ). For seeking the shortest trees we use four Markov-chain Monte-Carlo (MCMC) chains for 10 million generations with the 'temperature' set to 0.2. The trees are rooted by including a sequence for the outgroup *B. alpinus* (Linnaeus, 1758). A sample of 10,000 resulting trees is examined for convergence using TRACER ver. 1.6.0 (<https://www.beast.bio.ed.ac.uk/Tracer>; Drummond & Rambaut 2007).

To examine support for species' gene coalescents, we apply Poisson-tree-process (PTP) models to the summary estimated evolutionary gene tree (Zhang *et al.* 2013). PTP analysis depends on fitting models to a metric gene tree in order to model: (1) low branching rates on the tree between species; and (2) high branching rates on the tree within species (Zhang *et al.* 2013); contrasted in terms of the numbers of substitutions between branching events (Zhang *et al.* 2013).

For the PTP technique to perform properly, the models in each analysis need to be fitted to data representing at least five separate and previously verified species (Reid & Carstens 2012; Fujisawa & Barraclough 2013; Talavera *et al.* 2013; Zhang *et al.* 2013; Leliaert *et al.* 2014; Dellicour & Flot 2015). Unfortunately, the *hypnorum*-group has too few *a priori* recognised species, with only three species in the tree by Cameron *et al.* (2007). Therefore, we need to add more species from a closely-related group with agreed concepts of species – this in effect calibrates the models on agreed inter-specific and intra-specific branching patterns. We choose to extend our analysis to include the species of the North American *vagans*-group (using the tree from Cameron *et al.* 2007: species in Table 1), a group that is relatively well studied and taxonomically stable (Stephen 1957; Thorp *et al.* 1983; Williams *et al.* 2014). Sequence data are available for the *vagans*-group in the BOLD database (<https://www.boldsystems.org>; Ratnasingham & Hebert 2007). For each of these species in turn, we examined the barcode variation within the BOLD TaxonID Tree for the corresponding BOLD BIN code (BOLD's candidate species: Ratnasingham & Hebert 2013) to identify a series of barcodes that represent the major known divergent subgroups within the tree. We then downloaded these example sequences to include in our analysis (Table 1). Evidence for initial candidate species as supported by species' gene coalescents is obtained using the online bPTP server with default options (<https://species.h-its.org/>; Zhang *et al.* 2013).

### **Morphology**

We scored morphological characters using a light microscope (Wild model M5A). Morphological terms follow Michener (2000) and Williams *et al.* (2009b), with terms for the components of the male genitalia following the 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.

### **Integrative assessment**

The procedure followed here has been to begin by comparing samples from across the entire range of the *hypnorum*-group and *vagans*-group to seek evidence of species' coalescents in the COI gene. The candidate species within the *hypnorum*-complex then become the focus for comparing specimens to discover diagnostic and conflicting patterns of states within morphological characters. The candidate species are accepted as species only if the two patterns of evidence coincide among samples to support 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 considered.

### **Assigning names to species**

We seek to represent the major formally named taxa of the *hypnorum*-complex in our analysis with COI 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). However, because data for gene sequences are usually unavailable from 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 identical with the primary

**Table 1.** BOLD sequences for species of the *Bombus vagans*-group accessed by BOLD BIN codes (Ratnasingham & Hebert 2013).

species	BOLD BIN code	number of conspecific sequences in the BOLD IDTree	sequences downloaded
<i>Bombus caliginosus</i>	–	(1)	BEECC847-09
<i>B. centralis</i>	ABZ6660	49	NGAAC2036 NGAAC2065 NGAAC2098 UAIC296
<i>B. flavifrons</i>	ACE3465	141	BBHYL272 BCBEES317-22 BCBEE336 BCBEE011-21 GMCVA044-16 GMVVB058-16
<i>B. vagans</i>	AAB1777	231	BBEC145 BBHYL271 BBHYL232-10 BEECB1061-07 CFNS132 SSGBB4381
<i>B. vandykei</i>	ACE3465	4	LRBBC1588

**Table 2.** List of selected available formal names in the species group for taxa of the *Bombus hypnorum*-complex (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 (#*n*) of the proxy type in the *hypnorum*-complex project database.

taxon name	species name	original type locality	barcode proxy locality	specimen ID
<i>bryorum</i>	<i>bryorum</i>	Kashmir	Nepal	#005
<i>calidus</i>	<i>hypnorum</i>	Siberia	Yakutsk	#012
<i>hengduanensis</i>	<i>hengduanensis</i>	Xizang	Xizang	#017
<i>hypnorum</i>	<i>hypnorum</i>	Sweden	Sweden	#010
<i>koropokkrus</i>	<i>koropokkrus</i>	Japan	Sakhalin	#014
<i>perplexus</i>	<i>perplexus</i>	Connecticut	Nova Scotia	#024
<i>taiwanensis</i>	<i>taiwanensis</i>	Taiwan	Taiwan	#001
<i>wolongensis</i>	<i>wolongensis</i>	Sichuan	Sichuan	#002

type specimen and are chosen here where possible by: (1) matching morphology and colour pattern of the hair; (2) proximity of the proxy collection locality to the original type locality; (3) having long COI sequences; and (4), for some taxa, it is desirable to match the sex and caste of the proxies with the original type specimens, because of occasional difficulties in associating sexes and castes among species from morphology alone. Our proxies are not intended to have any formal or persistent nomenclatural status 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.

## Results

### *Species recognition*

#### Sampling

From the GenBank and BOLD databases, an initial sample of 161 sequences of the *hypnorum*-group was downloaded, which was supplemented by 29 new sequences from the authors. The majority of these sequences is either identical to one another or did not meet the in-frame length criterion.

#### Species' gene coalescents

As new sequences were gradually accumulated over 12 years, a series of coalescent analyses for nine successive data sets was run until stable results were obtained. TRACER showed that the last MRBAYES analysis of the 42 unique COI haplotypes over 10 million MCMC generations after a 10% burn-in had converged on stable traces.

There is evidence of population structure from the PTP results that show values of less than 0.9 for some of the species' gene coalescents within the *hypnorum*-group (for the candidate taxa *bryorum*, *hypnorum* s. lat., *hengduanensis*, *perplexus*). These scores are similar to those for several previously accepted species of the *vagans*-group (*centralis*, *flavifrons*, *vagans*) (Fig. 1).

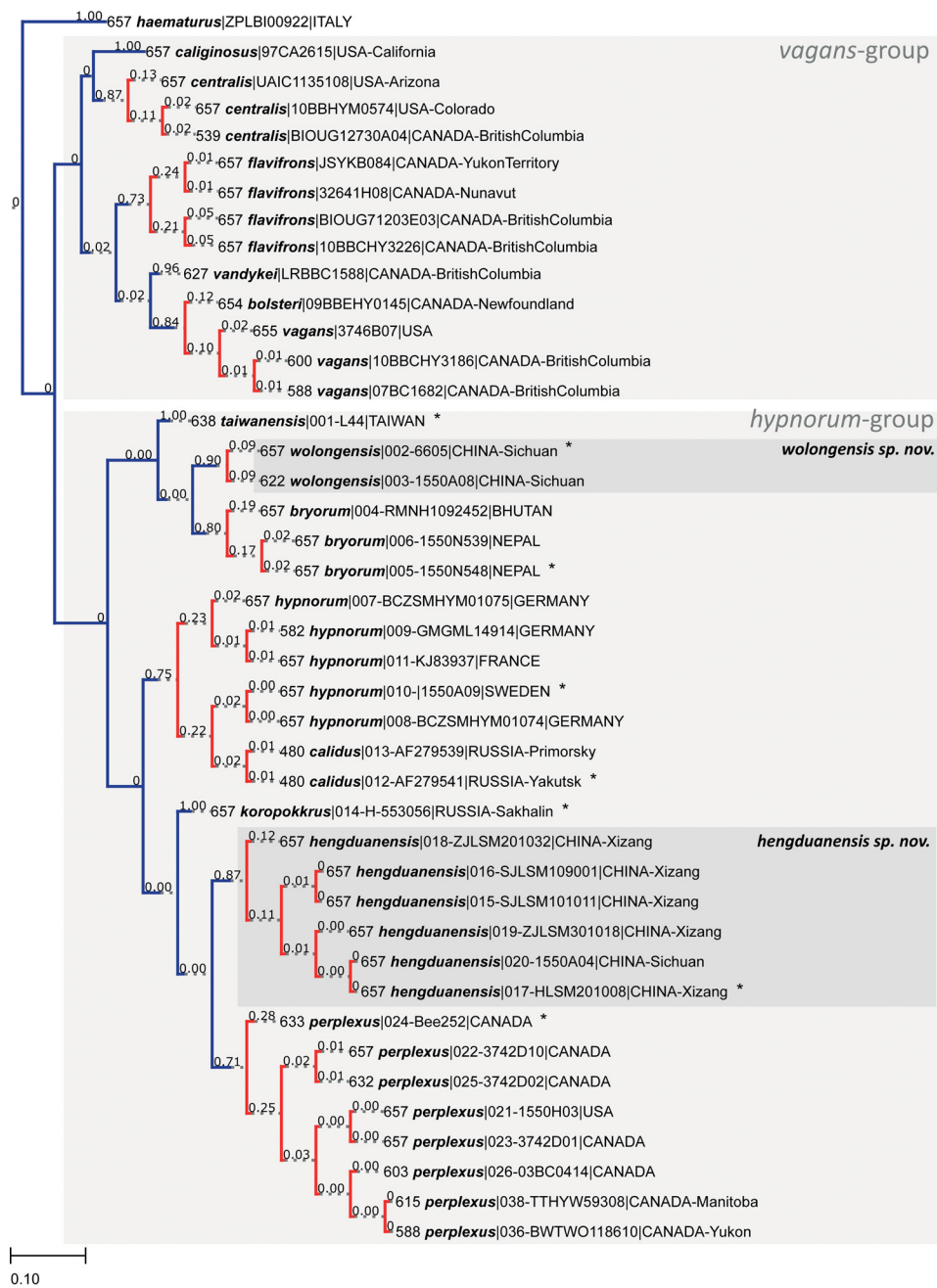
#### Morphology and integrative assessment

The *vagans*-group is the first large group at the top of Fig. 1, although two of the species are represented by only the single unique haplotypes that are known. The five candidate-species' coalescents from PTP analysis of barcodes (Fig. 1) have been distinguished by morphology (Williams *et al.* 2014) and match the established species. These candidates are accepted as separate species.

For the *hypnorum*-group, the second large group occupying the lower part of Fig. 1, seven candidate species' gene coalescents are then recognised. Of these seven candidates, two are represented by single unique haplotypes. Among these, the two new candidate species are represented by two and six haplotypes respectively. The seven candidates can also be distinguished by morphology as described in the key below. The differences among them in sculpturing of the exoskeleton are subtle, so some of them must be considered close to the threshold for accepting separate species (especially within the group of candidate species *koropokkrus*, *hengduanensis*, *perplexus*). Maps show that the distributions of the seven candidate species from the sequenced samples (Fig. 2) are spatially coherent, in the sense that they do not show the very wide, trans-continental disjunctions that might (in some cases) indicate artificially lumped species. Some of the different candidate species are also overlapping while maintaining their distinct character (*wolongensis*, *hengduanensis*), which is likely to indicate a lack of interbreeding (a necessary, but no longer sufficient, property of species). Therefore, within the *hypnorum*-complex, the seven candidate species (Fig. 1) are all accepted as species. Each of these species shows variation within it (e.g., for colour pattern, Figs 3–50).

#### Assigning names to species

The seven species of the *hypnorum*-complex 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. 1. The nomenclature of species is summarised in outline in the Synopsis section below.



**Fig. 1.** MRBAYES estimate of phylogeny as a metric tree (outgroup *B. alpinus* (Linnaeus, 1758) not shown) from COI barcodes from GenBank and BOLD databases for the *vagans*-group and *hypnorum*-group, with additions from the authors for the *hypnorum*-group of bumblebees, filtered to remove duplicate and short sequences. Each sequence is labelled with: sequence length; a taxon name from the database; 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). The scale bar is calibrated in substitutions per nucleotide site. Results of Bayesian Poisson-tree-process (PTP) models applied for assessing support for species' gene coalescents by maximum likelihood are shown as PTP scores above the branches: scores approaching 1 and where branches change from blue to red indicates are where the most likely species' gene coalescents are detected. Asterisks mark sequences used as informal proxies for the type specimens of each of the taxon names in Table 2.



## Synopsis of world species

Order Hymenoptera Linnaeus, 1758  
Family Apidae Linnaeus, 1758  
Genus *Bombus* Latreille, 1802  
Subgenus *Pyrobombus* von Dalla Torre, 1880

### *hypnorum*-complex

*Bombus taiwanensis* Williams, Sung, Lin & Lu, 2022

*Bombus wolongensis* Williams, Ren & Xie **sp. nov.**

*Bombus bryorum* Richards, 1930 **stat. rev.**

= *fletcheri* Richards, 1934

*Bombus hypnorum* (Linnaeus, 1758)

= *calidus* Erichson, 1851

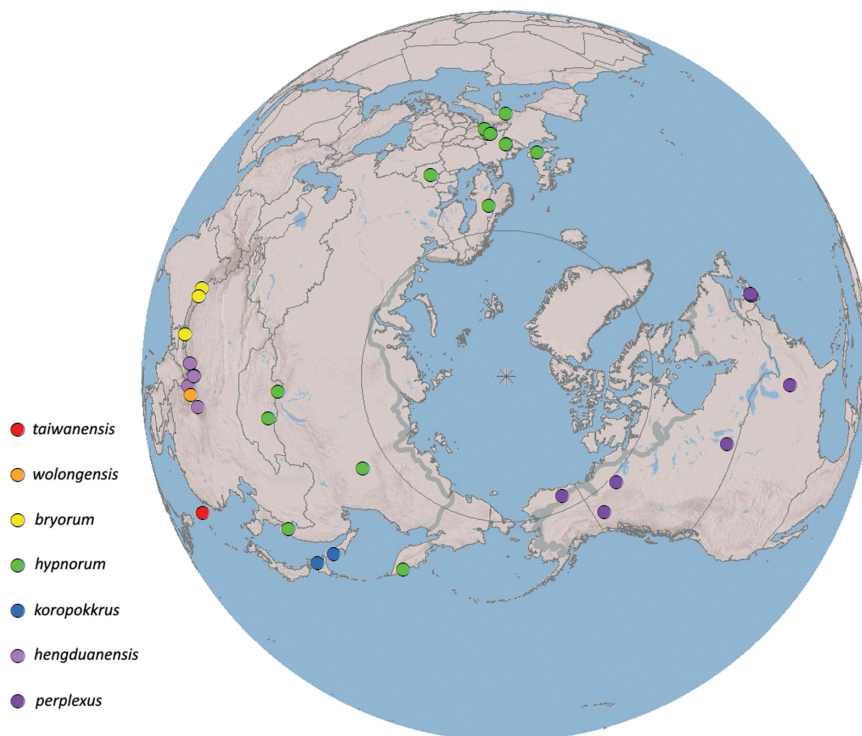
*Bombus koropokkrus* Sakagami & Ishikawa, 1972 **stat. rev.**

= *insularis* Sakagami & Ishikawa, 1969, not of Smith (1861)

*Bombus hengduanensis* Williams, Ren & Xie **sp. nov.**

*Bombus perplexus* Cresson, 1863

= *hudsonicus* Cresson, 1863



**Fig. 2.** Distribution of barcoded samples of the *hypnorum*-complex and *B. perplexus* Cresson, 1863, with the interpretations as separate candidate species from Fig. 1 shown as different coloured spots as per the colour key on the left. Relief map with hill shading, polar projection (north pole shown as a star), the international boundaries and the Arctic Circle are shown as narrow grey lines, and the northern tree line shown as a broad grey line. Image created in ArcGIS using World\_Shaded\_Relief basemap (© 2014 Esri).

**Key to species for females of the *hypnorum*-complex**

Future identification of the species of the *hypnorum*-complex recognised here will be most reliable for specimens when made from COI-barcode data, which are available for comparison of nucleotide differences with the reference data in BOLD. A key using morphological shape, surface sculpturing, and hair-colour-pattern characters follows below, with the most reliable characters placed at the beginning of each couplet. Our results imply that in many cases we should be able to assign most reliably the specimens with locality labels to species on the basis of their collection locality alone. All identifications of species from the key or from the figures should be checked against the species' diagnoses within the accounts for each species.

Diagrams showing the variation in the colour-patterns of the dorsal hair are presented in Figs 3–50. These diagrams summarise only the major differences (Williams 2007) rather than the details (e.g., Williams 1991: figs 311–316). 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.

1. Head with the ocello-ocular area along the inner eye margin with only one row of larger medium punctures; clypeus in the central area with scattered widely-spaced small punctures and the very large punctures spaced by more than three times their own diameter ..... 2
  - Head with the ocello-ocular area along the inner eye margin with a broad band of scattered larger medium punctures; clypeus in the central area with a longitudinal band of small punctures and with very large punctures, some spaced by just twice their own diameter ..... 4
2. Thoracic dorsum with the hair black; midleg and hindleg basitarsi with integument orange-brown (Taiwan) ..... *B. taiwanensis* Williams, Sung, Lin & Lu, 2022
  - Thoracic dorsum with the hair predominantly brown or yellow; midleg and hindleg basitarsi with integument dark brown or black ..... 3
3. Thoracic dorsum predominantly brown, in the centre of the scutum without black hair; labral lamella broad and shallowly rounded, almost rectangular (Himalaya) ..... *B. bryorum* Richards, 1930
  - Hair of the thoracic dorsum dull yellow, in the centre of the scutum with a dense central spot of black hair; labral lamella narrow and deeply rounded, almost pointed in the middle (Sichuan, Yunnan) ..... *B. wolongensis* Williams, Ren & Xie sp. nov.
4. Head with the ocello-ocular area along the inner eye margin with a broad band of small and medium punctures, in the posterior shining gap opposite the ocelli the small punctures spaced by about their own breadths; T5 posteriorly in the middle, anterior to the smooth posterior margin, with a narrow band of close large punctures extending for less than an eighth of the length of the tergum ..... 5
  - Head with the ocello-ocular area along the inner eye margin with a broad band of medium and small punctures, in the posterior shining gap opposite the ocelli the small punctures spaced by much more than their own breadths; T5 posteriorly in the middle, anterior to the smooth posterior margin, with a broad band of close large punctures extending for at least a quarter of the length of the tergum . 6
5. Hair of T4 *either* the posterior half white *or* white at least in a continuous band along the posterior margin; labral tubercle on its broad outer lateral and anterior-facing surface in the centre smooth, with large punctures only along the dorsal and lateral edges (Palearctic) ..... *B. hypnorum* s. str.
  - Hair of T4 *either* the posterior half black *or* with only a few white hairs along the posterior margin; labral tubercle on its broad outer lateral and anterior-facing surface in the centre with a few very large punctures scattered throughout (Hengduan, North China) ..... *B. hengduanensis* Williams, Ren & Xie sp. nov.

6. Clypeus in the centre with widely scattered large punctures with more numerous small punctures between them; scutum with the hair usually dull yellow (sometimes dull pale brown), T5 hair usually entirely black, but sometimes white or cream posteriorly and occasionally throughout (Nearctic) ..  
..... *B. perplexus* Cresson, 1863
- Clypeus in the centre with widely scattered large punctures with fewer small punctures between them; scutum with the hair orange-brown, T5 hair usually entirely white, but sometimes only along the posterior margin (Japan, Sakhalin) ..... *B. koropokkrus* stat. rev.

### Accounts of the species

Accounts of the seven accepted species of the *hypnorum*-complex follow below. Square brackets [*Bombus xus*] are used to indicate transliterations, translations, interpretations and unavailable names outside the species group (sensu ICZN 1999), including selected misspellings, misidentifications, and infrasubspecific names.

### *Bombus (Pyrobombus) taiwanensis* Williams, Sung, Lin & Lu, 2022 Figs 1–4

[*Bombus* sp. non descripta Chiu 1948: 71.]

[*Bombus (Pyrobombus)* nr. *hypnorum* Starr, 1992: 149.]

*Bombus (Pyrobombus) taiwanensis* Williams *et al.*, 2022: 438. Holotype by original designation: ♀, Mt Hehuan, Taiwan (TFRI). Examined.

### Diagnosis

#### Female

Distinguished by: clypeus in the central area smooth and shining with only a few large punctures, mostly spaced by much more than their own widths; ocello-ocular area with the inner eye margin mostly shining with few small punctures and the few larger, medium punctures forming a single row parallel to the eye margin; front, middle and hind leg basitarsi all with the exoskeleton lighter brown than for the tibiae; hair predominantly black but with metasomal T4–6 a dull sandy-brown or pale orange.

#### Male

Distinguished by: front, middle and hind leg basitarsi all with the integument lighter brown than the tibiae; genitalia with the gonostylus inner anterior (basal) projection separated from the gonocoxa by less than the breadth of the recurved hook of the penis-valve head.

### Material examined

#### Material sequenced or examined

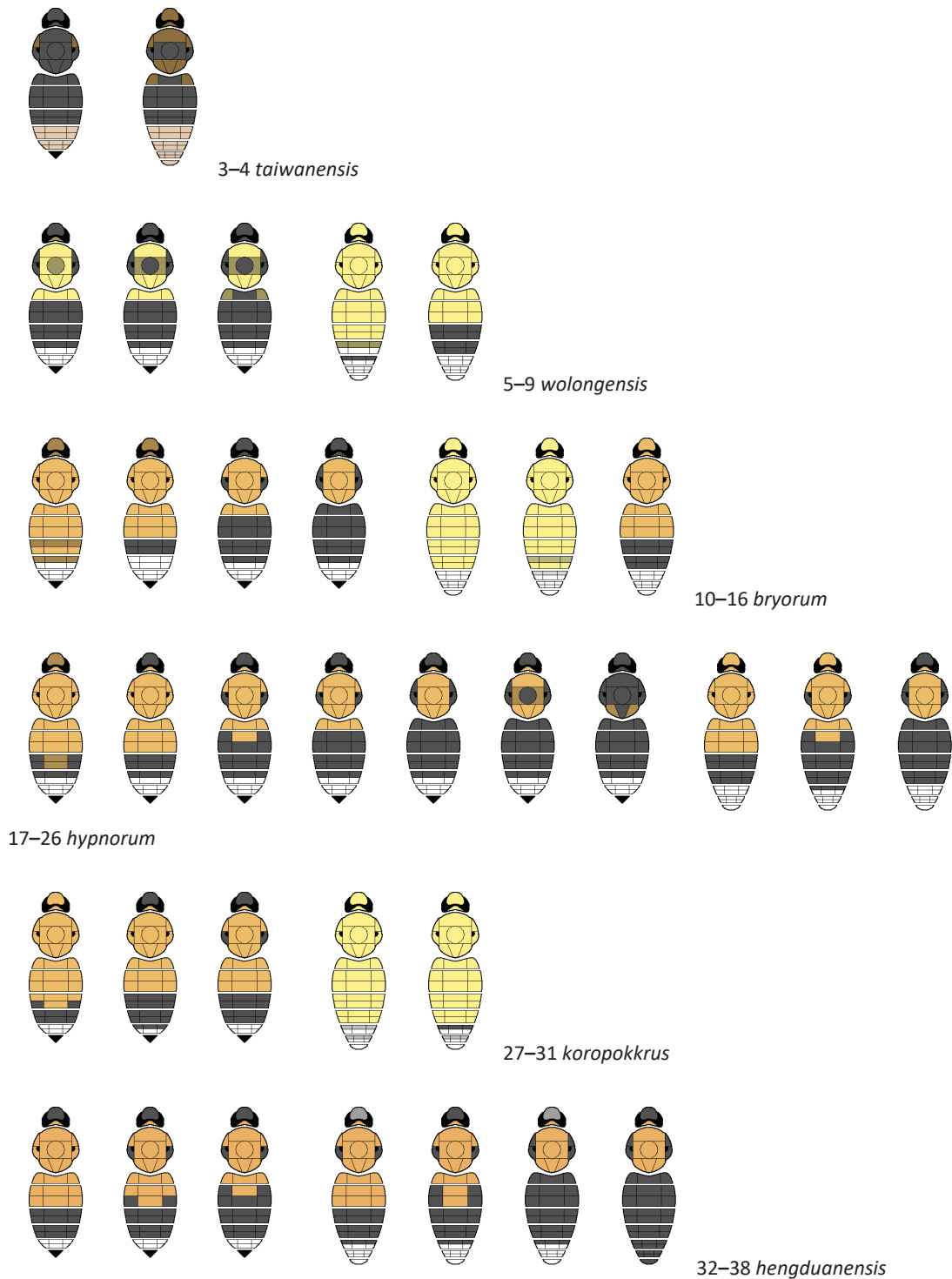
CHINA – Taiwan • 1 ♀ (worker); Nantou Hsien, Tsuifeng [Cuifeng]; 24.1060° N, 121.1988° E; alt. 2300 m; 23–25 Jun. 1983; K.S. Lin and C. Lin leg.; BOLD-1550A06-TWN; PW • 1 ♂; Hualien Hsien, Tayuling; 23.9767° N, 121.5206° E; alt. 2560 m; 9–16 Jun. 1980; K.S. Lin and B.H. Chen leg.; BOLD-1550A07-TWN; PW.

#### Other material sequenced

GenBank: MZ831884, MZ831885, MZ831886, MZ831887, MZ831891, MZ831892.

### Distribution

Endemic to the mountains of Taiwan, where it is extremely rare, at elevations of 2300–3100 m (Williams *et al.* 2022).



**Figs 3–38.** Simplified diagrams for the colour patterns of the hair on the dorsum for ♀♀ (left) and ♂♂ (right) of the *Bombus* species from Fig. 2. 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 (precise shades vary), with olive indicating a mixture of black and yellow hair, and grey indicating a mixture of black and white hair.

***Bombus (Pyrobombus) wolongensis*** Williams, Ren & Xie sp. nov.  
urn:lsid:zoobank.org:act:944777F5-62DD-416A-A778-7C6D1E189572  
Figs 1–2, 5–9, 51

[*Bombus (Pyrobombus) hypnorum* (Linnaeus, 1758) – Williams *et al.* 2009b: 157, (in part) misidentification.]

### Diagnosis

Female distinguished by the combination: labral lamella narrow and deeply rounded, almost pointed in the middle; clypeus in the central area with scattered widely-spaced small punctures and the very large punctures spaced by more than three times their own diameter; ocello-ocular area along the inner eye margin with only one row of larger medium punctures; thoracic dorsum with the hair predominantly dull yellow with a dense central spot between the wing bases of black hair.

Male distinguished by the combination: hair of the thorax and metasomal T1–2 yellow, T3–4 black.

### Etymology

Named for its occurrence near the area named Wolong, in Sichuan Province.

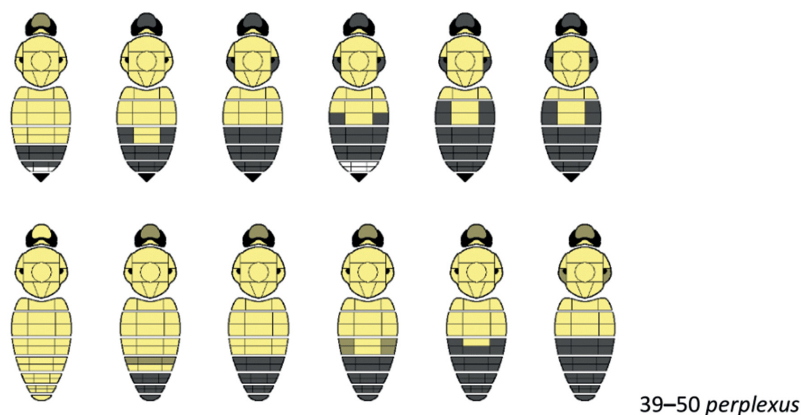
### Material examined

#### Holotype

CHINA • ♀ (queen) pinned; [four labels]; [(1) white hand-written in red] ‘6605’; [(2) white printed in black] ‘CHINA: Sichuan / Leibo Co, Gudui 1711m / 28.47056N 103.31884E / J Wang’; [(3) green printed in black] ‘BOLD# / (BEE-BOL/BBW/PHW) / 596G12-6605-CHN’; [(4) red printed in black] ‘HOLOTYPE ♀ (q) / *Bombus wolongensis* / Williams, Ren & Xie / det PH Williams 2022’; IOZ.

#### Material sequenced or examined

CHINA • 1 ♀ (queen); Sichuan, Leibo Co., Gudui; 28.4706° N, 103.3188° E; alt. 1711 m; 8 Apr. 2007; Z. Xie leg.; [#6603]; BOLD-596H01-0012-CHN; PW • 1 ♀ (queen); Sichuan, Leibo Co., Gudui;



**Figs 39–50.** Simplified diagrams for the colour patterns of the hair on the dorsum for ♀♀ (above) and ♂♂ (below) of *Bombus perplexus* Cresson, 1863. 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 (precise shades vary), with olive indicating a mixture of black and yellow hair, and grey indicating a mixture of black and white hair.

28.4706° N, 103.3188° E; alt. 1711 m; PW • 1 ♂; Sichuan, Litang Co., Litang-Yajiang; 30.0079° N, 100.3137° E; alt. 4382 m; 10 Jul. 2003; Y. Tang leg.; BOLD-1550A08-CHN; PW • 1 ♂; Sichuan; Y. Tang leg.; [TY0700189]; PW • 1 ♂; Yunnan, Lijiang; 29.0025° N, 100.1825° E; alt. 3200 m; 27 Jul. 2018; Z. Ren leg.; PW.

## Description

### Female

Habitus illustrated in Fig. 51, body size small (queen body length 15–17 mm, worker: no workers available to hand), hair (pubescence) moderately long, wings lightly clouded with brown. Mandible with the distal notch anterior to the posterior tooth (incisura) very shallow. Oculo-malar area (‘cheek’ sensu Williams *et al.* 2014; not the gena) of medium length,  $1.0 \times$  as long as the breadth of the mandible at its base (length measured between the ventral edge of the compound eye and the edge of the malar area at the articulation of the mandible midway between the mandibular condyles; breadth measured between and including the mandibular condyles). Labral lamella narrowly rounded and almost pointed in the middle. Clypeus weakly swollen, its raised area nearly flat, the central area with few widely scattered large, medium, and small punctures with intervening areas shining, few punctures especially medially and ventrally adjacent to the labrum. The area between the inner edge of the compound eye and the outer edge of the lateral ocellus occupied in just more than its outer third by widely spaced medium and small punctures, spaced by more than their own widths, the medium punctures in a single row. Mid basitarsus with the distal posterior corner broadly rounded; hind tibia outer surface with a corbicula, the surface sculpturing weakly reticulate so that the surface appears slightly matt; hind basitarsus in the distal three quarters covered with short branched decumbent and weakly overlapping hairs with golden reflections; metasomal T6 posteriorly rounded and not divided medially, with a small subapical dorsal



**Fig. 51.** *Bombus wolongensis* Williams, Ren & Xie sp. nov., ♀ (queen), holotype (IOZ), habitus, lateral view (image reversed). Scale bar: 10 mm.

boss. Colour pattern of the hair of the body predominantly black. Head entirely black, except for orange hairs anteriorly on the labrum and laterally on the mandibles, and a yellow fringe posteriorly on the occiput. Thoracic dorsum dull yellow (the exact shade varies but is lighter than for unfaded *B. bryorum*), this pale hair not extending down the side of the thorax anteriorly, with black hair as a small or large dense central spot between the wing bases and often a few black hairs scattered laterally and especially anteriorly; the front, middle and hind leg tibiae all with the hairs predominantly black, the basitarsi all with the integument brown-black like the tibiae. Hair of T1 yellow, T2–3 and T4 anteriorly black, T4 posteriorly and T5–6 cream-white.

#### Male

Body size small (body length 11–13 mm), hair (pubescence) moderately long, wings very lightly clouded with brown. Colour pattern of the hair of the body predominantly yellow. Front and top of the head with some black hair intermixed. Hair of metasomal T3–5 with some black hair at least anteriorly, T5–7 predominantly cream-white. Male genitalia with the gonostylus nearly triangular, the inner anterior (basal) projection separated from the gonocoxa by a distance equal to the breadth of the recurved hook of the penis-valve head; the volsella scarcely projecting beyond the gonostylus; the penis valve with the head recurved as a flattened sickle-shaped hook that is not tapering at the mid-point of its length.

#### Distribution

In the mountains of Sichuan and Yunnan, at elevations 1711–4382 m (Williams *et al.* 2009). Uniquely for species pairs within the *hypnorum*-complex, this species shows an overlap in distribution range with *B. hengduanensis* in Sichuan and Yunnan.

*Bombus (Pyrobombus) bryorum* Richards, 1930 stat. rev.  
Figs 1–2, 10–16

[*Bombus hypnorum*] var. [not subsp.] *bryorum* Richards 1930: 650, but not infrasubspecific after Tkalců (1974: 328) (ICZN, 1999: Article 45.6.4.1). Holotype by original designation: ♀ (not ♂) Kashmir, India (NHMUK). Examined.

*B.[ombus] fletcheri* Richards, 1934: 90. Holotype by original designation: ♀ Gulmarg, Kashmir, India (NHMUK). Examined.

[*Bombus (Pyrobombus) hypnorum* (Linnaeus, 1758) – Williams 1991: 70 — Williams *et al.* 2010: 127, misidentification.]

*Bombus (Pyrobombus) bryorum* Richards – Williams 2022a: 97.

#### Diagnosis

##### Female

Distinguished by the combination: labral lamella broad and shallowly rounded, almost rectangular; clypeus in the central area with scattered widely-spaced small punctures and the very large punctures spaced by more than 3 × their own diameter; ocello-ocular area along the inner eye margin with only one row of larger medium punctures; thoracic dorsum with the hair brown in the centre between the wing bases without black hair.

##### Male

Distinguished by the combination: hair variable, from the thorax and T1–4 yellow (western Himalaya), to thorax and metasomal T1–2 brown and T3–4 black (eastern Himalaya).

**Material sequenced or examined**

INDIA • 2 ♀♀ (queens); Kashmir, Gulmarg; 34.0343° N, 74.3678° E; alt. 3100 m; 1986; P. Williams leg.; PW • 2 ♀♀ (1 queen, 1 worker), 1 ♂; Kashmir, Gulmarg; 34.0343° N, 74.3678° E; alt. 3100 m; Aug. 1985; P. Williams leg.; PW • 1 ♀ (worker), 2 ♂♂; Kashmir, Gulmarg; 34.0343° N, 74.3678° E; alt. 2700–3200 m; 16 Aug. 1980; P. Williams leg.; PW.

NEPAL • 1 ♀ (worker); Karnali, Maharigaon; 29.337° N, 82.387° E; alt. 3250 m; 8 Jul. 1999; M. Hartmann leg.; BOLD-1550B09-N539; NME • 1 ♂; Mahakali, Charmaliya Khola; 29.746° N, 80.801° E; alt. 3100 m; 10 Jun. 2005; J. Weipert leg.; BOLD-1550B12-N548; NME.

BHUTAN • 1 ♀ (queen); Thimpu, Phajoding Gompa; 27.479° N, 89.595° E; alt. 2850 m; 25 Apr. 2018; J. Smit leg.; sequence-RMNH-1092452; RMNH • 1 ♀ (queen); Wangdue, Phodrang, Dangchhu; 27.546° N, 90.203° E; alt 3380 m; 5 May 2018; J. Smit leg.; RMNH.

**Distribution**

Himalaya (from Pakistan to Arunachal Pradesh), at elevations of 2286–3900 m (Williams 1991; Williams *et al.* 2010).

***Bombus (Pyrobombus) hypnorum* (Linnaeus, 1758) s. str.**

Figs 1–2, 17–26

*Apis hypnorum* Linnaeus, 1758: 579. Lectotype by designation of Day (1979): ♀ Sweden (LSL). Examined.

*Bombus calidus* Erichson, 1851: 65. Type not seen, but identity not in doubt.

**Diagnosis****Female**

Distinguished by the combination: labral tubercle on its broad outer lateral and anterior-facing surface in the centre smooth, with large punctures only along the dorsal and lateral edges; clypeus in the central area with a longitudinal band of small punctures and with very large punctures some spaced by just twice their own diameter; ocello-ocular area along the inner eye margin with a broad band of close small and medium punctures; hair of T4 either white in the posterior half or at least white in a continuous band along the posterior margin; T5 posteriorly in the middle anterior to the smooth posterior margin with a narrow band of large punctures extending for less than an eighth of the length of the tergum.

**Male**

Distinguished by the combination: hair variable, from the thorax and metasomal T1–2 hair brown and T3–4 black, to T1–4 black.

**Material examined****Material sequenced or examined**

SWEDEN • 1 ♂; Dalarna, Kopparberg; 61.979° N, 12.981° E; alt. 614 m; 20 Aug. 2006; P. Williams leg.; BOLD-1550A09; PW.

UNITED KINGDOM • 1 ♀ (queen); Buckinghamshire, Whiteleaf; 51.731° N, 0.816° W; alt. 153 m; 7 Jun. 2008; R. Goodson leg.; BOLD-1550H04; PW.



AUSTRIA • 1 ♀ (worker); Tirol, Seefeld; 47.3227° N, 11.1894° E; alt. 1100 m; 30 Jul. 1972; P. Williams leg.; PW.

NORWAY • 1 ♂; Larvik, Yttersøveien; 59.0615° N, 10.0573° E; alt. 58 m; 14 Jul. 1978; J. Stenløkk leg.; PW.

MONGOLIA • 1 ♀ (worker); Hövsgöl Aymag, Hövsgöl Nuur; 51° N, 100° E; alt. 2000 m; 18 Jul. 2004; D. Sheppard leg.; BOLD-1550A02; PW • 1 ♀ (worker); Hövsgöl Aymag, Hövsgöl Nuur ; 51.05° N, 100.73° E; alt. 1645 m; 20 Jul. 2004; D. Sheppard leg.; BOLD-1550E03; PW • 1 ♀ (worker); Hövsgöl Aymag, Hövsgöl Nuur; 51.05° N, 100.73° E; alt. 1645 m; 24 Jul. 2004; D. Sheppard leg.; BOLD-1550E02; PW • 1 ♀ (worker); Hövsgöl Aymag, Hövsgöl Nuur; 51.0628° N, 100.7320° E; alt. 1645 m; 28 Jul. 2004; D. Sheppard leg.; BOLD-1550A03; PW.

#### Other selected material sequenced

BOLD: BCZSMHYM01074, BCZSMHYM01075, BIOUG17229E02, BIOUG36732G05.

GenBank: AF279539, AF279541, AF279542, AY181110, GU674484, GU674503, GU705903, KJ839370.

#### Distribution

The PTP results in Fig. 1 show that the taxon *calidus* is a part of the species *B. hypnorum* s. str. and not a separate species, confirming its status as a part of the species, which is treated as a synonym here.

Widespread boreal Palaearctic in the north (from northern Europe to Primorsky, Kamchatka, and Anadyr) and in the south in the temperate mountains of the Pyrenees, Alps, Balkans, Caucasus, and Mongolia, at elevations of 0–2050 m (Reinig 1939; Rasmont 1988; Williams 1991; Rasmont *et al.* 2021).

#### *Bombus (Pyrobombus) koropokkrus* Sakagami & Ishikawa, 1972 stat. rev.

Figs 1–2, 27–31

*Bombus (Pyrobombus) hypnorum* [ssp.] *insularis* Sakagami & Ishikawa, 1969: 180, not of Smith (1861) (= *B. (Apathus) insularis* Smith, 1861). Type not seen, but identity not in doubt.

*Bombus (Pyrobombus) hypnorum* [ssp.] *koropokkrus* Sakagami & Ishikawa, 1972: 610, replacement name for *insularis* Sakagami & Ishikawa (1969).

#### Diagnosis

##### Female

Distinguished by the combination: clypeus in the centre with widely scattered large punctures with fewer small punctures between them; ocello-ocular area along the inner eye margin with a broad band of sparse medium and small punctures; thoracic dorsum with the hair orange-brown; T5 hair usually entirely white, but sometimes only along the posterior margin; T5 posteriorly in the middle anterior to the smooth posterior margin with a broad band of large punctures extending for at least a quarter of the length of the tergum.

##### Male

Distinguished by the combination: hair of the thorax and metasomal T1–4 yellow.

## Material examined

### Material sequenced or examined

RUSSIA • 1 ♀ (queen); Sakhalin, Sokol; 47.2553° N, 142.8062° E; [alt. 69 m]; 17 Jul. 2001; D. Bennett leg.; BOLD-1552F02; PW • 1 ♂; Sakhalin, Yuzhno-Sakhalinsk; 46.7148° N, 142.7338° E; [alt. 8 m]; 16 Aug. 2000; K. Blackhart leg.; BOLD-1552F05; PW.

JAPAN • 1 ♀ (worker); Hokkaido, Rausu spa; 29 Jul; 1959; K. Moriya leg.; PW • 1 ♀ (worker); Hokkaido, Yukomanbetsu; 8 Jul. 1967; M. Ito leg.; PW • 1 ♂; Hokkaido, Kawayu; alt. 650 m; S. Martin leg.; PW.

### Other material sequenced

GenBank: AF385815, HQ553056.

## Distribution

Islands of Japan (Hokkaido) and Sakhalin (Sakagami & Ishikawa 1969), at elevations of 0–650 m.

*Bombus (Pyrobombus) hengduanensis* Williams, Ren & Xie sp. nov.

urn:lsid:zoobank.org:act:4D8DB502-0822-4A83-BB73-2F1F869F3EA2

Figs 1–2, 32–38, 52

[*Bombus (Pyrobombus) hypnorum* (Linnaeus, 1758) – Williams *et al.* 2009b: 157, (in part) misidentification.]

## Diagnosis

### Female

Distinguished by the combination: labral tubercle on its broad outer lateral and anterior-facing surface in the centre with a few very large punctures scattered throughout; clypeus in the central area with a longitudinal band of small punctures and with very large punctures some spaced by just twice their own diameter; ocello-ocular area along the inner eye margin with a broad band of close small and medium punctures; T4 hair either black in the posterior half or with only a few white hairs along the posterior margin; T5 posteriorly in the middle anterior to the smooth posterior margin with a narrow band of large punctures extending for less than an eighth of the length of the tergum.

### Male

Distinguished by the combination: hair variable, from the thorax and metasomal T1–2 brown and T3–4 black, to T1–4 black.

## Etymology

Named for its occurrence in the Hengduan mountain region (in the provinces of Yunnan and Sichuan).

## Material examined

### Holotype

CHINA • ♀ (queen), pinned; [four labels]; [(1) white printed in black] ‘RWM101074’; [(2) green printed in black] ‘C1iBES221’; [(3) white printed in black] ‘CHINA, Xizang / Ranwu Lake 3910 m / 29.4849°N 96.6425°E / 24.vii.2018 Z. Ren’; [(4) red printed in black] ‘HOLOTYPE ♀ (q) / *Bombus hengduanensis* / Williams, Ren & Xie / det PH Williams 2022’; IOZ.

### Other material sequenced or examined

CHINA • 1 ♀ (worker); Sichuan, Zhegu Shan; 31.852° N, 102.672° E; alt. 4180 m; 2 Aug. 2002; P. Williams leg.; BOLD-1550A04; PW • 1 ♀ (worker); Sichuan, Zhegu Shan; 31.852° N, 102.672° E;

alt. 4180 m; 2 Aug. 2002; P. Williams leg.; BOLD-1550A05; PW • 1 ♀ (queen); [in Chinese: Yunnan, Zhongdian County]; 20 Aug. 1981; PW • 1 ♂; [in Chinese: Yunnan, Dêqên County]; alt. 4200 m; 30 Jul. 1982; PW • 1 ♂; Xizang, Sijilashan; 29.6416° N, 94.6982° E; alt. 4019 m; Z. Ren leg.; KIB-SJLSM101010; KIB • 1 ♀ (worker); Xizang, Sijilashan; 29.6416° N, 94.6982° E; alt. 4019 m; Z. Ren leg.; KIB-SJLSM101011; KIB • 1 ♀ (worker); Xizang, Sijilashan; 29.6416° N, 94.6982° E; alt. 4019 m; Z. Ren leg.; KIB-SJLSM109001; KIB • 1 ♂; Xizang, Honglashan; 29.2245° N, 98.6785° E; alt. 3909 m; Z. Ren leg.; KIB-HLSM201008; KIB • 1 ♀ (worker); Xizang, Zhujiashan; 31.1088° N, 96.8847° E; alt. 3953 m; Z. Ren leg.; KIB-ZJLSM201032; KIB • 1 ♀ (worker); Xizang, Zhujiashan; 31.11821° N, 97.0175° E; alt. 4029 m; Z. Ren leg.; KIB-ZJLSM301018; KIB.

BURMA • 1 ♂; Adung valley; alt. 3658 m; 23 Jun. 1931; F. Kingdon-Ward leg.; NHMUK.

## Description

### Female

Habitus illustrated in Fig. 52, body size small (queen body length 13–15 mm, worker 10–11 mm), hair (pubescence) moderately long, wings very lightly clouded with brown. Mandible with the distal notch anterior to the posterior tooth (incisura) very shallow. Oculo-malar area ('cheek' sensu Williams et al. 2014; not the gena) of medium length,  $1.0 \times$  as long as the breadth of the mandible at its base (length measured between the ventral edge of the compound eye and the edge of the malar area at the articulation of the mandible midway between the mandibular condyles; breadth measured between and including the mandibular condyles). Labral tubercle on its broad outer lateral and anterior-facing surface in the centre with a few very large punctures scattered throughout. Clypeus weakly swollen, its raised area nearly flat, the central area with few widely scattered large, medium, punctures with



**Fig. 52.** *Bombus hengduanensis* Williams, Ren & Xie sp. nov., ♀ (queen), holotype (IOZ), habitus, lateral view (image reversed). Scale bar: 10 mm.

intervening areas shining, with a longitudinal band of small punctures. The area between the inner edge of the compound eye and the outer edge of the lateral ocellus occupied in just more than its outer third by closely spaced medium and small punctures, the medium punctures scattered across this band. Mid basitarsus with the distal posterior corner broadly rounded; hind tibia outer surface with a corbicula, the surface sculpturing weakly reticulate so that the surface appears slightly matt; hind basitarsus in the distal three quarters covered with short branched decumbent and weakly overlapping hairs with golden reflections. Metasomal T6 posteriorly rounded and not divided medially, with a small subapical dorsal boss. Colour pattern of the hair of the body predominantly black. Head black except for orange hairs anteriorly on the labrum and laterally on the mandibles and a short hair brown on the top of the head around the ocelli. Thoracic dorsum bright orange-brown, this pale hair extending half way down the side of the thorax anteriorly, without black hair between the wing bases or scattered; the front, middle and hind leg tibiae all with the hairs black, the basitarsi all with the integument brown-black like the tibiae. Hair of T1 and T2 anteriorly orange-brown, T2 posteriorly and T3 and T4 anteriorly black, T4 in either posterior half black or with only a few white hairs along the posterior margin, and T5–6 white.

### Male

Body size small (body length 11–13 mm), hair (pubescence) moderately long, wings very lightly clouded with brown. Colour pattern of the hair of the body predominantly black. Front and top of the head with short hair brown. Thoracic dorsum bright orange-brown, this pale hair extending half way down the side of the thorax anteriorly, without black hair between the wing bases or scattered; the front, middle and hind leg tibiae all with the hairs black, the basitarsi all with the integument brown-black like the tibiae. Hair of metasomal T1–4 black or sometimes T1, or sometimes T1–2 brown, T5–7 with at least some white, but sometimes predominantly black. Male genitalia with the gonostylus nearly triangular, the inner anterior (basal) projection separated from the gonocoxa by a distance less than the breadth of the recurved hook of the penis-valve head; the volsella scarcely projecting beyond the gonostylus; the penis valve with the head recurved as a flattened sickle-shaped hook that is scarcely tapering at the mid point of its length.

### Distribution

In the mountains of the eastern Qinghai-Tibetan Plateau, extending into Sichuan, Yunnan, and Burma, at elevations of 3600–4200 m (Williams *et al.* 2009). From their distribution and the colour pattern of the hair, this is likely to be the species that occurs slightly further north in North China (An *et al.* 2014: at elevations of 780–2923 m), extending eastwards from Gansu through the Qin mountains to Ningxia, Shaanxi, and Shanxi, although it is not possible to confirm this here from barcode sequences. Uniquely for species pairs within the *hypnorum*-complex, this species shows an overlap in distribution range with *B. wolongensis* in Sichuan and Yunnan.

### *Bombus (Pyrobombus) perplexus* Cresson, 1863

Figs 1–2, 39–50

*B.[ombus] perplexus* Cresson, 1863: 91. Type not seen (believed lost, Cresson 1916), but identity not in doubt.

*B.[ombus] Hudsonicus* Cresson, 1863: 92. Type not seen (believed lost, Cresson 1916), but identity not in doubt.

## Diagnosis

### Female

Distinguished by the combination: clypeus in the centre with widely scattered large punctures with more numerous small punctures between them; ocello-ocular area along the inner eye margin with a broad band of sparse medium and small punctures; scutum with the hair usually yellow; T5 hair usually entirely black, but sometimes white or cream posteriorly and occasionally throughout; T5 posteriorly in the middle anterior to the smooth posterior margin with a broad band of large punctures extending for at least a quarter of the length of the tergum.

### Male

Distinguished by the combination: hair variable, from the thorax and metasomal T1–6 yellow, to T1–2 yellow and T3–6 black

## Material examined

### Material sequenced or examined

CANADA • 1 ♀ (queen); Ontario, Toronto High Park; 43.6460° N, 79.4679° W; alt 95 m; 11 May 1983; P. Williams leg.; PW • 1 ♀ (queen); Nova Scotia, Kings County; 45.1298° N, 64.7383° W; 13 Jun. 2003; C. Sheffield leg.; BOLD-Bee25-3; PW.

USA • 1 ♀ (worker); Kentucky, Camp Ernst; 38.9974° N, 84.7141° W; alt. 246 m; 1 Jun. 2006; P. Williams leg.; BOLD-1550H03; PW • 1 ♂; New York, Catskill Mts Highway 17; 41.650° N, 74.683° W; 28 Jul. 2004; P. Williams leg.; PW.

### Other material sequenced

BOLD: 3742D01, 3742D02, 3742D10, Bee25-2, 03-BC-0414, 6706C01, 6717D10-YT, BIOUG45105A07, 08BBHYM-0560.

## Distribution

Widespread in boreal North America in the north (from Alaska to Quebec) and extending southwards along the Appalachian mountains (Williams *et al.* 2014), at elevations of 0–1852 m (L. Richardson, pers. comm.).

## Discussion

Our estimate of phylogeny generally met expectations (Hines *et al.* 2006; Cameron *et al.* 2007) with few exceptions. In particular, the position in Fig. 1 of the sequence for *B. haematurus* (and of the other four matching sequences for this species examined from BOLD) as the sister to the rest of our tree does not match the position within the *hypnorum*-group expected from the tree from five genes by Cameron *et al.* (2007). This position in our tree might be explained if all of the *B. haematurus* barcode sequences we use were numts (Magnacca & Brown 2010). Fortunately, the precise interpretation of our results for *B. haematurus* does not affect the inferences made here for the other species (our inferences are unaltered if the analysis is run without any sequences for *B. haematurus*).

Preliminary test analyses including not just the *hypnorum*-group and *vagans*-group but also the closely-related Asian *lepidus*-group show the same relationships and recognise the same lineages as species within the *hypnorum*-complex as are shown here. However, the presence of numerous unresolved candidate species within the *lepidus*-group warrants further data gathering to ensure that the species recognised within that group are reliable. Problems in revising the *lepidus*-group are likely to include: (1) cryptic species; (2) unsampled variation within large inaccessible regions for some species; and (3) numts. Despite more than two decades of work already, further progress in revising the *lepidus*-group

will require yet more samples of these rare bees, especially from the mountains in the subtropical and tropical regions in the south of their range that are difficult to access at present.

The lack of strongly distinctive morphological character states to diagnose the species within the *hypnorum*-complex defines them as near-cryptic species. Weakly developed as these diagnostic morphological characters may be, we still consider them sufficient to support the recognition of likely separate species. Further lines of evidence (including cephalic labial gland secretions of the males) deserve further study.

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## References

- An J.-D., Huang J.-X., Shao Y.-Q., Zhang S.-W., Wang B., Liu X.-Y., Wu J. & Williams P.H. 2014. The bumblebees of North China (Apidae, *Bombus* Latreille). *Zootaxa* 3830: 1–89. <https://doi.org/10.11646/zootaxa.3830.1.1>
- Baker A.J., Tavares E.S. & Elbourne R.F. 2009. Countering criticisms of single mitochondrial DNA gene barcoding in birds. *Molecular Ecology Resources*: 9 (supplement 1): 257–268. <https://doi.org/10.1111/j.1755-0998.2009.02650.x>
- Barrowclough G.F. 1982. Geographic variation, predictiveness, and subspecies. *Auk* 99: 601–603.
- Baum D. & Smith S. 2012. *Tree thinking: an introduction to phylogenetic biology*. Roberts and Company, Greenwood Village, USA.
- Biella P., Cetkovic A., Gogala A., Neumayer J., Sarospataki M., Sima P. & Smetana V. 2020. Northwestward range expansion of the bumblebee *Bombus haematurus* into Central Europe is associated with warmer winters and niche conservatism. *Insect Science* 28: 861–872.
- Cameron S.A., Hines H.M. & Williams P.H. 2007. A comprehensive phylogeny of the bumble bees (*Bombus*). *Biological Journal of the Linnean Society* 91: 161–188.
- Chiu S.C. 1948. Revisional notes on the Formosan bombid-fauna (Hymenoptera). *Notes d'entomologie chinoise* 12: 57–81.
- Cresson E.T. 1863. List of the North American species of *Bombus* and *Apathus*. *Proceedings of the Entomological Society of Philadelphia* 2: 83–116.
- Cresson E.T. 1916 The Cresson types of Hymenoptera. *Memoirs of the American Entomological Society* 1: 1–141.
- Crowther L.P., Hein P.-L. & Bourke A.F.G. 2014. Habitat and forage associations of a naturally colonising insect pollinator, the tree bumblebee *Bombus hypnorum*. *PLoS ONE* 9: e107568. <https://doi.org/10.1371/journal.pone.0107568>
- de Queiroz K. 2007. Species concepts and species delimitation. *Systematic Biology* 56: 879–886.

- Dellicour S. & Flot J.-F. 2015. Delimiting species-poor data sets using single molecular markers: a case study of barcode gaps, haplowebs and GMYC. *Systematic Biology* 64 (6): 900–908. <https://doi.org/10.1093/sysbio/syu130>
- Dellicour S., Michez D. & Mardulyn P. 2015. Comparative phylogeography of five bumblebees: impact of range fragmentation, range size and diet specialization. *Biological Journal of the Linnean Society* 116: 926–939. <https://doi.org/10.1111/bij.12636>
- Dellicour S., Kastally C., Varela, S., Michez D., Rasmont P., Mardulyn P. & Lecocq T. 2017. Ecological niche modelling and coalescent simulations to explore the recent geographical range history of five widespread bumblebee species in Europe. *Journal of Biogeography* 44: 39–50. <https://doi.org/10.1111/jbi.12748>
- Drummond A.J. & Rambaut A. 2007. BEAST: Bayesian evolutionary analysis by sampling trees. *BioMed Central Evolutionary Biology* 7: 214. <https://doi.org/10.1186/1471-2148-7-214>
- Erichson W.F. 1851. Hymenoptera. In: Middendorff A.T.v. (ed.) *Reise in den Äussersten Norden und Osten Sibiriens, während der Jahre 1843 und 1844 mit allerhöchster Genehmigung auf Veranstaltung der kaiserlichen Akademie der Wissenschaften zu St. Petersburg ausgeführt und in Verbindung mit vielen Gelehrten herausgegeben. Band II. Zoologie. Theil 1*: 60–65. Buchdruckerei der Kaiserlichen Akademie der Wissenschaften, St Petersburg. Available from <https://www.biodiversitylibrary.org/page/37047877#page/74/mode/1up> [accessed 8 Nov. 2022].
- Fujisawa T. & Barraclough T.G. 2013. Delimiting species using single-locus data and the Generalized Mixed Yule Coalescent approach: a revised method and evaluation on simulated data sets. *Systematic Biology* 62: 707–724. <https://doi.org/10.1093/sysbio/syt033>
- Goulson D. & Williams P. 2001. *Bombus hypnorum* (Hymenoptera: Apidae), a new British bumblebee? *British Journal of Entomology and Natural History* 14: 129–131.
- Hebert P.D.N., Cywinska A., Ball S.L. & DeWaard J.R. 2003. Biological identifications through DNA barcodes. *Proceedings of the Royal Society of London B, Biological Sciences* 270: 313–321. <https://doi.org/10.1098/rspb.2002.2218>
- Hebert P.D.N., Penton E.H., Burns J.M., Janzen D.H. & Hallwachs W. 2004. Ten species in one: DNA barcoding reveals cryptic species in the neotropical skipper butterfly *Astraptes fulgerator*. *Proceedings of the National Academy of Sciences of the United States of America* 101: 14812–14817. <https://doi.org/10.1073/pnas.0406166101>
- Hines H.M., Cameron S.A. & Williams P.H. 2006. Molecular phylogeny of the bumble bee subgenus *Pyrobombus* (Hymenoptera: Apidae: *Bombus*) with insights into gene utility for lower-level analysis. *Invertebrate Systematics* 20: 289–303. <https://doi.org/10.1071/IS05028>
- Huml J.V., Ellis J.S., Lloyd K., Benerfer C.M., Kiernan M., Brown M.J.F. & Knight M.E. 2021. Bucking the trend of pollinator decline: the population genetics of a range expanding bumblebee. *Evolutionary Ecology* 35: 413–442. <https://doi.org/10.1007/s10682-021-10111-2>
- Hyde K.D. & Zhang Y. 2008. Epitypification: should we epitypify? *Journal of Zhejiang University SCIENCE B* 9: 842–846. <https://doi.org/10.1631/jzus.b0860004>
- ICZN 1999. *International Code of Zoological Nomenclature*. 4<sup>th</sup> Edition. London, U.K. International Trust for Zoological Nomenclature. London, UK. Available from <https://www.iczn.org/the-code/> [accessed 3 Nov. 2022].
- Lecocq T., Dellicour S., Michez D., Lhomme P., Vanderplanck M., Valterova I., Rasplus J.-Y. & Rasmont P. 2013. Scent of a break-up: phylogeography and reproductive trait divergences in the red-tailed bumblebee (*Bombus lapidarius*). *BMC Evolutionary Biology* 13: 263. <https://doi.org/10.1186/1471-2148-13-263>

- Lecocq T., Gérard M., Michez D. & Dellicour S. 2016. Conservation genetics of European bees: new insights from the continental scale. *Conservation Genetics* 18: 585–596. <https://doi.org/10.1007/s10592-016-0917-3>
- Lecocq T., Biella P., Martinet B. & Rasmont P. 2019. Too strict or too loose? Integrative taxonomic assessment of *Bombus lapidarius* complex (Hymenoptera: Apidae). *Zoologica Scripta* 49 (2): 187–196. <https://doi.org/10.1111/zsc.12402>
- Leliaert F., Verbruggen H., Vanormelingen P., Steen F., Lopez-Bautista J.M., Zuccarello G.C. & de Clerck O. 2014. DNA-based species delimitation in algae. *European Journal of Phycology* 49: 179–196. <https://doi.org/10.1080/09670262.2014.904524>
- Linnaeus C. 1758. *Systema Naturae. Editio Decima, Reformata*. Salvus, Holmiae [Stockholm]. Available from <https://www.biodiversitylibrary.org/item/10277#page/3/mode/1up> [accessed 1 Nov. 2022].
- Løken A. 1973. Studies on Scandinavian bumble bees (Hymenoptera, Apidae). *Norsk entomologisk Tidsskrift* 20: 1–218.
- Magnacca K.N. & Brown M.J.F. 2010. Mitochondrial heteroplasmy and DNA barcoding in Hawaiian *Hylaeus* (*Nesoprosopis*) bees (Hymenoptera: Colletidae). *BMC Evolutionary Biology* 10: 174. <https://doi.org/10.1186/1471-2148-10-174>
- Martinet B., Ghisbain G., Przybyla K., Zambra E., Brasero N., Kondakov A.V., Tomilova A.A., Kolosova Y.S., Bolotov I.N., Rasmont P. & Potapov G. 2021. Distant but related: genetic structure in the circum-boreal bumblebee *Bombus jonellus* (Kirby, 1802). *Polar Biology* 44 (10): 2039–2047. <https://doi.org/10.1007/s00300-021-02937-x>
- Michener C.D. 2000. *The Bees of the World*. John Hopkins University Press, Baltimore.
- O'Donnell M. 2018. Tree bumblebee (*Bombus hypnorum*) (Hymenoptera, Apidae): a bumblebee new to Ireland. *The Irish Naturalists' Journal*: 36: 50–51. <https://www.jstor.org/stable/45181554>
- Phillips J.D., Gillis D.J. & Hanner R.H. 2018. Incomplete estimates of genetic diversity within species: implications for DNA barcoding. *Ecology and Evolution*: Ecology and Evolution 9 (5): 2996–3010. <https://doi.org/10.1002/ece3.4757>
- Prŷs-Jones O.E. 2014. The tree bumble bee (*Bombus hypnorum*) as a house sparrow equivalent? Comments on colonizing success in Britain in the context of declining native species. *Bee World* 91: 98–101. <https://doi.org/10.1080/0005772X.2014.11417623>
- Prŷs-Jones O. 2019. Preadaptation to the vertical: an extra dimension to the natural history and nesting habits of the Tree Bumble Bee, *Bombus* (*Pyrobombus*) *hypnorum*. *Journal of Apicultural Research* 58: 643–659. <https://doi.org/10.1080/00218839.2019.1634462>
- Prŷs-Jones O.E., Kristjansson K. & Olafsson E. 2016. Hitchhiking with the Vikings? The anthropogenic bumblebee fauna of Iceland – past and present. *Journal of Natural History* 50: 2895–2916. <https://doi.org/10.1080/00222933.2016.1234655>
- Rasmont P. 1984. Les bourdons du genre *Bombus* Latreille sensu stricto en Europe occidentale et centrale (Hymenoptera, Apidae). *Spixiana* 7: 135–160. Available from <https://www.biodiversitylibrary.org/part/66953> [accessed 8 Nov. 2022].
- Rasmont P. 1988. *Monographie Écologique et Zoogéographique des Bourdons de France et de Belgique (Hymenoptera, Apidae, Bombinae)*. Faculté des Sciences agronomiques de l'Etat, Gembloux.
- Rasmont P., Ghisbain G. & Terzo M. 2021. *Bumblebees of Europe and Neighbouring Regions*. NAP Editions, Verrières-le-Buisson, France.



- Ratnasingham S. & Hebert P.D.N. 2007. BOLD: The Barcode of Life Data System (<http://www.barcodinglife.org>). *Molecular Ecology Notes* 7 (3): 355–364. <https://doi.org/10.1111/j.1471-8286.2007.01678.x>
- Ratnasingham S. & Hebert P.D.N. 2013. A DNA-based registry for all animal species: the Barcode Index Number (BIN) System. *PLoS ONE* 8 (8): e66213. <https://doi.org/10.1371/journal.pone.0066213>
- Reid N.M. & Carstens B.C. 2012. Phylogenetic estimation error can decrease the accuracy of species delimitation: a Bayesian implementation of the general mixed Yule-coalescent model. *BMC Evolutionary Biology* 12: 196. <https://doi.org/10.1186/1471-2148-12-196>
- Reinig W.F. 1939. Die Evolutionsmechanismen, erläutert an den Hummeln. *Verhandlungen der Deutschen zoologischen Gesellschaft (Supplement)* 12: 170–206.
- Richards O.W. 1930. The humble-bees captured on the expeditions to Mt. Everest (Hymenoptera, Bombidae). *Annals and Magazine of Natural History (Series 10)* 5: 633–658. <https://doi.org/10.1080/00222933008673177>
- Richards O.W. 1934. Some new species and varieties of oriental humble-bees (Hym. Bombidae). *Stylops* 3: 87–90. <https://doi.org/10.1111/j.1365-3113.1934.tb01552.x>
- Ronquist F. & Huelsenbeck J.P. 2003. MRBAYES 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* 19: 1572–1574. <https://doi.org/10.1093/bioinformatics/btg180>
- Sakagami S.F. & Ishikawa R. 1969. Note préliminaire sur la répartition géographique des bourdons japonais, avec descriptions et remarques sur quelques formes nouvelles ou peu connues. *Journal of the Faculty of Science, Hokkaido University (Zoology)* 17: 152–196. Available from <http://hdl.handle.net/2115/27480> [accessed 9 Nov. 2022].
- Sakagami S.F. & Ishikawa R. 1972. Note supplémentaire sur la taxonomie et répartition géographique de quelques bourdons Japonais, avec la description d'une nouvelle sous-espèce. *Bulletin of the National Science Museum, Tokyo*: 15: 607–616.
- Schlick-Steiner B.C., Steiner F.M., Seifert B., Stauffer C., Christian E. & Crozier R.H. 2010. Integrative taxonomy: a multisource approach to exploring biodiversity. *Annual Review of Entomology* 55: 421–438. <https://doi.org/10.1146/annurev-ento-112408-085432>
- Smith F. 1861. Descriptions of new genera and species of exotic Hymenoptera. *Journal of Entomology* 1: 146–155.
- Starr C.K. 1992. The bumble bees (Hymenoptera: Apidae) of Taiwan. *Bulletin of the National Museum of Natural Science* 3: 139–157.
- Stephen W.P. 1957. Bumble bees of western America (Hymenoptera: Apoidea). *Technical Bulletin, Oregon State College, Agricultural Experiment Station* 40: 163.
- Talavera G., Dinca V. & Vila R. 2013. Factors affecting species delimitations with the GMYC model: insights from a butterfly survey. *Methods in Ecology and Evolution* 4: 1101–1110. <https://doi.org/10.1111/2041-210X.12107>
- Tamura K., Stecher G., Peterson D., Filipowski A. & Kumar S. 2013. MEGA6: molecular evolutionary genetics analysis version 6.0. *Molecular Biology and Evolution* 30: 2725–2729. <https://doi.org/10.1093/molbev/mst197>
- Thorp R.W., Horning D.S. & Dunning L.L. 1983. Bumble bees and cuckoo bumble bees of California (Hymenoptera: Apidae). *Bulletin of the California Insect Survey* 23: 79.
- Tkalčič B. 1974. Eine Hummel-Ausbeute aus dem Nepal-Himalaya (Insecta, Hymenoptera, Apoidea, Bombinae). *Senckenbergiana biologica* 55: 311–349.

- Williams P.H. 1985. A preliminary cladistic investigation of relationships among the bumble bees (Hymenoptera, Apidae). *Systematic Entomology* 10: 239–255. <https://doi.org/10.1111/j.1365-3113.1985.tb00529.x>
- Williams P.H. 1991. The bumble bees of the Kashmir Himalaya (Hymenoptera: Apidae, Bombini). *Bulletin of the British Museum of the Natural History Museum Entomology* 60: 1–204. Available from <https://www.researchgate.net/publication/230668921> [accessed 1 Nov. 2022].
- Williams P.H. 1994. Phylogenetic relationships among bumble bees (*Bombus* Latr.): a reappraisal of morphological evidence. *Systematic Entomology* 19: 327–344. <https://doi.org/10.1111/j.1365-3113.1994.tb00594.x>
- Williams P.H. 1998. An annotated checklist of bumble bees with an analysis of patterns of description (Hymenoptera: Apidae, Bombini). *Bulletin of the British Museum of the Natural History Museum Entomology* 67: 79–152 [update available from <https://www.nhm.ac.uk/bombus/>, accessed 3 Nov. 2022]. Available from <https://www.researchgate.net/publication/230668913> [accessed 3 Nov. 2022].
- Williams P.H. 2007. The distribution of bumblebee colour patterns world-wide: possible significance for thermoregulation, crypsis, and warning mimicry. *Biological Journal of the Linnean Society* 92: 97–118. <https://doi.org/10.1111/j.1095-8312.2007.00878.x>
- Williams P.H. 2021. Not just cryptic, but a barcode bush: PTP re-analysis of global data for the bumblebee subgenus *Bombus s. str.* supports additional species (Apidae, genus *Bombus*). *Journal of Natural History* 55: 271–282. <https://doi.org/10.1080/00222933.2021.1900444>
- Williams P.H. 2022a. *The Bumblebees of the Himalaya*. AbcTaxa, Belgium. Available from <https://www.researchgate.net/publication/361184342> [accessed 11 Nov. 2022].
- Williams P.H. 2022b. Novel splitting/lumping index reflects the history of species concepts applied to bumblebees (Insecta, Apidae). *Zoological Journal of the Linnean Society*: 196 (2): 704–719. <https://doi.org/10.1093/zoolinlean/zlab123>
- Williams P.H., Cameron S.A., Hines H.M., Cederberg B. & Rasmont P. 2008. A simplified subgeneric classification of the bumblebees (genus *Bombus*). *Apidologie* 39: 46–74. <https://doi.org/10.1051/apido:2007052>
- Williams P.H., Colla S. & Xie Z.-H. 2009a. Bumblebee vulnerability: common correlates of winners and losers across three continents. *Conservation Biology* 23: 931–940. <https://doi.org/10.1111/j.1523-1739.2009.01176.x>
- Williams P.H., Tang Y., Yao J. & Cameron S. 2009b. The bumblebees of Sichuan (Hymenoptera: Apidae, Bombini). *Systematics and Biodiversity* 7: 101–189. <https://doi.org/10.1017/S1477200008002843>
- Williams P.H., Ito M., Matsumura T. & Kudo I. 2010. The bumblebees of the Nepal Himalaya (Hymenoptera: Apidae). *Insecta Matsumurana*: 66: 115–151. Available from <http://hdl.handle.net/2115/44628> [accessed 9 Nov. 2022].
- Williams P.H., Brown M.J.F., Carolan J.C., An J.-D., Goulson D., Aytakin A.M., Best L.R., Byvaltsev A.M., Cederberg B., Dawson R., Huang J.-X., Ito M., Monfared, A., Raina R.H., Schmid-Hempel P., Sheffield C.S., Sima P. & Xie Z.-H. 2012. Unveiling cryptic species of the bumblebee subgenus *Bombus s. str.* world-wide with COI barcodes (Hymenoptera: Apidae). *Systematics and Biodiversity* 10: 21–56. <https://doi.org/10.1080/14772000.2012.664574>
- Williams P.H., Thorp R.W., Richardson L.L. & Colla S.R. 2014. *Bumble Bees of North America. An Identification Guide*. Princeton University Press, Princeton, New Jersey.
- Williams P.H., Byvaltsev A.M., Cederberg B., Berezin M.V., Ødegaard F., Rasmussen C., Richardson L.L., Huang J.-X., Sheffield C.S. & Williams S.T. 2015. Genes suggest ancestral colour polymorphisms

are shared across morphologically cryptic species in arctic bumblebees. *PLoS ONE* 10 (12): e0144544.. <https://doi.org/10.1371/journal.pone.0144544>

Williams P.H., Huang J.-X., Rasmont P. & An J.-D. 2016. Early-diverging bumblebees from across the roof of the world: the high-mountain subgenus *Mendacibombus* revised from species' gene coalescents and morphology (Hymenoptera, Apidae). *Zootaxa* 4204: 1–72. <https://doi.org/10.11646/zootaxa.4204.1.1>

Williams P.H., Huang J.-X. & An J.-D. 2017. Bear wasps of the Middle Kingdom: a decade of discovering China's bumblebees. *Antenna* 41: 21–24. Available from <http://hdl.handle.net/10141/622626> [accessed 9 Nov. 2022].

Williams P.H., Altanchimeg D., Byvaltsev A., De Jonghe R., Jaffar S., Japoshvili G., Kahono S., Liang H., Mei M., Monfared A., Nidup T., Raina R., Ren Z., Thanosing C., Zhao Y. & Orr M.C. 2020. Widespread polytypic species or complexes of local species? Revising bumblebees of the subgenus *Melanobombus* world-wide (Hymenoptera, Apidae, Bombus). *European Journal of Taxonomy* 719: 1–120. <https://doi.org/10.5852/ejt.2020.719.1107>

Williams P.H., Sung I.-H., Lin Y.-J. & Lu S.-S. 2022. Discovering endemic species among the bumblebees of Taiwan (Apidae, genus *Bombus*). *Journal of Natural History* 56: 435–447. <https://doi.org/10.1080/00222933.2022.2052991>

Wilson E.O. & Brown W.L. 1953. The subspecies concept and its taxonomic application. *Systematic Zoology* 2: 97–111. <https://doi.org/10.2307/2411818>

Zhang J.-J., Kapli P., Pavlidis P. & Stamatakis A. 2013. A general species delimitation method with applications to phylogenetic placements. *Bioinformatics* 29: 2869–2876. <https://doi.org/10.1093/bioinformatics/btt499>

Zink R.M. 2004. The role of subspecies in obscuring avian biological diversity and misleading conservation policy. *Proceedings of the Royal Society of London (B)*: 271: 561–564. <https://doi.org/10.1098/rspb.2003.2617>

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