

**Species-coalescent analysis of bumblebees of the subgenus *Megabombus*  
von Dalla Torre, 1880 world-wide with the description  
of *Bombus hongyuanensis* Williams, sp.n. (Hymenoptera: Apidae) from China**

**Коалесцентный анализ шмелей подрода *Megabombus* von Dalla Torre,  
1880 мировой фауны с описанием *Bombus hongyuanensis* Williams, sp.n.  
(Hymenoptera: Apidae) из Китая**

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**Key words:** barcode, *Bombus*, taxonomy, synonymy, integrative, new species.

**Ключевые слова:** штрих-код, *Bombus*, таксономия, синонимия, интегративный подход, новый вид.

**Abstract.** Bumblebee species of the genus *Bombus* Latreille, 1802, subgenus *Megabombus* von Dalla Torre, 1880, are re-assessed world-wide with a species-coalescent analysis of COI barcodes. An integrative analysis of this evidence together with morphological characters shows (1) support for the widespread Eurasian species *B. consobrinus* Dahlbom, 1832 including as synonyms the taxa *B. yezoensis* Matsumura, 1932, **syn.n.** (from Japan) and *B. przewalskiellus* (Skorikov, 1933), **syn.n.** (from North China); (2) support for *B. tichenkoi* (Skorikov, 1926) s.l. as a widespread but under-recognised species in Asia that includes as synonyms the taxa *B. saltuarius* (Skorikov, 1931), **syn.n.** (from Russia), *B. sushkini* (Skorikov, 1931) **syn.n.** (from Central Asia and Mongolia), *B. morawitzianus* Pittioni, 1939, **syn.n.** (from Mongolia), *B. pseudoligusticus* Podbolotskaya, 1988, **syn. n.** (from Kamchatka), and *B. kurilensis* Sakagami, 1954 (from the Kuril Islands); and (3) support for *B. hongyuanensis* Williams, **sp.n.** as a previously unrecognised vicariant sister-species from the eastern Qinghai-Tibetan Plateau.

**Резюме.** Проведен коалесцентный анализ по COI шмелей подрода *Megabombus* von Dalla Torre, 1880 (род *Bombus* Latreille, 1802) мировой фауны. Интегративный анализ этих данных вместе с морфологическими признаками показывает: (1) валидность широко распространенного евразийского вида *B. consobrinus* Dahlbom, 1832, включая в качестве синонимов *B. yezoensis* Matsumura, 1932, **syn.n.** (из Японии) и *B. przewalskiellus* (Skorikov, 1933), **syn.n.** (из Северного Китая); (2) валидность *B. tichenkoi* (Skorikov, 1926) s.l. как широко распространенного, но недостаточно изученного вида в Азии, который включает в качестве синонимов *B. saltuarius* (Skorikov, 1931), **syn.n.** (из России), *B. sushkini* (Skorikov, 1931), **syn.n.** (из Центральной Азии и Монголии), *B. morawitzianus* Pittioni, 1939, **syn.n.** (из Монголии), *B. pseudoligusticus* Podbolotskaya, 1988, **syn.n.** (с Камчатки) и *B. kurilensis* Sakagami, 1954 (с Курильских островов); (3) подтверждение того, что *B. hongyuanensis* Williams,

**sp.n.** является ранее нераспознанным викириантным сестринским видом с восточного Цинхай-Тибетского плато.

## Introduction

Because bumblebees are brightly-coloured, large, and day-active insects they attract a lot of attention. It often seems to be assumed that because bumblebees show many different colour patterns that the species should therefore be easily identified from these colour patterns. For example, this has led to the production of species' identification charts by colour patterns for citizen-science projects in Europe and North America [e.g. by the UK Bumblebee Conservation Trust: <https://www.bumblebeeconservation.org/learn-about-bumblebees/species-guide/>; and in the US, by the Xerces Society's Bumble Bee Atlas: <https://www.bumblebeeatlas.org/pages/field-guide/>]. Unfortunately, it has long been known among specialists that colour patterns alone are often insufficient for identifying bumblebee species if the results are to be reliable [e.g. Morawitz, 1881; Radoszkowski, 1883, 1884; Friese, 1905; Vogt, 1909, 1911; Tkalců, 1968; Williams, 1998, 2007; Carolan et al., 2012].

Bumblebees all belong to a single genus *Bombus* Latreille, 1802. Within that group it has been found useful to label some of the principal subgroups with subgeneric names [Williams et al., 2008]. Their evolutionary relationships are now reasonably well agreed [Cameron et al., 2007; Sun et al., 2020; Williams et al., 2026a], providing a useful framework for many kinds of comparative studies. The subgenus *Megabombus* von Dalla Torre, 1880 is one such subgroup that includes some of the most striking and variable species world-wide in their brightly

coloured dorsal patterns of the hair (Fig. 1). Within the same geographic regions, these species appear to have converged with species (often in different subgenera) on closely and deceptively similar colour patterns, presumably driven by Müllerian mimetic convergence among the females, which can sting vertebrate predators that also have good visual acuity [Tkalců, 1968; Plowright, Owen, 1980]. This has had the secondary effect that the same species have often diverged in different geographical regions into confusingly different colour patterns [Tkalců, 1968, 1989; Hines, Williams, 2012]. Both the convergence within regions (among species of different subgenera) and the divergence among regions (within species) contribute to some very substantial difficulties in understanding bumblebee taxonomy at the species level when focussing on colour patterns [e.g. Hines, Williams, 2012; Williams, 2022b].

This raises questions of what is a species in theory and how can they be discovered in practice, which have

proved surprisingly difficult to answer [Wilkins, 2018]. This ‘species problem’ for bumblebees has long been appreciated by specialists [as ‘das Artproblem’: Vogt, 1909, 1911]. Here I adopt an interpretation that defines species in theory as evolutionarily independent lineages [de Queiroz, 2007]. In practice these species are recognised by looking for corroboration among multiple criteria, each derived from different steps in the speciation process [Schlick-Steiner et al., 2010]. This approach has been considered especially well-suited to applications in taxonomy [Maddison, Whitton, 2023] and has already been applied to many groups of bumblebees [e.g. Williams et al., 2012, 2020, 2026b; Martinet et al., 2019; Brasero et al., 2021].

The subgenus *Megabombus* is also notable for having the bumblebees with the longest tongues (proboscides) world-wide. Long tongues allow them to reach the deepest (longest corolla) flowers that are the most rewarding for nectar sugars [Harder, 1983] that can be used by

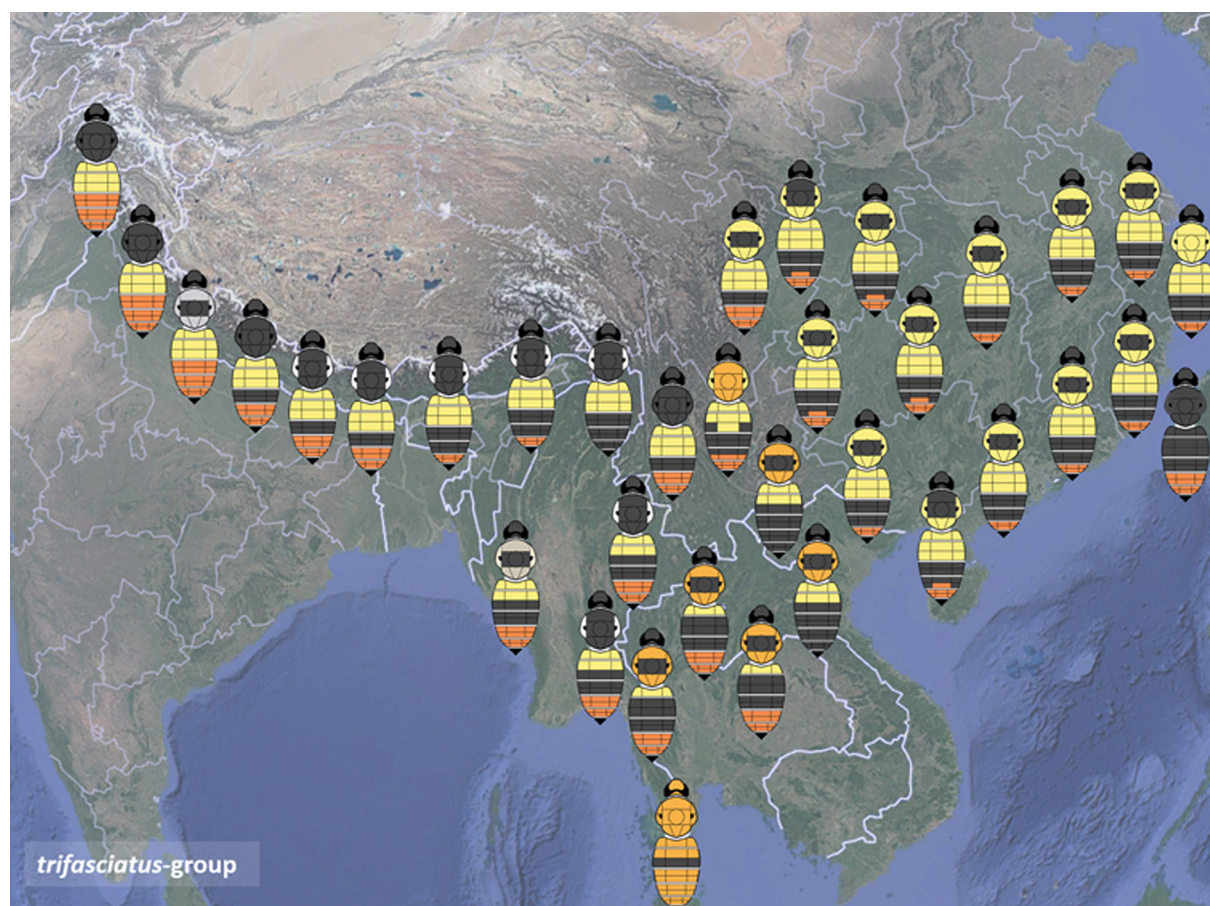


Fig. 1. Geographical variation across Asia in colour patterns of the dorsal hair summarised as simplified diagrams for bumblebees of the *trifasciatus*-group, including (Table 1) the species *B. albopileuralis* (Himalaya), *B. burmensis* (Sichuan/Yunnan), *B. montivagus* (Southeast Asia/Himalaya), and *B. trifasciatus* (China). The diagram for the predominantly orange taxon *maxwelli* (of *B. montivagus*) in the far south of the map is shown displaced north from the Cameron Highlands of Malaysia where it occurs. Updated from [Williams, 1991: his fig. 11]. Background image of vegetation from GoogleEarth showing national (white) and provincial (grey) boundaries.

Рис. 1. Географическая изменчивость окраски волосков груди у шмелей в Азии представлена в виде упрощенных диаграмм для группы видов *trifasciatus*, включая (Табл. 1) виды *B. albopileuralis* (Гималаи), *B. burmensis* (Сычуань/Юньнань), *B. montivagus* (Юго-Восточная Азия/Гималаи) и *B. trifasciatus* (Китай). Диаграмма для преимущественно оранжевого таксона *maxwelli* (*B. montivagus*), расположенного на крайнем юге карты, показана смещенной к северу от Камеронских высокогорий Малайзии, где он встречается. Обновлено по [Williams, 1991: рис. 11]. Фоновое изображение растительности из Google Earth, показывающее национальные (белые) и провинциальные (серые) границы.

bumblebees without robbing by biting holes in the flowers [reviewed in Williams et al., 2023]. This results in greater flower specialisation by the long-tongued bumblebees and consequently in the deep flowers being pollinated more successfully [Darwin, 1877]. The Eurasian subgenus *Megabombus* is interpreted here in its broader sense [Williams et al., 2008], which combines the smaller former subgenera *Diversobombus* Skorikov, 1914 and *Senexibombus* Frison, 1930, from Asia. The larger group remains monophyletic but is easier to recognise.

The species of the subgenus *Megabombus* s.l. have never been fully revised. Despite comparisons of many of the Asian species based on morphology [e.g. Skorikov, 1926, 1931, 1933; Tkalců, 1960, 1961b, 1968, 1974a, b; Sakagami, 1976; Ito, Sakagami, 1980; Ito, 1985; Lelej, Kupianskaya, 2000], recognition of some species has remained problematic. Relationships among these species have been clarified to some extent by analysis of gene sequences world-wide [Cameron et al., 2007; Williams et al., 2026a]. Relationships among closely related taxa are best informed by fast-evolving genes like mitochondrial COI [Lunt et al., 1996; Trunz et al. 2016]. However, even with species-coalescent analysis of fast-evolving COI barcodes, initially with General Mixed Yule-Coalescent (GMYC) analysis, several Asian taxa have remained of uncertain status [Huang et al., 2015]. Fortunately, it is now possible to add DNA sequences from the remaining taxa, as well as to apply improved Poisson-Tree-Process (PTP) analytical techniques to identify species' coalescents, which in combination with morphology allows a better evidenced appreciation of species' status.

## Material and methods

Earlier published studies with sequencing of COI barcodes (the COI-5P region of the cytochrome *c* oxidase subunit 1 gene) have made many of these sequences available for use here [Hines, Williams, 2012; Huang et al., 2015; Ding et al., 2019; Williams et al., 2022].

Two important taxa from Sumatra and Peninsular Malaysia regarded previously as species [Williams, 1998] were missing from the earlier analyses: *B. melanopoda* Cockerell, 1910 and *B. senex* Snellen van Vollenhoven, 1873. For *B. melanopoda*, the only specimen known is the holotype in the NHMUK collection, believed to date from 1882 [Williams, 1998]; whereas for *B. senex* the most recent specimen in the NHMUK collection is from 1929. For this study, both of these old specimens were barcoded with assets and benefit sharing permission from respective government offices in Indonesia and Malaysia by the NHMUK Ancient DNA Laboratory [Williams et al., 2026c] using specialised techniques [Meyer, Kircher, 2010; Dabney et al., 2013].

The data set was filtered to remove duplicate haplotypes and short sequences (< 600 nucleotides), to reduce biases that can interfere with PTP model fit and recognition of species [Williams et al., 2020; Williams, 2022a]. This requirement was relaxed for unique sequences for taxa that are especially rare in collections: for the taxa

*Bombus maxwelli* Pendlebury, 1923, *B. senex*, *B. tichenkoi* [Skorikov, 1926], and *B. yezoensis* Matsumura, 1932) (in these cases, particular care must then be taken to avoid over-interpretation as separate pseudospecies). The remaining sequences had the frequencies of the nucleotides adenine (A) and thymine (T) counted at the third codon position (AT3%) using the MEGA software [Tamura et al., 2013], because low values of AT3% are one indicator of paralogous nuclear copies of barcodes (known as 'numts') that can mislead estimates of evolutionary trees [Williams et al., 2023, 2024, 2026b].

Evolutionary relationships among barcode-like sequences were estimated using the MrBayes software [Ronquist, Huelsenbeck, 2003] for Bayesian estimation of evolutionary trees. This was applied with a GTR+Γ evolutionary model to run over 50 million MCMC generations, with the 'temperature' set to 0.2. *Bombus haemorrhoidalis* Smith, 1852 was included as the outgroup to root the tree. Convergence within the MCMC trace files was examined using the Tracer software [Drummond, Rambaut, 2007].

Species' gene coalescents were identified using the Poisson-Tree-Process (PTP) procedure online [<https://species.h-its.org/ptp/>] with maximum likelihood to fit the PTP models [Zhang et al., 2013].

Species are accepted here only when an integrated assessment [Schlick-Steiner et al., 2010], comparing results from species' gene coalescents and from morphology, finds supporting evidence from both sources. In this context, failure to find support from either source constitutes failure to find support for separate species so that such taxa have to be regarded as conspecific.

The present work is registered in ZooBank ([www.zoobank.org](http://www.zoobank.org)) under urn:lsid:zoobank.org:pub:9F33B939-6744-4741-9D94-7E9C2F1F78AD.

## Results

### APIDAE: *Bombus*:

#### *Megabombus* von Dalla Torre, 1880

**Remarks.** The initial data set from Huang et al. [2015] included 106 *Megabombus* sequences, to which 20 sequences were added from GenBank and 2 sequences from the NHMUK Ancient DNA Lab. Within this total of 128 sequences, filtering of identical and short sequences reduced the number of sequences suitable for analysis to 81 (as listed in Fig. 2).

The AT3 % scores in Fig. 2 show that 72 of the *Megabombus* sequences fall below the threshold suggested from other subgenera of ca 97 %, so that many are likely to be low-divergence paralogous copies of the COI gene from the nucleus ['numts': Williams et al., 2026b]. However, they are expected to provide only slightly less reliable evidence for species' status unless their degree of divergence is substantially larger (expected to be indicated by even lower AT3%, e.g. six sequences have AT3 % < 91 %, all belonging to the taxon *B. trifasciatus* Smith, 1852) or they support PTP pseudospecies that are not corroborated by morphology.

After 50 million MCMC generations with MrBayes (and a 10 % burn-in), the combined traces had converged on a stable solution. The lowest effective sample size (ESS) for any of the

trace statistics is very high, at 1761. All candidate groups for species have Bayesian support values for their groups from MrBayes close to 1.

Fig. 2 shows the most likely evolutionary tree for the 81 sequences. The PTP species' gene coalescent results are superimposed on this tree. The estimated number of candidate coalescent species is 24 (interval estimate between 20 and 38) as listed in Table 1. The Bayesian tree and PTP analyses were repeated twice with the same result. A few results are noteworthy and are discussed below.

### The taxon *melanopoda*

The greatest surprise in the results for the subgenus *Megabombus* has been that the full-length COI barcode sequence for the taxon *melanopoda* is identical to another sequence from Spain for *B. ruderatus* (Fabricius, 1775). The colour pattern of the hair is also identical to that of some near-melanic queens of *B. ruderatus* from the UK, even down to the orange hairs intermixed in the corbicular fringes (as mentioned in the original description of *melanopoda*) and to the very slightly paler, sooty-coloured hair on metasomal T4–5 (common in near-melanic British *B. ruderatus*, which has been named as the local infrasubspecific colour variation *perniger* (Harris, 1776)). I infer that this individual, although labelled Sumatra, is most likely to be a queen of *B. ruderatus* that is most likely to have originated from the UK. It may have been included in error with NHMUK specimens for accession to the collection over a century ago [Williams et al., 2026c].

### The *montivagus*-complex

Hines' specimens from the Rakhine/Arakan mountains (T415, T405 from 21.21°N 93.96°E) of western central Myan-

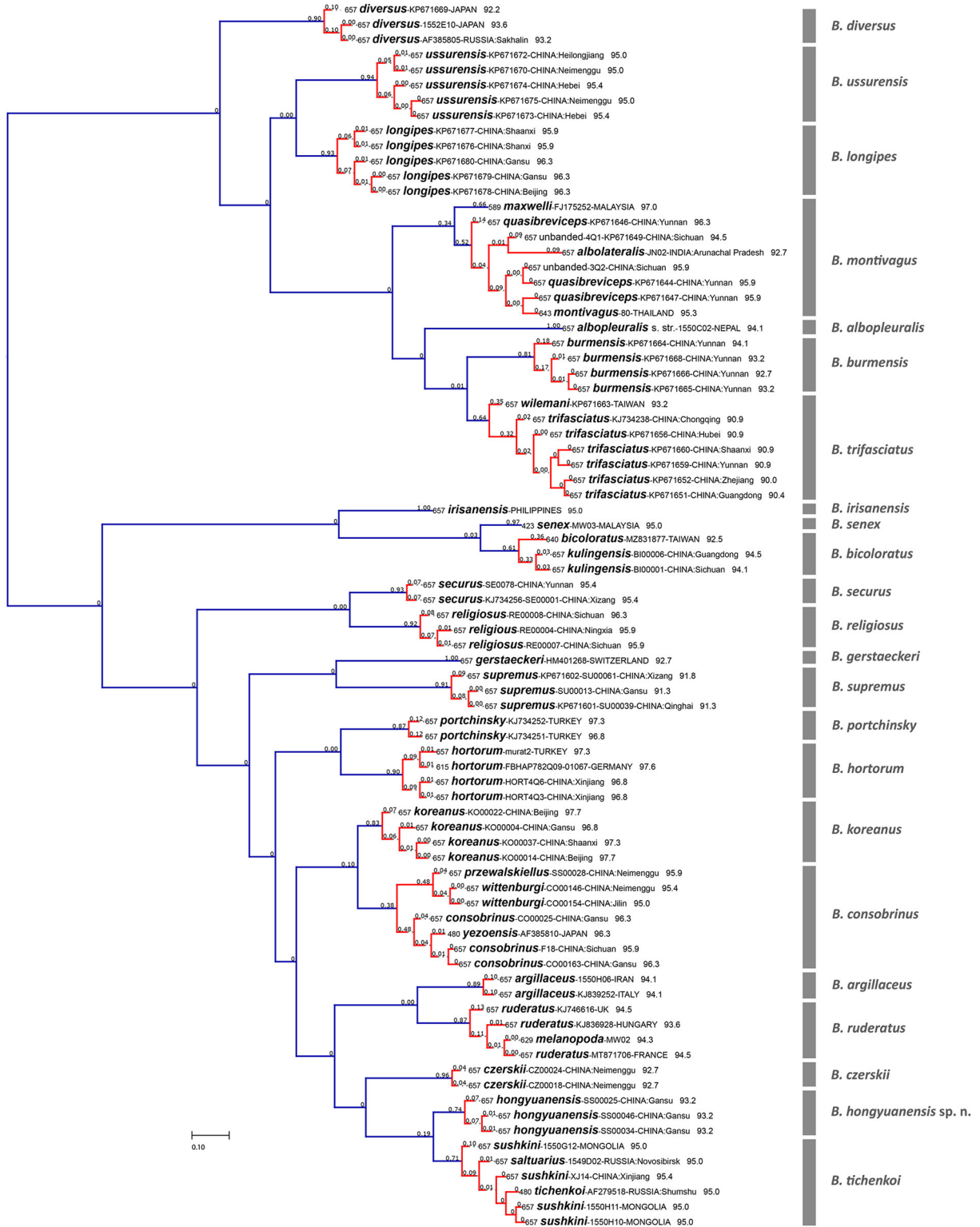
mar that resemble *B. (Pyrobombus) avanus* (Skorikov, 1938) in colour pattern had been considered by her as a possibly undescribed species separate from *B. montivagus* Smith, 1878 [Hines, Williams, 2012]. Their GenBank sequences (FJ175261, FJ175254) group here as the sister group to the *B. albopleuralis* Friese, 1916 sequence, although the PTP analysis supports them as possibly a separate candidate species. These are not shown in Fig. 2 because the sequences are so short (which can cause sequences to appear to be appear as separate species in the PTP analysis as an artifact). Furthermore, because few *B. albopleuralis* samples are available, therefore the broader variation within that species is not well understood. For the present, these samples continue to be treated as conspecific with *B. albopleuralis*, although this will need to be reviewed as soon as more variable material of this species' complex becomes available.

Short sequences from the specimens with the colour patterns of the taxa *quasibreviceps* (Tkalcu, 1968) from Yunnan and *albolateralis* (Richards, 1931) from Arunachal Pradesh group within *B. montivagus*, which identifies these taxa as likely to be conspecific with *B. montivagus* s.l.

Uncertainty in the PTP results is high (low support values) for the candidate species *B. montivagus* (0.52) and for the disjunct taxon *maxwelli* in Peninsular Malaysia (0.66). The one *maxwelli* sequence that is available is short (which can cause sequences to appear to be separate species as an artifact) and only weakly divergent. At present, no consistent discrete morphological variation has been found to corroborate the taxon *maxwelli* as a separate species (other than colour pattern, which is considered hypervariable and insufficient on its own). Therefore at present the taxon *maxwelli* does not meet the requirement here that both coalescent and morphological

Table 1. Summary alphabetic list of the valid names of species within the subgenus *Megabombus* recognised in this paper (shown in bold) and their synonyms (indented) from the named taxa assessed here with COI-gene coalescents and morphology  
Таблица 1. Краткий алфавитный список валидных названий видов подрода *Megabombus*, признанных в данной работе (выделены жирным шрифтом), и их синонимов (с отступом) из названных таксонов, оцененных здесь с помощью коалесцентных моделей генов COI и морфологии

|                                                        |                                                            |
|--------------------------------------------------------|------------------------------------------------------------|
| <b><i>albopleuralis</i></b> Friese, 1916               | <b><i>montivagus</i></b> Smith, 1878                       |
| <b><i>argillaceus</i></b> (Scopoli, 1763)              | <i>maxwelli</i> Pendlebury, 1923                           |
| <b><i>bicoloratus</i></b> Smith, 1879                  | <i>albolateralis</i> Richards, 1931                        |
| <i>kulingensis</i> Cockerell, 1917                     | <i>quasibreviceps</i> (Tkalcu, 1968)                       |
| <b><i>burmensis</i></b> Williams, 2020                 | <b><i>portchinsky</i></b> Radoszkowski, 1884               |
| <i>malaisei</i> (Skorikov, 1937) not of Bischoff, 1930 | <b><i>religiosus</i></b> (Frison, 1935)                    |
| <b><i>consobrinus</i></b> Dahlbom, 1832 s.l.           | <b><i>ruderatus</i></b> (Fabricius, 1775)                  |
| <i>yezoensis</i> Matsumura, 1932, <b>syn.n.</b>        | <i>melanopoda</i> Cockerell, 1910                          |
| <i>przewalskiellus</i> (Skorikov, 1933), <b>syn.n.</b> | <b><i>securus</i></b> (Frison, 1935)                       |
| <b><i>czerskii</i></b> Skorikov, 1910                  | <b><i>senex</i></b> Snellen van Vollenhoven, 1873          |
| <b><i>diversus</i></b> Smith, 1869                     | <b><i>supremus</i></b> Morawitz, 1887                      |
| <b><i>gerstaeckeri</i></b> Morawitz, 1881              | <b><i>tichenkoi</i></b> (Skorikov, 1926) s.l.              |
| <b><i>hongyuanensis</i></b> Williams, <b>sp.n.</b>     | <i>sushkini</i> (Skorikov, 1931), <b>syn.n.</b>            |
| <b><i>hortorum</i></b> (Linnaeus, 1761)                | <i>saltuarius</i> (Skorikov, 1931), <b>syn.n.</b>          |
| <b><i>irisanensis</i></b> Cockerell, 1910              | <i>morawitzianus</i> Pittioni, 1939, <b>syn.n.</b>         |
| <b><i>koreanus</i></b> (Skorikov, 1933)                | <i>kurilensis</i> Sakagami, 1954                           |
| <b><i>longipes</i></b> Friese, 1905                    | <i>pseudoligusticus</i> Podbolotskaya, 1988, <b>syn.n.</b> |
|                                                        | <b><i>trifasciatus</i></b> Smith, 1852                     |
|                                                        | <i>wilemani</i> Cockerell, 1911                            |
|                                                        | <b><i>ussurensis</i></b> Radoszkowski, 1877                |



criteria need to be met in order for it to be considered a separate species. Consequently, from the present evidence I consider that the taxon *maxwelli* is part of *B. montivagus*.

### The *bicoloratus*-complex

The synonymy of the Asian continental taxon *kulingensis* Cockerell, 1917 with the island species *B. bicoloratus* Smith, 1879 proposed by Williams et al. [2009] based on morphology is supported here by the coalescent analysis in Fig. 2.

### The *consobrinus*-complex

For the names below, square brackets enclose unavailable names that are either infrasubspecific, or published without description, or misidentifications; whereas angle brackets are used for parts of names that are interpolated by interpreting the context of the name. Because species' gene coalescents are not supported by PTP for the taxa *yezoensis* and *przewalskiellus*, then the integrative analysis as applied here necessarily fails to support their status as separate species and the nominal taxa are regarded as a synonyms.

#### *Bombus (Megabombus) consobrinus* Dahlbom, 1832

*B. <ombus> consobrinus* Dahlbom, 1832: 49. Neotype female (Sweden) by designation of Løken [Løken, 1966], not seen but identity not in doubt.

*Bombus yezoensis* Matsumura, 1932: 45. Type (Japan) not seen but identity not in doubt. **Syn. n.**

*H. <ortobombus> przewalskiellus* Skorikov, 1933: 59. Syntype queen (China 'Ordos') ZIN examined. **Syn. n.**

The taxa *yezoensis* from Japan and *przewalskiellus* from North China have previously been regarded as distinct species. However, Fig. 2 groups them within the single species' coalescent for *B. consobrinus*. They also share the female clypeus centre without large or medium punctures of *B. consobrinus* when compared with the sister species *B. koreanus* (Skorikov). Therefore the names *yezoensis* and *przewalskiellus* are considered to be synonyms of *B. consobrinus* s.l. (**syn. n.**), as parts of this widespread north Eurasian species.

Within *B. consobrinus* s.l., there is also weak evidence for divergence between a northern, Palaearctic group and a southern group in the hills of Gansu and Sichuan (Fig. 2: with PTP support of 0.48, 0.48). However, these two are grouped together by the species' coalescent weakly as a single species

(Fig. 2: 0.38), with no known morphological distinctions between the two.

### The *tichenkoi*-complex

#### *Bombus (Megabombus) tichenkoi* Skorikov, 1926 Figs 3–5.

[<*Hortobombus*> *saltuarius* Skorikov, 1923: 156, published without description, in part.]

[<*Hortobombus*> *tichenkoi* Skorikov, 1923: 156, published without description.]

*Hortobombus tichenkoi* Skorikov, 1926: 115. Type (Russia: Kamchatka mainland) ZIN images examined.

[<*Hortobombus tichenkoi* var. *pseudoligusticus* Skorikov, 1926: 116, infrasubspecific.]

<*Hortobombus*> *saltuarius* Skorikov, 1931: 235. Syntype males and females by indication of Skorikov [Skorikov, 1923 (Pechora [Komi], Siberia, not specimens from Gansu, Tibet = *B. hongyuanensis* sp. n.)] ZIN images examined, NHMUK queen and worker syntypes examined, in part. **Syn. n.**

*Hortobombus sushkini* Skorikov, 1931: 235. Lectotype queen (Kazakhstan: Saur mountains) by designation of Podbolotskaya [Podbolotskaya, 1988] ZIN images examined. **Syn. n.**

<*Bombus (Hortobombus)*> *sushkini* <subsp.> *saltuarius* (Skorikov, 1931); Bischoff, 1936: 21, in part.

*Bombus (Hortobombus) hortorum* <subsp.> *morawitzianus* Pit-tioni, 1939: 244, not of Popov, 1931 (= *B. morawitzianus* (Popov)). Lectotype queen (Mongolia) by designation of Tkalců [Tkalců, 1974a] NHMUK examined. **Syn. n.**

*Bombus (Hortobombus) tersatus* <subsp.> *kurilensis* Sakagami, 1954: 92. Type (Russia: Paramushir Island) not seen but identity not in doubt.

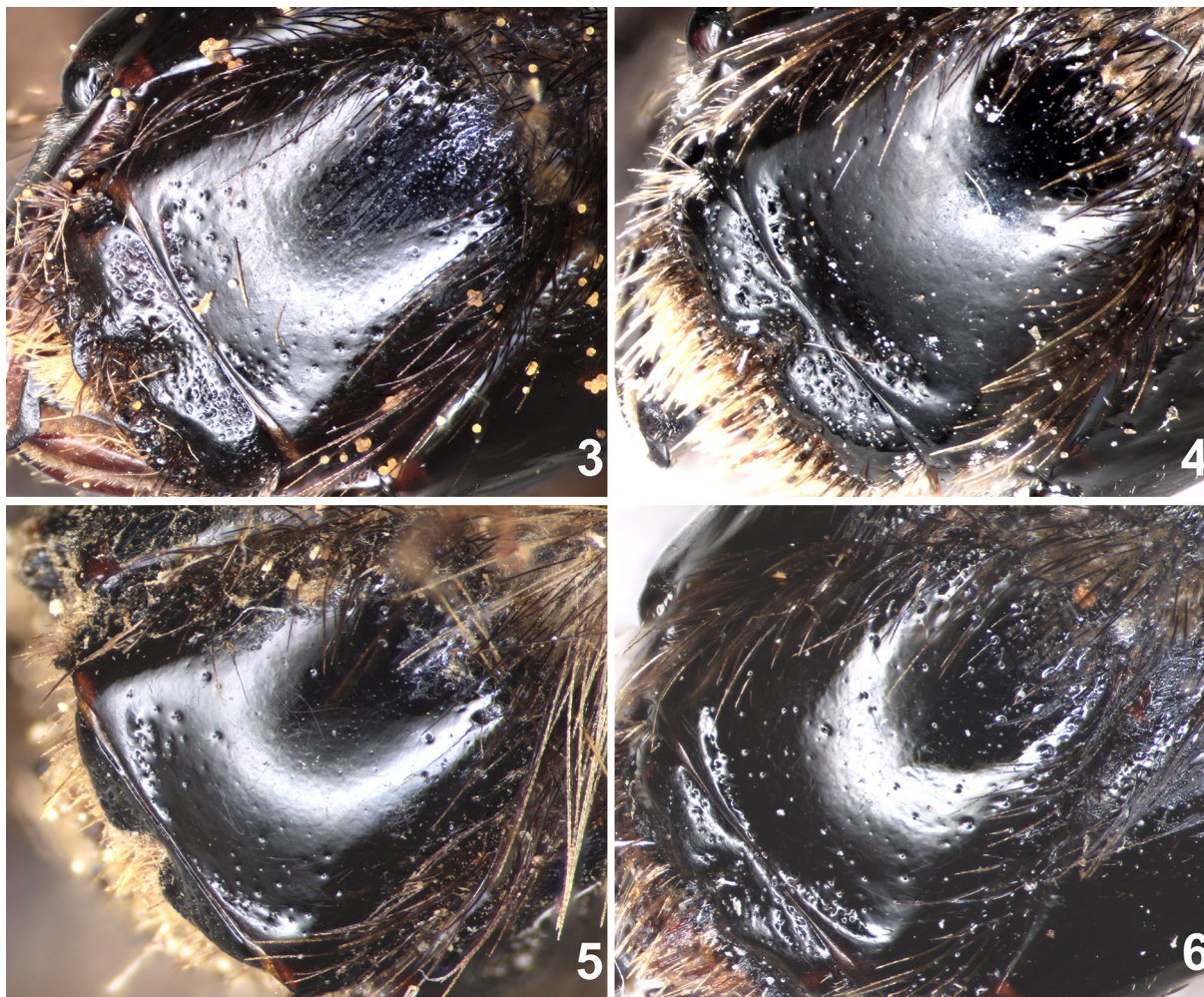
*Megabombus (Megabombus) sushkini* (Skorikov, 1931); Tkalců, 1974a: 51 in part (Mongolia, not 'Kan-su' [=Gansu]).

*Bombus (Megabombus) hortorum* ssp. *pseudoligusticus* Podbolotskaya, 1988: 113. Holotype queen (Russia: Kamchatka, Karajinsky Island) by indication of Skorikov [Skorikov, 1926]. Type not seen but identity not in doubt. **Syn. n.**

The names *tichenkoi* and *saltuarius* were published first by Skorikov [1923], but lacked a description or indication for the taxa, rendering the names unavailable [ICZN, 1999]: Article 12.1. *Bombus tichenkoi* s.str. has long been accepted as a species narrowly distributed in Kamchatka, Karajinsky Island, and the Kuril Islands [Skorikov, 1926; Ito, Sakagami,

Fig. 2. Estimate of the evolutionary tree for COI barcode-like unique haplotypes of bumblebees of the subgenus *Megabombus* in the broad sense showing Bayesian support values for potential species' gene coalescents on the tree. The tree for this gene is estimated with MrBayes and shows maximum likelihood fit of Poisson-Tree-Process (PTP) models, supporting 24 candidate species (of which only the taxon *maxwelli* is not also supported by morphology). Numbers at each node show the probability that all daughter sequences to the right are parts of a single species. Branches change from blue to red at the node with the best fit for the change from inter-species to intra-species branching PTP models (i.e. the species' gene-coalescent nodes). Sequence labels include: sequence length in number of nucleotides; taxon name; sequence number from GenBank or BOLD; country of origin in capitals and province in lower case within larger countries; followed by the percentage of the nucleotides A+T at the third codon position (where low scores (< 97%), these are likely to indicate low-divergence numts). The scale bar represents branch length on the tree in substitutions per nucleotide site. To the right in grey is the interpretation as the 23 accepted species (see the text) using the oldest available names (for details of inferring the species' nomenclature see Williams et al., 2012).

Рис. 2. Оценка эволюционного дерева уникальных гаплотипов COI шмелей подрода *Megabombus* в широком смысле, показывающая значения байесовской поддержки для потенциальных коалесцентных последовательностей генов видов на дереве. Дерево для этого гена построено с помощью MrBayes и показывает соответствие максимального правдоподобия моделям Пуассона-древовидного процесса (PTP), поддерживающим 24 вида-кандидата (из которых только таксон *maxwelli* не подтверждается морфологически). Числа в каждом узле показывают вероятность того, что все дочерние последовательности справа являются частями одного уникального вида. Ветви меняют цвет от синего на красный в узле с наилучшим соответствием для перехода от межвидового к внутривидовому ветвлению в рамках моделей PTP (т.е. узлов коалесцентных последовательностей видов). Метки последовательностей включают: длину последовательности в нуклеотидах; название таксона; номер последовательности из GenBank или BOLD; страну происхождения заглавными буквами и провинцию строчными буквами в пределах крупных стран; Далее следует процентное содержание нуклеотидов A+T в третьей позиции кодона (низкие значения (<97%), вероятно, указывают на низкую дивергенцию нуклеотидов). Масштабная линейка представляет длину ветви на дереве в замещениях на нуклеотидную позицию. Справа серым цветом показана интерпретация 23 признанных видов (см. текст) с использованием самых старых доступных названий (подробности определения номенклатуры видов см. в работе Williams et al., 2012).



Figs 3–6. Female (queen) clypeus photographed from a frontal oblique left angle showing the central area for: 3 — taxon *tichenkoi* s.str. from Shumshu, Kuril Islands, Russia; 4 — taxon *saltuarius* (with more extensive black hair on the thoracic dorsum and T2) from Bulgan, Mongolia; 5 — taxon near *sushkini* (with more extensive yellow hair on the thoracic dorsum and T2) from Bulgan, Mongolia; 6 — *Bombus hongyuanensis* sp.n. from Sichuan, China.

Рис. 3–6. Клипеус самки (королевы), сфотографированный с фронтального косого левого ракурса, показывает центральную область для: 3 — *tichenkoi* s.str. из Шумшу, Курильские острова, Россия; 4 — *saltuarius* (с более обширными черными волосками на спинке груди и T2) из Булгана, Монголия; 5 — близкого к *sushkini* (с более обширными желтыми волосками на спинке груди и T2) из Булгана, Монголия; 6 — *Bombus hongyuanensis* sp.n. из провинции Сычуань, Китай.

1980]. For *B. tichenkoi* s.str., a COI-barcode sequence from a specimen from Shumshu Island (Kurils) is considered representative here (Fig. 2).

The name *saltuarius* appears on individual labels in Skorikov's handwriting for a series of specimens in the ZIN and NHMUK collections that Skorikov listed as originating from Pechora [Komi], Siberia, Gansu, and Tibet. This is not sufficient as an indication, but it appears to represent syntypes from a broad area. No holotype was published for the name *saltuarius* when it was later made available with a description [Skorikov, 1931] (Podbolotskaya labelled specimens as lectotype and paralectotypes in the ZIN collection but did not publish this lectotype designation). The implication of the material listed in Skorikov's 1931 paper and of labels on the Skorikov specimens in the ZIN and NHMUK collections appears to be that the name *saltuarius* was applied to the more northern individuals (from Komi and Siberia) which tend to have less yellow hair, contrasting them with individuals named in the same paper as *B. sushkini* ([Skorikov, 1931]) from the Saur mountains (the lectotype's origin by designation of Pod-

bolotskaya), Semipalatinsk, and Kara-Su (Altay mountains). Specimens of the taxon *sushkini* have more extensive yellow hair (especially on metasomal T2 and between the wing bases) than the taxon *saltuarius*. The specimens from Gansu and Tibet are considered separately below.

The name *pseudoligusticus* Skorikov, 1926 was described as a variety, but because in the same paper Skorikov described other names as applying to subspecies and no additional justification is present, it must be interpreted as having infrasubspecific rank [ICZN, 1999: Article 45.6.4].

The species status of the taxa *saltuarius* and *sushkini* has long been uncertain, with only subtle and vague differences given in the first validly published descriptions [Skorikov, 1931; Bischoff, 1936; Tkalců, 1961a, 1974a; Williams, 1998; Williams et al., 2009]. Skorikov himself [Skorikov, 1931] had described the females as not always distinguishable and then only by the evenness of the hair length. Tkalců [1974a], after examining Skorikov's material, considered that the taxa *sushkini* and *saltuarius* were at least partly sympatric, and that he could distinguish only between the males of the two taxa by the

breadth of the volsella. However, Skorikov's illustration (1931: his fig. 39) of the male genitalia of the taxon *saltuarius* is very similar in the breadth of the volsella to the specimens to hand from Mongolia, which have often been identified as the taxon *sushkini*, so the difference remains unclear. The diagnostic value of this character was questioned by Bischoff. In asserting this difference in volsella breadth, Tkalců [1974a] referred to the illustration by Yasumatsu [1935: his text-fig. 8], although Yasumatsu's figure appears to be approximate in several details and may not be reliable. The significance of any variation in the breadth of the volsella for diagnosing these taxa is not immediately apparent and will need to be assessed from larger samples. It may require quantitative morphometric analysis.

The interpretation of the taxon *saltuarius* here is based primarily on Skorikov's queen (undated) and a worker (dated 1907) from northern Komi, northern Russia, labelled as *saltuarius* and sent in an exchange of material with O.W. Richards (NHMUK) (these collection sites are consistent with the European distribution of the species given by Rasmont et al. [2021 in their fig. 154]). These specimens are likely to have been among Skorikov's syntypes. A closely similar worker (dated 2008) from Novosibirsk was kindly identified as *saltuarius* and sent by A. Byvaltsev, who has made a study of all of Skorikov's *Bombus* type material in the ZIN collection. This was sequenced as a proxy.

The interpretation of the taxon *sushkini* here is based on images of Podbolotskaya's lectotype queen from the Saur mountains made by Yu. Astafurova and by A. Byvaltsev (a paralectotype queen from Kazakhstan had previously been sent on loan from the ZIN by M. Podbolotskaya, but may differ in some characters, see below). A queen with a similar extensively yellow colour pattern (with a narrow thoracic black band, T2 predominantly yellow, and with some yellow hair medially on metasomal tergum 3) is also available from Mongolia (46.37°N 91.10°E). A COI-barcode sequence is available from another specimen (KP671625) from a site in the Xinjiang Altay (47.99°N 88.24°E), which is only ca 200 km from the lectotype locality of the taxon *sushkini* in the Saur mountains. It is possible that these are different species, but I know of no convincing evidence for this at present.

A species' gene coalescent in Fig. 2 groups the sequence of *B. tichenkoi* s.str. from the Kurils together with the sequences from the present interpretations of the taxa *sushkini* (Xinjiang) and *saltuarius* (Russia, Mongolia). It appears from a corroborating morphological character state of females (central area of the female clypeus with few or no medium and large punctures: Figs 3–5) and another for males (penis valve head with only 12–14 lateral teeth) that they are likely to be conspecific. Therefore, the names *sushkini*, and *saltuarius* are interpreted as junior synonyms of *B. tichenkoi* s.l. (**syn.n.**), as parts of a widespread Asian species. From their shared morphology and distribution, the taxa *morawitzianus* Pittioni (Mongolia), *kurilensis* (Kurils), and *pseudoligusticus* Podbolotskaya (Kamchatka and the Kurils including Paramushir and Shumshu) are also likely to be conspecific with *B. tichenkoi* s.l. (**syn.n.**).

The broader species *B. tichenkoi* s.l. is rare in collections. I have seen a male from Baikal (Russia) and Bischoff [Bischoff, 1936] records females from the Sayan mountains (Russia). Taking all of these observations together, the species *B. tichenkoi* s.l. appears to be widespread from the western Russian Arctic [Skorikov, 1923; Levchenko et al., 2017; Rasmont et al., 2021: their fig. 154], via Siberia [Skorikov, 1923; Byvaltsev 2008, 2009; Levchenko et al., 2017], eastern Kazakhstan [Skorikov, 1931; Podbolotskaya, 1988], Sayany [Bischoff, 1936], Mongolia [Pittioni, 1939; Peters, Panfilov, 1968; Tkalců, 1974a], Baikal (PW), to Kamchatka, Karaginsky, and the Kurils

[Skorikov, 1926; Sakagami, 1954; Lelej, Kupianskaya, 2000; Levchenko et al., 2017] in the east. A thorough search of collections and a much more detailed study of variation within this species is clearly needed.

One specimen does not match with the interpretation above: there is an additional paralectotype queen [by designation of Podbolotskaya, 1988] of the taxon *sushkini* from the Saur mountains (Kazakhstan). This queen has a similar colour pattern to the taxon *sushkini* s.str. lectotype but has a slightly more heavily punctured centre of the clypeus [A. Byvaltsev pers. com. and image]. However, it is not best practice to rely on such subtle and individually variable characters to distinguish species *when based on just one specimen*. To resolve this question, ideally an expedition to the Saur mountains is needed to secure more specimens from which to establish COI-barcode data and male morphological data in order to assess this taxon properly.

In addition, a taxon resembling *B. tichenkoi* s.l. has also been recorded from the Qinghai-Tibetan Plateau (under the names *B. saltuarius* and *B. sushkini*) [Skorikov, 1923; Bischoff, 1936; Panfilov, 1957]. However, this has recently been suggested to be a hitherto unnamed taxon closely related to the widespread north Asian species with divergent morphology [Williams et al., 2009: pages 142–144] and barcodes [Huang et al., 2015: their fig. 3]. This species can now be described and named:

*Bombus (Megabombus) hongyuanensis*  
Williams, sp.n.

Figs 6–10.

urn:lsid:zoobank.org:act:8974DC9D-816A-41C2-8281-E219A3F51ADE

[<*Hortobombus*> *saltuarius* Skorikov, 1923:156, published without description, in part (Gansu and Tibet), not (Pechora [Komi] or Siberia), misidentification.]

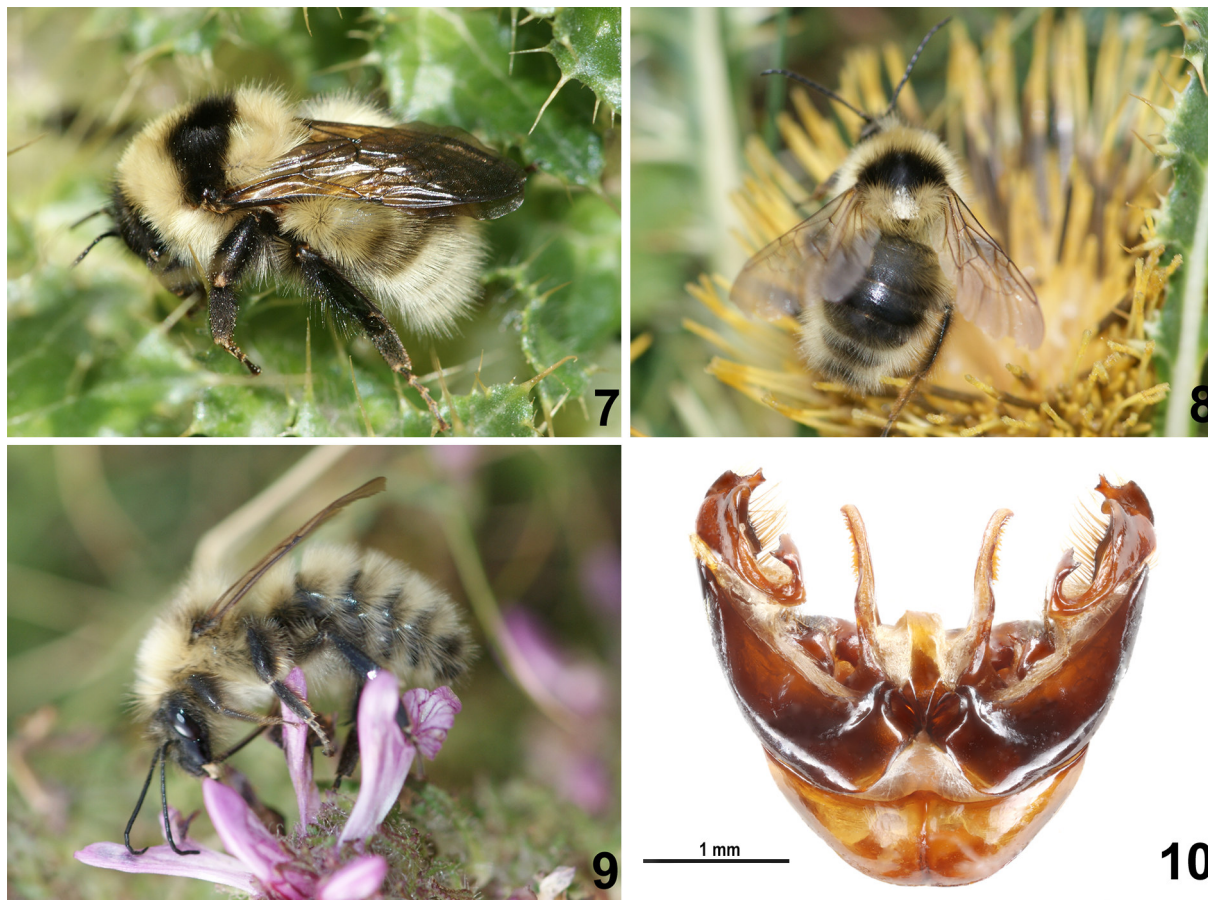
[<*Bombus (Hortobombus)*> *sushkini* <subsp.> *saltuarius* (Skorikov, 1931); Bischoff, 1936:21 in part ('Kansu' [=Gansu]), not ('Sajan'), misidentification.]

[*Bombus (Hortobombus) sushkini* <subsp.> *saltuarius* (Skorikov, 1931); Tkalců, 1961a:362 in part ('Gan-su'), misidentification.]

[*Bombus (Megabombus) sushkini* (Skorikov); Williams et al., 2009:142 in part, misidentification.]

**Material.** Holotype: ♀ (large worker) pinned; three labels: (1) white printed in black 'CHINA Sichuan (Aba Pr.) / (11) N Hongyuan 3458m [a.s.l.] / N 32° 06' 12.8" / E 102° 36' 14.9" / 5.7.viii.2002 P.H.Williams'; (2) white printed in black 'Bumble bees of Sichuan / DB#858. det. PHW / *Bombus sushkini*'; (3) red printed in black 'HOLOTYPE ♀ (w) / *Bombus hongyuanensis* / Williams 2026 / det. PH Williams 2026'. Holotype deposited in the collection of the Chinese Academy of Science Institute of Zoology (IZCAS), Beijing, China. Paratypes: ♀ (large worker) pinned; three labels: (1) white printed in black 'CHINA Sichuan (Aba Pr.) / (11) N Hongyuan 3458m / N 32° 06' 12.8" / E 102° 36' 14.9" / 5.7.viii.2002 P.H.Williams'; (2) white printed in black 'Bumble bees of Sichuan / DB#849. det. PHW / *Bombus sushkini*'; (3) yellow printed in black 'PARATYPE ♀ (w) / *Bombus hongyuanensis* / Williams 2026 / det. PH Williams 2026'; PW. Paratype: ♂ pinned; three labels: (1) white printed in black 'CHINA Sichuan (Aba Pr.) / (11) N Hongyuan 3458m / N 32° 06' 12.8" / E 102° 36' 14.9" / 5.7.viii.2002 P.H.Williams'; (2) white printed in black 'Bumble bees of Sichuan / DB#852. det. PHW / *Bombus sushkini*'; (3) yellow printed in black 'PARATYPE ♂ / *Bombus hongyuanensis* / Williams 2026 / det. PH Williams 2026'; PW.

**Description. Female.** Habitus Fig. 7, body size medium (queen body length 17–19 mm, worker: 11–16 mm), hair (pubescence) moderately long, wings very lightly clouded with brown. Mandible with the distal notch anterior to the posterior tooth (incisura) so shallow as to be almost absent. Oculo-malar



Figs 7–10. *Bombus hongyuanensis* sp.n. photographed in Qinghai, China: 7 — female (queen) 36.37170°N, 100.90852°E at an elevation of 3572 m a.s.l. on 30.VIII.2010; 8 — dark male, same location as for 7; 9 — light male 36.34402°N, 98.24853°E at an elevation of 3519 m a.s.l. on 31.viii.2010; 10 — male genitalia from the dorsal aspect, anterior towards the lower part of the image (the length of the volsellar distal inner processes is variable).

Рис. 7–10. *Bombus hongyuanensis* sp.n., сфотографирован в Цинхай, Китай: 7 — самка (королева) 36.37170°N, 100.90852°E на высоте 3572 м н.у.м. 30.VIII.2010; 8 — тёмный самец, то же место, что и для 7; 9 — светлый самец 36.34402°N, 98.24853°E на высоте 3519 м н.у.м. 31.VIII.2010; 10 — гениталии самца с дорсальной стороны, передняя часть изображения направлена к нижней части (длина дистальных внутренних отростков вольселлы изменчива).

area ('cheek' sensu Williams *et al.* 2014; not the gena) long, 1.8× longer (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) than the breadth of the mandible at its base (breadth between and including the mandibular condyles). Labral lamella narrowly rounded. Clypeus weakly swollen, in its central area irregular and with widely spaced small and medium punctures (Fig. 6), laterally with widely separated large punctures with the intervening areas shining, the clypeus in its dorsal third with a broad median groove within which the surface is irregular and with small punctures. The area between the inner edge of the compound eye and the outer edge of the lateral ocellus occupied in just less than its outer third by dense small and large punctures, spaced by less than their own widths. Mid basitarsus with the distal posterior corner acute and spinosely produced; hind tibia outer surface with a corbicula, the surface nearly smooth; hind basitarsus in the distal three quarters covered with short branched decumbent and slightly overlapping hairs with golden reflections; metasomal T6 posteriorly rounded and with a weak narrow median longitudinal groove. Colour pattern of the hair of the body predominantly black. Head black except for orange hairs anteriorly on the labrum and laterally around the clypeus, the face and top of the head with the short hairs

yellow. Thoracic dorsum cream pale yellow (the exact shade varies but is often a lighter cream than for unfaded *B. tichenkoi* s.l.), this pale hair extending down the side of the thorax where it is nearly white at the leg bases, with black hair as a band between the wing bases, the breadth about one third of the length of the thorax; the front, middle and hindleg femora all with at least some hairs yellow, the tibiae with the hairs black, although at least some with white tips, the basitarsi all with the integument brown-black like the tibiae. Hair of T1 yellow, T2 in the anterior half yellow and the posterior half black, T3 anteriorly narrowly yellow, across the middle black, and posteriorly cream-white, T4–6 cream-white.

*Male.* Habitus Figs 8–9, body size medium (body length 13–16 mm), hair (pubescence) moderately long, wings very lightly clouded with brown. Eye unenlarged relative to the female and the antenna long, reaching posteriorly to the wing bases. Colour pattern of the hair of the body predominantly cream-yellow (the exact shade varies but is lighter than for unfaded *B. tichenkoi*). Front and top of the head with some black hair intermixed. Thoracic dorsum with black hair as a band between the wing bases, the breadth about one third of the length of the thorax. Hair of metasomal T3 anteriorly black, T3 posteriorly and T4–5 a paler cream-white, T6–7 predominantly black with some cream hair at the sides. Male genitalia with

the penis-valve head unflared laterally with 16–18 regular teeth (Fig. 10). Gonostylus longer than broad, with a broad inner proximal process with one large and several smaller triangular teeth. Volsella broad with the inner hooks close to the distal (posterior) corner, with the distally directed hook spinose, the proximally directed hook reduced to a right angle but sharply pointed (from the available material the volsellar inner hooks are variable in this species, with some reduction in Fig. 10 possibly indicating wear or damage).

**Differential diagnosis.** The female of *B. hongyuanensis* Williams, **sp.n.** is distinguished from its sister-species *B. tichenkoi* s.l. by the combination: female clypeus in the centre with the surface uneven and with widely spaced small and medium punctures (cf. *B. tichenkoi* s.l., which has the surface smooth and shining, almost without punctures), the hair of the face and of T2 often predominantly yellow and of T3 often predominantly yellow or white (cf. usually more extensively black for *B. tichenkoi*); all of the yellow hair is cream-coloured (cf. lemon yellow for *B. tichenkoi*).

The male is distinguished from the sister species *B. tichenkoi* s.l. by the combination: the penis-valve head laterally with 15–18 teeth (cf. 12–14 teeth for *B. tichenkoi* s.l.); T2 hair predominantly yellow and T3 with at least some white hair; all of the yellow hair cream-yellow.

**Etymology.** Named for its common occurrence in tall, flower-rich meadows near the town of Hongyuan (Hongyuan County), in Sichuan Province, China.

**Notes.** The recognition of the new southern species is supported by a species' gene coalescent (Fig. 2: PTP values 0.71, 0.74) and from the corroborating morphological character states for both females (female central area of the clypeus with widely-spaced medium and large punctures) and for males (male penis valve head with 15–18 lateral teeth). The colour pattern of the hair varies from the dark pattern described for the holotype (and Fig. 8, most similar to *B. tichenkoi* s.l. from Mongolia) to individuals of both sexes with the hair of the metasoma predominantly yellow-white (Fig. 9). Such pronounced colour variation is common among bumblebees from Asian mountains [Williams, 2022b].

*Bombus hongyuanensis* **sp.n.** is a species distributed to the south of the Taklamakan and Central Asian deserts in the Oriental Region of the wetter eastern Qinghai-Tibetan Plateau. It is therefore vicariant with the widespread Palearctic *B. tichenkoi* s.l. found to the north of these deserts. *Bombus hongyuanensis* **sp.n.** is endemic to China, occurring in the wetter grasslands of eastern Xizang, eastern Qinghai, northern Yunnan, western Sichuan, Gansu, and southern Ningxia [Williams et al., 2009; An et al., 2014].

## Discussion

This review is the first to complete the representation of all known likely species world-wide for the bumblebee subgenus *Megabombus* and to include an estimate of the evolutionary relationships from their COI barcodes. Species'-coalescent analysis supports the existence of 24 candidate species, of which 23 are corroborated in an integrated comparison of morphological diagnoses as likely separate species (confirmed here). More evidence is still needed to understand better especially the species of the Himalaya (*B. albopleuralis* and *B. montivagus*) and the vicariant taxon of Peninsular Malaysia (taxon *maxwelli*).

The older (deeper) branching pattern of the tree in Fig. 2 may be unreliable as an estimate of the older evolutionary

relationships among the species [cf. Williams et al., 2026a] because of over-writing of older nucleotide patterns that can occur with more recent changes in a fast-evolving gene. This should not be expected to compromise the interpretation of this tree for identifying species' coalescents among the most recent branches of the tree, where the over-writing is less likely to affect the estimates of recent branching patterns.

The barcode-like sequences used here may include both sequences from the orthologous mitochondrial gene and sequences from paralogous nuclear copies (numts). Figure 2 shows the AT3 % scores for each sequence after each sample label, which reflects the time since they were copied to the nucleus. Almost all of the sequences in Fig. 2 meet an approximate criterion (AT3 % < 97 %) that has been suggested previously to identify most likely numts [Williams et al., 2023]. Figure 2 shows no obvious strong effect of high-divergence older numts on the results in the form of pseudospecies, in which a morphological or colour-pattern taxon (indicated here by the taxon names) occurs in more than one larger COI-barcode group on the tree [Williams et al., 2023, 2024]. Therefore there is no obvious reason to reject any of these candidate species as high-divergence numts, even when the AT3 % scores are low. Low-divergence numts sequences may be less reliable as evidence for species' status. But if their degree of divergence is small (i.e. still with relatively high AT3 %), then they are likely to retain sufficient genealogical information (in 'parsimony-informative sites') to indicate species' relationships [Williams et al., 2023, 2024, 2026b]. Nonetheless, inferences here must to some extent be provisional until reliably orthologous sequences can be obtained.

The results for the subgenus *Megabombus* from Hines and Williams [2012] are similar to those obtained here, although their results were based on a smaller subgroup of taxa and for a smaller sample of sequences. The tree in Fig. 2 for the reduced set of included sequences is broadly similar to the tree obtained by Huang et al. [Huang et al., 2015]. The 23 species recognised here from a larger sample match Huang et al.'s results for which they used a GMYC approach to discover species' gene coalescents. Their results include as 'unnamed' the divergent taxon from Sichuan first described (but not named) by Williams et al., 2009 (their page 143) and described in more detail here as *B. hongyuanensis* Williams **sp.n.** In addition, their species *B. malaisei* now has a replacement name *B. burmensis* [Williams, 2020]. The Sumatran species *B. senex* can at last be added and the enigmatic '*B. melanopoda*' is resolved as a synonym of the European *B. ruderatus* [Williams et al., 2026c].

Some species of this subgenus *Megabombus* are well known for being strongly polytypic in colour pattern, forming parts of mimicry complexes in different regions of Asia [Tkalců, 1968; Williams, 2007; Hines, Williams, 2012; Ding et al., 2019]. However, the pattern is more complex than had been thought (Fig. 1). At one extreme had been an interpretation that there might be different colour patterns of a single species, *B. trifasciatus*, for the subgenus *Megabombus* in the different regions of Asia [Williams, 1991]. Others have considered that there might be three separate species in this taxon complex:

one in Southeast Asia, one in the Himalaya [Tkalců, 1968], and one in China. This is an interpretation that was largely consistent with genetic data [Hines, Williams, 2012], although their study lacked a coalescent analysis. Its interpretation included only one species of the subgenus in the Himalaya, although it added another for Sichuan (*B. malaisei* = *B. burmensis* [Williams, 2020]). In contrast, the results in Fig. 2 now show that alongside a central Chinese species (*B. trifasciatus*) and a Himalayan and Myanmar species (*B. albopleuralis*), the Southeast Asian species (*B. montivagus*) not only extends into southern China with a widely distributed orange-banded pattern, but also into southern Sichuan and into the Himalaya with an ‘unbanded’ black-thorax pattern (including the taxon *albolateralis* in Arunachal Pradesh). The distributions in the Himalaya of the species *B. albopleuralis* and *B. montivagus*, both of which may show ‘unbanded’ black-thorax patterns in this region, are not, as yet, well diagnosed [Williams, 2022b]. All three species are morphologically closely similar, so a lot more sequencing of samples will be needed to clarify an understanding of the distributions of the three species and of any consistent subtle morphological characteristics.

The new synonyms proposed here for the species *B. consobrinus* s.l. and *B. tichenkoi* s.l. provide some resolution to the uncertain taxonomy of these widespread and variable species. No doubt more work could still add a lot to our understanding of these bees, especially those from the Saur mountains.

The sample size available for this study of the subgenus *Megabombus* is larger than for previous studies. When including especially the collections examined shown in Table 2, and the many individuals examined in the field, this amounts to a total sample of thousands of individuals, from which 128 were selected for sequencing. This is far larger than the 28 *Megabombus* sequenced specimens used by Hines and Williams [Hines, Williams, 2012] and larger also than the 117 sequenced specimens used by Huang *et al.* [Huang *et al.*, 2015].

Nonetheless, for these broadly distributed bumblebee species that are not only very variable in colour patterns but also in barcode sequences, samples that are far larger still and from a broader and more dense sampling coverage will very likely be needed in order to achieve stable and fully representative results [Williams, 2022a]. Furthermore, all sequences for future analysis should ideally be orthologous barcodes [Williams *et al.*, 2023, 2026b], if the results are to be reliable, so better sequencing techniques would be highly desirable.

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Table 2. The material upon which this study is based is deposited in the collections of the following institutions, using acronyms based on GRSciColl [<https://scientific-collections.gbif.org/>]

Таблица 2. Аббревиатуры учреждений, в коллекциях которых хранится материал, использованный в данном исследовании [согласно GRSciColl — <https://scientific-collections.gbif.org/>]

|           |   |                                                                                      |
|-----------|---|--------------------------------------------------------------------------------------|
| AMNH      | = | American Museum of Natural History, New York                                         |
| IAR       | = | Institute of Apicultural Research, Chinese Academy of Agricultural Sciences, Beijing |
| IZCAS     | = | Institute of Zoology, Chinese Academy of Sciences, Beijing                           |
| KUN       | = | Kunming Institute of Botany, Chinese Academy of Sciences, Kunming                    |
| Naturalis | = | National Museum of Natural History, Leiden                                           |
| NHMK      | = | Natural History Museum, London                                                       |
| PW        | = | Author’s research collection, Tunbridge Wells                                        |
| USNM      | = | United States National Museum of Natural History, Washington DC                      |
| YT        | = | Y. Tang, Chengdu                                                                     |
| ZIN       | = | Zoological Institute, Russian Academy of Sciences, St Petersburg                     |
| ZMB       | = | Museum für Naturkunde an der Humboldt-Universität, Berlin                            |
| ZMMU      | = | Zoological Museum of the Moscow State University, Moscow                             |

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